TOPICAL REVIEW

The role of internal and external constructive processes in evolution

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Abstract The architects of the Modern Synthesis viewed development as an unfolding of a form already latent in the genes. However, developing organisms play a far more active, constructive role in both their own development and their evolution than the Modern Synthesis proclaims. Here we outline what is meant by constructive processes in development and evolution, emphasizing how constructive development is a shared feature of many of the research developments central to the developing Extended Evolutionary Synthesis. Our article draws out the parallels between constructive physiological processes expressed internally and in the external environment (niche construction), showing how in each case they play important and not fully recognized evolutionary roles by modifying and biasing natural selection.

Introduction

The architects of the Modern Synthesis (henceforth MS) viewed development as an unfolding of a form already latent in the genes. For instance, Mayr (1984, p. 126) writes:

> All of the directions, controls and constraints of the developmental machinery are laid down in the blueprint of the DNA genotype as instructions or potentialities.

Mayr's (1961) distinction between 'proximate' and 'ultimate' causes led him to insist on a dissociation of evolution and development (Amundson, 2005; Laland *et al.* 2011), a stance that led to development being viewed as largely irrelevant to understanding evolution:

> The clarification of the biochemical mechanism by which the genetic program is translated into the phenotype *tells*

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us absolutely nothing about the steps by which natural selection has built up the particular genetic program (Mayr, 1980, pp. 9–10, our italics).

Throughout the 20th century, most leading evolutionary biologists took the same line (e.g. Dobzhansky, 1951; Maynard-Smith, 1982). In contrast, several of the more progressive elements to emerge within evolutionary biology in the last decade or so emphasize, in different ways, how developmental processes, traditionally disregarded as solely relevant to proximate questions, are in fact highly germane to evolutionary issues. These include the 'developmental bias' arguments emerging from evo-devo (Arthur, 2004; Brakefield, 2006; Muller, 2007), the 'genes are followers, not leaders, in evolution' argument emerging from the study of developmental plasticity (West-Eberhard, 2003), related arguments deriving from the theory of 'facilitated variation' (Kirschner & Gerhardt, 2005), and niche construction theory (Odling-Smee *et al.* 1996, 2003). The arguments from developmental bias, developmental plasticity and facilitated variation have in common the view that developmental processes systematically channel the generation of phenotypic variants along certain pathways, and thereby bias the direction and rate of evolution by, in part, determining the variants that are subject to selection. Gould (2002) refers to this channelling as 'active genetic constraints'.

Niche construction theory (NCT) makes a related argument: it emphasizes how developing organisms modify external environments in a manner that systematically biases the selection pressures acting on the constructing population, their descendants, and other populations (including other species) that inhabit their local environment. The parallels are self-evident: niche construction is a manifestation of an externally expressed developmental bias, or conversely, developmental bias is the outcome of an internal constructive process. All of these processes are viewed as central to the emerging Extended Evolutionary Synthesis (henceforth EES) (Pigliucci & Muller, 2010).

Thus, from the perspective of an EES, developing organisms play a far more active, constructive role in both their own development and their evolution than has been traditionally conceived. In this article we elaborate on what is meant by constructive processes in development and evolution, illustrating the parallels between processes that change physical states within and outside of the organism.

The term 'constructive development' (Laland *et al.* 2013) is designed to capture the idea that the developing organism shapes its own developmental trajectory by constantly responding to, and altering, internal and external states. Developmental systems respond flexibly to internal and external inputs, most obviously through condition-dependent gene expression, but also through exploratory behaviour (among microtubular, neural, muscular and vascular systems), which enables somatic selection of diverse functional states in response to local demands ('facilitated variation'; Kirschner & Gerhardt, 2005).

Developmental biologists emphasize how organisms possess active regulatory mechanisms that involve explorative and selective processes (Baldwin, 1902; Waddington, 1959; Gilbert, 2003; Schwenk & Wagner, 2004; Kirschner & Gerhardt, 2005; Gerhardt & Kirschner, 2007; Gilbert & Epel, 2009). These mechanisms are fundamental for maintaining phenotypic stability by buffering the effects of variation in the internal and external environments (Waddington, 1959; Turner, 2000; Kirschner & Gerhardt, 2005; Gilbert & Epel, 2009). Those same mechanisms also enable coordinated and functional responses to novel conditions (West-Eberhard, 2003; Gerhart & Kirschner, 2007). Moreover, some forms of epigenetic inheritance (i.e. prion-based or self-sustaining-loop-based) are constructive rather than replicative (Jablonka & Lamb, 2005). Constructive development is therefore a shared feature of 'facilitated variation' (Gerhart & Kirschner, 2007), 'developmental plasticity' (West-Eberhard, 2003) and 'inclusive inheritance' (Jablonka & Lamb, 2005). For the EES, because development is not simply the execution of a genetic program but a dynamic process that relies on a multitude of resources, the origin of adaptive variants cannot be reduced simply to mutation. Instead, an evolutionary explanation needs to address how existing developmental processes can give rise to novel phenotypic variants, whether those variants will be biased in any particular direction, or appear in response to particular conditions, and consider how those variants adjust external environments to meet their requirements.

In parallel with developmental biologists' emphasis on regulation of the internal environment, physiologists also emphasize how organisms regulate their external environment (Turner, 2000). Turner points out that many of the structures built by animals do physiological work, capturing and channelling chemical and physical energy. Earthworms' soil environment, termite mounds and countless animals' burrows effectively function as externalized organs of physiology. Developing organisms change, and frequently regulate, external environments, often in ways that are adaptive to themselves and to their descendants (Odling-Smee *et al.* 1996, 2003; Laland *et al.* 1999; Turner, 2000).

This process of environmental modification is known as 'niche construction', and it has also been subject to investigation by evolutionary biologists for its roles in evolution and ecology (Lewontin, 1983; Laland *et al.* 1996, 1999; Odling-Smee *et al.* 1996, 2003, 2013). Advocates of NCT have argued that niche construction is an

important, but hitherto neglected, evolutionary process (Odling-Smee *et al.* 2003). In this article we first describe NCT and then illustrate its evolutionary credentials with two empirical examples of niche construction, in earthworms and termites, drawing on Turner's (2000) conception of the 'extended organism.' The examples illustrate in different ways how the structures used and built, and other environmental modifications made, by animals are actually extensions of their internal physiology, which harness and control the flow of energy, thereby imparting an 'extended physiology' to external environments. NCT can therefore be effectively melded to one of physiology's cardinal principles, the dynamic phenomenon of homeostasis, which in turn brings a new twist to the phenomenon of adaptation. In so doing, these acts of niche construction leave evolutionary signatures by modifying selection pressures. We end by considering more generally how internal and external constructive processes affect evolutionary processes, and their role in the emerging EES.

Niche construction and the EES

'Niche construction' refers to the process whereby the metabolism, activities and choices of organisms modify or stabilize environmental states, and thereby affect selection acting on themselves and other species (Odling-Smee *et al.* 2003; see also Lewontin, 1983, 2000). Organisms can modify selective environments externally, for instance, through constructing nests, burrows, mounds, selecting habitat and essential resources, relocating in space (e.g. migration), and leaving ecological legacies for future generations. Niche construction also influences development, and constitutes an important way in which environmental factors imprint upon normal development.

Ecological inheritance refers to the accumulation of environmental changes, such as altered soil, atmosphere or ocean states that previous generations have brought about through their niche-constructing activity, and that influence the development of descendant organisms (Odling-Smee *et al.* 2003; Erwin, 2008).

A body of formal evolutionary theory has shown that niche construction can strongly affect evolutionary dynamics in a variety of ways (e.g. Laland *et al.* 1996, 1999; Lehmann, 2007, 2008; Kylafis & Loreau, 2008; summarized in Odling-Smee *et al.* 2013). The evolutionary significance of niche construction stems from that fact that (i) organisms modify environmental states in non-random ways, thereby imposing a systematic bias on the selection pressures they generate, (ii) since organisms modify the environments of their descendants, niche construction generates an additional form of inheritance ('ecological inheritance'), which has been shown to strongly affect evolutionary dynamics, (iii) acquired characters become evolutionarily significant by modifying

selective environments, and (iv) the complementarity of organisms and their environments (traditionally described as 'adaptation') can be enhanced through niche construction (modifying environments to suit organisms), not just natural selection.

Niche construction is both universal to, and obligate for, living creatures. Living organisms are far-from-equilibrium (strongly out-of-equilibrium) systems relative to their physical or abiotic surroundings. They can only survive and maintain their far-from-equilibrium status by constantly exchanging energy and matter with their environments. Organisms feed on molecules rich in free energy, in the process generating outputs largely in the form of molecules that are poor in free energy. The energy harvested is used to do work. Such work is necessary to allow organisms to produce and maintain a specified orderliness, be it inside their bodies or in their external environments. Indeed, organisms do not just modify environments, they confer their own physiology on their local environments (Turner, 2000). In order to survive, organisms must act on their environments and, by doing so, change them. One consequence of this imperative is that all living organisms *must* engage in 'niche construction' – that is, they must modify their environment to some degree, however small-scale and transient. Of course, it is immediately apparent that humans are niche constructors *par excellence* (Laland *et al.* 2000; Smith, 2007; Kendal *et al.* 2011), and there is evidence that their cultural practices, including domestication of plants and animals, generated selection for countless alleles, for instance, expressed in the digestion of milk and dairy products, the metabolism of carbohydrates, starch, proteins, lipids and phosphates, and the detoxification of plant secondary compounds (Laland *et al.* 1995, 2010; Richerson *et al.* 2010). However, while humans may be unusual with respect to the scale and impact of their niche construction, the fact that we modify our environments is not in itself exceptional: niche construction is a process generally present across all forms of life.

Work in the thermodynamic sense is only done when energy flows (Turner, 2000). Hence, for biologists, work can be defined as the processes that organisms engage in that allow them to exchange energy with their environments, to channel energy through their bodies and to create orderliness in their world. One ramification of the fact that niche construction ultimately functions to harvest energy is that niche construction cannot be random, since random niche-constructing acts could not provide organisms with a basis for sustained life (Odling-Smee *et al.* 2003, chap. 4).

Niche construction is the expression of genetic and acquired (e.g. learned, brain-based) semantic information, information specifying how organisms should operate in their local environments in order to

satisfy their requirements, and that information would be eradicated, by selection, or through learning, if its average effect on fitness was negative. It follows that niche construction is a selective process (albeit very different in form to natural selection), since it requires an ability on the part of organisms to discriminate and actively sort between environmental resources, and hence to change the physical state of some factors in their environments in beneficial ways (Odling-Smee *et al.* 2003).

This reasoning, which derives directly from the laws of thermodynamics (Odling-Smee *et al.* 2003), implies that organisms must modify environmental states in a systematic and directional way. For instance, niche construction disproportionately generates environmental states that are likely to match – that is, be coherent and integrated with – the constructing organism's phenotype and its developmental needs, or those of its descendants. These environments are therefore adaptive for the constructor or its descendants, at least in the short-term (Odling-Smee *et al.* 2003). This implies that organism–environment complementarity is not simply the outcome of selecting genes for 'apt function' in particular environments: niche construction 'adapts' environments to organisms too. This directionality derives from the fact that niche construction has been shaped by prior selection, as well as learning and other aspects of plasticity.

Much of the reasoning underpinning NCT can be derived from Ashby's (1956) 'Law of Requisite Variety'. This law specifies that, if it is to be stable, the number of states of the control mechanism of a system (e.g. the variant states available to an organism) must be greater than or equal to the number of states in the system being controlled (e.g. the variant environmental states with which the organism must cope). Ashby (1956) describes the main insight of the Law as 'only variety can destroy variety'. This is germane to living organisms: if it experiences an environmental state or states with which it is unable to cope (either by changing itself through internal physiological adjustment, or by changing the environment, either through dispersal i.e. environmental escape, or environmental perturbation), it will die. Under such circumstances, environmental variation will have 'destroyed' organismal variation.

In order to survive, the control system must act in such a way as to 'protect an essential variable' by ensuring that key parameters remain within bounds that the system can tolerate. For a living organism, the essential variable is its niche relationship, which means it must remain within its fundamental niche, the range of conditions and resource frequencies that the organism can tolerate. Where the organism is able to counteract or exploit environmental variation, either by responding to it adaptively or by changing the environment to suit itself (i.e. niche construction), then that enhances

the organism's capacity to survive and reproduce and contributes to the subsequent evolution of its population. Hence, through this niche construction, the fundamental niche itself may be adjusted.

In practice, this adaptive regulation demands not just the protection of multiple variables simultaneously and successively (akin to Hutchinson's *n*-dimensional hypervolume of ecological variables), but also their adjustment towards values that maximize fitness, which makes it a niche management problem. If adaptive regulation is successful, and the multi-dimensional organism–environment relationship (henceforth 'niche relationship') is successfully protected by the organism, then we end up with a dynamic and evolvable homeostatic relationship between the organism and its environment.

The evolvability of the niche relationship is based in part on genetic mutations but also on the two different ways niche-constructing organisms can affect their environments, through 'perturbation' (physically changing environmental states) or 'relocation' (actively moving in space to experience other environmental states) (Odling-Smee *et al.* 2003). The evolvability of the niche relationship is therefore based on changes in the niche relationship rather than solely genetic mutations. This evolutionary dynamic is driven by the purposive (i.e. goal-seeking) activities of organisms in pursuit of their fitness goals: it stems from the 'purpose' of organisms to stay alive and reproduce by doing work to oppose the depredations of the 2nd law of thermo-dynamics (Schrödinger, 1944; Odling-Smee *et al.* 2003; Pross, 2012). It follows that the evolutionary dynamic cannot be adequately described as 'linear causation', where the properties of environments shape the properties of organisms, through natural selection. Rather, Ashby's Law of Requisite Variety demands 'reciprocal causation': the idea that developing organisms are not solely products, but are also causes, of evolution (Laland & Sterelny, 2006; Laland *et al.* 2011).

With sufficient flexibility (i.e. variance) in its repertoire of phenotypic strategies, an organism can 'destroy' or drive down variance in the environment by modifying natural selection pressures in its environment (e.g. dispersal, temperature regulation). This applies equally to the *potential* variation in phenotypic state conferred by developmental plasticity, which allows the organism to 'destroy' (i.e. cope with) a range of environmental states (West-Eberhard, 2003), and to the internal environment too, where exploratory processes generate variation, which is retained or lost on demand (Kirschner & Gerhardt, 2005). These processes allow adaptive regulation by organisms to contribute to supporting Dynamic Kinetic Stability within their population relative to their environment (Pross, 2012). Conversely, if environmental variation causes the organism to be in a maladaptive

state, it harms or kills the organism and may thereby destroy organismal variance. At the population level, this may actually enhance Dynamic Kinetic Stability, but may alternatively contribute to population extinction.

Environmental regulation to bring about an adaptive dynamic homeostatic relationship between organisms and their environments can be brought about equivalently through both phenotypic and extended phenotypic means. For instance, some species of termites that live in hot, dry environments may adapt phenotypically (by evolving physiological tolerance to high temperatures and thick cuticles to limit desiccation), or through the organism's 'extended phenotype' (by building nests that damp temperature or humidity). These should be viewed as alternative means to the same end. The fact that organisms must protect their niche relationship relative to multiple selection pressures has apparently led to the sharing out of the adaptive regulation problem across diverse modules and sub-systems within and outside of organisms on a division of labour basis. That implies a recursion of the adaptive regulation problem relative to different within-organism (or extended phenotypic) modules. Populations of metazoans have evolved specialized modules (e.g. physiological sub-systems) to cope with different aspects of their over-all niche management in response to natural selection pressures in the external environment. Examples are the vascular system, including the heart, the digestive system, including the liver, the stomach and the pancreas, and the urogenital system, each of which has to cope with a particular sub-component of the organism's overall adaptive regulation problem. Yet in each case the fundamental problem remains how to protect an essential variable, and the solution remains through the environmental adaptation, environmental regulation or environmental change options available to the system, be the environment internal or external. In each case causation is fundamentally reciprocal, since organs and physiological sub-systems do not just respond to selective environments but also modify internal and external environments through niche construction. Once again, any homeostasis is both dynamic and flexible (i.e. open to developmental adjustment). While in healthy organisms these sub-systems typically operate in harmony, in sick (e.g. cancerous) organisms the niche-constructing activities of physiological subsystems may actually compete with or stress one another, and may disrupt each other's activities, disrupting dynamic homeostasis, and reducing the fitness of the metazoan host. Likewise, changes in hygiene and eating practices will alter the microbiome. The same logic applies at a finer scale. At the level of the cell, there is another recursion of the adaptive regulation problem, since each cell too must protect an essential relationship, relative to its extracellular micro-environment.

Hence, at multiple levels, there is a recursion of the adaptive regulation problem as described by Ashby's Law of Requisite Variety. At each level, successful adaptation implies the establishment and maintenance of homeostasis, which ultimately feeds through to the metazoan organism's adaptive regulation of its niche relationship relative to its external environment. Ultimately, the same logic applies, whether the adaptive regulation occurs internally through 'physiological processes' or externally through 'niche construction'. Indeed, we emphasize that these are alternative means to the same end: niche construction *is* externalized physiology, and physiology as traditionally conceived involves internal constructive processes with an identical function to niche construction.

This directional or systematic quality of niche construction is central to the argument that it should be regarded as an evolutionary process. The MS tacitly assumed that environmental states modified by organisms are not systematically different from environments that change through processes independent of organismal activity. On the basis of this assumption, niche construction could be regarded as a background condition to selection, rather than an evolutionary process in its own right (Scott-Phillips *et al.* 2014). The conventional MS stance is that evolution is change in gene frequencies over time, and hence that evolutionary processes are those phenomena that directly change gene frequencies; on this view, niche construction is not an evolutionary process.

The EES, in contrast, embraces a broader notion of evolution: evolution is transgenerational change in the distribution of heritable traits in a population. The notion of an evolutionary process is correspondingly broadened to encompass any phenomena that systematically bias the direction or rate of stable heritable variation, including processes that bias selection. Into this category fall niche construction and developmental bias, which the EES recognizes to be important in evolution because of the manner in which they channel and direct natural selection.

Niche construction as extended physiology

An extended view of physiology challenges the commonplace notion of the organism as a discrete entity partitioned from its environment by a boundary (Turner, 2000). Such a conception is inconsistent with basic principles of conservation of mass and energy. To sustain an internal environment of, say, high sodium concentration implies that work is being done to concentrate sodium from the environment. Doing so means that the external environment must, to a degree, be depleted of sodium (Turner, 2004*a*). It follows that sodium homeostasis in an organism's internal environment imparts changes in sodium concentrations to the external environment as well. Therefore, an organism's 'internal physiology' can imply a degree of 'external'

physiology, as in some, but not all, cases such environmental changes are themselves regulating and homeostatic. This means that extended physiology is both nestable and scalable in ways that are not readily accountable under the gene-selectionist scheme of the MS. Thus, physiology is both intensive *and* extensive (Turner, 2002). It is more proper, therefore, to speak of an organism's *extended physiology*, and to conceive of the organism, not as a physiological entity embedded in a physical environment, but as an *extended organism*, consisting of environments partitioned by adaptive interfaces that control the flow of matter and energy across them, including through niche construction. It is the cardinal principle of physiology, homeostasis, that distinguishes NCT and the extended organism from Dawkins' concept of the extended phenotype (Dawkins, 1982, 2004; Turner, 2004*b*). Rather than simply being an externalized projection of the genotype, the extended organism with its constructed environment frequently *is* an integrated homeostatic system (Turner, 2013).

In conventionally defined organisms, these adaptive interfaces constitute the various epithelial boundaries that manage the flows of matter and energy between the 'internal' and 'external' environments: the epithelia of the gastrointestinal and urogenital tracts, the lungs (or gills) and skin. Extended physiology in these instances is embodied in the internalization of the external environment: the 'interiors' of the lungs and the gastrointestinal and urogenital tracts are topologically 'external' environment, albeit enfolded 'internally.' This reflects an often-unappreciated fact about extended physiology. Exposing the adaptive interface to an unpredictable, capricious and capacious external environment increases energy costs of homeostasis and it makes those costs unpredictable. Costs of homeostasis can be brought under control by imposing homeostasis on both sides of the adaptive interface. This can be accomplished in a variety of ways: the elaborate infrastructure of the lung, for example – the infolding, the control of ventilation and so forth – internalizes the atmosphere in a way that regulates conditions on both sides of the epithelial boundary of the alveolus where respiratory gas exchange actually occurs. In short, the lung's structural and mechanical infrastructure constitutes a self-fabricated adaptive boundary that encapsulates and manages the environment across the adaptive boundary of the alveolus. Adaptive boundaries are thus nested within adaptive boundaries, the sum total of which constitutes the extended organism.

Niche construction follows inevitably from this analysis, as niche construction can often be construed as the construction of new adaptive boundaries that have nested within them other adaptive boundaries (Odling-Smee & Turner, 2011). However, niche construction also comprises changes in environments, such as depletion of resources, or dumping detritus, that have a negative

impact on the organism's fitness (Odling-Smee *et al.* 2003), although they may well benefit other organisms. By this logic, the architecture of, say, the lung, is niche constructing, providing a controlled environment where the exchange of respiratory gases across the pulmonary epithelium can be managed. Niche construction is the physiological expression of the extended organism. The logic also leads to an intriguing hypothesis: that there is no outward boundary to the extended organism and to niche construction, save the boundaries of the biosphere itself (Lovelock, 1987; Schneider *et al.* 2004; Turner, 2004*b*). In practice, researchers will usually need to impose boundaries on their systems, and the notion of individuality, while problematic, retains utility. Moreover, it does not follow that the niche construction of multiple organisms must sum to be well-regulated or functionally integrated, as the Gaia hypothesis implies, although it does not negate the possibility either. This extensive principle is evident in the emerging realization of social insect 'supercolonies' with geographic extents of thousands of kilometres (Moffett, 2012).

The extended organism has evolutionary implications because it connects niche construction to the core Darwinian phenomenon of adaptation (namely the adaptive coalition between organism and environment). Two examples will suffice to illustrate this.

The first is the familiar example of the earthworm, mentioned above. Physiologically, earthworms are freshwater aquatic annelids: their water balance organs, the nephridia, are structurally and physiologically geared toward the production of the copious and dilute urine that is the physiological signature of life in fresh water (Boroffka, 1965; Oglesby, 1978). In many lineages, the evolution of terrestriality involved an elaborate restructuring of the organs of water balance. The mammalian kidney, for example, has been restructured through time toward water conservation mechanisms that are beyond the capabilities of the ancestral, and aquatic, fish kidney (Schmidt-Nielsen, 1979). This is an essential component of the suite of physiological adaptations that have enabled vertebrates to live on land.

Earthworms, which evolved from freshwater oligochaetes, nevertheless exist in terrestrial environments, not by restructuring their nephridia, but by extending their physiology outward, by restructuring the soil environment to enhance water retention and accessibility. Through their digging and tunnelling, earthworms increase the incidence of soil macropores, which fosters the infiltration and capture of rain water (Edwards *et al.* 1992; Joschko *et al.* 1992; Trojan & Linden, 1992). Their mulching activities reduce the soil's clay fraction, which weakens soil matrix potentials, making soil water more accessible to the worms (Hoogerkamp *et al.* 1983). Finally, the increased loft and thermal capacity of earthworm-worked soil both enhances percolation of respiratory gases through the

soil and moderates the soil's daily march of temperature. Physiologically, restructuring the soil environment in this way creates a new adaptive interface for earthworms, one that is more suited to the earthworms' essentially aquatic physiology (Turner, 2000). In turn, this has altered the selective regime for earthworms and their descendants (not to mention the myriad of other organisms that inhabit the soil environment): whatever selective advantage that might accrue to modifying the physiology of the nephridia to the worms' dryer physical environment now accrues to adapting the soil environment to the worms' existing physiology. Because the modifications to soil by earthworms lasts longer than an earthworm's own typical lifespan, this constructed niche serves as a form of external hereditary memory, an ecological inheritance (Laland *et al.* 1996; Odling-Smee *et al.* 1996; Odling-Smee, 2010).

The second example concerns colonies of mound-building termites (Lüscher, 1961; Ruelle, 1964; Darlington, 1985; Turner, 2000, 2001). A mound-building habit is evident in many termite families, but it reaches its most elaborate expression in the fungus-cultivating termites of the family Macrotermitinae (*Macrotermes* spp., *Odontotermes* spp.). These termites construct compact subterranean nests that house the colony (Harris, 1969; Collins, 1979; Darlington, 1985; Turner, 2000). The workers harvest woody plant material from a defended territory that can extend as far as 70 m from the colony (Inoue *et al.* 2001). They return macerated forage to the nest, which is then composted by a symbiotic fungus (*Termitomyces*) that is grown on structures, called fungus combs, that are constructed by the workers (Abo-Khatwa, 1978; Batra & Batra, 1979; Wood & Thomas, 1989; Aanen *et al.* 2002).

Above the subterranean nest, the termites construct a massive mound, several metres tall, which is permeated with an elaborate network of tunnels that culminate in a finely porous mound surface. The mound is a dynamic structure. It sheds about 250 kg of dry soil *per annum* to erosion, which is replaced by termites depositing wet soil to the mound surface (Turner *et al.* 2006). Mound structure is thus a dynamic balance between patterns and rates of soil erosion, and soil deposition. Because of this, the mound is an adaptive structure, which can change through time, via the agency of termite swarms that decide the patterns and rates of soil deposition (Turner, 2005). This makes the mound and its associated structures a colony-constructed adaptive interface between the colony superorganism and its broader external environment. The mound is involved in managing fluxes of mass and energy for at least two aspects of the nest environment: water balance and perturbation of respiratory gas concentrations, including water vapour partial pressure (humidity).

Colony water balance is regulated by at least two mechanisms, one short-term and the other long-term (Turner *et al.* 2006). The fungus combs damp short-term fluctuations of humidity by acting as 'humidity sponges': they store roughly 50 l of liquid water in structures that have an extraordinarily large surface area for liquid–vapour exchange. The combs are also hygroscopic, adsorbing water vapour at local humidities above roughly 80% and evaporating liquid water when local humidity falls below 80%. This has the overall effect of 'clamping' nest humidity (at about 80% relative humidity) against short-term fluctuations of water flux between the broader soil environment and the nest.

Stability of nest moisture is ensured over the longer term by active transport of water by termites. These termites commonly inhabit environments with strong seasonal variation in environmental moisture: wet summers with torrential rainfalls alternating with very dry winters (Turner, 2006). During the winter, termites mine water from perched water tables below the surface and transport it to the nest, carried either in the abdomen as imbibed water, or in dollops of wet soil (West, 1970; Abushama, 1974; Sieber & Kokwaro, 1982; Lys & Leuthold, 1994). During the wet summers, termites transport excess water from the nest into the mound in the form of wet soil. This is how the mound is initially constructed. We see here a direct example of extended physiology in action: the water homeostasis of the nest extends upward into the dynamic construction of the mound. Furthermore, mound construction reflects the homeostatic imperative of the nest: experimentally increasing the inputs of percolated water enhances the upward transport of soil into the mound (Turner *et al.* 2006).

The termite mound is also interesting in that multiple homeostatic imperatives operate upon it (Turner, 2011). The initial building of the mound is motivated by the homeostatic demands of colony water balance, but once constructed, the mound is then extensively remodelled. This remodelling is biased by the demands of a second homeostatic imperative: maintaining a steady nest atmosphere. Termites will tolerate a wide range of steady conditions in their mounds and nests, but are disturbed by rapid perturbations of atmospheric (e.g. CO_2) conditions (Turner, 2011). By building the mound upward into the turbulent boundary layer, the mound and nest environment are then exposed to turbulence-induced transient perturbations, which the termites offset by remodelling the mound. The result is a structure that filters the transient energy in turbulent wind, allowing it to be captured for driving the colony's respiratory gas exchange. From this comes the mound's other function: acting as a regulated wind-driven 'lung' for the colony.

As in earthworms, this extended physiology of termites has evolutionary implications. Water and gas regulation are examples of counteractive niche construction by the termites, which neutralizes prior natural selection pressures in their environment (Odling-Smee *et al.* 2003).

Termites inhabit a variety of tropical habitats, but one salient feature of the Macrotermitinae is that they can inhabit much dryer and hotter habitats than can other types of subterranean and mound-building termites (Deshmukh, 1989). This is made possible because the Macrotermitinae are masters of the constructed niche (Dangerfield *et al.* 1998). As long as subterranean water is available, these termites can create a humid and stable sub-environment that is embedded in a very dry physical external environment (Turner, 2006). This changes the selective regime: selective advantage that might have accrued to evolving internal organs of physiology that better handle water scarcity now accrues to the ability to construct an environment where water is more abundant.

Internal and external constructive processes and the developing EES

It can be seen that niches and environments exist inside the body, whilst physiological processes operate outside it. The active construction of selective environments suitable for subsequent developmental events emphasized by NCT parallels the thinking explicit in the exploratory behaviour of core processes and the demand-based nature of development envisioned in the theory of facilitated variation and in developmental plasticity research (West-Eberhard, 2003; Gerhardt & Kirschner, 2007; Gilbert & Epel, 2009; Moczek, 2012). In each case, organisms, or their parts, actively construct new environmental interfaces through physiological processes that enable subsequent adaptive responses.

A central theme of the EES is the notion that developmental processes have evolutionary consequences. Developmental bias is the non-random generation of phenotypes by developmental systems, with variants sometimes channelled towards functional goals. Examples include the highly biased numbers of limbs, digits, segments and vertebrae across a variety of taxa (Arthur, 2004, 2011; Galis *et al.* 2010) and correlated responses to artificial selection resulting from shared developmental regulation (Beldade *et al.* 2002). With the above parallels in mind, it becomes easier to see how developmental bias and niche construction may be viewed as essentially the same phenomena expressed inside and outside the organism. Both arise because organisms construct internal or external states in ways that modify the match between their developmental and functional environments, often in a process of active regulation (Odling-Smee, 2010). Constructive development biases the action of natural selection, either by operating internally to bias the pool of variants, or operating externally to bias how well those variants fit to their environment.

Niche construction disproportionately generates environmental states that are matched to (coherent and well-integrated with) the constructing organism's phenotype,

and hence adaptive for the constructor (Odling-Smee *et al.* 2003), as a result of which selective environments modified by niche construction are projected to differ systematically from other environmental changes (Odling-Smee *et al.* 2013). Even the more destructive aspects of niche construction, for instance the production of detritus, are the product of informed metabolism (for instance, the expression of naturally selected genes), and hence can impose directionality on environmental conditions (witness the dramatic ecological effects of seabird guano on the Aleutian Islands, Croll *et al.* 2005). The construction of internal and external environments need not be separate phenomena: for instance, symbionts play critical roles by constructing internal environments of their hosts and external environments for themselves.

What the above considerations establish is that constructive physiological processes, whether they be expressed internally to generate plasticity, developmental bias and facilitated variation, or expressed externally to generate niche construction, are potentially of evolutionary significance. One strength of the EES framework is that, unlike the MS, it recognizes and encourages investigation into these phenomena. As a result, the EES will make a valuable contribution to the integration of evolution, ecology and physiology.

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Additional information

Competing interests

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