The Matrix Account of Niche Construction

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Abstract

Niche construction theorists standardly understand niche construction to occur through organisms modifying their selection regimes. Niche construction is also commonly characterized as organisms playing an active role in the evolution of their species. In this article, we argue that these characterizations do not amount to the same thing. Organisms can take an active role in the evolution of their species without changing their selection regimes. This article describes all the ways organisms can do so. The result is a 3x3 matrix detailing all nine forms of niche construction.

1. Introduction

When thinking about evolution, it is common to characterize the environment as posing a problem—such as surviving as a large mammal in a sparse, patchy environment—and the species evolving a solution: fat-filled humps as energy stores in the case of the camel. In the parlance of evolutionary biology, the environment creates selection pressures and species evolve adaptations in response. This framing views the environment as *active* and the species as *passive*. The species is clay, the environment the sculptor.

On this understanding, the things organisms do—their behaviors and development—are triggered by evolved traits. They are evolutionary outcomes; they are part of the evolved solutions to the problems posed by the environment. They are consequences, not sources, of selection pressures.

This view of organisms as passively responding to their circumstances has been famously criticized by Waddington (1959) and Lewontin (1983), as well as, more recently, by a body of research known as *niche construction theory*, NCT (Odling-Smee et al. 2003; Odling-Smee 2024; Laland et al. 2016). The basis of NCT is the realization that organisms are not merely passive subjects of evolution, but their actions can steer the course of evolutionary processes. Organisms can run, fly, burrow, swim, they can till soil, fell trees, spread fires. All of these have ecological impacts, and many of these impacts have evolutionary consequences.

NCT is, by now, well established (see, e.g., Hui et al. 2004; Laland et al. 2016; Odling-Smee et al. 2013; Tanaka et al. 2020), although its revolutionary consequences for evolutionary biology remain contested (see, e.g., Scott-Phillips et al. 2013; Fábregas-Tejeda and Vergara-Silva 2018; Uller and Helanterä 2019). The puzzle is not whether organismic activities can have evolutionary impacts, but *how*, precisely, their activities are translated into evolutionary outcomes. Organisms can do lots of things and species can evolve in many ways. To gain ground in evolutionary biology, NCT needs to offer a general framework for how specific kinds of activities can produce particular sorts of evolutionary outcomes.

As we will see, the main way NCT conceptualizes the link between organismic activity and evolution is to claim that the class of activities that lead to selection pressure changes are the ones that have evolutionary consequences. Organisms thus construct their niche by changing their selection pressures. These pressures, in turn, affect the pace and direction of evolution. This can occur through subtle organismic activities that merely stabilize or prompt minor evolutionary changes, but can also spur more significant changes to form and function through exploring very different niches—what Ramsey and Tao (2026) label *niche prospecting*. While it is clear that organisms can play the role of changing their population's selection pressures, and that this is *bona fide* niche construction (NC), what is not well supported is the premise that changing selection pressures is the *only* way organisms can take charge of their species' evolution.

We hold that limiting NC to altering selection pressures (or selection regimes more generally) is an overly restricted conception. In other words, organisms can do other things that have evolutionary consequences. In light of this, we offer here an expanded account of NCT. We call it the *matrix account*. It organizes NCT into a 3x3 matrix, providing a total of nine forms of NC. We argue that this is a comprehensive account—it outlines all the ways organisms can influence the evolutionary future of their species through the modification of the organism-environment relationship. This novel account thus fills an important gap in evolutionary theory: a full articulation of the causal impact of organisms on their species' evolutionary fate.

2. The blue pill

The received account of NC takes organismic activities to count as NC *if and only if* they change selection pressures (Laland and O'Brien 2011, 193; for a more stringent construal, see Matthews et al. 2014).[1] Importantly, NC theorists often define an evolutionary niche in terms of selection pressures and NC as changes in these pressures (for discussion, see Trappes 2021). For instance, in the founding monograph on NCT, Odling-Smee et al. (2003) say that they "will treat the niche of any population as the sum of all the natural selection pressures to which the population is exposed" (40).

The focus of NCT has not been on whether there are ways of engaging in NC in the absence of selection regime changes, but, instead, to articulate the variety of ways that organisms can construct their selective niche and what impact this has on the evolutionary trajectories of species. We will explore the ways that NC can occur in the following section. But first, we want to point out a tension at the heart of the received view of NCT.

The characterization of NC as organisms modifying their selection pressures is not its only characterization. Another way of conceptualizing NC, which has become increasingly common, is as organisms taking an active role in their evolution (see Laland et al. 2019; Lala et al. 2024; Odling-Smee 2024). For example, Laland et al. (2008) claim: "*With niche construction*, both evolution and development are perceived as interactive processes in which *the developing organism is itself a codirector of change*" (553; emphasis added). Of course, you might think that these characterizations are equivalent: How else would an organism take an active role but through changing selection regimes?

We will argue below that there is not one, but *three ways* organisms can take an active role in their evolution. These are the three *strains* of NC. Before we describe the strains, however, we must first articulate another tripartite distinction in NC, which we call the three modes of NC.

3. Three modes of niche construction

Odling-Smee et al. (2003) proposed that perturbation and relocation—organisms changing the physical properties of their environments and moving through them, respectively—are central categories of NC. However, in recent years, NC theorists have recognized that these categories are not comprehensive and that there are different paths to selection pressure modification that subsume them—three *modes* of NC, as we term them. These modes have been variously characterized by NC theorists (see, for instance, Chiu 2019; Baedke et al. 2021). We will adopt the formulation given by Aaby and Ramsey (2022). Aaby and Ramsey didn't use the 'modes' label but instead discussed three 'kinds' of NC. We adopt 'mode' language to avoid the generic

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[1] NC theorists sometimes argue that niche-constructing activities can also influence genotype-by-environment interactions that, although they do not involve direct changes in selective pressures, matter for selection regimes and thereby shape the evolutionary trajectory of the constructor's own population (see, e.g., D'Aguillo et al. 2022; Fogarty and Wade 2022). (We thank Caleb Hazelwood for this observation.) For expository simplicity, we mostly speak about selective pressures here. What matters is that the standard account of NCT is deeply tied with selection.

talk of kinds and to contrast the three modes with the three strains we will introduce later in this paper.

To understand the three modes, consider that, within the ontological scope of NCT, there are (1) organisms, (2) environments, and (3) organism-environment relations. There are three modes of NC because each of these three can be altered in ways that carry evolutionary consequences. Consider first how organisms changing themselves can change the selection pressures they experience.

Organisms can transform themselves in a variety of ways over a wide range of time scales. A raccoon can puff out its hair when threatened, making it appear larger than it is. An octopus can change its color, allowing it to blend into the background and avoid predation. In each case, the organism is changing itself—its constitution—in a way that has an impact not just on its life but on the selection pressures that may redound upon the evolutionary dynamics of its species (Chiu 2019; Baedke et al. 2021; Aaby and Ramsey 2022). Organisms can do this relatively rapidly (through behavior) or more slowly (through development). This is what Aaby and Ramsey (2022) label *constitutive niche construction*.

Next, consider that organisms can change the physical properties of their environment in ways that have consequences for the evolution of their species. When sloths need to defecate, they climb to the ground, possibly in order to fertilize the trees they feed on (Voirin et al. 2023). By doing this, sloths increase food availability and relax selection pressures related to nourishment. Aaby and Ramsey label the modification of environments by organisms as *external niche construction*.

An organism can thus influence evolution by changing itself or its environment. But it is also possible for an organism to change its *relation* with its environment in the absence of a change to itself or its physical environment. An obvious way is movement. A mountain goat could change its grazing elevation over the seasons, grazing at lower elevations during times of snowpack and higher elevations in the summers. A monkey could dive to the ground at the sight of an eagle. A bird could follow the advance of army ants as they flush insects.

Each of these activities may have some effect on the organism's constitution or their environment. But the way organisms are changing selection pressures is by changing their organism-environment relation. (For discussion on the epistemic and ontological dimensions of organism-environment interactions, see Fábregas-Tejeda 2026). For this reason, Aaby and Ramsey (2022) labeled it *relational niche construction*. This category of NC, besides encompassing relocation (sensu Odling-Smee et al. 2003), includes cases of what has been christened 'experiential NC' (see, e.g., Lewontin 2000; Sultan 2015; Chiu 2019; Baedke et al. 2021)—organisms changing their *experience* of their surrounding conditions in ways that redound upon the evolutionary trajectories of their population.

These three modes of NC can affect evolution by affecting selection pressures. But as we will now argue, changing selection pressures is but one of the three strains of NC.

4. Three strains of niche construction

The modes of NC capture the loci of change of organismic activities. We will now describe the *three strains* of NC—the potential consequences of organisms engaging in the three modes. The strains are individuated in relation to the evolutionary effects organismic activities bring about by modifying the organism, the environment, or the organism-environment relation.

4.1 Selection-adaptation

We will begin with the standard strain. This is the familiar case of organisms modifying selection regimes through the three modes of NC. The changes in selection pressures result in adaptation—the detectable evolutionary response to this form of NC (see Matthews et al. 2014). Thus, this is a case in which organismic activities have an effect on their adaptations (see Day et al. 2003).[2] The effect can be the modification of existing adaptations or the generation of new ones through directional selection. Or, if the selection is stabilizing, the effect could be the preservation of an adaptation that would otherwise change through drift. Because this is the received strain of NC, backed by considerable empirical evidence and theoretical reflection, we will not offer new arguments for its place in the NC matrix (see section 5).

4.2 Driftability-drift

While it is clear that organisms can change selection regimes, and that this has effects on evolution, what is less obvious is that organisms can also affect how their populations *drift*. Since drift is an evolutionary outcome, if organisms can affect drift, they can thereby affect evolution through a pathway distinct from selection. We have previously introduced the idea that NC can operate in this way (see Fábregas-Tejeda and Ramsey 2024) and we argue here that this is indeed a strain of NC.

There are two important variables that affect drift: driftability and effective population size. Consider first driftability. This is a notion introduced by Ramsey (2013). To understand

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[2] We acknowledge that other evolutionary outcomes, beyond adaptation, can be obtained through NC modifying selective regimes, e.g., disruption of evolutionary equilibria, time-lagged effects in populations evolving after selection has ceased, range expansions, and even the evolution of new niche-constructing capabilities (see, e.g., Laland et al. 1996, 1999; Odling-Smee et al. 2003; Kylafis and Loreau 2008; Silver and Di Paolo 2006). We focus on adaptation because it is the main evolutionary outcome of the selection strain.

driftability, it is useful to examine the propensity interpretation of fitness (PIF; see Brandon 1978; Mills and Beatty 1979). The idea behind the PIF is that organisms have a range of possible reproductive outcomes and that these outcomes have probabilities associated with them. An elephant might have a probability of 0.15 of having 0 offspring, a probability of 0.2 of having 1 offspring, and so on, over its lifetime. Under the PIF, the fitness of the elephant is the probability-weighted average of these possibilities.

In this example, there is a heterogeneity of possible reproductive outcomes for the elephant (no offspring, one offspring, and so on). While fitness is an important variable linked to the average of this distribution in possible outcomes, there is another important variable: the *variance* in the offspring distribution. Ramsey (2013) argued that driftability just is variance in reproductive outcomes.[3] To see the connection with drift, imagine if the elephant had a probability of 1 of having two offspring. A population of such individuals cannot drift—even if the population is arbitrarily small. Only a population composed of members with nonzero driftability will drift. And the higher the variance in their reproductive output—the higher their driftability, that is—the larger the expected drift.

Organismic activities can affect both driftability and effective population size (Fábregas-Tejeda and Ramsey 2024). A bird that is disposed to lay a very large clutch may have higher driftability than one that lays a moderate number of eggs. The reason is that the large clutch may have a big payoff, but if egg predators find the nest, the mother bird may have spent so much laying the large number of eggs that she is not able to lay another clutch that season. A mother that lays fewer eggs may be able to lay another clutch. Even if the two bird types have the same average reproductive output (the same fitness, that is), they may differ in their variance in reproductive outcomes. If they do, they differ in driftability.

Organisms can control effective population size by, for instance, affecting population density or structure. If a bird species forms flocks, the individuals can affect flock size by, for instance, controlling the threshold when a flock divides into two flocks. By reshaping environmental parameters, organisms can also reduce or increase carrying capacities and thus modulate effective population sizes (see, e.g., Gurney and Lawton 1996).

Because organismic activities—the very same that may affect selective regimes—can control drift probabilities through driftability and effective population size, we are justified in seeing the driftability-drift link as a genuine strain of NC. (For empirical examples and additional theoretical arguments for how this unfolds, see Fábregas-Tejeda and Ramsey 2024.)

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[3] If fitness is about average offspring number and driftability is linked to variance in the possible offspring distribution, for fitness and driftability to be independent variables, variances in offspring number must not affect fitness. Some philosophers (such as Beatty and Finsen 1989) have argued that variance affects fitness, while others have countered this claim (Ramsey 2026).

4.3 Channeling-dappling

The third strain we are positing has heretofore not been systematically identified as a strain of NC and will therefore require a bit more discussion.[4] Ramsey and Villegas (2024) explored the question of how to characterize, in a highly general way, the role of development in evolution. For adaptation and drift *qua* evolutionary responses, there are individual-level properties—fitness and driftability, respectively—that underlie these population-level evolutionary outcomes. The project of Ramsey and Villegas was to analogously identify the individual-level property and evolutionary outcome in the case of developmental activities affecting evolution. They identified *developmental channeling* as the evolutionary cause and *evolutionary dappling* as the outcome. Thus, to make the case that channeling-dappling is a third strain of NC, we need to show that organismic activities impact channeling and dappling.

Think again of the set of possible life histories of an organism. These life histories are heterogeneous in their reproductive outcomes. The distribution of possible reproductive outcomes serves as the basis of fitness and driftability. But these life histories vary not just in the heterogeneity of their *reproductive* outcomes, but also in the *phenotypes* of the organisms. Going all the way back to the beginning of its ontogeny, a developing organism makes countless "choices," developing along one possible trajectory while foreclosing others. In making these choices, organisms produce phenotypes capable of impacting evolutionary outcomes.

Ramsey and Villegas (2024) identified the key evolutionary outcome of channeling to be *evolutionary dappling*. To understand dappling, picture a morphospace for a taxon. A morphospace is a space of possible forms (for discussion, see McGhee 2006). The concept was introduced by Raup (1966), who offered a three-dimensional space for coiled shells based on translation rate, expansion rate, and distance of generating curve from coiling axis. The beauty of a morphospace is that it allows us to place actual forms within the space of possible forms. As Raup found, and as others who have created morphospaces for other taxa have discovered (e.g., Roelants et al. 2011; Chartier et al. 2014; Smith and Donoghue 2022), the space of possible forms is incompletely filled by the actual. The possible is *dappled* by the actual. This is the dappling of Ramsey and Villegas. This dappling can extend beyond morphospaces and is a property of phenotype spaces more generally, including behavioral and physiological spaces.

Some of this dappling will be due to fitness valleys. That is, the reason that there are no phenotypes is not that such variants never arise, but that when they do so, they don't fare well. But much of this dappling will be due not to fitness valleys, but to developmental channeling. By 'channeling', Ramsey and Villegas (2024) mean to capture both the negative aspects of developmental *constraints* (Maynard Smith et al. 1985) and the positive aspects of

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[4] We note that Lala (2024) has argued that NC can be a source of developmental bias and has explored the consequences this might have for selection regimes. Uller and Helanterä (2019) have also suggested that NC could impact development (see also Lala et al. 2024).

developmental *drives* (Arthur 2001). Thus, channeling is a term for the way that the developing organism moves itself through and stakes out regions of phenotype space.

The development of an organism involves an interplay between the state of the organism and its genetic and environmental inputs. Thus, if an organism modifies inputs into its development, it can affect channeling. One way to do so is to modify development-relevant environmental variables. Consider, for instance, gazelle dung beetles. They exemplify a case of both the modification of the physical parameters of the environment and the vertically transmitted inheritance of symbionts via fecal pedestals. These alter the developmental conditions under which the phenotypic traits of larvae emerge. Rohner and Moczek's (2023) experimental results show that disruption of the external mode of NC leads to reductions in overall body size, in male-limited head horn development, and in dimorphic limb traits. This evidences a role for environmental modification in shaping the sex-specific morphospace of trait variation.[5]

Organisms can also modify themselves, changing their possible developmental trajectories. For instance, as shown by studies in *Arabidopsis thaliana*, plants can change their germination and flowering timing (which have many ripple effects on developmental traits), thus determining which seasonal environments will impinge upon them and their offspring (Donohue 2005; 2014; see also Sultan 2015; Stotz 2017). In general, there is mounting evidence that phenotypic plasticity—the capacity that organisms have to change themselves in response to environmental cues—can generate non-random variation and thereby initiate developmental bias (Parsons et al. 2020). This is the constitutive mode of NC in action.

Finally, organisms can modify their relationship with their environment, changing their channeling. For instance, organisms can relocate to different environments, becoming exposed to a different suite of abiotic and biotic factors that steer their developmental trajectories in different directions (e.g., favoring certain phenotypes while precluding others). If those relocation-prompted phenotypes become stabilized and are transmitted across generations, this could mark the beginning of the exploration of new regions of phenotype space. Additionally, in animals, learning can be a way of altering organism-environment relations and is thus a source of developmental bias (see Laland et al. 2020), especially when interactions with conspecifics lead to the production of different developmentally grounded phenotypic patterns. These are cases of relational NC influencing channeling.

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[5] The external mode of NC can eventually lead to dappling. If NC alters the environment in a way that restricts certain phenotypic outcomes, it could create a scenario where some regions of the morphospace are left unoccupied. For example, if the constructed environment disproportionately favors larger male traits (like head horns) at the expense of traits that would otherwise be more variable, this would result in a lopsided morphospace that is not fully filled across all trait dimensions.

By affecting channeling, organisms are affecting the dappling of their species. Thus, this is another strain on NC since it is one more way in which the same organismic activities are translated into evolutionary outcomes (for additional discussion and examples of this NC strain, see Fábregas-Tejeda and Ramsey, *in preparation*).

5. The red pill

We have argued that there are three strains of NC as well as three modes. The claim of the matrix account is not only that there are these strains and modes, but that each mode can be combined with each strain, resulting in nine forms of NC (table 1).

Three Strains of Niche Construction

Three Modes of Niche Construction	Selection Strain	Drift Strain	Channeling Strain
Constitutive Mode	Changing selection regimes by changing one's constitution	Changing drift probabilities by changing one's constitution	Changing channeling by changing one's constitution
External Mode	Changing selection regimes by changing one's external environment	Changing drift probabilities by changing one's external environment	Changing channeling by changing one's external environment
Relational Mode	Changing selection regimes by changing one's relation(s) with their environment	Changing drift probabilities by changing one's relation(s) with their environment	Changing channeling by changing one's relation(s) with their environment

Table 1. The niche construction matrix formed by combining the three modes with the three strains.

Our discussion of the three strains in section 4 shows us that each of the nine forms of NC are possible. With the selection strain, all three modes are part of the standard understanding of NC. The drift strain is well supported by Fábregas-Tejeda and Ramsey (2024), and we outlined above how changes to driftability or effective population size can affect drift. Finally, the channeling strain is the most provocative. While the channeling-dappling framework has already been offered, we are the first to point out that this can be a strain of NC. As we have shown, organisms can modify themselves, their environment, or the relationship between themselves and their environment in a way that affects developmental channeling—and thus dappling.

While we have established that each of the three strains and modes of NC is genuine NC, we have not yet made the case that this is all there is to NC. Might there be a fourth strain or mode? First, consider mode. The modes pertain to the thing that is modified. The organism and its environment can both be altered. And the relationship between them can be modified, even in the absence of modifying the environment or organism. This is all there is within the ontological scope of NCT. Organism, environment, and organism-environment interaction. Thus, the three modes are complete.

The completeness of the three strains is somewhat more challenging to argue for. To make the argument, let us reflect on how evolution occurs. Evolution by natural selection requires phenotypic variation, that some of the variants fare better in surviving and making offspring, and that there is inheritance—that like tends to make like. The selection process is imperfect, since evolutionary outcomes can deviate from expectation values. That is, populations can drift.

Thus, we have four elements: variation, inheritance, selection, and drift. The selection strain clearly concerns selection and the drift strain is about drift. This leaves variation and inheritance. Does this mean that there are two more strains, not one? Both variation and inheritance relate to phenotype space. Variation concerns what variants occur, and inheritance is about how the occupation of one place in phenotype space in one generation relates to the place in phenotype space occupied by a descendant. Channeling is about how organisms come to occupy the place they do in phenotype space through their developmental trajectories. How they come to occupy their place in phenotype space has implications for variation as well as inheritance. For instance, development can be more or less buffered against changes in particular genes or environmental factors. This affects variation as well as the degree to which inheritance results in phenotypic constancy. We therefore hold that the three strains are complete and that the nine forms of NC exhaust the possibilities (for additional arguments, see Fábregas-Tejeda & Ramsey*, in preparation*).

Even if completeness could be disputed, our account would still offer epistemic benefits. In empirical scenarios, for instance, it could be mobilized to investigate how an organismal activity (instantiating a mode) might have consequences for selection regimes, drift probabilities, and developmental trajectories. The strains are conceptually distinct but not mutually exclusive in terms of potential causal sources: a single organismic activity could affect more than one strain simultaneously. The NC matrix can thus serve as a reference for investigating the relative significance of evolutionary factors in a process of interest and could eventually open new ways to model the interactions between various modes of NC, selection, drift, and development.

A final point we would like to make is that we are not arguing that everything an organism does is a form of NC. On the contrary, NC is a subset of organismic activities, many of which don't have evolutionary consequences. The matrix account is, admittedly, expansive. Many more activities count as NC under the matrix account than the traditional account. Nevertheless, we hold that if NC is about how organisms affect the evolution of their species, we need to identify all the ways that organisms can accomplish this.

6. Conclusions

There has been a recent surge in research concerning the active role of the organism in evolution. Niche construction is taken to be a causal process by which organismic activities can be translated into evolutionary outcomes. We agree about the importance of NC but have argued that existing accounts of NC are incomplete and overly fixated on selection.

To complete NCT, we have argued that there are three strains and three modes of NC. Together, these compose nine forms of NC. We have established that each of the nine forms is a genuine instance of NC and that the nine exhaust NC. We hope that the reader will swallow the red pill and join us in exploring the full extent to which organisms can affect the evolutionary trajectories of their species—seeing the matrix for what it really is.

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