Driftability and niche construction

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Abstract

Niche construction is the process of organisms changing themselves or their environment—or their relationship with their environment—in ways that affect the evolutionary trajectory of their population. These evolutionary trajectory changes are traditionally understood to be triggered by changes in selection pressures. Niche construction thus necessarily involves organisms altering selection pressures. In this paper, we argue that changes in selection pressures is not the only way organisms can influence the evolutionary futures of their population. We propose that organisms can also affect drift probabilities, and that such changes should be considered niche construction. Drift probabilities can be modulated by altering population size or by affecting driftability (individual variance in possible reproductive outcomes). We consider both and provide examples of how niche construction can stabilize, increase, or dampen drift probabilities. Finally, we revisit and broaden the traditional definition of niche construction. We hold that organismic activities that modify drift probabilities should count as niche construction, even if selection pressures remain unaltered.

Keywords Drift · Niche construction · Selection · Evolutionary causation · Driftability

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1 Introduction: debating evolutionary causation

In recent decades, many theoretical disputes on evolutionary causation have emerged in biological science and the philosophy of biology. One important cluster centers on natural selection and drift—their relative importance, differentiability, and causal status. Along these lines, one of the longstanding debates in evolutionary biology has pitted selection against drift as two sources of evolutionary change (see Skipper, 2002). Scientists and philosophers have tried to disentangle their purported separate contributions to trait evolution and microevolutionary dynamics, and have put into question the scope of application and the overall explanatory adequacy of these evolutionary causes. These discussions usually take the form of *relative significance controversies* (on this notion, see Beatty, 1997; Kovaka, 2021), for instance, in ascertaining or blurring their relative strength as widespread evolutionary causes (e.g., Brandon & Fleming, 2014; Clatterbuck et al., 2013) or in accounting for phenotypic divergence in concrete empirical scenarios (e.g., Mutumi et al., 2017).

Assessing the relative significance of selection and drift requires these to be conceptually distinct. A foundational debate thus considers how—or even if—selection and drift can be distinguished. Some scholars argue that this distinction should be drawn by appealing to evolutionary outcomes (e.g., Brandon, 2005) or to underlying causal processes (e.g., Millstein, 2002, 2005). Others are skeptical that selection and drift can be individuated as separate outcomes or processes (Matthen & Ariew, 2002; for discussion, see Abrams, 2007; Jeler, 2024). This skeptical response arises from a faction in the philosophy of biology known as the *statisticalists*. Statisticalists hold that some of the central concepts that underwrite the theory of evolution by natural selection—fitness, selection, and drift—cannot be given a coherent causal construal and should be understood as convenient (abstract) statistical summaries of the manifold causal processes impinging upon individual organisms in their struggle for existence (Walsh et al., 2017). The opposing faction, known as *causalists*, holds that fitness differences, for example, can *cause* evolutionary changes (e.g., Brandon & Ramsey, 2007; Ramsey, 2013a, 2013c; for overviews, see Otsuka, 2016; Pence, 2021).

Another cluster of disputes on evolutionary causation considers the extension of evolutionary theory (see Laland et al., 2014, 2015), one facet of which involves niche construction and the idea that organisms can actively modify their environments and thus the selection pressures that shape their population's evolutionary trajectories. This idea has been formalized in niche construction theory (NCT), which "explicitly recognizes environmental modification by organisms ('niche construction') and their legacy over time ('ecological inheritance') to be evolutionary processes in their own right" (Odling-Smee et al., 2013, p. 4; see also Odling-Smee et al., 2003). Importantly, fending off substantial skepticism (e.g., Scott-Phillips et al., 2014; Gupta et al., 2017), scholars have argued that NCT motivates conceptual change in evolutionary biology as niche construction contributes to selection, development, and inheritance in meaningful ways (Uller & Helanterä, 2019). For instance, by partly determining the selection pressures to which a given group of organisms and their descendants will be consistently exposed to, niche construction can lead to adaptation, contributing to organism–environment fit (Day et al., 2003). Furthermore, sustained rounds

of niche construction can have numerous ecological and evolutionary ramifications across different timescales (see, e.g., Laland et al., 1996, 1999; see also Odling-Smee et al., 2013; Laland et al., 2016). In general, NCT underscores the epistemic import of the tenet of *reciprocal causation* between organism and environment when explaining evolutionary processes (for discussion, see Fábregas-Tejeda & Vergara-Silva, 2018; Baedke et al., 2020, 2021).

In connecting these two coexisting clusters of large-scale debates on evolutionary causation, we hold that while niche construction is indeed important because of its role in shaping selection pressures, it also has an overlooked essential role: it can modify drift probabilities. In this paper, we consider the role of niche construction in shaping drift probabilities and argue that this role (1) can have significant implications for evolutionary outcomes and (2) calls into question how niche construction has traditionally been defined.

We start by outlining the life history framework of Ramsey (2015), which will help us to uncover how niche construction can affect drift and influence evolutionary trajectories (Sect. 2). Drift has a dual nature: It can be a *deviation* from expected evolutionary outcomes and *a cause* of these deviations. Drift-as-cause is understood as an organism-level cause and is labeled *driftability*. Driftability concerns the variance in life history reproductive outcomes for an individual organism. The higher the variance in the outcome space, the higher is the probability that the outcomes will deviate from fitness-based expectations. This framework offers the advantage of characterizing drift and selection under the same causal terms (namely, variance in possible life history outcomes). Next, we present the received view of niche construction in evolutionary biology, which requires modifications in selection pressures for niche construction to occur, and we offer reasons to be wary of it (Sect. 3).

Against this background, we recount common scenarios in which niche construction changes drift probabilities (Sect. 4). We argue that niche-constructing activities can modify drift probabilities by either changing population size or by affecting driftability (even in the absence of population size change). We cover each route and provide some examples of how different kinds of niche construction bear on drift outcomes. We posit that some kinds of niche-constructing activities can (i) stabilize, (ii) increase, or (iii) dampen drift probabilities—and this has different consequences for evolutionary dynamics.

Finally, we revisit the traditional definition of niche construction in terms of organismic activities that modify *selection pressures* (Sect. 5). In light of our argument for the importance of the modification of drift probabilities via niche construction, we hold that the very conception of what niche construction is should be expanded so that for activities to count as niche construction, selection pressure changes are not necessarily required. Instead, niche construction can also operate by changing *drift probabilities*.

2 Fitness, selection, and drift: a common life history framework

To make our argument that changing drift probabilities—not just changing selection pressures—is a criterion for niche construction, we need to bring niche construction, selection, fitness, and drift within a common conceptual structure. We will do so by using Ramsey's (2015) life history framework. The basic idea is this: Every organism lives one life, and in so doing realizes a life history. But this life history is just one of many possible life histories. The features of this set of possible life histories form the basis of core evolutionary properties and processes.

Let's begin with fitness. An organism's fitness is based on its set of possible life histories—in particular, the average number of offspring over the space of possibilities (Ramsey, 2006). This is the basis of the original account of the propensity interpretation of fitness, which characterizes fitness as expected number of offspring (Brandon, 1978). To motivate the idea that fitness is expected number of offspring, consider the "fitness" of a die. If you roll a die, one side will land up. If it lands with 5 up, it is incorrect to retroactively say that its fitness is 5. This is instead its "realized fitness." Its fitness is 3.5, which is the average over all possibilities. If you want to place bets in a game of chance, 3.5 is the important number, not 5. With organisms, instead of pips on a die, the outcomes are offspring numbers. And unlike a fair die, which has a 1/6 probability for each outcome, organisms vary in the probabilities associated with their outcomes. For instance, an organism could have a 0.3 probability of having no offspring, a 0.2 probability of having one offspring, and so on. The probability-weighted average offspring number is the fitness of the organism.

If organisms vary in fitness, they differ in their set of possible life histories. When this occurs, we can inquire into what organismic properties bring about the fitness differences. The properties causally linked with higher fitness values are those that are selected *for* (for discussion, see Sober, 1984). If a fleeter antelope variant is fitter due to its fleetness, then fleetness is selected for. We can, of course, go further, asking what environmental features—such as large cats—account for fleetness being advantageous. And we can be more precise about the fleetness trait: Is it top speed that is important? Or it is the ability to maintain a speed over a certain threshold for longer? Such details matter for individual cases, but what is important here is to understand that the concept of *selection for* is based on the properties tied to differences in the space of possible reproductive outcomes.

Now consider drift. Drift is generally understood to be a population-level phenomenon that refers to *random fluctuations* in allele or trait frequencies (for discussion, see, for instance, Matthen, 2009; Masel, 2011). This can occur through a sudden natural hazard, such as an avalanche striking a population, sharply reducing its size. The remaining population will likely not have the same proportion of alleles or traits as before the hazard merely due to the random nature of the event. But drift need not involve bottlenecks such as this. Instead, there is always some degree of randomness in the lives of organisms, randomness that plays out in their reproductive outcomes.

One way of characterizing this randomness is as deviations from expectation values: fitness values provide expectations for allele or trait frequencies. If types A and B are equally fit, they have the same expectation values. This is *expectation* in the mathematical sense, which is an *average* over possible reproductive outcomes. It is

not necessarily what we would *expect* to occur. This is because frequencies can and do deviate from fitness expectations.

This way of understanding drift may lead us to think that drift is simply a population-level phenomenon, not based on organism-level properties. But what is missed in such a view is that a population cannot deviate from expectation values unless there is organism-level variance in the distribution of possible offspring number. To see this, if every organism had a probability of 1.0 of having the number of offspring they have, then there can be no deviation from expectations. Similarly, if every side of your die has 5 pips, there can be no deviation from the expected outcome of a set of rolls, independently of the number of rolls. Ten rolls of the die will result in 50, for instance. No drift from this value is possible.

Not only are population-level departures in expectation values made possible by organism-level variances in offspring number, but the magnitude of population-level departures is modulated by these organism-level variances. Ramsey (2013b) identified this individual-level cause of drift and labeled it 'driftability' in order to distinguish it from the population-level outcome, which is labeled 'drift.' To better understand how drift probabilities are affected by driftability, consider two six-sided dice. On one, the sides are 0, 10, 20, 30, 40, 50 and on the other, 22, 23, 24, 26, 27, 28. The expected number of pips for both dice is the same (25), but their variance is radically different. Roll the low variance die twice and the total will range from 44 to 56. Do the same for the high variance die and the range is from 0 to 100.

The degree to which variance matters for deviations from expectation depends on the number of rolls. Roll each of those dice 1,000 times and the cumulative total for each will be close to 25,000. But roll each die once and only the low variance die will likely be close to 25. Analogously, population size matters for drift. Just as deviations in the case of the dice are due to two things—variance and number of rolls—population drift is due to two things: variance and population size. The analogy is strong since an organism living its life is like a die being rolled. Many rolls of dice decrease deviations from the mean for the exact same reason that a large population experiences little drift.

Drift probabilities are thus to be understood as the probabilities that a given population will experience a particular kind of evolutionary outcome in the next generation: drift (that is, a deviation from expected trait or allele frequencies due to fitness). These probabilities are modulated by both the degree of variance in offspring production numbers—driftability—and effective population size. Both driftability and population size always matter for drift probabilities—remember that there simply cannot be drift if there is no variance in a population—but their relative importance varies depending on the context. For instance, with very large population sizes, differences in driftability can make little difference. Conversely, with low population sizes, driftability values can take the upper hand in determining drift outcomes. Though the details of the quantification of drift probabilities need not worry us here, we should note that when we speak of "drift probabilities" in what follows, it is not merely the probability of drift occurring that we are referring to, but magnitude-weighted probabilities: changing the magnitude of the possible deviations from expectations counts as a change in drift probabilities irrespective of the probability of drift (in some form or another) occurring.

With this understanding of fitness, selection, and drift, we are now in the position to consider niche construction.

3 Niche construction: the received view

Organisms are not mere passive objects bending to the whims of external forces. Instead, they act on the world, changing themselves and their environment. Bacteria, for instance, cluster together, flee degrading conditions, release waste products, and decompose organic matter. Animals move in space to find new habitats and they build nests, burrows, webs, pupal cases, and mounds. Plants increase humidity, alter the cycling of nutrients in the soil, and some can even emit volatile compounds that attract the predators and parasitoids of their own herbivores (Clavijo McCormick et al., 2012). In general, organisms modify their environments in manifold ways through their metabolism, activities, and choices—with potentially significant ecological and evolutionary consequences. Proponents of NCT consider the environmental modifications by organisms, and their protracted legacies across generations (i.e., *ecological inheritance*), to be evolutionary processes in their own right (Odling-Smee et al., 2003, 2013).[1]

Under this perspective, organisms, as either contributors or goal-driven agents (Aaby & Desmond, 2021), are taken to influence their own population's evolution by affecting natural selection regimes. Scholars have argued that niche construction alters and stabilizes environmental states in non-random ways, thereby imposing systematic statistical biases on the selection pressures acting on a given organismic population and even on other species that are also affected by those (constructed) environmental states (Laland et al., 2016, 2017).[2] It is in this sense that niche construction is said to have a *co-directive effect on adaptive evolution* (Laland et al., 2017). Countering the traditional asymmetrical, externalist view of adaptation (for discussion, see Godfrey-Smith, 1996), organisms can achieve *adaptive fit* by the niche construction route, such as by modifying conditions in their environments to better suit their traits and lifestyles (Laland & Sterelny, 2006).

Moreover, by modifying selection pressures, niche construction can generate causal feedback at different levels of organization and timescales (Laland & O'Brien, 2011; see also Baedke et al., 2021). For instance, sustained rounds of niche construction might have important ecological consequences by creating habitats and resources used by species other than the constructors', as well as altering ecological community structure, composition, and diversity, and hence shifting the general flow of matter and energy through ecosystems (Hastings et al., 2007; Jones et al., 1994).

As we have seen, in the existing literature, the evolutionary consequences of niche construction are always framed through the lens of impacts on natural selection. Proponents of NCT define the *evolutionary niche*, that which is partially constructed by

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[1] On the notion of ecological inheritance, see Odling-Smee and Laland (2011).

[2] For instance, Clark et al. (2020) have shown that in cases where niche construction acts to buffer environmental variation, selection gradients can exhibit reduced temporal and spatial variation, and even weaker magnitudes of selection compared to abiotic sources that are not the product of organismic action.

organismal actions, by referring explicitly—and exclusively—to selection: "We will treat the niche of any population as *the sum of all the natural selection pressures* to which the population is exposed. This includes both selection pressures that are likely to cause the occupant population to evolve further, as happens in directional selection, and selection pressures that are likely to stop it from evolving further, as in stabilizing selection" (Odling-Smee et al., 2003, p. 40; emphasis added). This definition of the evolutionary niche entails that not everything an organism does to modify its environment should be deemed an instance of bona fide niche construction. Instead, only the organism-caused environmental changes that have an effect on selection pressures are to be construed as niche construction (for discussion, see Trappes, 2021). This is especially evident in the three criteria proposed by Matthews et al. (2014) to test the presence and evolutionary impact of niche construction:

1. An organism (i.e., a candidate niche constructor) must significantly modify environmental conditions.
2. The *organism-mediated environmental modifications must influence selection pressures* on a recipient of niche construction.
3. There must be a detectable evolutionary response in a recipient of niche construction that is caused by the environmental modification of the niche constructor. (p. 247; emphasis added)

It seems, then, that niche construction has only been made intelligible through its interplay with selection. Following along these lines, Aaby and Ramsey (2022) argue that there are three ways that niche construction can occur: (1) *Constitutive niche construction* involves organisms changing selection pressures merely by changing their constitution. By growing, for example, an organism changes what and when it can eat. (2) *Relational niche construction* involves organisms changing selection pressures by changing their relation with their environment (and not necessarily the environment itself or themselves). Migration is one such example. Finally, there is (3) *external niche construction*, which involves the organism directly modifying selection-relevant factors of the environment. Building a burrow, for instance.

This taxonomy helps to clarify the various forms of niche construction but doesn't question the assumption that the fundamental currency of niche construction is the selection pressure.[3]

However, there is no principled reason why selection pressure change should be the sole currency of niche construction. If niche construction is to be construed as an evolutionary cause in its own right, the full scope of its *evolutionary consequences* needs to be spelled out. We shouldn't a priori stipulate that the consequences cannot extend beyond selection consequences. After all, the causal structure underlying evolutionary processes encompasses more than what fitness differences and selection amount to.

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[3] For other niche construction taxonomies, see Chiu (2019) and Trappes et al. (2022). For discussion on the overlaps and differences of these taxonomies, including the traditional one by Odling-Smee et al. (2003), see Baedke et al. (2021). For a targeted discussion on the different processes by which individuals can increase their organism-environment fit, see Edelaar and Bolnick (2019).

Against this background, we argue that it is important to make a distinction between the *niche-constructing activities* that individual organisms engage in and the *evolutionary outcomes* (whenever these exist) of said niche construction. For instance, the evolutionary outcome of a population of organisms modifying some physical factors of their environment could be a change of trait frequency that *deviates* from selection-based expectations due to a shift in *drift probabilities*. This would be a bona fide evolutionary outcome emerging from the same kind of external niche-constructing activities that can bring about alterations in selection pressures. By excluding drift-related outcomes, the received view of niche construction overly restricts what counts as niche-constructing activities. For this reason, we think it should be challenged.

In what follows, we put the relation between niche construction and drift into full view (Sect. 4). This will allow us to put flesh to the bones of the claim that niche construction should not be entirely defined through the selection pressure currency (Sect. 5).

4 How niche construction can affect drift probabilities

Recall from Sect. 2 that deviations from fitness-related expectations—i.e., population drift—can emerge from two factors: population size and driftability (individual variance in possible reproductive outcomes). We argue that niche-constructing activities can modify drift probabilities by changing population size (subsection 4.1) or by affecting driftability (subsection 4.2). We cover each route separately and provide examples. With this, we intend to show that niche construction matters for evolutionary outcomes that involve some form of drift.

4.1 Changing drift probabilities by changing population size

Evolutionary biologists commonly model drift by appealing to classic chance processes. A recurring analogy has been used to illustrate this concept: blindly drawing beads from one urn, representing one generation, and placing them into a second urn, representing the next generation (see Dobzhansky, 1937; for discussion, see Beatty, 1984). The beads in this analogy could stand for particular alleles or organisms with a specific trait constitution. The frequencies of these beads will likely differ from one urn (generation) to the next because of the random sampling. The magnitude of this difference is inversely proportional to the sample size. Taking three beads from an urn will likely result in a sample that is not representative of the contents of the urn. A sample of one hundred beads will likely be a more representative one. Similarly with populations of organisms: the smaller the population, the smaller the probability is that the sample is representative.

Due to this relationship, population size is assumed to play a crucial role in modulating drift probabilities. For example, if you randomly sample individuals from a very small population to create a new population, the subsequent population is likely to deviate from the original trait frequency distribution, independently of fitness differences. Beatty (1984) famously argued that random sampling could occur through

various means, including *indiscriminate parent sampling*. This refers to processes that influence which organisms of one generation will become parents of the next without any fitness-mediated sorting. Some environmental events, such as a forest fire or a flood, for instance, might kill or spare potential parents indiscriminately, without regard to particular phenotypes and their fitness differences. In all finite populations, but especially in those with a small effective population size, there will always be some non-negligible chance that trait frequencies will diverge from fitness-related expectations (Walsh et al., 2002).

So how could niche construction affect population size and have an impact on drift probabilities? For some authors, evolutionary explanations based on population size compete against explanations relying on niche construction as a causal force (see, e.g., Collard et al., 2011). However, one way in which niche construction bears upon drift through changes in population size has already been recognized by the proponents of NCT, albeit only in passing (see Laland et al., 2016, p. 196). This occurs when organisms change the physical properties of environmental factors that directly abate carrying capacities and thus correspondingly alter effective population size (see Gurney & Lawton, 1996). If environmental modifications from niche-constructing activities diminish the carrying capacity of a given population, then its composition will be more prone to deviate from fitness-related expectations in the next generation.[4]

Importantly, the opposite of this can also happen, since external niche construction can increase the carrying capacities of populations, resulting in larger population sizes (see, for instance, Krakauer et al., 2009). In this way, niche construction can also reduce drift probabilities.[5] At present, most mathematical models of external niche construction do not consider scenarios in which niche-constructing activities alter population sizes, but some scientists recognize that this could be feasible to implement and interesting to explore (see, for instance, Scheiner et al., 2021, p. 1662). Likewise, many cases in the literature discuss drift outcomes prompted by abiotic factors (such as the recurrent formation and destruction of riverbank habitats due to natural conditions, which can lead to reductions in population size in certain species of grassland plants, see Van Looy et al., 2009) without taking into account that organismic activities can also affect population size through constructed environmental conditions.

Beyond cases of external niche construction that could curtail or augment carrying capacities, and accordingly raise or lessen drift probabilities, respectively, other kinds

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[4] Here, we restrict our exposition to how niche-constructing activities affect the carrying capacities of one's own species, but it is important to stress that external niche construction can also impact population sizes of other species besides the constructor's. For instance, there is mounting evidence that so-called 'anthropogenic niche construction' (for an overview, see Boivin et al., 2016) led to, among other things, a gradual decline in effective population sizes of different plant species during their domestication (see Purugganan, 2019).

[5] Population size can also (indirectly) impact the *strength* of niche construction. For instance, even if individual organisms have small per capita effects on a given environmental setting through their external niche-constructing activities, important ecological and evolutionary effects can still accrue if population size is large enough and population density is high enough. In this paper, we will only focus on the causal arrow from niche construction to population size, but we mention that the latter variable has widespread amplifying effects on niche-constructing activities as well (see, for instance, Fuentes et al., 2010).

of niche construction can also have effects on population size. Consider relational niche construction. A group of organisms could physically relocate to a new, unfamiliar habitat, leaving many of their conspecifics behind, and one of the outcomes of this translocation in space could be an alteration of effective population size. Specifically, think of *founder effects*, so widespread in evolution, whereby new populations are established by a small number of individuals from a larger ancestral population (for discussion, see Keller & Taylor, 2008). The drift consequences of this could include drastic changes in allele frequencies, leading to fixation of deleterious alleles, depletion of allelic richness, or even to speciation or extinction (see Santos et al., 2012; Templeton, 1980).

We are not, however, implying that all cases of population bottlenecks are cases of niche construction. Niche-construction-based bottlenecks differ from, say, cases of contaminant-driven bottlenecks, where a high concentration of a contaminant in the environment is sufficient to randomly eliminate a large proportion of individuals in a population of exposed organisms (see Ribeiro & Lopes, 2013). Drift probabilities can thus change in response to both niche-construction-driven and contaminant-driven reductions in population size.

While organismic movements can increase drift probabilities, they can also have the opposite effect. For instance, by being highly mobile, a bird species could link what would have been separate small populations into fewer large ones. In so doing, they are likely to reduce drift probabilities.

Furthermore, there are cases in which relational niche construction acts upon population size without involving relocation. Consider killer whales (*Orcinus orca*), a species for which cultural specializations are well known. They are divided into ecotypes that differ in their diet due to what they have learned from other group members. Particular ecotypes, for example, can concentrate on a single prey species, despite the fact that closely related and often more abundant species are easily found in their surroundings. In this sense, killer whales are constraining and molding the relations they have to one another and to other environmental factors (e.g., by establishing culturally stable groups with particular dietary preferences and foraging methods). This has evolutionary consequences and is a case of relational niche construction sensu Aaby and Ramsey (2022). In fact, Foote et al. (2016) have shown that, in an instance of gene-culture coevolution, the plastic behavioral responses of killer whales, perpetuated by social learning, bring about the rapid divergence of ecotypes, which exhibit genome-wide differentiation despite their recent shared ancestry. This is because, among other consequences, these culturally transmitted specializations *dwindle population size* (see Whitehead, 2020). Population genomic data suggests that recent killer whale population differentiation has likely been facilitated by founder effects and drift (Moura et al., 2015). Scientists explicitly hypothesize that dependence on culturally stable, learned foraging behavior serves to isolate populations of killer whale resource specialists and this "may lead to local adaptation through disruptive selection and differentiation by drift among populations whose foraging behavior determines different spatial and temporal patterns of dispersion" (Moura et al., 2015, p. 53). This is thus a clear case in which relational niche construction shapes evolutionary trajectories and drift probabilities by impacting population size.

Sometimes organisms are in a position to choose to eat different things by altering their relations to resources and conspecifics, as we saw with the orca example. Such dietary shifts can have important physiological and morphological consequences that impact population growth. These changes to organismic constitution are cases in which, through constitutive niche construction, organisms can alter effective population size. Niche construction-driven dietary specialization can have an effect in population density in at least two contrasting ways. On the one hand, it can increase population density by reducing competition among conspecifics for particular resources, thereby preventing overexploitation and exhaustion of these resources. On the other hand, when a particular life stage of a species becomes specialized to consume a limited resource, this may decrease population density and carrying capacity. This can occur because the maximum sustainable population becomes constrained by the availability of that specific resource required during that life stage. For example, juvenile organisms might depend on a rare or scarce food source because they lack the skills or morphological traits needed to access more abundant food sources that adults can utilize.[6] Thus, constitutive niche construction (sensu Aaby & Ramsey, 2022) can affect drift probabilities by affecting effective population size.

Consider an additional example: according to Donohue (2005), for plant species such as *Arabidopsis thaliana*, niche construction frequently takes place through plasticity in developmental phenologies, and markedly influences the evolution of dispersal and generation time (more specifically, of flowering and germination timing). Taken together, dispersal and generation time are "extremely important determinants of the ability of mobile species to persist, *grow in population size*, and expand their range" (Donohue, 2005, p. 90; emphasis added). One could say that constitutive niche construction in *A. thaliana* might partially have contributed to building up population sizes (and hence potential abatements of drift probabilities). As with the case of external niche construction, constitutive niche construction can modulate carrying capacities (e.g., through physiologically induced diet specialization or reproductive specialization, for instance, in populations that have 'sneakers,' 'breeders,' and 'helpers').

In the next section, we will see that altering effective population size is not the only way in which niche construction could impact drift probabilities. The niche-constructing activities of organisms are part of what determines their driftability.

4.2 Changing drift probabilities by changing driftability

As discussed in Sect. 2, organisms vary not only in their potential for reproductive success (fitness), but also in their variance in their possible reproductive outputs (driftability) (Ramsey, 2013b). High variance in the reproductive outcome space of organisms will tend to result in a population deviating from fitness-related expectations to a greater degree; in other words, if driftability is high in individuals composing a population, drift probabilities will be correspondingly high. The opposite is also true: if driftability is low, the outcome space in terms of offspring production

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[6] We thank an anonymous reviewer for this suggestion.

numbers will be much more homogeneous and there will be a lower probability for population drift.

As a dynamic product of organism-environment interactions, niche construction influences how individual life histories are realized. On this basis, it can play a role in determining the reproductive variance that can be important in population-level drift outcomes. Let's revisit the potential evolutionary trajectories opened by relational niche construction.

In the previous section, we argued that many instances of relocation can instigate founder effects that might magnify the probabilities of population drift. But there can also be evolutionary scenarios whereby relocation affects drift probabilities *without* the mediation of the waxing or waning of population size. This could be the case, for instance, if all organisms from a given population physically move to a new habitat that exposes them to different conditions, and these conditions have an impact on the variance of possible life history outcomes for the individuals and their offspring. Driftability can thus be affected by niche-constructing activities without any change in effective population size.[7]

We can offer biological examples of this. Some caribou populations, which can be made up of thousands of individuals, undertake mass migrations. For instance, the entire Porcupine Caribou (*Rangifer tarandus arcticus*) herd completes the longest annual land migration by a mammal, covering around 4,000 km from the arctic coastal plain of Alaska and Yukon to the forested valleys and plains of north-central Yukon and western Alaska (Russell et al., 1993). The changing conditions that thousands of migratory caribou experience between their winter habitat in boreal forests and their calving grounds on the Arctic tundra considerably affect the heterogeneity of possible individual life histories and offspring numbers. While effective population size might change during migration, what is important to point out is that by having this migration as part of their life history, the variation in the reproductive outcomes of these organisms is likely different than it would be were they to stay in one region. Niche construction-affected driftability could thus have an impact on drift probabilities independently of population size.

Whether relocation has a positive or negative impact on driftability depends on the details of the situation. For instance, relocating to a better seasonal habitat could mean a lower variance in reproductive outcomes by decreasing perceived environmental heterogeneity. On the other hand, if staying put in an adverse situation means all organisms will die, then migrating would be linked to higher driftability. Relocating can also have a stabilizing effect, acting as a driftability buffer. It is also worth

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[7] Technically, an individual cannot change their driftability values (just as they cannot change their fitness values, see Ramsey, 2006). This is because driftability is based on possible life histories and such possibility spaces are not altered by realizing one of these possibilities. Similarly, rolling a die does not change its chance of landing six. For a fair die, this is 1/6, despite the fact that the instantaneous probability of landing 6 can change over the course of the toss. (It will collapse to either 1 or 0 depending on whether it lands on 6.) Thus, by pointing out that niche construction affects driftability, we are pointing out the roles that niche construction plays in determining variances in the space of possible life histories. Additionally, organisms from one generation can modify the possibility space that the next generation will have. Thus, talk of "changing driftability" values is shorthand for (1) the counterfactual role that niche construction plays in determining driftability or (2) changing the driftability values that offspring will have.

noting that the energetic cost of migration is an important factor in how drift probabilities are affected (see, e.g., Linek et al., 2024).[8]

Another potential example of relational niche construction that affects driftability, but this time without involving physical relocation, is the mate choice of turnip sawflies (*Athalia rosae*). Adults of this species collect anti-predator and antimicrobial defense clerodane diterpene compounds (clerodanoids) directly from the cuticle of plants, but also indirectly through a highly aggressive behavioral interaction, nibbling on conspecifics that have already procured clerodanoids for themselves. Consequently, any clerodanoid-free individual may be the potential mate or energetic attacker of an organism of the opposite sex which already acquired clerodanoids. Scientists have shown that females, in particular, are able to choose a mate that either has or hasn't obtained clerodanoids, making themselves more or less attractive for social interactions via nibbling (Paul & Müller, 2022). This change of social relations via niche construction (for discussion, see Kaiser et al., 2024) helps determine the potential number of offspring that each individual female chooser might have in its lifetime. In other words, niche construction is tinkering with the outcome space via driftability, and this again does not (necessarily) involve a change in population size.

We contend that the other two types of niche construction that fall under Aaby and Ramsey's categorization, namely external and constitutive niche construction, can also help to determine driftability values. Through external niche construction, organisms might modify environmental factors that could have an impact on reproductive events and the conditions influencing the prospects of reproduction. For instance, affecting environmental factors through external niche construction could have a stabilizing effect on organismic variance in possible reproductive outcomes. Earthworms modify the soil in such a way that it becomes more hospitable for themselves. For instance, they accelerate leaf litter decomposition and soil mixing in the upper layers, and these changes affect nutrient and moisture availability and lead to warmer soils with improved drainage (Frelich et al., 2019).

If when the soil becomes compacted (from being trampled by large animals, for instance), earthworms restore it to its previous state (see Piearce, 1984), this behavior can play important roles in determining their driftability values. By making driftability values lower than they would otherwise be, the behaviors help to keep drift probabilities relatively constant in the face of environmental perturbations. In other words, niche-constructing organisms can be said to *stabilize* drift probabilities if they restore environmental factors to conditions similar to those experienced by previous generations or in cases in which they aid in keeping them constant. This ensures that the conditions that influence offspring production are roughly the same, without engendering additional variance (driftability), from one generation to the next.

Caching food is another way that organisms can affect driftability through external niche construction. While creating food caches has fitness benefits, it can also have driftability effects. If caching means that the organisms are less dependent on resource heterogeneity—if the cache acts as a resource buffer—then the reproductive outcomes will tend to be of lower variance. The size, nature, and number of the caches play a role in determining variance in reproductive outcomes. A small number

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[8] We thank an anonymous reviewer for this suggestion regarding the energy expenditure of migration.

of large caches that are subject to being discovered by others will likely involve a high variance in life outcomes compared to a larger number of caches, or ones that are unlikely to be discovered.

Constitutive niche construction can also play a role in determining driftability values. Consider seasonal weight gain. Arctic grizzly bears typically gorge on summer resources—such as berries and salmon—rapidly gaining weight. Mature females can gain as much as 70% of their spring weight by the time they are ready to hibernate (Kingsley et al., 1983). The more weight they put on, the lower the chance is that they will die of starvation during the winter. Thus, weight gain can be a factor that depresses the variance in reproductive outcomes—meaning that organisms disposed to gain ample weight will have lower driftability than ones not disposed to gain as much weight. However, at the other end of the scale—not gaining weight at all—starvation will be certain. This is also a low driftability outcome. An intermediate level of weight gain—all else being equal—might therefore be associated with the highest driftability values.[9]

As we have seen, some kinds of niche-constructing activities can change drift probabilities. This can be accomplished via organisms affecting driftability values or effective population size. Because drift probabilities have important evolutionary effects, we propose redefining niche construction to take them into account.

5 Redefining niche construction

Niche construction is fundamentally about organisms taking their evolutionary fates into their own hands by changing themselves, the external environment, or the relations that hold between themselves and their environment. We have seen that one manner in which organisms can accomplish this is by changing drift probabilities. These probabilities are based on driftability values and effective population size, either of which can be affected by organismic activities. Despite these ways organisms can have evolutionary effects, niche construction is typically defined in terms of selection pressures alone. We propose taking the three kinds of niche construction identified by Aaby and Ramsey (2022) and expanding the definition of niche construction to include drift probabilities:

> Niche construction occurs if organisms modify selection pressures *or* drift probabilities through a modification of (1) their constitution, (2) the constitution of their environment, or (3) the relationship between themselves and their environment.

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[9] The relationship between weight gain and driftability might be considerably more complex, however. For example, being well-fed might prompt a grizzly bear to engage in risky fights with other conspecifics, therefore having a negative instead of positive impact on driftability values. Beyond the weight gain example, the assumption that more hospitable conditions or a better-fitting physiology not only will improve an organism's chances of survival and reproduction, but also will reduce the variance in possible life histories for its offspring, might not always hold for cases in which external and constitutive niche construction affect driftability. We thank an anonymous reviewer for making this point.

Our call for expanding niche construction is not the first such call. Uller and Helanterä (2019), for instance, have argued that niche construction, in addition to shaping selection pressures, has further impacts on development and inheritance. They have in mind cases like parents transferring extragenetic resources to their offspring, which helps to ensure the development of species-typical features, to produce variation and maintain heritable differences, and, in general, to increase parent–offspring resemblance (see also Badyaev & Uller, 2009; Flynn et al., 2013). Indeed, many scholars have recently warned against conflating 'selective niche construction' with 'developmental niche construction,' and hence disregarding the latter by foregrounding only the former (see Stotz, 2017). In these cases, developmental niche construction is deemed to have relevant evolutionary consequences (such as enhancing organism–environment fit) without these redounding directly on selection pressures (see, e.g., Rohner et al., 2024; Schwab et al., 2017).

By arguing that modifying drift probabilities should be a sufficient criterion for niche construction, we are not claiming that niche construction cannot also be expanded in other ways. One route may be identifying a distinct "developmental niche construction," as just mentioned. It might seem that we are building on the selective vs. developmental framework, simply adding a third source of niche construction. We resist this conclusion. One important reason is that at least some of what falls within the scope of developmental niche construction—such as buffering the development of offspring—affects drift probabilities. Selection, development, and drift are thus not mutually exclusive categories of niche construction. In fact, it has already been recognized that developmental niche construction can have selection consequences. Larval dung beetles belonging to the genus *Onthophagus*, for instance, engage in brood ball modifications that, among other consequences, consistently shape scaling relationships in fitness-related traits (such as changing the allometric slope of—or trait investment in—legs, eyes, and horns compared to general body size), alter degrees of sexual dimorphism, and influence their reproductive success (see Schwab et al., 2017). Thus, even a clear-cut developmental-selective distinction should be questioned.[10]

At its root, niche construction concerns organisms taking some control over the evolution of their population. If we stick with the idea that niche construction is about organisms affecting evolution, they can clearly do so through changing selection pressures, developmental trajectories, *or* drift probabilities—with the proviso that these should be individually understood as *sufficient* conditions, not *necessary* conditions for niche construction to occur.

Along these lines, the three kinds of niche construction that organisms engage in—external, relational, and constitutive niche construction—can have three kinds of evolutionary consequences: altering selection, drift, and development. It was our contention here that niche construction-prompted changes in drift probabilities, in

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[10] A fully fledged clarification of the relationship between 'niche construction' (in our broad view that also encompasses changes to drift probabilities) and 'developmental niche construction' falls outside the purview of this article, whose focus has been untangling the links between niche construction and drift. However, we recognize that such clarification is of central importance for grasping the conceptual scope of niche construction and its causal consequences in evolutionary dynamics. We reserve this analysis for ulterior work on the topic.

particular, should not be overlooked by evolutionary biologists and philosophers of biology.

We should note that our call for redefining *niche construction* has implications for how we should understand the concept of a *niche*. As Trappes (2021) notes, niche construction theorists typically employ an *evolutionary niche* concept and define it based on selection pressures alone. This is opposed to an *ecological niche* concept, which is generally more expansive. Just as we hold that drift needs to be incorporated into the definition of niche construction, it is also important to the evolutionary niche concept itself. We will leave it to another project to review and rework the concept of a niche that is suitable for an enlarged conception of niche construction theory.

Our discussion holds theoretical value beyond updating the standard definition of niche construction, particularly regarding the nature of drift. Recognizing that many drift outcomes hinge on organismic activities should make us wary of associating drift solely with abiotic chance events that decrease population size (namely, earthquakes, floods, droughts, wildfires, and other natural hazards). There is a close tie between organismic activities and variances in life history outcomes, with non-negligible consequences for how fitness-related expectations might be upturned in some scenarios. Our work has thus shown the importance of inquiring into the underlying *causes* that lead to population drift and recognizing that organismic activities are central to this evolutionary outcome.

New research directions emerge from our analysis. In connection with scientific practice, it could be explored how best to operationalize and model the interaction between various kinds of niche construction and drift (in particular with driftability). Moreover, Clark et al. (2020) have shown that selection gradients differ between constructed and non-constructed sources of selection: when environmental variation is buffered by niche constructing activities, selection gradients exhibit reduced temporal and spatial variation, and even weaker selection, compared to abiotic sources. Following this, it would be important to investigate if there are significant differences between *constructed* and *non-constructed sources of drift* that could have epistemic value for explaining evolutionary dynamics and trajectories. For instance, deviations from fitness-related expectations stemming from niche constructing activities might be more reliably obtained across a wide range of actual and counterfactual scenarios, compared to non-constructed, abiotic sources of increased drift probabilities (e.g., chance events, such as tsunamis or landslides). In this sense, our linking of niche construction and drift might also suggest that not all divergences of allele or trait frequencies that move away from fitness-related expectations are adequately construed as *random* or *accidental* fluctuations—some are due to specific organismal actions in particular ecological and developmental contexts. In this sense, not all causal readings of drift should construe this process as referring only to non-interactive, non-pervasive, indiscriminate causal influences over the reproduction of variant types in a population, as some authors have argued in the past (see Gildenhuys, 2009).

In closing, we want to stress that our reconceptualization of niche construction does not fully depend on adopting Ramsey's (2015) life history framework, in which the notion of 'driftability' becomes salient as an individual-level cause distinct from the population-level outcome of 'drift.' Our argument that different kinds of niche construction can alter drift probabilities still holds even when adopting divergent

theoretical understandings of what drift amounts to. For one, virtually all conceptions of drift underline the tight link between population size and drift. Jeler (2024) has recently surveyed philosophical debates on drift and postulated the cogency of two distinct forms of this evolutionary process that have been defended by different authors in the past: 'circumstantial drift' involves a process wholly distinct from natural selection in which differences in a circumstantial trait cause differences in the reproductive output of organisms, while 'probabilistic drift' is a process that cannot be decoupled from natural selection, as it hinges on probabilistic causal relations between heritable traits and reproductive outputs, the same relations on which natural selection could potentially act. Importantly, for both circumstantial drift and probabilistic drift, population size is a crucial deciding factor (Jeler, 2024), and we have offered sufficient reasons to consider that niche-constructing activities impact population size. Along these lines, it is reasonable to argue that niche construction could affect drift probabilities in both scenarios of circumstantial and probabilistic drift—thus fulfilling the sufficient causal conditions for niche construction to occur according to the revised definition. After all, the notion of 'population size' can be easily cashed out outside of life history frameworks.

This notwithstanding, the advantage of adopting our preferred life history framework over other conceptions of drift is that it clarifies why population size matters for drift outcomes and allows exploration of other causal avenues that could lead to shifts in drift probabilities, regardless of effective population size—namely, changes in driftability values. By understanding drift probabilities as the joint product of two factors—population size *and* driftability—we gain a better and more fine-grained understanding of how different niche-constructing activities could lead to divergences from fitness-related expectations. This, we think, is a substantial epistemic gain that a life history framework brings to foundational debates on evolutionary causation.

In this sense, our framework also paves the way for understanding how different kinds of niche construction interact with and influence other evolutionary causes beyond selection and drift. This is an important direction to pursue in future work on the topic.

6 Conclusions

In this article, we connected two nodes of evolutionary theory that have never been systematically linked before: niche construction and drift. To integrate debates over selection, niche construction, and the dual nature of drift—as cause and effect—we have embraced the life history framework of Ramsey (2015). Against this background, we challenged the received view of niche construction, which requires *sine qua non* modifications in selection pressures for any organismic activity to count as niche construction. In contrast, we hold that while the importance of niche construction rests largely on its role in shaping selection pressures—and thereby helping to guide adaptive evolution—it also has an overlooked essential role in evolutionary dynamics: it can modify drift probabilities.

External, relational, and constitutive niche-constructing activities can modify drift probabilities by altering population size or by affecting driftability values. We cov-

ered each route separately and offered some examples of how different kinds of niche construction stabilize, boost, or reduce drift probabilities. Importantly, niche construction-induced shifts in organismic variance in possible reproductive outcomes—driftability—can happen even in scenarios where there is no change in population size.

By expounding the role of niche construction in shaping drift probabilities, we called into question how niche construction has traditionally been defined. We contended that for organismic activities—specifically those that alter organisms, their environment, or the relations between organisms and their environments—to qualify as niche construction, selection pressure modification is not the only possibility. Instead, drift probability modification can also be a form of niche construction. This broadened conceptual understanding of niche construction expands its domain of application and is an important step in articulating a comprehensive, thorough appraisal of all the possible evolutionary outcomes of niche construction.

Declarations

Conflict of interest The authors have no conflict of interest to disclose.

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