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Scaffold: A Causal Concept for Evolutionary Explanations

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Abstract

The concept of scaffold is widespread in science and increasingly common in evolutionary biology. While this concept figures in causal explanations, it is not clear what scaffolds are and what role they play in those explanations. Here we present evolutionary scaffolding explanation as a distinct type of explanatory strategy, distinguishing it from other types of evolutionary explanation. By doing so, we clarify the meaning of “scaffold” as a causal concept and its potential contribution to accounts of evolutionary novelty and major transitions.

1. Introduction

The concept of scaffold is widespread in science and increasingly common in biology (Bickhard 1992; Black et al. 2020; Caporael et al. 2014; Chiu and Gilbert 2015; Holton and Clarke 2006). While this concept often figures in causal explanations, it is far from clear what scaffolds are or the causal role that scientists believe they play. Indeed, one might suspect that when scientists use “scaffold” they are simply employing a suggestive metaphor that amounts to nothing more than a synonym for “cause” or “interactive phenomena” (Charbonneau 2015). In this article, we expand on our previous work and present evolutionary scaffolding explanation as a distinct type of explanatory strategy, distinguishing it from other types of causal explanation in evolutionary biology (Jones et al. 2023; Neto et al. 2023). By doing so, we clarify the meaning of “scaffold” as a causal concept and its relevance in evolutionary explanations.

First, we survey some traditional explanatory strategies in evolutionary biology (Brown 2014; Calcott 2009; Sterelny 1996). These strategies differ in terms of focus (population or other nonpopulational focus), process driver (internal vs. external), causal robustness (robust-process vs. actual sequence), and causal character

(stochastic/statistical, mechanistic, or dispositional). Second, relying on previous work, we define “scaffold” and describe how scaffolding processes figure in explanations of evolutionary transitions (Neto et al. 2023). In so doing, we show that such explanations are distinct from the strategies previously surveyed. We conclude that scaffold is a distinctive causal concept with a specific epistemic payoff in evolutionary biology that can be particularly illuminating in accounts of major transitions and the evolution of novelty.

2. Varieties of evolutionary explanations

Due to the prominence of selection-based explanation, evolution is typically construed as a populational phenomenon. That is, it involves changes in the frequency of traits within a single population of individuals over time (Godfrey-Smith 2009; Lewontin 1970). Paradigmatically, natural selection is the differential reproduction of variants within a population, as those heritable traits that confer higher fitness tend to make their bearers increasingly numerous. In contrast, evolution by genetic drift typically occurs when some contingent factor (e.g., an extinction event) sufficiently reduces the size of a population so that random accidents concerning reproduction and death override fitness differences between members (Millstein 2021). Unsurprisingly, when contemporary natural selection or drift explanations are given for various evolutionary outcomes, the analysis is typically statistical as the process is understood to be stochastic.¹

Not all evolutionary explanations focus on populations. Instead, some scientists focus on how the structure and function of specific traits change over time. These *nonpopulational explanations* are exemplified by so-called lineage explanations (Calcott 2009). Lineage explanations describe the successive transformative steps leading to a particular phenotypic trait in a specific clade and the underlying biological (genetic or epigenetic) mechanisms that brought the organism to its current form. A classic example of this is the stepwise process through which a patch of photosensitive cells is thought to have transformed into the vertebrate eye. This kind of explanation is mechanistic in character rather than statistical. Often, they derive a significant part of their explanatory force from a series of pictorial representations of, say, the basic form or inner workings of morphological traits, rather than from statistical analyses or results (e.g., figures 2 and 3 in Calcott 2009).

Along with selection-based explanations and lineage explanations, we also find evolvability explanations (Brown 2014; Love 2003) that describe how populations are likely to change toward a particular outcome given a particular starting point. In other words, the population has a certain disposition to evolve the outcome. This outcome can be a population- or group-level trait (e.g., diversity, speciation rate) but it does not have to be (e.g., the camera-type eye). The distinctive feature of evolvability explanations is their *internalist* character; members of population X possess internal (phenotypic or genotypic) traits, mechanisms, or constraints in virtue of which outcome O will be more or less evolvable in X than population Y

¹ Explanations citing natural selection can vary in several ways and do not have to be statistical. An exhaustive typology of such explanations is beyond the scope of this article. Instead, we focus on the type of statistical explanation that has been described by Walsh, Ariew, and Matthen (2017) and is common in population genetics.

(Brown 2014, 560). Hence, evolvability explanations focus on the internal constitution of organisms. Lineage explanations are also internalist in this sense. In contrast, explanations involving drift and selection are *externalist*; population X evolves outcome O because of environmental conditions (the presence or absence of selective pressures) shaping subsequent generations (Godfrey-Smith 1998, 30). For selection-based explanations the focus is on how organisms interact with their surroundings.

Along with focusing on populations, selection-based and evolvability explanations both share another characteristic, namely, they are *robust-process explanations* (Sterelny 1996). This type of explanation identifies causal factors that give rise to a certain trend that makes a specific evolutionary outcome more or less likely to happen. Instead of giving a detailed account of how this outcome happened (as in lineage explanations), robust-process explanations suggest that the outcome would likely happen, to a greater or lesser degree, under a variety of different circumstances.² For instance, consider the fact that bats are the only mammals capable of flying. How can one explain that bats evolved wings that enable them to fly? If one appeals to selection-based explanations, one will describe the type of selection pressure acting on the ancestral populations of bats. The specificity of this selection pressure explains why bats evolved wings while closely related mammals did not. Implicitly, the selection pressure is taken to be robust to a certain degree. Even if ancestral bat populations were somewhat different, they would still likely evolve wings given the relevant selection pressure.

Interestingly, evolvability explanations also fall under the category of robust-process explanations (Brown 2014, 560). Consider again the example of wings in bats. One might argue that ancestral populations of bats had important traits that were lacking in other mammal populations, such as elongated forelimbs and their underlying genetic mechanisms (Cooper and Tabin 2008). Those traits may have made it more likely that ancestral bats, rather than other relevantly similar mammals, would evolve wings capable of flying. Furthermore, even if the environmental conditions were somewhat different, bats may have evolved wings that enable them to fly. Hence, selection-based and evolvability explanations have some degree robustness, but the former highlights external causes and the latter highlights internal ones.

Some explanatory strategies do not convey any counterfactual information about what would likely happen under similar but importantly different conditions, but instead focus on the actual sequence of events leading up to an evolutionary outcome. So, following Jackson and Pettit (1992), one should distinguish robust-process from *actual-sequence* explanations. For instance, when scientists offer a lineage explanation of the vertebrate eye, they are trying to reconstruct the actual steps of morphological, genetic, or developmental transformations that might have resulted in that trait (Calcott 2009, 58). Likewise, one might reconstruct the actual chain of developmental transformations in bone structure that resulted in bats having wings. In both examples, there is no information concerning the likelihood of transformations or what would have happened were the environmental conditions different.

² Woodward (2003) offers an articulation of this notion of robustness through the notion of invariance. According to him, X is robustly sufficient for Y if, given that X occurs, Y would still occur, even under various changes to the background circumstances.

Let's take stock. So far, we have distinguished three types of evolutionary explanations, namely selection-based, lineage, and evolvability explanations. These explanatory strategies differ regarding certain characteristics: explanatory focus (population or other); process driver (external vs. internal); causal character (statistical, mechanistic, or dispositional); and causal robustness (robust-process vs. actual-sequence). Our analysis is far from exhaustive.³ Nevertheless, it is enough to show the variety of explanatory strategies in evolutionary biology and how they address distinct causal characteristics. These explanatory strategies provide a useful contrast class against which the distinctive aspects of scaffolding explanations come into sharp relief (see section 4). Before direct comparisons can be made, however, we must first look more carefully at the kind of explanatory projects in which “scaffold” has been employed.

3. Scaffolds in evolution

In ordinary contexts, the term “scaffold” refers to physical structures that help workers build, repair, or clean buildings. These structures are temporary and enable workers to complete tasks that would otherwise be difficult, more time-consuming, or perhaps impossible. So, the function of scaffolds is to support and direct an activity to reach otherwise inaccessible outcomes. The same idea is present in the scientific uses of the concept. For instance, developmental psychologists and cognitive scientists refer to scaffolds when describing factors that support agents in completing tasks that would otherwise be developmentally and cognitively more challenging (Bickhard 1992; Clark 1997; Holton and Clarke 2006). For instance, an adult might serve as a scaffold for a child that is daunted at the prospect of crossing a street by helping them manage their anxiety. Furthermore, repeating a particular scaffolded activity enables the agent to acquire new skills that not only help them achieve the task at hand, but may also prove useful for other tasks. In our example, through successive repetitions of being helped across the road by an adult, the child might glean the meaning of various street signs and learn to pay attention to traffic. The acquisition of these capabilities not only help them to cross the street safely in the present but will also be useful when they learn how to drive in the future. Once the agent acquires the relevant skills, the scaffold is no longer necessary to achieve the goal. However, if the scaffold is removed too early (e.g., if the adult stops helping the child before they reach the other side of the street), they may fail both to complete the task and to acquire the new skills that would enable them to achieve it unassisted in the future.

In part inspired by developmental psychologists, scholars have applied the concept of “scaffolding” in both biological and cultural evolution explanations (Caporael et al. 2014; Sterelny 2003). Most recently, the concept has figured prominently in Paul Rainey and colleagues' efforts to develop experiments (in vivo and in silico) that shed light on the evolution of multicellularity (Black et al. 2020; Doulcier et al. 2020). Their work is part of a long tradition of investigating the evolutionary transition from unicellular to multicellular organisms that treats the evolution of cell cooperation as a necessary step (Maynard Smith and Szathmari 1995). The novelty in Rainey's work

³ For instance, we omitted discussion regarding the nature of historical explanations. We also do not consider the metaphysical debate whether natural selection is a statistical pattern or causal process.

is the explicit appeal to scaffolds when explaining the evolutionary origin of cooperation. Instead of focusing solely on the genetic composition and mechanisms internal to cells, Rainey and his collaborators indicate how changes in the environmental conditions could create a scaffold that produces and sustains a population-level selection process that results in the origin of cooperation. As we discuss in the following text, this exemplifies what we call “evolutionary scaffolding explanations” (Neto et al. 2023).

In “Ecological Scaffolding and the Evolution of Individuality,” Black et al. (2020) present a computer simulation that shows how ordinary individual-level selective processes can be redirected by an externally imposed scaffold to produce cooperation, an outcome that would otherwise be highly unlikely. They present a collection of connected living spaces, or “patches,” each of which is supplied with a fixed quantity of growth-limiting nutrients and seeded with a single cell. Cell replication within each patch is exponential for a time, but the size of a cell population in a patch eventually declines toward extinction as the nutrient is exhausted. Extinction results in empty patches that can later be colonized during “dispersal events,” where cells come in from populated patches. The probability of a population colonizing empty patches is proportional to the number of cells it contains at the time of colonization. Selection at the level of individual cells within a population favors mutants with higher replication rates, but this is opposed by another selection process at the level of the populations within the metapopulation that favors populations whose size is not declining at the time of dispersal. In other words, populations whose replication rates are synchronized with the period of dispersal such that the number of cells they contain is maximized when dispersal occurs are more likely to be selected. It follows that a lower replication rate (i.e., a slower climb toward maximum population size), which corresponds to lower individual-level fitness, is increasingly favored by population-level selection as the time between dispersal events increases. Cooperation between cells is thereby selected, in the sense that competition to maximize individual-level fitness within a population by maximizing replication rate is curtailed for the benefit of the dispersal of that population.

Rainey and collaborators use the expression “ecological scaffolding” to describe the set of parameters that they impose on the metapopulation to produce cooperation. These conditions include the distributed structure of populations into a collection of patches, the imposition of a limited nutrient supply, the stipulation of time for dispersal events, and how populations are chosen for colonization. These conditions are “ecological” in the sense that they are part of the external environment in which individual cells are embedded. Without such conditions, population-level selection would be less likely to arise among cells. In effect, Black et al.’s scaffolds force “Darwinian-like properties” onto populations, causing them to exhibit variation, reproduction (i.e., dispersal), heredity, and fitness. The suppression of individual-level selection in favor of population-level selection would be extremely unlikely without the imposition of the “ecological” conditions imposed by the scientists. Moreover, if these conditions were removed from the experiment, selection at the population level would disappear, and cooperation would stop evolving.

As we have argued elsewhere (Jones et al. 2023; Neto et al. 2023), the work of Rainey and collaborators illustrates the general features of evolutionary scaffolds.

Scaffolding explanations identify some agent or system and an outcome of interest for that system, which is contrasted with an alternative default outcome. The system, under ordinary conditions, will typically move toward the default outcome. Scaffolds are structures external to (or in some sense independent of) the system that redirect it toward the otherwise less likely outcome of interest. In the experiment described in the preceding text, the system is the population that, under individual selection, drives toward the default outcome of maximizing replication rate. However, under the specific conditions regarding the patch structure, amount and timing of nutritive influx, and the timing and character of dispersal events, the system gets redirected toward an otherwise unlikely outcome—population-level selection and cooperation. Notice that these different ecological features have a range of possible values only a subset of which, when appropriately coordinated, will produce this outcome of interest; in this sense, the scaffold is a structure comprising multiple parts that must be in the right configuration for the scaffolding process to take place. The success of this process depends on these multiple parts interacting with the system. This interactive process is importantly gradual; the scaffold does not merely trigger a change but instead redirects the ordinary activity of the system. If the scaffold is removed during the process or even after the cooperative outcome is attained, the system will likely move toward the default outcome again. Once the outcome is attained, the transformed system has a new set of characteristics and capacities providing possible evolutionary paths that would have been unavailable prior to the scaffolding process. This means these characteristics may be endogenized by the system, thus remaining once the scaffold is removed (Bickhard 1992; Bourrat 2022).

4. Evolutionary scaffolding explanations, causation, and evolutionary novelties

Treating the work of Paul Rainey and colleagues as a kind of paradigm case, how do evolutionary scaffolding explanations compare to those presented in section 2? Before specifically addressing each characteristic in turn, it is important to emphasize the distinctive contrastive character of scaffolding explanations. Crucial to our account is the idea that the population (or more generally, the system) under investigation has a default process that drives it toward a default outcome (Neto et al. 2023). These are the population dynamics of a population that is left to evolve according to ordinary evolutionary processes (e.g., models based on mutation, selection, and drift in a single unstructured population; in Black et al.'s experiment, the gradual increase of replication rates). The scaffold is an external structure that redirects the population away from this default outcome toward some other outcome of interest that otherwise would be unlikely or practically impossible to achieve. Interestingly, selection, lineage, and evolvability explanations do sometimes depend on contrasts between populations, traits, or outcomes, but this is not essential to the logic of these explanation types.

Moving on to the characteristics previously summarized, scaffolding explanations focus on *populations*. They explicitly refer to population dynamics and gradual changes in the distribution of traits over time. Rainey and collaborators are not primarily interested in explaining the composition and inner workings of particular traits. The

structure and function of such traits may figure in evolutionary scaffolding processes, but they are not the relevant target of these scaffolding explanations.

Relatedly, scaffolding explanations are externalist. A comparison with evolvability explanations is instructive. The distinctive feature of evolvability explanations is their typically internalist character; outcome *O* is more evolvable in population *X* compared to population *Y* because of certain traits, mechanisms, or constraints that exist in members of *X* rather than *Y* (Brown 2014, 560). The environment plays a relevant role because many of these traits, mechanisms, and constraints depend on it to be realized (Love 2003). However, these features of the environment are, in effect, background conditions that allow causal factors internal to the system to be fully expressed. In contrast, the role of the environment and its specific configurations are of central interest to evolutionary scaffolding explanations. Scaffolds are external structures that drive a population to an outcome that is otherwise unexpected, given the population's initial state. In this respect, evolutionary scaffolding explanations resemble selection-based explanations in that they explain certain evolutionary outcomes that occur by virtue of external environmental factors. Nonetheless, in a certain sense evolutionary scaffolding explanations also recognize the importance of internal factors of a system. It is the activity of the population, as redirected by the scaffold, through which the otherwise unlikely outcome is achieved. As with a literal scaffold used by builders, the internal composition, features, and activity of populations enable them to "climb" the scaffold, thus achieving the otherwise unlikely outcome. While this interaction between internal characteristics of the population and external environment might be presupposed in the statistical explanations of natural selection, it is central to evolutionary scaffolding explanations.

This brings us to the causal character of scaffolding explanations. Here, we see some important similarities with selection-based explanations. Both are stochastic and are best modeled through statistical methods, which is entirely unsurprising given that both focus on populations. However, whereas selection-based explanations often reduce the processes that shape the evolutionary trajectory of a population to some mathematical expression of a selection coefficient or average fitness, scaffolds cannot be so reduced. A scaffolding explanation articulates the parts and configuration of environmental conditions with multiple components that must fit together in a particular way to enable the system to achieve the outcome.

In the experiment by Black et al., there are several distinct parameters that must be coordinated for cooperation to evolve. The metapopulation comprises a patch structure, there must be dispersal events that are in some way coordinated, and the nutrient supply must be limited, with nutrient influxes happening with a certain regularity. There is a certain range of options for each of these parameters that will produce (with more or less likelihood) the outcome of interest—though what exactly the range of any given parameter must be to get this result depends on the values of the others. To return to the analogy with the scaffolds employed by builders, there will be multiple different lengths and positions for the standards, ledgers, braces, and boards that could create a structure that enables builders to climb to the top. However, which configurations are most likely to work or will work best depends, in no small part, on who the workers are and how they are able to climb it. Moreover, the "correct" position of any given part depends on the position of the other parts.

Table 1. Distinctive features of evolutionary explanations

	Selection-Based Explanation	Lineage Explanation	Evolvability Explanation	Evolutionary Scaffolding Explanation
Explanatory Focus	Population	Not population	Population	Population
Process Driver	External	Internal	Internal	Internal and External
Causal Robustness	Robust-process	Actual-sequence	Robust-process	Robust-process
Causal Character	Stochastic/Statistical	Mechanistic	Dispositional	Mechanistic and Statistical

Likewise, the parts of ecological scaffolds need to be configured in a particular way to enable the populations to realize the outcome of interest (for Black et al., the first step in the evolution of cooperation). This kind of complex of mutually constraining structures of difference makers that together direct a particular type of causal process shares a good deal with mechanistic accounts of causation. In this sense, evolutionary scaffolding explanations are not only statistical/stochastic but also mechanistic.

It should now be clear that, like evolvability and selection-based explanations, evolutionary scaffolding explanations are robust-process explanations. They identify a set of causal factors that make a specific evolutionary outcome likely to happen in a variety of different configurations and with various background conditions. Were it not for the introduction of the scaffold, ordinary selection pressures would, most likely, prevent the outcome of interest—in the Black et al. study, the evolutionary of cooperation.

The preceding analysis enables us to better understand what is distinctive about evolutionary scaffolding explanations (table 1). As exemplified by the work of Rainey and collaborators, evolutionary scaffolding explanations focus on populations and are robust-process explanations where both internal processes and an external structure interact to drive an evolutionary process. While, like most explanations that focus on populations, the account is statistical/stochastic, the scaffold has an importantly mechanistic character due to the specificity of the scaffold's configuration.

This analysis also reveals the distinctiveness of scaffold as a *causal* concept. Scaffolds are causes in the sense of difference-makers, something that can be expressed using counterfactual and interventionist accounts of causation (Woodward 2003). But more than this, they interact over time with a system (i.e., a population) to both create and sustain the outcome of interest (Neto et al. 2023). No mere trigger, if scaffolds are removed too early, this process will end, and the outcome of interest will not be realized. In this sense, scaffolded processes are initially revertible (Ross and Woodward 2022), at least, within a certain time frame. In the process of interest to Rainey and colleagues, removal of the scaffold will lead the system to revert to individual-level selection, unless some other evolutionary process endogenizes the cooperation created by the scaffold first. Hence, while scaffolds produce initially revertible changes, the sustained interaction between scaffolds and the system can lead permanent or long-lasting transformations, which then open new possible evolutionary paths.

Given this transformational capacity of scaffolded processes, it is no surprise that evolutionary scaffolding explanations are useful when explaining major transitions in evolution, such as eukaryogenesis or the evolution of multicellularity (Black et al. 2020; Bourrat 2022; Douclier et al. 2020). The puzzle posed by such major transitions is that they seem to require fundamental changes in how evolution works or the levels at which evolutionary processes operate. For instance, a new level of selection appears to rely on a new level of entities with selectable properties, but how can these entities evolve without already assuming a new level of selection? As Griesemer (2000) aptly notes, the problem is that new levels of selection presuppose what they are supposed to explain.

Evolutionary scaffolding explanations offer a solution. They may explain how evolutionary novelties can first arise from the interaction of a population with an ecological scaffold that radically redirects its evolutionary trajectory, overcoming ordinary selection processes to produce entirely novel characteristics that significantly alter the future possible evolutionary paths and outcomes. Relatedly, scaffolding explanations may be particularly informative for evolutionary events that are otherwise difficult to explain. Indeed, ecological scaffolds may be quite uncommon. After all, to get a sustained scaffolding process, the components of the scaffold must be in the right configuration for some time and there may not be any causal connection between the components that makes this probable. Some reflection on the kinds of natural processes that are analogous to Black et al.'s nutritive influx frequency, patch structure, and dispersal events should make the point. Doubtless, one might come up with a just-so story where all parts of a scaffold are co-occurring and mutually coordinating, but it is just as likely (arguably, more likely) that the occurrence of the components and configuration of the scaffolds that have driven the evolution of major transitions or striking novelties are historical accidents. These are, however, empirical questions and thus beyond the theoretical goals of this article.

5. Conclusion

The concept of scaffold is not uncommon in the biological sciences, but its meaning and relevance has been unclear. Building on our previous work, we have clarified the meaning of scaffold as a causal concept in evolutionary biology. Evolutionary scaffold are environmental structures that, through their interaction with a population, redirect ordinary evolutionary processes to produce otherwise unexpected outcomes. The concept figures in a distinctive explanatory strategy, namely evolutionary scaffolding explanations. We have distinguished this strategy from traditional modes of explanation in evolutionary biology—selection-based, evolvability, and lineage explanations—and we have briefly suggested why it is a promising approach to explaining evolutionary novelty and major transitions.

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