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Scaffolds and scaffolding: an explanatory strategy in evolutionary biology

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Abstract

In recent years, the explanatory term "scaffold" has been gaining prominence in evolutionary biology. This notion has a long history in other areas, in particular, developmental psychology. In this paper, we connect these two traditions and identify a specific type of explanatory strategy shared between them, namely scaffolding explanations. We offer a new definition of "scaffold" anchored in the explanatory practices of evolutionary biologists and developmental psychologists that has yet to be clearly articulated. We conclude by offering a systematic overview of the various dimensions of scaffolding explanations that further suggests both their usefulness and range of application.

Keywords Scaffolds · Scaffolding · Development · Evolutionary explanations · Causality · Multicellularity · Evolutionary origins

Introduction

In ordinary language, scaffolds commonly refer to physical structures that help workers to build, clean, and repair buildings. These structures are typically temporary and enable workers to complete tasks that would otherwise be beyond their reach, or, at least, much more difficult or time-consuming. Alongside this ordinary use, the term "scaffold" appears in a variety of scientific contexts, such as ecology, developmental psychology, cognitive science, biotechnology, and cultural studies

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(Bickhard 1992; Clark 1997; Sterelny 2003; Caporael et al. 2014; Chiu and Gilbert 2015; Love and Wimsatt 2019). Nevertheless, it is unclear what these contexts have in common and whether the term "scaffold" plays a robust explanatory role or is merely an evocative metaphor.

The scientific use of "scaffold" first gained traction in developmental psychology. Lev Vygotsky (1978) has been credited as a pioneer in this regard (Reiser and Tabak 2014), while the work of Mark Bickhard (1992) is often used as the main source for discussing developmental scaffolds and their role in human development. For these psychologists, scaffolds are resources that are exploited by agents to accomplish a learning task or solve a problem. These resources help the agent deploy or acquire a set of skills and competencies that might otherwise be beyond them. In this sense, scaffolds assist agents in achieving learning outcomes that they would be incapable of (or, minimally, have difficulty) accomplishing on their own.

In recent years, the terms "scaffold" and "scaffolding" have made their way into evolutionary biology. Here, scientists are interested in examining how particular types of changes in the environment can result in otherwise unlikely evolutionary changes in populations (whether of conspecifics or of multispecies communities). For instance, while the evolution of cooperation might be hard to obtain from standard conditions of individual-level selection, the imposition of particular environmental structures, specifically configured as *ecological scaffolds*, render such transitions considerably more likely (Black et al. 2020; Doulcier et al. 2020).

Despite being increasingly popular in scientific contexts, "scaffold," as an explanatory term, has, as yet, received no adequate definition or characterization. Often, it is used to generically refer to any temporary conditions that causally facilitate or contribute to the accomplishment of a complex outcome (Wimsatt and Griesemer 2007; Caporael et al. 2014). As one critic has complained, scaffolding processes seem to encompass "pretty much any interactive phenomena above physics and inorganic chemistry" (Charbonneau 2015, p. 230). In other words, a number of scientists and philosophers use the term "scaffold" so loosely that it does no real explanatory work.

The few attempts to define the term depend on merely suggestive metaphors or are peppered with problems. For instance, Bickhard (1992) describes scaffolding in developmental psychology using evolutionary terms, such as "selective pressure" (1992, p. 168), yet fails to explain them, so it is unclear whether he means it purely metaphorically or has some literal cumulative selective process in mind. More recently, Veit (2022) defines "scaffold" as the external induction or support of a property Y in a process/system Z, such that Y should at some point become part of the process/system (i.e., Y should be internalized or "endogenized") (p. 171). Requiring internalization makes his definition overly narrow in the context of evolutionary biology, as we discuss below.

Of course, the lack of a clear definition for "scaffold" is not necessarily a problem. It is widely accepted that many useful concepts in science are ambiguous, metaphorical, or resist traditional definition (Keller 2009; Brigandt 2012; Neto 2020; Novick and Doolittle 2021; Reynolds 2022). However, rather than simply assuming this or even dismissing the term as mere rhetoric or little more than a synonym for "cause" or "causal process," it is worth carefully considering whether the various uses share a common meaning. When scientists talk about "scaffolds" and "scaffolding" might they be gesturing at a type of explanation that has not yet enjoyed careful philosophical analysis?

In this paper, we identify the commonalities between developmental psychologists' and evolutionary biologists' usage of "scaffold," identifying a common explanatory strategy—*scaffolding explanations*—associated with these uses. In recent work, we have very briefly described some aspects of this strategy, but here we offer an account of scaffolding explanations that is both conceptually and historically robust (Neto and Meynell forthcoming). In Sect. 2, we describe how developmental psychologists employ the term "scaffold." In Sect. 3, we introduce the work of Paul Rainey and collaborators (Black et al. 2020; Doulcier et al. 2020) as examples of recent discussions of scaffolding in evolutionary biology. In Sect. 4, we draw from some philosophical analyses of causal explanation to articulate the common features of scaffolding explanations in developmental psychology and evolutionary biology (Sects. 4.1 and 4.2). Our general analysis of scaffolding explanations lends itself to a definition of "scaffold" (Sect. 4.3). This definition has modest aims: it is meant to highlight how scaffolds figure in those explanations rather than to offer a single, correct, and ultimate characterization of what scaffolds are. We also compare our definition with alternative characterizations present in the literature. In Sect. 5, we address the specificity and potential of scaffolding explanations in evolution. This potential comes from the way that scaffolding explanations offer a promising strategy for investigating evolutionary origins.

Developmental origins

The use of "scaffolds" in scientific explanations can be traced back to Vygostky's (1978) notion of the *zone of proximal development*. This refers to the range of problem-solving activities that a human agent can only successfully perform with the help of more capable peers (1978, p. 86). Building on Vygotsky's view, developmental psychologists discuss cases in which an agent relies on someone or something to accomplish a certain developmental or learning outcome (Wood et al. 1976; Ratner and Bruner 1978; Rogoff 1990). Mark Bickhard (1988; 1992) discusses the role of scaffolding in human developmental psychology extensively. According to him, psychological development is a gradual process in which humans actively interact with their environment to acquire new skills and behaviors. Interestingly, Bickhard employs evolutionary terms to describe this process. Each agent naturally "varies" their behavior in specific environmental contexts, e.g., a classroom. The environment establishes a "selective pressure," in other words, a context in which certain human behaviors might be advantageous or disadvantageous (1992, p.169). Advantageous behaviors are those that lead to successful outcomes. Development is the gradual process of acquiring these behaviors through trial and error.

Scaffolds have an important function in this view of development. As the agent actively engages with an available resource, certain aspects of the selective pressure can be "blocked" (1992, pp. 169–170). The process of scaffolding occurs when the introduction of a distinct resource—a scaffold—modifies the conditions under which an agent can successfully engage with specific resources within their environment, increasing the likelihood that the agent will achieve a particular outcome. (To clearly distinguish the resources that constitute the scaffold from scaffolding *processes*, we find it useful to restrict the noun "scaffolding" to refer to the process in which the agent actively employs or engages with the relevant resource or resources. In contrast, the noun "scaffold" refers to the set of resources in the particular configuration that makes the process of scaffolding possible. We adopt this use of "scaffolding" and "scaffold" from here on.)

Bickhard notes that anxiety management is an important issue that children face when they confront novel situations (1992, p. 170). Imagine a child trying to cross the street for the first time. The child has to master several skills to successfully do this by themselves. Being in an anxiety-inducing environment is part of the "selective pressure" acting on the child. A caregiver might serve as a scaffold in this scenario. The mere presence of the caregiver during the crossing might give comfort and reduce the anxiety of the child, who then is much more likely to reach the other side of the street safely. In this example, the presence of the caregiver modifies the child's environment in a way that reduces the obstacles to the child's achieving their goal.[1]

Now imagine that the caregiver helps the child to cross the street multiple times. The caregiver might teach the child how to read street signs or how to pay attention to the traffic—perhaps employing easily remembered heuristics, like "Stop, look and listen" that the child can repeat to themselves. In this way, the scaffold/caregiver not only provides a means of reducing anxiety but supplies other resources, which, in concert with anxiety reduction, make it far more likely that the child will attain the capacity to cross the street safely than if the child were simply left to their own devices. Each time the child successfully crosses the street with the adult, they are in the process of gaining new skills and over time they may depend on the adult less and less. Furthermore, the skills acquired—the capacity to read street signs and pay attention to the traffic—will serve the child later on by providing the basis for the acquisition of further skills, as for example, when they try to get a driver's license. In this way, scaffolds and scaffolding processes facilitate the continuous acquisition and emergence of new human competencies. So, if we want to explain how this child developed the capacity to cross the road, the presence of the scaffold and the scaffolding process play a key role.

From this overview, we can glean eight central features present in *scaffolding explanations*. These are features of the explanations themselves, the scaffolding processes, the scaffold resources, or the system (in our case, the child) that engages with the scaffold (Table 1).

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[1] Some readers might balk at the treatment of a caregiver as a developmental scaffold given the complex and long-term dependency of children on their parents. However, notice that different adults (non-parents) can function as developmental scaffolds in the example above. Furthermore, there are countless other examples of developmental scaffolds in child development. For instance, the inclusion of training wheels on a bicycle increases the ease and probability of a child learning to ride a bicycle through removing the intermediary obstacle of not being able to balance on the bicycle. We thank an anonymous reviewer for this suggestion.

Table 1 Central features of scaffolding explanations

Feature	Description
(i) Contrastive Explanation	Scaffolding explanations contrast different outcomes
(ii) Probability Increase	Scaffolding explanations identify the increase in probability of an outcome in the presence of the scaffold
(iii) Independence	The scaffold is independent of or external to the system that interacts with it
(iv) Responsiveness	The system is active and adjusts and responds to the presence the scaffold
(v) Causal Sustenance	The scaffolding process continuously sustains the activity of the system
(vi) Temporality	The scaffold can become redundant after some time
(vii) Transformation	The system acquires traits or capacities during the scaffolding process that are novel to that system
(viii) Cumulative	The outcomes achieved by a scaffolding process often allow new possibilities of transformation unachievable from the system's pre-scaffolding state

First, explanations involving scaffolds are *contrastive*. At least implicitly, they contrast an outcome of interest (e.g., the capacity to cross the street successfully) with a *default* outcome (e.g., failing to cross the street successfully). Such explanations also contrast two ways of achieving the outcome of interest—through the presence of the scaffold and scaffolding process or despite their absence. The second feature is a further specification of the first; scaffolding explanations identify processes that facilitate the successful completion of an otherwise unlikely, outcome. In short, scaffolds *increase the probability* of the outcome of interest. Third, the scaffold (in our case, the adult caregiver) is in some sense *independent* of or *external* to the system. Fourth, the system must actively *respond* to the presence of the scaffold, interacting with it, using it or at least adjusting to it. The point is that it is through the system's activity, directed by the scaffold, that the outcome is achieved. This entails the fifth feature; the process of scaffolding is a *causally sustaining* one. It is thorough the interactive process that the scaffold sustains the system's transformation over time, producing the outcome. If the scaffold (in our case, the caregiver) is suddenly removed during the scaffolding process before the outcome is achieved, this process stops and the outcome becomes, concomitantly, less probable. Sixth, scaffolding is typically *temporary*, lasting only until the system achieves the outcome, at which point the scaffold may become redundant. Seventh, the process of scaffolding is *transformative*. In developmental psychology, the child is transformed through the acquisition of a skill or capacity that they did not possess before. In many cases, this transformation is necessary for the acquisition of other skills and capacities, pointing to the eighth feature of scaffolding explanations—they are often one step in a larger explanation of *cumulative* change. Scaffolding processes facilitate the achievement of otherwise unlikely outcomes, which shift the possibility space for the system, enabling new transformations, perhaps through additional scaffolding processes, which in turn shift the possibility space and so on. Significant changes might result from this dynamic.

In recent decades, scaffolds and scaffolding explanations, inspired by those in developmental psychology, have begun to appear both in philosophy of biology and several scientific contexts (Clark 1997; Griesemer 2000; 2014; Sterelny 2003; Caporael et al. 2014; Chiu and Gilbert 2015; Love and Wimsatt 2019). We are going to discuss some of this work later, contrasting it to our definition of "scaffold" (Sect. 4). However, before doing so it is useful to familiarize ourselves with some cases of scaffolding explanations that have already enjoyed some philosophical scrutiny (Veit 2022; Bourrat 2022). These are cases of scaffolds in evolutionary biology, which, as we will see, share the features identified in this section.

Scaffolds in evolutionary biology

Paul Rainey and colleagues have recently adopted the notion of scaffolding as a key explanatory idea (e.g., Rainey and Kerr 2010; Libby and Rainey 2013; De Monte and Rainey 2014; Rainey and De Monte 2014; Rainey et al. 2017; Rose et al. 2020; Doulcier et al. 2020; Black et al. 2020). Their primary objective is to investigate mechanisms and processes that can explain the evolution of multicellularity—how populations of single celled organisms might evolve into populations of multicellular individuals. Their efforts are predicated on a theoretical framework that asserts that explaining the evolution of multicellular individuals requires explaining how heritable variation in fitness can be established at the level of groups of cells (Rainey and Kerr 2010; Hammerschmidt et al. 2014). They employ computer simulations and in vitro experiments involving populations or communities of microbes upon which scaffolds are imposed.

Any account of the transition from single-cellular to multicellular life must at a minimum explain how individual cells evolve cooperative functions that benefit the collective. Explanations that appeal to pre-existing traits of individual cells (e.g., by quorum sensing, Abisado et al. 2018) or that consider a single population (e.g., kin selection, Hamilton 1963, 1964) or community (e.g., by biotic–abiotic feedback, Williams and Lenton 2007) already exist. Scaffolding explanations, by contrast, are based on the imposition of external ecological factors that curtail individual fitness in exchange for the persistence of the collective in the context of a "population of populations" (Levins 1969)—a metapopulation (Levins 1970; Wade 2016).

Black et al. (2020), for example, propose a computer simulation in which individual living spaces or "patches" are each supplied with a fixed quantity of growth-limiting nutrient and seeded with a single cell. Cell growth within each patch is exponential for a time, but the size of a population eventually declines toward extinction as the nutrient is exhausted. Selection at the level of individual cells within a single population favors mutants with higher growth rates, but this is opposed by the imposition of dispersal from one patch to another. With each dispersal event a population has some probability of being selected that is proportional to the number of cells it contains. When a population is selected, an individual cell is drawn from its numbers and placed into an empty patch with a fresh nutrient supply. Thus, the single cell founds a new population and dispersal constitutes a form of population-level reproduction. Populations whose growth 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 growth 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 growth rate is curtailed for the benefit of the dispersal and persistence of that population's genotype.

Rainey and collaborators use the expression "ecological scaffolding" to describe the set of external conditions under which cooperation between cells—the first step toward the evolution of multicellularity—can more likely emerge. These conditions include the distributed structure of populations (i.e., their occupation of patches in a metapopulation), the imposition of a limited nutrient supply, and the means by which populations are selected for population-level reproduction. These conditions are "ecological" in the sense that they are part of the external environment in which individual cells are embedded. Black et al. (2020) argue that the imposition of an ecological scaffold can force Darwinian-like properties onto populations, such as population-level variation, reproduction, and heritability (Lewontin 1983).[2]

Scaffolds play a central role in Rainey's studies, since it is the scaffold alone that imposes Darwinian-like properties of variation, differential reproduction, and heritability onto collectives of cells, which overrides individual-level selection. Importantly, the curtailment of individual-level fitness can only be maintained while the scaffold is in place. This means that the cooperation that evolves by scaffolding in these studies represents an intermediate state of organization but does not fully explain the emergence of multicellularity. Presumably, some other process is required to make this a permanent or stable collective-level property and secure a major evolutionary transition. Rainey and collaborators do not specify any such process, but they recognize that some type of stability or internalization ("endogenization") of that property is necessary for completing the transition (see also Bourrat 2022).

Rainey and collaborators do not claim originality for their use of the scaffold concept but cite Godfrey-Smith (2009) and James Griesemer (2000), who discuss scaffolds in the context of virus replication and developmental biology, respectively.

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[2] In another study (Doulcier et al. 2020), Rainey and collaborators employ a different set of external conditions to promote cooperation, this time in a multispecies microbial community. In this case each patch in a population of communities or "metacommunity" is occupied by two species, one that is red in color and one that is blue. Both feed on the same nutrient, which is continuously supplied. Selection within a community consequently favors the species with the higher growth rate. In the absence of the scaffold this would yield a single-species population of one color or the other. However, following each period of community growth, communities that are closer to purple in color, corresponding to an equal number of red and blue cells, are artificially selected. The remaining communities are culled. Collectives of cells are then drawn from selected communities to colonize empty patches. This process opposes individual-level competition and favors the reproduction of communities in which the growth rates of the two species are balanced in a way that generates approximately equal numbers of red and blue cells. Once again, the ecological scaffold generates a kind of cooperation, this time between different species. This, they argue, is the first step towards the permanent evolution of collective-level heritability.

As Godfrey-Smith points out, viruses do not have all the necessary machinery to replicate by themselves but must rely on mechanisms of the host cell. These external resources serve as scaffolds because they enable virus replication (2009, p. 88). Similarly, Griesemer indicates that organisms can only develop if they rely on material parts transferred from their parents during reproduction. In this sense, external resources provided by the parent serve as a scaffold for organismal development (see Sect. 4.3). Rainey and his collaborators conclude "that Darwinian-like properties can be scaffolded by the environment in much the same way that reproduction in viruses is scaffolded by the host cell or that development can be scaffolded by overlap of parts between parents and offspring" (Black et al. 2020, pp. 431–432).[3]

It is worth noting that other studies in evolutionary biology rely on the same or similar ideas of scaffold and scaffolding processes. For instance, Michael Sieber and colleagues investigate the evolution of host–microbe associations (2021). They discuss how specific environmental conditions ("scaffolds") can impose and drive population dynamics that facilitate the early evolution of those associations. These conditions increase the probability of hosts housing slow-growing microbes that do not benefit them, a scenario that is initially considered to be unlikely. Such conditions are supposed to be orchestrated and work together to help populations reach and maintain a certain evolutionary outcome. We suspect that such reliance of de facto scaffolds to explain evolutionary outcomes might be more prevalent and older than the recent appearance of the term "scaffold" in the literature might suggest.

At this point, one might ask what the use of "scaffold" in evolutionary biology and developmental psychology have in common and whether scaffolding constitutes an illuminating, useful, or distinctive explanatory strategy.[4] We answer these questions in the remainder of this paper.

Explicating scaffolds

In Sect. 2 (Table 1), we described eight notable features present in scaffolding explanations in developmental psychology: (i) the outcome of interest is contrasted with a default outcome and the presence and absence of the scaffold are also compared; (ii) the presence of a scaffold makes an outcome of interest more likely to happen; (iii) the scaffold is independent of or external to the system; (iv) the system actively

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[3] By referring to the examples of virus replication and organismal development, Rainey and colleagues indicate what is most relevant for them in the metaphorical content of "scaffold." Scaffolds are external supports that enable activities and processes that would be impossible or hard to obtain otherwise. The exact nature of this support (e.g., whether is sort of environmental constraint) is not addressed. This point will become clearer in Sects. 4 and 5.

[4] We do not assume that evolutionary biologists only use "scaffold" in the way exemplified in this section. Rather, we just point out one prominent way in which evolutionists employ the term. Our project is very much in the spirit of a Hempel-style explication (1962, pp. 15–6), albeit only of one type of explanation, rather than scientific explanation *in toto*. Explications elucidate vague pre-theoretical uses of terms and refine these concepts them so that they are more precise and better able to convey their meaning and more open to useful analyses. The key with explication is not to radically change the meaning and no longer applies to key cases, which is why we return to these paradigm examples.

responds to the presence of the scaffold, using it or adjusting to it to produce the outcome of interest; (v) the scaffolding process causally sustains the activity of the system; (vi) the scaffolding process is temporary; (vii) it typically transforms the system, providing new skills, properties, or capacities that it did not have before; and thus, (viii) it opens up a new space of possibilities, inaccessible to the system in its previous state.

We argue that each of these features has an analogue in the work of Rainey and collaborators, described in Sect. 3. They are interested in the way the presence of their ecological scaffold increases the probability of the emergence of cooperation (ii, vii). The scaffold itself is clearly external to the system and directs its reproductive activity over generations (which, otherwise, would evolve according to individual-level selection) to reach the outcome of interest, (i, iii, iv, v). Once cooperation has been achieved through the imposition of the scaffold the scaffolding process is complete (vi, vii). New evolutionary processes and outcomes then become possible, such as the endogenization of the trait, and ultimately the many other evolutionary possibilities associated with multicellularity (vii, viii).

What is less clear is how scaffolding explanations relate to other accounts of causal processes in the philosophy of science. While it might appear that we are suggesting a totally novel explanatory strategy, in fact, we think that the distinctive character of scaffolding explanations may have been overlooked because of their continuity with other approaches to explanation. In this section, we show how scaffolding explanations share features with two other approaches to explanation but are more specific, pertaining to a more limited set of phenomena. In doing so, we both elaborate the features discussed above and further elucidate the commonalities between the uses of scaffolding explanations in evolutionary biology and developmental psychology. We conclude the section by discussing some current definitions of "scaffold" and by proposing a new definition.

Probability, contrastive explanations, and causally sustaining processes

A scaffolding explanation is meant to explain how a system—such as a developing human or evolving population or community—might acquire a new state in the form of features or capacities that are novel to that system. Such explanations are only valuable when the new state would be unlikely or even impossible without the presence of the scaffold and scaffolding process (thus the necessarily contrastive and probabilistic character of scaffolding explanations). For example, it is more likely that the child will learn to manage their anxiety and develop the capacity to successfully cross the road if a caregiver has helped them acquire the relevant skills. Likewise, the imposition of an ecological scaffold curtails the effects of competition between individual cells allowing the emergence of cooperation—a result that might be so improbable without the scaffold that it would effectively be impossible. The outcome of interest is typically merely probable, not certain, even when the relevant scaffold is present and even if the scaffolding process is initiated. In other words, the outcome is stochastic rather than necessary.

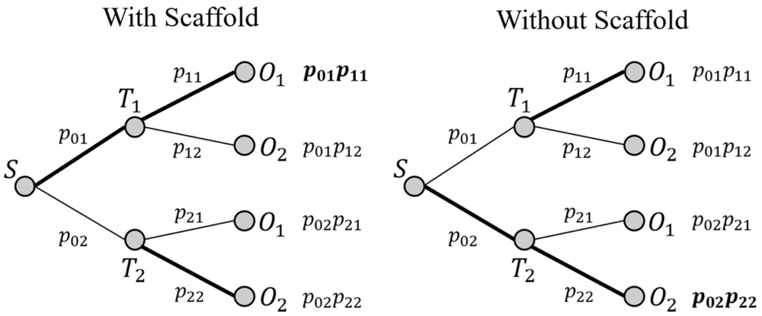

Fig. 1 The probabilistic aspect of scaffolding explanations

The contrastive and probabilistic nature of scaffolding explanations can be represented using the kind of diagram common in discussions of narratives and historical explanations (Beatty 2016; Desjardins 2011; Ereshefsky and Turner 2020). Such diagrams represent dependence relations among changing states and their paths (Fig. 1).

Nodes correspond to states or outcomes. The node S represents a system in its initial state, node O_1 the outcome of interest and node O_2 the default outcome. Node T_1 represents the transient state that is more likely when the scaffold is in place (left image) and T_2 the transient state that is more likely to be realized when the scaffold is not in place (right image). The thickness of each branch is proportional to probability, and each bifurcation corresponds to a probability distribution. The probabilities p_{01} and p_{02} are therefore assumed to add to one, and similarly for other pairs of probabilities. The figure shows how the probability that the outcome of interest will be realized is greater when the scaffold is in place compared to when it is absent, $P(O_1|\text{with scaffold}) > P(O_1|\text{without scaffold})$. S represents the initial state of the system—in our developmental example, a child who means to cross the street. T_1 represents a transient state that is associated with the scaffolding process—the suspension of the child's anxiety—and T_2 a default state—the child remains anxious. Each has some probability of occurring (p_{01} and p_{02}) that depends on whether the scaffold (an accompanying adult) is in place. It is assumed that the suspension of anxiety is more likely when the scaffold is in place (i.e., $p_{01}|\text{with scaffold} > p_{01}|\text{without scaffold}$). In either case, outcome O_1 (the child crosses successfully) is more likely given T_1 (the suppression of anxiety), i.e., $p_{11} > p_{21}$. It follows that the probability that the outcome of interest will be realized is higher when the scaffold is in place: $P(O_1|\text{with scaffold}) > P(O_1|\text{without scaffold})$.

Viewing Fig. 1 in the context of our evolutionary scenario (Black et al. 2020), S represents an unstructured population of cells, all genetically identical. The transient state T_1 is a structured population with diversity in the mean growth rate between groups arising from mutation and drift within groups. The transient state T_2 is a single unstructured population with limited diversity because mutants with lower growth rates are likely to be eliminated by purifying selection. In this instance, T_1 is much more likely when the scaffold (the imposed population structure, dispersal process, and nutrient regime) is in place ($p_{01}|\text{with scaffold} > p_{01}|\text{without scaffold}$).

The outcome O_1 (the emergence of cooperation) is similarly more likely given $T_1(p_{11} \gg p_{21})$. It follows that cooperation is much more likely to evolve when the scaffold is in place: $P(O_1|\mathit{with\ scaffold}) > P(O_1|\mathit{without\ scaffold})$.

The probabilistic nature of scaffolding explanations is closely connected to their contrastive nature. These explanations imply two types of contrasts. First, as illustrated by Fig. 1, there must be at least two possible outcomes in question (O_1 and O_2), which typically are assigned different probabilities. Second, as illustrated by the probabilistic equation, scaffolding explanations compare the probability of the same outcome (O_1) with and without the presence of the scaffold. The contrast between the presence and absence of the scaffold is the contrast between different environmental conditions. In this sense, scaffolding explanations are fundamentally about the effects of such conditions on the developing or evolving system. We expand on this point in Sect. 5.

Attaining the outcome of interest depends not simply on the scaffold as a causal trigger but as a structure with which the system interacts in a sustained and continuous way. If the scaffold is removed too early or the interaction stops for some reason, it is less likely the outcome will be achieved. The system will, in effect, shift from T_1 to its default state T_2 (see Fig. 1). In this sense, the ongoing changes in a system might be reversed (Ross and Woodward 2021). This is clear in our evolutionary and developmental examples. Without a sustained metapopulation structure and dispersal process cooperation stops evolving and the default state of individual-level selection is re-established. Likewise, if the caregiver and the child crossing the street stop engaging with one another, the default state would be re-established—the child's anxiety would increase, and the desired outcome (crossing the street safely) would become harder to achieve.

Interventionism, contingency, transformation, and temporality

While Fig. 1 illustrates the contrastive and probabilistic character of scaffolding explanations (features i and ii from Table 1), it does not elucidate the causal relationship between the scaffold and system. Happily, interventionist approaches to causal explanation usefully clarify this and related features, capturing the complex, contingent interrelationships that characterize many scaffolding processes. As we will show, scaffolding explanations correspond to a subset of causal explanations sensu interventionism. The toy example below helps us to make this point.

Figure 2 presents a paradigmatic example of the interventionist approach—a block sliding down an inclined plane, presented by James Woodward (2003, p. 12). When explaining the acceleration of the block, one must consider the interaction of the different forces and other factors at play. Acceleration is a function of a gravitational force due to the mass of the block (mg), a normal force perpendicular to the inclined plane (N), and a frictional force opposed to the motion of the block (F_k). Woodward's account invites us to consider how changing the value of one variable (e.g., increasing the friction) would result in different acceleration. As he notes, "the information that is relevant to causally explaining an outcome involves the identification of factors and relationships such that *if* (perhaps contrary to fact)

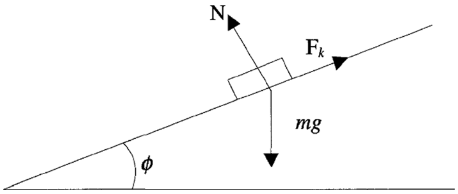

Fig. 2 Block sliding down an inclined plane. Source: Woodward (2003, 13)

manipulation of these factors *were* possible, this would be a way of manipulating or altering the phenomenon in question" (Woodward 2003, p. 10, emphasis in the original).

Scaffolding explanations have a similar character. Most obviously, the contrast between the presence and absence of scaffold entails considerations about "what-if-things-have-been-different." More interestingly, the interventionist lens brings into focus the precise character and relations of the components of the scaffold and how slightly different configurations have a better or worse chance of bringing about the outcome of interest. For instance, Rainey and colleagues, especially in the computer simulation of Black et al. (2020), investigate the particular parts of the scaffold and their specific interactions with the system to detail *how* they direct the system to the outcome of interest. In their work, scaffolding explanations invite one to explore how manipulating elements of the scaffold may alter the probability of the outcome of interest. Just as changing the angle of the slope would affect the acceleration of the block in Fig. 2, altering the metapopulation patch structure or the time between dispersal events could affect the probability of the evolution of cooperation in Black et al. (2020).

This feature of scaffolds, the complexity and interdependence of their structure, is not so obvious in the developmental contexts described by Bickhard but is key to the explanatory power of evolutionary scaffolds. To revert to the analogy with building structures, there are several components—such as the platforms, the poles, and the couplers—and a limited number of ways (though there are a *number* of ways) that they must go together if the builders are going to be able to effectively use them. Similarly, in the experiment by Black et al., scaffolds have several components with complex relationships among them. Scientists are not only interested in how changes in one component (e.g., dispersal times) influences changes in the outcome, but how the same outcome can be obtained from intervening in a set of components together (e.g., dispersal times, material influx, patch distribution, etc.) and when the scaffold will effectively break, reverting to the default outcome.

Such explanations are compatible with interventionism but not particularly suggested by it. Thus, scaffolding explanations can be understood as causal explanations in the interventionist sense, but they are a special type within this larger category that highlights features that are absent or backgrounded in most explanations as understood through an interventionist lens.

Other aspects of scaffolding explanations are likewise compatible with interventionism but not particularly suggested by it. First of all, the scaffold is crucially external to or independent of the system and, what is more, it transforms the system. In scaffolding explanations, the outcome of interest involves the acquisition of properties or capacities that change what the system can do in the future. Often, these remain part of the system permanently or, at least, long after the scaffolding process is over. For instance, as a child crosses the street successfully, they will also learn how to manage their anxiety and read traffic signs correctly. Similarly, population will evolve cooperative genotypes over time and, thus, will change genetically and phenotypically in significant ways. These transformations are important because they change the very space of possibilities for subsequent development and evolution. In contrast, remembering Fig. 2, no part of the model suggests that the block is significantly transformed by its traveling down the slope or that its future possibilities are informed by this passage.

Associated with transformation, the scaffolding process is, as a rule, temporary (feature vi in Table 1), having a distinct beginning and typically ending once the system is transformed, rendering the scaffold redundant. For instance, if a cooperative genotype evolves through a scaffolding process and gets fixed in a population, the structure of patches and dispersal times that scaffolded its emergence could be erased from the environment without immediately destroying the outcome of interest.[5] This suggested redundancy of the scaffold is implicit in scaffolding explanations but is of no particular interest for interventionism in general.

As we hope we have shown in these last two subsections, scaffolding explanations have significant continuities with both the probabilistic counterfactual approaches, common in historical and narrative explanations, and interventionism. Moreover, both of these accounts are useful in better understanding scaffolding explanations. Indeed, depending on their theoretical proclivities, readers may prefer to think of scaffolding explanations as types or special cases of either one of these approaches. What is important from our perspective is expanding on those approaches to articulate what is distinctive about the scaffolding explanatory strategy.

Redefining scaffolds

To date, proffered definitions of scaffolds in the scientific and philosophical literature have been notoriously vague and problematic (Bickhard 1992; Clark 1997; Wimsatt and Griesemer 2007; Sterelny 2010; Caporael et al. 2014; Chiu and Gilbert 2015; Love and Wimsatt 2019). For example, Bickhard characterizes scaffolds functionally in terms of how they block, reduce or mute “selective pressures,” enabling the survival and gradual transformation of the scaffolded system (1992). This definition is highly metaphorical and uses evolutionary terms to describe scaffolding processes in human development without adequate explanation. Drawing on this definition, Caporael and collaborators define scaffold as “the facilitation of a process that would otherwise be more difficult or costly without it” (2014, p. 14). Scaffolds, on

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[5] It must be noted that without some subsequent process of endogenization, the population of cooperators is vulnerable to a “selfish” mutant, and which would create a situation of “subversion from within,” ultimately destroying the cooperative type. However, if the scaffold has selected all selfish types out of the population one could reasonably expect a period of stability before a selfish mutant appears.

their view, are temporary structures that facilitate processes of maintenance, growth, or development.

Clearly, this definition is too broad. The seriousness of the problem comes into sharp relief when we ask, What causal factor is *not* a scaffold? Carporael and colleagues note this difficulty but don't provide a particularly satisfactory solution. They refer to "productive resistance or challenge" (Caporael et al. 2014, p. 15) as a necessary feature of the unscaffolded system. However, this merely restates the requirement that a scaffold must facilitate a process that would otherwise be difficult. By this standard, automatic doors scaffold one's entry into a drug store. Any temporary part of the environment that makes an outcome of interest less difficult or more probable counts as a scaffold.

As noted above, the lack of clear and precise definitions is not necessarily a problem in science. Carporael and collaborators (2014) are well-aware of the striking breadth of their definition, which they apply to explanations of phenomena ranging from evolution to culture and cognition. As they describe them, scaffolds and scaffolding processes are highly diverse (2014, p.9) and they discuss three distinct types of case that exemplify this diversity. First, cultural and biological reproduction scaffolds developmental systems (Griesemer 2000; 2014). Second, repeated patterns of social interaction scaffold human cognition and its evolution (Carporael 2014). Third, structures get "entrenched" in a biological or cultural system and scaffold later changes in it (Wimsatt 2014). In exploring these processes, Carporael and colleagues are more interested in characterizing the diversity of scaffolds than providing a narrow definition or characterization that captures what is distinctive about them.

Nevertheless, the approach of Carporael and colleagues makes it difficult to glean the common thread that these diverse kinds of scaffolding all share. Without this, "scaffold" plays a merely suggestive metaphorical role rather than helping us understand a distinct set of phenomena. Allegedly, the processes discussed by Carporael and colleagues are ways to counteract prevailing gene-centric narratives in evolution, culture, and cognition (see also Wimsatt and Griesemer 2007; Love and Wimsatt 2019). This negative role of "scaffolds" is important and finds some parallel in developmental psychology.[6] While we are sympathetic this move, it is simply not specific enough to ground a useful account of this distinctive explanatory strategy. Hence, although there is much to recommend Carporael and colleagues' wide-ranging exploration of scaffolds and scaffolding, it does not help us if we want to understand their explanatory role.

More recently, Veit (2022) has attempted to articulate a rather more precise definition of scaffold, albeit limited to evolutionary biology. According to him, "X is a scaffold iff: (1) X exogenously induces or supports the realization of property Y in

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[6] What seems to unite these approaches to scaffold is a reaction towards internalist explanations. In the case of cognition, they react against explaining human knowledge purely in terms of internal representation. In the case of evolution, scaffolds react against explaining change purely in terms of changes in genetic frequency. We return to the topic of internalist explanations in Sect. 5 and our recent work on scaffolding explanations (Neto and Meynell, forthcoming).

process/system Z. (2) X vanishes from or becomes part of the system, while property Y in process/system Z becomes endogenized" (p. 171). Like us, Veit is taken by the work of Rainey and collaborators (see esp. p. 167 ff.) and intends his account to capture their usage. There are, however, several problems with Veit's definition. First, the definition of scaffold becomes overly narrow if it requires internalization. Rainey and collaborators do not actually investigate how cooperation and collective-level properties would eventually be endogenized in their experiments, although they do suggest that it might be important to complete the evolution of multicellularity (Black et al. 2020; see also Bourrat 2022). The scaffolding process itself is prior to this internalization.

While we allow the possibility (even the likelihood) of some kind of internalization at the end of the scaffolding process and we agree that once the outcome is achieved the scaffold may disappear without the system reverting to its prior state, nonetheless, the scaffolding process itself precedes endogenization and would do so regardless of how the process ends. Importantly, Rainey and colleagues focus on how scaffolds, as external ecological conditions that are present in early stages of the evolution of multicellularity, effectively facilitate the initial fixation of cooperative genotypes. The role of scaffolds in bringing about this outcome is not conditional on the future internalization of this property. So, to require endogenization as a definitive component of scaffolds entails rejecting the paradigmatic cases provided by Rainey and colleagues as bona fide examples of scaffolding.

Even as Veit's definition is too narrow, it is also too broad and is prone to counterexamples. A snowball (X) that melts after shattering (Y) a bottle (Z) seems to fit Veit's conditions as does a sperm (X) that fertilizes (Y) an egg (Z), yet neither snowballs nor sperm would be well described as scaffolds in these circumstances. The problem is that Veit's definition simply misses key features, such as being probabilistic, multifactorial, and causally sustained, that are characteristic of paradigmatic cases of scaffolding.

As we hope we have shown, when theorists deploy scaffolding explanations, they are often after something more specific and distinctive than previous attempts to define the term have allowed. So, our task is to characterize "scaffold" in a way that brings out these specific and distinctive aspects of scaffolding explanations. In this sense, our definition of "scaffold" is parasitic on (and secondary to) the scaffolding explanations that inspire it. We do not pretend that the definition below is the final word on the matter. Nor do we present it as a descriptive account of what all users mean or intend when they talk about developmental or evolutionary scaffolds.[7] Other definitions appropriate to various contexts are, of course, possible. We see our contribution as modest in scope. We only hope to capture what is distinctive about scaffolding explanations and the role of "scaffolds" in them. We hope this definition illuminates why evolutionary biologists and developmental psychologists might be

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[7] In this way, one can interpret our project as somewhat akin to Hempel's method of explication (1962, pp. 15–16), albeit far more modest in scope—a project of conceptual articulation and clarification in the service of elucidating the character of scaffolding explanations so as to facilitate more careful analysis and assessment of them.

attracted to the terminology of “scaffold” and “scaffolding” and that it may facilitate the effective employment of these concepts in the future.

As should now be clear, the utility of our approach to definition is first and foremost *epistemic*—it indicates what epistemic goals scientists share when deploying scaffolding explanations. This point relates to Ingo Brigandt’s discussion of the “Dynamics of Scientific Concepts” (2012). Here, he argues that the usefulness of many scientific concepts is not limited to their capacity to delineate certain phenomena. There are other roles that a scientific concept performs, such as highlighting or encapsulating certain epistemic goals. For example, some definitions articulate a research problem for scientists or a type of explanation that needs development. In this spirit, the intended utility of our definition of scaffold is making explicit a type of explanatory strategy shared by different fields that draws attention to particular characteristics of these phenomena and suggests particular directions for research and analysis. The use of “scaffold” as an explanatory term invites various avenues of investigation, such as specifying the different components of the scaffold, the configurations of the scaffold under which the scaffolding process will or will not start, the likelihood of reaching the outcome of interest, the conditions under which the outcome becomes irreversible, the various probabilities associated with all these things, and so forth.

Our definition rests on a necessary background assumption that specifies the default state against which the scaffolding process is contrasted:

> **Background assumption**: For a given system S, the interaction of S with its environment will probably lead to a default state T_2 and will probably result in a default outcome O_2. An outcome of interest O_1 that significantly transforms S is unlikely in this default condition.
> **Definition**: A scaffold SC is a set of conditions (objects, processes) that are (relatively) independent from or external to S that, once introduced to S’s environment and in continuous interaction with S, raise the probability of directing S to an otherwise less probable state T_1, which in turn increases the probability of achieving an alternative outcome O_1. The interaction between SC and S causally sustains the transformation of S, which will realize new skills or capacities that can be either continuously sustained, revertible or internalized by S in the future.

According to this definition, objects and processes count as scaffolds insofar they add to pre-existing environmental conditions, changing the relationship between the system and its environment. This change shifts the probability distribution of possible evolutionary outcomes, raising the probability of the outcome of interest. Moreover, scaffolds contribute to the change of the system by enabling it to instantiate new properties. The interaction between scaffolds and the system is a causal process that sustains those properties and, thus, can be revertible if the scaffolds is removed too early. Alternatively, such properties can be internalized by the system, which renders the scaffold obsolete or redundant.

In the next section we compare this strategy to other types of explanation in evolutionary biology. This comparison provides a more careful analysis of some of the features of evolutionary explanations only briefly discussed in our recent work (Neto and Meynell forthcoming). Hence, the present analysis will complement the previous analysis while narrowing down what is distinctive and special about scaffolds and scaffolding explanations in evolution.

Why scaffolding explanations matter in evolution

In Egypt there are columns dating from the classical period called monolithic obelisks. They are made from a single stone weighing hundreds of tons and can reach thirty meters in height. It is not known how these artifacts were erected. Archeologists can nevertheless infer that there must have been building scaffolds combined with simple machines involved in these processes (e.g., Kato 2021). After all, such artifacts would be impossible to erect without scaffolds. Ancient Roman arches and Gothic Cathedrals provide further examples of structures that could not have been constructed without scaffolding of some sort. The point is that we can infer that the construction of these edifices required a scaffold without directly observing the way they were actually built.

Similarly, in biology we often see features or traits the evolution of which seems implausible under standard models of natural selection based on mutation, selection, and drift within a single Wright–Fisher population (e.g., Fisher 1930; Wright 1931; Moran 1958; Kimura 1962). According to these models, the contingencies of biological reproduction and death combined with the environment favor those individuals that generate more offspring. When we observe evolved traits that reduce the expected reproductive success of individuals, it is like seeing a monolithic obelisk. On the face of it, such traits contradict the biological imperative to maximize reproduction and, thus, it is hard to imagine how those traits evolved without moving beyond the standard models of selection for single populations. Similar considerations ground the circularity problem that confronts the evolution of any truly novel trait. Selection for a novel trait seems to presuppose that it already exists (Griesemer 2000; Veit 2022).

Currently, most efforts to explain these kinds of surprising or novel traits rely on characteristics that are internal to the population. Consider the puzzle of evolutionary altruism—i.e., any behavior that reduces the fitness of the individual exhibiting it but increases the fitness of others in the same population (Sober 1988). The prototypical scenario is sentinel behavior, where some individuals stand watch over a group of conspecifics and issue a warning call when a predator is detected. Such behavior exposes the sentinel to an increased risk of death by predation but also reduces that risk to others in the group. The classical explanation for this kind of behavior is kin selection (Hamilton 1964), which appeals to individual-level traits that increase the likelihood that the benefit of altruism will be conferred to other altruists (i.e., traits that positively assort altruists, Fletcher and Doebeli 2009). Such traits include the tendency to limit dispersal so that kin remain in proximity to one another, and the ability to discriminate kin from non-kin. Thus, these explanations are internalist—internalism being the strategy of explaining a certain evolutionary phenomenon in terms of internal traits of individuals in a population (Godfrey-Smith 1998)—as proximity usually depends on ancestral relations and discrimination capacity is a trait of the organisms themselves.

Interestingly, aside from some means of positive assortment, kin selection explanations effectively take the environment for granted or consign it to the background of the model. Environmental conditions are highly idealized or abstracted away. If they are included in mathematical models they are typically subsumed within a single fitness coefficient. At the same time, kin selection theory, like any other theory committed to the importance of evolution by natural selection, operates under the assumption that the environment has a central explanatory role in evolution, even when it is not the focus.

All selection-based explanations are externalist insofar as it is the environment that determines fitness; however, many models radically idealize the environment. Consider the classic diffusion approximation (Kimura 1962). The probability that a mutant is fixed is a function of the effective size of the single unstructured population in which it is assumed to exist plus a selection coefficient that represents the difference between the fitness of the mutant compared to the wildtype. The selection coefficient is typically thought of as a consequence of a feature (or set of features) of the environment that interacts with the phenotype producing a fitness difference between the mutant and wildtype. In this way, the role of the environment is both essential and highly idealized and unspecified.

Now consider the studies conducted by Rainey and colleagues, discussed above. Like the kin selection case, Black et al. (2020) are interested in explaining the fixation of cooperative genotypes. However, the explanation doesn't rest on specific characteristics of the organisms in the population but is entirely externalist. It focuses on how changes in the population are driven by complex and specific environmental conditions—i.e., a certain patch structure, timed dispersal, and periodic nutritive influx. These carefully specified conditions can lead to the evolution of genotypes that are not only truly novel to the system but are all but impossible to produce in standard models of selection in a single population. In the words of Black et al. (2020), they show how certain environmental conditions can cause individual cells to be "unwitting participants in a selective process … as part of a larger (collective-level) entity" (p. 426). In this way, they hope to offer an origin explanation of a major evolutionary transition.

Rainey and colleagues explicitly contrast their approach with internalist origin explanations (Rainey et al. 2017; Doulcier et al. 2020; Black et al. 2020), which appeal to co-option. According to this approach, a new phenotypic trait arises when parts of the genome are put to new uses. This genomic material is internal and already present in individuals of a determinate population, yet the new uses help to explain how phenotypic traits can first arise. In contrast, Rainey and colleagues argue that the "goal is to explain a certain outcome of interest *without* appealing to or co-opting individual-level traits" (Rainey et al. 2017, emphasis ours). Instead, the origin of phenotypic traits is explained by appeal to specific environmental conditions, i.e., the scaffolds.

We are now in position to recognize the significance and promise of scaffolding explanations in evolutionary biology. This explanatory strategy is particularly well-suited to accounting for the origins of novel traits in a lineage through the characterization of complex and specific environmental conditions, rather than some underlying internal feature of the organism that is co-opted. Analogous to the example of monolithic obelisks, the evolution of some traits is difficult to explain because their emergence is highly unlikely when viewed through traditional models of evolution. These models tend to idealize the environment, often reducing to a simple mathematical expression for fitness. Scaffolding explanations, in contrast, specify key components of the environment and focus on the ways in which specific configurations of these components can drive a population to outcomes that are highly unlikely from the perspective of more traditional approaches to evolutionary and selection-based explanation. The likelihood of these outcomes depends on the complex interdependent relationship of the components of the scaffold (reflecting characteristics familiar from interventionist accounts of causal explanations). In other words, the importance of scaffolding for evolutionary explanations is that they offer a new way of accounting for the significant transformation of a population through an externalist explanation that centres a specific and complex set of environmental conditions. Just as the origins of monolithic obelisks may seem inexplicable until one begins to consider the type of scaffold by which they could have been erected, so the evolution of certain novel traits that have no clear precursor in the lineage of the organism—like the evolution of cooperation or multicellularity from single-celled organisms—can be explained by the right kind of scaffold.

Conclusion

In this paper, we have examined the role of "scaffolds" in evolutionary explanations. This notion has a long history in other areas, in particular, developmental psychology (Wood et al. 1976; Ratner and Bruner 1978; Rogoff 1990; Bickhard 1988, 1992) and has been put to work by philosophers of science in discussions of biological and cultural evolution (e.g., Wimsatt and Griesemer 2007; Caporael et al. 2014; Griesemer 2014; Chiu and Gilbert 2015). Here we have identified a type of explanatory strategy—scaffolding explanations—with roots in developmental psychology that connect to recent work in evolutionary biology. We have identified the commonality between these traditions and offered a definition of "scaffold" that articulates the main features of scaffolding explanations. This definition is not intended to offer precise criteria for what counts as a scaffold but rather highlights the features of those explanatory practices that employ the notion of scaffolding. From there we focused on scaffolding explanations in evolutionary biology, contrasting them to selection-based explanations and indicating the potential of this approach as a type of externalist origin explanation. We hope the present analysis can serve as a basis for assessing the merit of scaffolding explanations given in evolutionary biology and other areas of science that employ this explanatory strategy.

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Declarations

Conflict of interest The authors declare that there is no conflict of interest in the production of this material.

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