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Scaffolding Natural Selection

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Abstract

Darwin provided us with a powerful theoretical framework to explain the evolution of living systems. Natural selection alone, however, has sometimes been seen as insufficient to explain the emergence of new levels of selection. The problem is one of 'circularity' for evolutionary explanations: how to explain the origins of Darwinian properties without already invoking their presence at the level they emerge. That is, how does evolution by natural selection commence in the first place? Recent results in experimental evolution suggest a way forward: Paul Rainey and his collaborators have shown that Darwinian properties could be exogenously imposed via what they call "ecological scaffolding". This could solve the 'black box' dilemma faced by Darwinian explanations of new levels of organization. Yet, despite 'scaffolding' recently becoming a popular term in the study of cognition, culture and evolution, the concept has suffered from vagueness and ambiguity. This article aims to show that we scaffolding can be turned into a proper scientific concept able to do explanatory work within the context of the major evolutionary transitions. Doing so will allow us to once again extend the scope of the Darwinian model of evolution by natural selection.

Keywords: Natural selection; Ecological scaffolding; Multi-level selection; Major transitions; Multicellularity; Individuality; Ecology; Group selection; Hierarchy; Selection analysis; Scaffolding

1 Introduction

Darwin (1859) provided us with a breathtakingly simple yet powerful tool to explain the evolution of living systems, that is the *Theory of Evolution by Natural Selection.* Out of all the principles in biology, natural selection appears to be the closest thing biologists have to something resembling a general ordering principle in physics, subsuming a vast range of diverse phenomena under a single theoretical framework (Okasha 2018). Externalist approaches relying on natural selection that explain organismal properties through recourse to properties external to the organism,[1] however, have often been considered insufficient to explain how levels of selection - i.e. the *major transitions* in evolution such as the origins of life and the evolution of multicellularity (Smith and Szathmáry 1995) - arise in their own right. That is, how does evolution by natural selection get started in the first place?

This problem has long been a major challenge for evolutionary biology. As James Griesemer (2000) argued early on, the very reason it has been so hard to explain the major transitions has been something like a problem of 'circularity'. Since Darwinian explanations invoking natural selection typically already assume the pre-existence of so-called 'Darwinian properties' at a level of spatial organization - such as Lewontin's (1970) preferred triad of variation, fitness differences, and heritability - there is an inherent challenge in offering hypotheses that explain the origins of these properties without recourse to the very properties we intended to explain in the first place. This is the most obvious for the origins of life, where the emergence of Darwinian entities is typically explained through non-Darwinian means (e.g. through appeal to principles of biochemistry and physics).

While there is now a very extensive literature (both theoretically and empirically) on such evolutionary transitions in individuality towards a new level of organization (so-called ETIs), the dominant view has simply assumed the existence of some higher-level Darwinian properties, without realising that they cannot just be taken for granted.[2] Despite significant progress hav-

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[1] Externalist approaches should be conceived as the opposite on a spectrum to internalist approaches that explain organismal features through recourse to other properties of the organism. In practice, the differences between these two modes of explanation is admittedly often only one of emphasis.

[2] While this is far from an exhaustive list, see Buss (1987); Michod (1999); Griesemer (2000); Queller (2000); Michod and Roze (2001); Okasha (2006); Grosberg and Strathmann (2007); Michod (2007); Koonin (2007); Hochberg et al. (2008); Godfrey-Smith (2009); Folse III and Roughgarden (2010); Clarke (2010); Calcott and Sterelny (2011); Bourke (2011); Ratcliff et al. (2012); Bouchard and Huneman (2013); Tarnita et al. (2013); Queller and Strassmann (2013); Niklas and Newman (2013); Fisher et al. (2013); Ratcliff et al. (2013); Hammerschmidt et al. (2014); Libby and Ratcliff (2014); Fisher (2015); Ratcliff et al. (2015); Pichugin (2015); West et al. (2015); Birch (2017); Van Gestel and Tarnita (2017); Bourrat (2019); Veit (2019a); Staps et al. (2019); Rose et al. (2020); Niklas and

ing been made, the literature remains far from reaching consensus regarding both general theoretical debates and in its mechanistic hypotheses. The black box dilemma forced upon us by the recognition that Darwinian properties are themselves derived traits in need of Darwinian explanations has been largely unaddressed. Recent work by the biologist Paul Rainey, however, suggest a new exciting path forward that could simultaneously offer both a general theoretical framework for the major transitions and a testable empirical program that may break the circularity problem entirely by employing natural selection itself in the emergence of Darwinian properties.

A New Proposal: Ecological Scaffolding

In his recent collaborative work, Rainey has developed his idea that Darwinian properties could be exogenously rather than endogenously imposed, through a process that he calls "ecological scaffolding", thus allowing natural selection to commence in something like an eco-evo feedback-loop (Rainey et al. 2017).[3] While a further mathematical explication of the idea by the physicist Andrew Black involved the philosopher of biology Pierrick Bourrat (see Black et al. 2020), there has yet been no discussion of the idea in philosophical circles, save for a brief mention in Veit (2019a). Yet, the idea of ecological scaffolding is already being applied and further developed elsewhere, such as in Doulcier et al. (2020) where it is explicated using mechanistic models in the context of egalitarian transitions (where lower-level entities are alike) to explain the origins of heredity.

This lack of attention among philosophers of biology is unfortunate for two reasons. Firstly, Rainey's idea of ecological scaffolds presents a unique merger of theoretical biology, experimental work, and philosophy of biology, in order to address the problem of major transitions that researchers in all three fields have long been wrestling with. Philosophers of biology may thus be interested in seeing an elegant case demonstrating how ideas from multiple disciplines can be turned into a new research program. Secondly, and perhaps more importantly, philosophers of biology are in a unique position to analyse and further explicate the notion of 'ecological scaffolding' in order to help it flourish into a novel research program on the major transitions. This idea is intriguing because it solves this circularity dilemma faced by

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Newman (2020).

[3] The idea was inspired by earlier experimental work on *Pseudomonas fluorescens* by the same group (Hammerschmidt et al. 2014), which I have discussed here (Veit 2019a).

Darwinian explanations relying on natural selection. In this paper, I will take the opportunity to further develop the idea here in order to make progress in our understanding of the major transitions within an evolutionary framework.

Despite the fact that the term 'scaffolding' has recently become a popular theme in the study of cognition, culture, evolution, and even science itself (see Sterelny 2010; Caporael et al. 2014; Chapman and Wylie 2015; Currie 2015; Walsh 2018 for a variety of interesting applications), the notion has generally suffered from vagueness, imprecision, and ambiguity. If one hears the term used in different contexts or by different scientists, it is often unclear whether there is any shared understanding. After all, there is no generally agreed upon definition, even within particular disciplines. This provides ample opportunity for philosophers of science to step in, as two of the most beneficial roles philosophers of science can play in the sciences are those of conceptual clarification and theoretical incubation. This paper aims to draw on the work of Rainey to show that the notion of 'scaffolding' can successfully be developed from a mere metaphor that is used in a vague sense describing environmental support, into a proper scientific concept able to do explanatory work within the study of the major transitions. By developing a general definition of scaffolding I aim to help Rainey's project to incubate a new set of ideas in the study of evolution. Doing so will allow us to address old philosophical questions on the scope and explanatory power of natural selection and open an array of research topics at the intersection of experimental biology, theoretical modeling, and the philosophy of biology.

Article Outline

In order to achieve these goals, the article is structured as follows: in ***Section 2***, I briefly illustrate the circularity problem that threatens the status and generality of natural selection as the unifying principle of the biological sciences. In ***Section 3***, I analyse Rainey's proposal of 'ecological scaffolding' as a solution to this problem and a potential explanation for the major transitions. In ***Section 4***, I explicate and improve their concept and its role in evolutionary thinking by linking it more closely to recent ideas in the philosophy of biology, such as Samir Okasha's work on the strategy of endogenization, Peter Godfrey-Smith's idea of scaffolded reproducers, and the scaffolding literature more generally. Finally, I conclude the discussion in ***Section 5*** and suggest further avenues for future research.

2 A Circularity Problem for the Generality of Natural Selection

Since Darwin's (1859) *The Origin of Species by Means of Natural Selection*, his concept of Natural Selection has fundamentally changed biology and our understanding of the world. Previously, no one had been able to provide a satisfying explanation of the design and apparent fine-tunedness of organisms to their environment. His perhaps most often quoted formulation of natural selection is offered in the latter part of the *Origin*:

> These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the external conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms.
>
> – Charles Darwin (1859, pp. 489-490)

As several authors have noted, Darwin emphasizes two special features of natural selection (see Dennett 1995; Godfrey-Smith 2009). The first one being the almost law-like form of natural selection: if the conditions for natural selection are satisfied, natural selection operates. This, importantly, does not require that evolutionary change or adaptation occurs, as other evolutionary factors such as drift may undermine the effect of natural selection. The second special feature of natural selection that Darwin emphasizes is the abstractness of the process. This feature allows for selection on different levels of organization than just the obvious case of organisms, leading to the fairly heated group selection debate on the proper level of selection (Wilson and Sober 1994; Okasha 2001, 2006; Leigh Jr 2010; Veit 2019a; Lloyd 2020).

As I indicated in the introduction, the principles of natural selection are often simply stated as the satisfaction of three conditions: (i) *variation*, (ii) *heritability*,[4] and (iii) *differential reproductive success*. In his paper "The Units of Selection", Lewontin (1970) has provided the most cited formulation of these three ingredients and the Darwinian 'algorithm' of natural selection:

> As seen by present-day evolutionists, Darwin's scheme embodies three principles [...]:

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[4] Or at least correlation between the phenotypes of parent and offspring (Godfrey-Smith 2009).

> 1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).
>
> 2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).
>
> 3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable).
>
> These three principles embody the principle of evolution by natural selection. While they hold, a population will undergo evolutionary change.
>
> – Richard Lewontin (1970, p. 1)

Naturally, it has been recognized that these three criteria can be satisfied at different levels of biological hierarchy, though there have been many disputes regarding the status of levels other than the organism, such as the group or the gene. Far from being solely tied to biology, many thinkers have also since used the tools of evolutionary biology to explain cultural evolution, giving these conditions cultural interpretations. As Godfrey-Smith emphasizes, the very "idea of an extension of Darwinism beyond its original domain is almost as old as Darwinism itself" (2009, p. 18).

But explanations employing natural selection will inevitably be faced with a problem of circularity that the Darwinian project has to address. Regardless of how the specific conditions for natural selection are explicated, these Darwinian explanations will still be insufficient to explain how these conditions themselves came into existence (especially in the case of the origin of life). The problem here is not that the conditions for natural selection we specified have been stated too strictly and would require a more relaxed form, though such an approach might be useful to provide a better understanding of natural selection itself (see for instance Godfrey-Smith 2009; Rainey and De Monte 2014) and the very first selection processes in the hierarchy of life. There is a deeper conceptual problem here that cannot be overcome by such an analysis since it lacks a mechanistic explanation for how this process comes to operate. In a previous paper, I have summarized the problem Rainey tries to address as follows:

> [M]odels already assuming a level in the 'hierarchy of life', the evolution of which we want to explain must conceptually prove insufficient for the purpose of explaining the evolution and persistence of new Darwinian individuals on a higher level. After all, one needs to explain

> the emergence of a mechanism of group reproduction, without such a mechanism already being present.
>
> – Walter Veit (2019a, pp. 4-5)

Similar points have been made by Griesemer (2000), who urges us to go into mechanistic detail in order to address this circularity problem. Hierarchical organization cannot be simply taken for granted as if it was just exogenously given, and yet, this fact is typically already assumed in evolutionary models (see Okasha 2006, 2018). The levels-of-selection question must address the origins of biological organization. So far, there have been numerous ingenious attempts to address the evolution of reproduction at a new level (often within a kin-selection framework), but this work has largely focused on the internal side of things - with Darwinian properties emerging as a result of interaction among parts - with relatively little attention to the ecological context as one might expect from the *externalist* model of natural selection (see Queller 2000; Michod and Roze 2001; Michod 2007; Hochberg et al. 2008; Fisher et al. 2013; Ratcliff et al. 2012, 2013, 2015).

I emphasize the term 'externalist' as important here more so than any other field, because evolutionary biology is dominated by an externalist mode of explanation in which features of a system (i.e. the organism) are explained in terms of properties of features external to it (i.e. their adaptive fit to their environment).[5] As the evolutionary biologist Arlin Stoltzfus (2019) elegantly puts it: "[t]he suspicion of internal causes in the dominant neo-Darwinian culture ran so deep that every internalist idea, no matter how reasonable, was treated as an appeal to vitalism" (p. 46). Yet, to explain the evolution of Darwinian properties in terms of external selective pressures has been precisely the source of the circularity problem, because it apparently presupposed the existence of the level of organization we are supposed to explain the first place. It is thus unsurprising that some, such as the cell biologist Stuart Newman, have emphasized the role of physical laws and constraints over the generality of natural selection and adaptive explanations in thinking about the evolutionary transition to multicellularity, despite the resistance to non-Darwinian explanations (Newman and Bhat 2008; Niklas and Newman 2013, 2020).

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[5] See Endler (1986); Godfrey-Smith (1996, 2001, 2002); Chiu (2019); Lewontin (1983, 2000); Mayr (1982, 1994); Gould and Lewontin (1979); Gould (1977, 2002); Walsh (2015); Williams (1966); Veit (2021b).

This is certainly one way to circumvent the circularity problem: employ a non-Darwinian explanation of the emergence of Darwinian properties. My goal is *not* to claim that this approach does not work. In fact, there may very well have been too little attention given to the possibility that multicellularity itself is not an adaptation, and I would be pleased to see a more pluralist approach to modeling the origins of multicellularity (see Veit 2019b, 2020, 2021c). Rather, my goal here is to demonstrate that the idea that natural selection may *itself* be scaffolded has the potential to once again extend the scope of natural selection as a general ordering principle in biology, by providing a non-circular Darwinian explanation of the emergence of Darwinian properties. Here, I explore Rainey's notion of 'ecological scaffolding' as an externalist and mechanistic solution to recover a Darwinian approach to the the circularity problem.

In contrast, the prevailing paradigm has been to explain the emergence of these properties in virtue of the interaction of lower-level particles (see Buss 1987; Smith and Szathmáry 1995; Okasha 2006; Godfrey-Smith 2009). Reproduction, for instance, is often considered as a simple byproduct of natural selection acting on particles at the lower level.[6] Yet, a mere assembly of single-cell organisms does not have a special group level mechanism of group selection. So where does it come from?

What ecological scaffolding allows, is for us to fill out these gaps and provide Darwinian explanations for the origin of Darwinian properties, i.e. the conditions under which natural selection acts. As Griesemer (2000) urged early on, we should recognize that reproduction is not a simple process, instead often being composed of the complex interactions between various parts (see also Wade and Griesemer 1998; Griesemer and Wade 2000; Griesemer 2014, 2016, 2018, 2019; Bourrat 2014; Wilkins and Bourrat 2020). Collective-level reproduction is not the same as reproduction at the level of individual cells, but something that requires an explanation of its own, a fact that is unfortunately often overlooked or idealized away. But to explain the evolution of multicellularity is, as Black et al. (2020) note, intimately linked to explaining the emergence of life-cycles, development, and a soma/germ-line distinction (see also Coelho et al. 2007; De Monte and Rainey 2014; Rainey and De Monte 2014; Staps et al. 2019; Miele and De Monte 2021).

It is nowadays not uncommon for people to think that natural selection

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[6] Though see Michod (2007) for more a more sophisticated attempt at solving the problem.

is an important force once its condition are satisfied, but then to hold that these Darwinian properties could only have been arranged through something like a higher-power (Nagel 2012). Recent work on scaffolding, however, may be able to undermine this leftover of pre-Darwinian creationist thought: from the origins of life to the evolution of multicellularity, ideas stemming from work in experimental evolution have offered a novel way to solve this omission in evolutionary biology. Though I suspect it unlikely that a scientific concept of scaffolding will turn creationists, it has the potential to at least remove this force of their argument, providing us with a simultaneously general, yet testable mechanistic framework for thinking about the major transitions. Let me thus now introduce Rainey's concept of 'ecological scaffolding' as an externalist solution to the circularity problem, one that does not rely on an internalist explanation seeking the emergence of Darwinian properties as an interaction between its parts.

3 Rainey's Solution: Ecological Scaffolding

Rainey has introduced his notion of 'ecological scaffolding' in three recent publications (see Rainey et al. 2017; Black et al. 2020; Doulcier et al. 2020), though precursors of the idea can be found in his earlier work (e.g. Rainey 2007). Above, I briefly sketched the idea as the exogenous imposition of Darwinian properties by the environment. And this is largely how Rainey et al. (2017) define the concept - seeing the environment as a crucial and neglected factor in the major transitions by "exogenously imposing Darwinian properties on otherwise 'unwitting' particles" (p. 104). Rainey himself sees his contribution as involving both a succinct statement of the essence of the circularity dilemma which he thinks has been ignored by many in the field and a straightforward solution, i.e. ecological scaffolding, which simply follows from the former clarification of the problem.[7] A more precise definition of this solution has been given in Black et al. (2020), where they maintain that "Darwinian properties can be [...] exogenously imposed in such a way as to cause lower-level entities (for example, cells) to become passive participants in a selective process that occurs over a longer timescale than the timescale over which cell-level selection occurs and as part of a larger (collective-level) entity" (p. 426). As I see it, Rainey's notion of ecological scaffolding is essentially a combination of three separate ideas: (i) an older suggestion by

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[7] From personal communication.

Wilson and Sober (1989) in their "Reviving the superorganism" that selection on groups could take place in virtue of the environment rather than properties internal to the group,[8] (ii) a general growing awareness of the importance of ecology, beyond population structure, within the study of major evolutionary transitions (see Wade 2016; Tarnita 2017; Veit 2019a), and (iii) the exploding usage of the term 'scaffolding' across the sciences to explain complex phenomena (see Caporael et al. 2014).

But the idea of ecological scaffolding is not merely intended as a theoretical contribution to debates in the philosophy of biology. While his career begun in experimental biology, Rainey developed an early interest in the more theoretical questions in biology. His research (Rainey and Rainey 2003; Rainey 2007; Rainey and Kerr 2010; Rainey and De Monte 2014; Rainey et al. 2017; Black et al. 2020) has long been concerned with the question of how multicellular organisms evolved from free-living single-celled organisms, serving as a paradigm example for an experimental biologist becoming engaged in a debate that was once the almost exclusive domain of evolutionary theoreticians and philosophers of biology. Rainey's introduction of the term ecological scaffolding builds on decades of (ongoing) experimental and theoretical work on the evolution of multicellularity and was explicitly intended to be operationalizeable and guide future empirical work.[9] The primary example used for ecological scaffolding is an experiment by Hammerschmidt et al. (2014). In this experiment they attempt to test Rainey's hypothesis of cheats as propagules or - in terms of the new terminology - a scaffold for group-level reproduction, variation, and heredity through a single-cell bottleneck (see Figure 1).[10]

If the bacterium *Pseudomonas fluorescens* is propagated in test tubes with a nutritious broth, mutations quickly arise that lead to adhesive cell-glue production that bind cells together. The cost of glue-production is two-fold: firstly, the costs of producing the glue itself, and secondly the costs of life in close proximity, as daughter cells cannot detach themselves from their parent. However, some such mutant assemblies are able to survive by taking over the interface between air and broth, attaching themselves to the walls of the 'microcosm', without which these non-buoyant mats would sink. They occupy a new niche rich in oxygen, a benefit that outweighs the costs

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[8] Wilson and Sober (1989) do not, however, apply this idea to the major transitions. [From personal conversation with Rainey.]

[9] From personal communication.

[10] First articulated in Rainey (2007); Rainey and Kerr (2010).

Figure omitted from preprint for copyright reasons. [See Rainey and Kerr 2010, p. 876]

Figure 1: "A putative life cycle for mat-forming bacteria. We start with a single bacterium (given in blue) capable of producing an extracellular adhesive. (1) It reproduces at the interface between liquid and air (in the case shown, starting at the inner surface of a glass tube). Daughter cells stick together because of the adhesive they produce. (2, 3) The resulting mat spreads over the liquid's surface as a single-cell layer. (4) Due to prime access to oxygen, a robust mat forms. Mutation generates "cheats" (green cells that do not produce any adhesive polymer and grow faster as a consequence). (5) These cheats spread like a cancer within the mat and contribute to (6) the collapse of the mat. Because the cheats do not produce the adhesive, they are liberated from the mat upon collapse. (7) Back mutation from one of these cheats to a mat-producing cell completes the life cycle. Of course, we do not imagine such a life cycle playing out in an environment where only a single mat can form (like a single tube). Rather, the back mutants from the liberated cheats could establish mats in different locations from their parent mat. Here the cell type leading to the death of the group also leads to its rebirth. The cheats amount to propagules ("germ line"), arising *de novo* from the mat-forming "soma" of an incipient multicellular individual." [Rainey and Kerr (2010), p. 876]

of glue production. In virtue of their access to oxygen these 'cooperative' groups achieve access to a limiting resource, taking over the entire surface. At some point, however, mutations lead to cheating cells living within the mat without producing glue themselves. These cheats prosper, as they have access to oxygen without the costs of glue production. The mat becomes heavier and loses structural integrity until the lack of cell-cell glue leads to the doom of the mat, i.e. the extinction of the 'proto-group' organisms.[11]

Of course, it is not meaningful to speak here of a Darwinian individual in its own right, unless it has some means of reproduction (see Godfrey-Smith 2009). But Rainey and Kerr (2010) suggest that the very cheats that spell doom for the mat could also be its saviour, by functioning as a sort of propagule - forming a new mat and thereby the beginning of a new life-cycle (see Figure 1). Hammerschmidt et al. (2014) facilitated a grand-scale experiment showing that a cheat-embracing regime in which a new life-cycle begins with a cheating cell[12] is able to decouple the fitness of groups from the fitness of individual cells. The lower level units become de-Darwinized, as Godfrey-Smith (2009) might put it, by becoming subservient to the life-cycle

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[11] The slime mold *Dictyostelia* may provide a similarly useful model system for the origins of multicellularity (Queller and Strassmann 2013; Kawabe et al. 2019).

[12] As opposed to a cooperating cell.

of the collective unit. The first steps towards multicellular organisms have been taken in the lab, successfully testing hitherto philosophical ideas.[13]

As I have previously argued, some may legitimately criticize the artificial nature of this experimental setup (Veit 2019a). The point here is not to claim that there is some deep metaphysical divide between artificially induced selection and 'real' ecological scaffolding in nature, but rather, that whereas it is comparatively easy to exogenously induce Darwinian properties so in the lab, aggregates of lower-level units in the word outside the lab rarely meet the conditions of evolution by natural selection, because they lack heritable fitness differences (Lewontin 1970; Godfrey-Smith 2009; Doulcier et al. 2020). One might thus criticise the the Hammerschmidt et al. (2014) work for lack of a plausible story of how their model could map onto the real world, but this would be to misunderstand the paper. Similarly to mathematical modellers, experimental biologists such as Rainey are often asked to provide us with a detailed story that maps the artificially induced selection onto natural selection operating in the real world. Such a requirement forces the abstract and generalized explanations presented in papers reporting the data of an experiment or model, to narrow to particular target systems. This then misinterprets the very point of the original paper, which was to provide a very general and idealized framework that would have to be filled out for the particular contexts we are interested in. When examples and narratives for such general explanations are provided, they are mostly suggestive, providing one possible way in which their explanation could be realized, not how they *must* be or how it actually happened. The lack of specific cases is thus not a flaw but a feature quite familiar from modelling in biology. The economist Robert Sugden (2011) has called such models fittingly "explanations in search of observations". I suggest the same applies to laboratory experiments exploring general mechanisms operating in living systems. Rainey et al. (2017) offer a supporting analysis: "the overarching goal of much experimental evolution [...] is to simplify in order to understand processes too complex to fathom in real world situations" (p. 106). Indeed, in Black et al. (2020) they further idealize from their already fairly abstract example to provide a general and simple model that highlights the important role of ecological factors as possibility proof for the imposition of Darwinian properties through proper-

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[13] For a more detailed and thorough analysis of the Hammerschmidt et al. (2014) experiment, its philosophical implications, and the role of cooperation in the evolution of multicellularity, see Veit (2019a).

ties of the environment, which has been corroborated in their experiments. Nevertheless, even if it is possible to scaffold Darwinian properties, we will still require plausible scenarios of how this could have happened outside the laboratory. In order to illustrate the importance of ecological scaffolding it is necessary to provide examples of how something analogous to the artificial scaffolds, such as beakers in the Hammerschmidt et al. (2014) experiment, could have been 'highjacked' by natural selection.

In Rainey et al. (2017) they provide *one* plausible story of how multicellularity could have evolved in the evolutionary past, or future for that matter. It is here that they introduce the idea of 'ecological scaffolding' using the case of reeds as an example for the imposition of Darwinian properties:

> Consider a pond with randomly placed reeds, each of which constitutes a scaffold around which a mat can form. Mats eventually collapse and go extinct due to their increasing mass, but provided a mat can re-establish at the original reed, or around one or more new reeds, then a process akin to collective-level reproduction occurs. With this comes the possibility of a Darwinian process at the level of mat collectives.
>
> – Paul Rainey et al. (2017, p. 104)

Instead of their 'artificial' set-up this scenario depicts a plausible scenario for how all three Lewontin conditions can be scaffolded at the collective level through patchily-distributed resources at reeds and means of dispersal that allow for competition between mats. This provides an interesting analogy to natural selection. Darwin's theory of natural selection has provided an explanation that drew on artificial selection to explain the appearance of purpose in the natural world, the diversity of living beings and their fit to the environment. Much the same applies for ecological scaffolding by externally inducing Darwinian properties to 'unwitting' particles. Instead of intentionally placed scaffolds for a specific purpose, ecological scaffolds are blind and random occurrences in the natural world that can nevertheless serve a 'purpose' in the evolution of Darwinian properties. Providing the following illustration (Figure 2), Rainey et al. (2017) argue that ponds could constitute a plausible scenario for ecological scaffolding outside the lab.

As Figure 2 illustrates, reeds could possibly enable the creation of a sort of proto life-cycle by exogenously imposing the necessary and sufficient conditions for evolution by natural selection. Given the right ecological conditions, mats then become subject to selection themselves. Take these reeds

Figure omitted from preprint for copyright reasons. [See Rainey et al. 2017, p. 105]

Figure 2: "Pond scum acquires Darwinian properties via ecological scaffolding. The illustration shows six reeds in a pond. Surrounding each reed is a set of different microbial mat- forming types. Reeds are sufficiently widely spaced as to prevent confluent growth of mats, thus ensuring variation at the level of mats. Consider that the yellow mat occupying the reed marked with the solid arrow collapses. Death of this mat provides opportunity for birth of a new mat, provided there exists a means of dispersal (by biotic or abiotic means) between reeds. In this example, cells from the red mat recolonise the vacant reed. The dispersal and recolonisation event is akin to mat-level reproduction and, because the cells founding the new mat came from the old mat, the offspring mat resembles the parental mat (there is heredity). Mats begin to take part in the process of evolution by natural selection by virtue of Darwinian properties that are exogenously determined. Additionally, selection sees two time scales: the doubling time of individual cells and the doubling time of mats. Continued selection under such ecological conditions allows the possibility that Darwinian properties become endogenised, that is, they come to be determined by the activity of the collectives themselves with no need for scaffolding. An early stage might be the evolution of a developmentally determined life cycle." [Rainey et al. (2017), p. 105]

away, and the mats no longer have the relevant Darwinian properties for natural selection to occur. Now it should be clear why they don't just use the widely used and imprecise metaphor of 'environmental scaffolding' to refer to any sort of environmental supporting relationship (Caporael et al. 2014), instead opting for the previously vacant term 'ecological scaffolding' which they intend to have a more precise meaning.

Reproduction can take place via biotic and abiotic means. While reeds are biotic components of the environments, nothing of course prohibits the occurrence of something roughly analogous to reeds as an abiotic component of the environment playing the same role. In the experiment this was the beaker, or rather the surface of the beaker at the interface between the broth and air. Consider for instance the case of stones in a pond peeking out of the water surface, as an abiotic scaffold. Though perhaps a less realistic scenario, we keep in mind that the evolution of multicellularity has independently taken place at least 25 times (see Smith and Szathmáry 1995). Hence, we should not be surprised that the actual evolution of multicellularity in eukaryotes may have been a fortunate interplay between extremely unlikely environmental conditions and the right mutations occurring in the required order. Proto life-cycles acting as marginal Darwinian individuals, far from being stable, are constantly threatened by extinction and this is the

Figure omitted from preprint for copyright reasons. [See Rainey et al. 2017, p. 106]

Figure 3: “Ecological scaffolding in a droplet-based evolution machine ensures droplets are units of selection. Parallel horizontal lines are walls of Teflon tubes containing an emulsion of oil and regularly spaced droplets harbouring bacterial cells. **(a)** At the start of operation all droplets are founded by identical types. (b) A period of cellular growth occurs within droplets. During this stage mutations within individual cells arise that affect the colour of each droplet. Droplets whose colour is not sufficiently bright are marked for extinction allowing the possibility that when the contents of the droplets are diluted in order to establish a new round of selection, the brightest droplets are split into two offspring droplets. **(c)** Selection thus works over two time scales — the doubling time of cells, and the doubling time of droplets. As in Figure [2], Darwinian properties are imposed (scaffolded) on droplets causing droplets to function as units of selection in their own right. (Rainey et al. 2017, p. 105)” [Rainey et al. (2017), p. 106]

fate we should expect almost all proto life-cycles in evolutionary history to have suffered. The multicellular lineages we observe today thus represent only those stable enough to persist.

The creation of such proto life-cycles in the lab - able to increase their stability before they eventually go extinct - is already quite the achievement. These experiments suggest ways forward, illuminating the ecological scaffolds that may have played important roles during the evolution of multicellular organisms. As Rainey et al. (2017) note: “ecology is everything: the structure of the environment permits realisation of Darwinian properties at the collective level even in the absence of these properties being endogenously determined” (pp. 104-105). Use of the term ‘ecological’ rather than ‘environmental’ scaffolding also highlights the importance of eco-evo feedback loops in ecological scaffolding that can lead to the evolution of genuine life cycles. Only in virtue of a cheat-embracing regime, which scaffolds mat reproduction, do we get a germ-soma distinction with cheating cells playing the role of proto germ-cells - a proto life cycle that can plausibly become a unit of selection. And with selection coming to act at the level of the mat, these exogenously imposed Darwinian properties can plausibly come under developmental control, i.e. become endogenized. The second example, Rainey et al. (2017) offer is perhaps less obvious (see Figure 3).

Unlike the previous thought experiment this one does not have a straightforward real-world analogy to the role of reeds in the development of mats and the construction of a building via scaffolds. The focus here is the general phenomenon of the exogenous imposition of Darwinian properties. Nevertheless, it could be made into a model for the evolution of multicellularity if each droplet was founded by single cell, which could be instantiated through pores in alkaline vents.[14] Doulcier et al. (2020) have developed a mechanistic model with this motivation in mind and show that egalitarian transitions can occur through ecological scaffolding. Consider the standard conditions for natural selection listed in Section 2: (i) phenotypic variation, (ii) differential fitness, and (iii) heritability. Upon closer inspection it turns out that all conditions for natural selection are here themselves being exogenously imposed by the experimenter. Without the experimental scaffolds, the Darwinian properties at the level of drops would cease to exist. In order to get distinct groups of individual cells, the setting above depends on "enclosure within a droplet surrounded by oil" (Rainey et al. 2017, p. 105), enabling the 'evolution' of group level variation. The oil can here be seen as a natural border for multicellular organisms, one that is abiotically scaffolded. If individual cells can freely move from one 'group' to the 'other' group level properties become diluted. While not strictly necessary for selection to occur at the level of groups, some form of boundedness is required to have natural selection 'conquer', or as Godfrey-Smith (2009) might put it, 'de-Darwinize' the lower level units in favour of the group. Boundedness strengthens the role of higher level selection since phenotypes have a higher correlation between generations, thus opening the possibility for group level beneficial adaptations at the level of individual cells. The scenario explored in Figure 2 similarly requires that the reeds are placed sufficiently far from each others for mats not to overlap, but close enough to enable differential reproduction. In addition, differential fitness of groups is here introduced by the introduction of an extinction process of darker groups, while the brightest groups are allowed to take over vacant 'niches' of now extinct groups. Both differential fitness and heredity at the group level are here imposed via the experimenter. But as Black et al. (2020) demonstrate in their follow-up study, these properties could nevertheless become endogenized.

I hope that this detailed analysis of Rainey's proposal, and the examples of its application, have given a good indication of the great potential it has for the interdisciplinary research among philosophers, experimentalists, and modelers. It's also an elegant example for how cooperation among these groups can lead to progress on a problem we have grappled with for decades. Philosophers of biology would be well-advised to help practicing biologists

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[14] I thank Rainey for this example.

to develop this research program further, and I hope that the next part of this paper will set the first stones for this exciting new avenue of research by attempting to make the notion of ecological scaffolding more precise and once again extend the scope of the Darwinian model of evolution by natural selection.

4 Scaffolding and Natural Selection

Black et al. (2020) exemplify the idea that "[e]volution is the control of development by ecology", an idea famously endorsed by the American evolutionary biologist Leigh Van Valen (1976, p. 180). Ecological scaffolds are exogenously imposed and can subsequently become endogenized - thus eliminating the circularity problem for the application of natural selection to explain the emergence of Darwinian individuals at a new level. This is an exciting proposal with compelling empirical evidence for the early stages of the edogenization of Darwinian properties, i.e. development, which deserves further philosophical analysis. In this section, I will draw on recent work in the philosophy of biology do to just that: offer a general, yet nevertheless simple definition of scaffolding as a distinctive phenomena in nature and clarify its importance within evolutionary biology. This will help us to conceive of natural selection itself as a scaffolded process.

A Simple Definition of Scaffolding

To begin with, we should get a firmer understanding of what scaffolding is. After all, the title of this article is 'Scaffolding Natural Selection'. Yet, this question is far from easy to answer, precisely because the term is often used in a deliberatedly vague and metaphorical way. I have noted that it has had an explosive growth in recent years, but its usage has varied widely due to the different areas in which it is employed. Nevertheless, substantial collaborative work across fields has already culminated in some progress, such as the volume *Developing Scaffolds in Evolution, Culture and Cognition* (Caporael et al. 2014), which arose from the 23rd Altenberg Workshop 'Scaffolding in Evolution, Culture and Cognition' at the *Konrad Lorenz Institute for Evolution and Cognition Research* (KLI). The prefix 'Developing' was deliberately added to emphasize the tentativeness of the project in attempting to make more sense of scaffolds across field. The volume explores conceptual and empirical questions on scaffolding across different disciplines and can here only be recommended for anyone seeking a broader overview across of this topic in fields beyond evolutionary biology. Caporael et al. (2014) argue that:

> The word scaffolding is both a noun and a verb; it names a structure and a process. The common meaning of scaffolding refers to a temporary structure of platforms and poles erected so that workers can build, repair, clean, or decorate a building. [...] Scaffolding is widespread, so widespread that its "attachment" to discourses in biology, culture, evolution, and human development indicates its centrality to processes of support and change of many kinds.
>
> – Caporael et al. (2014, p. 2)

Indeed, scaffolding processes understood in this sense are ubiquitous in nature. We can distinguish 'scaffolds' as structures from 'scaffolding' as a process, although the distinction can admittedly get blurred. But the way they are loosely described here in terms of an environmental supporting relationship, provides us with hardly any purchase on how to make them useful scientific concepts. It would turn a coffee cup into a scaffold in the same way as a beaver uses logs as a scaffold to build a dam. That the environment always plays a role in evolution would hardly constitute an interesting or novel thesis; it is almost universally accepted. Nevertheless, the ubiquity of scaffolds will remain an important for feature for several reasons, once we turn to the relationship between scaffolding and natural selection.

The most interesting property of scaffolding in relation to natural selection is undoubtedly, as the example of Rainey's work illustrates, its alleged usefulness for explaining 'black boxes' in traditional research paradigms. Caporael et al. (2014) likewise point out that:

> [S]caffolding is a "missing concept," perhaps because its primary virtue is that it is commonly temporary: it is often external, and either falls away or becomes assimilated to or part of the scaffolded relation.
>
> – Caporael et al. (2014, p. 2)

Now, this is precisely the sort of relationship we discussed with Rainey's thought experiment concerning reeds at which mats could form and his experimental work on the origins of endogenization. Here, Darwinian properties are in an important sense, induced from the outside. While one might expect scaffolding to differ widely from one context or target system to another, there is a straightforward analogy here to familiar cases in engineering where the term originated. At construction sites, scaffolds serve as temporary structures to enable or at least aid the creation or maintenance of a physical structure such as cranes and metal frames used to construct buildings. The common language use allows for a straightforward definition, once any intentional notions such as the purpose of the scaffold is eliminated. I propose the following working definition for scaffolding:

X is a scaffold *iff*:

1. X exogenously induces or supports the realization of property Y in process/system Z
2. X vanishes from or becomes part of the system, while property Y in process/system Z becomes endogenized

The important notions in my definition of scaffolds are (i) the exogenous realization of properties relevant to a process of system - such as Rainey's external imposition of Darwinian properties - and (ii) the endogenization of these properties, i.e. when they become part of the system itself or fall away without the important properties or effects thereby being lost. It is this second part of the definition that is unfortunately sometimes neglected, with the mere modal possibility of endogenization seen as sufficient for treating something as a scaffold. But as I shall demonstrate below, this would make the notion too permissive to be used as an explanatory concept in its own right, making it an almost trivial consequence of the fact that few if any processes occur independently from their environment.

Given the excessive usage of the terms 'scaffold' and 'scaffolding', being perhaps not always justifiably applied in multiple diverse domains, one may worry that my attempt to provide a general definition is doomed to failure and that perhaps the only unifying usage would a be a vague metaphorical usage. But if this were true, the vigour with which philosophers have joined the numerous debates embracing the position would appear quite strange. Doubly so, because unlike traditional philosophers of science, many of these philosophers have actually used it to probe new research programs, an undertaking that can only serve as exemplary.[15] But there is a tension in recent

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[15] See again Caporael et al. (2014) for an overview.

work that tries to (i) highlight the ubiquity of scaffolds in nature, and (ii) use it as an explanatory concept. Scaffolding can either be understood broadly as any kind of entity standing in a supporting relationship, or as a more precise concept that relies on the eventual endogenization or elimination of the scaffold. My definition rests on the motivation that it is only the latter understanding that can do genuine explanatory work. The former has far less explanatory value, as supporting relationships can be found almost anywhere, without thereby providing any further explanatory understanding of a target system. And since I am here primarily interested in naturalist conceptual engineering (see Veit and Browning 2020), rather than a mere conceptual analysis of the term, my focus is on endogenization. Unfortunately, many famous proponents of scaffolding seem to defend the much broader former notion, including Rainey. Here, one may object that my reservations against a broad usage of the term scaffolding are biased by my focus on major transitions.[16] But as I shall argue, such an unconstrained usage of scaffolding fails to distinguish it from other processes and obscures a unique role that scaffolds play in nature. Kim Sterelny, for instance, has been one of the most fervent users of the term scaffolding, but that very feature may also explain his apparently very broad definition of the term. Consider his example of Canberra's road signs:

> These cue names, directions to important locations, speed limits and rights of way. They are not deceptive; they are regularly present; their content is highly reliable. This set of resources scaffolds navigation around Canberra's confusing street network.
>
> – Kim Sterelny (2010, p. 475)

Road signs, of course, are here to stay. When Sterelny speaks of *environmental scaffolding* he uses the term interchangeably with *environmental supports.* Perhaps, scaffolding is the more attractive name for seemingly providing a novel position, but this can also serve to create an illusion, applying a new term for a point that would otherwise appear somewhat trivial. My point here, is not that the term scaffolding cannot be used in these circumstances, but rather that it would make the notion explanatory hollow and mix it up with a scientifically useful, but more restrictive application of the term. After all, the claim that many processes in the natural world, such as navigation, perception, cognition, and the development of organisms are supported by

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[16] I thank an anonymous reviewer for pressing me on this point.

the environment is far from novel nor particularly interesting. In fact, it is doubtful that anyone would object to such a weak version of scaffolding. More so, it raises the question of why the term was used to begin with if all it states is the existence of supporting relationships. Scaffolding, rather than a scientific concept in its own right, seems to be used as a mere analogy to strengthen the idea of *niche construction*, i.e. a process in which the organism alters its own selective environment to its own benefit (Odling-Smee et al. 2013; Scott-Phillips et al. 2014; Laland et al. 2015), in both the biological and cultural realm. While this metaphorical use is not problematic in its own right, indeed, can play an important role in science (see Veit and Ney 2021), my definition above is intended to provide a simple account that has the following triad of useful features: i) it is generalizeable across different contexts and domains, ii) it can be used in actual scientific work, and iii) it closely tracks common language use of the term.

Caporael et al.'s volume did not attempt to provide us with a general definition, with its contributors using the terms in widely different ways - sometimes solely metaphorically, sometimes with a precise and narrow meaning, fitted to the particular target of their investigation - and this was certainly admissible in the first collected volume on the topic. The goal was to let a hundred different flowers bloom and a deliberately vague use of the term was the ideal scaffold to accomplish just that. But in order to make the notion a precise scientific concept, there is an eventual need to provide a more precise and general definition that is applicable to the myriad scaffolding phenomena in nature, with their different time-scales and levels of organization - even if such an attempt at 'policing' the usage of the term will strike some as unwelcome. Admittedly, my definition may very well fail in due course and be replaced with a better one. Perhaps it will be demonstrated that the various phenomena conceived as scaffolding processes are too disunified as to allow for a useful general scientific concept. This is not too much a problem, as it is beyond the scope of any single stand-alone paper to survey an entire literature and prove that the definition stretches across all important instances of scaffolding processes. Nevertheless, if such an objection can be brought forth against my constrained definition of 'scaffolding' as a process of endogenization, it is even less likely that an much broader definition can play a useful role in science. For the present purposes of turning 'scaffolding' from a metaphor into an explanatory concept, my general definition will enable us to think about natural selection itself as a scaffolded process, enabling us to explain the major transitions in a non-circular, yet nevertheless Darwinian manner.

Darwinizing Natural Selection

Previously, I have mentioned that the idea of ecological scaffolds comes in the form of an externalist explanation, forming a break from the usual internalist explanations of Darwinian properties arising at a higher level in virtue of the interactions of parts (cells). As I have emphasized in Section 2, despite the general reluctance among contemporary neo-Darwinian evolutionary biologists to consider internal causes as a source of evolutionary change, many have nonetheless drawn on internalist patterns of explanations to avoid the circularity problem of explaining the emergence of Darwinian properties.

One popular example for an internalist explanation of a transition in Darwinian individuality is the idea of *co-option.* In co-option, pre-existing traits of particles become relevant for the collective entity, turning it into a Darwinian individual in its own right. Black et al. (2020) give the example of the colonial volvocine green algae, where groups can form by co-opting the retinoblastoma cell cycle regulatory pathway in the unicellular *Chalydomonas* (see Hanschen et al. 2016). Similarly, they point to exciting work of the Ratcliff lab on snowflake yeast (*Saccharomyces cerevisiae*) able to generate collective-level reproduction through co-option of the programmed cell death (apoptosis) to create propagules, thus showing that Darwinian properties can emerge from the interaction of parts (Ratcliff et al. 2012).

Nothing about this need be vitalist or mysterious. The point of Rainey's idea of ecological scaffolds is decidedly not to say that it is a competitor to co-option explanations. It will be exciting to see where these experimental research programmes on possible co-option processes will lead us in the next decades. We may start to think the actual evolution of multicellularity could have been a result of both co-option and ecological scaffolding, resisting a neat fitting into either category. Here, it would be a mistake to restrict ourselves to only one model. As I have previously argued: "for almost any aspect x of phenomenon y, scientists require multiple models to achieve scientific goal z" (Veit 2019b, p. 91).[17] But to restrict ourselves to co-option may force us to miss the important role of ecology. As Rainey would put it, we attempt to strip the problem to its bare bones, taking nothing for granted, and see how far we can get.[18]

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[17] See also Winther et al. (2013).

[18] From personal communication.

Unfortunately, the debate often reflects a higher-order commitment to kin-selection in the co-option of almost clonal cells and to multi-level selection in the scaffolding approach. But these shouldn't be seen as mutually exclusive, such that co-option necessarily 'beats' ecological scaffolding. This is easily recognized when we look at the very emergence of life, when there are no Darwinian units whose properties could become co-opted, and why Rainey's idea is even more useful outside of his work on multicellularity. It is at the origin of life - as a process - that ecological scaffolding provides us with a Darwinian view of how Darwinian properties emerge. It Darwinizes natural selection. Ecological scaffolding may provide us with a highly fruitful framework to develop plausible explanatory sketches of how natural selection could itself have gradually emerged in an eco-devo feedback loop. While Black et al. (2020) only talk in a few places about the transition to life from non-living matter, the idea of scaffolds finds a natural place within recent work on the origins of life. I will not go into any empirical detail on this issue here, since I am treating ecological scaffolding at a fairly general level as something that can explain the emergence of Darwinian properties in a non-circular, yet Darwinian way.[19]

In order to Darwinize natural selection in this way, I will introduce a concept that I shall dub 'evolutionary scaffold' as a broader conceptual framework in which to understand Rainey's notion of ecological scaffolding. Drawing on our general definition of scaffolding, we can define 'evolutionary scaffolds' straightforwardly as follows:

X is an evolutionary scaffold *iff*:

1. X exogenously induces or supports the evolution of property Y in process/system Z
2. X vanishes from or becomes part of the system, while property Y in process/system Z becomes endogenized.

Importantly, this is not how Rainey sees ecological scaffolding. For Rainey, it is scaffolding regardless of whether the properties induced by the environment become engodenised or not.[20] He effectively gives up the second part

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[19] Damer and Deamer (2020), however, may provide a useful hypothesis about the origins of life that may be explicated in terms of ecological scaffolding.

[20] From personal communication.

of my definition since endogenization need not be realized. But this is then returning to the overly expansive usage of the term scaffold as a mere environmental supporting relationship, a criterion that is notably weak due to its broadness. Whereas simple models of the origin of life and multicellularity may idealize all environmental factors away, merely consisting of the replication of units, almost all actual biological processes involve feedback between organism and environment. The real power of Rainey's idea of ecological scaffolding I suggest, is thus not this environmental role *per se*, but rather the process of endogenization.

To make this clear, it will be helpful to elaborate further in an evolutionary context what is meant by 'endogenization'. Borrowing the term from the economic modeling literature - where exogenous and endogenous variables are typically distinguished and the former are treated as given inputs, whereas the latter as outputs determined by the model - Okasha (2018) suggests that a similar distinction can be drawn in evolutionary models. Applied mathematicians switching from economics to biology may be surprised to learn that the role of endogenization has been given little attention in evolutionary models. Yet, this omission can simply be seen as an artefact of the modeling choices inherent to any evolutionary model: some factors are taken as mere inputs, whereas other can be influenced by the model itself. In Section 2, we saw that natural selection is often treated as a law-like ordering principle of biology. This largely owes itself to the procedural subsumption of more and more phenomena under the general explanatory scheme of evolutionary theory. Okasha (2018) describes this historical trend as a strategy of endogenization: "[i]t involves devising evolutionary explanations for biological features that were originally part of the background conditions, or scaffolding, against which such explanations took place" (p. 2). In the language of modeling, we can see this trend as the subsumption of phenomena under a more general model of evolutionary change. There are thus two senses of the term endogenization: one about a phenomena being subsumed/integrated into an explanatory program, the other about a phenomenon being endogenized over evolutionary time into the development of the organism. Both Wimsatt and Griesemer (2007, p. 245) and Caporael et al. (2014, p. 377) briefly talk about the "internalization" of scaffolds as an important factor involved in the evolution of complex forms of organization (both in biology and culture), but unfortunately treat this as optional. Whereas these authors see such a process as an important role for scaffolds, I see endogenization of Darwinian properties at the very heart of what makes something an evolutionary scaffold. This distinction provides us with an interesting further question of how well the endogenization of variables into an explanatory model can serve as an adequate representation for endogenization of scaffolds in nature, such as Rainey's reeds, that I will further address in this section.[21] Despite this ambiguity in the usage of the term endogenization, I expect that it will nevertheless be useful to think about our attempts at modeling the origins of Darwinian units and exogenous variables becoming endogenized. The explanatory reach of evolutionary theory has constantly pushed its limits, though this has often been criticized as too 'adaptationist'. Yet, Okasha (2018) elegantly demonstrates that evolutionary theory has been extended to explain many phenomena formerly considered to be outside the purview of - or at least obstacles to - Darwinian explanations such as the origin of variation, biological sex or anisogamy, altruism and population structure, niche construction, the genotype–phenotype map, and the origins of hierarchical organization. This is not to say that these phenomena have been fully explained in Darwinian terms, but rather that we are developing evolutionary models where these phenomena are treated as outputs, rather than just take them for granted. These points help to illustrate what Rainey has in mind when he speaks of the endogenization of Darwinian properties. Internal factors (development) become more important, with life becoming more 'autonomous' from external forces in the process.

In 2006, Okasha distinguished between the 'old' approaches to the levels of selection question as "synchronic" approaches that treated hierarchical levels as given in the explanation of adaptations on that level, whereas he considered the growing evolutionary transitions literature to constitute a "diachronic" approach to the levels of selection question. Here, the level of selection itself is explained through recourse to Darwinian explanation, which as Okasha (2018) points out in his recent paper, can be understood as the endogenization of the "hierarchical organization itself" (p. 12). Hierarchy is no longer seen as a necessarily exogenous factor in evolutionary models. This binary way of describing the growing major transitions literature can be misleading, however, since it may be interpreted as suggested that we have already subsumed these phenomena under the scope of the principle of natural selection. Partially, this is due to the origin of the endogenous/exogenous distinction that Okasha draws on from the modeling literature in economics. In economics, either a variable is an input of the model or it is an output. But

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[21] I thank an anonymous reviewer for pressing me on this point.

in nature we find gradations and endogenization as a natural phenomenon should not merely be understood as as a feature of our models and explanations. It is a real phenomenon in nature and it is the very origins of this endogenization process, i.e. the origin of development, that we should pay attention to since it is here that natural selection emerges in an eco-devo feedback-loop. It is because of this that ecological scaffolding ought to include endogenization in the sense of ecological properties becoming organismal ones - i.e. the second component of my scaffolding definition - in order to turn it from a mere metaphorical notion into an explanatory concept.

Much in the above discussion of Rainey's work has focused on reproduction, but other Darwinian properties face the same problems (for a discussion of heredity see Doulcier et al. 2020). Nevertheless, as Okasha (2018) describes it, Darwin's worries about the origins of variability in populations have been solved, and to some extent this is certainly true. We no longer treat variation as a black box. We have come up with both short-term and long-term macroevolutionary explanations for why variability itself can be explained as an adaptation. Indeed, this work elegantly overlaps with work on evolvability (see Pigliucci 2008). But debates about the role of evolution, or rather natural selection, in the emergence of a phenomenon rarely focus on the question whether or not natural selection is *part* of the story. The question is *how important* natural selection is in the explanation of a particular phenomenon as opposed to other factors such as physical or chemical constraints on the possibility of 'perfect' replication. This is why the abbreviated Van Valen quote in Black et al. (2020) about development being controlled by ecology must not be misunderstood as suggesting that we need either a developmental *or* an evolutionary explanation. Rather, Rainey defends the idea that development and evolution are two sides of the same coin. They are both in control of each other. There is no interesting thesis here about one beating the other and we need to pay more attention to the evolution of development. As Griesemer (2000) noted, development has long been a weak link in evolutionary theorizing and ought to be integrated in our thinking rather than idealized away (p. 29). Similarly, Van Valen maintained that despite the possibility of thinking about evolution in terms of ecology controlling development, "neither area has figured importantly in evolutionary theory since Darwin, who contributed much to each" (1973, p. 48). And it is this more important point by Van Valen that makes Rainey's ecological scaffolding framework such an interesting proposal, through integrating development, evolution, and ecology in an eco-devo feedback loop. Even at the longest possible time-scales, it suggests that development is a factor that cannot be idealized away. Rather, it is a process that underlies the very endogenization of Darwinian properties in their own right. Ecological scaffolding explains the very origins of internalist developmental explanations, without taking anything for granted. I am thus not here interested in claiming that development controls evolution through the endogenization of Darwinian properties. There is as much truth to this statement as there is to Van Valen's.[22] Indeed, Okasha warns us not to confuse the widespread prevalence of endogenization in evolutionary biology with a reductionist view of natural selection as a "universal acid" (see Dennett 1995). Even if we want to treat natural selection as something like a 'first principle of science', we can defend a more nuanced view that likewise makes use of the idea of endogenization.

> The alternative is this. It is not the core Darwinian principles themselves that bear the explanatory burden in evolutionary biology, but rather those principles as they operate in specific biological settings, in the presence of additional contingent biological features.
>
> – Samir Okasha (2018, p. 18)

Naturally, there is a myriad of ways background features can play a role in specific explanations that make use of natural selection. If these can in turn be explained through natural selection it is tempting to buy into Van Valen's dictum. But Okasha (2018) rightfully maintains that even if we can provide an evolutionary explanation for the background features of a particular phenomenon we want to explain, this does not entail that the phenomenon can be explained without an explicit appeal to the background features (p. 19). What is important for the purposes of this paper, is simply to recognize that background assumptions often serve as a scaffold in biological theorizing, only to later become part of a Darwinian explanation. But in ecological scaffolding, as I aim to more narrowly definite it here, it is not these background

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[22] Consider an egalitarian marriage of the 21st century. Historically, marriages were sometimes jokingly described as a man being chained by a woman, suggesting that women are in control of their husbands. But this would be a gross misrepresentation of the patriarchal and sexist power structures we found in marriages in the past (and unfortunately in many in the present). Such statements have largely been abandoned or at least come to be scrutinized due to their sexist nature. In an egalitarian marriage, however, it need not be the case that either partner has power over the other. Unless we want to define the term 'control' as whoever has more causal power, we can legitimately say that each partner has control over another. And so it is with development and natural selection. We do not have to defend a view in which one side must 'win'.

conditions of an explanation that become endogenized, but the phenomenon itself.

By understanding ecological scaffolding as an externalist attempt to endogenize Darwinian properties, we can tease apart this duality in Rainey's discussion of ecological scaffolding between what can be understood as an *explanatory scaffold* and what I have called an *evolutionary scaffold*. This distinction is subtle, but important. On the one hand, ecological scaffolding can be understood as an externalist - as opposed to internalist - mode of explanation, in which Darwinian properties are induced by Darwinian means in a non-circular fashion. Here, we rely on natural selection (environmental filtration) as an explanatory scaffold for explaining the origin of Darwinian properties. We subsume these phenomena in a Darwinian model of life. On the other hand, the environment itself is an evolutionary scaffold, a genuine scaffold in nature that induces Darwinian properties that are then able to become endogenized across evolutionary time. One is a tool for coming up with new explanations for Darwinian individuals, the other is a natural phenomenon that we are trying to make sense of here. In trying to understand the role of scaffolds in nature, we can also recognize a someting of a 'reverse' process of evolutionary scaffolding in which Darwinian properties become exogenized rather than endogenized, with organisms losing autonomy and becoming more dependent on special ecological conditions. Such an idea has been hinted at in Godfrey-Smith's discussions of viruses, that while brief, can be elegantly co-opted:

> Simple reproducers need not be the lowest-level reproducing entities in a hierarchy, however. A third category I will call scaffolded reproducers. They might even be called reproducees, or at least many of them could. These are entities which get reproduced as part of the reproduction of some larger unit (a simple reproducer), or that are reproduced by some other entity. Their reproduction is dependent on an elaborate scaffolding of some kind that is external to them. However, these entities do have parent–offspring relationships, hence they form lineages or family trees.
>
> – Peter Godfrey-Smith (2009, p. 88)

Viruses straightforwardly use other organisms for the continuation of their own life cycle. They depend on the reproduction of other living entities, in order to facilitate their own reproduction. Without this scaffold the life-cycle is 'stuck'; an evolutionary dead end. It is not, however, evolutionary scaffolding as I constrained the term. While viruses did evolve via other reproducers they did not discard or endogenize them. Only if a virus were to evolve the ability to reproduce without the need to high-jack the reproductive capacities of other organisms would there be a case of evolutionary scaffolding. It may thus be worthwhile to draw a distinction to *developmental scaffolding* which better describes Godfrey-Smith's notion of a scaffolded reproducers. Nevertheless, in thinking about evolution something very much like a *reverse* ecological scaffolding process must have been at the origins of virus life-style (and perhaps more generally at the evolution of parasitism), whence autonomy was lost.

Hence, we should recognize that the role of scaffolds in evolution can go in two ways: endogenization and exogenization. In the former, scaffolds become endogenized or discarded (e.g. the origin of life and plausibly the origin of multicellularity), and in the latter, organisms introduce scaffolds into their life-cycles that make it evolutionary viable to exogenize Darwinian properties such as reproduction (e.g. a virus). These two should not be confused and it is for this reason why the scaffolding metaphor in the latter is bound to be misleading, since there are two quite distinctive processes going on. Perhaps a better way of distinguishing the two processes would be between endogenized scaffolding as a process of autonomization (from external forces) and the exogenization of development as a loss of autonomy (reliance on external factors).[23] Nevertheless, in both it is the role of the ecology that is the crucial key to understand the evolutionary dynamics these systems take and we can see my narrower concept of evolutionary scaffolding as enabling us to distinguish these two directions evolution can take organism. I hope that my refinement of Rainey's idea of ecological scaffolding as a process of endogenization will help to highlight the importance of this simple fact: natural selection is an ecological process and should therefore be studied in terms of the external ecological scaffolds that gave rise to the eco-devo feedback loops of life. Before we move to the conclusion, however, I hope that this section has provided something of a proof that Caporael et al. (2014) were right in their prediction for the usefulness of a developed concept of scaffolding:

> A more highly analyzed and developed concept of scaffolding will high-

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[23] The relation of these processes to niche construction and the role of agency would be a further interesting topic to explore; see Veit 2021a for some initial thoughts on the subject.

> light the role of temporal and temporary resources to development, broadly conceived, across concepts of culture, cognition, and evolution.
>
> – Caporael et al. (2014, p. 3)

5 Conclusion and Further Avenues for Research

The theory of natural selection is the most impressive theoretical development in the biological sciences. No other theoretical framework has achieved the striking explanatory breadth and growing list of successes of this basic Darwinian idea. Yet, the major transitions have continued to resist this Darwinian imperialism. The aim of this article has been to offer the first philosophical analysis of Rainey's idea of *ecological scaffolding* as an ambitious attempt to once more push the boundaries of externalist Darwinian theorizing to encompass the major transitions, including the very origins of life.

Firstly, I have argued that Rainey's work constitutes a beautiful example for the possible fruitfulness of collaboration between philosophers of biology, theoreticians, and experimental biologists, since it provides both a general theoretical framework and an empirically testable hypotheses that can be implemented in the lab with plenty of possibilities for feedback between both. Collaboration between philosophers and evolutionary biologists is, of course, not a new phenomenon (see Lloyd et al. 2008 for a particularly elegant case); they have worked together on the nature of evo-devo (Wagner et al. 2000; Love and Raff 2003; Love and Travisano 2013) and on how theoretical, field, and lab work interacts in practice (Winther et al. 2015). Naturally, this is far from an exhaustive list and many more examples could be given once we extend our view to experimental evolutionary ecologists such as Robert Brandon and Janis Antonovics. But what I hope this paper has shown, is that philosophers of biology would do well to keep up to date with this exciting new work in experimental biology, addressing old philosophical problems with exciting new experimental tools. In this, I can only echo a recent critique by Pradeu (2017):

> Clearly evolution offers one unifying framework for all biology, and some aspects of evolution are highly theoretical, but this should not

> hide the fact that evolution has also a key experimental component. Recent major advances in evolution have come from studies in "experimental evolution", such as those of Richard Lenski, Michael Travisano, and several others (Lenski et al. 1991; Lenski and Travisano 1994; Sniegowski et al. 1997). An exclusive focus on the theoretical dimension of evolution might lead philosophers of biology to miss the importance of these experimental approaches to evolution .
>
> – Thomas Pradeu (2017, pp. 159-160)

Secondly, I have tried to offer an analysis and explication of ecological scaffolding, an idea that while highly useful and fruitful for the illumination of old biological problems in the major transitions literature, could benefit from further refinements by philosophers of biology. While usage of the term 'scaffolding' has exploded in recent years, it has often been used in rather imprecise, vague, and merely metaphorical ways. Here, I have attempted to give both a precise, yet general definition of scaffolding and evolutionary scaffolding, that restricts Rainey's idea of ecological scaffolding to only those circumstances in which exogenously imposed properties come to be endogenized, since it is here that we come to observe the dawn of development. In addition, I have argued that this emphasis on edogenization allows us to distinguish a reverse 'scaffolding' process, with organisms becoming less autonomous, that must have occured during the evolution of viruses and other parasitic life-cycles. Future work may attempt to model the adaptive dynamics leading to exogenization or endogenization. The greatest strength of the inherently Darwinian explanatory strategy of scaffolding may indeed lie outside of its original application, i.e. at the origin of life, when there are no lower-level units with Darwinian properties that could be co-opted. It is in this sense, that the very origins of natural selection may very well have required something like a complex ecological scaffold. Indeed, this recognition may help us to explain why the origins of life research has failed to make much progress: a partial neglect of ecology. While one may legitimately reply that the study of the chemical conditions for life has been about the ecological conditions of proto-life forms, this work does seems to have been dominated by an internalist mode of explanation which focused on the minimal conditions of living systems without a role for ecological scaffolding. This is why I have titled this paper 'Scaffolding Natural Selection'. The origins of life may require appropriate ecological conditions in order to scaffold Darwinian properties onto non-living systems, in something like an original eco-devo feedback loop in which natural selection selection itself gradually emerged alongside the process of life itself. However, I have also argued that we should resist the temptation to label any environmental support found in nature as environmental scaffolds, as this would make the explanatory concept hollow. Scaffolding can indeed be developed into a genuine scientific concept with explanatory power, but only if we restrict it as I have argued to processes that contain the very origins of the endogenization of Darwinian properties.

Further directions that deserve exploration are the connections between development, ecological scaffolding, and natural selection. While this paper has aimed to address these issues, I have only taken some of the first steps, and there is much further work that needs to be done. Using the framework suggested here, many puzzling problems about the evolution of multicellular organisms and even the origin of life may come to be illuminated. The scaffolding of natural selection offers an exciting new research area within experimental evolution, and it is likely to play an important role in future research on the major transitions. Unfortunately, it has been common among evolutionary biologists to ignore the role of development at the time-scale of the major transitions. But this is is a mistake. In evolutionary scaffolding processes (whether endogenizing or exogenizing) much hinges on the development of complex life-cycles. I expect that future work inspired by Rainey's experiments will show the need to distinguish between what we may call *developmental scaffolding* as a process within a life-cycle and *evolutionary scaffolding* as a process across life-cycles, and how these forces can pull in opposite directions in the cases of multi-level selection. Unfortunately, a proper treatment of these further problems will be a task for another day (though see Griesemer (2016, 2018, 2019) for a set of interesting ideas). Nevertheless, this need to distinguish different scaffolding processes only further emphasizes the need for greater conceptual clarity.

Finally, I hope that there is at least some kernel of truth to be found in the analysis I have offered, and that it will be useful to philosophers, experimentalists, and theoreticians alike in our joint goal to further progress our understanding of evolution. To conclude: scaffolding is a natural phenomenon, one that plays a myriad of underexplored, yet, important roles in evolution. We can be Darwinians about the Darwinian process of natural selection itself, thus once again broadening the scope of natural selection as a 'first principle' of biology as expressed in Theodosius Dobzhansky's famous dictum that "nothing in biology makes sense except in the light of evolution"

(Dobzhansky 1973).

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