

How Ecosystem Evolution Strengthens the Case for Functional Pluralism

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Abstract Evolutionary explanations appear to necessitate etiological theories of function. As Amundson and Lauder have shown (Amundson R, Lauder GV. Function without purpose: the uses of causal role function in evolutionary biology. *Biol Philos* 9:443–70, 1994, reprinted in Allen et al. *Nature's purposes analyses of function and design in biology*. The MIT Press, Cambridge, MA, 1998), current biological practice is in fact more pluralistic in its choice of functional explanations, using etiological functions as well as ahistorical causal functions. Here, I will examine how some functional descriptions in ecology and how they are imported into evolutionary explanations strengthen the case for the use of ahistorical functional theories in biology in general but in ecology and evolutionary biology in particular. I will focus on the case of ecosystem evolution where I will argue that fitness is better understood as differential persistence. We shall see that this type of evolutionary phenomenon demands nonhistorical functional explanations. This will be described as a potential vindication for forward-looking functional theories, otherwise known as propensity account of functions. In a more general way, I will show how this vindicates pluralistic account of functional explanations in biology.

1 Introduction

In this chapter, we will examine how some functional descriptions in ecology and how they are imported into evolutionary explanations strengthen the case for the use of ahistorical functional theories in biology in general but in ecology and evolutionary biology in particular. I will focus on the case of ecosystem selection and evolution

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and how it demands nonhistorical functional explanations. This will be described as a potential vindication for forward-looking functional theories, otherwise known as propensity account of functions. In a more general way, I will argue that this vindicates pluralistic account of functional explanations in biology.

The discussion about functions in biology has focused mainly on evolutionary biology for a few distinct reasons. Let us briefly examine two of these reasons.

First, philosophers of mind were looking for a way to offer some sort of teleological or quasi-teleological grounding for functional ascriptions in a way that constrained the types of structures that could instantiate the functional systems. Teleofunctionalism in philosophy of mind seemed able to evacuate problems that functionalism had with, for example, inverted qualia, or malfunctioning traits in general. This teleofunctionalism was cashed out in evolutionary terms.

Another reason for the focus of functional arguments on evolutionary biology is that, and this is more a sociological point than a philosophical one, most philosophers of biology for the last 40 years have focused their inquiry evolutionary theory, in part because it appears *prima facie* to be the best candidate for a unifying theory of biological explanations, something that developmental biology or cell biology cannot hope to achieve.

In this context, it is not surprising that theories of function grounded on history have been favoured: evolutionary history appears to get philosophy of mind out of theoretical binds while warranting philosophy of biology's focus on evolutionary biology instead of focusing on other biological disciplines.

What is not always recognized however is that evolutionary history will not always vindicate historical functional theories. Even though evolutionary biology has to look at selection history which seems to warrant a Wright-like function theory (Wright 1973, 1976), some evolutionary explanations necessitate nonhistorical functional ascriptions. For most readers of this book, this is probably not a novel point although it is still somewhat controversial. Amundson and Lauder in their oft-quoted 1994 paper (reprinted in Allen et al. 1998) argue for functional pluralism, that is, we should entertain both historical and nonhistorical functional theories since they are both necessary for biological discovery; Amundson and Lauder use examples from physiology and other biological fields that cannot be said to use historical functional concepts and show that they are necessary for evolutionary explanations. More recently, Griffiths (2006) has offered a similar argument using developmental biology (although he uses this example not to defend a pluralist view but something more akin to a monist nonhistorical functional theory). After briefly discussing this pluralist line of argument, I will use examples stemming from ecology to show that nonhistorical functions are necessary for biological explanations.

But I will add a twist; I will show how these nonhistorical functions are necessary not only for ecology but for evolutionary biology and play an even larger role than what was described by Amundson and Lauder. This result is somewhat ironic since it would show that some aspects of evolutionary explanations do not depend on past history... Propensity accounts (or dispositional, or forward-looking accounts) of functions are truly necessary, which reduces (but does not eliminate) the relative importance

of historical functions in evolutionary explanations. As we shall see, this point has been made before, but the support provided here is novel and more importantly shows the scientific urgency of thinking about these questions.

2 Diversity Rules

Wright (1973, 1976) famously described an etiological thesis where the function must be understood as an explanation of the persistence of an entity through time. As many have pointed out (e.g. Boorse 1976; Godfrey-Smith 1998; Millikan 1989), notice that this description does not entail that historicity only concerns biological entities although evolutionary theory puts this historicity in a plausible natural context. Non-biological entities also exist for a period of time; anything that contributes to the object's continuing existence is to be considered functionally. Millikan's account of proper functions (Millikan 1989, 1993) may be a good example of Wright functions but one that wishes to be geared towards biological entities. Millikan, herself, rejects the idea that she is merely exposing a refined Wright function.¹

The difference between the two theories would be concerning the concept of origin. According to Millikan, Wright speaks of etiology without talking about specific origins of the entities and their functions. Whether this is enough to distinguish Millikan's thesis from Wright's is arguable. I am inclined to say that Millikan's proper functions are but a special case of Wright functions: this special instantiation could be seen as purely biological. This point will not be examined further here. Whatever the degree of similarity or affinity between Wright's and Millikan's account, the fact remains that both rely on a notion of past selected effects and therefore on processes that have unfolded in the past, that is, historically. Neander and Godfrey-Smith (among others) have added further precisions to this account but the details will not concern us here.

The other functionalist camp rejects this historicity. Cummins (1975) argues that it is the *now* that science is interested in, and as such, it would be misleading to understand functions exclusively relative to their origin. Evolutionary theory is not needed to identify biological function. This is not surprising per se since Cummins himself is interested only in the concept of function as it is used in psychology, but others have used his concept in biology. In Cummins' view, functional explanations reflect the contribution of a capacity to the overall capacity of the system. The understanding of such capacity is ahistorical because actual capacities do not necessarily reflect the original goal or the purpose of the system. This means that we should only examine how the system is working at moment t1 and try to figure out how the different parts of the system work together at t1.

¹ See a comment to that effect in note 5 of Millikan (1989).

According to this functional theory dichotomy, one may *prima facie* believe that evolutionary biologists would focus on historical Wright functions (because of the focus on evolutionary history) and other biologists would focus on ahistorical Cummins functions.

This dichotomy (at least in the case of evolutionary biology) may be overly simplistic. Amundson and Lauder show that both functional theories underpin evolutionary explanations, that is, it is false that evolutionary biology only concerns itself with historical functions.

The bias of many evolutionary biologists (or rather, philosophers interpreting biological theory) is to see functions in evolutionary explanations exclusively as Wright functions, what Amundson and Lauder call selected effects (SE) functions. Amundson and Lauder defend the idea that evolutionary biology is also concerned with Cummins functions that they call causal role (CR). By describing subfields of evolutionary biology that do not put any relevance in the SE thesis, Amundson and Lauder show that CR is necessary for evolutionary biology. This is significant because, if Amundson and Lauder can show that some evolutionary biology research cannot be served exclusively by SE, and actually sometimes doesn't require it, and that, inversely, some other evolutionary biologists cannot do without SE, a pluralistic functional account will be necessary to account for functional explanations in evolutionary biology: different functionalisms will be needed in different subfields. It appears that this conclusion is intended both as a descriptive claim (i.e. evolutionary biology *is* actually pluralistic) and a normative claim (i.e. evolutionary biology *should be* pluralistic with regard to functional explanations).

As an example of a CR proponent, Amundson and Lauder use the case of functional anatomists who look at bone structures and organisms ahistorically – they consider all the possible capacities of a structure in an engineering-like way. If we accept the relevance of their work and more importantly the necessity of this work, for example, in the trait identification in palaeontology, we must accept that SE functions will not be sufficient in evolutionary biology. Some of the critiques of the CR view have questioned the antecedent in the previous conditional by questioning the relevance of functional anatomists. CR functions are painted as playing with trivial hypothetical descriptions. Amundson and Lauder show that this characterisation is unfair: functional anatomists, while considering possible capacities, are examining possible capacities of *actual* systems. Their explanations are not the trivial description of science-fiction cases as their opponents would make them out to be. The example I will describe later will hopefully be another argument in favour of nonhistorical functional analyses.

One must stress the point that Amundson and Lauder are not rejecting a SE view of function. Rather, they are arguing that an exclusive SE view gives an impoverished view of the field of evolutionary biology.

Conversely, they argue, a purely CR view of function cannot do the whole job. That is the reason a pluralistic account of function is needed, one where SE is useful in certain cases and CR is useful in others. Amundson and Lauder argue that reducing one to the other doesn't give a true characterisation of evolutionary biology as a whole.

3 Looking Ahead

As it has often been pointed out, Wright wasn't concerned with evolution per se. In fact, his descriptions of functions were devoid of any biological criteria, even though they would be compatible with a biological framework. The non-biological framework Wright described showed certain weaknesses. Boorse showed² that the way Wright functions are construed, one could ascribe trivial functions to systems that could be described as having a 'purpose', but that would be described as such only because of circumstantial evidence.

Take Wright's definition of function:

The function of X is Z *means* that (a) X is there because it does Z. (b) Z is a consequence (or result) of X's being there. (Wright 1973, p.161)

Boorse, Godfrey-Smith and Millikan among others note that 'the problem here is with the broad range of "X" and "Z" [which are the variables in Wright Functions]' (Godfrey-Smith in Allen et al. 1998, p. 455). Without any biological criteria (or in fact any other type of criteria), there is no way to determine what are the relevant entities that need to be explained functionally and what functional explanations are not trivial. Millikan, for example, wishes to use biology insofar as it constrains the domain of application of functional inquiry in a meaningful way. By doing so, we eliminate a priori many trivial cases of hypothetical teleology.

As previously noted, SE functions (and the explanation they provide) are not rejected by Amundson and Lauder. Rather, they argue for the importance of physiology and functional anatomy and the nonhistorical functional explanations they provide and their significant role in evolutionary explanations. For SE functions, one needs a past history of selection to identify the process and its 'real' function. As Amundson and Lauder point out, a purely engineering view is sometimes necessary when history is not available. But is that merely an epistemic point? The fact that our study of the fossil record, because of its relative poor quality, leads to nonhistorical description may say more about our access to evidence than about functional explanations per se.

In other words, a genuine worry is that functional pluralism might only be a temporary state of affairs: given more information about the living world, we could eliminate the instrumental use of nonhistorical causal functions and revert to historical functions simpliciter. Basically CR functions could be seen as instrumentally necessary for now, but ultimately disposable in favour of the 'real' SE functions.

I will now offer some hope that this worry is overstated: at least in some biological cases, the use of some sort of nonhistorical functions is not merely instrumental and does not merely depend on our epistemic constraints.

I wish now to examine an evolutionary case where there is no past history.

The problem of past versus future history is the core of the problem here.

²Boorse (1976), or see Griffiths in Allen et al. (1998), p. 445 for a detailed summary of the argument and a thoughtful discussion of this issue.

As Bigelow and Pargetter (1987 reprinted in Allen et al. 1998) point out, SE functions are purely backward-looking descriptions. A given trait has a specific function if that function contributed *in the past* to the persistence of that trait. But as they point out, some sort of forward-looking accounts play a large role in conventional accounts of fitness. At their core, propensity accounts of *fitness* are causal accounts. The probability of an organism to have a certain number of offspring is grounded on the physical, biological and behavioural features of the organism and how it interacts, causally interacts that is, with its environment. But propensity accounts are interested in probable offspring contribution, not actual offspring contribution. In the same way that propensities allow fitness to avoid the tautology problem, Bigelow and Pargetter argue that a propensity account of functions gives the explanatory force of functional explanations.

And they come up with this suggestive conclusion:

The etiological theory describes a character now as serving a function when it did confer propensities that improved the chances of survival. We suggest that it is appropriate, in such a case, to say that the character *has been serving that function all along*. Even before it had contributed (in an appropriate way) to survival, it had conferred a survival-enhancing propensity on the creature. And to confer such a propensity, we suggest, is what constitutes a function. Something has a (biological) function just when it confers a survival-enhancing propensity on a creature that possesses it. (Bigelow and Pargetter in Allen et al. 1998, p. 252)

Similar accounts have been given by Wimsatt (1972) for instance. The nice thing about propensities is that for better or for worse, one does not need past history. One could have a propensity even if a system and its functions appeared *ex nihilo*. This is not the case for SE functions and this will be crucial for the rest of my argument.

I will now show how ecosystem evolution can be understood and how, because of the abiotic part of ecosystems, one needs some sort of nonhistorical account of functions and of fitness. As it will become clear in the following pages, we will be relying on highly unorthodox ways of understanding evolution by natural selection. Yet, the hope is that payoff of adopting them outweighs the cost of changing our evolutionary framework.

Leo Buss's description of somatic selection (Buss 1983) is an inspiration for this part of the argument: Weismannism describes how only changes in the germ line can be passed on to the next generations. But as Buss points out convincingly, the evolution of protists, fungi and some plants which are in large part the result of selection on somatic changes cannot be accommodated by Weismannism. Buss uses this idea to justify a hierarchical view of selection broader than the usual modern synthesis view. Many of the examples given by Buss literally do not reproduce. Buss is correct in explaining how, in the cases he presents, evolution can happen via selection on sub-organismal variation. As we will see for some cases of evolution, the notion of component or part is more relevant than the notion of offspring. This insight has found some support in more orthodox understanding of evolutionary theory.

In his exhaustive survey of natural selection experiments, John Endler (1986) pointed out that many studies in evolutionary biology focus exclusively on intragenerational success and phenotypic selection. Although obviously fecundity and fertility

are keystones of evolutionary explanations, survival and the means by which organisms survive are a necessary aspect of the story.

Elsewhere (Bouchard 2004, 2007, 2008, 2011) I argue in details that *differential persistence* should replace *differential reproductive success* for a unified understanding of fitness. I can't give the whole argument here but the broad motivation is straightforward: what is necessary is a broader understanding of evolution to cover the evolution of strange entities like corals, huge integrated clones and, the example I will examine here, ecosystems.

This insight is inspired in part by Van Valen:

It is just as good, and maybe better, for a massive coral or a tree to stay alive, occupying the same good site, as it is for it to reproduce into an uncertain world.

(...)

Persistence is an important component of fitness and is ultimately related to the spatiotemporal heterogeneity of the total environment. (Van Valen 1989, p. 5)

For many biological systems, differential success does not perfectly match differential reproductive success. This is a controversial claim, especially since allelic frequencies are the current key metric of adaptive success in our evolutionary explanations. Yet the problems are well known: for many plants, for example, it has always been difficult to distinguish asexual reproduction that can count as differential reproductive success, from vegetative growth that concerns development more than evolution. Philosophers have assessed this difficulty by arguing that reproductive success while central may not be exhaustive to account for evolutionary success. Ariew and Lewontin (2004) have highlighted the problem of asexual reproduction for a reproductive-based account of fitness while Sober (2001) has described the dual understanding of fitness, the first usually focusing on reproductive success, while the other facet focuses on survival. In my previous work, I develop this last aspect to encompass all others. Fitness is usually understood as a composite of survival and reproduction, yet, in most models, survival is only included as instrumentally necessary to get the organism to the reproductive phase. I turn this relationship on its head to argue that reproduction is a means to increase the lineage's persistence (equivalent of survival). This idea is inspired by similar moves stemming from ecology.

The focus on persistence has been around for a long time in ecology (often under the guise of stability). Persistence was not seen by most ecologists as an evolutionary property. This is not surprising given that ecosystems do not have their own genetic systems (and therefore heritability at the ecosystem level is *prima facie* a non-starter). But, once one identifies ecosystem-level property (e.g. stability, complexity, species-richness), it is but a small leap to hypothesize that this property is the result of selection-like forces. Ecosystems obviously do not reproduce but they do persist, some better than others, giving us the building blocks of differential success. Many advocates of the idea that whole ecosystems could evolve quickly realize that persistence, not reproduction, will be the key to understand ecosystem evolution.

Theoretically, the idea of ecosystem evolution is interesting but the problem has always been to identify real cases of ecosystem evolution. Ecosystem evolution had until very recently not been identified as a genuine evolutionary

process (although many believed it was at least a theoretical possibility). It was believed to be epiphenomenal (Hoffman 1979) or at least very unlikely (Hull 1980). But within ecology, the judgement has not been so pessimistic. A few texts stand out as evolutionary descriptions of ecosystem creation, maintenance and transformation. Ott (1981) in his assessment of marine ecosystem writes that ‘Although the basic features of evolution can be found in ecosystem development, the mechanism is quite different from Darwinian evolution. Ecosystem fitness is not determined by differential reproduction but rather by differential persistence (survival)’ (Ott 1981, p. 144). Dunbar (1960), also focusing on marine ecosystems, arrives at a similar conclusion. ‘As to the mechanisms by which selection might take effect at this [ecosystem] level, they are of the ordinary Darwinian sort except that the criterion for selection is survival of the system rather than of the individual or even the species’ (Dunbar 1960, p. 134). Cropp and Gabric (2002) focus on the evolution of resilience as an ecosystem-level adaptation. Darnell (1970) goes further by placing ecosystem evolution at the heart of all evolutionary process. Many other ecologists have entertained the idea that ecosystems can evolve by natural selection, but this research programme is fraught with obstacles.

Part of the operational difficulty in testing the ecosystem evolution hypothesis is a problem of physical scale. How can one go about ‘measuring’ the evolutionary fate of whole ecosystems? Ecosystems are usually construed as relatively large, and it is very difficult to account for all the species constituting it and the interactions between them. But when one realizes that ecosystem or communities do not have to be ‘large’ relative to human scale, testing evolutionary hypotheses becomes much more manageable.

In artificial selection experiments (Swenson et al. 2000a, b), a good case for artificial ecosystem selection is provided. I will refer to the experiments as David Sloan Wilson’s experiments since he was, as far as I can understand it, the principal investigator in all three studies. Wilson and others describe three experiments where artificial selection is used to shape the phenotype of whole ecosystems. In all cases, they use mud samples and try to select for a certain phenotype.

Let me briefly describe one of their experiments.

They take 2 ml of sediment (full of dirt, bacteria, etc.) and 28 ml of water from a pond and fill 72 test tubes, which are then incubated. Each tube is then measured for pH level, which was the arbitrary trait they decided to select on, but a good trait to measure phenotypic change in ecosystems since the pH level is a feature of the physical substrate, the dirt, and the water, as well as a phenotype of the microorganisms living in the dirt. They then take the six test tubes with the highest pH. From each of these six test tubes, they take 5 ml of mud and add 25 ml of autoclaved pond mixture. And repeat. They observed an increase in pH level in the ‘winning test tubes’. As strange as it seems, the mud samples produced the phenotype that enabled them to ‘survive’ in this artificial selective environment. And more importantly, the phenotypes were stable enough so that the increase in pH level actually was retained across ‘generations’ and amplified across time.

By showing how small malleable ecosystems could be artificially selected to ‘get’ a particular trait, they show that at least in theory, we could observe the same thing in nature. Goodnight (2000) and Penn (2003) examined the heritability involved in these experiments (focusing on the community aspect more than the ecosystemic nature of the system), while Williams and Lenton (2007) reprise this idea to assess evolutionary optimization in ecosystems.

Many ecologists have focused on energy transfers/control or on entropy in general in ecosystems and how selection can act on ecosystems to maximize this control. This is implicit in Fath et al. (2004), explicit in Van Valen (1991) and offers for Loreau (2010), in his rich volume on the desirable dialogue between community ecology and ecosystem ecology, the best hope of unifying ecology and evolution (see also Felsenstein 1978; Fussmann et al. 2007 and Loreau 2009). In Bouchard (2004), I argue why energy control while offering a common-currency control for fitness has its own disadvantages. I focus instead on differential persistence of the system, but the idea remains that ecosystems can evolve.

To make sense of ecosystem evolution, defining fitness in terms of offspring numbers will only take us so far. There is internal competition between microorganisms in the mud sample, but they argue that the causal explanation at the ecosystem level however remains: microsystems with higher pH persisted better than microsystems with lower pH. The pH level is a trait of the ecosystem and a trait of the whole system is selected for.

The only way for the ‘mud’ to persist is if it changes its pH (the teleological connotation is merely a manner of speaking), and it does so without reproducing. But its phenotype changes thanks to environmental pressures, and this change persists and increases over time.

Again I am not claiming that reproduction is not involved at all here, but I am claiming that it is not the salient feature to explain the transformation of the phenotype of the ecosystem as a whole. Think of it this way. Let’s say that a higher pH lead to slower erosion. The patches of mud with a higher pH would persist, whereas the ones with lower pH would erode. There is natural selection here. But is there evolution? If the patch only gets smaller and smaller, there is just natural selection.³ If the patch eventually stabilizes, and moreover may grow thanks in part to reproductive success of some of its microorganisms but also possibly to the chemical reactions of the physical substrates AND if the pH increases (leading to less erosion), then it seems we have evolution by

³This is not surprising in itself since, as Van Valen points out, even non-biological structures may be subject to natural selection ‘When granite weathers, the feldspars and micas become clays but nothing much happens to the quartz grains. They are most resistant and get transported down streams or along shores. Thus most beaches are the result of differentially eroded granite. This is an example of natural selection in the nonliving world. Quartz grains survive longer than feldspar grains, and there is a progressive increase in the average resistance to weathering, of the set of grains that have still survived. This action of natural selection is even creative, as we see by the formation of a beach’ (Van Valen 1989, p. 2).

natural selection even though offspring contribution might not be the best way to describe the evolutionary change. But intuitively, we have a way to define the fitness of that patch. It ‘offered’ a better solution to a design-problem! It can still be a propensity (a propensity to have a higher pH in this case), but it isn’t defined in offspring contribution since the patch may expand (or minimally persist) without really reproducing. To understand the fitness of the ecosystem, one will have to understand how components of that ecosystem contribute to the capacity to persist.

Thoday in 1953 suggested that to be fitter is to have a higher propensity to leave at least one offspring in 10^8 years offering an understanding of fitness grounded in long-term persistence. But why should we talk about offspring at all? If we wish to examine two ecosystems, couldn’t we compare their relative fitness in terms of their capacity to still be there in x number of years? Couldn’t we say that *if* this propensity (which will fluctuate over time) is the result of environmental pressures, then what we have is evolution by natural selection? Ecologists have been suggesting concepts like differential persistence for ecosystems for many years. My suggestion is to extend this to other evolutionary phenomena.

Not surprisingly, this comes very close to the definition of function offered by Bigelow and Pargetter (1987 and reprinted in Allen et al. 1998). They focus on individual survival, but persistence is the more general feature of interest here.⁴

If one wishes to understand the evolution of ecosystems, one will have to explain the role of various components of those ecosystems. The biotal component of these components may be explainable via SE functions – after all they are the result of descent with modification of other species. It’s not obvious however that community evolution (i.e. interaction between different species) will always have such past histories. But more crucially, ecosystems are not just biotal (i.e. living) material. As the mud case hints, ecosystems are also geological, chemical and physical in nature. This means that significant components of these evolving entities cannot have SE functional role even though they may play a crucial role that will explain the capacity of that given ecosystem to persist longer than other similar ecosystems. With ecosystems, we have entities that may be evolving, do so *sans* differential reproductive success and where differential persistence is the measure of evolutionary success. More importantly, ecosystems are entities whose components do not always have SE functions in the strictest sense. However, these components are a necessary part of the explanation of ecosystems’ increased persistence. Therefore, SE functions are not sufficient to understand the functions of subsystems in evolving ecosystems.

In Swenson et al.’s example, we have a feature of a system (here the increased pH level of an ecosystem) that is the result of changes in selection pressures. Such feature does not have a past history, although it may have a ‘bright’ future ... so to ascribe functional explanations, one needs some type of engineering analysis to make sense of the functioning of the system.

⁴ As a side remark, thinking in terms of persistence instead of survival might help them extend their framework to artefacts, which is something they hope to achieve....

4 Conclusion

Is this merely another item on the list of items that cannot be accounted for by SE functions alone? Well yes and no.... If one retraces some of the history of the vindication of CR functions, one could say that Amundson and Lauder started by showing that physiology and functional anatomy exclusively use CR functions. Then Griffiths argued that developmental biology was another CR discipline. One of my goals is to add ecology as another functional orphan (relative to SE accounts)....

But there is more to the story than this. The claim here is more subtle. Following ecologists' theoretical work and recent empirical work, I am claiming that ecosystems evolve, but these ecosystems will not be part of lineages (as they are usually construed).... One could argue that some ecosystems may have been evolving for a long time, and the succession of states they have gone through will in some sense constitute some sort of lineage.

But more controversially, I would argue that new ecosystems 'appear' all the time and will start evolving. A landslide creates new ecosystems that will respond to selective pressures and could possibly evolve. A hurricane will redraw marshes and put species in new relationships. When trying to understand how these ecosystems evolve, one will not have access to past history and selected effect to understand the various functions of components of ecosystems. And this is not an epistemic blind spot as the case of the fossil record. It is the result of the coming into being of new entities. Ecosystems appear and disappear in much more transient fashion than other biological systems do.

The problem of novelty has always been a genuine worry for evolutionary biology. One can use evolution by natural selection to explain the maintenance and the transformation of a given trait, but it's not obvious how completely novel traits can appear (and they must at some point). This problem inspired many to argue for an increased look at developmental biology and its fusion with evolutionary biology in evo-devo. This is in part what motivates Griffiths to entertain nonhistorical functions. With ecosystem evolution, we seem to get the novelty problem in spades: new ecosystems and new components of ecosystems without any selection history appear all the time. Since those ecosystems may be evolving, it means we need, *at least for these cases*, nonhistorical functional explanations in evolutionary explanations: propensity accounts of function like the one suggested by Bigelow and Pargetter might be a good candidate. Ironically, what Bigelow identify has a possible pitfall of their account is exactly the type of opportunity I wish to explore. After describing the advantages of their account, they identify some 'less comfortable results'.

Suppose a structure exists already and serves no purpose at all, Suppose then that the environment changes, and, as a result, the structure confers a propensity that is conducive to survival. Our theory tells us that we should say that the structure now has a function (Bigelow and Pargetter in Allen et al. 1998, p. 246).

Of course, this whole discussion is moot if ecosystems cannot in fact evolve. But as I have pointed out, promising empirical results indicate that they can. Ecosystems display adaptive change as a response to the selective environments, and these

changes accumulate and are fine-tuned over time in order to increase the system's capacity to survive. However, these systems' evolution is not adequately captured by a concept of evolutionary fitness that is defined solely in terms of differential reproductive success, and a fortiori it will be difficult to make sense of intergenerational change. More importantly new ecosystems come into being all the time. To make a truly bad analogy (and a worse jeu de mot in this context), we have the equivalent of philosophy of mind's Swampman (Davidson 2001). If this is the case, one will need some sort of nonhistorical functional description to understand how they work and how they evolve.

The claim here is not that nonhistorical functions are sufficient for evolutionary explanations, but rather that ecosystem evolution vindicates some sort of functional pluralism in biology: we can use nonhistorical functional explanation as the only foundation of some evolutionary explanations when there is no available history (again not merely an epistemic point like in some of Amundson and Lauder's examples, but a metaphysical point: there exists no history).

As some of you may know, Leigh Van Valen often ends his talks with a song. It is only appropriate to end from a line from a song that he recommended to me when we were discussing these issues.

The Hippopotamus Song by Flanders and Swann

Mud! Mud! Glorious mud!
 Nothing quite like it for cooling the blood.
 So, follow me, follow, down to the hollow,
 And there let us wallow in glorious mud.

Maybe mud can help us better understand fitness and functions as well.

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