

Title: Do Transposable Elements Have Functions of Their Very Own?

Abstract: Philosophers who study the problem of biological function often begin their deliberations by reflecting on the functions of parts of animals, or the behavior of animals. Applying theories of biological function to unconventional or borderline cases can help us to better evaluate and refine those theories. This is the case when we consider whether parts of transposable elements (TEs) – bits of “selfish” DNA that move about within a host genome – have functions of their own, that is, whether the parts of TEs have the function of helping the TE move about within the genome. Here I argue that whether or not the parts of TEs have functions depends crucially on whether collections of TEs form “populations,” by which I mean, here, a group of individuals of the same type that impact one another’s chances of persistence or multiplication, by impacting one another’s access to a shared resource. I think there is suggestive, but not conclusive, evidence that some TEs have functions of their own. Considering the problem of TE functionality, then, has value both for philosophy and for biology.

Acknowledgements: I wish to thank the participants of the workshop, Evolutionary Roles of Transposable Elements: the Science and the Philosophy, held in Halifax, Nova Scotia on Oct 20-21, 2018. I particularly wish to thank the organizers, Stefan Linquist and Ford Doolittle, for their valuable feedback on an earlier draft, as well as comments from an anonymous reviewer.

1. Introduction

When one asks after the functions, or the purposes, of transposable elements (TEs), there are a number of different questions one might be asking, and we must distinguish them from the start. First, do TEs sometimes have a function for the individual *organism* (Orgel and Crick 1980)? That is, do they ever promote the organism’s evolutionary goals in a non-accidental manner, in a manner that would be worthy of the appellation “function?” Second, do TEs have a function for the host *species*? It is true that TE transposition is a source of genetic variation on a par with mutation, recombination, and duplication; we know, as well, that genetic variability can promote the species’ ability to adapt to novel challenges (McClintock 1984). In this respect, TEs plausibly have a “function” for the species itself. But these are not the questions at issue here. At issue here is the question of whether TEs have *functions of their very own*. Can a part, or a component, of a TE be said to non-accidentally promote the evolutionary goals of the TE itself? Are TEs the kinds of things that can have goals? Or is this just a loose and metaphorical way of speaking?

Consider, for example, a certain family of TE, the R1 family, which inhabits the 28S rRNA gene of some animals. When R1 successfully inserts itself into the genome, it appears to modify the structure of the neighboring region of DNA in such a manner as to prevent members of another family, the R2 family, from inserting themselves. This action plausibly contributes to the differential replication of R1 over R2, by allowing R1 to

secure a larger number of insertion sites for itself (Ye et al. 2005). Is this activity a proper function?

The question of whether TEs have functions of their very own is interesting both for philosophy and for science. Philosophically, pursuing this question can enhance our understanding of the nature of biological functions. One time-honored method of sharpening our concepts, such as the concept of natural selection, causation, or reproduction, is to think carefully about the implications of our concepts for true-to-life but unconventional or borderline cases. Theorists of biological function have, often enough, taken the *parts of animals* as paradigmatic function bearers: lungs, hearts, livers. Sometimes, when we attempt to apply those conceptions of function outside of the paradigm case of body parts, we strain those conceptions in a manner that reveals some interesting but latent structure. (Do *groups* have functions? Do *ideas* have functions?) This is the case when we attempt to think through whether TEs have functions of their very own. In particular, it draws attention to the need to restrict functions to members of *populations*, and it gives us some clues as to how to explicate this notion. TEs can, in this regard, be seen as nature's thought experiment.

The question is also important scientifically, for at least two reasons. First, some geneticists have sought to articulate, rigorously, the analogy between genomic environments and ecosystems. In this analogy, bits of DNA in their genomic surroundings are likened to individual organisms attempting to survive in a complex and often hostile ecosystem (Brookfield 2005; Le Rouzic et al. 2006; Venner et al. 2009; Linquist et al. 2013; Linquist et al. 2015). Leonardo and Nuzhdin (2002, 155) give voice to this analogy quite succinctly: "Transposable elements (TEs) are tiny organisms...that survive by spreading their progeny on host chromosomes." The question of whether TEs have functions of their very own pertains directly to the goodness of the analogy. If TEs are, in fact, a bit like tiny organisms, then we should expect their parts or components to have functions, and to acquire new functions by virtue of how they further the TEs mission to propagate itself within the host's genome. Conversely, if TEs do have functions, that would tend to promote, affirm, or vindicate the goodness of the analogy. If, on the contrary, TEs do not have functions, that would tend to undermine or otherwise put into question the goodness of the analogy.

Second, for several years, there has been a lively debate among geneticists about what proportion of the human genome is functional. This debate pits theorists of the ENCODE Project Consortium, who hold that most of the human genome is functional, against so-called "junk DNA" theorists who claim that the majority of the genome is not functional (e.g., Doolittle 2013; Graur et al. 2013; Kellis et al. 2014; for philosophical discussion see Germain et al. 2014 and Kaiser 2018). It is often taken for granted in these debates that the functions in question here are functions *for* the organism, that is, that the organism is the beneficiary of the correct performance of the function (Elliott et al., 2014). Thinking through the question of whether TEs have functions of their very own would help us to clarify the nature of this debate more sharply. It is possible, after all, that much of the genome *does* have a function – but that the organism itself is not the beneficiary of this function, but rather, the TE.

The following will proceed through four parts. In order to approach the question of whether TEs have functions of their very own, we have to know what functions themselves are. Here, I adopt, in a provisional way, the selected effects theory of function (Section 2). But the selected effects theory, as many critics have shown, is beset by apparently trivializing counterexamples. I show how we can avoid those counterexamples by restricting functions to the members of populations, which I here define in terms of a group of individuals of the same type that impact each other's prospects for persisting or multiplying, by impacting each other's access to a shared resource (Section 3). With these ingredients in place, we can begin to answer the question of whether TEs have functions of their very own: while the data is, for the most part, inconclusive, there is suggestive evidence that at least some of them do (Section 4). I then come back around to draw out some implications for philosophy and science (Section 5).

A word about parts and wholes is in order before moving on to the main argument. Functions are, paradigmatically, functions of *parts* (aspects, properties, behaviors) of organisms, not of organisms themselves. Thus we can ask about the function of the zebra's stripes, the function of the goblin shark's snout, the function of the silverfish's wiggling movement. But we don't talk about the functions of *zebras*, the functions of *silverfish*, the functions of *goblin sharks*. We generally reserve the term "goal" to point to the future-directedness of the individual as a whole ("how does the goblin shark's elongated snout serve the shark's goal of catching prey?") Or if we do give functions to whole organism, we usually are thinking of the whole organism as a part of a larger system ("what's the function of the goblin shark in the marine ecosystem?") In the following, I'll cleave to conventional usage: my ambition here is to ask about whether the parts of TEs (that is, sub-segments of DNA that constitute the TE, or the characteristic activities of those sub-segments) have functions. Perhaps another way of putting the question is to ask whether TEs are the sorts of things that have *goals*. But that's a question for another occasion.

2. What are functions?

The function of zebra stripes is, at least according to one current theory, to deter biting flies. The function of the beaver tail's splash is to alert other beavers to danger. The function of the eyespots on butterfly wings is, quite likely, to deter predatory attacks away from vital organs. Functions abound in the living world. So, do parts of TEs have functions, too?

In order to know whether TEs have functions of their very own, we have to know what functions *are*. A natural starting point for discovering what functions are is to consider how biologists use the term, that is, what sorts of things in the world they habitually apply the term "function" to. (By analogy, if I wanted to learn what neurotransmitters are, I'd probably begin by considering the ways that neuroscientists use the term "neurotransmitter.") For better or for worse, biologists use the term "function" in different ways on different occasions, so there's no single correct answer to this question.

This point has been recognized in the literature for decades under the label of “function pluralism.” (See Sterner and Cusimano 2019 for a recent entry into this expanding literature.) My goal here, then, cannot be to initiate a lively debate about the *true* meaning of the term “function.” My goal is rather to specify which kind of thing in the world I use the term “function” to pick out.

In the following, I will accept, provisionally, the selected effects theory of function, which holds that a function of a trait is whatever it was recently selected for by natural selection or some comparable selection process (Neander 1983; 1991; Millikan 1984; 1989; Griffiths 1993; Godfrey-Smith 1994). To be more specific, it holds that a function of a trait is some activity that contributed, in the recent past, to its differential reproduction within a population of like entities. Roughly, *functions are just adaptations*. So, suppose the function of zebra stripes is to deter biting flies. According to the selected effects theory, what that implies is, very roughly, something like this: at some point in the past, there was a population of ancestors to modern zebras, some of which had stripes and some of which didn't have stripes. The ones with stripes were able to out-reproduce the ones without stripes, and this historical fact is one reason that zebras, by and large, have stripes today.¹ While I can't defend the theory here, a core justification is that it illuminates how function statements can possess the explanatory force that they often carry in ordinary biological usage (see Garson 2019 for that defense). A noteworthy feature of the theory is that it hangs together with a *realist* worldview. Whether or not something has a function, and what function it has, doesn't depend on one's perspectives, goals, or research interests. Functions are as real and mind-independent as causation or mass.

Crucially, the selected effects theory does not *only* attribute functions to the parts of organisms by virtue of the fact that they undergo a selection process at the level of the organism itself. Proponents of the selected effects theory recognize, at least in principle, that selection can operate at multiple levels and in multiple domains; for example, antibody selection, group selection, chromosomal selection, and perhaps even memetic selection either do, or would, create new functions. As one might imagine, there is some disagreement about just how broadly we should construe the relevant notion of a “selection process” in the selected effects theory of function, but many of those fine details are not relevant here.² With this account of function in mind – that is, having specified what kind of thing in the world I use the term “function” to pick out – we can be more precise about the guiding question of this paper: do transposable elements have *selected effect* functions of their very own?

¹ Note that the selected effects theory, as traditionally conceived, is neutral between directional versus stabilizing selection. Whether the selection process in question causes a trait to spread through a population, or merely to be maintained at a certain level, it can acquire a selected effect function. This point is emphasized by Linquist, Doolittle, and Palazzo (2020).

² Garson (2021a) gives an overview of different construals of the notion of a “selection process” among theorists of function.

At first glance, the answer would appear to be a straightforward “yes.” Consider the example I mentioned earlier of the competitive struggle between the R1 and R2 families. Here, we have two types of TE that appear to compete over the same insertion sites in the genome (such as the 28S rRNA genes of arthropods). As I noted, there is some evidence that when R1 inserts itself into the genome, it changes the conformation of the DNA directly upstream of the insertion site in such a manner as to block the insertion of R2. In doing so, it secures a larger proportion of insertion sites for itself, which promotes its differential reproduction over R2. That would appear to satisfy the basic strictures of the selected effects theory. The selected effects theory would, then, allow us to say that the parts of TEs do, in fact, have functions. A certain activity of R1, namely, *altering the conformation of neighboring DNA*, has a function, *preventing the insertion of R2*, and it has that function because, in the past, that activity led to the differential reproduction (replication, multiplication...) of R1s over R2s.

At least, it *would* allow us to say that, but for certain well-known and problematic counterexamples that the selected effects theory has traditionally faced. Critics of the selected effects theory have argued that there are processes in nature, and certainly in systems that humans have created, that have all of the characteristics of a selection process (understood broadly in terms of exhibiting variation, inheritance, and differential reproduction), but that do *not* create new functions. One clever example comes from Bedau (1991), who discusses the case of clay particles. Clay particles quite possibly undergo something *like* natural selection. But people typically don’t think that clay particles have functions, or at least they don’t have functions in the same sense in which zebra stripes or goblin shark snouts have functions. Therefore, he concludes, I think rightly, that being the product of a selection process is insufficient for acquiring new functions.

I’ll take a moment to develop his argument, because it can be used as a template for similar kinds of objections.³ Examined under an electron microscope, clay particles exhibit a crystalline structure. What that means is that they are composed of layers of molecules, like sheets, where each layer has a very specific and regular pattern. Each layer provides a template for the next layer: as new molecules are added, new layers with the same pattern are formed upon the older layers. Crystal growth merely consists in the accumulation of new layers.

Now, when the clay crystal reaches a certain size, it can cleave into two crystals, and each new crystal can continue to grow. In this way, clay particles exhibit something like reproduction, which we can loosely think of as parent-offspring relations. The layers of the “offspring” particles, moreover, will generally share the same molecular pattern as the “parent” particle, so they exhibit something like inheritance, too. Finally, environmental conditions can change the structure of these molecular layers, so that crystals can differ from one another in the molecular “shapes” of their layers. So, groups of clay crystals show variation. But notice that we now have all the ingredients in place for a form of

³ For more details on selection in clay particles, see Cairns-Smith (1985). For extraordinary images, see Christidis (2011).

natural selection. From there, it's a short step to imagine that certain molecular patterns could dispose a crystal to grow and divide more quickly than others, thereby increasing its frequency in a group of like particles.

Still, the parts of crystals don't have any functions. It would seem strange, at the very least, for a crystallographer to say, "the function of *this* molecular pattern is to help the crystal grow more quickly, since that's what enables it to divide more rapidly than its competitors," or, "the purpose of this particular lattice structure is to help the crystal particle withstand environmental changes that would hinder its rapid growth." For that matter, it seems counterintuitive to say that parts of a crystal can *malfunction*. Suppose an environmental change induces a novel variation in the crystal structure that stunts its growth. Should we say that the crystal is dysfunctional or malfunctioning? Can there be *disorders* of clay crystals? (There can certainly be *irregularities* in crystal growth, and we might prefer some crystals over others on account of lacking such irregularities. But disliked irregularities of development aren't disorders.) Bedau summarizes the point:

Merely having a population of replicating entities will not produce teleology [i.e., functions], not even if the entities have random variations that are heritable, not even if those variations can affect the degree to which those entities proliferate. What happens on the [hypothetical] dead planet has no purpose and is for the sake of nothing; it is merely a physicochemical process. Therefore, contrary to those versions of the etiological approach to teleology which are couched in terms of natural selection, natural selection is not sufficient for teleology. (1991, 654)

One might, of course, reject the intuition that drives Bedau's argument, but doing so has consequences which I'll address shortly.

Similar counterexamples can be multiplied without end. Schaffner (1993, 383) asks us to imagine a "cloner machine" that causes ball bearings to be differentially reproduced on account of their smoothness. Effectively, a bunch of ball bearings of slightly different shapes roll down an incline with gaps in it; the smoother ones, being faster, tend to jump over the gaps and the rougher fall in. Those ball bearings that make it to the bottom of the platform are used as a template for creating a new batch of bearings, and the process is repeated. Schaffner argues that even in such a scenario, smoothness would not become a function of ball bearings *merely* on that account. (I am assuming that the ball bearings would have *artifact* functions, but their artifact functions would come from the intention of the maker and not from the fact that there happens to be something like a selection process taking place.)

Such counterexamples are particularly pressing for the version of the selected effects theory that I accept, which I call the *generalized* selected effects theory. As I said, the traditional selected effects theory assumes that this "selection process" must take place over entities that *reproduce*, or multiply. But that strikes me as an arbitrary restriction. In my view, even among a population of entities that don't reproduce – but merely persist for a certain amount of time and then vanish – a trait can acquire a function simply because it helps its bearer *out-persist* others. According to the generalized selected effects

theory of function, a function of a trait is an activity that, in the past, contributed either to the trait's *differential reproduction*, or *differential retention*, in a population. It agrees with the traditional theory that the ordinary sort of natural selection that happens by way of reproduction can give rise to new functions, but it also holds that this other sort of thing, differential retention, can do the same.⁴

A plausible example of how differential retention alone can create new functions can be found in populations of neurons. Neurons in a population can differ from one another in terms of their size, shape, and connectivity, and these differences can cause some neurons, synapses, or even entire groups of neurons, to persist better than others. In my view, this is sufficient to give them new functions. I suspect that this generalized account of function can also make sense of the practice of attributing functions to *groups* (what is the function of V-formation in geese?) and to ideas (what is the function of the idea of divine retribution in agricultural society?), but I will not pursue that line of thought here.

My ecumenical version of the selected effects theory, as one might imagine, creates even *more* counterexamples along the lines of the ones Bedau and Schaffner devised. Imagine a bunch of rocks scattered along a beach that differ in their hardness. (The example comes from Kingsbury 2008). The harder ones will withstand erosion for a longer period of time than the softer ones. Over time, only the harder ones remain – they have successfully “out-persisted” their neighbors. There is a differential retention of rocks on account of their hardness. But hardness isn't a function of rocks. We wouldn't say things like, “the *purpose*, that is, the *function*, of hardness in rocks is to withstand erosion.” And when one of the harder rocks eventually erodes, we wouldn't say that there must have been a *malfunction* in the rock that caused its erosion. Function, malfunction, and dysfunction, just aren't the sorts of properties that rocks (clay crystals, ball bearings) can have.

The conclusion that we must draw is that differential reproduction, or even “differential retention,” is not enough for creating new functions. Rather, the kind of selection process that yields new functions must have some *further* property, some mysterious ingredient that selected effects theorists have traditionally overlooked. There must be some special principle that separates *real* functions, that is, the sorts of functions that zebra stripes, eyespots on butterfly wings, and beating hearts have, from *fake* functions, the sorts of pseudo-functions that clay crystals, ball bearings, and rocks have. I think the idea of a *population* can supply just the principle we need.

Before considering this solution, there's an objection we need to confront right away: what if properties of rocks (crystals, ball bearings) really *do* have functions? Why is that such an unacceptable conclusion? After all, philosophical definitions of terms like “function,” “causation,” “disease,” and so on, often force us to reconsider the extensions of those terms. I assume that someday, when psychologists are in possession of a clear, consensus definition of “mental disorder,” they might conclude that certain conditions that were traditionally thought of as mental disorders, such as ADHD, aren't mental

⁴ See Garson 2011; 2017; 2019.

disorders at all, but just normal variations in cognition. Why can't a philosophical definition of "function" have equally surprising results – for example, that properties of rocks have functions, too? (See Bourrat 2021 for this objection.)

This objection would take some time to respond to adequately because it brings us to rather subtle questions about what exactly the *point* of a philosophical definition is. (Sometimes these are called "meta-analytic" or, more arrogantly, "metaphilosophical" questions.) When I offer a "philosophical definition of function," what exactly am I trying to do? Am I trying to give a conceptual analysis? That is, am I trying to say what ordinary folks have in mind when they use the word "function?" Or only what a limited subset of folks (e.g., biologists) have in mind? Or am I trying to say what functions *really are*, regardless of how folks think about them, as in "water is H₂O?" Or am I recommending that we adopt a new meaning of "function" altogether, one that's only loosely related to ordinary biological usage?⁵

This question is closely related to another. Any philosophical definition of function will probably have some revisionary consequences – that is, it might lead us to realize we were mistaken in some respects about how we've traditionally used the term. We expect philosophical definitions to be a *little* bit revisionary. But if it's *too* revisionary, then it's not really a definition of *function*, but of something else. For example, if I define the word "function" to mean the same thing as "effect," so that all of a trait's *effects* are its *functions*, then I've just redefined the term altogether – I've changed the topic of the conversation – and it'd be best for everyone if I just select a different word to convey what I mean (such as "effect").

These considerations bring us to a very hard problem: *how* revisionary may a definition of "function" be before it's no longer a definition of *function*, but something else altogether? How can we tell when someone has just changed the topic? The problem is that different theorists disagree about where, or better, how, to draw the line. Although philosophers have set out various guidelines for answering this question, one rather obvious guideline is this: to what extent does one's philosophical definition of function respect *paradigm* cases of things that do, and things that do not, have functions? For example, suppose I devise a definition of "mental disorder," and it turns out that, on my definition, depression, schizophrenia, and bipolar disorder *aren't* "mental disorders," but racism, truancy, and speaking with an accent *are* "mental disorders." In my view, such a definition would, by virtue of its wanton violation of paradigm cases of things that are and are not mental disorders, represent a change of topic.⁶

⁵ See Millikan (1989), Neander (1991), Schwartz (2004), and Garson (2016, Chapter 1), for discussion of these meta-analytic questions.

⁶ See Cappelen (2018), for an extensive treatment of the general problem. He suggests, following Railton, that paradigm cases might be one part of a more comprehensive account of topic-switching (p.120). Garson (2021b) and Wakefield (2021) discuss the problem as it pertains to definitions of mental disorder.

In my mind, a philosophical definition of “function” that lets rocks have functions would represent a change of topic. (I’m setting aside artifact functions, like using a rock as a paperweight and such. The case at issue doesn’t involve anything like that.) And if someone *doesn’t* consider it to represent a change of topic, I’d be interested in learning what that person *would* consider a change of topic. Moreover, given that there are different (and equally legitimate) senses of the term “function,” I’d encourage them to consider the possibility that, over the course of their deliberations, they’d accidentally switched from one legitimate meaning of the term to another legitimate meaning.

3. Functions and populations

Let’s begin again. Natural selection, or the more general notion of a selection process, is an attractive starting point for a theory of function for various reasons that I haven’t fully set out here. But as we have seen, the notion of a *selection process*, all alone, is too general; it yields counterexamples that contravene the very usage it seeks to capture. Here, then, is our question: what must we *add* to the bare idea of a selection process to restrict functions appropriately? What magic ingredient must go into the theory to make its entailments hang together with reality? Somewhat crudely put, we are trying to fill in the variable of a simple formula: selection + x = function. What is x ?

Here is a rather obvious candidate: the examples that struck us as having *real* functions (zebra stripes, eyespots on butterfly wings, etc.) all come from the living world; the examples of things with *fake* functions (clay crystals, piles of rocks) come from the non-living world. So perhaps we should say that in order for something to have a function, it must be a part or property of *something that’s alive*. This is a sensible solution given that much of the focus of philosophical discussion has to do with defining the notion of *biological* function, rather than *artifact* function. Biological functions are, by definition, functions of living creatures; *ergo*, rocks don’t have biological functions. Problem solved.

I’m hesitant, however, to take this step, for two reasons, one less significant and one more so. First, defining “function” in terms of “life” would be a textbook example of *obscurum per obscurius* – defining something that’s difficult to explain in terms of something that philosophers have all but given up trying to define. Of course, *obscurum per obscurius* isn’t strictly a fallacy of reasoning, and sometimes we might have no choice but to define something perplexing in terms of something even more so. But it’s best to avoid it when possible, given that the goal here is to illuminate functions, rather than to further shroud them in mystery.

A more serious objection is that we sometimes attribute functions to things that aren’t, technically speaking, *alive*, such as groups or ideas. What is the function of V-formation in a flock of geese? A flock of geese isn’t a living organism per se. What is the function of the idea of *divine retribution* in agriculturalist society? I take it that in this context we’re not saying that the idea has a function for the individual organism (the individual

member of society), but that the idea has a function for society as a whole.⁷ I don't want my theory of function to simply foreclose the prospect that groups, or ideas, can have functions in the same way that zebra stripes can. So while *life* surely has something or other to do with *function*, it remains unclear just what they have to do with one another.

A clue to the correct solution can be found by reflecting once more on the very definition of the selected effects theory of function. As I said above, according to the selected effects theory, in order for zebra stripes (say) to have the function of fly-deterrence, there must have been a population of ancestors to modern zebras, some of which had stripes and some of which didn't, and the striped zebras must have out-reproduced the stripeless ones on account of the fly-detering power of stripes. The crucial idea, here, is that of a *population*. What I'd like to say is that a bunch of clay crystals proliferating by a creek, or a bunch of rocks strewn across a shore, or a bunch of ball bearings rolling down an incline, isn't a population. It's just an aggregate (collection, multiplicity...). So, even though something like differential reproduction or differential retention is happening, those processes don't create new functions because the differential reproduction (retention) doesn't take place within a population.

What, then, is a population? What makes a collection of individuals a population, and not just an aggregate? Suppose you have a large field and there are many different ant colonies spread out across this field. How would you decide how many populations there are? Is each colony a population? Or are all of the colonies together a population? Or are all of the colonies part of an even larger population that includes the ants in neighboring fields?

At this point I can imagine someone rolling their eyes and saying, "Look, there's no deep metaphysical fact of the matter about how many populations there are. It all depends on the interests of the researcher. If a biologist is interested in *all* of the ants in the field, then all of the ants make up a single 'population.' And if she's interested in the dynamics of ant colonies, then each colony is its own 'population.' And if she's interested in, say, the migration of ants across a larger region, then the ants in the field are just one subset of a larger 'population.' Effectively, when a biologist calls a group of individuals a 'population,' she's drawing an arbitrary border around that group, and that 'population' will grow or shrink depending on how exactly she draws that border."

I can't accept this solution. The reason, as has been pointed out by others, is this: natural selection, according to standard definitions, takes place within a population. In order to decide whether a certain biological process counts as "natural selection," then, we have to

⁷ One might protest that the idea of divine retribution in agriculturalist society is an example of an *artifact function*, and not the sort of *natural function* I'm interested in here, but that's not obvious to me. Just as striped zebras might out-reproduce stripeless ones on account of their fly-detering power, communities with certain religious ideas might out-persist others by virtue of their power to minimize conflict (Wilson 2002). In that case, I'd be inclined to say that those ideas have functions in the same sense that zebra stripes do.

say exactly what the relevant population is. But if there's no "deep fact of the matter" about what populations are, then there's no "deep fact of the matter" about whether or not a certain process counts as "natural selection," either (Millstein 2009, 268; 2010). Whether or not a certain process in nature is an instance of "natural selection" would depend on rather subjective and arbitrary facts about how we choose to draw lines around groups of individuals. Although some of Darwin's critics have advanced arguments along these lines, I don't think that's a kind of relativism that biologists should flirt with.⁸ Whatever it is that transforms a mere aggregate of individuals into a population, it's not just that they happen to be located inside of the same arbitrarily-drawn boundary.

A better solution would be to say that what makes a collection of ants into a *real* population is the fact that the individual ants in the collection have the right kind of *impact* on one another. Millstein (2010) calls these "causal-interactionist populations." Put differently, in order for me and you to be part of a single population, my actions must have some impact on your welfare, and your actions must have some impact on my welfare. The things you do can help me or harm me in my quest to persist, to survive, to reproduce – and vice versa. (From here on, I'll just use the term "survival" as short for "survival, persistence, or reproduction"). This seems to be something like the emerging consensus among the philosophers who have reflected on the matter (e.g., Millstein 2009; Godfrey-Smith 2009; Matthewson 2015; Schulte 2021), though the biologists who use the word "population" haven't yet agreed about how exactly to define the term (Bourrat 2021).

One benefit of this way of defining populations is that, right away, without even diving into the details of what *else* populations are, we can see that a bunch of rocks eroding at different times on a beach is not a *function-bestowing* selection process, even if it's a selection process in some loose sense of the term. That is because the rocks on the beach don't impact each other's chances of survival (here construed as mere persistence). The rate at which one rock erodes has no bearing on the rate at which others erode. By the same token, we can imagine a bunch of clay crystals growing by the side of a creek. As long as there is an ample supply of silicic acid molecules in the creek, the rate at which one crystal "reproduces," if you will, has no impact on the others. We are not talking about real populations and so we do not have real function-bestowing processes – and hence, no real functions, only fake ones.

But what do I mean, precisely, by saying that the individuals in a population must have the "right kind of impact" on each other's survival prospects? Examples of interactions that transform aggregates into populations include competition, cooperation, and parasitism. Having sex, fighting over food, sharing a meal, and hunting a wild boar together, are ways that individuals impact each other's survival prospects. Additionally, the populations at issue here, the ones that play a role in giving rise to new functions, must be composed exclusively of individuals of the same *type* – the paradigm being members of the same species. If a group of hunters is cooperating to stalk a wild boar, the hunters certainly have an impact on the boar's survival chances, and vice versa, but the

⁸ Fodor and Piatelli-Palmarini (2010) develop this skeptical point of view.

collection that consists of *hunters* + *boar* is not itself a population, since its members don't belong to the same type (here, the same species). Obviously, the problem of how we are to individuate *types* will get progressively more difficult as we move away from good and proper species, toward reproducing entities that do not fall clearly into species, such as our TEs. I leave it to the scientists who actually work on the problem to *tell us* how TEs are to be partitioned into types.

There is one final subtlety in understanding, precisely, what populations are (that is, the sorts of things I use the word "population" to pick out). Some critics of my theory of function have argued that my theory actually *fails* to properly distinguish real functions and fake functions. For you can modify the rocks example slightly to make it look like the rocks really *do* form a population in the sense at issue. Suppose instead of having a bunch of rocks scattered across a beach, we have a heap of rocks by the shore. Suppose, moreover, that every time the waves come crashing in, the rocks rub against one another, and the harder rocks contribute to the eventual erosion of the softer. Then we have the differential retention of the harder rocks, *and* this process takes place within a population, that is, a group of entities of the same type that impact one another's survival prospects. But it still strikes me as unacceptable to attribute functions to rocks for the reasons I outlined above. (I owe this critique to Karen Neander.) In the past, I sought to avoid this embarrassing outcome by emphasizing that populations generally have a high degree of connectivity, and while I still think this is true, and that it solves Neander's worry, it doesn't entirely get me out of the muddle, as several critics have been quick to point out.⁹

Recently, Schulte (2021) recommended an important clarification to my view. As he puts it, in a heap of rocks by the shore, there's nothing like a competition over resources taking place. Although I don't agree with all of the details of his amendment, and I think the idea of a competition over resources is far too limited, I think his core insight is correct. I noted that among the ways that individuals can impact one another's survival prospects, we have competition, cooperation, and parasitism. But competition is always *competition-over-X*: a competition over some resource that both parties rely on for survival. And cooperation is always *cooperation-to-obtain-more-X*. Two lions can compete with one another *over* the same scrap of meat, or *over* the same female, or they can cooperate with one another *in order to* take down a zebra. But they don't just compete (cooperate) with one another *full stop*. When we examine the rocks example carefully, we see nothing like this. Although the rocks do impact each other's survival prospects, there's nothing like a competition (or cooperation) over resources. They never impact each other's survival by impacting each other's chances of obtaining some critical outside resource.¹⁰

⁹ Garson (2019, Chapter 6) offers a solution in terms of connectivity. For criticism, see Conley (2020); Schulte (2021); Bourrat (2021); also see Matthewson (2020) for discussion.

¹⁰ This brief discussion must suffice for now. Garson (in prep) develops this point, and responds more extensively to critics.

I can now state, much more specifically, the account of function I wish to offer: a function of a trait is any activity that, in the past, contributed to that trait's differential reproduction, or differential retention, in a population, *by which I mean* a group of individuals, of the same type, that impact each other's persistence/survival/reproductive prospects, either by facilitating, or hindering, each other's access to some shared resource.

Bourrat (2021) recently criticized an earlier version of my proposal on the grounds that biologists don't have any real agreement about how to use the word "population." (Lewontin, for example, doesn't think that populations require anything like a group of individuals impacting each other's survival prospects.¹¹) Fortunately, I'm not claiming that there is only one correct use of the term "population" in biology. My justification for using the causal-interactionist notion of population here is that it does a great job solving the problem of distinguishing real from fake functions, and it does so in a way that meshes with the selected effects theorists' predilection for *realism* about functions. As I noted, one core virtue of causal-interactionist populations is that there's a mind-independent fact of the matter as to whether or not any given collection of entities counts as a population.

We can, at long last, return to our primary question. Do TEs have functions of their very own? That depends not only on whether they undergo something like differential replication in the genome, but also *whether they affect one another's survival prospects*. More specifically, if I belong to one subtype of TE, does my behavior, that is, those actions by which I increase my own fitness, affect the survival or replication prospects of other subtypes? For example, do I purchase my power of replication at your expense? In replicating, do I exploit some common, limiting resource – transposition machinery, genomic insertion sites – and thereby decrease your replication odds? Or are TEs merely like clay crystals growing on the side of a creek, replicating at their own pace, with nary a care for the replication prospects of the other?

4. Do TEs have functions of their own?

The question of whether TEs have functions of their very own can now be restated more precisely. There are two questions at issue. First, do TEs undergo differential replication in the genome, that is, in their "genomic environment?" Second, in the course of this, do they impact one another's survival prospects? By "impact," I do not mean to focus narrowly on competitive interactions. These interactions can be cooperative or parasitical,

¹¹ Lewontin (1970, 1) asks us to envision two strains of bacteria multiplying at different rates in a test tube. He claims that even if they don't impact each other's survival chances, this is still an example of natural selection. I am not convinced that this actually is an example of natural selection at all, but that is beside the point (for discussion, see Lennox and Wilson 1994, 70; Godfrey-Smith 2009, 48). My point here is that I'm not resting my case for my account of function on the claim that the way I define "population" tallies with the way all biologists define it.

too.¹² Still, the competitive kind is an interesting kind of interaction that I will focus on here for the sake of developing an example. As Godfrey-Smith (2009, 52) memorably put the point, when it comes to constituting populations, “competition is an especially Darwinian glue.”

What does the biological literature tell us about competition in groups of TEs? Many theorists have considered the possibility, at least in the abstract, that TEs compete with one another over the resources that they need to replicate. Much of this literature has a self-consciously speculative character, and so if we want to be safe, we should probably say that this question of whether TEs, as a rule, do or do not have functions of their very own, remains inconclusive, but it appears that at least some of them do.

If TEs impact each other’s survival prospects, and more narrowly, if they compete over the same resources, over what, precisely, must they compete? What is the limiting resource, if you will, over which they struggle? Venner et al. (2009, 3) helpfully summarize three possible resources: *insertion sites*, *transposition machinery*, and *avoidance of host-defense mechanisms*. I will describe each in turn.

One possible answer that has been presented in the literature is that TEs compete over insertion sites, that is, space in the genome in which they can insert themselves. But this is not a competition for just *any* kind of space. There are better or worse genomic regions for TEs. There is a competition over what Linquist et al (2013, 581) call “high-quality genomic ‘niches’.” What makes one genomic region better than another? One possibility is that gene-poor regions of DNA are preferable. If a TE inserts itself into a gene-rich region, it is much more likely to be silenced or eliminated by host removal mechanisms, such as RNA interference (Brookfield 2005, 132). So, we might imagine that TEs sometimes compete over a limited number of gene-poor insertion sites in the genome.

It is also possible that TEs compete with one another over the limited amount of cellular machinery that they need to transpose. In this context, consider the well-known parasitism between autonomous (LINE) elements and parasitical (SINE) elements. LINES are TEs that code for their own transposition machinery, while SINEs do not. Rather, SINEs replicate themselves by coopting the transposition machinery of LINES. Le Rouzic et al. (2007, 216) use these facts to suggest that “both subfamilies [LINES and SINEs] compete for the same transposition resource.”

Finally, we should consider whether TEs sometimes compete in order to avoid host silencing mechanisms. TEs are constantly at risk of being silenced by the host, that is, of encountering so-called “cross-reactive TE silencing mechanisms.” What that means is that, for TEs, any property or trait that allows it to escape these silencing mechanisms could give it the *edge*, as it were, in the proverbial struggle for existence. Abrusán and Krambeck (2006, 368-9) ask us to imagine these silencing mechanisms as a kind of filter that forces different types of TE to compete. Suppose, for example, there are two types of retrotransposons (a kind of TE that uses a “copy-and-paste” type mechanism to

¹² Kremer et al (2020) describe a possible case of a cooperative interaction between TEs.

proliferate within the host genome), one with a rapid transposition rate and one with a slow transposition rate. A TE with a fast transposition rate is more likely to get copies of itself past this “filter” than those with slower rates, simply because there are more of them around. (This applies whether we’re describing TEs that accumulate within the germ line or those that merely accumulate in the soma.)

I will close by describing one case that may be a compelling example of competition between TEs. This is the competition mentioned above, that between R1 and R2 families for insertion sites in the 28S rRNA gene of arthropods (among other animals). In particular, when R1 successfully inserts itself, it appears to change the conformation of the DNA directly upstream of it, in such a manner as to prevent the insertion of R2 elements. In this way, it secures a greater portion of insertion sites for itself than R2. Now, suppose it is true that R1 successfully changes the conformation of the DNA directly upstream of itself, and thereby blocks the insertion of R2 elements. Suppose, moreover, that by doing so, it contributes to its own differential replication in the genome, that is, its replication over R2. Then it seems we have all the elements in place to apply the selected effects theory straightforwardly: R1 engages in an activity that promotes its differential replication over other elements in the same population. As a consequence, a *function* of the R1’s activity of changing the conformation of DNA is to block the insertion of R2 elements. This appears to be at least one plausible case in which a subtype of TE has a function of its very own.

There is, however, an important reason why this might not be a *compelling* case of TE functionality. We said that in order for new functions to arise, there must be competition (etc.) within a group of individuals of the same *type*. If a group of coyotes and bobcats compete for the same hare, that doesn’t make the collection of coyotes and bobcats a single population. What, then, constitutes *types* when it comes to TEs? How do we “individuate” TE types? As an anonymous reviewer noted, R1 and R2 have been separated evolutionarily for millions of years. If that’s right, it might be a mistake to treat R1 and R2 as two different variants of the same type, rather than two completely different types. That is, their competition over space might be more like a competition between bobcats and coyotes, rather than between two different varieties of coyote. What I hope to have accomplished here is to have sketched the *kind* of questions that must be posed, and answered, in order to answer our leading question.

5. Conclusion

We have considered whether TEs have functions of their very own, and concluded, in a tentative and provisional way, that some of them do. In reaching this conclusion, we have made a certain advance both for biology and for the philosophers who reflect on biology, in at least four ways.

First, philosophers of biology have had long-standing debates about the nature of biological functions. One way to develop these theories and to decide between them is to apply them to borderline or unconventional cases of function. In thinking about the functions of transposable elements, we have been forced to devote attention to the precise

question of when, and under which conditions, a collection of entities can constitute a population. Doing so has drawn our attention to the role of populations in creating new functions – and opened a host of questions about how such populations should be defined and identified.

Second, asking the question of whether TEs have functions of their own draws attention to a phenomenon that has perhaps been underappreciated by biologists. Leonardo and Nuzhdin (2002) suggest that while biologists who study TEs have devoted ample attention to the question of how TEs might impact selection at the level of the organism, that is, how they might differentially impact the *organism's* fitness, they have devoted relatively little attention to the question of whether and how different subtypes of TEs impact *each other's* fitness. What sorts of fitness-relevant impacts – competitive, parasitical, or cooperative relationships – might TEs have with one another? Asking the question of TE function points our attention, in a laser-like way, to this intriguing phenomenon.

Third, we have made some modest progress on a question that biologists consider. Understanding the mechanics of TE competition and selection can help to evaluate the “goodness-of-fit” of the ecosystem paradigm when it comes to studying the genome. Put somewhat simplistically, *if* TEs have functions of their very own, that would tend to support or reaffirm the goodness of the analogy between ecosystems and genomic environments and, in particular, Leonardo and Nuzhdin's claim that “transposable elements (TEs) are tiny organisms.”

Finally, considering the question of whether TEs have functions helps us think more carefully about the issue of what proportion of the human genome is functional. In some ways, it complicates the debate substantially. As Elliott et al. (2014) point out, it may be true that much of the genome *is* functional, but not for the organism, but for the TE itself. This is the *cui bono* problem – who benefits? This question would have to be resolved before solving the problem of what proportion of the human genome is functional.

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