Breaking news from genome-level ecology: Not everything that is a Darwinian individual should be scientifically regarded as such.

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When evolutionary thinking is extended to some novel domain – be it cancer cells, human culture, or ecological communities – the default tendency is to ask whether there are any Darwinian individuals present. This term refers to entities that are capable of forming populations that exhibit some degree of heritable variation which differentially impacts their expected rates of reproduction. In recent years, there has been an active metaphysical debate over the appropriate definition of Darwinian individuality. For instance, by substituting the requirement of differential replication for the more general condition of differential persistence, it is possible to view ecological communities as Darwinian individuals (Bouchard 2011, Doolittle 2013). Others propose that selection might not require a population of interacting entities. Instead, a single process could conceivably evolve to become increasingly articulated by a process that, arguably, qualifies as a form of natural selection (Doolittle and Inkpen 2018). This entire line of investigation falls under the heading of Universal Darwinism: an ontologically-driven research program that extends the definition of natural selection to its most abstract limits so that every possible phenomenon can be studied as an adaptation at some level or other. I offer pragmatic advice for Universal Darwinians: not everything that qualifies as a Darwinian individual should be regarded as such for scientific purposes. A central worry with this strategy is that it encourages researchers to posit adaptations where none in fact exist. In place of Universal Darwinism, I outline an alternative, epistemically motivated methodology. The eco-evo partitioning framework assesses the relative contributions of ecological and historical factors to some pattern of variation. Selection is posited as a causal factor only when a significant interaction is detected between these two types of factor. This paper first outlines some problems with Universal Darwinism and presents the partitioning framework as a theoretical alternative. I then provide a general introduction to the topic of transposable elements (TEs) and the field of genome-level ecology. The final section documents an empirical application of the eco-evo partitioning framework to communities of transposable elements. Although TE communities qualify as Darwinian individuals, I explain why (in this case) it would not be profitable to scientifically regard them as such.

1. Introduction

Charles Darwin's discovery of natural selection has been described by Daniel Dennett (1995) as universal acid that eats through everything. Once we recognize that selection is a substrate-neutral process, he suggested, we start to view familiar systems in a new light. Entire areas of scientific study are transformed into something more organismal-looking upon discovering that, all this time, they have been populated by Darwinian individuals. This is the term that Godfrey-Smith (2009) coined for entities capable of evolving and adapting by natural selection. On his refinement of Lewontin's (1970), Darwinian individuality is a matter of degree. It is affected by the fidelity with which the "intrinsic" properties of an entity are inherited, the amount of variation among entities in their reproductive success, and the extent to which they form interacting populations. Everything from human culture, to cancer, to ecological communities have been molded to this form. In some cases, this has required revisions to Godfrey-Smith's already permissive framework. For example, reconceptualizing persistence as a form of reproductive success makes it easier to view ecological communities as Darwinian individuals. (Bouchard, 2014; Dussault & Bouchard, 2017). Thinking about ecosystems as networks of processes (i.e. as "songs, not singers") allows one to view these even more inclusive entities in a Darwinian guise (Doolittle, 2017; Doolittle & Inkpen, 2018). This body of philosophical work is intellectually stimulating and often insightful. However, it pays surprisingly little attention to the relevant epistemic issues. What would it mean to empirically test adaptationist hypotheses about an ecological superorganism? More generally, how should scientists reconfigure their approaches to these entities, now that we appreciate their essential Darwinian natures?

George Williams (1966) notoriously described adaptation as a "special and onerous concept that should be used only where it is really necessary." Steven Gould and Richard Lewontin (1979) elaborated on some of the relevant challenges. They noted that trait individuation is deceptively simple. It is too easy to mistake some arbitrary structure as a genuine trait unless one has grasped its developmental origins. If this is true for biologists studying normal organismal phenotypes, what problems lie in store those who will investigate the emergent traits of superorganisms? Gould and Lewontin (1979) further identified a number of alternative processes besides natural selection that are capable of giving rise to apparent adaptations. These include phenotypic plasticity, developmental linkage, and drift. Analogous processes exist for ecological communities (Linquist 2019). If we are to avoid the temptation of Panglossian story-telling in the case of organisms, then we should be on the lookout for non-Darwinian processes that might give the appearance of adaptation at higher levels of organization as well.

When it comes to conventional organisms, it is already difficult to determine whether certain traits have indeed evolved by natural selection. Meticulous experiments by John Endler (1980) on guppies (*Poecelia reticulata*) or Rosemary and Peter Grant (1999) on Galapagos finches (*Geospiza*) remind us of the epistemic challenges (see Brandon, 2014). However, even these systems were relatively experimentally tractable. Mountain streams in Trinidad contain reproductively isolated guppy populations, allowing Endler to exclude migration as a factor influencing population-level phenotypic change. Likewise, the Grants were able to tag and reidentify individual birds, even tracking their relative reproductive success. Moreover, in both systems it was possible to rule out phenotypic plasticity as an alternative explanation for phenotypic change. It is said of Gregor Mendel that he got lucky in his choice of the pea plant (Pism sativum) as his model organism (Sturtevant 1971, Burian, 2022). It so happened that the phenotypic traits that he was able to measure occurred mostly on different chromosomes, making it relatively easy to identify the phenomena of segregation and independent assortment. In a similar way, our best available examples of evolution by natural selection have relied on relatively uncomplicated systems. It is easy to overlook these pesky epistemic limitations when speculating about the prospects of Universal Darwinism as an explanatory strategy.

The central thesis of this paper is that not everything that qualifies as a Darwinian individual should be regarded as such for scientific purposes. Universal Darwinism is an ontologically motivated research program. It extends the definition of natural selection to its limits so that a maximally diverse range of phenomena can be studied as adaptations at some level or other. The first order of business is to circumscribe the relevant individuals at a particular level of organization (see Clarke, 2010; Skillings, 2016 for a catalogue of options). Once a mode of individuation has been selected, the Universal Darwinian goes looking for candidate explanada: potential adaptations that might have been selected at that level. This procedure confronts all of the epistemic worries that were outlined by Williams, Gould, and Lewontin. In place of Universal Darwinism I recommend an alternative, epistemically motivated approach. This method has been described as the *eco-evo partitioning framework* (Linquist, 2019) and has been proposed elsewhere as a strategy for comparing the relative contributions of evolutionary versus ecological factors to community composition (Govaert et al., 2016). This method begins with an identification of the explanandum (the thing to be explained), which is ideally a pattern of variation among some type of focal entity. Unlike the Darwinian individualist approach, there are few ontological conditions placed on focal entities. For instance, there is no requirement that they must remain spatiotemporally bounded. It is possible for a population of entities to coalesce at one point in time, then disperse into a general population, only to reconfigure into distinct groups or communities at some later stage. This sort of process, characteristic of trait-group selection (Wilson, 1979), has no bearing on whether an entity can be analyzed using the eco-evo partitioning framework. The only ontological requirement for this analysis is that we are able to gauge the effect of historical processes on observed variation in the focal trait. For example, in a population of entities that occasionally disband and reconfigure after mixing, it is only necessary that we are able to determine the extent to which this historical process impacts variation in the population-level trait.

Once some pattern of variation among focal entities has been identified as an explanatory target, the next step is to partition the variance into “purely evolutionary” and “purely ecological” factors. This distinction is discussed in more detail in the third section on this paper. For now, the basic idea can be illustrated with an example.

Some patterns of variation among ecological communities are due entirely to local environmental factors. For example, suppose that oxygen availability varies across a range of tidepool habitats. Each tidepool contains a community of organisms with a given level of species diversity and abundance. It is easy to imagine that these tidepool-level traits would vary in response to O2 levels, with more oxygenated pools supporting greater abundances and levels of diversity. This pattern of variation would call for a purely ecological explanation since, by hypothesis, historical or evolutionary factors had no influence[1]. Other patterns of variation are driven entirely by historical factors. For example, imagine a similar scenario with a tidepool

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[1] There is a trivial sense in which evolutionary factors had an influence on pattern of variation caused by O2 levels: all of the organisms in question are products of evolution. However, differences in the distant evolutionary past do not contribute to variation among tidepools. It is important when considering the explanatory value of some variable to remain clear about the explanadum.

meta-community, except no variability in O2 levels nor any other local ecological factor. Differences in diversity and abundance could nonetheless arise through a historical founder event, where community members arrived from some other location and differentially populated each tidepool at random. In this case, variability in tidepool diversity and abundance are explained entirely by this historical factor which could continue to have an inertial effect on tidepool variability.

In reality, circumstances are rarely so cut and dry. It is almost guaranteed that both ecological and evolutionary factors would interact to some extent. Local ecological conditions are never identical. After the initial dispersal event, some of those ecological differences would presumably affect community diversity and abundance. For example, a particular tidepool that started with high diversity and abundance might evolve to lower levels because of relatively little oxygen. Other pools might increase in diversity and abundance thanks to high O2. In these cases, it might seem that both ecological and historical factors should play an explanatory role in accounting for the observed pattern of variation. However, this depends on additional pragmatic considerations. Suppose that ecological factors contribute to only a very small proportion of the variability compared to history. At this point, a researcher must consider the practical, financial and other costs associated with exploring the ecological factors and their interaction with historical influences. It is conceivable that this would pose more challenge than it is worth. In this case it would makes sense to treat the system as if ecological factors were absent, even though they exert a minor causal influence on the focal pattern.

What if there is a significant causal contribution from both types of factor? These are cases where differences in individual history impact the ways that systems interact with their local environments. In these cases, a researcher must work out how the two types of factor causally interact. This is no simple task. Even within a single species there will be individual variation in O2 sensitivity. Identifying the traits that make individuals more or less fit in a given range of O2 levels would involve a demanding research program. To carry this out at the community level would involve a research project reminiscent of George Van Dyne's ill fated ecosystem project (Kwa, 1993). It would likewise be an experimental challenge to determine the influence of different historical starting points on community development. Now, just imagine the difficulty of gauging the interactions between these two types of processes. Ontological discussions about the nature of Darwinian individuals can easily lose sight of the empirical challenges associated with developing a selectionist explanation of some system. This is not to say that such challenging projects should always be avoided. However, there is a reason that the disciplines of ecology and evolution have, in practice, engaged in a division of epistemic labour (Linquist 2019). It is reasonable that a researcher should seek empirical assurance –beyond the mere presence of a Darwinian individual—as to whether some pattern indeed calls for a combined, eco-evolutionary approach.

A few features of the tidepool example are important to highlight at this point. Notice, firstly, that cases where both types of factor interact are precisely the kinds of cases that the Universal Darwinian hopes to identify and investigate. Each tidepool community qualifies as kind of Darwinian individual provided that differential persistence through growth is permitted as a measure of its fitness (Dussault & Bouchard, 2017). To see this, we can think of historical inertia in abundance and diversity as the tidepool-analogue of heritable traits. Specifically, differences in these traits at time slice T is a function of the historical lineage to which each tidepool belongs. Individual tidepools resemble their antecedent time slices more closely than they to the average value of the tidepool metapopulation. Along a similar line of thinking, the ecological influence of oxygen serves as a selective factor, effectively creating indirect competition among the tidepools. To be clear, I am not endorsing this rather strained way of looking at things unless doing so provides some epistemic payoff. The whole point of the eco-evo partitioning framework is to gauge the extent to which such a framework is insightful. To detect whether there is such a benefit, we look for an interaction between ecological and evolutionary factors with respect to the focal pattern of explanatory interest. If no interaction exists, then a simpler framework is recommended.

There is something else to notice about the tidepool example: just because it qualifies as a kind of Darwinian individual does not necessarily mean that it should be investigated as such. As we have seen, pragmatic considerations play a role in determining whether ecological or evolutionary factors should be ignored for the sake of simplicity. This conservativism is not borne out of an arbitrary preference for parsimony, as some historical opponents of multi-level selection theory have embraced (see Sober, 1987 on the parsimony argument). Rather, it stems from a sensitivity to the pragmatics of scientific explanation. It is empirically very difficult to work out the causal interactions between both ecological and evolutionary factors. The few cases where this has been done in detail relied on exceptionally tractable systems and an incredible amount of challenging work. It stands to reason that if a particular type factor exerts only a small causal influence on the pattern of interest, then it should be excluded from the investigation and ultimately from the explanation. This argument mirrors Philip Kitcher's (1984) "gory details" objection to reductionism: sometimes the addition of causal complexity detracts from the quality of an explanation (Linquist 2019). The eco-evo partitioning framework provides a method for gauging the magnitude of a causal factor before deciding whether to investigate its significance and ultimately incorporate it into a scientific explanation. In contrast, the Universal Darwinian framework encourages us to regard every possible process as a selectionist process, no matter how complex. This is why the eco-evo partitioning framework does a better job of heeding Williams' cautionary warning.

A third noteworthy feature of the partitioning framework is that it requires a researcher to be explicit about the explanadum (the pattern to be explained) up front. This contrasts with Universal Darwinism, where the identification of superorganism-level phenomena requiring a higher-level explanation has taken a back seat to the ontological project of identifying Darwinian individuals. Indeed, Universal Darwinism seems to get things backwards. It erects an explanatory framework before determining whether there is any honest work for it to do. Especially given the tendency for mishandling adaptationist reasoning, this approach seems error prone. If one begins with the assumption that some entity qualifies as a Darwinian individual, there is an implicit commitment to a kind of adaptationist project that could be self fulfilling (Lloyd, 2015). In contrast, the eco-evo partitioning framework is designed so that a selectionist explanation is invoked only once it is deemed necessary.

At this point it might sound as if the eco-evo partitioning framework is nothing but a speculative proposal. Sounds good in theory, but can it ever work? In the third section of this paper, I describe a case study in which the eco-evo partitioning framework was successfully applied to collections of transposable element communities (Linquist et al., 2012). This provides some optimism that the partitioning framework can be applied to a certain type of superorganism (albeit a very microscopic one). Before presenting this case, it is important to say a few things about what transposable elements are, their relationship to the host genome, and how they qualify as Darwinian individuals at multiple levels.

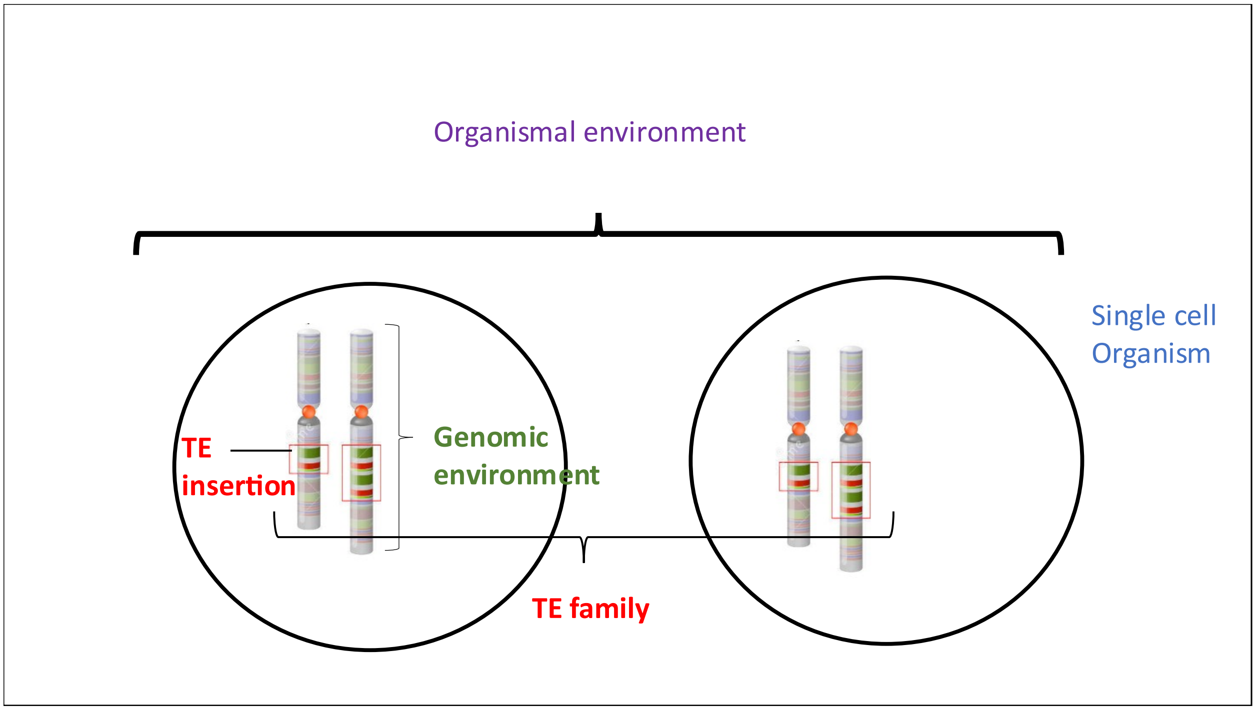
2. Transposon ecology and the individuality question

Transposable elements (TEs) are strands of DNA interspersed throughout the genomes of most, if not all organisms. Also known as “jumping genes,” their distinctive feature is an ability to self-replicate and insert into new chromosomal locations. This occurs either by a cut-and-paste or a copy-and-paste process. TEs that employ the cut-and-paste strategy contain a limited number of protein-coding genes. These genes encode enzymes that snip the element out of its current home and chaperone it to a new location. This leaves a temporary gap in the chromosome where the cell’s DNA repair mechanisms fill in the space with an identical TE, copied from the adjacent strand of DNA. This is how cut-and-paste TEs replicate and translocate independently of cell division. The other strategy of replication involves a copy-and-paste process. In this case, the “parent” element does not move from its location on the chromosome. Its DNA sequence is transcribed by the same cellular mechanisms that normally work on organismal genes to generate RNA and then DNA. Copied daughter elements are inserted back into new chromosomal locations by chaperone enzymes, as with DNA transposons. These replication and insertion processes can happen several times in the lifespan of a single cell. When it occurs within gametes, TE insertions form part of the “immortal” germline that is replicated by meiosis and passed on through sexual recombination. Over time, this process can generate an abundance of TE copies in the host genome. For instance, a particular copy-and-paste element called *Alu* has colonized the genomes of primates. Behaving in a manner reminiscent of an invasive species, the *Alu* element comprises over 45% of the human genome (Koning et al., 2011). To put this in perspective, a mere 2% of the entire human genome is comprised of protein-coding genes (Piovesan et al., 2019), and the total proportion of organism-functional DNA in humans, taken together, is roughly 10-15% (Ponting & Hardison, 2011). From a genomic perspective, we are mostly transposons.

A few terminological guidelines help to facilitate communication about TEs (Figure 1). An individual *TE insertion* is a token transposable element located at a specific spot on a particular chromosome in an individual organism. Some insertions are shared or *fixed* across all members of a “host” species or higher taxa. A given TE insertion can either be active, if it is capable of moving and/or producing new copies; or it can be inactive, if it lacks these abilities. A *family* of TEs is a group of ancestrally related insertions, including both active and inactive copies, that have a high degree of sequence identity. Note that a single TE family can be endemic to a single species or shared across a higher taxon. For example, *Alu* is shared (in different proportions) across primates, while another retroelement called *Line 1* is shared across mammals. A TE-*community* is an assemblage of distinct TE families located in the genome of a single species or higher taxon. Members of the same sexual species tend to share a TE community, because they exchange TE insertions through sexual recombination. When we examine higher taxa, where genetic exchange rarely occurs, the composition of TE communities becomes increasingly divergent.

A TE *environment* can be defined as all of the cellular and genomic structures with which a given TE family or community directly interacts. These include host genes, features of the chromosome such as centromeres and telomeres, DNA regulatory regions, the cell’s replication machinery, its DNA repair machinery, the three-dimensional structure of the chromosome, and so on. It is important not to confuse genomic environments with organismal environments. Whereas a physically distinct genomic environment exists within each cell, organisms share a common physical environment. It is the set of biotic and abiotic features with which they interact.

Figure 1. TE insertions are located at a specific chromosomal location in a token organism. TE families are distributed populations of TEs closely related by common descent and sharing a similar sequence. The genomic environment includes all of the intra-cellular and genomic structures that a TE family or community directly interacts with. Different token organisms of the same species have type identical (or nearly identical) genomic environments. The organismal environment includes all of the physical structures that the organism directly interacts with.



Confusion can sometimes arise when considering interactions across levels. For instance, a change in the host organismal environment might impose a selection pressure on the host population, causing an increase in the frequency of a particular allele. That allelic change qualifies, at the same time, as a change in the genomic environment. It is also possible that this change in the genomic environment might affect the replication rate of some TE family. For instance, the new allele might produce a protein that interferes with the RNA transcripts used by some family of copy-and-paste TEs to replicate. This would be a case where selection at the organism-level has a "downward" effect on a TE family through a change in the genomic environment. It is also possible to imagine a case of "upward" causation, from the TE environment to organismal fitness. For instance, a particular TE family might acquire some mutation that allows them to avoid detection and methylation by the cell. This could cause a burst of TE replication activity, thus increasing the rate of mutational damage to organismal genes and a decrease in host fitness.

Importantly, genome-level ecology tends to abstract away from processes occurring at the organism level. It focusses instead on those occurring intra-cellularly. This should not be understood as an ontological claim about the reducibility of all organism-level evolutionary phenomena to the genome (e.g. Kerr & Godfrey-Smith, 2002; Sterelny & Kitcher, 1988). Instead, genome-level ecology is an idealization strategy (see Section 3, below). It is successful to the extent that intra-genomic ecological and evolutionary processes can be causally "screened off" from organism-level processes (Sober, 1992). There are at least three prima facia reasons for thinking that such screening off is feasible.

At first, it might seem implausible that the proliferation of TEs within the host population could be semi-independent of their effects on host fitness. When a new TE insertion lands close to or within a host gene, it will most likely be disruptive. Hence, many TE insertions are effectively identical to deleterious point mutations. Over time, one might expect them to be removed by purifying selection from the host population. If that were all that was happening in the genome, then it would indeed be possible to view all TE activity through the lens of organismal fitness.

However, theoretical models of TE/host interactions demonstrate that, due to their ability to bias their representation in gametes, it is almost impossible for the host population to purge itself of TEs. As long as most TE insertions are non lethal, they tend to persist and accumulate even under strong selection against them (Charlesworth & Charlesworth, 1983; Hickey, 1982). Hence, even though the absolute fitness of a host population will decrease with the accumulation of TEs, it remains impossible for selection to eliminate them entirely.

It has long been assumed that this negative-fitness accumulation effect is limited to sexual species (Hickey, 1992). In sexually recombining populations, organisms that inherit extremely deleterious combinations of TE insertion are removed by selection, while those inheriting relatively benign combinations of TE insertion increase in frequency. By contrast, asexual populations are burdened by Muller's ratchet. All things being equal, a linage of asexual organisms has no means of purging highly deleterious combinations of TE insertions and will eventually suffer genetic meltdown. This is one of the reasons why it is thought that procaryotic genomes have lower overall abundances of TEs compared to eukaryotes. Selection among host organisms is more efficient at removing TEs, as their deleterious effects tend to compound over time. However, recent theoretical work shows that it is at least possible for TEs to accumulate to very high levels even in asexual genomes. By creating a certain number of inactive insertions for each active insertion, a TE family can effectively cerate its own "habitat" – neutral insertion sites for active TE copies to inhabit without affecting the host fitness. The authors describe this process as TE-level "ecosystem engineering" (Kremer et al., 2020, 2021).

I have argued that even if most TE insertions are mildly deleterious, TE communities can nonetheless multiply and persist in eucaryotic and (possibly) procaryotic genomes. This alone justifies a genome-level perspective that investigates ecological and evolutionary processes at the intra-genomic level, while backgrounding effects on the organism's fitness. Further justification for this approach comes from the fact that many TE insertions are actively neutralized by the cell. Eukaryotic organisms, with their large genomes packed with TE communities, have evolved a number of strategies for detecting and silencing their activity. For instance, the process of DNA methylation involves adding a molecule to the DNA strand which causes it to bind tightly together, making it difficult for DNA transcription to occur at the site. Although methylation is most commonly recognized as a mechanism for gene regulation, this process is thought to have evolved as a suppression mechanism against TE replication (Lisch & Bennetzen, 2011), a role that it continues to play in many species (Zemach et al., 2010). Another TE suppression strategy involves RNA interference. RNA transcripts produced by the TE are identified and disrupted in the nucleus by another type of RNA molecule called piRNA (Czech et al., 2018). These are only two of several strategies used by cells to dampen TE activity. However, they are enough to make the theoretical point that, because of such buffering mechanisms, a lot of TE/host interactions occur below the level of organismal fitness. An entire family of TEs could, in theory, appear and spread throughout a host genome with only minimal effects on host fitness. It is therefore sometimes profitable to study the ecology and evolution of TEs by focussing primarily on their local interactions within the genome (see also Abrusán & Krambeck, 2006; Brookfield, 2005b; Flores-Ferrer et al., 2021; Kidwell & Lisch, 2001; Linquist et al., 2015; Mendoza-Galindo, 2022; Saylor et al., 2013; Venner et al., 2009).

A third argument for focussing on the genome as a site of ecological and evolutionary processes involves an analogy between TE communities and microbiotic communities. Microbiotoc communities are multi-species assemblages of bacterial cells that often coexist intimately with some host organism (e.g. gut bacteria in mammals). If it is possible to view microbiotoc communities as ecological and evolutionary systems in their own right (O'Malley et al., 2015), then a similar approach ought to work for TE communities.

To elaborate on this analogy, some microbiotic communities are physically contained within the host, much in the way that TE communities are encapsulated in the nucleus. Just as specific microbial communities tend to be associated with particular host species (Zhang et al., 2021), so do TE communities tend to travel with particular hosts However, in both cases the communities are not perfectly isolated. Some microbiotic lineages jump across hosts (Mosites et al., 2017) just as certain TE families are horizontally transmitted across host species (Leaver, 2001; Lohe et al., 1995; Pinsker et al., 2001). A further similarity involves ecological interactions among community members. It is no surprise that ecological interactions exist among bacterial species within a microbiome (e.g. Guégan et al., 2018). Interestingly, similar interactions are known to occur among TE families. For instance, the *Alu* family that was mentioned earlier have come to depend for their replication on a more ancient family of TE called *Line 1* (Price et al., 2004). *Alu* transposons are much shorter – they have lost the genes encoding enzymes that would otherwise facilitate their transposition – and would be unable to replicate if there were no other types of TE present in the genome. *Line 1* transposons, which are distantly related to Alu, have retained the genes necessary for their own transposition and Alu has evolved the ability to hijack those proteins to facilitate their own movement. Somewhat surprisingly, a phylogenetic reconstruction of these two element families suggest that they have not coevolved (Wagstaff et al., 2013). Instead, the Alu element appears to have adapted to an available ecological "resource" (transposition enzymes generated by Line 1) that tends to be present in its local genomic environment. The more general point is that transposon communities exhibit ecological interdependence among families resembling ecological relations found in other communities, such as microbial communities.

There are a few noteworthy respects in which TE communities differ from microbiotic communities. However, many of these differences suggest that TE communities are an even more experimentally tractable. For instance, TE communities are highly spatially organized along a chromosome. This makes it relatively easy to compare the abundance and diversity of TE communities. The growing list of high-resolution genomic databases provide the raw data for innumerable comparative studies in genome-level ecology. By contrast, obtaining reliable data about microbial abundance and diversity tends to rely on the lower-resolution and more inferential process of meta genomics (Faust et al., 2015).

Indeed, it is even possible to track the physical movements of individual TE insertions by sequencing a host genome over successive points in time (Wessler, 2001). No such fine-grained analysis of individual microbial movements appears to be on the horizon. A further dissimilarity between transposon and microbial communities surrounds the tendency for TEs to persist in the genome long after they have been silenced. This provides a basic for reconstructing ancestral TE communities. For example, suppose that transposon invades a genome at some point in time, but its active copies gradually become silenced by methylation or other such mechanisms. The elements remain frozen in the genome, slowly accumulating point mutations that can be used to date them (Wagstaff et al., 2013). Microbial ecology would be a much more experimentally tractable discipline if fossilised community members persisted indefinitely alongside living individuals.

I have presented three arguments for viewing the genome as a site of evolutionary and ecological processes, somewhat independent of those which impact the organism as a whole. First, even when TE insertions tend to be moderately deleterious for the organism, they can accumulate and persist indefinitely – especially in the case of eucaryotic organisms. This makes it possible to study the origin and accumulation of TE families and communities while backgrounding their effects on organismal fitness. Second, eukaryotic species possess a diverse range of TE surveillance and neutralization systems that mitigate their effects on host fitness. These mechanisms give rise to a dynamic interaction at the TE level that is largely shielded from organism-level fitness consequences. Finally, if it is possible to analyze microbial communities from an eco-evolutionary perspective, then similar investigations of TE communities are even more promising given their high degree of experimental tractability. Let us now turn to the ontological question of whether TE insertions, families, or communities qualify as Darwinian individuals.

Starting with the individual TE insertion. When an insertion occurs in the germline it will spread by drift through the host population unless it has an effect on host fitness. Deleterious insertions will be removed from the population by selection on the host, though often not before making several copies that are inserted elsewhere. The occasional beneficial insertion can become fixed in the host population (Bourgeois & Boissinot, 2019). Such cases, where selection acts on an insertion via its host-level effects, qualify these insertions as a kind of Darwinian individual. A more interesting question perhaps is whether the production of TE "daughter" copies should be regarded as a case of TE replication, or, alternatively, whether this should be regarded as a case of a single TE individual growing within the host genome. I can see no principled reason for preferring one interpretation over the other.

Turning to TE families. An important consideration is that TE insertions belonging to the same family can have radically different effects on host fitness, depending where they land. It is therefore important not to infer from the beneficial or detrimental effects of one insertion that the entire family has a similar effect (Brunet & Doolittle, 2015). However, there are some examples where an entire TE family has been "domesticated" by the host to perform some specific function. The poster-element for TE domestication is a family of transposons that create telomeres in a particular species of Drosophila. Telomeres are repetitive DNA sequences at the ends of chromosomes that often get compared to the waxy tips at the end of a shoestring. Telomeres gradually degrade over successive replication events, a process thought to be related to senescence. In at least one Drosophila species, the task of generating new telomeric ends has been taken over by a family of TEs that insert preferentially into chromosome end points (Levis et al., 1993). This famous example shows that TE families can function as Darwinian individuals, even though many of them have more diffuse effects on fitness. In this case, the TE family promotes its own survival by effectively cooperating with the host genome. However, it is also possible to image a family of TEs being under selection to evolve properties that promote its own selfish replication. It is reasonable to assume that TE families are in competition with one another for genomic resources such as space, transcription factors, and favourable insertion sites (Abrusán & Krambeck, 2006). A particular TE family might acquire an ability to, for instance, preferentially insert into a location where the cell has a difficult time eliminating it, this gaining a competitive advantage over its rival community members. Such competition among TE families within the genome qualifies these entities as Darwinian individuals[2].

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[2] Godfrey-Smith (2009) reserves the category of scaffolded individuals for entities that depend on some other type of individual for their replication. Since TEs harness the transcription machinery of the cell to varying degrees (depending on the type and family of TE), I suppose that they fall into this category. However, it is unclear whether this undermines their qualification as bona-fide Darwinian individuals. Within the science of TE evolutionary dynamics, it is certainly possible to assign fitness values to individual insertions. I have further argued that TE families and communities have a semi-autonomous ecological and evolutionary dynamic. It should perhaps also be borne in mind that all organisms are dependent to some extent on other types of individual for their replication (Griesemer, 2016).

What about TE communities? One way that these collectives might qualify as Darwinian individuals is through their effects on host speciation (Brunet & Doolittle, 2015; Rebollo et al., 2010; Ricci et al., 2018; Serrato-Capuchina & Matute, 2018; Zeh et al., 2009). The accumulation of TEs in a genome can cause large scale mutations, such as chromosomal rearrangement. Such rearrangements can potentially be a source of reproductive isolation. Hence, it has been proposed that TE communities enjoy a sort of positive fitness by generating new organismal species (Doolittle, forthcoming). At the same time, TE communities have potentially deleterious effects on host populations. When TE replication gets out of control, it can drive a population extinct. This process could give rise to TE communities that evolve to become gradually less virulent within host genomes. It is also conceivable that two or more TE families could symbiotically co-evolve. One TE family might provide a useful resource such as the production of transposition enzymes, while the other provides a supply of neutral insertion sites. To my knowledge, few community-level interactions have been experimentally identified, but genome-level ecology is a very young discipline and the basis for such interactions (such as in the Alu / Line 1 relationship) are present.

Taken together, these considerations suggest that there are a number of different Darwinian individuals at play in the field of transposon biology. But what is an experimentally-minded researcher supposed to do with this ontological framework? A tempting prospect is to go looking for the associated adaptations at each respective level of Darwinian individuality. The assumption funding this approach is that everything that qualifies as a Darwinian individual (everything that is capable of undergoing selection) will ultimately give rise to adaptations. However, we know that this generalization is false. Selection can be a relatively weak force, such as when fitness differences among individuals is small, or when differential sampling (or "drift") is overwhelming. At the same time, there are various processes that generate apparent adaptations. At the population level, phenotypic plasticity and migration can cause a strong correlation between an adaptive trait and some ecological variable. Only rigorous experimentation can exclude these alternatives. It would be a sensible idea, before undertaking such experiments, to gauge whether there is likely to be some explanatory payoff.

3. A case study in genome-level ecology

The growing realization that TE dynamics within the genome resemble ecological interactions at a larger scale has led several researchers to call for a community ecology of the genome (Abrusán & Krambeck, 2006; Brookfield, 2005; Rouzic & Capy, 2006; Venner et al., 2009). In 2011, an interdisciplinary group of researchers at the University of Guelph set out to clarify this approach (Linquist et al., 2013). In particular, they aimed to explain what is distinctive about an ecological approach to transposons that might distinguish it from the more familiar co-evolutionary models that have been applied to TEs since the 1980s (Doolittle & Sapienza, 1980; Orgel & Crick, 1980). What follows is an interpretation of their framework, written for a philosophical audience.

There are three basic steps to the eco-evo partitioning framework. The first involves a view of the relationship between ecology and evolution as distinct idealization strategies. The second step is set of operational definitions outlining the differences between a purely ecological, a purely evolutionary, or a combined eco-evo framework. The third step involves an estimate of the extent to which each type of factor covaries with some pattern of explanatory interest. Using this framework it is possible to gauge, empirically, the extent to which a given pattern calls for either a purely ecological, a purely evolutionary, or a combined eco-evo explanation.

Starting with the idea of a simplification strategy. The aim of simplification generally is to create a tractable representation of a target system that explicitly foregrounds certain properties while ignoring others. This idea is familiar to philosophers and biologists who think about scientific models as simplifications (Weisberg 2013). Somewhat more novel is the suggestion that entire disciplines can be understood as simplification strategies (Linquist et al 2013). This departs from the conventional view of disciplines as defined in terms of their proprietary subject matter. Although the latter view of disciplines might apply to many fields such as chemistry, molecular biology, or physics, the field of evolutionary biology has been shown to apply to a wide range of entities ranging from memes to cancer cells. Along similar lines, it is noteworthy that the discipline of ecology is being similarly applied to a similar rage of unconventional entities. This suggests that ecological processes, too, are substrate neutral. Researchers working within ecology often regard themselves as taking a different approach to their subject matter than evolutionary biologists. Historically, this difference has been cashed out in terms of Hutchinson's (1965) metaphor of the ecological theatre and the evolutionary play.

This two-speed model holds that ecological processes occur over a shorter timescale than evolutionary ones. Although this analysis of the eco-evo distinction is somewhat helpful, it runs into problems in accounting for ecological and evolutionary processes that occur over similar time scales. For instance, in the introduction to this paper we imagined a tidepool example where a historical founder effect interacted with an ecological factor to differentially impact community diversity and abundance. This could in principle unfold over a single period. However, in understanding this process it is reasonable to distinguish historical or evolutionary factors from ecological ones. Therefore, the distinction between ecology and evolution cannot entirely boil down to a matter of time scale. An alternative way of distinguishing theses disciplinary approaches is captured by the following definitions.

> A **strictly ecological approach** regards some class of focal entities (e.g. TE communities) as a fixed type, or a limited number of such types, which possess certain intrinsic causal properties. Changes in the abundance or distribution of those entities are explained exclusively in terms of their relationships to specific features of their environments. Although feedback from the environment can potentially change the intrinsic causal properties of the focal entities over time, such changes are ignored for the purposes of simplification.

According to this definition, ecology in its “pure” or “strict” form adopts a typological view of its subject matter. This should be understood not as a denial of Darwinism, but rather as a strategic idealization. When it comes to certain patterns in nature, ecological processes are much more salient than evolutionary ones (as in one of the tidepool scenarios). Ecology as a distinct discipline can be understood as an idealization strategy that focuses on just the effects of environmental influences on population or community composition. Importantly. The strategy of ecology is to focus on the effects of specific ecological factors (e.g. the effect oxygen on community composition) as opposed to collapsing various ecological factors into a single variable called “the selective environment.” This distinguishes it from a purely evolutionary approach:

> A **strictly evolutionary approach** views the focal entity as a population of individuals with intrinsic properties that vary and are heritable to some significant degree. The explanatory aim of this approach is to account for changes in the focal population over

> time. Later stages of the population are explained entirely in terms of its earlier stages (including relationships among individuals at earlier stages). However, relationships to specific features of the environment are ignored for simplicity.

Much of the work in population genetics provides an illustration of how this approach is profitably applied at the level of alleles. Each allele is defined in terms of certain intrinsic properties such as fitness value and mutation rate. Early stages of the population such as allele frequency and effective population size explain how later stages arise. This is done without any reference to specific ecological factors. Even more explicit examples of a purely evolutionary explanation involve no mention of the environment whatsoever – not even in general terms. For instance, explanations of trait persistence that appeal to generative entrenchment (Schank & Wimsatt, 1986) or to constructive neutral evolution (Stoltzfus, 1999) very clearly attempt to explain the later stages of a system in terms of its earlier stages, while making to reference to influences of the environment.

Finally, it is possible to combine these two approaches:

> A **combined eco-evo approach** views the focal entities as members of a population with intrinsic properties that vary to some degree. Relationships between those variants and specific features of the environment are explicitly represented in order to explain, not only how the population changes over time, but potentially also the effects of such changes on features of the environment.

Work by Ender (1980) on guppies or by the Grants (1999) on Galapagos finches exemplify this strategy. These are cases where Darwinian individuals not only exist, but are doing clear explanatory work. The focal entities in these examples are populations of organisms that exhibit some degree of heritable variation that is recorded by the experimenters. Likewise, specific ecological factors (e.g. predation level or food abundance) are shown to vary systematically with changes in some focal property (tail colour, beak size). There is no idealization of either the population variability nor the specificity of ecological factors: both dimensions play significant causal roles in explaining change in the population over time.

One potential objection to this framework surrounds the use of "evolutionary." This term is already used to describe a wider range of investigations than those being singled out by these definitions. For instance, Endler's work is often described as an exemplary evolutionary study, whereas according to the aforementioned definitions it is an eco-evolutionary (or selectionist) explanation. Further confusion might stem from the fact that the focal entities are sometimes collectives. It can be difficult for some researchers, who define "evolution" in terms of gene frequency, to make this leap in thinking. I therefore sometimes use "purely historical" as an alternative expression for what was defined earlier as a purely evolutionary explanation.

A more substantive objection to this framework claims that there is no fundamental ontological difference between ecological and evolutionary processes as I have defined them. This point can be made in the context of the tidepool example. Earlier, I classified the historical founder event, where different communities started off with different initial abundances and distributions, strictly as an evolutionary (not an ecological) process. Conceivably, however, one might insist that this founder event could just as easily qualify as an ecological influence. The only difference is that the founder event is a token, one-off occurrence. Whereas changes in O2 level are a persistent influence that gradually changes community composition over successive generations. If these distinctions merely come down to a matter of perspective, specifically if they come down to a preference for longer duration processes over shorter ones, then the distinction is not ontologically real – or so it might be argued.

In reply, this objection misses the point of the partitioning framework. The aim is not to classify processes into fundamentally distinct ontological categories. Rather, the aim is to capture in general terms an expedient way of investigating complex systems. The disciplines of evolutionary biology and ecology (in their "pure" forms) have respectively hit upon distinct investigative strategies. One idealizes away from specific features of the environment and focuses on how earlier stages impact later ones. The other treats the focal entity as an idealized (unchanging) type and focuses on how such types increase or decrease in frequency in the presence of specific environmental factors. It doesn't matter whether these processes are ontologically distinct in some fundamental sense, so long as there are productive explanatory benefits in separating them (see Linquist 2015 for a comparison to the separation between "genetic" and "environmental" influences on development). A similar issue arises in discussions about the distinction between natural selection and sorting (Jablonski, 2008). Fundamentally, there is no ontological difference between a selective process that happens gradually over successive generations (natural selection) and another that that happens rarely, but with great effect, in the history of a lineage (sorting). However, in explaining the evolution of complex systems it is often expedient to distinguish the two. Admittedly, more philosophical work needs to be done on this issue. However, it is important to keep in mind that the eco-evo partitioning framework is an epistemically (as opposed to an ontologically) motivated approach for determining when it is profitable to use a selectionist (eco-evo) framework for explaining some pattern. It is not a metaphysical thesis about what a Darwinian individual really is.

The final step of the eco-evo partitioning framework is to estimate the prospects of each explanatory strategy by measuring the extent to which ecological and evolutionary factors covary with some dependent variable that is of explanatory interest. This framework was employed by Linquist et al. (2013) to evaluate the extent to which patterns of TE distribution and abundance in genomic communities called for each type of explanation. More specifically, the explanadum in this study is a very general pattern found across eukaryotic species: marked differences in the distribution and abundances of TE families and lineages among the genomes of different species. Like in the tidepool example, the authors identified specific ecological factors that are likely to influence these variables. One ecological factor was the sheer size of the genome. In conventional ecological systems, there is a strong positive correlation between geographic area species richness. Since this relationship holds across a wide range of taxa (Whittaker & Triantis, 2012), it is expected to obtain intra-genomically as well. The second ecological variable that the authors investigated was the proportion of GC content (guanine and cytosine content) in each genome, a factor that varies considerably among species' genomes. These two base pairs tend to be positively correlated with host genes, locations where TEs tend to be unable to insert without harming the host. However, some families of TE are found preferentially in GC rich regions. It is therefore possible that differences in GC content mark a kind of "habitat" difference that favours some TE families over others. To determine the explanatory prospects of these two ecological proxies, the authors measured the covariation between genome size and GC content and two sets of TE communities. One set of ten Drosophila TE communities were relatively closely related, the other set of fifteen mammalian TE communities were more distantly related. This comparison allowed the authors to compare the explanatory prospects of their ecological proxies at two temporal scales. The authors further evaluated the effects of ecological factors are two levels of TE classification.

A similar analysis was undertaken to evaluate the prospects of a purely evolutionary explanation of the TE communities. Since TE communities inhabit the genomes of eukaryotic species, they become geographically isolated when their host populations undergo speciation. This makes it possible to reconstruct the pattern of historical divergence for different communities by using host phylogeny as a proxy (Figure 2). Hence, the authors were able to evaluate the extent to which host phylogenetic distance covaries with differences in TE community diversity and abundance. Again, this analysis was conducted for two temporal scales. The ten TE communities inhabiting drosophila genomes had a maximum divergence time of 15 million years. The fifteen TE communities inhabiting mammalian genomes had a maximum divergence of 165 million years. Purely evolutionary factors are inferred to be of explanatory relevance to the extent that they covary with community diversity and abundance over these two scales.

This analysis also allowed the researchers to evaluate the explanatory prospects of a combined eco-evo (selectionist) approach. A statistical interaction between the ecological and evolutionary factors would indicate that both historical and ecological factors combine to influence TE community abundance and diversity. In other words, if there was no statistical interaction between these factors, then it was inferred that Darwinian selection is not a viable explanatory strategy for this pattern. Note that a lack of statistical interaction does not imply that selection was absent. TE communities might be under weak selection from their local environments. Or, perhaps properties of TE communities are not highly heritable (for e.g. in cases where they are aggressively removed from the genome by deletion bias). However, under these circumstances it would not be profitable to investigate the interaction of ecological and evolutionary factors.

The partitioning framework should also not be mistaken for an explanation in its own right. It is able to detect, under the appropriate circumstances, patterns of correlation between different types of variable. It would be a further question – to be decided by more refined experimentation—exactly how those evolutionary or ecological factors influence community composition. To draw again on the analogy from conventional ecology, merely showing that there exists a positive relationship between geographic area and species richness does not explain the mechanism(s) sustaining that pattern. All that the partitioning framework can tell us is whether there is a strong enough causal signal to pursue a particular mode of explanation.

Notably, Linquist et al (2013) found no statistical interaction between the ecological and evolutionary factors that they investigated and the distribution or abundance of TE communities. Among the relatively closely related drosophila genomes, these community properties covaried with only ecological factors. Among relatively distantly related mammalian genomes, variation in community and diversity and abundance were explained entirely by historical/evolutionary factors. This finding is extremely important for the future study of TE community dynamics. Genome-level ecology (in its pure form) attempts to understand the influence of specific ecological factors on TE communities. Our study reveals that this mode of investigation should restrict its focus to relatively closely related TE communities. Moreover, when it comes to explaining the abundance and distribution of more distantly related TE communities, one ought to idealize away from local environmental influences and focus on the ways that earlier states of the system bring about later states. The important philosophical lesson to draw from this study is that not everything that qualifies as a Darwinian individual on an ontological level should be scientifically regarded as such.

An obvious objection to this argument takes issue with the drawing of causal inferences from an analysis of variance. There are at least two general ways in which this inference could lead one to underestimate the relative significance of a particular type of factor. The first scenario involves a case where the observed pattern of variation does not reflect the relative causal contributions of each factor more generally. For instance, suppose that instead of mosquitos, we had compared TE communities across a more phylogenetically distant group of winged insects. It is plausible that at this level of analysis, an interaction between ecological and evolutionary factors would have emerged. Hence, it might be argued, this entire methodology is flawed because its outcome is contingent on the empirical pattern one chooses to investigate.

This objection can be dealt with in one of two ways, depending on how we understand the focal pattern of variation. One possibility is that the focal pattern simply is the explanadum. A second possibility is that the focal pattern is meant to be representative of the explanadum. Consider first the former possibility. Suppose that our explanatory interest is just in the exact same pattern that is being used to conduct the eco-evolutionary analysis. In this case, if it turns out that both types of factor covary with TE community composition in the new group of winged insects, then it is it is true that a selectionist explanation should be pursued in this case. By the same token, it would still remain true that a purely ecological approach should be pursued for drosophila, and a purely evolutionary one for mammals. Put simply, I am assuming that when it comes to Darwinian systems, the appropriate type of explanation is determined partly by one's explanatory goals and not entirely by the ontological category to which a system belongs. When the explanadum changes in the relevant respects, so should the explanada.

Now consider the other possibility, where the target of our explanation is some more general pattern to which we do not have perfect experimental access. Suppose, in this case, that we are interested in the relative contributions of ecological and evolutionary factors to TE community composition across all animals. In this case, the worry is that the two systems that we investigated (drosophila and mammals) misrepresent the more general pattern. Does this possibility mean that the partitioning framework is inapplicable to such cases?

There are a few things to say about this situation. First, that it might turn out to be a bad question whether one type of factor or the other is "more significant" when it comes to all TE communities in animals. This could be the case simply because there is no general answer: ecological factors dominate some systems, evolutionary factors dominate others, and in yet other systems the two interact. The failure to provide a simple causal answer is not a shortcoming of the framework. A second thing to note about this objection is that it tends to be misplaced. The problem is not with the analysis of variance per se, but rather with the sample that one uses to conduct the analysis. If we are interested in all animal genomes, then it might well turn out that an inference drawn from just one genus of insect and only 15 mammals is too small and unrepresentative to support a reliable inference to animals generally. Of course, one can never know with certainty that one's sample is representative. Science is an iterative process and causal generalizations are naturally revised in light of additional evidence. The empirical question of how to know whether one has selected a representative sample is not a problem for the framework per se. The eco-evo framework is only as reliable as the sample to which it is applied.

4. Conclusion

Depending on how permissive researchers are willing to be about their definition of a Darwinian individual, we can expect a proliferation of these entities across a growing number of scientific domains. However, it is one thing to classify entities according to this framework, quite something else to explain how ecological and evolutionary processes interact to shape and maintain their forms. It is widely received that scientific explanations should idealize away from extraneous processes. By definition, an explanation that combines ecological and evolutionary processes is more complex than one that idealizes away one type of factor or the other. It is only reasonable that a researcher would evaluate the explanatory prospects of a Darwinian framework before launching into a more complicated explanation than is perhaps necessary. At the same time, there exists a psychological tendency to project apparent adaptations onto the world. Universal Darwinism contains no corrective for this tendency. In contrast, the eco-evo partitioning framework is designed to explore a selectionist explanation only after empirically evaluating its prospects. Biologists studying communities or other complex systems would do well to define their explananda and evaluate the respective influences of history and ecology before invoking Darwinian individuals as key players in their causal stories.

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