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SYMBIOSIS, LATERAL FUNCTION TRANSFER AND THE (MANY) SAPLINGS OF LIFE

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ABSTRACT: One of intuitions driving the acceptance of a neat structured tree of life is the assumption that organisms and the lineages they form have somewhat stable spatial and temporal boundaries. Symbiosis that such 'fixist' assumptions does not correspond to how the natural world actually works. The implications of Lateral Gene Transfer (LGT) have been discussed elsewhere; I wish to stress a related point. I will focus on Lateral Function Transfer (LFT) and will argue, using examples of what many would call 'superorganisms', that the emergence of symbiotic individuals revives the importance of functional and adaptationist thinking in how we can think of how to organize the lineages of biological individuals. The consequence of the argument is that, if we really want to hold on to tree of life thinking, we had better accept that new saplings appear and disappear all the time.

Keywords

Evolution, Symbiosis, Individuality, Adaptation, Tree of Life, Web of Life

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Introduction

Questions concerning the best way to organize genetic data into information concerning the genealogy of species have been transformed in large part because of Ford Doolittle's (and others) work which has lead to broad reassessment of the Tree of Life metaphor (e.g. Doolittle 2000).

As others in this issue argue, two related developments of microbiology have led many to question the usefulness of a tree of life perspective and more broadly the way in which lineages form and change.

1- Endosymbiosis, in its narrow sense (intra-cell; i.e. one organism living within the cells of another organism in some sort of interdependent fashion) or in its broader sense (intra-individual; i.e. one individual living within the physical boundaries of another individual), forces us to reconsider our concepts of outer and inner (i.e. What constitutes an organism's environment), forces us to reconsider our understanding of biological individuality (i.e. are unitary organisms the only way that structured individuals evolved in nature?), and forces us to reconsider our intuitions about heredity and its mechanisms and how they translate in lineages.

2- Lateral Gene Transfer (LGT a.k.a. Horizontal Gene Transfer, HGT) forces us to consider the fuzziness of at least some lineages.

A more inclusive web of life perspective (or network approach) has been offered to better account for these developments in microbiology (Doolittle and Bapteste 2007). We have seen in this issue how these developments have been defined and analyzed. It is relatively safe to say that, whereas these scientific advancements were initially rejected as genuine (or significant) biological phenomena, they have now been accepted to various degrees as part of significant biological processes that have *at least sometimes* changed the course of natural history. Concerning the first development, it is now generally accepted that endosymbiosis (in its narrow sense) has happened and that endosymbiotic theory provides the best account of the evolution of mitochondria and chloroplasts. But the broad consensus is that it has been extremely rare (estimates are that narrow endosymbiosis has happened twice in prokaryotes in the last 4 billion years, See Martin in Sapp 2005). Many argue that because of the rarity of endosymbiosis, it should not be seen as an exception worthy of toppling some fundamental assumptions about how we construct phylogenies. As we shall see, this rarity may simply be the result of an overly narrow characterization of endosymbiosis.

Concerning the second development, the consensus is still evolving concerning the pervasiveness and the significance of LGT to our understanding of the biological world. One can find advocates of rampant LGT, others are more conservative, while others accept the theoretical possibility but don't believe it has had a significant impact (Andrew Roger discussed the issue at the Halifax workshop). The disagreements are in part traceable to subdisciplines (e.g. non-bacteriologists will often downplay LGT) but also a question of scale (a strict definition of LGT may ‘easily’ apply to close relatives but not necessarily so easily to the whole phylogeny of all microbes).

Given the assumed rarity of (narrow sense) endosymbiosis, it is the possible ubiquity of LGT that garners the most attention concerning how we view the organization of lineages. LGT is the real point of contention for it has the largest potential of reorganizing our understanding of the tree of life not only in the past as is the case for endosymbiosis but in current evolutionary scenarios.

But, as many articles in this issue show, accepting the possibility of LGT and accepting the theoretical consequences of its effects are two separate things. If LGT events occur at some significant frequency, some genes for at least some types of organisms are exchanged during ontogeny, muddling up our efforts to reconstruct a neat linear evolutionary history based on gene lineages. This would entail that a ‘simple’ tree based on strong Weismannian intuitions is probably not accurate and any organization of lineages based on genetic data should reflect a structure more akin to a web or a network of life.

As with most radical transformations of underlying assumptions concerning our theories (especially those as loaded as the metaphor of a tree of life), strong resistance emerged even when faced with strong corroborating empirical data. Many non-bacteriologists would offer some sort of compromise that tries to include the findings of endosymbiosis and LGT while maintaining neat structured lineage trees. Or to put it differently, faced with these challenges to well established metaphors of life, a more conservative middle road is often prescribed. Carl Woese offers what is probably the emergent consensus:

« Darwinian Threshold ». It separates a pre-Darwinian (progenote) world, in which organismal genealogies are fluid and ephemeral, and evolution is primarily a collective affair, from the Darwinian world we know, in which individual lineages and vertical evolution dominate, and speciation occurs » (Woese, in Sapp 2005 p.116)

This way of framing the issue may be agreeable to many non-microbiologists for it seems to offer a compromise between what we are finding out about the microbial world and what most non-microbiologists believe about the macrobial world (in fact, as Jan Sapp pointed out during the workshop, the progenote, as Woese conceived it, is even antecedent to the microbial world, but Woese's suggestion is more often than not interpreted as referring to a microbial progenote). This way of framing the issue allows for inclusion of the effects of LGT while restricting it to a part of natural history that many if not most evolutionary biologists do not focus on. As we shall see, evolutionary biologists who adopt such an account are blackboxing a process that in fact occurs in the macrobial world as well. To put it another way microbiology offers significant lessons for evolutionary biology.

Many of the participants to this workshop have discussed how the molecular data reshaped our knowledge of the structure of life's domains and how Woese's view does not go far enough since it still assumes a neat structured tree of life. As these advancements in molecular data gain acceptance, biologists are attempting to assess how they will reshape our understanding of natural history. This work is especially relevant for the microbial world where LGT arguably may have a large impact. I will let the other contributors to this issue explore these issues: I will not discuss molecular data here or even Lateral Gene Transfer. My silence on these issues is not meant as a rejection of these findings, rather I wish to make a different point.

I suggest that by recognizing the pervasiveness of symbiosis, we see that what Woese calls the 'pre-Darwinian world' is still among us but not restricted to the microbial world. Woese's description of the pre-Darwinian world obtains at higher level of organization than the microbial world as well. As we shall see, symbioses often lead to temporary coalition of organisms that could arguably be qualified as emergent individuals. Fluid and ephemeral individuals are still around us and therefore fluid and ephemeral lineages that appear and disappear all the time are still a large part of our evolving world: to employ the metaphoric language pervasive in these discussions, we need to recognize all the small wondrous saplings growing (and dying) in the shadow of the more visible tree of life. New trees of evolving systems appear and disappear all the time making the attempt to unify all of evolving systems into a single unified structured phylogeny quixotic. What symbiosis also teaches us is that the characterization of these individuals cannot be reduced to the genomic makeup of these individuals. Examining how the adaptations involved in these systems work, we get a new appreciation for functional characterization essential to define these individuals. As we will see a strong adaptationist heuristic is not helpful but necessary to understand many symbioses. This has profound consequences for how we may assess tree of life or web of life claims. One of the goals of tree of life (TOL) structuring of lineages is exhaustiveness of the natural world. Web of life (WOL) proponents argue that TOL fails at this goal because it excludes many of the genetic changes found (mostly) in the microbial world. Although WOL proponents embrace the fluidity of lineages on which my argument will build, the question I raise is whether they go far enough in recognizing the wild ways in which evolutionary individuals emerge (i.e. are they as inclusive as they think they are?).

This move is in part motivated by Éric Bapteste's exhortation (this issue) to adopt what he calls "lateral thinking" and the natural chimerism (i.e. organism lineages as multiple fluid genome constructs) it models. He argues that lateral thinking needs to be embraced to account for the purported ubiquity of LGT in the natural world. In this article we will see how radical lateral thinking forces us to reconsider biological individuality in ways that are sympathetic to the rejection of a conservative tree of life metaphor but goes beyond what most WOL proponents would argue for. This reshaping of our understanding of individuality and lineages is also prompted by O'Malley and Dupré's call to arms to reshape philosophy of biology to include the promise and challenges offered by microbiology (O'Malley and Dupré 2007 and elsewhere). With these issues in mind, I will focus on how "lateral function transfer" plays an integral role in how symbiosis creates biological individuals in ways not often appreciated in organismal biology.

Provisionally I will define lateral function transfer (or horizontal adaptation transfer) as any adaptive trait acquired during the ontogeny of the individual by other means than the genotype with which the organism began. Implicitly or explicitly, something like LFT appears all over symbiosis research (e.g. Saffo 2002) and similar concepts have emerged in the context of Niche Construction (Odling-Smee et al. 2003) and Epigenetic Theory (Jablonka and Lamb 2005). All these research frameworks focus on how the phenotype is created in part by the genotype, but how vertical genetic inheritance cannot exhaust the sources of adaptive change in biological systems.

This definition of LFT is provisional and only for discussion. Greg Morgan (in workshop discussion) cogently argued that to define LFT explicitly in terms of adaptive traits is prejudging the issue of the positive benefit of the interaction and that more needs to be said to avoid just-so stories. He is correct. As we shall see later in this article, the nature of the symbiotic interaction is highly ecologically dependent, meaning that an acquired trait may be very adaptive in one context or in a segment of the life-cycle while it is maladaptive in other contexts. I will provisionally maintain the adaptationist account of LFT but qualify the definition (in a later section) to account for the special role it plays in cases of symbiosis.

I wish to discuss a few examples of LFT to help us rethink about adaptation, fitness and individuals beyond what has been the Modern Synthesis (or as O'Malley, this issue, would put it, Mayr's take on the Synthesis). Looking at adaptive traits in symbiotic individuals we will see that many evolving biological individuals are much more transient than we often recognize. If that is the case, then any organization of the tree of life is at best a decent characterization of some evolutionary individuals but cannot encompass all the wonders that the biological world displays. Beyond the molecular data, I think that reviving a broad adaptationist way of thinking gives us even more reasons to reconsider the adequacy of tree of life.

This will not be a surprise to anyone interested in symbiosis research (see Sapp 1994 for the best historical survey of the issues involved) but the consequences of how symbiosis research transforms our view of the biological world are often downplayed in mainstream evolutionary theory. After examining some of the issues related to definitions of biological individuality and symbiosis, we will see how LFT allows us to consider the implications of symbiosis for the tree of life debate.

Individuality: One against the world

Lineages are grounded in the idea that biological individuals have relatively stable spatiotemporal locations, that they extend through time in a relatively organized fashion with distinct (but most of the time overlapping) generations and so on (Hull 1976 takes this idea to the conclusion that species are genuine individuals). Things however are not that simple. Jackson, Buss, and Cook (1985), in arguing for a reappraisal of the challenges of studying clonal organisms correctly point out that most theoretical work in evolutionary biology has focused on sexual organisms with easily recognizable boundaries.

> Ever since Darwin, the development of theory in ecology and evolution has been implicitly constructed for fruit flies, birds, and people, unitary organisms whose populations comprise readily distinguishable, sexually derived individuals of approximately determinate adult body size and life span. Grasses, vines, sponges, corals, and other clonal organisms, which commonly dominate much of the land and sea and do not commonly display such characteristics, have been largely ignored by theorists (Jackson, Buss and Cook 1985, p.ix)

Many biological individuals do not have the type of boundaries that we observe in mammals for example. As most contributors to this issue can attest, this assessment is even more appropriate for the microbial world. We often equate individual and organism, but this zoological-centric intuition has been weakened in various ways for centuries: intuitively many recognize that herds appear to have emergent behaviors bestowing a semblance of emergent superorganism status. . Such claims have been made in various ways before, mostly in the group selection literature (e.g. Sober and Wilson 1998, Okasha 2006). Based in part on intuitions about frequency-dependent selection, and trait-group selection, the general idea is that some groups possessing certain distributions of given traits do better than groups with other distributions the same traits. Clonal and colonial organisms (e.g. Portuguese man-o-war) are emblematic of the difficulties of establishing what a biological individual is. How are we to assess the sophisticated integration of differentiated zooids into a larger whole? How are we to assess the fundamental physiological differences between members of a colony? This type of 'puzzle' has led many biologists and philosophers to question how we define what it means to be a biological individual (see Wilson J 2007 and Wilson RA 2007 for some thought-provoking surveys of the issues involved). We need to realize that whereas all organisms are individuals, not all individuals are organisms. Although the claims presented in this paper are sympathetic to group selection claims (or hierarchical approaches to evolution) the ultimate goal is more radical. Since we will be talking here about individuals that are communities (i.e. many-species individuals), usual metrics of evolutionary success (i.e. fitness in terms of differential reproductive success) will not always be the most appropriate metric for their fitness. As we shall discuss later, the biological individuals considered here are more complex than the single species individuals concerned in the majority of the group selection literature and this affects how we construe their individuality and their natural history. Putting this point aside for now, we can recognize some of the many common issues have arisen in this broader literature.

First, Janzen (1977) famously argued that, in the case of many clonal plants, the physiological functions usually encompassed in a single organism in the case of most animals, are in fact spread out across many organisms. Janzen argues that the

“Evolutionary Individual” (for short the genetic individual) need not have physical continuity to be a genuine individual. “At any time, [the Evolutionary Individual, in the case of genetically homogenous dandelion patch] is composed of parts that are moving around (“seeds” produced by apomixes), growing (juvenile plants), dividing into new parts (flowering plants), and dying (all ages and morphs). Natural selection could just as well have produced an organism with all these parts in physiological contact (…)” Janzen 1977 p.586.

In other words, physical continuity is not a requisite for biological individuality. It should be noted, that the view defended by Janzen focuses on fitness as the marker of evolutionary individuality, and implicitly equates evolutionary individuality with genetic individuality.

A similar genetic notion of biological individuality has made large inroads in the botany literature. Harper (1978) makes the oft-quoted distinction between ramets (which correspond to the apparent morphological individual) and genets (as the genetic individual). Since ramets are not substantially different from the organs of an animal, the assumption is that ramets are what we may refer to as pseudo-individuals (or quasi-individuals) whereas the ‘real’ individual is the genet. A clonal grove of Quaking aspen may include thousands of ramets (what look like individual trees) but only a single genet (see Bouchard 2008 for a detailed discussion of this particular case).

As we shall soon see in the case of symbioses, the focus on genetic individuality can only take us so far. Since symbiosis research deals with communities of intertwined genomes ‘travelling’ through selective regimes at different temporal and spatial scales, a genetic notion of individuality may not be as helpful as it is in botany. Before examining this specific problem, let us adopt a provisional definition of biological individuality.

One way of avoiding a strictly genetic account of biological individuality while providing an account tractable in evolutionary terms has been suggested by Wilson DS and Sober (1989). Arguing for a richer multi-level selection approach to evolution, they come up with an intuitive definition of what it means to be a biological individual (my paraphrase).

A biological individual is to be a functionally integrated entity whose integration is linked to the common fate of the system when faced to selective pressures of the environment.

Wilson DS and Sober argue that, in the case of some social insects (as well in the case of other groups of same species organism), superorganisms (or emergent biological individuals of sort emerge; see Hamilton, Smith and Haber 2009 and Bouchard *forthcoming* for a discussion of their ideas as it relate to eusocial insects). What I wish to focus on is the notion of common fate. What does it mean to have a common fate when faced to selective pressures of the environment? Elsewhere (Bouchard and Rosenberg 2004) I argued that fitness applies to whole individuals (and not individual traits, or individual alleles) and in other texts (Bouchard 2008) I extended the notion to lineages. The intuition driving the application of common fate in cases of symbiosis is the same. If fitness is in part survival, than whatever system that falls as one is one. Emergent fitness becomes a tracker for biological individuality, which implies that evolution and biological individuality are necessarily linked. Much more deserves to be said on the issue of biological individuality (and we will come back on these themes later) but this brief discussion suffices to show that inclusive notions of individuality are necessary to account for non-standard individuals. As we shall see, defining a biological individual in terms of what functions and perishes as wholes in the face of selective pressures allows us to consider the biological individuality of ecological communities (for our purposes here symbiotic communities) in a novel and fruitful fashion.

Symbiosis: E pluribus unum

As Sapp (1994) has convincingly shown, the phenomenon of symbiosis has been unfairly downplayed through the development of biology in the contemporary era. It is therefore not that surprising that few philosophers of biology have looked seriously at the phenomenon (notable exceptions include Sterelny 2004 and O'Malley and Dupré 2007 from which many elements of this argument are inspired). Based on the work of symbiosis researchers (e.g. Saffo 2002, Paracer and Ahmadjian 2000) we can provisionally categorize definitions of symbiosis in two classes.

1- Associations of individuals of different species in which both partners derive a benefit within the context of a given environment.

2- Associations of individuals of different species that interact in a persistent fashion even if one of the partners derives no apparent benefit from it (commensalism) or is demonstrably harmed by the interaction (parasitism).

The former definition basically reduces symbioses to cases of mutualisms where both 'partners' derive a benefit from the interaction. But as most biologists recognize, this definition is much too restrictive. First, it is often difficult to establish the fitness 'costs' and 'benefits' of the interaction, and a fortiori to establish whether both partners get something from the interaction. Second, the fitness 'costs' and 'benefits' are almost always of completely different nature for both partners. How does one compare or weigh energy transfer with physical protection? For symbioses we are often trying to compare what seems incomparable. Third, many symbioses start out being parasitic and evolve into commensalist or mutualist interactions. Some symbioses revert from a mutualistic state to a parasitic one. The fluidity in the type of interaction is largely a factor of the ecological context (more on this important point later in this paper).

These problems push most symbiosis researchers to adopt the latter definition that is seen as more inclusive. The spectrum of interactions (parasitism, commensalism, mutualism) and the dynamic nature of many community interactions along this spectrum in ecological time are taken as a given. In symbiosis research, what deserves notice is not the mutualism itself but the persistence of the interaction that the mutualism maintains. Not surprisingly, the problem with this more inclusive definition of symbiosis is that it may be too inclusive. But as will become clear, the 'perils' of inclusiveness seem less problematic than the appeal of parochialism.

For all of these reasons, we will adopt the broader definition of symbiosis and see how it helps us better understand biological individuality and LFT. To do so, it is helpful to examine a specific case of symbiosis.

We will focus on the oft-referenced symbiotic association between squid and bacteria. The Hawaiian Bobtail squid (*Euprymna scolopes*) possesses light organs (called photophores) that contain about 10^9 bacteria (*Vibrio fischeri,* related to *V. cholera*). *V. fischeri* form a symbiosis with the Bobtail squid (McFall-Ngai 1994): the squid provides nutrients to the bacteria, while the bacteria allow for bioluminescence in the squid's mantle. The bioluminescence occurs through quorum sensing on the part of *V. fischeri*: when the *V. fischeri* are in high enough densities (when 'quorum' is attained) the chemical cascade leading to bioluminescence is initiated. These threshold densities are possible outside of the interactions with other organisms (the squid in this case) but in fact they do not obtain in 'free living' bacteria because these densities are not advantageous in the marine habitat[1]. These densities are easily achieved within the squid's mantle. So, to adopt the usual teleological adaptationist framing of the issue, what purpose does this bioluminescence serve? It is believed that this bioluminescence allows the squid to avoid its predators. The squid's potential predators hunt by identifying the shadows of the preys above them. The squid forages at dusk, and the light emitted by the bacteria creates countershading, making it invisible to predators when they are located underneath the squid.

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[1] An anonymous reviewer of this paper suggested that since these bacteria are enteric that get defecated out of most hosts and re-eaten (or in the case of the squid may survive the host's death) being bioluminescent might give a slight advantage to a glowing population on a dead squid or a clump of feces to be quickly re-ingested. Although this is a plausible reading of the situation, I think there are good reasons to doubt that they achieve the right density in these "non-squid-mantle" contexts (i.e. I doubt that the quorum kicks in these contexts since the high enough densities are probably not attained).

It is a horizontally transmitted symbiosis involving a bacterial symbiont colonizing extracellular apical surfaces of epithelial cells at each generation (the squid 'let's itself be' colonized after birth and maintains the same bacterial colony throughout its lifecycle even though it flushes out about 80% of the bacteria everyday, most likely to reduce the possibility that the symbiont would evolve a pathogenic response as many other *Vibrio* have done). The colonization triggers deep developmental change for the squid. It develops a lens type surface that allows it to direct the light generated by the bacteria. The developmental changes are triggered by the presence of these specific bacteria. Symbiosis of this sort highlights the interplay between genetic and non-genetic means of inheritance. The developmental pathways are genetically coded in the genome of the host, and triggered by a specific phenotype of its symbiont. The symbionts' phenotype is also genetically determined. So one should not downplay how much genetic inheritance affects how symbionts interact through generations. But since the symbionts are in interactions only in specific ecological circumstances, and since those ecological circumstances are 'passed' on as well from one generation to the next (by merely staying in the same environment, the squid pass on the 'possibility' of being colonized), one also gets the type of non-genetic inheritance that many biologists and philosophers have tried to make sense of (see Sterelny 2004 and Mameli 2004 for a better appreciation of issues related to non-genetic inheritance and development).

The squid may survive in an environment without *Vibrio fischeri* and if it is not colonized by it, it will not develop the mantle it usually develops when in contact to these bacteria (i.e. the development needs to be triggered at each generation). But the squids' fitness would be greatly reduced because of the higher success of predation on them. If however the squids remain in the same environments, environments with *V. fischeri*, they will develop the type of mantle that takes advantage of the bioluminescence.

In this case, as well as most case of symbiosis, how are we to analyze the new trait? How to distinguish between non-genetic traits and environmentally triggered traits? In the case of this symbiosis it is both. One could argue that it belongs solely to the bacteria (and their genes), but since the trait plays little purpose in non-symbiotic bacteria (or so it assumed right now) and that we don't observe it frequently in non-symbiotic bacteria it is reasonable to assume that it is not a significantly fitness enhancing adaptation for the *V. fischeri* colony. In this case, bioluminescence 'belongs' to the ecological interaction between two species and not to one species alone. To put it more starkly, I am claiming that the bioluminescence is community-level trait that is passed on by non-genetic and genetic means. An adaptation is linked to the fitness of a system. 'Silencing' an adaptation should therefore reduce the fitness of a system. If the bacteria weren't bioluminescent (which is actually the case for most of them for most of their life history), their fitness does not suffer too much (again, since the quorum attaining conditions are so peculiar, it is plausible to assume that the bacteria's survival doesn't depend on the bioluminescence). The squid itself is not bioluminescent or to be more precise, the squid's genome doesn't code for bioluminescence, but for traits that may take advantage of another species' bioluminescence. So if the bacteria alone doesn't often glow, and the squid alone cannot, who or what is bioluminescent and what benefits by being bioluminescent? Let's assume for a moment that we have an emergent trait (i.e. not reducible to single genome), what is the bearer of that trait? What is the biological individual bearing that trait if not the system comprising both squid and bacteria?

Cases such as the Bobtail squid are numerous in the natural world and test our best intuitions about biological individuality. Symbiotic associations obviously need an inclusive notion of biological individuality. As mentioned earlier, there is a large debate about what constitutes a biological individual (beyond our intuitions about organisms). The notion of biological individuality that was devised to account for eusocial insects (Wilson and Sober 1989) seems useful in many cases of symbiosis and was earlier paraphrased as such: *A biological individual is a functionally integrated entity whose integration is linked to the common fate of the system when faced to selective pressures of the environment.*

Earlier, I pointed to the idea that common fate and fitness are related (in the stark light of natural selection, only things that can be said to have a fitness, can be said to exist). Fitness is usually defined as a composite of survival and reproduction. For most animals, biologists focus on the reproduction, the survival being merely instrumental to reaching the reproduction events. Elsewhere (Bouchard 2008) I argued that in many biological cases (specifically many species of clonal plants), the survival component of fitness is all there is since the only proxy for reproductive success is actually merely vegetative growth. Thinking more broadly, if we are to consider that communities (multi-species individuals) can and do evolve, persistence will be a better tracker for their success than their (absent) reproductive success. There is change within communities that increases the communities' ability to persist, but this change does not necessarily translate in differential reproductive success. I argue (Bouchard 2004, 2008 and forthcoming) that fitness is best understood as differential persistence of lineages.

This type of approach applies in the cases of symbiosis as well, since these communities as wholes may not reproduce but may differentially persist, i.e. communities have differential persistence potentials that act as markers of common fate and therefore biological individuality. So, using survival potentials as markers of individuality, let us wonder, how many individuals are there in the case of the bobtail squid. Let's consider a few possible answers.

- Considering that the squid can survive without the bacteria, do we have 1 squid + a multitude (10^9) of *V. fischeri* = a billion and one individuals?
- Considering that the bioluminescence, because of the quorum sensing, is a group property of the bacteria, do we have 1 squid + 1 Vibrio superorganism = two individuals ?
- Considering that the symbiotic community has its own additional survival potential (i.e. its own emergent common fate) should we say that we have 1 squid + 1 billion Vibrio + 1 Vibrio superorganism + an emergent Squid/colony superorganism? = a billion and three individuals
- Etc.

These speculations may seem purely academic (in a pejorative sense…) but this question has some scientific urgency: if we can't agree on the boundaries and number of individuals, we cannot obtain meaningful notions of populations. Without clear and non-controversial population structures, assessing the evolution of these systems is difficult at best. Thinking solely in genetic terms (genes of bacteria and genes of bobtail squids) may seem more helpful but the genes alone don't track the symbiosis we wish to account for in the first place. As is the case in many symbioses, only the ecological context tells us whether the genotype leads to parasitic phenotypes or mutualistic phenotypes. Taking any given volume of sea water and identifying the allelic frequencies of *V. fischeri* and squid cannot lead to any conclusive claims about whether there is any bioluminescent individual. For that type of claim we would need to know where exactly are the bacteria (in the squid's mantle or outside, and at what point in the developmental cycle did the colonization occur) in what density in which organ and so on. Moreover, alleles alone will not track whether adaptations obtain or not, since the alleles of one of the symbionts will not code for the complete phenotype of the adaptation, in this case the bioluminescence, since it only appears within the squid's mantle when a certain density of bacteria is attained. It is only through specific functional integration (in an ecological context) that the adaptation emerges. Finally, alleles alone will not tell us, what are the entities involved, what are the individuals. As it has been known for a long time, carving out the number of biological individuals is very complicated in cases of symbioses. The problem will affect how we think of populations of these individuals as well and therefore how to think about the evolution of these systems.

In the case of the Bobtail squid/ *V. fischeri*, traits are acquired in ways not strictly reducible to genotypes: individuals (whatever they are) are acquiring survival increasing traits from their environment. I argue that this is the type of LFT that was suggested earlier. But what is interesting is not the LFT alone, but what it may help us identify. As we have seen with the difficulty of figuring the number of biological individuals (because of the multiple common fates and functional organization involved within a single community), it may be the case that LFT is the mark of genuine emergent individuals i.e. that LFT may result in emergent biological individuals.

Sapp (in discussion) rightly points out that if we are to take seriously the idea that an emergent individual appears, then we may not in fact have LFT since it is not the case of an individual acquiring or co-opting another individual as a functional trait but rather the temporary coalescence of two individuals in the first place. He is making a correct point. LFT is not necessarily about stable traits, but about new (often relatively ephemeral) individuals. Most nascent cases of mutualism begin as genuine LFT before the species involved evolve the right type of functional assemblage that warrants considering the community as a genuine emergent functional evolutionary individual. Functional integration is a question of degree (see McShea and Venit 2002 for a characterization of this question in the cases of coloniality). Let us reconstruct a theoretical history of some emergent individual. Individual 1 of species A is next to Individual 2 of species B. By chance, 2 is not detrimental to 1. In fact in some ecological contexts 2 is beneficial to 1. Here we have something like LFT, but we probably do not have common fates (I have said nothing of the fate of 2 in this interaction). With enough generational change, 1 and 2 may co-evolve to take better advantage of the community interaction. What began as LFT may evolve into a tightly integrated functional system with a common fate. What began as LFT may evolve into an emergent individual. This characterization is functional, focusing on how in the right ecological context, organisms function together, irrespective of how this functioning may or may not be passed on genetically. This being said, many of the structures involved will probably be genetically-coded and more importantly will transform the symbionts' genomes. Many obligate symbioses display significant gene attrition in the symbionts' genomes. Because the proximity between the symbionts and the increased possibility for LGT, some of the original genes in each symbiont's genome may become redundant and be lost through the generations, thereby 'cementing' the symbiosis by making it increasingly difficult to disentangle from the symbiotic.

It should be noted that pointing to the common fate of the community does not erase the individual fates of its constituting components. A squid has its own individual fate, and the colony has its own individual fate (and the bacteria composing it as well). When the squid dies, the bacterial colony goes on (maintaining its own fate). The claim is rather that in specific interactions an additional individual with its own fate appears (the symbiotic whole), not negating its parts' fate (i.e. the symbionts' fates) but adding another fate to the mix (by analogy, a termite colony may 'die' with or without all of its constituting termites dying as well: these are individuals at different levels, subject to different selective regimes). This type of multi-level selection has been described before (e.g. Brandon 1990), but it usually focuses on a single species' levels of organization (alleles vs. alleles, organisms vs. organisms, groups vs groups, but all of the same species). By decoupling fitness from reproductive success one can focus on multi-species assemblages and how their persistence (their fate) fluctuates in various selective environments. This means however that at least in the case of these emergent symbiotic individual, one exists only if one can be the subject of natural selection. If common fate is the foundation of individuality and if this common fate is ultimately the fitness of that individual, to be biological individual means to be an evolutionary individual. This is not intended as a strong metaphysical claim but a descriptive claim concerning what types of entities inhabit the world studied by biologists.

Minimizing the significance of genetic data as a guide to biological individuality is not without costs. If we focus on function instead of genetic identity, do we lose the ability to talk about adaptation? After all, adaptation is related to fitness, and fitness is usually defined in terms of differential reproductive terms (usually tracked indirectly by changes in allelic frequencies). To say that bioluminescence is 'good for' the squid (or the emergent individuals it is a part of) means that it's adaptive, not necessarily that it is the result of adaptation by natural selection. If we wish to understand these emergent traits as adaptations while minimizing the reliance of genetic identity, we need other ways to define and measure fitness. As I have suggested earlier, I do just that by defining fitness in terms of differential persistence of lineages. Differential persistence remains a relative notion. We are comparing the relative fitness of let's say two lineages in terms of their capacity to still be there in x number of years. For many 'simple' biological systems (most mammals for example) this may translate into differential reproductive success, but this will always be so for all species. I argued that we need to understand evolution by natural selection in more abstract terms to account for somewhat problematic cases of biological evolution such as symbioses.

As I write elsewhere (Bouchard 2008) some biological systems (e.g. certain clonal organisms, certain colonial organisms, symbiotic communities and ecosystems) appear to be evolving; by that I mean they display adaptive change as a response to the selective pressures from their environments and these changes accumulate and are fined tuned over time which results in an increase the system's capacity to survive. This adaptive change occurs in response to selection on the parts of the system (often these parts are whole organisms, or even communities; see Godfrey-Smith 2009 for a related account). Change among parts of a system, I argue, reflects the fundamental structure of evolutionary processes in general and is more in line witht the type of adaptive response observed in cases of symbiosis. Symbiotic communities' evolution is not adequately captured by a concept of evolutionary fitness that is defined solely in terms of differential reproductive success; moreover allelic frequencies will not track all adaptations by natural selection. These are strong claims, but thinking in terms of parts of a system is not only plausible but necessary to fully account for at least some adaptive traits emerging in symbiotic interactions.

Adaptationism: when just-so stories are actually the best ones to tell

Various evolutionary research projects have heuristics grounded in the idea that one should look for (at the onset of the inquiry) adaptations in nature. Gould and Lewontin 1979 offered a famous critique of such heuristics and labeled such approaches pan-adaptationist thinking. For brevity's sake, I will use the terms adaptationist thinking (contra Gould and Lewontin, I do so non pejoratively) as any research project that focuses on identifying adaptations in biological systems. Adaptationist thinking (of some kind) is essential in symbiosis research and is implicit in many notions of biological individuality (after all, functional integration and common fate are linked to the adapted nature of individuals). However, in the first section I raised the difficulty of focusing exclusively on adaptive traits especially in cases of symbiosis where a trait or a type of interactions may be beneficial in certain ecological contexts while deeply maladaptive in others. This will also weaken the appeal of the original definition of LFT offered in the introduction. There is a way to restrict the types of scenarios that LFT will focus on (italics correspond to the amendment to the original definition).

Lateral Function Transfer (or Horizontal Adaptation Transfer) corresponds to any adaptive trait acquired during the ontogeny of the individual by other means than the genotype, *that in part explains the increased persistence of the individual.*

In departure from LGT which has inspired LFT, there is no explicit mention that what is transferred (some trait in the case of LFT) comes from an organism (or biotic material for that matter). LFT makes no assumption about the origin or nature of the trait acquired laterally. In many cases of symbiosis, the laterally acquired trait is organic (the trait is often a distinct organism). But in other cases (not discussed in details here), an organism may be using abiotic structures as organs (e.g. A termite colony using its mound for gas exchanges, see Turner 2000, 2004 and Bouchard 2004 and forthcoming for discussion). It is not the origin that is relevant but whether the trait *increases* the capacity for persistence of the system. The mound is maintained but not re-created through the generations. Maintaining mutualistic relationships may have a similar structure (for after all, a symbiont doesn't know nor care whether the stuff it interacts with is biotic or not). If generations of organisms use some external structure (be it another organism or a non-living structure) that increases its potential to persist, then there is an indication that some trait function is accomplished by something other than the initial organism.

For many readers, this characterization of LFT and how it is applied to symbiosis will smack of pan-adaptationism. A few points need to be made regarding this adaptationism and why it's not necessarily a bad thing. As I have pointed out earlier, Gould and Lewontin offered a famous rebuttal of pan-adaptationist thinking (Gould and Lewontin 1979) [2]. Aside from the detailed criticism concerning how traits are identified and understood, their argument offered an important reminder of the complexity and integration of biological individuals. An important part of their argument focused on the non-modularity of biological organisms, or rather, about the arbitrary nature of our carving out biological individuals into neat modules that could be said to constitute adaptations. They argue that it is wrong to focus on adaptations since such an approach mistakenly assumes some sort of modularity of organisms into isolated modules -for the adaptations to evolve relatively independently one from the other they need to be constituted of isolated modules. Organisms, they argue, are undividable wholes. But if we shift our theoretical focus away from organisms onto individuals in general we may see that the holistic characterization of nature does not always apply as readily to other types of biological organization: it may be time to reassess the degree to which biological *individuals* (contra Gould and Lewontin's organisms) are as integrated as the holistic Baupläne organisms they describe.

As we have pointed earlier, for many biologists (not concerned with microbiology) and many philosophers the term "individual" has been treated as a synonym for "organism" but this is seen more and more as a simplistic manner of defining the issue. The fact that mitochondria and chloroplasts are the result of the symbiotic associations means that most organisms we are usually interested in were at some point collections of organisms from different species. If at least some individuals are composed of many organisms, couldn't we see each organism in these relationships as a component, and therefore an 'objectively' modular component of a larger whole? Couldn't we conceive of these modules being selected relatively independently?[3] If this is the case, large parts of Gould and Lewontin's argument lose their pertinence. They argued that adaptationist heuristics were misguided in part because of, in their view, the non-modularity of organisms. They argued that to have widespread adaptations one would need independent modules in order for selection to act on individual traits without disrupting the whole organism. By shifting our understanding from organisms to individuals, and that by recognizing that some of these individuals are collections of organisms, then single organisms are in a real sense modules on which selection can act without necessarily changing anything about the other components (other organisms in this case) of the overall system (the symbiotic community). An indication of this process is the asymmetry in how genomes respond to continued symbiotic interactions. One symbiont's genome may lose redundant genes (when the function is realized

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[2] I will not offer a detailed analysis of Gould and Lewontin's argument and its consequences, but I will question some of the heuristic prescriptions that arise from their argument. For a detailed analysis of the implications of their argument see Lewens 2009.

[3] Sterelny 2004 shows how the issues of modularity and evolvability play out in some cases of symbiosis.

by the other symbiont) without any changes occurring in the partner's genome. Symbiosis being a question of degree, modules are relatively independent from another and can therefore vary in ways that may not always provoke corresponding changes in the other partners involved. Ironically however, LFT does show that Gould and Lewontin were right about the pervasiveness of 'good' traits (what was later called exaptation) that may not have a *traditional* story of evolution by natural selection (inter-generational response to selective pressures via differential reproductive success). My take-home message however is not that evolution by natural selection is not sufficient to explain 'good' traits but rather that we need a better characterization of evolutionary processes and the types of entities that are involved in evolution.

As I have tried to show, natural selection often leads to the evolution of complex individuals beyond biological organisms. Those individuals, groups, species, community, ecosystem, etc, do not always display the holistic nature that, according to Gould and Lewontin, makes it impossible and wrongheaded to try to carve up nature in neat little modules.

If, as I and others have argued, some symbiotic communities are emergent individuals, we will need to adopt an adaptationist heuristic (at least sometimes) to understand strange features such as bioluminescence. And contrary to Gould and Lewontin's argument, it will be 'easy' in such cases to talk about the modules and how they contribute to the whole's persistence. The adaptation talk is not only possible -thanks to the modularity of these symbiotic associations- but it is the most reasonable way to approach the continuing association between members of different species. To what entity is this trait good for? How is it related to the 'success' of the individual.

Gould and Lewontin paint adaptationist thinking as not giving any power to ecological, developmental and other types of constraints that shape the form of traits. They show how the understanding of such constraints is necessary to understand specific extant traits. Their challenge was and is still welcomed and has provided impetus for many fecund research projects (e.g. evo-devo). I would argue that the pendulum now needs to go back towards adaptationist projects, mainly because many biological systems are in fact modular in ways that Gould and Lewontin rejected.

For those acquainted with symbiosis research this result is somewhat ironic: many scientists investigating symbiosis were doing so in an anti-darwinian fashion. Spencerian excesses and neo-darwinians's focus on competition conflicted with the world view of some scientists for whom cooperation was a more important natural process than competition (see Sapp 1994 for discussion). But as we have seen in the last thirty years the dichotomy of competition-cooperation is an artificial one (as most dichotomies...): natural selection can favor cooperation regimes (another hint that Woese' view of the natural world was a bit too neat). In many cases, this cooperation may translate into the specialization of the partners to the point that the symbiosis generates novel traits. I have argued that such symbiotic communities are in fact individuals. But caution is necessary: how are we to understand the traits of such individuals without reverting to some sort of overly enthusiastic adaptationism? We need to focus on traits that affect persistence (i.e. fitness). If there is a strong correlation between the introduction of trait and an increase in the capacity of an entity to persist, the trait is "good for" the bearer and may be selected upon.

Gould and Lewontin wanted to show that both for metaphysical reasons and epistemological reasons, adaptationism was a misguided programme. A charitable interpretation of their salvo is that they are merely arguing for pluralism (which I argue is necessary for evolutionary biology to flourish), but in fact they are arguing for a stronger claim. They are detailing the intrinsic inadequacy of the adaptationist research programme because it is based on a modular view of nature that does not correspond to how the world actually is. I have argued that in cases such as symbioses, it may be relatively easy to carve up in modules, because they are whole distinct organisms with somewhat distinct ontologies. Adaptations will sometimes be the result of the interaction of multiple modules (the bioluminescence here is the result of the interaction of a vibrio module and the mantle module), while in other symbioses the adaptation will be constituted of whole organism qua module (this is probably the case of many bacteria involved in their host's digestive process).Carving up of traits is not always a flight of fancy. But to see this we need to contemplate the possibility that some individuals are much stranger than the ones we are used to. LFT leads to a much broader bestiary with transient overlapping individuals.

Of course one could deny that we have emergent individuals and emergent adaptations. Rejecting these emergent symbiotic individuals would be as arbitrary and ill advised as rejecting the endosymbiotic origin of prokaryotes... But to fully appreciate this, when trying to identify individuals in the case of symbioses, we need to accept that the best heuristic tool we have won't be exclusively genomic, but it can be adaptationist.

What is needed however is a broader understanding of adaptation. Adaptation is defined by Brandon (1990 pp.41 reprising insights from Williams, Lewontin and others) as the product of the process of evolution by natural selection. I have argued for a broader understanding of the process to include responses to selective pressures that do not necessarily translate into changes in allelic frequencies. There can be differential success of parts in given environmental contexts and these successful parts may be passed on without changing the number in offspring of organism. Moreover, some biological systems (such as communities) may not reproduce differentially but may be replaced by similar individuals within which there may be differential reproduction of its parts (the number of Vibrio fischeri for example). Symbiosis tells us that some traits increase the persistence of a system in a way not necessarily directly related to reproductive success of the emergent individual. What is meaningful is how certain types of response to pressures of the environment increase the ability to persist for these systems. Emergent Individuals acquire traits in various ways (one of them is via LFT), and the question is whether those traits increase the potential for survival of said systems.

Conclusion: Novus ordo seclurum

What does this mean for our organization of the tree of life? Thanks in large part to WOL proponents, we already know that the microbial world is "messy". But do they appreciate how truly “messy” it is? The problem is much worse than most WOL proponents believe insofar as adaptations are passed on without necessarily changing the molecular hereditary material above and beyond the microbial world. Since the tools used by WOL proponents are strictly based on the molecular data (a caricature of course but a somewhat accurate one), they may (also) be blind to the evolution of emergent evolutionary individuals and the lineages they create.

One emerging compromise in the TOL vs. WOL debate is that for large segments of the evolutionary history of large chunks of life (mostly Metazoans), a tree of life structure may capture the branching patterns of lineages subjected to diversifying forces of drift and natural selection. For the rest of the natural history of life a web of life structure may be more appropriate to account for how genes are passed on between branches, between lineages (still a Darwinian story but a much more complicated one). What both fail to appreciate (in their own way) is how both these accounts leave out many evolutionary individuals. At the intersection of the branches are other evolutionary individuals that come and go and we can see this by looking for traits that change the persistence of systems. To put it starkly the TOL is too parochial by focusing on strict Weismannian continuity, but the WOL is not inclusive enough because it focuses strictly on genes and their bearers.

As symbiosis dramatically shows us, new individuals appear (and disappear) all the time, which means new lineages (in a broad sense) appear all the time. It also means that, because of the ephemeral nature of many of these biological individuals, many if not most of these lineages disappear before leading to nice structured evolutionary histories that may translate in genetic changes.

We may be tempted to say that because they are so ephemeral we do not have to care too much about them (in the same way that many biologist which to dismiss endosymbiosis and LGT because it assumed to be rare) but keep in mind that everything in evolutionary biology is relative. There is no absolute short or long term when considering how nature operates. To speak of some individuals as ephemeral or long-lived is of course only a matter of point of view. The fact that we may wish to dismiss some emergent individuals as being too transient merely means that their life-cycle does not correspond to temporal scales that usually we find interesting. If they do sometimes respond ‘positively’ to changes in their environment in ways that increase their relative success, they evolve. And that’s all that should matter.

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