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Causal processes, fitness and the differential persistence of lineages

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ABSTRACT: *Ecological fitness has been suggested to provide a unifying definition of fitness (Bouchard and Rosenberg 2004). Fitness is to be understood in terms of how individual organisms interact with their selective environment and how organisms solve design problems posed by the environment. However, a metric for this notion of fitness was in most cases unavailable except by proxy with differential reproductive success. In this paper, I show how differential persistence of lineages can be used as a way to assess ecological fitness sans reproductive success. This view is inspired by a better understanding of the evolution of some clonal plants, colonial organisms and ecosystems. I will argue that differential persistence shows the limitation of a purely ensemblist non-causal understanding of natural selection. I will show that causal explanations are necessary to understand the evolution by natural selection of these biological systems.*

1. Introduction

We may have to ‘tweak’ evolutionary theory for both philosophical and scientific reasons. Why? Because current accounts of fitness do not seem to adequately describe the evolution of some biological systems. In the case of some clonal species, social insects, and ecosystems, differential reproductive success cannot be successfully applied in trying to explain the adaptations we observe. Differential persistence will be presented as an alternative account of fitness to account for these adaptations. In this format, the argument will be unavoidably programmatic, but the actual existence of the cases presented in this paper forces us to consider the urgency of revising our accounts of fitness and natural selection.

Ecological fitness

There have been recent philosophical attempts to make evolutionary success solely a matter of changes in population focusing exclusively on the changes in reproductive success. In recent arguments (Matthen and Ariew 2002; Walsh, Ariew, and Lewens 2002) one gets accounts of natural selection and fitness in purely populational terms, the idea being that natural selection is merely the statistical effect of underlying non-evolutionary processes. In this story, natural selection loses any causal efficacy. Although a purely central tendencies approach may be intuitive to some, it cannot give a full picture of evolutionary processes and more importantly for many philosophers of science, it puts biology in a strange place for it would mean that natural selection merely describes past population changes but doesn't truly explain anything.

In recent articles, (Bouchard and Rosenberg 2004; Rosenberg and Bouchard 2005; Bouchard 2006) the theoretical difficulties and the diminishing returns such views offer are detailed. Contra the populational account, “ecological fitness” is put forth, a notion of fitness that in some sense puts the explanatory burden on the qualitative features of organisms, putting causation in the center of the evolutionary story, instead of the resulting demographic changes. We get something like this

> *a is fitter than b in E = a's traits result in its solving the design-problems set by E more fully than b's traits.*

This formula (or any of its terminological equivalents) provides a definition of what some label "ecological fitness".

Fitness as design-problem solution is however famously unattractive to philosophers and biologists (Lewontin 1978, 257-265). The problems vexing this definition include at least the following ones: a) it is not obvious how to individuate and count distinct design problems; b) nor is it clear how to measure the degree to which they are solved by individual organisms; and c) aggregating solutions into a overall level of fitness is difficult in the absence of a common unit to measure ecological fitness.

I will sketch a possible way of understanding fitness that could flesh out the ecological fitness account in a way that could solve those difficulties and that makes measurement possible while not resorting exclusively to demographic changes. Ecological fitness was argued for in response to the aforementioned acausal populational accounts, but there other reasons that demand a return to the fitness of individual organisms qua individuals.

In his exhaustive survey of natural selection experiments, John Endler (Endler 1986) pointed out that many studies in evolutionary biology focus exclusively on intra-generational success and phenotypic selection. Although obviously fecundity and fertility are keystones of evolutionary explanations, survival and the means by which organisms survive are a necessary aspect of the story. Population thinking loses this essential perspective (or recasts it as 'merely' instrumental in identifying populations, or merely part of the developmental story). I will argue that not only we need to give some attention to the survival story but that in some cases it might be the only story to give.

2. When there are no populations

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. However these systems' evolution is not adequately captured by a concept of evolutionary fitness that is defined solely in terms of differential reproductive success. This difficulty has been identified for a long time.

In the preface of an oft-cited book on the evolution of clonal organisms the editors (Jackson, Buss, and Cook 1985) correctly point out that most theoretical work in evolutionary biology has focused on sexual organisms with easily recognizable boundaries. They argue that more interest should be given to clonal organisms that lack many of the usual features of organisms studied in evolutionary biology.

> *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)

I argue that for clonal systems and many other systems, the adaptive change is obtained through slow accumulation of changes among the parts of the system, not through inter-generational change. For these organisms, there is natural selection, but natural selection on parts of the organism. A description of this change has to be explicitly causal, for it relies on an engineering analysis of the structure of these systems, not fluctuation in offspring number. This will have to be so since the systems examined here do not have (or very rarely) offspring per se.

As part of a larger research project I argue that for many species, Persistence Through Time of a lineage (hereafter PTT) is the property maximized by evolution by natural selection: maximization of relative reproductive success is only one strategy for persistence of a lineage but for many asexual species (but not all) reproductive success is actually minimized if not eliminated. I will now sketch some of the impetus behind PTT.

Thankfully, existing organisms can help us redefine our theories. An organism like the quaking aspen (part of the willow family) which can both reproduce sexually and asexually becomes a fascinating test case to examine our evolutionary intuitions. The quaking aspen turns the adage 'can't see the forest for the trees' on its head. What looks to be a normal forest with multiple individual trees is actually one huge clonal tree with 'branches' that appear to be individual trees but are in fact extensions of the clone still functionally integrated as a grove. The size of the organism relative to our usual encounters with other plants boggles the mind. The largest aspen grove/clone is believed to be in Utah. Grant (1993) describes the grove he named Pando (Latin for 'I spread') as such:

> *Made up of 47,000 tree trunks, each with an ordinary tree's compliment of leaves and branches, Pando covers 106 acres and, conservatively, weighs in excess of 13 million pounds, making it 15 times heavier than the Washington fungus and nearly 3 times heavier than the largest giant sequoia* (Grant 1993, 84)

As Mitton and Grant note, some groves of the quaking aspen, *Populus tremuloides*, may reach ages in excess of 1 million years (Mitton and Grant 1996).

What is more interesting however is its reproductive cycle. As it is the case for many plants, the quaking aspen can reproduce both sexually (in the aspen's case by seeds) and asexually (by cell-division, creating runners).

The sexual reproduction aspect is not relevant for our purposes, for when the quaking aspen sexually reproduces by sending out seeds, it seems to fit the received view of evolutionary theory. In theory the aspen could evolve through differential reproductive success of these seeds but, as Mitton and Grant point out (1996, 26), the vast majority of seeds die before germination mostly because of lack of water and inadequate sunlight.

The success of the aspen depends on suckering and the different type of variation that it provides. Suckering happens during the clonal growth of the aspen. Any given stem's root system can shoot out what are called runners (or suckers) underground which will in time pierce the surface and grow as a new above-ground stem. A root may travel 100 feet before sprouting up a new stem (Grant 1993) although the particular distance (and therefore the ramet density) varies greatly depending on the particular selective environments (Olejniczak 2003; Tamm, Kull, and Sammul 2002).

The conceptual problem becomes one of individuation (and therefore this is ultimately a metaphysical question). If new stems are merely growth of older stems and if they remain structurally interdependent, should we describe what we observe as one big individual or a population of smaller individuals? Clonality or asexual reproduction is not always problem for evolutionary theory (after all, many plants use asexual reproduction for most of their life-history), the problem is understanding and explaining the nature of evolutionary change when the clones remain structurally integrated.

Following the usual nomenclature (Harper 1978), the genetic individual is referred to as a 'genet' while the apparent morphological individuals are referred to as 'ramets' (Cook 1980 for discussion). The problem is that the genet-ramet language does not really distinguish between functionally, morphologically, physiologically distinct ramets and the ramets that are connected together exchanging water and nutrients. A variety of terms has been used by botanists to describe the various ontological relationships between ramets and genets but none have really taken root. Some (Oborny and Kun 2002) refer to genets as 'splitters' when the genet fragments into individual clones and 'permanent integrator' when all the ramets remain functionally integrated via their common root system.

The permanent integrator is the genet that will interest us most in this project. By clonal growth, a grove can insure that it maximizes the utilization of a patch making any other species seedling more difficult. The quaking aspen, increases the likelihood that it will not be overtaken by other species, by growing instead of creating other groves by seedling. There is even an internal pressure to minimize the use of sexual reproduction. Not only is successful seedling rare but it is slow, whereas an integrated ramet quickly grows to adult size using resources that could have helped the autonomous seedling beat the selective pressure of ungulate browsing (i.e. moose and deer 'grazing'). Basically the grove 'does' better by growing bigger than by producing offspring. The grove, by replacing its dying parts, increases its capacity to survive.

Let me stress once again that clonality does not always lead to the integrated growth of one huge genet. The lesson here is not that asexual reproduction is never adequately accounted for by the received view. When the clones are not integrated, the received view, in terms of differential reproductive success, might be adequate. However, cases such as the aspen show that some organisms using clonal growth and remaining structurally cohesive are not really reproducing. Nonetheless, they seem to be doing something right and we need new ways to explain their evolution.

One reason to distinguish the ontology of a fragmented clone (a 'splitter' clone) from a cohesive integrated one (permanent integrator) is that they seem to have different evolutionary fates –even though they might occupy the same surface area and therefore a somewhat similar selective environment. An integrated genet can send off ramets in more competitive areas (i.e. dense vegetation): the nutrients for the 'explorer' ramets are passed on from the 'mother'. A ‘splitter’ clone is not as successful because the new seedlings have only the nutrients that each new individual ramet’s root system can access. Some have actually tested the hypothesis that the high costs of integration are offset in that way (Gough et al. 2002). An integrated clone, as an ever ‘fattening’ organism, can change its phenotype by growing more rapidly in a dense environment than a population of fragmented ramets can, and therefore the integrated clone can occupy new micro-environments with new resources. The costs and benefits of ramet integration have been studied for many years.

According to Harper (1978) the costs of ramet integration include the risk that local stress may affect the entire clone, and faster spread of disease. The benefits of integration include faster exploration of new environments, benefits to the whole clone in cases of successful exploration, and reallocation of resources.

To treat the integrated clone simply as a population of individuals is to erase the distinction between different evolutionary strategies. But to understand the difference between these evolutionary strategies, a causal explanation about individuals (not a description of population wide demographic changes) will be necessary. After all, the numbers of ramets might be exactly alike over many years, while the adaptive trajectories would diverge tremendously. In a populational approach of evolution, the change would be absent of the explanation, whereas it would be central if one focuses on the causal interactions between the organism and its environment.

How then should we describe the fitness of an integrated clone? Gil and Halverson’s focus is the *Hamamelis virginia* L. (Gill and Halverson 1984) but most of their conclusions are applicable to the case we are interested in here. They are attempting to make the case that individual branches of trees have individual fitnesses and that those fitnesses are relevant to our evolutionary explanations. Gil and Halverson identify three criteria for this to be the case (Gil and Halverson 1984, 106) a) there must be significant phenotypic variation among branches b) Differential survival or reproduction of modular parts must occur c) the traits that confer the differential fitness must be inherited.

First, notice that, in b), ‘success’ is a function of reproduction or survival. The idea that survival is sufficient will play a significant role in our subsequent argument. Second, notice that Gill and Halverson are describing branches as modular parts. Their view is very close to the one I will defend: offspring contribution is not necessary to measure evolutionary fitness since components’ fate is sufficient to measure the adaptation of a system.

It should be noted that the most crucial criterion, the inheritance criterion, is not explicitly argued for in their article. Without such a defence, their argument falls short of truly showing how the components can be selected on to get adaptations. But, as I shall argue the analogous case of the quaking aspen can show how Gil and Halverson could have described inheritance in cases of intra-generational tree evolution.

The problem with intra-generational change is that many central concepts need some adjusting. I have spoken of the accumulation of small changes, implying some sort of inheritance. Coming back to the phenotypic selection, in the case of the growth of the grove there is a kind of inheritance. A ramet (a component of the grove) will have a phenotype closer to the phenotype of its originating ramet than the phenotype of other ramets in the grove, in part because a significant aspect of the phenotype of ramets is their spatial position: a ramet’s spatial position determines which micro-environment it can explore. This spatial position is passed on reliably between ramets because of physical constraints: in the same way that the apple never falls far from the tree, a 'daughter' ramet can only grow within a certain radius from the 'mother' ramet.

A good position means that ramet A has a higher likelihood of surviving, and since the ramets that ramet A will produce can only steer away so much from the originating ramet, 'daughter' ramets will inherit a position close to 'parental' position by mere physical and developmental constraints. This idea that spatial position can sometimes be part of the phenotype and be inherited has been described in other contexts in biology (namely as ecological inheritance in niche construction, (Odling-Smee, Laland, and Feldman 2003)) and in some projects in philosophy (Mameli 2004).

Spatial position is part of the phenotype since you can select on position in the same way that you can select on height. If that position is passed on to future 'generations' –or in the case of the grove, passed on to itself- then one has a case where non-genetic phenotypic variation that natural selection can act upon, is selected for and passed on differentially to its parts.

A grove that fragments (or splits) is different from one that does not, the difference being that fragmented ramets have the potential to become individual genets with individual evolutionary fates whereas ramets in unfragmented groves are 'merely' parts of the grove, part of a single genet. Most valiant attempts to accommodate asexual reproduction or clonal growth shift the semantics of offspring to the notion of copies, which seems less loaded. But if 'copies' is an acceptable semantic shift, why not move further to include 'parts' or 'components' as well?

As we can see, for cases such as the quaking aspen, it may be more helpful to put the notion of offspring/copies aside, in favour of the idea of 'parts' of a single organism, and when examining the question of parts, the question of how they contribute to the overall persistence of the whole system will be crucial.

I have argued that one needs a persistence approach, not a reproduction approach to understand the evolution of some plants, but this way of thinking can help us better appreciate the evolution of species of social insects and symbiotic communities as well.

E.O Wilson describes the problem that colonial organisms pose:

> *At what point does a society become so well integrated that it is no longer a society? On what bases do we distinguish the extremely modified members of an invertebrate colony from the organs of a metazoan animal*? (Wilson 1974, 54)

Social insects such as ants, wasps, bees and termites, can foster what he refers to as 'social homeostasis', defined as "The maintenance of steady states at the level of the society either by control of the nest microclimate or by the regulation of the population density, behavior, and physiology of the group as a whole."(Wilson 1971, 469)

Turner (2000) writes eloquently about colonies and how they attain some very complex forms of social homeostasis. To fix the terms of discussion we will employ Turner's suggested nomenclature:

> *I shall use the term colony to describe the assemblage of individual organisms that make up a familial unit. For example, a termite colony represents the*

> *descendants of a single queen, as well as the symbionts associated with them. The nest is the structure in which a colony is housed. (...) Among termites, the nest often has associated with it ancillary structures, the most spectacular being a mound.* (Turner 2000, 180 n.2)

In the case of *Macrotermes michaelseni*, we see that a termite colony consumes oxygen and produces carbon dioxide. It is also in a symbiotic relationship with fungus that it harvests within the mound that it has built. Consuming that fungus aids its digestion of cellulose, which termites are unable to digest by themselves (it is also believed that the fungus helps in controlling the atmosphere within the mound).

In order for the colony to grow, it needs to evacuate some of the carbon dioxide and let oxygen in from the outside. Turner's suggestion is that a colony of termites creates a mound in order to control the CO_2 present for the colony. The convection produced by the pressure differential of the spire of the termite mound sucks CO_2 out and sucks oxygen in. The colony in some sense creates a lung for itself. Turner's more general point is that certain organisms (or collections of organisms) extend their physiological processes outside of their 'normal' bodily boundaries. They build external organs that allow them to interact and survive in their environment.

If, as Turner argues, some physical structures (e.g. mounds) should be understood as organs built by organisms, then we have to include abiotic structures in our definition of an evolving individual. If an evolving individual may be in part non-biological, then it is plausible that its evolution will not be fully accounted for via differential reproductive success, since the adaptive external structures that Turner describes cannot be passed on genetically and the number of these structures does not always covary with the number of the organisms building them.

In the case of superorganisms such as colonies, there is no intergenerational change to speak of (or at least no intergenerational change at the colonial level). So the question of differential reproductive success is moot (at the colonial level). But there is variation in the phenotype of the colony.

In the case of the quaking aspen, I suggested that there is variation in the phenotype of the parts of the grove, an important aspect of the phenotype of the components of the grove being their spatial location. The spatial location of individual components was then passed on non-genetically (epigenetically) to the future ramets by virtue of the fact that the future ramets are outgrowth of the preexisting ramets and therefore can only grow in proximity to the previous ramets.

In the case of the termite colony the phenotype of the superorganism is in part the shape of the termite mound, and in part the fungus it harvests as a symbiont. But this phenotype is not 'passed' on through individual termites and their genes, therefore differential reproductive success will not be the full story.

To understand the evolution of some clonal organisms, colonial organisms and symbiotic communities, fitness in terms of offspring number will not take us very far. The success of these systems is in their overall survival, not in the reproduction of some of their members. Thinking of evolution in terms of persistence instead of reproduction allows us to entertain complex cases of evolution.

For some clonal plants, social insects and ecosystems, there can still be competition between parts, but the number of these parts won't be the measure of their success. The number of ramets or the numbers of termites will not be able to tell us how we obtained increased survival for the system.

Leigh Van Valen while examining various definitions of fitness makes this rather intuitive comment:

> *It is just as good, and maybe better, for a massive coral or a tree to stay alive, occupying the same good site, as it is for it to reproduce into an uncertain world. (...) Persistence is an important component of fitness* (Van Valen 1989, 5)

Cases such the quaking aspen and termite colonies highlight how notions of individuation of organisms strain our concept of differential reproductive success and inheritance.
Implicit to my argument so far has been the idea that **differential persistence** should replace **differential reproductive success**.

We see that differential reproductive success is a weak foundation for an evolutionary account for the cases presented here. Ecological fitness mentioned earlier in this paper might be better apt to translate their evolution. But what about Lewontin's problems concerning its metric?

One way that has been suggested is of persistence through time. In some sense, persistence is seen as the one and only over arching design-problem of which each adaptation is a partial solution. Moreover we can measure time and compare expectations of persistence over various time intervals. Thoday (Thoday 1953) suggested that to be fitter is to have a higher propensity to leave even only one offspring in 10^8 years. But why should we talk about offspring at all? If we wish to examine two aspen groves, couldn't we compare their relative fitness in terms of their capacity to still be there in x number of years? Couldn't we say that if this propensity (which will fluctuate over time) is the result of environmental pressures then what we have is evolution by natural selection? Ecologists have been suggesting concepts like differential persistence for ecosystems for many years (Tansley 1935; Barbault and Blandin 1979; Blandin 1979; Blandin and Lamotte 1989). But what about applying it to the evolution of 'simpler' biological systems. I argue that persistence might be necessary to understand the evolution of some clonal species like the aspen or colonial and symbiotic communities.

3. Conclusion

There is a real biological urgency in adopting differential persistence as a definition of fitness. If we are to take cases such as the aspen seriously, purely populational accounts of natural selection and fitness will be blind to many cases of evolution by natural selection. These organisms do not evolve via changes in population but via the differential persistence of their components. This should worry population accounts advocates for it shows that in addition to other philosophical arguments against their positions, there are biological cases that do not behave in ways accommodated by their story. At least some organisms' evolution cannot be adequately understood if we focus exclusively on reproductive success and on populations. Since these organisms, according to our intuitions, are obviously doing something 'right' (i.e. they have been around for a long time thanks to changes in their phenotype following pressures from their environment) we need to see how our understanding of fitness can be modified.

One fact remains clear. When we carefully examine some cases of biological evolution, from ecosystems, to colonial organisms to some asexual organisms, we quickly realize that nature does not ‘care’ what is selected (parts or wholes) and so we might wish to replace the ‘struggle for survival’ by the ‘struggle for persistence’.

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