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EVOLUTION, FITNESS AND THE STRUGGLE FOR PERSISTENCE

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Frédéric Bouchard

Department of Philosophy
Duke University

Date:___________________________

Approved:

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Alexander Rosenberg, Supervisor

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Dissertation submitted in partial fulfillment of the requirements for the
degree of Doctor of Philosophy in the Department of Philosophy in the
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ABSTRACT

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Abstract

I provide a new definition of evolutionary fitness. In my account, fitness is based on the idea that all lineages are selected for solving the same design-problem, namely Persistence Through Time (PTT). Current ‘head-counting’ conceptions of fitness provide fine-grain microevolutionary descriptions in some cases. My analysis improves on these accounts of fitness by making it possible to integrate biological cases in which head-counts do not reflect fitness. I argue that by acknowledging these ‘exceptions’ and changing our account of fitness, a more general description of evolution can be obtained. Indeed we may secure a nomic description of evolutionary processes.

I examine biological systems (e.g. quaking aspen groves, certain colonial organisms and symbiotic communities) that appear to be evolving; they display adaptive change as a response to the selective environments and these changes accumulate and are fined tuned over time. However these systems’ evolution is not adequately captured by a concept of evolutionary fitness that is defined in terms of differential reproductive success. I argue that for these systems and many others, the adaptive change is obtained through slow accumulation of changes among the parts of the system not through inter-generational change. Moreover, I argue that this novel view can be applied to reproductive organisms as well.

I argue that Persistence Through Time of a lineage is the property maximized by evolution by natural selection: maximization of relative reproductive success is only one strategy for persistence of a lineage. It is of course an empirical fact that most biological

systems use replication as a means to persist but other systems use other strategies to persist. In order to bring both systems under the same evolutionary mechanism, we need to focus away from inter-generational adaptive change. We need to concentrate on how their strategy for survival constitutes along with reproduction, mechanisms of evolutionary change.

À Amélie, Caroline, Monique et André

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Acknowledgments

There are so many people without whom it would have been impossible to get to this point that, strangely enough, writing this section has proven to be one of the most difficult parts of my dissertation. I would like to take here the opportunity to thank some of the people who have had an especially important role to play in the last few years.

Duke's Philosophy Department as a whole has made the last five years fruitful, enjoyable, and more intellectually stimulating than I could have hoped for. In particular, I would like to thank Larry Russell for all the small and big things he does that hold this department together, David Sanford and Owen Flanagan which over sandwiches and scones respectively have given me over the years much food for philosophical thought, and Dan McShea for leading me to some of the most exciting possibilities in this project often against my own preliminary intuitions. He and other members of Duke's Biology Department have been shining examples of what inter-disciplinary research can create. Duke's Center for Philosophy of Biology via its participating students and professors has been an invaluable source of inspiration as well. I would also like to thank François Duchesneau at the Université de Montréal who correctly predicted years ago that philosophy of biology would exert an implacable appeal to my philosophical tastes, and prepared me accordingly.

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Introduction

This dissertation is about fitness and how, by focusing on survival (or as I will call it, persistence) instead of differential reproductive success, we can describe a greater proportion of natural phenomena in evolutionary terms, phenomena currently not truly accommodated by received Darwinian views. Evolutionary fitness has usually been defined in terms of offspring contribution: the more offspring one can have, the fitter that organism is. If an organism can survive and reproduce in greater numbers than its competitor, it means that it is better adapted to the environment in which it lives. As we shall soon see, the picture is more complicated than this (of course) but the general point remains clear. Replication has been at the core of our understanding of evolution by natural selection since Darwin.

But this focus on replication creates certain problems for Evolutionary Theory. First, it cannot account for all adaptations: certain systems seem to respond to pressures from their environment in a way that increases their potential to survive, but they do so without reproducing. Are we to deny that these systems are evolving? I will argue that in fact Evolutionary Theory is flexible enough to encompass these systems' evolution. In my account, reproductive success is still a powerful mechanism for evolution to occur, but it is recast, not as the goal of fitness maximizing, but as one of many strategies by which a system can better respond to pressures from its environment. Reproduction shifts from being the exclusive engine of adaptation to being just another adaptive strategy.

The natural phenomena we will be concerned with, in this dissertation, are biological in nature and I will argue that their evolution is not easily accommodated by a ‘reproductive’ view. Thus there is a certain urgency about revising our most powerful biological theory in order to be able to explain these phenomena.

There is another reason we might wish to loosen the grip of reproduction on evolutionary theory: a ‘reproductive’ view of evolution has difficulty explaining how the replicating entities came to be in the first place. When we say that evolution is contingent, we usually mean that there isn’t a unique possible outcome that can occur as a response to selective pressures: a rise in water temperature might push some aquatic species to slowly evolve surface-dwelling capabilities or it might change its internal metabolism to be able to deal with the environmental fluctuation. Natural selection does not always select for a definite type of adaptation.

But evolution, as it is usually understood, is contingent in a much more fundamental sense: the consensus is that a necessary condition for evolution to occur is differential reproductive success: better adapted organisms have more offspring surviving and reproducing then the less well adapted. But if that is the case, then evolution might not have occurred at all. If we are to follow the received view of evolution, evolution started at some point in the universe’s history when reproducing entities appeared on earth[1]. Before that ‘moment’ there were no evolutionary phenomena in the universe. That few find this problematic for current accounts of evolutionary theory is somewhat

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[1] For simplicity’s sake I assume that ‘life’ exists only on Earth, but nothing hinges on this undefended assumption for my argument.

disconcerting. *Right before* it started reproducing what sort of thing was the first reproducing entity?

When does a living entity go from having components to having descendants? How does an entity go from changing via growth to changing via descendants? Shouldn't we expect this transition to be the result of evolution?

This is intended as a rhetorical question: there is nothing especially interesting about offspring (versus components) in the eyes of natural selection (which many would concede) but more importantly, one can conceive of evolution by natural selection *sans* differential reproductive success, in a fashion that remains compatible with Darwin's theory.

By shifting the focus away from offspring numbers, one is able is to see a continuous transition between lifeless non replicating molecules and the replicating macromolecules that make up RNA and DNA, instead of an abrupt chasm between a universe before evolution appeared to a universe which is suddenly Darwinian in nature. This project will not explain the 'origin of life' –in fact I won't talk further about this subject- but it aims at providing amendments to Darwin's theory of evolution to make it compatible with a continuous progression of organization from the inorganic to the organic.

Darwin's theory of evolution was mainly an organismal view of evolution: individual organisms live and die and the differential reproductive success of these organisms and the accumulated inter-generational change lead to the complex adaptations that demand explanation in the first place[2]. Subsequently, the distinctive role of individual organisms was minimized through the Modern Synthesis with its emphasis on population genetics. Suddenly the relevant actors were not solely individual organisms but genes and populations as well. This was a major advancement, since it permitted us to explain the origin of variation and the mechanisms of inheritance that had proven to be such a problem for Darwin's original theory.

Various accounts tried to unite all evolutionary phenomena at a single level of selection. Purely organismal views *à la* Darwin have difficulties explaining individual-fitness-reducing traits (e.g. altruism). Organismal views also face difficulties with cases such as the non-standard ontology of colonial organisms.

Inspired by the explanatory success of Neodarwinism, others –Dawkins being the best known proponent- advocate a gene or macro-molecular reductionist view which hypothetically offers a unified explanatory framework where the 'fundamental' causality is all at the macro-molecular level, but it does so at the cost of dismissing apparent ecological interactions[3]. Moreover, the lack of consensus (see Stotz and Griffiths, *forthcoming*) concerning the seemingly simple question of 'what is a gene?' weakens the case of genetic reductionism.

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[2] It should be noted that, in The Descent of Man, Darwin also endorsed some form of group selection to explain complex behaviors.

[3] Such reductionism may not have to devolve into eliminativism but Dawkins 'extended phenotype' idea does seem to be a first step on the slippery slope to dismissing most ecological interactions as merely epiphenomenal. As Hull notes, quoting Dawkins (1976) (Hull 1980, 315) "Dawkins argues that from the point of view of selection [organisms, population and species] are all amorphous aggregates, as ephemeral as "clouds in the sky or dust-storms in the desert"".

This leaves what is in many respects the consensus view. A hierarchical view of evolution by natural selection is even more flexible in what it considers to be units of selection. This view, which has always been part of evolutionary theory in some vague way, became a more focused understanding of evolution when Hull (1980) developed the interactor/replicator distinction, providing a framework to describe how various levels of organization could evolve[4].

Hull reprising Dawkins definition, defines a replicator as "an entity that passes on its structure in replication" (Hull 1980, 318) and defines interactor as an entity that "directly interacts as a cohesive whole with its environment in such a way that replication is differential" (Ibid.). Putting these two things together we get the Hierarchical view's understanding of evolution by natural selection:

> Evolution by natural selection involves two steps (we will ignore development for now). One step involves the direct replication of structure, and the other involves some interaction with the environment so that replication is differential (Brandon 1990, 81)

This view allows various levels of organization to play the role of replicator and of interactor, permitting in theory to explain gene level evolution where genes may be both the replicators and the interactors, organismic level evolution where organisms are the interactors and genes the replicators, etc.

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[4] I will use 'units' and 'levels' interchangeably in this dissertation. In this, I follow Sober and Wilson's (Sober and D.S. Wilson 1994, 545) usage which is adequate for this project. Although Brandon (1990) argues that the unit question and the level question or two separate issues, the level question possibly the more important question for biology, the distinction will not be crucial for my purposes.

The hierarchical view has empirical adequacy and theoretical richness on its side, and so, it seems it behooves us to side with the angels. This being said, there are hierarchical views and there are hierarchical views. The first distinction is of course hierarchy of interactors versus hierarchy of replicators and while many support a rich hierarchy of interactors where many levels of organization can interact with the environment, few find non-genetic replicators to be more than a logical possibility and few think these non-genetic replicator could play a significant evolutionary role[5].

It is interesting to note that the open-mindedness as to what constitutes an interactor has not been paralleled as to what constitutes a replicator. Although most pay lip service to the idea that some non-genetic material could act as replicator (Hull and even Dawkins wanted to allow for that possibility –ergo the use of 'replicator' instead of 'gene'- but they remain skeptical about its actuality[6]) few believe that these non genetic replicators could be an effective source of evolution by natural selection. Even advocates of what some would call very liberal hierarchical view, do not question the genetic nature of replicators. In their review of the unit of selection debate, Sober and D.S. Wilson (1994) go to great lengths to extend the notion of interactor, without seriously reexamining the notion of replicator. And even though they allow for different kinds of replicators, the possibility is not seriously assessed.

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[5] Here I focus on genetic for simplicity. More appropriately the 'accepted' hierarchy of replicators also includes lengths of RNA and DNA, chromosomes, genome and genes.

[6] "In my definition, a replicator need only pass on its structure largely intact. Thus entities more inclusive than genomes might be able to function as replicators. As I argue later, they seldom if ever do." (Hull 1980, 319).

In some sense my project is in the spirit of some criticisms of the replicator concept (see Godfrey-Smith 2000 for discussion). Work on epigenetics, evo-devo, DST (Developmental Systems Theory) and various other projects have questioned the nature and mechanisms of heredity and as such transformed preconceptions about replicators. The problem identified by many is that although the definition of replicator can be satisfied by various entities, genes are more often than not described as being the best replicators or replicators with a 'special' causal power. But the DST proponents argue that, the dichotomy between replicators and interactors (especially if replicators are construed as genes) is arbitrary and obscures many complex mechanisms.

By transforming the concept of replicator, one changes the notion of interactor as well; since replication is at the heart of the definition of interactor, the conceptual ricochet should not surprise us. The outcome of such theoretical flexing of fundamental concepts in this project will be to show that reproductive success is not the only measure of evolutionary success. The problem with differential reproductive success is that it does not describe the evolution of many natural phenomena. Although my project does not aim at providing a detailed analysis of replicators (such analyses can be found in Godfrey-Smith 2000, Griffiths 1997 and many others), I will add a few nicks to the death by a thousand cuts of a too-strong replicator concept. I will do so by recasting the *raison d'être* of reproductive success.

In some strange way, this project is the next step that the hierarchical view should take. By allowing various levels of organization to count as interactors, the hierarchical view rightly extended the range of natural selection beyond individual organisms. The replicator concept however has remained largely intact in its genetic identity despite the aforementioned attacks of DST, evo-devo or other ‘epigenetics’ projects. My project will offer a way to recast inheritance in an evolutionist framework in a way that accommodates all biological evolution. Oyama, Griffiths and Gray point out that “DST rejects the attempt to partition causal responsibility for the formation of organisms into additive components.”(2001, 1). My project intends to make some partition: genetic processes remain relatively more significant means of inheritance but the difference between their efficacy and the efficacy of other inheritance mechanisms is a difference of degree not a difference of kind.

Whereas DST aims to abolish the distinction between replicator and interactor (e.g. Jablonka in Oyama, Griffiths and Gray 2001), I argue that revamping of replication does not dilute the content or reduce the utility of distinguishing between inheritance and interaction with the environment. All the tools are there for extending the reach of Darwin’s theory to explain the evolution of more biological processes.

This dissertation is mainly about fitness. By redefining fitness we also redefine the principle of natural selection. This redefinition will lead us to questions concerning the nature of evolutionary explanations. The ambitious nature of the project implies that the exact focus will spill over into various areas. I therefore ask for the reader’s leniency: although the argument will move from one potential conceptual quagmire to another, the provisional goal will hopefully remain clear. I wish to provide a framework where all biological evolution can actually be explained by our theory of evolution and I will argue that focusing on the capacity of a lineage to persist can achieve just this. This ‘simple’ aspiration will demand that we transform some key factors of our theories but as I will argue, the upshot will be beneficial for biological inquiry.

The first chapter of this dissertation examines some standard accounts of fitness, their strengths and limitations. I will show that the received view, a propensity view of fitness, is the least problematic conception of fitness currently available but I will also show that its sub-optimal nature, legitimizes a reconsideration of another sub-optimal possibility, ecological fitness. The problem with ecological fitness is that no measurement unit of fitness is readily available. The rest of this dissertation will aim to fill that void.

The second chapter of this project will describe cases where a focus on components instead of focus on offspring contribution offers new evolutionary explanations. The systems that I will present in this chapter all share one thing in common: selection acts on components not offspring. Those components can potentially be identified at all levels of organization. Sometimes components and offspring will overlap (offspring are components of a lineage for instance) but sometimes they do not (e.g. ramets are not really offspring of a genet). More importantly, I will argue that this selection on components leads to evolution, without explicitly referring to replicators. This is not to say that replication is not involved at all. But rather that the differential replication is not how evolution is effected in these cases. Differential reproductive success is not the sole mechanism of evolution by natural selection.

I will argue that in order to describe accurately the change that some systems undergo in response to pressures from their environment (e.g. change in growth pattern of a huge aspen grove), we need to think about how the particular features of those components (e.g. each stem may have a high tensile strength) increase the ability of those systems to persist. Time is of the essence in more ways than one.

By framing evolution in temporal terms, the hope is to provide a unifying framework for evolution, possibly a law of evolution. Succinctly but in a sophisticated manner Leigh Van Valen expresses the doubts and hopes of finding a law of evolution, in the context of his own attempt to provide one:

> It is not fashionable to speak of laws in evolutionary biology or for historical processes generally. I think this is based on both a misunderstanding of the regularity of actual processes and on an over-reaction to poorly formulated laws of earlier workers. Laws are propositions that specify sufficient conditions for a result; given the conditions, the result will occur, although some of the conditions (the bounds of the domain) may be implicit. The degree of confirmation of a laws is of course a different matter from whether a proposition is (or represents) a law in this sense. Any general statement of the nature of a causal process states a law. (Van Valen 1973, 16)

As we shall see in chapter 3, Van Valen provides a candidate for a law of evolution. What will interest us about his attempt is not so much the law itself but the extension of some of Van Valen's premises. Laws are generally understood to be universal generalizations. Van Valen ultimately advocates an energetic paradigm of evolution, according to which *all* evolution is ultimately an attempt to increase control over available energy. Although I will explain why I am, in many respects, sympathetic with Van Valen's attempt, I will ultimately reject it: energy control is not universally maximized as Van Valen claims.

Using considerations from the first three chapters, chapter 4 will try to provide a definition of fitness focusing on persistence. As we shall see, the main inspirations for this account are Thoday (1953) and Van Valen (1973): both, in their own way, have emphasized how survival should inform our understanding of evolution by natural selection. It will be argued that differential persistence is the best way to explain all previously described phenomena and possibly provide us with a useful universal characterization of evolution by natural selection. Leo Buss's (1983) description of somatic selection is another inspiration for my project: Weismannism describes how only changes in the germ line can be passed on to the next generations. But as Buss points out convincingly, the evolution of protists, fungi and plants which are in large part the result of selection on somatic changes cannot be accommodated by Weismannism and by the Modern Synthesis relying on it to be true. Buss uses this idea to justify a hierarchical view of selection richer than the Modern Synthesis. Many of the examples given by Buss literally do not reproduce. I wish to take this idea and try to extend the means of evolution of Buss' cases and extend it to all organisms. Buss is correct in explaining how, in the cases he presents, evolution can happen via selection on sub-organismal variation; I want to see whether we can recast *all* response to selection as response to selection intra-unit changes… that unit, the lineage in my argument, being most of the time much 'larger' than the organism. My main point will become much clearer as we progress of course, but for now, let me just say that in some sense organisms should be seen as parts, selection on which can lead to evolution of lineages. The advantage is that thinking in terms of parts and persistence gives us a more unified picture of evolution by natural selection. By offering such a universal characterization the hope is to provide the foundations for a law of evolution.

The status of laws in biology has been seriously examined by many philosophers of science[7] and it will *not* be our purpose here to fully argue for how the principle described in chapter 4 constitutes a 'real' law. However, this project aims at removing one of the stumbling blocks to nomic projects in biology, namely the absence of a genuinely contingent universal generalization about evolutionary phenomena. This project's main intention is that by explaining how to unify all evolutionary phenomena, one will be better equipped to pursue the nomic project in evolutionary theory.

After providing such a universal generalization, the concluding chapter will sketch possible future developments of this project beyond biological cases. By focusing on persistence instead of reproduction, the possibility to extend evolutionary explanations beyond 'strictly' biological phenomena becomes more than some buoyant evolutionist rumination.

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[7] Beatty (1997), Brandon (1990 and 1997), Mitchell (2000), Rosenberg (1984 and 1985), and Thompson (1989) among many others.

Chapter 1 Unsatisfactory Definitions of Fitness

1.0 Introduction[1]

The Modern Synthesis is less and less modern, and is not as synthetic as it once was. Although the seminal work of Wright (see Wright and Provine 1986), Fisher (1930), Dobzhansky (1937), Mayr (1942), Simpson (1944), Haldane (1932 reprinted 1990) and others still provide us with fundamental insights into evolutionary processes, what is the role of genetic mechanisms in evolution, and the source of the variation that natural selection can then act upon, we are in many respect entering a post-modern Synthesis stage[2]. The projects of evo-devo (introduced and argued for by Waddington 1953 and others) and neutralist theories have recast the relative importance of natural selection not by denying that natural selection actually occurs but rather by highlighting how other processes are involved beyond natural selection and the resulting change in gene frequencies.

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[1] Parts of this chapter are taken from work done in the context of various publications with Alex Rosenberg.

[2] The use of 'Post-modern' is intentionaly tongue-and-cheek, please do not quote out of context! Jest aside, throughout this project, I will use 'Modern Synthesis' and 'Neodarwinian paradigm' interchangibly even though such an equivocation might be unfair: there is no consensus concerning the synonymy (or not) of the two expressions but Simpson (1978) implies that there is a difference. I will leave to others this exegetical question.

One of the weaknesses of the received accounts of evolution by natural selection is its difficulties in defining fitness. The *raison d'être* of this thesis is to redefine fitness and examine the resultant consequence for evolutionary theory. Optimally, this redefinition will allow us to state a law of evolution, but minimally, we will obtain a more adequate statement of the theory of evolution by natural selection.

This chapter mainly focuses on some philosophical and conceptual shortcomings of some of the most widely accepted accounts of fitness (Chapter 2 will examine shortcomings of these accounts when faced with some actual biological cases).

Through this chapter we will highlight three points:

1) A propensity account of fitness is the most serious contender currently available.

2) Although powerful, most propensity accounts are weakened by their common reliance on offspring contribution.

3) Going back to the intuitive notion of fitness as design-problem solution (a.k.a. ecological fitness) might be necessary to provide an adequate account of evolutionary biology.

As we will see the third point is something of a Pyrrhic victory. Our current incapacity to measure ecological fitness –except by its effects on reproductive success- makes it unoperational. I will argue that the lack of an operational measure is not an unavoidable outcome for ecological accounts of fitness. We will use this last conclusion to think of possible universal design-problems later in this dissertation. If we can establish a universal currency of fitness (i.e. a property that is universally maximized) we will avoid some of the measurements difficulties that usually plague the design-problem-solution views of fitness. As Van Valen so aptly put it: “Fitness is the central concept of evolutionary biology, but it is an elusive concept. Almost everyone who looks at it seriously comes out in a different place[3]” (Van Valen 1989, 2-3).

1.1 The Problem of Defining Fitness

Darwin’s theory of evolution by natural selection is often summarized in terms first coined by Herbert Spencer as the claim that among competing organisms the fittest survive. If there is random variation among the traits of organisms, and if some variant traits fortuitously confer advantages on the organisms that bear them (i.e. enhance their fitness), then those organisms will have a tendency to live to have more offspring, which in turn will bear the advantageous traits. But Darwin’s explanation’s success turns on the meaning of its central explanatory concept, ‘fitness’.

What is fitness and how can one tell when a trait enhances fitness, or more to the point, when one organism is fitter than another? Some critics of the theory of evolution by natural selection have long claimed that by defining fitness in terms of *actual* rates of reproduction the proponents of evolutionary theory are unknowingly condemning the principle of the survival of the fittest to triviality: if one wants to define fitness in terms of actual reproductive rates, one is actually making the tautological claim that those

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[3] Note as well that my use of ‘universal currency’ comes from Van Valen (ibid).

organisms with higher rates of reproduction leave more offspring. This is obviously an empty, unfalsifiable tautology without explanatory power[4].

Evolutionary theory requires a definition of fitness that will protect it from the charges of tautology, triviality, unfalsifiability, and consequent explanatory infirmity. If no such definition is in fact forthcoming, then what is required from the theory's advocates is an alternative account of the theory's structure and content or its role in the research program of biology (see section 1.6).

1.2 Ensemble Properties and Population Biology

Since the Modern Synthesis, evolution is usually described in terms of "change in gene frequencies" and the theory of evolution by natural selection is applied to the explanation of such changes through the vehicle of population genetics. The subject matter of population genetics is evidently populations, ensembles of organisms, or genes, and not individual biological organisms, or pairs of them. This has suggested to more than one philosopher that the theory of natural selection is better understood solely as a theory about ensembles and not individuals. As Sterelny and Kitcher put this view, "…evolutionary theory, like statistical mechanics, has no use for such a fine grain of

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[4] I am using 'tautology' somewhat loosely. Some have argued that there isn't really a tautology in the first place (Sober 1993) but regardless of the exact logical status of the statement, it is obvious that actual reproductive success can only be explanatory to a very limited extent by fitness so defined.

description [as the biography of each organism]: the aim is to make clear the central tendencies in the history of evolving populations." (Sterelny and Kitcher 1988, 345)

On this view, though the word 'fitness', and the symbol '*w*' which names the property, both figure in the theory, they are to be understood as exclusively expressing probabilistic reproduction rates for populations. The theory is then treated as a set of claims about how populations' and subpopulations' sizes change over time as a function of differing reproductive rates at some initial time, holding environments constant. Since, according to that account, the theory makes no claims about the local adaptation of individual organisms to their particular environment or for that matter about the local adaptation of populations to their environment, it does not provide a local causal explanation of these changes in organism or gene frequency. Explanations for these changes are to be sought elsewhere.

A recent extension of this ensemble view was provided by Matthen and Ariew (2002). The inspiration for their project is, as the previous quote made clear, the explanation of entropy changes in statistical mechanics. Entropy is not a property of individual gas particles, but of ensembles of particles. Even when we remain ignorant about individual particles, entropy provides us information about whole ensembles[5].

Matthen and Ariew distinguish the "vernacular" concept of fitness and the "predictive" concept. "Vernacular fitness" is a matter of adaptation or design-problem

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[5] This is not to say that our predictions are function of our ignorance but rather that individual properties are in some sense irrelevant to probabilities of ensembles. Some emergent properties (e.g. entropy increase) can only be predicated of ensembles.

solution–what I call later in this chapter “ecological fitness”. On Matthen and Ariew’s view, vernacular, or ecological fitness, plays no role in the fundamental generalizations of the theory about natural selection. Indeed, it has no role in the theory at all: vernacular or ecological fitness simply drops out as a cause of evolution by natural selection.

Matthen and Ariew define predictive fitness as

> A statistical measure of evolutionary change, the *expected* rate of increase (normalized relative to others) of a gene, a trait, or an organism’s representation in future generations, or on another interpretation, its *propensity* to be represented in future generations, suitably qualified and normalized.(Matthen and Ariew 2002, 56)

This is inspired by R.A. Fisher’s characterization of fitness in his fundamental theorem[6] (Fisher 1930). But then they qualify their claim: “We do not mean to insist on the expected-value interpretation; there are many ways of defining predictive fitness within population genetics.” (Matthen and Ariew 2002, 56)[7].

Deciding which population statistic it is best to employ as a measure of fitness all too often depends on what the biologist’s data shows about the distribution of traits in successive generations. It will accordingly be no surprise–and no prediction either–if the measure which data leads us to employ then enables us to retrodict this data. The varying measures which Matthen and Ariew name “predictive fitness” are the biologists’ means

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[6] Fisher’s fundamental theorem was originally defined as ‘The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time’.

[7] Moreover, in a footnote one author, Ariew, dissents altogether, arguing that the Fisherian interpretation is “misleading as a definition of statistical fitness.”(Matthen and Ariew 2002, 74, n.30). Ariew’s discomfort is understandable: Fisherian fitness cannot deal with nonlinear population change such as frequency-dependent selection, and it makes the selective process of heterozygote superiority invisible. See Brandon 1990, 29-30 and 151-153 for fuller discussion.

of quantitatively comparing fitness differences in terms of their demographic effects, usually *after* these effects have been recorded, not before they have been realized in nature. “Predictive” fitness *per se* is rarely if ever predictive.

Matthen and Ariew argue that, unlike vernacular or ecological fitness, “predictive fitness is not a cause of selection, or of evolution for that matter.” (Matthen and Ariew 2002, 56). They are trivially correct: it cannot be a cause, for it is an effect, a demographic statistic that measures ecological fitness. They seek to deny a causal role to fitness (something that the “vernacular” or ecological concept of fitness reflects); their view is that natural selection is what they call a purely “ensemble” process. Matthen and Ariew hold that “the theory of evolution abstracts away from concrete individual events (...) in order to isolate the causal factors that make a probabilistic *difference* to evolution.” (Matthen and Ariew 2002, 62).

These probabilities at the level of ensembles or populations are not to be related to natural selection at the level of individual organisms. There is no selection at the level of individual organisms: as they candidly admit, their explanation “tells us nothing about causes of [population] growth: it is a general truth about growth regardless of how it is caused”. (Matthen and Ariew 2002, 74) Moreover, selection is not a cause of growth (or of the change in population characteristics) in this conception; “it is the mathematical aggregate of growth taking place at different rates.” (ibid)

Their explanation deprives Darwinian Theory of its explanatory role with respect to evolution altogether and they admit as much:

> The distinction between evolution (the total change in gene frequencies due to all causes), and natural selection (the portion of evolution due to

> differences in competitive advantage) is unmotivated. (Matthen and Ariew 2002, 78)
>
> Fitness and natural selection have no reality except as accumulations of more fundamental events. In our conception, it makes dubious sense to hold evolution is different from natural selection, much less that it is caused by it." (Matthen and Ariew 2002, 82)

Reversing the order of nature, they conclude, that on their conception, "Natural selection is (...) the aggregative result over time over time of differential growth rates in a population." (Matthen and Ariew 2002, 78)

Their view is unattractive for a few reasons. It argues that individual fitness is a non-starter except in a vague heuristic metaphor, merely a useful instrument that should be discarded at the first opportunity. This description draws a very narrow view of what evolutionary biology sets out to do: ecological genetics for instance tries to make out particular fitness contribution to organisms (trait q increases fitness by x, this other trait r by y, etc.) the idea being that there is a relationship between individual fitness and population fitness. Whether this relationship is additive or multiplicative (or some other function) is another issue. Suffice it to say that in a large part of evolutionary biology, the working assumption is that ensemble properties could be derived from the individual properties.

The number of offspring is a very good indicator of fitness for most organisms since a higher number of offspring yields a larger number of different alleles, a larger potential to 'survive' in a fluctuating environment, a higher potential to improve existing adaptations. If counting the number of offspring is the only way to measure fitness, we need to retain individual fitness in our explanations for it is what 'produces' subsequent population in the first place. Ensemble fitness then becomes a way of tracking average fitness values in a group of individuals.

This being said, a population approaches offers distinct explanatory benefits. Standard accounts of population genetics refer only to the success of genotypes. Expected offspring numbers might not be sufficient to fully describe an organism's fitness, especially when confronted with traits such as altruistic behavior. Discussions of altruism and kin selection build in part on Hamilton's idea of inclusive fitness (Hamilton 1964). Some population structures in some species (e.g. some colonies of social insects) 'encourage' sterility among some of its members to increase the numbers of the overall population. As Sober puts it: "According to [organismal fitness notion], a sterile organism will have 0 fitness, since its chances of reproducing are nil" (Sober 1984, 135). If the focus is shifted from the organism to its genes, and if these genes are shared by other organisms, we may get a different view of fitness. An organism might have a better chance of having its genes represented at a later generation if it foregoes its own reproductive success to help other bearers of its genes increase their own reproductive success.

Kinship is used as a tracker to 'estimate' the degree to which two organisms 'share the same genes'. In this light, an organism might actually increase its [inclusive] fitness by reducing its own reproduction or eliminating it altogether. This view demands a new way of understanding individual fitness: Hamilton suggested that inclusive fitness should be understood as the sum of the individual's fitness and the individual's effect on the fitness of other related individuals. '*r*' represents the proportion of genes that two individual organisms share (e.g. homozygotic twins would have $r = 1.0$ whereas other siblings or parents would have $r = 0.5$, and so on). The benefit to other individuals weighted by the r (the higher the relatedness, the higher the probability that a significant proportion of genes is shared between the benefactor/donor and the recipient) has to be greater than the costs to the donor. That is, it could ‘make sense’ for an organism to forego reproduction if it is to ensure that its homozygotic twin (or other close relative) has many offspring, but helping a ‘stranger’ would not increase the donor’s inclusive fitness. The net effect in terms of the donor’s genes being passed on could be greater by helping relatives reproduce than by reproducing itself. Therefore, evaluating the expected number of offspring for an individual is clearly not sufficient to determine the fitness of that given individual. The ‘gene’s eye view’ might be more useful. However, taking this ‘view’ shifts most of the explanatory burden from individuals on to populations.

Interpreting fitness exclusively as a population level property denies that the individual differences are actually fitness differences. This interpretation is viewed by some philosophers as making the concept of ecological fitness (further defined below) superfluous in evolutionary theory even though it does in fact play a role in fields such as evolutionary ecology. But as we shall see later in this dissertation, ecological fitness (or some variant of it) is necessary to make sense of evolutionary change in very small populations. Since such populations can theoretically occur for all species (at least at the origin of new species and at the moment close to its extinction), ecological species will have to be included in the theory.

1.3 Solution to a Design-Problem: ecological fitness

Suppose, following Darwin, Gould (1977), Lewontin (1978) and more recently Dennett (1995), one characterizes the relation ‘x is fitter than y’, as follows:

> x is fitter than y if and only if *x*'s traits enable it to solve the ‘design-problems’ set by the environment more fully than *y*'s traits do.

Call this concept ‘ecological fitness’. One can find an exposition of it in Endler’s (1986) examination of the idea of intra-generational success. Evolutionary ‘success’ depends in part on organisms surviving long enough to reach reproductive stages. As such, survival will have to be factored in some way to the notion of fitness. The ‘ecological’ definition is fraught with difficulties (see Lewontin 1978). What are the design-problems an organism or lineage faces? How many of them are there? Is there any way of measuring the degree to which x exceeds y in its solution of one design problem? How do we aggregate, combine and balance various solutions to design problems?

To begin with, the notion of “design problems” is vague and metaphorical. Suppose that to be fitter means that an organism finds a better ‘solution’ to a design-problem and better fills an ecological niche. How is this differential success measured in any other way than by measuring higher offspring numbers? Thus the definition may simply hide the original problem of distinguishing fitness from reproductive rates, instead of solving it.

Second, the number of design problems is equal to the number of distinct environmental features that affect survival and reproduction, and this number is probably uncountable. It is therefore no wonder that many biologists have favored defining ‘x is fitter than y’ in terms of quantitatively measurable reproductive rates. As we will see later, these difficulties do not necessarily doom the ecological fitness concept but they show that some important modifications will be necessary to make such a definition acceptable to biologists (and, for that matter, acceptable to many philosophers of biology).

1.4 The Propensity Interpretation of Fitness

Among philosophers of biology there has been a wide consensus that the solution to problem of defining ‘fitness’ is given by treating it as a probabilistic disposition. The most popular probabilistic propensity accounts of fitness have been propensity accounts in terms of offspring contribution what will be referred to here as the ‘standard’ account or ‘received view’ (note that there are other propensity accounts that aren’t ‘offspring-centric’-more on this below). As such the propensity causally intervenes in the relationship between environments and organisms, that cause it, and the actual rates of reproduction, which are its effects. Thus an organism can have a probabilistic disposition to have *n* offspring and yet “unluckily” never actually reproduce (or produce a number of offspring different from *n*).

Comparative fitness differences are dispositions supervening on the complex of relations between organisms’ and environments’ manifest properties (Rosenberg 1978), and will give rise to differential reproductive rates. Thus, definitions such as the following were advanced (Brandon 1978, Beatty and Mills 1979):

> *x* is fitter than *y* in E iff *x* has a probabilistic propensity to leave more offspring in E greater than *y*'s probabilistic propensity to leave more offspring in E.

If fitness is a probabilistic propensity, then the fitter among competing organisms will not always actually leave more offspring. The theory will have to be understood as making the claim that fitness differences result in reproductive differences not invariably but only with some probability (since the theory allows thus for drift, this qualification on its claims will be a welcomed one). However, the probability of leaving more offspring (the effect) will have to be distinct from its cause - the probabilistic propensities that constitute fitness differences. This is a problem that all probabilistic accounts have to face (not just propensities to leave more offspring). One candidate that may do the work required is the interpretation of probability as long run relative frequency. The idea here is that chances explain long run frequencies: if *x* has a probabilistic propensity to leave more offspring than *y* in every generation, then the long run relative frequency of *x*'s having more offspring than *y* in any generation is greater than *y*'s long run relative frequency to leave more offspring that x.

But there must be at least a theoretical difference between the chance and the frequency if one wishes the former to causally explain the latter. There are philosophers of science who deny that such a distinction between probabilistic propensities in general (not just biological propensities) and long run relative frequencies is possible (Earman 1985, 149).

Others have argued that, as in the case for quantum mechanics, there are such independent chancy probabilistic fitness propensities that generate the long run relative frequencies. Proponents of ‘standard’ propensities accounts in biology have envisioned two possibilities here. One is that probabilistic propensities at the levels of phenomena that constitute the biological are the result of quantum probabilities “percolating up” in Sober’s (1984) phrase; the second is that there are brute unexplainable probabilistic propensities at the level of organismal fitness-differences (Brandon and Carson 1996). Few doubt that quantum ‘percolation’ of some kind *could* have an effect at the biological level. It may well be a source of mutation (see Monod 1971,111-115, for support of this idea or Stamos 2001 for a recent defense). But the claim that it has a significant role in fitness differences is not supported by any independent evidence (see Millstein 2000 for discussion) Even if quantum effects could ‘percolate’ up, they probably would do it so infrequently that they cannot help us ground all biological propensities. The claim that there are brute probabilistic propensities at the level of organismal fitness differences is also controversial: this view largely depends on one’s acceptance of emergent autonomous propensities at the macro-level. But, no one has adduced any evidence that, for instance, the probabilistic generalizations about the behavior of animals that ethology and behavioral biology provide are irreducibly ‘chancy’.

There is however a much more serious issue facing the propensity definition of fitness: it turns out to be difficult to pin down the specific probabilistic propensity that is supposed to constitute fitness altogether. The difficulty reflects features of natural selection that must be accommodated. And it leads inexorably to the conclusion that far from providing the theoretical meaning of fitness, the probabilistic propensity "definition" is a set of an indefinitely large number of operational *measures* of fitness. The 'standard' propensity interpretation will need to be qualified.

It might have to be qualified temporally: as Thoday (1953) suggested in his analysis of the various components of fitness, it might be necessary to understand fitness as the propensity to leave descendants in 10^8 years (time frame identified by Thoday) if we want to accommodate the notion of evolutionary progress. The exact number of years is arbitrary, but it implies that the emphasis should be put on very long-term outcomes instead of on the short-term time frame (which is what most standard propensity accounts focus on). I believe that the main difficulty with such a definition is not as Brandon argues (1990, 24-25) that such an account is 'forward-looking'. Brandon argues (1990 reprising Brandon 1978) that since natural selection acts only on actual organisms at any given time in actual environments, there can't be selection for 'forward-looking' traits or persistence. We often think selection events as thin time-slices during which something horrible happens to an organism. But selection or extinction patterns are much more complex than this picture. There is no such thing as the *instant* natural selection acts on an organism and its phenotype. Natural selection is a process not an event. Therefore the idea that selection is *never* forward-looking is wrong (and to be fair Brandon admits as much). How long in the future selection can act on is still open for debate but in some sense the near future is all temporal accounts *analogous* to Thoday's accounts needs. As such, the ‘forward-looking’ accusation looses some of its bite. Brandon’s critique of the scale of Thoday temporal scale still holds however. By making fitness into a far reaching temporal property it cannot be operational. Moreover the account rejects any notion of short-term fitness which should actually be preserved in the theory (see Sober 2002). The operational difficulties of measuring most of the components of fitness that Thoday identifies are not close to being resolved by Thoday; these components are adaptation to contemporary conditions, genetic stability, genetic flexibility, phenotypic flexibility and the stability of the environment. The fact that definitions of stability and flexibility are not offered in detail further reduces the possibility of operationalizing Thoday’s account of fitness.

This being said however, Thoday’s account has the advantage of characterizing offspring number as only one of many aspects of fitness, instead of seeing offspring contribution as fitness itself, as ‘standard’ propensity accounts do. Thoday provided a probabilistic propensity account of fitness that is not a ‘standard’ propensity account per se, and as such they offer ways to avoid the tautology problem without resorting exclusively to propensities to leave certain number of offspring. As we will see later in this dissertation, Thoday’s account will strongly influence my own definition of fitness.

But any standard probabilistic propensity account also faces the problem identified above: what are the propensities grounded on? Leaving aside Thoday’s propensity account and the long-term view it provides other more urgent qualifications to the ‘standard’ propensity account will need to be offered. As Gillespie (1977) has shown, the temporal and/or spatial variance in number of offspring may have significant selective effect. To take Brandon's example (Brandon 1990, 20), if organism *a* has 2 offspring each year, and organism *b* has 1 offspring in odd numbered years and 3 in even numbered ones, then, ceteris paribus, after ten generations there will be 512 descendants of *a* and 243 descendants of *b*. The same holds if *a* and *b* are populations, and *b*'s offspring vary between 1 and 3 depending on location instead of period. The mean number of offspring is the same at every generation but the total number of offspring at the end differs greatly.

Accordingly, the "definition" needs to be changed to accommodate the effects of variance. We would get something like this 'formulation':

> x is fitter than y = probably x will have more offspring than y, *unless* their average numbers of offspring are equal and the temporal and/or spatial variance in y's offspring numbers is greater than the variance in x's, or the average numbers of x's offspring are lower than y's, but the difference in offspring variance is large enough to counterbalance y's greater number of offspring.

It is also the case that in some biologically actual circumstances –for example, in circumstances in which mean fitnesses are low– increased variance is sometimes selected for (Ekbohm, G., Fagerstrom, T., and Agren, G. 1980). As Beatty and Finsen (1987) further showed, our "definition" will also have to accommodate "skew" along with offspring numbers and variance. Skewness 'appears' when one of the 'tails' of the distribution contains more observations and the median is therefore shifted away from the normal. Our "definition" of fitness must take these conditions into account on pain of falsity. One simple way to do so is to add a ceteris paribus clause to the definition. But the question must then be raised of how many different exceptions to the original definiens need to be accommodated? If the circumstances under which greater offspring numbers do not make for greater fitness are indefinitely many, then this “definition” will be unsatisfactory.

Some proponents of the propensity definition recognize these difficulties and are prepared to accept that at most a ‘schematic’ definition can be provided. Thus Brandon writes (1990, 20):

> We can … define the adaptedness [a synonym for expected fitness] of an organism O in an environment E as follows:
> $A^* (O, E) = \Sigma P(Q_i^{OE})Q_i^{OE} - f(E, \sigma^2).$

Here Q_i^{OE} are a range of possible offspring numbers in generation *i*, $P(Q_i^{OE})$ is the probabilistic propensity to leave Q_i^{OE} in generation *i*, and most important $f(E, \sigma^2)$ is “some function of the variance in offspring numbers for a given type, σ^2, and of the pattern of variation” (idem, 20) Brandon means “some function or other, we know not what in advance of examining the case.” Moreover, we will have to add to variance other factors that determine the function, such as Beatty and Finsen's skew, or the conditions which Ekbohm, Fagerstrom, and Agren identify as making higher variance adaptive, etc. Thus, the final term in the definition will have to be expanded to $f(E, \sigma^2, \ldots)$, where the ellipses indicate the additional statistical factors which sometimes combine with or cancel the variance to determine fitness-levels.

But how many such factors are there, and when do they play a non-zero role in fitness? The answer is that the number of such factors is probably indefinitely large. The reason for this is given by the facts about natural selection as Darwin and his successors uncovered them. The fact about selection which fates our “definition” either to being forever schematic is the “arms-race” strategic character of evolutionary interaction. Since every strategy for enhancing reproductive fitness (including how many offspring to have in a given environment) calls forth a counter-strategy among competing organisms (which may undercut the initial reproductive strategy), the number of conditions covered by our ceteris paribus clause is equal to the number of strategies and counter-strategies of reproduction available in an environment. Brandon writes, “in the above definition of $A^*(O, E)$, the function $\mathrm{f}(E, \sigma^2)$ is a dummy function in the sense that the form can be specified only after the details of the selection scenario have been specified” (Brandon 1990, 20) Brandon acknowledges that the function f will differ for different O and E: f will have to be expanded to accommodate an indefinite number of further statistical terms beyond variance. Schematically, it will take the form $\mathrm{f}(\mathrm{E}, \sigma^2, \ldots)$. Again, adapting Brandon's notation, none of the members of the set which express his generic “definition” of “adaptedness” or “expected fitness,” $[\mathrm{P}(Q_i^{OE})Q_i^{OE} - \mathrm{f}_1(E, \sigma^2, \ldots), \mathrm{P}(Q_i^{OE})Q_i^{OE} - \mathrm{f}_2(E, \sigma^2, \ldots), \mathrm{P}(Q_i^{OE})\, Q_i^{OE} - \mathrm{f}_3(E, \sigma^2 \ldots), \ldots]$, is in fact a definition of either term. It is the set of operational measurements of the property of comparative fitness.

It is for reasons such as these that the standard propensity account endorses a schematic view that accommodates all the ceteris paribus clauses that could appear (whether from variance, low mean fitnesses, kin selection effects, etc.). But since the number of these clauses may be indefinite, the propensity view may not truly offer a definition of fitness.

1.5 Fitness as a Subjective Probability

One alternative not yet canvassed is that the probability in the definition of fitness be treated as a Bayesian or subjective probability instead of a probabilistic propensity. This ploy (advanced in Rosenberg 1985) will enable one to avoid many of the problems canvassed for the probabilistic propensity interpretation, but only at a cost. The benefits are evident. There are no special metaphysical problems associated with subjective probabilities like those to which ungrounded probabilistic dispositions give rise; nor would the generic nature of the probabilistic schema be problematic. It is obvious that the right, best, or most well grounded subjective probability estimate of reproductive rates will incorporate all relevant available local information about a population and its environment, and that the factors to be taken note of will differ from case to case. Indeed, the probabilistically expected reproductive rate is most naturally viewed as a measure of fitness. As such, it does not of course provide a definition of fitness. And this is its principle defect. Viewed as an account of the *operational* measurement of fitness, probabilistically expected reproductive rates are unobjectionable, indeed attractive. But viewed as part of the *conceptual* content of fitness –a relationship between organisms and environment– the approach is flawed.

On a realist interpretation of the theory of natural selection, treating fitness as a subjective probability would commit the theory to the existence of sentient creatures having cognitive states and prepared to place bets in light of them: the theory of natural selection would be in part a psychological theory about such creatures along with the processes of heritable random variation and natural selection. Such an interpretation may not trouble the working biologist, but then the whole problem of giving a definition of fitness is a problem many biologists might reasonably treat as "academic." Anyone seeking to employ the theory within a naturalistic philosophical agenda, for example to give a reductive account of cognition, must reject a subjective probability interpretation of fitness or seek an alternative to Darwinian accounts of teleology in nature and the mind.

1.6 Models, Ecological Fitness and the Problem of Evolutionary Drift

Biological problems daunt any attempt to turn a generic probabilistic schema for fitness into a complete general definition that is both applicable and adequate to the task of vindicating the truth of the theory of evolution by natural selection. These problems suggest to some philosophers that we need to rethink the cognitive status of the theory altogether.

Some (mainly Williams' 1970 argument, later reprised by Rosenberg 1983, 1985) have argued that *if* one strives for an axiomatic formalization of evolutionary theory, one will have to understand fitness as being a primitive notion: a definition of fitness is not available from within the theory itself. Only operational 'definitions' of fitness will be available. These 'definitions' are only provisional characterizations to help us guide our investigations and not definitions in the strict sense since fitness can only be characterized "by appeal to the phenomena that it is employed to account for"

(Rosenberg 1985, 141). In other words, fitness can only be characterized through its actual causal role (in analogy with the concepts of ‘force’ or ‘charge’). The problem is that biologists do not use a ‘primitive’ notion of fitness in their inquiry but a more empirical notion better reflected in semantic accounts of the theory.

Trying to address these pragmatic concerns, others have argued that the theory of natural selection should not be viewed as a body of general laws, but as the prescription for a research program. As such, its central claims need not meet standards of testability, and fitness need not be defined in terms that assure the non-triviality, testability, and direct explanatory power of the theory of natural selection. Evolutionary theory remains a scientifically respectable, but nevertheless untestable, organizing principle for biological science. On this view, in each particular selective scenario, a different specification of the schematic propensity definition figures in the antecedent of a different and highly restricted principle of natural selection that is applicable only in that scenario.

The notion that there is a very large family of principles of natural selection, each with a restricted range of application, will be attractive to those biologists uncomfortable with a single principle or law of natural selection, and to those philosophers of science who treat the theory of natural selection as a class of models. On the “semantic approach” to the theory of natural selection, each of the substitution instances of the schematic principle of natural selection generated by a particular specification of the propensity definition of fitness is treated as a definition of a different Darwinian system of population change over time. The evolutionary biologist's task is to identify which definition is instantiated by various populations in various environments[8].

The difficulties that the probabilistic propensity definitions of fitness face (the 'standard' account and others) are serious enough to make the notion of "ecological fitness" worth revisiting. Recall that on this view, *a* is fitter than *b* in *E*' is defined as ' *a*'s traits result in its solving the design-problems set by *E* more fully than *b*'s traits.' The terms in which this definition is couched are certainly in as much need of clarification as is 'fitness'. There does appear to be important biological work that the ecological fitness concept can do, and which no definition of fitness solely in terms of differential reproductive rates –actual, expected, or dispositional– can do.

Suppose one measures the fitness differences between population *a* and population *b* to be in the ratio of 7:3 (e.g. *wa* = 1, *wb* = .428), and suppose further that in some generation the actual offspring ratio is 5:5. There are two alternatives: (i) the fitness measure of 7:3 is right but drift explains the deviation; (ii) the fitness measure of 7:3 was incorrect AND drift occurred.

In the absence of information about the initial conditions of the divergence, there is a way empirically to choose between (i) and (ii). This way requires that there are ecological fitness differences and that they are detectable. Suppose that fitness differences were matters of probabilistic differential reproductive success. Then the only access to fitness differences is via population censuses in previous generations (since

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[8] See Lloyd (1994), Beatty (1980), and Thompson (1989) for exposition of this position.

these form the bases of the probabilities). Suppose that this census does indeed show a 7:3 ratio between *a*s and *b*s in the recent past. In order to exclude the absence of fitness differences instead of drift, as the source of the current generation's 5:5 outcome, one needs to be able to establish that the 7:3 differences in previous populations were not themselves solely the result of drift. But this is the first step in a regress, since the original problem was in discriminating drift from mismeasures of fitness. Of course the problem does not arise if we have access to fitness differences independently of previous population censuses. And this access we have, at least in principle, if fitness is a matter of differences in the solution of identifiable design-problems, that is, if there is such a thing as ecological fitness and it is (fallibly) measured by probabilistic propensities to leave offspring.

If there is access to ecological fitness differences, one can, at least in principle, decide whether the divergence from predicted long-run relative frequencies is a matter of drift or reflects our ignorance either of ecological fitness differences or the unrepresentativeness of the initial conditions of individual births, deaths, and reproductions.

As alluded to earlier, another reason that we need such a conception of ecological fitness to truly make sense of drift is for explaining deviation from expectations for very small populations. Whether or not small populations are the most prevalent population structure behind most evolutionary change as Wright's shifting balance theory (1931, 1932 in Wright and Provine 1986) argued contra Fisher's large panmictic populations theory (1930), an ideal account of fitness should be able to make sense of both extremes.

In some sense both Wright and Fisher can accommodate both extremes. In Fisher's account it is acknowledged obliquely that his fundamental theorem held "except as affected by mutation, migration, change of environment and the effect of random sampling." (in Provine 1986, 272) Conversely, in later versions of his Shifting Balance theory, Wright acknowledges that qualitative environmental changes alone could shift a population from its adaptive peak without migration (see Provine1986, 284-286, especially figure 9.2 C)[9]. When looking at very small population we quickly realize that an ecological notion of fitness of some kind is necessary to compare the evolutionary success of organisms. I will attempt to show this through a thought experiment.

First, let's imagine that the most salient feature of the environment is its acidity (measured by the pH level). It's the most salient feature, for hydrogen is the source of nutrient for our imaginary organism, and, the lower the surrounding pH around our organism, the lower the predation is. So an organism's ability to be in a lower pH milieu is adaptive for two reasons: nutrition and to reduce predation risk.

Imagine a clonal species with two closely related individuals that each produce two 'offspring'[10] at every reproductive stage followed by the 'parent's' dying immediately after giving birth. Imagine that in response to selective pressures tied to availability of nutrients only one offspring for each parent can survive longer than 5 minutes. By mere chance, the clone that is in the slightly more acid milieu survives while

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[9] The Fisher-Wright debate goes beyond the purpose of this project and I will therefore not address this issue in the depth that it might deserve.

[10] The raison d'être of scare quotes will be explained in chapter 2.

the other genetically identical sibling dies. That surviving clone then reproduces and the offspring in the slightly more acid milieu survives while the other falters. And so on for many generations. The population of each lineage at any given time varies between 1 and 2. The organism that survives is always the one born in slightly more acid milieu and its offspring because they are produced adjacent to the parent in some sense inherit that acid milieu.

Now let's say that one has two lineages that are almost identical except for the distance between clone offspring and parent (that distance could be root length). Lineage 1 shoots off clonal offspring at 20 cm while lineage 2 shoots clonal offspring at 15cm. After 4 generations, lineage 1 has had 4 'opportunities' to shift 20cm per generation towards lower pH zones while lineage 2 has had 4 'opportunities' to shift 15 cm towards a lower pH milieu. Can we say that one lineage is fitter than the other? Of course we can: some features of lineage 1 (in this case longer distance between clones) permits it to move to environments with lower predation. But notice that reproductively they do not differ, or rather, lineage 1 is not fitter because it can produce more offspring which it can't. It is fitter because it is designed better. It takes advantage of an ecological niche better than lineage 2 does.

In this case, there are no new mutations and no new genetic variation so, in some orthodox sense, there is no adaptation, no descent with modification (the difference in distance regime is the result of past evolution by natural selection in the orthodox sense). The lineage is 'merely' moving in time and space towards more acidic areas. But as we will see in chapter 2, the boundary between organism and environment is not as clear cut as we often wish to believe. In an important sense, part of an organism's environment belongs to its phenotype –as was shown by Lewontin with his idea of niche construction (Lewontin 1983 reprinted with a new foreword in Oyama, Griffiths and Gray 2000). If the location of our organisms, or rather if the immediate surrounding pH around our organisms belongs to the phenotype of the organisms then these organisms are still adapting: the phenotype of lineage 1 and that of 2 are changing (decreasing surrounding pH) in response to selective pressures involved in sustenance and predation. I am not claiming that those ideas are new of course, but rather, I wish to argue that cases such as the one presented are more significant in determining an organism's fitness that we have been led to believe. We may need ecological fitness for certain 'fringe' cases, moreover, as was briefly argued, it might permit us to explain the nature of drift. But given the epistemic problems related to ecological fitness highlighted earlier, can we truly say that we have access to ecological fitness differences?

1.7 Conclusion

The problem of defining fitness remains. Or at any rate, it does so if biology cannot live with an imperfect definition of fitness in terms of over-all design-problem solution or an understanding of fitness as a research program for building models. But David Hull describes the necessity of an 'engineering' view of some kind: "As difficult as it is to apply such engineering criteria of fitness in particular cases, I see no way in which such difficulties can be circumvented without evolutionary theory degenerating into an empirically empty formalism." (Hull 1980, 319). As we will see in the following chapters, a measure of ecological fitness is available and tractable, and permits us to account for actual empirical cases of evolution that cannot be explained by other accounts of fitness.

Chapter 2 Letting Nature tell us how evolution works.

2.0 Introduction

In the previous chapter we examined various conceptual reasons why some popular accounts of fitness need to be reassessed and altered, or rejected in favor of more inclusive accounts of fitness. This chapter will focus on some biological cases where there is –at least according to some intuitions- evolution by natural selection but not in a way accommodated by standard 'differential-reproductive-success' accounts of fitness. If, by definition, evolution is exclusively defined in terms of differential reproductive success, then the cases that will be presented here are not instances of evolution by natural selection. This, however, might not be a lesson about the world, but rather an indication that our definitions are inadequate to describe all instances of evolution.

Arguably, the main contribution of Darwin's theory was to provide an explanation of the apparent adaptation of traits/individuals to their particular ecological circumstances. This explanation was 'designer-free' contra Paley and all the biological theorizing that preceded him. In this chapter we will examine three cases of what seem to be instances evolution by natural selection. The cases discussed in this chapter suggest that contrary to common Darwinian belief, adaptation is not necessarily the result of slow accumulation of phenotypic change through intergenerational culling of offspring by environmental pressures broadly construed. I will argue, using these three empirical cases, that, as Darwin recognized, adaptation must be understood as the slow accumulation of phenotypic changes through differential success. But contrary to received views, differential success is better understood (at least in some systems) as the differential success of some internal *parts* of systems *not* differential success of *offspring* of that system. This will have to be so since the systems examined here do not have offspring per se. I am not the first to make this observation (e.g. Gil and Halverson 1984) but the generalization that I will draw from it is, I believe, novel.

We will begin by examining the case of the quaking aspen. Most of the time, the aspen ‘foregoes’ sexual reproduction in favor of growth. Its growth is adaptive in a significant way and does not depend on differential reproductive success. This case provides the first example of why evolutionary theory needs to be expanded to better accommodate at least some clonal systems. Note that I am not arguing that all asexually/clonally reproducing systems demand a reinterpretation of evolutionary theory to make sense of their phenotypic change. As we shall soon see, cases such as the aspen are ‘special’ since the structural interdependence of the clones hints that the ‘individual’ stems -that *appear* to be individual organisms- are no more individual organisms than ‘individual’ florets are to the broccoli. The examination of the aspen will be the most detailed and assured since the two other cases rely on more speculative interpretation of the facts at hand.

Whereas the first case examines how one biological individual evolves without reproducing, the second case will show how whole ecosystems can evolve. A description and analysis of two recent artificial ecosystem selection experiments will be given

(Swenson et al. 2000a and 2000b). Evolution in these cases cannot be solely the result of differential reproductive success for it depends in part on purely geological features of the system (i.e. non-biological non-reproducing components of the system). If reproduction is a fundamental feature of life, if evolutionary theory in its offspring-centric form can only describe reproducing system, and if there seems to be evolution in systems that are partly non-living, then we might have to reassess the role of differential reproductive success within our explanation of the evolutionary process that produces adaptations.

The third case takes the ecosystem selection case even further. Using Turner's (2000) description of termite colonies and mound interaction, we will see how a system that is much more than biotic (i.e. the termite mound) has evolved a way to ensure its persistence using termite colonies. Basically, an example such as this one (others will be alluded to) shows that Darwinian evolutionary theory liberated from an offspring-centric conception of fitness can be extended beyond to which it is generally limited. Adaptation will also turn out to be the result of differential success of parts and the accumulation of the changes in these parts to lead to adaptation given particular selective pressures.

The first indication that reproductive success (expected or realized) might not be the sole focus of evolution is historical. Darwin's eureka was basically the formulation of an inference based on two observations. The first observation (expounded towards the beginning of Chapter 1 of the Origin) was that individuals in any given population vary in phenotype in multiple small but sometimes significant ways. The second observation, inspired by Darwin's reading of Thomas Malthus' "Essay on the Principle of

Population"(1798 reprinted 1993) was that any population, whether a population of plants or animals, will produce much more offspring then will survive. Darwin coined the expression the struggle for existence to express these observations. Together, these observations led Darwin to infer that differential reproductive success would produce adaptation, and the conclusion that differential reproductive success is the engine of evolution. I am not arguing that Darwin was wrong about the empirical facts he described. However, this project will show that to this day the Darwinian over-emphasis on such mechanisms overshadows other real cases of evolution.

Darwin himself left the door open to other sources of variation beyond the scope of reproduction and differential reproductive success. These other mechanisms were seen as possible causes of evolution. Chapter 5 of the *Origin* focuses on what Darwin calls 'Laws of Variation'. One can find in these laws a hint of Lamarckianism (see the section on 'Effects of Use and Disuse') often downplayed by readers because of the bad taste presupposed Lamarckian heresy leaves in the mouth. Even though our project does not aim for a Lamarckian revival we should leave the possibility of inheritance of acquired traits open. Waddington, one the founders of what is now called evo-devo, characterized our prejudices succinctly.

> Lamarck is the only major figure in the history of biology whose name has become to all intents and purposes, a term of abuse.(…) Lamarck has, I think, been somewhat unfairly judged. (Waddington 1975, 38)

He goes on to offer a partial defense of certain aspects of Lamarck's theory. Recent work by Jablonka and Lamb (1995) aims at establishing the reality of Lamarckian processes to varying success.

Even though Darwin clearly downplays the role of such sources of phenotypic change, he never claims that random variation followed by struggle for existence and differential reproductive success was the only way to achieve evolutionary change. The exegetical quality of this first historical indication is not the main issue here, for after all, Darwin was sometimes wrong (ironically enough, wrong about mechanisms of inheritance). But it is important to keep in mind that one of the main reasons why Darwin's formulation of the theory was maintained through all the developments of biological sciences in the 20th and 21st century was the theory's generality and flexibility in the face of radical scientific changes. These features are what made the Modern Synthesis possible at all. Darwinian evolution was not discarded as a vestigial theoretical apparatus for it did allow for fundamental reformulation of the mechanisms involved: Darwin's evolutionary theory does not presuppose a special kind of inheritance, does allow for competing mechanisms such as use and disuse, etc. We shall leave Darwin aside for now, but note that even though Darwin does not expressly advocate a non-differential reproductive success view of evolution, his theory is flexible enough to accommodate it.

The second indication that reproductive success is not the only evolutionary way to go comes from a better understanding of inheritance. As alluded to earlier, Darwin did not have a clear or correct understanding of how inheritance works. The advent of genetics provided the next piece of the puzzle in that regard. If genetics is the only medium of inheritance, then an offspring-centric view of how change can accumulate over time to provide adaptation is more plausible than the alternatives. After all, organisms live and die, those that have ‘good’ genes (i.e. genes that lead to phenotype that perform better under given selective pressures) will over time leave more descendants.

One then gets between generations mutations (or recombinations) which may or may not accumulate over generations to provide adaptations. The Modern Synthesis of evolution and genetics emphasizes reproductive success for it reflects the plausible role genetics plays in evolutionary change. I am not denying that genetics is a powerful mechanism of slow cumulative change as a result of selective pressure. However, as evo-devo and DST try to show, mechanisms of inheritance should be construed in a more inclusive fashion. DST defines evolution as “changes in the life cycles of organisms in their co-constructed niches, tracked by differential reproduction and distribution of developmental systems” (Jason Scott Robert in Hall and Olson 2003, 97). DST goes too far in diluting the importance of genetics in its causal relativism (or causal democracy as as DST’s proponents call it). But DST and evo-devo explain how changes during ontogeny affect the formation of phenotype and how these changes can constrain future phenotypic formation without being part of the ‘program’ passed on through DNA. This insight tells us that the transmission of adaptive traits does not depend on DNA alone. When Dawkins wrote that “genetics factors replicate themselves, blemishes and all, but non genetic factors do not” (Dawkins 1982, 98-99) he was wrong: non-genetic factors can be replicated as well. This was recognized to some degree by multi-level selectionists, but the extent of Dawkins error is not always fully appreciated.

The multi-level selectionists thought that Dawkins error was in focusing exclusively on genes as the unit of selection (which is a somewhat uncharitable interpretation of Dawkins if we are to take his "The Extended Phenotype" seriously). But Dawkins' error, which the multi-level selectionist sometimes makes as well, is that of treating evolutionary change as resulting from differential reproductive success exclusively. If Dawkins is really wrong about genes, it might be because he is wrong about the special status of inter-generational change. Changes in non-genetic[1] material constrain future phenotype, and can be 'passed on' forming changed future phenotype that will be selected on. As well see, the success of some epigenetic changes does not depend on higher reproductive success of their bearers. This is a significant indication that reproductive success might be too exclusive to fully take advantage of what evolutionary theory can offer. But this latter point will be defended later on in this project.

The thread of the chapter will be as follows: we begin by showing how some purely biological cases (e.g. Quaking aspen) require a reformulation of the theory. This section will include a brief discussion of the concept of inheritance and how it could be modified. We will then examine how such a reframing might be helpful to understand some more complex/contentious cases of biological evolution (e.g. ecosystem evolution). Finally we will assess future possible dividends of this type of analysis and how they

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[1] 'Epigenetic' has very different uses in various biological disciplines, in part because epigenetic can refer to the mechanism beyond or over (the etymology behind the prefix 'epi') genes, or it can refer to the processes beyond or over birth (genesis). This being said most of the evolutionary biology literature uses the word 'epigenetics' as implying "non-DNA-based mechanisms of inheritance" (Müller and Olsson in Hall and Olson 2003). Therefore the context of this dissertation warrants the use of the word as such.

provide a basis for describing changes in non-exclusively biological systems as cases of evolution by natural selection (e.g. termite mound formation and maintenance).

2.1 Quaking aspen

> I grew strong
> I learned how to carry on
> (…)
> It took all the strength I had
> not to fall apart
> kept trying hard to mend
> the pieces of my broken heart
> (…)
> you think I'd crumble
> you think I'd lay down and die
> Oh no, not I
> I will survive
>
> Gloria Gaynor

Reproduction even though central is recognized to be problematic for evolutionary theory for many reasons. The costs of sexual reproduction, and its evolution as an adaptive strategy demand explanation. The consensus is that the ‘costs’ for a parent to pass on only part of its genome are compensated by the benefits of having new variations introduced at every generation. So although the original appearance of sexual reproduction is difficult to explain, its maintenance and its ‘success’ across many species may not be. Asexual reproduction is problematic as well. Asexually reproducing organisms were a problem at the onset of the Modern Synthesis because of their reproductive isolation: if one advances a biological concept of species as Dobzhansky and Mayr did, how will one identify species in asexual organisms? Many philosophers and biologist recognize the difficulties that at least some cases of asexual reproduction pose. Sterelny and Griffiths (1999, 188) and Gould and Lloyd (1999, 11907) describe how asexual reproducing organisms pose a problem for defining the concept of species and lead to a seemingly undesirable consequence for the biological species concept. On this notion, a species consists "of a group of organisms connected to one another by actual or possible reproductive links, and reproductively isolated from other organisms" (Dupré in Keller and Lloyd 1992, 315), and therefore asexually reproducing organisms have to be treated as 'paraspecies' (Mayr 1987) or pseudospecies (Ghiselin 1987), for an asexually reproducing organism may be completely reproductively isolated from all other organisms.

If one shifts from a phylogenetic plane to a morphological plane other problems arise. When the clones are functionally autonomous from each other, they seem to fit somewhat neatly into accepted views of species: each independent clonal copy can be seen as an offspring in this view. But what is the entity supposed to do the differential reproducing is not evident even in those easy cases. When the clones are not functionally autonomous as in the case of many plants, the difficulties become obvious: why should we consider the clones to be individual offspring and not simply growth? And if we are presented with growth and not reproduction, where is the evolution? Buss (1983) describes convincingly how the Weismannism on which the Modern Synthesis depends leaves out the somatic mutations that can in fact be selected on and constitute the response to selection in protists, fungi or plants. This selection is on *within*-individual parts, not offspring. Although this fact is accommodated by hierarchical views of selection (Brandon 1990, 90), I will argue later that they do not go far enough to accommodate these cases.

Some argue that even if we wish to see asexual reproducing species as problematic for evolutionary theory, it is merely a transient problem that will disappear as asexuality is slowly but surely selected out. Stanley (1975) describes the overwhelming advantage of sexual species over asexual species in occupying diverse ecological niches rapidly and claims that this advantage will extend to clades as well. But the facts may not be as simple as they appear. In trying to understand the evolution of sexual reproduction, Hull describes how depending on how one defines the concept of species, asexual reproductive species are rare or much more prevalent than sexually reproductive species.

> For example, Stanley cites White's estimate that about one in a thousand animal species is asexual; but if we take him at his word and agree that asexual organisms neither form species not are capable of speciating, then clones and species are not comparable. (…) If like is to be compared to like, asexual lineages should be compared to sexual lineages, and in such a comparison, sexual reproduction becomes as rare as it should be. (Hull 1980, 330)

Many simply assume that sexually reproductive species are much more prevalent than asexually reproductive species because of the obvious benefits of making new genetic combinations at every reproductive event. But if we are to give even just a hint of credence to Dobzhansky's biological species concept (extended by Mayr) then we have to consider the possibility that every genet is a 'species' of sort since it is not capable of interbreeding with other genets.

All this to say that we should not assume that asexual reproduction is going the way the dodo simply because its apparent prevalence is decreasing. In fact, it might not be decreasing: it all depends on how one counts. I will not argue this point further for the relative contemporary prevalence of asexual reproduction is not the true issue here: since all species originated from, *have evolved from*, asexual species, evolutionary theory needs to provide a framework that can truly accommodate growth and fission. As I alluded to in the introduction of this project, if evolution only 'kicks in' once systems have developed a way of producing offspring, then we cannot describe the development of the reproductive system as the result of evolution. If an organism makes the transition from a growing organism to reproducing one, and if evolution can only be described in terms of differential reproductive success, then we are left with the counter-intuitive -and ultimately false- conclusion that organisms did not make this transition as a result of selective pressures. There is therefore an urgent need to describe evolution by natural selection in a way that does not depend on differential reproductive success. If we fail to do this, our most fundamental biological theory is making the strange claim that evolution appears ex nihilo *only when* production of offspring appears. Whatever has lead to that production of the first offspring is evolutionary theory's blind spot.

Note that the received view of evolution is not the only one that has difficulties with asexual reproduction. Non-standard evolutionary accounts have difficulties with asexual organisms as well. In their reconsideration of the punctuated equilibria idea, Eldredge and Gould place asexual organisms in a strange position in their theory:

> We predict more gradualism in asexual forms on biological grounds. (…) Their unit is a clone not a species. Their evolutionary mode is probably intermediate between natural selection in populations and natural selection in clades. (Gould and Eldredge 1977, 142)

Assuming Darwinism is a gradualist theory, this would make asexual species more Darwinian than most species in Eldredge and Gould's eyes! And if we wish to see asexual species as more prevalent, because of their reproductive isolation, than sexual species, then gradualism applies to the majority of cases of evolution contra Eldredge and Gould. Asexual reproduction is a problem for everyone for it tests the boundaries of our criteria of individuation.

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. By analogy, imagine burying a broccoli so only the top florets stick out of the dirt. Now imagine that you are the size of an ant. It would look like you are faced with a forest when in actuality there is a single organism growing beneath your feet. The size of the organism relative to our usual encounters with other plants boggles the mind. The largest aspen grove/clone is believed to in the Wasatch Mountains of 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, the quaking aspen, *Populus tremuloides*, seems to merit a plethora of superlatives:

> [The quaking aspen] is North America's most widely distributed native tree species and the second most widely distributed in the world (Barnes and Han 1993, Jones 1985). The world's most massive individual organism is a quaking aspen (Grant et al. 1992). Individuals may reach ages in excess of 1 million years (Barnes 1966, Grant 1993, Kemperman and Barnes 1976). And quaking aspen may also be the most genetically variable plant studied to date (Cheliak and Dancik 1982). (Mitton and Grant 1996, 25)

Even though the spatial and temporal distribution of the quaking aspen are impressive and will deserve some of our attention here, the interesting features of the quaking aspen for now are ontological in nature. The quaking aspen appears in various morphological forms depending on the environment: its ramet can grow into 'bush' shorter than a meter up in height or it can grow to a tall 'tree' 30m tall[2]. 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. A single stem (what we wrongly identify as the individual 'tree') can produce up to 94 million seeds per year (Shopmeyer 1974). But the success of these seeds is rare (at least in more arid environments). In theory the aspen could evolve

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[2] Here 'bush' and 'tree' are in scare-quotes to highlight that the use of the words is only mean to track the apparent morphological form not a deeper ontological nature of the entities at hand.

through differential 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 (quaking aspens are very shade intolerant, a feature that will be important later in this argument).

The ideal circumstances for new seedling are following a forest fire. The fire destroys most of the competition for the quaking aspen (by destroying the conditions creating the shade): quaking aspen are easily top-killed (DeByle 1985) and of course the fire destroys surrounding trees. But the conditions leading to the fires reduce the likelihood of the conditions necessary for successful seedling: the lack of water making fire more probable also makes it hard for new seedling to take. For these reasons and others explained below, sexual reproduction is not the main reproductive strategy of the aspen. But as Mitton and Grant put the question "If seedling success is so rare, why are aspen so abundant and widespread in the semiarid West?"(Mitton and Grant 1996, 27)

Although seedling might explain some of the genotypic variation in aspen, 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[3]. 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

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[3] Richtsmeier in Hall and Olson 2003, 162, defines growth as "change in the arrangement of component parts with increase in spatial dimensions occurring over time". This is what the grove is doing when sending out roots to produce new ramets and as Richtsmeier points out (Ibid. 163) "growth plays an important role in evolution by generating diversity during ontogeny". This will be significant for my argument.

therefore the ramet density) varies greatly depending on the particular selective environments (Olejniczak 2003, Tamm et al. 2002).

The conceptual problem becomes one of individuation. If new stems are merely growth of another stem and if they remain structurally interdependent, should we describe what we observe as one big individual or a population of smaller individuals? The task is complicated by the fact that, because the stems merely are different stages of a shared growth process, they are relatively identical genetically except for somatic mutations that can occur. Clonality or asexual reproduction is not a novel 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 linked.

Epistemological prejudices might be at play here[4]. We tend to individuate organisms relative to our own scale (a problem also faced in group-selection arguments see Sober and D.S. Wilson 1998 for analysis). For that reason a 30 meters stem is not considered as merely an appendage to an existing stem whereas we have much less difficulty seeing the stem as growth when it is merely a 1 cm short extrusion of an existing root system. Stephen J. Gould, when considering the ontology of another 'exotic' clonal organism, the famous 30 hectares mushroom mat fungus *Armillaria bulbosa*, describes such epistemological limitations.

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[4] As Hull put it "Given our relative size, period of duration and perceptual ability, organisms appear to us as reasonably discrete entities developing continuously in space and time. Each organism is spatiotemporally localized and as such is unique." (Hull 1976, 176) Or as Gould more famously put it "We are prisoners of the perceptions of our size, and rarely recognize how different the world must appear to small animals."(Gould 1977, 173)

> Since these rhizomorphs grow and extend underground (in and around tree roots), a human observer sees nothing of this interwoven subterranean mat except for the occasional and spatially discontinuous mushrooms that poke through the forest floor. Since we mistake an individual mushroom body for a discrete organism, we might look at the area of this Armillaria clone and, seeing nothing of the underground continuity, view the species as consisting of a few widely scattered, entirely separate items–a population of several insignificant individuals.(Gould 1992, 10)

Following Smith, Bruhn and Anderson (1992) Gould goes on to describe the mat as one unified organism. Clearly our intuitions can only take us so far to individuate organisms of that kind[5]. A priori it seems unjustified to 'atomize' the fungus or an aspen grove into smaller individuals only because the smaller unit 'looks like' other more paradigmatic organisms we usually deal with. Although individuation is a serious ontological question that has a significant import on the question at hand (see J.Wilson 1999 for a thorough analysis of the question), we will limit ourselves to a cursory examination of the topic in this chapter. Clearly genetic identity is an inadequate criterion since clones by definition are genetically identical to their 'parent'. Even though there are some differences between clones, these differences are often trivial. It is safer to not include genetic identity as the main criterion. Functional morphological notions might be more useful for individuation criteria.

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[5] As we shall see, although the case of the fungus could have been used for the argument I am making, the case of the quaking aspen was preferred, for intuitions concerning aspen 'trees' lend themselves much more readily than the case of a huge fungus patch taking over Pennsylvania. Also I wish to avoid counterarguments that the generalizations I hope to identify only apply to only a certain exotic kingdom and not to life in general. Species that have life cycles similar to those of the aspen are many and so my argument will apply to many organisms.

The study of clones lead to a new vocabulary to describe this genetic individual and what appears to be a collection of morphological individuals. The genetic individual is referred to as a 'genet'[6] while the apparent morphological individuals are referred to as 'ramets' (see Cook 1980 for discussion). This nomenclature permits botanists to refer to a grove as a population of individual ramets or as one genet with many component ramets (depending on the structural integration). The evolution of the phenotype of the quaking aspen could be described as the differential reproductive success of ramets and the additive changes of somatic mutations that are passed through generations of ramets. However such a characterization hides some significant processes that the grove uses to survive. The problem is that the genet-ramet language does not really distinguish between functionally or morphologically physiologically distinct ramets and the ramets that are connected together exchanging water and nutrients[7].

A quaking aspen is usually a successional species (i.e. an early species occupying an area, later supplanted by other communities) but it can actually create the circumstances leading to its being a climax species (the mature 'final' community). By clonal growth, a grove can insure that it maximizes the utilization of a patch making any other species seedling more difficult. In some sense, there is selection for fatness in the

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[6] Not to be confused with the spotty carnivorous mammal of *Genetta* family or the political trouble maker Edmé-Jacques Genet.

[7] 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. Oborny and Kun (2002) refer to genets as 'splitters' when the genet fragments into individual clones (sometimes called 'clumpers' because after the fragmentation the ramets still remain in proximity to the other ramets), 'transient integrators' when there are various integrated mini-groves in a shared area, and 'permanent integrator' where 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.

case of the quaking aspen since it increases the likelihood that it will not be overtaken by other species, by growing instead of creating other groves by seedling[8].

There is even an internal pressure to minimize the use of sexual reproduction. Not only is successful seedling rare but it is slow, whereas a 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'). By growing quickly, the grove minimizes the effects of moose and deer, reduces the successful seedling of other species, increases the control it has over nutrients that are exchanged via the root system, etc. Basically the grove 'does' better by growing bigger than by producing offspring. This shift towards exclusively asexual reproduction is not a 'necessary' outcome of organisms that have access to both modes of reproduction. Bengtsson and Ceptlisis (2000) model how in relatively stable environments dual-reproduction species will tend to overwhelmingly use only one of their modes of reproduction –which one will depend on the specific selective pressures at hand. Highly variable environments are the conditions necessary to maintain balanced mixed reproductive systems where both asexual and sexual reproduction are 'used' by the biological system. Most large integrated aspen are in relatively stable environments and the aspen attenuate the effect of some selective pressures that could destabilize their environment.

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[8] For a thorough examination of spatial dynamics modeling in plant communities see Bolker et al. 2003. Note also that 'growth' in most clonal plant species is horizontal and not vertical because of the costs of moving water (i.e. hydraulic cost) from roots to canopy beyond a certain height -costs that are obviously much lower for horizontal water transport. See Midgley 2003 for examination of hydraulic costs and their relation to increase in size in plants (and the possible extension of this idea to animals as well) and Sachs 2002 for more on the developmental constraints of clonal plants and how it affects their height.

Let me stress once again that clonality does not always lead to the integrated growth of one huge genet. As pointed out above, genetic identity is not the main criterion of individuation. The lesson we hope to learn here is *not* that asexual reproduction is never adequately accounted for by the received view. When the clones are not integrated, I think the received view, in terms of differential reproductive success, *might* be adequate. Rather, cases such as the aspen should teach us that organisms using clonal growth but remaining structurally cohesive are not really reproducing. The expression "asexual reproduction" should only be used to describe clonal growth that is followed by fragmentation.

One reason to distinguish the ontology of a fragmented clone (a 'clumper' clone) from a cohesive integrated one is that they seem to have a different evolutionary fate – 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 'clumper' clone is not as successful with the new ramets because they have only the nutrients that each new individual ramet's root system can access. Gough et al. (2002) have actually tested the hypothesis that the high costs of integration are offset in that way. 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 can occupy new micro-environments with new resources.

Changes in the ontogeny of the grove are possible not only in the phenotype but in the genotype as well. Somatic mutations are still possible and can be transmitted through the cloning process to other stems. As Gill and Halverson (1984) point out in another related context:

> The term ‘somatic mutation’ as applied here may be misleading to ecologists from zoological backgrounds. In animals, mutations that occur in somatic tissues and exclusive of the germ line have no heritability and are irrelevant in an evolutionary context. In plants mutations that arise in meristems during development have the dual potentiality of being expressed phenotypically in the somatoplasm and reproductively in the gametophytes. That such mutations persist vegetively after grafting and may be transmitted through pollen and seed show that they are heritable both asexually and sexually. Hence somatic mutations can have evolutionary importance in plants. (1984, 105)

Gil and Halverson’s focus is the *Hamamelis virginia* L. 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 contributions are 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 defense, 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 describe inheritance in cases of intra-generational tree evolution.

Let us now ponder how evolutionary theory seems to apply to the aspen case. The quaking Aspen is clearly subject to natural selection. This is not surprising in itself since, as Van Valen points out, even non-biological structures may be subject to natural selection

> When granite weathers, the feldspars and micas become clays but nothing much happens to the quartz grains. They are most resistant and get transported down streams or along shores. Thus most beaches are the result of differentially eroded granite. This is an example of natural selection in the nonliving world. Quartz grains survive longer than feldspar grains, and there is a progressive increase in the average resistance to weathering, of the set of grains that have still survived. This action of natural selection is even creative, as we see by the formation of a beach. (Van Valen 1989, 2)

There is discriminate sampling of mineral objects, by virtue of their chemical bonds and other chemical and physical properties: the landscape is transformed in response to pressures from the environment. The same is true of the quaking aspen. Wind patterns, bugs, and other selective forces determine the shape of the grove, its growth pattern, which paths will runners explore, which runners will be more successful, etc. Of course this is a different use of the expression ‘natural selection’ than many biologists’ use. It conflates some sampling with natural selection. But such a conflation does not seem inappropriate. Imagine ten trees planted in the soil with simple root system extending under the surface. Winds will push over the trees with shallow root systems. That is natural selection. Now replace the trees with posts planted to various depths. Winds will push the shallow posts in the same way. Features from the environment permit some entities to persist while others are ‘washed away’. That is the essence of natural selection.

In these cases, there is natural selection, but is there response to natural selection, is there *evolution* by natural selection? If evolution is, as the Modern Synthesis put it, changes in gene frequencies, then the erosion case is not evolution because there are no genes in the granite. But this is obviously not a sufficient rebuttal. Notice that Van Valen does try to describe the composition of the soil in terms of relative frequencies as if he were trying to convince a synthesist that evolution remains change in frequencies, the ‘only’ thing given up being ‘genes’. There are changes in molecule frequencies which puts us in very similar scenario as a change in macro-molecules/genes frequencies. More will need to be said to explain that, while erosion is the result of natural selection, it is not evolution by natural selection.

Brandon (1990, 7) reprises Lewontin’s (1978) formulation of the three conditions of evolution by natural selection:

1- *Variation*. There is variation in phenotypic traits among members of a population

2- *Inheritance*. These traits are heritable to some degree, meaning that offspring are more like their parents with respect to these traits than they are like the population mean

3- *Differential reproductive success*. Different variants leave different numbers of offspring in succeeding generations.

Let us try to accommodate these three features to the quaking aspen case. I will argue that the same three conditions seem to obtain *sans* offspring in the case of the aspen. I will offer a brief overview of some 'accommodations' and then explore the three points in more details.

There clearly is variation within the grove:

> An electrophoretic survey of protein variation revealed that more than 90% of the enzymes analyzed were genetically variable (Cheliak and Dancik 1982), in comparison with the average of 50% for all plant species that have been analyzed (Hamrick and Godt 1989). Surveys of DNA markers are consistent with the survey of proteins, indicating high levels of genetic variation (Mitton and Grant 1996, 28).

Even if the variation were not genetic, we can assume that some developmental constraints would affect differently various regions of the grove (some parts are older than others, they may senesce or react differently to shared environments, etc.). In fact the amount of nutrients passed on from one ramet to another depends in part on the age of the ramet. There is *internal* variation within the grove. The conventional use of variation is to convey differences between individuals in a population. If, following Mitton and Grant, the grove is an individual, *not* a population, how can the concept of variation truly apply?

Just as Gil and Halverson (1984) had suggested, there is variation among the parts of the whole grove. These parts are the ramets. Nature does not care whether the ontology makes these ramets full-fledged autonomous individuals or parts. Selection acts on differences and the parts of the grove show differences. As hinted above, there are genetic differences but I do not wish to base my whole argument on this type of differences: if the ramets are that genetically variable, then it might be harder to be convinced that it is really a single genet. In other words, if most of the clonally produced ‘offspring’ mutate, why consider the ‘parent’ a single organism in the first place? More importantly, Mitton and Grant do not describe the type of genetic differences that they observe: those differences might not affect the phenotype in any significant way. Finally, we have already put aside genetic identity as the individuation criterion for even if the aspen were ‘interestingly’ genetically variable, there are numerous other clonal organisms (most that do not have meristematic growth, i.e. cells actively dividing in growth regions, permitting ‘continuous’ indeterminate growth) where such genetical variability is less significant and I wish my argument to be applicable to them as well.

More interestingly, in some respect there are phenotypic differences. The ramets show a great phenotypic diversity. This diversity or variation is amplified once we understand that the spatial location of individual ramet/part is part of the phenotype of the part and by extension, part of the phenotype of the grove. We will come back to this point in our discussion of inheritance.

As we will see, in the case of the aspen, inheritance and reproductive success are linked.

It is more difficult to address differential reproductive success in the case of the quaking aspen since, if one accepts the description offered above, there are no offspring (at least in the case of permanent integrators, i.e. unfragmented clones). Linhart and

Grant (1996) might be of more help here in determining where something like an offspring might come in. When discussing differentiation in clonally reproducing taxa they allude to the success of the quaking aspen: “Fragmentation of clones *may*[9] produce physiologically independent individuals, which then more or less successfully exploit their own micro-environment.”(Linhart and Grant 1996, 262).

Imagine a grove covering 500 km^2 of a 501 km^2 circular valley encircled by steep unwelcoming mountains. Imagine further, that a meteorite crashes down cutting a straight swath, bisecting the grove (deep enough to completely cut through the root system). We now have two independent individual groves. The traits that were beneficial for the grove were roughly equally present in all parts of the grove and will now be present in two groves (assuming that the environment in the valley is roughly homogeneous). Assume the harmful traits were probably less evenly represented throughout the grove and the chance that they will be as equally present in both smaller groves is low (keep in mind that this is a thought experiment, and is not meant to be close to an actual empirical case).

Reproductive success (aside from the rare sexual episodes) may be thought of as a capacity in the case of the aspen. Since there are no compelling reasons to fragment *sans* meteor strike, the large grove, being able to commandeer vast resources and to reduce the risk of extinction, will remain one integrated grove. *However* if it were to employ the offspring strategy, reproductive success would apply in the classical sense. In some sense, the quaking aspen displays a counterfactual adherence to Lewontin’s reproduction

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[9] My emphasis.

condition. If things were different, it would play by the ‘rules’, but as things are [generally] the aspen’s best strategy is *not* to fragment if the optimal outcome is to persist. Different variants *would* leave more offspring if fragmentation *were* to happen.

In some sense this is massaging the grove into the propensity view. If externally induced fragmentation of the grove counts as reproduction, the grove has potentially as many offspring that can inherit the traits selected as there are ramets. But since the fragmentation is never as efficient as that possibility, how many offspring should we count when the meteorite creates not two independent groves but three. What if these fragmented clones have different numbers of ramets. How many individuals are there, what is reproducing at the moment of the fragmentation and more importantly in the future? The questions highlight the difficulty of applying reproductive success notions to the grove. Even if, as in the possibility entertained above, we see the reproductive success as being a capacity of the grove given fragmentation –which would prima facie put it in line with the propensity view– the distinct ontology and functional integration of the grove, makes ‘head-counting’ difficult.

There might be a way to make integrated clonal systems fit the propensity view but only by relying heavily on a suspect notion of counterfactuals. Looking at how the three conditions could apply however shows something important however: if one looks at what these conditions are really meant to describe, one may be able to extend those conditions to enable evolutionary theory to explain more phenomena. Variation is easily accommodated since we merely go from variation in phenotype in a population to a variation in the aspect of component/parts. Nature does not care whether it is sampling components or individual entities. Reproductive success is harder to accommodate. If one truly wanted to find offspring, one could count individual ramets and offer a group selection argument but since fragmentation is never complete, the formation of different sized mini-groves makes that kind of ramet-individuation somewhat suspect. In the same way that we might be comfortable seeing variation in phenotype of parts replacing variation in phenotype of individuals in a population, we might have to think of differential success not reproductively. I will come back to this point after discussing the third condition not yet examined.

Inheritance is trickier but it still can be accommodated. Recall that inheritance has occurred when the offspring are more like their parents with respect to the supposed inherited traits than they are like the population mean. But this is exactly what occurs when considering the components and how they differ to one other.

A ramet 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: their spatial position determines which micro-environment they 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 in a certain radius from the ‘mother’ ramet.

Thus to reprise the conditions identified by Lewontin, a good position means that component/ramet A has a higher likelihood of surviving, and since the components/ramets that ramet A will produce can only steer away so much from its preceding ramet, ‘daughter’ ramet will inherit a position close to ‘parental’ position by mere physical and developmental constraints.

Mameli (2004) offers a somewhat similar ‘epigenetic’ argument with what he calls the lucky butterfly effect: a genetically homogeneous population of butterflies will have different phenotypes depending on which leaf they grow on (different leaves give different phenotypes). If a lucky butterfly happens to fall on a nutrient super-rich leaf, it will develop a very different phenotype and might be more successfully represented in the overall population even though there has been no change in gene frequencies.

My description of the quaking Aspen differs from Mameli’s example since his is translatable into a norm of reaction case where genes are expressed differently depending on environmental cues. But there can be selection for different norms of reaction.

My use of ‘inherited’ spatial position and the difference in phenotype that it provides (leading to inheritable non-genetic variation) is different from Mameli’s in that the expression of the gene in the case of the aspen remains constant. The quaking aspen’s change in phenotype will not be captured by norms of reaction. If one accepts that position is part of the phenotype -which is the case since you can select on position in the same way that you can select on height- and 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 on is selected for and passed on differentially but non-genetically. We will come back to the importance of spatial position as part of the phenotype later in this section and in our examination of Turner’s argument later in this chapter.

The example of the quaking aspen was employed to show that counting offspring needlessly limits the scope of evolutionary inquiry. In some sense, counting offspring is much too parochial. This hang-up will be hard to give up. It requires a different unit of selection. After all nothing of the original grove persists forever[10]. Paradoxically, this bewilders us but should not surprise us. Individual human cells do not survive for our complete life cycle –they are *all* continuously replaced (or destroyed)–, meaning that in some sense 'I' am not the same Frédéric I was 10 years ago. Frederic is an entity of sorts, just like the aspen grove is. Every part is replaced over time, but the entity remains. The Ship of Theseus problem is a serious metaphysical problem that I cannot fully address here: Individuality is a complicated matter. I hope that our intuitions will be sufficient to continue the debate.

I have highlighted the asexual nature of the quaking aspen. But since it also has access to sexual reproduction, the quaking aspen does not necessarily have to be a counter example to offspring centric fitness. It does reproduce sexually after all. The growth strategy might simply be treated as a very long latent stage that permits it to take better advantage of the next sexual event. This seems like a cop-out: when sexual events are so effectively rare, can we really talk about actual or expected offspring[11]?

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[10] "No physical tissue such as root or stem or leaf presently in existence would have been in existence from the original seedling." (Mitton and Grant 1996, 28).

[11] "Biologists most familiar with aspen dynamics propose that these western clones are ancient, perhaps on the order of 10,000 years (Kemperman and Barnes 1976), and conceivably as much as 1 million years (Barnes 1966, 1975), and potentially immortal. Part of the rationale behind current age estimates for aspen clones is that sexual reproduction is effectively frustrated by the rarity of a favorable suite of conditions in semiarid environments. Clonal age, in the strictest sense, truly applies only to the individual gemome, which is the single element of clone identity that would be continuous across time spans." (Mitton and Grant 1996, 28).

A compromise, identified above, could be that the definition of the quaking aspen fitness will have to include an entity's *potential* to have some offspring (which strictly speaking is different from the propensity to have a specific number of offspring). Fragmentation could be seen as a reproductive mechanism leading to descendants of different size depending on the degree of fragmentation. Moreover, those potential offspring would act as regular offspring under Lewontin's three conditions of evolution by natural selection. I don't think this would satisfy the propensity proponents, but it would be a way to keep the three conditions while recognizing the fact that entities like the aspen don't meet these conditions in actuality although they could in potentiality.

The problem for such a compromise is that the aspen's evolution is more than a mere possibility. There is evolution by natural selection for the aspen.

Most valiant attempts to accommodate asexual reproduction or clonal growth shift the semantics of offspring to the notion of copies, which seems less loaded. It is still assumed that as long as 'copies' remain isolated and incompatible with other types of copies, speciation obtains. But if 'copies' are an acceptable semantic shift, why not move further to include 'parts' or 'components' as well? A grove that fragments is different from one that does not, the difference being that fragmented ramets have the potential to become individual genets (by somatic mutations) whereas ramets in unfragmented groves are 'merely' parts of the grove, part of a single genet.

As we can see in cases such as the quaking aspen, but also vividly in colonial organisms examined later in this chapter, it might be more helpful to put the notion of

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offspring/copies aside, in favor of the idea of 'parts'. There can still be competition between parts, but their numbers won't be the measure of their success. Whether they are still represented at a later time is a more informative measure of success. The idea of differential success of parts is not new; it is in the background of many macro-evolutionary projects[12]. The difference here is that I wish to make differential persistence of parts a condition of at least some micro-evolution as well.

In this sense, each runner is a part of the grove (not an offspring, not a copy) and some parts help the grove more than others since there is some genetic and phenotypic diversity between runners. Genotypic differentiation has been addressed earlier: there can be slow accumulation of somatic mutations in ramets but as I pointed out earlier I do not wish my case to rest to heavily on the ability of the aspen to accumulate somatic mutations. More significantly, phenotypic differences that can be passed on play a significant role in the aspen's evolution. As I have already alluded to, the phenotype is not solely question of color, chemical structure, etc, but also geographical emplacement, direction of growth, etc. This is an important aspect of the phenotype for our account since it can explain how one can find gradual accumulation of changes in the phenotype (e.g. does the grove grow more eastward) that is selected for (e.g. eastward is better than westward) without necessary genetic change.

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[12] "The species-individual, as a Darwinian interactor in selection at its own level, operates largely with cross-level exaptations arising from unsuppressed evolution of subparts (primarily organisms) at lower levels within itself. Such nonsuppression acts as a source of power by permitting species to draw upon a wider pool of features than organisms can access (for the organismic style of individuality enjoins active suppression of most selection at lower levels within itself)." (Gould and Lloyd 1999, 11909).

If the eastward runners persist longer than the westward runners, if this persistence is favored gradually (the first eastward runner persists longer than the other runners, and produces other runners –copy/offspring account- OR simply grows larger and stronger increasing its survivability), this accumulation of changes leads to an adaptation for the lineage (eastward phenotype for the whole grove). This adaptation is passed on genetically but also non-genetically.

Botanists have already been toying with this idea. Pan and Price (2002) suggest measuring the fitness of a whole genet as a function of its growth since rates of ramet production impact the genotype in the grove (slight mutations in a sections of the grove might not persist while other sections slightly different genetically might persist longer). They then suggest that clonal growth be integrated to seed production to measure a clones overall fitness. They identify two components of a genet's fitness. First is the persistence of the genet, second is the fecundity or ability to create to create new genets (new groves) estimated via seed production

They also show that, in predicting a genet's survival, at least as important as the number of ramets in a genet, is the surface area occupied by the genet. In other words, a genet might create the same favorable survival conditions by having a dense grove in smaller area or a less dense (and smaller absolute number of ramets) covering a larger area. If growth becomes more significant in assessing a genet's fitness, the rate of growth is significant. However, *pace* Pan and Price, the spatial position of the grove becomes supremely important as well: how and in what direction the grove grows has to be significant since they determine which environments are explored.

Seed production is for all intents and purposes irrelevant in most selective environments in the case of the quaking aspen. Persistence of the grove and what affects it will be the sole components of its fitness. Since the growth ‘success’ of a genet and how it impacts its survivorship is not strictly demographic, reproductive success cannot be the measure of evolutionary success.

When in chapter 4 we offer a new account of fitness, it will be helpful to remember that intuitively we might want to see evolution by natural selection as persistence through time (PTT). Such persistence may be accomplished via differential reproductive success (in most biological cases) or via differential persistence of its constitutive parts (in cases such as the aspen or potentially some colonial organisms). The important lesson here is that the means to achieve survival or persistence should not be prejudged a priori. In different context, Van Valen in 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 and is ultimately related to the spatiotemporal heterogeneity of the total environment (Van Valen 1989, 5)

Why should survival be only a question of reproduction? In the same way that we see Darwin’s account as flexible insofar as it casts selection as blind to internal structure, we should favor an account that does not presuppose one means of shaping and transmitting adaptations over time. The advantage of this outlook is that reproduction is not seen as the sine qua non mode of evolution.

Before we move on to the other cases, let me briefly allude to one possible reply to the quaking aspen case. Let's imagine that our theoretical opponents grant us that the aspen is evolving, that it does so without offspring production. Let us imagine that they grant us every point in this analysis. They may still argue that even though we have these exceptions, evolutionary theory in its received view does the work in the vast majority of cases.

First of all, as pointed out at the onset of this section, the quaking aspen is not a rare organism. It is 'special' granted, but that doesn't warrant its exclusion from evolutionary thinking. The platypus is a strange organism, but does that allow us to exclude it just because it doesn't fit nicely in our phylogenic pictures? Of course not: our best theories (and evolutionary theory is clearly on of those) are not in the business of explaining solely the frequent phenomena or the most tractable cases but the difficult fringe cases as well. These fringe cases need to be understood for they impact garden-variety cases both in the theory but also in the practice of science. For example, if autecology is in fact concerned with the ecology of single individual organisms, questions concerning the ontology of integrated clonal systems as an evolutionary individual (as well as that of the systems we will now examine) will have to be answered to properly describe the field and its role with in ecology at large.

The quaking aspen does not constitute a single rare exception to the received view of evolution. If evolutionary theory has to describe problematic cases of evolution, then, as we shall soon see, the aspen is the least of its worries.

2.2 Artificial ecosystem selection

Mud, Mud, glorious mud
Nothing quite like it for cooling the blood!
So follow me, follow
Down to the hollow
And there let us wallow
In glorious mud

‘Hippopotamus Song’
Flanders and Swann

The quaking aspen case highlights how notions of individuation of organisms strain our concept of differential success and inheritance. Even if we could individuate all these ‘exotic’ systems into reproducing entities, which *might* be possible in cases of fragmentation or through sexual reproduction, we will still have to account for the interactions between species and interactions of species and their immediate abiotic surroundings. We also have to account for how those interactions may lead to higher level organized systems that will not be individuated in a way that translates into an offspring view of evolutionary success.

Community or ecosystem evolution (i.e. the evolution of a group of different species not reducible to the evolution of individual species composing the community or the ecosystem) had until very recently not been identified as a genuine evolutionary process (although many believed it was at least a theoretical possibility). It was believed to be epiphenomenal (Hoffman 1979) or at least very unlikely (Hull 1980)[13]. Some,

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[13] Maybe surprisingly the question is rarely whether communities or ecosystems exist (i.e. they have a distinct ontology) but solely whether they evolve. There is a real question concerning the boundaries of

including Lewontin, were much more optimistic about the possibility of ecosystem evolution but ecosystem selection (and response to it) never got more than a theoretical nod[14]. Part of the operational difficulty in testing the ecosystem evolution hypothesis was a problem of physical scale. How can one go about 'measuring' the evolutionary fate of a whole ecosystem? Ecosystems are relatively large and it will be very difficult to account for all the species constituting it and a fortiori the interactions between them. But when one realizes that ecosystem or communities to not have to be 'large' relative to human scale, testing evolutionary hypothesis becomes much more manageable.

In recent artificial selection experiments, a good case for artificial ecosystem selection can be made. Consider the experiments of Swenson et al[15]. In the journal "Environmental microbiology" (Swenson, Arendt and D.S. Wilson 2000) and in the "Proceedings of the National Academy of Science" (Swenson, D.S. Wilson and Elias 2000), Swenson and others describe three experiments in which artificial selection shapes the phenotype of whole ecosystems and those ecosystems seem to evolve through time.

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these ecosystems and whether these entities can evolve. Just as it will be the case in our exposition of the termite mound case, the boundary question and the evolution question are intertwined.

[14] "At yet higher levels, the species and the community, natural selection obviously must occur. (…) The same is true of communities whose stability of composition depends upon the interaction among their constituent species." (Lewontin 1970, 15). It should be noted that Lewontin's support of the idea is mitigated by the relative silence concerning operational details (whereas he is more explicit concerning lower levels of organization). Lewontin in fact did not think that evolution above the organism would play a significant evolutionary role because of the difficulty of having heritable fitness differences above the organismic level.

[15] It should be noted that David Sloan Wilson is involved in both experiments as well which is not surprising given his involvement in the group selection debate (see for example Sober and Wilson 1998). See also Johnson and Boerlijst 2002 who provide a good survey of the community selection debate and how it is related to the group selection debate.

In all cases, Swenson et al. chose mud samples as ecosystems and try to select "intergenerationally" for a certain phenotype.

Let me briefly describe one of their artificial ecosystem selection experiments: 2ml of sediment (full of dirt, bacteria, etc) and 28 ml of water from a pond are placed in each of 72 test tubes. Those test tubes are then incubated. Each tube is then measured for pH level (which is the arbitrary trait the authors chose to select on). pH level is a good trait to measure phenotypic change in biotas since its level is not solely a feature of the micro-organisms living in the dirt but is also a feature of the physical substrate, the dirt, and the water as well; this fact reduces the likelihood that fluctuations in pH level can easily be reduced the individual species' fluctuation in pH level. From the 6 test tubes with the highest pH, 5 ml of mud are removed and 25 ml of autoclaved pond mixture are added to each 5ml sample. This selection was repeated for 40 3.5-day 'generations'. An increase in Ph level was observed at every 'generation'. As strange as it seems the mud samples produced the phenotype that enabled them to "survive" in this artificial selective environment. And more importantly the phenotypes were stable enough so that the increase in pH level actually was retained across 'generation' and amplified across time.

Swenson et al. aimed at showing that higher level units of selection could in fact evolve in a way not reducible to individual component species fitness increases. By showing how small malleable ecosystems could be artificially selected to obtain a desired trait (in this case higher pH level) Swenson et al. suggest that, at least in theory, we could observe the same thing in nature. To make sense of biotal evolution, defining fitness in terms of offspring numbers will only take us so far, since ecosystems do not reproduce–

we will come back to this question in much more details in the next chapter when we examine Van Valen's framework and its application to biotal evolution. There is internal competition between micro-organisms in the mud sample, but Swenson et al. argue that the overall phenotype is not reducible to the addition of individual pH level of the micro-organisms: a trait of the whole system (i.e. higher pH) is selected for. Moreover, ecosystems are defined as the interaction between biotic components and abiotic components[16]. Since the abiotic components cannot reproduce, community evolution probably cannot be reduced to reproductive success.

In a teleological caricature we could say that the only way for the mud to increase its likelihood to persist is if it changes its pH level… and it does so without reproducing. Again I am not claiming that reproduction is not involved at all here (contrary to the aspen case), but I am claiming that reproduction is not the sole salient feature to explain the transformation of the phenotype of the biota as a whole.

Consider the following thought experiment (not part of Swenson's et al. work). Imagine for a moment that a higher pH leads to slower erosion. The patches of mud with a higher pH would persist whereas the ones with lower pH would erode. There is natural selection here in the same way that there was natural selection in Van Valen's granite example.

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[16] As Hoffman puts it: "communities are claimed to be real biological units each of which is defined by its particular taxonomic composition and ecological structure. The latter term encompasses both biotic (i.e. trophic, behavioral, allelochemic, etc.) interactions among all community members and the totality of autecological relationships of community members to their physical environment." (Hoffman 1979, 364).

But is there evolution? If the patch of mud only gets smaller and smaller there is just natural selection. Suppose the patch eventually stabilizes, and then grows thanks in part to reproductive success of some of its micro-organisms but also possibly the chemical reactions of the physical substrate surrounding it[17]. Suppose further that the pH increases (leading to even less effects of erosion). Then it seems we have evolution by natural selection –we observe a response to selection- even though offspring contribution might not be the best way to describe the evolutionary change. But intuitively there is a way to define the fitness of that patch. The patch "offered" a better solution to a design-problem. The patch's fitness may still be a propensity (it may be a propensity to have a higher pH in this case) but it isn't defined in offspring contribution since the patch may expand (or at least increase its capacity to persist) without really reproducing.

If an ever changing phenotype (in this case the change in pH) permits an entity (in this case the mud patch) to fight eradication and that phenotype is changing in response to pressures from the environment, and that those changes in phenotype are passed on and 'accumulate' over time ever increasing the entity's persistence, the question should not be whether or not it evolves, but how should we construe its evolution.

Swenson et al. have artificially selected for a phenotype at the ecosystem level. What in fact remains debatable is whether this experiment validates the conclusion (which they do not explicitly make) that the ecosystem is evolving in a non-reproductive way. As I have already pointed out, there is differential reproduction here (in the

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[17] The pH differential could help bond new dirt to the existing patch while the more acidic portion of the mud patch erodes away: or maybe the more welcoming basic milieu could attract new organisms which would increase the volume of the patch.

organisms inhabiting those patches) but the pH is in a very significant way a feature of the abiotic substrate as well. It would actually be surprising if the increase in pH could be reduced to the increase reproduction of some species in the ecosystem without any changes in the pH level being caused by non-biological chemical interactions.

The most controversial aspect of this thought experiment is the idea that the patch could increase in size (in analogy to the growth of the aspen) via non-biological processes, making reproduction of biological organisms ancillary or at least insufficient to explain the persistence of the patch. But the argument would hold even if we rejected the possibility of the 'growth' of the patch. The section of the patch with the higher pH could remain the same in size while other sections erode. If the size of the patch remains constant, and the pH increases, reducing the possibility of the erosion, there is adaptation of some kind (in the same way that a population of organisms can adapt even if the absolute number of constituent organisms remains constant).

Swenson et al.'s data is more suggestive than really conclusive (they admit as much), and therefore, my thought experiment derived from their experiments is only intended to suggest possibilities of extending our understanding of evolution. My intention is to shift our intuitions away from reproduction: if a population of 1 (1 patch) with many components (biotic and abiotic) changes its features (via changes in its components) in response to pressures from the environment and if those changes reduce the possibility of the patch disappearing, we should not try to look for 'daughter' patches in order for us to have a reproductive handle on the evolution and we should be comfortable with describing such change as evolution by natural selection.

A provisional conclusion is that offspring numbers may not be adequate to explain all evolutionary phenomena. To adequately define fitness we need to expand our perspective of it, to include persistence through time. Indeed we may go further and view persistence as the one and only overarching design-problem to which each adaptive trait is a solution. If we wish to examine two biotas, couldn't we compare their relative fitness in terms of their capacity to still be there in x number of years?

By definition, if fitness is defined in terms of reproductive success expected or otherwise, then we have to say, that the biota is not evolving (unless it is in fact reproducing). But if the biota's phenotype is changing, and that change contributes to its persistence, it seems, our theories have to adapt, just as the mud patch did.

This artificial ecosystem selection example is interesting for it highlights how complex interactions between multiple species and non-biotic material can lead to seemingly a higher level of organization. The resulting system appears to be responding to selective pressures in a way that may go beyond the reproductive success of any given participant species. But as Swenson et al. recognize this case lacks important information about mechanisms:

> A second criticism is that we do not know the species composition (or the genetic composition within species) of the ecosystems that we have selected. If we haven't identified the actual strains of microbes and how they interact with each other, isn't our research sloppy? Again, most artificial selection experiments at the individual level are conducted entirely in terms of phenotypes without detailed knowledge of the genetic and physiological mechanisms that underlie the response to selection. Details of the phenotypic response to selection often are used to infer underlying mechanisms (e.g., particulate inheritance in the case of Mendel, or additive vs. epistatic genetic interactions in the case of modern quantitative genetics research), but this is also true in the case of our experiments, which point to complex interactions as a source of

> phenotypic variation and heritability. Mechanistic knowledge is always desirable but is not required to conduct an artificial selection experiment. Indeed, it is strength of evolutionary thinking in general that it can proceed so far in the absence of mechanistic understanding. Darwin's theory of natural selection was developed in complete ignorance of the mechanistic basis of inheritance. Following Darwin, it is a legitimate research strategy to first demonstrate the existence of heritable phenotypic variation at the ecosystem level, and only then to attempt to understand its mechanistic basis. (Swenson et al. 2000, 9113)

The question may ultimately be whether the evolutionary success of the ecosystem as a whole screens off (in Salmon's 1971 sense[18]) the aggregation of phenotypic changes in individual species. This is not a recent worry; in fact evolution was seen by some as the criterion for recognizing the ontology of communities in the first place:

> If the community concept is to resist Occam's Razor, selection value assigned to communities as to be considered as irreducible to or indeducible from characteristics of the component populations and even more so from those of individuals. This implies that there exist some ecological and evolutionary processes acting directly upon communities which through their mediation affect the component populations and individuals. (Hoffman 1979, 366)

Hoffman ends up finding no selection value for the communities he is looking at, but it isn't clear that the artificial ecosystem selection experiments examined here suffer the same fate.

Remember, my claim is not that reproductive success is not involved at all in the increase of pH level, rather, it is that in some sense we cannot attribute partial increases

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[18] Brandon in applying Salmon's concept to evolutionary explanations describes screening off as such: "if *A* renders *B* statistically irrelevant with respect to outcome *E* but not vice versa, then *A* is a better causal explainer of *E* than is *B*" (Brandon 1990, 82-83).

of pH solely to the creation of particular offspring. The pH of the ecosystem is more than the sum of the pH of its offspring parts since the ecosystem also includes abiotic material that has its own pH level, and this value may change by virtue of chemical interactions alone.

But how are such changes in pH passed on from ‘one’ ecosystem/test-tube to another beyond the success and failures of its constitutive species? The problem of heritability is of course urgent. It is one thing for Swenson et al. to say they haven’t identified the genetic mechanisms of inheritance involved in this phenotypic change, but another to say that anything beyond the genetic is inherited. Although the abiotic portion of the ecosystem has its own pH level, it hasn’t been shown that the abiotic contribution in the pH fluctuates at all. Without such fluctuation, the ecosystem trait might in fact be reducible to the pH level of component species.

In the quaking aspen section I have already alluded to the possibility that in some sense, the spatial location (and the benefits or disadvantages it provides) is inherited by individual ramet. Future changes can only depart from the position at the present. Such inheritance is not available to the ecosystem selection case. A more complex chemical story is needed. For this reason, the ecosystem selection remains speculative, but suggestive nonetheless. But once again, we should see Swenson et al.’s experiment for its programmatic value. They have found good indication that community level adaptation is possible and such adaptation if truly a community level phenomenon does not depend on differential replication of the ecosystem itself. If as I have suggested the fluctuations in pH level may in part be due to the abiotic material, then persistence might be a better way to describe the adaptive strategy.

Whereas the aspen was a case that demanded a non-offspring centered view of evolution by natural selection, this is not necessarily apparent in the ecosystem case. The reason ecosystem selection was presented was to show how dropping the differential *reproductive* success condition, in favor of differential success of parts might permit us a more appropriate description of the evolution happening in these cases.

Thinking about ecosystem evolution and community evolution weakens the rigidity of the reproductive success condition. As such, Swenson et al.'s experiments are another indication that a new account of fitness is needed.

The next section will take the notion that abiotic material should be taken into consideration as part of the community, one step further.

2.3 Turner extended organism

In a recent book, Turner (2000) argues that some physical structures that are built or co-opted by organisms should be understood as external 'organs' used by those organisms to survive. Turner is advocating that we reject the absolute separation of organisms and their environments: some elements of the environments should be seen as integral parts of the organisms not solely as the external medium that molds organisms by natural selection. This argument is useful for our purposes since it strengthens the case for a non offspring centric view of fitness: if, as Turner argues, some physical structures (e.g. a nest) should be understood as an organ built by an organism, then we have to include non-biological materials and structures in our definition of an evolving individual. If an evolving individual may be in part non-biological, then it is possible 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. Our ultimate argument will be more sophisticated than this but for now simply keep in mind that Turner's case suggests that system that aren't exclusively biological can evolve. Since it is usually believed that reproduction is a property exclusive to biological system, Turner's suggestion might lead us to question the *raison d'être* of reproduction in evolutionary processes.

Turner argues that there is a selective environment distinct from the organism but he argues that its boundaries should not always be drawn at the 'skin' of the organism. As Turner himself acknowledges (and as is intimated from the title of the book itself), the book's impetus is given by Dawkins' description of the extended phenotype of the genotype. At the very onset of the book, Turner remarks that "the idea that external structures are properly parts of the animals that build them really is not a new idea: the notion of an "extended phenotype," as Richard Dawkins has so aptly termed it, is well established" (Turner 2000, 2). As becomes clearer throughout the book however (and becomes evident in the last chapter where he entertains the Gaïa hypothesis), the physical structures that he describes cannot all be genetically inherited. It is therefore doubtful that Dawkins would be happy with this type of 'extension' of his theory.

Turner embraces the Neodarwinian shift away from the exclusive focus on the organism, but he cannot coherently embrace the genetic reductionism that seems to be linked to some degree or another to Neodarwinism[19]. After all, Turner's account, as we will see in this section, demands some sort of epigenetic inheritance mechanism which cannot be fully incorporated in an orthodox Neodarwinian framework.

Not all of Turner theses will be discussed here: his whole argument is multi-faceted and goes from boundaries of organisms, to evolutionary success as a fight against thermodynamic loss of organization, to the Gaïa hypothesis. But the central theme that will be examined here is that the unfolding of certain physical structures is the result of evolution by natural selection not merely as an effect of organisms' behavior on their environment but as the development by the organisms of non-biological adaptive external structures as organs. For brevity of exposition I will only describe some of the most salient features of Turner's example. One should not infer from my exposition that the mechanisms involved are simple. Turner scrupulously goes through the details of all chemical and ecological mechanisms involved in all the cases he presents. Any exposition of his views will necessarily gloss over the detailed mechanics of each of his cases. I will begin by examining homeostasis in beehives which Turner uses as an example of how a superorganism can maintain its own emergent homeostasis. This section will highlight some of the difficulty colonial organisms pose for the received

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[19] The claim that Neodarwinism is gene-reductionism might be surprising to some but insofar as neo-Darwinism describes evolution in terms of change in gene frequencies, and insofar as genes are viewed as the best if not only efficient means of inheritance, there is some reductionist impetus (in a loose sense) to this understanding of evolution.

view of evolution. Building on these ideas, we will then examine the termite mound, where such homeostatic mechanisms in colonial organisms achieve new heights of sophistication: the construction of a termite mound as an external organ for the colony.

Finally, we will use the interaction between the mound construction and the termite colony of an example of how a system can evolve *sans* reproduction. The upshot will be another indication that capacity to persist might be the property that we need to examine in order to account for all cases of evolution by natural selection.

2.3.1 Physiology, colonies and homeostasis

The main issue is energy transfer. This idea will be extended in the next chapter with Leigh Van Valen's argument detailing how biotal-level organization is used to manage various energy transfers. Turner, self-described physiologist, defines physiology as "essentially how animals (…) use energy to do order-producing work" (Turner 2000, 24). Turner often uses the fluid meaning of the word 'work' to his advantage. When he defines physiology as the study of how organisms work, he uses 'work' to describe how organisms 'mechanically' function (the standard use in physiology) but elsewhere he uses 'work' in physics' sense, work as transfer of energy. By co-opting that second meaning he implies that physiology has always been about energy transfer which would surprise many physiologists. With this generous definition of physiology as energy used to do order producing work, it will not be surprising that external features of the environment will be seen as part of the organism's physiology.

What is latent in this definition however is that organisms basically try to fight the rise of disorder, or entropy, in the universe[20]. Thus homeostasis, insofar as it fights fluctuation in the 'internal' environment of the organism is a crucial aspect of physiology for Turner. Individual organisms clearly have homeostatic mechanisms, but can the same be said of certain colonies of organisms or social insects?

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? These are not trivial questions. They address a theoretical issue seldom made explicit in biology: the conception of all possible ways by which a complex organism can be created in evolution. (E.O. Wilson 1974, 54)

Turner is sympathetic to this line of questioning and argues that some social insects such as ants, wasps, bees and termites, can foster what he refers to as 'social homeostasis', "referring to the supposed regulation of the physical environment of the nest, social homeostasis is the superorganismal analogue of homeostasis (or, as I shall call it from here on, organismal homeostasis)." (Turner 2000, 180).

Turner is not the first to suggest the idea of social homeostasis. E.O. Wilson defines it (1971, 469) 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,

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[20] A connection between thermodynamics and evolution has been suggested as early as Peirce 1877, Fisher 1930 and more recently by Matthen and Ariew 2002. I wish to bracket any discussion of the evolution/entropy idea. First of all, they are not necessary to evaluate most of Turner's descriptions of organized systems. But more importantly, even if they had been central to his claims, his description of how structures are used to manage energy would still remain instructive for orthogonal reasons which we will now examine.

behavior, and physiology of the group as a whole." What is new in Turner's work is the interpretation of the outcome that such social homeostasis can lead to.

To fix the terms of discussion we will employ Turner's suggested nomenclature[21]:

> 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)

Homeostasis as Turner describes it is the result of a regulatory process to maintain a steady internal state for the colony as a whole. He would argue that it should be distinguished from stability simpliciter which is not necessarily the result of such a process. Although a rock retains its internal structure, Turner my claim that it is not homeostatic for there is no internal structure 'fighting' external environmental fluctuations. Although prima facie, Turner's characterization seems reasonable, I am not certain it warrants a rigid divide between stability and homeostasis. Homeostasis usually refers to the maintenance of some 'ideal' internal temperature, but this restriction is not always respected and the concept is sometimes used to refer to the maintenance of optimal hormonal level for example. If homeostasis can be extended beyond the regulation of temperature, the divided between stability and homeostasis is weakened. After all, the type of chemical bonds that bind molecules do respond to some degree to

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[21] The only exception to our following his nomenclature will be the conflation of nests and mounds. The distinction is not significant in the context we will be developing here, although the distinction is useful when one delves more deeply in the architectural details of mound construction.

micro perturbation of the surrounding electrical field surrounding these molecules and permit the rock to maintain its structure. In a strict sense, rocks are not completely inert objects. This is not to say that they are living systems, but rather that their chemical dynamics might permit them to instantiate a loose definition of homeostasis. I will use the fact that some forms of stability can be understood as homeostatic later in this chapter.

Let us examine how Turner applies the concept of homeostasis to the colony as a whole instead of applying the concept solely to individual organisms as is generally the case.

In order to prepare the ground for the termite mound case, Turner begins by strengthening the case for the superorganism: Turner examines the case of a bee hive well known for its supraorganismic behavior. The bees while in the nest have their own individual body temperature affected by the internal temperature of the nest. The internal temperature of the nest is affected conversely by the external temperature. For the colony to instantiate autonomous social homeostasis, there should be internal hive processes that regulate the internal temperature of the nest as a response to changes in the external environmental temperature. Moreover these regulatory processes should not be reducible to the internal homeostatic processes for each individual bee. In other words, if Turner wishes to argue that there is such a thing as social homeostasis for the whole colony then the overall colony temperature should not be purely dictated by the homeostatic processes of the individual organisms.

The search for autonomous higher level mechanisms resonates in various ways in group selection literature. The problem as Brandon puts it “if the fitness of a group is simply a linear function of the sum of the fitness values of its members, then group “adaptedness” does not screen off all non-group properties from group reproductive success. In particular it does not screen off the aggregate of the individuals’ adaptedness values” (Brandon 1982 reprinted in 1996, 61). In the case of colony evolution, the peculiar reproductive nature of the hive makes the screening off question both more complex and moot: not all ants, bees, wasps, etc. reproduce (the queen reproduces with a only a few selected males) and therefore the individual fitness of individual ants cannot be assessed without recourse to inclusive fitness (see chapter 1).

But it’s not clear how to add up those inclusive fitnesses in a linear way especially given the fact that queens can be numerous within a single nest and replaced, making genetic relatedness very difficult to assess. We will therefore assume that there is a group or colonial level fitness independent or emergent from the aggregation of individual member’s fitnesses. It should be noted that this argument will not apply to all cases of purported group selection but the assumption seems appropriate for complex superorganism like beehives and termite colony. The purported homeostatic mechanisms of the colony should to some degree screen off the individual homeostatic mechanisms. Turner alludes to this problem of identifying truly emergent processes at the colony level:

> Keep in mind also that the stability of hive temperature is not simply a consequence of a large numbers of bees all individually regulating their own body temperatures. (…) on cool mornings bees tend to huddle into a compact cluster. (…) Huddling confines heat within the cluster, and huddling more closely restricts heat loss more. (…) [some bees] located at the outer margin of the cluster, adopt postures that interweave the

> chitinous hairs of each bee with its neighbors, forming a kind of downy coat that helps insulate the cluster. This social differentiation into shivering [to generate heat] and down weaving bees cannot be explained as organismal homeostasis *en masse*. (Turner 2000, 187)

Turner has to show that there is some homeostatic feedback loop emergent at the colony level that is autonomous in some way from the individual homeostatic feedback loops found in each individual bee. Turner begins by noting that the air inside the nest is "more humid, richer in carbon dioxide, and poorer in oxygen than the outside air" (Turner 2000, 187-188) Moreover the relative concentrations of these gases are relatively constant even with fluctuating external conditions. This maintenance of internal nest conditions is in large part the result of an often found behavior of social insects to rapidly and wildly spread alert signals, which Turner calls the 'little big bang'. The defensive swarm of a bee hive is the result of this positive feedback loop: one disturbed bee sends an alarm signal which is relayed and amplified by each bee: one disturbed bee 'tells' the neighboring bee that they should be 'annoyed' and now three annoyed bees (3 x the disturbed signal) tell their neighboring sisters to be annoyed and so on. The 'message' is carried on with surprising speed, the intensity of the signal being amplified exponentially throughout the hive[22].

This positive feedback loop is not only found in fright response. Natural nests have only one opening at the bottom of the nest permitting worker bees to leave and enter

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[22] Let me offer an analogy: one person might be running with a frightened expression, scaring two bystanders who now begin to run as well with that same expression, and now we have three scared 'runners' which scares other bystanders. Bystanders will be 'convinced' to run more effectively by these three runners than by this initial lone 'runner', and so on, and very quickly one scared individual creates a stampede of frightened individuals running away for no well understood reason.

but also permitting some gas exchange. As Turner stresses: “Oxygen and carbon dioxide must move through the hive’s entrance at a rate adequate for the colony’s needs” (Turner 2000, 190). Those needs are a function of the oxygen consumption of the individual bees but if oxygen consumption alone were the driving force, the oxygen flow would be passive. Turner describes how by positioning ‘fanning’ bees at the nest entrance a positive convection of oxygen is created. These ‘fanning’ bees are placing themselves in a cooler environment which is unfavorable for their own individual homeostatic mechanisms. This convection fanning is a very precise mechanism possibly leading to a very finely tuned colony wide homeostatic mechanism:

> Because the ventilatory flux depends upon the number of bees fanning (n_b) and how energetically each individually fans (q_v), the flux of oxygen can be modulated minute-by-minute simply by altering the number and activity of bees recruited to do the fanning. (…) If fanning could be modulated by a meta-loop coupled to oxygen demand, then variation of the hive’s oxygen consumption could be supported with no disruption in the gas consumption of the hive atmosphere: in short, social homeostasis. (Turner 2000, 191)

What makes this case interesting is that the recruitment of fanning bees is regulated by the internal proportion of CO_2. By increasing the internal proportion of carbon dioxide which is easily done artificially we observe an increase in the number of fanning bees. This in part explains why artificial beehives are constructed with two holes (one at the bottom, one on top) reducing the number of bees that have to remain inside the ‘nest’ to maintain the optimal convection but this type of structure demands active participation of the beekeeper in regulating the upper entrance when faced with external temperature fluctuations. The type of complex behavior that the bees at the nest opening exhibit cannot really be understood without a colonial-level perspective on the system involved.

As we shall soon see, the termite mound argument presupposes that the colony is the ‘organism’ that evolves the mound as an external organ. But in order to make the case, Turner needed us to convince us that colonies exist as emergent beings not reducible to the aggregation of their constituent organisms. Bee hives are exhibit A. The intricacies of the beehive activity do not stop there but the ones offered briefly here will suffice for now. To sum up, bee colonies, the closest thing we have to well recognized superorganism seem to demonstrate superorganismic wide homeostatic processes. If one accepts the existence of superorganism the next question is of course a question of morphology. What does a superorganism ‘look like’? Or to put it differently what are the boundaries of the colony?

Turner explains why the beehive makes his case only to some point:

> A bee hive is a relatively passive component in its inhabitants’ social homeostasis. Bees may seal off holes here and there, but the structure of the hive itself does not alter dramatically with the metabolic demands being placed on it-most of the adaptation involves recruitment of workers to particular tasks. (Turner 2000, 194)

Beehives are an excellent example of super-organism but Turner wishes to go further with his termite mound example that we will now examine. Note that Turner does not address the evolution of the beehive, only the current utility of its behavior, assuming a certain selective environment vaguely defined.

To employ the functionalist language so aptly analyzed by Amundson and Lauder[23], Turner (as any physiologist would do) is 'merely' describing the ahistorical causal-role function (or Cummins function[24]) while most evolutionary accounts focus on etiological selective effect functions (or Wright functions[25]). While, following Amundson and Lauder's conclusion, I agree that causal-role functions may have an essential role to play in evolutionary biology, the beehive case (clearly described exclusively in causal-role terms) does not provide a conclusive argument that the nest has evolved as an adaptive structure to the colony. The particular nest structure described by Turner might only be the result of other constraints. The colony then learned to 'deal' with the result of these constraints. Although the case for the nest as a tool for the colony can easily be made (after all the nest *is* used as a shelter) Turner has not shown that it is an organ that has evolved. To show that, Turner would need to provide a selected effect account of the evolution of nest formation.

Turner has offered an intricate description of how a colony regulates its 'internal' milieu, what he called social homeostasis, but he hasn't proven that the nest is more than part the environment of the colony. In other words, the nest is not necessarily an 'organ' built by a superorganism. Insofar as it makes sense to speak in such terms, the boundaries of the superorganism could still be at the surface (skin) of the biological 'components'

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[23] Amundson and Lauder *in* Allen, C., Bekoff, M., and Lauder, G. V. 1998.

[24] See Cummins 1975 and 1983.

[25] See L. Wright 1972, 1973, 1976 (not to be confused with S. Wright).

(termites) which constitute it. What Turner wants to show however is that the boundaries of some organisms extend beyond their ‘skin’.

2.3.2 Termite mound

Turner’s most impressive (in his assessment) example of external physical physiology is the termite mound. One way to understand Turner’s case is to see the mound as merely an external organ produced by the colony. Colonial evolution is itself an indication that offspring-centric views might be incomplete and incapable of describing the evolutionary change going on in these peculiar cases: after all, colonies do not always reproduce per se and their ‘success’ is not measured by the number of daughter colonies they can produce. The problem is in part the complex population structures where multiple queens can inhabit the colony and be replaced at various times making any attempt to offer a complicated kin selection story that could be accommodated by received views less likely.

Aside from the difficult aspect of describing the population structure, social insects in particular exhibit very complex and sophisticated behaviors, one of them being nest/mound construction.

While Turner’s is not the first attempt to understand the *raison d’être* of the nest, most previous accounts of superorganisms have focused on the social aspect of the colony. My decision to focus on Turner instead of more comprehensive studies of social insects such as E.O. Wilson classic 1971 work stems from the fact that the latter focuses almost exclusively on the social nature of the interactions while Turner’s focuses on the physiological nature of the interaction. Although E.O. Wilson does mention external physical structures such as termite mounds, he does not see them as integral parts of the social colony but as more efficient tools or barriers produced by the colony. This distinction is more than merely a semantic squabble since as we will see, Turner’s case is in some sense not interested in the specific social structure of the colony, since various caste structures could evolve the same ‘external’ organs. This is not to say that Turner dismisses E.O. Wilson (in fact the Turner’s discussion of the honeybee examined in this chapter is heavily inspired from chapter 16 of E.O. Wilson 1971) but rather that he understands the ‘external’ physiology as being as important as the sociality in understanding the evolutionary success of the colony, whereas E.O. Wilson understands the mound as being a by-product of the social colony.

Other examples of explanations of the existence of the nest can be found in Gordon (in Oyama, Griffiths and Gray 2001) whose work on social insects is used to bolster DST claims: the social colony is actively changing the environment (following Lewontin’s 1983 description of niche construction). As previously noted, Turner offers one of the first serious account of mound as genuinely being a part or organ of the colony.

For the physical structure to be an adaptive structure, it has to be able to be fine-tuned in the organism or superorganism that possesses it in response to selective pressures from the environment. Turner offers such an account with the termite mound case, by describing the dynamic nature of mound formation: by describing how both the mound and the termite colony change in response to external environmental pressures and those changes are beneficial to the survival of the termite colony, Turner is describing a selective effect functional account for the mound. He needs such an account to show that the mound is an evolved physical external organ of the colony as a whole.

It will be difficult to prove that any structure is the result of adaptation for a group of social organisms since, since social behaviors are difficult to fossilize (but not necessarily impossible[26]) and therefore it will be difficult to prove that those structures are the result of a slow accumulation of small changes in phenotype of the colony as a whole. On a much smaller timescale however, if it can be shown that some physical structures are beneficial to a group and if those structures may replace the long term evolution of more intricate internal biological structure, and more importantly that those external structures are constantly 'tweaked' by the colony in response to environmental cues, then Turner might have a case that some physical structures are to be understood as evolved organs, as adaptive structures.

Turner's use of termites as the ultimate test case for his idea of 'external structures as organs' is partially historically motivated. As he notes, termite mounds as a an example of superorganism were described in details in the work of the entomologist Martin Lüscher (1961). Lüscher claimed that "the mounds of *Macrotermes natalensis*, a

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[26] Human artifacts are good example of this. Archeologists infer complex social behaviors by 'simple' artifacts found in archeological digs. But the quality of the inference provided depends on the richness of the site in those socially produced tools. The American constitution or some other social contract is a very instructive tool that could be used as grounds for inferring (rightfully or not) the existence of some superorganism. But not surprisingly such contracts cannot be found for other species and therefore the evolution of superorganism and a fortiori the evolution of physical structures as organs for these superorganisms is mostly theoretical which is not to say that they should be rejected as such.

southern African termite, functioned as colossal heart-lung machines for the colony" (Turner 2000, 195). Although Turner arrives at a slightly different conclusion concerning the role of the mound, he does endorse the type of analysis presented by Lüscher. Turner rejects Lüscher's conclusion for it wrongly assumes that the external surface of the mound will be cooler than the mound interior (which is empirically false) and more importantly, Lüscher describes the mound as a way for the colony to isolate itself *completely* from the external selective environment. This is a fatal flaw, in Turner's opinion, for "if the mound cannot interact energetically with the outside environment, how can the performance of the mound be assessed and adjusted?" (Turner 2000, 197).

This idea of constant assessing and adjusting is necessary for Turner's claim that the mound is an evolved organ: for the mound to be an adaptive structure it needs to be modified in response to selective structure. For both rhetorical reasons (Turner *wants* the mound to be adjusted), and empirical adequacy (Lüscher is wrong about the thermal makeup of the mound structure), Turner offers his own novel description of mound structure and the dynamic processes that guide its development and maintenance.

First, Turner argues that most termite species do not actually isolate themselves completely from the external world: for example most mounds are built with large holes to increase airflow. Lüscher's termite species (*Macrotermes natalensis*) do built better insulated mounds than its sister species but Turner will make the case that completely closed mounds such as those of *M. natalensis* do in fact interact energetically with the external environment. Turner's species of interest is a closely related termite *Macrotermes michaelseni*: "The principal difference between the two is a tall cylindrical spire that tops the conical mound of *M. michaelseni*. This spire, which has a pronounced northward tilt, can extend the mound to substantial heights, as high as 9 meters." (Turner 2000, 198)

The northward tilt is a good hint that thermal regulation is part of the explanation for the architectural 'preference'. Turner does not address this crucial scientific point but Boy Scout folk science tells us that moss grows often on the north side of trees (and moss can therefore be used as an emergency compass of sorts). In fact there is some empirical evidence for this and the explanation is simple. In the middle latitudes of the northern hemisphere (where incidentally most Boy scouts go camping!) the southern portion of any standing object will get slightly more sunlight than the northern surface. Since moss grows more easily on damp cooler surfaces, we observe slightly more moss on northern surfaces than on southern surfaces. Is there some type of similar thermal bias in spire formation in termites? Since those mounds are to be found in the middle latitudes of the *southern* hemisphere, we know that it will not be exactly the same story. In fact, Turner does not explain this peculiar orientation fact although he does explain how the particular shape of the mound is significant and how it is shaped by wind patterns.

Turner's explanation is intriguing: the explanation is to be found in Bernoulli effects. We know that when "air is accelerated around an object, a negative suction pressure results" (Turner 2000, 198). By extending the spire high enough, the mound creates a complex pressure field around its surface. Turner offers a detailed description of these fields.

> Positive pressures develop at the mound's upwind or leading face, and negative pressures develop at the mound's trailing and lateral faces. (…)

> [The pressures at the top of the spire] can be quite substantial, reaching as high as a few hundred pascals. At the porous walls separating the surface conduits from the outside, the pressures can drive air flow into or out of the surface conduits. If a surface conduit is at the mound’s leading face, fresh air is driven into it. If the surface conduit is at the lateral or trailing face of the mound, air is sucked out of it. (Turner 2000, 198)

Intuitively one could imagine many reasons why this air circulation is ‘good for’ the colony and the individual termites that constitute it, but more needs to be said to make this structure into an adaptive structure for the colony. Without going too deep into the elaborate description Turner offers, suffice it to say that the mound is segmented into stable and unstable ‘atmospheric zones’. The colony consumes oxygen and produces carbon dioxide. In order for the colony to grow, it needs to evacuate some of the carbon dioxide and let in oxygen from the outside. The convection produced by the pressure differential of the spire sucks CO_2 out and sucks oxygen in. The height of the spire is not the only design feature that the colony has to ‘assess’: wind energy insofar as it affects the pressure and convection around the spire is a significant design constraint. In other words, structures that have the ‘right’ orientation to optimize the convection and subsequent gas exchange, while not being toppled by the prevailing winds, will persist longer than others. In some sense this is where aerodynamics meets evolution: some structures will do better to combat erosion or toppling *and* they will be maintained by the colony in such a way as to combat erosion or toppling caused by the external elements. Turner describes the benefit of an appropriate architectural sense as such:

> Consider what must happen as the colony grows. From its inception (the queen and a few hundred workers in her nuptial brood) to its maturity, the colony’s collective metabolic rate increases by six orders of magnitude. Despite this large increase in demand for oxygen, the composition of the

> nest atmosphere stays pretty constant, with CO_2 concentrations hovering between 2-5 percent of all stages of colony growth. Such large increases of respiratory flux are supported mostly by the upward extension of the mound into sufficiently energetic winds to power a sufficiently high rate of ventilation. (Turner 2000, 200)

The mound is a protection against predators of course, but more importantly it is also a wind turbine permitting the colony to grow in this protected environment while not jeopardizing the metabolic rate of the individual termites. The colony can grow ‘thanks to’ the increase in height in the right direction of the spire that the colony creates through the work of some of its termite members. As was alluded earlier, in Turner criticism of Lüscher’s hypothesis, it is doubtful that the mound is used mainly as a barrier against weather changes. Turner notes that there is wide variation between and within termite species in the degree of isolation created by the mound structure (Turner 2000, 196-197). The mound obviously plays many roles for the colony but what is salient here is that the particular shape of the mound is dictated in part by the metabolic needs of the colony as a whole.

I have not given all the mechanical details but this broad stroke description gives a good idea of Turner’s argument: these spires are created by termite colonies. The particular shape and height of these constructed spires affects the fitness of the colony. This fitness increase translates into the growth of the colony, which in turn affects the shape of the development of the spire. The last claim is the most interesting point in many respects: it reveals the true homeostatic process. If the spire is not built in a way to ‘take advantage’ of the type of winds present in the external environment and the Bernoulli effect they create, CO_2 will not be dissipated at a rate matching the colony’s growth. In other words, if the colony does not build the right spire it will choke and limit its growth to maintain previous gas concentrations.

But how is the feedback loop initiated or how does the colony ‘know’ that it should build spires and how in what shape it should build them? In one respect this is an unfair question: we do not ask how a butterfly knows how to evolve a particular wing pattern. Darwin’s gift to us was to allow for non-teleological explanations of natural processes. On the other hand, it is a fair question in light of the fact that Turner is suggesting that a *superorganism* is evolving in this away adapting by building these wondrous structures. For the butterfly case, we know how they ‘learn’ these wing patterns. Intergenerational change and selection on individual butterflies weeds out the unsuccessful patterns, fostering slightly better patterns. But in the case of the superorganism, there is no intergenerational change to speak of (or at least no intergenerational change at the colonial level). The genetic makeup of the colony remains relatively constant. So how does the ‘learning’ process occur?

We encountered a similar problem with the quaking aspen. Usually the question is posed in terms of inheritance. In sexually reproducing organisms, and many asexually reproducing organisms, the variation within the population followed by the differential reproductive success of the variants, and the somewhat reliable inheritance mechanisms, provide a ‘learning’ mechanism at the species level. But as we have seen in the case of the quaking aspen, variation, inheritance and reproductive success are less straight forwardly applicable and that is also the case for the termite colony. When the population has a size of 1 how can the concept of variation even apply? 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 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 but this phenotype is not 'passed' on through individual termites and their genes. Imagine that ramets grow on a grid and that ramet A has a location of (5,5), imagine that ramets cannot grow farther than one unit way from the previous ramet. Ramet B, an outgrowth of A, could have a position of (5,6) or (6,5) etc. The future phenotype of the ramet *if* that phenotype includes its spatial location is determined in part by the spatial location of the previous "generation" (or more precisely, previous instantiation) and this is passed on by non-genetic means: developmental and, more importantly for the case we now want to examine, physical constraint. Now if it is granted that non-genetic information can be passed on through time, then we can see how the colony learns to build 'good' spires.

The crucial aspect of the 'learning' process is the lack of oxygen as the colony size increases: the 'choking' factor is the regulating process. Let's assume for a moment that bigger colonies are fitter than smaller colonies[27]; let's assume that increase size

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[27] This is not an obvious assumption since remember that not all colonies have offspring colonies per se, or rather it is not appropriate to measure the fitness of these colonies by the potential number of daughter colonies that a colony creates. The number of termites might increase but the number of colony remains relatively constant at 1. A bigger colony contains has more termites than a smaller colony but it does not

minimizes the effects of predation (or the effects of being crushed by hooves). The colony 'tries' to grow to reduce effect of predation and it can only do so if it expels the CO_2 produced in the mound. The way it does so is by building a taller spire that faces the wind in an optimal fashion. The better the spire is at regulating the gas exchange the more the colony can grow, and the more it grows the more it can sustain the development of the spire. This will not go on indefinitely of course; the spire could topple at some point (a physical constraint). There is self-regulation of the growth of the colony in part because of the geological features of the terrain. In a different kind of soil, perhaps the spire could be taller (owing to mud of a different composition, or a different humidity gradient in the air) but basically, the colony is growing an external physical lung and the particular way it does so impacts its fitness.

The spire is built on its previous stage; just like a ramet it cannot grow at any arbitrary position. Let's imagine, for simplicity sake, that a spire is a line in a two-dimensional plane. The spire starts at (3,0). As Turner describes, also assume that there is selective pressure for the colony to raise the spire in a way that maximizes gas exchange. It can then grow towards (2,1) or (3,1) or (4,1). If (2,1) does not actually improve gas exchange for the colony inside the mound, then there is 'choking' and the colony cannot grow which means that spire cannot be raised any further. But since the oxygen needs of the colony do grow, the spire has to be raised in a way that maximizes the gas exchange: spire raising is an outcome of colony behavior. The spatial location of the spire growth is

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necessarily have more offspring colonies than a smaller colony. Complex population structures involving multiple concurrent queens in a single colony, make the idea of 'daughter' colonies more difficult to assess.

a form of variation and this variation is selected on by the metabolic needs of the colony and the physical constraints of the external environment. The resultant spire is in some sense passed on through time since future developments can only build on previous spire stages -termites cannot create a free-floating spire in a better position regardless of the previous stages of the spire. The position is 'inherited' through its mere physical location and the constraints it imposes on future developments of the spire. In this sense, we are close to "an entity that passes on its structure in replication" (Hull 1980, 318). The structure is passed on to future builders and how they modify the plan of the mound will affect the survival of the colony.

There is variation in phenotype but it is in the phenotype of just one individual, namely the colony-mound system (more on this 'individual' later in this chapter). This variation is selected on and the better solutions are passed through time. Thus there is evolution by natural selection but not in the standard sense. We have selection on components of an entity *not* selection on imperfect copies of an entity.

Turner wants to argue that some organisms build external physical 'organs' and that the termite case is the most impressive example of this. But in many respects, the termite case is a strange culmination for his argument. The claim that termite colonies have external physiology is in some sense trivial; either ant colonies are not integrated organisms (and therefore do not have physiologies internal or otherwise), or they are super-organisms but, since super-organisms in general do not have well-recognized boundaries (or a definite ontological status for that matter), why be surprised that they could have external physiology?

Turner is on much firmer footing when examining cases where the organism has well accepted boundaries AND where he can show that it has external ‘organs’. The example of the worm presented much earlier in his book is such a case[28]. In these cases, Turner can show how by a relatively standard application of evolution by natural selection, organism evolve physical structures instead of evolving internal organs.

Turner’s description of how some structures are external physiology raises the question of distinguishing environments, tools and organs. Should the mound be understood as a tool developed by the colony, in some sense ‘merely’ a behavior of the colony or an organ? And insofar as the mound constrains the growth of the colony isn’t it the selective environment as well? Let us address the former question first. Even if the mound were to be described as ‘merely’ a behavior, that would make it part of the phenotype as much as the organs of an organism are. If there can be selection on height, there can be selection on behavior that places you in higher locations, or if someone is uncomfortable with the word ‘behavior’ in this context, replace with ‘position’. If there can be selection for height, there can be selection for certain higher spatial positions of a

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[28] In chapter seven, Turner describes how “by burrowing as they do, I shall argue, earthworms co-opt the soils they inhabit and the tunnels they build to serve as accessory kidneys, ensuring their survival in an essentially uninhabitable environment.”(Turner 2000, 100) Turner explains how the common earthworm does not actually have the physiology necessary for terrestrial life: terrestrial life is desiccating and earthworms do not have the type of kidneys that would allow them to maintain the right water balance inside their bodies. Basically –the full story is much more intricate of course- by living in a particular soil horizon, worms use the features of the soil to maintain a properly hydrated environment that will not extract all the water out of them. This is not a question of merely choosing the best environment in which to live: the worm is actually transforming the environment in order to not have to develop the organs necessary to survive in a terrestrial environment. This quick description is not intended to be convincing for although I believe it is more crucial to Turner’s case than the anthill mound, it is not crucial to my project.

system. Since such spatial system cannot be strictly genetically inherited, other inheritance mechanisms must be involved.

The tool/organ distinction is not as rigid as some would like to believe. Ultimately it comes down to question of inheritance: if the behavior is reliably passed on, then it can be selected on and become an adaptation. Behavior can be phenotype and as such the mound is part of the phenotype of the colony. Turner's argument however shifts our intuitions away from viewing the mound solely as a tool or a barrier, by showing how the shape of the spire changes in response to the needs of the colony in the same way that organs are shaped by natural selection in 'normal' cases of evolution. The mound is more than a tool. The termite mound is the result of what Turner calls a meta-feedback loop. Note however that Turner is not arguing that all animal-built structures are external organs (if this were the case, the mere existence of Beanie babies would be an evident reductio).

As I have pointed out, internally to Turner's argument, the worm case is more helpful; it does in fact show that we need to extend the boundaries of the organism. The anthill case 'merely' shows that we need to redefine what constitutes an organism in the first place. In other words, the worm shows us that what we believed to be a simple 'normal' organism actually has 'external' organs. The anthill case shows us that a system that was previously recognized as ontologically problematic (as all colonial organisms are) has problematic boundaries!

For our purposes however, the colony case remains primary, for it highlights the fact that evolutionary theory is not solely in the business of explaining individual reproducing organisms. This has already been recognized; the novelty is that Turner explicitly includes abiotic material in the definition of the organisms studied. The termite mound case shows us that colonies which were already recognized as being problematic are even more problematic than we have recognized before, for they might be parts of a more complex, non fully biological system.

Let me co-opt the word symbiosis for a moment. Try to imagine the anthill and the ant colonies as two symbionts in a mutualistic symbiotic relationship. The mound cannot reproduce but it can persist; the ant colony can in some fashion reproduce into other ant colonies but it is probably a more appropriate description to say that ants reproduce but the colony grows and persists. We have a relationship between a physical structure and a biological organization that can both benefit (i.e. increase their persistence) if they both develop in a concerted way.

Not surprisingly, Turner is very close to this analysis in the termite mound case: he does entertain the Gaïa hypothesis in the final chapter of the book. The Gaïa hypothesis does claim that the whole planet Earth including its non biological constituents is one integrated homeostatic system/organism. In this context, it is not a leap to conceive of the anthill as one integrated organism constituted of mud and termites. But even if Turner had not been willing to go as far as entertaining the Gaïa hypothesis which after all will be seen by some uncharitable readers as a reductio ad absurdum of his whole argument, a more conservative interpretation of his argument still provides the framework to see the mound-colony interaction as an integrated organismal unit. Turner defines superorganism as “any association of living things that through the coordinated actions of its members, behaves with all the attributes of an organism" (Turner 2000, 179). It seems a fair question, especially in light of his inclusion of external physical structures in the organism's constitution, to ask why limit the association to *living* things. In other words, if, as he recommends throughout the book, we should see beyond the biological to better understand the physiology of organism, what's to stop us from defining superorganism as any association of things that through the coordinated actions of its members, behaves with all the attributes of an organism? By this definition, the anthill-ant symbiotic complex could be seen as a super-organism.

The worry here will be that this semantic shift dilutes the meaning of organism in an unhelpful way. After all, 'organism' is a supremely useful category in evolutionary biology and we should somehow preserve its integrity. But if Turner is correct its integrity should be reexamined.

For nomenclature purposes let us provisionally maintain the current usage of organism as an individual living biological entity. A superorganism however has to be understood as in some cases more than the interaction of living things. Once again, the hierarchical view might again be of help. Some of its defenders provide a definition of interactor that might provide help us extend the nature of superorganisms. Gould and Lloyd (1999), in trying to defend macro-evolution at the species level and beyond, examine some definitions of interactor and hope to find one that can accommodate higher level of organizations. They entertain and then reject a group-selectionist notion of interactor framed by Sober and Wilson as ''level (or levels) at which natural selection actually operates, producing the functional organization implicit in the word 'organism' "

(Sober and D.S. Wilson 1994b, 606). An organism being ‘‘any biological entity whose parts have evolved to function in a harmonious and coordinated fashion’’ (Ibid). Gould and Lloyd reject this definition since it puts the burden on functional integrity. Since Gould and Lloyd are entertaining the possibility of species-individuals, functional integrity is not generous enough a criterion for the higher levels of selection they wish to examine[29]. Provisionally however, functional integrity is sufficient for our purposes: it seems an adequate description of the aspen, the mud samples and the termite case. Ultimately however, if Gould and Lloyd are correct, it might not be sufficient to accommodate all cases of evolution.

In the end, Turner's emphasis on *living* things, in defining superorganisms, might be misguided. Let me anticipate here: Evolutionary Theory describes evolving systems, some of which are biological systems, some of those systems are 'simple individual' organisms. Sometimes evolving biological systems are superorganisms in Turner's sense, and sometimes evolving systems, because they aren't exclusively constituted by living things, are not strictly biological. This idea ultimately could lead us to the conclusion that evolutionary theory is not exclusively about the biological and as such should not be grounded on differential reproductive success. We will come back to this idea in the conclusion of this project.

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[29] "[Sober and Wilson's definition] suggests that if higher units operate as vehicles of selection, then they must work like organisms in the harmony and coordination of their parts. But this claim cannot be supported, for the argument confuses one potential outcome or product of a causal process with the causal process itself. Higher-level selection processes do not necessarily require, nor do they invariably produce, functional organization or harmony of parts." (Gould and Lloyd 1999, 11905).

2.3.3 From fuzzy boundaries to fuzzy definitions of organisms

Turner has argued that organisms do not always have the fixed boundaries that we often attribute them. Moreover, sometimes organisms interact in a way that ‘creates’ a super-organism with its own emergent evolutionary fate. These superorganisms sometimes use physical structures as ‘organs’. What Turner described as an organ (i.e. the anthill) of a superorganism (i.e. the termite colony), I have described as components of symbiotic relationship between a physical structure and a biological community co-dependent on each other in their evolutionary fate. Good symbiotic relationship between mounds and termites persist longer than those that do not, and good relationships can be observed when the phenotype of the whole complex changes ‘appropriately’ in response to pressures from the selective environment (in this case, wind, temperature, predators, etc.) In some weird way, both the mound and the colony persist better when they cooperate and reproductive success will not fully accommodate the success of this cooperation.

2.4 Conclusion

This chapter showed that there can be evolution by natural selection without differential reproductive success. One of the consequences of emphasizing a community approach (as was the case for the ecosystem case) or a societal approach (as was partly the case in the termite colony case) is that the possibility of more complex interactions questions the relative importance of individual organisms: if communities can evolve why demand that an individual organism's fitness can only be tracked by looking at that organism reproductive success. Again, the hierarchical view of evolution needs to be kept at the forefront of our evolutionary inquiry. The claim is not that *all* evolution happens at the ecosystem level and that therefore, individual organisms and their reproduction merely become ancillary processes; rather the claim is that *when* ecosystem evolution happens, it is not reducible to component species evolution. This case as well as the others presented here aimed at reducing the grip of reproduction on our thinking of evolutionary processes.

If complex systems such as mound-colony, clonal systems and whole ecosystems can evolve, we need a metric of some sort for their evolutionary success and reproductive rates cannot play that role. By examining what is increased by the changes in those systems we might find a metric of evolutionary change. In the next chapter, we will examine one relatively good case for a universal metric for fitness –other than reproductive- fares.

Chapter 3 Will it really take time AND energy?

3.0 Introduction

The previous discussion aimed to show how thinking beyond differential reproductive success can be beneficial in explaining at least certain cases of evolution. In this chapter, we will see how one insight derived from paleontological data may provide us with a way to describe the evolutionary cases described in the previous chapter without using offspring contribution. My general argument aims at reducing the foundational appeal of differential reproductive success as defining fitness. As such, paleontology and paleobiology insofar as they look at species which cannot straightforwardly be understood as reproducing in an obvious fashion may provide a source of inspiration.

When thinking in terms of extinction rates or speciation rates, the mainstay of paleobiology, the timescale lends itself to attempts to provide general abstract characterizations that surpass the special localized nature of ecological explanations or the spatio-temporally localized populations of population genetics.
Van Valen suggests that evolution may be better understood in terms of energy control. And such thinking arises in the context of unifying a macro-evolution hypothesis (the Red Queen) to a micro-evolution hypothesis (biotal evolution).

In this chapter, we will examine three Van Valen papers. The first (1973) establishes the notion of a resource space in the context of a new evolutionary law, the second (1989) offers a view of this resource space in energetic terms while the third (1991) presents the study of evolution of biotas as a reason for adopting an energetic framework. I have argued that offspring numbers are not universal measures of fitness. In this chapter, I will argue that the more general metric of energy control suggested by Van Valen is not universal metric sought either and a fortiori cannot be the foundations of our definition of fitness. But before examining Van Valen's work, let me raise a few considerations about macro-evolution and the epistemic point of view that it provides Van Valen. I do not intend a complete survey of macroevolutionary hypotheses, but rather an indication of what such hypotheses might offer evolutionary theory in general.

3.1 Synthesis from top to bottom

Although I have tried to distinguish myself from the Modern Synthesis in some ways, I wish to adopt the scalability of their project (i.e. using the same process to explain both the micro and the macroevolutionary). In the same way that they see change in gene frequencies as explaining all evolutionary change up to the macro-evolutionary species level (Simpson 1944 reprinted 1984), the use of persistence and success of parts in this project is intended as explaining change on many temporal scales and on many levels of organization. So, insofar as most macro-evolutionary projects try to identify autonomous emergent trends at the species level, my project is more in the spirit of the Modern Synthesis which tries to account for all evolution (not just evolution at or above the level of species). But past macro-evolutionary projects are an inspiration as well in that their object is not truly reproductive success.

Serious consideration of macro-evolutionary hypotheses is necessary[1]: aside from the useful epistemic vantage point of looking at large scale trends, any attempt to provide a synthesis of evolutionary explanations demands that we look at all levels of supposed evolution. Theoretical generality demands that any candidate for a law be scalable to all levels of organizations including species, clades and possibly higher levels if evolution occurs. While macroevolution refers to species-level or higher levels of evolutionary change, evolution simpliciter (or microevolution) usually refers to all the evolutionary changes below the level of species. Of course, while the existence and effectiveness of microevolutionary processes is universally accepted (except by creationists of course), macroevolutionary processes is widely contested.

What is most often contested is not the logical possibility of species-level evolutionary change, but the actuality of such change. The consensus imposed by the Modern Synthesis is that the difference between microevolution and macroevolution is a difference of degree and not a difference of kind. As Dobzhansky puts it in the 3rd edition of <u>Genetics and the Origin of Species</u> "The words "microevolution" and

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[1] The renewed interest in macro-evolution is heralded in evo-devo as well After all, Waddington who laid the foundations of evo-devo was trained as a paleontologist which influenced his later work (see Waddington 1953, 1975). Gilbert, Optiz and Raff (1996) describe how macro-evolution, probably the most important casualty of the synthesis is getting a new chance to explain biological phenomena and that it easily fits in to the evo-devo project.

"macroevolution" are relative terms, and have only descriptive meaning; they imply no difference in the underlying causal agencies." (1951, 17). Or as he put it in a less forthcoming fashion in the first edition

> …we are compelled at the present level of knowledge reluctantly to put a sign of equality between the mechanisms of macro- and micro-evolution, and, proceeding on this assumption, to push our investigations as far head as this working hypothesis will permit. (Dobzhansky 1937, 12)

The reluctance, born out of the ignorance of how to make macroevolution 'fit' into the synthesis, was dissipated between the first and third edition thanks to the intervening publication of Simpson's 1944 *Tempo and Mode in Evolution* (reprinted 1984) where Simpson showed how seemingly autonomous macroevolutionary phenomena could be integrated into the 'genetical' understanding of natural selection of the Modern Synthesis. Simpson's efforts to synthesize both macro processes (species and super species level) and micro processes as one continuous progression of organization are not so much a synthesis as a complete elimination. He does not really explain macro-processes via micro-processes but, rather, explains away the apparent phenomena. What seems to be a reduction of macro-evolution to micro-evolution is in fact an elimination of the data that had interested paleontologists in the first place: in Simpson's treatment macro-evolution becomes a mere artifact of large temporal scale data

According to some supporters of macroevolutionary ideas, Simpson glossed over important phenomena to achieve 'his' synthesis. For instance, Raup (1995) describes as somewhat surprising that Simpson does not include extinction as an important process of evolution. That other founding Neodarwinians focused on speciation instead of extinction as a force of evolutionary change is not surprising, but as the 'token' paleontologist, Simpson should have seen how extinction would need to play a part in this 'new' evolutionary theory. As Raup puts it "For an evolutionary biologist to ignore extinction is probably as foolhardy as for a demographer to ignore mortality." (Raup 1994, 6758). Although, to support his own project[2], Raup rhetorically downplays how Simpson did in fact examine extinctions –after all they are the flip-side of his famed survivorship curves- he is correct in that Simpson does not give it an important evolutionary role (which places Simpson's view in sharp contrast with Darwin).

Raup argues that extinction should have been added to Simpson's list of the determinants of evolution (*variability, mutation rate, character of mutations, generation length, population size*, and *natural selection*) Since extinction is exclusively a species level (or above) property, maybe the synthesis between macro and microevolutionary processes would not have been so easy to achieve if Simpson had included extinction as a determinant. Ultimately Raup argues that such mass extinction cannot be 'derived' from or reduced to microevolutionary processes. (See Raup 1992).

Because macroevolution is concerned with species-level (and higher) properties, it might provide us with a degree of generality that we could use to provide a general account of fitness. While the Modern Synthesis was trying to scale up the processes it identified at the micro-level, it might turn out to be more fruitful (at least in some cases) to scale down the processes identified in macro-evolutionary explanations.

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[2] Raup's general programme emphasizes the signification of mass extinctions as a source of evolutionary change.

Many projects in paleobiology and paleontology have attempted to explain fundamental evolutionary phenomena using autonomous species-level trends. Stanley (1975, 1976, 1979) argued that micro-evolution is too slow to explain the observed diversity and adaptation in the organic world and posited that a process *analogous* to natural selection operated at the species level, 'favoring' species that have higher rates of speciation over species with lower rates of speciation. Stanley defended a 'rectangular' (Stanley 1975, 646) view of phyletic change over the 'gradual' view of the usual radiating 'tree of life' representation of phyletic change. As he puts it, evolution proceeds in a "step-wise pattern"[3] (Ibid.).

> The assumption that gradual change within established species is the dominant process of evolution has led many workers to predict that differing rates of evolution among taxa should correlate with generation time because the fate of each generation represents, in effect, a single event of natural selection. The demonstrated absence of such a correlation (19, 20) can be taken as a failure of the gradualistic model. If speciation is the dominant source of evolutionary change, however, rate of evolution should be related not to generation time, but to an equivalent parameter of speciation. (Stanley 1975, 648)

Stanley's attack is obviously misleading. We should not expect generation time alone to be a good indicator of the number of selective event (Simpson 1944 had argued for a similar point). After all, natural selection does not work solely serially but also in parallel: a generation time of 20 years does not give a complete picture of the selection process, for natural selection acts on the individuals forming the population. Therefore, a generation comprising 500 members will offer natural selection much more restricted

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[3] Such 'abrupt' changes followed relative stasis has of course been vocally defended by Eldredge and Gould (1972)

variation than a generation of 10000 members. Generation time is insufficient to describe the extant to which natural selection can cull 'favored' organisms. This being said, Stanley's criticism highlights an important point: if generation time is to be a factor in describing the capacity of a lineage to change in response to natural selection, it will be necessary to show how generation time is linked to the 'life-history' of the whole lineage. This issue will be explored further in the next chapter.

Certain features of Stanley's macro-evolutionary project seem especially relevant to our argument. Stanley points out that "Species selection (…) is most analogous to natural selection in asexual organisms". (Stanley 1975, 648) This last statement is very telling since the Modern Synthesis has, as previously noted, not handled asexual organisms very well. It's not that there isn't any possible way to account for asexual organisms in the Modern Synthesis but rather that in virtue of their 'strange' reproductive cycles they show the possible limitations of some key concepts of the Modern Synthesis. A large contribution of the Modern Synthesis was the concept of biological species offered first by Dobzhansky and then popularized by Mayr. But biological species are individuated by reproductive isolation. Since many clonal organisms are completely reproductively isolated from any other organisms, they, strictly speaking, are species-individuals (i.e. an individual organism being a singleton species).

Whether this constitutes or not a *reductio* of the biological species concept is debatable but the lesson remains: asexual species demand serious accommodations in our best theories. If there is only a difference of degree between species and asexual organisms, then the trends identified at species level may scale down first to asexual organisms and then maybe to sexual organisms as well. For these reasons paleontological inspired projects need serious consideration.

Instead of assuming that *everything* can be explained from the bottom up, let's entertain the possibility that macro-evolutionary data can actually inform our micro-evolutionary explanations. The hope is however to offer a synthesis of a different directionality than the one offered by the Neodarwinists 80 years ago (i.e. synthesizing from top-bottom instead of bottom-up). In some sense this is exactly what Van Valen attempt to do.

3.2 Van Valen's project

In chapter 2, we were confronted with biological cases in which the notion of 'offspring' becomes, if not suspect, mysterious. Depending on whom you ask, growth and clonal reproduction are anomalies that merely stretch the offspring model of fitness, or they are powerful counterexamples of organismal selection. These biological examples have been described earlier in this dissertation (chapter 2) and, together with the limitations of offspring accounts of fitness (see chapter 1), they give the consideration of alternative definitions of fitness a certain urgency.

We are now at an interesting crossroad: I have argued that we should take a second look at macroevolution. Stanley in the end does endorse a reproduction-centric view of fitness by focusing on speciation rates as a measure of the evolutionary success of a species or a taxon: species that have more daughter-species are fitter. But if that is truly his argument, his account cannot be the foundation for the more inclusive explanation of evolutionary change that I am trying to provide. If macro-evolution is to be instructive for our purposes, it needs to not focus on the ‘pseudo-reproduction’ of species.

Leigh Van Valen has been one of the few trying to provide such an alternative account. We will now examine some his suggestions. Although he has offered seemingly disparate evolutionary generalizations, they have over the years gravitated with ever increasing centripetal force towards an account of evolution in terms of increase in energy control (hereafter EC). I will begin with the Van Valen’s 1973 *A New Evolutionary Law* and then move on to related projects developed a few years later. The endpoint of Van Valen’s ideas is the idea that fitness could be construed as increasing energy control (EC). In Chapter 1 we noted that “solving-a-design-problem” definition of fitness is difficult to quantify beyond the measure provided by offspring contribution. If we wish to avoid the measurement problems of the solution-to-a-design-problem account of fitness, we need a definition of fitness that is quantifiable and that permits relevant objective comparisons between entities. Van Valen’s interest in EC is an especially interesting candidate definition of fitness in that it is at least theoretically quantifiable for any given system without counting offspring the metric.

Bock and Wahlert (1965) proposed that energy is the correct measure of fitness. More specifically, they suggested energetic efficiency be used as the means of measuring relative adaptedness. This efficiency is relative to the amount of energy necessary to maintain the organism’s ecological niche. In more conventional terms (see Brandon 1996, 20) we get a definition of relative adaptedness that looks something like this

> *A* is better adapted than *b* in *E* iff *a* requires less energy to maintain successfully its niche in *E* than does *b.*

A major problem as Brandon points out is that this efficiency is ultimately measured by offspring contribution (and Bock and Wahlert seem to admit as much, 1965, 287). By making energy ultimately reducible to offspring contribution, Bock and Wahlert reduce any interest we may have in their energetic view: the cost of adding their theoretical layer to our evolutionary explanations is not offset by any true explanatory benefit. If energetic success were relatively autonomous from reproductive success (even though they might be highly correlated in many cases) then the advantage of shifting away from the consensus view would be more apparent. Van Valen ultimately proposes an energetic metric of fitness independent from –but in many cases overlapping with-offspring contribution.

In chapter 2 we concluded that offspring contribution cannot be the only fitness quantity, since it isn’t general enough to measure all cases of evolution. The criterion of generalization seems intuitive: we seek laws and theories that can encompass as many relevant phenomena as possible. We will see whether energy is a useful way of quantifying fitness demanded by our own account. In the end EC will be rejected but important lessons will be retained.

3.2.1 A New Evolutionary Law

> Death....a great Leveler – a king before whose tremendous majesty shades
> & differences in littleness cannot be discerned – an Alp from whose
> summit all small things are the same size.
> by Mark Twain- Letter to Olivia Clemens, 10/15/1871

In 1973, Leigh Van Valen advanced the now famous Red Queen's Hypothesis. What interests us here is how the Red Queen discussion of 1973 lays the foundations for Van Valen's subsequent projects. Sepkoski offers a useful overview of the magnitude of Van Valen's project: "In [the 1973] paper, Van Valen presented more than 100 taxonomic survivorship curves for approximately 35 phyla, classes, and orders of animals, plants, protists with good fossil records." (Sepkoski 1975, 343) Moreover for an examination of the Red Queen's Hypothesis per se, we might have been better served comparing it with Rosenzweig competing 'Rat Race' hypothesis (1975) and subsequent reformulations of the Red Queen (e.g. Stenseth and Maynard Smith, 1984). It's not even clear that the data identified by Van Valen holds water: For instance McCune (1982) and Salthe (1975) argue that the survivorship curves are not truly linear and that even if they were, Van Valen is 'merely' identifying patterns not genuine new processes.

For Van Valen, the data demanding explanation are the apparent constant extinction rates for given groups[4]. Van Valen suggests the Red Queen's Hypothesis to explain these patterns: in ecological terms, the environment for a given group is stochastically deteriorating at a constant rate. One should understand deterioration of the

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[4] As Van Valen notes however, even though extinction rates are constant over the majority of temporal scales, they are not constant over geological time (see Van Valen 1973, 10-12).

environment in adaptive terms: the environment at t2 has degraded from the environment you were adapted to at t1. If the environment is constantly degrading, one has to adapt simply to stay at the same 'coordinate' in a fluctuating adaptive landscape (defined in resource space), or as Van Valen quotes Lewis Carroll's *Through the looking Glass*: "Now here you see, it takes all the running you can do, to keep in the same place" (Van Valen 1973, 25, n.32). This hypothesis is intended to explain the apparent linearity of extinction curves across taxa.

> The method[5] is an application of the survivorship curve of the population ecology (including demography). It is a simple plot of the proportion of the original sample that survives for various intervals. (…) A logarithmic ordinate, standard in ecology, gives the property that the slope of the curve at any age is proportional to the probability of extinction at that age. (Van Valen 1973, 1)

Van Valen observed uniform linearity of the extinction curves. As he also points out, the linear pattern of constant extinction rate holds even if you include pseudo-extinction, i.e. the evolution of a taxon into another taxon in a succession pattern. He does identify some exceptions but attempts to explain them away either by invoking sampling error or by describing the fluctuations as events of complete destruction of a selective environment (he identifies such massive environmental changes as different in kind from the other more 'normal' environmental fluctuations). Van Valen's law of extinction has in his opinion no actual exceptions and few possible exceptions. "The pattern is therefore sufficiently general that the minor exceptions are best explained by

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[5] See Fig.1 below for an example of the data Van Valen is examining.

unusual circumstances peculiar to each case.” (Van Valen 1973, 10) If one group does not have a linear slope of survivorship, Van Valen assumes that truly unexpected events (e.g. mass extinction or complete environmental shift) shift the curve away from his ‘expected’ linear curve. Basically the exceptions are explained by them not belonging to the appropriate reference class.

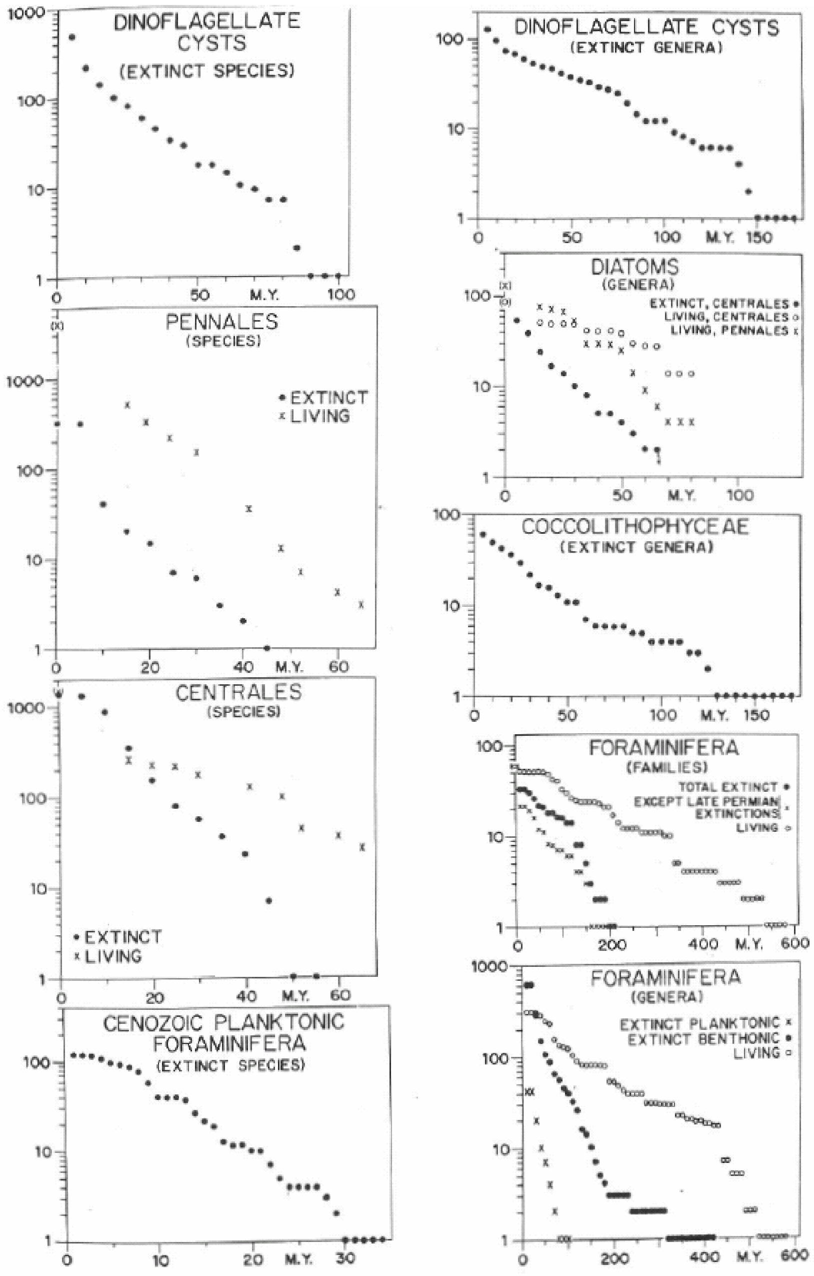

Fig. 1. Taxonomic survivorship curves for protists.

Figure 1: Examples of Van Valen's data

From Van Valen (1973, 2). Some examples of the "linear" data that Van Valen wishes to explain. The X axis is divided in millions of years (NOT chronological but duration), while the Y axis represents the surviving proportion from the original group.

He offers the ‘macarthur’[6] or *ma* as the unit of extinction rate or more generally the rate at which the probability of an event per 500 years is 0.5. These *ma* are found to be constant for all the taxa he examined[7]. The problem is that ‘perfect’ linearity should not be expected: concave survivorship curves should be expected. Taxa occupying larger spatial area –in real space *not* in resource space- are harder to stamp out and therefore, older taxa are ‘probably’ harder stamp to out since they have had more time to increase the area they occupy. We should therefore have declining *ma* for extinction since with time the probability that the taxa will occupy a larger area increases[8]. In other words, the linearity observed in the survivorship graphs, does not match ecological assumptions concerning the difficulty of younger, less spread out, taxa to persist: in fact the whole project makes the strong Markhovian assumption that present survivorship probability is independent from previous probabilities. As Van Valen points out, his data implies that “The probability of extinction of a taxon is then effectively independent of its age” (Van Valen 1973, 17)

After examining (and ultimately rejecting) various explanations to explain the linearity as merely data artifacts, Van Valen concludes that “extinction in any adaptive zone occurs at a stochastically constant rate” (Van Valen 1973, 16). This is actually a

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[6] In honor of Robert H. MacArthur and his work on extinction and ecology.

[7] See Reed McCune (1982) for various ways of interpreting this notion of ‘constancy’.

[8] Although Van Valen does not make the connection in this paper, the assumption of increasing probability of increase area control is analogous to the predictions made in statistical mechanics: larger volumes in some hyperspace are more probable at later times. I do not defend any strong claim in drawing this analogy. I find it merely interesting that the thermodynamical language keeps rearing its ugly head…

reformulation of what he sees as the new ‘law’ namely that “The effective environment of the members of any homogeneous group of organisms deteriorates at a stochastically constant rate” (ibid). Since he does not believe his law is exceptionless, it is doubtful that his law is as robust as laws found in physics, but his principle can be seen as an attempt to provide a principle more general than any previous attempt[9].

The constancy of the extinction rates is the result of the constant ‘attempt’ of individuals and the groups they are aggregating in to resist the changes in the resource environment. But since every group is in competition for limited resources, there is a deterioration of the ‘initial’ selective conditions for any given group, making past adaptations less and less advantageous.

> We can think of the Red Queen’s Hypothesis in terms of an unorthodox game theory. To a good approximation, each species is part of a zero-sum game against other species. (…) Furthermore, no species can ever win, and new adversaries grinningly replace the losers. (Van Valen 1973, 21)

This is the first step towards Van Valen’s EC account: environmental degradation is described in terms of shift in controlled resources. Ultimately he attempts to apply some sort of game theory literally to extinction cases.

> The adaptive landscape is a resource space. The amount of resources is fixed and can be thought of as an incompressible gel neutrally stable in configuration, supporting the peaks and ridges. If one peak is diminished there must be an equal total increase elsewhere, in one related peak or more uniform. (Van Valen 1973, 19)

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[9] Van Valen actually wrote on the subject of generalizations and laws (see Van Valen 1972) and argues for the value historical laws that will not meet more positivist notions of laws. His case is too vague to be addressed here. For a more thorough related argument see Rosenberg (2001).

Although the leap to energy is not explicitly made in the 1973 paper, the foundations for an energy-account are all there. Van Valen in facts only offers a somewhat hand-waving definition of ‘resource’ in terms of predation, food source, etc. but in later papers he focuses more on energy for it seems to be the best way to provide a unified resource landscape in which different kinds of species could be represented. As will become salient later in our analysis of Van Valen’s project, he points out (Ibid. 19) that the ‘momentary fitness’ of a species corresponds to the amount of resources controlled at that time i.e. actual energetic control at t. This will be a problem in his subsequent accounts for Van Valen makes no room for efficiency as adaptational; more generally, in Van Valen’ theory, there is no ‘premium’ for *potential* access to energy. The issue of efficiency will be explored in the next section.

With our limited examination of the Red Queen’s Hypothesis, we can see how the energetic paradigm is foreshadowed in Van Valen’s paleontological work. By looking at very general trends, Van Valen reaches the conclusion that at any given time, there are limited resources (which probably can be measured in energetic terms), and that those resources are fought over by all species sharing a given adaptive zone[10]. This struggle changes the energetic environment in a way that make past adaptations less advantageous than they were. This constant catch-up battle between evolving species and the changing environment cannot be avoided or won which ultimately leads to extinction.

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[10] For a thorough discussion of the concept of adaptive zone, see Van Valen (1971). Most of the discussion is however not crucial for our purposes. The zones are section of the resource space. That resource space is inspired explicitly (Van Valen 1971, 420, n.1) from Wright’s adaptive landscape.

Given the highly theoretical nature of the language used by Van Valen, some potential confusion needs to be addressed. Van Valen is not arguing that there is no adaptation or phenotypic change in the face of an inexorable culling. When Van Valen points out that a species is running to stay in place, the race is not in morphological space but in resource-control space. What this means is that adaptation is still possible, for it is the way that species try to fight a changing resource space (and by their adaptation they are shifting the resource space for other species and so on). In fact the given capacity of a species to adapt explains in part the particular slope of each extinction curve.

The constant arms race described by Darwin means that yesterday's solution has affected how your competition adapts, which changes their response which makes your past solution less optimal than it might have been before. The branching by species means that new competitors are always there to make one's past 'successes' less adequate. Basically Van Valen is claiming that all species have a fixed expiration date…

The biggest benefit I hope to extract from this complicated attempt at a quantitative evolutionary law is the realization that in order to provide any universal statement of evolution, a universal metric must be obtained. The best way to explain the constant extinction rates described by Van Valen is in terms of decaying resource environment for particular species. The implied metric is energy and, depending on how you define the 'size' of the resource space, the metric suggests the possibility of comparing the fitness between species and even between non-contemporary species.

Van Valen implies that the size of the overall energetic 'pie' remains relatively constant through time. The idea that the resource space is an "incompressible gel" (see quote above) implies the immutability of the resource pie[11]. But more importantly Van Valen rejects (without empirical justification) the possibility that the resource space could shrink or increase (Van Valen 1973, 19). Or rather he rejects the idea that such fluctuations have a significant evolutionary effect: only the relative size of the resource slice that any given species controls at any given time matters.

This idea leads us to the surprising conclusion that Van Valen is defending an idea of absolute fitness. Although he claims that fitness is a relative notion since it is 'merely' the proportion of the resource space controlled by a species at a given time, it is actually an absolute notion if the resource space as a definite and unchanging size. In other words, if species A is controlling X % of a resource space, that species is controlling Y joules of that resource space. But if that resource space is unchanging in total size then we can make absolute fitness comparisons across species and time since what matters is how much resource is controlled not the specific date at which one controls it[12]: a bigger slice of pie is *always* better and if the pie does not change in size you can compare slices at different times. Species A is fitter at t1 than Species B at t2 because it is controlling Y joules more than Species B *regardless* of the time one is interested in. A caricature of this could be that in extending Van Valen's model we can

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[11] *Pace* a current political leader, one cannot 'make the pie higher', if one means increasing the size of total available resources.

[12] This difficulty with Van Valen's account was pointed out to me by Dan McShea in conversation.

say that Stegasauri are fitter than French poodles[13]! Although one may want evolutionary theory to provide such interspecific across time fitness comparisons, they do not seem truly informative for it washes out the importance of specific selective environments, i.e. context, in evolution.

Aside from the fixity of the resource space, another problematic assumption in Van Valen's argument is that any loss for a given species is maximally utilized by the other species 'instantly'. Although this might sometimes be the case, it isn't clear why there shouldn't be unutilized resources, 'unclaimed' spoils of war, for certain periods of time.

A charitable interpretation could be that Van Valen is wrong about the relative unimportance of the mutability of the size of the energetic pie. The energetic pie does fluctuate in the amount in total energy available –if only by the increase of entropy- and as such only comparisons in a shared temporal frame are relevant, because the identification of the specific temporal frame is the only way to identify the resource space and the relative control each species has[14]. If Van Valen wants us to focus on extinction rates *not* fixed quantities, he cannot also contend that the total available quantity available remains constant for that makes rates less interesting since we would now have access to

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[13] This reductio rests on the undefended assumption that Stegasauri controlled more resources than poodles have controlled and control now: although I guess a smart aleck could point out that a poodle in Louis XIV's court probably controlled –indirectly- more resources than most dinosaurs…

[14] Interestingly, Van Valen dismisses the physical environment as a source of selective pressures and emphasizes exclusively (at least in the 1973 paper) the coevolution of different species as being the source of evolution. Zero-sum game in resource space is exclusively biotic for Van Valen which might explain why the entropic energetic fluctuations are not considered as affecting the size of the resource pie.

fixed quantities (i.e. why focus on 13% control at t1 when we could focus on X joules sub specie aeternitas?).

Our cursory examination of the Red Queen's Hypothesis and some of its consequences show the benefit and possible perils of finding universal generalizations for biological phenomena: by showing how fitness is related to resource control, Van Valen can establish a universal metric concerning extinction rates, but in doing so, he overemphasizes the importance of an unfluctuating resource pie which makes fitness absolute and reduces the importance of specific ecologic context. I will now put the problem of absolute fitness aside and delve further in Van Valen's more explicit energetic paradigm.

3.2.2 EC as increase in fitness

In two subsequent articles, Van Valen explicitly describes his EC account of evolution. The first paper "Three paradigms of evolution" (Van Valen 1989) describes the superiority of an energetic paradigm over a reproductive paradigm (the current consensus) and a strawman, informational paradigm. In "Biotal evolution: a manifesto" (1990) Van Valen describes a possible application of this energetic paradigm to a 'new' level of selection. I will present both papers jointly, for in many respect they constitute a single argument. Van Valen's account is interesting for our purposes for it is attempting to provide a universal currency of evolutionary success, different from reproductive success. Such an account might be able to describe the evolutionary success of the three evolutionary systems described in chapter 2 along with other systems previously unexplained. Moreover, insofar as the attempt is intended to describe universal features of evolution, it may serve as a useful canvas on which to draw our own nomic account.

Part of Van Valen's motivation for proposing an energetic paradigm is his dissatisfaction with the lack of interaction between genetics and ecology (Van Valen 1989, 1). In ecological cases, reproductive success loses its primacy (or so Van Valen argues). As he points out (in a similar vein as my exposition of the aspen), size is important to natural selection and although this fact often translates into population size, Van Valen argues that physical size in a single organism whether it be a coral or a plant says much more about its evolutionary fate than its (often absent) reproductive success. Van Valen clearly has selection for 'fatness' in mind when he writes that "Rather than saying that natural selection is expected differential reproduction, we should say that it is expected differential expansion" (Van Valen 1989, 7) But spatial position will not be what is always expanding.

In trying to link growth cases to normal reproductive cases, Van Valen suggests that the only feature uniting them is increase in energy control. Van Valen argues that energy control is the only thing being maximized in nature by all species and that sometimes it translates into higher reproductive numbers, whereas sometimes it translates into higher growth. Notice how this links to Van Valen Red Queen's Hypothesis: one of his assumptions was that the resource space and the species living in it were in a zero-sum game where each species' loss translates immediately into a competing species' gain. In that framework, it should not be surprising that maximization of energy is the way to understand evolution since it is the only way to stave off extinction a bit longer.

This energy control has two forms: maintenance energy, and reproductive or growth energy depending on the system[15]. Van Valen believes that reproductive energy is always maximized in any environment whereas there is no such maximization for maintenance energy.

The fact that we do not always observe such a maximization of reproductive energy is, according to Van Valen the result of conflicting levels of selection. This energy control is not only level-relative but temporally relative: a certain amount of energy control maybe sufficient to be fitter in a given time interval but not in another different time interval.

Van Valen advocates the energetic paradigm not only because it seems to him a more coherent understanding of all cases of evolution but also because it permits novel applications of evolutionary theory. Using comparisons of amount of energy available to a species (i.e. controlled by the species), one can compare the fitness of different communities and ecosystems. This application will be more compelling to biologists than the other application identified by Van Valen. In the previous section I described the comparison between the fitness of Stegasauri and French poodles as a reductio. But this

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[15] Even though Van Valen sometimes equates growth and reproductive energy, he also points out (Van Valen 1973, 12) that they might not be equivalent quantities. He might have examples similar to the aspen in mind where growth energy via ramets and reproductive energy via seedlings have to be different and where maintenance energy will be radically different given the integration cost for remaining unfragmented.

is exactly the type of fitness comparisons that Van Valen is interested in.: “We can compare the fitness of a bird with that of a fungus” (Van Valen 1989, 13).

Although the interspecific fitness comparisons might be a genuinely interesting subject of inquiry, I will temporarily put them aside because of the extreme difficulty of quantifying energy for a single system, let alone comparing the energy between two vastly different species operating in different spatial and temporal scales.

Rather let us return to the idea of community evolution, an interesting application of an energetic paradigm. I will use ‘biota’, ‘community’ and ‘ecosystem’ interchangeably in part to reflect Van Valen’s usage: while a biota refers to all the species in a particular area, community refers to all *interacting* species in a particular area. Since it is plausible for Van Valen to assume that all organisms in a particular area interact with all others however remotely and indirectly, the synonymy will be maintained for our purposes. The major difference between ecosystems on the one hand, and biotas and communitys on the other, is that ecosystems are defined as well by the abiotic (i.e. non-living) features of the environment where the community occurs.

Community evolution is examined in much more detail in the aptly named “Biotal Evolution: a manifesto” (Van Valen 1990). Here, Van Valen explores the application of his energetic paradigm to ecosystem evolution (or biotal evolution). As Van Valen points out “The usual view, as expressed by May (1978) is that, “strictly speaking, ecological systems as such do not evolve.”” The reason, as identified by Van Valen, is that an ecosystem does not have a genetic inheritance mechanism. The component species do have such mechanisms but these mechanisms can only explain their own infra-ecosystem evolution. As in the previous paper, Van Valen argues that this view reflects the unwarranted predominance of genetics in received views more than it reveals about the nature of evolutionary processes.

Part of the difficulty for Van Valen's research project is in identification of the biota itself. Most of the time biotas do not have clear spatial or temporal boundaries. However, as we have seen in the previous chapter, Swenson et al. experiments showed it is not necessarily the case that biotas a large boundaryless entities (recall that Van Valen's paper precedes those results by ten years). At the time Van Valen wrote, ecosystems under consideration were much larger. Ecosystems do not have to have vague boundaries and even when they do, that is not necessarily a problem: many objects created by evolution have fuzzy boundaries as well. The question is not epistemic -of course it may be difficult to identify ecosystems and their successes- but ontological: do ecosystems really exist as unified entities involved in particular causal chains? If the only causal chain we wish to look at is the one leading to reproduction then the answer will probably be an emphatic no. But, just as I have argued in the previous chapter, ecosystems do exist and Van Valen focuses on them in aiming to reduce the relative importance of reproduction. In doing so, biotal evolution might find a place in our evolutionary explanations.

The control of energy is what isolates and bounds ecosystems and Van Valen explicitly identifies this control as being causal in nature and not just a measurement or bookkeeping tool (*pace* his use of the metaphor 'universal currency'). The type of causal mechanisms Van Valen think exists autonomously at the ecosystem level (i.e. not reducible to success and failures of underlying species) is similar to D.S. Wilson's trait-group selection, or as Van Valen calls it patch selection. Van Valen does not give details for how biotal evolution would occur, and ultimately we are left with not much more than a programme for future research. Biota spatial distribution is the most likely candidate for a trait of the biota that could be selected on. A biota increases its fitness by increasing its control of energy and, most of the time, it does so by expanding physically, whereas individual species does this by increased fecundity (which also often coincides with physical expansion).

But ecosystem selection, as Van Valen describes it, is problematic. Earlier in this dissertation, I quoted Van Valen on the analogy between erosion and natural selection[16] and pointed out that although most would grant that erosion can be thought of as a type of natural selection, few would believe that that erosion can cause evolution by natural selection in the geological 'entity'. In the same fashion, although charitable readers may grant that natural selection of ecosystems can occur few will grant that this may lead to evolution of ecosystems. Van Valen goes on to defend the idea that erosion is actually a case of evolution by natural selection. He sees reproduction not as a *sine qua non* for evolution by natural selection but as "modifier" of evolution, i.e. what type of adaptation

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[16] "When granite weathers, the feldspars and micas become clays but nothing much happens to the quartz grains. They are most resistant and get transported down streams or along shores. Thus most beaches are the result of differentially eroded granite. This is an example of natural selection in the nonliving world. Quartz grains survive longer than feldspar grains, and there is a progressive increase in the average resistance to weathering, of the set of grains that have still survived. This action of natural selection is even creative, as we see by the formation of a beach." (Van Valen 1989, 2).

will obtain[17]. In this I am very sympathetic to Van Valen: reproduction is a way to evolve, but not the only way to do so, and if that is the case, an account of fitness should not depend solely on differential reproductive success. But if Van Valen is truly arguing for increase in energy control, he will have to explain how the eroding rock is increasing its energy control –which he does not.

The difficulty of testing the biotal evolution hypothesis is not the biggest liability of Van Valen's project. With no notion of efficiency[18], Van Valen's suggestion is intrinsically flawed. A sudden cataclysmic drop in energy availability may hurt the big guzzler much more than the small efficient entity. One couldn't even argue that such a doomsday scenario is so improbable that energy guzzling will be a better evolutionary strategy in most environments. *If* evolution by natural selection were really about ever increasing energy guzzling, the arms race may create highly fluctuating energy availability close to the radical scenario first described: a new vastly improved way to control energy would disturb significantly surrounding energetic 'regimes'.

Van Valen assumes that any resources lost by one species are immediately utilized by other species in a zero-sum game. But if there can be selection for efficiency, then we should expect some resources to be left unutilized (not forever but for some period of time). When other species 'notice' that some resources are left unused for a

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[17] "The lack of reproduction imposes constraints on the flexibility of evolution here (…) We do have here a common sort of evolution by natural selection and there are many other nonliving examples." (Van Valen 1989, 2)

[18] He actually rejects the idea explicitly: "But if they get more expansive energy by wasting more, that is what is selected for. Efficiency per se in not maximised." (Van Valen 1989, 9)

long duration they would utilize them: if efficiency could be selected on, we would expect jagged survivorship lines where the resource space goes from being underutilized to maximally utilized, making the result of co-evolution in resource space less ‘linear’.

Van Valen backtracks slightly on the idea that efficiency is irrelevant (see p.13); he accepts the *possibility* that efficiency be maximized through evolution, even though he then goes to say that it is probably an irrelevant factor in actual cases. Much more would need to be said to support that claim. But the reason that he might not want efficiency to come into play is that it would interfere with the idea of a zero-sum game in the resource space. If species could increase their efficiency, the linear patterns might not be explained by the Red Queen’s Hypothesis for the resource space would not be incompressible as Van Valen describes it in 1973; if a species could increase its efficiency, the resources controlled by it would in some sense ‘squeeze’ more energy out of the quota it controls, without necessarily taking any energy from another species. He seems to admit as much when he writes that “[energetic] wastrels reduce the total realized fitness of their community” but then reduces the importance of this by writing that “wastrels are rarely an energetically major components of their communities”(Van Valen 1989, 13). He does not justify these claims in any way.

3.3 Conclusion

An analogy might be useful. Let's compare country A where the expected number of children is 6 children per family unit, and the expected lifespan is 50 years with that of country B where the expected number of children is 1.6 with a life expectancy of 80 years. Do we want to say that that population A is 'fitter' than country B? Maybe, maybe not. The only thing that such an analogy tells us is that counting offspring is a limited way of measuring fitness (although it might be the best in many cases). That's why another component of fitness is survival. Although survival is always recognized as a component it often plays second fiddle to the fecundity aspect; survival is understood as being instrumental to reproduction and the post-reproduction survival is irrelevant on the received view- the primacy of population genetics in contemporary evolutionary biology reflects this bias. But again, do we measure fitness solely by counting offspring because other measures are too difficult to obtain or because we think it corresponds to the truth of the matter? If, as Van Valen suggests, resource control (i.e. energetic control) is the route to stave off extinction then the sociological example presented above needs to be recast. How much energy does a small long-lived family control over a large short-lived family?

Ultimately, Van Valen suggests a way of thinking about all entities' fitness in energetic terms. I use the word entity since the units of selection become muddled in Van Valen's work. Although he is clearly 'counting' a group of similar genomes as part of one large individual, he wants to put the emphasis on ecology where individual organisms are more significant than large abstract populations of gene. In Van Valen's later papers, the entities in question are whole ecosystems. The lack of precision concerning the specific unit of selection is not surprising since Van Valen is, after all, out to provide a law. By providing a mechanism general enough to encompass many levels of organization, the hope is that a universal principal will be obtained.

Van Valen's attempt to provide a universal currency of fitness although fascinating is problematic for many reasons. The first one is a problem of operationalisability. How could we measure energy control for a whole ecosystem? Let us be charitable and assume that we could measure all the relevant joules. Which joules would we be leaving out? First, there is a question of causal closure: ecosystems (or any system for that matter) are not completely closed off energetically from other systems and as such, the fuzzy boundaries are not only spatial and temporal but energetic as well. That is not a death blow, for as we have seen in chapter 2 fuzzy boundaries are not a problem unique to Van Valen, but it shows the necessity for Van Valen to offer some more explicit individuation criterion.

However, there is another measurement problem that is much more significant. An ecosystem or community might in actuality control little energy but have the *potential* to control vast quantities of existing and non yet available energy. Another socio-political analogy might be instructive. Let's see atomic weapons as quantities of 'controlled' energy, not a huge stretch since they are after all 'contained' nuclear energy. The number of deployable joules themselves is not overly instructive since what is truly a measure of the deterrent power is not their energetic capacity but *where* this power will be unleashed.

The megatonnes are not sufficient to describe the force of these weapons since their effectiveness depends on the nature of their targets. X joules used on a deserted landscape are radically different from their use on a village or a highly populated city. Since there are an infinite number of potential targets with the accompanying infinite number of total energy ‘controlled’, it is doubtful that energy be the universal ‘currency’ sought. Again, the ecological description underlying the energetic description is the relevant story that needs to be told. Controlling x amount of energy is only relevant given a certain context and this context will not be captured in energetic terms.

Also we do not want EC to be solely an *actual* measure of controlled energy since this is merely moving the tautology problem to another level: if to be fitter means to control more energy, we do not want the principal of natural selection to make the empty claim that A controls more energy than B if A controls more energy than B. So we want EC to be a capacity of some sort. Maybe I wrongly interpreted Van Valen’s take on the issue. Maybe the quantity of energy controlled by a species should include not only the energy actually controlled at a certain time but the energy that *could be* controlled at that time. But by making EC a capacity, we realize that there is no finite number of possible energy uses. How much energy does an ecosystem control if we understand this control to be in part only potential? Since the energy that a system *could* control depends on the interaction between it and other systems and that the number of the possible interaction is indefinite, emphasizing the dispositional aspect of EC reduces its theoretical value. Let me offer an analogy. I can answer the question “How much energy I am expanding at any given time?” it will be a certain numbers of joules given the context at t. But how could I answer the questions “How much energy I *could* expand at any given time?” What will be the constraints permitting us to separate likely cases (e.g. energy needed to run at a certain speed) from the silly but still possible cases (e.g. energy needed to run at a certain speed if gravitational pull suddenly dropped by 50%). What will be the ‘relevant’ contexts to determine the potential energy that an ecosystem could control. Any ecosystem could control 500 times more energy that it does control at a given time, given the right changes in circumstances.

Maybe *actual* EC is a good predictor of fitness in the same way that *actual* offspring numbers are a good predictor of evolutionary success for many biological cases. But ultimately, efficiency and potential energy control distort the resource landscape that makes energy such an attractive as a metric in the first place.

Moreover, as we have seen in chapter 2, increased energy control will not always be the right measure of success even in actual cases of ecosystem selection. Although Swenson et al. might have chosen to select increase EC in his mud samples, in fact they selected for an increase in pH level which does not necessarily correlate with increase in EC. If we are to take seriously the possibility that fitness is a matter of solving design problems posed by the environment, we should not expect to measure it by measuring increase energy control. This can’t be the solution to *all* design problems. We can easily imagine design-problems that do not implicate energy-control in any obvious non ad-hoc way.

An increase in EC is often translated into an increase in spatial control (at least for ecosystems). By increasing one’s size, one is often reducing the availability of energy for one's competitor. But, although there might be selection for 'fatness' in many cases (e.g. the aspen described in chapter 2 might be such an instance), increase spatial control cannot be the universal currency either since there are many cases where decrease in spatial control can actually be beneficial: the survival of mammals in the context of the extinction of dinosaurs is a chilling reminder of that fact.

Spatial location is very important to understanding fitness but only insofar as it determines an aspect of the selective environment. As we have seen in the previous chapter, spatial location should also be understood as an aspect of the phenotype and part of the inheritance mechanism.

If offspring numbers, EC and spatial control are not universalizable measures of fitness and a fortiori cannot be the foundations of our definition of fitness how do we move beyond the apparent measurement intractability of ecological fitness? As has been hinted many times throughout this dissertation and as we shall see in the next chapter, time is of the essence. In some sense, this takes us back to Van Valen 'new evolutionary' law where the significant data were survivorship curves. In the end what matters is how long you survive and how what you are doing increases the likelihood you will survive for various time durations.

As I pointed out earlier in this chapter, if Van Valen wishes to argue that an eroding rock is evolving, he has to show how such supposed evolution is increasing control of energy. It is doubtful that an eroding rock is increasing its energy control. An easier way to define the erosion as a case of evolution is to focus on the increased persistence that the weathering provides. Van Valen seems almost there when he writes that there is an “increase in the average resistance to weathering, of the set of grains that have still survived” (Van Valen 1989, 2). The erosion itself is the result of natural selection: if there is change in the way the rock is eroding in response to erosion and that that change is increasing the future persistence of the rock then there is evolution by natural selection[19]. Increasing persistence is the idea we will now explore and develop as the foundation for an extended account of fitness and of evolution by natural selection.

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[19] I should note that prima facie I do not think there is that type of evolutionary change in the eroding rock.

Chapter 4 Struggle for Persistence

4.0 Introduction

In Chapter 1 I provisionally conceded that the propensity view was probably the least problematic operational definition of fitness we had. The only alternative was an ecological notion of fitness construed as design solution. But depending on how one looks at it, it isn't an alternative at all since either it can be operationalized only by demographic descriptions already present in the propensity view or is an unmeasurable property of limited use to biologists. Ecological fitness might be necessary to the theory as it seems to describe an essential aspect of actual evolution by natural selection, but our inability to measure ecological fitness in a way independent of reproductive success will make it unattractive to evolutionary biologists.

Chapter 2 hinted at a way to measure ecological fitness without resorting to reproductive success. I described real biological cases in which offspring-number do not provide the explanation for the adaptive change. These biological entities are ones which do not meet the offspring-centric approach of evolution by natural selection. This conclusion leads us to a few inexorable conclusions. The quaking aspen and other similar entities

1) do not evolve.

OR

2) they evolve but *only* in very rare occurrences of functional differentiation (sexual reproduction episodes or asexual reproduction leading to 'production' of separated

autonomous individuals, such as the fragmentation of the clonal organism).

OR

3) they are evolving but only if you consider the functionally integrated ramets to be the relevant individuals relative to natural selection (i.e. the evolution of the grove is then understood with a modified group selection argument).

OR

4) the grove is evolving but our notion of evolution by natural selection needs reformulation.

As is it has been made clear in Chapter 2, I favor the fourth alternative. The reasons each of the other alternatives are excluded are as follows. The fact that groves persist for such long period and that they do so by decreasing local competition and that the way they decrease competition changes in response to environmental changes makes the denial of the possibility that that evolution occurs implausible. The fact that many groves discard sexual reproduction altogether without any negative effect on their persistence reduces the plausibility of the second possibility. Forcing the aspen case into a reproductive description obscures the benefit of the individual maintaining integration and wrongly associates growth and the rare sexual reproduction events, dismissing the genuine differences between the two processes.

Biological systems that do not straightforwardly reproduce, yet change in response to pressures from their environment in a way that improved their chances of survival led us to two points (1) change within a lineage could be achieved by differential success of parts (2) success of parts and of the lineages that they compose can be measured by durations in time. In this chapter we will flesh out both of these ideas.

Although time may be an attractive unifying framework to evaluate evolutionary success, a more predominant suggestion over the years has been energy. Chapter 3 examined whether time *and* energy would be necessary. Van Valen, in the context of his explanation of constant extinction rate data, provided a way to explain some cases that an offspring-centric view could not. Van Valen did not explicitly attempt to formulate a law of evolution in energetic terms but provided a more general framework from which a likely law could emerge[1]. According to Van Valen, when thinking in terms of biotal evolution, the relevant parameter becomes ever-increasing energy commandeering, *not* increased offspring numbers (expected or otherwise).

Endorsing Van Valen's idea, we could describe the aspen as increasing its energy control instead of increasing its offspring. Energy might be a good way to measure ecological fitness in non-reproducing entities (and in many reproducing entities as well), but energy cannot be the universal metric. Although Van Valen held that increasing energy control is the evolutionary end of all system, I argued that this is not the case. Efficiency, which enables organisms to reduce the actual control of energy (i.e. reduces the amount of energy controlled at any given time), cannot fit neatly into an energetic maximising paradigm. Just as lower reproduction will sometimes be selected for, indeed just as *no* reproduction will sometimes be selected for, similarly sometimes decreased

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[1] In his own words, he was 'merely' establishing "An organizing principle" (Van Valen 1990, 5).

energy control could be selected for as well. By reducing one's share of the resource space, one may avoid predation, or reduce one's vulnerability to energy fluctuation. Van Valen's programme implies that actual energy control is the measure of success. There might be way to provide an energetic paradigm that avoids this problem but, as I have argued in the previous chapter, the redescription of EC in terms of *capacity* to control energy would actually weaken the energetic paradigm or be incompatible with the data presented by Van Valen.

It's not obvious what would be the purpose of this increased efficiency. If efficiency is to be dispositional, efficiency means control of *future* energy. This may mean that what is important is not energy control per se but what a good energy management offers. I argue that ultimately efficiency (or in other cases wasteful energy management) is a means to increased longevity.

Both increase in energy control and increase in offspring numbers are means to a more universal end: increased persistence. Energy is not a universal metric, for decreased energy control for various time intervals can actually increase the potential to survive. Since increase in survival is ultimately the only relevant goal, other factors have to be seen as accessory. The energy commandeering paradigm was incomplete (just as the propensity view was) but remains an elegant example of what non offspring-contribution generalizations could look like.

Two interesting lessons were drawn from examining Van Valen's project:

a) Evolution might sometimes be better understood from way above the level of paradigmatic organisms (or even cohesive entities like groups). After all, much of the energetic paradigm is derived from examining taxon-level data. When looking at competition at the macro level, persistence is crucial and reproduction is just one way to achieve it. Van Valen saw increase in reproductive success as a proxy for increase in energy control. Instead I wish to see both reproductive success and increase in energy control as means to increased persistence.

b) For evolutionary theory to be truly general (and have a chance of nomological expression) we need to identify a universal currency of evolution that isn't exclusively reproductive. Biological phenomena are so heterogeneous (especially when examining vastly different levels of biological organization) that some other type of unifying property –energy, a physical property, for Van Valen- might be the only unifying feature.

There can be evolution in biological systems *sans* differential reproductive success. If replication is not general enough, and if increase in energetic control is not general enough, what else is there? If, as I have argued, increased reproduction and increased energy control are means for increased persistence, then perhaps persistence itself is the common currency of evolution.

4.1 Legal considerations

We have now reached the point where we can provide a new definition of fitness and the principle it fits into. Let us provisionally identity four characteristics of an *ideal* scientific law:

1- a law is an exceptionless contingent universal generalization

2- a law includes no spatially or temporally limited predicates

3- a law supports counterfactuals

4- a law's credibility increases dramatically with only a few confirmed positive instances.

Although this conception of law is not without problems, it may be the most common understanding of scientific law to be found in philosophy of science[2]. Let us keep these characteristics in mind when describing the principle. Some contenders for a general principle/laws of evolution by natural selection have been identified.

The first one, adopting a strong population genetics view, focuses on central tendencies of ensembles:

> PNS_{pop} (x) (y) (E) [If x and y are competing populations and x is fitter than y in E at generation n, then probably, (x's size is larger than y in E at some generation n' later than n)][3]

As I pointed out in chapter 1, what this candidate gains in generalization power, it loses in applicability for it jettisoned any *genuine* appeal to ecological fitness. Focusing solely on ensemble properties divorces the theory from the causal interactions it is trying to explain. Aside from being theoretically suspect, it draws an unbridgeable gap between ecology and genetics, which is highly undesirable for the actual inclusion of this principle in the practice of biology.

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[2] After noting the lack of consensus in philosophy of science for lawhood, Brandon offers some general desiderata that he presents as being relatively non-controversial:"laws of empirical sciences are to be empirically testable universal statements. It is also highly desirable, whether or not definitionally necessary, that laws be empirically correct or at least nearly true. One cannot just look at the surface logic of a statement in order to determine whether or not it is a scientific law."(Brandon 1978 reprised in Brandon 1996, 11). He goes to describe the schematic principle identified in Chapter 1 as being as close to a law as evolutionary theory can hope to get since there will always be a trade-off in the desiderata.

[3] See Matthen and Ariew (2000), or Sterelny and Kitcher (1988).

The more serious attempt to provide an evolutionary law is the most stable candidate so far, ironically because of its weakness: Brandon's schematic view (1990) provides a *principle* of natural selection that may be as close to a law as we can get, but, as Brandon points it out himself, not a full-blown law (in a positivist sense). It is closest to having all the properties of a scientific law described earlier but does so by thinning out the actual content of the principle: variables, specific causal relationships, etc. are not defined in the principle he offers. Whether the law I shall offer can go beyond the schematic view remains to be seen. But it will account for more evolutionary phenomena than Brandon's schematic view and as such needs to be seriously entertained. I will argue that focusing on persistence as universal currency gets us closer to universalizability than differential reproductive success view can. My account may provide the closest thing to a law that evolutionary theory can hope for.

As I pointed out at the onset of Chapter 2, the first requirement for a truly general theory of evolution is to account for all evolving biological systems. Cases such as the aspen demand an explanation of evolutionary success that does not rely on offspring number. One might suppose that this is the group-selectionist conclusion all over again. This would be inaccurate: most credible group-selectionist arguments rely on a notion of reproduction: a group is doing 'well' *if* it can produce new groups. But the whole point of the chapter 2 was to show that an organism, a group, or a system, can do well evolutionarily without producing other individuals: the aspen can be successful without creating new groves or new seedlings; colonies can be fit without creating new autonomous colonial individual, etc.

Even if one wishes to be generous in one's definition of offspring –accepting groups, colonies, species, etc. as satisfying the definition of what a reproducing individual can be– one will not be able to explain all biological cases. Some biological entities literally don't reproduce or rather have even stranger reproductive cycles: social insects offer rich examples of this (as E.O. Wilson, 1971, has famously shown). For many social insects, the potential number of daughter colonies alone only establishes the fitness of the queen for, after all, the daughter colonies represent individual queens that the mother queen as produced. But to understand the fitness of a colony as an integrated organism, one has to look beyond reproductive success since the caste structure, population density, number of idle workers, etc. play a significant role in explaining the adaptive advantages of the social behavior.

Other colonial organisms have an even more problematic ontology. Bryozoans are integrated colonies[4], in which one of the 'individual' constituent organisms (zooid) can pass on nutrients to other non-feeding constituents. Individual zooids can be 'specialized' to occupy various roles in the colony: the degree of polymorphism of zooids varies from one species of Bryozoans to another but even when that degree is low, some zooids will basically be non-feeding, structural modules, while others will be the ones gathering the nutrients for the rest of the colony. These colonies display an irreversible division of labor: all zooids become completely non-autonomous when they 'enter' into the colony. Individual zooids are basically organs of a very large individual.

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[4] See McShea and Venit (2002).

The resulting colonial organism is, *in theory*, immortal since the budding of other modules can replace non-functional parts indefinitely[5]. The last two examples presented in chapter 2 were intended to show possible extensions of evolutionary explanations once one surrenders the focus on reproductive success. Ecosystem selection and mound-colony evolution are not well-established phenomena, but they suggests that Darwin's theory, once amended, may be able to account for even stranger phenomena than organs of extreme perfection.

4.2 *What* is really evolving?

Although clearly, all the cases examined in this project shared a lack of replication, the other 'property' they shared is a contentious ontology. What is the individual or the unit doing the changing at any given time? Individuality is a central problem of most biological projects –most scientific projects for that matter. The problem is often left unsolved, scientists preferring to adopt intuitive accounts of individuality often based on functional individuation however crude[6]. Not surprisingly, the problem is thornier.

The first problem is that there is an asymmetry between biological individuality

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[5] I should note that senescence for these systems is not well understood; 'indefinitely' should therefore be understood loosely to mean 'a very long time barring catastrophes'.

[6] The criteria for functional individuation are more intuitive than anything else: what *seems* to be the main causal interactor in any given causal chain is the relevant individual.

and evolutionary individuality. The reason is obvious for anyone who admits a multi-level or pluralistic conception of evolution by natural selection. *If* selective pressures operate at various level of organizations (genic, organismal, group, species, etc.), then the same biological individual will be part of many selection stories, where the individual animal for example is not always the central unit of selection. Since groups sometimes favor group-traits that don't directly benefit any given individual member of the group, we have to assume that the units of selection do not always correspond to biological individuality[7].

As Cook puts it "The laws of natural selection are not constrained by human notions of individuality."(Cook 1980, 92). But it *could* be argued that even the aspen is a relatively 'simple' case, for it remains amenable to an organismal evolution description – an amended description of course- where ramets are individual organisms. I have argued that such a view does not correspond to the actual processes at play. But even if we accepted their characterization, there are many cases where such a translation will be even more counterintuitive: an ant colony is a much more significant unit of natural selection than any individual ant. Ants have been well studied for a long time and their cohesive behavior, their division of labor[8], etc. demand a view of selection that goes beyond the single individual organism. One suggestion, following accounts in line with J. Wilson' s argument (1996), is to try to solve the problem by using the term of spatio-

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[7] For a recent thorough group-selection argument to explain the existence of altruism see Sober and D.S. Wilson (1998). For good opinionated primer concerning the unit of selection debate see Sober and D.S. Wilson (1994).

[8] See Oster and Wilson (1978).

temporal individual to refer to biological entities instead of the term ‘organism’. That individual may be an organism, a group, a species, a clade, etc. as long as it belongs to a substantive kind. Which kinds are relevant depend on the research interest[9].

‘Individual’ might do but I suggest using a different concept. An individual does not have to persist, or rather one can be an individual for only a short instant in time. The individuation problem (biological or evolutionary) is a real problem that deserves attention, but it might be possible for evolutionary theory to shift the focus from individual organisms, groups, etc. onto a unit that doesn’t demand an immediate answer to the individuation problem. Our problem is two-fold. Individualization will necessarily be a problem since as we have seen, in the termite mound and the other examples presented by Turner (2000), the boundaries of individuals are not as fixed in the ways we often think. The second problem is that as in any hierarchical view, adopting criteria for individuation that are too strict (at least in the evolutionary context) will miss interesting cases of evolution such as the aspen presented in this thesis. I will bracket the individuation problem and use lineage as my unit for I wish to use a term that allows succession of states and stresses the temporality of the process. The world ‘lineage’ might be a better choice than ‘individual’ to convey the importance of time in the process that I am trying to describe. ‘Lineage’ may also shift the problem from one of individuality to one of membership in the lineage. Since membership has always been seen as more interest-relative than the inexorably ontological problem of individuality, we might be

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[9] Wilson (1996) mentions developmental individual, functional individual, genetic individual and unit of selection.

able to temporarily bracket some real philosophical problems by employing lineages.

Common definitions of lineages are flexible enough to accommodate all the biological examples given so far. A lineage is generally understood as a descent group with a common ancestry back to a single parent. Hull defines lineage as “an entity that changes indefinitely through time as a result of replication and interaction” (Hull 1980, 327). Hull’s definition is given in the context of his seminal paper on levels of selection, in which he stresses that lineages can evolve.

Hull views the lineage as the highest level of organization that can evolve: “they are the most inclusive entities that are ‘actively evolving entities’ to use Wiley’s phrase” (Hull 1980, 328). If Hull is correct, then reproduction can not be the core of fitness increases, for lineages do not all ‘really’ reproduce. They may split and as such have parts (species, sub-species, populations, individual organisms) but a lineage that evolves does not necessarily ‘do better’ if it leads to more lineages than another lineage. Lineages are inherently genealogical or historical items. They include individuals or classes across many generations.

The notion of lineage is inclusive enough for our purposes since we want to be able to say that an entity may belong to various lineages depending on the time-scale one is interested in, something that is allowed by the definition of lineage. I belong to many lineages, one that includes only the Bouchards in Quebec since the 17th Century, one that crosses the Atlantic and the Centuries to France, one that includes the entire Human race, one that includes most primates, etc. Lineages are carved up temporally, which, as we will soon see, permits us in theory to make evolutionary comparisons at any temporal scale we wish to (e.g. lineages over 100years, 1000years ,100000years, etc.).

Another advantage of thinking temporally is that it does not put much importance on actual physiological integration. Although I have focused on functionally integrated entities, Gould and Lloyd pointed out that non-cohesive entities may be able evolve as well[10]. Lineages are not defined in terms of spatial continuity (although we may want spatial features to be acknowledged in some way) but in terms of temporal continuity. There might not actually be evolution by natural selection on lineages on a given temporal scale (i.e. evolution at the clade level might not actually occur), but that is an empirical fact that needs to be established after the comparison has been chosen. Minimally we want an account to allow for the possibility of the macro-evolution as described by Gould and Lloyd.

How far back in the past, how far ahead in the future, or to what degree of relatedness, branches should count as part of the same lineage *is* to a large degree interest-relative. If membership to a lineage is partly a function of our interests, this is no reason to reject the account: the same 'problem' appears in traditional evolutionary theory and it doesn't hinder the theory's development or its practical applications.

As Sober puts it:

> Darwin thought of speciation as the result of a slow accumulation of modifications within a lineage. Phyletic gradualism, as it is now called, presents obvious line-drawing problems. Marking off where one species ends and another begins will be rather like determining the number of hairs that marks the difference between being bald and not. According to Hull, the Aristotelian idea that species may be informatively characterized

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[10] See section 2.3.3 for discussion of functional integration.

> in terms of necessary and sufficient conditions set biologists on a two-thousand-year wild-goose chase. Aristotle thought of species as discrete, whereas Darwinian theory sees evolution as continuous. (Sober 1984, 162)

The same lesson applies to the notion of lineage employed here. Furthermore, if all biological systems have evolved from a common origin, then they are all related to some degree and could therefore be identified on one scale as one sole lineage evolving thereby confirming Sober's characterization of the issue.

The relevant lineages are identified on the basis of the relevant comparison. The objects may well be real, but their boundaries are function in part of our research interests, or rather, as the hierarchical view pointed out with force, the same entity may be selected on directly or be selected on indirectly as a part of a larger entity that is selected on.

Intrinsic to the idea of lineage is the idea of succession. Succession need not be strictly generational, since, as I have argued, reproduction is not always necessary. Modifying Hull's definition of lineages, we could treat them as any entities that change indefinitely through time as a result of differential persistence of their components. When those components are offspring, we get a definition of lineage in line with Hull's definition. In non-reproducing lineages, the persistence of the components becomes more important a measure of fitness.

4.3 PTT: it's about time

We can now begin to identify some of the features of fitness as persistence through time, PTT.

1) Our account should not focus exclusively on any specific unit of selection as they are generally understood. In some sense, contemporary pluralist accounts (i.e. multi-level selection accounts), such as Brandon's or Sober's and Wilson's, meet this non-exclusivity requirement.

However, their reliance on offspring numbers make their formulation pluralistic *not* vis-à-vis what constitutes a real unit of selection per se but rather what constitutes an organism. In the end, most multi-level selection models treat whatever unit of selection they pick, to function as a reproducing organism (or a reproducing super-organism). But as we have seen throughout this dissertation, reproduction is much too restrictive a fitness measure for clonal systems, colonial organisms and ecosystems. I suggested the use of lineage as a general all purpose unit. Defined as an entity that changes indefinitely through time as a result of differential persistence of its components, a human being is a lineage of cells on one time scale, a group may be a lineage of organisms as well, as of course a species or clade may be. If one dislikes the extension of the concept of lineage in this way, one can provide an equivalent neologism (maybe 'persistors'?)

2) Our account should not employ the concept of offspring-production. This is not to deny that offspring-production plays a crucial role in many biological cases of evolution by natural selection but rather that offspring production is merely an effective (if not *the*

most effective) strategy to becoming fitter. Offspring-production is itself just another solution to a design problem. This suggestion is not as radical as it may seem; reproductive patterns have already been studied as specific design solutions. The *r* and *K* selection research project[11] in evolutionary ecology focuses on density dependent selection: in unstable environments, there is a selection for smaller organisms, lower energy needed for offspring production, large number of offspring, early maturity, etc. while a stable environment will select for larger organism, with higher energy needs for offspring production, smaller number of offspring, late maturity, and so on.

Theoretically, extreme K selection could lead to very long-lived offspring-less singletons. A somewhat analogous conclusion is obtained in arguments for the evolution of sterility in certain clonal organisms. Eckert argues that in the same way that selectively neutral traits will tend not to be maintained, sexual reproduction will be selected out in stable environments in favor of clonal growth (Eckert 2002). My model takes this conclusion seriously: if maximizing offspring numbers is sometimes not the best way to respond to selection pressures, offspring numbers cannot be the core of evolutionary fitness.

3) Our law (or principle) should rely on a metric of some kind for fitness. As we have seen in chapter 1, although fitness may be better construed theoretically as a overall-solution to design problems, the measurement problems (identified by Lewontin 1973 and others) make this definition unuseful to biologists. For our principle to have any

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[11] See Roughgarden (1979).

chance at being testable, explanatory and useful there needs to be there should be a way to measure and compare entities. In this respect I depart from Van Valen's opinion that "A law need not be quantitative (although the law of extinction is). The contrary tradition is a myth derived, as Egbert Leigh has said, from physics envy." (Van Valen 1973, 25, n.31). Not for the first time, I embrace this physics envy, at least as a good heuristic principle for identifying a *useful* law or principle.

Given these constraints, we can start defining fitness. Let us begin with a popular definition due to Brandon[12]. Brandon defines relative adaptedness (relative fitness) as:

> (RA): *a* is better adapted than *b* in *E* (i.e. fitter) iff *a* is better able to survive and reproduce in *E* than is *b*

RA is seen as a reformulation of the Principle of Natural Selection[13]. As we have seen in chapter 1, the crucial aspect of the definition is the *propensity* to leave a higher number of offspring not the *actual* number of offspring. We may have to find a way to leave some sort of propensity operator in the final definition as well.

If, following the argument of chapter 3, we accept that the notion of offspring should be dropped from the definition altogether, we can transform the definition to a first provisional statement. I call this statement PTT (Persistence Through Time). PTT is meant to be a reformulation of the Principle of Natural Selection to accommodate

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[12] I wish to use Brandon's view for various reasons. Chief among them is the fact that it was one of the first to express the propensity view of fitness that aims to avoid the tautology problem. Brandon is also one of the only philosophers who clearly explains how and why the principle remains schematic. It will therefore be useful to compare PTT to his principle to see if my account really leads to a law, remains merely schematic or is schematic but less so than current propensity views of fitness.

[13] Brandon 1990, 15.

evolution of non-reproducing systems. The reader should note that each restatement of PTT will be numbered to show that it is a ‘temporary’ suggestion that will be refined throughout the rest of the chapter.

PTT1 *a* is better adapted/fitter than *b* in *E* iff *a* is better able to survive in *E* than is *b*

The reproductive expectations are left out explicitly from the principle since, as we have seen reproduction is ‘merely’ a way to persist and not an independent condition of fitness. Intentionally, this first formulation is close to the definition of ecological fitness described in chapter 1.

We must now say more about *a* and *b*. What is the relevant unit of selection if natural selection is to apply equally to lemurs, colonial organisms, human societies, aspen groves and the rest of the strange and wonderful biological systems that evolve over time? I have suggested that the concept of lineage might be useful and inclusive enough to include all the cases described in this project. Modifying Hull’s definition of lineage, I defined lineage as entity that changes indefinitely through time as a result of differential persistence of its components. When we introduce lineages in our principle we get

PTT2 Lineage *a* is fitter than Lineage *b* in *E* iff Lineage *a* is better able to survive in *E* than is Lineage *b*

The careful reader will notice that I dropped “better adapted” from the previous formulation of PTT: in Brandon's view (1990), relative adaptedness and relative fitness are used interchangeably. I favor the latter for esthetic reasons: Spencer coined 'survival of the fittest' not 'survival of the relatively better adapted'.

The notion of environment (*E*) is problematic since, at least in some cases, we are looking at a longer periods. It is hard enough to characterize the relevant environment when thinking in terms of 'paradigmatic' organisms, but the problem is magnified if the relevant unit of selection goes beyond 'usual' time frames. In what environment(s) does a lineage evolve? Environments, however construed, change over time. The lineages that PTT may range over *may* span million of years. What notion of environment will be appropriate for such a timescale? What is the selective environment for an evolving clade?

One should note that this is not a problem for all evolutionary comparisons; the lineages we are interested in could span only a thousand years (or much less) and the environment could be relatively constant for that duration. But on longer time scales, the multiple changes in environments would pose problems in defining the relevant environments[14]. It should be said that the same measuring problem exists in macro-evolutionary explanations and the environments do become sketchier as the features of the relevant selective environment become more abstract. In the case of macro-evolutionary explanations, the environment is not characterized in terms of specific predators, number of food-sources, etc. but rather in terms of massive catastrophes,

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[14] The 'relativity' of time scale will be examined in the next section.

climatic changes spanning thousands of years, etc. The scale issue and how it affects the definition of the relevant environment is a problem my account shares with traditional evolutionary theory: this is more an epistemic problem than not an ontological problem.

That being said, there might be a more useful way to put aside this problem. We could make *E*, the selective environment, part of the definition of the relevant lineages. In the same way that an adaptation is defined (at least intuitively) by the niche it is 'meant' to fill, maybe the lineage can only be defined by explicit reference to the selective environment that shapes it. If the selective reference becomes part of the definition of the lineage, we can delete explicit reference to it in PTT.

PTT3 Lineage *a* [defined in part by its environments] is fitter than Lineage *b* [defined in part by its environments] ~~in *E*~~ iff Lineage *a* is better able to survive ~~in *E*~~ than is Lineage *b*.

To simplify exposition we get

PTT4 Lineage *a* is fitter than Lineage *b* iff Lineage *a* is better able to survive than is Lineage *b.*

The attentive reader will notice two things: first we are very close to Spencer's slogan for evolution as "survival of the fittest". This is not surprising. As a response to Paley's argument, Darwin's theory is often described as attempting to explain complexity, diversity and adaptation. Darwin originally expressed these features of the world via variation in offspring phenotype and subsequent selection on these traits and organisms. But I argue that the idea of modification with descent is not solely expressible in reproductive terms. After all, to explain adaptation and complexity one only needs to explain how traits develop over time in response to environmental cues. The fact that an efficient way of evolving is via selection on offspring variants is a contingent fact about the world. Another contingent fact about the world is that certain organisms do not in fact need to use this process. Our law should accommodate both strategies.

I intentionally left diversity out in the last enumeration of the explananda. This is a difficulty that my account has to face. As is, PTT does not explicitly provide an explanation of the diversity of phenotypes in the world. One possible way out of this problem is to argue that implicitly PTT can explain diversity since our model is meant to be compatible with or to include differential reproduction explanations previously identified in traditional evolutionary theory.

But more importantly, we must recognize that diversity and complexity are results of contingent features of the world[15]. Take a very simple universe with only two relatively similar organisms. Evolutionary Theory can tell us that given limited resources, the organism better adapted to the environment will persist (and possibly flourish) while the other will eventually disappear. Natural selection simpliciter can produce adaptation but it does not inexorably lead to diversity or complexity. Diversity and complexity are

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[15] See McShea (1998) for an argument against an active trend of increasing complexity.

contingent consequences of environmental variation over space and time, which shape adaptations. In this light, diversity can still be seen as a possible consequence of the effect of natural selection but not a necessary outcome.

The biological world *is* complex, *is* diverse and *is* full of relatively well adapted systems but the first two features are not necessary outcomes of evolution by natural selection alone. They are highly likely characteristics natural selection will ‘produce’ in a changing environment. Accordingly, PTT’s formulation need not incorporate these contingent features of the world; if the environment had not been fluctuating, there might not have been complexity and diversity to explain). Accordingly, PTT leaves out features of the world that may be beyond the genuine explanatory grasp of evolutionary theory in the first place.

Second this formulation of PTT seems to make absolute fitness comparisons possible: if the selective environment is not an autonomous part of the principle, can I compare lineages that do not belong to the same selective environment? I will come back to this difficulty later when I address the relative nature of PTT.

The *ability* to survive expressed in PTT4 can be put into terms that will be more amenable to avoiding the tautology problem: if fitness is to be understood in terms of persistence, we do not want to offer the statement that if a lineage persists longer it will persist longer. Exploiting the strategy of the propensity view, we may express PTT as

PTT5 Lineage *a* is fitter than Lineage *b* iff Lineage *a* has a higher propensity of persisting x years than Lineage *b*

The notion of 'life-expectancy'[16] is important and deserves clarification: as pointed out in the beginning of this dissertation the most popular way to avoid the tautology problem is to include a notion of propensity factor in the consequent of our principle. The asymmetry between propensity of persistence and actual persistence is sufficient to void the accusation of tautology. PTT becomes a non-tautological principle of evolution by natural selection by using expectancy to reflect propensity in the consequent. What PTT5 describes is the principle that lineage *a* is fitter than *b*, fitness defined as persisting longer than your competitor, *iff* lineage *a* has a higher *likelihood* of persisting for a certain duration than lineage *b*.

4.4 Relative and Absolute persistence

What is an attractive aspect about focusing on likelihood of persisting is that it offers a natural metric for comparing lineages. Biologists have always sought a metric for fitness. On the offspring view of fitness, the units are the cardinality of offspring. As we have seen, that type of project leaves out much relevant information: environments have a bound carrying capacity that cannot be exceeded. If a given environment can sustain only 100 organisms, producing 150 organisms only to surpass your competitor is not

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[16] I use 'life-expectancy' loosely: since we are interested in lineages, the notion of the duration of 'life' might be misleading. Hopefully the reader will understand that 'life expectancy' here refers to expectation concerning duration of existence. Survival may have been appropriate but I wish to avoid confusion with the use of the word in paleontology.

necessarily a good idea: in the same way that there can be selection for energetic efficiency there might be selection for lower numbers of offspring. In a more sophisticated reproductive view of fitness, what is sought is a notion of fitness according to which a higher fitness level is a matter of higher *expected* number of offspring[17]. The organisms are creating more variants on which selection acts, they are creating more units that may survive selection events, etc. But this notion of fitness is relative. 10000 offspring is not intrinsically better in all selective environments than 9000 offspring. What we quickly discover is that *even if* all biological cases could fit the offspring model, the offspring model can only describe evolution by introducing countless redescriptions of the principle of natural selection to accommodate all the ceteris paribus clauses given by how nature actually works.

But, contrary to having a higher number of offspring or controlling more energy, having the probability (q+1) to persist x years is *always* ‘better’ than having a probability q of persisting x years. Earlier, by making the environment part of the definition of the lineage, I seemingly made the environment unimportant in the fitness comparison. In other words, if the environment belongs in the individuation of the lineage and not in the context of comparison, then could we compare lineages in radically different environments? Or could I compare radically different lineages in the way that Van Valen suggested with birds and fungus?

We will now examine how PTT is absolute and relative.

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[17] As we have seen in Chapter 1, there are many circumstances in which the organism of greater fitness fails to have the higher number of expected offspring than the less fit organism.

PTT is relative in two ways. It is always used when *comparing* two lineages (existing or hypothetical[18]). PTT is relative in so far as fitness is always comparative: One is not fit: a lineage can only be fit*ter* than some other lineage. But PTT is relative in a more fundamental way that relates to fluctuating fitness, through time.

Suppose that Lineage A and lineage B are closely related. Lineage A has a propensity of 0.2 of persisting through the next thousand years, but, if A makes it beyond those first thousand years, it has 0.6 chances of still being in existence in a million years. Lineage B has a propensity of 0.5 of persisting through the next thousand years, but, if it makes it through those first thousand years, it has 0.3 chances of being present in a million years. Which is fitter?

In some sense the question is incomplete: more would need to be said about why the probabilities (0.2, 0.6, 0.5 and 0.3 in this case) are higher (or lower). This is a point similar as the one made in Chapter 1 in defense of ecological fitness. Without fuller causal stories provided by ecological fitness differences one cannot arbitrate.

The ecological fitness information is crucial for two reasons:

1) Pragmatically, our predictions about the near future are by orders of magnitudes more accurate than those for the far future n part because we have access to more specific ecological information.

2) Ecological properties correspond to the specific causal stories and interactions

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[18] An example of hypothetical competition: quaking aspen grove A might be thousands of miles from another grove B. These two groves are not in actual competition even though we might want to compare their likelihood to persist through time if they were in similar environments. *Actual* competition is not a necessary part of evolutionary explanations.

organisms have with their environment. When trying to pin down how specific design solutions interact with specific design problems, we quickly realize that, beyond our epistemic limitations in accurately describing the evolutionary scenario playing out at any given moment, *dynamic* interactions are at play. Those dynamics, stemming in part from stochastic effects[19] on the unit of the selection, the nature of the physical/external environment, the development environment and the selective environment[20] affect all of the selection processes, all the time (the same is true of the response to selection, adaptation or otherwise).

The implication of this randomness is that the fitness propensities are always changing *in actuality*. Take the example discussed earlier: Lineage A has a propensity of 0.2 of persisting through the next thousand years, but, if A makes it beyond those first thousand years, it has 0.6 chances of still being in existence in a million years. These probabilities are ‘appropriate’ only at t1. They would have to be altered at t2 (let’s say 500 years later) following the appearance of unlikely occurrences, *not* because we know more, although new knowledge will of course change our scientific predictions, but because the world has *really* changed following highly unlikely interactions. Fitness coefficients in this model as well as in the received view are dynamic: most contemporary accounts of fitness do describe fitness as a changing property of the organism over its lifetime[21]. A lineage that is relatively fitter than its competitor is only

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[19] See Chapter 1 for a brief discussion of stochastic effect on evolutionary processes.

[20] See Brandon (1990, 47-49) for an examination of the differences between these notions of environment,

[21] It should be noted that some recent projects (Ramsey, G.) try to redefine fitness in terms of fixed-at-birth

relatively fitter given its higher propensity for persistence -this propensity being a function of the particular interactions between that individual and its environment. Since that environment continually changes and that at least some of these changes are in some way stochastic, the fitness coefficient of a given organism will have to be changed over time.

Since time is the metric of my account, what fluctuates over time is not the expected number of offspring but the 'life-expectancy' of the lineage measured as a probability of surviving for given amount of time. Since long-term persistence demands different design solutions than short-term survival solutions, PTT is necessarily time-relative. Our definition of what is fitter will depend on the time scale we are interested in. The question then shifts from 'is lineage A fitter than B?', to the time-relative and more accurate question, is 'lineage A fitter than B for a context of 1000 years?'

When taking these temporal contexts into account PTT is transformed into:

PTT6 Lineage *a* is fitter than Lineage *b* iff Lineage *a* has a longer life-expectancy than Lineage *b over temporal duration T*

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coefficient that doesn't fluctuate over time. Although at first glance that type of endeavor seems to provide the scientist with a tractable way to establish fitness coefficients by making fitness a one-time expectation that is then 'thrown in the world', it is in actuality a much more radical claim than my offspring-less view. First of all it focuses, still, on offspring numbers (which, as I have shown is in itself problematic), but more importantly it presupposes that the probability attributed to the organism depends on a time-slice description of the whole-world that is beyond the biologists' tools. The implication of such a project is that in Wesley Salmon sense *everything* is potentially statistically relevant to everything else all the time. This point would need further exposition, but we will wait for these projects to come to fruition before commenting further.

T is a variable in the same way that A and B is. The duration is necessarily limited in the same way that physical laws concern, in most cases, objects with limited mass. Interestingly, time becomes the explicit comparison context whereas *E*, the selective environment in Brandon's formulation, was the comparison context in propensity view.

More importantly, the predicate is not really temporally limited. This takes us to the absolute aspect of PTT. Since the environment is now part of the definition of each lineage, the lineages compared do not necessarily have to be in the same environment. A fortiori, they do not have to be contemporaneous. This takes us closer to the reproach against absolute fitness briefly addressed in the previous chapter. There is absolute fitness in that it is *always* better to be able to have a higher propensity to persist. That is if lineage A in has a propensity 0.6 of persisting between 10 A.D and 1010 A.D., it is accurate to say that it is fitter than lineage B which has a propensity 0.4 of persisting between 1000 A.D. and 2000 A.D even though they are not in the same environment.

A nice upshot of PTT defined as such is that we will be able to compare one species' fitness through time. Intuitively, we wish we could compare the fitness of a given species for different stages of its evolution. We now have a framework allowing us to establish whether lemurs were more or less fit for a period of X years two thousand years ago, than a period of same length contemporary to us. In other words, we can compare the fitness of a species at different stages of its evolution and determine whether it was fitter at for some period of its evolution.

A possible confusion needs to be addressed. This does not mean that one can claim that lineage A is fitter at t1 than lineage A at t2. Since lineages are in part defined by their environments and by the period they persist in, the two lineages cannot be identical for they are not in the same period. We may want to follow one species' evolution through time. But because we need to carve up the species temporally, we are in fact comparing two different lineage-segments even though we may be examining two temporal segments of one and the same species. The correct fitness comparison for non contemporaneous lineage-segments would be to say that lineage A of species alpha is fitter at t1 for period X than lineage B of the same species alpha at t2 for the same time period X without those periods being contemporary to each other.

PTT is relative in that there isn't a privileged temporal frame or scale, and it is relative in that lineages as defined above do not privilege a priori a specific level of organization: we may examine lineages of 2 generations or 50, or species, or clades, etc. But PTT is absolute in that one is able to compare non-contemporaneous lineages as long as we compare their propensity to persist for a given length of time.

One may be in fact be able to compare the fitness of a lineage of Stegasauri to the fitness of a lineage of French poodle for a given time duration.

This being said, most *interesting* fitness comparisons will be between contemporaneous lineages in similar environments (or in the same selective environment). Those comparisons will be more instructive because, since they share similar selective environments, we will more likely be able to tease out how the specific ecological interactions between organisms and their environments increase or decrease the propensity to persist for a certain period of time. If I compare, let's say, an asexually growing aspen clone lineage to a contemporary sexually reproducing aspen lineage, I might be able to establish that clonal growth is ‘better’ for increase persistence over a certain time period but not for another. And I can explain this in terms of design problems. PTT allows for non-contemporaneous inter-specific fitness comparisons, but I believe most instructive work will be done in contemporaneous intra-specific fitness comparisons where we are better equipped to establish the propensities in the first place.

Remember that in Chapter 1 I argued for an ecological fitness ‘revival’. With PTT, I claim to provide a way to compare ecological fitness. We will still need to individuate the problems and consider how well the lineages solve them: the measurement problems identified by Lewontin have not completely disappeared, but we now have a way to establish the relative fitness of a lineage at least for past evolutionary cases without identifying and summing all the solutions to design problems. In other words, it is at least possible in theory to compare the fitness of two lineages non-demographically (therefore allowing the inclusion of non-reproductive entities) in terms of the likelihood of their persisting over a certain time frame *even* though we have not completely identified how each little design problem impacts on this probability.

As Van Valen wished, we may be able to compare the fitness of a bird with that of a fungus, but in survival terms, not in energetic terms. We may be able to say that the fitness of a fungus lineage is higher than the fitness of a bird lineage B because the propensity of lineage A to persist for 1000 years between 1000 AD and 2000 AD is higher than the propensity of lineage B persisting 1000 years between 2000 BC and 1000 BC. I’m not sure how scientifically useful that comparison is because of the difference in environment, species, etc. But the usefulness (or uselessness) is not mine to predjudge.

Knowing *how* a lineage solves a design-problem is crucial just as I pointed out in chapter 1 but oftentimes it may be an intractable problem. But we can still compare the overall success of lineages in terms of differential persistence. And this differential persistence is not solely a function of differential reproductive success: it can also be evaluated by the persistence of an individual's components. To draw a very simple picture, imagine an entity with only two roughly identical components. The entity's persistence is function of the persistence of the two components (the exact nature of that function will vary from one system to the other). Those components can change (e.g. by growing), they will affect the future persistence of the entity. If the growth is affected in some way by external pressures, and that the growth changes in a way that increases the persistence of the components and the overall entity, the entity is evolving.

If the probability of a lineage to persist for a given time frame increases, then the lineage is probably adapting/evolving. We can still measure the fitness of a lineage that isn't evolving, but when we see a positive increase in the probability to persist, we can infer that changes in components (often in the differential reproductive success of its members when applicable) lead to a better solution of the design problems posed by the environment. But ultimately I am suggesting, at the most abstract level, survival is the only overall-design problem.

Using the word lineage may be misleading: it gives the impression that we are only concerned with long term macro-evolutionary events spanning thousands or millions of years. But that is not what is really at stake. Long*er* life expectancy is not relevant only when talking about million of years. A lineage with an only slightly higher probability to persist even for a short time period than its closest competitor is fitter. This may be seen as making evolution forward-looking but such forward-looking is already part of some evolutionary biology projects (e.g. grand-mothering effect). The search for mechanisms of evolvability is another similar example. In some real way, evolutionary biology is already somewhat sympathetic the idea that an organism with the ability to have *some* forward-looking is advantaged. The fact that it has only been proven to be relatively short term should not detract us. The forward looking aspect of our account is to be in the spirit of how it is applied elsewhere in evolutionary explanations. In its long form PTT becomes

PTT [entity *A* that changes through time as a result of differential persistence of its components] is fitter than [entity *B* that changes through time as a result of differential persistence of its components] iff *A* has a higher propensity than *B* to persist for *time duration T*

For reproductive biological systems, this formulation will be very similar to Brandon’s propensity view.

PTT$_{\text{reproductive}}$ Lineage A (changing via differential reproductive success of its members) is fitter than Lineage B (changing via differential reproductive success of its members) iff A has a higher propensity than B to persist for time duration T (propensity established in part demographically)

Moreover, our PTT is very close to Thoday's original definition of fitness, except that by making it explicitly temporally relative, I avoid some of the difficulties identified by Brandon and others: PTT, because it doesn't privilege long term persistence, can accommodate both micro-evolution and macro-evolution.

4.5 Conclusion

The Aspen Grove is not a community of ramets, but rather a single entity responding to selective pressures from the environment. The ramets could become individual groves only if they were to all be separated physically: they would actually have to be permanently separated, for if left in proximity, the ramets' root system would eventually reconnect into a single grove. Consider the teleological question, why is there such a tendency to reconnect and become a single organism? This remains an enigma on any offspring view, or even in biotal evolution/energy commandeering paradigm[22]. If the relevant unit is the grove itself (or actually its lineage), regardless of the number of autonomous groves it actually produces, why, *for evolutionary reasons,* selection

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[22] This is an empirical point that needs confirmation, but theoretically 1000 individual ramets *trying* to grow into 1000 large groves could in the end commandeer more energy than 1000 ramets becoming one integrated grove. However, the unified large grove would persist longer because of its resistance to extinction. Only mass-extinction events like rapid decline in temperature, *massive* fire, meteorites or immense pressure from humans (the size of the grove makes it more 'human-resistant' than most organisms botanical or zoological). In some sense, although the grove seems to validate Van Valen's claims, it is plausibly less energy-guzzling than it *could* be if it were to sprout actual individual autonomous units. This empirical claim demands testing that is beyond the scope of this project.

‘favored’ its integration instead of its fragmentation? Because integration increased its persistence. Or more accurately in a non-teleological language, integrated groves, big ‘fattening’ groves persist longer than reproducing aspen: integration is more fitness enhancing than reproduction.

Again let me stress that integration will not always be favored. My project aims to provide a framework where both no-offspring systems and many-offspring systems can be accommodated. In a nutrient poor environment or in certain fluctuating environments, the aspen’s growth (by contrast to the sexual reproduction strategy it has ‘access’ to) wouldn’t necessarily have been favored. PTT provides a way of describing the fitness of non-reproductive systems like the Aspen as well as reproducing systems. With PTT we get a principle of natural selection that takes this new view of fitness.

If one adopts PTT, we can still apply intergenerational change accounts via differential reproduction and inheritance when appropriate. But for the ‘non-standard’ cases of evolution, like the aspen, the classic story can only take us so far. There are “intra-generation” mutations (somatic mutations) that are passed on insofar as the mutated runners ‘pass-on’ the mutation in their creation of other runners. More abstractly however, the transmission lies in the persistence itself. As we saw in Chapter 2, the aspen’s growth pattern is a response to natural selection. Growth in the optimal direction will flourish while disadvantageous growth patterns will eventually disappear. Subsequent growth will start from the previous successful growth patterns and so on. The growth pattern is directed by previous growth successes and future environmental changes. And growing ‘in the right way’ will increase the persistence of the grove.

There is in some sense modification with “descent” without genetic inheritance. The scare quotes are intended to highlight that since we are examining parts instead of descendants, speaking of descent or generations may not always be appropriate. What this implies however is that we need to understand the notion of phenotype in a less-restrictive way. This is not a novel requirement, as any group-selectionist will readily agree: the notion of group-trait goes beyond what Darwin understood as the trait of a single individual organism. The growth pattern or the directionality of growth is part of the phenotype of the aspen grove, as much as the color of the leaves, or the structure of the root system. The supremacy of genetic inheritance has already been somewhat ‘reduced’ in the evo-devo project, which identified an important role for epigenetic inheritance. Reaping the benefits of this project, we should realize that genetic transmission in particular and reproduction in general are not *sine qua non* conditions for evolution by natural selection. Reproduction is ‘merely’ the most efficient way of adapting rapidly for most biological systems. PTT provides a way to describe fitness that is both inclusive and more general about how evolution works in nature.

Conclusion

As is often the case in philosophy of biology, David Hull provides guiding wisdom:

> The reader may now be tempted to agree with Hamilton that “common usage’ is preferable to all these “metaphysical” ruminations. As understandable as the temptation is, I suspect that sooner or later common usage will have to be sacrificed if we are to understand the evolutionary process. (Hull 1980, 331)

It is doubtful –or rather it remains to be seen- whether we have identified a ‘physics’ grade law of evolution, although the necessary programmatic steps have been made.

As shown in Chapter 1, evolutionary theory demands a notion of ecological fitness. If fitness has to be ‘exclusively’ ecological, the worry is that it robs biology of the true operational concept it has with fitness defined in terms of differential reproductive success.

We have seen in Chapter 2 that the notion of ‘organism’ having this ecological fitness is more complex than thought prima facie –not a novel point. We have also seen that for those individuals, the notion of population is at best suspect since they do not reproduce. This is a more controversial point because of its implication for the received view of evolution. I have argued that the problem is with the theory, not with these non-reproducing biological systems. Finally, using the examples given in chapter 2, I have hinted at a new metric of ecological fitness, namely time. The struggle for persistence can explain those problematic cases of evolution.

In some sense, how long a lineage fights extinction is the only crucial fact –in this respect I am heavily inspired by macro-evolutionary and paleontological projects in general and Van Valen's work in particular.

Our examination of some of Van Valen's work in chapter 3 showed us the use of looking at survivorship to identify general trends. In was also instructive in that it suggests us with an ambitious universal currency of fitness, increase in energy control. Although the account has some flaws and limitations, I sympathize with Van Valen's motivation: Van Valen rightfully thought that evolution is more prevalent than normally believed and that there might be a way to unify all the motley types of evolution under a heading other than changes in gene-frequency. He correctly thought that reproduction might not be inclusive enough. In the same way that *specific* design solutions can play no role in the general description of adaptation, offspring numbers might turn out to be convenient for identifying some evolutionary processes but a flawed and incomplete theoretical foundation to build all of evolutionary theory upon. How an entity does in fact persist (i.e. which type of adaptation will prevail) remains maybe of deep scientific interest but, as I argue, it is a different issue from what constitutes the core of the theory of evolution by natural selection.

Surviving means 'persisting through time'. Having more offspring in the long run is generally a great way for a lineage to persist through time. As I pointed out earlier with more offspring, chances are you will get more variation and therefore, possibly, the novel phenotype that will be permit survival in tomorrow’s ‘new’ environment. Or a large number of offspring will be harder to stamp out, etc.

A large number of offspring is generally ‘good’ in facing selective pressures. But even this received view is always implicitly qualified to accommodate variance, skew, etc. We quickly learn that a high number of offspring is not always absolutely good *per se*. Then why keep it as a general definition of what fitness is? When digging a little deeper around the received view, we find a slew of ceteris paribus clauses qualifying the definition. As we get further and further from the schematic view of the principal of natural selection we see that, although expected numbers of offspring are a good measure, it cannot be the core of what fitness means.

In our examination of the three cases of non-reproductive evolutionary systems, the intended message was that reproduction is a means not an end. That means can be occupied by other mechanisms. What makes offspring so special in evolution by natural selection is that through them we achieve increased variation. But the same feature can be obtained through differential persistence of parts.

Variation can be obtained by changing the ‘external’ phenotype during an individual’s lifetime: a point that evo-devo has been pressing on in last decades. Passing on reliably ‘good’ structure so they can ‘accumulate’ in a way that could explain the apparent adaptation of organisms to their surroundings is prima facie more complicated, but only when we expect all traits to be passed by the same mechanism.

My proposal is in many ways simple: by recognizing the role of extended inheritance, we realize that some systems evolve without differential reproduction but via differential persistence of components instead. These systems are still molded by the environment and it is at least theoretically possible to parse out the relevant forces in play in that molding. As such, evolutionary theory to encompass more phenomena while retaining some meaningful empirical content.

Spatial position, when treated as part of the phenotype, can be passed on very reliably through ‘mere’ physical or developmental constraint. That ‘new’ phenotype can then be selected on, and the selective pressures can then push the organism towards having a very different phenotype, in part by changing its position, by ‘pushing it’ into different environments that it can explore in a way that may enhance its propensity to persist in one way or another.

There are two ways to evaluate the argument given in this project. The first possible interpretation could be that PTT may provide a *model* for the evolution of some non-sexual-reproducing species, ecosystems and colonial organisms. According to this view, there is no single causal process of evolution in the first place. So perhaps we should not expect reproductive success to be part of the evolutionary explanation for all systems in the first place. My account could then be cast as useful to explain a small number of exceptions that cannot be easily accounted by contemporary evolutionary theory. As such my analysis describes the evolution of non-standard biological systems but leaves evolutionary explanation for all the rest of biological systems intact. In some sense, the received reproductive propensity view can coexist with PTT.

A second more interesting interpretation of my account is that it unifies all cases of evolution by natural selection by treating high fecundity not as the only way to increase one's fitness but as a local response to local selective pressures: it is a contingent fact about the world, that high fecundity is an oft traveled evolutionary path in the same way that photosynthesis is very prevalent in plants. High fecundity becomes an adaptation just like any other evolved trait. The background context for its appearance is increased persistence. PTT may help to explain the 'difficulty' the propensity view has with skew, variance, etc, by showing how increased reproductive success should not always be expected even in reproducing biological entities.

From a macroevolutionary viewpoint we could say that lineages that have increased their persistence, by increasing the number of autonomous components they have (i.e. individuals), have strengthened their propensity to persist more then lineages that have not increased the number of their components.

The reader more interested in 'coexistence' of both models may ask the fair question as to whether one should let the fringe redefine the core of evolutionary theory. In some sense we are not interested in 'merely' fringe phenomena. Mayr (1987), when biting the 'biological species concept' bullet, contends each genet is its own species (or paraspecies) because of its reproductive isolation. But then there are actually much more aspen type cases than there are 'garden variety reproductive' organisms. Every reproductively isolated clone could count as an individual species and then, there will be numerous cases of biological evolution that the current evolutionary accounts cannot fully account for.

More importantly, if biotal evolution is a real process, then there is a whole level of organization that evolves by natural selection but that does not reproduce. It is doubtful that such evolution can be described in energetic terms. Perhaps Swenson et al.'s ecosystems might possibly be understandable from some energetic perspective. But our critique of Van Valen's framework shows that increased energy control might not always be selected for as well. Persistence however is always 'good'. So, first, the biological facts that inspired this project can hardly be written off as merely 'fringe'. And second, *even if* the cases described in this dissertation belonged only to a small collection of outliers, the PTT they lead to permits us to identify more cases of previously unrecognized cases of evolution.

This idea leads us to the final potential reason why we may prefer the second interpretation and let the 'freak' cases change our understanding of the whole theory. In their defense of punctuated equilibrium, Gould and Eldredge point out that even if they are potentially only identifying trends and not novel processes, the 'mere' identification of trends may reorient the empirical project of paleobiology[1]. Similarly PTT (and future fleshing out of it) may motivate more inquiry in how components/parts affect persistence. Just as evo-devo has emphasized the significance of developmental in evolution and therefore demands more integration of developmental biology in evolutionary inquiry, PTT demands that we increase the role of morphology, physiology and indirectly to paleontology in evolutionary research. By exploring these three fields we will uncover novel cases of evolution invisible through a population genetics lens. Genetics will remain a crucial aspect of evolutionary inquiry, but a return to our naturalist roots might

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[1] "We knew that we were proposing a reorientation of empirical work in evolutionary paleontology-away from the search for gradualism in selected species within local sections, towards the quantitative study of evolutionary pattern in all members of fauna" (Gould and Eldredge 1977, 117).

be of help here: by examining form, classifying patterns, trying to look at the phenotype without immediately looking for a genetic mechanism and the differential reproductive mechanisms associated to it, we will be able to understand more cases of evolution. A very Darwinian turn indeed…

Ultimately, Lewontin provides an important word of caution when reintroducing his "Gene, Organism and Environment":

> We are constantly being urged to see the world of living phenomena in a different and better way, using new organizing principles (…). But the question that must always be asked of such proposals is how the practice of biologists would be changed in a way that would allow us to answer previously unanswerable questions. (…) The biological philosopher only interprets the world; the point, however, is to change it. (Lewontin in Oyama, Griffiths and Gray 2001, 55)

Aside from Lewontin's nod to Karl Marx, the challenge is real. Are we merely suggesting the drawing of unnecessary epicycles? Is a shift away from the exclusive focus on reproductive success in favor of differential persistence a truly useful organizing principle? I have argued that the dividends for accepting my view are numerous: first and foremost, it provides a metric for a definition of fitness (ecological fitness) that was previous unacceptable for epistemic reasons. Chapter 1 argued that the need to revisit a design-problem view of fitness was necessary for various theoretical and empirical reasons. But ecological fitness insofar as it doesn't provide any intuitive measuring scheme aside from reproductive success is not a viable stopping place. Persistence does however provide a way to deal with all the measurement problems by allowing us to get away from independent from 'head-counting' when it fails to measure fitness.

The second upshot of adopting my view is that it permits us to understand some real change in biological systems in an evolutionary framework. Some of these changes are more intuitively evolutionary (such as the quaking aspen case) while others demand more massaging of the theory (e.g. ecosystem selection). But in all cases described in chapter 2, shifting away from offspring number permits us to provide a Darwinian explanation of how some systems change and adapt in response to selective pressures from the environment.

There is a third more speculative upshot to my project. First let me go back to the ellipse in my last Lewontin quote. Here is what I had left out of his cautionary question: "What new experiment, what new testable hypothesis, what explanation of a previously mysterious or contradictory observation will flow from a change in point of view?" (Ibid. 55) If evolution does not necessitate differential reproduction, it may not necessitate life. Evolution becomes a process that can *in theory* be found in non-living systems. This was hinted in the discussion of ecosystem selection and termite mound evolution, but PTT may take us much further. My account could possibly be applied to game theory, cultural evolution, formation of star systems, etc. There is no good reason to preclude us from trying to make sense of other types of changes in evolutionary terms. In the past, most 'apparent' evolutionary changes have been forced into a reproductive framework (or simply dismissed as being non evolutionary). Memetics is a good example of this. It was thought that replication was necessary to make sense of apparent cultural evolution, but it was always difficult to identify what was evolving, through the replication of what, etc. In my framework, those questions are avoidable. Differential persistence will be much easier to find than differential reproduction. Aside from cementing the role PTT can play for biology, I wish in the future to see where else outside biology, we can identify genuine evolutionary processes. In the same way that natural selection does not care whether one is an offspring or a component, it does not care whether one is a living system or not. As such, a persistence approach to evolutionary theory might lead us to a more inclusive description of the evolution research field.

Ironically a project initially motivated as a reductionist project ends up being the ultimate autonomist manifesto. Evolution may turn out to be a process as basic as other foundational ones in chemistry or physics. Notice that in saying that evolutionary theory might be an autonomous non-reducible theory, I am not arguing that biology is autonomous or non-reducible. It might be the case that in the end most biological processes will be reducible to macro-molecular interactions and then to chemical and then physical interactions. But any biological process (and obviously they will be many) that are evolutionary processes will be non-reducible. Or to put differently, many aspects of biology might in the end be macromolecular, but the evolutionary aspect of biology will be non-reducible to macromolecules. That of course deserves a more robust argument, but provisionally, we can agree that evolution is an established fact about the world and that *if* differential replication is not necessary for evolution to obtain, evolution will be found beyond the living world. If so, evolutionary theory is not ‘simply’ the story of some quirky associations of carbon, oxygen, hydrogen and nitrogen on the third planet from the sun. Anything constituted of parts might be subject to evolutionary inquiry. It becomes a general theory about some interactions of systems with their surroundings and how some of these interactions increase the persistence of those systems. As such evolutionary theory might be as foundational as our most fundamental theories in science.

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Biography

Frédéric Bouchard was born in Montréal, Québec, March 13th 1975. He obtained his *diplôme d'études secondaires* as well as his *diplôme d'études collégiales* from Collège Jean-de-Brébeuf. He went on to earn a Bachelor of Arts in Philosophy (1997) and a Master of Arts in Philosophy (2000) from the Université de Montréal. During his studies at Duke University he held doctoral fellowships from the Social Science and Humanities Research Council of Canada as well as from the *Fonds pour la formation de chercheurs et aide à la recherche (Gouvernement du Québec).* At Duke University, Bouchard was Evan Frankel Fellow and the William Bernard Peach Instructor of Philosophy during the 2003-2004 academic year. Prior to instructing at Duke University, Bouchard has taught philosophy at Collège André-Grasset and Collège Jean-de-Brébeuf. Bouchard has recently been appointed assistant professor in philosophy at the Université de Montréal.

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