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Adaptive landscapes:
A case study of metaphors, models, and synthesis in evolutionary biology

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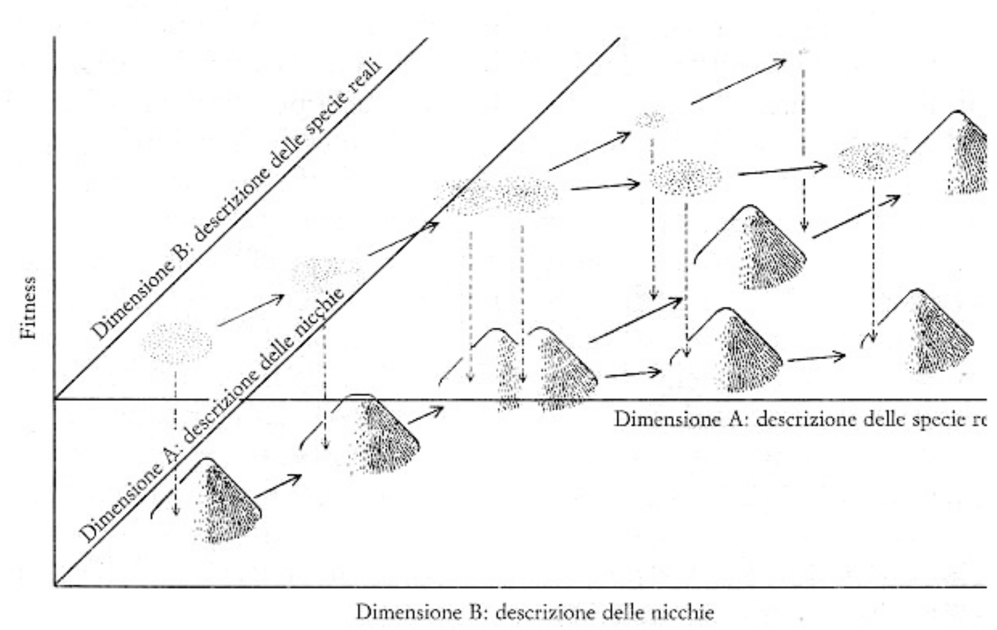
INTRODUCTION

I met adaptive landscapes as an undergraduate, reading Niles Eldredge's *Reinventing Darwin* (1995). In this beautifully enlighting book, Eldredge was celebrating the historical, epistemological, and empirical milestones of evolutionary biology. At the same time, he was no less than educating his reader to seeing how evolutionary biology had been conflating ecology and genealogy, epistemologically "smashing" the former into the latter. In the ever-changing flow of biological evolution, where everything moves in all directions at all scales, biologists had established a solid ground on genes. Among organisms moving on planet Earth, forming competing or somehow cooperating groups, phenotypes shifting from averages to averages yielding minor and major transformations, genealogies splitting and carrying over a flow of inherited genes, individual genes forming dynamical trajectories in these flows, the grand dynamics of global ecology and climate change...



among all this, and much more, the movement of genes had offered a locus (and focus) of study to biologists.

Eldredge showed Theodosius Dobzhansky's picture of the adaptive landscape (1937, reported by Lewontin) citing him at length. Dobzhansky's hilly, moderately rugged adaptive landscape featuring peaks and valleys was a landscape of genotypes, suitable for representing genealogical continuity and fitness, but silently endowed with the ability to reflect also the physical movement of organisms in space, the dynamics of their phenotypic transformations, the changing influence of environments.

I learned what an adaptive landscape was, and how important it was. But above all, and more deeply, I learned that words and pictures can aggregate a world for us to know and, at the same time, constrain our thought, channel it in certain ways of thinking. In science as in everyday life.

Eldredge's thought then became a major organizing guide for my understanding of evolution and for my undergraduate dissertation (2003) on cichlid fishes and evolutionary pluralism. The core messages were that the most fascinating cases of evolution require epistemological pluralism, mainly intended as articulation between ways of looking, each typical of some disciplinary fields (and not others); and that pluralism is not easy “anything goes”, demanding rigor and imagination, exercise and flexibility. Eldredge’s ideas on the Modern Synthesis, an “unfinished synthesis” (1985), were another theme I was about to find again in recent years. It is developed here as well, indeed.

For one who studies evolution and philosophy of biology, adaptive landscapes are a discreet, but constant, presence. They appear in scientific literature, here and there, in various “clothes”, and they also put on their “public dress” when, as in Richard Dawkins’s book *Climbing Mount Improbable* (1996), they are used to explain and spread (sometimes, defend) evolution to the public in an appealing and persuasive way.

So when I, Telmo Pievani and our group and the University of Milano Bicocca started a research program on “adaptation”,[1] we promptly decided that adaptive landscapes could never ever be left out, being among the most effective and influential representations of adaptation (a phenomenon, in turn, at the heart of evolutionary biology since its dawn in Darwin’s work). So we opened the “historical box”, and read the original papers by Sewall Wright (1931, 1932) where the landscape was originally proposed (cf. Provine 1986).

It was then, in 2008, that my attention was drawn to a monographic issue of *Biology and Philosophy* - the leading journal in its field - right about

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[1] PRIN 2007: The Adaptive Behaviour of Biological Systems and the Scientific Method, 2008-2010.

adaptive landscapes! Titles and abstracts sounded like “the end of the adaptive landscape metaphor” (Kaplan), “the rise and fall of the adaptive landscape” (Plutynski), “the metaphor can have misleaded biologists for decades” (Pigliucci), “it is time to drop the metaphor” (Kaplan), “the landscape revolution” (Pigliucci & Kaplan 2006), “is landscape a metaphor? is landscape a model?”. The issue was pervaded by the resonance of “holey landscapes” proposed by Sergey Gavrilets (1997, 2004), more similar to Swiss cheese than to a hilly countryside (by the way, I knew Gavrilets because he had been among the authors of fascinating mathematical models of speciation in cichlid fishes). Another, almost irresistible hook was the appearance of Massimo Pigliucci and his proposal of an Extended Evolutionary Synthesis (Pigliucci 2007), that had raised interest in the Italian evolutionary community.

I put myself to work and read the papers, and then again, and I was puzzled and surprised: I did non understand, exactly. Yet, I had known adaptive landscapes for a while. By my reading of Eldredge I thought I had grappled its main epistemological trick. I was studying adaptive landscapes more and more, reading the papers by its inventor. I missed many points of the debate, and moreover, I perceived that there was something “out of gear” in that debate. I read also other papers, like Robert Skipper (2004), and Michael Ruse (1990). I have a large intellectual debt with all these people debating the problems I address here.

All revolved around what adaptive landscapes are. That is, not how they are, what shape do they have, how are they to be used: these issues were left to scientists (although philosophers tended to slip a bit into the third one). *What adaptive landscapes are?* The words “model” and “metaphor” were surely central. I wanted to think about it, to bring a contribution to that debate, but I simply did not know enough. So, I had to take time to make a journey in the philosophical thought on metaphor and model. Much of such time was spent at the University of Utah, Department of Philosophy, Salt Lake City. The “U of U” - as they call it - gave me time and food for thought on these arguments - but actually on many, many more. It was there that, perhaps with a cosmic coordination, I met met personally one of the authors of that *Biology and Philosophy* issue: Anya Plutynski, professor of philosophy at the U. I am so grateful to her for patience and time spent with me exploring evolution, philosophy and, most of all, my thoughts.

This dissertation brings a contribution to the philosophical debate on adaptive landscapes. I think there are some elements of innovation, for example: the distinction between native and migrant metaphor; a processual and communicational idea on what the Modern Synthesis was, and on what role a metaphor could have played in it; a view (taken by Richard Lewontin) of the disunity and theoretical structure of population genetics; the distinction between “adaptive surfaces” (mainly metaphors) and “combination spaces”, two terms normally conflated in the word “landscape”; an analysis of what bridges (including heuristics) may be cast between equations of gene frequency and the genotype space that, due to its huge dimensionality, cannot be handled by mathematics; a specified vocabulary to be used to clear the adaptive landscapes debate, accompanied by a plea in favor of a pragmatic approach - for example, the plurality of available notions of model forces us to choose one notion and see where it brings, otherwise we get stuck in confused, endless debates; an updated analytical comment of recent landscapes - Dobzhansky, Simpson, Dawkins but also the proliferation of combination spaces used in evolutionary biology to address a great variety of problems; the vision (got by Sergey Gavrilets) of a patchwork of tools finally making Mendelian population suitable model *also for* speciation; the exact position of holey landscapes in this patchwork, and the idea that scientists's questions - like "how possibly" questions - matter in accessing this patchwork and in deciding "what explains" and "what describes" what in the world; the direct response to some mistakes Massimo Pigliucci made, I think, in his assessment of the adaptive landscape; an analysis of the Extended Evolutionary Synthesis project at its present stage, and some reflections on the conditions that will allow such a project to give a fair treatment and a good position to tools from the past, like the adaptive landscapes.

All this would have not been possible without the support of a landscape of wonderful people. Already mentioned Anya Plutynski but also Steve Downes, at the University of Utah, have made possible my research stay, and donated me care and attention, leaving me free of exploring my sometimes tortuous trails. I owe them fundamental comments that put me on the right way. I also thank Brett Calcott at the Australian National University for his amazing work on a paper of mine, a summarized version of this dissertation. At the University of Utah, I have to thank a few true friends: above all Monika Piotrowska, David Drake, Ravi J. Cerar, and Roxana

Arauco. A terrific context of learning was the Philosophy of Biology Lab Group, led by Matt Haber, who I want to thank very much, along with all participants like Joe Dickinson, Mariam Thalos, Jim Tabery, Patrick Forber, and Steve Peck, and guests Peter Godfrey-Smith and Frederic Bouchard. A particular appreciation to Chris Jenson and Cinnamon Wuthrich for having involved themselves in the reading group on the Extended Synthesis. In Italy, I have to thank very much prof. Marco Ferraguti for his support on this project. And in our University of Milano Bicocca, thanks to all our Department, but especially to young researchers I luckily worked with, like Chiara Ceci, Francesca M. Rossi, Fabrizio Panebianco, and Edoardo Datteri. And finally, my advisor Telmo Pievani, for all the trust and knowledge he gave me through the last decade. May we have the pleasure (and sometimes pain) to work together for many years to come! There are no words to thank all my family for valuing and trusting me, my acquired family for loving (and logistical) support, and well above all my lovely wife Anna, my life.

CHAPTER I

Adaptive peaks and valleys in the big picture of evolution

1. Introducing adaptive landscapes

Landscape pictures with peaks and valleys have been present and influential in evolutionary biology for many decades. They appear in Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937), George Gaylord Simpson's *Tempo and Mode in Evolution* (1944), and Julian Huxley's *Evolution The Modern Synthesis* (1942), which are among the most authoritative and widely cited books in evolutionary theory. They belong to the foundational works of the Modern Synthesis, so the very presence of the landscape picture therein may be seen as a clue for a theoretical role the picture may have played in the making of it. Indeed, I argue for such a possibility in section 3, where I also unveil the picture's diffusion (3.1) and origin (sect. 4, cf. also chapter II). In section 2, I present Simpson's and Dobzhansky's landscapes, commenting on their "evolutionary scope" (i.e., "how much" they are meant to show of evolution) which leads me to label the adaptive landscape a "big picture" of evolution. I also present the wide-scope landscape picture offered in *Climbing Mount Improbable* (1996) by Richard Dawkins, certainly one of the main popularizers of evolutionary theory in the Twentieth Century. The presence of a landscape picture as the central organizing image of his 1996 book may not be a reliable sign of theoretical importance of the metaphor, but it is of its communicational virtues.

All my chapter revolves around adaptive landscapes seen as a scientific *metaphor*, a definition widespread in literature but requiring, in my view, further specification. On the one hand, I propose a reading of adaptive landscapes as a *migrant* metaphor, a figure of speech important to build bridges between biological fields in a communicational view of the Modern Synthesis *à la* Ernst Mayr (cf. 3.2, 3.3). On the other hand, in section 5, I suggest looking at landscapes in their *native* theoretical context, i.e. mathematical population genetics. The peculiar definition of what a metaphor is *in* mathematics reveals the necessity of thinking of adaptive landscapes there as "metaphors for models". Such peculiarity of the *native metaphor* might trigger deeper reflections on the migrant metaphor, too: what would it imply for different biological fields to think to "metaphors for models" instead of metaphors and models as competing descriptions of the world? When an *altered* metaphor is delivered from the native context, like in the case of holey landscapes by Sergey Gavrilets sketched out in section 4, weighing properly the native metaphor is useful and necessary.

But, first of all, it is fundamental to say very briefly what does it mean to draw a landscape picture of evolution. There are many interpretations and uses of the landscape picture (cf. this chapter, and chapter III) but, according to my analysis, the following *three shared features* need to be presented first in order to correctly introduce the topic. They will be recalled throughout the chapter, so I name them synthetically "no environment" (1.1), "virtuality" (1.2), and "higher is better" (1.3) features.

1.1 No environment

Contrary to what is probably first evoked by the word "landscape", a landscape picture *does not directly depict environment*. And this doesn't have to do with the fact that any representation is, in fact, an abstraction.[2] The point is that, given that a landscape picture of evolution *is* an abstraction, it is an abstraction *of something else* than the geographical environment: the landscape is a picture of *something that lives in* an environment, e.g. a population of organisms, a species, a set of species, a population of molecules and so on, according to the theoretical context from time to time. So, an evolutionary landscape is not - in any case - the portrait of geographic landscapes (like e.g. Figure I.1) we can walk through and observe. It is an abstract representation of the living "stuff" that is evolving, distinct from the environment which is, in a strong sense, not represented, because "external".

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[2] Many philosophers have reasoned about representational value and limits of evolutionary landscapes and other ways of representing or modeling evolution, cf. II.3.

Figure I.1. *Hills, peaks and valleys in a geographical landscape we could walk through and explore. Evolutionary landscapes* do not *directly represent geography and the environment.*

1.2 Virtuality

A landscape picture shows on a more or less rugged surface *a whole space of possibilities* of the entity that "that lives in" an environment, mentioned in point 1.1. Each location on the surface represents a configuration which is *virtually* possible within the evolving entity. If the represented evolving entity is, e.g., a population of organisms, any location of the surface will stand for an individual *virtually possible* within such a population. Virtuality is a fundamental feature: the landscape typically represents a huge number of possibilities, and a few of them (or, in some versions, one) *at a time* are effectively realized. Time dimension is thus introduced: evolution as represented on a landscape is the *exploration through time* of different locations on the surface, of different possibilities for the evolving entity. Movements on the landscape are evolutionary movements, represented as explorations of possibilities. The landscape is then the synchronic representation of all the possibilities for an evolving entity; such possibilities have to be (always partially) explored diachronically, through time. Getting back to the example in which the evolving entity is a biological population, every birth of an organism will be the exploration of a new location on the surface, the realization of an individual which was virtually possible (a spot on the landscape) but yet to be realized. If, instead, we are using the landscape to represent all the possible versions of a morphological trait, a linear path starting from a point on the surface might represent the evolutionary change of the trait through a series of intermediate forms.

1.3 Higher is better

Vertical dimension of the evolutionary landscape represents "adaptedness", fitness,[3] or (in some versions we will see) more absolute and intrinsic values, like complexity or perfection or "harmony". As seen in 1.2, each location of the landscape represents a possibility, but the location's elevation is not supposed to be randomly or aesthetically determined: rather, it is supposed to depend on the fitness of that possibility *in an environment* which - as seen in point 1.1 - is *absent* from the picture. The environment is thus extremely

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[3] Fitness (Haldane 1924) is actually the technical term for many expressions used in the text, including fitness value, adaptedness, and adaptive value. The very expression "adaptive landscapes" is, in some theoretical contexts, incorrect or at least inexact (see Gavrilets 1997, 2004, and chp. III), and should be replaced by "fitness landscapes". In most of this work which is philosophical, not scientific, the terms are used interchangeably according to the context - unless differently specified.

important because it *influences the whole shape* of the surface by determining the elevation of each and every location. The supposed environment is the same for the whole surface, it is *the* environment which every possibility must confront with, getting its particular fitness value. Accordingly, peaks and valleys respectively accommodate the fittest and the least fit possibilities. Paths or courses moving from any location of the surface and arriving on peaks would be rightfully called *adaptation* in the postulated environment.

Adaptation is the most fundamental organizing concept for the landscape pictures of evolution.[4] That is why I am willing to acknowledge the term *adaptive landscapes* in the title of my dissertation and throughout it. The term is widespread in the scientific and philosophical literature and evokes the right area of reflection. But the term is also problematic and problematized in many respects, as I am showing in what follows.[5]

Evidently, a landscape picture of evolution - an adaptive landscape - is not at all a picture of a natural landscape we can contemplate by looking out of the window, or by going for a walk in the countryside. Natural landscapes are *products* of evolution, and they can bear the *traces* of evolution, as Charles Darwin had understood and poetically wrote at the end of *On The Origin of Species*:

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[4] There is a less immediate, but at least equally important, organizing principle that will be presented in chapter II: neighborhood (II.2.2).

[5] For example, adaptive landscapes has, for some authors, a restricted reference to *one kind* of landscapes, with “fitness landscapes” indicating a different kind (Gavrilets 1997, Kaplan 2008, Pigliucci & Kaplan 2006). On the other hand, the very term “landscape” conflates, in my view, the ideas of a combination space and a surface, I try to disentangle in chapter II.

> It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us (Darwin 1859).[6]

Adaptive landscapes are abstract pictures set out with the aim of depicting the evolutionary *process*. They represent a virtual space of possibilities for one evolving entity - for example, a population. Different entities will have different landscapes. Landscape pictures do not depict Darwin's "entangled bank", i.e. the environment in which many entities live, interact, and evolve. Rather, the external environment determines the shape of the landscape because every possibility's elevation depends on its own fitness *in* the given environment. The exploration of possibilities through time can draw paths, figures, and courses on the landscape.

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[6] An interesting notice: "Darwin's Landscape Laboratory" is the house, gardens and countryside near London where Darwin lived and worked for the forty years of his scientific maturity including his work *On The Origin of Species*. *This* landscape is of outstanding universal value because of its unique cultural significance as the open-air laboratory in which the theory of evolution by natural selection was developed. It provided unique insights into the scientific understanding of natural life and biodiversity. The character of the neighbourhood is conserved and many of the settings that Darwin lived and worked in for forty years; with the many plant, insect and animal species that were observed there can still be seen in existing habitats today (http://www.darwinslandscape.co.uk).

2. Three bigs

I present now the most important landscape pictures, and moreover argue for their big scope conveyed by the term "big picture" Their authors - Theodosius Dobzhansky, George Gaylord Simpson, and Richard Dawkins - will be presented in sections 3 and III.1

2.1 Dobzhansky's landscape

The book *Genetics and the Origin of Species* (Dobzhansky 1937, 3rd ed. 1951) begins with an appreciation of the diversity of life (e.g. pp. 3, 6), and with the explicit declaration of a strong correlation between *diversity and adaptedness* (p. 3).[7] Diversity in Dobzhansky's main focus is not among individuals, that vary in a continuous fashion. Rather, focus is group diversity,[8] which appears discontinuous and hierarchically nested. In Dobzhansky's argument the structure of such diversity is related, through adaptedness, to the discrete variation of habitats:

> The enormous diversity of organisms may be envisaged as correlated with the immense variety of environments and of ecological niches which exist on

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[7] «The adaptedness of organisms to their environment is striking. [...] Every organism is adjusted to occupy and to exploit certain habitats» (Ivi, p. 3).

[8] «The structures, functions, and modes of life of every *species* are at least tolerably consonant with the demands of its environment» (p. 3, my emphasis). Actually - Dobzhansky remarks - groups themselves reflect *clustering* of individual variation. «If we assemble as many individuals living at a given time as we can, we notice at once that th observed variation does not form any kind of continuous distribution» (Ivi, p. 4). To recognize a group is to recognize a cluster of individuals which, however all different and unique, form a cluster in a much larger array of individuals. It is *in* individual variation that «a multitude of separate, discrete, distributions are found» (Ivi, p. 4).

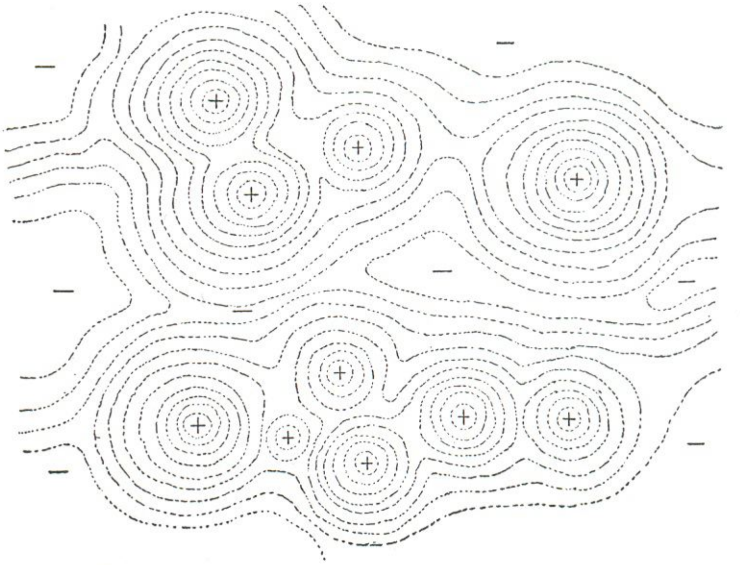

FIG. I. The "adaptive peaks" and "adaptive valleys" in the field of gene combinations. The contour lines symbolize the adaptive value (Darwinian fitness) of the genotypes. (After Wright.)

Figure I.2. *Dozhansky's symbolic landscape picture of the relations between the organism and the environment (with original caption). The picture is a topographic map in which the "contours" symbolize the adaptive values of various combinations. Plus signs mark "adaptive peaks", while minuses "adaptive valleys".*

> earth. But the variety of ecological niches is not only immense, it is also discontinuous (p. 9).[9]

So, groups differ because they are adapted to different habitats and, conversely, environment variation in time and space corresponds with variation in organisms. Indeed, the blotched condition of adaptedness is «a product of evolution, an outcome of a long historical process of development» (Ivi, p. 4).[10] The process of adaptation brings about diversity because:

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[9] Another quote, more about the nested hierarchical organization: «The hierarchic nature of the biological classification reflects the objectively ascertainable discontinuity of adaptive niches, in other words the discontinuity of ways and means by which organisms that inhabit the world derive their livelihood from the environment» (p. 10).

[10] How discontinuity can emerge from a continuous process was one of the main focuses of the Modern Synthesis, faced by theoretical innovations such as "allopatric speciation" (cf., e.g., Mayr 1980).

> The evolutionary changes not only enable life to endure the shocks emanating from the environment; they permit life to conquer new habitats, and to establish progressively firmer control of the older ones (p. 4).

The tight link between organic diversity and diversity of habitats, due to the process of adaptation (which produces a condition of adaptedness), is well expressed by Dobzhansky when he states that:

> It is a natural surmise as well as a profitable working hypothesis, that the diversity and discontinuity on one hand, and the adaptation to the environment on the other, are causally related (p. 8).

Then the landscape picture in Figure I.2 is presented by Dobzhansky as «a symbolic picture of the relations between the organism and the environment» (p. 8). As much as relations of adaptedness are dignified as foundational for the hierarchical organization of organic diversity,[11] I argue, the landscape picture representing those relations is elevated to be *a* big picture in evolutionary theory, if not *the* big picture of evolution. Some more elements suggest the latter statement.

An important topic is what Stephen Jay Gould would probably call the picture's *scope*,[12] i.e. "how much" of evolution does the picture portray: how

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[11] Dobzhansky's idea of adaptation as a possible mainstay of biological classification reflects the philosophy of the "New Systematics" (Huxley), a taxonomical school contemporary to Dobzhansky and integral part of the Modern Synthesis (cf. 3.2), aimed to ground taxonomy and systematics on evolution. Adaptation has been questioned and refuted as a taxonomic criterion by contemporary taxonomic philosophies (cf. e.g. Haber). Niles Eldredge (e.g. 1995) pointed out the inconsistent logical, epistemological, and empirical outcomes of the conflation between genealogical (phylogenetic) and ecological information in Dobzhansky's landscape. More on this in III.1.1.

[12] Gould (2002).

many groups, how large, how comprehensive, how large is the time span, and so on. Information can be clearly discerned in Dobzhansky's argument:

> *Each living species* may be thought of as occupying one of the available peaks in the field [...]. The adaptive valleys are deserted and empty (p. 10, my emphasis).

So, the landscape represents all the existing species. According to Dobzhansky's vision of the coupling between habitat and species diversity, species can be found occupying peaks, i.e. they are well adapted to environments. Moreover - in accordance with the characteristic "virtuality" seen in section 1.2 - the landscape represents all *non*-existing species too: valleys are represented in the landscape, and they are «deserted and empty», because no actual species nor individuals exist there. In the following quotation, virtuality is well expressed, together with the view of an individual as a combination of traits (which will be important for subsequent arguments):

> Every organism may be conceived as possessing a certain combination of organs or traits, and of genes which condition the development of these traits. Different organisms possess some genes in common with others and some genes which are different. The number of conceivable combinations of genes present in different organisms is, of course, immense. *The actually existing combinations amount to only an infinitesimal fraction of the potentially possible, or at least conceivable, ones.* All these combinations may be thought of as forming a multi-dimensional space within which *every existing or possible organism may be said to have its place* (p. 8, my emphases).

In sum, Dobzhansky’s landscape picture strives to encompass nothing less than every existing or possible organism. Organisms are clustered in groups within which organs or traits are shared. Some of these groups actually exist because they rest on peaks (i.e., they are adapted to some existing environment), and some others not, because «...the valleys symbolize the gene combinations the adaptive values of which are low in the existing environments» (p. 277). In accordance with the “no environment” criterion (section 1.1), environments are not directly represented the landscape picture, but they are a determining factor of its shape, so we can talk about an environmental scope of the landscape picture, and logically derive that it matches the *complete* set of *all* the existing environments.

> The existing and the possible combinations may now be graded with respect to their fitness to survive in the environments that exist in the world. Some of the conceivable combinations, indeed a vast majority of them, are discordant and unfit for survival in any environment (p. 8).

No virtuality is allowed for environment, though: virtual environments, unlike virtual species and organisms, do not have place in the landscape picture - at least in Dobzhansky’s.

Let me now return to the *taxonomical* scope of Dobzhansky’s landscape picture. Not only the landscape stretches to display all the existing and possible living species: the picture is meant to show higher categories (e.g. Genera, Orders) as groupings of peaks on the landscape. In Dobzhansky’s own words:

> ...the adaptive peaks and valleys are not interspersed at random. "Adjacent" adaptive peaks are arranged in groups, which may be likened to mountain ranges in which the separate pinnacles are divided by relatively shallow notches. Thus, the ecological niche occupied by the species "lion" is relatively much closer to those occupied by tiger, puma, and leopard than to those occupied by wolf, coyote, and jackal. The feline adaptive peaks form a group different from the group of the canine "peaks." But the feline, canine, ursine, musteline, and certain other groups of peaks form together the adaptive "range" of carnivores, which is separated by deep adaptive valleys from the "ranges" of rodents, bats, ungulates, primates, and others (p. 10).

Peaks are arranged in ranges, representing higher taxa. All is environment-driven because of adaptation, but we should not forget[13] the "no environment" criterion (1.1), i.e. the fact that this is *not* a geographical landscape, and species that are piled together on a "mountain" range do not necessarily live nearby. On the contrary, they are likely to live geographically far removed one from the other, but genetically related and adapted to analogous habitats.

Dobzhansky's landscape picture is, according to my analysis, his big picture of evolution. The living world, including the existing and the possible organisms and spanning all the way up the taxonomical categories, *is* for Dobzhansky «...a great array of families of related gene combinations, which are clustered on a large but finite number of adaptive peaks» (p. 10).

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[13] Dobzhansky seems to forget it sometimes, cf. e.g. II.2.3.

The idea of *organisms as gene combinations* comes directly from Dobzhansky's field of study: "genetics of populations".[14] The scope of population genetics is, for Dobzhansky, no less than evolution. Stated very explicitly:

> Evolution *is* a change in the genetic composition of populations. The study of mechanisms of evolution *falls within the province* of population genetics (p. 16, my emphases).

Population genetics studies the "rules governing the genetic structure of populations" and its change through time. So, basically, the "evolving entity" on Dobzhansky's landscape is a biological population.[15] But since species are made of populations, the same rules are seen as governing also «the genetic constitution of species» (p. 16). In sum the scope of population genetics is, for Dobzhansky, evolution itself. Individual organisms are viewed as gene combinations, and change in the populations' genetic composition - in accordance with environments - creates diversity and discontinuities at all taxonomical levels:

> ...changes observed in populations may be of different orders of magnitude from those induced in a herd of domestic animals by the introduction of a

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[14] Dobzhansky (pp. 12-17) clarifies the distinction between the two major subdivisions of genetics: one is "genetics of populations", and the other studies the problem of heredity that, although the main laws of transmission are understood, aims to clarify «the whole of individual development during which the genes exert their determining action» (p. 13; on the concept of "gene action" seen as an explanatory metaphor for development see Keller 2002, section 2). The latter is variously labeled genetics of realization of hereditary characters, phenogenetics, or developmental genetics. Population genetics will be largely addressed here, see e.g. sect. 3.2 and chapter II.

[15] There are different definitions of population. Here the term may be intended in a very broad sense, as a group of organisms linked by reproduction and ecological cohabitation.

> new sire to phylogenetic changes leading to the origin of new classes of organisms (p. 16).[16]

The possibility for Dobzhansky's landscape diagram to have an omni-comprehensive evolutionary scope comes then from it being a visual projection of population genetics which, in his argument, embraces all the organic world. Every spot on the landscape will correspond to a particular individual - being it actual or potential. Two individuals on the same peak will grossly belong to the same group (population, or species), while two individuals on the same "range" will belong to a same higher taxon (genus, or family for example).

What about elevation? This measure is very clear in Dobzhansky's thought:

> The relative capacity of a given genotype to transmit their genes to the gene pool of the following generations constitutes the adaptive value, or the Darwinian fitness, of that genotype. The adaptive value is, then, a statistical concept which epitomizes the reproductive efficiency of a genotype in a certain environment (chapter IV, "Selection", p. 78).

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[16] Dobzhansky's pleas about the sufficiency of population genetics mechanisms to the exclusion of any other are, at least in some editions, really strong. This is probably due to the presence of competing (and largely discredited) anti-darwinian theories for the origin of macroevolutionary novelties (e.g. Goldschmidt 1940). Dobzhansky credits the conciliation of macro- with micro-evolution to authors like Simpson (1949), Schmalhausen (1949) and Rensch (1947). Consider the following (with my emphases): «Experience shows [...] that *there is no way toward understanding* of mechanisms of macro-evolutionary changes, which require time on geological scales, *other than through understanding of micro-evolutionary processes* observable within the span of a human life-time...» (p. 16) and we «*find nothing* in the known macroevolutionary phenomena *that would require other than the known genetic principles* for causal explanation. The words "microevolution" and "macroevolution" are relative terms, and have only descriptive meaning; they imply *no difference in the underlying causal agencies*» (p. 17).

Elevation of a genotype will depend on its adaptive value, which is a measure of its genetic contribution to the following generation. So, by definition, individuals with a high fitness, i.e. close to peaks, will contribute most to the following generation, and this will perpetuate the population's peak position. In a word, peaks represent combinations favored by natural selection.

But, if *natural selection* is the main mechanism of equilibrium on Dobzhansky's landscape, it is also a mechanism of evolutionary change. In the last chapter of *Genetics and the Origin of Species*, "Patterns of evolution", Dobzhansky (re)proposes the picture in Fig. II.8 in order to show varied evolutionary dynamics on the landscape: peaks can move due to environmental change, and movement depends on several factors beside natural selection, like mutation, population size and population subdivision. All these factors together determine movement on the landscape, which can be other than inflexible and close-ended climbing to the top of peaks.

2.2 Simpson's landscapes

George Gaylord Simpson was a paleontologist. His book *Tempo and Mode in Evolution* (1944) is a manifest attempt to synthesize (mainly) paleontology and genetics by the illustration of «the basic evolutionary phenomena» and «the grand pattern and great processes of life» (p. xxvii) liable to be overlooked due to increasing disciplinary fragmentation and specialization. Accordingly,

> The topics treated in the present study do not embrace the whole subject of evolution, but they are fundamental in nature and broad in scope (Ibidem).

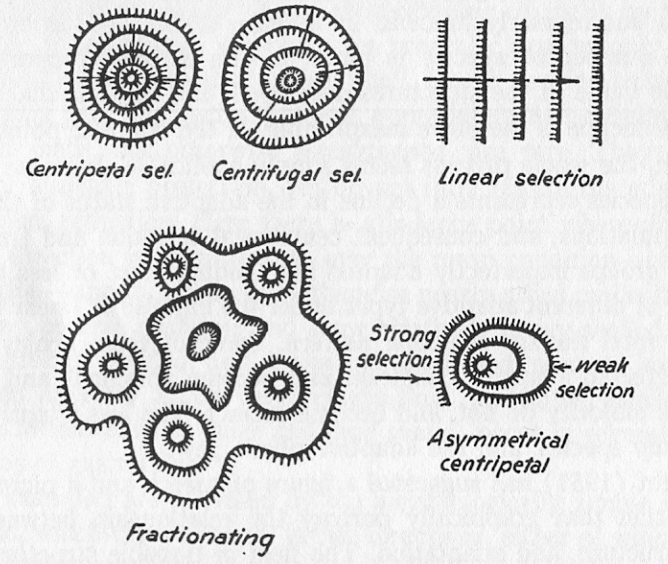

FIG. 11.—Selection landscapes. Contours analogous to those of topographic maps, with hachures placed on downhill side. Direction of selection is uphill, and intensity is proportional to slope.

Figure I.3. *Simpson's graphical portrait of the relation between selection, structure, and adaptation in five cases: (a)* ***centripetal*** *- the adaptive optimum is the "typical" character, selection concentrates the population towards a point; (b)* ***centrifugal*** *- the "typical" character is ill-adapted, selection favors divergence; (c)* ***linear*** *- selection drives to an optimum which is out of the actual adaptive range of the population; (d)* ***fractionating*** *- centrifugal towards five different optima; (e)* ***asymmetrical-centripetal*** *- see text (and also original caption) for explanation.*

Simpson's book focuses in particular on two topics on which «the paleontologist enjoys special advantages» (p. xxix): the first is suggested by the word "tempo" of evolution, and it

> ...has to do with evolutionary rates under natural conditions, the measurement and interpretation of rates, their acceleration and deceleration, the conditions of exceptionally slow or rapid evolutions, and phenomena suggestive of inertia and momentum (p. xxix).

The second topic is labeled "mode" of evolution, and it has to do with macro-evolution, as seen in the previous section where I pointed out Dobzhansky's ideas on how organisms come to be distributed not only on evolutionary peaks but also on groups of peaks ("ranges"), or groups of groups of peaks, and so on. With Simpson's study on modes of evolution:

> The purpose is to determine how populations became genetically and morphologically differentiated, to see how they passed from one way of

> living to another or failed to do so, to examine the figurative outline of the stream of life and the circumstances surrounding each characteristic element in that pattern (p. xxx).

Importantly, tempo and mode in evolution aren't to be explained, for Simpson, *despite* population genetics models, exposed for example in Dobzhansky's book, but *by means of* them[17] (expanding where necessary with models specifically designed to answer macro-evolutionary questions).[18] Indeed, after the first chapter on paleontological data and models on rates of evolution, Simpson devotes a long chapter to the "Determinants of evolution" studied by population geneticists[19] - i.e. factors like variability, mutation rate, character of mutations, length of generations, size of population, and selection - trying to use them in explanatory hypotheses of paleontological patterns.

Simpson's book features many diagrams. Figure I.3 appears in the section on the direction of selection, and is meant to

> ...graphically portray the relationship between selection, structure, and adaptation. The field of possible structural variation is pictured as a

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[17] The relationship between population genetics and paleontology (together with other "naturalistic" disciplines) in the Modern Synthesis will be thoroughly explored in section 3. The role of the adaptive landscape metaphor - and of authors such as Dobzhansky and Simpson who reported the metaphor in their books - will be focused.

[18] In the last chapter, "Modes of evolution", Simpson writes: «The same general forces are operative throughout the whole of evolution, and they bring about similar processes and sequences wherever and whenever they occur. Their *predominance*, *balance*, and *interaction* do, nevertheless, vary greatly, and quite different sorts of evolutionary patterns may result» (p. 197, my emphasis). Three "major styles" of balance and interactions are recognizable by the patterns they generate: "speciation", "phyletic evolution", and the pattern of "quantum evolution" originally introduced by Simpson.

[19] Simpson refers especially to Fisher (1930), Wright (1931), and Haldane (1932).

> landscape with hills and valleys, and the extent and directions of variation in a population can be represented by outlining an area and a shape on the field. Each elevation represents some particular adaptive optimum for the characters and groups under consideration, sharper and higher or broader and lower, according as the adaptation is more or less specific. The direction of positive selection is uphill, of negative selection downhill, and its intensity is proportional to the gradient. The surface may be represented in two dimensions by using contour lines as in topographic maps (p. 89).

Notice thay Simpson's landscape is about *structure*, *structural variation*, whereas Dobzhansky's landscape was about about genes.[20] In contemporary terms, we are in presence of a phenotypic landscape vs. a genotypic one.[21]

In section 2.1, I argued for the large scope of Dobzhansky's adaptive landscape, embracing all the existent and virtual organic forms, in all the existing environments, depicting all taxonomical levels and unifying micro and macroevolution thanks to the sufficiency of population genetics. Dobzhansky's adaptive landscape is - I argued - his big picture of evolution. What about the scope of Simpson's landscape pictures? Are they to be seen as a big picture of evolution? Looking at Figure I.3, I see *a repertory of landscape-depictions* of various cases. Here is an elucidation of them: (a) *when* a peak is

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[20] It is true that Dobzhansky *moved from* a description of the organism made by a combination of "traits and organs", but it is equally true that *the passage* from there to gene combination is *immediate* and transparent in his argument (Dobzhansky 1937, p. 8, see section above). The relation between genotypic and phenotypic landscapes will be taken up again in chapter III.

[21] I see also another, perhaps minor, difference: Simpson has a more immediate attention to directional dynamic aspects, whereas in Dobzhansky we have to wait for the last chapter, "Patterns of evolution", to see the dynamics on the landscape. In some way, I think, this has to do with the different stances and time scale of paleontology and genetics. Also, it could be related to population genetics explanations as "equilibrium explanations".

in the center of the population it means that the «typical character» is favored (remember the "higher is better" criterion, 1.3) and selection is "centripetal", concentrating the population towards a point that represents the typical character; (b) *when* a valley is in the center of the population the typical character is disadvantaged and selection is "centripetal" driving the members of the species away from the typical but maladaptive condition; (c) *in cases where* there are no peaks in the population - i.e., no optimums in its immediately possible (see 1.2) characters - but the population is on a slope - i.e., there is an adaptive tendency in a particular direction - there will be linear selection, probably driving the population towards a new, previously unexplored peak; (d) *when* a valley is surrounded by peaks, selection will not only be generically centrifugal but will also drive different parts of the population on distinct adaptive peaks (fractionating selection); (e) *sometimes* the slopes surrounding a peak may not be uniformly steep, i.e. variations of an optimal character in a direction may bring to maladaptive situation faster than in other directions; in such cases, centripetal selection will be asymmetrical: more severe on some variations and more permissive on others.

Apparently, Simpson's landscapes do not constitute a "big picture" of evolution in Dobzhansky's sense, whereas they reveal themselves a flexible tool for representing a variety of evolutionary scenarios. Notice, furthermore, that Simpson talks about *a* "typical character".[22] Simpson's character-talk seems to make his picture's scope even narrower compared with

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[22] All Simpson's explanation of his figure (my Fig. I.3) centers on «the modal condition of a character in the population» (p. 83).

Dobzhansky's, who considered adaptation as a result of *all* of the organism's traits. In his first chapter on "Rates of evolution", Simpson affirms that although

> [considering] whole organisms, as opposed to selected characters of organisms, would be of the greatest value for the study of evolution [...] it cannot be said that the problem is quite insoluble, but certainly it is so complex and requires so much knowledge not now at hand that no solution is in sight at present (pp. 15-16).

Simpson employs the concept of a *character complex*, bringing forth that «in any phyletic series various different characters are changing over the same period of time» (p. 4). Some characters appear to be genetically related and to change in a correlated way, although this relation may be stable only for a period and then change. Some characters seem not to be completely under genetic control, rather depending in different ways from the external environment. In sum, by argumented necessity, Simpson's adaptive landscapes are of *limited scope* in the sense that they must deal with a few characters or a character complex, chosen and weighted case by case. The "evolving entity" (see sect. 1) in Simpson's landscape is a population *considered as all the existent variations of the chosen character or character complex*, and the landscape represents, in accordance with its known virtuality (1.2), also those variations which are non-existent but possible, and it is such virtuality that allows it to represent change through time (as a realization of previously virtual possibilities).

Simpson's expressed ideas on adaptation limit furthermore his landscapes' scope. Simpson's adaptive landscapes have, as usual, adaptation as their central organizing principle (1.3), and they represent adaptive dynamics. However, Simpson is much less radical than Dobzhansky[23] in seeing adaptation as a central organizing principle *of evolution*.

> No theorist, however radically non-Darwinian, has denied the fact that natural selection has some effect on evolution. An organism must be viable in an available environment in order to reproduce, and selection inevitably eliminates at least the most grossly inadaptive types of structure. Aside from this obvious fact, theories as to the role and importance of selection range from belief that it has only this broadly limiting effect to belief that it is the only really essential factor in evolution [...]. The last word will never be said, but all these disagreements can be reconciled, and the major discrepancies can be explained. In the present synthesis adaptation, preadaptation, and nonadaptation all are involved, and all can be assigned immediate, if not ultimate, causes (pp. 74, 77).[24]

Until now I have cumulated arguments diminishing the scope of Simpson's adaptive landscapes, and therefore against seeing them as a big picture of evolution: such landscapes visualize single cases, they deal with one or a few characters, and they describe adaptive dynamics where such dynamics are not granted to be the central evolutionary phenomenon. Now I will propose two

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[23] The reader will remember the primacy of the link between organic diversity and adaptedness, all the way up through higher taxonomic categories (Dobzhansky 1937, chp. 1).

[24] About preadaptation (Cuénot 1921, 1925, cit. in Simpson) it must be said that it *can* be suitably represented in Simpson's adaptive landscapes (e.g. p. 91; see also Figure 4 here).

Figure I.4. *Simpson's landscape of the evolution of horses from browsers (right) to browsers and grazers (left). From bottom:* ***(1)*** *in the Eocene browsing and grazing represented for the Equidae two well-separated peaks, but only the browsing peak was occupied by members of the family;* ***(2)*** *throughout the Oligocene the browsing peak moved toward the grazing peak;* ***(3)*** *in the late Oligocene and early Miocene the two peaks were close enough and this asymmetrical variation was great enough so that some of the variant animals were on the saddle between the two peaks;* ***(4)*** *a segment of the population broke away under selection pressure and climbed the grazing peak with relative rapidity during the Miocene.*

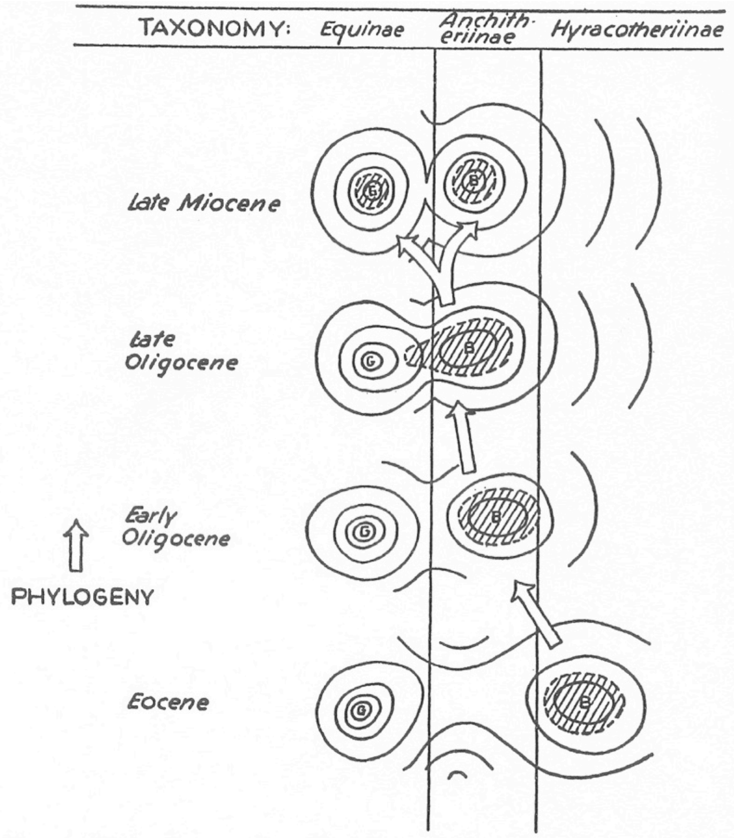

FIG. 13.—Major features of equid phylogeny and taxonomy represented as the movement of populations on a dynamic selection landscape. For fuller explanation see text.

arguments in favor of seeing Simpson's landscapes, if not as *the* big picture, at least as *big* pictures: the first goes through Simpson's representation of an episode in horse evolution (Figure I.4), and pushes the fact that landscapes reveal fundamental evolutionary patterns; the second emphasizes the bridge landscapes seem to constitute from micro to macroevolution. More argumentation on this will come in section 3.

Figure I.4 is the adaptive landscape of the evolution of horses in Oligocene and Miocene. The landscape has the already recognized features: it is, indeed, *adaptive* in that it considers the evolution of food habit, «an essential element in the progress of the Equidae» (p. 90). It considers the characters that directly or indirectly relate to food habits, to begin with the height of teeth and including many others. It is a dynamic model, articulated in four phases, and portraying natural selection as a vector on the local landscape which changes with dynamics of its own. The model employs the patterns seen in Fig. I.3: in I.4, phases 1-2-3, the direction *opposite* to grazing (right, in the picture) was for Simpson «more strongly selected against» (p. 92), and this resulted in weak asymmetrical centrifugal selection towards grazing (left-hand), pictured as an asymmetry of the browsing peak (cf. Fig. I.3.e). Character correlation plays an important role because in phase 2 an adaptive increase in the animals' size brings about «secondary adaptations to a large size» such as, e.g., higher teeth crowns (p. 93), that are incidentally in the direction of grazing adaptation. This fact is represented as one peak approaching the other. In phase 3 the animals on the "saddle point" between the two peaks were relatively ill-adapted and subject to centrifugal selection in two directions (fractionating). With relative ease, selection created a branch of grazers, once again because of the peaks' asymmetry: «the slope leading to grazing [...] is steeper than those of the browsing peak, and the grazing peak is higher (involves greater and more specific, less easily reversible or branching specialization to a particular mode of life)» (p. 93).

Simpson's landscapes do not represent the whole organic world or evolution. Neither they deal with all the characters of organisms and populations. However, they constitute a flexible tool for describing a vast array of evolutionary events. In this operation, according to some authors and

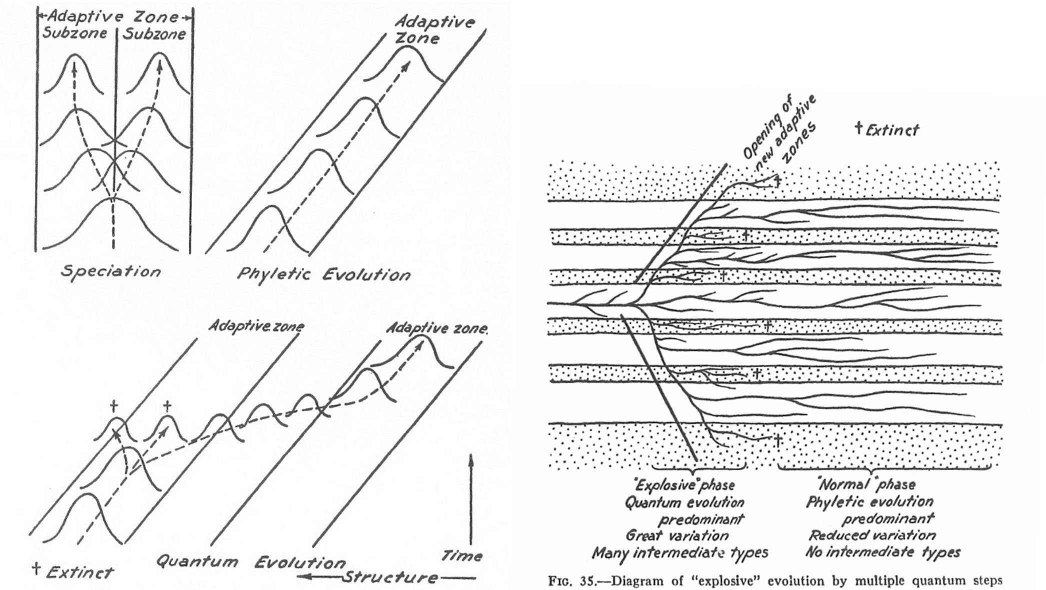

FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.

FIG. 35.—Diagram of "explosive" evolution by multiple quantum steps into varied adaptive zones, followed by extinction of unstable intermediate types and phyletic evolution in each zone. The pattern is like that of South American ungulates, although the diagram does not attempt to show their actual phylogeny in detail.

Figure I.5. *Two pictures by Simpson showing the possibility, seemingly allowed for by the adaptive landscape, of a unified picture of evolution.* ***(a)*** *left: landscape pictures of the thre major modes of evolution (speciation, phyletic, quantum);* ***(b)*** *right: «diagram of explosive speciation» similar to more traditional tree-diagrams drawn in paleontology.*

Simpson himself, his adaptive landscapes can reveal fundamental evolutionary patterns. Natural selection, determined by the changing local environment and constrained by correlations among characters in the considered character complex, is the leading mechanism of differentiation.

Finally, Simpson's adaptive landscapes were also a way to link microevolution to macroevolution, as it should be clear from Figure I.4. Adaptive events are time-limited evolutionary patterns. On one side, they can be described and explained in terms of the "determinants" of population genetics. On the other side, they are part of «the figurative outline of the stream of life» (Simpson, cit., p. xxx), the picture of macroevolution which was already represented by paleontologists and morphologists in ways alike Fig. I.5.b. The adaptive landscape, an atypical representation of population genetics, seems to have been particularly consonant with representations typical of paleontology. A unified account of evolution seems to be suggested by a unified way of depicting "the pattern of evolution" (Eldredge 1999) and «circumstances surrounding each characteristic element in that pattern» (Simpson, cit., p. xxx).

2.3 Dawkins on Mount Improbable

Richard Dawkins's popular book *Climbing Mount Improbable* (1996) proposes a vision of evolution as "mountain climbing".[25] Seen from a low altitude, the most perfected forms may seem high and unreachable. Like in mountain hiking, however, *there are* gradual paths allowing to reach the highest peaks. Taking the fig tree as an example of a particularly complex and perfect organism, Dawkins writes:

> …the fig tree stands atop one of the highest peaks on the massif of Mount Improbable. But peaks as high as the fig's are best conquered *at the end of the expedition* (pp. 1-2, my emphasis).

And further:

> …the story of the fig is, at the deepest level, *the same story as for every other* living creature on this planet [...]. We shall reconstruct the *slow, gradual evolution* of wings and of elephant trunks [...]. We shall program computers to assist our imagination in moving easily through a gigantic museum of *all the*

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[25] In some points (e.g. where he contrasts Mount Rushmore and «curiosities of natural weathering», p. 3) Dawkins seems to talk about the process *giving shape to* the mount. But the core argument of the book sees a pre-existing mount climbed by organisms. In other words, metaphor of the process of evolution is climbing, not shaping.

> *countless creatures* that have ever lived and died, and their even more numerous *imaginary* cousins, who have never been born. We shall wander the paths of Mount Improbable, admiring its vertical precipices from afar, but always restlessly seeking the gently *graded slopes on the other side* (p. 2, my emphases).

The main concern of Dawkins's book is indeed the clarification of the classical "problem of design" (cf. p. 2). The "big picture" of Mount Improbable answers the problem by giving an imaginary pictorial shape to the classical argument of "chance *and* necessity" (cf. Monod 1970). Evolutionary paths are linear trajectories of exploration of forms which amount to series of gradual modifications, where each form is a slight modification of the previous. Scientists have to restlessly seek graded slopes on hidden sides of the mountain.

The moving force on the landscape is natural selection, described by Dawkins as a cumulative process of *finding* (also called "exploration", "discovery", "expedition"), where the accidental improvements found are cumulated because of heredity. The resulting vector on Mount Improbable is one that *always pushes upwards*. This is also the reason why when the climbing of a mountain is started it has to keep going, as well as why, when a peak is reached, there will be no possible improvements and no changes from a kind of structure to another. Dawkins is very clear on this point: natural selection cannot accept downhill movements. Valleys cannot be crossed. Rather, through small steps, structures that are more simple and probable can turn into complex and improbable ones.

Every step along the Mount's slopes consists in the discovery of a solution (shapes, mechanisms, functions) which is slighly but significantly more complex, perfect, improbable, "designoid" than the previous steps. Dawkins's idea of designoid is well explained in the following quotation:

> Accidental objects are simply found. Designed objects aren't found at all, they are shaped, moulded, kneaded, assembled, put together, carved: in one way or another the individual object is pushed into shape. Designoid objects are *cumulatively found*, either by humans as in the case of domestic dogs and cabbages, or by nature in the case of, say, sharks. The fact of heredity sees to it that the *accidental improvements found* in each generation are accumulated over many generations. *At the end* of many generations of cumulative finding,

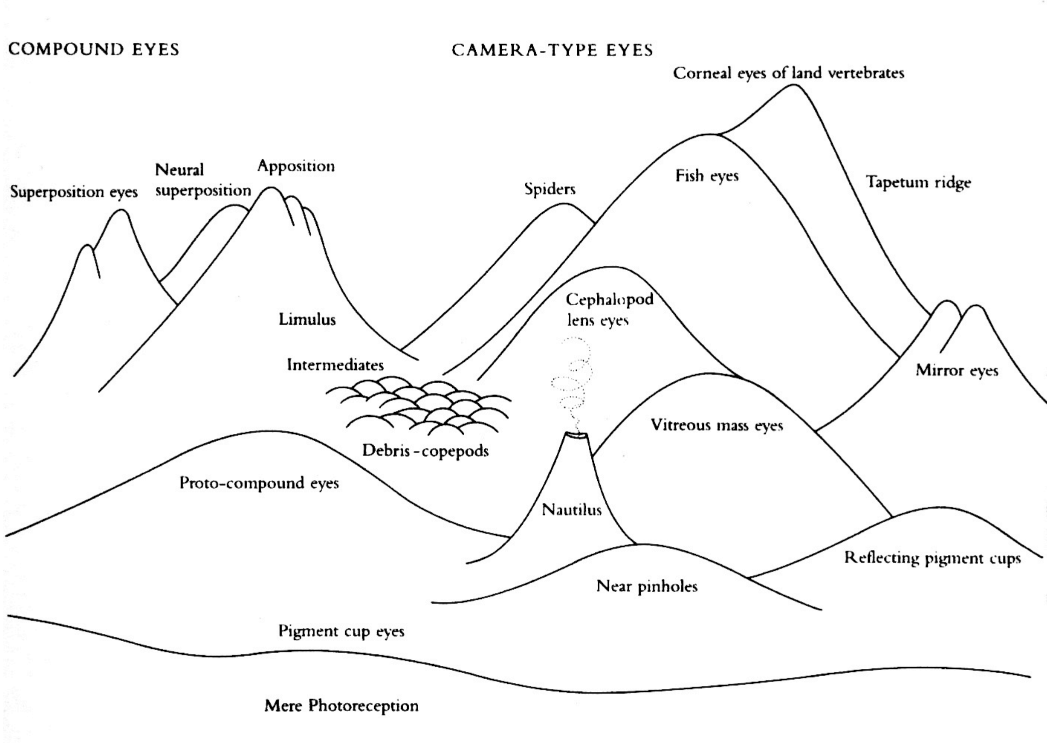

Figure 5.30 The eye region of the Mount Improbable range: Michael Land's landscape of eye evolution.

Figure I.6. *According to ethologist and evolution writer Richard Dawkins (1996), this landscape depicts «the eye region of Mount Improbable» (p. 177).*

> a designoid object is produced which may make us gasp with admiration at the perfection of its *apparent design*. But it is not real design, because it has been arrived at by a completely different process (pp. 22-23, my emphases).

Figure I.6 is based on a map of the alternative forms of eye structure found in different living and extinct species. In the bottom part of the drawing, for instance, we find the simplest form of photoreception - a slight photosensitive spot on the surface of the body. At the top, instead, we find the most perfect forms, divided in two comprehensive groups - "composite" and "photographic" eye. The vertebrate eye is the most perfect form of photographic eye: (1) it has specialized cells with many strata of pigments that effectively capture a huge percentage of photons; (2) single cells are sensitive to the direction of light, and they are arranged as a concave surface (our retina) with a small, pinpoint opening (*pinhole*) that projects a single image on the surface itself; (3) it has a transparent lens which reduces diffraction and improves the image through an appropriate refraction index; (4) it is provided with muscular apparata capable to modify focus, regulate pupil size and move the eye, as well as with neural systems necessary for controlling the eyes and elaborating information from them. In the space between the top and bottom boundaries of the landscape, many other more or less complex eye forms - at least forty[26] - are possible. And actually they are found in different species. For example, *Nautilus* - a marine cephalopod so ancient to be considered a living

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[26] «It has been authoritatevely estimated that eyes have evolved no fewer than forty times, and probably more than sixty times, independently in various parts of the animal kingdom. In some cases these eyes use radically different principles. Nine distinct principles have been recognized among the forty or sixty independently evolved eyes. I'll mention some of the nine basic eye types - which we can think of as nine distinct peaks in different parts of Mount Improbable's *massif* - as I go on» (Dawkins, cit., p. 127).

fossil - has a particularly perfected pinhole eye, depicted in the center of the drawing as a vulcan; picking from the above list of vertebrate eye's characteristics, *Nautilus* has only (1) and (2), but the structure is arranged in such a way to obtain images which are rough but efficient for that particular species (cf. Saunders & Landman 1987, Muntz 1999, Warrant 1999, Colicchia 2006).

With the vertical dimension of Figure I.6 Dawkins aims to represent several things: perfection, but also complexity, improbability, and the time dimension as well, portraying evolutionary processes that bring to the present variegated situation. In the Figure, eye structures mapped on the bottom are supposed to be the early evolutionary precursor of all the more complex forms. An initial path of improvement may split into different alternatives, leading to peaks in rather different directions - like the "composite" and the "photographic" mountain ranges. Within each of them, different alternatives are possible, leading to the single particular local peak. Alternatives are legitimate and viable forms, brought about by living species that are adapted to their respective environments and other characteristics.

The taxonomical scope of Dawkins's landscape of eye evolution is definitely broad, including lampreys to vertebrates. Differently from Dobzhansky, though, the landscape focuses only a character "complex" (cf. Simpson), i.e. the eye. Groupings on the landscape (namely, "ranges") are thus assembled according to the eye form (the taxonomical relevance of such groupings is not addressed). Just like in the majority of his other bestsellers,[27]

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[27] e.g. Dawkins (1976, 1986, 1989, 1995).

Dawkins aims to convey his “big picture” of evolution by using examples and the communicational virtues of simple and powerful metaphors.[28] Mount Improbable is undoubtedly one of those metaphors. In section 3 I will advance the hypothesis of a role carried out by the adaptive landscape metaphor in the Modern Synthesis thanks to quite the same virtues exploited by Dawkins in *Climbing Mount Improbable*. A critical examination of Dawkins’s landscape is, instead, postponed to chapter III (sect. 1.3).

2.4 Summing up: the big picture of evolution

Throughout the chapter I repeatedly referred to adaptive landscapes as a “big picture” of evolution. The adjective “big” refers certainly to the authority acknowledged to its drawers - Dobzhansky, Simpson, and Dawkins - but it is actually mainly a statement about the evolutionary *scope* granted to such a picture. By scope, I mean “how much” of evolution these pictures are supposed to portray.

I quoted Theodosius Dobzhansky to demonstrate that his landscape picture was meant to represent, in principle, all the organic world, with species and higher taxa arranged in mountain ranges on the landscape, such an arrangement being coupled with the whole existing diversity of environments. Universal scope was supported by the postulated importance and sufficiency of population genetics (the landscape is, indeed, a genotypic landscape) to explain diversity at all levels as well as the centrality of

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[28] see Elsdon-Baker (2009), Sterelny (2001).

adaptation as an organizing principle of organic diversity (and the landscape is adaptive because adaptation is its organizing principle, cf. 1.3).

Roughly the same scope is recognizable in Richard Dawkins's landscape, Mount Improbable, although his particular example - the landscape of eye evolution - reduces the scope by using only a character complex as the sorting principle, whereas Dobzhansky's landscape considered all the organisms' traits. Using only a few characters also reduces the scope by sorting out only the species (and higher taxa) *actually having* a form of that particular character. Expressing their characteristic virtuality (1.2), both Dobzhansky's and Dawkins's landscapes are even more inclusive: besides existing organisms, they portray potential populations and species that do not exist due to the absence of suitable environments for them. They are represented as deserted valleys, and they may come into existence by natural selection, should the landscape be modified by the appearance of novel, different environments. The latter, acting from "outside" (cf. 1.1), would create peaks in place of valleys (such dynamicity of environment is much more explicit in Dobzhansky). The scope of adaptive landscapes extends thus also through time, towards the future.

George Gaylord Simpson's landscapes seem to have a more limited scope. They are not meant to represent all biodiversity in all existing environments, rather, Simpson's adaptive landscapes are each devoted to tell a particular episode in the evolutionary history. They focus on a specific taxon or group, and - like Dawkins's - on a set of traits. But, differently from what happens with Dawkins, such set of traits does not operate as a sorting principle upon the considered taxa; in other words, the scope is not augmented by the inclusion in the landscape of all the taxa having the considered trait(s). On the contrary, *traits are chosen* because they are adaptively relevant *in the context* of the particular story (e.g., the evolution of horses from browsers to grazers and browsers), a context that stands still. Moreover, not only the scope of Simpson's landscape is limited to a particular adaptive story: Simpson - as opposed to Dobzhansky - declares that adaptation is *not* to be considered the general organizing principle of organic diversity.

If Simpson's landscapes cannot be considered *the* big picture of evolution as Dobzhansky's and Dawkins's, they maintain - I argue - at least the status of *a* big picture of evolution, and in a way that assures them a remarkable scope along the dimension of micro- to macro-evolution. As noted above (sect. 2), Simpson wanted to show that the same «determinants of evolution» which had been formalized by population genetics were at work in phyletic diversification. Simpson's landscapes *are* then big pictures in that they give the sense of including a population genetics description - using, indeed, a picture *drawn from* population genetics - re-proposing it in phenotypic, morphological terms as an explanation of how some large groups of organisms «passed from one way of living to another or failed to do so» (p. xxx), and linking all this to more inclusive pictures that show «the grand pattern and great processes of life» (p. xxvii).

Lastly, Simpson's landscape is a big picture in that it displays a particular history *as an instance of a general pattern*: many other cases would be captured by the same picture (or, at the very least, by the same *way* of picturing). Simpson's adaptive landscapes are thus big pictures, I would say, *by recurrence* (or repetition) rather than by inclusiveness, as they serve to the author's aim to illustrate «the basic evolutionary phenomena» (p. xxvii). Moreover, Simpson's landscapes graphically suggested a connection between evolutionary patterns at different time scales, which were previously seen as separate or even incompatible.

3. Landscape metaphor and evolutionary synthesis

Throughout the chapter I argued for seeing adaptive landscape as a "big picture" of evolution by emphasizing the wide scope of the picture in its main proponents' intentions. But what is to be intended with "picture of" evolution? Many authors in the philosophical and theoretical debate consider the adaptive landscape a *metaphor*. This is apparently in line with what Theodosius Dobzhansky, George Gaylord Simpson, and Richard Dawkins themselves explicitly said. According to Dobzhansky, indeed, the adaptive landscape is «a symbolic picture» (1937, p. 8) of the relationship between the organism and the environment. For Simpson (1944, p. 89) the landscape is «a figure of speech and a pictorial representation» that graphically portray the relationship between selection, structure, and adaptation. As for Dawkins (1996), he declares Mount Improbable as a «parable» and a «central metaphor» (p. 2).

Many scientific papers referring to the adaptive landscape metaphor take the term “metaphor” for granted. Many stress the importance of distinguishing a metaphor from a model. Some philosophical papers address more or less extensively the issue of metaphors by taking adaptive landscape as a case in point.

I think that an important distinction has been overlooked in the debate. Roughly speaking, the distinction is between the metaphor viewed in its *native* context (i.e., mathematical population genetics, cf. sect. 5), and the metaphor viewed in research contexts other than that. I will refer to this second view as the *migrant* metaphor. The migrant metaphor is the topic of the present section, where I take it as a linguistic entity that was “injected” by Sewall Wright (1932) into the Modern Synthesis. I examine its genealogy (3.1), its context of operation (3.2), and some hypotheses about its effects and importance (3.3). In section 5, on the other hand, I analyze the *native* adaptive landscape metaphor, tackling the very meaning of metaphor in that context, not without “spillover effects” for reflecting on metaphor migration.

3.1 The landscape’s simple family tree

In 1989 philosophers James Griesemer and William Wimsatt, adopting a populational view of scientific diagrams inspired by David L. Hull (1988),[29] attempted a «quantitative evolutionary analysis» of the genealogy of diagrams

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[29] In Hull’s vision the best way to study conceptual change in science is to delimit social groups of interacting scientists on the basis of genealogical descent relations and then to analyze variation in the style, content and structure of ideas and arguments within and among social groups. For Griesemer and Wimsatt (1989) the same can be done, indeed more easily, for *diagram* phyletic continuity and change. For analogous approaches cf. Bellone (2006).

of Weismannism.[30] Beginning with original pictures by Weismann himself (1893), they gathered as much pictures as they could from textbooks, papers etc. dating back to different years, trying to establish genealogical relationships among them. «In some important cases - they wrote - diagrams appearing in published scientific works are conceptual organisms» (p. 76): they are copied one from the other, novelties are introduced for various reasons (e.g., to reflect theoretical innovations) and preserved in subsequent descendants.

A complex history of descent with modification awaited for Griesemer and Wimsatt in the many diagrammatic versions of Weismannism. Adaptive landscapes, despite their importance and success (documented, e.g., in section 2 of this chapter) would not offer as much an interesting story, I suspect.[31] I wrote "despite" their success, but I should probably say "due to" it: the originator of the diagram was famous geneticist Sewall Wright in 1932, and most part of the story is reknown mainly through the biographical and historical work on him by William B. Provine (1986). Theodosius Dobzhansky was present at Wright's 1932 talk at the 6th Congress of Genetics at Cornell University, and Dobzhansky's book *Genetics and the Origin of Species* (I.1.2 and Fig. 1.2) was such a successful "branch" that almost all copies of the diagram came directly from there. Relying on his own

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[30] Briefly, the central message of Weismannism is the division between germline and soma, which entails the "central dogma" of inheritance: somatic changes cannot be inherited because only cells in the germline are causally and physically involved in reproduction. Diagrams of Weismannism illustrate this concept and other kinds of related information, also reflecting theoretical and empirical novelties cumulated over time.

[31] I cannot be completely sure of it, but I have some support since I tried to gather material to probe the possibility of undertaking a study similar to Griesemer & Wimsatt (1989) on adaptive landscapes. With not much success.

experience as well as on literature, philosopher of biology Michael Ruse (1990) wrote:

> Dobzhansky's book had immense influence. It has fair claim to having been the most important work in evolutionary theory since the *Origin*. And with the influence has gone the Wrightian landscape - reproduced again and again, in work after work (p. 70).

From a genealogical, populational point of view - i.e. one considering the number of copies as offspring - adaptive landscapes enjoy undisputed success. Their story is known too, so much that already cited Griesemer and Wimsatt (1989, p. 130) brought it as an example of diagram genealogy everybody should be aware of. They report two more observations that - equally widespread in literature - worth noting, i.e. the difficulty of Wright's mathematics, and the detrimental effects that are expected from the transmission of the diagram with no understanding of the underlying mathematics:

> Provine (1986) documents how Wright's mathematical theory failed to spread rapidly because few evolutionary biologists had the mathematical ability to understand it, or to understand Wright's self-taught mathematics, often idiosyncratic notation, and sometimes torturous derivations. The substantial influence it had (through Dobzhansky and a few others) was often propagated without transmission or understanding of its mathematical apparatus, and this led many evolutinary biologists to believe incorrectly that the evolutionary synthesis was accomplished without need or benefit of the

> mathematical theory, or led them to often bowdlerized and incorrect renditions of Wright's views (Ivi, p. 130).

More than mistakes, equivocations, or «incorrect renditions» of Wright's adaptive landscapes in scientific and popular literature, my interest will go to *conceptual changes* that could possibly have occured in their genealogy, leading to Dobzhansky's, Simpson's, Dawkins's and others' landscapes. But conceptual changes will be spelled out in chapter III, since tackling them requires a thorough analysis of Wright's work (chp. II). The theme here, however, is the role the landscape metaphor (a migrant metaphor, as I dubbed it) may have had in evolutionary synthesis.

3.2 The Modern Synthesis

Julian Huxley's fundamental book, *Evolution The Modern Synthesis* (1942) does not feature a picture of the adaptive landscape, but offers a clear verbal description of it in chapter 3, "Mendelism and evolution". Huxley is talking about theoretical and empirical cases where the selective pressure relaxes in a population, allowing an excess of variability, and when the pressure is restored the "stable type" differs (although slightly) from the starting point. Huxley draws upon the Wrightian idea of a "peak shift":

> Sewall Wright (1932). in discussing such problems in more general terms, concludes that there must be available to most species a number of gene-combinations all of about the same survival value, he compares them to peaks separated by "valleys" of intermediate combinations which are less favourable. Normally it is difficult or impossible for selection to shift the type

> from an established peak to another, although this might be equally satisfactory if reached: but when the intensity of selection is reduced (or when low size of population promotes the accidental survival of genes and gene-combinations), many “valley” combinations are realized, the species can cross dryshod to other peaks, and it will be a matter of chance on which Ararat the type eventually remains perched when the rising tide of selection again floods out the valleys (Huxley 1942, p. 113).

The meaning and mechanism of this “peak shifting” explanation will be clarified, I hope, in the next two chapters. It is probably obscure now, due to the conceptual changes the landscape underwent along its short “family tree” (3.1). Conceptual changes will be pointed out in III.1.

What is important for me here is the clear presence of the adaptive landscape in Huxley’s important compendium to the Modern Synthesis, of which - as said earlier - Dobzhansky’s and Simpson’s books were also foundational. The appearance of the landscape all over the “Modern Synthesis” pushes to me the question of what role, if any, the landscape picture may have played *in* the synthesis.

The Modern Synthesis (MS henceforth) is an elusive object of study. By far the most important and rich work on it is the book *The Evolutionary Synthesis* (Mayr & Provine 1980) which is a partial account of a conference organized by Ernst Mayr at the end of 1970s. In the book’s epilogue, William Provine reports:

> One certain conclusion emerged from the conference. All participants [...] agreed that a consensus concerning the mechanism of evolution appeared among biologists during the 1920-1950 period (1980a, p. 399).

But, he also advances the grounded suspect that such unanimity concealed a variety of meanings of the word "synthesis".[32] Accordingly, while I try to reflect upon the role that adaptive landscapes metaphors may have had in MS, I have to give at least some coordinates to specify what synthesis I have in mind.

To begin with, here I consider MS as a *process* as opposed to a product of a process.[33] The former perspective is not more correct than the latter - and indeed in chapter IV I will adopt the second.[34] Simply, here I want to consider the role adaptive landscapes can have played *in the process* of synthesis. But again, there are no unanimous accounts and intepretations of the process: *The Evolutionary Synthesis* (Mayr & Provine, cit.) demonstrated that MS occurred simultaneously and at different rates on many different levels (from chromosomes to higher taxa), in different fields (like e.g. genetics, cytology, or botany), and in different countries, «or even in the same fields in different

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[32] The conference itself may have had the pragmatic effect of diminishing the differences: «Although all participants seemed to agree that an evolutionary synthesis had occurred, they may have had different syntheses in mind. The evolutionary synthesis may therefore have appeared more cohesive during the conference than it actually was» (Ivi, p. 408).

[33] As Dudley Shapere (1980) points out, «"Synthesis" is one of those words that involve what philosophers call a "product-process ambiguity"» (p. 395). Another word like that is "adaptation" (cf.).

[34] I will do it by following Massimo Pigliucci and the advocates of the Extended Evolutionary Synthesis in seeing the MS as a "conceptual framework" for biological research. A framework is a static object, the outcome of a process. Other approaches will be cited that see MS as an outcome.

divisions of the same university» (Provine 1980a, p. 405). Again, with historian William Provine:

> The evolutionary synthesis was a very complex process; its historical development cannot be encompassed accurately by any simple thesis [...] No simple historical thesis, however brilliant, can describe all essential elements of the evolutionary synthesis (1980a, p. 405).

Agreed that we can think about MS as a complex process, even the time span of its realization can be put into question. Before 1980, the origins of MS had never been exposed. Finding no trace of origin in any of the major works *of* MS,[35] Provine (1980a) cited Thomas Kuhn (1962) saying that «the actual origins of a scientific field generally will not be found in the major books that embody the fundamental beliefs of the field» (Provine 1980a, pp. 400-1). Provine even expressed the feeling of evolutionary synthesis having «been a part of biology for a long time, almost since Darwin» (p. 400). Most authors, however, recognize the existence of two main phases of MS. They have several names, but I shall call them *early* and *second* syntheses.

The early synthesis (1910s, '20s) will be a topic of chapter II. Sewall Wright was undisputedly one of the main figures in such phase. Another name for this phase is Darwinian-Mendelian synthesis because it reconciled the Darwinian theory of natural selection with the Mendelian theory of inheritance: the latter was increasingly supported by experimental evidence

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[35] Besides the already cited Huxley (1942), Dobzhansky (1937), and Simpson (1944), Provine studied: Fisher (1930), Wright (1931), Ford (1931), Haldane (1932), Darlington (1939), White (1945), Rensch (1947), Jepsen, Mayr & Simpson (1949), Stebbins (1950), Huxley, Henry & Ford (1954). Most of them are recalled again and adain in philosophy and biology.

featuring discrete variation (called “mutation”), in turn considered as opposed to the requirements for natural selection. In the early synthesis population genetics introduced a «particulate theory of inheritance» (cf. Mayr 1980): continuous variation was considered as the product of a huge array of the discrete variation of discrete genetic elements. Populations were seen as having a “gene pool” on which small fitness differences between factors can yield major impact. Population genetics was essentially a powerful mathematical theory, modeling factors like selection, mutation, drift, population size, allele frequency. In the early synthesis it guided laboratory experiments and (limited) agricultural applications (Provine 1980b). Sewall Wright was undisputedly one of the main figures in this phase. For Lewontin, Wright’s «synthesis», based on the importance of gene interactions (cf. a characterization in II.1.1), was particularly important as a step to the subsequent synthesis because it considered a number of factors (e.g. random processes), their balance, and configurations possibly leading to outcomes like speciation or extinction. For Richard Lewontin, «Only in the synthetic work of Wright do we get hints (and only hints) of the way in which both speciation and extinction can flow mechanically from the processes of modulation of variation» (1980, p. 61).

The second synthesis (1930s, ‘40s) was characterized by the involvement in evolutionary theory of a larger and larger group of previously separated fields, like systematics and taxonomy, zoology and botany, paleontology and morphology, cytology and embryology. In early 1930s all these fields were dominated by theories that were incompatible with or irrelevant to evolutionary theory. Ernst Mayr (1980) recalls a "Princeton conference" in 1947 where scientists of all fields were present and there was «an essential agreement among all the participants on the gradual mode of evolution, with natural selection as the basic mechanism and the only direction-giving force» (p. 42). Mayr considers it as a documentation that a synthesis *had* occurred. In the time between, books like Dobzhansky's, Simpson's, and Huxley's had been published. Geneticists and those whom Mayr calls "the naturalists" were somehow unified by evolutionary theory.

Granted MS as a complex, two-steps historical process that took place between 1910s and 1940s, different views (and very interesting discussions) were held about *the nature* of each step and about the *relationship* between the two. Indeed, the main reason why Ernst Mayr organized the "Evolutionary Synthesis" conference was his view on these topics, completely different from the dominant (Mayr 1959, 1973) he wanted to revise. It is in Mayr's view that I will put my discussion of the adaptive landscape metaphor.

At face value, Mayr's disagreement was about the relative contributions brought by different professionals to the second synthesis. The standard view[36] held *geneticists* as the main contributors to the synthesis, with a minor or even passive involvement of those who Mayr called the "naturalists", e.g., systematists and paleontologists. As Provine reports very clearly:

> ...most geneticists in the 1950s [...] believed that the evolutionary synthesis was a function or product of advances within the field of genetics and that these advances were applied to other fields like systematics, paleontology,

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[36] E.g. Dunn (1965), Sturtevant (1965), Wright (1967), cit. in Provine (1980a), p. 402.

> embryology, cytology, and morphology. [... that] the real advances took place in genetics and were exported to other fields of evolutionary biology, thus creating the evolutionary theory (1980a, pp. 402-3).

Mayr did much to obtain a revision of this view of synthesis as an export from genetics.[37] After the conference, Provine gave as acquired that the evolutionary synthesis had been «more than a simple application of new concepts in genetics to other facets of evolutionary biology, as earlier accounts have suggested» (p. 405).[38] The previously standard view was overcome.

One of the conference participants, however, strongly defended the rival view: it was Richard Lewontin (1980). I shall expose his main arguments and his view of synthesis before going into Mayr's view of MS with more detail.

Lewontin held a standard view on the second synthesis, i.e. he saw it as an extension, an "export" as it has been said, from genetics to other fields. Lewontin insisted on the importance of (mathematical) theory and on the tight relationship between theory and observations:

> Theory generally should not be an attempt to say how the world is. Rather, it is an attempt to construct the logical relations that arise from various

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[37] The view had been best epitomized by Dobzhansky (1955, p. 14): «The foundations of population genetics were laid chiefly by mathematical deduction from basic premises contatined in the works of Mendel ad Morgan and their followers. Haldane, Wright, and Fisher are the pioneers of population genetics whose main research equipment was paper and ink [...]. This is theoretical biology at its best, and it has provided a guiding light for rigorous quantitative experiment and observation». Mayr challenged the view that geneticists, especially Fisher, Haldane and Wright, were entirely responsible for the synthesis, and among Mayr's targets was also a book by Provine himself (1971).

[38] However, he regarded as open the question about the relative contributions of genetics compared to each disciplinary field (1980a, pp. 408-9).

> assumptions about the world. It is an "as if" set of conditional statements [...] theory acts as a guide for perplexed experimentalists (p. 65).

For Lewontin, the models of population genetics *would have* been able to guide the naturalists' work, by providing detailed predictions, and means to subtly distinguish among competing hypotheses for the explanation of observations in nature.[39] But Lewontin lamented the *incompleteness* of such a synthesis, blaming the scarce knowledge and understanding by most biologists:

> ...a tremendous amount of understanding and synthesis of evolutionary ideas could have been derived chiefly from the theoretical work of Fisher and Wright. These insights were explicit in the writings of Fisher and Wright, but simply unavailable to most biologists for reasons of literacy (p. 58).

For Lewontin, e.g., systematics and paleontology made use of too simple models[40] within the much more advanced genetic theory. Lewontin had written in 1974:

> For many years population genetics was an immensely rich and powerful theory with virtually no suitable facts on which to operate. It was like a complex and exquisite machine, designed to process a raw material that no one had succeeded in mining [...] for the most part the machine was left to the engineers, forever tinkering, forever making improvements, in anticipation

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[39] Lewontin remarks also that the power of theory goes as far as to calculate error estimates of the observations (p. 68), another use that in his opinion was overlooked by biologists.

[40] «...the Mendelian population genetics of single genes of fixed effect» (p. 60)

> of the day when it would be called upon to carry out full production (Lewontin 1974, p. 189).[41]

The limited use of a subset of the powerful genetic theory made the synthesis incomplete, and deprived evolutionary hypotheses of sufficient support. The use of too simple models

> ...only shows consistency, not entailment. As an evolutionary geneticist, I do not see how the origin of higher taxa are the necessary consequence of neo-Darwinism. They are sufficiently explained, but they are not necessary consequences (p. 60).

The genetical theory with all its refined development - being a way to drive observations that allow discrimination among hypotheses - was exploited, for Lewontin, to a tremendously limited extent. It was not "correctly incorporated" in the work of other biologists, so, if theory had to say something, it was: «we have not yet found the observations sufficient to distinguish among the [evolutionary] hypotheses» (p. 66).

At the "Evolutionary Synthesis" conference Richard Lewontin thus argued for his own version of the "export" view of synthesis, consisting in a more and more extensive use of population genetics models as a powerful guide to observations in all biological fields, with the potentiality to pick in each field those evolutionary hypotheses necessarily entailed by the observations. Aside from the fact that *such* a synthesis was incomplete for Lewontin, and that he saw a serious problem here, the important point for my

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[41] Thanks to Steve Downes for this reference.

argument is that *it would be difficult to imagine a role for metaphors in such a view of synthesis* based chiefly on an export of exact mathematical models.[42] So different was Mayr's view from Lewontin's, that the former asked:

> Wasn't the evolutionary synthesis possible *on the basis of a very minimal agreement* that there are small genetic changes and that the phenotypes produced by even every small genetic changes may differ and probably usually differ in their selective values? [...] *perhaps we should not complain* about the failure of application of the sophisticated and advanced theoretical analyses... (in Lewontin 1980, p. 67, my emphasis)

Lewontin's answer began as follows: «I really disagree».[43]

So, what is Mayr's idea of synthesis which, I believe, would allow a greater role for the adaptive landscape metaphor? A core aspect is the construction of a *common language* between specialists in different fields who had become more and more separated - mainly experimental biologists vs.

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[42] There is, actually, a role for "mathematical" metaphor as auxiliary to mathematical models. It will be subject of section 5, and chp. II.

[43] Lewontin went on defending the empirical value of *all* in population genetics theory: «I can think of very little in the theories of Fisher and especially of Wright and even of that much-maligned gentleman Kimura that is irrelevant to the question of what can be inferred from the observations» (1980, p. 67).

«naturalists», but with several other subdivisions.[44] Terminological inconsistencies needed to be fully resolved, like in the case of "mutation":

> Most naturalists described phenomena concerning the phenotype; the geneticists, those concerning the genotype. The use of the same terms, such as mutation, to describe aspects of the phenotype by naturalists and to describe aspects of the genotype by geneticists led to endless confusion (1980b, p. 14).

The construction of *a new, shared vocabulary* was, for Mayr, a mainstay of MS:

> The creation of a new evolutionary terminology greatly contributed to the eventual synthesis. At least some of the misunderstandings resulted from the lack of an appropriate and precise terminology for certain evolutionary phenomena. Nearly all the architects of the new synthesis contributed terminological innovations (p. 29).[45]

MS had to fill in communication lags between specialists throughout the world who weren't aware of each others' work and advancements: before

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[44] E.g., theoretical population geneticists and experimental geneticists, although they were, for Mayr, and e.g. Provine (1980b, p. 54), already on a way of unification by the straightforward and successful application of theoretical models to agriculture and experimental genetics. Other subdivisions came from the different organisms and levels of study dating back to Darwin's years: «The rise of evolutionism after 1859 coincided with an increasing separation of zoology and botany into new special fields, such as embryology, cytology, genetics, behavioral biology, and ecology. Simultaneously, the gap widened between the experimental biologists and those anatomists, zoologists, botanists, and paleontologists who had been raised as naturalists and who worked with whole organisms» (p. 6).

[45] Dobzhansky (1937) coined the term isolating mechanisms for the totality of the barriers maintaining the reproductive isolation of species; Rensch, the term Rassenkreis, subsequently designated by Huxley polytypic species; Serebrovsky coined genofond, subsequently referred to as gene pool; I revived Poulton's term sympatric and provided the antonym allopatric. Balanced polymorphism, climatic rules, founder principle, gene flow, introgression, isolate, sibling species, stabilizing selection, and taxon are some other helpful terms coined or adopted during this period (see Mayr, 1978).

synthesis, for example, the many advances made by experimentalists had «percolated only very incompletely» (p. 28) to the naturalists, and vice versa.[46]

> The conceptual advances made by either group were not perceived by their opponents; in fact, they were usually unknown to them. As a result, the construction of a unified and comprehensive theory of evolution during the first three decades of the century was impossible. The naturalists had wrong ideas on the nature of inheritance and variation; the experimental geneticists were dominated by typological thinking that resulted in their distrust of natural selection and a belief in the importance of pure lines and mutation pressure. Like the naturalists, the geneticists had many misconceptions about the nature of variation. They had at least as great an ignorance of the excellent taxonomic literature on species and speciation as the naturalists had of the genetic literature (p. 13).

So, the Modern Synthesis was primarily *establishment of communication* allowing for shared awareness and familiarization with the advancements that were being made in different fields.

Communication and commonality of language enabled, for Mayr, the clarification of distinctions (e.g., between proximate and ultimate biological

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[46] While, e.g., «post-Mendelian genetics» was overcoming a "macro-mutational" and "essentialist" concept of species and of their evolutionary origin, many naturalists in the U.S., England, and Germany «still argued against the obsolete interpretation of evolution by the mutationists even though the new insights of the younger geneticists had already refuted the mutationists' arguments» (p. 32). Conversely, «the Mendelians not only ignored the comprehensive findings on speciation made by [...] systematists, but they also took a dim view of natural selection» (p. 7).

causes),[47] resolving long-standing oppositions into complementarities, allowing for untroubled division of work. Importantly, for example, it was clarified that «the naturalists and the experimental geneticists were concerned with different levels» (p. 11) of the biological hierarchy, whereas in earlier years much confusion was brought about by «discussions that made no distinction between phyletic evolution (temporal genetic changes in populations) and the multiplication of species - that is, the splitting of a phyletic line into two or more reproductively isolated lines» (p. 35).[48]

In Mayr's account, MS seems to be understandable as a convergence on the idea that *different fields of biology were actually working on the reconstruction of the same story*, although with different methods and from different points of view; and on the idea that they all were doing it with *one* theory, the Darwinian theory, ruling out five or six competing theories that featured *inconsistent* concepts and observations.

A key concept in Mayr's view of synthesis is *consistency*: authors like Haldane (cf. p. 39), Simpson, Huxley, Mayr, and Dobzhansky (cf. p. 38) showed consistency between experiments and field work, genetics and

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[47] Mayr explains: «The functional biologist is interested in the phenotype and its development resulting from the translation of the genetic program within the framework of the environment of the respective individual. It is this interaction between the translation of the genetic program and the environment that we refer to as proximate causes. The evolutionist is interested in the origin of the genotype, in the historical reasons of antecedent adaptation and speciation responsible for the particular genetic program that now exists. This analysis deals with ultimate causes. There are few biological problems for which we cannot study either the proximate or the ultimate causation» (p. 9, see also Mayr 1961).

[48] «Speciation is not a phenomenon of genes or genotypes but of populations» (p. 35). To explain speciation it is not sufficient to explain the origin of variation or of evolutionary change within populations. It is the origin of reproductive isolation between populations that must be explained. Speciation is not so much the origin of new types but of protective devices against the inflow of alien genes into gene pools. In retrospect, the solution of the problem of speciation was simplicity itself (Mayr, cit., p. 36).

phenotypic data in the wild, theoretical and field genetics, microevolution and macroevolution. Contextually, an unprecedented, limited but strong *agreement on natural selection* was reached, with the diffusion of experimental and mathematical evidence of its agency and efficacy.[49] A real unifying phenomenon was, for Ernst Mayr, the spread of what he calls a *neo-Darwinian or population thinking*,[50] characterized by the centrality of variation and by the importance of ecological factors and population structure. In such a spread, Mayr vindicates the important contribution by naturalists who developed a new (evolutionary) systematics and a populational understanding of species.

In summary, Mayr's account describes the Modern Synthesis as a process engaging separate fields of research by virtue of common language, communication, reciprocal awareness and familiarity, resolution of oppositions into complementarities yielding a sense of a single theory potentially explaining in a consistent way a unified set of phenomena, and the spread of a very general way of thinking. The complexity of such process is often summarized by its results, that is

> ...the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes ("mutations") and recombination, and the ordering of this genetic variation by natural selection;

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[49] Artificial selection was demonstrated as a highly effective method through the brilliant selection experiments by Castle (Castle and Phillips, 1914), MacDowell (1917), Sturtevant (1918), Payne (1920), and the work of numerous animal and plant breeders.mathematical geneticists (Norton, Fisher, Haldane, and others) showed that even very small selective advantages can have a major evolutionary impact if selection is continued over a sufficiently long period.

[50] The interpretation of macroevolution in terms of neo-Darwinian mechanisms consisted not merely in generalized assertions, but also in attempts to apply neo-Darwinian thinking to specific phenomena and problems (Mayr, cit., p. 38).

> and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms (p. 1).

A consideration of the *process* of MS is necessary, I think, to figure out the successful role of Sewall Wright's migrant metaphor.

3.3 A view of a metaphor in evolutionary synthesis

Aside from the historical evidence of the adaptive landscape appearing in major foundational works of MS (Dobzhansky, Simpson, Huxley, see sections 2, 3.1), and beyond the advocacy of its intended wide evolutionary scope (sect. 2), philosophical analysis can specify what role the migrant metaphor could have played in the Modern Synthesis, as defined by Mayr (not by Lewontin, cf. sect. 3.2).

Let me start by a dictionary definition and go straight to the points of interest for adaptive landscapes:

> a metaphor is defined as a figure of speech concisely comparing two things, saying that one is the other.[51]

The adaptive landscape can be easily assimilated to a figure of speech. Not only because a picture can be seen as "iconic language", rather, landscape pictures - as it is evident also in my presentations, sect. 2 - *always went along with verbal descriptions*, and indeed words replaced the picture altogether in some cases, like Julian Huxley (1942, see 3.1). Furthermore, in today's

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[51] Note that Simpson (1944, p. 89) used exactly the same expression, "figure of speech". Dawkins used "parable", and Dobzhansky "symbolic picture".

evolutionary literature it is common to find terms like "peaks", "valleys", "climb", "rugged"[52] or, more recently, "ridges",[53] referring to an adaptive landscape which is rarely drawn actually. This, I think, demonstrates that during the Modern Synthesis adaptive landscapes opened up an enduring semantic area for verbal description of evolutionary phenomena. Adaptive landscapes can thus be rightfully seen as a metaphor, a linguistic object, a figure of speech, important in the development of a new, common, and shared language for speaking about evolution, a central aspect of the Modern Synthesis.

In the visual realization of landscapes, as we have seen in Simpson's work (2.2), the metaphor was particularly catchy for paleontologists and morphologists among others, who routinely made pictures of macroevolution (cf. Fig. I.5.b). Here the sense of a shared language was amplified.

The metaphor was proposed by Wright in 1932. As will be shown in chapter II, it was an ambitious metaphor, aimed on the one hand *to summarize* what went on most generally in the meta-model of population genetics, i.e. a Mendelian population; on the other hand, it presented the topic *in a form understandable* to other biologists, *emphasizing* furthermore *the relevance* that population genetics potentially had for biologists of all fields, who typically regarded mathematical models as abstract and obscure. The English "metaphor" derives from the 16th c. Old French *métaphore*, from the Latin

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[52] E.g. Kauffman (1995), Godfrey-Smith (2009, pp. 57-9).

[53] See Gavrilets further on in this chapter. Keller (2002, p. 113) notices how «successive stages of narratives» usually embed earlier meanings, with partial preservation of language in the common knowledge.

metaphora “carrying over”, and in Greek (μεταφοϱά) metaphorá “transfer”, from (μεταφέϱω) metaphero “to carry over”, “to transfer” and from (μετά) meta “between” + (φέϱω) phero, “to bear”, “to carry”. If the Modern Synthesis has not to be intendend, *à la* Lewontin, as the rigorous transfer of highly mathematized theory to control experiments and field work, then probably transfer and sharing *of metaphors* can have had a central role.[54]

The connection between metaphor and mathematical models can be seen as simultaneously weak and strong. It was *weak* because, in fact, no exact understanding of mathematics was necessary in order to get a hold on the metaphor. Indeed, understanding of the visual metaphor could lead to an intuitive grasp of the peculiar meaning of concepts employed in mathematical models, such as genetic combinations, mutation pressure, selection pressure, drift, and so on. Furthermore, the metaphor would have allowed biologists to start figuring out what meaning, if any, those concept could have in their own research fields.[55] *Context-independence* is, indeed, a characteristic of metaphors, and one that makes them powerful tools for knowledge. Rather than a direct

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[54] Ideas on more candidate metaphors: from older metaphors like the “tree of life” (e.g. Baum et al. 2005, Rieppel 2010) or “dominance” (Allchin 2005, Plutynski 2008), to more recent ones like the “evolutionary arms race” (Dawkins & Krebs 1979, cf. Kopp & Gavrilets 2006), “the Red Queen” hypothesis (van Valen 1973, cf. Kopp & Gavrilets 2006).

[55] For Evelyn Fox Keller (2002), metaphors are terms borrowed from other domains where they exploit an explanatory function, and the introduction of metaphors can be a fundamental operation for scientific research, especially - I understand - in some crucial phases: «scientific research is typically directed at the elucidation of entities and processes about which no clear understanding exists, and to proceed, scientists must find ways of talking about what they do not know» (p. 118).

transfer of mathematical concepts, this seems a way of engaging new, open-ended but seemingly promising research questions.[56]

The connection between metaphor and mathematical models was *strong* because it was pragmatically emphasized: indeed, *the authority* of the metaphor came from the fact that it was explicitly based on mathematical models, *and* from a shared confidence in such models. Such a confidence was rather recent if, as Mayr tells, for many years experimental scientists

> ...insisted that the solution to the problems of evolution would have to be found by asking entirely different questions and by using entirely different methods. They insisted that the hypothetico-deductive approach was pure speculation and that the looked-for laws could be found only by induction from experiments (1980, p. 27).[57]

An ingredient of the Modern Synthesis was, in Mayr's account, the gain of confidence of scientists in the methods used in each other's fields. And if confidence in mathematical models can be seen as a prerequisite for the efficacy of the adaptive landscape metaphor, it could be also said that *the metaphor might have itself aided the increase of confidence* by showing that mathematical models could be consistent with, and relevant to, observations in other fields.

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[56] Once introduced, metaphors constitute, for Keller (2002, cf. p. 113), a particular kind of explanation: the process of readaptation generates *explanatory force*, i.e. the two meanings metaphor brings together are both *consonant* and *discordant*, and this creates cognitive tensions fueling explanation.

[57] An idea that - Mayr speculates - divided experimentalists *from naturalists* as well as from theoreticians.

In his account Mayr emphasized the role in Modern Synthesis of scientists he defined “bridge builders”, who were necessary because in many cases the communicational gap between fields had changed into real hostility.[58] I find it strange the absence of Sewall Wright from Mayr’s list of bridge builders[59] since, as a mathematician and (to a limited extent, cf. II.2.4) laboratory scientist, he was he was *already* thinking to (for) naturalists. For example, his “shifting balance theory” (cf. III.3.1, III.3.2) and observations he drew by the naturalists were explicitly mutually reinforcing, «an early direct link» between the shifting balance and speciation theory (Pigliucci 2008, p. 596). Another «astoundingly early recognition» was the compatibility with the fossil record. Wright’s metaphor was thus an *intentional* communication, purposefully tailored to an audience of naturalists.

I expressed the idea of adaptive landscape as a unifying metaphor in the Modern Synthesis. Both metaphor and synthesis are seen here in a communicational perspective, where synthesis consists in an improvement of a common language (iconic but in most cases verbal) among once disparate fields. The metaphor had the merit of summarizing in an understandable form the researches in mathematical population genetics, and indeed in a form that seemed to be consistent with the naturalists’ observations, and to open possibilities of research by tentative reconceptualizations. The enthusiast

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[58] «When I read what was written by both sides during the 1920s, I am appalled at the misunderstandings, the hostility, and the intolerance of the opponents» (Mayr, cit., p. 40).

[59] And indeed Wright’s name is very rarely cited throughout *The Evolutionary Synthesis* (Mayr & Provine 1980). Wright was not at the conference either, although still alive at that date. The issue would require further inquiries, since in my view Wright was one of the mathematical population geneticists most early and decidedly oriented to the synthesis. See also Provine (1986).

acceptance of the metaphor may be seen as a consequence of the esteem mathematical models had begun to have among biologists, *but also* as a contribution to such esteem, by virtue of its communicational effectiveness. The use of the metaphor in a popular book by Richard Dawkins (2.3) is perhaps the exploitation of the same communicational virtues, such as comprehensiveness, conciseness, context-independence.

I should mention a stronger view of metaphors as *explanatory* devices in their own right.[60] In the years preceding the synthesis, naturalists and experimentalists (as well as other groups) had shown little involvement in refutation and/or explanation of each other's domain. The "shifting balance theory", a qualitative account presented by means of a visual representation, could be considered for some authors *as an explanation* of some observations of naturalists. I am not sure that such a strong view would hold for adaptive landscapes, though.

4. Altering the metaphor: holey landscapes

Adaptive landscapes were introduced by mathematical geneticist Sewall Wright (1932) at the dawn of Modern Synthesis. Adaptive landscape pictures featuring peaks and valleys were then reproduced, along with verbal descriptions, in major books such as Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937), Julian Huxley's *Evolution The Modern Synthesis*

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[60] Thinking to metaphors in developmental genetics - such as "gene action", "genetic program", "feedback", or "positional information" - Keller (2002) argues for the continuing and productive action of linguistic metaphors: «...much of the theoretical work involved in constructing explanations of development from genetic data is linguistic - that it depends on productive use of the cognitive tensions generated by multiple meanings, by ambiguity, and, more generally, by the introduction of novel metaphors» (p. 117).

(1942, only verbal description), and George Gaylord Simpson's *Tempo and Mode in Evolution* (1944), often gaining so a wide evolutionary scope to constitute a "big picture" of evolution, and one of the most influential metaphors in the history of evolutionary biology. In *Climbing Mount Improbable* (1996), to argue for the power and sufficiency of natural selection as an explanation of the most complex adaptations in the living world, Richard Dawkins took advantage of the communicational virtues (e.g., simplicity and context-independence) that - I argued - made the migrant adaptive landscape metaphor remarkably important in the Modern Synthesis. *The shape* of adaptive landscapes served as a pivot for the growth of a metaphorical vocabulary including terms like "peak", "valley", "climbing", "crossing", "rugged" etc. for speaking about evolution. Natural selection was seen as a force pushing "upwards" on the landscape, away from valleys and towards adaptive peaks. Peaks depend on the environment and represent combinations of traits that are far too improbable for being due to chance alone. Actually, peaks themselves represent selective pressures and natural selection, and the upwards movement is part of a tautology: "by definition", peaks *are* those possibilities that are favored by natural selection.

In all this story, I would point out, the shape of adaptive landscapes was preserved and treated as *inherent* to it.

Recently, mathematical biologist Sergey Gavrilets began to draw landscape pictures with a radically different shape - Figure I.7.b - describing them as "holey landscapes" as opposed to Wright's "rugged". Notably, Gavrilets chose to use and enrich the existing metaphorical vocabulary,

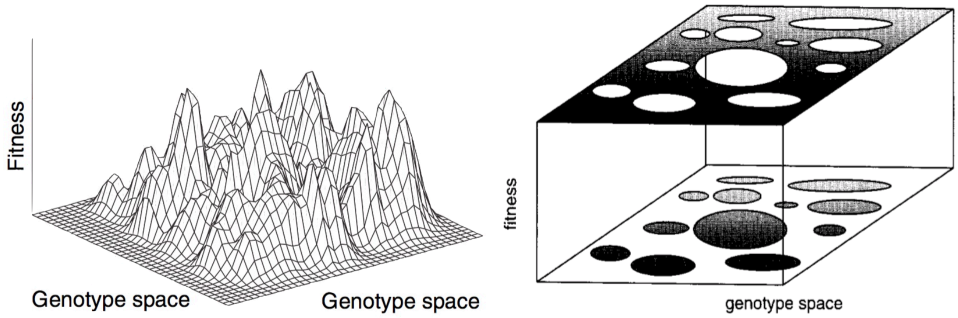

Figure I.7. (a) Redrawing of the 1932 original landscape by Sewall Wright (from Gavrilets 2004, p. 35). Actually, in Wright's original figure the perspective was perpendicular to the landscape base, i.e. the landscape was seen "from above" (1932, p. 358) - a choice, I guess, trivially bound to the difficulty of 3D manual drawing contrasted with the fact that the picture was meant to be just a sketch. Anyway the new perspective does not substantially alter the shape of the landscape. (b) Picture of a "holey" landscape, first appeared in Gavrilets (1997). Similarity of perspective in (a) and (b) allows to best appreciate differences between the two three-dimensional landscapes.

talking about "ridges" and "holes" in a landscape with no peaks and valleys. Adaptive landscapes can thus exist with a shape different from that given by Wright. This means that the particular shape is not inherent to the landscape metaphor: the two are decoupled.

Gavrilets's pictures were based on new mathematical analyses, and holey landscapes were presented as «a multidimensional alternative to the conventional view of rugged adaptive landscapes» (1997, p. 307; mainly based on Gavrilets & Gravner 1997). The statement conveys, in my opinion, the idea that the "conventional view" of the landscape as characterized by hills and valleys has now an *alternative*: a view that finally considers - through suitable mathematical tools - the huge number of dimensions that a genotype space is supposed to have.

In section 3.3, I presented the adaptive landscape *migrant* metaphor in Modern Synthesis as capable of summarizing what happens in the mathematical entities studied by population geneticists, giving biologists an insight into them with no immediate need for technical mastery of mathematical models; I also argued that the migrant metaphor could trigger researches in different fields, aimed to develop the implications of concepts like mutation, selection, drift, peak, etc., to reconceptualize them and probe them in new contexts. Accordingly, now I imagine biologists working in the Modern Synthesis dealing with the new metaphor of holey landscapes just like they did with rugged landscapes. Holey landscapes would suggest, I think, major inferences concerning the influence of evolutionary factors like natural selection.

A hilly landscape seems to allow selection pressure to drive the population uphill, or to keep it on a peak; on the contrary, a flat and holey landscape seems to leave the population wander free on the surface, with selection doing nothing but keeping it out of maladaptive holes. A flat surface suggests a situation of *neutralism*, where most changes are adaptively neutral. Where have the peaks gone? If, like in Dawkins's or Dobzhansky's landscapes, different spots on the surface correspond to different and unlikely conditions, how can natural selection be the causal mechanism for the population reaching them, in absence of adaptive differences? And, if natural selection cannot drive adaptation, can chance alone do? Must alternative evolutionary mechanisms be looked for? And what all this can mean for a biologist working on the fossil record, a particular case of speciation, or the phylogenetic history of a higher taxon? What can it mean in general for the origin of complex structures like the eye? Does it invalidate adaptive explanations of events like the evolution of grazing in horses?

Actually, there is, in holey landscapes, variation in adaptive values (between the surface and the holes), but it is abrupt and discontinuous. There is no smooth distribution natural selection may work on. This seems to point to *saltational* theories, where selection is seen only as a passive "paper pusher" of individual discontinuities, not as an active and creative evolutionary mechanism. Again, many questions rise on the meaning of holey landscapes for various biological fields and inquiries.

As I will argue in chapter III, all the questions I raised here are misplaced:[61] the *native* context of the two different-shaped landscapes is quite the same, but at the same time the relationship between them is subtler than replacement (III.3). Here in the next section. I only reflect on the epistemological importance of looking at the native metaphor.

5. Native metaphor: a metaphor for a model

Sergey Gavrilets works in the same context as Sewall Wright: population genetics. In the book where Gavrilets treated most extensively his new-shaped adaptive landscapes, *Fitness Landscapes and the Origin of Species* (2004), he defines explicitly a metaphor, i.e. *what a metaphor is*:

> One has to realize that there is a clear distinction between a *fitness landscape* [...] and the *metaphor of fitness landscape* by which one means a two- or three-

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[61] By the way, no biologists as far as I know posed them seriously, or more seriously than they were already doing, e.g. for neutralism or morphological discontinuity. This could indicate that while adaptive landscapes may have played a central role in MS (as I argued in section 3), in the years that followed they became only one of many representations of the shared and established evolutionary theory. According to such a hypothesis, different shapes of the landscape would have been decisive only in early phases of the synthesis.

> dimensional visualization of certain features of multidimensional fitness landscapes. The former is defined in a precise mathematical sense. The latter is necessarily a simplification that emphasizes only those specific features of fitness landscapes [models] thought to be most important while neglecting many other features. The requirements for metaphorical pictures are much less strict than for exact mathematical constructions (p. 34).

There will be space in the next two chapters to appreciate what Gavrilets means by "fitness landscape". Provisionally, it can be defined as *a model* of «the relationships between multilocus genotype and fitness» (p. 33), defined in a precise mathematical sense. A metaphor, on the other hand, is a simplification emphasizing specific features *of* the model. Gavrilets seems thus to assume a hierarchical layout of metaphor and model: metaphor is metaphor *for* a model. The relation is even more clear in the following quotation, that assumes severe limitations hanging over the visualization of a fitness landscape *model*:

> ...because of the huge discrepancy between the number of dimensions necessary to define a fitness landscape and the number of dimensions for viewing, fitness landscapes *cannot be graphically described in their entirety*, *even if they were known*. One needs [...] three-dimensional geographic landscapes as *a metaphor for* multidimensional relationships between genotype and fitness (pp. 33-34, my emphases).

In its native, mathematical context the adaptive landscape is a metaphor, *not* only meant as simpler and less demanding than models, *nor* as a candidate substitute for a model - I summarized the latter ideas (inappropriate to the

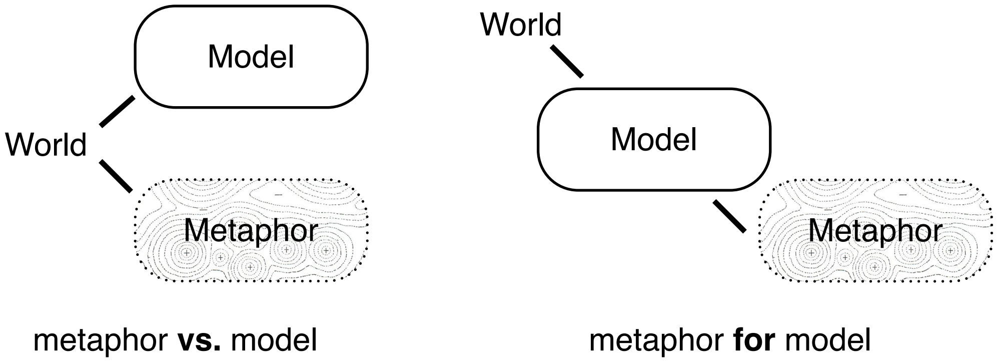

Figure I.8. *Two views on adaptive landscapes as a metaphor.* ***Left:*** *landscapes metaphorically represent real populations, potentially in (disadvantaged) competition with models.* ***Right:*** *landscapes are metaphors of population genetics models.*

native context) in the "metaphor vs. model" view, in Figure I.8. In the native context we are considering, there is instead a "metaphor for model" view: the model has too many dimensions to be represented, so a metaphor is necessary to express some of its features.

Many philosophers in the adaptive landscapes debate stress the importance of marking the distinction between metaphors and models.[62] Sometimes, however, the distinction seems to be set out in terms of the "metaphor vs. model" view. Yet, features like abstraction, simplification, idealization, provisionality, and limited validity apply to models as they do to metaphors. Brett Calcott, for example, writes:

> We may be misled by the models (rather than metaphors) when we have made inappropriate assumptions relevant to the question we are asking [...]. If both models and metaphors are simplified representations *of the world*, then it

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[62] Talking about holey landscapes, John Wilkins for example makes it clear: «...but the more recent metaphor, *and I must point out that it is indeed a metaphor not a model*, is of a holey landscape» (2007, p. 251, my emphasis).

> is difficult to see what distinguishes the two. It can't be just that one is misleading, while the other is not (Calcott 2008, pp. 642-641, my emphasis).

Many philosophers of biology agree that the adaptive landscape metaphor might be (and have been) *misleading*. In a "metaphor vs. model" view, this would be translated into a sense of limited validity and reliability of metaphors, appearing as "not so good" models. Wilkins & Godfrey-Smith (2008) claim that they «use the metaphor to illustrate features of the biology itself» (p. 201), therefore they try to improve its formalization,[63] being however aware of the metaphor's lability.[64] At heart, in their paper they «make a point that does not depend on taking this spatial landscape metaphor fully seriously» (Ibidem). Communicational virtues of the metaphor exceeds, for these authors, its lack of governability - which in turn requires caution. Some authors suggest to drop the metaphor as soon as possible for its liability to mistake (Pigliucci & Kaplan 2006, Pigliucci 2008a, Kaplan 2008).[65]

Sometimes metaphors are seen as *preliminary* to exact mathematical models.

All the problems set out in a "metaphor vs. model" view, might perhaps apply to the adaptive landscapes *migrant* metaphor, as seen in the transdisciplinary dynamics of the Modern Synthesis (sect. 3). After its arrival in a new field of research, the metaphor might be seen as an ancestor of a

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[63] E.g. by coding precisely what the horizontal axes of the landscape are meant to represent.

[64] E.g. problems of incommensurability get more and more acute as long as one "zooms out" to encompass a more and more diverse set of organisms

[65] Plutynski (2008) and Calcott (2008) are more cautious.

model, susceptible to subsequent specification and probe; as a provisional, potentially misleading hint for more rigorous researches with no guarantees of success; above all, the metaphor would be seen as a metaphor *of the world* - that portion of the world studied by the receiving field.

All these problems do *not* apply in the same way, I argue, to the *native* metaphor, because metaphor in the native context is intended as "metaphor for model".

Many philosophers actually do assume the "metaphor for model" view. Some of them make it explicit, like John Kaplan (2008) talking about «the *metaphorical understanding of the models* in terms of "landscapes"» (p. 632, my emphasis) related to «our inability to generate visual images that accurately portray more than a very few significant aspects *of the models*» (p. 637, my emphasis). Pictures or images of landscapes can, for Kaplan, give insights *into the theory*.[66]

It is not - immediately - that biological populations *are as if* there were peaks and valleys in their fitness distribution. Rather, *population genetics models* are as if there were peaks and valleys in *their* fitness distribution. The possible relation between metaphor and the world is thus mediated by the model. It is not im-mediate.

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[66] Kaplan's thought is actually more complicated and, I think, convoluted and obscure. The exact quotation is: «But if the "landscape heuristic" refers to the uses to which the physical pictures or diagrams of landscapes are put, then the usefulness of the heuristic depends on for example the degree to which such pictures provide meaningful insights into the systems they are supposed to represent. Here, there is an additional ambiguity, in that we might wish for insights into the more or less concrete models/images produced from the theories, or we might wish for insights into the world. In the latter case, we might for example wish to compare aspects of the pictures produced using a particular (semi-concrete) model to some aspect of the world» (p. 631).

“Metaphors for models” should not be judged like models, e.g. by using rigorous mathematical criteria:[67] they express *some* properties of the considered model. They become powerful and delicate tools to reveal and communicate features of models, the latter being too complex to allow a complete cognitive grasp. Metaphors can stimulate hypotheses and researches - where and when possible - *on* the models (Plutynski 2008, Skipper 2004). For a single model, *several* metaphors can be chosen, and changed, and they can also be *misleading*, but about that particular model’s properties.[68]

Many philosophers do not make it explicit whether they are talking about the adaptive landscape *migrant* or *native* metaphor. This creates confusion, because they have very different properties. When adaptive landscapes are called a metaphor in their native context, the reference is *not* to the fact that the landscapes “are alike” or “resemble” or “share some features with” *actual, real, living* populations; rather, the reference is to the fact that the landscapes share *some* features, bear *some* resemblance *with models* that are complex, and for which it is possible to offer only partial representations. Perhaps controintuitively, actually the majority of philosophical and

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[67] Gavrilets notes that some of Provine’s (1986) criticism of adaptive landscapes stems from Provine’s attempt to judge a metaphor using rigorous mathematical criteria. The “impossible packing” objection and the related “apparent continuity” objection are exposed in II.2.3.

[68] In the case of adaptive landscapes, however, Kaplan thinks that visual metaphors are *so much* insufficient to be almost always misleading about the characteristics of population genetics models. The final recommendation of his paper, entitled “The end of the adaptive landscape metaphor?”, is: «Finding a better way to talk about the models and the results generated from those models - a way that does not encourage the use of misleading images - may prove to be difficult, but that should not stop us from trying» (pp. 637-638). Is he thinking about non-visual, but still metaphorical, representations? In other words, would the metaphorical *function* or *role* survive to the replacement of landscape pictures with some non-visual representation?

theoretical literature assumes that *adaptive landscapes are metaphors for population genetics models*. Chapter II addresses the ambiguity of the word model (sect. 3) and, in particular, what is to be intended with “population genetics models”, an issue which I diverge upon from mainstream literature.

The migrant metaphor, instead, can be seen as representing *the world*.[69] When in *Climbing Mount Improbable* Dawkins specifies that metaphors are good for some purposes only, and that we have to be prepared to drop or modify them when or where they are not good anymore, he could well be referring to how well our metaphor describes the biological world and the actual course of evolution. Looking closely, however, it would be completely different and philosophically stimulating to reflect on the fact that perhaps the migrant metaphor is a “metaphor for models” *also* in fields where it migrates; the metaphor is accepted exactly because it is also a good metaphor for the models found *there*; and that we never have access to the world but build metaphors of metaphors of models, and so on. Important and in-depth works have been done on scientific metaphors (e.g. Black 1962, Hesse 1966, 1980, 1987, 1993, cf. also Gadamer 1975), and they arrive to quite radical conclusions, presenting scientific language as metaphorical “through and through” (cf. Keller 2002, p. 119).

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[69] As long as this is imagined as possible, see Godfrey-Smith (2008).

CHAPTER II

Surfaces and spaces: on the origin of adaptive landscapes

The adaptive landscape was a *migrant* metaphor, I hypothesized. Since 1932, for several years, it served well the Modern Synthesis in assisting communication and convergence across field boundaries, the main of which (for Ernst Mayr) had kept apart geneticists from naturalists. But much can be

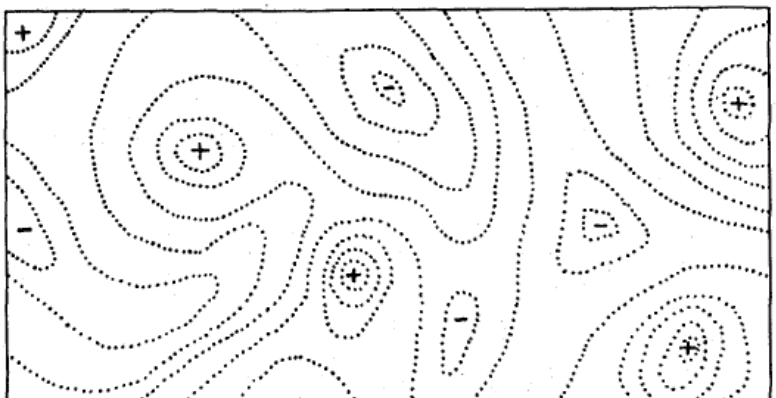

Figure II.1. *The first adaptive landscape (Sewall Wright, 1932). The caption claims «Diagrammatic representation of the field of gene combinations in two dimensions instead of many thousands […]». The landscape is framed from above, pluses represent "adaptive peaks", while minuses are "valleys".*

said on the *native* metaphor (I.5), i.e. on the metaphor as it was intended in Sewall Wright's work in mathematical population genetics, its original context. As said in the previous chapter, the native adaptive landscape was surely a "metaphor for" some model. But *exactly what model was the adaptive landscape metaphor for?* Saying - as often happens in literature[70] - that the adaptive landscape was a metaphor "for complicated mathematical models of population genetics" is, I show here, *formally* vague and misleading, and *substantially* wrong.

The debate on adaptive landscapes is probably gripped into lack of a sufficiently articulated and shared language, I make a dispassionately pragmatic proposal (3.2, Table II.1). I stress the idea of pragmatism (3.1, 3.3) because we have for example a richness of notions of model in philosophy of biology, but richness can become poverty if we refuse to make choices on the aims of our analyses, and accordingly on the most useful notions to reach them.

To set out an answer to the question "what model was the adaptive landscape metaphor for", it is of primary importance to clarify the difference and relationship among elements that are ordinarily conflated in the debate, also due to a inaccurate terminology (see Fig. II.3). First, I emphasize the

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[70] Griesemer and Wimsatt (1989, p. 130) seem convinced that Wright's diagram was «propagated without transmission or understanding of its mathematical apparatus» because «Wright's mathematical theory» was crammed with «Wright's self-taught mathematics, often idiosyncratic notation, and sometimes torturous derivations». For Robert Skipper (2004, p. 1185), Wright used the landscape to evaluate the «dynamical behavior of population genetics models», obtaining different «dynamical behaviors» by manipulating model assumptions. In Skipper's account, later authors used the landscape likewise to assess the dynamical behaviors of «alternative population genetics models» (p. 1186). Pigliucci and Kaplan (2006, p. 204) think that «Wright proposed the [landscape] metaphor because the underlying math was abstruse». And so on.

radical difference in Mendelian population genetics between population genetics *equations*, dealing with gene frequencies (1.3), and *Mendelian population*, a combination space (1.2). I deal with such distinction in section 1. Native adaptive *surfaces*[71] are, in my view, *metaphor for the entire Mendelian population*, for which *no* tractable equations were (and still today are) available (cf. 2.4). Using the term "model" to refer both to equations for gene frequencies *and* to the Mendelian population space - although acceptable in principle - blurs these clear distinctions in the debate. Therefore, I advance the proposal to focus Mendelian population as a model.[72] Another source of confusion is the habit of using the word "landscape" to simultaneously point at combination space and surface.[73] I propose to safeguard the space-surface distinction by terminological specificity (*combination space* vs. *adaptive surface*). This is absolutely necessary to avoid confusion.

Under these clarifications, adaptive surfaces will be rightfully "metaphor for a model", as it was preliminarily said in chapter I (sect. 5).

The combination space of Mendelian population is enriched with the notion of fitness, with notions about distance (making the space a "metric space"), and movement (2.1, 2.2). All is set then to understand the native metaphor in all its epistemological complexity and implications. I look at the dynamics Wright wanted to show by using the diagram (2.3). I give my

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[71] I will call "surface" the visual metaphor henceforth (cf. 2.3), by the way mutuating the term from Wright's paper, "Surfaces of selective value revisited" (1988).

[72] I intend model as a «stable target of explanation», see 3.2, and 3.1, 3.3.

[73] Landscape models in scientific literature are a heterogeneous ensemble of combination spaces similar (but not identical) to Mendelian population. I address them in III.2, where I hypothesize that their name, "landscape models", is partially due to the force of the landscape metaphorical verbal language invented by Sewall Wright.

hypothesis on how Wright managed to cross the *epistemological gap* separating his equations from the Mendelian population as a whole, for which no equations were (and are) available (2.4). How did Wright get the information he conveyed with the metaphor? He built a "bridge" by means of his limited laboratory experience, intuition, and heuristics. The epistemological gap is another thing often overlooked in the debate, perhaps also due to a lack of clarity by Wright himself (Provine 1986, see 1.4).

1. Mendelian population vs. equations of population genetics

1.1 Genetics of populations

> If the entire field of possible gene combinations be graded with respect to adaptive value under a particular set of conditions, what would be its nature? (Wright 1932, p. 357).

The paper entitled "The roles of mutation, inbreeding, crossbreeding and selection in evolution", published in the Proceedings of the 6th International Congress of Genetics held at Cornell University in 1932, is the written version of a talk by Sewall Wright that - as described in chapter I - influenced evolutionary biology to a remarkable extent.

Wright was one of the most brilliant makers of population genetics, a field that in 1910s and 1920s had realized a neo-Darwinian synthesis by building mathematical models that reconciled the Mendelian mechanisms of heredity[74] with the theory of natural selection by Charles Darwin (1859). Still in 1980, however, in commenting the Modern Synthesis (cf. I.3.2), Richard Lewontin expressed his view of population genetics as persistently *split into two* «traditions» or «theoretical structures» or «schemes» the MS had not brought really together (1980, p. 59). Here I follow Lewontin's suggestion.

One tradition was mainly grounded in important works by Ronald Fisher (e.g. 1918)[75] and had been developed in what Lewontin calls *biometrical genetics*. In such theoretical structure, «everything is dealt with in terms of phenotype», whose variation is continuously distributed, and partitioned in genetic (heritable) and nongenetic components. Fisher's scheme «talks about rates of changes of means and of variance» (p. 63). There is no specific reference, in this tradition, to the frequencies of genes:

> ...the genes get lost in the shuffle. They get absorbed into mysterious parameters like the heritability or the average effect (Lewontin, cit., p. 59).

An example is Fisher's fundamental theorem of natural selection, establishing that the rate of increase of fitness in any organism is equal to its genetic

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[74] On Mendel's work and achievements, see Orel (1984), Henig (2000), and Lloyd (1988) who expressed a relevant model-based view of his "laws".

[75] Fisher also dealt with gene frequencies, e.g. in his researches on balanced polymorphisms, but he is by far most known for his fundamental theorem of natural selection, see further. Lewontin remarks how the two parts of Fisher's work were not well integrated: his biometrical genetics works «did not cope with the conflict between the utilization of variation by natural selection» and the consequent destruction of variation. They said «nothing about balance, only evolutionary progress» (p. 60).

variance in fitness at that time (Fisher 1930).[76] Another example is the Price equation.[77]

Interaction among genes is a fundamental phenomenon giving rise to continuous variation, that can be studied by further partitioning genetic variation «into additive, dominance, and epistatic components» (Lewontin, cit., p. 59).[78] But gene interaction is a difficult object of study: Fisher's 1918 paper was an immense advance in the tradition of biometrical genetics because it considered *two* genes for a trait.

In the other tradition, most interesting for Wright and adaptive landscapes, «everything was dealt with in terms of the frequencies of genes». For Lewontin

> Mendelian population genetics - that is, dealing with gene frequencies - is impossible unless something about the phenotype of the genotypes - their fitnesses - can be asserted. But those phenotypic transformations get lost in the shuffle because they are assumed constant; a given genotype has a given fitness (Lewontin, cit., p. 59).

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[76] For recent analyses see Plutynski (2006), Okasha (2008).

[77] See Okasha (2006), where the Price equation is commented and used in a multilevel expansion of natural selection.

[78] See references to the G-matrix for trait variance-covariance in IV.2.2. Notably, recent studies, e.g. on evolvability, are an extension of the Fisherian theoretical framework. This will be important since some commentators try improperly to relate new developments to the landscape, tied instead to the Wrightian theoretical structure (IV.2).

The exemplar work by Sewall Wright (e.g. 1931)[79] in this theoretical structure is «more ambitious» than Fisher's in Lewontin's view, because it deals with more factors, not only natural selection, and their balance.[80]

Although Sewall Wright's work was not at all a pure form of Mendelian population genetics, following Lewontin's distinction and characterization I claim that Wright devised adaptive landscape essentially *inside* the theoretical structure of Mendelian population genetics. Accordingly, when I talk about population genetics (models, equations etc.) in this chapter I am referring to *Mendelian* population genetics, as a sub-part of population genetics where gene and allele combinations, interactions, and frequencies are the focus.[81]

In 1931 Wright had published a long state-of-the-art paper entitled "Evolution in Mendelian Populations" (Wright 1931), reaffirming in the introduction that «the evolutionary process is concerned, not with individuals, but with the species», and that population genetics is related to the genetics of individuals by means of *statistics* (Ivi, p. 98). If the genetics of a biological individual can be formalized as an array of *discrete* inherited factors, the huge

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[79] Debates between Wright and Fisher (cf. an excellent review in Provine 1986) continue to generate theoretical discussions. There has been, for example, a recent debate opposing so-called neo-Wrightians vs. neo-Fisherians (Wade & Goodnigh 1998, Coyne et al. 1997, see e.g. Plutynski 2005). The groups, however, do not coincide with biometric and Mendelian population geneticists.

[80] Some evolutionary forces preserve variation and others destroy variation. Wright for example brought into the theory of evolution the role of random processes as part of the former category.

[81] The two camps were nonetheless interrelated. Fisher, for example, *justified* biometrical genetics by means of conditions *in* Mendelian genetics, such as that the effective population size of most populations was the entire breeding population, that the latter was on the order of infinity, or that there was only one adaptive peak.

number and above all the *statistical distribution* of Mendelian factors in the population re-establishes the necessary *continuity* for natural selection to work. Mendelian population genetics is the shift from individual genetics to (statistical) genetics of populations, dealing with gene frequencies. And it is founded on (and made possible by) the crucial formal notion of a Mendelian population.

1.2 Mendelian population: a combination space

As shown in the title of the already cited important paper “Evolution in Mendelian Populations” (Wright 1931), the notion of a Mendelian population is a fundamental and necessary notion of population genetics since its birth (it is a *space* population genetics equations are *about*, cf. 1.3). My understanding is that the phrase «the entire field of genetic combinations» in Wright’s quotation above (1.1) points exactly to nothing less than Mendelian population in its entirety. So, I want to confute the idea - expressed in literature - that adaptive landscapes refer to population genetics equations I will refer to Mendelian population interchangeably as a space or as a model (cf. II.3.2).

The space consists of a collection of individuals, every individual consists in a *combination*,[82] i.e. an array of *alleles* - two for each genetic *locus*. *Genetic loci* are the same, in number and identity, all over the population, i.e.

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[82] I purposedly avoid the term genoTYPE, although unanimously used in literature. The term indeed evokes *repeatability*: a genoTYPE is repeated in more individuals. While when we consider one, two, three or a number of loci the recognition of a TYPE with its frequency is perfectly acceptable, it is not in Mendelian population, where *each combination is, by definition, unique*.

every individual in the space has exactly *the same* loci as any of the others, but it has a unique combination of *coupled* alleles occupying each locus. Conversely, for every genetic locus *a number* of different alleles are available, and *any combination* of them is allowed in the space, including the *homozigous* combination (i.e., two copies of the same allele in a locus). So Mendelian population is the space of all possible individual combinations given a number of loci and a number of alleles.

A correct label for Mendelian population is, I think, a *combination space*. The term is borrowed from logics, but to see clearly a Mendelian population *is* a logical structure, defined by the sequence of loci and by the array of available alleles for each locus, plus combinatory rules and operations like "sexual reproduction" (see below). Each individual combination, being a combination of alleles, occupies a (logical) *position* in the combination space. Mendelian population is indeed a *metric space*,[83] because of some properties that will be addressed in section 2.2 regarding the distance between elements in the space.

An assumption coming along with Mendelian population is that *only some positions* in the combination space are actually occupied at a certain time.[84] That is, at any time, only a number - conventionally designated with the letter N - of individuals are considered existent, and N is exceedingly small compared to the number of possible combinations in the combination

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[83] See Bryant (1985), Searcóid (2006). Thanks to Fabrizio Panebianco for useful discussions on the notion.

[84] Whether this assumption (finite population size) changes the properties of the space was debated in population genetics, e.g. by Wright vs. Ronald Fisher (cf. Provine 1986).

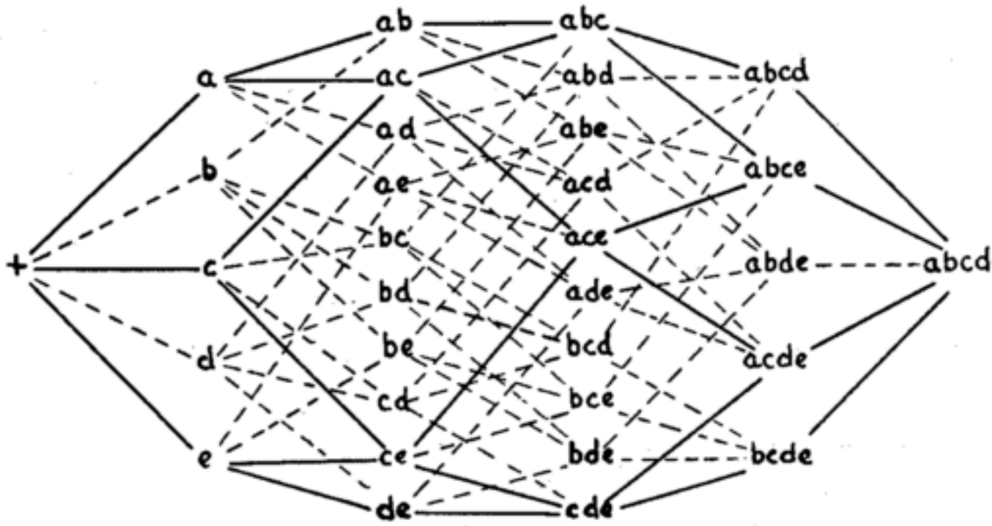

Figure II.2. *Part of the first figure appearing in Wright (1932), giving an idea of a Mendelian population as a combination space. Letters are alleles, organized in all their possible combinations.*

space. This creates what I will call simply a *population* (without the caption "Mendelian").[85] Its finite number is a property shared with real, living populations.[86]

Individuals are *sexually reproducing* in a population, and reproduction consists in the production of novel individual combinations in the space by random *recombination* between parents. Generations are "non-overlapping": whereas in biological populations individuals of different generations are simultaneously alive and interacting, in a Mendelian population it is assumed that a generation of the population disappears in giving birth to the next. In each generation population size (N) remains constant.[87]

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[85] In my proposed vocabulary (3.2), population will be called a dynamical system *in* the model.

[86] This also reminds the "virtuality" feature seen in section I.1.2 about adaptive landscapes, but I will get back on the issue in the next sections.

[87] Constant number N is, in Darwinian theory, the condition for operation of natural selection. So limited number is a theoretical condition justifying, e.g., selective pressures.

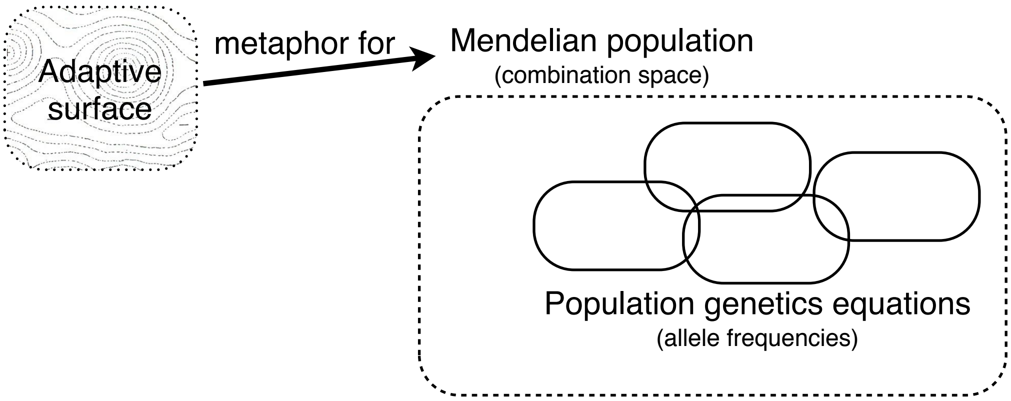

Figure II.3. *View of adaptive landscape as a metaphor for Mendelian population, not for population genetics equations. Mendelian population is the combination space that frames population genetics equations (statistical equations of allele frequency in the population).*

What I argue is that Wright's talk in which he famously proposed his idea of adaptive landscapes (1932) had Mendelian population not only as a theoretical framework *but also* as its *argument*, differently from most population genetics equations (see 1.3). Fig. II.2 - the first in Wright's paper - gives an intuitive idea of what a combination space is.[88]

The argument of Wright's paper was a Mendelian population suitable for hosting a population which be as proximate as possible to a natural population. Relying on knowledge and estimates of the time, he imagined a Mendelian population with 1000 genetic loci and 10 alleles per locus.[89] The number of combinations in such a space is astronomically large.[90]

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[88] The Figure is perhaps a little obscure in its notation, so see sect. 2.2 for some clarifications.

[89] «Estimates of the total number of genes in the cells of higher organisms range from 1000 up […]. Presumably, allelomorphs of all type genes are present at all times in any reasonably numerous species. Judging from the frequency of multiple allelomorphs in those organisms which have been studied most, it is reasonably certain that many different allelomorphs of each gene are in existence at all times. With 10 allelomorphs in each of 1000 loci the number of possible combination is 10^{1000} which is a very large number. It has been estimated that the total number of electrons and protons in the whole visible universe is much less than 10^{100}» (Wright 1932, p. 356).

[90] In a few passages of his works, Wright remarks how unlikely (practically, impossible) would be, due to the huge number of possibilities, the appearance by chance of two identical individuals (e.g. 1932, p. 356).

A Mendelian population is a *combination space* and it is, in my view, *the* model of population genetics (at least of Mendelian population genetics), it is the space of the population *which equations are about* (cf. 1.3), and it is directly referred to by the adaptive surface metaphor (Figure II.1). I fixed these relations in Figure II.3.

1.3 Population genetics equations

Population genetics equations realized quantitative, statistical analyses of allele distributions across generations of a population inhabiting a Mendelian population space, *but* such equations did *never* deal with the Mendelian population as such.

The statistical study of the stochastic dynamics of alleles distribution in populations inhabiting Mendelian population space - *modified* for example by *selection pressures* favoring some alleles and opposing others - was the essence of population genetics, and in 1931 the field had reached a remarkable degree of refinement. Wright and the other mathematical geneticists had shown how the *balance* among factors such as *size* and *degree of subdivision* of a population, or allele *frequencies*, can determine allele frequency. This was the theoretical context in (or better, to) which Wright was working[91] when he was invited to give a talk at the 6th Congress of Genetics. A talk which he would have concluded as follows:

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[91] Remarkably, the theoretical structure worked out by Wright and colleagues has been the foundation of population genetics, largely until today (Hartl & Clark 2007).

> The most general conclusion is that evolution depends on a certain balance among its factors. There must be gene mutation, but an excessive rate gives an array of freaks, not evolution; there must be selection, but too severe a process destroys the field of variability, and thus the basis for further advance; prevalence of local inbreeding within a species has extremely important evolutionary consequences, but too close inbreeding leads merely to extinction. A certain amount of crossbreeding is favourable but not too much. In this dependence on balance the species is like a living organism (1932, p. 365).

The available mathematical equations in 1931-32 were complex and refined but, to remain mathematically tractable, they were limited to *single-locus, diallelic* settings: they calculated either the changes in *frequency of a single allele* (Fig. II.4.a), and/or the *overall frequency spectrum* of all diallelic loci in the population (Fig. II.4.b).

In diallelic equations, equilibrium at the considered locus consists of a particular frequency of fixation in the population, named q, for one of the two «allelomorphs» (the other allele, of course, gets the complementary frequency 1-q).[92] Due to the Mendelian mechanism of inheritance, the two alleles are expected to reach the Hardy-Weinberg equilibrium, which is modified by relevant parameters such as mutation[93] and selection "pressures",

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[92] Population genetics models were (and are) essentially equilibrium models (Sober 1983; cf. Plutynski 2004, p. 1204): they calculated the change of allele frequencies over time in a population in the Mendelian space, and the reach of equilibrium or, better, "moving equilibrium" (Wright 1931, p. 146) of those frequencies depending on a number of factors included as model parameters.

[93] A tractation of mutation in Mendelian population genetics is found in III.1.1.

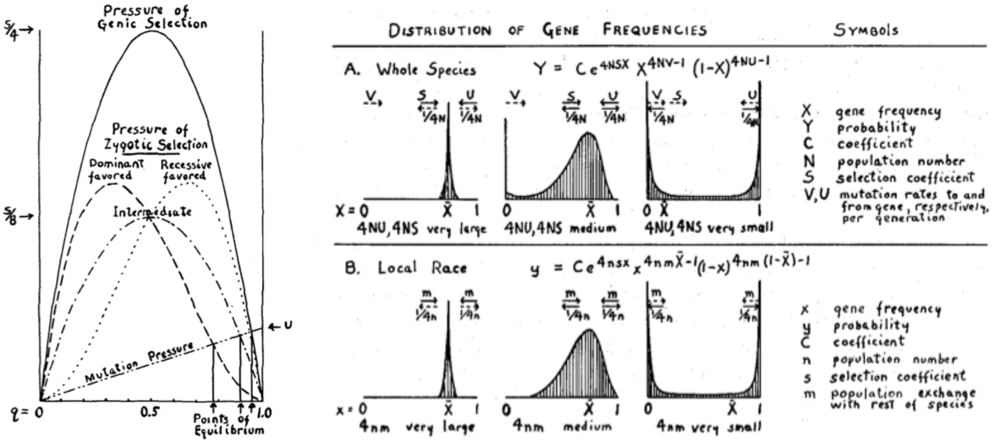

***Figure II.4.** Wright's graphs representing the two kinds of diallelic equations which were available and mathematically tractable in population genetics. **(a)** on the left, graph of a single-locus, diallelic case (Wright 1931, p. 104): selection and mutation pressures on a particular allele are function of its frequency* q *in the population; the frequency of fixation depends on an equilibrium between mutation and selection, and is different in a zygotic situation (and, within it, if the allele is dominant, recessive, or intermediate); the frequency of the alternative allele (or of the whole set of alternatives) is assumed to be* 1-q. ***(b)** on the right, frequency spectrums in different cases of mutation pressures, selection, and population size (Wright 1932, p. 359): each value for gene frequency* X *is supposed to capture a number of loci in the population that will reach that value at equilibrium.*

migration rate, population size,[94] and drift. Zygotic equations - limited to a single locus as well, but with selection acting on zygotes rather than on alleles[95] - allow to take into account the difference between recessive and dominant alleles and between heterozygotes and homozygotes (Fig. II.4.a).[96]

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[94] «There remains one factor of the greatest importance in understanding the evolution of a Mendelian system. This is the size of the population. The constancy of gene frequencies in the absence of selection, mutation or migration cannot for example be expected to be absolute in populations of limited size. Merely by chance one or the other of the allelomorphs may be expected to increase its frequency in a given generation and in time the proportions may drift a long way from the original values» (Wright 1932, p. 106). See also 1.2.

[95] Different values of s are assigned to heterozygotes (Aa) and to the two homozygotes (AA and aa). This displaces the point of equilibrium, and allows for example unfavoured, recessive alleles to stably remain in the population, explaining «a marked correlation in nature between recessiveness and deleterious effect» (Ivi, p. 103) and other laboratory observations.

[96] Dominance has a large effect on the dynamics of natural selection on alleles. E.g., unfavored or even lethal recessive alleles will have the chance to remain in the population carried by heterozygotes. The influence of selection on a single allele's frequency is more indirect: «There may be equilibrium between allelomorphs as a result wholly of selection, namely, selection against both homozygotes in favor of the heterozygous type» (Wright 1931, p. 102).

The way of treating simultaneosly all the loci in a population was to look at them as a collection of independent, diallelic loci, analyzing their "statistical situation" (Fig. II.4.b). Frequency spectrums[97] - whose charts were reported in Wright (1931) and copied in Wright (1932) - represent *how many* alleles are expected to come to a fixation for each value of q, and the modifying influence of selection and other factors on such a curve.

It was not that Wright considered diallelic equations satisfactory: the exact opposite, indeed. He gave warnings and methodological solutions to *the unbridgeable epistemological gap between statistical population genetics equations and Mendelian population as a space for which no mathematically tractable equation is available* (cf. Fig. II.3).

Wright observed, for example, that zygotic equations «quickly become complicated» (Wright 1931, p. 102), and not all the conceivable relations between the two alleles in the zygote can be easily modeled. He cited the "multiple series" of allelomorphs that were known in all the main experimental systems of the time, like guinea pigs and fruit flies, and he considered very likely that *all* series were potentially multiple. He knew that «each gene has a history which is not a mere oscillation between approximate fixation of two conditions» (p. 105), and that diallelic equations were a strong simplification.[98] However, including multiple alleles would have been too

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[97] Cf. e.g. Nielsen 2005, p. 202.

[98] For example, the presence of more than two alleles would require the model to decouple the complete loss of an allele and the homozygosis of the locus. Instead, «...it has been assumed for simplicity that each locus was represented by only two allelomorphs in the population in question and that either complete fixation or complete loss of a particular gene means homozygosis of all individuals with respect to the locus» (p. 110).

complicated, so these situations were methodologically reduced to the available diallelic equations.[99] Wright was also well aware - and, indeed, a supporter - of the modifying interactions among genes: he recognized[100] the limitation of considering each locus separately, but he brought forth diallelic equations as the best mathematical tools available and tractable. Frequency spectrums treated the whole combination (i.e. all loci simultaneously), but they were nothing more than statistical descriptions of a collection of independent, diallelic loci without any reference to interactions between genes, nor to *which* loci were likely to become fixed at a certain frequency. And they certainly did not go through (and tell anything about) gene *combinations*.[101]

Despite all such limitations of the available equations, the ambitious subject of Wright's 1932 paper was the whole space of Mendelian population: «If the entire field of possible gene combinations be graded with respect to

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[99] This was done by considering a gene with its frequency (q), and treating the group of all its alleles as a single, alternative allele with complementary frequency (1-q): «The effects of the various kinds of evolutionary pressure on the frequency of each gene may be treated as before by contrasting each gene with the totality of its allelomorphs» (Wright 1931, p. 105). The multiplicity of alleles was to be considered as the n-th cause influencing the variation of s (the selection pressure on the considered gene) which, in turn, was "modeled away" for mathematical simplicity by holding a fixed value of s (selection pressure). «The existence of multiple allelomorphs merely adds another cause of variation» (Ivi, p. 106).

[100] «It does not seem profitable - Wright had admitted in 1931 - to pursue this subject [the modifying interactions among genes] further for the purpose of the present paper, since in the general case, each selection coefficient is a complicated function of the entire system of gene frequencies and can only be dealt with qualitatively» (p. 102).

[101] A mathematical model of gene combinations should be able to calculate the fitness of a whole individual combination as a function of all its alleles, be capable to model what happens to fitness of a combination if we change individual alleles, and to model the effect of fitness on the production of new individual combinations over time. The mathematical and computational tools that would allow to build such a model never existed. These limitations were shared - as Provine (1986) pointed out - with all the other major authorities of the field, above all Fisher (1930).

adaptive value under a particular set of conditions, what would be its nature?» (Wright 1932, p. 357). The central part of the paper «consider[ed] briefly the situation with respect to a single locus» (p. 359), thus laying down on the table the mathematics that was actually available, and which I have briefly summarized above. But *equations and space, based respectively on frequencies and combinations, are - I argued - separated by an uncrossable epistemological gap.*

1.4 If only the entire field of possible gene combinations...

My claim is that there was, in fact, *no* math behind Wright's landscape. There is an epistemological gap between equations and space: population genetics equations were (and are) statistical equations of what happens to one, two loci in a population inhabiting an oversimplified diallelic Mendelian population space. Above all, *equations work with frequencies, not with combinations*.

Nonetheless, many times in literature the adaptive landscape metaphor is said to «refer to population genetics models», where with "models" the authors evidently intend the complicated equations of population genetics. To call equations "models" would not be necessarily wrong (section 3 examines some criteria for identifying a model). However, there is evidence of a generalized missing of the fact that Mendelian population space is *the* specific model the adaptive surface is metaphor for. Mendelian population is certainly not one among the many, ordinary mathematical tools in population genetics. Therefore, at present I think that *calling both equations and Mendelian population "models" does nothing but hide the epistemological gap that separates the space from* *the statistical equations referring to it*. For this reason, my pragmatic proposal relative to this debate will be (in sect. 3) to drop the term "models" for equations, saving the term model to point at the Mendelian combination space equations are about (exemplified in section 1.3).

There would be many examples of the errors induced by the ambiguous comfort given by the term model.[102]

In what follows, I add fitness (cf. 2.1) and mechanisms of movement (cf. 2.2) to Mendelian population combination space, making it exceedingly complex but also recalling situations that can be (and are) handled by mathematical equations, although in much more simplified situations. As I show in section 2.4 - *mathematics was not* the way Wright arrived to his conclusions about Mendelian population. His mathematical equations were *among* his inspirations to *guess* the properties of Mendelian population. However, a misconceived assumption in literature is that Wright *had* some sort of computable mathematical model of a Mendelian population underlying his adaptive landscape, perhaps a kind of very complicated derivation from population genetics models like those in 2.3. But neither he nor anyone after him ever had such a model: only qualitative appraisals are available for Mendelian population as such. William Provine (1986) argued that Sewall Wright, together with Ronald Fisher and others, omitted explaining the limitations of quantitative derivations «at the crucial stage of advancing beyond the strictly formal models to discussions of evolution in

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[102] Some examples are given at the very beginning of this chapter.

nature» (p. 280).[103] For Provine, the clear-cut line between two grounds of work - quantitative, mathematically tractable equations, and qualitative reflections on the model - was not adequately flagged by Wright and the other architects of population genetics. This might have been the origin of the misconception, but I believe that its perpetuation may be due to a non-pragmatic and non-practical use of the term "model" in philosophy and theory, grouping space and equations under the same flag. Refer to section 3 for a defense of a still liberal, but *pragmatic*, approach to models in philosophy of science.

2. Adaptive landscape for Mendelian population

2.1 Enter adaptive value

In section 1.2, I reported that Wright, at the outset of his 1932 paper, imagined the parameters of a Mendelian population proximate to living populations, with 1000 loci and 10 alleles per locus. After that, Wright posed the question quoted at the beginning of section 1:

> If the entire field of possible gene combinations *be graded with respect to adaptive value under a particular set of conditions*, what would be its nature? (Wright 1932, p. 357, my emphasis).

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[103] Provine also argues that several antagonisms to population genetics would have been avoided if «Fisher, Wright, and Haldane [...] had discussed more frankly and fully the limitations of their quantitative analyses and the precise relations of these analyses to their qualitative theories of evolution» (Ibid.). Is this observation limiting towards the thesis I argued for in I.3 about the role of adaptive landscape in MS?

Now I want to stress analogies between Mendelian population and the generally intended adaptive landscape, presented in I.1. The combination space (Mendelian population) exhibits the feature of "virtuality" seen for adaptive landscapes at the beginning of my work (sect. I.1.2): the system called "population" is the partial and dynamically changing realization of the time-independent space. And Mendelian population has features related to environment and adaptation that are strongly analogous to the others seen for adaptive surfaces (sections I.1.1 and I.1.3).[104]

In section I.1.1, I described the adaptive surface as a picture *of something that lives in an environment*. Even if such environment is not directly portrayed in the picture ("no environment" feature, I.1.1) it is nonetheless extremely important because it influences the whole landscape. Each location on the surface represents a possibility ("virtuality", I.1.2) and there is *a single environment every possibility must confront with, getting its particular adaptive value* (I.1.3). The adaptive value of each possibility depends on the environment (which is invariable all the way around the picture) although more absolute and context-independent values, like complexity or perfection,[105] can be considered.

A Mendelian population is assumed to be placed in an environment. Every combination in the combination space is assumed to have an adaptive

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[104] The term "suface" lowers also the risk of confusion with real, natural landscapes, already pointed out in I.1.1, and more technically specified in II.2.3).

[105] Wright (1932) talked about «harmonious» combinations (e.g., p. 358). There are some landscapes used for speciation (III.2.3) for which "sterility" or "unviability" (independent from environment) are important. The most prominent example of an absolute idea of adaptedness is Richard Dawkins (I.2.3, III.1.3).

value *which is relative to* that environment. Environment is not represented directly in the system, but it influences the whole system altogether: it determines the adaptive value of each and every combination.

If I did a good job, it will be no surprise that *Mendelian population and adaptive surface have so much in common*. In this chapter indeed I am trying to argue for the tight relation between the two objects, at least at the origin of landscape surfaces in Sewall Wright's initial creative thought (1932). My view is that the adaptive surface must be seen - at least at its dawn - as a *metaphor for Mendelian population*.[106] And arguably good metaphors have much in common with what they are metaphor of.

A few more words on adaptive value in Mendelian population. As seen in 1.3, *population genetics equations* study the statistical situation of alleles *within* a population: they consider one or a few alleles at a time and, in doing it, they typically assign an adaptive value (or, better, a selection pressure) *to an allele*. But in the Mendelian population combination space single alleles *cannot* have adaptive values. As Sewall Wright had written in 1931:

> Selection, whether in mortality, mating or fecundity, *applies to the organism as a whole* and thus *to the effects of the entire gene system* rather than to single genes (Wright 1931, p. 101, my emphasis).

In a Mendelian population, an allele will probably be more favorable than its alternatives in some *combinations* and not others. Population genetics

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[106] For the definition of "metaphor for model" cf. I.5. For terminological consequences see here sect. 3.

equations that assign adaptive value to single alleles are, for Wright, *justified* simplifications:

> The selection coefficient for a gene is thus in general a function of the entire system of gene frequencies. As a first approximation, relating to a given population at a given moment, one may, however, assume a constant net selection coefficient for each gene (Ibidem).

In my view, ingenious and powerful methodological solutions by population geneticists do not fill the epistemological gap between equations and combination space (again, Fig. II.3). Rather, the gap is confirmed. In a population genetics equation, an allele can have an adaptive value. In the combination space, only full individual combinations can. And *the latter* is the system adaptive surfaces are metaphor of, at least in their original version.

2.2 Neighborhood, dimensionality, and movement in the combination space

Figure II.1 by Wright (1932) gives the idea of a Mendelian population as a combination space. What do *the lines* connecting the combinations represent? Two combinations which are connected by a line are, as it is often said in literature, *one-step neighbours*. That is, they differ by *one substitution* only. In other words, one combination of the couple can be obtained by *substituting one allele* in the other. The relation is symmetrical.

To better illustrate neighborhood relation and other concepts (dimensionality and movement) concerning combination space, I will now avail myself of the simple model diagram in Figure II.5, devised by Stuart A.

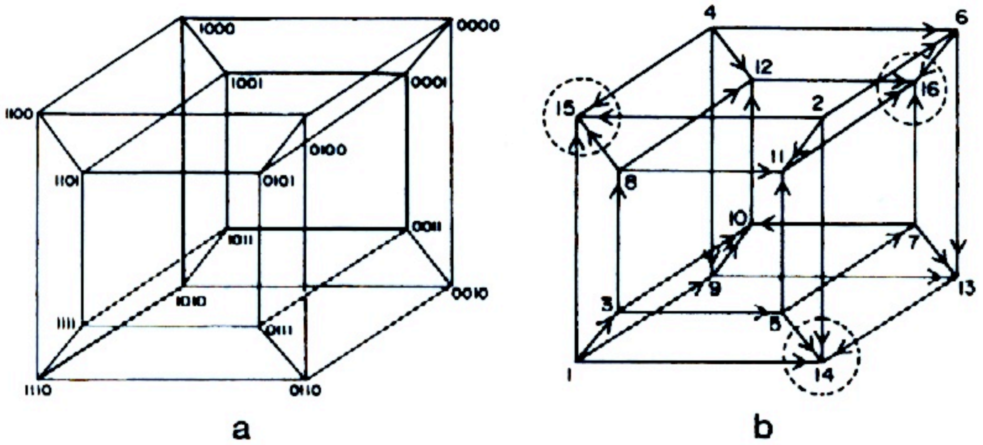

Figure II.5. (a) *Four binary-digit combination space represented as a hypercube, with lines connecting one-step neighbor "gene" combinations;* ***(b)*** *the same hypercube endowed with a fitness value for each "gene" combinations, with circled "local optima".*

Kauffman (1995). Kauffman's model is "haploid", so it is simpler than Mendelian populations where individual combinations have *two* alleles for each locus (diploidy) and this entails that one-step neighbors can be obtained by substituting one *or* the other of the alleles in any locus. Kauffman's model is anyway sufficient to illustrate the concepts of neighborhood and dimensionality, and moreover its notation is clearer than Wright's (Fig. II.2).

Figure II.5.a represents a combination space with four binary loci. It is analogous to a Mendelian population featuring four diallelic loci, where for all loci the available alleles are 0 and 1. There are sixteen combinations in such a space, and each combination *is one-step neighbour* to those from which it differs in only one of its four genes. For example, 0000 is neighbour to 0001, 0010, 0100, and 1000. Kauffman arranges combinations in a hypercube that shows by means of connecting lines all the *neighborhood* relations among them.[107]

Dimensionality, which is another general characteristic of combination space frequently evoked in literature, derives directly from neighborhood.[108] *Dimensionality of a combination space is equal to the number of one-step neighbours each combination has in the space*. With 4 diallelic genetic loci, dimensionality is 4, and a hypercube like Figure II.3.a is necessary for every combination to be graphically connected with its 4 neighbours. In a system with *many* alleles per locus, dimensionality (i.e. the number of one-step neighbours) increases exponentially, and graphical representation becomes more and more complicated. In 1988 Sewall Wright himself as an old man, looking back at the invention of adaptive landscapes under analysis here, wrote:

> The multidimensionality, both among and within loci, would seem to make any pictorial representation impossible. It would, indeed, seem practically impossible with as few as five pairs of alleles [32 haploid combinations] […]. For each of the 243 different diploid genotypes, the selective values should be exhibited [...]. An intelligible representation depends on some enormous simplification (Wright 1988, p. 116).[109]

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[107] Neighborhood becomes the unit for calculating distance between two points. The exact distance between two combinations will be the number of one-step substitution necessary to go from one to the other. This characteristic makes Mendelian combination space similar to a metric space (cf. Bryant 1985, Searcoid 2006).

[108] «The dimensionality of genotype space can be defined as the number of genotypes that can be obtained from a given genotype by changing single genes. In other words, this is the number of one-step neighbors of each genotype» (Gavrilets 2006, p. 27).

[109] This makes Wright's caption to Fig. II.1 more understandable: «...in two dimensions instead of many thousands».

Consider now Figure II.5.b, in which hypercube vertices (corresponding to the same sequences of Fig. II.5.a) are assigned *adaptive values*. It is now possible to compare neighbour combinations by their adaptive value (or fitness): an arrow is drawn on each neighborhood relation, pointing towards the higher-fitness combination.

Stuart Kauffman's work on "adaptive walks" (Kauffman & Levin 1987, Kauffman 1995, see also Kauffman 1989, 1993, 2000) gives me now the hook to talk about *movement* in the combination space, as anticipated in sections 1.2 and 2.1. As I wrote there, combination space has a "virtual" character: only a small part of the possible combinations is realized at a time, and such part changes through discrete time steps. In Kauffman's space, *only one* combination is realized at a time indeed. He programs computer simulations called "adaptive walks" that, starting from a combination chosen at random in the space, "explore" it by following a simple iterated algorythm: (1) randomly choose a one-step neighbour; (2) if the chosen combination's fitness is higher than the present, move there (i.e. release this combination and realize that one), otherwise, stay; (3) start again from 1. In Figure II.3.b, an adaptive walk would follow the directions of the arrows until it reaches one of the circled vertices, where it will stop.[110] Circled vertices are indeed "local

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[110] If adaptive walks end on a local optimum which is not *the global* optimum (i.e. the combination with the highest fitness in the space) it is often said that they "get stuck". This is a debated theoretical problem, and there is a huge literature in diverse fields about complex and reliable *optimization algorythms*. Occasional random mutation in the present model - i.e. one extra gene changing from 0 to 1 or vice versa by chance - can be seen as a possible part of the solution to the problem, resuming a stuck adaptive walk (cf. Orzack & Sober 2001) .

optima", i.e. those combinations whose adaptive value is the highest compared with each neighbour's value.

Although generically sharing "virtuality", Kauffman's space is different from Mendelian population for what concerns the rules of movement. In Mendelian population *a number N*, however relatively small, of combinations is realized at a time.[111] Individuals "sexually reproduce" and give birth to a subsequent generation in which N new combinations are realized, assembled through random *recombination* of previous generation's combinations. The two spaces of course differ also by dimensionality: as already noticed - by Wright himself in my 1988 quotation - the dimensionality of a Mendelian population is so high that an endeavour of visualizing neighbourhood relationships would not be conceivable.

Now all is set for me to tackle the solution Wright envisaged in 1932 for overcoming this problem.

2.3 A surface for a space

Wright was invited to the 6th Congress of Genetics by E.M. East, his doctoral supervisor. He was asked to participate in a forum with the other two great theorists R.A. Fisher and J.B.S. Haldane, and - importantly - to keep his

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[111] «...the population in which an elementary evolutionary process is to be illustrated must be indicated in some way, as by encircling the genotypes that are supposed to be the most abundant» (Wright 1988, p. 116). The quotation is taken from the same block as the previous, on the difficulty of graphically representing multidimensional spaces. I think the quotation shows, on the one hand, Wright's graphical imagination at work and, on the other hand, his population genetics view that does not really strive to handle the whole Mendelian population: 5 loci represent, in any case, only a tiny part of the genotype in the ideal Mendelian population; accordingly, combinations are not unique, they are in copies, they have a frequency, they have to be treated statistically.

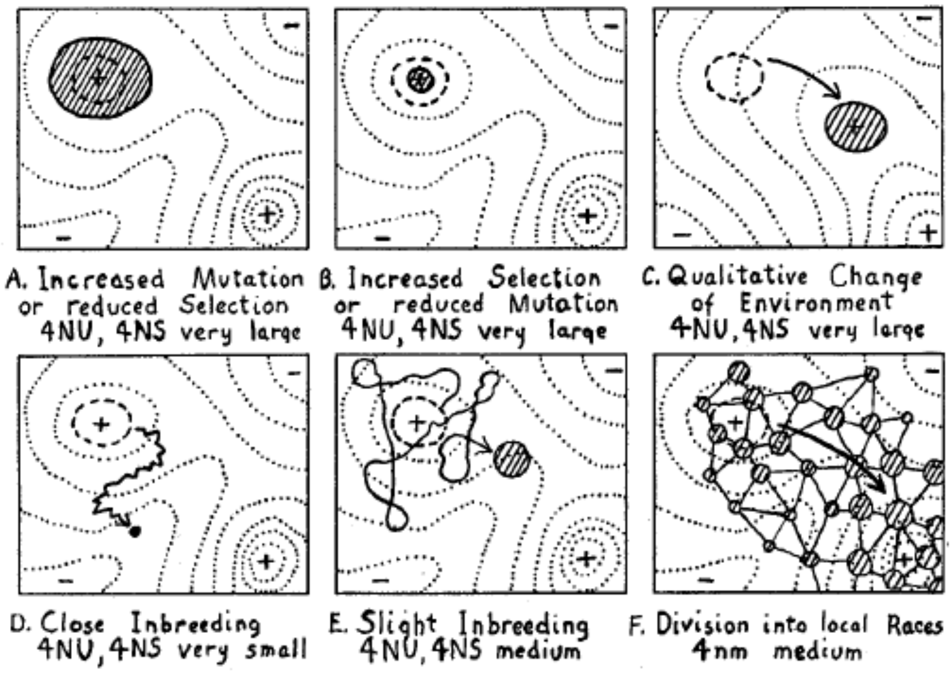

Figure II.6. *Possible courses on Wright's adaptive surface, depending on demography (number of individuals, spatial subdivision) and genetics (number of loci, number of alleles, topography of the landscape) of the population, as well as on selection pressures, on the environment influencing fitness of genotypes, and on the (extremely low) rate of viable mutations that modify the topography. The circular dotted line is the initial boundary of the population (Wright 1932).*

presentation short and simple. It was then that he conceived (and then showed) Figure II.2: Wright's adaptive landscape, the first, the original.

Figure II.2 is, in Sewall Wright's words, a «diagrammatic representation» of «the entire field of possible gene combinations [...] graded with respect to adaptive value under a particular set of conditions» (1932, pp. 357-358). If my analysis is correct, "the entire field of possible gene combinations" concides with Mendelian population (see sect. 1), and the "particular set of conditions" designates the environment where the population "lives", influencing simultaneously the adaptive values of each and every genetic combination (see 2.1).

Figure II.6 (Wright 1932, p. 361) is the use of the *static* diagrammatic representation of Fig. II.2 to show the *dynamics* happening in the «field of possible gene combinations». At any time, only a part of the combination space is actually realized in the much larger combination space: i.e. a *population* of N individuals vs. the "Mendelian population". In each case except F,[112] the dotted empty circle represents the initial population and the filled circle represents the population in a subsequent time. Cases A and B show a population remaining on a peak, with an increase (A) or decrease (B) of genetic diversity due to a changed balance between selection pressure and mutation rate; there is also a corresponding decrease (A) or increase (B) of mean adaptive value; case C shows a population tracking a peak which is moving due to environmental change (and consequent change of adaptive values in the unchanged combination space); cases D and E show that a reduction of population size N (= increased inbreeding)[113] determines an increase in the incidence of chance, bringing to non-adaptive random wandering (E) with a low likelihood of reaching a new peak, or even to a high probability of extinction in the bottom of an adaptive valley (D); case F shows the simultaneous realization of clusters of combinations ("local races") in

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[112] F is, for Wright, the most likely normal condition for natural populations. The idea relates to Wright's "shifting balance" theory, i.e. «the trial and error mechanism» likely to «solve "the problem of evolution"», cf. III.3.

[113] As Wright often remarks, no matter how high the degree of inbreeding, the possibility of the chance appearance of two identical genotypes is practically 0.

many spots of the combination space,[114] with limited inter-racial reproduction.

With all the concepts and distinctions introduced in this chapter, understanding Wright's captions should be straightforward. Conversely, I think, understanding Wright's picture *would not be straightforward at all without a comprehension* of Mendelian population, as distinct from population genetics equations, along with all the related concepts. Lastly - and I think this would be a guideline for philosophical and theoretical literature on adaptive landscapes - *disagreements or different catches of the terms* hereto exposed would result in largely, often implicitly different intepretations of the adaptive *surface*.

The surface is a metaphor of the space of Mendelian population, so it is ideally constituted by points that stand for whole individual genetic combinations. Now, there is an assumption about the surface that was left

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[114] See previous footnote. This is, I believe, a point with a *high risk of conflation*, leading astray to a logical *inversion* of the whole interpretation of the landscape in a geographical - and *only secondarily* genotypical - key (vs. I.1.1, "no environment" characteristic). Yes, geographical subdivision is - in Wright's view - likely to *cause* a clustering in the genotype space: small, isolated groups with limited interbreeding will drift to different areas of the combination space. *But*, wait, *only if* groups continue to be exposed to *the same environment* (or, to environments that are identical in all aspects relevant to fitness) they can be still depicted together on the same surface (i.e., be part of the same adaptive space). Moreover, *also without* geographical disjuction, some clustering in the genotype space can be imagined, e.g., by the subdivision in land-sharing tribes found in some animals (but many other examples could be thought of). In sum, talk of "local races" may induce the idea that subdivision on the metaphorical adaptive surface *requires* (inversion) and even *is* (conflation) geographical subdivision. It doesn't, and it isn't. Indeed, clustering can happen, in principle, without geographical departure, and this in turn may *break* the landscape by exposing groups to different environments (yielding different adaptive peaks and valleys). Some authors - like Dobzhansky (III.1.1) with his "global" landscape - seem to have missed the point.

somehow implicit in Wright's 1932 paper.[115] I put forth the assumption by means of retrospect words by Wright himself (1988):

> In Figure [II.2], it is assumed that the genotypes are packed, side by side [...] in such a way that each is surrounded by genotypes that differ by only one gene replacement (Wright 1988, p. 117, my emphasis).

For both "Wrights" (1932, 1988) and for our understanding it is fundamental to get the assumption: the surface is supposed to be structured in such a way that points representing *neighbour* combinations in space (cf. 2.2) *are contiguous* to each other on the surface.

The relationship between neighborhood in the space and contiguity on the surface brings out three issues I want to remark. One is a frequent criticism to adaptive surfaces which I will name the "impossible packing" objection. The second is that the organized *continuity* of the surface doesn't come for free: for the surface to be continuous (*sensu* Lewontin 1985a, Godfrey-Smith 2009) contiguity must go along with slight differences in adaptive value, but contiguity depends on *neighborhood* among genetic combinations in the space, and neighborhood is, in principle, unrelated to adaptation. Third, *movement* "on" the surface doesn't come for free either: mechanisms for movement are needed, and they reside in the "metaphorized" system, not on the surface.

The "impossible packing" objection. I wrote that in reading Wright's paper (1932) it seems intuitively obvious that proximity relations are preserved in the

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[115] I think that Wright's silence on this assumption in 1932 can be explained by the fact that he presented the surface as a natural development of combination space (Fig. II.1) and it seemed intuitively obvious that proximity relations are preserved.

transition from combination space to surface. This is not exact, or at least what seems intuitively obvious can be revealed wrong. One of the most iterated criticisms to the adaptive surface is that it would be impossible to "pack" a space with thousands dimensions in only two, preserving their neighorhood relations. Kaplan (2008), for example, explains: «The problem [...] is that this compression misrepresents the distances between most of the genotypes - accurate representations of distance cannot survive the packing of many dimensions into a few» (p. 630). Pigliucci (2008) writes: «there is no metric that allows one to "pack" genotypes side-by-side» (p. 593).[116] Sewall Wright was actually in agreement with the "impossible packing" objection: «The two dimensions […] are a very inadequate representation of such a field» (Wright 1932, pp. 356-357), and a surface picture «cannot accurately represent relations that are multidimensional» (Wright 1988, p. 116). But, while he would probably have considered it a killer objection for a geometrical model, he shielded the surface picture by declaring the latter «useless for mathematical purposes» (Ibidem). The surface is not to be considered a point-by-point map of the combination space: it captures and displays some general

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[116] A less frequent criticism, which I see as the exact opposite, could be called the "apparent continuity" objection: the surface is made of discrete points, so it is «dense but fractioned, not continuous». But it *looks* continuous due to the acknowledged high density. More than an impossible, it seems then a "hard but well done" packing, so a funny name for this criticism would be the "too good packing" objection. Pigliucci (2008) sees the apparent continuity as a risk for interpretation: it «may induce a modern reader to think that it is analogous to most modern representations, where the non-fitness axes are gene frequencies» (p. 593). In the next paragraph on "continuity of the surface", the term "continuity" is used with a slightly different meaning - more rigorously coded in literature: see below and Lewontin (1985a), Godfrey-Smith (2009).

features of the space. It is, indeed, a *metaphor* of it.[117] If this view answers the "impossible packing" objection, I don't think it eliminates the need for a general, qualitative (if not point-by-point) reflection on the following two points: contiguity and movement on the surface.

Continuity of the surface doesn't come for free. Several times throughout this work I declared adaptation (or fitness) as the central organizing principle of adaptive landscapes (cf. section I.1.3).[118] My analysis of Wright's adaptive surface, however, brought to light another equally determinant organizing principle: neighborhood (2.2). Adaptive values of gene combinations[119] certainly influence the shape of the surface by determining *the elevation*, we may say the "vertical position" of its points. But *the "horizontal" position of such points on the surface* is determined by neighborhood among gene combinations in the (not visualized) combination space. Adaptive values depend on the environment, neighborhood relations do not: they are engrained in the structure of the combination space.

To appreciate the concurrence and reciprocal independence of the two organizing principles, I think it would be useful to imagine a visual animation

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[117] Kaplan (2008), like others, accepts Wright's defense of metaphor in general, but then he criticizes this particular metaphor as poor and misleading in respect to the complexity of the space it represents. My observations hereafter about the metaphor hiding important elements are, I think, in consonance with Kaplan's view. Other authors (e.g. Gavrilets 1997, 2004) accept Wright's idea of metaphors *and* the clarity of this particular metaphor, but think that its messages are *wrong*, i.e. that the genotype space is not like Wright thought. On the messages conveyed by the adaptive surface metaphor see 2.4.

[118] The claim was used in particular when considering the scope of adaptive landscapes in Dobzhansky, Simpson, and Dawkins (sect. I.2), where the centrality of adaptation in the adaptive landscape was seen as an argument for seeing it as "big picture" evolution in views that see adaptation as central *to evolution* too.

[119] Values are relative to the non-represented environment, see I.1.1 and 2.1.

of a process in which the adaptive surface is built *by aggregation* of points: the points representing all the gene combinations in the Mendelian population come in a scrambled ordered cloud, then they aggregate on a horizontal plane with the criterion that each combination must be «surrounded by genotypes that differ by only one gene replacement» (Wright 1988, p. 117); in other words, they aggregate using neighorhood as a criterion; *then* each point is elevated to its vertical position which is preventively fixed by its adaptive value. Here it is: our adaptive surface. But imagine that, unexpectedly, in many spots of the surface contiguous points are thrusted to dramatically different elevations. This would be perfectly possible because elevation depends on an organizing principle - adaptation - which is different and independent from the principle determining that the two points are contiguous - neighborhood. Normally, we assume that neighbour combinations, differing by only one substitution, are similar in fitness, too. But here is what it is, in fact, *an assumption*. If, for example, we imagine a combination space in which changing an allele has always (or normally) a dramatic effect on fitness, we will obtain a rather unfamiliar surface.

Now, here is something the adaptive surface metaphor hides: in natural landscapes, like the one in Figure I.1, *we know* that contiguous points differ infinitesimally in elevation. Horizontal contiguity *entails* vertical contiguity, there. On the adaptive surface, this characteristic - called “continuity” by Lewontin (1985a) and taken up by Godfrey-Smith (2009)[120] - doesn’t come for free: it *requires an extra assumption, i.e. that neighbour combinations always have*

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[120] See especially section 3.5 (pp. 57-59).

similar adaptive value.[121] The adaptive surface metaphor, in sum, induces the conflation of two shaping principles (again, neighborhood and adaptation) and in doing so it hides that, in order to obtain a surface with a certain shape, an extra assumption (called "continuity") is required (and Wright had it, see 2.4).

Movement doesn't come for free. Rules for movement are another structural aspect the adaptive surface metaphor conceals or, at least, misleadingly simplifies. Rules for a walk in a natural landscape are evident by the land itself: to begin with, if we are climbing a mountain we will want to go up as much as possible; there will be trails, and easy passages we can walk through; there will also be dangerous or difficult areas we will try to avoid. Movement, in sum, is largely constrained and ruled by terrain. This is not true for populations on adaptive surfaces, because *rules and constraints for movement reside elsewhere, i.e. in the combination space*. Moreover, linguistic expressions suggesting that a population moves "on" the adaptive landscape can be misleading:[122] *a population does not move* on *the landscape, a population* is *the realization of parts of the landscape*, changing through time. Instead of a person, or a group of hikers, choosing where to move their steps and climbing on the landscape's peaks, the population should be visualized as a series of clouds of points (one for each generation) appearing on the surface according to rules of

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[121] Note that Dobzhansky (1937), in presenting his landscape, specified in passing that «related gene combinations are, on the whole, similar in adaptive value» (p. 8).

[122] Unfortunately, these include nice expressions like «a population [...] sits on an adaptive peak» (Pigliucci 2008, p. 595).

the combination space. At every generation, new points will appear on the surface, replacing those of the previous generation.

In a Mendelian population each new individual originates from two parent combinations by allele recombination, therefore new points will usually appear in proximity of the pre-existing cloud or somewhere inside the cloud, the individuals being genetically intermediate between the two parents.[123] That is why, I think, the cloud can supposedly be concentrated in a limited area of the surface like, e.g., the area surrounding a peak. A phenomenon on the adaptive surface I would call “cloud cohesion” is, then, due to the reproductive mechanism. Such mechanisms, of which there is no evident trace on the surface, explain why points representing individuals are not scattered all the way around through the adaptive surface as one might imagine (excluding, of course, valleys).

As early population geneticists established (e.g. Wright 1931), several factors influence change in the genetic composition of the population through time - and, as a consequence, movement of the cloud on the surface. Selection pressure, for example, is one of those factors, favoring the survival of individuals with relatively high fitness. By definition, selection interacts with fitness in affecting the direction of change: in presence of a selective pressure *and* of suitable fitness difference *and* of suitable population size, gene combinations will be biased towards higher fitness values, and the cloud will be seen “climbing” a neighbouring relief on the surface. Mutation, and drift

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[123] This observation is important for Gavrilets’s extension of the Bateson-Dobzhansky-Muller model (BDM), formalizing reproductive barriers as genetic incompatibilities (cf. III. 2.3).

(resulting in part from Mendelian random recombination) will oppose selection, preventing the population to gather too tight at the top of a peak,[124] and making the cloud "pulsate" back and forth in the surrounding area.

Population size, environment, mutation pressure, drift, allele frequency, selection pressure and many others are the factors that shape movements of the population in its space of possibilities (and thus on the adaptive surface). Sometimes populations "climb", pushed to "go up", but it is not necessarily so. Movement is a product of a balance of factors.

The metaphor shows, the metaphor hides. It hides the necessity of an assumption for continuity, and of mechanisms of movement that, in a natural landscape, come for free. What the metaphor *shows* is the topic of next section.

2.4 What did the surface tell about the space and how did Wright know

Throughout all this chapter I argued for viewing the adaptive surface (as I want to call it) introduced by Sewall Wright (1932) as a metaphor for Mendelian population, seen in turn as a combination space (1.2) with high dimensionality (2.2). The metaphor tells that the combination space is "as if" it had many peaks and valleys. In this section I briefly point out what properties of the combination space this image should reveal, and most importantly how did Wright arrive to such revelations.

There is in my view - today as in Wright's times - an epistemological discontinuity, an unbridgeable gap between equations and space (Fig. II.3).

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[124] As Gavrilets writes (2004, p. 103), "tips" are largely irrelevant, see III.3.1.

Mendelian population is about gene combinations (with many loci and alleles), whereas population genetics equations are about allele frequency in one or a few diallelic loci. There is, in sum, no mathematical model of Mendelian population as a whole, although the system can be approached statistically and piecemeal. Now, Sewall Wright's job was to create, refine, and perfection population genetics models (cf. 1931), hence the question: *how did Wright know what he knew about the genetic space?* Where did Wright get the features he wanted to deliver with his adaptive surface metaphor? This seems an epistemologically interesting theme, and represents a further focus of this section.

> If the entire field of possible gene combinations be graded with respect to adaptive value under a particular set of conditions, *what would be its nature?* (Wright 1932, p. 357, my emphasis).

The question, appearing at the beginning of Wright's 1932 paper, may seem rethorical but has to be read, in my view, as a genuine one. The answer about the static structure of the space was not going to come from the available mathematical equations, so it demanded an effort to transcend the state-of-the-art single-locus, diallelic equations Wright had exposed just a year before (Wright 1931). I think he strived to bridge the gap by means of his limited *laboratory experiences*, *intuition* and *heuristic rules*.

In section 1.4, I reported a criticism William Provine (1986) made to Wright and Fisher. According to Provine, they didn't do enough to mark the boundary between conclusions of their quantitative models and their qualitative reflections. I translated Provine's criticism, seeing such boundary as the one between population genetics equations and the mathematically intractable Mendelian population. In 1.4, I agreed with Provine because of a perceived obscurity-effect in the literature. In Wright's 1932 paper the marks of intuition *may* in fact be found, yet in the form of just clues, and only in the first part.

Suggesting the depart from diallelic models, for example, Wright specified that, «presumably» and «reasonably», numerous alleles for each locus are present in a species (1932, p. 356). The estimate number of possible combinations being greater than «the total number of electrons and protons in the whole visible universe» by a magnitude order, Wright tried to guess - I think this is the appropriate word - the number of peaks in the combination space. He saw «one possibility» of assuming the presence of a single peak (p. 357), an idea that was defended by Fisher (cf. Provine 1986). But he also observed: «*it is possible* that there *may* be two peaks, and the chance that this may be the case greatly increases with each additional locus» (p. 358, my emphasis).

The presence of multiple peaks was - I argue - one of Wright's intuitive attributions to the combination space. As Anya Plutynski pointed out (2005b, p. 600), «Wright had been a laboratory scientist before he turned to the problem of mathematical population genetics. He used guinea pigs as a model system to investigate the inheritance of coat color in mammals». In his experience, traits like coat color resulted from the interaction among several loci, and several, separate combinations of alleles were most favorable among all the others in between. Wright's limited laboratory observations had influenced his intuition about evolution, where «highly adapted systems of genes [...] become dissociated and [...] reform into a new, more favorable combination» (Ibidem). When Wright introduced the peak shifting problem (see III.3.2), he observed that, besides the peak the population is kept upon by selection, «there *may* be innumerable other peaks which are higher but which are separated by "valleys"» (1932, p. 358, my emphasis).

Epistasis was - I argue - another characteristic of the combination space which was due to Wright's intuition, shaped by his experiences. Lab work had «forced him to think not only about genes as simple factors, but the physiology of genetics: how genes were expressed and interrelated» (Plutynski 2005b, p. 600). The genome-wide interaction between genes implied, for Wright, that no privileged loci or alleles can, alone, impact fitness in a significant way. Due to epistasis, no single substitution can have dramatic fitness effect. Accordingly, similar combinations will always be close in fitness, and the landscape will feature smooth reliefs (*continuity*, cf. 2.3) rather than canyons or ridges.[125] The influence of Wright's convictions coming from his laboratory experiences contributed in shaping his intuition in the wading from quantitative models to qualitative reflections and the imaginary model we are considering.

The central part of Wright's 1932 paper «consider[ed] briefly the situation with respect to a single locus» (p. 359), thus bringing to the table available population genetics equations results (cf. 1.3 and Fig. II.4). But from

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[125] An assumption explicited by also by Dobzhansky (1937, p. 8). See 2.3.

there, Wright turned again «to the field of gene combinations» (p. 360) and tried to intuitively extrapolate the results of diallelic equations to the whole genetic space, and, yes, I am not able here to find warnings by Wright that he is using intuition. It could be argued that such warnings would have been important, if we consider that Wright was speaking to a heterogeneous audience of biologists, and that - as Provine puts it - even «most geneticists at that time had so little preparation in quantitative analysis that Wright's [1931] paper took a mystical tinge» (1986, p. 277).[126] Perhaps the line between mathematical treatments and intuitive, qualitative reasoning should have been drawn more clearly when Wright finally proposed shifting balance as a solution for the peak shifting problem (III.3.2), and speculated about conditions to be found in nature. The extrapolation is (intuitively) convincing, but there is no actual mathematics allowing calculations.

I have argued, with Plutynski and Provine, that Wright's laboratory experiences influenced his intuition in bridging the gap from diallelic models to an imagined model of the whole genetic space. I think that a careful analysis of this "leap" would also reveal Wright's prolonged use of *heuristic rules* that were already at work - with successful results - in his mathematical workings. These rules have to do, I guess, with the extrapolation from simple to increasingly complicated mathematics.[127]

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[126] «No other geneticist in the United States had the quantitative and biological background to even attempt such analysis; thus Wright's paper was immediately viewed by geneticists as a major achievement» (1986, p. 277), and «few geneticists worked their way through all of the mathematics» (p. 278).

[127] Could Wright's calculation of the number (!) of peaks result from these procedures?

The concept of heuristics in science was analyzed by philosopher William Wimsatt (e.g. 1985, 1997, 2006, 2007a, b), who took advantage of elaborations in the fields of artificial intelligence and cognitive psychology (works by Herbert Simon and others). For Wimsatt heuristic procedures, or heuristics, have four important properties (1986, pp. 76-77).[128] I cite them, though not conserving order, because I think that they apply well to Wright's case.

First, *heuristics are cost-effective* «in terms of demands on memory, computation, or other resources in limited supply» (p. 76). The model of a whole Mendelian population space is a desperate case of limited resources: still today, after 80 years, no machine has the computational capacities to even approach the suitable huge dimensionality and number of combinations of Wright's space, and no formal system is able to handle and analyze a population in that space.[129] Yet, in this desperate situation probably Wright stuck to some rules that, in much more limited cases in his experience of

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[128] Also: Wimsatt (2007) pp. 345-346; Griesemer & Wimsatt (1989) pp. 98-101.

[129] Take, for example, one of the most recent and established handbooks in population genetics (Hartl & Clark 2007): «The presence of multiple alleles complicates the analysis» (p. 223), creating «surprising situations» (p. 224) and difficulties in modeling. When modelers try to take epistasis into account, «complications abound» (p. 240), even among few loci. Where possible, models are reconducted to a single-locus type by considering a "type of gamete" (e.g. a combination of alleles) as a single allele (p. 239). The use of a landscape picture - called «adaptive topography» - to visualize the mean fitness of the population (ϖ) as «a function of the allele frequencies at many loci» (p. 225) is evidently far from Wright's original idea (see section 1), and reflects - I think - the enduring untractability of Wright's model of the genotype space. Aswill be seen in the next chapter, Gavrilets's high-dimensional analyses establish very general characteristics of the genotype space, but then his "spontaneous clusterization" models in stage two of analysis are low-dimensional. To date, Stuart Kauffman's (1993) formal models are those that handle the highest number of genetic dimensions: up to 24 - still very far from the thousands dimensions (and dozens of alleles per each) of a Mendelian population.

lower-dimensional mathematical modeling, had economized resources and yielded good results.

Second, *heuristics make no guarantees* «that they will produce a solution or the correct solution to a problem». In this respect, heuristics differ from «truth-preserving algorithms», where results exactly follow from axioms. The case of the link between "single-locus diallelic models" to "all-loci frequency spectrums" (Fig. II.4) seems to me as a truth-preserving algorithmic one. Wright's leap to the combination space certainly not.

Third, *the cases where heuristics break down are not random*. The errors produced using a heuristic happen in a systematic direction and in certain classes of cases and not in others. I don't know how the direction of errors could be conceptualized in Wright's leap to the combination space, but certainly there was some error (III.3), and I firmly think Sergey Gavrilets is speaking about a heuristic breakdown when he frequently states that «Properties of multidimensional adaptive landscapes are very different from those of low dimension» (e.g. 1997, p. 307).[130]

Fourth, «The application of a heuristic to a problem yields a transformation of the problem into a nonequivalent but intuitively related problem. Most important this means that answers to the transformed problem may not be answers to the original problem» (Wimsatt 1986, p. 77). Some authors have argued that the landscape picture has transformed a

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[130] However, I am not sure if I agree with Gavrilets when he seems to argue that the heuristic rules that break down come from our experience in a three-dimensional world. Rather, I would encourage Gavrilets to think to heuristic rules for the extrapolation from one locus, to more loci, to many loci (where multidimensionality comes out), and see where and how they break down.

mathematical problem into a visual one.[131] This is not the kind of transformation at issue here, since we are dealing with the passage from population genetics equations to combination space. A deeper formal analysis would probably reveal important discontinuities in such a transformation: the one I can figure out is the passage from problems of allele frequency to problems of allele *combinations*.

Wimsatt mostly studied heuristics in the context of *reduction*, i.e. in cases where «we don't have lower-level description of higher-level systems» (1976a, b, 1979, 1980b, 1997b, 2000, 2006, 2007a, b pp. 347-352).[132] In Wright's case the "direction" of heuristics seems to be opposite, as we do have lower-level descriptions of gene frequencies, and want to extrapolate from there the higher-level system. Following again Wimsatt (2007a, upon Levins 1970), Wright's heuristics go perhaps in the direction of a "composed system", "engineered" from its lower-level parts.

My use of heuristics, I guess, is completely different from Skipper's (2004) who sees the landscape diagram as a «theory evaluation heuristics» (p. 1176). In my use of it - and in Wimsatt's, at least for what concerns the points

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[131] I agree with this point for what concerns the migrant metaphor, and its effect of transformation onto evolutionary biology. Not about the native.

[132] Although reductionist heuristics do not apply here, they would apply very well to an analysis of the previous stage in Wright's work: to yield mathematically tractable, single-locus and diallelic models, simplifications and assumptions were needed everywere (Wright 1931). About selection pressure, for example, Wright clearly recognized that «Selection [...] applies to the organism as a whole and thus to the effects of the entire gene system rather than to single genes. A gene which is more favorable than its allelomorph in one combination may be less favorable in another... The selection coefficient for a gene is thus in general a function of the entire system of gene frequencies. As a first approximation, relating to a given population at a given moment, one may, however, assume a constant net selection coefficient for each gene» (1931, p. 101).

reported here - heuristics are cost-effective algorithmic procedures that make no guarantees of the solutions they yield: they systematically break down in face of particular challenges (e.g. too many dimensions?) and transform problems in different, but intuitively related, problems. With this definition, I don't think that the landscape diagram can be considered a heuristic, least of all for theory evaluation: rather, it is the graphical visualization *that owes* its existence to heuristics that from single-locus, diallelic models help to work out the "composed system" which is the whole genetic space. Those heuristics are, more than a tool for evaluating, something that *needs* evaluation.[133]

We should not be misguided by the lack of explicit warnings: Wright attempted to guess the properties of the whole space of Mendelian population, by using his single-locus diallelic equations, intuition, limited laboratory experiences, and probably heuristic procedures. Wright conveyed these properties through the adaptive surface metaphor, a smooth landscape with many peaks and valleys. What does the metaphor say on the genetic space? It says that there are massive epistatic interactions among genetic loci, and they result in a smooth and graded distribution of fitness, since similar genotypes probably[134] differ slightly in fitness; also, there are many "favorable", "harmonious" combinations in the genotype space, and the population can somehow reach them through adaptive evolution.

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[133] In III.3 I consider a case where new mathematical analyses substitute heuristics.

[134] Again, this is the "continuity" assumption (Lewontin 1985a, Godfrey-Smith 2009, cf. 2.3).

3. Models and adaptive landscapes

3.1 A pragmatic approach to models for the philosopher of biology

Models are a relatively late object of study of philosophy of science, but a huge literature on them is now growing. Although general philosophical issues continuously rise from models, literature is mainly case-based - the present section of course isn't an exception. Cases often come from sciences outside biology (mainly, physics and economics), but in philosophy of biology, too - after a boom of interest in models with the "semantic view of theories" in the '80s - more and more works focus on the importance of models in theorizing. Several accounts (e.g. Downes 1992, Godfrey-Smith 2008, Thomson-Jones working paper) have shown that such movement of extension yielded in fact a multiplicity of notions of model.

In earlier versions of my work I had acritically assumed that, if Sewall Wright's 1932 idea could be split in a formal and a pictorial part, the former would have been the "true" model, with the picture relegated to an ancillary role. I assumed that the idea of a model required something more than a "simple picture", which I defined simply as «a chart derived through a mapping function from a population genetics mathematical model», «like a bell curve». For the same reasons I criticized the picture's migration to other contexts of research where it was used as a metaphor of something else: «this is an improper use of a chart - I wrote - just like if we were impressed by a bell curve, finding it physically resemblant to a phenomenon or situation of our interest, and begin reasoning upon the latter phenomenon calling it "bell curve"» (Serrelli 2009). Later, I wrote again that «Wright's landscape was not a model. My idea is that Wright's landscape was a diagram, a graphical presentation of parameters' and variables' values of an *underlying* mathematical model. The static image of the hilly surface wanted to *display* numerical features *of* the model. The dynamics of the "cloud" on the landscape was meant to show the behavior of the *underlying* mathematical model of a population. Confusion between the model and its graphical presentation yields confusion» (Serrelli 2010, p. 7, emphasis original).[135]

Some philosophers who read my papers, then, *questioned the opportunity of restricting the label of a "model" to the formal part*. Is it legitimate - they asked - to draw the math out of landscapes and to consider math as a good model, relegating the pictorial part to being "just a metaphor"? At the very least, can this be done for free? Rather, may not we consider the fitness surface - thus, a pictorial object - as a *fundamental part* of a model, or even as *a model in its own right*?[136] That is, even assuming that "the math does all the job",[137] is not the *pictured* dynamical behaviour of a population on a fitness surface used as a good model of evolutionary dynamics of the biological population(s) we are modeling?

I still think that «confusion between the model and its graphical presentation yields confusion», but I took the criticism completely: I don't think anymore that confusion should be avoided by apriori adoption of one,

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[135] Notice the unclarity brought about by a lack of distinction between surface and space.

[136] I have to thank Steve Downes and Anya Plutynski at the University of Utah for having pushed this point to me.

[137] Again Steve Downes, and Brett Calcott at the Australian National University.

clear-cutting notion of a model, to the exclusion of others. On the contrary, I am now convinced that *the plurality* of notions of a model should be adopted and taken care of, by having the patience to spell out whether, how, and why each valuable notion applies (or doesn't) to each and every element in an epistemological analysis; and, when choosing a model notion to the exclusion of others (an operation I think necessary for a clear and meaningful analysis), by making it explicit and argued for. I would call this a pragmatic approach to models *for the philosopher of biology*. This is neatly distinct from a pragmatic approach a scientist can (or, must) have: since pragmatics means "context sensitivity", a pragmatic approach to models for a scientist will likely mean the choice of the most appropriate model or modelling technique for the considered problem; a scientist *chooses* (or accepts) something to consider a model of the studied phenomenon, and she can *change* her mind about that, and this is the pragmatic dimension of models for a scientist; the philosophical context is, instead, made all researches, or fields, or theories and so on, where philosophers think (or accept) models to play a role, and they will have to choose the *notion of* a model best describing the case(s) he or she is presently studying. For philosophers, modeling scientists are the cases.

Something else than my fellow philosophers' arguments has dissolved my naive "default mathematical view of model": a situation (Fig. II.3) at the end of my in-depth analysis of Wright's work, which is slightly more complex than I figured out earlier. I don't have just a mathematical model and a picture; rather, I have the series of mathematical equations in population genetics, which are about the formal system of Mendelian population, for which it turns out there is no mathematics; so, pictures (Figg. II.2, II.6) cannot at all be considered charts mechanically flowing from mathematical models (unlike those in Fig. II.4), indeed they do not derive from those equations at all; instead, surface pictures are about the formal system, the combination space, but they do not mechanically derive from that either; on the contrary, they add information on its structure and fitness distributions, and indeed they are yielded through an integrative process (2.4).

So, how many and what models, if any, are there? Are some objects models and others not? And why? Do two or three objects group together to form a model? Or also, is any of these objects a model for (or model of) another? Answers to these questions are absolutely not trivial. I appreciate more and more the criticism against my naive "default mathematical view of models": I need to consider the existence of many notions of models, with different sets of criteria for an object to be labeled (and, also, evaluated as) a model. A pragmatic approach to plurality, accepting that answers are always partial, tentative, is also open to the possibility for local conventional agreements, allowing for the choice of the notion(s) of model that fit best with the considered problem. And just the multiplicity and popularity of different notions of a model make agreements necessary: in this pluralistic situation, if in philosophy of biology we talk about "the landscape model" without explicitly defining a model (we could dub it a "no choice" strategy), there will be trouble; and an equally confusing situation will happen if we start saying «since a model is... then the landscape model...» ("implicit choice").

3.2 Statement

As required by a pragmatic approach to models in philosophy of biology (cf. 3.1), here are statements (and some justifications) of how "model" and related words will be used henceforth (and have been used as much as possible above). The resulting vocabulary is reported in Table II.1.

Mendelian population is a model, intended as a «stable target of explanation» (Keller 2002, p. 115). Although Mendelian population is certainly a formal system, in my approach it is likened for several epistemological characteristics to *model organisms* in experimental biology. According to Evelyn Fox Keller, for example:

> ...the primary meaning of the term model in experimental biology is an organism, an organism that can be taken to represent (that is, stand in for) a class of organisms. A model in this sense is not expected to serve an explanatory function in itself, nor is it a simplified representation of a more complex phenomenon for which we already have explanatory handles. Rather, its primary function is to provide simply a stable target of explanation (p. 115).

According to Creager et al. (2007, p. 5)

> A model system in biology refers to an organism, object, or process selected for intensive research as an exemplar of a widely observed feature of life.

For the same authors, "model-systems" constitute answers to the challenge of producing lawlike knowledge in fields such as experimental biology, and their stability is due, amongst other things, to a *self-reinforcing quality*:

Term	Kind of object	Synonyms
Mendelian population	Model as «stable target of explanation», similar to model organisms in experimental biology	- Combination / genetic / metric space - Space (with fitness)
Mendelian population genetics	Theoretical structure	Wrightian population genetics (opposed to Fisherian or biometrical)
Population	Dynamical system Realized (N individual) subset of the model Function of time	
Environment, phenotypes, and interactions among them	Compressed self-evident truths	
Population genetics equations	Equations of gene frequencies (one or few diallelic loci, frequency spectrums)	Equations
Landscape language	Metaphorical verbal language, vocabulary to communicate features of the model	Includes peaks, valleys, ruggedness, ridges, climbing etc.
Landscape models	Combination spaces built on imitation of Mendelian population. These models are «stable targets of explanation» in their own right.	Landscape spaces, combination spaces, spaces
Adaptive surface	3D visualization - metaphorical in case of high-dimensional spaces - exact in case of low-dimensional spaces	- Fitness surface - Surface - Surface picture - Landscape picture

Table II.1. *Pragmatically-stated vocabulary for the debate on adaptive landscapes.*

> ...the more the model system is studied, and the greater the number of perspectives from which it is understood, the more it becomes established as a model system. Even for the many biologists who do not study one of the canonical model organisms, these systems tend to serve as benchmarks and methodological guides when they turn to other organisms and objects as researchers (Creager et al. 2007, p. 6).

Another strength of a model - in the present sense - is constituted by the "experimental resources" associated with it, i.e., those elements that ease its study by making it, e.g., cost effective.

A difference between Mendelian population and model organisms like, e.g., *Drosophila melanogaster* or *Caenorhabditis elegans* lays in its complete artificiality. Mendelian population is a formal system built up from some simple rules of inheritance, discovered and coded by Mendel, scaled on a large number of factors and alleles, and provided with fitness, a value coming from the Darwinian theory of natural selection. But this architectural artificiality does not rise a discontinuity between Mendelian population and experimental biology, because different degrees of (and also complete) artificiality is inherent to models also in the latter. In reconstructing the history of developmental biology, for example, Evelyn Fox Keller studies scientists like Jaques Loeb (1912), Stéphane Leduc (e.g. 1906, 1910), E.A. Schäfer (1912), and she found that:

> To many authors writing in the early part of the twentieth century [...] the question of what life is was to be answered not by induction but by *production*, not by analysis but by synthesis (Keller 2002, p. 18, my emphasis).

Artificial production does not move Mendelian population away from the notion of a model used in experimental biology. Moreover, the artificiality of Mendelian population does not imply at all that such a model is completely known (another feature that would separate it from model organisms). On the contrary, the behavior of Mendelian population is *unknown*: various, non-exhaustive methods have to be devised and tried in order to approach it. This feature once again relates Mendelian population to model organisms:

> ...although model organisms are standardized in order to facilitate highly controlled biological experimentation, their inherent complexity means that the systems are never fully understood and can continue to generate surprising results (Creager et al. 2007, p. 7).

A single notion of a model, one that does not imply exhaustive knowledge even in case of complete artificiality, seems then to capture effectively Mendelian population *and* model organisms.

Many authors (Creager et al. 2007, Morgan & Morrison 1999) insist today on the *autonomy* of model as a direct object of research. Such "stubborn autonomy" is two-fold: from theory, and from outside data input. A model as a «stable target of explanation» - the notion I'm adopting here - is, by definition, autonomous in both respects. Models are *targets* of explanation, not immediately tools for explaining (moreover embedded in other kinds of explanation, e.g. theories). The already quoted passage by Lewontin on population genetics may be useful to express the autonomy of Mendelian population:

> For many years population genetics was an immensely rich and powerful theory with virtually no suitable facts on which to operate. It was like a complex and exquisite machine, designed to process a raw material that no one had succeeded in mining [...] for the most part the machine was left to the engineers, forever tinkering, forever making improvements, in anticipation of the day when it would be called upon to carry out full production (Lewontin 1974, p. 189).

Autonomy of model from data creates epistemological questions (dilemmas?) about, at the very least, *representation* and *explanation*.

If, as several authors point out (e.g., Creager et al. 2007), models are not chosen because they are *typical* of a certain set of systems, nor they are built *to represent* some other system by reduction, deduction, encoding (Casti & Karlqvist 1989, Rosen 1989) or the like, *how can they represent?* Creager and colleagues (2007, p. 2) talk about models *for* (as opposed to models *of*), acting as "representatives", not "representations":[138] their similarities to other systems stand to be always better explored. In this exploration the model might, e.g., exploit a classificatory function for the organization of knowledge, and instances of *unpredictable relevance* (Hubbard 2007) might well happen. Context-dependent similarity has been proposed by several authors (e.g. Giere 1988, Plutynski 2006b). Autonomy from data and from theory depends on the model's self-consistency: in discussing self-organizing complex models, for example, Oreskes (2007) and Dahan Dal Medico (2007) emphasize the

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[138] According to Hughes (1999, p. 141), some models in physics can act as «representative, as well as a representation». This allows models like the Ising model to be used as representative of a large and varied ("universal") set of systems.

possibility of experimental exploration *of* them in search of aspects that *produce* complexity, a strategy to obviate the impossibility of miming complex natural systems. For Evelyn Fox Keller:

> To be sure, a model is expected to bear some resemblance to that which is being modeled, but in science as in art, the degree of resemblance is generally understood to be a matter of perspective. The more critical question is whether it is a "good" model, and in both science and art the measure of how good a model is varies notoriously (2002, p. 46).

The possible decoupling of model and explanation is well expressed in the following quote by John von Neumann: «the sciences do not explain… they mainly make models» (cit. in Creager et al. 2007, p. 11). Models can explain, for von Neumann, only with the addition of verbal interpretation and narratives containing assumptions. Like resemblance, explanation is, for Keller (2002), a context-dependent use of models: what counts as an explanation (and as knowledge) depends on values, so that for example many biologists could reject physical or mathematical models of life as valid explanations by (cf. e.g. E.B. Wilson 1934).

Models can also be predictive (Oreskes 2007, Dahan Dal Medico 2007), but prediction is conveniently outside the notion of a model I am using here.

The fantastic degree of *idealization* of Mendelian population has been topic of much philosophical literature (cf. also Cartwright 1983 for physics).[139] This literature focuses on *representation* and *explanation* relationships Mendelian population should, may, or may not have with other systems (real populations). Such a relationship is obviously important (it will be focused in III.3 about Gavrilets's work), and my personal view would be pragmatically inclined (like Keller, Plutynski, cit.).[140] But the point is that discussing such relationships is not essential *within* a notion of a model as a stable target of explanation. That is, if we choose this notion of model we can provisionally remain silent on how and what the model represents and explains. We can concentrate on what the model *is*, its structure, *assuming* that it is an adequate description of some object of study.[141]

Let me remark once again that I am considering *one* of the two "theoretical structures" or "research traditions" in which population genetics is split according Richard Lewontin (1980). Such theoretical structure[142] - that

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[139] By the way, idealization is a studied feature in model organisms research, too. In the case of *Caenorhabditis*, for example, Ankeny (2007) finds at least two levels of idealization: the "wild type" that serves as biological "norm" for genetic comparison; and description, that is an idealized version of actual worms, abstracted in a diagram. Both idealizations might be (and are) called models, but - importantly - *naming them this way is excluded* by the notion of model I am using here. This is a little example of how a pragmatic terminological choice may help in avoiding confusion.

[140] «Typically, explanations in the biological sciences are provisional and partial, and the criteria by which they are judged are, and always have been, as heterogeneous as their subject matter [...]. Just as the diversity of life, rather than its unity, has historically commanded the respect of life scientitst, so too, I propose, the epistremological diversity of their aspirations demands our respect as historians and philosophers of science» (Keller 2002, p. 2). The representational and explanatory use of Mendelian population will be topic of III.3.2-3.

[141] That this is a legitimate and autonomous question is agreed upon by Martin Thomson-Jones, for whom «To call something a model [...] is partly to ascribe a certain role to it, and partly to classify it as a certain sort of thing. There is a job to do it, and a kind of thing doing it» (Thomson-Jones, draft, p. 2).

[142] I retain here Lewontin's term. Formal system (Rosen 1989) would be an equally good term, but I want to avoid confusion with what I call "dynamical system", the population in the Mendelian population space.

can be called Mendelian or Wrightian (as opposed to biometrical or Fisherian) - population genetics deals with gene frequencies and, less effectively, with gene combinations.

In analyzing the theoretical structure involved in modeling, many authors in literature (e.g. Willem 1989) provide it with a *hierarchical organization*. In the Mendelian formal system I recognize at least Mendelian population as a model and as a metric *space* provided by fitness, and, as a subset of such a space, a *population*. The latter is not a model itself, rather it is the *part* (N individuals) of the Mendelian population model that is realized either at a certain time *t* or seen as a diachronical sequence in a time interval. I call the population a *dynamical system*[143] within the model. It is function of time (measured in discrete steps, i.e. generations) whereas the model is time-invariant. Dynamics of the population depends, as we know (2.3), on the static features of the model.

Mendelian population model can be tuned by means of a few parameters like numbers of loci and alleles. And another component of the theoretical structure is *environment*, that acts by influencing the distribution of fitness. As Willem (1989) writes:

> we postulate, in effect, that the system is isolated from its environment [but] what this assumption actually means is that we postulate that we know, or think we know, how the environment will act on the system, what the boundary conditions are, how external influences are generated; thus, in

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[143] I agree in this definition with Skipper (2004).

> modelling ...we find ourselves in the absurd situation of having to model the environment as well! (Willem 1989, p. 108).

If we look for a moment at what the model should be suitable to represent, i.e. the gene pool of a biological population, what is called the “environment” in the model appears actually as a *compression* (Casti & Karlqvist 1989), not only of any feature and event of the environment, but also of the interaction between *phenotypes* and environment. Compression in modeling is the “omission of self-evident truths” which are summarized into a more malleable and understandable form (Casti & Karlqvist, cit., p. 4). Everybody knows the self-evident truth that alleles do not float free in environments: rather, phenotypes live and are naturally selected. Good modeling should avoid the “drastic and probably disastrous” consequences of overlooking or compressing incorrectly some of these self-evident truths.[144]

The population dynamical system is embedded in the Mendelian population space (and model), this being a larger universe of virtual facts (Thom 1989). Mendelian population has thus the characteristic of *virtuality*, which I put forth at the beginning of my work (I.2.1), and which is seen by some authors as an important aspect of theoretical science:

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[144] Casti & Karlqvist (1989, p. 4) cite a case of self-evident truth to be omitted by good modeling of social organization: «Hägerstrand [Swedish geographer] notes the fairly obvious facts that a person can be only at one place at a given point in time, and that such a person must be at some spatial location at all times. Despite their self-evident nature, these facts have very definite and often profound implications for how societies are organized. As a result, their omission from the encoding of N into M will have drastic and probably disastrous consequences for the explanation/prediction properties of any mathematical model of a social organization N».

> Theoretical biology will exist only insofar as biologists are able to construe a set of theoretical developments generated according to a constructive definition, and to specify how reality propagates among this set of virtual processes. ...That the consideration of virtuality is necessary to science was clearly perceived by Aristotle, who systematized it with the distinction between potentiality and actuality (Thom 1989, p. 40).

Equations describing gene frequencies and factors such as selection pressure, mutation rates, migration, drift, and so on will be simply called *population genetics equations*. I understand that my choice of depriving these equations of the title model goes against almost all the literature on (and in) population genetics. But again, I insist on all the implications of a pragmatic approach: the chosen notions (e.g., the model notion) are not at all considered “better” or “more right” than others, and the choice is not supposed to be valid for all (or many) contexts of discussions. Rather, the explicit choice of notions is aimed to ease a *particular* debate (and not others). The condition for success of such facilitating task is *conceptual coherence*, even if initially puzzling and countertrend. I chose a notion of a model as a «stable target of explanation». Population genetics equations seem definitely not to be covered by such a notion. Rather, they are descriptive (if not explanatory) tools used to approach the model. They are always infinitesimally partial (one locus, diallelic, with frequency spectrum as the most comprehensive type of equation). Moreover, they describe the dynamical system in the model (i.e., the population) in a statistical fashion, and we should not confuse the deterministic and combinatorial nature of the model with the statistical description of its realizations (cf. Willem 1989).[145] There is an epistemological gap (cf. 1.3) between model and equations.

The landscape language is a metaphorical, verbal vocabulary used to approach and communicate some inferred features of the model - for which no mathematical equations are available -, to share discussions and even stimulate research on it (cf. Gavrilets in III.3). The vocabulary includes terms like ruggedness, peaks, valleys, ridges, holes. There are also words for describing the model dynamics, such as walking, climbing, crossing.

Landscape models will be subject of the next chapter (III.1, III.2). They are combination spaces provided with fitness, which are built "from scratch" and have a structure analogous to Mendelian population model. These spaces include not only low-dimensional allelic spaces, but also, e.g., nucleotidic or phenotypic spaces (cf. III.2). Such combination space models are, I repeat, completely autonomous from Mendelian population, but the landscape metaphorical language which was worked out for Mendelian population is used also with all these spaces/models, arguably because it was so strong, portable, and useful. Moreover, the language was probably itself an important part of the inspiration to those models, along with the influence of the fitness surface. However the story went, these combination models are collectively addressed in literature as "landscape models".

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[145] «For good historical reasons and some impressive success stories, statistics has transformed the problem of modelling into a problem of stochastics, and has chosen the question of reconstructing a probability law from a finite sample as the basic question in modelling from data. This vantage point is very restrictive, and in our opinion plays much too central a role. [...] the stochastic nature of the phenomena is questionable and certainly not compelling [...] the field of modelling from data has been totally dominated by a philosophy which equates uncertainty with stochasticity, which identifies unknown with random, and which reduces data to samples» (Willem, cit., p. 113).

Finally, *adaptive surface* or *fitness surface*, deeply analyzed in the present chapter, is a metaphor in cases of high-dimensional landscape models; it is an exact visualization in lower-dimensional spaces. Model dynamics can be depicted on it. It is interesting to notice that, in the present *liberal* situation of models in philosophy of biology (cf. e.g. Downes 1992, Godfrey-Smith 2008, Plutynski 2006b, Griesemer 1990), *there are notions of model* (different from the one chosen here) *that would capture the adaptive surface*, with or without depiction of the dynamics. Steve Downes (2009), for example, has carried out an analysis of a notion of model as a representation based on similarity (cf. Baigrie 1996, Perini 2005a, b). This notion tries to unify models and pictures:[146]

> What some scientific images have in common with most scientific models is that they are taken by scientists to stand for some physical system or pattern in a data set (Downes 2009, p. 420).[147]

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[146] Downes's conclusion, anyway, is against this notion: «Scientific models may have other roles than representing reality and those models that have a representational function may not represent in virtue of their similarity (or isomorphism) to their objects» (2009, p. 419).

[147] «The images that scientists invoke range from photographs taken in good light of medium sized live organisms - such as those used to illustrate species typical features of birds or butterflies - to highly abstract and schematic diagrams - *such as biologists' diagrams of adaptive landscapes*. An image can often be data, for example, images from f-MRI's in neuroscience; and just as often be the way of presenting a model or a theoretical construct, for example, the iconic diagram of the Bohr model of the atom» (Ivi, p. 419, my emphasis). An approach accounting of each of the many and varied ways in which images contribute to successful scientific practice has been adopted, according to Downes, by e.g. Odenbaugh (2003), Suarez (2004), Woody (2004), Odenbaugh (2005), Weisberg (2007).

In some views, then, pictures like the surface can be seen as models, intended as representations of empirical systems. In more classical semantic views, pictures can also be seen as models *of theory*.[148]

I already motivated my choice of the notion of a model as a «stable target of explanation», and I don't think the notion would easily apply to the adaptive surface.

3.3 A last plea for careful analysis and pragmatics

I think that much of the debate on the adaptive landscape have been hindered by a lack of pragmatic attitude towards making an explicit choice of a fit notion of model among the multiplicity of available notions. I do not claim at all that the solution I proposed in 3.2 and summarized in Table II.1 is the best way to set the debate. Other, equally acceptable notions of model might organize the debate in different ways.

First of all, however, *there are* some distinctions, in the historical and epistemological topic of adaptive landscapes, that *must* be recognized and properly emphasized in order to develop a meaningful and correct debate. This has not always been the case. Several authors, for example, arguing

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[148] Van Fraassen (1980) used "the Seven Point Geometry" (Wylie 1964) to introduce the semantic view. Axioms were interpreted as being about some geometrical object (points and lines), a simple geometric structure of which axioms are (or are not) true. The geometrical object, a model of the theory, is used to present theories (in a semantic form) and to work with them. For example, the Seven Point Geometry is embedded in the Euclidean plane, and since the Euclidean plane is a model of T2, we can detect a different relation between T1 and T2 beyond a simple syntactical inconsistency. Despite some (still ongoing) endeavors, however, population genetics was never axiomatized. The first axiomatization of population genetics was famously attempted by Mary B. Williams in 1970. Her system raised several reactions, e.g. Ruse (1973), Thompson (1989), Rosenberg (1985), Lloyd (1988). Then again Rizzotti & Zanardo (1986), Zanardo & Rizzotti (1986), Magalhães & Krause (2000).

through sentences like "the adaptive landscape was a metaphor for population genetics models" missed the fundamental distinction and epistemological gap between Mendelian population and equations of gene frequencies (1.3), as well as between Mendelian and biometrical population genetics (1.1). Many treated the metaphor as a simple way to convey complicated mathematics (1.4), failing to recognize Wright's tentative filling of the gap between space and equations by means of intuition, experience, and heuristics (2.4). Even the clear distinction between space (2.1, 2.2) and surface (2.3) is rarely found.

But, when all this analysis is done and agreed upon, confusion can still come from the use of unclear, heterogeneous, or ill-chosen notions of model. The notion of model is involved, I see, in different kinds of philosophical endeavours: first of all, model is a conceptual pillar of some very general approaches to what science is (e.g., among the most cited, Bas van Fraassen, and Ronald Giere). Particular notions of models are built and defended with close interest in the defense and elaboration of those very general theories. Other studies, called "model-based science studies" by Godfrey-Smith (2008), aim to understand the concept of model for its importance in science practice. Such studies are usually carried out with a case-based approach (e.g., Morgan & Morrison 1999, de Chadarevian & Hopwood 2004, Daston 2004, Creager et al. 2007), where the case study is a means to look for some general feature of models and modeling. But, model is also a part of a very fundamental grammar used to describe and discuss a case, where the aim is just to gain better understanding of *that* case. In this latter situation, I think, general background pressures on models can favor “no choice”, “implicit choice” or simply wrong choice of the best notion of model to employ.

Expressions like “the adaptive landscape model” or “the adaptive landscape metaphor”, variously and implicitly including picture, verbal descriptions, combination space, equations, dynamics and almost anything whatsoever, have made the debate a real mess. I hope that even who does not endorse my choices will accept the necessity, and urgency, *to choose*, and to do it with a pragmatic sensitivity.

CHAPTER III

Landscapes today

As seen in chapter I, adaptive landscapes are a migrant metaphor. Migration implies an explicit or implicit redefinition of some or all native meanings in non-native research fields, like e.g. paleontology or morphology. This tension and necessity, I argued, is exactly the stimulating aspect of the migrant metaphor. But clear redefinition is also a difficult task that can lead to inconsistencies, and what's worst, in lack of an appropriate analysis such inconsistencies can go overlooked, concealed by the metaphor's intuitive and rhetorical force. My in-depth analysis of Wright's native metaphor (chapter II) has mainly brought to an emphasis on the distinction between surface and space: Wright's surface was metaphor for Mendelian population metric space, and the former was meant to communicate some features of the latter (while ignoring others). I analyzed the properties of Wright's combination space, i.e. classical Mendelian population, spelling out the meaning of terms like genotype, allele, locus, position, population, reproduction, recombination, generation, fitness, neighborhood, distance, movement, selection, and epistasis. Interpreting the native metaphor, I think, requires knowing the exact definition of such terms more than of some complicated "underlying" mathematics. Taking advantage of this, and especially of the distinction between combination space and surface, here I "assess the migration" in Dobzhanky's, Simpson's, and Dawkins's cases. Then I consider the vast and varied use of combination spaces in today's evolutionary biology. The landscape language is routinely used to describe these spaces: could it also have had a causal role in their existence? Particular interest bear for me the combination spaces and statistical analyses used to understand and model speciation by means of population genetics (2.3). Gavrilets's review of such studies (2004) gives an idea of contemporary population genetics as a "patchwork" of numerical models and statistical analyses, yielding fascinating results from the same disciplinary field Wright contributed to establish. No migration here. Section 3 is devoted to the famous holey landscapes (anticipated in I.4). I try to correctly locate them into the "patchwork", and to give a philosophical account of why and how elements are chosen by scientists to represent and explain, i.e. to answer "how possibly" questions. Such account complements well the notion of model as a stable target of explanation exposed at the end of chapter II (cf. II.3.2).

1. An assessment of the three big pictures

Theodosius Dobzhansky (1.1) was a population geneticist like Sewall Wright. His landscape (space and surface) was a genetic landscape, so the two versions would be supposed to be the nearest. Analyzing them, however, I point out a few crucial differences that, I think, hinder the very consistence of Dobzhansky's landscape (1.1). George G. Simpson's landscape, on the other hand, might be expected to be problematic, being about a few, phenotypic characters instead of whole genotypes. My analysis, however (1.2), shows the consistency of Simpson's space and surface. New versions of Simpson's landscape, indeed, found applications in contemporary research (section 2), and were accordingly defended by other authors. As for Richard Dawkins (1.3), his landscape inherits features from the other two, adding the idea of an absolute measure of complexity or perfection, conflating phenotypic and genotypic spaces and considering the latter as a sort of universal, decontextualized space on a vast time scale. Dawkins's use of the metaphor is, I think, purely rethorical in response to the classic "problem of intermediate stages". But, evolutionary biology in fact answers the problem in a much more advanced and integrated way, already set out by Darwin himself.

1.1 Dobzhansky

One difference between Dobzhansky's and Wright's space concerns the mechanism for movement. For Dobzhansky, such mechanism is declared to include *mutation*. When a peak moves due to environmental change, for example, «the species may become extinct, if no genetic elements *(mutations)* *necessary to produce the new adaptive genotypes* are available...» (p. 277, my emphasis). Mutation works together with recombination, as it is evident from how Dobzhansky goes on: «...or if the requisite constellations of these elements do not appear in time» (Ibidem), but *mutation is present and essential* in his space. In Dobzhansky's account, the Wrightian "trial and error" mechanism for the population to explore the landscape space

> ...is provided *primarily by mutation* and sexual reproduction, which are able to generate a practically limitless variety of genotypes (p. 278, my emphasis).

What I want to point out here is that for Sewall Wright mutation was a rare, most of the times lethal event. In 1932 in presenting dynamics on the landscape he had *excluded* mutation as a major evolutionary mechanism:

> Under the above conditions [i.e. equilibrium on a peak] further evolution can occur only by the appearance of wholly new (instead of recurrent) mutations, and ones which happen to be favorable from the first. Such mutations would change the character of the field itself, increasing the elevation of the peak occupied by the species. Evolutionary progress through this mechanism is excessively slow since the chance of occurrence of such mutations is very small and, after occurrence, the time required for attainment of sufficient frequency to be subject to selection to an appreciable extent is enormous (Wright 1932, p. 360).

In Wright's population genetics, although the general rate of mutation may increase for some reasons (e.g., cosmic rays as suggested by some authors), mechanisms like that «do not appear adequate to explain evolution to an important extent» (Ivi, p. 361). Mutation is not at all a mechanism for movement in Wright's space, not only for its rarity, but importantly because *its effect is primarily the modification of the landscape space*, and only as a secondary effect the movement of the population.

A clarification of the expression «recurrent mutations» will be useful to understand the notion of mutation Wright had, and its role in his landscape. Mutation was formalized in Wright's population genetics equations (e.g. 1931) as *mutation pressure* acting on the frequency *of one allele*, in two distinct components: mutation *to* the considered allele, randomly changing different alleles *to* the considered allele, yielding an increase of its frequency; and mutation *from* the considered allele, decreasing its frequency by changing it in other alleles.

What is most important is that in Wright's population genetics *mutation is conceptualized in terms of alleles*: recurrent mutations change one allele in another, one which is *already present* in the population's genotype space; non-recurrent, «wholly new» mutations, which are very rare, *introduce novel alleles* in the combination space, modifying the space and, consequently, the surface. That is why mutations do not directly fuel the movement of the population in the combination space, but rather they modify the space.

Recombination was for Wright the one and only mechanisms of movement in the Mendelian space. What he calls "mutation pressure" *does not generate novelties* in the combination space (the Mendelian population), it only influences the frequency of an allele in the population. *The space includes most of the possible evolutionary change*, because such a change consists in the realization of different combinations *in the same* space. Only «wholly new» mutations modify the space, by introducing brand new alleles in it, adding a number of new possible combinations.

For Ernst Mayr (e.g. 1980), underemphasis of mutation by Wright and others in the first decades of the Twentieth Century can be straightforwardly explained by the fact that macro-mutations were studied by authors (such as Hugo DeVries) who considered it as the non-Darwinian mechanism for the origin of species. Recombination was thus seen as the major genetic evolutionary mechanism for neo-Darwinian population genetics. The redefinition of mutation was, for Mayr, a late achievement due to the Modern Synthesis (cf. I.3.2). Only then, mutation - reframed in population genetics - was seen as a major mechanisms for the origin of evolutionary novelties in those years when Dobzhansky worked and wrote. But *the absence (almost "eclipse"?) of recombination* in those works was, for Ernst Mayr, an «astonishing» fact:

> It would be decidedly whiggish to suppress the fact that even [many biologists] slighted recombination in the 1930s. Dobzhansky, who later did much to establish the evolutionary importance of recombination, hardly referred to it in the first edition of his book (1937) [...]. Recombination was, of course, well known since 1900 as one of the basic Mendelian processes and described in every genetics textbook. Remarkably, only a few evolutionary geneticists used it as a source of material for selection (1980, p. 23).

Dobzhansky's landscape introduced the concept of mutation - still seen like in classical population genetics, as the origin of alleles - as a mechanism for movement on *Wright's* landscape. But mutation - intended as the origin of novel alleles - and recombination can hardly be *both* seen as mechanisms for movement in the completely defined allele space envisaged by Wright. What this introduction is supposed to mean is, I think, hard to understand even though in today's evolutionary biology mutation is seen as a major evolutionary mechanism.

Mutation in contemporary evolutionary biology has been re-conceptualized again, thanks to the development of molecular biology and DNA sequencing. Mutation is, very roughly speaking, DNA sequence alteration. On the one hand, from the point of view of alleles, mutation can still be seen as the origin of brand new elements, as a "different rules" mechanism altering the combination space. But, on the other hand, molecular biology has shown lower-level combination spaces: *sequence spaces* (cf. 2.1). Sequence spaces can be seen, I think, as analogue to Wright's allele spaces, where individuals are sequences of nucleotides (instead of alleles), the number of loci is substituted by the number of nucleotides in the sequence, and the number of possible states for each nucleotide is, of course, four. In a sequence space, mutation can, at least in some cases (e.g., simple point mutation), be treated as a form of movement in the sequence space: it is not the origin of a brand new factor in the combination space, rather, it is the realization of a possibility which was already specified in the space. Of course, should whole individual organisms be represented in a sequence space with all their genome, the dimensionality of the sequence space would be absurdly greater than the dimensionality of Wright's allele space:[149] a human sequence space, as an example of an average genome, would feature 2.9 billion dimensions. One should also imagine to be able to calculate the fitness effect of every nucleotide in the sequence, and of any single-nucleotide substitution. In sum, it seems to me that it would make probably more sense to accept and take advantage of the descent to a lower-level space by building meaningful lower-dimensional sequence spaces. This could be made - and is being made, cf. 2.2 - by isolating a short genetic region for which it could make sense to calculate fitness, for example a protein-coding gene. With this methodology, knowing the properties of low-dimensional spaces (cf. 2.1, 2.2) would prove useful, contrarily to what Massimo Pigliucci (2008) affirms:

> [biologists] simply cannot assume that the intuitive properties of low-dimensional landscapes are a reliable guide for the real thing (p. 599).

Reference to "the real thing" is misleading because what we need are reliable guides *to our models*: for low-dimensional models, low-dimensional guides are far enough; and we should not think that high-dimensional models are "the real thing". As I shall review below (2.2), intuitive properties are not the only thing we have about low-dimensional spaces.

A related issue is what I called the big scope of Dobzhansky's landscape. A wide environmental scope is a problem, since it is difficult to imagine to sum up all selection pressures on Earth as pressures acting on a

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[149] Sergey Gavrilets accepts this kind of space in his analysis of high-dimensional spaces (cf. 2.3).

single gene pool. But the real problem is the taxonomic scope, making Dobzhansky's landscape inconsistent. Why? In Wright's genotype space (i.e., in classical Mendelian genetics) genetic loci are formalized with a *fixed* number and order in a population. Order is not necessarily physical, it is essentially logical: it means that alleles for one locus cannot appear in another.[150] Fixed number and logical order is what is today called a *genetic map*. A fixed genetic map is the prerequisite for neighborhood: how could we measure step-wise distance between genotypes if they have different numbers of loci, or if alleles can equally be in a locus or another with no general rule? Dobzhansky did know that the genetic map of different taxa is absolutely different. He proposed the landscape anyway, but making it - in my view - inconsistent.

Certainly we don't need all these in-depth analyses to judge the role of the landscape metaphor in the Modern Synthesis. But we do benefit from them to better understand ideas about the genotype space and related concepts, such as mutation. Also, I should say that I disagree with Michael Ruse (1990): I don't see the landscape metaphor as an integrated part of Dobzhanksy's work. The metaphor appears in the first and last chapter, like a metaphorical framework for low-dimensional models. The epistemological gap between model and equations (II.1.3, II.1.4) returns again and again. But more will be said on the structure of population genetics in 3.3, thanks to Sergey Gavrilets's work.

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[150] The rule in the model is full of exceptions, in the natural world, as Dobzhansky (1937) already knew and studied.

1.2 Simpson

Simpson's landscape is *local* in scope, both environmental and taxonomical, differently from Dobzhansky's and more similarly to Wright's. Local ecological conditions determine selective pressures, causing that different structures may fall "under the influence" of a new peak, causing the local population to adaptively split.

But Simpson's landscape is limited in scope also for what concerns the considered characters. Whereas Wright and Dobzhansky defined the individual organism as an assembly of *all* its (genetic) traits, Simpson's concept of character complex operates a strong reduction of the number of traits considered. Individuals are represented and distributed on the landscape only according to their variation *in* the considered character complex.

In chapter II (1.1) I presented Lewontin's idea of a binary structure of population genetics. A half, i.e. Wrightian or Mendelian, deals with gene combinations and gene frequencies. The other, Fisherian or biometrical, deals with phenotypes, heritability, variance and covariance of traits and their response to natural selection. Well, if Wright's landscape has to be seen well into the first theoretical structure, Simpsons's is, I think, a landscape picture of the second tradition: still population genetics, still legitimate, *and* exquisitely phenotypic.

The concept of character complex brings about not only a limited set of characters, but also a set of *constraints* among them: values for the various characters in a character complex cannot come in any combination, they constrain each other, so that, e.g., in horse evolution body size influences teeth structure, so a change in one character causes a correlated change in the other.[151] Constraints among characters are not considered by default universal, nor stable on a long evolutionary time: Simpson specifies that such constraints change over time. This points once again to the spatiotemporal locality of Simpson's landscapes: they are worked out to describe and explain singular evolutionary events. *Within* the scope of the considered evolutionary event, the combination space is completely defined (and this avoids the problem of undefined possibilities found in Dobzhansky's landscape), also by constraints among characters in the character complex.

As for the mechanism of movement, it can be supposed that Simpson's landscape may integrate rules for reproduction and inheritance among individuals, so that the character complex in an individual could still be seen as a recombination of the parents' traits. The rules of inheritance and movement of phenotypic measures would be more complicated than random recombination between parents.

But another peculiarity of Simpson's landscape needs to be evaluated: the fact that it is a *phenoypic landscape*, i.e. a phenotypic combination space. How different is a phenotypic from a genotypic combination space? How much relevant are such differences? Sewall Wright (1988), for example, in reviewing Simpson's landscapes thought that

> Phenotypes are, no doubt, more appropriate units for dealing with selection, whether between individual or groups, but genotypes seem more appropriate

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[151] A concept of positive, channeling evolutionary constraint was worked out by Stephen Jay Gould (cf. 2002).

> for mutation or random drift. The choice, however, is practically irrelevant in connection with pictorial representation of changes that occur in populations (p. 120).

Massimo Pigliucci (2008) criticized Wright for such a simplicism and considered the transition from a genotypic space «a bold and questionable move»:

> Wright acknowledges that Simpson took the idea of adaptive landscapes - defined in genotypic space - and translated it with little fanfare at the phenotypic level. This is actually a bold and highly questionable move (p. 597).[152]

A phenotypic landscape considers all the possible combinations of a limited number of *distinct* characters, *but the variability of any of them is continuous*. Whereas a genetic locus in classical population genetics can assume a number of discrete "values" (i.e. the alleles for that locus), in a phenotypic space any trait - e.g., body size - can assume any value in a continuous range. Could it be defined as a continuous, as opposed to discrete, combination space? What is certain is that *the concept of neighborhood* as defined in II.2.2 *is not applicable* - and the same is true of dimensionality. Different, *continuous measures of phenotypic distance* must be devised in Simpson's space, and the transition between space and surface may perhaps be subject to an exponential version of the "impossible packing" objection (cf. II.2.3).

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[152] See also Pigliucci & Kaplan (2006), chp. 8. In IV.2, I comment on what I think are mistakes and unappropriateness of this criticism.

1.3 Dawkins

Richard Dawkins's adaptive landscape of the evolution of the eye (I.2.3) inherits characteristics from both Dobzhansky's and Simpson's.

Like Simpson's landscape, indeed, it is a phenetic landscape, and it isolates a few characters - those that relate to the function of vision. But like Donzhansky's landscape, its taxonomical and environmental scope is universal: it includes species from all the natural world. The chosen character complex (the eye) operates an epistemological taxonomic sorting: all and only the groups having any form of eye are represented and placed in the landscape.

A novel characteristic in Dawkins's landscape concerns the measure of adaptiveness: not only different species are distributed and grouped according to the particular eye form that is fit in the environment they live in; some peaks and ranges are higher than others, giving the landscape a kind of "staircase" shape. So, fitness is not only *relative* a measure to a particular environment: there is an absolute component in it.[153] Dawkins calls perfection or complexity. The perfection component prevails, indeed, because for example organisms with "mere photoreception" or "pigment cup-eye" are represented at the bottom of a valley, regardless they are probably adapted and well fit to their own environment of life. No landscape before Dawkins had ever introduced this idea of perfection and progress.

The ideas of a universal scope and of the primacy of function as major organizing principle of the living world (shared with Dobzhanky), with the

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[153] Thanks to Anya Plutynski who made it as a first observation when I showed her Dawkins's picture.

significant addition of a measure of complexity and perfection, remind other works by Dawkins, like the essay "Universal Darwinism" (1983), where he wrote:

> I shall be an adaptionist in the [...] sense that I shall only be *concerned* with those aspects of the morphology, physiology, and behaviour of organisms that are undisputely adaptive solutions to problems (p. 17).

Adaptive characters are thus an epistemological choice of what is most in need for an evolutionary explanation. Dawkins calls the vertical dimension "adaptive complexity", and he thinks it could be rigorously measured:

> A complex thing is a statistically improbable thing [...]. Living things are not just statistically improbable in the trivial sense of hindsight: their statistical improbability is limited by the a priori constraints of design. They are *adaptively* complex (Ivi, pp. 16-17).

Natural selection is the mechanism for movement on Dawkins's landscape: it is a force driving constant and small improvements towards adaptive complexity. Borrowing Wright's landscape picture, Dawkins recognizes intellectual debt, with no special mention of the various differences separating their two metaphors. In *Climbing Mount Improbable* there is little if no mention of the possible mechanisms by which a species could descend a peak and reach a higher one, but again in "Universal Darwinism" we find:

> The phrase 'random genetic drift' is often associated with Sewall Wright, but [...] he clearly sees selection as the driving force of adaptive evolution. Random drift may make it easier for selection to do its job by assisting the

> escape from local optima, but it is still selection that is determining the rise of adaptive complexity (1983, p. 31).

In Dawkins's exposition of drift we see his idea that, although the landscape is a phenotypic one, underlying genetic mechanisms drive the movement on it. Drift and natural selection are thought by Dawkins in genetic terms, and I shall return on it in a few lines.

By introducing the concept of "design" in an evolutionary view, and indeed by tackling the very case of eye evolution, Dawkins recalls a case which was very important in the development of the theory of natural selection by Charles Darwin. The eye was a classical case by which natural theologists built the "argument from design", advocating the need of an intelligent designer to account for the most "adaptively complex" structures, like the eye. William Paley was the champion of this school of thought, and he had defended the argument from design in his influential book, *Natural Theology*:

> As far as the examination of the instrument goes, there is precisely the same proof that the eye was made for vision, as there is that the telescope was made for assisting it. They are made upon the same principles; both being adjusted to the laws by which the transmission and refraction of rays of light are regulated (Paley 1828, p. 17).

When Darwin was developing the theory of natural selection, and perceiving that the theory would have needed the demonstration of gradual implementation of complex structures, he looked at the eye with some worry, and in his notebook C (1838) he wrote:

> We never may be able to trace the steps by which the organization of the eye, passed from simpler stage to more perfect, preserving its relations. The wonderful power of adaptation given to organization. This really perhaps greatest difficulty to whole theory.

And again, in the *Origin of species*, Darwin declared:

> To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree [...]. If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down (1859, Sixth Edition, 1872, pp. 143, 146)

The demonstration of the existence and viability of several intermediate forms is then, for Dawkins, a way of *defending darwinism* (Elston-Baker 2009). The solution to the eye “dilemma”, however, is carried on in today’s evolutionary biology by means of the integration of phylogenetic and adaptive approaches, where adaptation is seen as a complex dialectic between structures and functions, with the chance - already realized by Darwin - of co-option of pre-existing structures to contribute to novel functions in different ecological contexts. None of this is (or can be) shown in Dawkins’s landscape. Dawkins’s metaphor is thus an effective but very simplifying one, conveying -

according to many authors - an oversimplified picture of evolutionary biology.[154] To give only an example, structures evolve in Dawkins's landscape with little trace of the complex and taxon-specific character correlations that were hinted to in Simpson's landscapes, and Dawkins's absolute measure of "adaptive complexity" hides, in fact, the configuration of selective pressures which explains specialization and speciation in Simpson's evolutionary episodes (cf. horse evolution, II.2.2).

Finally, let me turn back to Dawkins's vision that movement on the landscape happens actually in a *genetic* space. If genetic drift can be seen as the mechanism for "peak shifting", natural selection is also to be intended, in Dawkins's view, as competition among genes or "replicators". His famous argument for this is that, to be relevant to evolution, the units of selection have to be stable in time, and genetic replicators are the only candidates for such a stability. By the way, the temporal scale (or scope) of Dawkins's landscape strives to cover a large part of evolution. At such time scale (very different from Wright's or Simpson's, more similar to Dobzhansky's) competition among replicators happens, I understand, in some universal genetic space, its *result* being shown in phenotypes. As far as I can imagine, there is no room in such a universal, n-dimensional space for a "balance of factors" (cf. II.2.3) like migration rate, population subdivision and size with consequent random fixation, plurality of equally fit combinations, epistasis (cf. II.2.4) implying that alleles (despite the necessary oversimplifications of

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[154] The "selfish gene" (Dawkins 1976) is probably the most famous of a set of extremely successfu metaphors used by Dawkins to defend Darwinism, or at least its own version of it (Elston-Baker 2009).

models, cf. II.1.3) can never be thought as actually having individual fitness value, and so on. It must be said that in some works (like "Universal Darwinism", cit.) Dawkins qualifies himself as an "epistemological adaptationist", so his views would apply only to those features that are adaptive (therefore, all the factors I just listed would be negligible *only fo*r complex adaptations). In many other works, however, he is not so cautious.

Concerning the adaptive landscape, I think, the main result is a complete *conflation* between a genetic and a phenetic landscape, which is typical of Dawkins's thought: there are "hidden rules" of movement, phenotypes are what we see, but they are completely *transparent* to their genotypes in evolutionary time. Perhaps it could be said, in almost ontological sense, for Richard Dawkins the phenotypic landscape is just metaphor of a genetic space.

2. Landscape models today

The success of the landscape metaphorical language is measured above all by the amount of researches on "fitness landscapes" in evolutionary biology. What is to be intended with fitness landscape *models*? And which are the most relevant differences among them, and between them and the original native metaphor by Wright? The metaphorical landscape picture opened up a semantic area for describing evolution, with terms like peak, valley, ruggedness and so no. The evocative landscape language lasted and permeated evolutionary biology until today. Many articles talk about landscapes: what is intended with that?[155] With the analytical and terminological effort made mainly in chapter II, I claim, it is not so difficult to answer these questions. Section 2 is devoted to a taxonomy of contemporary research on adaptive landscapes.

A survey of literature reveals consistently that “landscape models” are combination *spaces* provided with fitness, whose static features and dynamics *may or may not* generate 2D or 3D visualizations. In all cases, the landscape vocabulary (peaks, valleys, ruggedness, etc.) is used to qualitatively describe features of the model. I propose some fundamental criteria for sorting out landscape models (2.1). Such criteria are tightly interrelated, but several different combinations of them are possible, and they could be exposed and considered in any order.

2.1 Sorting out fitness landscape models

I think that a major qualifying element about what kind of space a study is dealing with is the nature of a point in the space, that is to say, *what kind of factors get combined* in the space. Wright’s space was an allelic space: individual points represented (large) combinations of alleles. Today, sequence spaces combine nucleotides (A, C, T, G); “complex trait spaces” combine factors influencing (each with its continuous or discrete value) the development of a phenotypic trait; phenotypic spaces (or morphospaces) combine continuously varying traits; and so on. Several landscape spaces are purposely generic,

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[155] Why and how can a metaphor be the focus of so many researches? Can it be - as Pigliucci & Kaplan (2006) argue - that all these researches are misleaded, especially after Sergey Gavrilets’s work on holey landscapes (I.4)?

aiming to clarify general properties of landscape models: points are arrays of factors, so that factors can be interpreted elsewehere in various ways, e.g. alleles, nucleotides, physical quantities or even bits in a computer program. There is also a kind of landscape space combining gene *frequencies*: this is the space properly called "adaptive landscape" (differentiated from fitness landscape, cf. Gavrilets 1997, 2004, 2010), where each point in the space represents *a whole population* with a certain combination of the considered gene frequencies.

Another parameter worth considering is *how many "loci"* are there in the space. Inverted commas are compulsory since proper loci are present only in case of allelic spaces, or at most in "complex trait" spaces if factors coincide with genetic loci. In all other kinds of spaces, an *equivalent* of "number of loci" will be, e.g., sequence length in sequence spaces, number of traits in phenotypic spaces, number of factors in generic spaces, and so on. *Dimensionality* of the space (see II.2.2) is proportional to the number of loci (or analogue).

How fitness is assigned to combinations is another distinctive feature of a landscape space. A rich literature deals with landscape models in which fitness values are assigned to combinations *at random*,[156] either with statistical independence or specified patterns and strengths of *correlation* (Kauffman & Levin 1987, Kauffman 1993, 1995, Gavrilets 2004, Frenken 2005). So there

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[156] Fitness attribution is random - possibly with a given frequency for different fitness values - and uncorrelated - that is, fitness is calculated for each genotype independently from neighbors. These are simplification respect to Mendelian population, in which fitness is a *function of* allele combinations. But models od this kind are used to investigate very general properties of combination spaces.

are random uncorrelated landscapes, and random landscapes with varying degree of correlation. In a growing number of spaces, instead, fitness is attributed *empirically*.

Another important feature to sort out landscape models is *dynamics*. In many models there is no dynamics: the static shape of the landscape is the main focus, and that is enough in order to make possibility/impossibility, or plausibility/implausibility statements by means of background assumptions on evolutionary dynamics. In many models the dynamics consists in *adaptive walks*, i.e. trajectories of an individual point in the space.

2.2 Examples

Much literature focuses on landscapes of high dimensionality with constrained randomization of fitness, and deals with issues such as the fitness ultimately achieved (Rokyta et al. 2006), the role of mutation bias (Stoltzfus 2006), noisy fitness mappings (Levitan & Kauffman 1995), genetic robustness (Kim 2007), and whether the likelihood of becoming stranded at a submaximal fitness peak is reduced at high dimensionality (Gravner et al. 2007).

The already cited studies by Kauffman (cf. 2.2, Kauffman 1993, Kauffman and Levin 1987) are an example of generic, low-dimensional landscape models used to study general space properties like the relation among correlation, ruggedness, and expected outcome of adaptive walks. NK models, with N genes and K fitness interactions between genes, are tunably “rugged”. Correlated landscapes have great K, i.e. many interactions among genes. They are smoother than completely random landscapes (i.e., they feature fewer local optima, Weinberger 1990), and this influences (probabilistically) the dynamics of adaptive walks therein.

In sequence spaces (Maynard Smith 1962, 1970), a DNA sequence recurrently mutates to a finite number of alternative sequences (also Gillespie 1983, 1984, 1991). The block model (Perelson and Macken 1995), another simple correlated and tunably rugged landscape model, envisions genes or proteins as composed of distinct functional domains. Orr (2006) studied the block model tackling the assumption that the initial sequence ("wild-type") is probably vastly more fit than the many, essentially random, sequences possible in the space. To study adaptation in sequence spaces, he used extreme value theory (EVT).[157]

Many landscape models in literature have a few dimensions. Their dimensionality is incommensurably lower than that of Wright's Mendelian population (cf. II.1.2), often compatible with exact mathematical tractability and numerical simulation. Still, high-dimensional spaces are a more and more interesting object of study, requiring methods different from the numerical.

RNA models (Schuster et al. 1994) are a widely cited as one of the first examples of biologically relevant sequence spaces, where the nucleotide sequence directly determines the RNA's secondary structure, which in turn can meaningfully be assigned a fitness value. RNA models show that one RNA structure is produced by many sequences in the sequence space. Common, equally fit structures are *distributed* over the sequence space, and

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[157] Accordingly, in Orr's model fitnesses of one-step neighbors are always randomly drawn from a distribution that *changes throughout* the adaptive walk.

they can be easily reached through chains of nearly-neutral steps: Schuster et al. wrote, anticipating words that will be in centre stage also in Sergey Gavrilets's work (cf. section 3), that «the sequence space is percolated by extesive neutral networks».

More and more *empirical* studies (cf. Poelwijk et al. 2007) take advantage of metrics and methods developed for artificial fitness landscapes. In combinatorial chemical spaces (e.g. Stadler & Stadler 2002), rules associated with neighborhood and fitness are directly applied to guide chemical synthesis. In biochemistry, fitness-related parts of a protein can be focused: the entire sequence space of an average protein is intractable owing to the 'hyper-astronomical' number of variants (Voigt et al. 2000), and considering a region of the protein allows «some measure of protein function or some proxy for fitness» (Carneiro & Hartl 2010, p. 1750). In a recent review, Carneiro and Hartl point out that low-dimensional protein space (Maynard Smith 1970)[158] are presently amenable to experimental investigation. For example, all proteins in a protein space can be engineered, including possible intermediates in evolutionary pathways, for example, to resistance. Engineered proteins can be put to work in organisms, and their function measured. Empirical fitness landscapes can then be compared to theoretical ones (see above): Carneiro and Hartl (2010), for example, found a landscape significantly less rough than that expected with random permutations, and verified consistency with other studies of empirical fitness landscapes that include more sites (Aita et al. 2001, Lunzer et al. 2005,

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[158] The model of protein evolution by Maynard Smith (1970) has been widely used and became known as the strong-selection, weak-mutation model (Gillespie 1984).

Poelwijk et al. 2007). Rowe et al. (2010) recently studied the relation between protein affinity (analogue to fitness) and the combination of a 10-base sequence in the protein: they experimentally determined fitness for each combination of the sequence space, and they also obtained 3D visualizations of results by means of “classical multidimensional scaling plot” (third dimension visualized with colors). Visualization is not metaphorical in cases like this: the chart is exactly calculated from experimental data.

Simpson’s phenotypic landscapes have been object of formalization and research, at first by Lande (1976, 1979) and then by many others (see Arnold et al. 2001, 2008) who called this kinds of landscape spaces “Simpson-Lande landscapes”.[159] They are essentially phenotypic, but taking advantage of the biometrical tradition of population genetics they not only track the movement of populations in phenotypic space but also - using tools like the the G-matrix - genotypic effects (heritability, variance-covariance etc.). The G-matrix is a multivariate version of classic heritability, h2, that measures the additive genetic variance and covariance of traits within a population. In theory, the evolution of the population can be studied by looking at how the G-matrix reacts to an adaptive landscape.

2.3 Fitness landscapes and the origin of species

Among current landscape models (described through the landscape vocabulary), the emerging mathematical theory of speciation deserves special

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[159] Thanks to S. Andrew Inkpen, University of British Columbia, Vancouver, for useful discussion on this.

mention. *Fitness Landscapes and the Origin of Species* by Sergey Gavrilets (2004) is an outstanding review of the state-of-the-art research in the field:

> ...a theoretical component of speciation research is emerging now that is becoming comparable in its breadth and depth to the mathematical frameworks developed for studying changes within populations. I believe that we really do now have a comprehensive and general mathematical theory of speciation (p. 418).

Reading Gavrilets's book is surprising for the quantity and variety of mathematical analyses that are possible in population genetics, applied to speciation. My impression is that basically they *all* pertain to the theoretical structure which I named (II.1.1) Mendelian or Wrightian population genetics, dealing with gene frequencies and gene combinations. Different kinds of models, analyses and their results are placed side by side and combined, and landscape models are among the most important and flexible in this "patchwork".

The Bateson-Dobzhansky-Muller (BDM) model (Bateson 1909, Dobzhansky 1936, 1937, H.J. Muller 1940, 1942) is an example of a *low-dimensional allelic* combination space, where two alleles at different loci are incompatible, in the sense that their simultaneous presence in an offspring's genotype or in the genotypes of a (potential) mating pair reduces a corresponding fitness component (viability, fertility, or sexual attractiveness). The assumption allows reproductive isolation (and therefore, speciation) to result from a series of allele substitutions, each of which is unopposed by selection (i.e., it is neutral). The BDM model received interest in the 1970s and early 1980s (Nei 1976, Maynard Smith 1983, Barton & Charlesworth 1984, Kondrashov & Mina 1986), and underwent “multidimensional generalizations” by the consideration of more alleles (still one or two loci, Nei et al. 1983) and more loci (Walsh 1982, Werth & Windham 1991). The BDM model - a low-dimensional allelic landscape model - is today a crucial element of any theory of speciation although, as Gavrilets remarks, there is no evidence that interactions between a single pair of genes underlie reproductive isolation in real species: they typically differ in many rather than just two genes (cf. Wu 2001). The BDM model is the keystone of a way of using fitness landscape models to handle natural selection, sexual selection, and speciation altogether within a single unified framework.

A fundamental divide I see in Gavrilets’s review is between, on the one hand, *numerical or analytical* models that are suitable for low dimensionality, and, on the other hand, *statistical* analyses. The BDM model, for example, shows that

> ...if the genetic architecture of reproductive isolation is known, the dynamics of speciation can be modeled, *at least in principle*. However, first, the genetic architecture of RI is never known completely, and, second, the mathematical treatment *becomes extremely complicated as the number of genes involved increases*. […] it becomes much more fruitful to look at the dynamics of speciation expected *on average* (Gavrilets 2004, p. 158, my emphasis).

In my understanding, there are two styles of analysis or modeling. Statistical analyses and their results are striking for their *portability*: they are *insensitive to many details*, so that, for example, a statistical analysis of the accumulation of underdominant chromosome rearrangements (Walsh 1982) can be applied to other situations, e.g. underdominant loci (Gavrilets, cit., p. 152). Modeling with one style or another is a matter of choice. If for some models genetic details are largely negligible, taking such details into account yields gains and losses. Introducing "Part III, Speciation via the joint action of disruptive natural selection and nonrandom mating", Gavrilets (2004) writes

> In this part, I consider models of speciation in which the population genetic state is described explicitly in terms of haplotype or genotype frequencies. [This] allows one to treat frequency-dependent selection and get additional insights into the dynamics of speciation driven by spatially heterogeneous selection. The price for these gains is that only a very small number of loci (one, two, or three) can be handled in analytical models, whereas detailed studies of numerical models are prevented because of a very large number of potentially important parameters, the values of which are generally unknown (p. 234).

Disruptive selection is modeled by means of landscapes that are altered as a result of changes in the population genetic structure or in spatial location of individuals.[160]

Statistical and numerical models are, evidently, deeply *interdependent*, since on the one hand low-dimensional models *require* to hypothesize, postulate, or know characteristics of the high-dimensional space (like Wright

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[160] This type of alteration of landscapes is then a fundamental element, whose modeling was prevented in Dobzhansky's version of the landscape, not to speak of Dawkins.

did, cf. II.2.4), and on the other hand large-scale statistical analyses aggregate a large number of cases assuming their repeated low-dimensional pattern.

In sum, in *Fitness Landscapes and the Origin of Species* Sergey Gavrilets presents the fascinating results of a patchwork of numerical and statistical analyses, where the high-dimensional space of Mendelian population as well as other, low-dimensional genetic landscape models (allelic, nucleotidic, and more), enjoy a prominent position.

3. Gavrilets and holey landscapes

But are fitness landscapes *rugged* as Wright had concluded (II.2.4), or not? From the debate that grew around Gavrilets's landscapes, one could easily get the impression that the ideas on the Mendelian population space conveyed by Wright's surface metaphor should now be *replaced* by the ideas showed by the holey landscape surface picture (Fig. I.7). The following quotations may not be that informative, since they are brief and out of context, but they can serve - with my emphases - to communicate my point. Skipper (2004, p. 1182) reproduced Figure I.7.b and stated that «On Gavrilets' view, the adaptive landscape in multiple dimensions will have neither multiple peaks nor a single peak. *Instead*, the landscape will be the holey one in Figure» (p. 1181). And he continued: «The holes represent locations of incompatible combinations of genes and *replace* the peaks» (Ibid.).[161] Advocating a revolution in the research on properties of fitness landscapes, Pigliucci and Kaplan (2006) wrote:

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[161] Skipper goes on: «That is, the higher the number of possible gene combinations in a field of gene frequencies, the higher the number of incompatible combinations in that field. The incompatible gene combinations cause reproductive isolation within populations, which cause genetically driven speciation events».

«Fitness landscapes *may be best thought of* as "holey" (as in having holes); that is, as characterized by loosely connected networks (or areas) of high fitness separated by areas of low fitness» (p. 190). Pigliucci (2008) emphasized that Wright's picture «is deeply flawed» in light of Gavrilets's models, and that «*taking adaptive landscapes seriously* leads to quite different evolutionary scenarios from those classically formulated by Wright» (Ivi, p. 591). Kaplan (2008, p. 634), like Skipper, reproduced Figure I.7.b and remarked that «for very high dimensional systems, our intuitions about the "shape" of the landscape might be very poor, and *the actual topology* quite different. There might not, for example, be anything like ''peaks'' separated by ''valleys'' at all» (p. 632).

3.1 Gavrilets's restricted space

First of all, it is true that between Gavrilets's and Wright's pictures there are elements of important, perhaps unique continuity. Indeed, they are both *metaphors* in the *same sense* (cf. I.4, I.5, II.2.3), and of the very *same space or model,* i.e. the Mendelian population. The two surface metaphors are aimed to summarize and convey features of the Mendelian population, so they are to be interpreted in the same way: they are thought as *discrete* surfaces, where *points* correspond to positions in the space (i.e., individual allele combinations), near points represent one-step *neighbour* combinations in the space, so that distance on the surface is proportional to the number of substitutions in the space, and a *population* is thought of as represented by a cloud of points on the surface, and change over generations by Mendelian reproduction (i.e., recombination). Of course, Wright and Gavrilets share a confidence in the usefulness of a surface metaphor,[162] differently from other authors (Pigliucci & Kaplan 2006, Pigliucci 2008, Kaplan 2008). A *methodological* difference is that whereas Wright had obtained ideas on the features of Mendelian population (cf. II.2.4)[163] by means of intuition, experience, and heuristics (Wimsatt e.g. 1986, 2006, 2007a, b), Gavrilets gained his information from a kind of statistical analysis of the space he added to the "patchwork" (cf. 2.3) of mathematical tools of population genetics: percolation analysis (Gavrilets & Gravner 1997). At this point it is possible to notice that, due to the portability and invariance to details which is typical of statistical analyses, the results of percolation analysis apply - as Gavrilets points out - to any combination space with sufficient dimensionality, therefore also to *sequence* spaces (where individuals are considered combinations of nucleotides rather than of alleles, cf. 2.1, opening the possibility to consider mutation among the sources of movement, vs. 1.1).

All that said, a major *representational* difference between Wright and Gavrilets which, I think, has not been sufficiently emphasized in literature (see quotations above) is the following: Wright's picture portrays the *entire* space of Mendelian population, whereas Gavrilets visualizes *only a tiny subset* of it. Gavrilets's work results indeed, through the first analytic stage of

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[162] «The set of all possible genotypes is referred to as genotype space. The relationship between genotype and fitness is one of the most important factors in determining the evolutionary dynamics of populations. This relationship can be visualized using the metaphor of 'adaptive landscapes'…» (Gavrilets 1997, p. 307).

[163] As Provine (1986) pointed out, Wright was probably not explicit enough in crossing the boundary between quantitative models and qualitative reflections, cf. II.1.4.

percolation analysis, in the isolation of “giant components” or “nearly neutral networks” into the genotype space, and *these* sub-spaces are the objects holey landscapes portray. The two pictures differ not only in their shape, but also in what they represent. It is necessary to read any of Gavrilets’s works a little carefully to appreciate that Figure I.7.b actually depicts a part of the Mendelian population space, namely all and only those combinations whose fitness has a certain value. The space of combinations is thus incredibly reduced down to an equal-fitness sub-space. Since the vertical dimension in the surface picture represents fitness, the surface will be flat by definition, and of course the tautology that combinations with equal fitness fall within a flat plane in the metaphor is not the main focus of Gavrilets. What is so interesting, then, about this picture? It tries to capture a relevant analytic result of percolation analysis: due to the high dimensionality of Mendelian population space - a space which is not shown in any of Gavriltes’s pictures - any chosen fitness value is likely to pick up a large number of genotypes forming a giant component, also called a neutral network,[164] that “percolates” in the genotype space. Within a neutral network any genotype is connected with any other by a chain (or, more likely, many chains) of genotypes belonging to the network and differing by single substitutions. Figure 1b thus depicts a neutral network or giant component, not the whole genotype space. Rather than flatness - that counts as an assumption - interesting results about the surface are the existence of holes and the fact that *it is* a surface. In order to appreciate the novelty of equal-fitness combinations forming a surface,

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[164] Neutral network = «a contiguous set of sequences (or genotypes) possessing exactly the same fitness» (2004, p. 82).

imagine to mark, in Wright's surface picture (Fig. I.7.a), all genotypes having a particular fitness value: this would mean to cross-cut horizontally the surface, obtaining nothing more than a closed "contour line" around each sufficiently high peak. Contour lines would be thin and disjunct. Such (instead of Figure I.7.a) would be the image to correctly compare with Gavrilets's holey surface.

The existence within the Mendelian space of significant surfaces of equal-fitness combinations - called "ridges" by Gavrilets (1997, p. 307) - results from the extremely high dimensionality. Either considering sequence or allele spaces (Gavrilets e.g. 2006, p. 101) dimensionality is very high. In the alleles case, one could obtain a one-step neighbor of a genotype by picking one among thousands genetic loci and exchanging the present allele with any of perhaps dozens of alternatives available in the population; in the nucleotides case, any one of the billions nucleotides could be substituted with any one of its three alternatives. In both cases, speaking of diploid populations, the number of possible substitutions is furthermore squared due to paired homologue chromosomes.

The extremely high dimensionality of the genotype space is crucial for the existence of giant components (or neutral networks) of equal-fitness genotypes. Speaking intuitively, *if a genotype has so many neighbors it is very difficult that all of them differ in fitness*: not so many fitness values are available, indeed. Fitness varies between 0 and 1, and even dividing such range in more and more infinitesimal (therefore, less and less meaningful) intervals, the number of possible fitness values will be astronomically small compared to the number of possible genotypes. As Gavrilets explained in 2010, «one should not expect [all combinations] to have different fitnesses - there should be a lot of redundancy in the genotype-to-fitness relationship, so that different genotypes must have similar fitnesses» (2010, p. 55). He went on: «The question is how these genotypes with similar fitnesses are distributed in the genotype space and whether high fitness genotypes may form connected networks expanding through the genotype space». That is, if these equal-fitness combinations form, metaphorically speaking, a surface or ridge.

Speaking now in terms of Gavrilets's mathematical analyses, a very high dimensionality determines a very low *percolation threshold*. Such a threshold - worked out in physics (e.g. Ballobás 1985; Grimmett 1989; cf. also Kauffman & Levin 1987) - concerns the size that a cluster of the genotype space must have in order to likely form a giant component. If the size of the cluster compared to the whole genotype space is above the percolation threshold, it will form a giant component.[165] Gavrilets's analyses show that the extremely high dimensionality lowers the percolation threshold so that the formation of giant components in the genotype space is unavoidable, with any chosen fitness value, including high ones.

In sum, with huge dimensionality, and a consequent dramatically low percolation threshold, the genotype space will consist - as a very generalized

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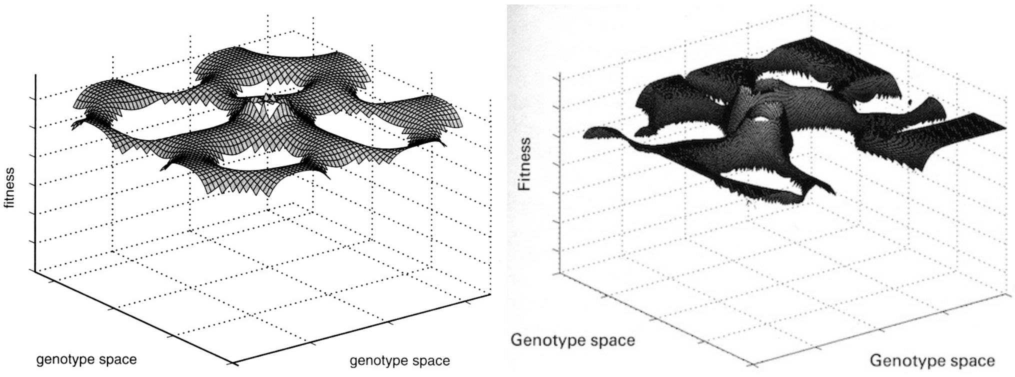
[165] The reason why I use terms like "cluster size" instead of the more used and correct term "frequency" is the same why I use "combination" instead of "genotype" as much as possible (cf. II.1.2): i.e., to avoid confusion. In the present context, the term frequency would exactly mean how often, in the genotype space, you run into genotypes that have the considered fitness value. Frequency quantifies identical fitness values that pertain to elements that are different, unique. In population genetics equations and in low-dimensional spaces, "frequency" means frequency of identical elements. Frequency-talk could then be misleading here (although technically more correct, in percolation analysis, as referring to "the frequency of a certain fitness value").

Figure III.1. *Holey fitness landscapes formed by genotypes within a narrow fitness band, forming a nearly neutral network (Left: Gavrilets 2004, p. 103; redrawn from Gavrilets 2003. Right: Gavrilets 2010, p. 59).*



condition - in a collection of neutral (or nearly neutral, see below) networks. Gavrilets's holey landscape represents a holey giant component, not a holey genotype space: every neutral network in the genotype space can be picked out and depicted as a surface.

Now there is an important move forward to be done. Gavrilets's early review (1997) actually defined two distinct combination spaces, the first highly unrealistic, the second more realistic. The first and unrealistic space was the only to be endowed with a pictorial representation: Figure I.7.b. Yet, the first space was only meant to «train our intuition» (p. 308) towards a comprehension of what the formation of a giant component is. I would call it the "1-0" Mendelian space since, by assumption, available fitness values in that space are only 0 and 1.[166] Well-fit genotypes (fitness = 1) will form a giant component if their frequency is above the percolation threshold - which is dramatically low when dimensionality is huge. And the giant component will

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[166] Fitness attribution in the "1-0" model is random - with a given frequency for 0s and 1s - and uncorrelated, cf. III.2.1.

be "drilled" with holes of genotypes whose fitness is 0. Above I ran over Figure I.7.b by interpreting it as if it was not about a whole Mendelian space. In fact, Figure I.7.b *can* represent the whole space in the "1-0" training case: the space there consists in a perfectly flat holey surface (fitness = 1) with holes set to 0. But that situation was not at all the main focus of Gavrilets's review.[167]

Gavrilets was much more interested in a space where fitness values *vary between* 0 and 1. Like in a realistic population, there is no clear-cut division between low-fitness and high-fitness individuals, rather, fitness is a continuous variable and an individual can have any fitness value in range. In such a space, Gavrilets set the arbitrary determination of a narrow interval of fitness, picking out only those combinations whose fitness is comprised between two values, w_1 and w_2. In a high dimensional space, percolation analysis yields that the caught combinations will likely form a giant

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[167] Gavrilets presents the "1-0" model over again with the aim of "training our intuition" (e.g. 1997, p. 307; 2004, p. 84; 2010, p. 57) but he makes short work of it as highly unrealistic, and quickly passes to the following, continuous distribution of fitness in the genotype space. However, I think that the "1-0" model could be of some interest beyond training intuition. Dividing the population in viable and inviable genotypes could indeed make some sense in the context of speciation, considering only a component of fitness which is relevant to it. The "1-0" model was worked out in Gavrilets & Gravner (1997), where they declared: «Evolution of reproductive isolation is influenced (at least potentially) by many genetical, ecological, developmental, behavioral, environmental, and other factors in different ways. If one wants to make the discussion less speculative, one should necessarily concentrate on only some of them while neglecting others. We will consider only post-zygotic isolation manifested in (and defined as) zero fitness of hybrids» (p. 52). More in general, «Different fitness components are described by very different fitness landscapes. Combining them in a single fitness landscape may not be easy» (2010, p. 47). The necessity of choosing some fitness dimension, and the particular interest of the "viability" component, was again expressed very recently by Gavrilets: «In the most common interpretation, a fitness landscape specifies a particular fitness component (e.g., viability, that is, the probability to survive to the age of reproduction)...» (Ivi, p. 46). The question whether the "1-0" model is realistic or not depends, I understand, on the component of fitness that one wants to consider. Viability could perhaps be modeled as a binary, "1 or 0" component.

component just like the 1s in the "1-0" model. And this will happen even if we set w_1 and w_2 to high values, thus picking up a relatively small cluster of the space where fitness varies slightly in a continuous fashion: a nearly neutral (as opposed to completely neutral) network will form,[168] which Gavrilets also calls a "band" that continuously extends throughout the genotype space.

Despite nearly neutral networks having been the main interest of Gavrilets's review, no picture of them was shown for some years, until pictures like those in Figure III.1 began to appear (e.g. 2003, 2004, 2010). Perhaps the delay was due to temporary lack of visualizing techniques. Meanwhile, Figure I.7.b was reproduced, and stood for the holey landscape. Interestingly, in 2008 Kaplan reproposed Fig. I.7.b observing in the caption that «More recent images by Gavrilets' depict the surface as "nearly flat" rather than flat, but are otherwise similar» (2008, p. 634). In opposition, I would claim that Fig. I.7.b picturing the "1-0" model *was not a good* visual metaphor for representing the nearly neutral networks that form in a Mendelian population where fitness varies continuously. And among the important characteristics emphasized by pictures like those in Fig. III.1, I would count the idea that holes consist in genotypes that are either below or above the w_1-w_2 fitness band, provided that they do not belong to the network.[169]

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[168] Nearly neutral network = «a contiguous set of sequences (or genotypes) possessing approximately the same fitness» (2004, p. 82).

[169] Why are fitness "tips" of Mendelian population left out? Mutation rate (Wrightian non-recurrent mutation, see 1.1), and Gavrilets says also "absence of right mutations" (2004, p. 103) and "recombination and gene flow" (p. 104).

> Overstating just to make the point, tips are largely irrelevant because the population is almost never able to climb there [...]. Valleys are largely irrelevant because natural selection will quickly move the population from there uphill, or the population goes extinct. What is most relevant for continuous genetic diversification and speciation are the ridges of high-fitness genotypes that expand [percolate] throughout the genotype space (2004, pp. 102-103).

Summing up, I would say that it is true that Sergey Gavrilets and colleagues have approached the genotype space with mathematical techniques capable of handling a biologically realistic number of dimensions. Indeed, these methods work *only* with a suitably huge number of dimensions. Brett Calcott recognizes in Gavrilets's work two «steps» in which different models are deployed: the first step (see Gavrilets 2004, chp. 4) deals with the static structure of the genotype space, and focuses on the likelihood of the presence of neutral ridges; the second step (Gavrilets 2004, chp. 5 and over) develops low-dimensional models in which - relying on step one - a neutral structure is assumed. Here I use the term "stage of analysis", I agree in seeing the two stages characterized by different orders of dimensionality. In what could be called a "stage one" of analysis Gavrilets and colleagues picked giant components out of the Mendelian space, picturing them as nearly flat surfaces, appreciating their connectedness and the presence of holes. What seems not true is that their analyses have blown away the rugged landscape to replace it with a flat, holey one. Indeed, no alternative picture of the *whole* genotype space came up.

3.2 Model, patchwork, and "how possibly" questions

In II.3.2, I proposed to consider Mendelian population as *the* model in a theoretical structure called Mendelian population genetics. The notion of model I employed is that of a «stable target of explanation», again and again approached and understood - but never exhausted - by scientists by means of statistical equations and analyses. In II.2.1 and II.2.2, I sketched out the existence of several other "landscape models", autonomous but built on imitation of Mendelian population (a fact favored, perhaps, by the success of the landscape language). In particular, low-dimensional genetic landscape models are combination spaces treating numerically two, three loci, and a few alleles at a time. In II.2.3, I described Gavrilets's book *Fitness Landscapes and the Origin of Species* (2004) as a fascinating patchwork of low-dimensional genetic landscape models and statistical analyses of high-dimensional Mendelian population. Importantly, *in many cases ideas about the high-dimensional space take part into the fundamental assumptions of low-dimensional models*.

In his book, Gavrilets announces an ongoing extension of population genetics to be accounting for speciation, an important phenomenon for which mathematical models have been lacking for several decades (pp. 417-418). I would like to re-describe this advocated extension in terms of my view of Mendelian population as a model. In II.3.2, I remarked that viewing a model as a target of explanation leaves open the problems of representation and explanation: while the model is studied more and more, what does the model represent? What does it explain? I hinted to a pragmatic solution to these problems: scientists decide when, how, and what the model they are studying describes or explains. Now, I think that the patchwork of statistical analyses and low-dimensional models presented by Gavrilets *is making Mendelian population a good model for speciation*, whereas before it was not. Low-dimensional BDM models (cf. 2.3) were endeavours to see if Mendelian population model could have been relevant for speciation: they formalized reproductive isolation as genetic incompatibility among alleles, and modeled its evolution. Gavrilets's percolation analysis showed sub-spaces in the Mendelian population space - i.e., nearly neutral networks - that, with their (metaphorically speaking) holey structure, would not only justify (the assumptions of) low-dimensional BDM models, but also opened the possibility of a large scale version of BDM incompatibilities in the high-dimensional Mendelian space.

A way by which a model (target of explanation) can become a model for some phenomenon in the world is through "how possibly" questions. Plutynski (2001, 2004, 2005, 2006a) repeatedly pointed out that mathematical models can be built as answers to "how possibly" scientific questions (cf. Brandon 1990).[170] This is exactly the case, I think, for Gavrilets's percolation analysis. His "how possibly" question could be formulated as follows: how is it possible that a population which is kept in a narrow range of fitness values splits in reproductively isolated groups, developing those genetic incompatibilities that are predicted by the biological concept of species? The

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[170] Based on Dray (1957). See also Lewontin (1985b, 2000), O'Hara (1988), Resnik (1991) and a recent elaboration by Forber (2010).

best place to look at in order to understand the source of such question is, once again, Sewall Wrights's landscape.

Wright was already aware of what has later become known as the "peak shifting" or "valley crossing" problem. In Wright's models the population - pictured as a cloud on the fitness landscape (Fig. I.7.a) - could have been found distributed around a peak. Selection pressure prevents the population from sliding down below a certain fitness value. At the same time, mutation and random drift prevent it from gathering tight at the very top of the peak. In sum, the population is kept in a range of fitness between two values, w_1 and w_2 if we use Gavrilets's notation. «A finite population subject to mutation is likely to be found on a fitness level determined by mutation-selection-random drift balance» (Gavrilets 1997, p. 310). And «Among different percolating fitness bands, those at relatively high fitness levels are of particular importance. If they exist, then biological populations might evolve along the corresponding nearly neutral network...» (2004, p. 102).

Wright wondered how, in this situation, the population could ever move from where it is to reach another peak. For example, a drastic reduction of population size (what we call a bottleneck today, see e.g. Hartl & Clark 2007, pp. 122-3) would increase the incidence of chance, allowing the cloud to slip off the peak and move to lower fitness values, but Wright's calculations yielded an inevitable result of such a movement: extinction down in the bottom of a low fitness valley. The same outcome was predicted for a relaxation of selection pressure, that would allow the cloud to expand down the slopes, but with null probability of finding and climbing up another peak.

How is peak shifting possible, if a population cannot outbound the narrow w_1-w_2 fitness band in which it is kept by a balance between natural selection and random factors, since any widening of such a band yields sinking in a valley of low fitness and extinction? The question must have been attractive to Gavrilets, who was interested in studying speciation. Indeed, the criterion of genetic reproductive isolation by hybrid inviability - employed by the Biological Species Concept - is clearly allowed and represented on a rugged landscape (Fig. I.7.a). It is sufficient to assume two sub-populations resting on separate peaks: their hybrids will likely fall in valleys of low fitness, just like in the BDM model,[171] thus enabling us to consider them different species according to the BSC. The problem is, again, the process of peak shifting: how is it possible that a population splits into multiple, reproductively isolated populations despite the barriers constituted by fitness valleys?[172]

In a sense, Wright and Gavrilets can be seen as puzzled by the same "how possibly" question, shaped by the same assumptions. In another sense, their questions are different: I would say that Gavrilets is more interested in valleys, whereas Wright in peaks. Gavrilets himself pointed out that the reach of a local peak raised «two important questions. The first is how fitness can be increased further. The second is how new species can be formed» (2004, p. 36). They represent, respectively, Wright's and Gavrilets's interests. Wright

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[171] Or, if they will fall on another peak by chance, they will result isolated and lost within a few generations.

[172] «...describing the splitting of populations» (Gavrilets 2004, p. 33). «...I will view the dynamics of speciation as the dynamics of genetic divergence between different populations (or between parts of the same population) resulting in substantial RI»; «...ultimately speciation is a consequence of genetic divergence»; «reproductive isolation is defined as reduction or prevention of gene flow between populations by some differences between them» (2004, p. 9).

was interested in adaptive evolution, as he famously wrote «The problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field. In order for this to occur, there must be some trial and error mechanism on a grand scale by which the species may explore the region surrounding the small portion of the field which it occupies. To evolve, the species must not be under strict control of natural selection. Is there such a trial and error mechanism?» (Wright 1932, pp. 358-359). Wright's "how possibly" question concerned the population finding the overall optimum on the landscape, as opposed to getting stuck on a local peak. He proposed a solution - the "shifting balance" process - that remained controversial, and the peak shifting problem stood.[173] Gavrilets linked this problem to speciation: "the problem of speciation as Gavrilets sees it" is that of a mechanism by which a population may split upon the fitness landscape, so that the resulting groups are

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[173] An important information, though not central for the problems at issue here, is that Wright used the adaptive landscape diagram to demonstrate the need for an apparently complicated process of "shifting balance" for the ideal conditions for evolution to be satisfied. Evolution on the shifting balance process occurs in three phases: Phase I. Random genetic drift causes subpopulations semi-isolated within the global population to lose fitness. Phase II. Selection on complex genetic interaction systems raises the fitness of those subpopulations. Phase III. Interdemic selection then raises the fitness of the large or global population. Gavrilets (e.g., 1997, p. 307) reported persistent controversy on shifting balance, which assumed a condition of subdivision of the population in "races" distributed on different peaks (Lande 1979, 1985; Barton & Rouhani 1993; Rouhani & Barton 1993; Gavrilets 1996; Coyne et al. 1997, 2000; Peck et al. 2000). Indeed, low-dimensional landscape models (e.g. one-locus two-alleles, two-locus haploid, cf. 2.2) allow peak shift only at exceedingly strict conditions (for e.g. population size, or depth of valleys). Overall, «It is highly improbable that stochastic transitions requiring the majority of the population to pass through the bottom of a fitness valley are a major mechanism of genetic divergence (and speciation) of natural populations on a large scale» (2004, p. 77). Similar counterarguments are reported by Gavrilets about another solution proposed through time to the same question: founder-effect speciation (cf. Carson 1968; Templeton 1980, 1996; Rice & Hostert 1993; Gavrilets & Hastings 1996). Gavrilets concludes that «there must be some kind of an error or a weakness in the chain of arguments...» (2004, p. 80) and the missing link is, of course, the existence of giant components in the genotype space brought to light by percolation analysis (3.1).

reproductively isolated by hybrid inviability, i.e. a valley. Gavrilets's interest focuses on how reproductive isolation can be attained.

Wright's and Gavrilets's "how possibly" questions have much in common, but they differ nonetheless. So much so that the existence of holey, nearly neutral networks is an excellent answer to Gavrilets's question, not at all to Wright's. Gavrilets is interested in holes, not in peaks: «Consider a genotype g_0 on the largest component. As we move along a chain [...] of viable genotypes away from g_0, where g_i and g_{i+1} differ in a single gene, after some i steps any offspring of g_0 and g_i will be inviable. In other words, sooner or later genotypes g_0 and g_i will happen to be on opposite sides of a 'hole' in the fitness landscape. According to the biological species concept, genotypes g_0 and gi can be considered as representing two different species» (Gavrilets 1997, pp. 308-309). The holey landscape gives an answer to a "how possibly" question about speciation: «Speciation occurs when a population evolves to a genetic state separated from its initial state by a hole» (Gavrilets 2004, p. 104). Problems about adaptive evolution are out of reach.

I called the percolation analyses of Mendelian population the "stage one" of Gavrilets's work. Stage one - a statistical analysis of high dimensional spaces - offers the theoretical possibility of genetic speciation under ordinary conditions where the population is kept in a narrow fitness band by selection and random factors. Stage one concludes that, by explaining how, «significant genetic divergence and speciation do not require overcoming strong natural selection» (2004, p. 105). The "how possibly" answer opens the way for a second stage, i.e. the building of a set of advanced (low-dimensional and analytical) speciation models that Gavrilets, in a recent essay (2010), calls "spontaneous clusterization" models (reviewed in Coyne & Orr 2004; cf. Gavrilets 2004, p. 105). They «can be imagined as population fragmentation on ridges in a holey fitness landscape with different clusters becoming reproductively isolated because they happen to be on opposite sides of a hole in the landscape» (Ivi, p. 62). «Spontaneous clusterization models include those describing the accumulation of Dobzhansky-Müller genetic incompatibilities, speciation by hybridization, divergence in mating preferences, or allochronic speciation via divergence in the timing of mating. Spontaneous clusterization can happen in any geographic context (i.e., allopatric, parapatric, or sympatric). The fitness differences between genotypes which may be present are not of particular importance» (Ibidem). As pointed out by Calcott (2008), spontaneous clusterization models (stage two of analysis) are low-dimensional,[174] and they make *the assumption* of neutrality which is supported by the high-dimensional analysis in stage one.

3.3 Conclusion

"Holey fitness landscapes", resulting from Sergey Gavrilets's statistical analyses, are undoubtedly a fascinating new element in the patchwork of instruments by which scientists are understanding better and better the

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[174] Brett Calcott (2008), analyzing Gavrilets's book (2004), noticed the discontinuity between the two stages of analysis, treated in different chapters: «Given the importance of high dimensions in the previous chapter, it is surprising that the model Gavrilets uses to introduce speciation on holey landscapes is one with very few dimensions» (p. 647). Seeing stage one as a legitimating answer to a "how possibly" question makes the discontinuity less surprising: models in stage two are low-dimensional models, whose assumptions are made possible by high-dimensional stage one. «An assumption of neutral change, rather than increasing the number of dimensions, is sufficient to make a difference in these models of speciation» (Ibidem).

Mendelian population, making it a model *also* for speciation, and also for those cases in which selection seems to *prevent* speciation. By mathematically demonstrating the existence of nearly neutral, holey networks within the genotype space, Gavrilets opens the "stage two" for himself and other modelers, that is, the building of "spontaneous clusterization" models in which a population - kept in a certain, narrow fitness "band" by standard population genetics factors - fragments in different clusters that become reproductively isolated because they happen to be "on opposite sides of a hole" of genetic incompatibility in the space.

A direct visual comparison between the two metaphors, Wright's rugged surface and Gavrilets's holey, is completely improper because Gavrilets's picture (whose most proper versions are alike Fig. III.1) portrays a tiny portion of it, i.e. a nearly neutral network *within* the genotype space. On the one hand, Gavrilets's analyses cast doubts on the results of Wright's use of intuition, laboratory experiences, and perhaps heuristic procedures up from the available, single-locus, diallelic models (cf. II.2.4). On the other hand, assumptions like epistasis and the existence of multiple optima are not directly challenged by Gavrilets's studies; moreover, the operation of natural selection and drift *are needed* among the *assumptions* of Gavrilets's analysis. The implications and openings of neutral networks for Wright's "how possibly” question about adaptation have to be explored further.[175] Gavrilets can be seen as demonstrating the irrelevance of the “peak shifting problem” posed by Wright’s landscape, but such irrelevance *is relative* to a “how possibly” question about speciation, not about adaptation, which was Wright’s concern.

Mendelian population stands there, as a «stable target of explanation» (cf. II.3.2), exposed to skill and creativity of mathematical geneticists who cannot calculate individual combinations, their fitness, and the influence of fitness on the production of new combinations in the population. They work with their patchwork of numerical models and statistical analyses, gently guided by “how possibly” questions on the biological world.

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[175] About adaptive evolution, Gavrilets does not always remain mute. With his lab, he recently got particularly interested in adaptive radiation (e.g. Gavrilets & Vose 2005, 2009). However, these are recent and less developed studies. Being mainly interested in speciation, for several years Gavrilets remained vague on adaptation, seeing it as a process happening on a smaller time scale than speciation, and hinting to a process called “extra-dimensional bypass” (from Conrad 1990), consisting in the passage from a giant component to another with higher fitness.

CHAPTER IV

Landscapes and the Extended Synthesis

> I will briefly examine how Wright's ideas have fared in the recent debate about the conceptual foundations of evolutionary biology and what, if anything, they may contribute to a forthcoming Extended Evolutionary Synthesis (Massimo Pigliucci 2008a, p. 592).

Recently, the adaptive landscape appeared several times associated to the Extended Evolutionary Synthesis (e.g. Pigliucci & Kaplan 2006 chp. 7, Pigliucci 2008 a, b, Kaplan 2008, Pigliucci & Müller 2010a), mainly in conjunction with Gavrilets's works on holey landscapes (see III.3). According to my analysis, however, the treatment of the adaptive landscape in such contexts suffers from some mistakes and conflations, both historical and epistemological. In this chapter, I answer precisely to Massimo Pigliucci's statements on adaptive landscapes (sect. 2), but I also examine the Extended Evolutionary Synthesis (sect. 1). Can the adaptive landscape play a role in the

Extended Evolutionary Synthesis (EES) as it did for the MS (cf. chapter I)? It *can* play a role, I argue (2.3), if correct and deep conceptual analysis is maintained, with no forcing of consolidated tools into new urgencies of research. Such a treatment, if demanding, should be *expected* from the ambitious project of EES. Arguments on synthesis are continued in the Conclusion of my work, where I let aside a view of synthesis as a product (the idea of a "synthetic theory"), recovering a *processual* view of synthesis, as an "approach" and a "continuing promise" in evolutionary biology. With the processual, communicational "approach view" of synthesis, I look once again at the utility of the adaptive landscape, updated with all its versions and developments seen in chapter III, and I also express some thoughts on the role of philosophy of biology.

The EES is a recent perspective on contemporary evolutionary biology, advocating - in face of the proliferation of new concepts, discoveries, and fields in evolutionary biology - the necessity of an *extension* of the Modern Synthesis (MS) that was carried out in 1930s and '40s (cf. I.3.2, II.1). One of the main EES proponents is philosopher and biologist Massimo Pigliucci. [176] One of his several steps in that direction was a paper entitled "Do we need an extended synthesis?" (2007), where he lamented that for many biologists «the

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[176] Pigliucci not only relies on scientific studies on evolvability, evodevo etc. (see below). He also reports *the call* for EES from many other authors like R.L. Carroll (2000), Love (2003a), Kutschera and Niklas (2004), Müller (2007), Rose and Oakley (2007), and S.B. Carroll (2008), prompting further scientific debate (Pennisi 2008, Whitfield 2008). An important step was the Altenberg meeting in 2008, resulted in proceedings (Pigliucci & Müller 2010a), where Pigliucci involved Beatty (2010), Gavrilets (2010), Wilson (2010), Wray (2010), Purugganan (2010), Jablonka & Lamb (2010), Odling-Smee (2010), Fernando & Szathmary (2010), Kirschner & Gerhart (2010), Newman (2010), Müller (2010), Jablonski (2010), Wagner & Draghi (2010), together with Pigliucci humself (2010), and the two philosophers Love (2010), and Callebaut (2010).

MS provides *the* framework for current and future evolutionary biology, with no need to revisit the fundamentals» (Pigliucci 2007, p.), whereas a series of concepts and research fields like evolvability, plasticity, evo-devo, modulatity and many others would *require* an extension of that synthesis.

In chapter I, I chose to view the MS as a process following Mayr's ideas and figuring out the possible role of the adaptive landscape metaphor. But, as Dudley Shapere (1980) observed, «"Synthesis" is one of those words that involve what philosophers call a "product-process ambiguity"», and indeed Massimo Pigliucci and the other advocates of the Extended Synthesis (e.g. Pigliucci & Müller 2010a, b) clearly view MS as *the product* of a process. They consider the MS a conceptual *object* fundamental for biological research. Here I ask about *the structure* of such an object, observing that structure (and even what is to be *intended for* a structure) is still to be defined in Pigliucci's project, for what concerns not only EES, but also MS. More philosophical work is needed on the general meaning of the EES, as this is perfectly understandable if we think about the scope of a process akin to MS (cf. I.3) granted the possibility to treat its results synchronically as a product. The advocates of the EES themselves admit:

> It took almost four decades for the Modern Synthesis to take shape, and we certainly do not expect to achieve an equivalent result with a single edited volume. Others, including many not represented here, have advanced along similar intellectual lines, and more will undoubtedly do so in the near future (Pigliucci & Müller 2010a, p. 14).

In section 1.4, I present some promising philosophical ideas towards a better understanding of the Modern Synthesis as a product, and of the process of its extension and revision: a neo-Lakatosian hypothesis being developed by Telmo Pievani (2010), bearing close affinities with Stephen Jay Gould's view (2002) of the structure of evolutionary theory.

In section 2, I discuss Pigliucci's treatment of the adaptive landscape. I notice some historical-epistemological mistakes, such as the idea that Wright would have been concerned with phenotypic evolution, or even evolvability, and that he should have worried about the genotype→phenotype mapping function and the relation between genotypic and phenotypic landscapes. I hypothesize that conflations depend not only by an insufficient articulation of the analysis (which I tried to obviate in this dissertation), but also from an urgency of defending the "conceptual pillars" of the Extended Evolutionary Synthesis.

1. The structure of Modern and Extended Syntheses?

1.1 Concepts

What kind of object is MS? Answering this question seems fundamental to understand what modifications should EES bring *to* MS - and also what a role the adaptive landscape might play thereby. In EES writings the MS is often qualified as a "conceptual framework". Pigliucci repeatedly manifested his primary interest in *conceptual* foundations:

> conceptual understanding informs lines of inquiry in biology (Pigliucci & Kaplan 2006, p. 10).[177]

So, what is to be expected from EES is a conceptual analysis of adaptive landscapes, with a direct relation to conceptual foundations of evolutionary biology.

Massimo Pigliucci often talks about "conceptual pillars", "building blocks", "pivotal novel concepts" of EES, seemingly adopting a very loose conceptual structure: the EES would presently be *a collection of concepts* including mainly evolvability,[178] phenotypic plasticity,[179] epigenetics, genotype-to-phenotype map, modularity, complexity, and evodevo.[180] There has been controversy on some of these concepts, and in some debates - as happened before the Modern Synthesis according to Ernst Mayr (1980, p. 29) - "the pendulum swings too far", and polarization of supporting and opposing positions take shape well beyond theoretical utility. For several years EES gathered around, promoted and defended concepts that are now also collected in the book *Evolution: The Extended Synthesis* (Pigliucci & Müller 2010a). But the MS as a process was allegedly much more than a collection of defenses of some debated concepts. Advocates of the EES agree - and indeed emphasize -

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[177] This line is from "Evolutionary biology and conceptual analysis", the prelude to Pigliucci & Kaplan's book (2006) which aspired already (like the EES) to «a more compelling overall picture of evolution» (p 11).

[178] Cf., e.g., Wagner & Altenberg (1996), R.L. Carroll (2002), Love (2003b), Wagner (2005), Hansen (2006), Hendrikse et al. (2007), Colegrave & Collins (2008); Pigliucci (2008).

[179] Cf., e.g., West-Eberhard (1989), Scheiner (1993), Pigliucci (2001), Schlichting & Smith (2002), West-Eberhard (2003), Borenstein et al. (2006).

[180] Cf. with special reference to the Extended Synthesis: Laubichler & Maienschein (2007), Müller (2007, 2008), Sansom & Brandon (2008).

that the *process* of MS yielded a conceptual *product* (again, MS). Will EES do the same? And what idea does it convey of MS as a product?

In their introduction "Elements of an Extended Synthesis", Pigliucci and Müller (2010a) take care of reporting a "textbook summary" of MS:

> The major tenets of the evolutionary synthesis, then, were that populations contain genetic variation that arises by random (i.e., not adaptively directed) mutation and recombination; that populations evolve by changes in gene frequency brought about by random genetic drift, gene flow, and especially natural selection; that most adaptive genetic variants have individually slight phenotypic effects so that phenotypic changes are gradual (although some alleles with discrete effects may be advantageous, as in certain color polymorphisms); that diversification comes about by speciation, which normally entails the gradual evolution of reproductive isolation among populations; and that these processes, continued for sufficiently long, give rise to changes of such great magnitude as to warrant the designation of higher taxonomic levels (genera, families, and so forth) (Futuyma 1986, p. 12).

Are textbook summaries good targets for philosophical arguments about the structure and extension of theories? Pigliucci and Müller seem to think that Futuyma's textbook summary effectively represents the MS as a vision, perhaps a narrow "tunnel vision" for evolutionary biology. But, in an essay in the very same book edited by Pigliucci and Müller, Alan Love (2010) uses another summary *by the very same textbook*,[181] to argue for the exact contrary:

> In Futuyma's second edition chapter on the origin of novelties, a brief defense of the Modern Synthesis perspective reveals a commitment to a broad rather than a narrow representation of evolutionary theory (Love 2010, p. 416).

So we have *two* summaries from the same textbook (Futuyma 1986). One, at the beginning of the book (p. 12), is used by Pigliucci and Müller to argue for the narrowness and closure of MS. The other, in an advanced point of the book (p. 416), is cited by Alan Love as an example of the openness and intrinsic integrative nature of MS. If the coexistence of divergent rethorical uses of the same textbook demonstrates something, it is that *textbooks and textbook summaries are unreliable sources, at least for gaining access to elements important for theory limitation and extension*. Summaries should perhaps be taken for what they are: oriented, partial descriptions, pragmatically directed to some communicational aim (pedagogic, didactic, introductory, defensive, or whatever).[182]

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[181] The summary by Futuyma cited by Love is: «The power of neo-Darwinism lies in its generality of explanation. But like most general theories, it is highly abstract. It gains full explanatory power when concepts such as gene frequencies and selection are given empirical content by applying them to real features of real organisms: behavior, life histories, breeding systems, physiology and morphology. When this is done, however, new questions appropriate to those particular features emerge and context-specific factors must be added to the theory» (Futuyma 1986, p. 440).

[182] For a similar problem, see Godfrey-Smith (2009), p. 17.

1.2 Structure

Is a (foundational) conceptual framework more than a collection of “conceptual pillars” as “building blocks”? Does it have some kind of *structure*? And if so, what is the structure of MS? The question was asked and answered by a few authors in philosophy of biology. One of them was Stephen Jay Gould. In his book *The Structure of Evolutionary Theory* (2002), Gould talked about a continuum between two extremes of being demanding towards theory structure. On one extreme Gould put the absence of structural requirements, which he assimilated to David Hull’s (1988) idea of historical continuity: in this extreme, evolutionary theory would have no structural, conceptual identity, rather its identity would derive exclusively from genealogical continuity (in a populational, or “conceptual lineage” view of theories). On the other extreme Gould put «the “too much” of long lists of ideological fealty, superficially imbibed or memorized, and then invoked to define membership in ossified cults rather than thoughtful allegiance to developing theories» (Gould 2002, p.). Between the “too little” and “too much”, between the purely *genealogical* and purely *essentialist* extremes, Gould claims to be choosing a “Goldilockean solution”.[183] Theories are historical entities with genealogical continuity, but

> Theories [...] also feature inherent “essences,” implicit in their logical structure, and operationally definable as minimal sets of propositions so

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[183] His particular solution is that «a Darwinian essence can be minimally (and properly) defined by *three central principles* constituting a tripod of necessary support, and specifying the fundamental meaning of a powerful system that Darwin famously described as the “grandeur in this view of life». The three principles are for Gould agency, efficacy, and scope of natural selection.

> crucial to the basic function of a system that their falsification must undermine the entire structure, and also so necessary as an ensemble of mutual implication that all essential components must work in concert to set the theory's mechanism into smooth operation as a generator and explanation of nature's order.

In advocating a Goldilockean solution, Gould fought against for example what he called the "hardening" of the Modern Synthesis (1983), but other views of the structure of evolutionary theory can be seen as occupying the essentialist extreme.

The semantic view (e.g., Lloyd 1984, 1988, Beatty 1981, Thompson 1989) tried to formalize evolutionary theory as a family of mathematical models growing out from population genetics. The semantic view cannot be seen as occupying Gould's essentialist extreme, I think, since theory is seen as constantly moving (although only through mathematical derivations, integrations and complications). On the other hand, however, the semantic view concentrated on a deductive, logic-mathematical structure, and (like, e.g., Lewontin 1980, see I.3.2) saw perhaps the Modern Synthesis as a one-way, progressively more complete application of that advanced mathematical structure to all biological fields. The semantic view of evolutionary theory, with a dynamic but mathematical-deductive conceptual structure, was anyway a very narrow project and it failed to capture the complexity of evolutionary biology.

After the semantic view, attention to models in biology was deepened and simultaneously unrooted from an attention to the general structure of evolutionary theory (and so, of MS). Margaret Morrison (2007) recently called for a «redress of the imbalance» between models and "theory". Although the concept of theory is polysemic and complex, Morrison's momentum recalls exactly the problem about the structure and nature of the Modern Synthesis possibly substantiating it beyond mere genealogical continuity of evolutionary theory and models.

1.3 Change

Where does the EES place MS and itself on Gould's essence-genealogy continuum? MS is frequently described as a "conceptual framework", as an "edifice" or "structure" built by "architects", a structure capable of including and excluding ideas as being parts of it or not:[184]

> ...being consistent with the MS is not at all the same thing as being part of the MS! (Pigliucci & Muller 2010a, p. 4).[185]

The MS is thus described as an "established framework" in evolutionary biology, featuring "tenets". Tenets and "assumptions" are not always detailed, but for example Pigliucci and Müller see "gradualism", "externalism", and "gene centrism" as «basic restrictions and methodological commitments» (p. 13) of the MS, i.e. tenets that have been necessary for the MS to work.

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[184] The exclusion/inclusion binomial emphasizes, I think, that product and process in synthesis are in continuity despite our analytical separation: exclusion begins in the process, and is then operated by the product (i.e. the achieved theory, cf. concept o positive and negative heuristics in Lakatos, 1978). Like Gould (1983), Pigliucci & Müller notice that MS's emphasis on gradualism and adaptation may have excluded some typically macroevolutionary patterns: «…the "synthesis" *was achieved* as much through exclusion as it was through integration» (p. 7).

[185] Notice the difference with Mayr's synthesis (1980), based on consistency and minimal agreement (cf. I.3.2).

Nonetheless, for Pigliucci and Müller, assumptions of the MS can be "relaxed" and tenets «can be modified, or even rejected, without generating a fundamental crisis in the structure of evolutionary theory» (2010a, p. 10).

But, if in some passages a *modification* of MS is evoked, in others Pigliucci and Müller seem to suggest just a *shift of emphasis*, in particular:

> [the] shift of emphasis from statistical correlation to mechanistic causation arguably represents the most critical change in evolutionary theory today (p. 12).

Pigliucci and Müller refer here to the possibility of addressing «the mechanistic conditions for the origin and innovation of traits» (p. 13), the mechanisms of trait generation, fixation and variation, through what they call "how" questions, as opposed to correlational questions of the MS.

Besides the EES as a modification of the MS, or as a shift of emphasis in the MS, at times the EES is presented as a *problem-based addition* to MS, a "conceptual augmentation" (p. 4), again *without* modification:

> ...one may ask whether any of the general principles of the population-dynamical core of the classical theory are compromised by these new views. Well no. The concepts we bring together in this volume for the most part do not concern population dynamics, our understanding of which is improved but not fundamentally altered by the new results. Rather, the majority of the new work concerns problems of evolution that had been sidelined in the MS and are now coming to the fore ever more strongly (p. 12).

There are perspectives that see the biological phenomena listed by EES proponents as symptoms of the need for an entirely new theory to supplant the neo-Darwinian synthesis (e.g. Fodor & Piattelli Palmarini 2010). Apart from these "perspectives", lying completely outside the scientific field of evolutionary biology, EES encounters resistance: some researchers are not yet persuaded that the the newly described phenomena have sufficient relevance and empirical support to justify a broad theoretical revision; at the opposite, more "continuist" perspectives see evolutionary theory as *already* grown, although perhaps in ways different from the establishment of a new synthesis.

All these views seem to elude a question: *does* the MS have a conceptual structure? What kind of structure is it? And how is it supposed to change into another structure, e.g. EES? In itself, the EES project (cf. Pigliucci & Müller 2010) appears still open and *in fieri* along theoretical and epistemological (as well as empirical) dimensions. I shall present in the next section a promising view on the structure of synthesis.

1.4 Research program

> Philosophers will certainly play an important role in the determination of what is even meant by the term "evolutionary synthesis" (Provine 1980a, p. 409).

The MS is alternatively defined by Pigliucci and Müller with terms coming from different schools in philosophy of science, the most notable of which are "standard theoretical paradigm" (2010a, p. 3, cf. Kuhn), and "research program" (Ibidem, cf. Lakatos).

Although Ernst Mayr (1980, 1993) had - as I repeadly recalled - a processual and essentially communicational view of evolutionary synthesis, he expressed some ideas on the philosophical view which would be more adequate to understand the Modern Synthesis. To begin with, no addition, augmentation, or conceptual novelty enabled the MS:

> What was the particular missing piece of information or missing theory that had previously prevented the synthesis, the discovery of which now made it possible? No such missing piece was involved (Mayr 1980, p. 39).

The MS was thus a kind of reorganization of theoretical and empirical elements that had been entirely available for years. To the question whether the MS should be considered a scientific revolution yielding a Kuhnian paradigm (Kuhn 1962), Mayr's answer was decidedly negative:

> The synthesis [...] evidently was not still another revolution but simply the final implementation of the Darwinian revolution (Mayr 1980, p. 43).

The distinctive marks of a paradigm shift are the *accumulation* of irresolvable anomalies and dogmatic hardenings, and *incommensurability* between previous and new explanations and scientific languages. This is definitely not the case of the MS nor of the EES. A much more adequate account is, for Mayr, Larry Laudan's (1977) idea of the synthesis between two "research traditions":

> ...the two camps of evolutionary biology, those of the experimental geneticists and of the population-naturalists, differed in their studies of

> causation (proximate vs ultimate), in the level of the evolutionary hierarchy with which they were concerned, and in the dimensions they studied. They represented two very different "research traditions" (Laudan, 1977). The evolutionary synthesis was a fusion of these widely different traditions. Such an event occurs only occasionally in the history of science, as Laudan writes: "There are times when two or more research traditions, far from mutually undermining one another, can be amalgamated, producing a synthesis, which is progressive with respect to both the former research traditions" (p. 103). What happened between 1937 and 1947 was precisely such a synthesis between research traditions that had previously been unable to communicate (Mayr 1980, p. 40).

Recently, philosopher Telmo Pievani (2010) has been formulating a hypothesis based on the Methodology of Scientific Research Programmes by epistemologist Imre Lakatos (Lakatos 1978, Lakatos & Musgrave 1974). Pievani agrees with Mayr and Stephen Jay Gould (2002) in seeing the history of evolutionary theory as characterized by a series of theoretical and empirical *extensions and revisions*, far from being radical changes of the Darwinian "paradigm", rather well described as the evolution of a *research programme* improperly called evolutionary "theory".[186] A research programme (RP) is made up by the scientific community's *decisions*. A set of fundamental theoretical postulates is ascribed to the *core* of the RP: such principles are declared methodologically, operationally *unfalsifiable*. Any *competing* RP, let us

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[186] The theory seems constituted by an integrated multiplicity of concepts and explanatory patterns (cf. Mayr 1991), with a heterogeneous empirical basis "from molecules to fossils" (Pievani, cit.).

call it RP_2, should attempt to disprove the core of the RP. Decisions about the constitution of the core - that is, the choice of *which* well-corroborated theories are to be taken as plausible - are made by virtue of a "conjectural inductive principle".[187] The core contains also philosophical ideas and untested assumptions, i.e. the influent "metaphysics" of the RP, explicated in a series of heuristic rules that channel research in some directions (positive heuristics) avoiding others (negative heuristics). Despite the Kuhnian influence, Pievani stresses an important difference from Kuhn, i.e. that the core of Lakatosian RPs *changes* dynamically over time, and such dynamics is rather continuous, without the radical breaks and incommensurabilities typical of Kuhn's scientific revolutions. The core gets modified by the scientific community in relation to uprising anomalies and challenges from any competing RP_2, and in harmony with the positive heuristics.

The Modern Synthesis have constituted, for Pievani, the Research Programme of evolutionary theory for a great part of the Twentieth Century. It exhibited a "synthetic force" around a core of generalized principles. With proponents of the EES, Pievani shares the feeling that some heuristic principles - e.g., explanatory extrapolation from micro to macroevolution - may have marginalized some problems and alternatives, such as the multiple rates of change and speciation, or the role of development and of non-genetic factors. These marginalizations, typical of a cohesive scientific community,

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[187] Inductive reliability has two criteria: a) acceptance1 = additional empirical content (prevision of novel facts); (b) acceptance2 = corroboration of the additional empirical content (so that predictions actually increase the RP's empirical content).

have been described as a "hardening" (Gould 1983) and as "quasi-paradigmatic" (Gould 2002).

How does a Research Programme evolve? For Pievani, the Modern Synthesis RP has shown a remarkable capacity for inclusion and "progressiveness" towards challenges like puctuated equilibria (Eldredge & Gould 1972),[188] neutralism (Kimura 1983), and ecology (Eldredge 1999).

More recent challenges, however, will probably require a renovation of the RP, although some of such challenges are waiting for a more thorough evaluation of relative frequency and incidence on evolution. Pievani's list largely overlaps with the challenges gathered by the project of the Extended Synthesis: Evo-Devo (Carroll 2005, Minelli 2007, Minelli & Fusco 2008), epigenetics and multiple ways of inheritance (Jablonka & Lamb 2005), phenotypic plasticity (Pigliucci 2001), Niche Construction (Odling-Smee, Laland & Feldman 2003), Developmental Systems Theory (Oyama, 1998; Oyama, Griffiths & Gray, 2001), evolvability (Kirschner, Gerhart, 2005) complexity and self-organization (Kauffman, 2000).

> The passage from MS and EES is to be seen as a shift from a Research Programme that is beginning to be regressive, to a new version of the Research Programme with strongly progressive characteristics due to its pluralistic explanatory set up (Pievani 2010, my translation).

What Pievani's neo-Lakatosian hypothesis might give to philosophy of biology, and to EES advocates in particular, is an apparatus - lacking at

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[188] The evaluation of relative frequencies of different patterns is a key integrative principle for the evolutionary RP (Pagel, Venditti, Meade, 2006)

present - for the structural analysis of the Modern Synthesis, its change and its extension. A clearer idea of the structure of the MS might alleviate problems like those I shall expose in the next section, where elements like the adaptive landscape are burdened with expectations of anticipation and charges of insufficiency. A clearer idea of the structure and organization this grand architecture we call evolutionary theory would perhaps help adaptive landscapes and the "universe of discourse" about them to find a proper, fitting if dynamical place.

2. A critique of Pigliucci's view of adaptive landscapes

> Sewall Wright introduced the metaphor of evolution on ''adaptive landscapes'' in a pair of papers published in 1931 and 1932 [...]. While the metaphor is flawed, some of the problems which Wright was attempting to address are still with us today, and are in the process of being reformulated as part of a forthcoming Extended Evolutionary Synthesis (Massimo Pigliucci 2008a, p. 591).

Massimo Pigliucci's paper "Sewall Wright's adaptive landscapes: 1932 vs. 1988" (2008a) compares the origins of the "adaptive landscape metaphor" with the positions expressed by Wright the year he died (1988),[189] demonstrating that Wright's ideas have impressively remained unchanged across 56 years. Pigliucci's main interest on the adaptive landscapes, however,

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[189] I reported and answered some terms and ideas by Pigliucci in chapter II on the origin of adaptive landscapes and III on Gavrilets's work.

seems to reside in «what, if anything, they may contribute to a forthcoming Extended Evolutionary Synthesis» (p. 592).

As far as I understand, Massimo Pigliucci's analysis of the adaptive landscape is essentially aimed to demonstrate the need for some conceptual pillars that are *already* present in his agenda for an Extended Synthesis, like the "genotype-to-phenotype map" and evolvability. Such urgency, I think, leads Pigliucci to commit historical and also epistemological conflations, coming to consider the adaptive landscape at times as a seriously deficient model, at other times as a (false) "friend" supposedly anticipating contemporary notions.

2.1 Landscapes and G→P map

Pigliucci quotes and criticizes the following comment made by Wright (1988) on Simpson's phenotypic landscapes:

> Simpson (1944) […] treated the local population in terms of the phenotypes, rather than the genotypes as in my work. Phenotypes are, no doubt, more appropriate units for dealing with selection, whether between individuals or groups, but genotypes seem more appropriate for mutation or random drift. The choice, however, is practically irrelevant in connection with pictorial representation of changes that occur in populations (Wright 1988, p. 120).

Pigliucci is surprised of Wright seeming «strangely unconcerned» about the difference between genotypic and phenotypic landscapes, because «the two landscapes are not at all easy to relate to each other» (Pigliucci 2008, p. 599). In Pigliucci's worry I see a misinterpretation of Wright's words. I think that, while Wright was marking a *difference* between himself and Simpson, he was not at all talking about *relating* two "landscapes". Rather, he was acknowledging two *autonomous uses* of the same diagram - i.e., the adaptive surface. As I have shown in chapter III, many landscape models[190] have been built, and provided with their own, autonomous dynamic rules, to address the most diverse problems in evolutionary biology. Some landscape models allowed legitimate use of 3D visualizations like the adaptive surface. Simpson-Lande landscapes (III.2.2) are an example of an autonomous (phenetic) combination space, allowing for the realization of adaptive surfaces, being them metaphorical (in case of high-dimensional spaces) or exact. In my interpretation of Wright, what is «irrelevant» to the pictorial representation is *which one combination space is represented*, *not* the *relationship* between genotype and phenotype. It could be argued that Wright was hypothesizing a visual similarity between surfaces obtained for distinct spaces. But anyway, *he was acknowledging the necessity of a plurality of combination spaces, each appropriate for dealing with a specific set of phenomena*.

By the way, Pigliucci seems not convinced about the autonomy of Simpson's landscape from genetic space.[191] He marks the distinction as follows:

> The first one [genotype space] can be described - albeit approximately - by mathematical population genetic formalisms, while the latter [phenotype

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[190] Combination spaces with fitness, see definitions in II.2.

[191] Also in his review on evolvability, Pigliucci writes: «George Gaylord Simpson talked of phenotypic, not genotypic, landscapes, *the two being related* only through the anything but straightforward genotype→phenotype (G→P) map» (p. 78, my emphasis). I found no statement of explicit G→P relation in Simpson's book. Who put it there?

> space] admits only of a posteriori statistical descriptions a la Lande and Arnold (1983).

There are two imprecisions in this statement, at least according to my analysis. Pigliucci's idea about the boundaries between disciplines does not coincide with mine. The idea of phenotype space being outside the domain of population genetics contrasts with the recognition of "biometrical genetics", i.e. all the theoretical structure *within* population genetics dealing with phenotypic variation and evolution (cf. II.1.1). If Simpson-Lande phenotypic landscapes bear on the biometrical tradition in population genetics, including tools as important as Fisher's fundamental theorem of natural selection, it is also incorrect that they must limit to "a posteriori" statistical descriptions: phenotypic landscapes are models in their own right, consisting in phenotypic combination spaces provided with fitness and with their own rules of movement (e.g., morphological constraints). The second imprecision is that the "genotype space" would be described by "mathematical population genetic formalisms". In Chapter II, I distinguished Mendelian population (a space) from population genetics equations (dealing with gene frequencies), and I argued for an epistemological gap between the two. In sum, genetic (allelic) and phenetic spaces appear to be equally valid and autonomous, bearing on two different research traditions.

The main of Pigliucci's worries here appears to be the "genotype to phenotype mapping function" (G→P, e.g. Alberch 1991). Relating genotype to phenotype is theoretically fundamental to Pigliucci, so he is brought to think that the same should have been true for Wright: «How can it be irrelevant?» (Pigliucci, cit., p. 597). How could Wright think about modeling adaptation and fitness in genetic terms, without knowing the relationship between genetics and phenotypes, being the latter the fundamental units of natural selection? But this projection by Pigliucci on Wright is an evident historical and epistemological conflation. Should I symbolize the complete mapping function Pigliucci seems to be figuring out, I would write:

$$G \rightarrow P \rightarrow \omega$$

Where ω stands for fitness. Genotype variation maps onto phenotypes, which in turn are units of natural selection, thus having an adaptive or fitness value.

This is *Pigliucci's* idea, and undoubtedly an important area of inquiry in contemporary biology. But the point is: did *Wright's* theoretical structure compel him to worry about phenotypes? Right the contrary, according to my analysis:[192] the theoretical structure framing the adaptive landscape, i.e. Mendelian genetics, did "skip" phenotypes, relating genotypes directly to fitness:

$$G \rightarrow \omega$$

Why shouldn't Wright have been «unconcerned» when just the theoretical structure of Mendelian population genetics *was based* on the abstraction from phenotypes? That «...something about the phenotype of the genotypes - their fitnesses - can be asserted» (Lewontin 1980, p. 59) is a very general theoretical assumption, and it would make no sense indeed to talk about fitness without such a theoretical assumption. But epistemological limitations and

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[192] Relying among others on Richard Lewontin (1980, see II.1.1).

methodological assumptions are also essential to modeling. Something about G→P map *might* be asserted, and of course (as Pigliucci claims) it would be of extraordinary importance for understanding evolution, but there is *methodological silence* on G→P map *in the theoretical structure* of the research tradition of Mendelian population genetics, where

> ...those phenotypic transformations get lost in the shuffle because they are *assumed* constant; *a given genotype has a given fitness* (Lewontin, cit., p. 59).

To have a G→ω map means to remain silent on phenotypes. This implies that we simply don't know and don't care how the phenotype, *produced* by G and *producing* ω, looks like. A smooth fitness surface means only that slightly different genotypes will differ slightly in fitness. As far as we know, there might be unexpected effects concerning phenotypes in some regions of the landscape: slightly different genotypes may map onto dramatically different phenotypes with similar fitnesses; conversely, largely different genotypes may map onto slightly different phenotypes that, however, have dramatically different fitnesses in the considered environment. Phenotypes are modeled away because their mediation between G and ω is not specified.

So little Pigliucci accepts such epistemological alterity by Wright, that he projects - I think - an exact continuity of the question on phenotypes even since Darwin:

> ...the crucial problem *Wright was attempting to address* remains: as Darwin (1859) noted, the theory of evolution does require an account of the intermediate steps taken by the evolutionary process in the production of new

> structures and functions. Obviously, Darwin was not talking about genotypic landscapes, but he was aware that one needs to explain *how movement in what is today called phenotypic space actually occurs* (Pigliucci 2008, cit., p. 599, my emphasis).

Pigliucci is removing the evident truth that Wright and his "school" studied the mathematics of evolution in Mendelian populations with no reference to phenotypes. An identical and contrary, concealed rejection by Piglucci hits phenotypic landscapes and biometrical genetics (and Darwinian, indeed), where - against Pigliucci's present worries - the genetic basis is "modeled away" and not studied directly:

> ...the genes get lost in the shuffle. They get absorbed into mysterious parameters like the heritability or the average effect (Lewontin, cit., p. 59).

In symbols, Darwinian, phenotypic landscapes rely on the following function:

$$P \rightarrow \omega$$

Pigliucci describes a study by Kavanagh et al. (2007) on the evolution of mammalian teeth as a developmental model addressing the G→P map. According to my criteria (III.2), Kavanagh et al. (2007) is classified as a "complex trait" landscape: a low-dimensional combination space with a few factors interacting to generate a phenotypic trait (cf. III.2). A complex trait landscape embeds a G→P map. But it is very far from Wright's high-dimensional Mendelian population. It does not meet the interests of students of high-dimensional spaces: should it be judged negatively for that?

2.2 Landscapes and evolvability

A further, puzzling thesis by Pigliucci is about evolvability. For Pigliucci, Wright's insistence that peak shifting is the problem of evolution was not probably due to his belief in optimality (cf. footnote in chp III). Rather,

> ...he may have been concerned, at least in some fashion, with what today is known as evolvability, i.e. with what makes it possible for evolutionary mechanisms themselves to evolve over time (Pigliucci 2008, p. 595).

The relationship between landscape and evolvability is obscure in Pigliucci's paper, since he does not deepen the latter idea. To compensate, I follow Pigliucci's citations of a review by himself on evolvability (2008b) and a paper by Conrad (1990).

In his clarifying review on *Nature*, Pigliucci explains the multiple meanings of evolvability ranging in a spectrum. On one side, evolvability is a refinement of the classic concept of heritability (e.g. Flatt 2005, Griswold 2006, Houle 1992), through the concept of genetic variability as distinct from variation (Wagner & Altenberg 1996). At the other end, evolvability refers to the evolutionary possibilities opened by some specific structural features (Brookfield 2001, Alberch 1991). Pigliucci notices that the different meanings are actually «a family of interconnected but partially distinct ideas» (2008b, p. 76), valid at different time scales, but considers particularly the Wagner & Altenberg (1996) concept a necessary building block of the EES. The crucial novelty of evolvability so intended is, Pigliucci reports, the distinction between standing variation (already captured by Fisher's fundamental theorem of natural selection) and variability:

> variability is the propensity of characters to vary (whether or not they actually do) and depends on the input of new genetic variation (2008b, p. 76).

The particular meaning of evolvability is tightly tied to such a distinction:

> ...evolvability is no longer seen as a matter of standing genetic variance but as a result of the propensity to vary that is afforded by the entire genetic architecture (Ivi, p. 77).

That *this* concept of evolvability and the related distinction are the reference for Pigliucci's discourse in the adaptive landscape paper (2008a) is corroborated by an explicit hint therein:[193]

> ...[Wright's] distinction between actual and potential genetic combinations anticipates the distinction between standing variation and potential variability (Pigliucci 2008a, pp. 592-3)

But it is really hard to understand how Wright's Mendelian population landscape could ever be relevant to genetic variation and variability.

First of all, the concept of variation employed in evolvability comes not from Mendelian genetics (II.1.1) but from a completely different theoretical structure: biometrical genetics (II.1.1). In *that* theoretical context "heritability" (Griswold 2006) or the "genetic coefficient of variation" (Houle

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[193] And that it is also the "time-scale" Pigliucci has in mind, is explicitly stated by him: «Considering how Wright continues his original paper [...] it seems unlikely that his primary concern was the evolution of evolvability in the long run [i.e., sensu Brookfield 2001, Alberch 1991]. At most, his goal was to provide an account of the current level of local evolvability of a given population».

1992) or a “genetic variance-covariance (G)-matrix” determines “the ability of a population to respond to selection” (Flatt 2005). The theoretical structure of biometrical genetics, I remind, works with continuously varying phenotypes, modeling away the genotype.

With the important theoretical addition of the G→P map, genotype (G) and development (→), according to their structure (more, less, differently, peculiarly *variable*), *react* to new mutations generating new ranges of variation in phenotypes (P), in ways that are indeducible by the previous distributions of variation. So the concept of variability seems to complement variation *in the same* theoretical context: genetic architecture and developmental constraints - which are *not* captured by G-matrix etc., *invisible* to them - determine the “reaction” of the genetic structure to mutations that may occur.

It is not necessary here to enter the debate on evolvability. I just want to argue that Wright’s landscape *cannot undertake* any of the evolvability-related observations and phenomena. For example, as I argued in the previous section, Wright’s landscape is completely phenotype- and development-free, whereas for Pigliucci:

> ...evolvability can be linked to the G→P map through the idea of adaptive landscapes (2008b, p. 78).

And Pigliucci is not talking about phenetic landscape spaces like Simpson’s and others’. He intends exactly Wright’s landscape, as updated by Gavrilets whose “extra-dimensional bypasses” (originally conceived by Conrad 1990) attract Pigliucci: he seems to think about *shifts of the population in the genotype* *space from a nearly neutral network to another* as cases of evolvability, that is as *events in which a genetic change gives rise to a largely different phenotypic space* of possibilities. But if this is Pigliucci's thought, he overlooks that both Wright's and Gavrilets's landscapes are silent on phenotypes: the entirely new spaces of possibilities opened by "peak shifts" or "extra-dimensional bypasses" are *genetic*, with no intrinsic phenotypic implication. And, in fact, such "new" spaces of possibilities *are not new* at all either in Wright's or Gavrilets's (virtual!) space. The combination space consists in all the combinations which are virtually possible *made up with the presently available* alleles. *Standing* genetic variation thus outlines the whole space of possibilities, and movement in the landscape - even in case of high-sounding "extra-dimensional bypasses" - is nothing but the realization of a different set of combinations in the same space. As I showed in Dobzhansky's case (III.1.1), even only introducing mutation as a mechanism for movement in Wright's landscape yields to inconsistent results. And the "genetic structure" of a Mendelian population (or a sequence space) is trivial: it is just a series of loci, with no way to conceptualize phenomena like modularity (e.g. Hansen 2003), or robustness (Wagner 2005), or neutral spaces (Wagner, cit.) in the genome that are so important for evolvability.[194] The conflation between phenotype and genotype and a series of improperly attributed concepts inherited from some version of

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[194] Some other evolvability-related phenomena, instead, have some counterpart in Mendelian population space, but their visibility is always through fitness, not by direct reference to phenotypes. Phenomena are, e.g., pleiotropy and epistasis (Carter et al. 2005), and neutral phenotypic evolution. The latter is important because evolvability in some meanings is not related to adaptive changes, but on phenotypic change decoupled from natural selection (Dichtel-Danjoy & Felix 2004, Schlichting & Murren 2004).

the landscape, make it a really "false friend" to Pigliucci to illustrate (if not support) evolvability.

2.3 Conclusion: landscapes (like others) in the EES

In several occasions, Massimo Pigliucci manifested that extending the Modern Synthesis should be done

> ...without resorting to anachronistic *post facto* reinterpretations of what that effort [Modern Synthesis] was historically about (2008b, p. 77).

But Pigliucci's treatment of adaptive landscapes appears to me as biased in just that direction. Pigliucci expresses discontent for the lack of correlation between Wright's genotypic and Simpson's phenotypic landscapes, and for the complete absence of a G→P map, but his complaints seem based on historical-epistemological conflations and on a blurred view of the involved theoretical structures. On the other hand, Pigliucci tries to put forth Wright as an anticipator of notions like evolvability and variability that, once again, do not fit at all in the proper theoretical structure where the landscape was conceived. It is hard, with such an analysis, to answer properly Pigliucci's questions like «Is there a future for adaptive landscapes?» or «What role, if any, will they play in the Extended Evolutionary Synthesis?». For me, fair and interesting questions on the adaptive landscape would have been the following: are the two traditions ("Fisherian" biometric and "Wrightian" Mendelian, see II.1.1) in population genetics flawed research traditions? If not, how could G→P maps be integrated into them, or, even better, serve as *integrative* tools between them? Can we find inspirations among the many kinds of established landscape (combination space) models for building completely new models of (or including) G→P maps? Will we be able to produce 3D illustrations (for example, surfaces of some sort) of the new models? And will we benefit from using the common landscape metaphorical vocabulary to describe some features of the new models?

Whatever idea of synthesis and urgency of extension guide philosophical reflection, I think that careful, sometimes painful and maybe boring conceptual analysis should not be overlooked. Clear working hypotheses on the structure of evolutionary theory (or of that object called MS) might help to give notions a (right) place (1.4). If philosophy of biology is, as in Pigliucci's view, essentially conceptual analysis, this is what is mostly required by it. In the case of adaptive landscapes - differently from other cases - I see lack of analysis, with potential large effects of confusion on the scientific literature. With my work here, I humbly tried to contribute to conceptual clarification.

CONCLUSION

> Synthesis continues to drive progress in evolutionary biology (Sidlauskas et al. 2010, p. 872)

Evolutionary biology and the Modern Synthesis are today unique, fascinating objects of study for philosophy of science, through the eyes of an autonomous and variegated discipline: philosophy of biology. The Modern Synthesis, seen by the majority of philosophers and historians as a two-step process concentrated between 1910s and 1930s, has given unprecedented articulation and momentum to biology, and to evolutionary biology as the most comprehensive theoretical structure for the scientific study of life.

For Ernst Mayr, the Modern Synthesis was deeply communicational in its nature: it consisted in the construction and tuning of a common language that allowed fields until then separated like paleontology, theoretical and experimental genetics, morphology, zoology, botany and many others to begin working to the reconstruction and recognition of a common story.

I hypothesized that a "migrant" metaphor like the adaptive landscape may have played a role in this process of bridge-building, allowing e.g. a geneticist like Theodosius Dobzhansky and a paleontologist like George G. Simpson to give a grand sense of unity embracing genes, phenotypes with their adaptations to different environments, speciations, micro and macroevolution, singular episodes and the general pattern of evolution. Simple and intuitive ideas seem to be at the base of the metaphor: that "higher is better", i.e. that best combinations and solutions rest on "peaks" and worst lay in "valleys"; that evolution can be thought of as the realization of possibilities over time; and that environment exerts its influence, whether this is evident or not.

Evidence of the force of the migrant metaphor of adaptive landscapes, regarding both communication and inclusiveness, may be found up to date, in its utilization in popular books defending and spreading evolution like Richard Dawkins's *Climbing Mount Improbable,* but also in persisting figures of speech used in biological research. In recent years, however, a differently shaped adaptive landscape metaphor has been spreading: holey landscapes, featuring no peaks nor valleys, but a flat plain with holes. What can it mean for evolution, and for evolutionary biology? Remarkable debate has been risen on the issue, but sometimes it yielded more confusion than clarification. It has been my task to try to settle some problems, to re-open some of them in a more productive way, and to see some more directions.

There is much to say about what scientific metaphors are, and how they work. For example, for adaptive landscapes I proposed a net distinction between migrant and native metaphor. In mathematical population genetics, which is its native context, the metaphor plays a peculiar and perhaps unexpected role: it is metaphor for a model. The hierarchical relation between the two terms is alternative to seeing them in competition, with metaphor as a "not so good model", and opens the reflection to the recursive nature of our knowing.

To understand the adaptive landscape metaphor it is of primary importance to answer in detail the question "what model(s) is the metaphor a metaphor of, exactly?". This is one of the most obscure and misleading *locus* in the debate, but the answer is easy if we enter very carefully in the brilliant work of the landscapes' inventor: Sewall Wright. This is also the occasion to clarify that "population genetics" - often presented as a solid body of knowledge - has a rather articulated theoretical structure. Mendelian and biometrical genetics are two distinct research traditions, consistent but not coincident. And in Mendelian population genetics there is - I claimed - a unique model, Mendelian population, which is a combination space provided with fitness values. The space is mathematically intractable, but liable to be approached with statistical equations. Sewall Wright's adaptive landscape metaphor is, I argued, metaphor of Mendelian population, which is too complex an object to be visualized exactly. Moreover, the epistemological gap separating Mendelian population and mathematical equations entails the fact that Wright had to use some other strategy than mathematical derivation to obtain information about the former. This has not to do with the metaphor anyway, which was used to display the (already) inferred features.

There are several objects in this story: the Mendelian population combination space; population (without the prefix "Mendelian") which is the partial realization of the space, changing over time; the "adaptive surface" which is a metaphor showing some characteristics of the space; population genetics equations describing gene frequencies in the population; and many others. This heterogeneous plurality of objects meets an equal plurality in the meanings of terms like "model" in contemporary philosophy of biology. I proposed a local agreement on a vocabulary to be used for discussing the fascinating story of adaptive landscapes, insisting very much on a "pragmatic approach for the philosopher of biology", because I think that indiscriminate use of words, above all "model", has fed confusion and consequent confusing clarifications in the discussion of adaptive landscapes.

I like the notion of a model as a «stable target of explanation» I proposed for grappling the Mendelian population combination space. It gives account of all the work done, and being done, *around* the model, to understand its characteristics and behaviours. It leaves open questions about how, when and what the model can represent or explain, but I like this aspect, too. It calls for a consideration of the pragmatic dimension of modeling, in a view that leaves scientists the authority to decide "what counts as a representation", "what counts as an explanation", "for what", and "to what extent".

Having deepened the history and epistemology of the native metaphor, and having fixed a vocabulary to deal unambiguously with landscapes, I turned back on the various instances of the migrant metaphor. I showed the retained features and internal inconsistencies of Dobzhansky's landscape; the novelties and consistency of Simpson's landscapes; and the simplifying, abstracting rhetorical thrust of Dawkins's views. Then I turned on landscape models that proliferate in today's evolutionary biology: they are not necessarily tied to Mendelian population or to an adaptive surface. They are combination spaces provided with fitness, differing by kind of combined factors, dimensionality, method for fitness assignment, kind of dynamics. Some combination spaces are presently addressing a problem that - according to Sergey Gavrilets - was left out of reach of mathematics: speciation.

Gavrilets's state-of-the-art book, *Fitness Landscapes and the Origin of Species* (2004), presents the population genetics of speciation as a "patchwork" (as I said) of low-dimensional combination spaces and statistical analyses that are beginning to make the Mendelian population model a description and explanation *also* of speciation. Seen in the context of this patchwork, percolation analysis produces results about the same model in the landscapes' native context, and these results are metaphorized by means of holey landscapes. They have to be properly understood and used, when required, to answer "how possibly" questions. Their implications are still to be fully developed.

Proper understanding and contextualization is not what I found, unfortunately, in the way adaptive landscapes are treated by Massimo

Pigliucci, the main advocate of the Extended Evolutionary Synthesis. Caring perhaps too much of contemporary concerns like evolvability or the genotype to phenotype map, Pigliucci operates some epistemological and historical conflations, asking too much from the adaptive landscape, neglecting its original aims and perhaps some inherent features of the activity of modeling. Pigliucci neglects, for example, the legitimate *compression* of phenotypes and environment in population genetics models, allowing this field to concentrate on genes, genotypes, gene frequency with a clarity of scope and problem definitions.

So, we are back to synthesis. The project of an Extended Evolutionary Synthesis will probably go on and further. To such a project I would recommend caution in treating models, metaphors and other tools that have secured impressive advancements in evolutionary biology over the past 150 years. Too much worry of proposing something new, or, at the opposite, to find precursors of present-day urgencies, can lead to distorted understanding (and also, I would add, to unnecessary opposition by scientists and philosophers to the project). From the point of view of the Extended Synthesis, Modern Synthesis is a product of that historical process reconstructed by Mayr, Provine, and other scholars. What exactly this product or "theoretical framework" is, whether it has some structure and how this structure has to change, these are all exciting questions for philosophy of biology. What Ernst Mayr called "minimal requirements" agreed upon during the Modern Synthesis - the belief in genetic mutation and natural selection - may have constrained some researches, but perhaps to a less extent than EES advocates claim. On the other hand, there have to be ways to acknowledge theoretical novelties and advancements. The most promising approach to the structure of evolutionary theory is, in my opinion, Telmo Pievani's neo-Lakatosian hypothesis - and this is not because he is my PhD advisor.

But in closing this work, I would like to quit again a view of synthesis as a "product", an entity, and get back to an equally interesting view of synthesis as a process, and as communication, i.e. synthesis as a "continuing promise" in evolutionary biology (Sidlauskas et al. 2009). Last year the National Center for Evolutionary Synthesis (NESCENT) published this paper where synthesis is presented as an *approach*, suitable for addressing complex questions (p. 872) from a «grand perspective» (p. 871). An approach of which the Modern Synthesis would have been a particularly successful example, but yet, only an example. The starting point of synthesis is always *fragmentation*, not only and not much as specialization, but as lack of communication of expertise and data. The key element to synthesis, in a scientific context, is *combination*:

> ...it is the extraction of otherwise unobtainable insight from a combination of disparate elements that best diagnoses synthesis (Sidlauskas et al., cit., p. 872).

Elements to be combined are concepts, data, methods, and/or results, either within the same discipline or across disciplines. Among the kinds of barriers that prevent synthesis (cultural, economical, academic), two illuminate my work on the landscape with particular brightness.

Technology may hinder as well as facilitate synthesis. Among the many technological solutions for data organization and sharing, *visualization* occupies a preminent role:

> As the amount of data available for synthesis continues to grow, so does the need for new methods to display and explore these increasingly complex data spaces. Successful data visualization promotes scientific discovery and communication by harnessing the power of human cognition to detect patterns within complex datasets (p. 877).

How not to think to our famous and troubled adaptive surface? It's been a long way since Sewall Wright used his pen and paper to write and solve equations, and to draw his landscape "diagrammatic representation" (Fig. II. 1). Today, computers run extremely complex simulations, and scientists are more and more collaborating with «specialists in the fields of informatics, technology, cognition, and graphic design» (p. 878) who provide visual tools and new media to be used for research and for science education. Perhaps we won't see an adaptive surface drawn from a Mendelian population, but we will surely know such model better and better, and avail ourselves of unexpected visualization techniques (some combination spaces already have them, cf. III.2.2). And this is expected to help synthesis.

Language barriers are another familiar topic. Here I stood much on the importance of the development of a common language for the Modern Synthesis. Sidlauskas et al. (cit.) agree on the necessity of common languages for collaboration and synthesis, and they remark:

> The lack of a common frame of reference can present a serious barrier to communication and effective collaboration, particularly when collaborators cross disciplines. Overcoming that obstacle often requires the development of new frameworks based upon a common language or ontology (p. 875).

Perhaps adaptive landscapes will do the trick again. Perhaps they are already doing it.

How can philosophy of biology contribute to synthesis? Well, there is a lively and always renewed debate on what philosophy of biology should and should not do (e.g., Hull 1969, 2002, Ruse 1989, Sterelny 1995, Callebaut 2005, Müller-Wille 2007, Pradeu 2009, Gers forthcoming). What I see - in theory and practice - is that there are many styles of doing philosophy of biology. Here I put forward a style of epistemological, conceptual and terminological analysis. The historical dimension here is more marked than the average, although I intend it at the service of other dimensions. The mathematical apparatus is much less developed than that of many successful works (e.g., Okasha 2006, Sober 2008a, b). But the plurality of philosophy of biology, even "against" mathematics, has its own defenders (cf. Downes 2006, 2008). My highest hope is that this essay in philosophy of biology, with its peculiar style, may contribute to synthesis by calling to a common language and to some conceptual distinctions that help to grasp and share the deep machineries of surface visualizations, landscapes models, and population genetics; and by pointing some feeble lights on the "deep machinery" that biology and science, with their metaphors and models, are.

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