Chapter 4
Selection

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Abstract One of Darwin's major contributions to our understanding of evolution, namely natural selection, seems a very simple idea. However natural selection is a very subtle concept and biologists and philosophers have been struggling for decades to make sense of it and justify its explanatory power. In this chapter, first I present the most general formulations of natural selection in terms of necessary conditions, and I argue that none of them capture all the aspects of the concept. Second, I question the explanatory status of selection, asking what exactly it is supposed to explain, and considering its relationship with stochastic factors (i.e. genetic drift). Second, I investigate its metaphysical status, asking whether it can be seen as a law, and to what extent it would deprive evolution of any contingency. The last section presents controversies about the units and levels of selection, and, after exposing the philosophical assumptions proper to various positions, sketches a pluralist conception.

Charles Darwin's *On the Origin of Species* advances two major ideas in 1859: *common descent with modification*, by which all species are connected into a tree of life; and *natural selection*, as an organizing principle and root cause of this tree of life. This second idea seems simple: according to Darwin, restating one of Herbert Spencer's formulas, the most apt survive best or longest (*survival of the fittest*), have more offspring, transmit their traits[1] to these offspring, which is sufficient for creating change in the frequency of traits and producing thereby an evolution of populations' overall profiles. Yet in reality, this notion contains within it serious epistemological and metaphysical[2] challenges. This chapter gives overview of these challenges in order to more clearly present the depth and richness of the idea of natural selection. The first part examines possible generalizations of the principle of natural selection;

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[1] Traits or "characters" in the sense developed by Véronique Barriel, Chap. 7, this volume. On Variation, see Heams, Chap. 2, this volume.

[2] Not "speculations", but rather questions about ontological engagement and rules for validating scientific theories (for example, the debate on realism versus instrumentalism, the interpretation of probabilities, etc.).

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27   the second part investigates specific forms and effects of natural selection; the
28   chapter concludes with an inquiry into the epistemological and metaphysical status
29   of the selective explanation and examines at which levels natural selection can
30   play a role.

1   The Principle of Natural Selection (When and Why Is There Natural Selection?)

1.1   The Selectionist Explanation

34   To begin, as Ernst Mayr (1959a, 1961) insisted in pointing out one of Darwinism's
35   originalities, the explanation by natural selection involves *populations* of diverse
36   individuals rather than a single individual or a type of individual. How does this
37   "populationist" explanation work?[3] According to Elliott Sober (1984), there are two
38   ways to explain why a ship's staff comprises people who know how to swim: either
39   retrace the individual history of each individual or point out that a condition for
40   belonging to this group was knowing how to swim. The first explanation is said to
41   be "developmental", adding up individual histories. The second is "selectionist",
42   considering the entire population and identifying a filter that separates those who do
43   from those who do not possess a property – therefore singling out a subpopulation
44   of a global population. This form of explanation does not therefore consist of
45   retracing an individual trajectory comprising a series of causes and effects that are
46   eventually subsumed into a law (as for instance in mechanics); in this sense, it will
47   present epistemological particularities. "*Natural* selection" is a particular instance
48   of the selectionist explanation, and one that is extremely fruitful in the biological
49   field due to conditions that I will now introduce in more detail.
50   As rich and sophisticated as his ideas are, Darwin's vision of selection could be
51   summed up as follows: organisms of a species are distinct from one another and bear
52   offspring that are different but generally more closely related to their parents than to
53   other conspecific individuals. Because of certain properties that they have – such as
54   the speed of land mammals like antelopes or leopards, the fast metabolism of
55   bacteria, birds' beaks – certain organisms succeed more than others in gaining access
56   to limited resources (the famous "struggle for life") and to sexual partners, thus
57   having more offspring that tend to resemble them and who therefore more or less
58   inherit these advantageous properties. These properties do not suddenly ensure better
59   differential reproduction, but in an important population of individuals on average
60   those with these properties will reproduce more often. With subsequent generations,
61   new advantageous properties become apparent, the same filtering process takes

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[3] Sober (1980), Ariew (2008) or Gayon (1998) argue that Darwin himself was not truly a "popula-
tion thinker", among other reasons because he used no statistics, but that changes nothing as far as
the argument here concerns the Modern Synthesis in evolution.

place, and so the general physiognomy of the species will be modified. This process 62
is analogous to the way farmers or breeders select the best plants or animals and 63
create a lineage by rejecting others. In biology it is nature itself that, due to the 64
scarcity of resources, plays the role of selector, an analogy that is extremely impor- 65
tant for Darwin.[4] Selection targets organisms, and the result is a transformation of 66
the average type of organism in the population and thus ultimately of the species 67
itself. Adaptation, meaning traits that are optimally adjusted to the environment,[5] 68
and diversity (different adaptations would result from separating a given population 69
into two different environments) are explained in this manner. 70

This process clearly operates on two levels: organisms *are selected,* that is, some 71
survive and reproduce more than others – **and** they are selected *because of* certain 72
properties they possess, which will then be redistributed in the following generation. 73
This difference within the structure of natural selection leads to the distinction 74
between *selection-for* and *selection-of.*[6] This duality is fundamental to the dynamics 75
of the process, and we indeed find it in certain general theorizations of selection. 76

When Darwin replaced *natural selection* by *survival of the fittest* in later editions of 77
The Origin following Spencer's suggestion and in order to avoid an anthropomorphic 78
reading of *selection*, he unfortunately folded the two dimensions into one. There is 79
no longer any dimension but that of the organisms (being fit is a property of organisms). 80
There is no mention of what these organisms could have been selected for 81
(and precisely what makes them more or less *fit*), which gave rise to the famous 82
"tautology" criticism: Who are the *fittest*? Those who survive. We know they are the 83
fittest because they have survived, therefore the principle is circular: it signifies the 84
survival of those that have survived…[7] 85

In reality Darwin's reasoning does not suffer from the tautology objection 86
because it of course meant to be probabilistic (the *fittest*, whoever they are, do not 87
always survive). But as probabilistic reasoning, it must certainly resolve certain 88
major objections: thus, if the population is large, and if heredity is such that when 89

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[4] Limoges (1977) maintained that the analogy with "artificial selection" mainly served a rhetorical and pedagogical purpose in Darwin (1959) and that biogeography was the much more true argument.

[5] See Sect. 4 below.

[6] Sober's distinction originally concerns selection *for some* traits and the selection *of* traits (or alleles, i.e. different versions of the same gene) correlated to precedents (and not for what they are in and of themselves). I mean here the relation between selection *of* organisms and selection *for* (or because of) these organisms' traits, but clearly there is selection-*of* traits correlated to traits *for* which there is selection because the former are in the same organism as the latter.

[7] Beyond highlighting the probabilistic nature of selection and hence of fitness (Beatty and Mills 1979), which is a rather weak defense that would leave open the possibility that empirical validity of the selectionist explanation depends on the weakness of our cognitive ability (Michod 1999), there are other responses to this "argument"; for example, to point out that "tautology" is not in and of itself bad: mathematics are a great tautology, and are the basic structure of physics. By the same token, the principle of natural selection would support all population genetics, which are essentially a set of mathematical models, and in this sense the tautological nature is in no way a serious objection. On tautology, see Brandon (1990).

sexual reproduction mixes the mother's and father's traits (*blending inheritance*), then won't the very advantageous traits be slowly diluted and lost, as the engineer Fleeming Jenkin objected in one of the first reviews of the *Origin*? Hence, the Darwinian hypothesis of natural selection only found its full realization with the evolutionary "Modern Synthesis" (MS), which (to put it very briefly) synthesized Darwinism and Mendelian genetics to offer answers to such objections (Gayon (1998), Mayr and Provine (1980)). Population geneticists (Haldane, Fisher and Wright, working in the 1930s[8]) showed with the help of appropriate mathematical probability theory[9] that in a Mendelian context, where inheritance is not mixing but rather comprises gene that are or are not discretely transmitted ("particular inheritance") to the descendent, an allele that offers even a little advantage in reproductive chances will be fixed within a population. The natural selection hypothesis will thus hold true thanks to Mendelian (particular) inheritance and to probability theory.[10] Darwin's terms "variation" and "transmission" were thereby explained by a theory (heredity as the transmission of genes; variation as mutation and recombination[11]). But at the same time, selection grew more complicated: organisms were no longer solely at play – there were also alleles, genes, genotypes and phenotypes. Evolution, for population geneticists, cannot be primarily a transformation of organisms (as it was for Darwin), but rather a change in gene frequency in populations, according to Theodosius Dobzhanski famous definition.[12]

How, in this context, do we understand the process of natural selection itself? The systematist Ernst Mayr, one of the architects of the synthetic theory, explains: "Darwin made it clear that natural selection was a two-step process, the first consisting of the production of heritable variation and the second of the testing of this variation (…). When an author asks, Is evolution due to molecular processes or due to selection?, it amounts to asking: "Is evolution a change due to step one or step two of natural selection?" Actually the two steps are completely inseparable and the question thus is quite meaningless." (Mayr 1984: 150). In this definition, it is striking that selection appears to play out twice: the *second stage* is selection strictly speaking ("As the second step in this process, selection sensu stricto is an a posteriori process dealing with the previously produced variation and not a process which itself produces variation," Mayr goes on), but *together the two stages also constitute* natural selection. One could then wonder if "natural selection" names a unique mechanism or if it

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[8] See e.g. Fisher (1930).

[9] Whose elaboration would run its course over three decades, through Galton, Pearson, Fisher – See Gayon (1998) for this story.

[10] Gayon (1998) insists on this point that Darwin indeed offers a hypothesis, that afterwards Darwinians will construct a test and justification.

[11] Wright (1932). See chapters "Heredity" (Thomas Heams and Andras Pàldi) and "Variation" (Thomas Heams), Chaps. 3 and 2, this volume.

[12] This does not hold true for all modern synthesis, see Mayr: "Evolution is not a change in gene frequencies, as is often stated, but the maintenance or improvement of the adaptation and origin of diversity. Changes in gene frequencies are a result of this evolution, not its cause." (Mayr 1998, 2093).

designates an explanatory principle that allows for the comprehension of diverse 123
processes involved in changes of gene frequencies within populations, but without 124
being by itself a genuine process. 125

1.2 Necessary and Sufficient Conditions 126

In order to clarify these problems, it is worth trying to state natural selection's form 127
in the most general way. Although MS deals with a natural selection that involves 128
genotypes and gene pools, nothing *logically* demands that natural selection involve 129
genes: Darwin was unaware of them; above all, the fact (discovered in 1953) that 130
genes are segments of DNA is quite contingent as far as natural selection is concerned.[13] 131
The issue is therefore to understand the fundamental properties of genes and 132
organisms that make it possible for natural selection to take place. It is in this sense 133
in 1970 that Lewontin formulates *necessary and sufficient conditions* (NSC) for 134
entities to enter into a natural selection process. This question of NSC for natural 135
selection becomes even more crucial to the natural selection explanation when we 136
try to apply it beyond the domain of organisms and genes, where it triumphed in 137
biology. Thus, it was invoked, for example, at the infra-genetic level to explain the 138
emergence of life in terms of macromolecules (Eigen 1983; Maynard Smith and 139
Szathmary 1995), as well as at the supra-organism level when discussing cultural 140
evolution, and even in discussions of computer programs as genetic algorithms.[14] 141
Lewontin (1970) thus writes: 142
"A sufficient mechanism for evolution by natural selection is contained in three 143
propositions: 144

C1. There is variation in morphological, physiological, or behavioral traits among members 145
of a species (the principle of variation) 146
C2. The variation is in part heritable, so that individuals resemble their relations more than 147
they resemble unrelated individuals and, in particular, offspring resemble their parents 148
(the principle of heredity). 149
C3. Different variants leave different numbers of offspring either in immediate or remote 150
generations (the principle of differential fitness)."[15] 151

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[13] Without mentioning here the difficulty that has appeared over time in drastically characterizing the notion of the gene. See Tendero (2006) and Keller (2001).

[14] See Shoenauer's, Chap. 28, this volume; and Holland (1995).

[15] Later, Endler (2006) recapitulates (by inverting C2 and C3): "Natural selection can be defined as a *process* in which: If a population has:

C1. variation among individuals in some attribute or trait: *variation*.
C2. a consistent relationship between that trait and mating ability, fertilizing ability, fertility, fecundity, and, or, survivorship: *fitness differences*.
C3. a consistent relationship, for that trait, between parents and their offspring, which is at least partially independent of common environmental effects: *inheritance*." The formulation is clearer and I will refer back to it at times.

152   The three conditions are thus variation with regard to certain traits, heritability of
153 these traits, and, finally, a connection between the expected number of descendents
154 and (varying and heritable) traits considered (the specified condition of *fitness*).
155 Note here that in the framework of population genetics, evolution is a conceivable
156 effect as a process that affects two levels, genotypes and phenotypes. Genotypes
157 condition phenotypes, and by natural selection the phenotypes themselves will have
158 an impact on the frequency of genotypes in the following generation.

159   Yet, Lewontin's formulation here is extremely general, since in any possible
160 world – even if it does not present an immediately identifiable genotype-phenotype
161 structure based on genes – , any population of entities possessing C1–C3 must
162 present some natural selection processes. Nothing, however, demands that these
163 processes lead to an evolution, or a defined modification in the frequency of initial
164 types. This precision is fundamental – in many cases selection does not change a
165 trait's (or allele's) frequency; it only protects it from constant mutations, even if in
166 many cases this uncovers underlying nucleotidic changes. In these cases there is
167 not, in fact, any evolution.[16] As Fisher famously said in the opening sentence of his
168 groundbreaking work *The genetical theory of natural selection* (1930), "natural
169 selection is not evolution." It is also worth noting that scarcity of resources, a
170 consideration Darwin had borrowed from Malthus to justify the struggle for life, is
171 no longer a necessary ingredient. In empirical evolutionary biology, competition
172 is certainly often the cause of differences between organisms in chances for
173 reproduction; generally, though, for natural selection to occur it is sufficient to have
174 this difference no matter the cause, and even with limitless resources.

175   Let me clarify then the three conditions, beginning with the second because it is
176 the least intuitive. *Heritability* (C2) does not equal transmission (as is generally
177 meant by heredity), but rather a statistical property involving classes of distinct
178 phenotypes. Roughly said, there is a correlation between the deviation from the
179 average value of a trait in individuals descended from given parents, and the devia-
180 tion from the average for this trait in parent individuals. A classic example is height:
181 tall individuals have in average tall offspring and short individuals have in average
182 short offspring, even if a short individual can have a tall descendent. All traits trans-
183 mitted via heredity are not equally heritable, since heritability supposes a variation
184 in trait values: a trait possessed to the *same degree* by all individuals, even if it is
185 hereditary, is not heritable, and therefore would not give rise to natural selection,
186 according to Lewontin.

187   The third condition (C3) of "*fitness*"[17] is perhaps the most controversial word in
188 the entire theory of evolution. Very generally said, it designates a mix or survival
189 and reproduction. In most neo-Darwinian models the focus is on the number of
190 offspring (survival essentially only has effects because it correlates with the number
191 of offspring who are raised). Fundamentally, if a trait causally correlates to the

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[16] Brandon and Mc Shea (2011) make a strong claim for drift (see below) being a cause of evolution
and selection being very often stabilising.

[17] It is more explicit in Endler's formulation.

reproductive success of its carrier, it contributes in a regular manner to the expected 192
number of descendents this carrier will have. This trait can thus be ascribed a fitness 193
value, because we can measure the contribution of this trait to the amount of off- 194
spring, or, more precisely, in the next generation, the relative number of offspring of 195
the organisms having this trait compared to organisms not having it. Of course, 196
fitness is a probabilistic magnitude – it could, for instance, be constructed as the 197
expectation of a probability distribution on the number of representatives of the trait 198
or of an allele underlying the trait[18] in the following generation. Fitness can thus be 199
attributed just as easily to traits and organisms as to genotypes or alleles. In the context 200
of population genetics, where the evolutionary dynamics of populations of alleles is 201
the main consideration, often on one or two loci,[19] it is also possible to measure fitness 202
as the number of representatives that a given allele or genotype will contribute to the 203
following generation's gene pool. However, some traits that would not have any direct 204
effect on reproductive success will have, from one generation another, a frequency 205
that only depends on these traits' initial frequency and on chances of reproductive suc- 206
cess in organisms that carry them. In this case, their evolution is not a matter of selec- 207
tion, since these traits cannot be said to have relative fitness. 208

The key feature of selection is therefore the difference an organism's traits bring to 209
chances of reproduction. Its driving force is in some ways *differential* reproduction. 210
If all variants of a trait now have the same effect on reproduction, then everything 211
occurs as if the traits were not correlated to reproduction, and there is no selection. 212
The essential fitness is, then, *relative* fitness rather than absolute fitness. An anecdote 213
illustrates this point: two men are in the jungle: the first sees a tiger and says, "A tiger! 214
Quick! Run!" and the second retorts, "What's the point? Tigers run faster than us 215
anyway," to which the first man responds, "My problem is not to run faster than the 216
tiger; it's to *run faster than you*…" 217

Fitness has a clear connection to adaption, in the intuitive meaning of the adjust- 218
ment of organisms to their environment, a connection that Brandon (1996) while 219
explaining the most general sense of adaption in MS defines as *relative adaptedness*. 220
The more an organism is adapted to its environment, the more chances it has for sur- 221
vival and reproduction; heritable traits that contribute to adaptedness thus have a high 222
fitness value (Burian 1983). This led to the general formulation of a principle of natu- 223
ral selection (Brandon 1996) that would reinterpret the condition of fitness (C3) in 224
terms of adaptation. According to this principle the most adapted organisms, having a 225
higher level of fitness, will probably reproduce more, entailing that the traits that make 226
them most adapted will then be better represented in subsequent generations. 227

The condition of heritability has, for its part, given rise to a series of discussions: 228
is this condition really necessary? If one simply looks at two generations of a popu- 229
lation (satisfying C1 and C3) – one can support the idea that there is selection even 230
without heritability, because there will be differential reproduction of individuals 231

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[18] Genes are not required to be single determinants of a trait. It is only required that the fact of having a gene makes a difference to the value of the trait (see Waters 2005).

[19] Locus (plural: loci): the physical location of a gene on a chromosome.

232 due to of differences in a varying trait. Yet, there will not necessary be evolution
233 (except in extreme cases such as sterility of recessive homozygotes in a population
234 of pure homozygote strains), but interesting cases for biologists are those where
235 evolution occurs. Following the same logic, if we consider that *cumulative* selection
236 (i.e. selecting for slowly modified values of a trait, which progressively can give rise
237 to a new trait) is one of the fundamental forms of creating adaptation, such selection
238 proves impossible without heritability (which conditions any accumulation of a
239 trait's values). Even if a definition of pure natural selection, independent of the
240 question of knowing whether it leads to an evolution, would not require heritability,[20]
241 we must still keep this definition in a theory of *evolution*.

242 Since heritability (h^2) is a statistical property, it can be quantified. It is easy to
243 see that the higher it is, the more selection will be at work. If, inversely, it is weak,
244 selective action will essentially depend on differences in relative fitness among
245 entities: when they are strong, selection will take place; if they are weak, selection will
246 be undetectable and obscured by stochastic variations that exist in all populations
247 (generally referred to as "drift" – see below). Quantitative genetics directly studies
248 variation in quantitative properties conditioned by genes like height, weight, etc.,
249 rather than studying allelic frequencies (Falconer 1960). Generally the genetic
250 make-up of the trait is unknown, the trait value being influenced by a network of
251 hundreds of alleles. In this type of study, the coefficient h^2 is defined as the fraction
252 of phenotypic variance caused by additive genetic variance,[21] and the actual inten-
253 sity of selection thus depends simultaneously on the selective value of traits and on
254 their heritability. This implies that, rather than finding the conditions in which there
255 is selection, the crucial question would be to understand the rules that govern the
256 intensity of selection: it replaces a binary question ("selection or not?") with a
257 question of degree.

258 In this context, the notion of "response to selection" arises, related to heritability.
259 Let us suppose that there is a population in a given environment. Any regular
260 environmental factor defines a selective pressure: each type of individual – types
261 being distinguished by the possession of an heritable trait – will have, related to this
262 characteristic trait, specific chances of reproduction that are a function of this
263 environmental factor (resources, sexual partners, etc.). Let us also suppose to
264 simplify the example that there is only one selective pressure. If the trait is not, or
265 very weakly, heritable, this selection will only have a small effect; that is, the benefit
266 received by the *fittest* individuals will not be allocated, on average, to their offspring
267 (for example, if the tallest have selective advantages, their offspring will be hardly
268 taller than average so the advantage of being tall will get lost). Thus, the way in
269 which a population evolves by natural selection due to selective pressures will

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[20] For one such argument in this controversy, see Brandon (2008), and also the discussion of heritability among CNS in Godfrey-Smith (2009).

[21] Additive variance is variance caused by the contribution of alleles whose effects are presumed to be additive. In reality they are only rarely additive, but this is only a model, that can be made more complex and allows us to define h^2. Recent findings on epigenetics call for a more sophisticated partition of h between genetic and epigenetic transmission variance (Danchin et al. 2011).

depend on heritability, which thereby measures "response to selection" in the 270
considered population (cf. Brandon 1990, 2008). In quantitative genetics, this 271
"response to selection" is formally the product of heritability h^2 and the selection 272
differential s, which is a measure of association between trait values and fitness.[22] 273

Last, there is C1, the seemingly simple condition of variation.[23] Variation has two 274
meanings: intragenerational, namely, individuals differ regarding a focal heritable 275
trait (e.g. people are more or less tall…), and intergenerational, namely, an indi- 276
vidual will have various offspring (regarding the focal trait). And variation is taken 277
by the Modern Synthesis to be due to genetic mutation or (in sexual species) recom- 278
bination. Even leaving this equivocation aside, there is still one difficulty, which has 279
emerged through debates over the random or directed nature of genetic mutations in 280
the constitution of the Modern Synthesis. Imagine that mutations are directed in 281
order to foster better performance vis-à-vis environmental demands. Natural selection 282
is then only superfluous for evolution; even the relative difference in fitness between 283
entities will spontaneously diminish. More generally, if variation is directed, it will 284
make natural selection impossible. Variation must, therefore, be "random" in the 285
sense that the form of the environment does not allow us to predict it – random here 286
means "not adaptively directed". Of course selection does not require that *any* 287
mutation be possible; evolutionary history constrains[24] the space of variations. This 288
constraint is, however, orthogonal to the (un)directed nature of the variation; that is, 289
to the degree to which the environment functions as a predictor of variation. 290

Technological evolution can illustrate this last point nicely: certain scholars 291
(Lumsden and Wilson 1981; Cavalli Sforza and Feldman 1981; Boyd and Richerson 292
1985; Dawkins 1976; see Lewens 2013 for a summary) have tried to apply a selec- 293
tive theory to culture and, more directly, to technology (Basalla 1988). For instance, 294
it would be possible to understand the evolution of air travel, from the hot-air 295
balloon to the A380, as an evolutionary process where public demand, technological 296
possibilities, and energy resources played the role of selective pressures. However, 297
even setting aside the difficulty of finding an equivalent for genes in this technological 298
field, the project runs into a major problem. Variations (which distinguish different 299
products of the same type created in a given time period) are not random in this 300
case; they are due to engineers working on ways to adapt their prototypes for 301
specific goals. Selection does not appear to play any role. 302

Yet this statement of incompatibility between selection and directed variation 303
should be weakened: when variation is not totally random (that is, when not all 304
places in the space of possible variations are equally likely, and moreover, a sub- 305

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[22] Quantitative genetics takes selection experiments as its paradigm: one selects a group of indi-
viduals who have a required phenotypic value and breeds them. The result, and thus the "response"
to the selection will be proportional both to the average of their phenotypic values and to the trait's
heritability. If this is 1, the following generation will have an average phenotypic value of the
selected parents; if it is ½, the average phenotypic value will be half, etc.

[23] See the chapter "Variation" for theories of variation; here we are only assuming the fact of
variation.

[24] On "constraint" see Grandcolas, "adaptation", Chap. 5, this volume; Gould and Lewontin (1979).

space closer than others from the subspace of optimal solutions is most probably occupied), but not totally directed, then there is room for natural selection.[25] Here again, it is a matter of degree rather than straightforward opposition.

1.3 Replicators and Interactors

The "necessary and sufficient condition" formulation, even if it outlines the most general functioning of natural selection, is not without its weaknesses. The first flaw as argued above is that it seems dichotomous ("is there or is there not selection"?) whereas each one of these conditions specifies in fact the degree to which the process involved is produced. In addition, recent research has shown that NSC is not general enough[26]; in particular, it imposes unnecessary conditions on natural selection (Okasha 2006, based on an analysis of Price's equation), which is a major flaw in a formulation that calls itself universal. Finally, there is a nagging ambiguity about exactly what the should be heritable: is it fitness, or phenotypes? Lewontin (1970) said "fitness", Endler (1986) corrected this with "traits", which seems more correct (of course the criterion of traits involves that of fitness), but in actually each of the two options defines different legitimate cases of selection (Godfrey Smith 2007).

There is in fact another extremely general concept of natural selection. In *The Selfish Gene* (1976), Dawkins described an all-powerful selection that acts upon everything from molecules to culture. Biological evolution is the easiest to understand, since it rests on the gene, whose control of inheritance we know quite well. It serves as a paradigm for analysis of the way in which other fields are also subject to the selection process. Dawkins calls genes *replicators*, since their fundamental property is to replicate themselves more or less identically through mitosis and meiosis. They are essentially the substrate of heredity. Other areas of evolution must also have their own replicators. In contrast, organisms are simply "vehicles" for these replicators. Developing this idea further, Hull (1980) suggested conceiving of entities involved in selection as belonging to two classes: replicators and interactors. The nature of selection then appears clearly: *it is a matter of the differential replication of replicators as a function of the interactions of interactors.*

Consider the usual cases of selection: some organisms reproduce themselves more than others as a function of their traits; genes that code for these traits increase or decrease in frequency and then the constitution of the gene pool progressively transforms. What allows us to speak of selection here is that not only the replicators are undergoing changes in frequency, but also that this change is due to what is happening at the level of the organisms (success in foraging, finding mates, etc.), namely the interactions that ultimately lead to more descendants of some organisms than of others.

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[25] As to the role of chance variation related to selection, and especially the importance of the order of random mutations (as well as the fate of this notion by Darwin and by the Modern Synthesis biologists) see Beatty (2011).

[26] See especially Godfrey-Smith 2009.

Hull's formulation captures this characteristic (seen above) of natural selection   343
as a process that plays out on two different levels. Moreover, it allows for the   344
extension of natural selection to many cases other than the usual ones. If it is most   345
often the case that genes are the replicators and organisms are interactors, nothing   346
requires it to always be so: interactors and replicators are not natural categories of   347
entities, but rather roles in a process. Think of the "selfish genetic elements" (Burt   348
[AU1]   and Trivers 2006), which were discovered in the work of Doolitle and Sapienza   349
(1980) – namely, sequences present inside the genome that are there because,   350
though they serve no purpose for the organism, they reproduce quicker or better or   351
to the detriment of other sequences on the genome. This is a case, then, where the   352
replicators are genes, but where selection involves the differential reproduction of   353
certain genes as a function of their interactions *with other genetic elements* (having   354
a more rapid replication speed that leads to overrepresentation after meiosis,   355
neutralizing other alleles during meiosis ("segregation distorters"), etc.), in a way   356
that here the genes are also interactors.   357

This perspective does, however, run up against a major problem: a general con-   358
cept of selection must account for all circumstances where a selectionist explana-   359
tion is possible; it must therefore be applicable to the inquiry into "major transitions   360
of evolution" that have produced the different types of individuals we know today   361
(Maynard-Smith and Szathmary 1995), such as multicellular organisms, unicellu-   362
lars, genes, etc. – individuals that are likely to be ascribed fitness properties   363
(i.e. selective advantage regarding their contributions to subsequent generations).   364
This research program (e.g. Michod 1999; Bouchard and Huneman (2013)) involves   365
speaking about selection on macromolecules, that are thought to have preceded the   366
RNA and DNA that are essential to life; but these molecules do not *replicate*. Insofar   367
as there is selection wherever replication is absent or, at least, controversial, like in   368
this case, the definition of selection in terms of interactors/replicators is not as broad   369
as it should be.[27] Moreover, reproduction, even if we allow for it in macromolecules   370
or cultural entities, is not always reliable: what degree of reliability is then required   371
in order to talk about replication? The formulation of Necessary and Sufficient   372
Conditions avoided this type of problem since heritability is quantifiable; the repli-   373
cators/interactors formulation, though it does have the advantage of uncoupling   374
natural selection from notions that were originally unique to population genetics   375
(fitness, inheritance) in order to create an absolutely general idea of selection, is   376
ultimately restrictive due to the essentially binary notion of the replicator (something   377
either is or is not a replicator).   378

To sum up, formulating a general outline of selection is a project that is both   379
illuminating and limited. In most cases, insofar as replicators ensure heritability and   380
the effects of interactions are statistically tracked in fitness values, the two phrasings   381
(NSC/interactors-replicators) are reciprocally translatable. Certain cases of presumed   382
evolution by natural selection can't be subsumed under one or the other conception,   383
as I have indicated earlier, so that ultimately neither attempt allows an absolutely   384
general formulation of natural selection. It is possible, moreover, that the fact that   385

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[27] Godfrey-Smith (2000) demonstrates with a thought experiment that the concept of replication itself is not essential for selection.

386 genes are entities created by evolution, presumably through natural selection itself
387 (Michod 1999), makes these formulations only partially correct: in their explanation
388 of natural selection they take for granted that which is a result of selection itself –
389 heritability or replication.[28]

390 　　The weaknesses of general formulations can also come from the presupposition
391 that, as is often the case when it comes to conceptualizing natural selection in its
392 generality, population genetics is the key to its understanding. Population genetics
393 has undoubtedly given way to the mathematical representation of selection, making
394 the hypothesis of natural selection testable. Yet selection involves several fields of
395 biology, and it is possible that the concept of natural selection takes on a different
396 tone according to the discipline studying it. There is already a fundamental differ-
397 ence between population genetics, which *assumes* fitness values relative to alleles
398 and to genotypes and follows their evolutionary dynamics, and ecology (population
399 ecology or community ecology, at least), which studies relationships between
400 organisms of different species. The *causes* of fitness (and therefore of selection,
401 cf. Wade and Kalicz 1990) for a given population are thus included in and studied
402 by ecology. It is therefore not clear that an analysis of natural selection carried out
403 within a population genetics framework will yield a final truth about selection.
404 In particular, investigating how different selective pressures combine to yield "the"
405 selection, namely a selection coefficient or fitness values, is supposedly settled once
406 we *ascribe* relative fitness to alleles, genotypes or organisms, but it remains a very
407 complicated issue (is it an addition? A product of conditional probabilities? etc.).[29]
408 To conclude, if a general concept of natural selection requires an answer to these
409 questions, then it cannot do so based on population genetics alone.[30]

2　What Does Natural Selection Explain, and How?

411 The ubiquity of the selectionist explanation arises from the fact that it explains
412 very different *explananda*[31]: adaptation (certain traits whose adjustment to their
413 environment seems obvious[32]), diversity (arising from the response to different
414 selective pressures), evolution – at least in the sense of changes of a population's
415 allelic frequencies, and, from there, of the replacement of one sort of organism
416 (defined by the possession of some alleles or some trait) by another in a population.

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[28] See Griesemer (2000) for an attempt at reinterpreting selection in general using the yardstick of works on evolutionary transitions.

[29] See Matthen and Ariew (2002), Bouchard and Rosenberg (2004).

[30] See Glymour (2006) for a radical critique of the notion that population genetics provides a general dynamic of selection.

[31] Group of statements corresponding to what is explained or to be explained (singular: *explanandum*).

[32] "Adaptation" refers both to the result of selection – a trait – and the process that leads to it. Here, this second meaning is completely set aside.

The accumulation of these replacements, or cumulative selection, thus explains the   417
emergences of novel traits (Mayr 1959b) as well as the appearance of certain trends   418
on the phylogenetic scale (for example, the increase in size observed in different   419
vertebrate lineages).   420

2.1 Types of Selection   421

One of the first empirical attestations of natural selection was "industrial mela-   422
nism". Some insects, the "peppered moths", existed as two types (black and white)   423
in a single region of England; the lighter ones were the majority, but after a certain   424
amount of time, the dark ones claimed the majority. As Kettlewell (1955) pointed   425
out, emissions from nearby industrialization changed the color of the trees, and the   426
dark insects became the favorite prey of predators, which had previously been the   427
role of the lighter ones. Selection had thus changed the population's color. Inversely,   428
cleaning up the air would lead to an inverse selection favoring the lighter insects.   429
This form of selection, perhaps the most striking case, is by no means the only one.   430
The selection process can effectively take many forms, some of which I will list   431
here. First, as in the case of industrial melanism, selection can favor mutations that   432
move in the same direction. This is "directional selection", and it is the concept that   433
most easily comes to mind when one considers novel appearances. There is also   434
"stabilizing selection", which broadly maintains given traits, adjusted to the envi-   435
ronment, and thus eliminates the most distant mutations or variants. Directional   436
selection acts on the trait's mean value; stabilizing selection acts on variance,[33]   437
without changing the average value (cf. Fig. 4.1). "Disruptive selection" is another   438
form, which concentrates the values taken by individuals in the population on two   439
values of traits and eliminates intermediate ones (Fig. 4.1c). In ecology, for instance,   440
a single population may have two different preys; disruptive selection will be the   441
process by which two types of individuals become the majority, each specializing in   442
one prey – the more generalist individuals being eliminated because they are less   443
skilled at catching each of the preys (of course, this example only holds in precise   444
conditions of frequency and lifecycle of the preys; Fig. 4.1c would show a disruptive   445
selection on a camouflage trait in a population with two types of predators, one that   446
sees the "lighter ones" and the other the "darker ones".)   447
   On the other hand, up until this point we have discussed the fitness of character-   448
istics as being the number of expected offspring *in the environment*. Yet other   449
individuals of the same species are also part of the environment, and it is thus   450
possible that the selective value of a trait is a function of the frequency of those   451
who carry it, which is the definition of *frequency-dependent selection*. Camouflage   452
is the perfect example of a trait that often depends on frequency: if many individuals   453
possess it, this raises the likelihood that predators will develop strategies of   454

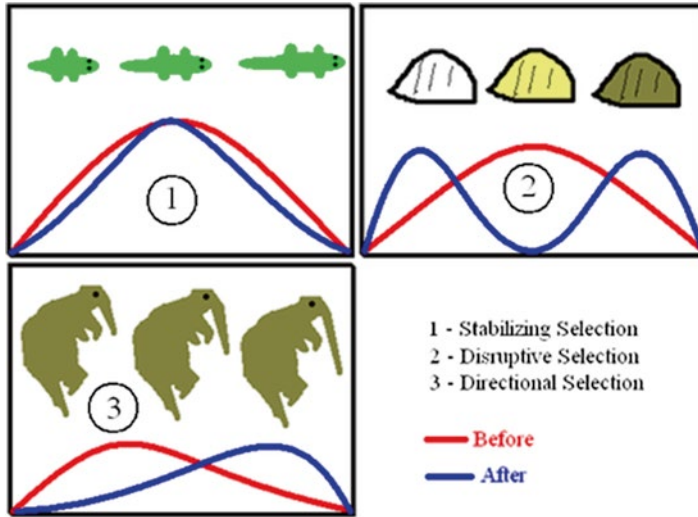[33]Variance: see footnote 10 in Christine Clavien's, Chap. 34, this volume.

Fig. 4.1 Schemas of stabilizing (*1*), Disruptive (*2*) and directional (*3*) selection

immunity to camouflage, which will then diminish its selective value. In the standard case, we presume that selection optimizes certain traits,[34] and thus model selection by optimization methods. With frequency-dependence, the trait which seems optimal may be counter-selected when it reaches some frequency. Calling "strategies" the traits that are competing,[35] the idea for understanding the dynamics of selection and predicting its outcome is to determine the strategies such that, if they are adopted by individuals in the population, no other ("mutant") strategies can invade the population. Maynard Smith (1982) called this "evolutionary stable strategy" (ESS), and behavioral ecology has made great use of it; often ESS are a mix of simple strategies (for example, in case of encountering an other individual, "fight with a probability 0.3 and flight with a probability 0.7"). Many traits are, in effect, dependent on frequency, but sometimes this dependence is so weak as to be negligible.

Beyond these forms of natural selection, Darwin (1999 [1871]) also pointed out "sexual selection", with its two modalities: the competition among males for females or the female choice. For him, many of the properties that make human races different, as well as those that are unique to each sex, come from sexual selection. Sexual selection greatly preoccupied evolutionists, since it sometimes seemed

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[34] See Philippe Grandcolas's chapter on adaptation, Chap. 5, this volume.

[35] The word "strategy" of course does not mean that organisms consciously deliberate and plan their actions; it just means a kind of determinate behaviour in given circumstances, distinct from another determinate behaviour, so that all strategies constitute a "strategy set" (for example: fight a competitor/ flight in the face of a competitor, care for the offspring after hatching/don't care for them and mate with other partners, etc.),

to be independent of natural selection because it has favored traits that were clearly 472
counter-adaptive (the peacock's tail, obviously chosen by females, seems to have 473
little adaptive value).[36] As for its principle, at its root it seems that sexual selection 474
does not differ from natural selection (e.g. Mayr 1965a), and one could combine 475
them in considering the relationship to females as a supplementary selective 476
pressure. Yet the existence of the sometimes counter-adaptive direction of sexual 477
selection, as well as the fact that it only applies to sexually reproducing species and 478
does not involve survival, makes it more pragmatic in many contexts to consider the 479
two separately. (Of course, on the most general level both forms of selection are the 480
same process of differential reproduction[37]). Amotz Zahavi has developed an 481
explanation of sexual selection along these lines with the concept of "costly signal- 482
ing": females prefer counter-adaptive traits since they are a reliable signal of the 483
male's having a higher fitness than others, since he is able to bear such extraneous 484
cost. This "handicap principle" defines, for Zahavi, another form of selection, which 485
he calls "signal selection" and which explains obviously non-adaptive traits that 486
natural selection does not explain (Zahavi & Zahavi 1997).[38] 487

2.2 Epistemology of Selection Explanations 488

How then does the explanation by natural selection work? Sober (1984) clearly 489
formulated the implicit understanding shared by population geneticists. Let us imagine 490
a population of organisms diploid at a single locus, with alleles having frequencies 491
p and $1-p=q$. If the population is infinite, panmictic,[39] without mutation, migration, 492
or selection, the proportions of each of the alleles in generation 2 and each thereafter 493
are simply calculated with the Hardy-Weinberg theorem: $F(AA)=p^2$, $F(Aa)=2pq$, 494
$F(aa)=q^2$ (they immediately follow from Mendel's second law).[40] 495

Thus, if these proportions do not hold, then something more must be at work. 496
Setting aside mutation and migration, selection explains this difference, exactly as 497
in the Newtonian mechanical model where forces explain the gap with respect to the 498
uniform trajectory predicted by the principle of inertia. If the fitness values of 499

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[36] Roughgarden (2006) goes as far as contesting the validity of the idea itself, in favour of what she calls "social selection", i.e. the forming of teams to raise offspring, but her views are controversial.

[37] Fitness is measured traditionally in the number of offspring, adaptedness (in the sense of adjustment to the environment allowing for a longer survival) and traits maximizing access to females are two ways of optimizing this fitness; the traits that are ultimately selected often appear as trade-offs between these two pressures.

[38] Grafen (1990) proposed a mathematical model of the handicap principle, which made a very powerful and explanation of it using behavioral ecology.

[39] A population where all mating between individuals are random; all individuals are potential partners.

[40] Note that in the expression of these frequencies, AA, aa, Aa are the genotypes. W is fitness; the assumptions are unrealistic of course, but this is a model; the inclined planes, with no friction, etc. in classical mechanics are the same type of unrealistic models.

genotypes are known, it is then possible to predict these deviations by plugging these fitnesses into frequency equations (in the second generation, $F(AA) = p^2$ $W(AA)$, etc.).

The problem of applying these predictions rests in the clause of infinite populations: if they are finite (and in practice, small), then there is a stochastic phenomenon of "random genetic drift" that occurs; Sewall Wright illustrated its importance. Genetic drift is easier to understand with a dice example: one die tossed millions of times will have, by the law of large numbers, a very high probability that the frequency of each one of the sides will equal 1/6. If the die is tossed only ten times, however, it is still probable that the 5 and the 6 each appear 4 times, or perhaps even not at all. The same goes for a very small population of organisms, where it is possible that the actual frequencies of alleles do not correspond to the expected frequencies (given the genotypic fitnesses) – the equivalent of 1/6 appearing 4 times in the dice example. Drift depends directly on the size of the population. If a population is small, it can overpower selection. More generally, the intensity of selection will depend on both the selection coefficient, the rarity of the allele under consideration, and the size of the population (e.g. Gillespie 2004).

The question of the relative importance of drift and selection was raised at the origin of the Modern Synthesis. Fisher maintained (via the fundamental theorem of natural selection, see below) that, nature being made up of large populations that could be treated as infinite, selection would always work upon it so that, generally, the population's mean fitness would grow. Conversely, Sewall Wright, who studied genetic drift in depth, thought that populations are often small and that genetic drift was more important. Drift plays a fundamental role in understanding evolution, since the possibility of drift prevents populations from stagnating at the local *optima* of fitnesses instead of reaching higher fitness peaks, according to Wright's "shifting balance theory"[41] (Fig. 4.2). The issue is still not settled (cf. Coyne et al. 1997) and partially rests on the empirical prevalence of small populations. Much later, Motoo Kimura's (1983) neutral theory showed that drift is an extremely intense force at the nucleotide level (rather than the trait level) and is responsible for a large part of the genome's composition.[42] One of the arguments for this is the fact that different

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[41] Sewall Wright elaborated the idea of "adaptive landscape", the surface defined by the frequencies of *n* possible alleles on *n* axes, and the average fitness of the population corresponding to the combination of these *n* frequencies on the final axis. Such a landscape clearly shows the local and global *optima*, and the question is: why don't all populations remain most often on local *optima*. The "*shifting balance* theory" mentioned here aims to resolve this problem. Moreover, the peaks are not really stable, since a population that reaches the local optimum loses genetic diversity and thus becomes more vulnerable to environmental changes. However recently Gavrilets has shown that since real landscapes are high-dimensional their mathematical properties are different from three-dimensional intuitive landscapes and allow for n-dimensional shapes that make possible shift between peaks without loss of fitness ("neutral network") (see Gavrilets 2011).

[42] For neutralists, it is not exactly an question of drift in the sense Wright uses it, since he would consider the alleles themselves whereas neutralists are more interested in the stochastic fluctuation of the nucleotide composition of alleles. In both cases, though, it is a matter of a selectively neutral stochastic alternative to natural selection.

Fig. 4.2 Adaptive environment. Note the local optima next to the global
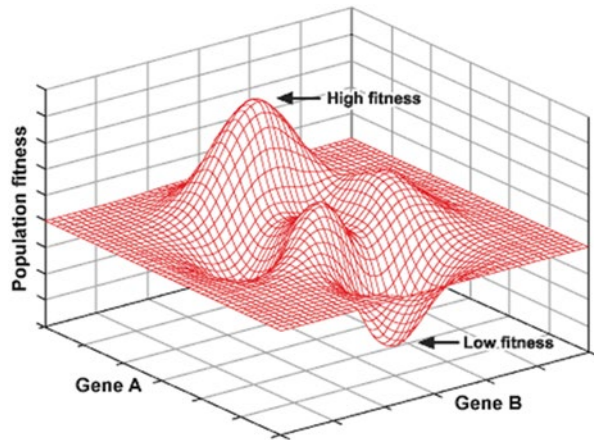
nucleotide triplets code for the same amino acid,[43] meaning that certain nucleotide substitutions are undetectable for natural selection since they contribute to the same phenotype. Only stochastic variation will then determine the evolution of these nucleotides (Gayon 1998). Molecular biology has developed many tests to determine which portions of the genome are due to selective action and which are due to drift. These tests rely fundamentally on the fact that the variation pattern in the case of a genetic sequence subject to selection differs from a case where it simply drifts (Voight et al. 2006; Pál et al. 2006).

Epistemologically, it is not always easy to differentiate between traits that are there essentially because of natural selection and those that are there because of genetic drift. One of the reasons for this is that we do not always have an extensive knowledge of selective pressures. Take the example of eye color distribution. At first stake, eye color seems irrelevant for adaptation, hence selectively neutral. If a population has a majority of blue eyes, we can assume it is due to genetic drift. Recently, however, it has been shown that blue eyes were subject to sexual selection bias in certain Nordic countries because men with blue eyes preferred women with blue eyes (Laeng et al. 2007). (The evolutionary hypothesis behind this is that preferring blue-eyed women – for a blue-eyed man – yields certainty in some instances where illegitimate offspring is possible[44]). This selective advantage is enough to raise the frequency of blue eyes (by raising the frequency of the allele that conditions men to prefer blue eyes…). This example illustrates that when it

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[43] What is called the degeneration of the genetic code.

[44] If a child of a blue eyed couple has brown eyes, then his real father is someone else, because the gene for blue colour is recessive.

552 comes to assuming that something exists because of genetic drift, one cannot be
553 certain that the phenomenon is not in fact due to a subtle selective pressure.[45]
554 Because of this epistemological difficulty, certain authors have denied the exis-
555 tence of drift (Rosenberg 1995) or have said that it is not objectively discernable
556 from selection (Walsh 2007). Nevertheless, drift and selection are *conceptually* dif-
557 ferent. To return to the previous example of eye color, if one is to say that blue eyes
558 are there because of genetic drift, one means that it is equally possible that it could
559 be brown eyes that arose, since it is random variations that made blue eyes the out-
560 come of drift. In other words, if one were to replicate the same population and
561 restart, "brown" could win out just as easily as "blue" – in the same way as a new
562 series of 10 dice tosses would yield a different leading number than the previous
563 one. On the contrary, arguing that "blue eyes" is the result of natural selection means
564 that eye color itself, and certain properties linked to it, are causally involved in the
565 increasing frequency of the trait, since having blue eyes (or not) makes a difference
566 in the individual's objective chances for reproduction (Huneman 2012). Hence per-
567 forming the experiment yet again with a relatively large population[46] would, most
568 likely, yield another blue-eyed majority. The concept of natural selection thus
569 includes *a causal efficiency of the nature (and effects) of the trait* in its frequency
570 variations, whereas the concept of drift signifies a causal indifference of this same
571 nature of the trait regarding its changes in frequency. Selection and drift therefore
572 differ conceptually, even if they may sometimes be epistemologically indiscernible,
573 and ontologically inseparable processes (see next paragraph).[47] Selection is also not
574 a purely stochastic process, contrary to drift; patterns of frequency change across
575 generations due to selection are not occurring randomly but are causally related to
576 the nature of the traits. Even if fitness is a probabilistic concept, selection remains,
577 compared to drift, a deterministic process.[48]
578 The problem of composing selection and drift still remains. Population geneticists
579 consider both as forces and add them together in the manner of classical mechanics.
580 Consider the dice again; suppose one die is hollowed out so that the expected
581 frequency of side 1 is ½. Now suppose that out of 30 tosses, the 1 appears 10 times
582 (rather than the expected 15 times). Would one then say that the weight (of the
583 hollowed-out die) is responsible for these 10 throws where 1 shows up, or that it is

[45]The compared importance of drift and selection is a crucial topic for modern evolutionary biol-
ogy. Recently, Lynch (2007) argued that drift has been a very important cause of the architecture
of eukaryote genome, especially because since eukaryote are often large-sized organisms, their
population tend to be small, therefore drift is powerful relative to selection.

[46]See Lenski and Travisano (1994) and Barberousse and Samadi chapter on this subject, Chap. 11,
this volume.

[47]It does happen that one can experimentally separate the two; see Millstein (2006) who studies
Lamotte's work on the evolution of snails.

[48]One can argue whether or not selection is deterministic, but here I am simply pointing out that
the stochasticity in the theory of evolution comes out of genetic drift and not natural selection. This
is less of an ontological argument than it is an observation concerning the mathematical modeling
of these concepts (see Malaterre and Merlin, Chap. 17, this volume).

responsible only for the 5 additional tosses where 1 showed up in addition to the   584
5 expected faces of a non-hollowed-out die ? And those stochastic fluctuations   585
preventing a frequency of 15 of side 1: for which occurrences are they responsible?   586
In classical mechanics, trajectories result from the addition of forces whose proper   587
result can be stated independently of other forces; now, given the analogy between   588
weight and fitness on one side, and stochastic fluctuations and drift on the other, it   589
becomes clear just how difficult it is to combine selection and drift in the same   590
way mechanics adds up forces – which makes selection and drift ontologically   591
inseparable.   592

In a series of articles (Matthen and Ariew 2002, Walsh et al. 2002), after Endler   593
(1986), Walsh, Lewens, Ariew and Matthen on the basis of such considerations   594
defended an idea of selection as a statistical construct resulting from an aggregation   595
of individual interactions and without any causal efficiency, much like entropy in   596
statistical mechanics, rather than as a force. This sophisticated controversy is still   597
open to debate, and even if the concept of force only has an analogical usefulness,   598
certain researchers continue to argue for natural selection as a cause (Millstein 2006;   599
Bouchard et Rosenberg 2004; Abrams 2007; Huneman 2013).[49]   600

But the *cause* of what, exactly? And, on a solely epistemological level, what is   601
precisely *explained* by natural selection? This last question (the only one I will   602
broach here) comes up once we focus on the notion that traits, which are adaptations in   603
the theory of evolution, are originally variations marked and maintained by natural   604
selection. In this sense, if natural selection does explain the frequency of traits   605
within a population, it does not appear to explain *why a trait exists* in the first place   606
(since that is a matter of variation mechanisms). This observation, simple though   607
it may seem, sounds deflationary with regard to most of pronouncements about   608
natural selection. Mayr (1965b), for example, thinks that natural selection leads to   609
essential characteristics of the living world, as diverse and complex. Dawkins (1982)   610
finds in natural selection the architect of all complex traits of the living world.[50]   611
If selection is only responsible for the diffusion of traits in a population and eventu-   612
ally of their maintenance, such judgments are overvalued. Neander (1995) thus   613
opposed a "creative" vision of selection to a "negative" view that would simply   614
make the prevalence of traits selection's only legitimate *explanandum*. From the   615
latter perspective, selection offers an explanation of *why a certain individual has a*   616
certain trait (it is explained by the prevalence of the allele in question in the popu-   617
lation), but not *why this certain trait exists*. Yet some arguments do exist that selec-   618
tion also contributes to the creation of traits, largely because in modifying the gene   619
pool, cumulative selection modifies the probabilities for this or that genotype – in   620

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[49] Lewens (2010) proposes a subtle analysis of the difference between "force of selection" and "selection for".

[50] As is often the case with Dawkins the metaphorical nature of formulations ("the blind watchmaker", the "selfish gene" etc.) affects the precision of his remarks; and yet on this point we can certainly classify him together with Mayr or Gould, as well as many authors of the Modern Synthesis, as someone who insists on the "creative" sense of selection – with this precision that the essential thing (from the explanation's point of view) is the complexity of traits generated by selection.

621 turn responsible for a given trait that one is attempting to explain. Of course, this
622 philosophy of science issue does not bear directly on biology; fundamentally, it only
623 concerns the nature of explanations for adaptations. The more one restricts the range
624 of possible *explananda* for natural selection, the more ground one yields to explana-
625 tions of adaptation in non-selective terms, whether these are developmental or even
626 self-organizational as in Kauffmann's "order for free"[51] (or both together): because
627 if selection only explains the *diffusion* of adaptations, it is still necessary to under-
628 stand their *emergence* (Walsh 2003).

629 Whatever the case may be, the principle of natural selection is crucial to all
630 evolutionary disciplines. The consideration of epistemological difficulties raised by
631 explanations using natural selection leads to the questions of the metaphysics of its
632 overall status.

3 The Status of Natural Selection

3.1 Is Selection a Natural law?

635 Evolutionary biology has often been subject to scrutiny regarding the status of laws
636 that it would formulate. These laws are never universal (for example, they involve
637 species, which are transitory[52]), and even the most general formulations, though
638 mathematical such as those of population genetics, require matters of fact that are
639 contingent. The Hardy-Weinberg equilibrium for instance assumes a sexually repro-
640 ducing Mendelian population, but sex is the result of evolution and most likely
641 historically contingent (see Gouyon, Chap. 23, this volume, Maynard-Smith 1978;
642 Williams 1975). All of this would justify what Beatty (1995) calls the "evolutionary
643 contingency" thesis.

644 In sum, such remarks underscore the fact that evolutionary biology is in part
645 historical – we could say that nothing in evolution has meaning without an historical
646 perspective (see Gayon 1993). Granted, many mathematical models exists
647 (Fisher-Wright models in population genetics, selection frequency-dependent
648 models such as those of Clarke and O'Donald, Lotka-Volterra equations in predation
649 ecology, etc.), but their application to real biology requires a knowledge of the
650 historical context, and, unlike physics, does not bring with it nomothetic generalities
651 similar to physical laws that link matter and energy.

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[51] Kauffmann (1993) studies properties of Boolean networks in order to see the emergence of stable ordered patterns from iterated interactions between nodes.

[52] But see Lange (2007) for an idea of a law the would give status to laws for observations such as "Cuckoos are parasites of other species' nests." See the chapter of Samadi and Barberousse, Chap. 8, this volume.

Yet whatever their weaknesses may be, the general formulations of natural   652
selection I outlined in §1 establish that it would take place in many other possible   653
worlds provided that certain very basic conditions were met. In this way, natural   654
selection is absolutely universal. Next to biological claims, which are all limited to   655
species, clades, or historical periods of life, it seems then that the principle of   656
natural selection – that is, if a collection of entities indeed fulfills such and such   657
conditions, it will undergo natural selection – resembles a natural law. Nevertheless,   658
there are doubts to draw from this hasty conclusion.   659

The principle of natural selection is certainly universal, and it certainly holds true   660
for other possible worlds besides ours, or in other words, in the parlance of philoso-   661
phers of science, it 'supports counterfactuals' (that is, if entities were not satisfying   662
one of the conditions for natural selection, they would not be undergoing selection;   663
and if there were no selection at all, then one of the conditions would not have   664
been met), which is one of the criteria required for natural laws. The universality in   665
question extends even beyond the possible worlds that are nomothetically identical   666
to ours (that is, sharing fundamental physical laws and differing in initial conditions),   667
a characteristics that would not hold about many laws of physics (think for example   668
of worlds where inheritance is not realized by DNA but by another physical sub-   669
stance, underpinned by different chemical laws). But if we look closer, does natural   670
selection behave in the same manner as familiar laws like that of gravity? The law of   671
gravity provides an absolute formulation of the behavior of two objects as a function   672
of two properties, mass and distance. In general, natural laws include in their formula-   673
tion a list of properties; having them or not, and the degree to which they are pos-   674
sessed, determines values of the variables contained in the law.[53] At issue with   675
natural selection is that its action is essentially context-dependent: in certain cases,   676
some properties will be relevant for defining selection pressures; for instance, color   677
when the environment has predators who can see color. In cases where the predator   678
cannot see it, though, color will not be relevant. Furthermore, these claims are only   679
valid for a given period of time – they depend on the group of available mutations   680
(if there were to be a mutation that renders some predators sensitive to color, then the   681
selective pressures would change). Natural selection works differently than the law   682
of gravity since we could not list all the properties that enter into its formulation.   683

Of course, it is possible to say that 'fitness' is the only property involved in   684
natural selection. This argument raises two important objections. First, fitness is not   685

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[53] Certain philosophers (Dretske 1977, or even Tooley and Armstrong) have argued that a law, before being a general statement concerning individuals, is a singular statement that links proper- ties (for example, gravity is a single statement that links mass and distance). This position avoids well known pitfalls that appear when trying to specify seriously what separates an accidentally true universal judgment ("there is no mountain higher than 10,000 km") and a nomothetically true universal judgment ("there is no liquid mountain"). The difficulty then boils down to understanding what constitutes an 'genuine' property (intuitively, "weighing 20 kilos" is an genuine property, "liking Brahms or having voted for Obama" is not; but finding the criterion that sets apart these two types of properties is tricky (see Shoemaker 1984)).

686 a property that is as natural or genuine as others. Rosenberg (2001) calls fitness
687 *supervenient,*[54] in the sense that certain esthetic or ethical properties "supervene" on
688 the material composition of objects to which they are ascribed. A disjunction of very
689 different biological properties (seeing far, running fast, etc.) can therefore realize an
690 identical fitness, which is always dependent on the environmental context (unlike
691 mass, a property shared by multiple diverse atomic structures but in itself context-
692 independent). Under certain views of what a law is, such properties are not ontologi-
693 cally robust enough to define natural laws.

694 The second objection admits that natural selection has the character of a law that
695 engages the property of fitness, but only emphasizes that such law is not essentially
696 biological. Natural selection is the population genetics dynamics in which alleles'
697 frequency, generation after generation, depends on their fitness, which is precisely
698 the probability of the differential reproduction of individuals carrying these alleles.
699 The truth of this assertion is grounded fundamentally in mathematics, more specifi-
700 cally probability theory, rather than in biology. The fact that Fisher (1930, 28) draws
701 a parallel between the dynamic of alleles with different fitnesses and the dynamic of
702 loans with various interest rates indicates that it is a matter here of something that is
703 not initially biological. The biological context comes after, when we start to look at
704 the causes of fitness (namely, the ecological interactions that explain why such trait
705 has chances of survival and reproduction higher than such other trait in a given
706 environment). From this perspective, natural selection is not a law of biology, but a
707 mathematical principle that yields a variety of possible biological generalizations of
708 a locally nomothetic nature. This principle implies, for example, a tendency toward
709 optimization at work in gene pools, and also supports most of the models of behav-
710 ioral ecology.[55] Optimization here means a sort of fit between organismal traits and
711 environmental demands, and it is indicated, at least in some models like behavioural
712 ecology's models, by fitness maximization.

713 Fisher (1930) introduced his "fundamental theorem of natural selection" as
714 "the law of evolution." Nevertheless, this statement requires a subtle interpretation.
715 Traditionally, the interpretation has been: the variation of population mean fitness
716 is equal to the additive genetic variance,[56] which implies that it is always positive,
717 hence that mean fitness increases. This interpretation immediately runs into some
718 counter-examples, such as cases of selection that are negatively frequency-
719 dependent. Think, for example, of the rise in frequency of "aggressive" in a

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[54] On this concept, See Kim (1993).

[55] The link between selection and optimization seems obvious; the far from trivial demonstration of this apparent truism is given in Alan Grafen's articles (2002, 2006).

[56] That is, variance due to the addition of alleles' contribution to the phenotypic value, ignoring the relationships that contradict this additivity: epistasis, dominance.

hawk-dove model.[57] Yet there have been recent[58] different interpretations of the 720
theorem, as an equality between the variation in mean fitness (directly) *due to* 721
natural selection and additive genetic variance. The theorem becomes correct but its 722
biological meaning remains controversial. 723

Fundamentally we can thus say that the principle of natural selection is in 724
general a mathematical principle from which many different models may be built, 725
(optimization in behavioral ecology, "evolutionary stable strategies" in behavioral 726
ecology when no optimal strategy is available because there is frequency-dependence, 727
models with one or two loci in population genetics, etc.). Each mathematical model 728
captures some aspects of the reality of selection in nature, but one can't say that 729
each model is a different take on the same law of biological nature.[59] 730

Brandon (1996) defends an analogous position and discusses the principle of 731
natural selection as an explanatory scheme – rooted in probability theory – rather 732
than as a law. In itself, natural selection is not a biological law, but its instantiation 733
within specific biological contexts – that require considering causes of the selection 734
(i.e. specific environmental demands) as well as constraints on possible variations 735
(hence, historical considerations) –transforms it into local biological laws.[60] For 736
instance the so-called Bergmann's rule, according to which birds in general become 737
larger when going up North -because the surface-volume ratio entails that larger 738
birds are less likely to lose heat, and temperatures decrease along a South/North 739
gradient – could be such a law. Applied to predator–prey situations, the principle of 740
natural selection can also give rise to extremely general statements in ecology like 741
the Lotka-Volterra equations, or even the "competitive exclusion principle".[61] 742

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[57] The "hawk-dove" game was popularized by Maynard-Smith 1982 (See Clavien, Chap. 34, this volume). Hawks fight doves and the doves flee the fight; the hawks' fitness is higher and so their fitness rises, but when there are too many hawks, it becomes more advantageous to be a dove (the hawks eliminate each other). In this sense, the mean fitness of the population does not rise, contrary to the theorem, since increasing the number of hawks increases mean fitness up to a point where hawks' fitness becomes lower than doves' fitness, and then population mean fitness decreases.

[58] See Frank and Slatkine (1992), Edwards (1994) (following Price (1972)).

[59] Following this line of argumentation leads easily to a semantic vision of the theory of evolution – and not a syntactic one, originally adapted for physical theories (See Thompson 1989). Since the 1960s philosophers have indeed distinguished between two conceptions: the traditional view, the syntactic one, for which sciences can be rendered axiomatically in language of first order logics, relying on semantic rules that allow for the construction of theoretical terms based on observations; and the recent alternative, the "semantic" view initiated by Bas Van Frassen, Patrick Suppes and Frederick Suppe, for which theories are structures defined in a formal language and satisfied by families of mathematical models. The most general statements under the first conception are laws of nature, whereas the second, insofar as it does not have the equivalent of "correspondence rules" between terms of observation and theory, gives no status to the idea of natural law (See Van Fraassen 1980).

[60] On the notion of constraint, see Gould and Lewontin (1979) and Grandcolas, "Adaptation", Chap. 5, this volume.

[61] See art "Ecology", Delord, Chap. 25, this volume.

3.2 Laws and Contingency

This dialectic of (local) lawlikeness and historicity that seemed to be proper to evolutionary biology invites a reconsideration of the metaphysical question of evolutionary contingency or necessity. Against spiritualist views of directed evolution, Stephen Jay Gould ardently defended the idea of evolutionary contingency, particularly at the level of mega-evolution.[62] At such a level, facts that are totally contingent regarding the selection pressures can create dramatic consequences; for example, the asteroid that struck Earth hundreds of millions of years ago, plausibly causing the extinction of dinosaurs, or even the mass extinction leading to the disappearance of most of the fauna represented in Burgess shale (Gould 1989). On this scale, according to Gould, if one were to replay the "tape of life", the same history would never repeat itself, since the particular contingencies causing mass extinction would not occur again. Biologists and philosophers of biology argue endlessly over this thesis. If one follows Gould, contingency fully plays out at the extreme levels of evolution, either mega-evolution or molecular evolution that forges the details of nucleotides (according to the neutralist theory), whereas selection, which is not stochastic, better explains the intermediate levels: organisms' traits, some long periods in phylogenesis (between two mass extinctions), etc. Yet others, like Dennett (1995), claim, on the basis of the non-stochastic nature of selection that, despite big changes, replaying the tape of evolution would find certain invariants, namely configurations of traits that would be like super attractors: in any possible world, selection would evolve parasites, anti-parasites, light detectors, movement trackers, motile organs, etc. A large part of the controversy rests on how narrow some descriptions are: to say that *human* eyes or intelligence are *necessarily* produced by evolution is absurd (imagine that dinosaurs never went extinct, so…); with a very broad description, however, it is plausible that light detectors, or some equivalents of immune systems, result from evolution in most alternative evolutionary scenarios… (Huneman 2010). Clearly, it is rather difficult to decide the issue with empirical arguments. Nevertheless, work in the field of Artificial Life, where researchers create computer programs that reproduce differentially according to their fitness value, provides a sort of replica of evolution, and their results can give an idea of what evolution would be in another possible world. To be sure, this Artificial Life effectively demonstrates major invariants (in Tom Ray's Tierra experiment, digital individuals developed parasites and anti-parasites, as did Holland (1995) famous Echo simulation); at the same time the open-ended creativity pattern unique to the biosphere's evolution has not yet been replicated (Bedau and Packard 1998), even if

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[62] Population genetics concerns microevolution in time periods that are not very long and with limited environmental variations; macroevolution, on a larger time scale, starts with speciation; and, with variations on an even larger scale (emergence and extinction of clades, etc.) one sometimes talk of megaevolution in the history of life.

sophistications of Artificial Life models including properties like niche construc- 779
tion (e.g. Taylor 2004) allow one to now approximate some open-ended evolution. 780
This is where the scientific approach currently lies when it comes to the issue of 781
contingency in evolution. 782

4 Units and Levels of Selection 783

After investigating the form selection takes and the conditions for it as well as what 784
selection explains and what makes it unique compared to other explanations, 785
whether it is a law or not, it is time to ask the big question: at its root, what is selec- 786
tion about? It is a question that has mobilized many philosophers of biology and 787
evolutionists for four decades. It involves two parts that I will handle here together 788
both for the sake of convenience and because some of the problems are identical in 789
both cases. In fact, the major issues were already raised with the formation of 790
Modern Synthesis – its founders were already fighting over what the true target of 791
selection is: alleles according to Fisher, integrated portions of genotypes according 792
to Wright, organisms according to Mayr… Modern controversy has reactivated 793
these debates starting with theoretical advances after the 1960s that involved 794
biological altruism, mutualism, or genome structure. 795

4.1 Settling the Question: Group Selection, Genic Selection 796

Until now I have only discussed organisms and genes. A classic misunderstanding 797
of natural selection is that people confuse it with a providential intervention for 798
the good of the species. It is nothing of the sort: selection favors variants with the 799
highest fitness, no matter what interest they may hold for their group or their spe- 800
cies, and no matter their long-term effect. Death is sometimes explained in 801
pseudo-Darwinian terms (for the good of the species: "the old have to yield space 802
to the young…"); as is sex (it is supposed to favor diversity, which is good – cf. 803
Gouyon and Giraud's article, Chap. 23, this volume). Such explanations are false: 804
one must find either a short-term selective advantage for sex or death, or an advan- 805
tageous individual trait that would have the collateral effect of favoring death or 806
sexuality (cf. Medawar 1957; Huneman 2009 for death; Williams 1975 for sex). 807
Selection is myopic: it favors individuals. The question, then, is who are these 808
individuals? 809

Ecologists have, however, often thought in terms of the good of the species. 810
When Wynne-Edwards (1962), explained the apparent self-limitation of resource 811
consuming in animal populations in terms of group selection, it raised a major 812
reaction from George C. Williams (the author of theoretical advances on question of 813

814 sex and death…), who published *Adaptation and Natural selection* in 1966. There,
815 Williams (1966) he showed that explanation by adaptation is less parcimonious than
816 an explanation by the laws of physics alone, and must therefore remain an alterna-
817 tive option, the default hypothesis being physics. Moreover, he argued that to postu-
818 late adaptation of groups is even more onerous (than that of organisms) and must
819 then be avoided whenever possible in favor of explanations that focus on the indi-
820 vidual's selective advantage, whether the individual in question is an organism or
821 even – advancing a suggestion that would be abundantly developed later on and will
822 be explored here in the paragraphs that follow – the gene.

823 Here, the questions of group selection and genic selection cross paths. For a long
824 time, altruistic behaviors in the evolutionary sense (i.e. behaviors that carry a cost
825 for the individual in terms of fitness and a benefit for other individuals[63]) have
826 remained mysterious for neo-Darwinism from the moment where it prohibits
827 recourse to group selection. Vervet monkeys that send out warning screams when
828 they see predators at the risk of being eaten, birds that help other birds to raise their
829 offspring, and sterile castes of ants or bees that help their sisters raise the queen's
830 offspring rather than produce their own descendents: it seems that natural selection
831 cannot explain any of it since the relative fitness of such individuals is weaker than
832 that of others. (For similar reasons, symbiosis – association between two individuals
833 which raises mutual benefits – has long remained inexplicable to Darwinians.)

834 Hamilton (1963) offered a simple explanation in 1964 with *kin selection*. The
835 idea is to consider the fitness of the alleles involved in behaviors rather than the
836 organisms' fitness.[64] Suppose that to save another individual from drowning,
837 X performs an action with a 1/10 probability of costing her life. X's relative fitness
838 is lower than that of X', who refrains to save the other individual. If now the drown-
839 ing individual is X's brother, he shares 50 % of his genes with X, in addition to
840 genes of the species that are common to all members of that species. We can call A
841 the altruist allele and S the selfish allele. If the S allele has a fitness W, A has a fit-
842 ness of W-1/10 W (risk of dying) + 9/10 (1/2 W) (probability of saving the brother
843 and stay safe, times the probability of the brother having an A allele) = W
844 $(1+7/20)>W$. Clearly, the A allele would be much more represented than S in
845 subsequent generations.[65] Hamilton generalizes this: an action is selected if its cost
846 c (for the actor) is less than its benefit b (for the receiver) multiplied by the coeffi-
847 cient of "relatedness". This coefficient measures the probability for an A-carrying
848 individual, of sharing the gene A in excess to the probability of sharing this gene

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[63] In reality, the notion of altruism is amended according to whether or not its beneficiaries include the author of the action or not (Kerr et al. 2004; Frank 2006).

[64] To make it simpler we speak of the altruism allele. In reality the reasoning, like any selectionist reasoning, never implies genetic determinism, which is an absurdity. It is simply enough that possession of the allele A makes a difference for altruism with regard to allele S in a fixed given environment in order for selection to take its effect. One can thus speak of an "altruism gene", but of course it's just a way of speaking, not the claim that altruism (or selfishness) is the expression of a given allele.

[65] This calculation only works if A is rare in a population.

with a randomly selected individual with whom the focal individual is competing.[66] 849
The rule is written c < br,[67] according to the usual formula. It explains the sterility of 850
hymenoptera insects (in their kinship system, sisters are closer to one another than 851
to their offspring, therefore selection will favor a behavior that sacrifices my own 852
descendents for the benefit of my sisters, since we all descend from the same 853
queen)[68]; this also explains vervet monkeys' warning screams, which will be more 854
frequent if the group comprises more relatives.[69] So basically, in this perspective 855
one determines the fitness of a behaviour as an addition of the fitness benefits 856
received by the focal actor (direct benefits), and the fitness benefits which are 857
received by the other ones, proportionately to the relatedness (indirect benefits). For 858
the altruist, indirect benefits are br and direct benefits are (−c). Hamilton called 859
"inclusive fitness" this fitness, which is computed by considering the reproductive 860
chances of the focal individual and all the related organisms. 861

Dawkins (1976) then constructed the *gene's eye view* of evolution from this 862
concept. Briefly, his idea is that selected entities are not organisms, but rather genes. 863
The case of ordinary selection is special because the organisms here have the same 864
interest as their genes. But the enigma of altruism reveals that sometimes these 865
interests diverge, and it is in such cases that we should look at the level of the gene; 866
genic selectionism maintains that this is the fundamental level of selection, even if 867
it is often the case that selection on the level of the organism is a good shortcut for 868
studying the former. The major argument is that, genes being replicators,[70] natural 869
selection mainly targets them: Dawkins developed this thesis in his famous work 870
The Extended Phenotype (1982), arguing that genes' phenotypes are not limited to the 871
organism that carries them, but extend to organisms that they manipulate; this entails 872

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[66] This last expectation explains why the calculation above was only valid if A is rare. In fact, r is approached by kinship relations, but its true value is defined here, so that its measurement is sometimes rather complicated. Grafen (1984) proposes two measurement techniques, and Frank (2006, p. 352) gives a more formal definition. In certain cases the probability that a shares a gene with b is higher than the probability that it is shared with c, even when a and c are relatives in the ordinary sense instead of a and b. In particular when the kinship structures are not as simple as they are in most mammal populations the calculation becomes increasingly complex. The straightforward way of considering r by starting with kinship is sometimes enough, but the most complete definition comes in terms of probabilities; with such a definition many of the controversies surrounding kin selection disappear, as I discuss further on (see also West et al. 2010).

[67] In a diploid system of reproduction such as ours, some brothers have 50 % of genes in common, so the probability of having an identical gene to one of mine by randomly choosing one of my brother's genes is ½. It is easier to understand the degree of genetic relatedness between individuals if it is defined by probability.

[68] This is only valid when there is only one queen and when she does not mate with many males; in other cases the explanations are more sophisticated.

[69] The monkeys' warning screams could have many explanations, which differ according to the species and are not exclusive to one; Charnov and Krebs (1975) have demonstrated that the effect of disorder that the shrieks have on the group play to the crying monkey's advantage, who is less easy to target by the predator thanks to the chaos. In this way the shrieking monkey's individual fitness also rises.

[70] See Sect. 1.

that the proper level for observing the natural selection process is not at all organisms – it is genes themselves.[71] This perspective has been extraordinarily fruitful for behavioral ecology and sociobiology (theory of parental investment according to sexes, inter-sibling and parent–child conflicts (Trivers 1971), *parental imprinting* (Haig 2000),[72] etc.); indeed, entire parts of phenomena were not visible under the organism-based view of selection.

The debate on genic selectionism has raged for nearly 30 years. Kin selection as a genuine biological process is, of course, not at risk; what is at stake is interpreting a group of phenomena in terms of selection acting upon genes. In addition, the last 15 years have seen some resurgence of group selection. Michael Wade had already developed an *experimental* approach to group selection (Wade 1977), letting groups of diverse types of flour beetles evolve; these animals were cannibals, so that individual selection favoring the most voracious individuals ended up reducing the number of flour beetles. Wade added an apparent form of group selection: he re-divides the flour beetles into groups and keeps the large groups; this induces a sort of selective pressure against cannibalism. In the experiment where this artificial group selection was present, the result in terms of average phenotype and total population size was different from experiments where no such group selection was added.

At the same time, the theoretical approach has come to rehabilitate group selection and casted doubts about its dissolution in kin selection. The theory of kin selection is certainly quite powerful: it predicts cooperation and conflict in animal societies down to the smallest details as a function of relatedness (Strassman and Queller 2007). This theory is also, however, theoretically problematic. For example (Taylor 1992), insofar as kin selection favors altruists that interact with related offspring, over time the number of altruists who are more or less neighbors will grow (altruists' offspring often stay in the same area); yet at the same time, competition between relatives is often more intense since they are more susceptible to having similar habits, thus the proximity will create more competition among altruists. In total, these two trends for and against related altruists will cancel out if we do not set any special condition on the population structure. Finally, Wilson and Dugatkin (1997) showed that if there is a correlation between altruist and the beneficiary of the altruistic act, whatever it may be (that is, if the altruistic act is not performed randomly), then altruism may evolve: genetic kinship is the simplest way to realize this selection, but it is not the only one. To summarize, in general altruism will evolve if its beneficiary has in principle a propensity (higher than average) to perform the altruistic action (which is obviously ensured by genetic relatedness, since such relationship is symmetrical).

Following Dawkins, biologists sometimes call this the "green-beard effect" (Dawkins 1982), an allusion to what would happen if green-bearded individuals

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[71] Dawkins gives selfish genetic elements as another argument; it is a matter of genic *selection* in which the organism has nothing to do, thus no controversy can exist. *Genic selectionism* is an argument concerning selection in general.

[72] See Heams, "Heredity", Chap. 3, this volume.

carried a gene for an altruistic action toward the other green-bearded individuals   912
they would meet.[73] But for West et al. (2007), this is a matter of a sort of extended   913
kin selection that they call "broad kin selection" They emphasize indeed that what   914
is crucial in relatedness is indeed the statistical correlation at the considered locus   915
(e.g. the locus of altruism). Kinship is a way to get this correlation, because kinship   916
creates a genome wide association; however the locus-correlation required for relat-   917
edness is something weaker, and can be obtained by other means, even if kinship is   918
the factor that would most easily allow for the correlation between an altruistic   919
tendency and propensity to take altruistic action. Hence relatedness produced by   920
kinship can be seen as yielding what one would call "narrow kin selection", and   921
differs from other cases of relatedness (which include green-beards for example)   922
(Grafen 2009; West et al. 2010).   923

David Sloan Wilson has developed an alternative to the kin selection explanation   924
of altruism, which is a type of group selection conceived a bit differently as a form   925
of multi-level selection (Wilson from 1975). The basic idea is that natural selection   926
can be understood as the addition of selection within a group and of selection that   927
acts upon the groups themselves, such as competition between groups (this is where   928
the idea of multi-level selection comes from: in/between groups). This appears as a   929
gloss of Price equation, which is a mathematical formulation of natural selection as   930
covariance between trait values and fitness.[74]   931

This equation, noted: 932

$$\Delta \overline{Z} = Cov(w,z)/\overline{W} + E(w\Delta z)/\overline{W}$$

933

says that the intergenerational change Δ of the average value of a trait (z) in a   934
population is the sum of *the variation caused by selection* (which is the covariance   935
of the trait's value and fitness (w)[75]), and of the *change due to transmission biases*   936
(expectation term $E(w\Delta z)$), the fidelity of transmission between parents and offspring.   937
If we now consider some individuals starting in several groups, the first term could   938
be understood as covariance of the group's mean fitness and the average phenotype   939
of groups, and the second could be analyzed as the bias introduced by the role   940

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[73] Keller and Ross (1998) first pointed out a "green-beard" effect in nature, with ants. Dawkins rejects the green-beard effect because he thinks it is vulnerable to cheaters who would have the beard without having the altruist gene; but Jansen and Van Baalen (2006) show that in theory, if there are several colored beards, the system remains stable.

[74] Price equation is one of the general mathematical formulas of natural selection. I did not include it in the review of principle statements of selection since, though it is no doubt less subject to counter-examples and more rigorous than Hull's definition of Lewontin's condition, the equation does assume that the entities in play present heritability and fitness, so the subsequent discussion would be the same as that of Lewontin's conditions.

[75] That is, the variation of a trait between two generations is correlated to the probability of repro-duction that the value of the trait confers to the organism who carries it, which is another way of stating the principle of natural selection articulated earlier – for example, the more the tallest ones have the tendency to have more offspring, the more height will rise in subsequent generations and size is under selection.

941 selection plays within groups in the transmission of the value of the groups' aver-
942 age traits. Price equation may thus be read as a natural decomposition of traits'
943 variation into an intergroup selection component and an intragroup selection com-
944 ponent, on the condition that one can identify the relevant groups. This is what
945 Sloan Wilson does with a very broad definition of group, as "*trait group*", the
946 ensemble of individuals that are affected (on their fitness) on the same basis by
947 interactions involving a given trait (for example, all beavers living near a dam are a
948 *trait group*), so that intergroup/intragroup decomposition is accessible in all cases
949 and as general as initial Price equation.

950   This view accounts for two of the antinomic properties of altruism: in a group, an
951 altruist always does less well than a selfish individual (by definition[76]); a group
952 comprising altruists will do better (will have more populous groups) than a group
953 comprising mostly selfish individuals.[77] Intuitively, we understand that a high degree
954 of competition between groups can generate altruism, whereas very few isolated
955 groups (those with less competition) will have less selection in favor of altruism
956 within each group.

957   From this, Sober and Sloan Wilson (1998) argue that kin selection is a special
958 case of multi-level selection (the *trait-groups* at play being defined by kin groups).
959 Such a definition is not, however, without its difficulties.[78] Thus, West et al. (2007)
960 demonstrate that the process at work in Sloan Wilson's multi-level selection formally
961 reduces to broad kin selection. Multilevel selection favors altruism when indeed you
962 raise the intergroup competition relatively to the intragroup competition; but this
963 means that you increase the intergroup variance relative to the intragroup variance,
964 which means in turn that you increase relatedness, hence you can consider this process
965 as a process where relatedness is the crucial causal variable – i.e. kin selection.[79]

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[76] The formal definition of the altruistic act A and selfish act S demands this: A has a cost for X and
a benefit for something other than X, S has not cost to X but only a benefit. The cost can be absolute
(when the act benefits another while costing the altruist) or relative – when the act benefits the
group of n individuals including the altruist himself: she then gets a benefit b/n, but her benefit is
smaller than that of the others (b/n-c instead of b/n). Obviously the costs are in fitness, and this
altruism is not psychological altruism, (see Clavien, Chap. 34, this volume).

[77] This is the basis of Darwin's explanation of moral sense, see Jérôme Ravat's, Chap. 35, this
volume.

[78] In a very close investigation of some of the diverse processes leading to cooperation, Frank
(2006) distinguishes between *actual kin selection*, which explains self-sacrifice that operates in the
casts of sterile workers in insects, for example, and the *behavioral correlation*, which explains
cooperation within groups. Whereas there is selective advantage in benefiting from cooperative
acts while others remain altruistic when one is in a group, in the second case cooperation benefits
the group in general, including the focal individual. Independently of the issue of knowing if these
two models perform the same process, Frank thus suggests that they are formally different contrary
to Sloan Wilson and Sober's thesis on the universality of multi-level selection. However, others
will say that in all cases, what is causally relevant is the relatedness, which compensates in terms
of indirect benefits the cost paid by the focal altruistic individual (West et al. 2010).

[79] Here we return again to Hamilton's rule (West et al. 2007, 423). From this perspective, opposi-
tion between two selections at work is a rhetorical artifact, since there is only one single process at
work, mathematically speaking.

Summing up, authors such as Lehmann and Keller (2006, 2008), advance the idea that   966
broad kin selection encompasses many of its supposed alternatives to explanations   967
of cooperation and altruism, at least from a formal perspective. Notwithstanding the   968
equivalence however, most of models of kin selection are more tractable than   969
multilevel selection ones. On the other hand, next to evolutionary questions of altruis- 970
tic behaviors that seem resolved, at least as far as modeling is concerned, multi-level 971
selection is commonly required – and rather naturally – in certain evolutionary   972
explanations; for instance, the issue of the emergence of collective individuals from 973
autonomous ones as in the advent of chromosomes, multi-cellular organisms or   974
sociality (e.g. Michod 1999; Frank 2006; Okasha 2006; Bouchard and Huneman   975
2013; Gardner 2013).   976

The debate is by no means settled, but it is useful to understand what is here at   977
stake philosophically: notions of causality and explanation, and questions of real-   978
ism, pluralism, and instrumentalism.   979

4.2   Units and Levels of Selection: Causality vs. Representation   980

Genic selectionism has often been wrongly interpreted because what is at its root   981
was never quite clear. We can oppose *gene* selection and *organism* selection, but   982
also *allele* selection and *genotype* selection. These two dichotomies have generated 983
two types of opposition to genic selectionism. Mayr and Gould immediately reacted   984
against Dawkins by pointing out that selection 'sees' phenotypes (thus, organisms)   985
and not genotypes. Brandon (1988) further clarified this point with the concept of   986
screening-off, borrowed from statisticians. Briefly, when A and B simultaneously   987
cause C, A *screens-off* B if a modification of A changes C, but a modification of   988
B does not necessarily change it. Modifying the phenotype will, in effect, change   989
the selective action, but a change to the genotype may not (if it yields the same   990
phenotype). The efficient cause of selection is found at the phenotype level, thus   991
the organism level.[80] This puts the question of the *level* of selection into play, that of 992
the causal processes – or, to put it another way, interactors. It is important to note that 993
for cases of segregation distorters, the level of selection is the gene itself.   994

The other argument, developed by Sober and Lewontin (1982), opposes allelic   995
selection to genotypic selection. Here, the discussion is among population geneti-   996
cists. Take the classic case of heterozygote superiority, illustrated by sickle-cell   997
anemia. Two alleles code for hemoglobin; in certain regions of Africa the recessive   998
allele, which makes one anemic (the red blood cells take the form of a sickle) gives   999
an advantage against malaria when coupled with the dominant allele: (with the   1000
usual notations) $W(Aa) > W(AA) > W(aa)$ (=0). We can certainly write the selection   1001
dynamics by considering the *allelic* frequencies and fitnesses ($W(a)$ and $W(A)$),   1002
these being given by each combination's fitness where each allele intervenes,   1003

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[80] See Huneman (2010b) for an analysis of the involvement of genotypes and of organisms in the controversies over genic selection.

weighted by the frequency of this combination; but in this case the cause of selection, namely the health advantage conferred by the heterozygote, is ignored. Nothing distinguishes this allelic model from an identical allelic model where the genotypic fitnesses from which they are derived would be different (for ex. $W(AA) > W(Aa) = W(aa)$, plugging in the appropriate initial frequency values) – since several genotypic fitnesses may determine the same allelic fitness. The allelic model cannot therefore pinpoint the cause at work in natural selection (even if it can correctly represent the dynamics). A similar argument also concerns what Brandon calls the *unit* of selection, the nature of the smallest entity such that its fitness remains *constant* in the environment under consideration (here, Aa, but not a or A, since the fitness of allele a or A depends precisely on its proximity at its locus, i.e. an A or an a). The questions of the unit of selection and of the level of selection are thus distinguished by Brandon, and by Burian (1983), as questions about, respectively, the *entities* targeted by selection, and the nature of the *causal process* through which it occurs.

Regarding the second issue, Sober's argument against allelic selectionism is fundamentally an epistemological one that opposes *description* (an allelic model is always an available representation) and *explanation* (causation is only effective at least at the level of pairs of alleles, i.e. genotypes). The same logic holds in Sober and Wilson's (1998) defense of multi-level selection. In substance, they say, those who refuse multilevel selection are committing "*averaging fallacy",* ascribing to individuals fitness values that are computed as an average of their fitnesses in their groups weighted by the proper frequency and fitness of these groups. This is a mathematical abstraction that can represent a dynamics, but which loses sight of any real causality in the competition between groups – exactly like the allelic model loses sight of the causal relevance of the difference between heterozygotes and homozygotes in the struggle against malaria. The issue of group selection and the critique of genic selectionism are therefore in the same boat: they assume a "realist" option through which science aims to explain effective causal relationships, and not only to describe variations. On the other hand, genic selection (or kin selection) is both more general and the most easy to work with mathematically; for these reasons it tends to prevail.

But this does not mean that, when it comes to understand altruism and the evolution of sociobiological organization, a realist stance commits one to multilevel selection instead of kin selection. Actually, supporters of kin selection can also argue that relatedness is what plays the major causal role in processes of biological organisation, and that modeling social evolution in terms of multilevel selection obfuscates this causal structure, notwithstanding the formal mathematical equivalence between kin selection and multilevel selection (displayed above). And therefore a focus on explanation does not ipso facto entail a rejection of kin selection, which is in general embraced because of its highest mathematical tractability. At the contrary, even with this focus, a pluralism seems plausible.

4.3   Pluralism   1046

In explaining the previous point, the similarity emerges between the two   1047
debates – that of genic selectionism *à la* Dawkins and Sober's responses, and that   1048
of multi-level selection à la Sloan Wilson vs. kin selection perspectives. In both   1049
cases, what is at issue is selection that acts on individuals (organisms, genes) and a   1050
selection that acts on collectives (societies, genotypes). This opposition raises the   1051
philosophical issue of *pluralism*. Pluralism means the recognition of several processes   1052
as legitimate explanation for the same phenomenon. This notion can, however, have   1053
several variants, two of which are of particular relevance to these debates. First is a   1054
"process pluralism"; the second is an "explanatory" pluralism. To be pluralist or not   1055
is orthogonal to issues referred to as conventionalism, instrumentalism, or realism   1056
that are debated in the philosophy of sciences.   1057

Process pluralism consists of accepting, in one way or another, both selection   1058
that acts on collectives and that on individuals. In the case of genic selectionism,   1059
process pluralism takes several forms. (i) *Each* selection process takes place on a   1060
specific level, since it puts into play specific interactors and replicators. Nothing   1061
therefore prevents group selection a priori, provided that the causal processes exist   1062
at the group level. This would be Brandon's (1988) solution. (ii) In *any* process,   1063
there are several explanatory models as legitimate as this one; this is the position   1064
defended by those ranging from Sterelny and Kitcher (1988) to Waters (1991) to   1065
Lloyd (2001). Nevertheless, Sterelny & Kitcher specify that the allelic level   1066
possesses a unique property, which is to be a causal explanation at least as complete   1067
as all the others, and always available, so that their pluralism is a sophisticated   1068
genic selectionism.   1069

Very generally, if we take the terms "individual" and "collective" as abstract and   1070
indeterminate, and if we define an individual's fitness as the average of its fitnesses   1071
in possible environments (thus the collectives…), Kerr and Godfrey-Smith (2002)   1072
have demonstrated that selection on individuals and multilevel selection (the addi-   1073
tion of selection on the individual and that upon the collective where it is found), are   1074
mathematically equivalent. This demonstration could justify a pragmatic explana-   1075
tory pluralism (namely, you might as well just take the most user-friendly model   1076
each time), as well as a kind of reductionism (if multi-level selection is equivalent   1077
to individual selection, then levels do not "really" exist…). Such a result will, how-   1078
ever, have less consequences for those who maintain that mathematical modeling   1079
does not resolve issues of the ontology of processes, but instead presupposes them.   1080

There is another specific type of pluralism that I call explanatory pluralism.   1081
It concerns the evolution of altruism and cooperation. Some, like Sober and   1082
Wilson (1998), argue that a single process leads to them; they oppose some   1083
explanatory pluralists (like Nowak 2006; Frank 2006) who make inventories of the   1084
various processes likely to foster altruism, including kin selection and intergroup   1085

1086 selection.[81] This explanatory pluralism also contradicts the supremacy of the most
1087 sophisticated kin selection (such as West et al. 2007, or Lehmann and Keller 2006).[82]
1088   In addition, the multi-level selection at issue here defines group fitness as *the*
1089 *number of members in a group* in each generation. Damuth and Heisler (1988) call
1090 this *multi level selection 1 (MLS1)*, in contrast to another type of selection, *multi*
1091 *level selection 2 (MLS2)*, where the fitness of a group is the number of *daughter*
1092 *groups* that it generates. A group that has some evolutionary success can in effect be
1093 a group that becomes larger and larger with each generation but also, via another
1094 process, a group that gives birth to more groups than those with which it is competing.
1095 In this second scenario, the measure of reproductive success is not the number of
1096 groups' members but rather the number of daughter groups. In other words, selection
1097 at the *supra-organism level is not logically homogeneous* (since it includes these
1098 two very different varieties). Considering what Gould called "species selection",
1099 this becomes evident. When a biologist says that species' properties have played a
1100 selective role in their evolution – for example, their polymorphism, or the extension
1101 of space that they cover – she is not saying that the species have become more
1102 abundant, but she claims that they have given rise to more speciation. The measure
1103 of evolutionary success here is the number of daughter-species. Clearly, Kerr and
1104 Godfrey Smith's equivalence demonstration then only holds true for MLS1. MLS2,
1105 if it is still empirically controversial (see Rice (1995), as a proponent of species
1106 selection after Gould; Williams (1992) rejects it but does accept clade selection[83]…)
1107 is in any case conceptually irreducible.

1108 ## 5   Conclusion

1109 The evolution of the concept natural selection in modern biology features several
1110 oppositions. On one hand, evolutionists have accumulated, through mathematics,
1111 theoretical proofs of what Darwin called the "*paramount power*"of selection, as well
1112 as, through experiments and field investigations, empirical evidences of its strength.
1113 The development of the field and the emergence of new disciplinary areas such as
1114 sociobiology, behavioral ecology, molecular biology, etc., demonstrated that natural

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[81] Of course, Sober and Wilson are part of the "pluralist" camp in the sense of those that think there are several levels of selection; but "explanatory pluralist" here means believing that there are several possible explanatory frameworks for altruism or cooperation, which is clearly not their case, since they think that the only explanatory process is multi-level selection.

[82] It remains important, however, to point out that pluralist models presented as different from kin selection (like Traulsen and Nowak 2008) are often reduced in mathematical terms to kin selection processes (Lehmann et al. 2008).

[83] Some clades persist more than others; if we think that the number of species inside a clade, or its level of branching, or any other property the clade itself has as a clade, contributed to it lasting longer than another clade, then there is clade selection, that is, selection of clades in virtue of clades properties.

selection has a major causal role at levels that were still unknown or not understood 1115
in Darwin's time, and regarding kinds of facts left aside by Darwin and his contem- 1116
poraries. On the other hand, the sophistication of evolutionary biology, especially 1117
population genetics, while shedding new light on the processes involved in natural 1118
selection and the conditions under which they occur, has raised new theoretical 1119
questions as well as impassioned controversies: at what level does selection act on, 1120
what exactly are its explananda, how does it fit with other types of explanations that 1121
are not population-based in order to account for broader biological phenomena? In 1122
particular, the general form of selection makes it clear that there is nothing about it 1123
that is unique to the living world, characterized by its structure (DNA molecules, 1124
etc.), a structure that partly results from historical contingencies. Still, a general 1125
theory of natural selection,[84] that would embrace biology, culture, economics, tech- 1126
nology, chemistry, neurology and so on, and which clearly is possible, has to 1127
overcome major obstacles: it assumes that these theoretical puzzles (sketched in this 1128
chapter), that evolutionary biology faced while striving to understand natural selec- 1129
tion, have been solved 1130

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[84] Darden and Cain (1989) outline such an attempt. It was also the meaning of what Dawkins (1982) calls 'universal Darwinism'.

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