Biology and Philosophy (2005) 20:343–353
DOI 10.1007/s10539-005-2560-0

Matthen and Ariew's obituary for fitness: reports of its death have been greatly exaggerated

ALEX ROSENBERG* and FREDERIC BOUCHARD
*Department of Philosophy, Duke University, Box 90743, Durham, NC 27708, USA; *Author for correspondence (e-mail: alexrose@duke.edu)*

Received 28 October 2003; accepted 31 October in revised form 2003

Philosophers of biology have been absorbed by the problem of defining evolutionary fitness since Darwin made it central to biological explanation. The apparent problem is obvious. Define fitness as some biologists implicitly do, in terms of actual survival and reproduction, and the principle of natural selection turns into an empty tautology: those organisms which survive and reproduce in larger numbers, survive and reproduce in larger numbers. Accordingly, many writers have sought to provide a definition for 'fitness' which avoid this outcome. In particular the definition of fitness as a probabilistic propensity has been widely favored.[1] Others, recognizing that no definition both correct and complete can actually be provided, have accepted the consequence that the leading principle of the theory is a definitional truth and attempted to mitigate the impact of this outcome for the empirical character of the theory.[2] Still others have argued that 'fitness' is properly viewed as a term undefined in the theory of natural selection (on the model of mass – a term undefined in Newtonian mechanics).[3] But few have contemplated the solution to this problem proposed by Mohan Matthen and André Ariew (hereafter, MA), in 'Two Ways of Thinking about Fitness and Natural Selection'.[4] Their way of dealing with these interpretive problems is to expunge altogether the concept of fitness from the theory of natural selection. No fitness, no fitness problem. In this paper we show that (1) MA's attempts to expunge fitness from a theory of natural selection for populations results in a serious misrepresentation of the structure of evolutionary theory, (2) that the parallel they allege to obtain between the role of fitness in the theory and the role of entropy in thermodynamics is nonexistent, and (3) that in any case the notion of fitness MA seek to expunge is indispensable to the theory, whether the theory is treated as a claim about ensembles or individual organisms.

---

[1] See for instance R. Brandon, 'Adaptation and evolutionary theory,' *Studies in the History and Philosophy of Science*, 9 (1978): 181–206, J. Beatty, and S. Mills., 'The propensity interpretation of fitness', *Philosophy of Science*, 46 (1979): 263-286, E. Sober, *The Nature of Selection*, Cambridge, Ma., MIT Press, 1984, but see also E. Sober, 'The Two Faces of Fitness', in *Thinking about Evolution: Historical, Philosophical, and Political Perspectives*, *New York*, Cambridge University Press, 2002 and J. Beatty and S. Finsen [Née Mills], 1987, 'Rethinking the propensity interpretation' in M. Ruse, (ed), *What Philosophy of Biology Is*, Boston, Klewer, 1989, for second thoughts.

[2] See R. Brandon, *Adaptation and Environment*, Princeton, University of Princeton Press, 1990, chapter one.

[3] See A. Rosenberg, 'Fitness', *Journal of Philosophy*, 80 (1983): 457–47. But see also E. Sober, 'Fact, Fiction, and Fitness', *Journal of Philosophy*, 81 (1984): 372–384, and A. Rosenberg, and M. Williams, 'Fitness as Primitive and Propensity', *Philosophy of Science*, 53 (1986): 412–418.

[4] *Journal of Philosophy*, 94 (2002): 55–83. Page references in the text are to this paper.

Predictive fitness is not predictive and Fisher's fundamental theorem is a theorem

MA begin by distinguish the 'vernacular' concept of fitness and the 'predictive' concept. 'Vernacular fitness' is a matter of adaptation or design-problem solution – what some biologists refer to as 'ecological fitness'. On MA's view vernacular, or ecological fitness, plays no role in the fundamental generalizations of the theory about natural selection. Indeed, it has no role in the theory at all. Vernacular or ecological fitness simply drops out as a cause of evolution by natural selection. MA's argument for why 'vernacular' fitness drops out is straightforward: they deny that there are what Sober calls 'source-laws' which identify the *causes* of ecological fitness differences, and they deny that there are what Sober calls 'consequence-laws' which identify the *effects* of ecological fitness differences.[5] If the only explanatory role for fitness is based on its presence in the consequents of the source-laws and the antecedents of the consequence-laws, then without such laws, it drops out of the theory of natural selection. Instead, natural selection directly connects the real causes of evolution, identified in what MA call 'substrate specifications', with predictive fitness, by-passing the detour through ecological fitness. The 'substrate specification' states the properties of populations, including 'properties of their members or of their parts, and/or the causes of differential growth rates… conditions of inheritance, development and environmental interaction that bring about changes in predictive fitness' (MA, p. 75). Accordingly, a description of natural selection should dispense with an intermediary notion of vernacular fitness that does no quantitative work. Indeed, it must do so, *if* there are no laws governing vernacular fitness that would enable us to link it systematically with what can be measured in population biology – subsequent reproductive rates.

MA define predictive fitness as 'a statistical measure of evolutionary change, the *expected* rate of increase (normalized relative to others) of a gene, a trait, or an organism's representation in future generations, or on another interpretation, its *propensity* to be represented in future generations, suitably qualified and normalized.' [p. 56] This is R.A. Fisher's characterization. But then they qualify their claim: 'We do not mean to insist on the expected-value interpretation; there are many ways of defining predictive fitness within population genetics.' [p. 56]. Moreover, in a footnote one author, Ariew, dissents altogether, arguing that the Fisherian interpretation is 'misleading as a definition of statistical fitness' [p. 74, n.30]. Ariew's discomfort is understandable: Fisherian fitness cannot deal with nonlinear population change such as frequency-dependent selection, and it makes the selective process of heterozygote superiority invisible.[6] But the real problem here is that there cannot literally be many ways of defining 'fitness' unless debate in evolutionary biology is to be

---

[5] See E. Sober, 1984, *The Nature of Selection*, Cambridge, MIT Press, 1984, chapter one.

[6] See Brandon, *Adaptation and Environment*, Princeton, Princeton University Press, 1990, p. 29–30 and 151–153 for full discussion

vitiated by ambiguity. MA mistake alternative specifications of how to measure fitness in different circumstances for incompatible definitions. What is more, once we see how biologists decide on which measure to employ in explaining evolutionary processes, it becomes clear that the adjective 'predictive' is at best a misleading way to characterize reproductive fitness measures. Deciding which population statistic it is best to employ as a measure of fitness all too often depends on what the biologist's data shows about the distribution of traits in successive generations. It will accordingly be no surprise – and no prediction either – if the measure which data leads us to employ then enables us to retrodict this data. The varying measures which MA style 'predictive fitness' are the biologists' means of quantitatively comparing fitness differences in terms of their demographic effects, usually after these effects have been recorded, not before they have been realized in nature. 'Predictive' fitness *per se* is rarely if ever predictive.

MA argue that, unlike vernacular or ecological fitness, 'predictive fitness is not a cause of selection, or of evolution for that matter.' [p. 56] Of course, they are right. It cannot be a cause, for it is an effect, a demographic statistic that measures fitness. But if the causal concept of ecological fitness drops out, then so too must a causal version of the principle of natural selection drop out of biology. Instead of a law like:

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

MA are forced to identify some *alternative statement* as fundamental to the theory of natural selection. This they find in a *modified* version of Fisher's fundamental theorem of natural selection (hereafter FFT). This theorem states that the fitness of a population increases at a rate proportional to the genetic variance in fitness present in the population. MA express the theorem as follows:

FFT In a subdivided population the rate of change in the predictive fitness of the whole population is proportional to the variance in the predictive fitness of the subpopulations. This formulation is simply the result of substituting the terms 'predictive fitness' for 'overall growth rate', in accordance with MA's definition,[7] in the following statement due to C.C. Li,[8] which MA describe as 'an extremely abstract characterization' of 'the formal properties of natural selection' [p. 72]:

> *Li's theorem*: in a subdivided population the rate of change in the overall growth rate [of the whole population] is proportional to the variance in the growth rates [of the subpopulations].

---

[7] In effect, our version of Li's theorem adopts their strategy of 'Taking growth rate as a surrogate for fitness' [p. 74]

[8] C.C. Li, *Population Genetics*, Chicago, University of Chicago Press, 1955.

But Fisher's fundamental theorem, from which MA's FFT follows, is just *that*, a derived consequence of what Fisher recognized as the more fundamental truth: the PNS. The theorem states something that Darwin explicitly recognized: the more the variation in a heritable trait, the more rapidly it will evolve under natural selection. Darwin however treated this fact as only a subordinate consequence of the PNS. Moreover, when we consider the Darwinian assumptions, about selection for ecological fitness, from which this theorem is derived, its derivative status as a theorem becomes evident.

As Fisher himself noted, the fundamental theorem only holds subject to important evolutionary assumptions: 'the rate of increase in fitness of any population at any time is equal to its genetic variance in fitness at that time, except as affected by mutation, migration, change of environment and the effect of random sampling.'[9] Moreover, the very expression of the theorem makes clear its status as derivative from one or more fundamental, dare one say, postulates or axioms of the theory of natural selection. For the theorem is a claim about changes in the rate of natural selection, which of course requires that there exist some amount of natural selection whose rate can change. The existence of this process is of course evinced in a principle like PNS above.

The reasoning from the PNS to Fisher's fundamental theorem is fairly direct and intuitive: As Depew and Weber note,

> Fisher is painting a picture in which natural selection speeds up as usable variation is fed into it. Moreover, he means to say that as natural selection acts on variation, it necessarily does so in such a way that it increases the fitness of the population from what it was at the instant before the integration of the action of selection on the genetic array. The system moves naturally towards a state of maximal fitness, even if it never quite arrives because as it approaches maximal fitness, it runs, by definition, out of fuel.[10]

Besides the independent prior assumptions about natural selection in general required to derive the theorem, there are other reasons to forego the theorem as a characterization, abstract or otherwise, of natural selection's general properties. Besides the controversies surrounding the meaning and significance of the theorem,[11] there are circumstances in which selection operates in but there is no response to selection. As Sober's treatment of Fisher's theorem and its implications shows, 'Selection may increase or decrease the value of w [the average fitness]. Once frequency dependent selection is taken into account, no

---

[9] R.A. Fisher, *The Genetical Theory of Natural Selection*, Oxford, Clarendon Press, 1930, quoted in W. Provine, *Sewall Wright and Evolutionary Biology*, Chicago, University of Chicago, Press, 1986, p. 280.

[10] D. Depew and B. Weber, *Darwinism Evolving*, Cambridge, Ma. MIT Press, 1997, p. 251.

[11] For a detailed discussion see Anya Plutynski, *Modeling Evolution*, University of Pennsylvania, Ph.D thesis, 2000 chapter IV.

general statement can be made as to whether selection tends to improve.'[12] As in the subversion of a population of altruists by a selfish organism, there are conditions of frequency dependence in which natural selection can lower average fitness of a population. It is easy to reconcile this and other such cases with Fisher's theorem by bringing them under the clause 'change of environment'; after all an individual's environment includes the population of its conspecifics. This is what a more basic principle of natural selection tells us in reference to the environment. The important conclusion is that Fisher's theorem cannot serve as the touchstone of a theory of natural selection, because FFT's truth is a qualified consequence of more fundamental truths about natural selection.

Why do MA substitute FFT for a principle like PNS? The answer is that since they seek to deny a causal role to fitness (something that the 'vernacular' or ecological concept of fitness reflects), MA's version of Fisher's theorem, FFT, is a convenient one for their purposes. This is owing to the fact that, as Fisher famously noted, the theorem parallels the second law of thermodynamics.[13] Like the second law, FFT does not make a causal claim, but states a relationship between events in a process. (This matter is taken up at greater length in section 2 below.) These events are presumably the successive consequents of an underlying causal process. Moreover, the FFT reflects their view that natural selection is what they call a purely 'ensemble' process. MA hold that 'the theory of evolution abstracts away from concrete individual events … in order to isolate the causal factors that make a probabilistic *difference* to evolution.' [p. 62]. These probabilities at the level of ensembles or populations are not to be related to natural selection at the level of individual organisms. There is no selection at the level of individual organisms: their FFT 'tells us nothing about causes of [population] growth: it is a general truth about growth regardless of how it is caused'. [p. 74] Moreover, selection is not a cause of growth (or of the change in population characteristics) in this conception; 'it is the mathematical aggregate of growth taking place at different rates. [p. 74]' Note if we decline to treat Fisher's theorem as an adequate characterization of the properties of natural selection, it becomes much more difficult to justify MA's claim that evolution of populations is independent from laws about the consequences of fitness differences among individual organisms.

Thus far, we may conclude at least three things. First, MA's preferred definition of predictive fitness is no definition but a set of non-predictive largely retrospective measures of fitness. Which of these measures should be plugged into a recognizable PNS is almost always something we can decide only after looking at the data 'predictive fitness' is purported to predict. Second, in arguing that 'predictive' fitness is a non-causal property, MA wrongly substitute one of the implications of the theory of natural selection – a version of

---

[12] E. Sober, *The Nature of Selection*, Cambridge, MIT Press, 1984, chapter VI., p. 182.

[13] See for instance, R.A. Fisher, *The Genetical Theory of Natural Selection*, Oxford, Clarendon Press, 1930, p. 36

Fisher's theorem – for a causal claim about how natural selection proceeds, such as the PNS above. Third, and perhaps most egregious, substituting FFT for a causal principle of natural selection deprives Darwinian theory of its explanatory role with respect to evolution altogether. MA admit as much, '... the distinction between evolution (the total change in gene frequencies due to all causes), and natural selection (the portion of evolution due to differences in competitive advantage) is unmotivated.' [p. 78] And further, 'Fitness and natural selection have no reality except as accumulations of more fundamental events. In our conception, it makes dubious sense to hold evolution is different from natural selection, much less that it is caused by it.' [p. 82] Reversing the order of nature, they conclude, that on their conception, 'Natural selection is... the aggregative result over time over time of differential growth rates in a population.' [p. 78] One philosopher's *modus ponens* may well be another's *modus tollens*, but the result of MA's attempt to solve the problem of fitness is not recognizable as the theory of natural selection at all. If, as we argue in the next two sections, MA's analysis of ''predictive fitness' on the model of entropy is mistaken and neither their version of the theory, nor any other, can do without 'vernacular' or ecological fitness, sufficient grounds will be available to treat their argument as a *modus tollens*: evolution is caused by natural selection, acting on individual ecological (or 'vernacular') fitness differences.

Fitness and entropy

How then, are population level statements in the theory of natural selection – the FFT, or the PNS for that matter – related to statements about the individual members of these populations? Here MA appeal to a parallel with thermodynamics: 'Like the theory of natural selection, statistical mechanics has a formal component: this is concerned with probability distributions on large ensembles of entities interacting with each other in certain ways.' [p. 71] More specifically, like entropy, predictive fitness is a property of 'a temporal sequence of aggregates, a running tally of lower-level events'. Just as entropy is a property of an ensemble, but not a property of any of its individual components, fitness is a property of an ensemble, but not a property of its individual members. Just as the increase in entropy is not a matter of earlier entropic states causing later ones, so natural selection is not a matter of earlier fitness-levels causing later ones.

> We may state the second law of thermodynamics as follows:
> 2nd law (x)(y)[x, y are states of a closed thermodynamic system and y is later than x → Probably (the entropy of y is greater than the entropy of x)

The 2nd law tells us that later entropy is probably greater than earlier entropy, but not that the earlier entropy caused the later. *Mutatis mutandis*, on MA's view, earlier distributions of fitness differences in sub-populations do not cause, they are merely succeeded by, later changes in population size. MA write: ‘natural selection is not a process driven by various evolutionary factors taken as forces; rather, it is a statistical ‘trend’ with these factors (vernacular fitness excluded) as predictors.’ [p. 57] MA are right to say that the 2nd law is not a causal claim: earlier entropic states do not cause later ones. Moreover, if MA can substantiate the parallel between fitness in the theory of natural selection and entropy in thermodynamics, they might after all provide some motivation for substituting their version of Fisher’s theorem, FFT, for the PNS. They might thereby ground the claim that evolutionary theory describes the relations of ‘predictive fitness’ differences among ensembles only, and not also the effects of ‘ecological’ fitness differences among individual trait-bearing tokens of biology – genes, individual genotypes, individual organisms, particular groups and so on. For, it will turn out that fitness is no more a property of individual organisms than entropy is a property of individual particles.

The trouble with this argument is that the features that make entropy an emergent property in the second law of thermodynamics are largely absent from the foundations of the theory of natural selection. The emergent character of the second law is generated by the fact that entropy is not a property of the individual components of an ensemble, but of the ensemble as a whole. The standard explanation of how entropy emerges from the behavior of the members of the ensemble remains highly problematical.

To see why consider the simplest case in which a thermodynamic system – say a quantity of a gas in a container – is treated as an ensemble of particles moving in accordance with Newtonian dynamical laws. Following Albert,[14] call a specification of which particles are where in the container, and what their specific momenta are, an ‘arrangement’ and a specification of how many particles are within a given region of the container and a given range of momenta, a ‘distribution’. The entropy of the system depends on the distribution of the particles and not the particular arrangement of them. Any one distribution is of course compatible with more than one arrangement of particles. The particles change position and momenta in accordance with deterministic Newtonian laws, and the number of physically possible arrangements of particles that realize any one distribution increases as the particles spread out in space and in momentum-values. The increase in entropy the 2nd law reports is a result of this fact about arrangements and distributions: in the long run later distributions supervene on a larger number of arrangements than earlier ones do. The larger the number of arrangements for a given distribution, the higher the entropy. Entropy is thus accounted for in terms of Newtonian concepts of position and momentum via the concepts of distribution and arrangement.

The flaw in this story is that we have no right to hold that the numbers of arrangements at the earlier time is less than the number of arrangements at the later time. Since Newtonian momentum and space-time location can take on a continuum of values, the number of arrangements compatible with (almost)

---

[14] See D. Albert, *Time and Chance*, Cambridge, Ma., Harvard University Press, 2000, pp. 43 for an illuminating introduction to this problem.

any single distribution is infinite, and there is no unique way to measure the size of these infinities. Within any given region of space and range of momentum values for any one particle, the position and momentum of the particle can take up a continuum of values. If the earlier 'smaller' number of arrangements compatible with a given distribution is infinite in number, and the later, larger 'number' of arrangements is also infinite in number, we cannot appeal to differences in the number of arrangements on which given distributions supervene to explain the increase in entropy the 2nd law reports. Thus, both entropy as a property and the second law as a regularity are said to be irreducible ensemble-level matters.[15]

But the theory of natural selection is not vexed by the problems that bedevil a reduction of thermodynamic properties to Newtonian dynamics. These problems, that make entropy an emergent property of an ensemble, prevent us from turning the schematic derivation of the second law into a complete explanation. In evolutionary theory, the derivation of population fitness differences from individual fitness differences is not similarly schematic. All we need in order to understand where the fitness-coefficients of populations come from is the 'concession' that there is such a thing as comparative differences in (ecological) fitness between pairs of individual organisms; and that these differences can be arithmetically aggregated into fitness differences between populations.

On this basis there is no difficulty explaining where 'comparative fitness' in the PNS 'comes from': it is just the average over the compared populations of the comparative fitnesses of the individual members of the populations. There is nothing at the ensemble level here emergent or autonomous from the properties at the individual level the way there is in thermodynamics. There is no new property of the whole ensemble – like entropy – utterly dissimilar from any properties at the level of the individual components of the ensemble. Nor is there an infinite number of equiprobable underlying states; there is just the average of actual relations among pairs of organisms. Even if 'predictive fitness' *could* be understood on the model of entropy, ecological fitness would still be required in population level evolutionary explanations as we now show.

Ecological fitness is indispensable

In evolutionary biology, selection is contrasted with drift. Since MA argue that selection due to fitness differences is not a cause of evolution, they must draw the same conclusion about drift: it does not 'really make sense to say that drift is a *force*, or more generally a cause of change that acts independently of

---

[15] The apparent insolubility of this problem of reductively explaining thermodynamics has been diagnosed by Lawrence Sklar, *Physics and Chance: Philosophical Issues in the Foundations of Statistical Mechanics*, New York, Cambridge University Press, 1993, and in 'The reduction (?) Of thermodynamics to statistical mechanics', *Philosophical Studies*, 95: 187–202. Sklar concludes that we must resign ourselves to building these probabilities into thermodynamics at the level of ensembes.

selection' [p. 60] Getting clear on how MA go wrong here enables us finally to see that ecological fitness is one concept the theory of natural selection cannot do without.

To explain why drift is not a cause, MA invoke coin-tossing. Suppose a fair coin is tossed four times and comes up heads twice. Explanation: 'the physical set up of the coin-tossing trials' [p. 61] Now, they ask,

> What would explain the outcome *four heads*? Answer:… the same set up explains both outcomes… Perhaps one might say that the four-head outcome was less predictable, therefore less well explained within this set up. However that may be, there is nothing available with which to strengthen the explanation of the four-head outcome.... For closely related reasons, 'drift' should not be regarded as a force that can be added to others acting on a population. [p. 61]

But coin-tossing is not like radioactive decay, where rare outcomes are explained by the same facts that account for frequent ones. We should reject MA's claim that 'there is nothing available with which to strengthen the explanation of the four-head outcome.' [p. 61]

Consider a 'coin-plus-thumb-and-fore-finger coin-flipping-device'. This physical system is (asymptotically) deterministic, and after a large number of tosses, say more than a 1000, we infer that the long-run relative frequency P (the coin comes up H on landing/ the coin is H-side up on the forefinger) = 0.5. We know perfectly well where this probability 'comes from': the initial conditions of the coin flipping, which deterministically bring about an outcome of H or T in each case, are distributed into two sets. One of these sets of initial conditions, together with the relevant Newtonian laws, determines a set of paths, from thumb to table top, which results in *heads*; the other set of initial conditions, determines paths resulting in *tails*.

Evidence that the whole set of initial conditions of a real series of coin-flips is divisible into two equal sets – one of which results in H and the other in T – will consist in the bilateral symmetry of the coin, the human coin flipper's inability to control initial conditions with sufficient accuracy, etc. Now consider MA's case. Suppose that among the set of 1000 tosses, however, the 20th through 23rd toss were four consecutive heads. Since we know that four consecutive heads comes up only 6.25% of the time, merely adverting to the very same physical set up that results in an equal split of heads and tails is either no explanation of why four heads came up when they did, on tosses 20–23, or only a small part of the explanation, or an explanation of something else (viz., that 6.25% of large numbers of fair-coin tosses result in four consecutive heads) or an explanation that satisfies very unstringent standards on explanatory adequacy. *Pace* MA, there is a stronger explanation for the departure from 50:50 that will appeal to the particular initial conditions of each of the flips that gave rise the four consecutive heads, showing how the particular initial conditions in tosses 20 through 23, together with the Newtonian laws, resulted in the four consecutive H's.

What does all this have to do with drift and selection? When organisms of lower fitness leave more viable offspring than fitter organisms in four consecutive mating seasons out of say, 1000, then the likely explanation is 'drift' – i.e., the initial conditions in those four seasons were not equally distributed among all the possible initial conditions. This is a causal explanation, and drift – the departure of these initial conditions from equality in proportion among all physically possible initial conditions – is the cause of the departure from the outcome that selection leads one to expect. So viewed, drift does reflect the operation of distinct causal processes, *pace* MA. But how can we tell whether the outcome in these four seasons reflect drift and not selection? This is where ecological fitness turns out to be a property the theory of natural selection cannot do without.

Suppose we measure the fitness differences between population x and population y to be in the ratio of 7:3, and suppose further that in some generation, the actual offspring ratio is 5:5. There are three alternatives: (a) the fitness measure of 7:3 is right but there was drift – i.e., the initial condition at this generation are unrepresentative of those which obtain in all relevant generations; (b) the fitness measure of 7:3 was incorrect and there was no drift; (c) both drift and wrong fitness measure. How do we discriminate among these three alternatives? The only way is via access to ecological fitness differences. In order to exclude equal fitness, instead of drift, as the source of the 5:5 outcome, we need to be able to establish that the 7:3 difference derived from previous population censuses was not the result of drift. But this is the second step in a regress, since we began with the problem of discriminating the 5:5 ratio as drift instead of mismeasures of fitness. To solve the initial problem of determining whether the current 5:5 census is a matter of drift or selection, we now have to assure ourselves that the 7:3 ratio in the past were not itself the result of drift. Whence the regress.

Of course the problem does not arise if we have access to fitness differences independent of previous population censuses. And this access we have, at least in principle, if there is such a thing as ecological fitness and it is (fallibly) measured by probabilistic propensities to leave offspring – one of the many measures of 'predictive fitness'. We can, at least in principle, decide whether the divergence from predicted long-run relative frequencies reflects our ignorance either of ecological fitness differences or drift – the unrepresentativeness of the particular initial conditions of individual births, deaths, and reproductions in these seasons.

Because populations are finite there is always some drift, and there is in the end no way to dispense with 'ecological' fitness in the theory of natural selection. And since comparative ecological fitness is ultimately a relationship between organisms taken two at a time, the theory is as much a set of claims about individuals as it is about ensembles. Even if 'predictive' fitness were more than a fallible measure, it still couldn't do all the theoretical work Darwinian Evolution requires.

Conclusion

MA’s suggestion that biology do away with the notion of ecological fitness should be resisted. Not only are the arguments for this conclusion flawed. Even if they were not, they would be out-weighed by the role of ecological fitness in guaranteeing the testability of the theory. This is an irony in light of the long history of suggestions that the notion of ‘fitness’ is what makes the theory of natural selection untestable.