31 On Genetics, Ecology, and the Role of Philosophy in Evolutionary Biology: A Reply to Distin

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Abstract

In this reply, I consider the valuable points raised by Distin in the light of the actuality of evolution as a population genetic process, and how philosophers of science may come to help evolutionary biologists tackle the problems that matter to them.

Keywords

Darwin · Evolution · Natural Selection · Philosophy · Population Genetics

Your philosophy,
    Is totally lost on me.

Impatience, *We Are Scientists.*

Alongside the welcome support for many of the points raised in my chapter, Distin provides important food for thought for evolutionary biologists. However, he also raises issues that need to be considered by the philosophers of evolutionary biology as well.

Distin and I are in strong agreement that the current body of evolutionary thinking, encapsulated by our rich and diverse body of evolutionary theory, tested and challenged every day by a richer and more diverse body of empirical work, remains a work in progress. As stressed in my chapter, what I have characterised as Standard Evolutionary Theory (SET; other characterisations are possible) is not

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some conceptual monolith of finished thinking, but rather a theoretical framework, one that is based around the notion of biological evolution as genetic change in populations over time. Here, genetic change refers to changes in frequencies of DNA sequences ("alleles"; or RNA sequences, as in annoying entities such as coronaviruses). Within that framework, new theories explaining the evolution of phenotypes, old and new, are continually being developed and tested. However, whether the framework itself needs tinkering with, as hinted at by Distin, is perhaps more contentious. In part this is perhaps down to the historical development of evolutionary biology from Darwin onwards.

I will make two brief comments in response to the insightful discussion by Distin. First, what is the role of population genetics in evolution? To address this, we need to be clear about what we are talking about in terms of population genetics. On the one hand, population genetics is a field that describes the genetic structure of populations and how the genetics of populations change over time (synonymising itself with evolutionary genetics as a field of study). On the other hand, population genetics can also be a shorthand for population genetic theory, the often-formidable body of theoretical work that has been developed to help empirical population geneticists go about their business (Charlesworth and Charlesworth 2010). This association between data and theory has been reflected in the development of population genetics since the very beginning however, with the ecological genetics of Dobzhansky (1951) and Ford (Ford 1964; see also Birch 1960) developing alongside the population genetic theory of Wright, Fisher, Haldane and others. We can therefore see that understanding the genetics of populations within a real-world ecological context ("putting ecology into population genetics") has always sat within some parts of population genetics, even if it is more typical to equate population genetics with equations. Now, it might be true that the birth of molecular population genetics (from the 1960s onwards, first of proteins, then of DNA) initially focused more on population genetics statistics (F_{ST} and the like) than the ecology of the populations being studied, but Distin is correct in saying that in recent decades evolutionary biology has been rather rarely undertaken naïve to the underlying ecology of the study organisms (the importance of model study organisms such as *Drosophila melanogaster* notwithstanding). Population genetics texts are quite maths-heavy, but that should not be over-interpreted as a reflection of what those equations are then used to explore. This is clear from a cursory reading of any of the major evolutionary biology journals today, and indeed the journal *Molecular Ecology*, which very much epitomises modern empirical population genetics.

More generally, there have been repeated calls for a greater synthesis of ecology and evolution, some of which are almost as old as the Modern Synthesis itself (see above). A longer view, however, shows that that the extent to which evolutionary biology and ecology have been bound together has varied over time, at times stronger, at times weaker. Darwin (1859, 1871) began the study of evolution with a deep-seated understanding of what we now call ecology, especially in terms of within- and among-species interactions, driving natural and sexual selection (what else is the "law of battle" for instance?). The natural history that provided Darwin with so much ecological insight was perhaps eclipsed to some extent by the rise of modern professional biology and the re-discovery of Mendelian genetics, generating the field of genetics and other aspects of molecular biology. However, the emergence of ecology as its own professional discipline, while obviously developing its own rich collection of ecological theory, also saw the more-or-less contemporaneous emergence of evolutionary ecology, for instance in terms of figures such as David Lack (e.g., Lack 1965). Alongside the ecological genetics of Ford, Dobzhansky, and others, the stage was set for what we now call molecular ecology. As such, calls for further synthesis can be frustrating in terms of this already rich history of the interaction between ecology and evolution, if only very lightly sketched here.

In addition, there is also something of an irony in the structure of population genetic theory itself. Whilst many of the models within the canon of population genetics theory might lack ecologically explicit assumptions or context, that lack can be viewed in two ways. On the one hand, it could be argued that population geneticists are patently oblivious to the ecological truths their theory wishes to speak to. On the other, it could be that the abstractions inherent in population genetics models in fact allow a vast array of ecological circumstances *into* population genetics models. Let us take the humble selection coefficient, s. A simple population genetics model that specifies selection on a given allele, as denoted by s, is in fact allowing that any plausible component of fitness, across any plausible ecological circumstance that influences that component of fitness, can be modelled and insight therefore gained, all through the abstraction of s. Therefore, how population genetics models deal with ecology, either explicitly or implicitly, is perhaps not a very good way to assess how well integrated ecology and evolution actually are.

Second, Distin touches on the philosophy of the theory of evolution, making the case – albeit briefly due to space constraints – that work remains to be done here. Indeed, more philosophical aspects of evolutionary theory (including how we do evolutionary biology, and what assumptions, explicit or otherwise, we make when we do it) enrich many of the chapters of this volume. But there is also a clear disconnect between the philosophy of evolutionary theory and what evolutionary biologists do – and care about, to be frank – day-to-day. For instance, debates about statisticalist versus causalist views of evolution continue well away from the mainstream evolutionary journals (see Otsuka 2016 for a review of the debate). For better or worse, philosophers of biology need to make a much stronger case that there are issues that need addressing by evolutionary biologists on the ground, for example something that is genuinely missing from their thinking, couched in language and with *empirical examples* that ground that absence in tangible terms. This will require a substantial appreciation of the corpus of modern evolutionary biology, as the thoughtful comments on evolvability by Distin clearly show. After all, as my chapter highlights, this failure to seem aware of, or accept the reality of, modern evolutionary biology is a crucial failing of the Extended Evolutionary Synthesis. And as with the EES, opinion pieces and self-citations will not sway many evolutionary biologists, but data and new phenotypes to theorise about and puzzle over, just might.

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