CORRESPONDENCE

Hanno Sandvik and I have different concepts of what constitutes the evolutionary synthesis. He focuses specifically on the nomothetic character of selection theory However, for me, the term synthesis applies more broadly to the integration of this concept with empirical data from the fossil record, the nature of species and speciation, and mendelian and population genetics, to form a unified explanation of evolutionary patterns and processes. The formulation of the evolutionary synthesis was extensively reviewed by Mayr and Provine⁶. Mayr⁷ specifically cited the concept of macroevolution that was promulgated at that time: '...all the available evidence indicates that the origin of the higher categories is a process which is nothing but an extrapolation of speciation. All the processes and

phenomena of macroevolution and the origin of the higher categories can be traced back to intraspecific variation...'. This concept of evolution is applicable primarily to sexually reproducing diploid organisms and can only be indirectly applied to prokaryotes, which dominated the first 2.5 billion years of life.

My call for a 'new' synthesis does not indicate a rejection of natural selection, but is a summons for broader recognition and integration of data from molecular developmental biology, and knowledge of the history of the earth and its biota, which were unknown to Darwin and those who framed the evolutionary synthesis.

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An evolutionary no man's land

The gap between evolutionary studies in laboratory versus natural populations is a persistent problem^{1,2}. In an attempt to bridge this gap, some researchers in the early 1980s studied the quantitative genetics of laboratory populations recently founded from the wild, with and without inbreeding^{3,4}. The dangers of such approaches were soon demonstrated experimentally^{5,6}. Inbreeding depression and genotype-by-environment interactions make such studies unreliable guides to the evolution of populations long-established in any environment. This conclusion is reiterated to some extent in Harshman and Hoffmann's recent TREE perspective2, where the authors state that, 'The nature of laboratory selection regimes is unnatural.' But, they then go on to propose complementing selection experiments in long-established laboratory populations with selection experiments in recently introduced ones. It is not clear how one could disentangle the causes of possible differences from the results of such disparate studies. Furthermore, from first principles and extant experimental studies, we expect a conflation of evolutionary effects in the recently introduced populations because of adaptation to the laboratory environment, and because of genetic and evolutionary disequilibrium. In particular, interactions between adaptation to the general laboratory environment and any particular selective regime under study could be a source of unresolvable evolutionary outcomes, as we will now explain.

Two evolutionary processes are at work in the transition from the wild to the laboratory. First, placing a population in a novel environment can cause a change in genetic variances and covariances between traits, as a result of genotype-by-environment interactions. Second, continued maintenance in this novel environment might bring about evolutionary change, perhaps because of new selection pressures or changes in breeding structure. A recently founded laboratory population will thus be in a 'no man's land'. We cannot use it to provide information about the original wild population, nor can we test evolutionary models that rely on the assumption that the newly transplanted population is near genetic or selective equilibrium. Surprisingly, like Harshman and Hoffmann, several recent studies have essentially repeated these mistakes^{7–9}.

Let us conclude with an example. The empirical challenge posed by the transition from wild to laboratory conditions led us to study the evolution of a newly founded laboratory population of Drosophila subobscura¹⁰. We found that adaptation to the novel, laboratory environment occurred at a relatively fast rate. As an illustration, fecundity around the age of reproduction increased steadily in the generations after establishment in the laboratory, showing convergence to the values of a longestablished population serving as a control (maintained in the lab for 24 generations before the foundation of the new one); the fecundity of the new population became similar to that of the long-established population after just 14 generations of adaptation to the laboratory. In this no man's land between the wild and the laboratory, the population evolved extremely rapidly. Instead of straining for dubious interpretations of the uncertain results afforded by studies of recently sampled populations, we might use the gap between the wild and the laboratory as an evolutionary tool - recognizing that, after all, the lab is just another environment to which populations adapt, albeit a very peculiar one¹⁰. To this extent, we can agree with Harshman and Hoffmann.

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