Evolutionary history and species interactions

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We celebrate this year the sesquicentennial anniversary of the publication of *On the Origin of Species* (1), one of the most important books ever written. The two great themes of *The Origin* are descent, with modification, of diverse species from common ancestors, and natural selection, which Darwin proposed as the chief agent of modification. He remarked, in Chapter VI, that "it is generally acknowledged that all organic beings have been formed on two great laws—Unity of Type, and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life. On my theory, unity of type is explained by unity of descent. The expression of conditions of existence…is fully embraced by the principle of natural selection." The two great laws are conjoined, he noted, because natural selection will have adapted the parts of each being "during long-past periods of time," so that "the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type" (ref. 1, p. 168).

Darwin thus described what we today consider the main subjects of evolutionary biology: the history of evolution, including that history embodied in "unity of type," the causal processes of evolution (including, but not only, natural selection), and the relation between them.

During the 1930s and 1940s, dialogue among geneticists, systematists, and paleontologists resulted in the "evolutionary synthesis," in which a chief point of agreement was that the phenomena of long-term evolution ("macroevolution," or "evolution above the species level") result simply from the prolonged and repeated action of the processes of mutation, recombination, and gene frequency change that occur in populations ("microevolution"). Despite this synthesis, evolutionary biology diverged into largely disjunct studies of evolutionary history (among species) and genetic processes (within species). Some inferences about evolutionary history could be made from comparative studies by systematists, but the fossil record was generally viewed as the chief source of historical information. Well into the 1970s, however, paleontology and systematics were viewed by students of microevolution as descriptive sciences that could contribute little to understanding evolutionary processes—-a view that some paleontologists sought to dispel, arguing that evolution includes processes above the population level, such as differential rates of speciation and extinction (2, 3). On the whole, the study of evolutionary history occupied a relatively marginal position in evolutionary biology, which tended to be more focused on population-level processes. The divide between historical, generally macroevolutionary study and process-oriented, genetic, microevolutionary study was substantial (4).

This situation has changed dramatically in the last 15–20 years, owing largely to the great growth in sophistication and reliability of phylogenetics, the first task of which is to infer a major component of evolutionary history, namely the sequence of divergence of lineages as portrayed in phylogenetic trees. Phylogenetic analysis of living organisms cannot entirely replace paleontology as a way of recovering the past; for example, it cannot reveal the existence of many extinct taxa. But it can provide insights into the history of taxa that are seldom fossilized. Moreover, it enables us to trace the evolution of characters—-their polarity of change, convergence, reversal, elaboration—-including molecular, physiological, behavioral, and ecological features that are seldom recovered in fossils. Time-calibrated phylogenies, incorporating not only the relative sequence but also the absolute time of lineage branching, enable us to relate evolutionary events to climatic and geological changes (complementing paleontological data); to estimate rates of character evolution; and to infer the time course of diversification, including rates of speciation and extinction (5). It has become clear that historical information can often be used to test hypotheses about evolutionary process, based on the patterns that the hypotheses predict, so the once-divided approaches are becoming united. For example, interspecific comparisons are commonly used to detect selection at the molecular level and to distinguish modes of selection; contrasts between the species richness of sister clades provide tests for the role of sexual selection in speciation; and "gene trees" for related species cast light on possible instances of founder-effect speciation. A phylogenetic framework is now *de rigeur* in addressing many, if not most, problems in evolutionary biology (6).

An important and most interesting effect of being able to more confidently infer history is that evolutionary biologists have become more aware of the role of historical explanation for the characteristics of living organisms. This seems odd, because one would suppose that of all biological disciplines, evolutionary biology should always have been most conscious of the impact of history. Nevertheless, an equilibrial assumption, that organisms are near their adaptive optima, has been widespread, arising in part from evidence that most characteristics are genetically variable and hence responsive to natural selection, and in part from many examples of rapid adaptation to human alterations of environments. This assumption, which is characteristic of much of physiology and functional morphology (7), carried over into ecology. For example, most community ecologists since the 1960s assumed that the species richness and species composition of ecological assemblages are near equilibrium, and could be explained by ecological theories framed in terms of current and very recent environmental conditions (8). Today, the theme of historical or "phylogenetic constraints" looms large in evolutionary biology, and "phylogenetic conservatism" of characters is thought to account for many taxonomic patterns in ecological features such as habitat associations (9). Likewise, community ecologists increasingly recognize that the diversity and identity of species in communities, and the interactions among them, may be fully explicable only if long-term history, including macroevolu-

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Author contributions: D.J.F. and A.A.A. wrote the paper.

The authors declare no conflict of interest.

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tionary history, is taken into account (10, 11). For example, among the many hypotheses advanced to account for the greater species richness of many taxa in lower than higher latitudes, those that include effects of long-term history appear to be gaining favor (12).

The connections between community ecology and macroevolution are nowhere clearer than in interactions among parasites and their hosts (13) and among herbivores and their food plants (14, 15), because many herbivores and parasites are highly host-specific, and their host associations are often phylogenetically conservative. More broadly, the diversity of herbivores, their host plants, and the defensive adaptations of plants to herbivory are postulated to have arisen by a long history of coevolution that has affected the food web links between these trophic levels (16). Using as data the host-plant associations and some physiological features of insects and the chemical and other defenses of plants—-features that are very imperfectly documented by fossils—-phylogenetic analyses enable us to describe some aspects of the macroevolution of these associations and relate them to contemporary interactions. Studies of herbivores and their host plants clearly show, as Reznick and Ricklefs (17) recently urged, that ‘‘understanding macroevolution requires the integration of ecology, evolution, and the role of history in shaping the diversification or decline of lineages.’’ Conversely, understanding the ecology of communities of species requires appreciation of evolution and the role of history.

Darwin, whom many view as a founder of ecology, appreciated that ‘‘plants and animals, most remote in the scale of nature, are bound together by a web of complex relations’’ (ref. 1, p. 61). Since his time, we have learned quite a lot about the processes and history whereby these relations have evolved. As the papers in this Special Feature attest, evolution and ecology are indissolubly joined in the study of interactions between plants and their herbivores, which offer a cardinal illustration of evolution as the unifying theory of biology.

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