Preface

This issue of the *Journal of the History of Biology* began with Arizona State University's celebration of its centennial in 1984–1985. The university sponsored a number of projects designed to bring nationally recognized experts to ASU for conferences and lectures. The three of us — historian, biologist, and philosopher — decided to invite a group of scholars to discuss historical and philosophical issues relevant to ecology and evolutionary biology. The way in which ecology has been informed by evolutionary biology, or has remained largely independent of it, was to be a central question. We agreed to ask predominantly younger scholars, who had not published extensively in the history of ecology and whose views were not so well known, rather than established experts. Thus on March 1–2, 1985, we held a conference at ASU on the topic "Reflections on Ecology and Evolutionary Biology." This collection of papers comprises an updated version of the talks presented at that conference. In addition to the authors represented here, Malcolm Kottler spoke about David Lack and his work and William Provine discussed ecological genetics.

Publication of this material has been sponsored by the Arizona State University Centennial Commission. We also received funding and moral support from Dean Charles Woolf of the Graduate College, to whom we are particularly grateful. The Zoology Department, the Department of Botany and Microbiology, the Center for Environmental studies, the Ecology Colloquium Series, the History and Philosophy of Science Colloquium Series, and the Philosophy Department all provided financial support for the conference and for this publication. We thank them most sincerely, especially Richard Creath and Michael White, who provided an outstanding meal for our guests, and Nita Dagon and Joy Erickson, who handled paperwork, mailings, checks, and generally helped to keep things running smoothly.

We are indebted to the conference participants, both speakers and listeners, for keeping the discussion lively and informative. Contributors to this volume deserve our warm gratitude for their prompt submission of excellent manuscripts. Douglas Futuyma performed an unusually heroic service: we asked him to do the nearly impossible, to listen to two days of papers and then to react

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spontaneously at the end. He succeeded impressively, with a fine survey of issues and contributions and by anticipating the remaining questions. We thank him for his willingness to undertake such a task and for performing it so well. We have included his comments here, with only minor editing, even though they consider essays that do not appear in these pages.

Finally, we thank the *JHB* staff, especially associate editor Shirley Roe, for her assistance in publishing this material. It is our pleasure to have the conference results appear in the *Journal of the History of Biology.*

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Introduction: Between Ecology and Evolutionary Biology

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Ecology emerged as a self-conscious discipline during the last decade of the nineteenth century, growing out of a heterogeneous mix of fields. Indeed, its roots are as different as field natural history and experimental physiology.[1] Given that ecology was (and remains) such a heterogeneous enterprise, it is unlikely that any single perspective will suffice to describe its history. Several very different approaches have already proved fruitful. Ronald Tobey has discussed the changing importance of applied versus non—mission-oriented research in the development of ecology. Sharon Kingsland has emphasized the relative merits of theoretical versus empirical research at various points in the history of the discipline. Robert McIntosh has taken the very heterogeneity of the discipline as his perspective on its history.[2] The papers that follow approach the history of ecology from yet another standpoint, namely, the changing role of evolutionary theory in the solution of ecological problems.

In *On the Origin of Species* Darwin frequently brought evolu-

1. Robert McIntosh, *The Background of Ecology* (Cambridge: University Press, 1985), p. 26.

2. Ronald C. Tobey, *Saving the Prairies: The Life Cycle of the Founding School of American Plant Ecology, 1895—1955* (Berkeley: University of California Press, 1981); Sharon E. Kingsland, *Modeling Nature: Episodes in the History of Population Ecology* (Chicago: University of Chicago Press, 1985); McIntosh, *Background*. See also R. Colwell, "The Evolution of Ecology," *Amer. Zool.*, *25* (1985), 771—777.

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tionary considerations to bear on the distribution and abundance of organisms, and on the relations of organisms to their environments. Inasmuch as these areas eventually constituted the domain of ecology, Darwin is often cited as an early advocate of evolutionary approaches to ecological problems. Not all subsequent ecologists have followed Darwin in this regard. We asked the authors of the following papers to consider why ecologists sometimes have found evolutionary concepts significant for their research and sometimes have not. In addition, some of our contributors have explored the degree to which evolutionary biologists have sometimes and sometimes not found ecological concepts significant.

The ensuing articles illustrate how complicated the answers to such questions can be. The complications undoubtedly reflect the diffuse and changing identity of ecology in the late nineteenth and twentieth centuries. Historians and philosophers are hardly in agreement on what constitutes a discipline, much less on how disciplines emerge and establish their indentities. The difficulties are compounded when it comes to studying the history of a young discipline like ecology.

During the late nineteenth century biologists most often sought explanations for the distribution and abundance of organisms through studies of natural history — especially biogeography. Those explanations were historical and evolutionary, and frequently incorporated the concept of adaptation via natural selection. By the very end of the century, however, botanical biogeographers in particular had begun to offer mechanistic, rather than historical, explanations for the distributions of species. Their objective was to account for distribution and abundance of plants not in terms of the evolutionary histories of those plants, but more directly, in terms of the physiological abilities of those plants to adjust to some environments but not to others.

Eugenius Warming was an early proponent of this new approach to the study of plant distribution — an approach that he called ecological plant geography. In his paper here William Coleman summarizes Warming's vision of this new geography as a departure from the more common methods of the time.[3] An

3. William Coleman, "Evolution into Ecology? The Strategy of Warming's Ecological Plant geography," *J. Hist. Biol.*, this issue.

ecological approach to plant distribution supposedly provided a better explanation of community structure. According to the physiological approach, communities of plants in different parts of a country, or even the world, might look quite similar (have a similar physiognomy) if they grew in comparable environments. Although having different evolutionary histories, species of plants in a community would look alike because environments with similar biotic and abiotic attributes would favor plants with comparable physiological capacities. Evolutionary history was not, therefore, of as much consequence for the study of community structure as was physiology. The concept of adaptation to the environment was very useful for Warming, although he was not much concerned with the historical, evolutionary process leading to it. For Warming ecology was the science of understanding how physiological plant-environment and plant-plant interactions resulted in groupings of organisms into communities that were unevenly distributed geographically.

The physiological relationship between plant and environment provided an important theoretical framework within which the new science of ecology could begin to develop and distinguish itself from the closely allied discipline of biogeography. Both relied on the background perspective provided by the concept of adaptation. But the biogeographers were more interested in the *evolution* of adaptation. In particular, biogeographic explanations for distribution and abundance depended on adaptive divergence of taxa within a region, and on subsequent migration. Fundamentally, such biogeographic explanations were historical and evolutionary. In contrast, ecologists argued that *present* environmental conditions could be invoked to account for plant distribution and abundance, that is, in a manner more analogous to a physiological explanation.

Joel Hagen also discusses the physiological roots of ecology, though not so much to point out the difference between physiological and historical approaches as to emphasize the lure of physiology's experimental approach.[4] Early ecologists such as Warming, Andreas Schimper, and Frederic Clements urged ecologists to use the rigorous, experimental methods of physiology

4. Joel B. Hagen, "Ecologists and Taxonomists: Divergent Traditions in Twentieth-Century Plant Geography," *J. Hist. Biol.*, this issue. See also Eugene Cittadino, "Ecology and the Professionalization of Botany in America, 1890–1905," *Stud. Hist. Biol.* 4(1980), 171–198.

effectively making ecology field physiology. Their new science was to be quantitative and experimental following the model provided by physiology, a model highly regarded by biologists of the time. As Garland Allen has argued, there was at the turn of the century a dramatic movement toward the use of experiments as exemplified by physiology. While the revolutionary nature of this shift remains debatable, it seems clear that more biologists, including ecologists, began to use experiments in their research.[5] Hagen demonstrates the importance of this experimentation, but shows also that this new approach did not completely replace traditional plant geographies, which continued to rely on historically oriented explanations.

The physiological interests of many early ecologists are well reflected, as Coleman and Hagen both note, in the "superorganismic" analogies that these researchers used when characterizing communities. Just as traditional physiology attended to the development and functioning of individual organisms, these early ecologists treated the development and functioning of individual, *superorganismic* communities.

We have thus far discussed only community-level investigations. One might expect to find more interest in Darwinian evolutionary theory among those investigating the ecology of individual populations and species than among those studying communities. Populations and species are, after all, the things that evolve by natural selection. If evolutionary biology is going to be relevant to ecology, one would expect to find it at least in population ecology. For the first two decades of this century, however, Darwinian evolutionary theory was under considerable attack.[6] In particular, it was seriously doubted whether evolutionary change could occur as a result of natural selection of small mutations. A number of alternative evolutionary agents, the most prominent including large-scale and directed mutations, were accorded great influence. So it is not surprising that evolution by natural selection was not the favored mode of explanation of population growth and composition.

5. Garland E. Allen, *Life Science in the Twentieth Century* (Cambridge: Cambridge University Press, 1975); Jane Maienschein, Ronald Rainger, and Keith Benson, "Introduction: Were American Morphologists in Revolt?" *J. Hist. Biol., 14* (1981); 83—87.

6. Peter Bowler, *Eclipse of Darwinism* (Baltimore: Johns Hopkins University Press, 1983).

There were notable exceptions. Among the several topics treated in his paper, William Kimler discusses the career of Edward Poulton, an entomologist and a staunch defender of Darwinism during the first decades of this century, when this was not such a popular position.[7] Poulton saw the science of ecology as a means of promoting studies of the role of natural selection in accounting for population composition, specifically intraspecific variation. He was especially interested in intraspecific differences in mimicry, which he denied were due simply to mutation pressure. He attributed the maintenance of such differences to selection instead. For Poulton understanding the selection pressures involved was an ecological problem.

Kimler's point is *not* that Poulton was representative of the general influence that Darwinism had on ecology in the first decades of the century. Poulton was exceptional in this respect. But he serves as a contrasting case, to show what sort of influence Darwinism might have had (and what influence it eventually had) in distinction to what prevailed at the time. After Poulton there developed in Britain a strongly pro-Darwinist school of ecological genetics. Among its members were R. A. Fisher, E. B. Ford, A. J. Cain, and P. M. Shepard. The Darwinian character of the British school was also exceptional in its time, a point to which we shall return shortly.

So-called theoretical population ecology developed considerably in the twenties and thirties, still prior to the general acceptance of selection of small mutations as a viable mode of evolutionary change. That population ecology should not have assumed a Darwinian character in light of the period of its initial development is understandable. The reasons for that fact are complicated, however, as Sharon Kingsland explains in her article.[8]

The attitude toward evolutionary theory differed among early population ecologists. W. R. Thompson, for one, positively eschewed evolutionary approaches to population dynamics and even grew suspicious of mathematical approaches to the subject because of the success of Fisher's mathematical population genetics, which in turn supported the importance of natural selection, which

7. William C. Kimler, "Advantage, Adaptiveness, and Evolutionary Ecology," *J. Hist. Biol.*, this issue.

8. Sharon E. Kingsland, "Mathematical Figments, Biological Facts: Population Ecology in the Thirties," *J. Hist. Biol.*, this issue.

Thompson did not accept. Although population ecologists like A. J. Lotka and Vito Volterra explicitly proposed to formulate general theories of "evolution," the equations of population growth that they (and Raymond Pearl, whom Kingsland discusses elsewhere) formulated — the equations that formed the theoretical core of population ecology — were hardly "evolutionary" in any standard sense of that term.[9] Truly evolutionary considerations of population dynamics (for example, notions of *r*-selection and *K*-selection) were much longer in coming.

Kingsland's article helps us to understand why a Darwinian perspective was not a point of convergence among Lotka, Volterra, Pearl, Thompson, and other population ecologists like R. N. Chapman, G. F. Gause, and A. J. Nicholson. Perhaps most important in this regard, these individuals had very different backgrounds in the sciences and very different goals. Certainly they did not all identify themselves as ecologists. Consider, for instance, that Thompson was an entomologist; Nicholson, also an entomologist, collaborated with V. Bailey, a physicist; Lotka was a demographer and mathematician, and Volterra a mathematician. Pearl's career is more difficult to categorize because of his interests in demography, biostatistics, genetics, and evolutionary theory.

The reasons that these investigators had for pursuing the mathematics of population dynamics were similar only in their shared quest to achieve some generally applicable theories. Lotka sought a law of evolution that would be as general as the laws of thermodynamics, especially the second law. Pearl pursued a general law of population growth. Volterra sought to develop a mathematical, general theory of evolution. Thompson wanted to understand in general terms the relationship between parasites and their hosts. In developing their theories, these researchers used analogies borrowed from different disciplines to motivate their mathematical reasoning. Lotka, as is clear from the point above, drew on physical chemistry, whereas Volterra and Pearl used analogies from physics, especially theory concerning movement of particles in a gas.

A significant improvement in the understanding of microevolution was accomplished in the twenties and thirties, thanks in large part to the pathbreaking studies of Fisher, Sewall Wright,

9. Kingsland, *Modeling Nature*.

J. B. S. Haldane, and Sergei Chetverikov. Applications of the theory by Theodosius Dobzhansky, Ernst Mayr, G. G. Simpson, Bernhard Rensch, and G. Ledyard Stebbins during the thirties and forties, represent the major empirical advances. This chain of developments has come to be referred to as the "evolutionary synthesis,"[10] The synthesis made it clear that natural selection of small variations *could* be effective in directing evolutionary change. It did not, however, establish natural selection as the *chief* means of evolutionary change — at least, not at first. As Steven Jay Gould has pointed out in a number of articles, proponents of the synthesis early on — in the thirties and early forties — attributed considerable significance to evolution by random drift. Only in the later forties and fifties did the synthesis "harden," to use Gould's term, in favor of the all-importance of evolution by natural selection.[11]

William Provine, in a talk at this conference (taken in part from a forthcoming book and a previous essay), used the fact of this further delay in the general acceptance of natural selection to account for the late impact of evolutionary thinking in ecology.[12] Provine did not neglect the pro-Darwinian character of the British school of ecological genetics, but pointed out that the position of

10. William B. Provine, *The Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 1971); Ernst Mayr and William B. Provine, eds., *The Evolutionary Synthesis* (Cambridge, Massachusetts: Harvard University Press, 1980); Ernst Mayr, *The Growth of Biological Thought* (Cambridge, Massachusetts: Harvard University Press, 1982); Mark Adams, "Towards a Synthesis: Population Concepts in Russian Evolutionary Thought," *J. Hist. Biol.*, *3*(1970), 107—129.

11. Steven Jay Gould, "G. G. Simpson, Paleontology, and the Modern Synthesis," in Mayr and Provine, *The Evolutionary Synthesis*; idem, Introduction to the Columbia Classics in Evolution Series reprint of the first edition of Theodosius Dobzhansky's *Genetics and the Origin of Species* (New York: Columbia University Press, 1982); idem, "The Hardening of the Synthesis," in *Dimensions of Darwinism*, ed. Marjorie Grene (Cambridge: Cambridge University Press, 1983), pp. 71—93.

12. William B. Provine, "Ecological Genetics: *Drosophila pseudoobscura*, *Cepaea nemoralis* and *hortensis*, and *Panaxia dominula*," unpublished paper presented at the conference "Reflections on Ecology and Evolutionary Biology," Arizona State University, Tempe, Arizona, March 1—2, 1985. See also idem, *Sewall Wright: Geneticist and Evolutionist* (Chicago: University of Chicago Press, 1986); and idem, "The Development of Wright's Theory of Evolution: Systematics, Adaptation, and Drift," in Grene, *Dimensions of Darwinism*, pp. 43—7.

the British school was, in the thirties and forties, not the position of general consent.

In a related paper at the conference (part of a much longer manuscript in progress), Malcolm Kottler discussed the career of the British ecologist and evolutionist David Lack.[13] Lack's analysis of "character displacement" among the various species of Galapagos finches is by now a legendary example of evolutionary ecology. Lack explained the differences in beak morphology of the finches in terms of selection for ability to utilize different food resources — that is, in terms of the advantages of escaping competition for the same resources. This combination of ecological thinking (such as his use of the notion of interspecific competition) and evolutionary thinking (such as his use of the notion of natural selection) has made Lack one of the most frequently cited evolutionary ecologists. But Lack originally considered the differences among the Galapagos finches to be a matter of random drift. Thus, he neatly reflects the changing attitude toward the importance of natural selection during the evolutionary synthesis. Indeed, his own work partially accounts for the change in attitude (a point made also by Gould).

James Collins, in his article in this issue, notes three more specific ways in which the evolutionary synthesis — in particular, the empirical work associated with the synthesis — affected the development of ecology.[14] First, by the early sixties, it became increasingly evident that genetics had a role to play in developing causal explanations in ecology. In general, genetic bases were being demonstrated for more and more traits of interest to ecologists, for example, traits having to do with population fluctuations. A second line of empirical evidence concerned the rate at which evolution, at least as construed in terms of changes in gene frequency, could occur. In 1945 Lotka argued that evolutionary

13. Malcolm Kottler, "David Lack: Ecologist to the Evolutionary Synthesis," unpublished paper presented at the conference "Reflections on Ecology and Evolutionary Biology," Arizona State University, Tempe, Arizona, March 1–2, 1985. The original report was David L. Lack, "The Galapagos Finches (Geospizinae): A Study in Variation," *Occ. Pap. Calif. Acad Sci., 21* (1945), pp. 1–59. Lack published the revised version of this report as *Darwin's Finches* (Cambridge: Cambridge University Press, 1947; reprinted Cambridge: Cambridge University Press, 1983).

14. James P. Collins, "*Evolutionary Ecology* and the Use of Natural Selection in Ecological Theory," *J. Hist. Biol.*, this issue.

change happened on a different time scale from ecological processes like population growth. H. J. Muller acknowledged this distinction in 1949 by recognizing "ecological" and "evolutionary" time scales.[15] By the early sixties, however, evidence had begun to accumulate that gene frequencies in natural populations could change relatively quickly, certainly within the time needed for some ecological processes to reach completion. The distinction between the two time scales broke down. During and immediately after the evolutionary synthesis, a third line of empirical evidence was provided by studies showing heritable morphological differences, within species, correlated with differences in habitat. This research demonstrated different selection pressures operating over small spatial scales, and made it clear that some cases of population distribution and abundance over such scales would require Darwinian explanations.

Collins also notes a conceptual development, not intrinsic to evolutionary biology, nor to ecology, nor to any specific biological discipline, but rather a conceptual development concerning the structure of biology as a whole, that has helped to articulate the relation of evolutionary biology to ecology. The distinction proved especially fruitful in the context of ecological research into population regulation.

During the fifties and sixties the problem of how population size is regulated (especially how animal population size is regulated) was a major focus of ecological research. Explanations fell into two classes. There were those based on evidence that immediate environmental factors such as temperature and humidity affect increases and decreases in population size. These were generally classed as density-independent explanations, in that the abiotic factors brought about changes in population size independently of population density. Alternatively, density-dependent explanations were formulated. Evidence was offered that population changes were often in proportion to population density. The question of whether density-dependent or density-independent

15. Alfred J. Lotka, "Population Analysis as a Chapter in the Mathematical Theory of Evolution," in *Essays on Growth and Form Presented to D'Arcy Wentworth Thompson*, ed. W. E. Le Gros Clark and P. B. Medawar (Oxford: Clarendon Press, 1945), pp. 355—385; Herman J. Muller, "Redintegration of the Symposium on Genetics, Paleontology, and Evolution," in *Genetics, Paleontology, and Evolution* ed. George L. Jepsen, Ernst Mayr, and George G. Simpson (Princeton: Princeton University Press, 1949), pp. 421—445.

factors regulate population size was central to ecology during this period.

In 1961 Mayr discussed two complementary explanatory strategies pursued by biologists: "functional" or "proximate" explanatory strategies, and "evolutionary" or "ultimate" explanatory strategies.[16] Proximate explanations, like physiological explanations, address the mechanisms causing expression of the characters an organism exhibits. Ultimate explanations address the evolutionary reasons why a population should come to be composed of organisms exhibiting a particular character.

Gordon Orians used this perspective in 1962 in discussing the question of population regulation.[17] He argued that there were actually two questions: "How is population size regulated?" and "Why is population size regulated?" He reasoned that studies of the effect of density-independent factors on population increases and decreases represented a search for proximate causes, reflecting an effort to answer the first question. In contrast, the second question elicited density-dependent explanations based on ultimate causes. For Orians these explanations remained complementary, that is, each contributed to a complete explanation for why populations seemed to vary within limits. During the sixties many scientists interested in using evolutionary theory to develop causal explanations for ecological problems either implicitly or explicitly used the proximate-ultimate distinction.

Issues of population regulation arise in another context in the articles that follow — with regard to the influence of "group" selectionist versus traditional Darwinian selectionist notions within ecology. Kimler and Collins both discuss the publication in 1962 of V. C. Wynne-Edwards' book *Animal Dispersion in Relation to Social Behaviour.*[18] Wynne-Edwards argued in this book that the density of a population was regulated in such a way as to benefit the population. What he called group selection was, he believed, quite distinct from Darwinian selection of individuals.

Criticisms of the group-selectionist account of population

16. Ernst Mayr, "Cause and Effect in Biology," *Science, 134* (1961), 1501—6.

17. Gordon H. Orians, "Natural Selection and Ecological Theory," *Amer. Nat.*, 96 (1962), 257—264.

18. V. C. Wynne-Edwards, *Animal Dispersion in Relation to Social Behaviour* (Edinburgh: Oliver and Boyd, 1962); see also Kingsland, *Modeling Nature*, p. 37, and "Mathematical Figments."

regulation were numerous, the most extensive and effective being G. C. Williams' *Adaptation and Natural Selection*, published in 1966.[19] According to Williams, accounts like those of Wynne-Edwards were just as fallacious as would be an account of fleetness among deer in terms of the benefit of fleetness to the whole herd. Williams believed that every purported case of group selection could be recast in terms of selection for alternative alleles in Mendelian populations. That is, he believed that apparent group traits, like the fleetness of a herd, could be reduced to individual traits controlled by specific alleles, and selection for those alleles in contrast to alternative alleles could account for the ubiquity of the traits in question. It was, he further argued, more parsimonious not to multiply the levels at which selection operates. And therefore he urged against explaining the presence of traits in populations in terms of group selection for groups with such traits.

It is important to note that Williams' argument concerns not only ultimate, evolutionary accounts of such phenomena as population regulation, but also proximate accounts of those phenomena. Accordingly, it encourages ecologists to seek the traits responsible for population regulation at the organismic level. The question of population regulation is still unanswered. But it is clear that not only a proximate approach to ecological problems, but also an evolutionary approach, will be necessary to find the solution.

Richard Michod's article on density-dependent and density-independent forms of evolution by natural selection illustrates what is now the frequent give-and-take between evolutionary biology and population ecology.[20] Not only are changes in population density affected by microevolutionary changes, but evolutionary changes are reciprocally influenced by factors like population density. As Michod noted in the discussion of his paper, the teaching of evolutionary biology today benefits as much from a consideration of issues in population ecology as the teaching of ecology benefits from evolutionary considerations. The interaction between ecology and evolutionary biology is becoming ever stronger.

19. George C. Williams, *Adaptation and Natural Selection* (Princeton: Princeton University Press, 1966).

20. Richard E. Michod, "On Fitness and Adaptedness and Their Role in Evolutionary Explanation," *J. Hist. Biol.*, this issue.

It has not been our purpose in this introduction to present detailed episodes from the history of ecology. That is done in the essays that follow. Rather, it has been our aim to underline some of the main themes, especially those bearing on the role of evolutionary thinking in ecology. There is, of course, much more to the articles than we have presented here — including many more themes for understanding the history of ecology. Douglas Futuyma, who was the general commentator at our conference, and whose remarks here represent his response to the original papers, provides a general consideration of the various contributions more in the spirit in which each was written.[21] His summary is styled as an overview of what has come to be called "evolutionary ecology," but it goes further. It also suggests a perspective on what may come to be.

21. Douglas J. Futuyma, "Reflections on Reflections: Ecology and Evolutionary Biology," *J. Hist. Biol.*, this issue.