Patterns, Models, and Predictions: Robert MacArthur's Approach to Ecology

Yoichi Ishida†‡

Robert MacArthur's mathematical ecology is often regarded as ahistorical and has been criticized by historically oriented ecologists and philosophers for ignoring the importance of history. I clarify and defend his approach, especially his use of simple mathematical models to explain patterns in data and to generate predictions that stimulate empirical research. First I argue that it is misleading to call his approach ahistorical because it is not against historical explanation. Next I distinguish three kinds of criticism of his approach and argue that his approach is compatible with the first two of them. Finally, I argue that the third kind of criticism, advanced by Kim Sterelny and Paul Griffiths, is largely irrelevant to MacArthur's approach.

1. Introduction. Robert MacArthur elegantly expresses his approach to ecology in his introduction to *Geographical Ecology*, written shortly before his death:

> To do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map. The person best equipped to do this is the naturalist. . . . But not all naturalists want to do science; many take refuge in nature's complexity as a justification to oppose any search for patterns. This book is addressed to those who do wish to do science. . . . Science should

†To contact the author, please write to: Department of History and Philosophy of Science, University of Pittsburgh, 1017 Cathedral of Learning, Pittsburgh, PA 15260; e-mail: yoi5@pitt.edu.

‡I am especially grateful to Thomas Nickles for encouragement and helpful comments on earlier versions of this paper. Thanks also to Guy Hoelzer, Stephen Jenkins, and Jay Odenbaugh for comments on an earlier draft, Kim Sterelny for clarifications of the Tasmania example, Gregory Mikkelson for references, and the audience at PSA 2006 for discussions.

Philosophy of Science, 74 (December 2007) pp. 642–653. 0031-8248/2007/7405-0008$10.00
Copyright 2007 by the Philosophy of Science Association. All rights reserved.

https://doi.org/10.1086/525610 Published online by Cambridge University Press

> be general in its principles. . . . The theme running through this book is that the structure of the environment, the morphology of the species, the economics of species behavior, and the dynamics of population changes are the four essential ingredients of all interesting biogeographic patterns. (1972, 1)

The search for patterns of species diversity and their underlying mechanisms was a major theme of MacArthur's work. In pursuing this theme, MacArthur built simple mathematical models to represent mechanisms he regarded as essential and made predictions to stimulate new empirical research. As a naturalist, he was interested in details of nature, but as a "machinery oriented" (MacArthur 1972, 239) scientist, he was interested in organizing and explaining the observed phenomena by developing general theories (Kingsland 1995; Brown 1999).

MacArthur's approach to ecology, according to Sharon Kingsland, is *ahistorical*, leading to "the eclipse of history" (Kingsland 1995). Her distinction between ahistorical and historical approaches and her characterization of MacArthur's approach are widely accepted in the literature (e.g., Ricklefs 1987; Brooks and McLennan 1991, 2002; Sterelny and Griffiths 1999; Cooper 2003); and the ahistorical aspect of MacArthur's work has been criticized by ecologists and philosophers who emphasize the importance of history (e.g., Ricklefs 1987; Ricklefs and Schluter 1993; Brooks and McLennan 1991, 2002; Sterelny and Griffiths 1999).

In this paper I clarify and defend MacArthur's approach to ecology. First, I argue that MacArthur recognized the necessity of natural history and historical ecology and that the ahistorical/historical distinction mislocates the difference between his mathematical ecology and natural history. Second, I distinguish three kinds of criticism advanced by historically inclined ecologists and philosophers and argue that two of them are compatible with MacArthur's approach. Finally, by clarifying the scope and role of simple models in MacArthur's mathematical ecology, I show that the third kind of criticism is largely irrelevant to his approach.

2. The Eclipse of History? In *Modeling Nature*, Kingsland considers the history of population ecology as "a conflict between historical and ahistorical thinking" (1995, 8). For Kingsland, mathematical modeling is ahistorical, because it does not aim at reconstructing history and offering historical explanations. Instead, she says, it aims at generating predictions based on the present state of a system (Kingsland 1995, 5). In this sense mathematical modeling is "forward looking" (Kingsland 1995, 5). This distinction is often useful for interpreting the historical development of population ecology; it can explain why historical biologists often resisted mathematical approaches imported from non-historical sciences. Al-

https://doi.org/10.1086/525610 Published online by Cambridge University Press

though she says that the goal of mathematical modeling does not conflict with that of historical explanation (Kingsland 1995, 5), she argues that MacArthur's interest in modeling "created a *bias against* historical explanations" (Kingsland 1995, 191; italics mine). She thus suggests that MacArthur's approach is not merely *a*historical but *anti*-historical. However, Kingsland mislocates the difference between MacArthur's approach and historical approaches of natural history and historical ecology; the ahistorical/historical distinction obscures his recognition of the necessity of historical explanation in ecology.

Kingsland contrasts MacArthur's mathematical ecology with historical ecology, without clearly distinguishing between natural history and historical ecology (see, e.g., Kingsland 1995, 217–225). Natural history, however, is different from historical ecology. Historical ecology offers explanation by reconstructing history; natural history accumulates facts about nature without necessarily offering explanation or reconstructing history. Indeed, 'history' in 'natural history' does not refer to time. Rather, it refers to "a systematic account (without reference to time) of a set of natural phenomena, as those connected with a country, some division of nature or group of natural objects, a species of animals or plants, etc." (*The Oxford English Dictionary* 2nd ed.). This is one of the traditional senses of the word 'history', which is now rare except in 'natural history'. Natural history so understood therefore means, among other things, "the aggregate of facts relating to the natural objects, etc., of a place, or the characteristics of a class of persons or things" (*The Oxford English Dictionary* 2nd ed.). And MacArthur's mathematical ecology should be contrasted to natural history in *this* sense; for, when he refers to natural history, MacArthur seems to mean natural history as a body of facts about nature. For example, MacArthur and Edward O. Wilson describe a "natural history phase" of biogeography as accumulation of information:

> Biogeography has long remained in a natural history phase, accumulating information about the distribution of species and higher taxa and the taxonomic composition of biotas. . . . Without doubt this descriptive activity will continue to be of fundamental importance to the science. . . . But biogeography is also in a position to enter an equally interesting experimental and theoretical phase. (MacArthur and Wilson 1967, 181)

Note also the carefully balanced contrast between the natural history phase and the theoretical or experimental phase. Both are equally important.

In *The Theory of Island Biogeography*, MacArthur and Wilson mention major differences between their approach to ecology and traditional natural history. First, they note that traditionally ecologists asked historically

https://doi.org/10.1086/525610 Published online by Cambridge University Press

oriented questions such as "What was the ultimate origin of the Antillean vertebrate fauna?" and "Did Central America develop a discrete insular fauna during the Tertiary?" (1967, 5) and that these questions did not motivate ecologists to seek generalizations (1967, 5). Thus, MacArthur and Wilson explicitly ask more theoretically oriented questions, that is, questions about patterns in data. One such question concerns the species-area relationship: Why do large islands support more species than small ones?

Second, not only do MacArthur and Wilson try to find patterns in data but they also try to explain them by identifying underlying mechanisms. For example, they begin their work (1963, 1967) by noting general patterns in species diversity: there are more species on large islands than on small ones, and there are more species on islands near the mainland "source pool" than on far islands. These relationships hold for many communities with striking regularity, suggesting that these patterns have some underlying mechanism. MacArthur and Wilson's equilibrium model, which I will introduce in the next section, is an attempt to explain these patterns.

Third, for MacArthur and Wilson, a theory is supposed to organize facts about nature by explaining them theoretically and to stimulate new empirical research by making novel predictions. As they say, a purpose of a theory is "to simplify our education by substituting one theory for many facts," and "a good theory points to possible factors and relationships in the real world that would otherwise remain hidden and thus stimulates new forms of empirical research" (MacArthur and Wilson 1967, 5). In Section 4, I will discuss how MacArthur and Wilson derive novel predictions from their model.

Despite these major differences between theoretical ecology and natural history, MacArthur and Wilson believe that traditional natural history remains fundamental to ecology (1967, 181). For one thing, they need to rely on data from natural history when they compare predictions of their model with data (1963, 1967). They also point out that certain questions require historical answers: "Of course the history of islands remains crucial to the understanding of the taxonomic composition of species" (1967, 64).

MacArthur also recognizes that even theoretically oriented questions sometimes require historical explanations. At one point in *Geographical Ecology*, he says:

> Some problems in numbers of species truly seem to be outcomes of a capricious history. That is, they are interpretable in historical terms and not in terms of the machinery controlling species diversity. (1972, 173).

He goes on to offer a historical explanation of the difference in the numbers of tree species in Europe and North America. Before the Pleistocene glaciations, Europe and North America had similar numbers of tree spe-

https://doi.org/10.1086/525610 Published online by Cambridge University Press

cies, but today Europe has fewer tree species than North America. MacArthur explains this difference in terms of glaciers and geographical barriers. On both continents, advancing glaciers pushed trees to the south; in North America, where mountains range north to south, the trees did not face barriers in moving to the south, but in Europe, where the Alps and the Mediterranean range east to west, many tree species were pushed to the barriers and went extinct. As MacArthur adds, "History, pure and simple, appears to be the only explanation for the difference between European and American tree diversities" (1972, 174).

The distinction between ahistorical and historical therefore mislocates the difference between MacArthur's approach and natural history, and obscures his sensitivity to historical explanation. Unlike natural historians, he looked for patterns in data and tried to explain them theoretically. In doing so, he preferred mathematical models to historical narratives, but it is misleading to call this preference as "a bias against historical explanations" (Kingsland 1995, 191). MacArthur was always prepared to accept historical explanations; indeed, his explanation of the difference in numbers of European and North American tree diversities is remarkably similar to narrative explanations in historical ecology (e.g., see Blondel and Vigne 1993).

3. Three Kinds of Historical Criticism. Many ecologists and philosophers today call for a broader perspective in ecology, one that incorporates the influence of large-scale and long-term (historical in our sense) processes on community diversity. Emphasizing the importance of history, these people often criticize MacArthur's so-called "ahistorical" approach. It is possible to distinguish three kinds of this "historical" criticism of MacArthur's approach as illustrated by the MacArthur-Wilson model. MacArthur and Wilson suggested that the number of species on an island depends primarily on the relative rates of immigration from the source pool and of extinction on the island. If so, the number of species on an island will reach equilibrium when the rate of immigration from the source pool is balanced by the rate of extinction on the island (MacArthur and Wilson 1963, 1967). Graphically, they represented the equilibrium number of species as an intersection of two curves, the decreasing curve for the immigration rate and the increasing one for the extinction rate (MacArthur and Wilson 1963, 376; 1967, 21). Mathematically, they described the equilibrium number of species thus:

$$\hat{S} = IP/(E + I), \tag{1}$$

where $\hat{S}$ is the equilibrium number of species on an island, E and I the rates of extinction and immigration, and P the size of the source pool

https://doi.org/10.1086/525610 Published online by Cambridge University Press

(MacArthur and Wilson 1967, 26). Once a community reaches equilibrium, the number of species can be predicted as a balance between immigration and extinction. Specific history of the community does not affect the prediction.

Let us now look at the three kinds of historical criticism of MacArthur's approach. The first kind of criticism emphasizes influence of regional, long-term processes on local diversity. Robert Ricklefs and Dolph Schluter, for example, see regional diversity as a source of local diversity: species in a local community are samples of species existing in a region (Ricklefs and Schluter 1993). This regional perspective is not incompatible with MacArthur's approach. Indeed, MacArthur anticipated this perspective: the MacArthur-Wilson model (equation (1) above) describes the influence of a regional process (immigration of species from the mainland source pool) on local diversity (the number of species on an island). Moreover, workers who emphasize the regional perspective often use mathematical models (e.g., Roughgarden, Gaines, and Possingham 1988). This perspective will be a criticism of MacArthur's approach only if his approach is interpreted as *anti*-historical.

The second kind of criticism emphasizes the existence of nonequilibrium communities and the importance of the sequence of historical events in determining their diversity. For example, James H. Brown, stimulated by MacArthur and Wilson's work, argues that the diversity of small mammal species on mountaintops of the Great Basin of North America cannot be explained as a balance between immigration and extinction, for there is no balance to be achieved. According to Brown, these mammals colonized their habitats during the Pleistocene, when there were no barriers between the now isolated peaks; and since the mountaintops became isolated, no new species have colonized these places. So there has been nothing but extinction (Brown 1971). But this kind of research is compatible with MacArthur's approach, for its goal is not to challenge his approach but to test the generality of an equilibrium model.

The third kind of criticism emphasizes the necessity of taking historical accidents into account. This is a general criticism of MacArthur's approach; for if it is necessary to take historical accidents into account, theoretical explanations in ecology become impossible, and explanation in ecology must take the form of historical narrative. Thus, Kim Sterelny and Paul Griffiths argue that "the inescapable importance of history" (Sterelny and Griffiths 1999, 260) undermines MacArthur's approach to ecology (see also Sterelny 2001).

Consider their example of the historical development of a mammalian community in Tasmania. Tasmanian devils arrived at the island probably because they were excluded from the mainland by dingoes. Devils were able to reach the island because, when they were pushed southwards by

https://doi.org/10.1086/525610 Published online by Cambridge University Press

dingoes, the Bass Strait was closed and did not form a barrier; but when dingoes reached southeastern Australia, the Bass Strait had already been formed again and blocked their way. Since their establishment in Tasmania, devils have been excluding foxes by preying on fox kits, and this has important downstream consequences for small mammals in Tasmania. So the character of the mammalian community of Tasmania is a result of interactions of these species and historical accidents. Thus, Sterelny and Griffiths argue that we must appeal to history to explain ecological characters of a community:

> If the ecological character of a community mainly depends on the causal roles of the organisms in it—on, for example, the fact that some organism or other is recycling dung—then the prospects are good for general theories of community types. But if the particular species composition is critical to the character of a community, then history must play a central role in explaining the nature of biological communities. For no one denies that history determines which particular species are found in a community. (Sterelny and Griffiths 1999, 261)

Unlike the second kind of criticism, this argument challenges MacArthur's approach in general.

4. The Scope and Role of Simple Models in Ecology. Sterelny and Griffiths' argument expresses general skepticism about theoretical ecology. Here I show that when the scope and role of simple models in MacArthur's approach are properly understood, their skepticism becomes largely irrelevant to his approach.

4.1. The Scope of Simple Models. Sterelny and Griffiths claim that "the ahistorical program is explicit" (1999, 258) in MacArthur's work. To support this claim, they quote (1999, 259) the following passage from MacArthur's *Geographical Ecology*:

> We are looking for general patterns, which we can hope to explain. There are many of these if we confine our attention to birds or butterflies, but no one has ever claimed to find a diversity pattern in which birds plus butterflies made more sense than either one alone. Hence, we use our naturalist's judgment to pick groups large enough for history to have played a minimal role but small enough so that patterns remain clear. (MacArthur 1972, 176–177)

The passage, however, is quoted out of context and does not support Sterelny and Griffiths' claim that MacArthur's approach is explicitly ahistorical. This passage appears in the section entitled "History or Equilib-

https://doi.org/10.1086/525610 Published online by Cambridge University Press

rium" in which MacArthur offers the aforementioned historical explanation of European and North American tree diversities. One purpose of the section is to explore ways to find general patterns in data by distinguishing species whose numbers can be explained by general models and those whose numbers must be explained by historical narratives. For example, immediately following the tree species example, MacArthur considers bird species in Europe and North America. He says that if we compare forests and fields in both places, we see that forests tend to support more bird species than fields. Thus, although the numbers of tree species in these places need to be explained by historical accidents, the numbers of bird species may be explained by systematic habitat differences (MacArthur 1972, 174). These differences may in turn be explained by theory. Given this context, MacArthur's point in the above passage is not that we should be ahistorical but that we should be aware of the role of history so as not to miss general patterns.

The above passage also implies that MacArthur understands that simple models, though apparently general, have characteristic domains of application. He says that diversity patterns may be restricted to particular species, and if so, models that explain such patterns are also restricted to those species. Thus, a model often comes with subtle assumptions and has a characteristic domain of application (for a general discussion, see Wimsatt 1980). Consider, for example, the logistic equation

$$dN/dt = rN[1 - (N/K)],$$

where N is the size of the population, K the carrying capacity, and r the intrinsic rate of growth. This model assumes that the individual birth and death rates (used to determine r) are constant, an oversimplifying assumption for most animals and plants. The model appears to be highly general, but the appearance is deceptive. For, as Charles Puccia and Richard Levins (1985, 9) point out, there is a subtle limitation to the domain of this model: if r is negative (e.g., unfavorable environment), and N is larger than K (i.e., overpopulation), the model predicts that the population will increase! As Puccia and Levins say, "This nonsense result is the consequence of taking the equation too seriously, of applying it to circumstances it was not designed to represent" (1985, 9). The logistic equation comes with our implicit assumption that the above situation does not occur; in other words, it is not designed for this situation.

Similarly, in building equilibrium models, MacArthur implicitly assumes that diversity of species in question will *eventually* reach equilibrium:

> History even leaves its mark on equilibria, although how long its influence will be felt is unknown. We have already seen (p. 91) how

https://doi.org/10.1086/525610 Published online by Cambridge University Press

> very hard it is for a second species to colonize an island containing a reasonably close competitor. In this sense whichever species arrives first is practically permanent, and the later arrival is virtually certain to remain missing. But this is not really stable. *Given enough time*, early species A will go extinct from some islands and B will certainly successfully invade some of them. By this time random processes will have erased most of the history. (MacArthur 1972, 247; italics mine)

In other words, his equilibrium models come with an assumption that a system in question will *eventually* reach equilibrium, at which point the number of species can be predicted as a balance between immigration and extinction. This assumption is violated if the system in question is a non-equilibrium system. It was thus significant that the first experimental work on the MacArthur-Wilson model tested whether or not islands reach equilibria (Simberloff and Wilson 1969). The conclusion that islands do reach equilibria suggested that the model is not totally wrongheaded (see also Simberloff 1976).

So the scope of the equilibrium model is sensitive to species in question (birds but not trees or birds plus butterflies) and the possibility of the diversity of a given community to reach equilibrium. For example, MacArthur and Wilson (1963, 1967) are mostly concerned about birds, insects, and plants. These organisms can disperse more rapidly or widely than nonvolant mammals, and MacArthur thinks that birds might be less sensitive to historical effects (MacArthur 1972, 172). But Sterelny and Griffiths seem to neglect the subtle limitations of the equilibrium model, for they are concerned about fairly large, nonvolant mammals, which are likely to be affected by historical accidents, including human action. The distribution of large mammals like cattle and sheep is strongly affected by human activity (Blondel and Vigne 1993), and the distribution of small mammals can be sensitive to climatic and geographical barriers (Brown 1971). In short, Sterelny and Griffiths' example does not seem related to the equilibrium model.

4.2. The Role of Simple Models. As we saw in Section 2, for MacArthur, one of the roles of simple models is to describe essential mechanisms underlying patterns in data. Ecological communities are highly complex systems; simple models of such systems necessarily leave out many factors that affect systems. In this sense, simple models are 'false' descriptions of the world (Levins 1966, 1968; Wimsatt 1987). Thus, they can often deal with only one aspect of communities (e.g., species diversity), but they can generate testable predictions that stimulate empirical research.

Consider, for example, MacArthur and Wilson's manipulation of the basic equilibrium model (equation (1) above). After deriving the model,

https://doi.org/10.1086/525610 Published online by Cambridge University Press

MacArthur and Wilson explore possible effects of area on the equilibrium number of species. They develop a model for the magnitude of the area effect, that is, the rate of change of $\hat{S}$ with respect to area A, by keeping I constant and using the logarithm of $\hat{S}$:

$$d(\ln \hat{S})/dA = (1/\hat{S})(d\hat{S}/dA) = [(E + I)/IP](d\hat{S}/dA). \quad (2)$$

Given that I is constant, $\hat{S}$ is a function of E, and E is hypothesized to be a function of A. Therefore,

$$d\hat{S}/dA = (d\hat{S}/dE)(dE/dA). \quad (3)$$

Differentiating (1) with respect to E, we have

$$d\hat{S}/dE = (-IP)/(E + I)^2. \quad (4)$$

Substituting (4) into (3) yields

$$d\hat{S}/dA = [(-IP)/(E + I)^2](dE/dA), \quad (5)$$

where (dE/dA) is always negative. Finally, substituting (5) into (2), we have the model for the area effect:

$$\begin{aligned} d(\ln \hat{S})/dA &= [(E + I)/IP][(-IP)/(E + I)^2](dE/dA) \\ &= -(dE/dA)/(E + I), \end{aligned} \quad (6)$$

where $-(dE/dA)$ is always positive (MacArthur and Wilson 1967, 26–27).

Equation (6) predicts that if the extinction rate does not vary, the magnitude of the area effect always increases as the immigration rate decreases. Since the immigration rate is hypothesized to be lower on islands far from the source pool, MacArthur and Wilson predict that the area effect is greater on far islands than on near ones (1967, 27–28). They also predict that differences in area do not strongly affect the equilibrium number of species on near islands. MacArthur and Wilson call this a "new and nonobvious prediction" (1963, 386) of their model and argue that it is apparently consistent with the data from Indo-Australian archipelagos (MacArthur and Wilson 1963, 1967).

MacArthur and Wilson are well aware that their model can only deal with one ecological character: species diversity or the number of species in a given community. They are also aware that the model cannot deal with other characters of a community. For example, it cannot answer questions about taxonomic composition of a community (MacArthur and Wilson 1967, 64) and hence properties that depend critically on taxonomic composition. To answer this kind of question, historical explanation is necessary.

Sterelny and Griffiths seem to confuse MacArthur and Wilson's ques-

https://doi.org/10.1086/525610 Published online by Cambridge University Press

tion about species diversity with the question about taxonomic composition and related properties. In ecology, patterns of species diversity refer to statistical patterns in numbers of species. MacArthur and Wilson are interested in one such pattern: the species-area relationship. Sterelny and Griffiths say that their example shows how "the character of a community" (1999, 261) is determined, at least in part, by a particular taxonomic composition of that community and historical accidents, but by "the character of a community" they mean devils' exclusion of foxes from Tasmania and its importance for the small mammals endemic to the island. But this character is not species diversity, and species diversity often remains constant despite changes in taxonomic composition (Brown et al. 2001). Thus, Sterelny and Griffiths' example is largely irrelevant to MacArthur's approach to ecology. (See also Mikkelson 2001, 2003 for similar arguments against Sterelny and Griffiths' skepticism about theoretical ecology.)

5. Conclusion. MacArthur's philosophy of ecology as summarized in his introduction to *Geographical Ecology* is subtler than it first appears. MacArthur tried to find general patterns in data and to explain them by constructing simple mathematical models. Models were supposed to explain patterns by identifying underlying mechanisms and generate nonobvious predictions that stimulate new empirical research. But MacArthur was not against natural history and historical ecology; he simply wanted to go beyond traditional natural history by finding and explaining patterns in data. Kingsland's ahistorical/historical distinction thus mislocates the difference between MacArthur's approach and traditional natural history.

There are three kinds of historical criticism of MacArthur's approach:

1. Large-scale historical processes have important effects on community diversity.
2. Species diversities of some communities cannot reach equilibrium because of historical accidents.
3. Explanation in ecology must take historical accidents into account.

The first two are compatible with MacArthur's approach in general, and the third one is largely irrelevant to his approach. Sterelny and Griffiths, who advance this kind of criticism, seem to overlook the subtle limitations of equilibrium models. Moreover, even though their example of Tasmania shows that certain characters of a community are determined by a particular species composition of that community, which in turn is determined by history, the example is not about patterns of species diversity, the main theme of MacArthur's approach to ecology.

REFERENCES

Blondel, Jacques, and Jean-Denis Vigne (1993), "Space, Time, and Man as Determinants of Diversity of Birds and Mammals in the Mediterranean Region", in R. E. Ricklefs

https://doi.org/10.1086/525610 Published online by Cambridge University Press

and D. Schluter (eds.), *Species Diversity in Ecological Communities: Historical and Biogeographical Perspectives.* Chicago: University of Chicago Press, 135–146
Brooks, Daniel R., and Deborah A. McLennan (1991), *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology.* Chicago: University of Chicago Press.
——— (2002), *The Nature of Diversity.* Chicago: University of Chicago Press.
Brown, James H. (1971), "Mammals on Mountaintops: Nonequilibrium Insular Biogeography", *American Naturalist* 105: 467–478.
——— (1999), "The Legacy of Robert MacArthur: From Geographical Ecology to Macroecology", *Journal of Mammalogy* 80: 333–344.
Brown, James H., et al. (2001), "Regulation of Diversity: Maintenance of Species Richness in Changing Environments", *Oecologia* 126: 321–332.
Cooper, Gregory J. (2003), *The Science of the Struggle for Existence: On the Foundations of Ecology.* Cambridge: Cambridge University Press.
Kingsland, Sharon E. (1995), *Modeling Nature: Episodes in the History of Population Ecology*. 2nd ed. Chicago: University of Chicago Press.
Levins, Richard (1966), "The Strategy of Model Building in Population Biology", *American Scientist* 54: 421–431.
——— (1968), *Evolution in Changing Environments.* Princeton, NJ: Princeton University Press.
MacArthur, Robert H. (1972), *Geographical Ecology: Patterns in the Distribution of Species.* New York: Harper & Row.
MacArthur, Robert H., and Edward O. Wilson (1963), "An Equilibrium Theory of Insular Zoogeography", *Evolution* 17: 373–387.
——— (1967), *The Theory of Island Biogeography.* Princeton, NJ: Princeton University Press.
Mikkelson, Gregory M. (2001), "Complexity and Verisimilitude: Realism for Ecology", *Biology and Philosophy* 16: 533–546.
——— (2003), "Ecological Kinds and Ecological Laws", *Philosophy of Science* 70: 1390–1400.
Puccia, Charles J., and Richard Levins (1985), *Qualitative Modeling of Complex Systems: An Introduction to Loop Analysis and Time Averaging.* Cambridge, MA: Harvard University Press.
Ricklefs, Robert E. (1987), "Community Diversity: Relative Roles of Local and Regional Processes", *Science* 235: 167–171.
Ricklefs, Robert E., and Dolph Schluter (1993), "Species Diversity: Regional and Historical Influences", in Robert E. Ricklefs and Dolph Schluter (eds.), *Species Diversity in Ecological Communities: Historical and Geographical Perspectives.* Chicago: University of Chicago Press, 350–363.
Roughgarden, Jonathan, Steven Gaines, and Hugh Possingham (1988), "Recruitment Dynamics in Complex Life Cycles", *Science* 241: 1460–1466.
Simberloff, Daniel S. (1976), "Species Turnover and Equilibrium Island Biogeography", *Science* 194: 472–478.
Simberloff, Daniel S., and Edward O. Wilson (1969), "Experimental Zoogeography of Islands: The Colonization of Empty Islands", *Ecology* 50: 278–296.
Sterelny, Kim (2001), "Darwin's Tangled Bank", in *The Evolution of Agency and Other Essays.* Cambridge: Cambridge University Press, 152–178.
Sterelny, Kim, and Paul E. Griffiths (1999), *Sex and Death: An Introduction to Philosophy of Biology.* Chicago: University of Chicago Press.
Wimsatt, William C. (1980), "Reductionistic Research Strategies and Their Biases in the Units of Selection Controversy", in Thomas Nickles (ed.), *Scientific Discovery: Case Studies.* Dordrecht: Reidel, 213–259.
——— (1987), "False Models as Means to Truer Theories", in Matthew H. Nitecki and Antoni Hoffman (eds.), *Neutral Models in Biology.* New York: Oxford University Press, 23–55.

https://doi.org/10.1086/525610 Published online by Cambridge University Press