

## 10

**SEARCHING FOR PATTERNS,  
HUNTING FOR CAUSES**  
ROBERT MACARTHUR, THE  
MATHEMATICAL NATURALIST

**INTRODUCTION**

Robert Helmer MacArthur was born in Toronto, Canada, on April 7, 1930, and died of renal cancer on November 1, 1972 (see figure 10.1). However, his legacy as an ecologist is not adequately represented by his mere forty-two years of life. MacArthur received an undergraduate degree in mathematics from Marlboro College in Marlboro, Vermont, where his father, John Wood MacArthur, was a geneticist. From there, MacArthur received a master's degree in mathematics from Brown University, and in 1957 he began a PhD program at Yale University starting in mathematics but quickly moving to ecology. At Yale, he studied with George Evelyn Hutchinson, the most important ecologist of the twentieth century, who influenced him both in style and substance.<sup>1</sup> During 1957 and 1958, MacArthur worked with ornithologist David Lack at Oxford University. From 1958 to 1965, he went from assistant to full professor at the University of Pennsylvania and finally became the Henry Fairfield Osborn Professor of Biology at Princeton University. In 1969, he was elected to the National Academy of Sciences.

In their memorial volume *Ecology and Evolution of Communities*, Martin Cody and Jared Diamond write:

In November 1972 a brief but remarkable era in the development of ecology came to a tragic, premature close with the death of Robert MacArthur at the age of 42. When this era began in the 1950s, ecology was still mainly a descriptive science. It consisted of qualitative, situation-bound statements that had low predictive value, plus empirical facts and numbers that often seemed to defy generalization. Within two decades new paradigms had transformed large areas of ecology into a structured, predictive science that combined powerful quantitative theories with the recognition of widespread patterns in nature. This revolution in ecology had been largely due to the work of Robert MacArthur.<sup>2</sup>

When ecologists consider MacArthur's work, they emphasize the use of simple analytic models with interspecific competition as the primary



**Figure 10.1:** Robert MacArthur.  
Photograph by Orren Jack Turner.

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mechanism structuring ecological communities, accompanied by an approach to hypothesis testing consisting of qualitatively comparing models and patterns.<sup>3</sup> MacArthur worked as a mathematician “outsider,” and not the customary biologist, identifying ecological patterns and providing simple models representing the causes of such patterns. As Eric Pianka notes, when MacArthur was with mathematicians he claimed to be a biologist, and when he was with biologists he claimed to be a mathematician.<sup>4</sup>

Some “insiders” denied these patterns exist, and some denied simple models could explain them.<sup>5</sup> Nevertheless, MacArthur’s mathematical approach was historically important. As the writer David Quammen recognized, his influence has been profoundly methodological; he changed the way ecologists asked and answered questions about populations and communities.<sup>6</sup> MacArthur, as an applied mathematician with a love of fieldwork, changed the face of ecology.

In this essay, we first look at an influential view of the nature of mathematics espoused by G. H. Hardy; namely, that it is a science of patterns. Second, we consider the views of MacArthur’s teacher G. E. Hutchinson and his emphasis on theory and pattern. Third, we explore the methodologies of co-members in the “Marlboro Circle,” Richard Lewontin and Richard Levins. Fourth, we directly engage MacArthur’s own views as a “mathematical naturalist.” Finally, I offer some speculative reflections on MacArthur’s role as an outsider.

**HETEROGENEOUS UNSTABLE POPULATIONS**

During the 1950s, vociferous but unproductive stultifying debates were occurring in ecology. In population ecology, ecologists argued intensely over whether populations are “regulated.” Many populations persist through time and vary moderately in abundance. The “biotic school,” of which David Lack was a member, argued that this was so because of density-dependent processes such as intraspecific competition.<sup>7</sup> Contrarily, the “climatic school” argued that populations minimally vary because of the abiotic environment (e.g., weather).<sup>8</sup> Confusions and complications appeared at every juncture in the debate. The facts were unclear, mechanistic explanations were often merely assumed, experiments were unrealistic, different groups used different model organisms, and terminology was ill defined. At the 1957 Cold Harbor Symposium, where the two sides epically clashed, G. E. Hutchinson suggested that the symposium itself was a “heterogeneous unstable population.”<sup>9</sup> To MacArthur, the debate appeared to be mired in terminological difficulties over terms like “carrying capacity,” “competition,” and “density.”<sup>10</sup>

He noted in his review of the volume in which Hutchinson's "Concluding Remarks" appears:

Science usually progresses faster when theory is able to keep abreast of facts; when the array of facts is as complicated as human demography already is, one despairs of finding a theorist who can set up a complete, adequate theory. It may be very true that demographers know too much.<sup>11</sup>

Likewise, he opined that an "almost religious fervor replaces objectivity in the symposium."<sup>12</sup>

Similarly, in community ecology, Frederic Clements and Henry Gleason, along with their respective followers, disagreed vigorously over succession and the nature of ecological communities. Clements argued that disturbed communities followed a very specific sequence of stages to a single "climax" community. In fact, he considered communities to be "superorganisms." Gleason argued Clements's views were empirically unfounded and that community properties were the result of individual species's "physiological" requirements; "every species of plant is a law unto itself" with no climax community.<sup>13</sup>

Like population ecology, MacArthur saw the state of community ecology as deeply problematic. With regard to Clements, he was very skeptical of the notion of superorganisms and their "emergent properties," since most scientists believe that properties of wholes are the result of the behavior and interactions of their parts.<sup>14</sup> With regard to Gleason, he argued that ecologists primarily interested in separate species "have never made any progress in unraveling community patterns."<sup>15</sup> More generally, he writes:

The question is not whether such communities exist but whether they exhibit interesting patterns about which we can make generalizations. This need not imply that communities are superorganisms or have properties not contained in the component parts and their interactions. Rather it implies simply that we see patterns of communities and that, at this stage of ecology, the patterns may be more easily related than the complex dynamics of the component species.<sup>16</sup>

Why couldn't ecologists leave behind fraught debates about population regulation and the nature of communities? In both disciplines, something new was needed. As we shall see, something new in ecology is exactly what MacArthur proposed.

**MATHEMATICS AS A SCIENCE OF PATTERNS**

To appreciate MacArthur’s mathematical approach, we should consider the nature of mathematics. E. O. Wilson and G. E. Hutchinson note that MacArthur “resembled very much in temperament and philosophy” the pure mathematician G. H. Hardy and shared his “conviction” that mathematics was a science of patterns.<sup>17</sup>

Hardy begins with the idea that a mathematician is, like a painter or a poet, “a maker of patterns.”<sup>18</sup> As an example of pure mathematics, Hardy considers pure geometries. He suggests that pure geometries are models; they are maps or pictures that are partial and imperfect copies of mathematical reality.<sup>19</sup> Pure mathematics is an attempt to describe mathematical objects, but not the physical world. Applied mathematics is an attempt to describe the patterns exemplified by spatiotemporal objects. He continues:

Applied mathematicians, mathematical physicists, naturally take a different view, since they are preoccupied with the physical world itself, which also has its structure or pattern. We cannot describe this pattern exactly, as we can that of a pure geometry, but we can say something significant about it. We can describe, sometimes fairly accurately, sometimes very roughly, the relations which hold between some of its constituents, and compare them with the exact relations holding between constituents of some system of pure geometry. We may be able to trace a certain resemblance between the two sets of relations, and then the pure geometry will become interesting to physicists; it will give us, to that extent, a map which “fits the facts” of the physical world. The geometer offers to the physicist a whole set of maps from which to choose. One map, perhaps, will fit the facts better than others, and then the geometry which provides that particular map will be the geometry most important for applied mathematics.<sup>20</sup>

Thus, for Hardy, mathematical and physical objects exemplify patterns respectively that can be “roughly” compared.

So, pure mathematicians study and prove theorems regarding patterns independent of any physical exemplification. Applied mathematicians study patterns too, but particularly ones that “fairly accurately, sometimes very roughly” are exemplified by spatiotemporal systems. For example, a pure mathematician studying differential equations is concerned with how a point “changes position” in a geometric space. However, an applied mathematician studies differential equations in order to model, say, how birds feed in a forest. Mathematics, then, is the science of patterns.

### G. E. HUTCHINSON, PATTERNS, AND NICHES

Remarkably, G. E. Hutchinson also wrote about the importance of patterns in his “The Concept of Pattern in Ecology.”<sup>21</sup> According to Hutchinson, the concept of “pattern” is fundamental to science because the “completely disordered is unimaginable,” and “if we are going to say anything at all, some structure is certain to be involved.”<sup>22</sup> Put simply, intelligibility in science requires that objects be patterned. He defines “pattern” in ecology as follows: “The structure which results from the distributions of organisms in, or from, their interactions with, their environments, will be called pattern.”<sup>23</sup>

Hutchinson also offered theoretical frameworks for investigating patterns in ecology; specifically, the concept of a “niche.” In his 1957 “Concluding Remarks,” he provided a commentary on the population regulation debates, with the hope that some clear theory could profitably redirect ecologists. In this essay, Hutchinson formalized the competitive exclusion principle: roughly, species with identical niches cannot coexist. Suppose that we have an  $n$ -dimensional hypervolume composed of independent variables, each affecting the abundance of species. This hypervolume has a nonempty area where the species persists; this is its “fundamental niche.” Similarly, the “realized niche” is the volume where a species persists given interspecific interactions. If the realized niches of species in a community overlap, but not completely, then they will coexist. Hutchinson controversially claimed that there were groups of species, such as the European insect species *Corixa affinis*, *C. macrocephala*, and *C. punctata*, that differed in size by a factor of 1.3 to avoid competitive exclusion.

Hutchinson also claimed the principle of competitive exclusion might be falsified by territorial birds whose population size was too low for competition to occur.<sup>24</sup> In his dissertation, MacArthur did extensive fieldwork on five warbler species in Maine.<sup>25</sup> In areas of feeding where competition would be most likely to occur, he found an amazing degree of niche specificity. Each bird species fed in different parts of the trees, thus avoiding competitive exclusion. Hutchinson impressed upon MacArthur both the importance of well-chosen patterns and mathematical theory. Ironically, MacArthur noted regarding Hutchinson that his most significant achievements occurred in part by using procedures from other sciences on ecological questions.<sup>26</sup>

### THE MARLBORO CIRCLE

The 1960s were an exciting time in theoretical biology. MacArthur, along with Egbert Leigh (another Hutchinson student), Richard Levins, Richard Lewontin, and E. O. Wilson, were conceiving of a new integrative mathematical biology.<sup>27</sup> The group informally met at MacArthur’s home in Marlboro,

Vermont. E. O. Wilson called this group the “Marlboro Circle” (Wilson 1994, 253). In his autobiography, Wilson notes that this group of five biologists met in July of 1964 to discuss their individual research agendas and to how they might jointly contribute to the future of population biology.<sup>28</sup> The question was how would they mathematically integrate population genetics, ecology, biogeography, and ethology into population biology:

For two days between walks in the quiet northern woodland, we expanded upon our common ambition to pull evolutionary biology onto a more solid base of theoretical population biology. Each in turn described his particular ongoing research. Then we talked together about the ways in which that subject might be extended toward the central theory and aligned with it.<sup>29</sup>

Interestingly, Wilson reports they considered publishing under the pseudonym “George Maximin” (254). However, though the group did not, Levins and Lewontin did write under a pseudonym, “Isadore Nabi,” criticizing systems ecology.<sup>30</sup> In the end, the group did not meet thereafter, instead pursuing their various interests in smaller groups.<sup>31</sup>

In the seventies, E. O. Wilson reminisced that they were interested in “simple theory.” They deliberately attempted to simplify natural systems in order to articulate mathematical principles.<sup>32</sup> Wilson compared their work with that of other systems ecologists like Kenneth Watt, C. S. Holling, and Paul Ehrlich, who devised “complex theory.”

They say that because ecosystems are so vastly complex, you must be able to take all the various components into account. You really must feed in a lot of the stuff that we simple theorists leave out, like sunsets and tides and temperature variations in winter, and the only way you can do this is with a computer. To them, in other words, the ideal modern ecologist is a computer technologist, who scans the whole environment, feeds all the relevant information into a computer, and uses the computer to simulate problems and make projections into the future.<sup>33</sup>

This juxtaposition between “simple” and “complex theory” was important for the Marlboro Circle’s members. Richard Lewontin similarly recollects,

Dick Levins and I had hooked up with Robert MacArthur, who was then at Penn but then went to Princeton, and the three of us had this idea that we ought to be able to build a science of population biology that would fuse the intrapopulation genetic variation aspect of biology with demography and population ecology, and so on. . . . Dick Levins and I and Robert MacArthur used to meet, and we had a sense of really building some new



science of population biology. We had contact with Ed Wilson, who was also interested in that, and with Lee Van Valen. We met a couple of times in Vermont at Robert's "in-laws" place and, in general, had a kind of zeal for founding a new field.<sup>34</sup>

To understand this group's methodological opinions, we can start with geneticist Richard Levins in his 1966 classic essay, "The Strategy of Model Building in Population Biology" and his 1968 classic *Evolution in Changing Environments*. As MacArthur himself notes, they shared ideas so continuously that it was difficult to trace their individual history.<sup>35</sup>

In Levins's 1966 essay, there are several issues in play. First, Levins, along with others in the "Marlboro circle," was convinced that ecological and evolutionary processes must be modeled together. Clearly, ecological processes like plant succession can occur over centuries, and evolutionary processes like pesticide resistance can occur over a few years. Thus, given their entwinement, they should be jointly modeled, contrary to traditional theory. This is the "fusing" of the "intrapopulation genetic aspect" with population ecology, Lewontin notes. Second, mathematical models that represent the dynamics of the ecological-evolutionary multispecies ensembles could not be "photographically exact."<sup>36</sup> Maximally general, realistic, and precise models would be analytically insoluble, their parameters would be meaningless, and they could not be measured. This sort of "FORTRAN ecology," which "Isadore Nabi" poked fun at, was being advocated by "complex theorist" Kenneth Watt.<sup>37</sup> Third, Levins claimed one could build models that maximized any two factors among generality, realism, and precision, but not all three. MacArthur and Levins preferred general and realistic models at the expense of precision.<sup>38</sup> He concluded famously that theories in biology were collections of models with "robust theorems"; he writes, "Our truth is the intersection of independent lies."<sup>39</sup> Curiously, according to Wilson and Hutchinson, MacArthur often claimed to quote Picasso when he would say, "Art is the lie that helps us to see the truth."<sup>40</sup> What Pablo Picasso actually said was,

We all know that art is not truth. Art is a lie that makes us realize truth, at least the truth that is given us to understand. The artist must know the manner whereby to convince others of the truthfulness of his lies.<sup>41</sup>

It seems likely that Levins's famous quote derives from Picasso via MacArthur.

In *The Genetics of Evolutionary Change* (1974), evolutionary geneticist Richard Lewontin articulates his own perspective on modeling systems, with a strong resemblance to that of Levins'.<sup>42</sup> At some time  $t$ , the system is in state  $E$ , and we want to predict the system's state  $E'$  at  $t + n$ . To do so, we must con-



struct laws that contain the relevant variables and parameters. For example, we might predict gene frequencies using parameters describing fitness, mutation rates, and so forth. Lewontin crucially notes that there may be states  $E$  and  $E'$  such that no law of transformation can be constructed to obtain  $E'(t+n)$  from  $E(t)$ .<sup>43</sup> For example, given merely the present position of a space capsule at some time, we cannot successfully predict its future position. However, given information regarding its velocity and acceleration in three orthogonal directions, a *dynamically sufficient* description can be given; that is, a set of laws such that given  $E(t)$ , we can successfully predict  $E'(t+n)$ .

Crucially, Lewontin notes dynamic sufficiency is relative to chosen variables and “tolerance limits.” That is, for each state  $E$  a *tolerance set*  $e$  is provided such that states in  $e$  are regarded as “indistinguishable”; we do not care about differences among states within  $e$ .<sup>44</sup> With broad tolerance limits, the required model dimensionality (i.e., the number of variables needed for dynamic sufficiency) will be low, and if the limits are narrow, the required dimensionality will be high. For example, if population ecologists explain the changes in population abundance “to one order of magnitude,” then net fecundity and mortality rates are sufficient. On the other hand, if fisheries biologists want to predict abundances to an accuracy of 10%–20%, this requires complete age-specific life tables. Human demographers’ attempt to predict population size within 1% requires knowledge of age, sex, socioeconomic class, education, geography, and so on.<sup>45</sup> Echoing Levins’s view of theories, Lewontin writes,

The building of a dynamically sufficient theory of evolutionary processes will really entail the simultaneous development of theories of different dimensionalities, each appropriate to the tolerance limits acceptable in its domain of explanation.<sup>46</sup>

Of course, models must be more than dynamically sufficient; they must be *empirically sufficient* too.<sup>47</sup> The variables and parameters must be measured. Otherwise, the theory becomes a “vacuous exercise in formal logic.”<sup>48</sup>

Lewontin extends his methodological discussion to ecology as well:

It is not always appreciated that the problem of theory building is a constant interaction between constructing laws and finding an appropriate set of descriptive state variables such that laws can be constructed. We cannot go out and describe the world in any old way we please and then sit back and demand that an explanatory and predictive theory be built on that description. The description may be dynamically insufficient. Such is the agony of community ecology. We do not really know what a sufficient

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description of a community is because we do not know what the laws of transformation are like, nor can we construct those laws until we have chosen a set of state variables. That is not to say that there is an insoluble contradiction. Rather, there is a process of trial and synthesis going on in community ecology, in which both state descriptions and laws are being fitted together.<sup>49</sup>

Community ecologists must find the right state variables for their laws to be dynamically sufficient. Only then, can they be empirically sufficient.

Thus, the methodological views of the evolutionary geneticists Levins and Lewontin have several features in common. First, both recognize the importance of theorizing in biology. Second, theories are judged relative to the task at hand. When we are not primarily interested in precision (i.e., “narrow tolerance limits”), we add to the generality and realism (i.e., dimensionality) of our models. Third, we need multiple models for adequate population biology. As we shall see, MacArthur accepts these points too.

#### **MACARTHUR’S MATHEMATICAL MIND**

After considering the most prominent influences, let’s finally examine MacArthur’s mathematical approach to ecology. His approach has four components: the search for patterns, the construction of simple theory, the testing of such theory with natural experiments, and a disregard for conceptual disagreements. Let’s consider each in turn. MacArthur infamously writes:

To do science is to search for general 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 who loves to note changes in bird life up a mountainside, or changes in plant life from mainland to island, or changes in butterflies from temperate to tropics. But not all naturalists want to do science; many take refuge in nature’s complexity in a justification to oppose any search for patterns. This book is addressed to those who do wish to do science.<sup>50</sup>

According to MacArthur, like Hardy and Hutchinson, science is the study of patterns. Ecologists study patterns that species and communities exhibit in space and time. Like Hardy, he claims that ecological patterns are importantly different from pure mathematical ones. First, ecological patterns admit of variation; they are seen with “blurred vision”:

Ecological patterns, about which we construct theories, are only interesting if they are repeated. They may be repeated in space or time, and they

may be repeated from species to species. A pattern which has all of these kinds of repetition is of special interest because of its generality, and yet these very general events are only seen by ecologists with rather blurred vision. The very sharp-sighted always find discrepancies and are able to say that there is no generality, only a spectrum of special cases.<sup>51</sup>

The “sharp-sighted” naturalist finds exceptions. Second, not only are the patterns “blurry,” they are sensitive to the morphological, economical, and dynamical properties of the species.

Science should be general in its principles. A well-known ecologist remarked that any pattern visible in my birds but not in his *Paramecium* would not be interesting, because, I presume, he felt it would not be general. . . . [A] bird pattern would only be expected to look like that of *Paramecium* if birds and *Paramecium* had the same morphology, economics, and dynamics, and found themselves in environments of the same structure.<sup>52</sup>

Ecology involves natural history, but it inescapably requires the construction of theory too.

Unraveling the history of a phenomenon has always appealed to some people and describing the machinery of the phenomenon to others. In both processes generalizations can be made and tested against new information so both are scientific, but the same person seldom excels at both. The ecologist and the physical scientist tend to be machinery oriented, whereas the paleontologist and most biogeographers tend to be history oriented. They tend to notice different things about nature. The historian often pays special attention to *differences* between phenomena, because they may shed light on the history. . . . [The machinery person] tends to see *similarities* among phenomena, because they reveal regularities.<sup>53</sup>

Reviewing Lawrence Slobodkin’s 1961 publication, *Growth and Regulation of Animal Populations*, MacArthur suggests that ecologists can be placed into two groups. One group pays the utmost attention to nature’s complexity, documenting it through observations at endless lengths. The other group proposes theories that are continuously patched up to account for as much data as possible. This latter group of theoreticians will sometimes have to ignore important observations in order to articulate generalizations that will have to be revised considerably. However, it is only through this constant revision of principles that ecology can have any hope of becoming a “respectable branch of science.”<sup>54</sup> The existence of “blurry patterns” undergirds MacArthur (and

Levins's) preference for general, realistic, but imprecise theories (and is similar to Lewontin's notion of broad "tolerance limits"). "Simple" as opposed to "complex" theory represents simple causal mechanisms that make qualitative differences, such as "fine vs. coarse-grained, pursuers vs. searchers, jacks of all trades vs. masters of one, *r* selection vs. *K* selection."<sup>55</sup>

Simple theory coupled with "blurry" patterns leads MacArthur to his "qualitative" view of theory evaluation.

The concept of pattern or regularity is central to science. Pattern implies some sort of repetition, and in nature it is usually an imperfect repetition. . . . The imperfection of the repetition gives us the means of making comparisons. We witness an event *A*, occurring under conditions *C*, then, under slightly altered conditions, *C'*, we witness a slightly altered event, *A'*. Now we have the seed of a scientific hypothesis: "the difference between *C* and *C'* causes (i.e., is always associated with) the difference between *A* and *A'*," which we test by further observations. In geographic ecology, we study patterns repeated in space, not time, and natural comparisons are those of events occurring in different places. Over and over again in what follows we compare the species on the mainland to those on an island, the species on one mountain to those on another, the species high on a mountain to those lower on the mountain, the communities of the tropics to those of the temperate, and so on.<sup>56</sup>

Thus, this approach lends itself to "natural experiments" where differences between mainland and island, temperate regions and the tropics, etc. allow one to look for these simple difference makers.

Interestingly, MacArthur was very skeptical of laboratory or "bottle experiments," considering their "dramatic failures" due to the difficulty of adding environmental heterogeneity.<sup>57</sup> But he also claimed we do not need them, since astronomy was a respected science even though Copernicus and Galileo "never moved a star."<sup>58</sup> As with Levins, he was skeptical of computer modeling, since he thought computers could never replace the good judgment provided by the training of a field naturalist.<sup>59</sup> As Levins suggested, using computers prematurely could "confuse numbers with knowledge."<sup>60</sup>

Finally, we have MacArthur's disregard for conceptual debates. Consider again his views on the nature of ecological communities (which highlight the concerns regarding empirical sufficiency and the choice of variables raised by Lewontin).

Humpty Dumpty told Alice, "When *I* use a word, it means just what I choose it to mean—neither more nor less." Irrespective of how other people use

the term “community”—and there are almost as many uses as there are ecologists—I use it here to mean any set of organisms currently living near each other and about which it is interesting to talk. . . . The question is not whether such communities exist but whether they exhibit interesting patterns about which we can make generalizations.<sup>61</sup>

MacArthur chose community-level properties like species diversity because there are interesting patterns to be found concerning interacting species, and, on his view, populations exhibit too much variation for simple theory (having learned this lesson in part from the population regulation debates).<sup>62</sup> MacArthur’s mathematical approach is now clear. First, he was an ardent defender of the search for patterns. Second, he forcefully proposes simple theories representing simple causes of those patterns. Third, qualitative theory capturing said mechanisms should be evaluated by natural experiments where the relevant causal factors naturally vary and produce the blurry patterns of interest. Finally, we should put to the side obscuring debates over conceptual issues.

**CONCLUSION**

MacArthur’s approach, though borrowing elements from an ecologist like Hutchinson and from geneticists Levins and Lewontin, was applied with his preeminent mathematical powers to population and community ecology, where they never had made an appearance. He chose a variety of ecological topics and offered remarkably novel mathematical theories (e.g., species abundance distributions, island biogeography, optimal foraging theory, limiting similarity). “Simple theory” appeared to have the resources to turn ecology into a quantitatively successful science like physics, and this prospect was extremely alluring. This was especially tantalizing for him and others against the background of stagnating debates over population regulation and the nature of communities, as we have seen. Given the dreary state of ecology, MacArthur envisioned a radical ecology of patterns, simple qualitative theory, natural experiments, and pragmatism about conceptual disputes.

Unfortunately, MacArthur’s “simple theories” ultimately had to be tested against ecological patterns, and here is where the critics demurred. First, in some instances, ecological patterns discovered were challenged as being mere statistical artifacts or explainable without interspecific competition.<sup>63</sup> Second, what started as analytically tractable theory eventually had the problems of the “complex theory” MacArthur originally opposed (e.g., the theory of limiting similarity).<sup>64</sup> Third, even in those cases where there are

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patterns and simple theory, the qualitative methodology sometimes fails. Schematically, suppose  $C$  causes  $A$  and  $C'$  causes  $A$ ; then we would assume observing  $A$  confirms  $C$  is the relevant mechanism. However, if sometimes  $C'$  causes  $A$ , then our simple theory and natural experiments can fail us. Different theories can lead to the same observations and thus precise predictions are required to discriminate between the theories (e.g., “broken stick” distributions and the equilibrium theory of island biogeography).<sup>65</sup> Of course, there were theoretical and empirical successes, but there have been challenges and failures too.

Presciently, MacArthur believed his theories, even if false, could be of great importance, writing:

A theory attempts to identify the factors that determine a class of phenomena and to state the permissible relationships among the factors as a set of verifiable propositions. A purpose is to simplify our education by substituting one theory for many facts. 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. Even a first, crude theory can have these virtues. (MacArthur and Wilson 1967, 5)

MacArthur thought that ecology “can never have too much theory.”<sup>66</sup> Likewise, the worst sin of a scientist is not to be wrong but to be trivial.<sup>67</sup> Robert MacArthur’s work, even if wrong, was never trivial. In Hutchinson’s “Concluding Remarks,” he wrote:

It is not necessary in any empirical science to keep an elaborate logicomathematical system always apparent, any more than it is necessary to keep a vacuum cleaner conspicuously in the middle of a room at all times. When a lot of irrelevant litter has accumulated the machine must be brought out, used, and then put away.<sup>68</sup>

In my estimation, MacArthur’s outsider approach attempted to remove “a lot of irrelevant litter” from ecology. Some of the litter was surely removed but some was merely swept under the rug.

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8. H. Andrewartha and C. Birch, *The Distribution of and Abundance of Animals* (Chicago: University of Chicago Press, 1954).
9. G. E. Hutchinson, "Concluding Remarks," in *Cold Spring Harbor Symposia on Quantitative Biology* 22 (1957): 415–427, 415.
10. V. Diether and Robert H. MacArthur, "A Field's Capacity to Support a Butterfly Population," *Nature* 21 (1964): 728–729, 728. Apparently, Theodosius Dobzhansky felt similarly; he wrote regarding the symposium, "To a non-ecologist, the controversy which has made our session so lively is, I confess, somewhat bewildering. I have had a feeling for several years now that this is a controversy chiefly about words, about 'semantics,' to use a fashionable word. Having tried to the best of my ability to understand the issue involved, I still continue to feel that way" (Gordon Orians, "Natural Selection and Ecological Theory," *The American Naturalist* 96 [1962]: 257–263, 257).



11. Robert MacArthur, "Population Studies: Animal Ecology and Demography," review of *Cold Spring Harbor Symposium Vol. XXII, Quarterly Review of Biology* 35 (1960): 82–83, 82.
12. MacArthur, "Population Studies," 83.
13. As Henry Horn humorously notes, "The many fragments of the traditional analysis of succession have been christened and described in detail, but the resulting jargon has added more to Freudian imagery than it has to a genuine understanding of successional patterns" (Henry Horn, "Markovian Properties of Forest Succession," in *Ecology and Evolution of Communities*, eds. Martin Cody and Jared Diamond [Cambridge: Harvard University Press, 1997], 196–211).
14. Robert H. MacArthur, *Geographical Ecology* (Princeton: Princeton University Press, 1972), 154.
15. MacArthur, *Geographical Ecology*, 55.
16. Robert H. MacArthur, "Patterns of Terrestrial Bird Communities," *Avian Biology* 1 (1971): 189–221, 190.
17. E. O. Wilson and G. E. Hutchinson, "Robert Helmer MacArthur 1930–1972: A Biographical Memoir," *National Academy of the Sciences Biographical Memoirs* 58 (1982): 319–327.
18. G. H. Hardy, *A Mathematician's Apology* (Cambridge: Cambridge University Press, 1992), 13.
19. Hardy, *A Mathematician's Apology*, 35.
20. Hardy, *A Mathematician's Apology*, 36–37.
21. G. E. Hutchinson, "The Concept of Pattern in Ecology," *Proceedings of the Academy of Natural Sciences of Philadelphia* 105 (1953): 1–12.
22. Hutchinson, "The Concept of Pattern in Ecology," 2.
23. Hutchinson, "The Concept of Pattern in Ecology," 3.
24. Kingsland, *Modeling Nature*, ch. 8.
25. Robert H. MacArthur, "Population Ecology of Some Warblers of Northeastern Coniferous Forests," *Ecology* 39 (1958): 599–619.
26. Slack, *G. Evelyn Hutchinson and the Invention of Modern Ecology*, 290.
27. Anne Chishom, *Philosophers of the Earth: Conversations with Ecologists* (New York: Dutton, 1972); R. C. Singh et al., eds., *Thinking About Evolution* (Cambridge: Cambridge University Press, 2001); E. O. Wilson, *Naturalist* (New York: Harper Collins, 1994).
28. Wilson, *Naturalist*, 253.
29. Wilson, *Naturalist*, 253.
30. Richard Levins and Richard Lewontin, *The Dialectical Biologist* (Cambridge: Harvard University Press, 1987).
31. The reasons the group did not meet again are complicated. At the time, Wilson was beginning his work on sociobiology and Levins and Lewontin would later oppose it. Levins writes, "Robert MacArthur, E.O. Wilson and I had planned a division of labor in which they would ask 'How many species are there on islands?' while I would ask, 'How many islands does a species occupy?' It was intended that both

approaches would converge in a continental biogeography. Although this program was thwarted by Robert's early death and disagreements with Ed over socio-biology, it remains a valid strategy" (Gry Oftedal, Jan Kyrre Berg O. Frillis, Peter Rossel, eds., *Evolutionary Theory: 5 Questions* [New York: Automatic Press, 2009], 120).

32. Chisholm, *Philosophers of the Earth*, 177.
33. Chisholm, *Philosophers of the Earth*, 181–182.
34. Singh et al., *Thinking About Evolution*, 37.
35. MacArthur, *Geographical Ecology*, vii.
36. Richard Levins, *Evolution in Changing Environments* (Princeton: Princeton University Press, 1968), 304.
37. Levins, *Evolution in Changing Environments*, 504.
38. Model properties generality, realism, and precision are controversial and complicated. Put simply, a model is general if widely applicable, is realistic to the extent that it represents causal information, and is more precise than another model if the set of predicted values of the former is smaller than that of the latter.
39. Richard Levins, "The Strategy of Model Building in Population Biology," *American Scientist* 54 (1966): 421–431, 423.
40. Wilson and Hutchinson, "Robert Helmer MacArthur 1930–1972," 321.
41. P. Selz, and H. Chipp, *Theories of Modern Art* (Berkeley: University of California Press, 1982), 264.
42. MacArthur had a great respect for Lewontin. E. O. Wilson writes, "Robert MacArthur told me, when we three were young men, that Lewontin was the only person who could make him sweat" (Wilson, *Naturalist*, 342).
43. Richard Lewontin, *The Genetic Basis of Evolutionary Change* (New York: Columbia University Press, 1974), 7.
44. Lewontin, *The Genetic Basis of Evolutionary Change*, 9.
45. Lewontin, *The Genetic Basis of Evolutionary Change*, 9.
46. Lewontin's and Levins's views are similar though importantly different given that Lewontin compresses generality and realism into the dimensionality of models. Lewontin merely commits himself to the claim that given different tolerance limits, models with different dimensionalities will be needed, and this is distinct from Levin's claim about tradeoffs.
47. Lewontin, *The Genetic Basis of Evolutionary Change*, 12.
48. Lewontin, *The Genetic Basis of Evolutionary Change*, 12.
49. Lewontin, *The Genetic Basis of Evolutionary Change*, 8.
50. MacArthur, *Geographical Ecology*, 1. Strangely, MacArthur writes, "It is a pity that several promising young ecologists have been wasting their lives in philosophical nonsense about there being only one way—their own way, of course—to do science. Anyone familiar with the history of science knows that it is done in the most astonishing ways by the most improbable people and that its only real rules are honesty and validity of logic, and that even these are open to public scrutiny and correction" (Robert H. MacArthur, "Coexistence of Species," in *Challenging Biological Problems*, ed. J. Benke [New York: Oxford University Press, 1972], 259).

51. Robert H. MacArthur, "The Theory of the Niche," in *Population Biology and Evolution*, ed., R. C. Lewontin (Syracuse: Syracuse University Press, 1968), 159–176, 159.
52. MacArthur, *Geographical Ecology*, 1.
53. MacArthur, *Geographical Ecology*, 238.
54. Robert H. MacArthur, "Reviewed Work: *Growth and Regulation of Animal Populations*," *Ecology* 43 (1962): 579.
55. Schoener and Boorman, "Mathematical Ecology and Its Place Among the Sciences," 390.
56. MacArthur, *Geographical Ecology*, 77.
57. MacArthur, *Geographical Ecology*, 193.
58. James Brown, "The Legacy of Robert MacArthur: From Geographical Ecology to Macroecology," *Journal of Mammalogy* 80 (1999): 333–344, 335.
59. MacArthur, "Patterns of Terrestrial Bird Communities," 220.
60. Levins, *Evolution in Changing Environments*, 504.
61. MacArthur, "Patterns of Terrestrial Bird Communities," 190.
62. One might be perplexed, given MacArthur's skepticism regarding population-level "repetitive" patterns, by his pursuit of theoretical population biology and that he was in fact a founder of the journal *Theoretical Population Biology*. Probably, "population biology" included much more than merely population ecology and genetics but community ecology and biogeography as well.
63. Strong et al., *Ecological Communities*, 316–331.
64. Robert H. MacArthur and Richard Levins, "The Limiting Similarity, Convergence and Divergence of Coexisting Species," *American Naturalist* 101 (1967): 377–385; Robert H. MacArthur and Robert May, "Niche Overlap as a Function of Environmental Variability," *Proceedings of the National Academy of the Sciences* 69 (1972): 1109–1113.
65. Robert H. MacArthur, "On the Relative Abundance of Bird Species," *Proceedings of the National Academy of Sciences* 43 (1957): 293–295; Robert H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton: Princeton University Press, 1967).
66. Brown, "The Legacy of Robert MacArthur," 335.
67. Brown, "The Legacy of Robert MacArthur," 335.
68. Hutchinson, "Concluding Remarks," 1957.