



How the Modern Synthesis Came to Ecology

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Abstract

Ecology in principle is tied to evolution, since communities and ecosystems result from evolution and ecological conditions determine fitness values (and ultimately evolution by natural selection). Yet the two disciplines of evolution and ecology were not unified in the twentieth-century. The architects of the Modern Synthesis, and especially Julian Huxley, constantly pushed for such integration, but the major ideas of the Synthesis—namely, the privileged role of selection and the key role of gene frequencies in evolution—did not directly or immediately translate into ecological science. In this paper I consider five stages through which the Synthesis was integrated into ecology and distinguish between various ways in which a possible integration was gained. I start with Elton's animal ecology (1927), then consider successively Ford's ecological genetics in the 1940s, the major textbook *Principles of animal ecology* edited by Allee et al. (1949), and the debates over the role of competition in population regulation in the 1950s, ending with Hutchinson's niche concept (1959) and McArthur and Wilson's *Principles of Island Biogeography* (1967) viewed as a formal transposition of Modern Synthesis explanatory schemes. I will emphasize the key role of founders of the Synthesis at each stage of this very nonlinear history.

Keywords Modern Synthesis · Ecology · Coexistence question · Population regulation · Elton · Hutchinson · Lack · Competition · Ecological community · Population biology

Introduction

Strikingly, in the section on different disciplines and the Modern Synthesis in the landmark volume on the *Evolutionary Synthesis* edited by Mayr and Provine (1980), there is no chapter devoted to ecology. Granted, one reason could be the that, at the conference on which the volume was based, the paper on ecological genetics

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was unable to be recorded. Still, the fact that no other aspect of ecology other than E. B. Ford's brief and largely autobiographical comments (1980) was considered in this volume is significant. Even though Julian Huxley listed ecology as a discipline whose fate was to be influenced by the Modern Synthesis, by the late 1980s the nature of such an impact was not obvious for people in the field.

Ecology is a set of disciplines whose unity is hard to grasp: objects, timescales, methodologies, and intellectual traditions are very diverse within ecology. This lack of unity is to some extent a central issue of the history I will tell here. No overarching theory exists that would unify all these fields without controversy. By contrast, on the side of evolutionary biology (which includes a set of disciplines ranging from population genetics to paleontology and systematics), the Modern Synthesis has been precisely constituted into such an overarching framework. As Smocovitis (1992) argued, unifying biology has been both a central concern and a major result of the Modern Synthesis, best understood as a process.

Yet an important contrast can be noted: at the time the Modern Synthesis emerged in the late 1930s, ecology was already well institutionalized, with journals, chairs, institutes, and societies (including the Ecological Society of America and the British Ecological Society). Evolutionary biology, by contrast, for many years had no chairs, no specialized curriculum, no journal (*Evolution* only launched in 1946), and no society.¹ Thus, while today ecology often seems to be much less unified than evolutionary biology—precisely because of the overwhelming presence of the Modern Synthesis as a theoretical framework—for most of the period examined here, ecology was much more unified institutionally than was evolutionary biology, even if theoretically divided. In comparison, evolutionary biology was only a “theory”—a set of studies rather than a discipline. Most evolutionary biologists worked in zoology and botany departments, natural history museums, or genetics labs. Huxley was indeed one of the first to use the phrase Modern Synthesis (1942), and this was undoubtedly instrumental in creating the discipline of evolutionary biology, as Smocovitis shows, by unifying other disciplines—genetics, systematics, paleontology, and botany, but not exactly ecology (1992). As Futuyama noted in his contribution to a special issue on ecology and evolution: “Foremost among [the roots of what will be called evolutionary ecology] is the legacy of the evolutionary synthesis: natural selection is not only real, it is powerful.” Yet, he added, this “ecology” only emerged in the 1960s. He then asked, “why was there a delay among ecologists in understanding and using the message of the new synthesis? It may be even more difficult to trace the historical causes of a nonevent than of an event, but this is certainly a critical episode in history that calls for explanation” (Futuyama 1986, p. 310).²

This paper analyzes this state of affairs by examining how and to what extent the Modern Synthesis came to ecology, presenting a different interpretation than that found in Mayr and Provine (1980). It examines the changing relationships between

¹ See, for example, Cain (1993, 2002) and Smocovitis (1994) for the societies that promoted evolutionary biology.

² In the introduction to a special issue on ecology and evolutionary biology, James Collins, John Beatty, and Jane Maienschein consider “the changing role of evolutionary theory in the solution of ecological problems” (Collins et al. 1986, p. 169). The present paper attempts to provide a more systematic account of the acclimatizing of the Modern Synthesis, in particular within ecology, over the course of five decades.

ecology and evolutionary biology from the late 1920s—with the rise of population genetics—up to the late 1960s, a period that defines the Modern Synthesis in the narrow sense. I argue that an incomplete acclimation occurred as follows: while the Modern Synthesis (hereafter, simply the Synthesis) unfolded, it progressively engaged with the concerns and problems of ecologists and contributed to shaping the way some addressed their research problems. On various topics and questions, some elements of the Synthesis informed ecological thinking, while at other points the Synthesis was removed from ecological theorizing. Thus, I speak of *acclimation* (of the Synthesis within ecology) rather than of unification (of ecology and evolution), integration (of ecology within the Synthesis), or synthesis (between ecology and the Synthesis), terms that I hope will become clearer within the scope of this paper. The disciplines labeled “behavioral ecology” (see Grodwohl, this issue) and “evolutionary ecology” are the most visible effects of such acclimation, but I will argue that the effects of the Synthesis within ecology have been more pervasive and followed an articulated sequence that I intend to unravel here.

To sketch such a story, however, it is first necessary to specify what is meant by the Synthesis. Clearly, one difficulty is the fact that, as Burian described it, the Synthesis is a “moving target”: what it is depends upon the time-slice one considers, the set of documents supposed to represent this Synthesis, and, finally, whether one sees it as mostly a theoretical or an institutional process or event (1988). Those difficulties are considered by all the essays in this issue, as well as addressed in the introduction. In this paper, I offer a statement and then consider in each section what exactly the Synthesis may have meant for the ecologists I discuss—given that the Synthesis was itself evolving while the story I am telling unfolded.

One way to begin is to examine the definition given by Julian Huxley, writing to Ernst Mayr in 1951 to present his plans for a volume on evolution. Huxley described how he viewed the core commitment of the Synthesis: “Natural selection, acting on the heritable variation provided by the mutations and recombination of a Mendelian genetic constitution, is the main agency of biological evolution.”³ Although expressed during the later period of the Synthesis, Huxley’s statement perfectly captures his long-standing views. The Mendelian basis was presented as the major recent advance of evolutionary theory. A short review of “Genetics and ecology in relation to selection” in *Nature*, which summarized the session Huxley organized for the 1936 meeting of the zoological section of the British Association for the Advancement of Science, noted: “One of the most striking features of post-War biology has been the reanimation of Darwinism on a genotypic, instead of a phenotypic, basis. That such an attitude to evolutionary theory derives strong support from modern genetic and ecological work is undoubtedly the chief fact which emerged from the discussion on selection” (Anonymous 1936, p. 748). Regarding natural selection, Huxley used the term “agency” in the paper he read in this session published in the same issue (Huxley 1936, p. 548), even if others preferred to speak of “factors” (Sewall Wright) or “causes” (J. B. S. Haldane) to avoid any intentionalist

³ Julian Huxley to Ernst Mayr, 3 September 1951. Papers of Ernst Mayr. HUGFP 14.15 Box 1. Harvard University Archives, Cambridge, MA.

connotations. By the late 1950s, the Synthesis itself included not only those core claims, but also the commitment to their foundational roles for other theoretical claims and modeling strategies regarding speciation, macroevolution, systematics, and paleontology (Smocovitis 1992).⁴

To present my argument, I divide the paper into six sections. In “[The Rise of the Modern Synthesis and the Issue of Ecology: Charles Elton and Julian Huxley](#)” section, I focus on the work of the prominent animal ecologist Charles Elton in 1927, even though his understanding of evolution contrasts with that entailed in the Synthesis. Next, I consider Ford’s ecological genetics, but show that this did not capture what ecologists do in practice (“[Fisher and Ford’s ‘Ecological Genetics’](#)” section). In the 1940s, the Synthesis started to solidify with the formation of the Society for the Study of Evolution and the founding of its journal. “[Making the Modern Synthesis Relevant to Ecology: Institutional Processes and the Animal Ecology Treatise by Allee, Emerson, and Colleagues \(the 1940s\)](#)” section thus examines Allee et al.’s *Principles of animal ecology* (1949), regarded as the landmark publication in ecology and the first attempt to introduce ways of thinking resulting from the Synthesis into ecology in the form of an alliance between Wrightian and Clementsian inspirations. This pathway, however, as shown in “[Another Avenue to Acclimatize the Modern Synthesis into Ecology: From ‘Natural Control’ to the Notion of ‘Evolutionary Ecology’](#)” section, was not pursued as such, and the debates on population regulation culminating in the 1950s introduced an evolutionary viewpoint in several respects. I argue in “[The Regulation Question Meets the Coexistence Question: Hutchinsonian Niches, Genetic Feedbacks \(1959–1968\)](#)” section that Evelyn Hutchinson’s “concluding remarks” at the 1959 *Cold Spring Harbor Symposium* on population biology (the collective apogee of those debates) introduced a new way of conceiving of the species co-existence question through Hutchinson’s concept of “niche” and its explanatory appeal to natural selection. The last stage (described in “[Theoretical Ecology and Biogeography as Last Result of the Acclimation](#)” section) was a result of the *acclimation* of some formal tools of the Synthesis to address the coexistence question at higher levels, namely the theory of “island biogeography” initiated by MacArthur and Wilson (1967). I will emphasize the extent and limits of those acclimations of the Synthesis into ecology.

Overall, I argue that different efforts to introduce the Synthesis in ecology failed until the debates on competition in population regulation led to theoretical tools likely to frame the ecological question of coexistence in ways involving modeling styles from the Synthesis. This occurred even though ecology was ultimately not unified as a science and integrated within evolutionary studies. Throughout this historical account, I refer to the constant presence of Synthesis biologists within (or behind) the efforts to bring evolutionary thought into ecology.

⁴ This dual core of the Modern Synthesis is also how Smocovitis characterizes Dobzhansky’s network activity, which fostered the Synthesis at Columbia in the late 1930s and early 1940s: “in so doing they began to bind the heterogeneous practices of evolution into an evolutionary network grounded in genetics and selection theory”(Smocovitis 1992, p. 29).

The Rise of the Modern Synthesis and the Issue of Ecology: Charles Elton and Julian Huxley

The Landscape of Ecology at the Time of the Ongoing Modern Synthesis

As Kimler noted, “There have been earlier evolutionary perspectives, implicit and explicit, in the works of major twentieth-century ecologists; but... a surprising lack of interest within the growing professional ecology, between 1930 and 1960, in studying adaptation and natural selection” (1986, p. 215). This was mostly due to what Peter Bowler termed the “eclipse of Darwinism”⁵ and the suspicion cast over natural selection.⁶ Even if I nuance this account, the contrast between Ernst Haeckel or Eugen Warming’s notions of the importance of evolution within ecology, and its status in major works by Frederic Clements or Victor Shelford, is striking.⁷ Cain (2002, 2009) insisted on the fact that a thread in what is (according to him) exaggeratedly lumped together under the label “Modern Synthesis” is the push towards a science of processes instead of a science of objects: turning away from natural history and going towards experimental and quantitative methods to unravel processes. Cain analyzed Huxley’s activity as a scientific entrepreneur in those terms, and the previous establishment of population genetics can be seen as the first step towards this “process orientation,” since R. A. Fisher, Sewell Wright, and J. B. S. Haldane provided template models for mathematically addressing evolutionary processes (Cain 2010).

While Smocovitis (1992) considers the methodological aspect of this trend (natural history versus quantitative/experimental biology), Cain (2009, 2002) insists on the domain of study (object versus processes), but these distinctions are clearly correlated. What is striking here is that ecology had already started to move towards experimental methods and away from natural history—Clements’s reference to physiology was decisively instrumental in this move. On the other hand, in the 1920s and the 1930s, evolutionary theory was rather mostly tied to natural history and what Cain calls “object orientation” (2010).

But in the 1920s ecology was not of one piece. Hagen (1989) identified two still competing trends in postwar ecology, namely, a mereological one and a more

⁵ Both Smocovitis (1992) and Cain (1993, 2009) concur in arguing that this eclipse relies mostly on the fact that, until the achievements of population genetics in the 1930s, evolution was addressed mostly in a natural history style and not through quantitative and experimental methods—which, in turn, were the hallmarks of genuine science. The rise of the Modern Synthesis should therefore be understood as a reaction against this eclipse, which set evolution among the scientific objects approachable through experiments and measures, especially because of its genetic material basis, as begun by Dobzhansky (1937).

⁶ Evolution was at the same time crucial and controversial for ecologists in the early twentieth century. As Ilerbaig indicates, this provided room for an emphasis on experimental physiology or natural history (2013) descriptions rather than evolutionary reasoning. “One common concern seemed destined to keep together this increasingly heterogeneous biological community: the centrality of the problem of evolution. However, the alignment of particular theoretical, methodological, and institutional positions fed the existing dismembering tendencies, making the study of evolution more a ground for dispute than an occasion for unification” (Ilerbaig 1999, p. 456).

⁷ On Warming’s Darwinism, see Coleman (1986, p. 192).

holistic one—the “hological,” using terminology proposed by G. E. Hutchison. He sees them as two “perspectives” on ecology that divided the whole field. In the hological view, communities, populations, or ecosystems are mechanical or organismic entities in which parts are functionally related. Clements’s idea of communities as organism-like wholes, whose “succession” is analogous to organismic development, is the initial figure in this perspective. Development, metabolism, and homeostasis are key concepts here, and this perspective may encompass evolutionary views as soon as selection operates on the whole. An example of this is J. C. Wynne-Edwards’s influential later views on group selection. The mereological perspective inversely starts from the individuals and uses a demographic approach to address ecological phenomena as the result of individuals’ and species’ proper dynamics. Hagen (1989, p. 439) argues that this mereological perspective initially was systematically articulated by Gleason in the 1920s but rediscovered in the 1950s. It embraced both “Gleasonian” views, where “every species is a law into itself” and where the ecosystem’s features are the aggregate result of those laws, and the views that community equilibria, species distribution, and abundances result from interactions of species that obey general laws. Here, Alfred Lotka and Vito Volterra’s models on predation or Georgy Gause’s experiments and models on competition stand as mereological approaches in the 1920s and the 1930s (Gause 1934, 1935). The two perspectives, I will demonstrate, interact later on in the acclimation of the Synthesis into ecology.

Three additional divides—orthogonal to Hagen’s capital distinctions—are important in the present story. In the 1920s, a division existed between plant ecology and animal ecology. (This divide, to some extent, still exists, especially in the training of scientists, but it is not structuring the field as it formerly did.) Both could be addressed, either as the ecology of one species, by studying its habitat and environmental habits, or as the ecology of a set of species, that is, as “autecology” and “synecology,” to use terminology introduced by the German ecologists Schröter and Kirscher (1902) in their book on Lake Konstanz (*Bodensee*). Plant ecology considered issues like the assemblage of plant species in a forest and whether or not there are laws for the succession of species. Clements elaborated a general pattern for the development of a community, inventing terms to name moments of these development (the “sere,” the “climax” as the apogee, mostly determined in nature by climate).⁸ Patterns like the relations between species number and area, or the specific species patterns proper to some biogeographical environments (forest, tundra, etc.), were described and questioned.

On the other hand, animal ecology was much less developed, and the relations between prey and predators, with the Malthusian-inspired logistic curve, and then the formulation of the Lotka-Volterra equations in late 1920s (Volterra 1926; see also Kingsland 1995), constituting the more theoretical part of it. Yet evolutionary concerns were still largely absent,⁹ while experimental physiology in the field was a

⁸ See van der Valk (2014) on Clements’s climax and its reception.

⁹ “The equations that formed the theoretical core of population ecology—were hardly ‘evolutionary’ in any standard sense of that term” (Collins et al. 1986, p. 174).

way to address ecological relations of animals in a sort of natural history mode. As Futuyama noticed, “much of early ecology was in essence a physiological approach to adaptation, and if the physiological ecologists were vague about mechanisms or skeptical of natural selection, they were nonetheless concerned with a central concept in evolutionary biology” (Futuyama 1986, p. 304). Relying on physiology to capture the relations between organisms and environments and then analyzing their distributions was pervasive across ecology.¹⁰

This divide between animal and plant ecology has been viewed as an obstacle to theoretical ecology. For instance, in *Bioecology* (1939), in which Clements and Shelford attempted to provide a theoretical approach to key principles of ecology, the authors began by complaining about the divide between plant and animal ecology.¹¹ Shelford was an animal ecologist at the University of Illinois who had studied at Chicago and became interested in aquatic environments. He was also the first president of the Ecological Society of America.¹² Their joint work—a combination of the forces of some of the most influential ecologists on each side of the ocean—relied on the juncture of their competences in plant and animal ecology, and they applied Clements’s ideas of succession and climax to marine environments.¹³ Clements’s idea of development of communities provides the object of ecology.¹⁴ But the unity of plant and animal ecology is rather seen in terms of a “general physiology.”¹⁵ By contrast, the Synthesis in the late 1940s had integrated plants and animals and formulated theoretical principles that should hold for both. Ecology was in a different position.

A third divide existed between mathematical ecology, illustrated by the Lotka–Volterra equations of predation cycles, and more biologically-oriented ecology, which would focus on specifics of one or two species. Chicago ecologist Thomas Park’s work on animal ecology, especially on flour beetles begun in the 1940s, is paradigmatic here (1948, 1954).¹⁶ It has been argued that the rise of

¹⁰ “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” (Collins et al. 1986, p. 171).

¹¹ “In contrast, the development of the science of ecology has been hindered in its organization and distorted in its growth by the separate development of plant ecology on the one hand and animal ecology on the other” (Clements and Shelford 1939, p. v).

¹² On Shelford, see Benson (1992).

¹³ “A signal extension of ecological ideas is involved in the application of climax and succession, that is of development, to lake and ocean” (Clements and Shelford 1939, p. 4).

¹⁴ “Development is the basic process of ecology, as applicable to the habitat and community as to the individual and species (Clements 1904, 1905). It recognizes that life constitutes a dynamic system and that static studies are valuable only as they throw light on development or serve some practical purpose in this connection.” (Clements and Shelford 1939, p. 3).

¹⁵ “Plant ecology is physiology carried into the actual habitat, and in consequence its paramount theme is stimulus and response. It confines itself primarily and exhaustively with the cause-and-effect relation between the habitat on the one hand, and the organism and the community on the other. All further relations arise out of this, and all other approaches are incomplete unless they lead back to it. With the inclusion of animals in the biotic formation (biome), this relation naturally becomes more complex, but it is none the less valid” (Clements and Shelford 1939, p. 3).

¹⁶ See also Smith (1952).

experimental methods to explore ecological relations was part of a strategy to legitimize the new science of ecology.¹⁷ On the other hand, the Italian mathematician Vito Volterra inspired a mathematical trend in American ecology in the first decades of the century, which was another strategy to legitimize ecology as a science.¹⁸ But, as Kingsland noted, this mathematizing trend ran in parallel with the mathematization of population genetics by Fisher, Ford, and Haldane at the same time.¹⁹ It first seduced William Thompson, a Canadian entomologist at the US Bureau of Entomology, in the 1930s, although he later became a critic, illustrated by his changing attitude toward the bipolarity of ecological science in the twentieth-century.²⁰ Yet such duality—mathematical versus empirical styles—has been crucial for the history that I am investigating here, because the question of reconciling mathematical and biological ecology was a longstanding concern for ecologists. The Synthesis, on the other hand, had already by the 1940s reached some unity between mathematical modeling and natural history, exemplified by the first major Synthesis book, Theodosius Dobzhansky's *Genetics and the Origins of Species* (1937).

The First Phase—Huxley and Elton

During the first stage of the Synthesis, namely, the elaboration of population genetics by Haldane, Fisher and Wright up to the publication of Dobzhansky's 1937 book, ecology witnessed several important realizations. These noticeably included Charles Elton's book *Animal Ecology* (1927), because of its actual ties with the institutional and personal elaboration of the Synthesis.

Elton was incontestably a major figure in ecology throughout the first half of the century. His ecology departed from the field with a way of considering the ecology of animals that did not consider populations of various species, but relied heavily on experiments on animals of one or two species (Cooper 2003). The animal ecology treatise indeed regarded Elton's book as the major achievement of the decade. This justifies my choice of focusing on this book as paradigmatic of ecology during the time of the first elaboration of the Synthesis.²¹

Elton's involvement in making animal ecology scientific by considering new issues, differing from ethology or experimental physiology, was consistent over the

¹⁷ On Shelford, see, for instance, Ilerbaig (1999, p. 457): "Physico-chemical reductionism and experimental manipulation, the hallmarks of physiology, were the bandwagon on which Shelford jumped in his attempt to make ecology more legitimate."

¹⁸ As Kingsland noted: "by providing ecology with a solid theoretical base, mathematics would raise the status of ecology to the level of the physical sciences" (Kingsland 1986, p. 243).

¹⁹ "In ecology the use of mathematics was parallel to, but mostly separate from, its use in population genetics" (Kingsland 1986, p. 237).

²⁰ Kingsland (1986) indicates that Thompson's skepticism was also caused by his defiance regarding the recently mathematized population genetics. "After 1930 Thompson feared that the mathematical arguments in population genetics put forth with such assurance by Fisher and Haldane were giving natural selection a new popularity, even though the lack of solid supporting evidence was almost as great as before" (p. 252).

²¹ "Since Elton's treatment of communities is without question the best of the decade, we can do no better than examine the state of this phase of ecology as seen through his eyes" (Allee et al. 1949, p. 58).

decades. Elton founded the *Journal of Animal Ecology* in 1931. As the director of the Bureau of Animal Populations from 1932 on, he launched the 20-year-long program of surveying the Wytham Hill estate that belonged to Oxford University. A crucial mission of the Bureau was to detect patterns of invasions of rodents like rats and to understand their acuity and their resistance. The results of this program led Elton to one of his major achievements, which became labelled “invasion ecology.” His landmark book, *Ecology of Invasions by Animal and Plants*, published in 1958, was based on his experience at the Bureau.²² 6 years later, Elton summarized his views on animal community ecology in *Patterns of Animal Communities* (1964).

Strikingly, the 1927 book included a foreword by Julian Huxley, one of the major architects of the first stage of the Synthesis. Elton had studied zoology with Huxley, and he accompanied Huxley on an expedition to Spitsbergen in 1923. This experience formed a key part of Elton’s elaboration in the book, and his views more generally. One of the main ideas defended by Elton was the concept of trophic chain (see Fig. 1); this was exemplified by his study of the relationships between predators and prey in the Spitsbergen ecosystem. The book went through seven reprints and made a major impression on many ecologists, including Hutchinson (see Hagen 1992).

Elton was commissioned to include *Animal Ecology* in the undergraduate book series Huxley edited on *Animal Biology*. Other books in the series were *Vertebrate Morphology* by Gavin de Beer, *Animal Morphology with Reference to Invertebrates* by Walter Garstang, *Comparative Physiology* by Lancelot Hogben, and *Experimental Zoology* by Huxley himself. The whole series was supposed to counter the belief, common at times, that comparative morphology was the backbone of biology. In Huxley’s introduction to Elton’s book, he challenged this idea—an endeavor representative of his longstanding commitment to separate biology from natural history by making it into a science of “processes” rather than “objects, thus including monographs on topics like comparative physiology or ecology in the series.”²³ He justified choosing Elton because of his knowledge of Arctic fauna, where “the web of life is reduced to its simplest and the complexities of the detail does not hide the broad outlines” (see Elton 1927, p. xiii). Ecology was also economically important, such as in improving crop yields. Knowledge of the natural cycles of predator/prey population sizes could, for example, lead to the avoidance of dangerous methods of pest control, e.g., overkilling predators, which leads to the prey population surpassing its carrying capacity.

In this book, Elton advanced the notion of a “pyramid of numbers,” which accompanied the notion of trophic levels built in the idea of trophic chains. Numbers at each level of the chain—primary producers, predators, superpredators, etc.—are, by definition, decreasing. The pyramid of numbers allowed one to address food cycle, and this became a central concern for what became functional ecology three decades later (see Hagen 1992).

²² This is sometimes considered as part of the foundation of the discipline, and volumes like Richardson (2011) are reflection upon its seminal impact and legacy.

²³ Cain (2010) developed this interpretation of Huxley’s trajectory by focusing on his career and activity as director of the London Zoo.

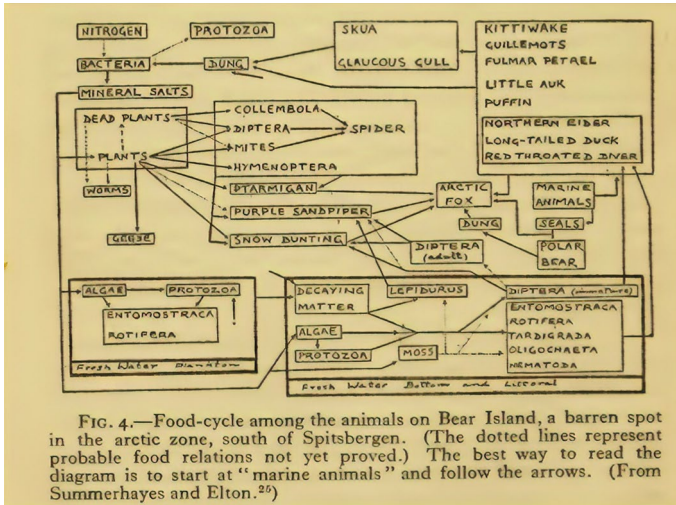


Fig. 1 Trophic Web on Bear Island, Spitsbergen (from Elton 1927, p. 58)

Elton also studied in detail variations in population sizes of animal species, both in the Arctic and in data about rodents and pests. Sizes were showing striking cyclical features, but the relations between species he described were not limited to models considering only two predator/prey species, as in Lotka–Volterra equations. Although he cited these equations, applying them was difficult because the chain had several components. That was why Elton supplied a general *qualitative* appreciation of the way the numbers varied, and why he concentrated on the periods where the dynamics pushed one species’ abundance far beyond its mean level.

More generally, Elton defined animal ecology as “the sociology and economics of animals, rather than the structural and other adaptations possessed by them” (1927, p. vii). Fisher soon compared the notion of fitness to a “loan” in *Genetical Theory of Natural Selection* (1930). In the preface of *Animal Ecology*, Elton noted that animal communities are “subject to definite economic laws” (1927, p. viii).²⁴ A main aspect of those laws is the regulation of animal numbers—namely, the fact that the variation of population sizes obeys some laws, even if only qualitatively captured. This issue came to lie at the center of animal ecology in the 1960s, as we will see (Fig. 2).

Animal Ecology ends with a chapter on “ecology and evolution.” Strikingly, Elton began by saying that the reader might be surprised to see a chapter on evolution in a book about ecology. However, he insisted, somewhat surprisingly, on the importance of ecology for *supplementing* Darwinian theory, especially concerning the existence of non-adaptive characters such as color dimorphism, pointing to the blue fox of the Arctic or the white eared cob of the Sudan. Because natural selection could not explain that particular character, Elton argues that ecology was able to account for this through the cycles of numbers.

²⁴ Another social metaphor through which he addressed animal communities was human industry (see Hagen 1992, p. 56).

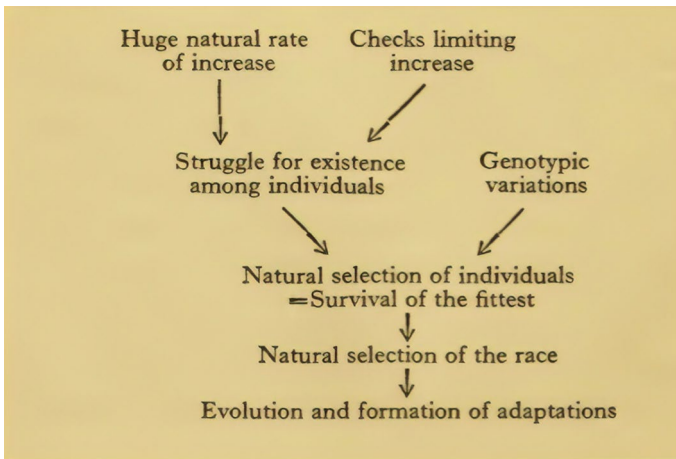


Fig. 2 Diagram of natural selection according to Elton (1927, p. 180)

Elton had an interesting view of evolution: he mainly argued that the “checks”—i.e., predation in general and limiting supply of resources that counter exponential population growth for a given species—were sometimes disappearing, so that “the struggle for existence tends to disappear almost completely” (1927, p. 186; see also Fig. 1). This is the case where a population of prey is somehow relieved, after it has been over-preyed by a predator, because as a result predators, having run out of resources, then tend to be very rare. Elton concluded that “the nature and severity of natural selection are periodic and constantly varying” (1927, p. 186). It is striking that, whereas ecology was supported by Huxley as an important field of biology to be developed, its relation with evolution was supplementary: ecology explains what natural selection could not explain, namely, cases of mismatch between organisms and environments.²⁵ However, unlike his interpretation of the Arctic fox cases, the explanation of the lack of adaptation would soon be integrated within population genetics, and the formalization of random genetic drift by Sewall Wright would

²⁵ For instance, in a book Elton published 3 years later that was wholly devoted to evolution and animal ecology, he noted that “in most cases of irregular migration on a large scale the migrants perish, [thus] the instinct to migrate cannot therefore have been produced by natural selection, since it is the butterflies which do not migrate that survive, and those that migrate that perish. If migration is a biological advantage to the lemmings, how is the instinct to migrate perpetuated in the species, since all the animals that carry and exhibit this impulse march downhill into the lowlands, to be eaten by dogs?” (1930, p. 36). From cases like these, he infers that migration is an irreducible animal impulse driving evolution in addition to selection. Given that migration can lead to habitat selection, he concludes that there are two processes at play in evolution, so that we see “a process which may be called the SELECTION OF THE ENVIRONMENT BY THE ANIMAL AS OPPOSED TO THE NATURAL SELECTION OF THE ANIMAL BY THE ENVIRONMENT. In evolution there are two variables—variations of the outer environment in place and time, and variations of the characters of species in place and time. From the interaction of these two variables, adaptation has been produced” (1930, p. 51). Notice how close this formulation is to the dual-process view of adaptive evolution vindicated today by niche construction theorists, even though, of course, Elton did not consider the same evidence and rather considered what we call habitat selection.

especially incorporate those cases where ecology could provide an evolutionary explanation.

Fisher and Ford's "Ecological Genetics"

The elaboration of "ecological genetics" by E. B. Ford, the only kind of ecology the Mayr and Provine volume acknowledged, was included in the section devoted to the Synthesis in various countries and traditions (in this case, the UK). If extant narratives of the Synthesis are taken seriously, one should see Ford's ecological genetics as the first locus of ecology in a Synthesis mode. Cain (2009), however, criticizes those narratives; below, I will address the exact challenge this criticism raises to my own account.

Ford was a student and collaborator of Fisher after completing his studies with Huxley in the early 1920s. He undertook the project of an ecological genetics—that is, a study of species and their interactions from a genetic perspective—by especially considering the way actual interactions were reflected in the change of gene frequencies. (Ford was also the supervisor of Bernard Kettlewell's major work on industrial melanism [1955], which is often considered one of the first rigorous empirical corroborations of the Synthesis.) To some extent, one may see the project of an "ecological genetics" as a direct translation of the Synthesis into ecology. However, it was a much more limited project, and may perhaps better be regarded as an extension of population genetics in the field than as a new framework to deal with issues raised by population ecology (and Lotka-Volterra modeling of abundance variations in preying contexts), Clementsian issues proper to plant ecology and successions, or Eltonian concerns related to the understanding of trophic chains emerging in animal ecology.

What "ecological genetics" intended was a set of investigations about the driving forces of trait change in the wild and, especially, the intensity of natural selection. It should be remembered that Fisher's take on the Synthesis was focused on natural selection and its role in forging the design of organisms; this distinguished him from the approaches of Wright (who emphasized the role of drift) or of those of Dobzhansky and others, influenced by Wright.

Together with another Fisher student, William Dowdeswell, and Fisher himself, Ford worked on *Lepidoptera* from the early 1930s until the 1960s. In studies on the moth *Triphanena comes* in England and *Lepidoptera Polyommatus Icarus* and *Maniola jurtina* (with Fisher) in Sicily, he specifically addressed polymorphisms, mimicry, and the founder effect (Fisher and Ford 1947; Dowdeswell et al. 1949; Dowdeswell and Ford 1952). His book *Ecological Genetics* summarized a good part of this research (1964).

Ford recalls that at the times he saw no "naturalist" as a "geneticist" and "subconsciously, was aware of the importance of taking that step" (Mayr and Provine 1980, p. 340). Ford applied Fisher's statistical method, especially in his treatment of marking, recapturing, and releasing individuals in populations of moths and following their survival rates. "Ecological genetics," as understood by Ford, is about "taking genetics into the field" (Mayr and Provine 1980, p. 338), especially to scrutinize

natural selection in real ecological settings. Ford had been a friend of Fisher since 1923, a connection that was stronger than that between Huxley and Elton. It is fair to say that Ford was indeed developing a Fisherian program in natural history. Ford's research complemented Fisher's theoretical modeling in the same way as, and almost in the same period, Dobzhansky allied with Wright. By turning from genetics to evolution, he used and corroborated Wrightian population genetic models to pursue evolution in the field.

Two of the key issues Ford dealt with were colonization and the explanation of polymorphism. Both concerned estimating the strength of natural selection. A distinction between "balanced polymorphism" and "transient polymorphism" served to separate cases in which a balance of selective agencies is realized (as in the case of heterozygote superiority) and cases where a previously disadvantageous gene replaces its allomorph (Ford 1964). In his view, polymorphism needed in principle a "selectionist" explanation. With regard to colonization, this is viewed from a mostly genetic point of view, which contrasts with the invasion ecology as developed by Elton, in which the units of invasion are species and not genes.

A major claim made by ecological genetics was that the intensity of natural selection in the wild was far higher—possibly twenty times higher—than what was theoretically estimated. This supported a generally adaptationist view of evolution and of phenotypes. A major conclusion of Ford's was that variation and differences in selection's direction are enough to account for major features of diversity of populations, which therefore significantly reduces the role of drift, as noted in the papers with Fisher and Dowdeswell on *Maniola lurtina* in Sicily (Dowdeswell et al. 1949; Dowdeswell and Ford 1952) and later ones summarizing the general consequences of these studies on drift. Chromosome inversions, for example, were rather subject to a "delicate balance of selective intensity" (Fisher and Ford 1947, p. 119).

Chance plays no role in the field, and appearance of chance patterns are due to variation of deterministic selection. More generally, and in a direct attack on Dobzhansky and Wright's views of evolution in the field, Ford noted that,

the conclusion that natural populations in general ... are affected by selective action varying from time to time in direction and intensity, and of sufficient magnitude to cause variation in all gene-ratios, is in good accordance with other studies of observable frequencies in wild populations. We do not think that it has been sufficiently emphasized that this fact is fatal to the theory which ascribes particular evolutionary importance to such fluctuations in generatio as may occur by chance in very isolated populations." (Fisher and Ford 1947, p. 171)

While Elton was opposing selection with what ecology can explain (the nonadaptive characters), here, on the contrary, ecological studies were confirming the paramount power of selection predicted by Fisher's theory, which showed how Ford's path contrasts with former ecological theorizing. In the same way, neither of the problems addressed by ecologists at the time—namely, the regulation of population numbers, the rules of plant succession or distribution of species generally, the food cycle, or the stability and instability of communities (e.g., Clements's climax)—were considered by Ford's ecological genetics.

With regard to Dobzhansky's contribution to the Synthesis, Beatty argued that while the core theoretical claim of the Synthesis is constituted by population genetics, "there is more to the synthesis than theory" and that Dobzhansky's use of Wrightian concepts in field observations and lab experiments was a contribution of another nature. It was not evidence for claims, but rather making explicit the fact that models and theories could indeed be used to handle real data.²⁶ By including the relative importance of various modes of evolution, based on such particular field or lab cases, biologists acknowledge such "additional contributions of experiments and field" (Beatty 1986, p. 130). To this extent, one can take Ford's contribution to the Synthesis as of the same nature—even though he relied on Fisher rather than on Wright and his contribution was less foundational than Dobzhansky's *Genetics and the Origins of Species*. This latter difference of importance is arguably mostly due to Dobzhansky's further involvement in making evolutionary biology into a unified science, as documented by Smocovitis (1992) and Cain (1993), an involvement that extends through his position at Columbia, his relations with Mayr, his patronage for the Columbia Classics Series that published key books by Mayr, Simpson, Stebbins, and himself—all things that were not part of Ford's career. The difference between Ford and Dobzhansky here may also be related to the cleavage between what Depew (2011) sees as a UK and a US version of the Synthesis, Ford being much more part of the former (with Fisher), while the post-1940 stage of the Synthesis mostly occurred in the US.²⁷

Thus, even though ecological genetics was a clear development of the Synthesis (in a Fisherian approach) within ecology, it was addressing its own agenda, mostly derived from Fisher's view, and therefore was not really impacting ecology itself as a set of various subdisciplines. Citations of Ford in the ecological literature are indeed much less numerous than in evolutionary literature. For instance, in Allee et al. (1949), he is much less cited than evolutionary biologists such as Dobzhansky, Wright, or Mayr. As McIntosh (1980, p. 261) notes, most of the references in Ford's landmark 1964 book come from evolution rather than ecology journals. However, the insistence on the genetic tracking of ecological changes in populations was influential two decades later, when some ecologists designed a project of "evolutionary ecology," of which a genetic-centered approach became one aspect, as emphasized by Collins (1986). But the emergence of such evolutionary ecology is due mostly to conceptual shifts that will be described below.

²⁶ "The core of the synthetic theory is pretty much just the theory of population genetics" (Beatty 1986, p. 125).

²⁷ A geographical comment: the fact that the Synthesis, at least in institutional terms, has been mostly elaborated in the UK and US explains why my story focuses on those two countries. Granted, there was development of the Synthesis in Russia, Germany, and many other countries (as Mayr and Provine acknowledged (1980) and many subsequent scholars confirmed), and major ecological work has been done in Russia, Denmark, and Germany, but asking about the Synthesis in ecology implies focusing on the US and UK.

Making the Modern Synthesis Relevant to Ecology: Institutional Processes and the Animal Ecology Treatise by Allee, Emerson, and Colleagues (the 1940s)

The Solidification of the Synthesis and Its Contacts with Ecology during this Period

Kingsland noted that with the coming of the Synthesis in the late 1930s through the mid-1940s, although “ecology’s main purpose was still to understand organism-environment relations and the principles of community structure and development,” these aims were joined by a “more explicit interest in evolution” (1995, p. 174). However, what the Synthesis means at this time, both institutionally and conceptually, was not exactly what Elton or Ford dealt with while working with Huxley or Fisher in the early 1930s. By the mid-1940s there had been a shift in the institutional and theoretical meaning of the Synthesis. The Columbia Classics in Evolution after Dobzhansky (1937)—namely Mayr (1942) and Simpson (1944)—progressively solidified the Synthesis, annexing systematics and paleontology. The Committee on Common Problems of Genetics and Paleontology was launched in 1942, merging paleontology and genetics on common themes, mostly speciation, and initially run by Simpson and Dobzhansky (Cain 1993). Pushed by Dobzhansky, Mayr took the lead when the Second World War broke out, leading to the founding of the Society for the Study of Evolution and the launch of the journal *Evolution* (Cain 2002; Smocovitis 1994).

Of course, Huxley’s *Evolution: The Modern Synthesis* had also appeared and received a favorable reception among biologists (see Smocovitis 1992, p. 29). Referring to the Evolution symposium in the Zoological Section of the British Association for the Advancement of Science that Huxley presided over, Cain (2010) describes Huxley as somewhat of a scientific entrepreneur. But while this session was a step towards institutionalizing the Synthesis, it did not yet include ecologists and ecology. At this time, Huxley was more attached to conciliating systematics, genetics, and evolution, which gave rise to the project of the new systematics and the book with this title (Huxley 1940).

In his symposium address, Huxley distinguished several “distinct heads” under which evolution should be thought of: “origin of adaptation,” “origin of species,” “long-term evolutionary trends,” and “extinction.” The distinction between adaptation and speciation indicates two things: first, that the study of selection by population geneticists did not exhaust the set of evolutionary problems; second, it sketches the issue of the relation between the timescales of those problems, an issue reinforced by the mention of the last heading, evolutionary trends. This question was directly tackled in Simpson’s 1944 book and, more generally, the three problems besides adaptation gesture towards the provinces of systematics and paleontology.

In the US another society involving evolutionists in the study of a topic much closer to the interests of ecologists, namely speciation (the “Origin of Species” sensu Huxley) emerged in 1939. After a session on speciation organized by

Dobzhansky at the 1939 meeting of the American Association for the Advancement of Science, and following Huxley's suggestion, the Society for the Study of Speciation was founded (Cain 2000; Smocovitis 1994, p. 245). This society thus predates the US National Research Council's Committee on Common Problems of Genetics and Paleontology (founded in 1943) and was one of the first institutional realizations of the Modern Synthesis. Created by Dobzhansky, Huxley, and ecologist Alfred E. Emerson, its aim was to facilitate information "between the fields of morphology, cytology, genetics, biogeography, ecology, paleontology, comparative psychology, comparative physiology, embryology, population biology, and taxonomy," as the notices announced (see Smocovitis 1994, p. 246). Speciation is a natural common object for a synthetic evolutionary theory, since it involves both systematics and population genetics and needs their collaboration to be tackled. The major books of the Synthesis explicitly addressed speciation, as their titles indicate ("X and the Origin of Species"). But the Society for the Study of Speciation had an ecologist as secretary—Emerson, who at the time was the editor of *Ecology*.²⁸ As Emerson wrote in his 1937 article on "Speciation," "The time seems ripe for the first comprehensive analysis of modern knowledge of evolutionary events which brings the recent discoveries of the taxonomists, animal geographers, *ecologists*, and geneticists into balanced relationship" (cited in Cain 1993, p. 6; my emphasis).

Cain (2009) argued that the Synthesis was not a single theoretical or institutional entity, but was rather a trend in science characterized for a while by a focus on speciation and an interest in moving science from a study of objects to a study of processes. This characterization of the Synthesis is critical and concurs with my analysis. Whatever the "Modern Synthesis" means, and even if this term connotes a moving target as is widely agreed, its promoters had been making connections with institutional ecology through the focus on speciation. Clearly speciation is a common object here.

In the decade of the 1930s, ecology was indeed not entirely removed from considerations of evolution. In his 1936 address, Huxley indicates that "an important difference will be found between abundant and scarce species. In the latter competition will be more with other species, while in the former it will be more between members of the species itself. In general this latter or intraspecific type of selection is more widespread than the interspecific" (Huxley 1936, p. 573). This is an early recognition of a major ecological theme, namely, the difference between intraspecific and interspecific competition, which resurfaced when ecologists came to consider the density-dependence theory of regulation. This point was emphasized by G. E. Hutchinson when he later ended these debates with his famous "concluding remarks" about the concept of niche (see "[Another Avenue to Acclimatize the Modern Synthesis into Ecology: From 'Natural Control' to the Notion of 'Evolutionary Ecology,'](#)" below). In 1946, the journal *Evolution*, launched by the new Society

²⁸ Smocovitis (1994, p. 277) suggests that the name of the journal *Evolution*—a single word—and its two column style was inspired by the journal *Ecology*; Mayr and Emerson were regularly corresponding during this period.

for the Study of Evolution, published in its first issue a paper by Dean Amadon that mentioned ecology in its title (“Ecology and the Evolution of Some Hawaiian Birds”). However, the important role that ecology had in the speciation society during the 1930s seems to have faded away in the 1940s in favor of the synthesis between systematics, botany, paleontology, and genetics, as pushed forward by the Committee on Common Problems of Genetics and Paleontology (in 1944 “Systematics” was added). Thus, from the viewpoint of the Synthesis in construction, the recognition of the relevance of ecology, as I mentioned, existed but was supplanted on the institutional level by the trajectory of the Committee on Common Problems, which left ecology on the margin.

However, Emerson, who was instrumental in the genesis of those Synthesis societies, worked in the 1940s together with Clyde Allee, Thomas Park, and Karl Schmidt on the monumental *Principles of Animal Ecology*, which constituted a substantial attempt to introduce the Synthesis of the time into ecology, as we will see. In the next section, I will trace the pathway which led ecology from this first attempt of acclimatizing the Synthesis into ecology to the formulation of the theory of the niche by Hutchinson through the recognition of the role of competition within ecology.

Much has been written on the scientists involved in the next stage of my story, although no systematic attempt has been made to place their work within the general history of the acclimation of the Modern Synthesis into evolution. Many of them were involved in distinct programs or were seminal for them: Hutchinson for ecosystem ecology (see Hagen 1992; Slack 2010), Calhoun for overpopulation issues (see Ramsden and Adams 2009), Emerson for speciation studies and the speciation society (Cain 1993; Smocovitis 1994), Lack for behavioral ecology (see Grodwohl, this issue; Anderson 2013; Borello 2003). They are considered here only to the extent that they played a role in this story, either by pushing novel concepts or models in a seminal way, or by developing in a representative way a theoretically novel attitude.

The Wright-Clements Connection: Clyde Allee, Orlando Park, Karl Schmidt, Thomas Park, Emerson, and the Principles of Animal Ecology

Clyde Allee and Thomas Park were animal ecologists, both at the University of Chicago (where Sewall Wright taught), whose work on the “Allee effect” (see below) and the experimental ecology of competition, respectively, obviously qualified them as authors of the major treatise synthesizing knowledge of the time in animal ecology. The other authors were also in Chicago, Orlando Park, a former student of Allee’s, at Northwestern and Karl Schmidt at the Field Museum. Indeed, they recognized that the time was ripe for formulating principles of ecology and started an ecology group that met weekly (Schmidt 1957). This echoed Clements and Shelford’s principles book *Bioecology* published 10 years earlier. The object itself was not dissimilar: Clements and Shelford defined ecology as “in large measure the science of community populations ... concerned with natural communities primarily, (including ...) a considerable fund of organized knowledge of plant communities and their dynamics, and a lesser body of similar knowledge on the animal side”

(Clements and Shelford 1939, p. 3). Allee et al. (1949) also devoted a long section to “community” following a section on “population.” Thomas Park, beside a focus on experimental ecology, had an interest in demography, justifying the tripartite division of ecology into individual ecology, population ecology, and community ecology (Park 1946). This structure shaped the 1949 treatise, which includes sections on “environment,” “population,” “community,” and, finally, “ecology and evolution.”

Clyde Allee himself was a student of Victor Shelford, whose work integrated Clements’s perspective on communities. Undoubtedly, the Clementsian approach was brought into the Chicago school via Shelford—who taught at the University of Illinois—and then Allee. Allee’s work in animal ecology devoted much attention to variations in population size; the “Allee effect” that he formulated specified a positive correlation between population density and individual fitness. For Allee, a Quaker concerned with issues of pacifism and social justice, this signified that the prosocial activities of animals were good for the group and larger groups thrived better than smaller ones (Schmidt 1957; Beatty 1988). The Allee effect has indeed been witnessed in many animal species and is still a topic of investigation (e.g., Courchamp et al. 2008).

The need for an *evolutionary* take on ecology was pervasive in *Principles of Animal Ecology*. “We stress ecological generalizations from two vantage points. First, there are those principles concerned with the functions or physiology of contemporary individuals and ecological assemblages of whatever rank. Second, there are those ecological principles concerned with organic evolution. We are not interested in helping to continue the separation between those two aspects of ecology. Rather, our aim is to point out their essential interrelation” (Allee et al. 1949, p. vii). This contrasted with Clements and Shelford’s earlier quest for principles of ecology; the kind of unity of ecology they strived for was not evolutionary but rather *physiological*.²⁹

Some of the founders of the Synthesis were closely involved in this highly influential book (later colloquially called “the great AEPPS”) at stages in its elaboration and diffusion. Closely associated with Wright, they reflected some of his ideas, and he commented on drafts of sections on evolution. Similarly, Mayr read and validated the chapter on “ecology and isolation” (i.e., on speciation). Reviewing the book in *Quarterly Review of Biology*, Dobzhansky praised it highly:

The inclusion in a treatise on ecology of a thorough account of modern theories of evolution connotes a most important development of ecological thought. ... Indeed it is the evolutionary idea that gives an internal unity to the field of ecology; and ecological investigations contribute basic data for an

²⁹ As for Shelford, Ilberaig shows how he decided for physiological viewpoints to animal-environment interactions against an evolutionary approach: “Shelford recognized two distinct points of view for biological investigation, namely evolution and physiology. In his opinion, the former had repeatedly failed to organize properly the facts of natural history. Thus, it was time to move along more physiological lines” (1999, p. 457). Regarding Clements, van der Valk notes: “Clements famously stated that ecology was ‘nothing but a rational field physiology.’ Even interactions among plants, like competition, could be explained by changes in the physical environment caused by the plants, like the reduction of available light or soil moisture” (2014, p. 3).

understanding of the mechanisms of evolution. If the book under review were to accomplish nothing more than the above propositions are true, its important role in the history of ecology would be assured. ... It is a most gratifying fact that in our day investigators who start from such diverse fields as ecology, genetics, paleontology, systematics or comparative and experimental morphology and embryology have arrived at concordant interpretations of the evolutionary process. (Dobzhansky 1950, p. 278)

Undoubtedly, for him this book realized the program of evolutionary biology in ecology.

Indeed, the involvement of Mayr, Dobzhansky, and mostly Wright guaranteed that such an ecological treatise would fit the views of the founders of the Synthesis. The authors claimed that evolution should provide a framework for ecology, and explicitly referred to the Synthesis. In a long and detailed historical review of the progress of ecology since the nineteenth century, the authors noted that until recently ecology and evolution had many commonalities: “(a) that the history of the rise of evolution in its modern biological connotation repeats much of the history of ecology in that many of the same men were involved, and (b) that the subject matter of each of these two aspects of biology strongly overlaps” (29). They also underscored that the shift that occurred in ecology since the 1920s was the emergence of populations as a problem per se—a shift that parallels the establishing of population thinking through the Modern Synthesis. As they noted, in the 1900s “the present discussion would have centered about the history of the ecology of species as distinct from that of individuals. Now, in the 1940s, it is concerned with populations.” That is, “For ecology, the supra-individualistic units are real entities. Aggregations, populations, societies, and various units at or near the community level present problems rarely recognized by physiologists working as physiologists” (11). However, as we shall see, this was not exactly an *integration* of evolution into ecology.

Alfred Emerson, who mainly wrote the chapter on evolution, was originally an entomologist and a world expert in termites, hired at Chicago in 1925 where he remained his whole career. Institutionally Emerson never distanced himself from evolutionary theory, and, even if he was outside the Committee on Common Problems, he quickly regained a major institutional role in evolutionary biology. He helped Mayr organize the Society for the Study of Evolution in 1946 (to which his coauthor Schmidt also belonged, serving as president for a while) and suggested that its nucleus should be officers of the Society for the Study of Speciation. He served as its president in the 1960s (Smocovitis 1994, pp. 255–257). Besides his institutional positions, Emerson supported the idea of superorganism in ecology generally, based on his knowledge of social insects, whose colonies are characterized by a “dynamic homeostasis” (1939). As Mitman (1988) established, like Allee Emerson was concerned by the analogy between ecological communities and human societies, justifying a positive use of ecological knowledge for improving the latter.³⁰

³⁰ In detail, however, their conceptions did not emphasize the same aspects: “Allee saw cooperation as a principle underlying the evolution of sociality and also embodying the tenets of his Quaker philosophy, while for Emerson, cooperation was important because it contributed to greater homeostatic control; it was homeostasis that was the phenomenon of interest” (Mitman 1988, p. 187).

If one glances at the last section of the *Principles*, “Ecology and Evolution,” many problems and theories belonging to the Synthesis are exposed, in a way quite faithful to the classical treatment. Mayr’s views on speciation are discussed as well as some of Dobzhansky’s experiments, and many pages include long quotations of Wright’s papers. Clearly, Emerson commits himself there to the major tenets of the Synthesis at the time. But in including the theory of speciation within this treatise on animal ecology, he also inversely affirms the relevance of ecology to the study of speciation, whereas ecology was not central within the earlier problem agenda of the Committee on Common Problems, crucially interested in speciation.

It was also claimed that adaptation should be seen in an evolutionary perspective. But this had more of the appearance of an insertion of classical evolutionary themes within an ecology book than an evolutionary framework to address ecological questions. Many of those pages addressed adaptation and argued that adaptation is in essence an evolutionary problem; then they cited the evolutionary treatment of the problem by Dobzhansky and Wright (rather than Ford and Fisher). The section’s scope ranges across wide ecological and evolutionary territory. In his review of the book, LaMont Cole (a former graduate student of Thomas Park’s who later became a prominent ecologist influential in developing life history theory and a pioneer in writing about the ecological crisis for a general audience) wrote: “The final section of the book is devoted to ‘ecology and evolution’ and is an extraordinarily effective amalgamation of genetic and ecological principles” (Cole 1950, p. 155).

Where evolution indeed appeared in the book, it is about *communities* and the pervasive attempt to establish a parallel between the organism, as a product of optimizing selection and the community. Both of these are shaped by natural selection and owe to selection their integration and fit with the environment. Emerson indeed subscribed to the idea that “selection could operate on various levels of organization, what appeared to be individual competition at one level might be group homeostasis on another” (Mitman 1988, p. 188). This explains the surprising view that communities are mostly integrated by “facilitation.” Indeed, even populations are viewed as analogous to organisms:

At least five general attributes are exhibited by population and organism alike. These are: 1. A definite structure and composition is constant for any moment of time, but fluctuates with age. 2. The population is ontogenetic. It exhibits (as does an organism) growth, differentiation and division of labor, maintenance, senescence, and death. 3. The population has a heredity. 4. The population is integrated by both genetic and ecologic factors that operate as interdependent mechanisms. 5. Like the organism, the population is a unit that meets the impact of its environment. This is a reciprocal phenomenon, since the population is altered as a consequence of this impact, and, in time, it alters its effective environment. (Allee et al. 1949, p. 264)

The concept of communities was described as “one of the most fruitful ideas contributed by biology to modern civilisation;” it was defined as “a natural assemblage of organisms which, together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self-sustaining” (p. 436). To this extent, a community—unlike

H. A. Gleason's critique of Clements in plant ecology—was for these authors an integrated and dynamic whole with a specific signature. “Since each kind of organism inherits a more or less specific arrangement of genes, the resulting protoplasmic demands are similarly more or less restrictive. It follows that communities are opposed, not of random assortment of species but of ecologically compatible species populations whose collective ecological requirements of food, shelter and reproduction are satisfied ... by a certain range of environment.... Upon this basis a community may be said to have a *characteristic anatomy, an equally characteristic physiology and a characteristic heredity.*”³¹ To this extent community is the “natural unit of organization in ecology” and the “smallest ... that can be ... self-sustained” (p. 437). The organization of the community is named a “Metabolism” (the object of chapter 27), which directly traces back to Clements's view of organisms.³² But the evolutionary reference here is necessary: the community is “*a resultant of ecological selection*” (my emphasis). In turn, this selection appeared as parallel to natural selection in evolution in that it supported this functional integrity and self-sustainability. The authors provided this parallelism in Table 30 (Fig. 3), in which they draw a parallelism between cell, multicellular organism, and community: at each level, concepts and processes are parallel. Hence, it is the selection of an entity of high-level (e.g., organism, community) that determines the low-level individuals (cells, species). In his review of the book, Cole recognized that this analogy was a major resource: “The emphasis of this section is on natural selection acting upon biological units which may commonly be more than individual organisms. The approach is convincing, even uncontested.... This postulate is supported by analogy solely, without discussion of possible selecting factors, relative rates of survival and fertility, or barriers to gene movement and with no attempt to define desirable objectives for ‘intelligent artificial selection of social units’” (Cole 1950, p. 155).

To sum up, in 10 years, between the publication of *Bioecology* and *Principles*, the concept of community as a superorganism shifted from a physiological to an evolutionary understanding of “organism.”³³ Even though Dobzhansky was not a

³¹ My emphasis. Granted, Elton (1930) had a similar systemic view, as when he says: “animal community forms a highly intricate system of interlocking parts, and the actions of any one species affect not only its next neighbor in the chain of food and other relationships, but through this neighbor, and its neighbors, all other species. Thus a wave of disturbance set up in one part of the system may produce unexpected reverberations in other parts of ramifying branches” (p. 16), but this is rather an insight than a developed theoretical articulation as presented in Allee et al (1949).

³² As Hagen (1992) established, this idea of the metabolism of a community—later, an ecosystem—has been foundational for “ecosystem ecology,” developed by Odum on the tracks of Lindemann and Hutchinson. However, this ecosystem ecology relaxed the ties to evolution, while here it is presented as a concept proper to an evolutionary framework.

³³ Elton already anticipated this view (even though he had a heterodox conception of the scope of selection) when he said that “the whole of an animal community can act as a biological unit, operated upon by natural selection so as to bring about the best compromise in the way of optimum population for all” (1930, p. 75). Also, that “adaptation is produced by the selection of whole populations rather than the selection of individuals, and whole it raises one huge difficulty by reopening the species problem, it does away with another huge difficulty, of seeing how in practice natural selection could ever be effective in picking out a single individual and succeed in leading it, as it were, through the perils of life in a fluctuating animal population” (p. 30). This “difficulty” shows once again that Elton was quite far removed from

vocal proponent of group selectionism (although neither a critic), he supported this view in his review: “No serious objection could be raised against this community as superorganism idea.” Actually, the authors were reflecting their colleague Sewall Wright’s views on interdemic selection, included in his shifting balance theory (even though Wright, strictly speaking, did not advocate “community selection”). This contrasts strongly with Ford’s ecological genetics, which initially was framed from a Fisherian standpoint and was intended to refute some of Wright’s views.

Allee and his colleagues held what we would now call a “group selectionist” view. Selection acting on communities is favoring cooperative interspecific and infraspecific behavior, a force they call *facilitation* (a word that has recently resurfaced in functional ecology; see Bruno et al. 2003). As a consequence, these forces are “in the long run somewhat stronger than those tending towards disoperation” (Allee et al. 1949, p. 11). Possibly alluding to this sentence, Dobzhansky’s review argues that the authors promote a more sophisticated understanding of Darwinian selection, which was often unduly restricted to the very idea of struggle.³⁴

The parallel between community and organism allowed the authors to conceive of the integration within a community in the same way as the physiological division of labor, and ecological succession as a kind of development (as Clements did in his physiological framework). The second chapter on “population” actually dealt with the question of why populations did not increase to too large a size before collapsing, often calling this “population integration.” This contested the idea that the sum of individual deaths and births was the ultimate explanation. “Population size is not explained when one merely discusses natality and mortality. These responses, as end products, are intimately under the control of the genetic and ecological factors that emerge from the reciprocal interaction between the population and its environment” (Allee et al., p. 390). Ultimately, selection acting on groups integrates the community; in so doing, it helps large populations of a given species to thrive, up to a point where they would stop expanding. *Hence the selection-based parallelism between community and organism allowed the authors to unify two major concerns for ecologists: namely, the community, with its the laws of succession, as investigated by Clements, and the question of the regulation of populations, which Elton deemed to be “really the chief scientific goal of pure ecology, since to do so is only possible after most of the other phases of ecological research have been covered in a fairly extensive way”* (1930, p. 51).

Such an evolutionary inspiration in ecology was not exactly an integration of the Synthesis: it is much more an injection of a “Wrightian touch” within ecology (since much about evolution in the book is Wrightian) that was compatible with a

Footnote 33 (continued)

the Synthesis understanding of natural selection, as the population geneticists initiated it. Unlike his 1927 treatise, this 1930 book was not influential.

³⁴ “The protooperation and cooperation of organisms of the same and of different species have great survival values. This is evidently an important corrective of the naive view that evolution is promoted exclusively by the struggle for existence. The ‘struggle’ involves cooperative as well as disoperative elements, and the former are adaptively more efficient” (Dobzhansky 1950, p. 279). “Disoperation” was coined by Clements and Shelford (1939) to “indicate organismic operations that have immediately harmful effects” (Mitman 1988, p. 181).

Cell	Multicellular Organism	Community
Composed of definitive protoplasm	Composed of definitive cells and tissues	Composed of definitive organisms and species
Has anatomy (cytological)	Has anatomy (tissues and organs)	Has anatomy (pyramid of numbers)
Has symmetry and gradients	Has symmetry and gradients	Has aspects of symmetry and gradients (stratification)
Has ontogeny (cell development)	Has ontogeny (embryology)	Has ontogeny (succession)
Has limitations of protoplasmic amounts (size, surface-volume ratio)	Has limitations of cell numbers (size, surface-volume ratio)	Has limitation of population numbers
Regeneration of parts	Regeneration of parts	Regeneration of parts
Division of labor between protoplasm	Division of labor between cells	Division of labor between organisms and species
Cycles of protoplasmic behavior	Cycles of cellular behavior	Cycles of organismic and species behavior
Self-sustaining organization (dynamic equilibrium)	Self-sustaining organization (dynamic equilibrium)	Self-sustaining organization (dynamic equilibrium)
Successful integration of whole determines survival of parts and repetition of parts	Successful integration of whole determines survival of parts and repetition of parts	Successful integration of whole determines survival of parts and repetition of parts
Homology of cytological parts	Homology of tissues and organs	Homology of phylogenetically related species in different communities
Senescence and rejuvenescence of cell	Senescence and rejuvenescence of organism	Senescence and rejuvenescence of community
Phylogeny of gene pattern	Phylogeny of cellular pattern	Phylogeny of species pattern
Selection of whole cell unit determines survival of gene pattern	Selection of whole organismic units determines survival of cell pattern	Selection of whole community determines species and organism pattern
Controls internal protoplasmic environment and establishes optima	Controls intercellular environment and establishes optima	Controls environment within community and establishes optima
Selects or rejects protoplasmic building materials	Selects or rejects tissue-building materials	Selects or rejects organisms (species) that harmonize or do not harmonize with community
Retgressive evolution of cytological structure (chloroplasts)	Retgressive evolution of tissue structure and of organs (eyes of cave fish)	Retgressive evolution through species elimination

Fig. 3 Table of parallels between organisms and communities (from Allee et al. 1949, p. 440)

Clementsian view of communities as superorganisms, presented through the Wrightian idea of an interdemic selection.³⁵

As previously mentioned, an important theme of *Principles of Animal Ecology* was the *regulation* of numbers in populations. This was already a concern for Elton, whose notion of “population cycles” reflected the practical interest of the Bureau of

³⁵ Such a Clementsian-Wrightian view of community ecology would be fatally affected by the demise of group selection in the 1960s, when Williams (1966) issued his devastating critique of Wynne-Edwards (1962), who in answer to Lack (1954) had made explicit the thesis of a selection on groups to explain the self-restricted consumption of organisms. On Lack and Wynne-Edwards, see the contrasting views of Kimler (1986) and Borello (2003). Interestingly, Borello traces Wynne-Edwards’s interest in population ecology to Elton’s influence, his mentor at Oxford (532). Kimler argues that Williams’s critique of group selectionism was a key advance in forming “evolutionary ecology,” though this is mostly valid for behavioral ecology; the integration of Synthesis views in ecology overall—addressed here—is a much more complicated story.

Animal Populations in controlling the causes of animal population growth. Shortly after the publication of the book, this area became the object of a controversy that facilitated the integration of some ideas of the Modern Synthesis into ecology. As we shall see, the founders of the Synthesis were not absent from these debates, even though they were less directly involved than they had been in the *Principles*.

Another Avenue to Acclimatize the Modern Synthesis into Ecology: From “Natural Control” to the Notion of “Evolutionary Ecology”

“Natural control,” Competition, and the Modern Synthesis

The debate about what process is the most important for controlling the abundance of populations spanned more than two decades. According to M. E. Solomon’s “Natural Control,” he intended to assess all the theories proposed and consistently used the label “control” to talk about the regulation problem: “Natural control will be taken to mean that regulation of the numbers of a natural population which keeps them within the limits of a more or less clearly definable though often very wide range of abundance” (1949, p. 2). Solomon was a researcher at the Pest Infestation Laboratory, Slough, Bucks (UK), thus the concern with regulating pests was still undergirding the theoretical interest in population regulation in the UK, as was the case with Elton in the US.

Allee et al. considered natural control in the “Population” section, mostly acknowledging the lack of data constrains towards a qualitative, hence less rigorous, approach (1949). In the 1950s such quantitative attempts flourished.

On one side of the debate on natural control, some argued that the major driver of population regulation were abiotic factors such as climate (directly and through availability of resources), whose regularity and fluctuations explain both the existence of population fluctuations and their limited range. These factors were density-independent, since direct and indirect effects of climate on death ratio will not be related to population size. Others, mostly in the wake of Nicholson (1933), claimed that those factors are on the average much less important than the effects of competition, which necessarily depend upon the size of the population. Two books instantiated this opposition: ornithologist David Lack’s *Regulation of Animal Numbers* (1954) and insect-oriented animal ecologists Andrewartha and Birch’s *Distribution and Abundance in Animals* (1954). Lack explicated the argument for density-dependence, summarizing his earlier work on clutch-size and population regulation among birds: “The comparative stability of natural populations is controlled dynamically, meaning that the farther that numbers rise or fall, the stronger is the tendency to return to previous levels. This can happen only through the operation of factors which vary with population density.... Such ‘density-dependent’ factors might influence either the reproductive rate or the mortality. Thus stability is favored if the reproductive rate is higher at low than high density, and if the death-rate is higher at high than at low densities” (Lack 1954, p. 19). This is why Nicholson’s statement on competition appears crucial: “Action of a controlling factor should be governed by the density of the population controlled, and competition seems to be the only factor that can be governed in this way” (1933, p. 176).

Indeed, Nicholson, a Birmingham-educated biologist who traveled to Sydney and pursued his career in Australia, was the first champion of competition theories of natural control.³⁶ As he said in a letter to Franck Egerton, the major intuition behind his view came from realizing that the number of insects on trees will be proportional to the available food—i.e., the available trees—but will remain inferior to that.³⁷

This controversy between density-dependence versus density-independence conceptions of regulation has often been viewed as a question of biotic versus abiotic regulation, though the former are not the only biotic processes and the latter not the only abiotic. Solomon wrote: “There has been (and still is) a general tendency to identify density-dependent action with biotic factors, and density-independent action with physical factors,” and this overlooks the fact that often abiotic factors operate through biotic factors (1949, p. 10). More generally, the notion that a population increase will be limited by its abiotic environment relies on a false dichotomy between environment and population, because, as he said, sometimes the population itself constitutes the environmental resistance: “Part of the restrictive processes (sometimes a major part) arises from activities of the population itself, such as cannibalism, intraspecific competition, spoiling of the environment.” Solomon intuited the insistence on biotic factors was more aligned with a Darwinian view of ecology (1949, p. 3).

Australian ecologist Herbert Andrewartha and his graduate student Charles Birch championed the density-independence thesis in their major 1954 book, *The Distribution and Abundance of Animals*. There, Andrewartha and Birch contested the importance of density-dependence for regulation: for them, “population phenomena are essentially responses to fluctuations in the conditions of life” (Cooper 2003, p. 54).³⁸ Though both men spent their careers in Australia, Birch during the 1950s came to have closer links with biologists in the US, especially with Ernst Mayr.

After the 1950s, interest in the natural control issue was always connected to practical issues, but less in the domain of pest prevention than connected to worry following Second World War about the future of humanity threatened by overpopulation.³⁹ Thus, understanding how animal populations regulated their numbers would help to identify what seems to go wrong in our own species: reaching the carrying capacity of our environment—and possibly to fix it. Many papers considered

³⁶ On Nicholson’s mathematical model, see Kingsland (1986) and Kimler (1986), who writes, “Nicholson, however, was typical of ecology in his focus on population-level questions; along with much of the new professional field he made population regulation the central phenomenon” (p. 223).

³⁷ “When the number of scales became exceptionally high, I argued, this constitutes an increase in the food supply of the enemies, which consequently increase in numbers and so collectively search the trees more intensively. Carrying on this type of argument, I concluded that the scale insects and their enemies would strongly tend to reach a balance at which the number of scale insects is just sufficient to support the right sized population of enemies and to destroy the surplus numbers of scale insects produced” (Egerton 2014, p. 157).

³⁸ Ironically, in the early 1930s Andrewartha had reviewed the manuscript of Nicholson’s intended book on natural control and rejected it, so Nicholson finally had published some of the materials as the 1933 paper on the “balance of animal populations.”

³⁹ Such a point was dramatically underscored in the short paper Sewall Wright published in *Science* to honor the accession of ecologist Thomas Park to the presidency of the AAAS in 1960: “Humankind question of the very persistence of mankind, or at least of civilized man, in the explosive situation

below will feature such dramatic connections, combined with a deep worry about humanity's future.⁴⁰

Throughout the 1950s, such debate on density-dependence involved the major ecologists of the decade and raised many new questions. It would have been surprising if all regulation phenomena in animal populations and plant population were due to a single factor. In fact, most of the attempts to theorize general regulation acknowledged that density-dependent and density-independent factors were at play and tried to identify conditions under which one rules out one or one swamps the other. As Stearns discussed in a paper reviewing the formation of community ecology, "this controversy [about density-dependence] subsided without any clear resolution, in the sense that few would now be willing to argue that we understand what generally regulates natural populations. Perhaps no resolution could be expected, because both processes affect the fitness of individual organisms and that, in turn, regulates the density of the population" (1982, p. 635). He emphasized that much of the progress made after 1956 was due to "precisely defined field manipulations."⁴¹

At the times of *Principles*, one of the major theoretical questions was about the concept of *succession* in ecological communities, and possibly the refinement of the concept of community. The latter involved Tansley's proposition about ecosystems (1935; see also van der Valk 2013) and was favorably considered by Allee et al. (1949) as well as by Solomon (1949), who viewed "ecosystem" as the appropriate level at which to enquire about population regulation. In the 1950s, the issue of "natural control" attracted more controversy and heated debates. The 1957 Cold Spring Harbor Symposium on population biology demonstrated the polarization on the issue, which may have contributed to making the question of "natural control" major structuring issue for the community of ecologists.

The importance of competition in this debate on population regulation played a key role in the story of acclimating the Synthesis into ecology. Kingsland indicated that this debate on competition occurred because "the wide-ranging viewpoints of the biologists who were emerging as the architects of the modern synthesis in evolution between the wars began to exert an effect on ecology as well as the other biological disciplines" (1995, p. 146). This is due to the logical ties between selection

Footnote 39 (continued)

brought about by the world-wide decrease in mortality rates and the lack of compensating decreases in birth rates. The alternatives are violent reduction or even extinction of the human species, perhaps by way of the hydrogen bomb: expansion to a violently fluctuating upper limit, controlled by the availability of necessities for bare subsistence; or attainment of ecologic equilibrium with the resources of the world at such a level that progress in civilization remains possible. Park brings a keen awareness of the population problem to the thinking of organized science" (Wright 1961, p. 502).

⁴⁰ As Palladino (1991) indicates, the status of ecology in the 1960s was deeply affected by the rising public concern about problems that were usually dealt with theoretically by ecologists: "The rapid expansion of theoretical population ecology and systems ecology during the 1950s and 1960s [was] indicative of a general desire to project an image of scientific respectability for the field as a whole. However, this depressed state of affairs began to change quite rapidly in the early 1960s in the wake of growing public concern over the degradation of the natural environment—radioactive fallout from the testing of atomic weapons and Rachel Carson's writings had done much to arouse public interest" (p. 233).

⁴¹ He refers to experiments by Paine on keystone species (1966) or Connell on barnacles (1961).

and competition, as is made clear by Lack in the introduction of his book: the facts under study are “organized round the biological concepts of competition, natural selection and the interactions of predators and parasites with their prey, he writes. For this reason, the best introduction to the subject is still that given in the Chapter 3 of the *Origin of Species*” (1954, p. 4). But the importance of this debate for acclimating the Synthesis into ecology also relied on advancing two side-questions that triggered the debates that I will consider now.

Mathematical versus Empirical Theories, and the Need for a Synthesis

A first concern in the debate was methodological. Solomon (1949) indicated that there are two takes on “natural control.” one of which was “hypothetical and deductive,” exemplified by Lotka on the predation cycles and by Nicholson and Bailey (1935), the other being “inductive” and based more on biological experiments and observations. “Perhaps the major cleavage is that between the upholders of a primarily deductive and of a primarily inductive approach to the subject. The mathematical theories of population interactions, such as the studies of Lotka, Volterra, or Nicholson and Bailey,” led to conclusions “that are the results of deductions from a few simple assumptions. Even when the assumptions are correct as far as they go (and this is not always certain), the conclusions tell us only what would happen in an extremely simple situation immune from the usual environmental disturbances. In relation to natural populations, they should be regarded only as suggestions” (Solomon 1949, p. 1). Solomon’s paper intended to conciliate those approaches, a methodological unification that is as important as the synthesis between density-dependence and density-independence approaches of natural control.⁴²

To some extent, mathematical models in population biology such as Lotka-Volterra’s equations have been good at formulating the patterns of annual variation in abundance. A debate about the logistic curve took place in the earlier decade, and it proved useful to predict patterns in various populations of animals. However, a growing concern arose regarding the explanatory nature of this curve. According to Lack’s formulations, the logistic curve would nicely *fit* the phenomena of abundance variation, but it did not provide an *explanation* of the regulation. He noted: “The Pearl-Verhulst logistic curve was valuable in introducing precision in a new field of biology, and its use has greatly stimulated further research on populations. But undue veneration has sometimes been paid to it and it does not, of course, ‘explain’ population growth” (Lack 1954, p. 17). Both families of ecologists, those who

⁴² In the same way, in his 1954 book, Lack worried about theory construction in population research: “The only theoretical concepts so far put forward are highly simplified, based on a priori arguments, and expressed in mathematical terms in a few abstract and difficult papers. These concepts have been distrusted by naturalists, as is both understandable and partly, but only partly, justified. In the early stages of a science a way has to be steered between two opposite dangers, on the one hand of theoretical ideas so simplified that they have no value in application, on the other hand of facts so disorganized that no coherent theme is apparent. The first danger is greatest when the ideas have been expressed mathematically, as has happened in population research” (1954, p. 3).

followed Nicholson and those who followed Andrewartha, agreed in the search for such an explanation.

This agreement between two schools in population ecology did not mean that a biological explanation should be substituted for a mathematical description of patterns, but rather the way mathematics may not have provided satisfying explanations about the phenomena under study. The philosophical message concerned the relations between patterns and mechanisms within explanations, and the fact that those categories, may indeed be relative to explanatory strategies and to question agendas. But, regarding our interest here, this shift in explanatory interest opened room for a discussion of the relevance of evolutionary theory, and that is where the Modern Synthesis entered ecology in a different manner than in the context of the Clementsian-Wright convergence proper to Allee et al. (1949).

LaMont Cole was among the former students of the Chicago School of Ecology at Cornell's zoology department. In his 1954 paper on life history and population regulation, which plays a role in this acclimation story, he shared the same methodological concern. For Cole, the divide between mathematical approaches and biology-based approaches were reflected in a divide between *continuous* models, such as Lotka's equations, and models in *discontinuous* time, as Thompson's models (Thompson 1939),⁴³ which counted offspring month after month and proposed discrete patterns of variation. Significantly, the paper integrated an evolutionary approach to life history: life history parameters are tuned by natural selection, because "any life history features affecting reproductive potential are subject to natural selection; and that such features observed in existing species should be considered adaptations" (Cole 1954, p. 104).

Moreover, the way Cole configured the population regulation problem acknowledges the evolutionary meaning of ecological variables; he stated that a simple formula for population growth is $dP/dt = r P f(P)$, where f is the resistance of the environment (notwithstanding the critiques by Solomon), and r an intrinsic rate of increase of the population of size P , which he traces back to Fisher's Malthusian parameter. It is the "rate of true compound interest at which a population would grow if nothing impeded its growth and if the age-specific birth and death rates were to remain constant," which corresponds to the way Fisher defined fitness (p. 107). This is at the same time Lotka's "intrinsic rate of increase" (p. 107). But while Lotka's equations of populations growth are continuous, the biological reality of reproduction, as emphasized by Thompson, is discontinuous. The issue therefore concerned conciliating those two approaches, and Cole argued that they can be derived from one another.

In this way, the differences made by changing life history parameters onto population regulation could be modeled. Cole noted, "the exceedingly important ecological questions of what potential advantages might be realized if a species were to alter its life history features have remained largely unexplored" (p. 108). His framework tackles this question, which concerns the impact of evolution on ecology. A difference in life history strategies was a simultaneous large reproductive output versus a

⁴³ On Thompson's views, see Kingsland (1995, pp. 166ff).

strategy repeating few offspring at regular intervals—which Cole labeled, respectively, “semelparity” and “iteroparity.” This idea has been influential on life history theory, which is an important part of behavioral ecology (Bryant 1971; Charnov and Schaffer 1973). His contributions also led in the 1960s to the fundamental epistemic role of the notion of “strategies” in the papers of R. H. MacArthur, E. O. Wilson, and Eric R. Pianka, and generally in behavioral ecology, which instantiates the same mathematical model-based approach of evolutionary problems.⁴⁴

The Role of Individual Differences in Population Regulation and Competition

Cole’s (1954) paper also exemplified a second concern: the role of *individual differences* in the production of population regulation, such as differences in life history. This directly introduces an evolutionary dimension into the natural control question. Individual differences producing regulation was arguably a major concern of ecologists in the 1950s. This may echo some of Allee’s conceptions about the role of prosocial behavior in producing group welfare and population regulation. In the 1950s, both US and UK ecologists began moving away from the idea of the community as a superorganism as depicted in the *Principles of Animal Ecology*. The change was due in part to the shifted focus on the ecological role of individual differences onto population regulation. Interestingly, the group-selectionist view proper to the Clements-Wright framework built by Allee et al.’s *Principles* was not really refuted, but rather sidestepped by ecologists working on population regulation—its real critique waited for Wynne-Edwards’s explicit formulation of group selection in 1962 as a reaction to Lack’s individual selectionist view (Borrello 2003).

At this time, John Calhoun, a zoologist trained mostly in ornithology, started to work on the “rodent project” at Johns Hopkins University. In a 1952 paper, he drew on his experiments on Norway rats,⁴⁵ in which the colony remained at 200 individuals in an environment with superabundant food that could have carried from 5000 to 10,000 individuals. Calhoun insisted on the effect of changes in individual behavior—social behavior of individuals—as causally contributing to population dynamics. As he noted: “If social behavior really does alter the character of population dynamics, it is just such an understanding of the role of the individual and his group which we must seek” (Calhoun 1952, p. 139). The paper rested on a hypothesis of *adaptation* in response to a failure of ecological equilibrium, described as follows: “Whenever the density of a population increased beyond that level to which the heredity-to-environment relationship provides optimum adjustment, then the individual and the group must forfeit some of their potentials of behavior if all members are to maintain an adequate state of health” (p. 140). Note that the population does not reach carrying capacity since resources are constantly provided; the individual rats feature abnormal behavior (cannibalism, poor parental care, murder, aggression, etc.). This adaptive response to overcrowding is causally related to “the manner in

⁴⁴ On Cole’s career as an ecologist, see Blomquist (2007).

⁴⁵ This follows a smaller identical experiment in Scotland a few years earlier (Ramsden and Adams 2009).

which animals perceive their environment,” which appeared to be “socially important because it largely determines the rate and manner in which animals contact each other, and the manner in which they utilize the space about them” (p. 144). Calhoun’s conclusions were oriented toward a worry about human overpopulation, and some of his later work addressed this issue directly.

Of course, Calhoun’s study was the inverse of the Allee effect, which implied a positive covariation of population increase and individual rate of increase; however, like Allee, Calhoun saw the social behavior of individuals triggered by a population size threshold as a major driver of population dynamics.⁴⁶ The nature of the causes of these changes was not clearly characterized by him; later developments would clarify the role of evolutionary viewpoints in this question. But in general, American ecology in the 1950s was concerned with “individual differences as a factor in population dynamics,” as William Wellington, an ecologist from British Columbia, captured in the title of his 1957 paper.⁴⁷

Wellington began by expressing an opinion shared by the writers previously mentioned in this section: “Populations are composed of individuals, and individuals differ. Nevertheless, our attempts to identify and evaluate factors regulating animal numbers frequently seem to include a tacit assumption that the populations thus regulated are monolithic, or else consist of well-nigh interchangeable units that respond uniformly to given biotic or physical pressures” (Wellington 1957, p. 3). The individual differences, reacting differently to environmental change, impact the effect of those changes and therefore play a key role in population regulation: this is something that an ecology that considers species as monolithic individuals—both in the sense of elements of a superorganism and in the sense of Gleason’s critique of Clements’s superorganisms—could not capture.⁴⁸

Due to catastrophic storms, natural experiments on populations of the tent caterpillar *Malacosoma pluviale* in British Columbia became the subject of Wellington’s paper. He demonstrated a hypothesis: changes in population density trigger changes in population composition (frequency of individual types), and this accounts for population regulation. In this matter, attention to individual differences

⁴⁶ Ramsden and Adams (2009) described the pathologies of the rats and how Calhoun’s notion of “behavioral sink,” used to label the shift in behavior due to overcrowding, resonated with contemporary social concerns about megacities in popular culture. They also note Calhoun’s lesser-known later work, devoted to the identification and understanding of the few individuals that manifested enhanced abilities to cope with overcrowding.

⁴⁷ Calhoun and Wellington are among the few names cited by pioneer behavioral ecologist Krebs in his paper about Denis Chitty and the evolutionary viewpoint within ecology in the 1950s (Krebs 1995).

⁴⁸ Gleason’s individualistic conception of communities is often claimed to have dismissed Clements’s superorganism. But on this precise issue, Gleason’s view of communities neglected individual differences within a species, to the extent that Janis Antonovics saw this concept as typically typological, and therefore not compatible with the Synthesis. “It seems that much ecological thinking is still a generation behind that of the systematist, in that it remains locked into a typological view of the species. The current ‘individualistic’ view of communities, first championed by Gleason, has embedded in it a view of a species that is remarkably typological: the ‘individualistic species’ is almost synonymous in usage with ‘typological species’” (Antonovics 1976, p. 239).

entered American ecology in the 1950s, partly through studies by Calhoun and Wellington, and was increasingly acknowledged to involve evolution in the sense of the Synthesis.

Lack's work on population regulation and clutch size focused precisely on the response of individuals to population variation and introduced a key shift by which the role of evolution in ecology changed status. After Lack, group selection ceased to be the only way to introduce natural selection in ecology (in contrast to the Clementsian-Wrightian explanatory scheme developed in Allee et al.'s *Principles*). A former student of Nikolaas Tinbergen, Lack by 1938 was already acknowledged as an evolutionary biologist; since 1945 had led the Edward Grey Institute of Field Ornithology at Oxford University (Anderson 2013).⁴⁹ After a trip to the Galapagos in 1940, Lack visited Mayr at the American Museum of Natural History in New York and the two became lasting friends. Lack's research on Darwin's finches in the Galapagos added a new brick to the Modern Synthesis edifice by acknowledging the role of competition for resources in the process of speciation (especially the case of the bills of finches), thus complementing Mayr's views on isolating mechanisms and insisting on the role of selection in speciation. As Beatty (1986) and Kimler (1986) remind us, Lack initially accepted the consensus view that random drift would account for minute differences between Galapagos species.⁵⁰ His research, however, convinced him that natural selection accounted for species divergence in islands. Lack's 1947 book thus propelled the Synthesis towards more explanatory power given to selection. Afterwards he intervened as an evolutionist in the population regulation debates, important enough to be credited as "the father of evolutionary ecology."⁵¹

Lack began his 1947 paper in *Evolution* by noticing that, even though studying natural selection in the wild is notoriously difficult, clutch size is an excellent character to consider, because "it directly affects the number of offspring" and thus fitness (p. 95). His hypothesis was that because clutch size cannot be explained by physiology (physiological limitation cannot explain why most starlings have four or sometimes five nestlings for a clutch size), it is "ultimately selected by the number of offspring the parents can raise, the latter being determined by the available food supply" (p. 95). Lack acknowledged that this hypothesis was "a priori acceptable to the population-geneticist" but "so difficult for the traditional ecologist." His reasoning was what we would call *optimality modeling*: "for broods above the average size, proportionate mortality among the young would rise as brood size increases... [then] a point is reached when an increase in the number of eggs is offset by the

⁴⁹ The Institute was near the Bureau of Animal Populations led by Elton, but the two groups apparently did not get along very well (Gay 2013).

⁵⁰ "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" (Collins et al. 1986, p. 176).

⁵¹ With "both *Darwin's Finches* and 'the Significance of Clutch-Size' in 1947, Lack inaugurated the application of the Modern Synthesis (the successful integration of Darwinian natural selection with Mendelian genetics that was forged in the 1930s and early 1940s) to the field of ecology" (Anderson 2013, p. vii).

increase in mortality, so that there is no increase in the number of young raised” (p. 95). This “turning point” is what selection determines as clutch size. His paper relied on experiments and data on Swiss passerine, great tits, and starlings to provide direct evidence of those facts. In the conclusion, Lack applied the language of optimality: “The commonest brood-size found in nature is also the size with optimum productivity” (p. 107).

These views would later be corrected by behavioral ecology (see Grodwohl, this issue), which was promoted by Lack’s clutch size work as well as by Cole’s paper on life history, among others. While Lack’s earlier work was intended for an evolutionary audience, his 1954 book introduced his theories into the major debate of contemporary ecologists about population regulation. He argued that population regulation in birds was due to two factors: reproductive rate being tuned by natural selection—shown by the theory of clutch size—and by density-dependent regulation of death rates.⁵²

As we have seen, earlier ecologists such as Allee and colleagues accepted the idea that natural selection was ultimately involved in the maintenance of communities and in population regulation. Lack, however, made detailed distinctions that shifted the way the topic of natural selection’s involvement in population regulation was handled, aligning closer to the Synthesis view of natural selection. To account for the clutch size, after excluding physiological causes such as the limit of eggs likely to be sat on or the number produced, he considered the option that clutch size was “adjusted by natural selection to balance the mortality of the species,” an idea that “rests on a mistaken view of both population balance and natural selection.” This functioned as a kind of “group selection hypothesis,” where selection fits the individual property to the welfare of the species. Lack argued that this was wrong for two reasons: empirically “it would achieve balance only if clutch size were much lower at high than at low population densities, which is not the case,” and conceptually, involving the nature of natural selection, which “operates on the survival rate of each individual or genotype.” Hence, if a larger clutch size were to appear, it would invade the population unless “for some unknown reasons the individuals laying more eggs leave fewer, not more, descendants” (Lack 1954, p. 22). This unknown reason is precisely what his enquiries about birds established, namely, that after some point one more nestling decreases the survival rate of all offspring. Hence the only hypothesis left to explain clutch size patterns is individual selection for the optimal clutch size.

But this reasoning neglected the concern for genetics that the Modern Synthesis introduced. Lack knew that heritability was needed for his reasoning to hold; he assumed that for clutch size, the hereditary control was probably influenced by a “number of genes, as in the case of other quantitative characters, such as body size” (1947a, p. 104). Yet this was still problematic for the argument, as he conceded in

⁵² “The reproductive rate of each species is a result of natural selection, and is not, as often supposed, adjusted to the mortality rate of the species; and the critical mortality factors are density-dependent, hence climate per se cannot be the primary factor controlling numbers” (Lack 1954, p. 8).

the conclusion of the 1948 paper: “The most important gap in knowledge, and one that will be difficult to fill, is the way in which clutchsize is inherited” (p. 107).

To sum up these developments, in the 1950s, the appeal of superorganism and a form of group selection progressively faded in favor of a focus on the role of individuals in groups as contributing to “natural control.” This new focus occurred in the form of life history differences or prosocial behavior and could be addressed in the evolutionary context of individual selection. As I have demonstrated, the population regulation issue addressed in terms of density-dependence paved the way for introducing some concepts of the Modern Synthesis within ecology.

Lack, trained by Tinbergen and supported by Mayr, was highly influential in introducing this intellectual shift. His rejection of group selection illustrates a turning away from the Clementsian view of communities expressed in Allee et al.’s treatise. And with this move, ecological considerations mostly focused on *population* ecology, namely, the regulation of one or two populations rather than the set of species involved in a succession proper to a community. The emphasis on community faded from view, which constitutes a move away from Emerson’s and Allee’s superorganism and the issue of succession and a reemphasis on mathematical models in population biology, such as those of Lotka or Gause.

Population Biology and “Evolutionary Ecology”

At times, there was a sense that ecology would make progress as population biology through quantitative and mathematical methods. For instance, G. Evelyn Hutchinson and his student Edmund Deevey noted in 1949 that ecology was the only branch of biology (besides genetics) that had undergone formalization and quantification in the last decade, and “developed an autonomous quantitative theory independent of the physico-chemical sciences” (Hutchinson and Deevey 1949, p. 327). Advocating for ecologists to follow this path and especially to rely on a “significant cooperation involving field naturalist taxonomist, experimentalist and mathematicians” that also affected “genetics and evolutionary studies,” the authors stressed the integrated character of population ecology. They pushed for the same kind of process of community ecology, with the Synthesis—“evolutionary studies and genetics”—presented as a paradigm or a model for the structuring of ecology (rather than a set of concepts that should be imported into ecology). Hutchinson’s survey of various aspects of ecology circa 1950 highlighted the call for mathematization and the parallel with the Synthesis. Some of the work I consider here dealing with density-dependence in population regulation illustrates these trends.

Refocusing ecology on population biology and appealing to mathematical modeling implied that an understanding of dynamics involving *many* species in a community (with reference to the concept of succession) was becoming harder to handle. For instance, in their landmark paper on replacement of species in a model of competition, Nicholson and Bailey (1935) already developed a mathematical model that mostly considered two species, and when several species were at stake, “in the formulation of the problem of interaction between several species of animals it is essential to consider the effects of age-distribution. The resulting complexity

introduced in the fundamental equations makes their full investigation a task to be undertaken only by professional mathematicians” (p. 597).

Density-dependence, however, was not the last word on evolution and ecology. In 1995, behavioral ecologist John Krebs argued that density-dependence was the received view of population regulation, but that this was mostly based on *pattern* and without clear mechanisms involved (Krebs 1995). He contrasted this to what he called a “mechanistic view” of population regulation, which proposed model mechanisms rather than density-dependence as explanatory.⁵³

Krebs, co-author of the first major textbook in behavioral ecology in 1991,⁵⁴ had been a student of Denis Chitty, so naturally for him the paradigmatic illustration of the “mechanistic view” of population regulation was what is known as the “Chitty hypothesis.”⁵⁵ Chitty’s work on voles, begun in his 1952 dissertation, helped expand his views on population regulation published in 1960.⁵⁶ Lack, who had been on Chitty’s dissertation committee, vetoed its earlier publication because he disagreed with the thesis, and it was only due to Peter Medawar’s intervention that it was published. Chitty tackled the constant problem of animal population cycles that was also Elton’s concern at the Bureau, initiating a wholly evolutionary approach that contrasted with his mentor’s understanding of the relations between ecology and evolution.

In density-dependence theories, researchers assumed some heritability like Lack, but did not take this as one of the problems to investigate. Rather, researchers would usually rather consider the phenotypic result of evolution, namely the clutch size, but not the process of changing gene frequencies. Thus, evolutionary change was somehow a black box in such theories. By contrast, Chitty hypothesized that populations regulate themselves, not by effects of competition that act on the size of the group, but by *changing the (genetic) individuals themselves via natural selection*, inducing in them a “spacing behavior” that ultimately decreases population density.⁵⁷

In this view, evolution was wholly integrated within ecology because it held the whole answer to population regulation. Contrasted with the works of Calhoun, Cole, or Wellington, Chitty theorized that what caused population regulation was not the differences between different individuals, possibly triggered to express other behavioral potentialities, but rather the genetic change brought into the population by the density change itself. As Krebs (1978) indicated, there was no definite proof of this hypothesis nor support for the extent of its validity, and it was even hard to devise a

⁵³ Once again, notice the shifting sense of mechanism versus pattern difference: now the whole density-dependence is the pattern and no longer the explanation.

⁵⁴ Krebs and Davies (1995).

⁵⁵ Chitty, a British-born ecologist, received his PhD at Oxford with Elton and then worked with him for 26 years at the Bureau of Animal Population before going to the University of British Columbia in 1960.

⁵⁶ Chitty (1952, 1957, 1960).

⁵⁷ “Voles probably exemplify a general law that all species are capable of limiting their own population densities without either destroying the food resources to which they are adapted, or depending upon enemies or climatic accidents to prevent them from doing so. If this is true, self-regulatory mechanisms have presumably been evolved through natural selection, and arguments in support of this view can certainly be advanced” (Chitty 1960, p. 111).

test that would not also corroborate antagonistic theories of population regulation. In contrast to Lack's views, Chitty's perspective was not rapidly adopted by most ecologists. This was despite the fact that such a perspective represented a genuine kind of integration of Synthesis thinking into ecology with regard to the problem of natural control, since it conceived of genetic change evolutionarily induced as a major ecological force.

In 1957, Chitty was among the presenters at the Cold Spring Harbor Symposium devoted to "population biology," together with Lack, Andrewartha, Birch, Hutchinson, Gordon Orians, and others (which led to a publication, Cold Spring Harbor Symposium 1957). Major evolutionary biologists and population geneticists such as Dobzhansky, Mayr, and Richard Lewontin (a member of the younger generation of population geneticists) were there too. The nature of the meeting attested to the importance of ecologists' debates on evolutionary biology and, inversely, of the evolutionary meaning of density-dependence debates about population regulation for ecologists. Clearly, although one section of the symposium was devoted to "Animal Populations, Experimental and Theoretical" and another to "Human Population Growth," generality was aimed at in the published proceedings, which included three sections on the "Ecology of Natural Populations." Here, the papers by Andrewartha, P. J. Wangersky and W. J. Cunningham, and Chitty are plainly general and formal. Another section addressed "The Structure of Communities," and the final one "The Population as a Unit of Evolution," including chapters by Lewontin and Dobzhansky. The ecological issues covered mostly concerned the question of population regulation, not community diversity, which had been a major focus of mainstream ecology until *Principles of Animal Ecology* (1949).

After the publication of the symposium proceedings, it became obvious that the ecological problem of population regulation involved evolution.⁵⁸ Lack had recognized this when he characterized his own approach, referring to Baker (1938), as dealing with the "ultimate factors" (concerned with survival value) and not "proximate factors" (concerned with "adaptations in physiology and behavior") (1954, p. 5).⁵⁹

In 1961, Lack's mentor Ernst Mayr wrote a brief paper that analyzed the distinction between ultimate and proximate causes in biology to stress the autonomous

⁵⁸ Although dated 1957, the volume did not appear until 1958. In 1959 another landmark work was the publication of an issue of *Ibis* on population regulation that included a paper by Wynne-Edwards and a paper on Lack, presenting opposed versions of the explanation of natural control based on natural selection (see Borello 2003). Here I focus on the Cold Spring Harbor Symposium, which mobilized many of the protagonists I consider here and presented a larger set of issues.

⁵⁹ "Some of the factors influencing animal numbers, such as size, the length of the breeding season, or migration, are products of evolution, and their causes can be considered under two distinct heads. For example, a bird may be said to breed in spring because the longer days stimulate the growth of its sex organs, and also because it is only in spring that there is enough food for it to raise young. In this example, daylength is a proximate factor helping to bring the bird into breeding condition at a suitable season; but the suitability of the season depends on the food supply, which has been an ultimate factor in the evolution of the breeding season of the species. Ultimate factors are concerned with survival value, proximate factors with adaptations in physiology and behaviour. ... An effective adaptation is often thus 'anticipatory,' but the anticipation is not, of course, conscious, nor a result of the immediate situation; it is a long-term product of evolution" (Lack 1954, p. 5).

character of evolutionary biology in the face of recent progress in molecular biology (Mayr 1961; see Beatty 1994). In his 1962 paper “Natural Selection and Ecological Theory,” Gordon Orians revisited the whole density-dependence controversy in terms of the distinction between ultimate and proximate causes. Andrewartha and Birch (1954), Orians declared, mainly considered the proximate causes of population regulation: they believed it was the “job of the ecologist to count auger-holes and so to predict the number of bees to be found and the job of the evolutionist to measure genetic change as a result of competition” (Orians 1962, p. 158). This was a *conceptual separation* that held that “evolutionary concepts have no place in ecological theory.”

The importance of natural selection is not disputed, for the final section of the book is devoted to evolutionary aspects of ecology, and Birch (1955, 1961) has made important contributions to the study of evolution. Rather it is claimed that a general and satisfying theory of ecology can and should be constructed without recourse to evolutionary thinking and concepts. (p. 158)

Orians contrasted this with Lack’s approach, whose work on clutch size was an excellent example of “selectionist thinking” similar to Fisher’s work on sex ratio—a clear example of the Synthesis—and to MacArthur and Pianka’s recent work on foraging.

Hence, the fundamental dichotomy in modern ecology, as illustrated by these two books (Andrewartha and Birch versus Lack), according to Orians, “can only be understood as a manifestation of the fundamental division of biology into two major categories—functional biology and evolutionary biology (Mayr 1961)” (p. 260). The consequence was that Orians distinguished two parallel fields in ecology—“functional ecology” and “evolutionary ecology,”⁶⁰ which were largely independent. He claimed that only evolutionary ecology had some unity, while functional ecology was rather a juxtaposition of autecological cases. Asking whether there was “any such thing as a general theory of ecology,” he responded that while there were descriptive generalizations in comparative anatomy, embryology, and physiology, “the only general theory which now seems possible is that of natural selection” and that “evolution would seem to be the only real theory of ecology today” (Orians 1962, pp. 261–262).

This interpretation of the debate pervaded the field of ecology in the 1960s, although the fate of the label “functional ecology” is not considered here. But Orians’s view became widely accepted, even beyond the domain of animal ecology. In 1967, John Harper, British plant ecologist and president of the British Society of Ecology, stated in his presidential address that “the theory of evolution by natural selection is an ecological theory—founded on ecological observation by perhaps the greatest of all ecologists” (Harper 1967, p. 247). He considered population

⁶⁰ Futuyama later made the same point: “In many of these fields [of functional ecology] the major questions were and are functional rather than historical in nature; evolution and history need not be invoked if we wish to know what immediate factors govern the course of succession, the rate of phosphorus turnover, or the distribution of a species, given its physiology” (1986, p. 306).

regulation in plants in terms of the “reproductive strategy of different species” (crucial for behavioral ecology; see Grodwohl, this issue), which indicates his Darwinian perspective (p. 254). Referring to Cole (1954), Harper pinpointed the key ecological role of the “strategy of the life cycle.” For him, this was the key to the future of plant ecology: “A whole branch of plant ecology lies almost untouched in attempts to understand the significance of the strategy of reproduction” (p. 255). He would himself pursue such questions, especially in a set of papers published in the *Journal of Ecology* on “the reproductive strategy of higher plants” (Ogden and Harper 1970). Harper transformed the problems ecologists faced into evolutionary terms as the trade-off between investing in seed number or investing in seed size (1967, p. 257), which exactly paralleled Lack’s treatment of clutch size as well as the recent considerations of K and r selective regimes by MacArthur and Wilson.⁶¹

Not all ecologists, of course, agreed with such a point of view. That Orians and Harper played such major institutional roles should not obfuscate the fact that many ecologists were simply unconcerned by these findings. In the early 1960s, for example, as William Hamilton worked on his major theoretical breakthrough in evolutionary biology, he recalled that nobody at the major ecological station at Silwood Park in Ascot (part of Imperial College, London) seemed interested in his work (see Gay 2013, p. 69).

Ecological Genetics Meets Evolutionary Ecology

Harper, like Lack and Orians, equated the evolutionary viewpoint to the principle explanatory role of natural selection. For these researchers, the genetic constitution was a kind of black box—which indicates that the Synthesis had not wholly penetrated ecology. However, around 1953 another approach to population regulation emerged in the mathematical tradition of Nicholson and Bailey’s model, but explicitly integrating the genetic constitution of the population into the models. It somewhat followed Ford’s project of an ecological genetics. However, instead of attempting to prove the major role of selection in the field, ecologists promoting this new approach intended to model the genetic underpinning of ecological processes of population regulation and species coexistence.

This began with Howard Levene’s model of competition in his 1953 paper “Genetic Equilibrium When More Than One Ecological Niche is Available,” in which genetic equilibrium is proven to support the ecological equilibrium of two populations. Levene, a statistician and geneticist at the Institute for the Study of Human Variation at Columbia University, had earlier collaborated with Dobzhansky on studies of *Drosophila* populations. Later the two published a study of the genetic differences between the head louse and the body louse (Levene and Dobzhansky

⁶¹ r - and K -selection are two modes of selection, distinguished by the ratio of offspring number and parental investment. r selection favors a strategy of leaving many offspring and not caring about them (e.g., laying thousands of fish eggs), while K selection favors the strategy of leaving a few mature offspring requiring substantial parental care (e.g., primates’ reproductive life). The environmental conditions, especially the frequency of predators, decide which selective regime dominates.

1959). Here again is a case in which Dobzhansky was involved in one of the threads in which evolutionary theorizing was used to address an ecological issue.

Levene's short paper featured a model that "disregarded drift" and inquired about the effects of selection alone. It showed how the ecological concept of niche (understood abstractly, as a space in which alleles and genotypes have a specific and proper "adaptive value") can be involved in an analysis of classical population genetics, which in turn may explain aspects of ecological coexistence. As Levene wrote:

It would seem that the existence of several ecological niches, with one allele favored in one niche and the other allele favored in another, might increase the possibilities for attainment of equilibrium with both alleles present in substantial proportions. Recently the question arose of whether it was in fact possible to have equilibrium without the heterozygote being superior to both homozygotes in any single niche. It is shown below that under certain assumptions the answer is yes. (Levene 1953, p. 331)

The model is as simple as possible, with random mating and no habitat choice. This makes it even more explanatory for equilibrium since it is the "worst possible case," given that nothing except individual fitness-based selection explains the equilibrium.

Levene and Dobzhansky, among others, had thought of using a genetic viewpoint to address ecological issues such as coexistence precisely because of the advances of the Modern Synthesis, which had shown that microevolutionary change can be as quick as ecological change. Indeed, one of the reasons for the divide between ecology and evolution until the 1950s was that evolutionary change supposedly occurred at a slower timescale than ecological change. Ecologists, in turn, "tended to focus on short-term changes" (Kingsland 1997, p. 424). But microevolution in the 1950s, as Collins notes, had proven this not to be the case: "The accumulating evidence of the evolutionary synthesis and post-synthesis research yielded a fuller understanding of the rate of evolutionary change. ... The repeated demonstration of 'microevolution' forced a reduction in the amount of time thought to be required for at least some kinds of evolutionary change. This reduction condensed what H. J. Muller called 'evolutionary' time to the timescale of some ecological processes" (Collins 1986, p. 275). Therefore, one of the lessons of the diffusion of the Modern Synthesis in this period was that the previous distinction between ecological time versus evolutionary time, was now viewed as "artificial and misleading." As Janis Antonovics noted, "changes of both kinds may be on any time scale: frequently genetic and ecological changes are simultaneous" (1976, p. 241). Hence, approaches to ecological problems through using simple genetics-based models began to emerge. Antonovics even claimed that "explaining the abundance and distribution of organisms"—which define the two major problems addressed by ecologists—"is basically a genetic problem," since "the ecological amplitude of a species (both within and among communities) has a genetic component" (p. 236).

In the early 1960s, the genetic viewpoint would prove to be crucial to the determination of ecological equilibria. Already the Berkeley geneticist Michael Lerner had published *Genetic Homeostasis* (praised by Dobzhansky), in which he developed an account of the properties of Mendelian populations evolved as a byproduct

of individual selection (Lerner 1954). This supported a view of polymorphism closer to Dobzhansky's. Along with his colleague Everett Dempster, Lerner revisited an experiment made by ecologist Thomas Park, which had shown that a system with two species of flour beetle, *Tribolium castaneum* and *T. confusum*, could not predict which one would dominate over the other (Park 1948).⁶² Park and colleagues had indeed set up the experiment to test Gause's theoretical views on competitive exclusion. However, after several decades of results and publications, they found a proportion of cases that would not fit the predictions and rather showed coexistence, or random exclusion of a species. But Lerner and Dempster argued that when controlling for genetic diversity, the indeterminism of the system disappeared and one could indeed predict the final composition (1962).⁶³ The genotypes of founder populations are causally relevant to the final outcome, and the authors referred to Mayr's "founder's effect." Mayr, who was in regular correspondence with Lerner, read the manuscript and agreed with their conclusions. He tied Lerner's results to his major concern at the times in genetics, namely, the compared effects of allelic and epistatic interactions on reproductive success. As he told him: "The outcome of Park's experiments were indeterminate under the conditions chosen by him, which included not only a set of environmental conditions, but also a specified breeding system. I am becoming more and more intrigued about the relative contribution of epistatic and allelic interaction to reproductive success". This, of course, is directly related to Mayr's contemporary critique of "beanbag genetics" and, therefore, his interpretation of the Synthesis, which Mayr tried at times to make less centered on population genetics than it usually was. Crucially, he related this genetic aspect to ecological conditions of the population's existence, telling Lerner: "My hunch is that epistatic interactions are the predominant factor in open populations and allelic interactions in closed populations with a comparatively homogeneous genetic background."⁶⁴

More generally, Lerner and Dempster's study showed how black-boxing genes, in models and even in the design of ecological experiments, prevented the adequate understanding of ecological phenomena. As in the case of Nicholson and Bailey (1935), the models involving genetics were not able to address succession in communities or situations in which many species coexist because of the complex mathematical tractability.

To some extent, contemporary labeling of "evolutionary ecology"⁶⁵ is often related to this tradition of using a priori genetic models to account for ecological experiments or data on regulation and coexistence. By contrast, a major heritage of

⁶² Lerner regularly corresponded with Dobzhansky (sometimes in Russian, their common native language). Dobzhansky relied on Lerner's mathematical ability to support him, for example, in the controversy about balanced versus classical accounts of polymorphisms.

⁶³ Actually, Park and colleagues continued to work on the experiment, integrating the genetic viewpoint and controlling strains; Leslie et al. (1968) still concludes that some cases are not explainable by competitive exclusion.

⁶⁴ Mayr to Lerner, 2 January 1962, I. Michael Lerner Papers, American Philosophical Society, Philadelphia, PA.

⁶⁵ See Roughgarden (1979) and Pianka (1983). As Kimler (1986) notes, in such instances evolutionary biology is used to structure the research questions, while in Elton's or Allee et al.'s treatises it was the object of the final chapter of the book.

Lack and Orians is referred to as “behavioral ecology” and essentially involves the use of a general adaptationist viewpoint to illuminate autecologies.⁶⁶

While Levene’s and Lerner and Dempster’s works merged ecology and genetics in a way reminiscent of Ford’s ecological genetics, by turning to the nature of the genes involved to explain ecological processes, Chitty’s hypothesis made evolution into a causal explanation of population regulation. Thus, in early 1960s, notwithstanding the final validity of a pure competition-based thesis, the debates on density-dependence indicated two lines of connections between the Synthesis and ecology. The first concerned natural selection: assuming heritability (which can be confirmed using a sort of circular process of justification), the ecologist could explain population regulation by invoking natural selection for traits related to reproduction. The second was about genes: here, ecological equilibria may not be understood without appealing to genetic constitutions. Both conceptual branches underwent further development.

The Regulation Question Meets the Coexistence Question: Hutchinsonian Niches, Genetic Feedbacks (1959–1968)

The New Concept of a Niche

The 1957 Cold Spring Harbor Symposium on Animal Ecology and Demography culminated with G. E. Hutchinson’s “Concluding Remarks,” in which he formulated his concept of niche and the difference between a fundamental and a realized niche. He acknowledged the crucial role of natural selection in shaping coexistence and biodiversity. Here I focus on this text because Hutchinson’s concept of niche was a consequence of the debates on density-dependent population *regulation*. These debates introduced another ecological key issue, *coexistence*, which was earlier addressed in the Clementsian-Wrightian framework of the *Principles of Animal Ecology* (see “[The Solidification of the Synthesis and its Contacts with Ecology during this Period](#)” section, above) through the ideas of succession and group selection. Yet this was eclipsed in the 1950s by the issue of “natural control.” Hutchinson made natural selection the underlying factor likely to explain *coexistence*, and in so doing finally paved the way for the last acclimation of ecology by the Synthesis.⁶⁷

G. Evelyn Hutchinson was only 2 years younger than Elton. A respected limnologist at Yale University, in the 1950s he gained prominence as the leader of the major research school in theoretical ecology (Slack 2003). Concluding the debates on population regulation (Andrewartha and Birch versus Lack, Chitty, and Orians), Hutchinson mostly ascribed the main driving role to competition, yet added an interesting

⁶⁶ Together with Eric Charnov, Gordon Orians in the 1970s authored a textbook on behavioral ecology of foraging that, although not published, was nonetheless circulated and was very influential.

⁶⁷ Gay, referring to the important historical role of this piece, states: “Judging from the flurry of work following Hutchinson’s ‘concluding remarks’ it appears that he gave ecology a considerable heuristic boost” (2013, p. 121).

nuance. He held that the respective impacts of competition on population growth and regulation depend on the autecology of species, primarily for reasons concerning the timescales of generation. For him, the differences between the views of Andrewartha and Birch, on the one hand, and Lack or Nicholson, on the other, were mostly due to the difference between insects and birds: “Much of the apparent extreme difference between the outlook of these investigators (Andrewartha and Birch) and a writer such as Lack (1954) ... is clearly due to the relationship to seasonal cycle which differs in the insect and the birds” (Hutchinson 1957, p. 420). The relation between the importance of site-specific competition (the one that matters for community dynamics) and intraspecific competition depended upon these parameters. This starkly contrasts with Orians’s interpretation, who explicitly stated that the difference between the two positions was not due to species selection (1962).

The debates on the importance of competition were thus reinterpreted by Hutchinson in terms of the *relation of interspecific to intraspecific competition*. When intraspecific competition was much more important, individuals are mostly affected by competition with conspecifics, and therefore the competition with other species was somehow swamped. This meant that environmental factors such as meteorology or seasonal changes were the major determinants of population regulation of the species: “In the situations described by Andrewartha and Birch in which the major limitation of numbers is the length of time that meteorological and other conditions are operating favorably on species, it is reasonable to suppose that interspecific competition is no more important than intraspecific competition” (Hutchinson 1957, p. 420).⁶⁸ This key difference, already emphasized by Huxley (1936), is decisive for understanding the respective merits of the main rival views regarding population regulation.

Hutchinson then formulated the important distinction between a *realized niche* and a *fundamental niche*. The latter is the hypervolume, in the hyperspace of environmental parameters,⁶⁹ where a species is likely to exist. However, if two species X and Y have overlapping fundamental niches—for example, on the dimension of resource A they forage the same kind of resource—then there is competition, and if X is a better competitor than Y, then the realized niche of species X takes over the part of the fundamental niche of Y that overlaps (see Fig. 4). Therefore, whereas the fundamental niche explained the possibility of finding two species around the same parameter values, competition explained the *realized* niches, those inhabited by a particular species, and ultimately the extant coexistence and diversity. Explaining why X_1, X_2, \dots, X_n coexist meant showing how they have n realized niches—natural selection being what explained how those realized niches differ from fundamental niches. It is the difference between fundamental and realized niches that explains coexistence of various species. In turn, this difference is accounted for

⁶⁸ The question of the inter/intraspecific competition ratio would remain a major concern for community ecology, and would re-emerge at the center of recent debates on the explanation of biodiversity by neutral versus niche models (e.g., Holt 2006; Leibold and McPeck 2006).

⁶⁹ A hyperspace is a mathematical abstract space with a high number of dimensions (much higher than 3).

by competition. Hence, natural selection appeared in the gap between fundamental and realized niches. Granted, *niches* was already a major concept in Elton and Grinnell's works (see Pocheville 2015); but, besides the fact that niche is a property of species rather than the environmental space, Hutchinson introduced two key changes. Niche became an abstract space (or subspace of a space of parameters), and it could also be explanatory, to the extent that fundamental and realized niches are decoupled. Earlier biologists would refer to various kinds of niches: "ecological niches" (Lerner 1953), "habitat niches" and "food niches" (Allee et al. 1949), but all those instances are unified in the parameter hyperspace where Hutchinson constructed his general concept of niche. Connell did a classical study that empirically established the difference between fundamental and realized niches of the clam *Chthamalus*, just by removing another species, *Balanus*, living on the same tidal rocks and sharing some of the former's fundamental niche (1961).

However, in this framework, researchers still had to explain why it seemed that many species coexist even though they have similar environmental requirements. Hutchinson would grapple with this question throughout his career, for instance, under the mode of what he called the "paradox of the plankton." Applying the purely competitive exclusion principle does not allow for many species, while there are thousands species of plankton, and the environmental parameters in which they exist seem to be very similar (factors like light, oxygen level, and temperature are all very homogeneous in oceans) (Hutchinson 1961).

Hutchinson proposed two kinds of solutions. The first option meant there could be minute environmental parameters that we do not see when we formulate the fundamental niches of all plankton species, which implies, in turn, that each species has a specific micro-realized-niche appearing when we take them into account. The second option originates from his "Concluding Remarks," in which he opposed an overarching explanatory role for competition, namely, the fact that "the direction of competition is never constant enough to allow elimination of one competitor" (1957, p. 420). So, given that the competitive abilities change in a quick timescale, limiting similarity cannot by itself explain coexistence because the competitive equilibrium is not fully reached.⁷⁰ This could also make sense of Park's experiments on flour beetles, which curiously sometimes showed stochastic results.

To sum up, through this theoretical framework sketched in Hutchinson's "Concluding Remarks," the competitive exclusion principle emerged as the core of community ecology and allowed the elaboration of an evolutionary perspective in synecology. This evolutionary perspective created a major theoretical space for natural selection and concepts related to natural selection addressed by population and quantitative genetics—i.e., stochasticity, drift, transient regimes, etc. The competitive exclusion principle, understood in the scheme of the difference between

⁷⁰ "The only conclusion that one can draw at present from the observations is that although animal communities appear qualitatively to be constructed as if competition were regulating their structure even in the best studied cases there are nearly always difficulties and unexplored possibilities. *These difficulties suggest that if competition is determinative it either acts intermittently, or it is a more subtle process than has been supposed*" (Hutchinson 1957, p. 419).

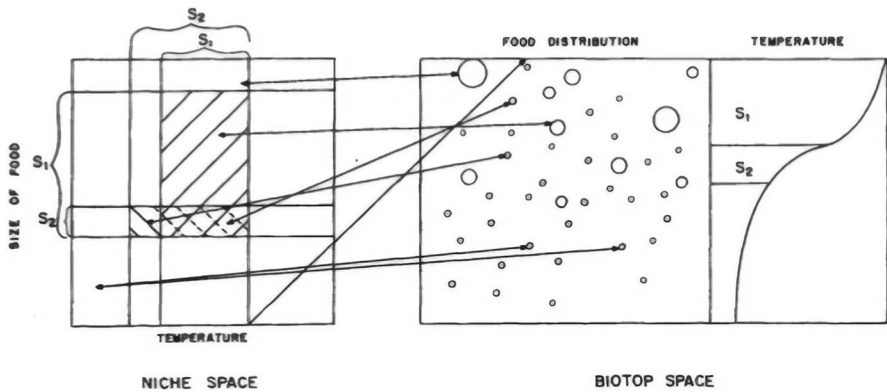


Fig. 4 Realized and Fundamental Niches. (The “circle” species is a better competitor than the “cross” species; Hutchinson 1959, p. 421)

fundamental and realized niche, made “natural selection” (and especially the rhythms, intermittences, and fluctuations of selective pressures) the key *explanans* for species *coexistence*. In addition, in the wake of ideas of density-dependent drivers of natural control defended by Nicholson (1933) and Lack (1954), it became a major explanation for the way in which *species may limit other species’ populations*, thereby controlling *population regulation*.

In this framework, which inherited the privileged explanatory role ascribed to natural selection by the Synthesis, the *natural control* issue and the *coexistence* issue were addressed together, in a perspective allowing for mathematical modeling.⁷¹ However, many of the major technical notions of the Synthesis—crucially, fitness and genes—were absent from this ecology, while the “evolutionary ecology” initiated by Levene, among others, had integrated them. Moreover, the absence of fitness was plausibly due to the fact that mathematical models used in subfields of ecology (and in Hutchinson’s construal of “niche”) were not using major theoretical models from population genetics.

Complexifying the Picture: “Genetic Feedback” and Competition as Coexistence and Regulation Yielding Processes

The connection between the coexistence question and the natural control issue realized by Hutchinson through his concept of a niche, independently of the consideration of genes, produced a very different view of the ecological role of selection than the “evolutionary genetics” that followed from Ford and from Levene and other geneticists “see section [Ecological Genetics Meets Evolutionary Ecology](#)”. However, during the 1960s these two approaches rejoined on several occasions. In

⁷¹ See Slobodkin and Slack (1999, p. 28) and Slack (2003, p. 524), on the inclination of Hutchinson and his students and coworkers towards generalization through mathematical modeling.

1968, the entomologist and limnologist from Cornell, David Pimentel, published a paper on “Population Regulation and Genetic Feedback” in *Science*. Pimentel theorized the notion of “genetic feedback” in this way: “High herbivore densities create strong selective pressures on their host-plant populations; selection alters the genetic make up of the host population to make the host more resistant to attacks; this in turn feeds back negatively to limit the feeding pressure of the herbivore. After many such cycles, the number of the herbivore population are ultimately limited, and stability results” (1968, p. 1433). This process combined with other processes, such as competition, to account for the patterns of variation of species abundances, including the specific patterns witnessed when a new species is introduced in a community. All these processes may occur successively to induce control: “Competition in the beginnings was the dominant control mechanism, operating in the experimental system, but genetic feedback became dominant with time and through evolution” (p. 1436).

Pimentel also undertook experiments on parasitic wasps and housefly hosts with a control group where evolving wasps were removed at each generation. The experiments matched the model: genetic evolution in the host stabilized the abundances of each species. But genetic feedback also accounted for several species competing in the same niche, based on the different values of interspecific and intraspecific competition across time. This demonstrated how genetic evolution provided a robust evolutionary explanation for coexisting species having a similar niche.⁷² Pimentel’s paper is thereby an excellent instance of bridging the gap between Hutchinsonian niche ecology and genetic approaches to evolutionary ecology. Most importantly, Pimentel viewed his model as an answer to the question of homeostasis of communities treated in Allee et al. (1949): “Population regulation by genetic feedback supports Emerson’s view (*Principles*, chap. 5) that evolution in natural populations is toward homeostasis (balance) within populations, communities and ecosystems” (1968, p. 1437). Hence, almost 20 years after Allee, Emerson, and colleagues formulated this view, in a context where the reference to selection for the community as a whole was no more likely to be used, some ecologists provided another evolutionary understanding of community endurance and stability as well as community composition.

Theoretical Ecology and Biogeography as Last Result of the Acclimation

Robert MacArthur, Hutchinson’s student, earned his PhD at Yale in 1958. He played a major role in reshaping ecology in the 1960s, both through his impact on the rise of behavioral ecology, coauthoring two seminal papers, MacArthur and Pianka

⁷² “Competing species seeking the same plant, prey or host, can coexist if their numbers are controlled by genetic feedback. For example, let assume that two aphid populations feed on sap from the same plant species. The two aphid species can coexist because the more abundant aphid species will eventually be controlled through the processes of genetic feedback” (p. 1436).

(1966) and MacArthur and Levins (1967), and through the *Theory of Island Biogeography*, coauthored with E. O. Wilson (1967). In a short time, the circle of ecologists around him began referring to themselves as “theoretical ecologists” (McIntosh 1986, p. 243) and to impact ecology at large.⁷³ MacArthur launched the population biology series at Princeton University Press, in which *Theory of Island Biogeography* appeared, and published Levins’s *Evolution in Changing Environments* (1968). This created a niche for monographs exploring the articulation between ecology, evolution, and genetics. Richard Levins characterized his own book as “a series of explorations in fields where ecology, genetics and evolutionary studies meet around the common theme of the consequences of environmental heterogeneity” (Levins 1968, p. v). The nature of the “meeting” mentioned here well captured the interest of the researchers who occupied this niche.

Recalling MacArthur, Wilson noted: “We became friends, and one of our common concerns was the growing decrepitude of our specialties (as we saw it), in dismaying contrast to the newly triumphant emergence of molecular biology. *Ecology and evolutionary biology seemed like the aforementioned rhinos and archaic carnivores*, surrendering university chairs and grants to the new wave of biologists coming out of the physical sciences. It was clear in the 1960s that their achievements were to be the hallmark of twentieth-century biology” (Wilson 2010, p. 4; my emphasis). The problem with ecology and its connection to evolution was its lack of theoretical formalizing, as well as disconnect to general and basic principles. *Theory of Island Biogeography* undertook such a project and began by underscoring its aim: “Biogeography has long remained in a natural history phase, accumulating information about the distribution of species and higher taxa and the taxonomic composition of biota. ... But biogeography is also in a position to enter an equally interesting experimental and theoretical phase” (MacArthur and Wilson 1967, p. 1). Granted, ecology in the early twentieth century tried to supersede its natural history core and access experimental knowledge. Clements’s reference to physiology played this role, as did Shelford’s. Midcentury evolutionary theory aimed at being so experimental and quantitative. As Smocovitis (1992) argued, the Synthesis partly instantiated such an endeavor.⁷⁴ Later, Hutchinson was also criticized for pushing for general mathematized models and explicitly trying to make ecology more theoretical than natural historical.⁷⁵ Thus, MacArthur and Wilson’s theory repeats the constant quest of ecologists and evolutionary biologists, but on the basis of adopting the latest theoretical tools.

Theory of Island Biogeography was designed to reformulate *biogeography*—an aspect of ecology originating in plant ecology’s concern for characterizing types of communities and environments—into a theory questioning the geographical patterns of stability among and across communities “in terms of the first principles of

⁷³ On MacArthur, see Odenbaugh (2013). See Ishida (2007) for a rebuttal of the idea that MacArthur models are excluding history and falsely always assume equilibrium.

⁷⁴ Kingsland speaks of a “shift away from descriptive or story-telling narratives to a more analytical, hypothesis-testing style, complete with attempts to mathematize the biological world” (1997, p. 417).

⁷⁵ Hagen (1992, 96ff.).

population genetic and ecology” (MacArthur and Wilson 1967, p. 7). The spatial and time scales of interest are noticeably much larger than problems dealt with by Pimentel or, earlier, by Lerner and Dempster and by Levene. At such stages, those genetic-based models could not work, hence MacArthur and Wilson’s book represent a new kind of acclimation of the Synthesis in another area of ecology.

Their theory relied on the very simple model of “island-mainland.” In this model, “island” is a territory that can be inhabited by a population of a species and where individuals can migrate from the mainland as well as from other islands. Immigration and population extinction are major processes that occur in this model, exactly like mutation and migration were basic processes in population genetics models. A further question concerned which species were likely to colonize and in which environmental conditions. This, of course, brought natural selection into the picture via the notion of “adaptive strategy” proper to a species (and not to an individual; the notion was already present in Cole (1954), as mentioned earlier). Their goal was described as follows: “From these a priori mathematical considerations, a biological portrait of the superior colonist is drawn, and matched against an empirical description of superior colonizing species made by previous biogeographers” (p. 151).

The island-mainland model can be viewed as equivalent to simple models like the Fisher-Wright model, the stepping stone model (Kimura), or the Moran model in population genetics. The commonality among models was the introduction of a methodology proper to population genetics at the highest ecological scales. These were very simplified representations of populations (considering only one or two loci, possibly skipping the fact that generations overlap, sometimes assuming asexuality, etc.) through which a mathematical treatment could be applied to make predictions and compare these with data.⁷⁶

Besides this formal parallelism with population genetics, the manner in which MacArthur and Wilson defined colonization and addressed the question of the best colonizer—defined in terms of largest increase in population rate—required taking on board *several concepts* that were directly drawn from population genetics and, more generally, from the theoretical understanding of speciation in the Synthesis. First, the rate of population increase in a species r corresponded to Fisher’s “fitness.” This concept allowed for distinguishing the best and the worst colonizers and therefore enabled predictions. Second, island biogeography models intended to account for the evolutionary divergence of species, to this extent considering the genetic basis of species’ characteristic traits. They asked how a species itself, in its behavior and phenotypic traits, is affected by its colonization success. Chapter 7 addresses these details by considering alleles. Such a question echoed Chitty’s earlier view of population regulation: individuals in species evolve genetic responses to

⁷⁶ A hypothetico-deductive method, drawing testable predictions from simple mathematical models, and identical to the method in population and quantitative genetics, is something MacArthur made pervasive in ecology through his influence. Fretwell notes that “prior to MacArthur’s 1957 paper on relative abundance, it had been little used in the study of natural history (about 5% of papers in biology from 1950 to 1956 tested predictions, compared to almost 50% nowadays)” (Fretwell 1975, p. 3).

ecological processes; but here the question is integrated within a general and formal interrogation of coexistence at the highest spatial scale.

MacArthur and Wilson (1967) therefore shaped a theoretical framework for regional scale ecology that finally introduced into ecology both a formal style that characterized the early times of the Modern Synthesis and major concepts proper to the Synthesis that were introduced in various explanatory projects developed in ecology in the 1950s but in separate places. This project echoed the Synthesis as an attempt to synthesize and ground a novel body of ecological knowledge, as Wilson indicated above; strikingly, it did it in a way parallel to some major theoretical principles and concepts proper to the Synthesis.

Conclusion

This paper constructs a story that explains the acclimation of the Synthesis within ecology. It is not linear in two fundamental senses: not all steps give rise to following ones—that is, pathways sketched by Elton or later by Allee et al.'s *Principles* were given up—and parts of the Synthesis were acclimatized differently in different areas of ecology—for instance, importing population genetics modeling style in biogeography is different than implementing the major role played by selection in post-Hutchinsonian niche modeling of coexistence and regulation.

A striking switch occurred that brought evolution by natural selection into ecology. Evolution and ecology are now acclimatized opposite of Elton's animal ecology: in the last avenues of integration of the Synthesis within ecology, all *concur* in explaining phenomena, instead of evolution by natural selection being supplemented by an ecological explanation. We have successively witnessed this in the Hutchinsonian niche concept, in the gene-oriented "evolutionary ecology," or in the emergence of the notion of "species strategy" that culminated in the *Theory of Island Biogeography* with the idea of "best colonizer."

Scholars often partition current ecology between "ecosystem ecology" and "evolutionary ecology," as Hagen (1992) did. Each famously bears the mark of Hutchinson's students: Lindemann and Odum for the former, MacArthur for the latter. But "evolutionary ecology" is much larger than what is usually encapsulated by that term—namely behavioral ecology and approaches like Lerner's or Pimentel's, which import a genetic viewpoint in community ecology. It is this multifaceted field of "evolutionary ecology"—which Hagen opposes to a functional or ecosystem ecology—that resulted from the *acclimations* of the Synthesis into ecology. I use the plural form of the noun because—besides the birth of "behavioral ecology" and the thread that runs from Ford to Lerner, Leven and Pimentel's approaches documented here and likely to be labeled "evolutionary ecology"—another acclimation of the Synthesis ran through the competition debates, the Hutchinsonian niche concept, and the models of MacArthur and Wilson. Thus, acclimation of the Synthesis has been plural and never complete.

Hence, against Kimler (1986), who reduced the birth of evolutionary ecology to "recognition of the existence of a theoretical question, namely, at what level of biological organization does natural selection act" (p. 232), I sketch the acclimation of

the Synthesis in ecology as a multifarious process. In this story, I have consistently underscored the key role of a few figures from the Synthesis, which documents their intertwining (both personally and institutionally) with ecology. All aspects of this integration were patronized to some extent by Synthesis biologists, in ways specified above. But the result was not so straightforward; the connections that I identified here were to some extent successive and did not merge altogether into an ecological synthesis. “Evolutionary Ecology” (in the sense of the textbooks so entitled that emerged from the thread presented here) remains a subdiscipline whose relation to biogeography is not tight. Therefore, integrating ecology within the Synthesis appeared as a project deemed crucial by the architects of the Synthesis, but which ultimately did not succeed either in providing a consistent extension to the Modern Synthesis, or an entire, structured reshaping of the field of ecology along its lines. In fact, it yielded various acclimations of the Synthesis into ecology.

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References

- Allee, W.C., O. Park, A.E. Emerson, T. Park, and K.P. Schmidt. 1949. *Principles of Animal Ecology*. Philadelphia, PA: W. B. Saunders Company.
- Anderson, Ted R. 2013. *The Life of David Lack: Father of Evolutionary Ecology*. New York, NY: Oxford University Press.
- Andrewartha, H.G., and L.C. Birch. 1954. *The Distribution and Abundance of Animals*. Chicago, IL: University of Chicago Press.
- Anonymous. 1936. Genetics and Ecology in Relation to Selection. *Nature* 138 (3496): 748–749.
- Antonovics, J. 1976. Plant Population Biology at the Crossroads. *Input from Population Genetics. Systematic Botany* 1: 234–245.
- Baker, J.R. 1938. The Evolution of Breeding Seasons. In *Evolution: Essays on Aspects of Evolutionary Biology*, ed. G.R. de Beer, 161–177. Oxford: Oxford University Press.
- Beatty, J. 1986. The Synthesis and the Synthetic Theory. In *Integrating Scientific Disciplines*, ed. W. Bechtel, 125–136. The Hague: Nijhoff.
- Beatty, J. 1988. Ecology and Evolutionary Biology in the War and Postwar Years: Questions and Comments. *Journal of the History of Biology* 21: 245–263.
- Beatty, J. 1994. The Proximate/Ulimate Distinction in the Multiple Careers of Ernst Mayr. *Biology and Philosophy* 9: 333–356.
- Benson, K. 1992. Experimental Ecology on the Pacific Coast: Victor Shelford and His Search for Appropriate Methods. *History and Philosophy of the Life Sciences* 14(1): 73–91.
- Blomquist, G. 2007. Population Regulation and the Life History Studies of LaMont Cole. *History and Philosophy of the Life Sciences*, 29(4): 495–516.
- Borrello, M.E. 2003. Synthesis and Selection: Wynne-Edwards’ Challenge to David Lack. *Journal of the History of Biology* 36: 531–566.

- Bruno, J.F., J.J. Stachowicz, and M.D. Bertness. 2003. Inclusion of Facilitation into Ecological Theory. *Trends in Ecology & Evolution* 18: 119–125.
- Bryant, E.H. 1971. Life History Consequences of Natural Selection: Cole's Result. *American Naturalist* 105: 75–76.
- Burian, R. 1988. Challenges to the Evolutionary Synthesis. *Evolutionary Biology* 23: 247–269.
- Cain, J. 1993. Common Problems and Cooperative Solutions: Organizational Activities in Evolutionary Studies, 1937–1946. *Isis* 84: 1–25.
- Cain, J. 2000. Towards a 'Greater Degree of Integration': The Society for the Study of Speciation, 1939–1941. *British Journal for the History of Science* 33: 85–108.
- Cain, J. 2002. Epistemic and Community Transition in American Evolutionary Studies: The 'Committee on Common Problems of Genetics, Paleontology, and Systematics' (1942–1949). *Studies in History and Philosophy of Biological and Biomedical Sciences* 33 (2): 283–313.
- Cain, J. 2009. Rethinking the Synthesis Period in Evolutionary Studies. *Journal of the History of Biology* 42 (4): 621–648.
- Cain, J. 2010. Julian Huxley, General Biology and the London Zoo, 1935–42. *Notes and Records of the Royal Society* 64 (4): 359–378.
- Calhoun, J. 1952. The Social Aspects of Population Dynamics. *Journal of Mammalogy* 33 (2): 139–150.
- Charnov, E.L., and W.M. Schaffer. 1973. Life History Consequences of Natural Selection: Cole's Result Revisited. *American Naturalist* 107: 791–793.
- Chitty, D. 1960. Population Processes in the Vole and Their Relevance to General Theory. *Canadian Journal of Zoology* 38: 99–113.
- Clements, F.E., and Shelford V. 1939. *Bio-ecology*. New-York: Chapman & Hall.
- Cold Spring Harbor Symposia on Quantitative Biology. 1957. *Population Studies: Animal Ecology and Demography*, vol. 22. Cold Spring Harbor, NY: Biological Laboratory. <http://symposium.cshlp.org/content/22>. Accessed 21 Jan 2016.
- Cole, L.C. 1950. Principles of Animal Ecology—An Appraisal. *Ecology* 31 (1): 153–155.
- Cole, L.C. 1954. The Population Consequences of Life History Phenomena. *Quarterly Review of Biology* 29: 103–137.
- Coleman, W. 1986. Evolution into Ecology? The Strategy of Warming's Ecological Plant Geography. *Journal of the History of Biology* 19 (2): 181–196.
- Collins, J.P. 1986. Evolutionary Ecology and the Use of Natural Selection in Ecological Theory. *Journal of the History of Biology* 19 (2): 257–288.
- Collins, J.P., J. Beatty, and J. Maienschein. 1986. Introduction: Between Ecology and Evolutionary Biology. *Journal of the History of Biology* 19 (2): 169–180.
- Connell, J. 1961. The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus Stellatus*. *Ecology* 42 (4): 710–723.
- Cooper, G. 2003. *The Science of the Struggle for Existence*. Cambridge: Cambridge University Press.
- Courchamp, F., J. Berencs, and J. Gascoigne. 2008. *Allee Effects in Ecology and Conservation*. New York, NY: Oxford University Press.
- Depew, D. 2011. Adaptation as a Process: The Future of Darwinism and the Legacy of Theodosius Dobzhansky. *Studies in the History of Biology and the Biomedical Sciences* 42: 89–98.
- Dobzhansky, T. 1937. *Genetics and the Origin of Species*. New York: Columbia University Press.
- Dobzhansky, T. 1950. The Science of Ecology Today. Review of Principles of Animal Ecology by W. C. Allee, Alfred E. Emerson, Orlando Park, Thomas Park, Karl P. Schmidt. *Quarterly Review of Biology* 25 (4): 408–409.
- Dowdeswell, W.H., R.W. Fisher, and E.B. Ford. 1949. The Quantitative Study of Populations in the Lepidoptera; *Maniola jurtina* L. *Heredity* 3: 67–84.
- Dowdeswell, W.H., and E.B. Ford. 1952. The Distribution of Spot-Numbers as an Index of Geographical Variation in the Butterfly *Maniola jurtina* L. (Lepidoptera, Satyridae). *Heredity* 6: 99–109.
- Egerton, F. 2014. A 1961 Letter from A. J. Nicholson. *Bulletin of the Ecological Society of America* 95 (2): 101–186.
- Elton, C. 1927. *The Ecology of Animals*. New York: Wiley.
- Elton, C. 1930. *Animal Ecology and Evolution*. Oxford: Clarendon Press.
- Emerson, A.E. 1939. Social Coordination and the Superorganism. *American Midland Naturalist* 21: 182–209.
- Fisher, R.A., and E.B. Ford. 1947. The Spread of a Gene in Natural Conditions in a Colony of Moth *Panaxia dominula* L. *Heredity* 1: 143–174.
- Ford, E.B. 1964. *Ecological Genetics*. London: Chapman and Hall.

- Ford, E. B. 1980. Some Recollections Pertaining to the Evolutionary Synthesis. In *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, 336–338. Cambridge, MA: Harvard University Press.
- Fretwell, S. 1975. The Impact of Robert MacArthur on Ecology. *Annual Review Ecology Systematics* 6: 1–13.
- Futuyama, D.J. 1986. Reflections on Reflections: Ecology and Evolutionary Biology. *Journal of the History of Biology* 19 (2): 303–312.
- Gause, G. 1934. *The Struggle for Existence*. Baltimore, MD: Williams and Wilkins.
- Gause, G. 1935. Experimental Studies on the Struggle for Existence. *Journal of Experimental Biology* 9: 389–402.
- Gay, Hannah. 2013. *The Silwood Circle: A History of Ecology and the Making of Scientific Careers in Late Twentieth-Century Britain*. London: Imperial College Press.
- Gleason, H.A. 1939. The Individualistic Concept of the Plant Community. *The American Midland Naturalist Journal* 21: 92–110.
- Hagen, J. 1989. Research Perspectives and the Anomalous Status of Modern Ecology. *Biology and Philosophy* 4: 433–455.
- Hagen, J. 1992. *The Entangled Bank: The Origins of Ecosystem Ecology*. New Brunswick, NJ: Rutgers University Press.
- Harper, J.L. 1967. A Darwinian Approach to Plant Ecology. *Journal of Ecology* 55: 247–270.
- Holt, R.D. 2006. Emergent Neutrality. *Trends in Ecology & Evolution* 21: 531–533.
- Hutchinson, G.E. 1957. Concluding Remarks: Cold Spring Harbor Symposium. *Quantitative Biology* 22: 415–427.
- Hutchinson, G.E. 1959. Homage to Santa Rosalia or Why are There So Many Kinds of Animals. *The American Naturalist* 93: 145–159.
- Hutchinson, G.E. 1961. The Paradox of the Plankton. *The American Naturalist* 95: 137–145.
- Hutchinson, G.E. 1965. *The Ecological Theater and the Evolutionary Play*. New Haven, CT: Yale University Press.
- Hutchinson, G. E., and E. S. Deevey, Jr. 1949. Ecological Studies on Populations. In *Survey of Biological Progress*, ed. George S. Avery, Jr., 325–359. New York, NY: Academic Press, Inc.
- Huxley, J. 1936. Natural Selection and Evolutionary Progress. *Nature* 138: 571–573.
- Huxley, J. (ed.) 1940. *The New Systematics*. Oxford: Clarendon Press.
- Ilerbaig, J. 1999. Allied Sciences and Fundamental Problems: C.C. Adams and the Search for Method in Early American Ecology. *Journal of the History of Biology* 32: 439–470.
- Ishida, Y. 2007. Patterns, Models, and Predictions: Robert MacArthur's Approach to Ecology. *Philosophy of Science* 74: 642–653.
- Kimler, W.C. 1986. Advantage, Adaptiveness, and Evolutionary Ecology. *Journal of the History of Biology* 19: 215–233.
- Kimura, M. 1985. *The Neutral Theory of Molecular Evolution*. Cambridge: Cambridge University Press.
- Kingsland, S.E. 1986. Mathematical Figments, Biological Facts: Population Ecology in the Thirties. *Journal of the History of Biology* 19 (2): 235–256.
- Kingsland, S.E. 1995. *Modeling Nature: Episodes in the History of Population Ecology*. Chicago, IL: University of Chicago Press.
- Kingsland, S.E. 1997. Neo-Darwinism and Natural History. In *Companion to Science in the Twentieth Century*, ed. J. Krige and D. Pestre, 417–438. London: Routledge.
- Krebs, C.J. 1978. A Review of the Chitty Hypothesis of Population Regulation. *Canadian Journal of Zoology* 56 (12): 2463–2480.
- Krebs, C.J. 1995. Two Paradigms of Population Regulation. *Wildlife Research* 22: 1–10.
- Krebs, J.R., and N. Davies. 1995. *Behavioral Ecology: An Evolutionary Approach*. London: Blackwell.
- Lack, D. 1947a. The Significance of Clutch-Size. *Ibis* 89: 302–352.
- Lack, D. 1947b. *Darwin's Finches*. Cambridge: Cambridge University Press.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Oxford University Press.
- Leibold, M.A., and M.A. McPeck. 2006. Coexistence of the Niche and Neutral Perspectives in Community Ecology. *Ecology* 87 (6): 1399–1410.
- Lerner, I.M., and E.R. Dempster. 1962. Indeterminism in Interspecific Competition. *Proceedings of the National Academy of Sciences of the United States of America* 48 (5): 821–826.
- Leslie, P.H., and T. Park. 1949. The Intrinsic Rate of Natural Increase in *Tribolium castaneum* Herbst. *Ecology* 30: 469–477.

- Leslie, P.H., T. Park, and D.B. Mertz. 1968. The Effect of Varying the Initial Numbers on the Outcome of Competition Between Two *Tribolium* Species. *Journal of Animal Ecology* 37: 9–23.
- Levene, H. 1953. Genetic Equilibrium When More Than One Ecological Niche is Available. *The American Naturalist* 87 (836): 331–333.
- Levene, H., and T. Dobzhansky. 1959. Possible Genetic Difference Between the Head Louse and the Body Louse (*Pediculus humanus* L.). *The American Naturalist* 93 (873): 347–353.
- Levins, R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton University Press.
- MacArthur, R.H. 1972. Coexistence of Species. In *Challenging Biological Problems: Directions toward Their Solution*, ed. John A. Behnke, 253–259. New York, NY: Oxford University Press.
- MacArthur, R.H., and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* 101: 377–385.
- MacArthur, R.H., and E.R. Pianka. 1966. On Optimal Use of a Patchy Environment. *The American Naturalist* 100: 603–609.
- MacArthur, R.H., and E.O. Wilson. 1967. *Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Mayr, E. 1961. Cause and Effect in Biology. *Science* 134: 1501–1506.
- Mayr, E., and W. Provine (eds.). 1980. *The Evolutionary Synthesis. Perspectives on the Unification of Biology*. Cambridge, MA: Harvard University Press.
- McIntosh, R.P. 1980. The Background and Some Current Problems of Theoretical Ecology. *Synthese* 43 (2): 195–255.
- McIntosh, R.P. 1986. *The Background of Ecology: Concept and Theory*. Cambridge: Cambridge University Press.
- Mitman, G. 1988. From the Population to Society: The Cooperative Metaphors of W.C. Allee and A. E. Emerson. *Journal of the History of Biology* 21 (2): 173–192.
- Nicholson, A.J. 1933. The balance of animal populations. *Journal of Animal Ecology* 2: 131–78.
- Nicholson, A., and V. Bailey. 1935. The Balance of Animal Populations—Part 1. *Proceedings of the Zoological Society of London* 3: 551–598.
- Odenbaugh, J. 2013. Searching for Patterns, Hunting for Causes: Robert MacArthur, the Mathematical Naturalist. In *Rebels, Mavericks, and Heretics in Biology*, ed. O. Harman and M. Dietrich, 265–281. New Haven, CT: Yale University Press.
- Ogden, J., and J. Harper. 1970. The Reproductive Strategy of Higher Plants, I: The Concept of Strategy with Special Reference to *Senecio vulgaris* L. *Journal of Ecology* 58: 681–698.
- Orians, G. 1962. Natural Selection and Ecological Theory. *The American Naturalist* 96 (890): 257–263.
- Paine, R.T. 1966. Food Web Complexity and Species Diversity. *The American Naturalist* 100: 65–75.
- Palladino, P. 1991. Defining Ecology: Ecological Theories, Mathematical Models, and Applied Biology in the 1960s and 1970s. *Journal of the History of Biology* 24: 223–243.
- Park, T. 1946. Some Observations on the History and Scope of Population Ecology. *Ecological Monographs* 16 (4): 313–320.
- Park, T. 1948. Experimental Studies of Interspecies Competition I. Competition Between Populations of the Flour Beetles *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecological Monographs* 18: 265–308.
- Park, T. 1954. Experimental Studies of Interspecies Competition II. Temperature, Humidity and Competition in Two Species of *Tribolium*. *Physiological Zoology* 27: 177–191.
- Pianka, E. 1983. *Evolutionary Ecology*. London: Harper & Row.
- Pimentel, D. 1968. Population Regulation and Genetic Feedback. *Science* 159: 1432–1437.
- Pocheville, A. 2015. The Ecological Niche: History and Recent Controversies. In *Handbook of Evolutionary Thinking in the Sciences*, ed. T. Heams, P. Huneman, G. Lecointre, and M. Silberstein, 547–586. Dordrecht: Springer.
- Ramsden, E., and J. Adams. 2009. Escaping the Laboratory: The Rodent Experiments of John B. Calhoun & Their Cultural Influence. *Journal of Social History* 42 (3): 761–792.
- Richardson, D. (ed.). 2011. *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*. London: Wiley.
- Roughgarden, J. 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. London: Prentice Hall.
- Schmidt, K.P. 1957. *Clyde Warder Allee: Biographical Memoir*. Washington, DC: National Academy of Sciences.
- Schröter, C., and O. Kirchner. 1902. *Die Vegetation des Bodensees. Teil II. – Schriften des Vereins zur Geschichte des Bodensees*. 31: 1–86.

- Slack, N. 2003. Are Research Schools Necessary? Contrasting Models of 20th Century Research at Yale Led by Ross Granville Harrison, Grace E. Pickford and G. Evelyn Hutchinson. *Journal of the History of Biology* 36 (3): 501–529.
- Slack, N. 2010. *G. Evelyn Hutchinson and the Invention of Modern Ecology*. New Haven, CT: Yale University Press.
- Slobodkin, L., and N. Slack. 1999. George Evelyn Hutchinson: 20th-Century Ecologist. *Endeavour* 23 (1): 24–30.
- Smith, F.E. 1952. Experimental Methods in Population Dynamics. *Ecology* 33: 441–450.
- Smocovitis, V.B. 1992. Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology. *Journal of the History of Biology* 25: 1–65.
- Smocovitis, V.B. 1994. Organizing Evolution: Founding the Society for the Study of Evolution (1939–1950). *Journal of the History of Biology* 27: 241–309.
- Solomon, M.E. 1949. The Natural Control of Animal Population. *Journal of Animal Ecology* 18 (1): 1–34.
- Stearns, S. 1982. The Emergence of Evolutionary and Community Ecology as Experimental Science. *Perspectives in Biology and Medicine* 25 (4): 621–648.
- Tansley, A.G. 1935. The Use and Abuse of Vegetational Concepts and Terms. *Ecology* 16: 284–307.
- Thompson, J. 1939. Biological Control and the Theories of the Interactions of Populations. *Parasitology* 31: 299–388.
- van der Valk, A.G. 2014. From Formation to Ecosystem: Tansley's Response to Clements' Climax. *Journal of the History of Biology* 47: 293–322.
- Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Memoria della Reale Accademia Nazionale dei Lincei* 2: 31–113.
- Warming, E. 1909. *Oecology of Plants*. Oxford: Clarendon Press.
- Wellington, W.G. 1957. Individual Differences as a Factor in Population Dynamics: The Development of a Problem. *Canadian Journal of Zoology* 35: 293–323.
- Williams, G.C. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Wilson, E.O. 2010. Island Biogeography in the 1960s. In *The Theory of Island Biogeography*, ed. B. Losos and R. Ricklefs, 1–13. Princeton, NJ: Princeton University Press.
- Wright, S. 1961. Thomas Park, President-Elect. *Science* 131 (3399): 502–503.
- Wynne-Edwards, J.C. 1962. *Animal Dispersion in Relation to Social Behavior*. New York, NY: Hafner.

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