Introduction

Why Philosophy of Ecology?

Dobzhansky's sweeping generalization, "nothing in biology makes sense except in the light of evolution" (1964, 449), provocatively captures the centrality of evolutionary theory in contemporary biological science (see also Dobzhansky 1973). But his indelible rally call is also revisionist history, and grievously partial. Although the term "ecology" was not coined until 1866 (Haeckel 1866), most of what would be deemed biological investigation that did not concern the interior of organisms since at least the time of the ancient Greeks, and long before a nascent awareness of evolutionary forces, falls squarely within the purview of ecology. The biological understanding that laid the groundwork out of which evolutionary theory emerged was largely ecological.

Ecology therefore casts the same indispensable light in biology, and particularly on evolution. Ecological insights were an integral part of early evolutionary thinking; they are at the core of Darwin's original theory; and they will remain crucial to theorizing about how evolutionary dynamics shape the biological world. Consider evolutionary theory's central concept, natural selection. Evolution by natural selection is traditionally thought to depend on three population-level factors: phenotypic variation, heritability, and differential fitness (see Lewontin 1970).[1] All three are biologically crucial components, and at least the latter two have garnered significant attention from philosophers of biology (on heritability, see Tabery 2014 and Downes and Matthews 2019; on fitness, see Rosenberg and Bouchard 2015).

[1] Interestingly, population structure poses problems for this concise characterization of evolution by natural selection (see Godfrey-Smith 2007). Besides its relevance to population genetics, population structure is obviously also an important research topic within population ecology.

But without a doubt fitness is the conceptual and explanatory core of evolution by natural selection, and by far the most philosophical ink has been expended on it. What has not been recognized as widely or thoroughly as it should be is that fitness is a fundamentally ecological concept. Without wading into the substantial controversy about how exactly it should be characterized, it is safe to say that fitness depends on the relations between the traits of an organism and the various aspects of the environment it lives in. That is vague, of course, and hence the philosophical controversy. But studies of how organisms make their living in their different environments are about as central to ecology as it gets.

Moreover, indefensibly ignoring an ecological perspective is arguably responsible for flawed conceptions of fitness that motivate defining it in terms of reproductive rates, thereby abetting the infamous Popperian charge that evolutionary theory is tautologically vacuous. Properly *defining* fitness requires considering the organism–environment relations at the core of ecology. Only by disregarding those relations to focus exclusively on measures of reproductive success does the triviality threat gain purchase.

Fitness, in turn, is at the heart of other important biological concepts and explanations of biological phenomena, for example, adaptation, speciation, multilevel selection, niche construction, and perhaps even biological individuality, to name but a few. If fitness, evolution by natural selection, and evolutionary theory in general are unquestionably in the wheelhouse of any competent philosopher of biology, ecology should be as well.

Apart from its contribution to evolutionary theory, ecology also endeavors to account for vast portions of the living world directly. It is, for example, canonically characterized as the study of interactions between organisms and the environment. Its explanatory scope therefore includes not only these interactions but also their causal ramifications: the distributions and abundances of species they produce throughout the globe. Any science with an agenda this ambitious, especially one that pursues it with such sophisticated mathematical models and complex statistical methods for empirically testing them, deserves significant attention from philosophers of science.

Thus far the title question has received two answers: (1) an ecological perspective underpins much of evolutionary theory, so competent philosophy of the latter, whose value is unquestioned, requires the same of the former; and (2) any science with such a global scope merits philosophical attention. Answer (2) is generic. Many other sciences are in the same camp, and like ecology, many are beginning to receive appropriate interest from philosophers of science: archeology (Chapman and Wylie 2016), chemistry (Hendry et al. 2011), paleontology (Turner 2011; Currie 2018), and others. Answer (1) is specific to ecology, and perhaps a few other biological disciplines that contribute directly to understanding evolutionary dynamics, for example, developmental and molecular biology. But answer (1) is also derivative. Philosophy of ecology's significance piggybacks on the philosophical significance of evolution. Dependency is not diminishment, but the value is not autonomous.

Fortunately, there is ample autonomous value to go around. For starters, the systems studied in ecology are unbelievably complex. Ecosystems contain a plethora of distinct kinds of entities, which interact in an untold number of ways, and do so on numerous spatial and temporal scales. Even the simple task of representing these systems in a model poses interesting philosophical issues about, for example, the nature and justification of (usually necessary) idealizations (Weisberg 2007), when inference under conditions of significant uncertainty is reliable (Justus 2012a), how the epistemic credentials of such (sometimes quite unwieldy) models can be evaluated (Winsberg 2018), the ultimate limits of representations in science (van Fraassen 2008; Weisberg 2013), and many others.[2]

The magnitude of this complexity does not mean it is necessarily unmanageable or that simple unifying principles will never be found. Imagine the natural philosopher-scientist well before Mendeleev and his predecessors. It understandably would have seemed preposterous that the seemingly innumerable types of substances exhibiting such a vast array of different properties were actually composed of only a relatively small number of elements, elements that in turn could be grouped into an even smaller number of categories that explained much of their nature. Despite its apparently dismal odds, the periodic table was created and this unruly diversity tamed.

But the stubborn fact is that an analogous ecological periodic table has not been uncovered, after a century and a half of continuous scientific inquiry since Mendeleev's breakthrough, and with cutting-edge technologies and statistical methods of data analysis that far exceed the investigative capabilities of anything nineteenth-century scientists could have imagined, let alone

[2] For an excellent overview of all these issues in an ecological context, see Odenbaugh 2019.

have had access to. We should not be surprised. The chemical world is complicated, but at the elemental level its compositional complexity is much less daunting. Chemical processes are also much more tightly tethered to numerous law-like regularities, conservation of matter, conservation of energy, principles of electromagnetism, and so on. These regularities govern ecological systems as well, of course, but the constraint they impose is much more slack. Biological communities as diverse as the Amazon rainforest, Saharan desert, and Siberian boreal forests all dutifully conform to the law-like regularities, but these and other epistemic triumphs from physics offer little to explain the stark ecosystem differences.[3]

With little mooring in physics below and no grand unified theory governing from above, economics, rather than physics or chemistry, seems to constitute a close disciplinary analog to ecology (see Shulz 2020). Economics, like ecology, trades in extremely sophisticated mathematical models. And, like ecology, it lacks anything remotely resembling a comprehensive *and plausible* theoretical framework.[4] And perhaps because both disciplines lack such a framework they often utilize concepts and methods developed in other fields, such as physics, to construct those sophisticated mathematical models, which itself raises interesting philosophical issues (see Justus 2008b). Although economic data are plentiful, acquiring the kind of data that would definitively confirm or disconfirm economic models is extremely difficult. The same challenge confronts ecological modeling. Being heavy mathematically and light on (relevant) data makes economics and ecology philosophically rich subjects in their own right (see Kincaid and Ross 2017).

There is another dimension to the philosophical significance of ecology. Sciences are human activities that occur in broader cultural and societal

[3] It should be stressed that the challenge complexity poses, which differentiates ecology from many but certainly not all other sciences, does not establish some *inherent* difference, that it possesses some fundamentally distinct, autonomous nature that necessitates different epistemological approaches and methodologies from most other sciences. The complexity of ecological phenomena partially explains the current epistemic and methodological character of the science, and that dependency is itself philosophically interesting. But it is far from establishing ecology as an autonomous special science, whatever that may mean. Chapter 4 in fact shows ecology can benefit greatly from practices developed in other sciences if deployed wisely, mathematical models being the case study. For a sustained critique of the autonomy line for biology and defense of the role mathematics has in unifying the sciences, see Thompson 1995.

[4] Here I follow behavioral economists in holding that the death knell of *Homo economicus* and the Chicago school rattled long ago (see Kahneman and Tversky 2000).

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contexts.[5] The latter always bears on the former, and the former sometimes on the latter, but not nearly with the same intensity across disciplines. The newest discoveries in carbon sequestration or cancer sequencing have a social potency that the latest findings in vampire bat mating strategies or astrogeology do not. Ecology is unmistakably toward the potent end of that spectrum. As the impacts humans have on the natural world magnify, ecological studies can reveal their full, horrific ramifications. And ecology's expansive investigative purview ensures it is uniquely positioned to expose the details of those ramifications across a wide variety of different kinds of ecosystems and spatial scales, as well as possibly identify how they can be mitigated. In a way, ecological knowledge might provide the scientific antidote to ultimately catastrophic societal tendencies.

Similarly, ecology has uniquely epistemic authority vis-à-vis environmental ethics. First, the revelatory function described above can assist ethical theorizing. Ecology furnishes scientific facts that ethicists must recognize and respond to. The details of how global warming will affect coastal communities, for example, raise daunting issues about inequity and the environmentally exacerbated ramifications of economic and political inequality. Independent of concerns about animal welfare, the ecological effects of factory farming should also inform ethical judgments about them.

But there is a second kind of link between the disciplines. Environmental ethics often trades in concepts and claims that have both normative and descriptive content. For example, whether a negative ethical appraisal of exotic or invasive species is defensible depends on what they are and what they are capable of (Elliot-Graves 2016). Ethicists alone cannot answer those questions; ecological input is essential. Sober's (1986) trenchant criticism of environmental ethicists' use of a "naturalness" concept showcases the salience of biological science, ecology in particular, in environmental ethics.[6] That input might influence the valence of an ethical judgment, or clarify that one basis for an ethical position is inferior to another or outright indefensible. Whether there is a

[5] Here it is crucial to sharply distinguish ecology the science from popular characterizations of the term 'ecology' associated with environmental and other sociopolitical views, such as that "everything is interconnected" or new-age versions of the Gaia hypothesis (see Ruse 2013). For those with little exposure to biological science, the two connotations are often conflated.

[6] "[T]o the degree that 'natural' means anything biologically, it means very little ethically. And, conversely, to the degree that 'natural' is understood as a normative concept, it has very little to do with biology" (p. 180).

"balance of nature" as Paul Taylor (1986) intends that phrase is another example of where ecological science should bear on theories of value in the natural world.

So far, I have described general features of ecological science that garner philosophical interest. But, as with any new and burgeoning field, focus has congealed around several broad areas:

1. conceptual issues in the history of ecology
2. characterizing problematically unclear ecological concepts, especially "biodiversity" and "stability"
3. whether there are distinctively ecological laws
4. reduction in ecological science and the reality of biological communities
5. the role of mathematical modeling in ecology
6. the relationships between evolutionary theory and ecology, and conservation science and ecology.
7. the role of non-epistemic values in applied sciences

Beyond a narrow focus on ecology, some of these areas offer novel insights into standard topics in general philosophy of science, such as emergence and reduction, the nature of laws of nature, conceptual content and concept determination, the status and function of models in science, and the status and function of values in sciences.

Others areas involve topics unique to ecology, and to which philosophers can make valuable contributions to scientific practice. Each area, in turn, covers numerous specific issues. With respect to item (4), for example, some ecologists and philosophers of science have recently proposed an analogy between Newtonian mechanics and ecosystem dynamics (Ginzburg and Colyvan 2004). Although the status and epistemic utility of this analogy remain controversial, this work suggests a close parallel should exist between modeling strategies in physics and ecology. But other analyses counter this parallel. For example, Hubbell's (2001) unified neutral theory of biodiversity primarily derives from theories developed within biology proper: MacArthur and Wilson's (1967) theory of island biogeography and Kimura's (1983) neutral theory of molecular evolution. And one concept of stability appropriated from physics and often employed in ecological modeling, Lyapunov stability, seems unable to capture the ecological phenomena it is intended to represent (Justus 2008b). Analyses of this unresolved issue shed light on the different role that models may have in biology and physics in general. With respect to item (1), to cite another prominent example, there are several concepts besides "biodiversity" and "stability" central to ecological science and in need of conceptual clarification, including "carrying capacity," "community," "complexity," "disturbance," "ecosystem," "habitat," "keystone species," "niche," "population," and many others. Like most concepts in developing sciences, fully adequate definitions of these and other ecological concepts have not yet been formulated. These and other issues provide rich conceptual grist for philosophers of ecology.

As these examples illustrate, ecology concerns a diverse conceptual terrain and an interesting set of theoretical and methodological issues, thus far underexplored by philosophers of science. The subsequent chapters describe its main contours and introduce readers to some of the most exciting topics in philosophy of ecology.

Chapter 1 scrutinizes the ecological unit thought to underlie the structure of biological communities and perhaps provide a "conceptual foundation" for the science: the niche. The history of the concept's origin and development is recounted, from its beginning with Joseph Grinnell and Charles Elton, and culminating in G. E. Hutchinson's highly abstract *n*-dimensional hyper-volume account. The niche is widely believed to be a fundamental abstraction in ecological theorizing, essential to ensuring its generality. For example, general accounts of the similar structure of communities composed of different species are only possible, it seems, if a shared underlying niche structure generates the similarity. Grasslands in the central plains of North America and Africa share a similar structure and exhibit similar dynamics because they instantiate roughly the same system of niches, it is claimed, albeit with different species. This is only one of many seemingly indispensable functions of the niche concept. Appeals to niche structure seem to provide the only explanation of convergent evolution, character displacement, as well as evolutionary convergence of ecosystems: remarkably similar biological communities emerging over geologic time scales (e.g., past communities with saber-tooth tigers as apex predators and present communities with *Canis* species functioning similarly).

But this paradigm has been challenged in at least two ways. First, "neutral" theories of community structure, particularly Stephen Hubbell's "Unified Neutral Theory of Biodiversity," pose a serious threat to the putative indispensability of niche thinking. By emphasizing the role of dispersal limitation, sampling effects, and stochasticity within a cohesive model of community dynamics, neutralists have formulated a cogent alternative to

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"rules of community assembly" based on niche structure. Second, niche constructionists' recent charge that many niches are made, not found, seems to make the standard account inapplicable. If organisms can modify their environments and thereby their niches to increase fitness, it is no longer clear the niche has explanatory priority. What explains community structure, convergent evolution, character displacement, and the like is no longer an extant niche structure that specific communities realize or that imposes a selection regime producing convergence and displacement. Rather, a locus of explanatory force resides within organisms that do the niche constructing. After carefully examining the content of proposed definitions of the niche, and the supposed contributions it makes to ecology theory, Chapter 1 also arrives at a negative assessment, but with a very different basis. Despite its supposed centrality, the analysis surprisingly concludes the niche concept is dispensable. It simply does not do the significant conceptual or explanatory work in ecology it is claimed to do.

Chapter 2 connects ecology with two central issues in general philosophy of science: what marks the real, and the nature of laws of nature. On the former, biological communities are the problem case. The question is whether they are anything more than the individual organisms of different species comprising them. If they are not, presumably they possess no independent existence. If they are, an account is needed of (1) this "something more" *and* (2) how it confers independent existence. Absent either, realist aspirations are frustrated. The first task requires a careful dissection of community structure, community dynamics, species distribution patterns, and what they reveal about how groups of species might assemble into communities. For example, individualists claim that species distributions along environmental gradients overlap continuously and significantly, and do not form discrete boundaries. But, the argument continues, communities are only real if they have such distinct boundaries. So they are not real. The second task involves delving into metaphysics, principally to determine whether the "something more" these ecological assemblages possess actually "cuts nature at its joints," the proverbial criterion for ontological credibility according to realists. These issues have catalyzed lively debate in several recent publications, and vetting the arguments contained therein is one of the two main goals of this chapter.

The second goal is addressing a similarly intricate and fundamental topic: whether there are laws in ecology. There are various challenges to the idea that there are such laws: ecology's relative paucity of predictive success, that its models and experimental results lack sufficient generality, that candidate laws are riddled with exceptions, and that ecological systems are too complex. But complexity is surely a surmountable obstacle. It is difficult to imagine a more complicated system than the entire cosmos, but no one suggests its complexity is not governed by relativistic and quantum mechanical laws, or that humans do not continue to uncover their form. Some philosophers have recently argued that other properties thought to preclude a discipline from trading in laws – limited predictive accuracy, generality, not being exceptionless – should be jettisoned, and that ecology indicates why. Ecology, they argue, has uncovered regularities, such as Gause's supposed law of competitive exclusion and numerous allometries, that possess a kind of necessity and therefore merit the label law of nature.

The idea there is a "balance of nature" in focus in Chapter 3 was a staple of the schools of natural philosophy from which biology emerged, long before the term "ecology" was even coined. Some early ecologists continued this tradition by attempting to derive the existence of a "natural balance" in biological populations from organismic metaphors and anthologies with physical systems. Not until the second half of the twentieth century was the concept of a balance of nature rigorously characterized as a kind of stability, and the predominantly metaphysical speculations about its cause superseded with scientific hypotheses about its basis. But significant uncertainty and controversy exists about what features of an ecological system's dynamics should be considered its stability, and thus no consensus has emerged about how ecological stability should be defined. Instead, ecologists have employed a confusing multitude of different terms to attempt to capture apparent stability properties: "constancy," "persistence," "resilience," "resistance," "robustness," "tolerance," and many more. This, in turn, has resulted in conflicting conclusions about debates concerning the concept based on studies using distinct senses of ecological stability.

Different analyses seem to support conflicting claims and indicate an underlying lack of conceptual clarity about ecological stability that this chapter diagnoses and resolves. In particular, a comprehensive account of stability is presented that clarifies the concepts ecologists have used that are defensible, their interrelationships, and their potential relationships with other biological properties, including diversity and so-called ecosystem functioning. Chapter 3 also evaluates the intriguing idea developed by some ecologists and philosophers of science that there *must* be a balance of nature given the claimed necessity of density-dependence and the negative feedback mechanism it imposes on population growth. Besides providing insights about how problematic scientific concepts should be characterized, it is worth noting that the issues addressed in this chapter have a potential bearing on biodiversity conservation. It seems that for most senses of stability, more stable communities are better able to withstand environmental disturbances, thereby decreasing the risk of species extinction. If there is a systematic positive feedback between diversity and stability, that would therefore support conservation efforts to preserve biodiversity.

To learn anything significant about the natural systems, ecologists have to represent them. The most common types of representation in ecology, and science in general, are mathematical models. Models of biological populations and communities take a wide array of functional forms and can contain many different types of variables and parameters. This complexity, the focus of Chapter 4, makes for fertile philosophical fodder and connects ecology to the extensive literature in general philosophy of science on modeling and scientific representation. To manage this complexity, ecologists sometimes borrow concepts and methods developed in other sciences. The fruits and perils of such cross-disciplinary fertilization is explored with two case studies: the methodological individualism of individual-based models, which connects ecology and social science, and defining ecological stability as Lyapunov stability, which connects ecology and physics. The first connection bears significant fruits, the second proves perilous.

Some biological communities are clearly more complicated than others. For example, tropical communities usually contain more species; there is evidence their species interact more intensely; these interactions are more variegated in form; and they exhibit more trophic levels than high latitude communities. Ecologists often invoke the concept of diversity to represent these differences in the "complicatedness" of communities: tropical communities are often said to be more ecologically diverse than tundra communities. Chapter 5 explains how "biodiversity" (coined as a simple shorthand for "biological diversity" in the mid-1980s) captures this notion of ecological diversity and much more, including developmental, morphological, and taxonomic diversity. Simply put, it designates the diversity of biological systems at all organizational levels, the population and community levels being the most common focus in ecology. How biodiversity should be characterized therefore depends on how these systems are represented, particularly on how their parts are individuated, classified, and distributed among those classes. Representations may vary with different explanatory or predictive scientific goals, and across types of systems, so characterizations of biodiversity may vary across these contexts as well.

Philosophers are drawn to the concept of biodiversity given its problematic complexity and the interesting theoretical and methodological issues the sciences studying and endeavoring to protect it raise. Its significance is common currency within environmental ethics, but biodiversity has only recently garnered broader attention from philosophers of science. This chapter describes the main contours of the concept and guides the reader through some of the growing scientifically oriented philosophical literature on biodiversity. It also makes the connection, explored in great detail in Chapter 6, between ecology proper and the kind of applied ecology conducted in efforts to conserve biodiversity, conservation biology.

Chapter 6 shows that the notion of progress for ethically driven applied sciences needs to be rethought. Conservation biology emerged as a rigorous science focused on protecting biodiversity, and as a discipline of applied ecology distinct from pure ecology, in the 1980s. Two algorithmic breakthroughs in information processing made this possible: place-prioritization algorithms and geographical information systems. They provided a defensible, data-driven methodology for designing reserves to conserve biodiversity. This obviated the need for largely intuitive and highly problematic appeals to ecological theory to design reserves at the time. They also supplied quantitative, largely critical assessments of existing reserves. Most reserves had been designated on unsystematic, ad hoc grounds and consequently poorly represented biodiversity. Demonstrating this convincingly was unsurprisingly crucial to ensuring biodiversity would be adequately protected in future policy-making contexts.

Despite these unquestionable advances, the notion that they constitute scientific "progress" has recently been criticized. Traditional ecological theory, such as island biogeography theory, it is claimed, is required for genuine progress about reserve design; algorithmic innovation in data processing is insufficient. Place-prioritization algorithms are also supposedly less scientifically grounded and produce reserves that poorly protect biodiversity. Chapter 6 argues that on all accounts this criticism is indefensible

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and involves numerous inaccuracies about the science, misconstrues the character of applied science, and relies on an untenable conception of progress for applied sciences with ethical objectives such as conservation biology. Although applied sciences are unquestionably science and employ scientific methods, what constitutes progress within them should not always be judged by the standards of classic descriptive sciences such as chemistry, evolutionary biology, and physics.

Chapter 7 attempts to clarify the *proper* role of ethical values in ethically driven disciplines of applied ecology such as conservation biology, invasion biology, and restoration ecology. Most sciences are principally concerned with discovering and explaining phenomena, but applied sciences sometimes have a different, explicitly ethical agenda. Some applied sciences pursue more immediately pressing goals, such as solving societal problems. Applied ecology and biodiversity conservation, and medical science and human health are two examples. Nonepistemic values concerning ethical goals seemingly permeate these "teleological" sciences. One of the most direct ways in which ethical and sociopolitical values bear on ecology (and vice versa) is in population viability analyses (PVAs). These are studies, usually model-based, of the dynamics of biological populations and how they would respond to various disturbance and management regimes. Whether the data are sufficient to show a regime adequately ensures a stipulated viability threshold usually requires a trade-off between minimizing type I and type II errors. This in turn seems to require the input of nonepistemic, ethical values. As such, PVAs have a significant bearing on conservation planning and action and seem to essentially incorporate ethical assumptions and considerations. Choices of scientific categories and terms, such as "carcinogen" and "endangered," seem to be similarly infused with ethics. Numerous other examples could be cited.

This influence has recently encouraged the view that they are value-laden in a strong sense: both ethical values and nonnormative facts contribute indispensably to teleological science, and their respective contributions cannot be demarcated. In fact, the inextricable suffusion of value supposedly challenges a clear fact/value distinction. Some have also argued that this influence begets an unacceptable relativism in scientific testing in applied ecology: which hypotheses are ultimately accepted or rejected will be determined by the ethical evaluation of the relevant states of affair, such as whether species conservation is worth doing. Chapter 7 describes these charges but also argues they are overstated. The value-laden character of these sciences does not challenge the fact/value distinction or the objectivity of hypothesis testing in applied sciences. Rather, although ethical values influence the general structure and methodologies of applied ecology, these influences can be demarcated from the factual status of claims made within it.

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