Philosophical Issues in Ecology

James Justus

1 Introducing Philosophy of Ecology

Dobzhansky's (1964) sweeping generalization, "nothing in biology makes sense except in the light of evolution," provocatively captures the centrality of evolutionary theory in biological science (see also Dobzhansky 1973). But his rally call is also grievously partial. Ecology casts the same indispensable light in biology, particularly on evolution. Although the term 'ecology' was not coined until 1866 (Haeckel 1866), ecological insight was an integral part of early evolutionary thinking, it is at the core of Darwin's theory, and it will be crucial to future theorizing about how evolution has shaped the biological world. Evolutionary theory's central concepts—e.g. adaptation and natural selection—and its compelling accounts of biological phenomena—e.g. the transmutation of species and fit between organisms and environments—all reflect an ecological perspective.

Apart from its contribution to evolutionary theory, ecology also endeavors to explain significant 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 the distributions and abundances of species they produce throughout the globe. Given these ambitious goals, the sophisticated experimental tests and mathematical theories developed to achieve them deserve much more attention from philosophers of science. And despite an ecological perspective underpinning much of evolutionary theory, even philosophers of biology have paid relatively little attention to ecology, largely due to disciplinary inertia. Similarly, the typical undergraduate exposure to biology for pre-medicine and non-biological majors often consists

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largely of evolutionary theory, at the expense of ecology. This has recently changed and philosophical and pedagogical interest is growing in the conceptually rich questions ecologists study.

Although the structure of the sub-discipline continues to evolve, several broad areas of interest have emerged:

1. conceptual issues in the history of ecology (Justus 2008a; Eliot 2011a);
2. characterizing problematically unclear ecological concepts, especially 'biodiversity' and 'stability' (Sarkar 2005; Justus 2008b; Maclaurin and Sterelny 2008; Justus 2011);
3. whether there are distinctively ecological laws (Mikkelson 2003; Lange 2005; Eliot 2011b);
4. reduction in ecological science and the reality of biological communities (Sterelny 2006; Odenbaugh 2007);
5. the role of mathematical modeling in ecology (Ginzburg and Colyvan 2004; Justus 2008b);
6. the management of uncertainty in ecological inference (Regan et al. 2002; Weisberg and Reisman 2008);
7. the relationships between evolutionary theory and ecology, and conservation science and ecology (Cooper 2003; Linquist 2008; Millstein forthcoming).

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 (see Lange, this volume); conceptual content and concept determination (see Depew, this volume; Forber, this volume); the status and function of models in science; and, the status and function of values in sciences (see Millstein, this volume; Plutynski, this volume; Gannett, this volume).

Others areas involve topics unique to ecology, and on which philosophers can make valuable contributions to scientific practice (e.g. [1] and [4]–[6] from above). Each area, in turn, covers numerous specific issues. With respect to (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 remains controversial, this work suggests that a close parallel should exist between modeling strategies in physics and ecology. But other analyses counter this parallel. For example, Hubbel's (2001) unified neutral theory of biodiversity primarily derives from theories developed within biology proper: R. 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 models may have in biology and physics in general. With respect to (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 largely unexplored by philosophers of science and underappreciated in liberal arts education. An exhaustive survey is impossible, but the following sections describe *some* of the main contours of the newly emerging field of philosophy of ecology. Section 2 describes how an ecological perspective shaped Darwin's theory, particularly the niche concept and the idea that there is a "balance of nature." Section 3 considers the debate between individualists and holists such as Fredric Clements about the character of biological communities as well as metaphysical issues about their reality. Section 4 surveys the perennial controversy about the nature of laws of nature that has recently emerged within ecology. Section 5 attempts to clarify a central, but also problematic concept: ecological stability. Section 6 briefly concludes that ecology holds largely untapped riches for philosophy of science, and should have a more central role in the teaching of philosophy of biology.

2 Ecology and Evolution: The Niche Concept and the "Balance of Nature"

Although ecology only emerged as a distinct biological science in the late nineteenth – early twentieth century, ecological ideas indispensably shaped Darwin's theory. Perhaps the most theoretically fertile issue at the intersection of ecology and evolution—and the key driver of evolutionary dynamics—is the adaptive fit between organisms and their environments (see Forber, this volume for the concept of adaptation).

Darwin's brilliance was to recognize how the austere conditions environments impose on organisms yield a selective mechanism of evolutionary change. Malthus identified the presumed biological predicament: populations grow geometrically but food supplies at best increase arithmetically. For Darwin, this pinpointed the inescapable struggle for limited resources confronting all organisms. In such a struggle, some heritable variations are favored, others prove detrimental. Ecology provides the relevant scientific window into the struggle underlying such natural selection: "ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence" (Ernst Hackel in 1869 as quoted in Stauffer 1957).

The struggle is not just between organisms and the abiotic environment. Darwin frequently emphasized that species realize different functional roles in ecological systems, which he often labeled 'places' and later ecologists termed 'niches' (Worster 1994). Generalizing what counts as a species' environment to recognize the significant selective impact of intra and interspecific interactions between organisms—interactions that may change in form and intensity over time—was one of the key insights the niche concept facilitated. As realizers of particular functional roles in an ecosystem, organisms face more than just a static environment composed of a suite of abiotic factors such as precipitation, temperature, nutrient availability, etc. Their niche is also the product of intraspecific interactions, and shaped by relationships with other species occupying different niches in the overall dynamics of the ecological system, which are also evolving. Species' efficiency in utilizing and expanding their niche, and the nature of relationships between inhabitants of different niches, would then explain why some species succeed and others fail in the struggle for existence. Natural selection then becomes a form of niche dynamics. These interactions and interspecific relationships could also, in turn, produce reproductive barriers that would catalyze the transmutation of species, even in the absence of geographic isolation (Darwin 1859, p. 103). Put in contemporary terms, the niche concept gave Darwin resources to explain speciation even in the absence of geographic barriers, so-called sympatric speciation (Coyne and Orr 2004).

Besides helping explain the origin of species, the niche concept also played a role in Darwin's account of how competition shapes ecological systems and his conception of a "balance of nature." Darwin, with most of his scientific contemporaries, was committed to the idea of such a balance:

> Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time, though assuredly the merest trifle would often give the victory to one organic being over another (Darwin 1859, p. 73).

The commitment to some type of balance was a staple of the schools of natural philosophy from which biology emerged, long before the term 'ecology' was even coined (Egerton 1973). Darwin and other early ecologists continued this tradition by attempting to derive the existence of a "natural balance" in biological populations from organismic metaphors and analogies with physical systems, although the analogical and metaphorical content often differed (see Kingsland 1995). For example, the ecologist Frederic Clements (1916) is best known for claiming to find functional integration within biological communities that resembled the physiological integration within individual organisms, and which justified conceptualizing communities as a kind of superorganism with analogous homeostatic properties (see §3). But Darwin (1859, pp. 115–116) employed the same metaphor several decades before,[1] with a much less problematic aim:

> The advantage of diversification in the inhabitants of the same region is, in fact, the same as that of the physiological division of labor in the organs of the same individual body [...] No physiologist doubts that a stomach by being adapted to digest vegetable matter alone, or flesh alone, draws more nutriment from these substances. So in the general economy of any land, the more widely and perfectly the animals and plants diversified for different habits of life, so will a greater number of individuals be capable of there supporting themselves. A set of animals, with their organization but little diversified, could hardly compete with a set more perfectly diversified in structure.

Although this conclusion plausibly holds for communities in relatively constant environments and thereby provides a plausible explanation of the greater species diversity found in the tropics than in more environmentally turbulent temperate

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[1] See Kohn (2009) for further analysis of Darwin's conceptualization of this metaphor.

regions (see Rosenzweig 1992), later ecologists would show that specialization often constitutes a handicap in fluctuating environments that favor adaptable generalists (e.g. Pianka 2000, Ch. 8).

There were two threads to Darwin's view on the character of this putative balance, particularly the causal forces responsible for it. Most scientists before Darwin did not fully appreciate the extent to which inter *and intra*specific competition shaped communities (Bowler 1976). A balance of nature was considered the result of a predetermined harmony that competition would only undermine. Darwin's balance was undergirded by a much more realistic dynamics. Interspecific competition constrains the populations comprising biological communities by limiting organisms' access to the resources they need to metabolize and ultimately reproduce. This curtails populations' geometric tendency to increase. Other forms of interspecific interaction have similar consequences. Predators and parasites, for instance, inhibit prey and host populations. Intraspecific competition produces the same inhibitory effect within a species, and it can inhibit other species through interspecific relationships. For example, intraspecific competition among prey limits predator populations.

But, as Darwin was well aware, these inhibitory relationships do not alone account for the kind of dynamic balance ostensibly exhibited in the natural world. The problem was the differential power and scope of intra and interspecific competition. Intraspecific competition is fully general: it arguably occurs in all biological populations (but see Cooper 2003, Ch. 3). But its power to restrain population growth is governed by the availability of resources. When resources are plentiful, little check on growth occurs. On the other hand, interspecific competition (predation, parasitism, etc.) can suppress population growth more effectively than intraspecific dynamics in such cases, but it is not universal: not all species seem to be connected in inhibitory interspecific relations. Thus, although intraspecific competition would limit all populations when resources were scarce and interspecific interactions would sometimes suppress growth further, if these were the only checks on populations, it seems that many species would exhibit unrealistic rates of growth for unrealistic periods of time.

For Darwin, the potential problem stemmed from under-appreciating a second important thread in his concept of a balance of nature, the vastly complicated and intricately complementary set of ecological interdependencies between species: "how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life" (Darwin 1859, p. 80). Although most species do not interact directly, Darwin believed they do indirectly through chains of intermediaries. The result is a "web of complex relations" (Darwin 1859, p. 73) in which species are highly ecologically connected. A specific species' position in the web indicates what other species curb or enhance its growth. Darwin described examples of several such food webs, perhaps the most well-known (and engaging) being the ecologically serpentine relation between a clover species (*Trifolium pratense*) and the common cat (Darwin 1859, pp. 73–74). Not all parts of this web and other complex sets of ecological relationships in nature exemplify an antagonistic struggle for survival. Some are beneficial, such as mutualisms benefiting both species. But through those relationships the population suppressing effects of competitive and predatory struggles are propagated throughout the web.

Unlike previous accounts that assumed a static, providentially predetermined pattern or structure, Darwin's web-based balance of nature concept was rooted in the struggle between individual organisms to survive and reproduce. Species were balanced at their current population levels through a complex array of checks and balances finely honed by natural selection. Darwin emphasized that the exact character of the balance could change as species evolved, so in this sense the niche structure of a community was not fixed. But note that even this kind of balance requires an equilibrium assumption: population levels at a given time reflect the homeostatic processes of a biological community at a point of equilibrium. Although this assumption has been supplanted with a recognition that non-equilibrium models with complex dynamics such as chaos, limit cycles, and so-called strange attractors may best represent many types of ecological systems (DeAngelis and Waterhouse 1987), the idea that there is, and perhaps must be, a balance of nature persists. Section 5 considers the contemporary account of this balance—characterized intuitively, but plausibly by Darwin and early ecologists—with the concept of ecological stability.

As the above discussion illustrates, the niche concept seems to be a fundamental abstraction in ecological theorizing, essential to ensuring its generality (Leibold 1995). For example, general accounts of the similar structure of ecosystems 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, 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 *Panthera* and *Canis* species functioning similarly) (see Sterelny and Griffiths 1999, Ch. 11).

But despite the significant work the niche concept is employed to do within current ecological theory, the somewhat opaque nature of the concept is worth highlighting. Its content, for example, has evolved significantly. Joseph Grinnell (1917), one of the first to use the term 'niche' in an ecological context, construed niches as portions of habitat in which species persist and reproduce. Abiotic environmental factors, vegetation, and food *supporting animal species* were the primary focus. So construed, plants fell outside the scope of applicability of the niche concept. In *Animal Ecology*, Charles Elton (1927) retained the focus on animals, but shifted perspective to the causal role of species within a broader biological community. Rather than environmental factors undergirding species, a species' niche was then its constellation of causal impacts on other species, its "way of making a living" in a biological community. This is the sense of 'niche' that seems to underlie Darwin's account of the balance of nature (see above). Hutchinson (1957) later returned to Grinnell's perspective, while broadening it to include all species, with his notion of a fundamental niche: a multi-dimensional hyper-volume, each dimension representing a relevant environmental factor (e.g. temperature, precipitation, etc.) and within which a species *can* persist indefinitely. Note the modality. The realized niche is the portion of the fundamental niche a species actually occupies, which competition and other interspecific interactions can often make much smaller.

This fluid conceptual landscape renders different, sometimes incompatible grounds for ecological theorizing. For example, although Grinnell and Hutchinson's conceptions emphasize environmental factors, Hutchinson relativized niches to species: niches are defined by persistence properties of species (Griesemer 1992). Grinnell's account is not similarly relativized. Niches are independently identifiable units of the environment. As such, niches can be occupied by species or be vacant, an idea Hutchinson's concept does not permit.[2] This stronger concept is committed to ecosystems possessing a niche structure irrespective of the species they contain, and is needed to underwrite judgments that an ecosystem is "saturated" with species or that an invasive species is successful because it has occupied a previously vacant niche (Lawton 1984). But these claims and the niche concept underlying them have received significant criticism (Colwell 1992). First, and perhaps more importantly, the growing literature on niche construction challenges the claim there typically is a species-independent niche structure to be found (see Odling-Smee et al. 2003). The recent charge of niche constructionists such as Richard Lewontin that many niches are made and are not simply found seems to make the standard approach inapplicable. If organisms can modify their environments and thereby their niches to increase fitness, it is no longer clear that the niche has explanatory priority. What explains ecosystem structure, convergent evolution, character displacement and the like is no longer an extant niche structure that specific biological systems 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. Second, and relatedly, some have argued that clear, defensible criteria for delineating such niches have not been formulated (Herbold and Moyle 1986). One general problem is that some of the modalities involved in these and other niche concepts seem intractable, for example, evaluating whether a species *would* occupy a reputedly vacant niche, or whether a species *could* persist indefinitely in this region of environmental parameter space. Third, "neutral" theories of ecosystem structure, particularly Stephen Hubbell's (2001) "Unified Neutral Theory of Biodiversity," pose an intriguing alternative 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 approaches based on niche structure, at least for plants.

Beyond its role in contemporary ecological theory, these worries about the niche concept also raise concerns about perhaps the strongest candidate for the status of a distinctively ecological law: species with identical niches cannot coexist. Before scrutinizing that claim's nomological status in Sect. 4, the next section considers the philosophically intricate issue of the reality of biological communities.

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[2] Elton's (1927) niche concept seems to also allow vacant niches, but with a very different sense. Vacant Eltonian niches would be unfilled nodes in the causal nexus of interactions between species.

3 Are Biological Communities Real?

At a minimum, a biological community is a set of populations of different species. Usually, the species are taken to interact in *some* way to *some* degree. Beyond these platitudes, controversy emerges. The difficult question is whether communities are "something more" than the individual organisms of different species comprising them. If they aren't, presumably they possess no independent existence. If they are, an account is needed of: (i) this "something more" *and* (ii) how it confers independent existence. Absent either, realist aspirations are frustrated.

Assessments of (i) primarily focus on the nature and intensity of interactions between species comprising candidate communities. This requires a careful dissection of the causal structure of these interactions, their dynamics, species distribution patterns, and what they reveal about how groups of species might be assembled into communities. Appreciating that this is a conceptual *and empirical* issue is essential. Assessing (ii) involves delving into the murky depths of metaphysics, principally to determine whether the additional causal structure these ecological assemblages possess actually "cuts nature at its joints," a proverbial criterion for ontological credibility according to most scientific realists. Ecological science seems to offer little or no new insights regarding the ontological question of whether causal novelty confers independent existence at issue in (ii), and most philosophical analysis has thus far concerned (i).

Different positions on (i) fall on a spectrum. At one extreme is the view that communities are simply aggregations of species at a particular location and time, and that their relationships with the abiotic environment, not other species, largely determines their co-occurrence. On this view, communities as distinct ecological units are no more real than a *collection* of knick-knacks on a mantel, as opposed to the knick-knacks themselves, is real. The contingency of co-occurrence and lack of significant interaction are considered marks of the unreal. At the other extreme is the view that communities are tightly causally integrated units that exhibit a degree of functional cohesion, similar to individual organisms. On this view, communities are as real as individual organisms that possess these attributes.

A long-standing debate about the mechanism(s) of ecological succession in early twentieth century ecology helped catalyze this question about the nature of biological communities. On one side were "holists" such as Fredric Clements with his climax account of succession. For Clements, the specific constellation of abiotic factors in a given locale—cloud cover, elevation, precipitation, soil type, temperature, etc.—yields a deterministic sequence of succession stages that usually culminates, if undisturbed, in a final climax community. Different constellations usually produce different sequences and climax communities: grassland, mangrove, marsh, pine forest, and so on. If the seemingly mechanistic determinism were not controversial enough, Clements added that climax communities were "superorganisms" with the teleology and functional integration among constituent species that that term suggests. On the other side of the debate were "individualists" such as H. A. Gleason, H. G. Andrewartha, and others who discerned much less structure to succession, less cohesion in reputed biological communities, and generally more contingency underlying ecological patterns.[3]

The extreme positions associated with this debate have largely been abandoned as implausible, but the theoretical contrasts it drew continue to reverberate throughout contemporary ecology. For example, although both sides of the dispute considered themselves respectable empiricists, one influential criticism of the climax, "superorganism" theory was that it departed significantly and unjustifiably from what observations of succession, species distributions, and dynamics in supposed biological communities actually indicated. Robert Whittaker made this kind of criticism based on very influential analyses of plant distributions along environmental gradients, such as elevation. Plant species distributions along environmental gradients seem to overlap continuously and significantly, and do not form discrete identifiable boundaries (see Whittaker 1956). But, the argument goes, communities are only real if they have such distinct boundaries. So they aren't.

The key claim being challenged is that species distributions display converging boundaries that communities must possess. Recently, Odenbaugh (2007) gave three responses to this argument. First, Odenbaugh rightly points out that Whittaker's results are inflated in claims such as: "Whittaker found, each species behaved totally independently […] there is no such thing, really, as a pine forest, or a mixed hardwood forest or a tall-grass prairie or a tundra," (Budiansky 1995, p. 86) and, "There are no discrete communities of plants. The reality is endless blending," (Colinvaux 1979, p. 72). These audacious claims simply assume Whittaker's results can be extrapolated to all plants. But it is worth noting that both of these assertions occur not in top-tier scientific journals, but in works of popular science where epistemically unwarranted flights of rhetorical fancy are less constrained. More measured assessment suggests Whittaker's results constitute strong *evidence* against the existence of the needed boundaries.

Odenbaugh's additional responses address this more reasonable interpretation. He claims that two implicit assumptions seem to underlie Whittaker's analysis:

> Interactions among species should be similar at *all* points along environmental continua. Thus, if two or more species interact in a certain way at a point, then if they interact at other points it is in the same way. […] Groups of species should be associated at *all* points on a gradient if interdependence is to be accepted. Thus, if two or more species interact at a point on a gradient, then they interact at *all* points on that gradient. (2007, p. 635; italics added)

Odenbaugh correctly notes that these assumptions are false, but it seems implausible that Whittaker or other respected ecologists would be foolish enough to endorse such categorical claims. Exceptionless patterns are a rarity in ecology, and biology generally. One should no more accept the conditional that species interact at *all* points on an environmental gradient if they interact at one, than one should accept that species do not interact at all points if they fail to at one. The same goes

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[3] See Eliot (2011a) for a historically engaging and conceptually rich account of this debate, one that locates the divergence more in methodological disagreements about how ecological research should be conducted than contrasting ontological commitments.

for the functional form of the interaction. The degree of continuity of species interactions across environmental gradients is obviously an empirical issue. But all that is required for Whittaker's results to constitute evidence of a lack of boundaries is that interactions persist and remain similar along sufficient portions of the environmental gradient sampled. What counts as 'sufficient' depends on the patterns Whittaker found and the species involved: the higher the turnover in species distributions, the smaller the portion generally required for sufficiency. Intraspecific variability exists, but organisms comprise a species in large part because they share a very similar ecological profile. One would expect, although data and sophisticated statistical analyses could only reliably confirm, that this similarity would ensure the sufficiency required.

Odenbaugh's last response is that Whittaker himself employed a "community-level" property, niche differentiation between two species, to explain the absence of boundaries in species distributions. This, Odenbaugh suggests, shows Whittaker was himself committed to the existence of communities. If Whittaker's contention was to show that no communities exist and two species interacting shows they do, Whittaker would have indeed blundered. But the worry is that this characterization of the debate construes the goal-posts too weakly. Surely what is at stake with respect to the reality of biological communities—and the target of Whittaker's analysis—is more than whether there are binary community-level properties such as predator–prey interactions between populations, and thus two-species-member "communities." If this were the issue, simply observing a population of lions consuming gazelles or parasitic mistletoes infesting a deciduous forest would be sufficient to resolve the debate. Even if they stop short of endorsing full Clementsian "super-organismal" status, proponents of the reality of biological communities have a more ambitious agenda. They believe there are many communities composed of many more than two species, that maintain some type of homeostasis, and that exhibit other kinds of causal integration that two-species interactions, which are often highly unstable, do not. Odenbaugh's criticism therefore seems to invoke an indefensibly weak burden of proof given what is at issue in this debate.

Against this more exacting standard, Sterelny (2001) gives a positive argument for the reality of communities based on paleoecological data and an analogy with organisms and species. What makes the latter real, according to Sterelny, is their internal regulation. For example, organisms maintain a boundary between themselves and the external environment, and they regulate their internal states against environmental changes. In particular, organisms exclude foreign objects and agents of disease through a complex array of processes. Species also regulate membership through behavioral, physiological, and genetic impediments to reproduction. Through an impressive regimentation of paleoecological data and scientific analyses to understand that data, Sterelny convincingly argues that there have been episodes of "co-ordinated stasis":

> Suites of species, drawn from quite different lineages, appear together quite suddenly in the fossil record. They persist together largely intact. The periods of persistence are evolutionarily significant: often a few million years. These species not only persist together; they do so maintaining both their morphological and their ecological characteristics. The commonest species stay common; the relatively rare stay relatively rare. Few new species migrate

> in, or evolve in place. Few of those in place at the establishment of an association disappear before the association breaks up. In general, *associations* persist, not just the individual taxa that make up those associations. Each seems to end with the association dissolving and many of its component species disappearing, to be replaced by a different but persisting assemblage. So the pattern is one of both evolutionary and ecological stability bounded on each side by a turnover event. (2001, pp. 438–439)

Most of Sterelny's analysis is concerned with scrutinizing proposed explanations of these periods of surprising constancy based on the best theories of community dynamics. None proves successful. It therefore remains a tantalizing prize for future theorizing. It is abundantly clear, however, that individualist approaches such as those associated with Whittaker uncontrovertibly fail to account for this phenomenon. The paleoecological data Sterelny considers therefore constitute strong evidence for the community-level internal regulation that, by analogy with the organismal and species cases, indicates the reality of biological communities. Sterelny does not over-extrapolate the significance of these results, and other paleoecological studies seem to provide countervailing evidence. For example, Davis and Shaw (2001) found that after the glaciers receded, individual tree species dispersed at different rates, in different directions, and from different origins. This seems to confirm the individualist view in which abiotic factors, not biotic interactions, drive species distribution patterns. As with most philosophical questions in ecology with an empirical component, the evidentiary issues involved are far from resolved.

4 Are There Distinctively Ecological Laws?

The philosophy of each special science such as biology, chemistry, economics, psychology, etc. inevitably grapples with whether it has distinctive laws (see Lange, this volume). Ecology is no different. And like the question of whether biological communities are real, the relevant issues involve a complex interplay of conceptual and empirical issues. Many take the possession of natural laws to be a signature mark of a science's objectivity, so the philosophical stakes are also significant.

Prima facie, there are various challenges to the idea that such laws exist: the relative paucity of predictive success in ecology, that ecological models and experimental results lack sufficient generality, that candidate laws are riddled with exceptions, and that ecological systems are too complex to name a handful. But complexity, to take the last first, 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 (Ginzburg and Colyvan 2004), or that humans do not continue to uncover its underlying law-governed physical and chemical dynamics. Some philosophers have recently argued that other properties thought to preclude a discipline from trading in laws—poor predictive accuracy and limited generality, not being exceptionless—should be jettisoned, and that ecology indicates why. For example, generalizations sometimes accorded nomic status, such as the latitudinal gradient in species diversity (see Rosenzweig 1992) and the so-called species-area power law (see Connor and McCoy 1979), are nevertheless known to have numerous exceptions. One suggestion is that these exceptions can be subsumed under a suitably crafted *ceteris paribus* clause, just as recognized physical laws, for example ideal gas laws and Coulomb's law of electrostatics, do not hold in some circumstances and thereby lack universality.

Even without fully entering the thicket of difficulties with *ceteris paribus* clauses (see Earman et al. 2002), the general inadequacy of this response is apparent. Absent clear and justifiable standards delimiting the extent of *ceteris paribus* clauses, this move is entirely *ad hoc*. No matter how unmotivated, potential counterexamples can simply be folded into the clause's scope in a facile ploy to preserve nomic status. By this rationale, it seems that *any* true claim can be made faux-nomological with a sufficiently well-chosen and comprehensive *ceteris paribus* clause. The important insight that laws possess a kind of natural necessity that simply true generalizations do not has little traction in this account.

The problems with this approach are compounded by the fact that most candidates for laws in ecology are based on models and theories that are *highly* idealized. That is, they incorporate unrealistic, i.e. *false*, assumptions about the systems they are intended to represent, largely to make model and theory analysis tractable. For example, they ignore some components and interactions of ecological systems, treat interactions as instantaneous and assume that their effects propagate similarly, represent discrete components with continuous variables, describe community structure non-spatially, etc. But these and other unrealistic idealizations make it uncertain whether modeling results demonstrate properties of the represented system or are byproducts of the idealizations. Since it is often unclear what properties are primarily responsible for system dynamics given their complexity, idealizations may significantly mischaracterize their most important features. An enhanced sense of understanding conveyed by an idealized model may therefore fail to be about the system it is intended to represent, thereby misdirecting rather than assisting in the discovery of ecological laws. This difficulty is exacerbated by the short supply of extensive and long-term ecological data required to empirically vet model results, in contrast with the usually highly-confirmed models found in physics and chemistry. An added concern is that mathematical ecologists have often uncritically emulated mathematically sophisticated models of physics to ensure their modeling is mathematically rigorous, but the emulation has sometimes led to serious misrepresentation of biological phenomena (see Justus 2008b). Models are the main conduit through which theorizing occurs in ecology, so high degrees of idealization pose a significant impediment to finding distinctively ecological laws. The same concern holds for other areas of biology, such as population genetics.

There is one class of empirical generalizations that avoid these model-based difficulties, and are also apparently very well confirmed, albeit with significant "scatter" of data around the proposed relationships. These are the so-called macroecological allometries (see Ginzburg and Colyvan 2004, Ch. 2). They include:

1. Kleiber allometry – basal metabolic rate is directly proportional ($\propto$) to a 3/4 power of body mass, i.e. (body mass)$^{3/4}$. First noticed by biologist Max Kleiber, the larger the organism, the greater (at a 3/4 power) its calorie consumption rate at rest.

2. Generation-time allometry – organismal maturation time $\propto$ (body mass)$^{1/4}$.
3. Fenchel allometry – maximum reproduction rate is inversely proportional to (body mass)$^{1/4}$; first studied by Tom Fenchel.

Other ecological allometries exist, but these are perhaps the most empirically vetted and thus strongest candidates for lawhood. Besides their high degree of confirmation, their broad scope also seems to evince nomological credentials. The Kleiber allometry, for example, has been verified for organisms with masses ranging from elephants to bacteria. For these reasons, Ginzburg and Colyvan (2004, p. 12) suggest these allometries "deserve to be called *laws*."

John Beatty's (1995) evolutionary contingency thesis (ECT)—that all distinctively biological generalizations describe contingent evolutionary outcomes—constitutes a formidable obstacle to this claim. The thesis presents a two-horned dilemma for proposed biological laws. If they are distinctively biological, then they are contingent because the evolutionary processes responsible for their existence are highly contingent. The unguided, largely random nature of genetic mutation, and the fact that natural selection acts with respect to environments that frequently (and contingently) fluctuate are two examples of such contingency. This contingency, Beatty argues, is incompatible with lawhood in the same way that, for example, the contingency of 'There are no 5 m^3 gold cubes' is incompatible with lawhood. This view is not without its detractors (e.g. Sober 1987), but the controversy need not detain us because regardless of whether the allometries fall to the first, they do fall to Beatty's second horn: they are not distinctively *ecological*.[4] Take Kleiber's allometry.[5] One recent credible explanation of the pattern is that it is a consequence of fluid dynamics and the geometric structure of circulatory, respiratory, and vascular systems of animals and plants (West et al. 1997). As such, whether or not this pattern should be accorded nomic status, it certainly does not seem to be a distinctively ecological generalization any more than the fact that all organisms have mass, or that organism body mass tends to scale with body volume are truths of ecology. Although these are truths concerning entities studied in ecology, ecological science seems to contribute nothing nomological.

But there is a famous and distinctively ecological generalization with pretensions to lawhood, the *competitive exclusion principle* (CEP). Although Grinnell (1917) drew upon Darwin's work to arrive at the same kind of exclusionary principle a few decades before (see Hardin 1960), CEP's origination is largely credited to the Russian biologist Georgyi Gause (1934). In a series of brilliant experiments, Gause (1934) studied competitive dynamics in *Paramecium* and yeast species, respectively. In constant ecological conditions (e.g. nutrient levels, water temperature, turbidity, *etc.*) and in the absence of refugia that would mitigate the effects of interspecific competition, one species inevitably outcompeted the other to extinction. On this

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[4] Marc Lange's (2005) recent analysis of what biological laws could be seems vulnerable to Beatty's first horn (see also Lange this volume).

[5] Ginzburg and Colyvan (2004) note that the Kleiber allometry is the most empirically well supported, and that the generation time and Fenchel allometries are likely based on it.

basis, Gause generalized the CEP: species with identical niches, i.e. two species that would compete for exactly the same resources, cannot coexist. The intuitive appeal of the idea and its apparently exceptionless status across many different biological systems has prompted its honorific designation as an ecological law, Gause's Law.

Apart from the extreme case of exclusion, the degrees and types of niche overlap that permit coexistence has become an important focus of contemporary attempts to explain species distribution patterns and dynamics in biological communities (Abrams 1983). The ecologist Robert MacArthur (1958) was one of the first to rigorously document this kind of phenomenon in his rightfully famous dissertation work on New England warblers. The objective of the study was to determine how so many behaviorally and physiologically similar bird species could coexist in boreal forests, which seemed to contradict the exclusion principle. With such similar properties, it seemed that interspecific competition would be especially strong between the birds and would eventually lead to the extirpation of all but one competitively dominant species. Through meticulous observation MacArthur uncovered the mechanism that eluded the exclusionary outcome: different species bred and fed in distinct spatial parts of coniferous trees and, furthermore, warblers exhibited strong territoriality towards those parts. He also found that nesting times differed across the warbler species. This affected the same minimization of competition as spatial partitioning. These behaviors effectively divided the homogeneous arboreal habitat into disparate sections, thereby partitioning (spatially and temporally) the niche space. This process curtails competition and allows the extant set of warblers to coexist.

Despite these successes, there are reasons to doubt that the CEP constitutes a natural law. First, it is of quite limited scope. For example, it is inapplicable when resources are abundant and species are not competing for them. Nor does it apply in fluctuating environments where niche contours are ephemeral, or changes in the direction of competition occur before exclusion can catalyze extinction. Since most environments nontrivially fluctuate, this is a serious limitation, and it recalls difficulties with *ceteris paribus* described above. CEP also seems to have numerous potential counterexamples. For example, migration into an area can prevent the predicted competitive exclusion. Another apparently recalcitrant counterexample was originally identified by MacArthur's advisor, G. E. Hutchinson (1961): the seemingly inordinate number of plankton species given their seemingly simple, homogeneous niche space. Known as the "paradox of the plankton," this issue remains an active area of contemporary ecological research and is yet to be conclusively resolved (see Tilman et al. 1982).

There is another threat to CEP as law, its empirical status. To appreciate the potential difficulty, first note that the relevant niche concept CEP invokes must be the Grinnellian, environmentally-based notion (see Sect. 2). In his seminal publication, Gause (1934) actually appeals to Elton's (1927) work, but Elton's functional niche concept would make CEP false. Different species often serve veritably identical roles in the causal nexus of interspecific interactions comprising a biological community. Different African grazers that migrate and ruminate together, and different pollinators, are but two plausible examples. In fact, ecological literature has labeled species with similar resource requirements that utilize them in similar ways a ‘guild’ to capture this commonality. Instead, what permits species with similar causal roles in a biological community to coexist, according to CEP, is their partitioning of the environment. For example, two fish eating water fowl, the great cormorant (*Phalacrocorax carbo*) and the European shag (*P. aristotelis*), exhibit approximately the same causal interactions with other terrestrial species, but they nest in different portions of cliffs (as well as consume fish from different sources, estuaries and harbors vs. the open sea, respectively) (Lack 1954).

But with ‘niche’ construed environmentally, the empirical content of CEP has been questioned. The problem begins with imprecision. For example, the CEP says nothing about what precise degree of niche differentiation is required to ensure coexistence. It seems that this can only be answered on a case by case, ecosystem by ecosystem, basis, if at all. The poor general guidance sets up a troubling scenario. The reasoning proceeds as follows. Suppose two species coexist but ecologically appear very similar. Then, by CEP, their niches must differ. Their ecological similarity initially suggested similar niches, so at what point does investigation of how the species utilize resources and interact with the environment that reveals no significant difference constitute a counterexample to CEP? Without precise guidance about what degree of niche differentiation coexistence requires, the worry is that the CEP is effectively immune from empirical challenge. For this reason, Pianka (2000, p. 248) calls CEP an untestable hypothesis “of little scientific utility.” The claim about utility should be rejected. As Slobodkin (1961) convincingly argued and the history of the science confirms, CEP has played a very useful role in ecological theorizing as a research heuristic. But scientific utility should not be confused for nomic status. The mechanistic world-view was extremely valuable in the development of science, but it was not a law, or true.

5 A Theory of Ecological Stability

With some legitimacy, Arthur (1990, p. 30) cites the balance of nature as ecology’s “number one” research priority, about which there is “near unanimity on its importance” (1990, p. 35). This priority is recent. Not until the second half of the twentieth century was the concept of a balance of nature rigorously characterized as ecological stability, and predominantly metaphysical speculations about its cause superseded with scientific hypotheses about its basis. But significant uncertainty and controversy remains 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.

One such debate, the stability-diversity debate, has persisted as a (perhaps the) central focus of theoretical ecology for half a century. The debate concerns the deceptively simple question of whether there is a relationship between the diversity of a biological community and its stability. From 1955, when Robert MacArthur initiated the debate, to the early 1970s, the prevailing view among ecologists was that diversity is an important, if not the principal, cause of community stability. Robert May, a physicist turned mathematical ecologist, confounded this view with analyses of mathematical models of communities that seemed to confirm the opposite, that increased diversity jeopardizes stability. The praise May's work received for its mathematical rigor and the criticisms it received for its seeming biological irrelevance thrust the SD debate into the ecological limelight, but subsequent analyses have failed to resolve it.

Different analyses seem to support conflicting claims and indicate an underlying lack of conceptual clarity about ecological stability that this section diagnoses and resolves. Below, 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. In particular, I argue that the concepts of resistance, resilience, and tolerance jointly provide an adequate definition of ecological stability. Roughly speaking, a community exhibits these concepts to a high degree if it: changes little after being perturbed (resistance); returns rapidly to a reference state or dynamic after being perturbed (resilience); and will return to that reference state or dynamic after most perturbations (tolerance).

Besides providing insights about how problematic scientific concepts should be characterized, it is worth noting that the issues involved in characterizing ecological stability 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. Positive feedback between diversity and stability would therefore support conservation efforts to preserve biodiversity. This yields a response to an influential criticism. As part of their argument that ecological theory has failed to provide a sound basis for environmental policy, Shrader-Frechette and McCoy (1993) have criticized that several proposed definitions of ecological stability are incompatible and that the concept is itself "conceptually confused" or "inconsistent." The account of ecological stability below answers this criticism.

Stability attributions must be made with respect to two evaluative benchmarks. The first is a system description (M) that specifies how the system and its dynamics are represented.[6] The second is a specified reference state or dynamic (R) of that system against which stability is assessed. In most ecological modeling, M is a mathematical model in which:

1. variables represent system parts, such as species of a community;
2. parameters represent factors that influence variables but are (usually) uninfluenced by them, such as solar radiation input into a community; and

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[6] In the following, 'ecological stability' designates stability of a biological community unless otherwise specified, though most of the discussion also applies to the stability of a biological population or an ecosystem.

3. model equations describe system dynamics, such as interactions among species and the effect that environmental factors have on them.

M therefore delineates the boundary between what constitutes the system, and what is external to it. Relativizing stability evaluations to M is a generalization of Pimm's (1984) relativization of stability to a "variable of interest" because stability is assessed with respect to (1)–(3) rather than a subset of (1).

The specification of M partially dictates how R should be characterized, and *vice versa*. A biological community, for instance, is usually described as a composition of populations of different species. R must therefore reference these populations in some way. For example, R is often characterized in terms of the "normal" population sizes of each species. Since ecological modeling in the late 1960s and 1970s was dominated by the development of mathematically tractable equilibrium models (DeAngelis and Waterhouse 1987), "normal" population sizes were often assumed to be those at equilibrium, *i.e.* constant population sizes the community exhibits unless perturbed. This is not the only possible reference specification, however. A community may be judged stable, for instance, with respect to a reference *dynamic* the populations exhibit. Common examples are a limit cycle—a closed path C that corresponds to a periodic solution of a set of differential equations and towards which other paths asymptotically approach—or a more complicated attractor dynamic (see Kot 2001, Ch. 8). Ecological stability can also be assessed with respect to some specified range of tolerated fluctuation. R may also be characterized solely in terms of the presence of certain species.[7] Only extinction would constitute departure from this reference state.

The details of M and R are crucial because different system descriptions—e.g. representing systems with different variables or representing their dynamics with different functions—may exhibit different stability properties or exhibit them to varying degrees relative to different specifications of R. Specifying R as a particular species composition vs. specifying R as an equilibrium, for instance, can yield different stability results. Similarly, different M can produce different assessments of a system's stability properties. Describing a system with difference versus differential equations is one example (May 1974). He showed, for instance, that the logistic *difference* equation:

$$N_{t+1} = \left(1+r\right)N_t - \frac{r}{K}N_t^2; \tag{1}$$

where t is time; r is the intrinsic growth rate; K is the carrying capacity; and N is the population size, exhibits dramatically different behavior than the corresponding logistic *differential* equation. For $r > 0$, the logistic differential equation has an asymptotically Lyapunov stable equilibrium $N^* = K$. This is also an asymptotically Lyapunov stable equilibrium of the logistic difference equation, but only for

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[7] To illustrate the partial dependence of M on R, notice that the species referred to in R must be part of the system description M.

$0 < r < 2$. For $2 < r < 2.526$ the system exhibits a 2-period limit cycle. As r increases beyond 2.526 a 4-period limit cycle emerges, and the system exhibits chaotic behavior for $r > 2.692$. Thus, although the logistic differential and difference equations appear to describe very similar dynamics, the seemingly inconsequential choice of representing time as a discrete or continuous variable has a substantial effect on evaluating stability properties of the system.

Details of M and R are also important because they may specify the spatial and temporal scales at which the system is being analyzed, which can affect stability assessments. Systems with low resistance but high resilience, for example, fluctuate dramatically in response to perturbation but return rapidly to their reference state R. Low resistance is detectable at fine-grained temporal scales, but systems may appear highly resistant at coarser scales because their quick return to R prevents detection of fluctuation. Similarly, significant fluctuations in spatially small areas may contribute to relatively constant total population sizes maintained through immigration and emigration in larger regions.

Once (and only once) M and R are specified, the stability properties of a system can be determined. These properties fall into two general categories, depending on whether they refer to how systems respond to perturbation (relative to R) or refer to system properties independent of perturbation response. A perturbation of an ecological system is any discrete event that disrupts system structure, changes available resources, or changes the physical environment (Krebs 2001). Typical examples are flood, fire, and drought. Perturbations are represented in mathematical models of communities by externally induced temporary changes to variables that represent populations, to parameters that represent environmental factors, and/or to model structure. Many, perhaps most, real-world perturbations of communities should be represented by changes to both variables and parameters. A severe flood, for instance, eradicates individual organisms and changes several environmental factors affecting populations. In the following, let P_v, P_p, and P_{vp} designate perturbations that change only variables, change only parameters, and those that change both, respectively.

Perturbations may cause other changes, such as alteration of the functional form of species interactions, that are not adequately represented by changes to variable or parameter values of typical community models, but which should be included in a comprehensive assessment of community's stability. Since these perturbations change community dynamics, they change M. How the altered community responds to these (and subsequent) perturbations must then be assessed against the new description of the community's dynamics as long as those dynamics remain altered. Although a completely adequate assessment of the ecological stability of a community requires consideration of all such changes caused by perturbations, most ecological modeling focuses on changes to variable and parameter values.

There are four plausible adequacy conditions for an account of ecological stability:

(A1) the ecological stability of a biological community depends upon how it responds to perturbation ([A2]–[A4] specify the form of the required dependency);

(A2) of two communities *A* and *B*, the more ecologically stable community is the one that would exhibit less change if subject to a given perturbation *P*;
(A3) if *A* and *B* are in a pre-perturbation reference state or dynamic *R*, the more ecologically stable community is the one that would most rapidly return to *R* if subject to *P*; and,
(A4) if *A* and *B* are in *R*, the more ecologically stable community is the one that can withstand stronger perturbations and still return to *R*.

Before considering these conditions in detail, a few remarks help clarify their general basis. First, (A2)–(A4) only place *comparative* constraints on the concept of ecological stability and therefore require only a rank ordering of the stability of biological communities, rather than a particular quantitative valuation. The reason for requiring only comparative constraints is that quantitative valuation of ecological stability depend upon the system description (*M*) and reference state or dynamic (*R*) specified for a community, both of which may vary. Second, conditions (A2) and (A3) order the stability of communities based on their behavior following a *particular* perturbation *P*. As adequacy conditions, they therefore do not require a measure of the strength of perturbations. This reflects the difficulties facing the formulation of a measure of perturbation strength (see below), although such a measure is needed to evaluate the resistance of communities when only their responses to perturbations of different strength are known. If a quantitative measure of perturbation strength for different types of perturbation were available, two further *non-comparative* adequacy conditions could be formulated:

(A2′) a highly stable biological community should change little following weak perturbations;
(A3′) a highly stable biological community should rapidly return to its reference state or dynamic following weak perturbations.

In contrast, condition (A4) does require a measure of perturbation strength.

Condition (A1) captures the idea that a community's behavior is a reliable indicator of its ecological stability only if the behavior reflects how perturbation changes the community. If unperturbed, a community may exhibit great constancy throughout some period, for instance, as assessed by a lack of fluctuations in the biomasses of species in the community. It may be, however, that if it had been even weakly perturbed, it would have changed dramatically. Constancy of this community surely does not indicate ecological stability when it would have changed substantially if perturbed slightly. Similarly, variability of a community does not necessarily indicate lack of ecological stability if it is the result of severe perturbations, perturbations that would cause greater fluctuations or even extinctions in less stable communities.

The reason for (A2) is that more stable communities should be less affected by perturbations than less stable ones. Communities that can withstand severe drought with little change, for instance, are intuitively more stable than those modified dramatically. The justification for (A3) is that more stable communities should more rapidly return to *R* following perturbations than less stable ones. This adequacy condition captures the idea that lake communities that return to *R* quickly after an incident of thermal pollution, for instance, are more stable than those with slower return rates following similar incidents. The ground for the last condition, A4, is that communities that can sustain stronger perturbations than others and still return to *R* should be judged more stable.

Three concepts—resistance, resilience, and tolerance—represent the properties required of ecological stability by (A2′)–(A4). **Resistance** is inversely correlated with the degree a system changes relative to *R* following a perturbation (P_v, P_p, or P_{vp}). Since perturbations vary in magnitude, resistance must be assessed against perturbation strength. Large changes after weak perturbations indicate low resistance; small changes after strong perturbations indicate high resistance. Resistance is thus inversely proportional to perturbation sensitivity.

Depending on *M* and *R*, changes in communities can be evaluated in different ways, each of which corresponds to a different measure of resistance. Community resistance is typically measured by changes in species *abundances* following perturbation. It could, however, be measured by changes in species *composition* following perturbation, or in some other way. Pimm's (1979) concept of species deletion stability, for instance, measures resistance by the number of subsequent extinctions in a community after one species is eradicated.

A simple example illustrates the contextual import of *M* and *R* in assessing resistance. Consider the classical Lotka-Volterra model of a one-predator, one-prey community:

$$\frac{dx_y(t)}{dt} = ax_y(t) - \alpha x_y(t)x_d(t); \tag{1a}$$

$$\frac{dx_d(t)}{dt} = -bx_d(t) + \beta x_d(t)x_y(t); \tag{1b}$$

where x_d and x_y represent predator and prey populations; *a* represents prey birth rate; *b* represents predator death rate; and $\alpha, \beta > 0$ in the second term of each equation represent the effect of prey individuals on predator individuals and *vice versa*. Equations (1a and 1b) are the description of the system, *M*. There is one nontrivial equilibrium, $x_d^* = \frac{b}{\beta}$ and $x_y^* = \frac{a}{\alpha}$, which is usually specified as the reference state, *R*.

For this M and R, resistance to a Pv perturbation that eradicates, say, half of x_y can be measured by how far x_d deviates from x_d^*. If M were different, the perturbation could obviously have a different effect on x_d. If x_d and x_y were competitors, for instance, x_d would increase rather than decrease after this perturbation. Similarly, if R were different, assessments of resistance may change. If R were the species composition x_d and x_y (i.e. $X_d, X_y > 0$) rather than their equilibrium values, for instance, resistance would be assessed in terms of changes from this composition, i.e. in terms of species extinction. The equilibrium $X_d^* = \frac{b}{\beta}$, $X_y^* = \frac{a}{\alpha}$ is globally stable for this simple community, so only a Pv perturbation strong enough to eradicate one of the species will cause extinction; this community returns to equilibrium after all other Pv perturbations. For communities with many species and more species dynamics, however, a Pv perturbation that eradicates half or less of one species may cause the extinction of that, or other species.

Different types of perturbations, moreover, yield different measures of resistance. Since evaluating resistance requires considering perturbation strength, strengths of different types of perturbations must be comparable for there to be a single measure of resistance for a system. Such comparisons are sometimes straightforward. If one perturbation eradicates half of species x in a community, for instance, another that eradicates 75 % of x is certainly stronger. If another perturbation eradicates 25 % of 3 species or 5 % of 15 species in the community, however, it is unclear how its strength should be ranked against the perturbation that eradicates 75 % of x. What criteria could be used to compare strengths of P_v, P_p, or P_{vp} perturbations, to which systems may show differential sensitivity, is even less clear. Systems that are highly resistant to P_v perturbations may be extremely sensitive to even slight P_p. Comparing the resistance of communities is therefore only unproblematic with respect to perturbations of comparable kind.

Resilience is the rate at which a system returns to R following perturbation (P_v, P_p, or P_{vp}). Like resistance, resilience must be assessed against perturbation strength unless, although unlikely for many types of perturbation, return rate is independent of perturbation strength. Slow return rates after weak perturbations indicate low resilience and rapid rates following strong perturbations indicate high resilience. If return rate does not depend on perturbation strength, however, resilience can be evaluated by the return rate independent of the perturbation strength, although the rate may vary across different types of perturbations. Systems may not return to R after perturbation, especially following severe perturbation, so, unlike resistance, resilience is only assessable for perturbations that do not prevent return to R. Note that resilience and resistance are independent concepts: systems may be drastically changed by weak perturbations (low resistance) but rapidly return to R (high resilience), and *vice versa*.

Resilience is commonly measured as the inverse of the time taken for the effects of perturbation to decay relative to R. For a specific mathematical model, this can be determined analytically or by simulation. For the community described by Eq. (1) above, for instance, resilience to a P_v perturbation that eradicates half of one species could be simply measured by $\frac{1}{\left|t_{eq} - t_p\right|}$ where t_p is the time at which the community is initially perturbed and t_{eq} is the time at which the community reestablishes equilibrium. Resilience to P_v perturbation is determined by the largest real eigenvalue part for systems modeled by linear differential equations if it is negative, and analytic methods have been developed to assess resilience to P_v perturbation for nonlinear models. Empirical measurement of resilience for communities in nature, however, is often thwarted by subsequent perturbations that disrupt return to R. This difficulty can be avoided if subsequent perturbations can be evaded with controlled experiments. If the return rate is independent of perturbation strength, estimation of resilience is also more feasible because only the decay rate of the perturbation effects need be measured before the system is further perturbed; measurement of perturbation strength is not required (Pimm 1984). Like resistance, furthermore, different types of perturbations yield different measures of resilience since return rate to R may depend upon the way in which systems are perturbed. A system may be highly resilient to P_v perturbation and poorly resistant to P_p perturbation, for instance, or more resilient to some P_v or P_p perturbations than others.

Tolerance, or "domain of attraction" stability, is the ability of a system to be perturbed and return to R, regardless of how much it may change and how long its return takes. More precisely, tolerance is positively correlated with the range and strength of perturbations a system can sustain and still return to R. The magnitudes of the strongest perturbations it can sustain determine the contours of this range. Note that tolerance is conceptually independent of resistance and resilience: a system may be severely perturbed and still return to R (high tolerance), even if it changes considerably (low resistance) and its return rate is slow (low resilience), and *vice versa*.

Similar to resistance and resilience, different kinds of perturbations yield different measures of tolerance. Tolerance to P_v perturbations, for instance, is determined by the maximal changes variables can bear and not jeopardize the system's return to R. With respect to P_v perturbations that affect only one species of a community, for instance, tolerance can be simply measured by the proportion of that species that can be eradicated without precluding the community's return to R. If a nontrivial equilibrium of Eq. (1) from above is globally stable, for instance, the community described by the equation is maximally tolerant to P_v perturbations relative to this reference state because the community will return to it after any P_v perturbation that does not eradicate one of the species. Variables of a system may be perturbed, however, in other ways. A P_v perturbation may change all variables, several, or only one; it may change them to the same degree, some variables more severely than others; and so on. How exactly variables are perturbed may affect whether the system returns to R. System tolerance must therefore be evaluated with respect to different types of perturbation. The same goes for assessing tolerance to P_p or P_{vp} perturbations.

Although resistance, resilience, and tolerance do not adequately explicate ecological stability individually, they do so collectively. In fact, they constitute jointly sufficient and separately necessary conditions for ecological stability, notwithstanding Shrader-Frechette and McCoy's (1993, p. 58) claim that such conditions do not exist. Consider sufficiency first. Since these three concepts represent the properties underlying conditions (A2)–(A4) [and (A2′) and (A3′)], communities exhibiting them to a high degree would change little after strong perturbations ([A2]), return to R rapidly if perturbed from it ([A3]), and return to R following almost any perturbation ([A4]). If R is a point equilibrium, moreover, a community exhibiting high resistance, resilience and tolerance will be relatively constant. As such, these three properties certainly capture ecologists' early conceptions of ecological stability, and there seems to be no further requirement of ecological stability that a community exhibiting these properties would lack.

Each concept is also necessary. Highly tolerant and resistant communities, for instance, change little and return to R after most perturbations. In regularly perturbing environments, however, even a highly resistant and tolerant community may be iteratively perturbed to the boundary of its tolerance range and “linger” there if its return rate to *R* is too slow. Subsequent perturbations may then displace it from this range, thereby precluding return to *R*. If this community rapidly returned to *R* after most perturbations (high resilience), it would rarely reach and would not linger at its tolerance boundary. In general, low resilience preserves the effects perturbations have on communities for extended, perhaps indefinite durations, which seems incompatible with ecological stability.

Similar considerations show tolerance and resistance are necessary for ecological stability. A highly resilient and tolerant but weakly resistant community rapidly returns to *R* following almost any perturbation, but changes significantly after even the slightest perturbation, which seems contrary to ecological stability. The dramatic fluctuation such communities would exhibit in negligibly variable environments is the basis for according them low ecological stability. A highly resilient and resistant but weakly tolerant community changes little and rapidly returns to *R* when perturbed within its tolerance range, but even weak perturbations displace it from this range and thereby preclude its return to *R*, which also seems contrary to ecological stability.

Resistance, resilience, and tolerance are independent concepts and thus biological communities may exhibit them to different degrees. Although the necessity of each concept for ecological stability does not strictly entail they are equally important in evaluations of a community’s stability, nothing about the pre-theoretic concept of ecological stability seems to suggest otherwise. As a concept composed of resistance, resilience, and tolerance, ecological stability therefore imposes only a partial, not complete, ordering on communities. Moreover, since communities may differentially exhibit resistance, resilience, and/or tolerance for different types of ecological perturbations, each property also imposes only a partial ordering on communities. This twofold partiality entails inferences from analyses of stability-diversity and stability-complexity relationships are limited by the property and type of perturbations analyzed, beside the particular system description (*M*) and reference state or dynamic (*R*) specified.

It is worth pausing over what the framework for ecological stability presented above shows about the general concept. It certainly shows that ecologists have used the term ‘stability’ to describe several distinct features of community dynamics, although only resistance, resilience, and tolerance adequately define ecological stability. This plurality does not manifest, however, an underlying vagueness, “conceptual incoherence,” or “inconsistency” of the concept, as Shrader-Frechette and McCoy (1993, p. 57) suggest in their general critique of basic ecological concepts and ecological theories based on them.

Two claims seem to ground their criticism. First, if ‘stability’ is used to designate distinct properties, this indicates the concept is itself conceptually vague and thereby flawed. Although terminological ambiguity is certainly undesirable, most ecologists unambiguously used the term to refer to a specific property of a community and accompanied the term with a precise mathematical or empirical operationalization. Since these were in no sense vague, in no sense was ecological stability “vaguely defined" (Shrader-Frechette and McCoy 1993, p. 40). Ecologists quickly appreciated this terminological ambiguity, moreover, and began explicitly distinguishing different senses of ecological stability with different terms (Odenbaugh 2001).

Shrader-Frechette and McCoy's second claim is that, "There is no homogeneous class of processes or relationships that exhibit stability," (1993, p. 58). The underlying assumption seems to be that concepts in general, and ecological stability in particular, must refer to a homogeneous class in order to be conceptually unproblematic. That ecological stability does not, and worse, that ecologists have supposedly attributed inconsistent meanings to it, shows the concept is incoherent, they believe, much like the vexed species concept (1993, p. 57). Shrader-Frechette and McCoy do not offer an argument for this assumption, and it is indefensible as a general claim about what concepts must refer to. Common concepts provide clear counterexamples. The concepts 'sibling,' 'crystal,' and 'field,' for instance, refer to heterogeneous classes, but there is nothing conceptually problematic about them. There is debate about the idea of disjunctive *properties* in work on multiple realization (Kim 1998), but criticisms raised against disjunctive properties do not necessarily apply to disjunctive *concepts*, nor were they intended to. Kim (1998, p. 110) emphasizes this point:

> Qua property, dormativity is heterogeneous and disjunctive, and it lacks the kind of causal homogeneity and projectability that we demand from kinds and properties useful in formulating laws and explanations. But [the concept of] dormativity may well serve important conceptual and epistemic needs, by grouping properties that share features of interest to us in a given context of inquiry.

Even if criticisms of disjunctive properties were sound, it therefore would not follow that the disjunctive concepts such as ecological stability are also problematic. Shrader-Frechette and McCoy's criticism of ecological stability is therefore indefensible. The conceptual and epistemic utility of a concept is enhanced, furthermore, if clear guidelines for its application exist, which the above analysis has attempted to provide.

Moreover, the definitional status of the concepts of ecological stability and species is not analogous. Biologists have proposed plausible, but incompatible competing definitions for the species concept because it is problematically ambiguous (Ereshefsky 2001; Reydon 2013). That resistance, resilience, and tolerance have been referred to under the rubric 'stability,' however, do not show ecological stability is similarly problematically ambiguous because they are conceptually independent and therefore compatible, as different senses of 'species' are not.[8] In addition, most ecologists recognized that there are several components of ecological stability, and individual stability concepts such as resistance, resilience and tolerance, or measures thereof, were rarely proposed as *the* uniquely correct definition of ecological stability. Rather, they were and should be understood as distinct features of ecological stability or ways of measuring it, not competing definitional candidates. Like many

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[8] As noted above, different quantitative measures of resistance, resilience, and tolerance may be incompatible. This does not establish, however, that the corresponding concepts are incompatible.

scientific concepts, ecological stability is multifaceted, and the distinct referents ecologists attributed to it accurately reflect this. Conceptual multifacetedness alone does not entail conceptual incoherence or inconsistency.

6 Conclusion

The discussion above confirms philosophy of ecology's proper place within the purview of philosophy of science. It should, and increasingly is, garnering the philosophical attention it should. Before concluding, the timely significance of the relationship between ecology and conservation science, and environmental science more generally, merits special consideration. Although ecology has received less attention from philosophers of science than other areas of the life sciences, this has begun to change as the severity and complexity of environmental problems, and ecology's potential role in helping solving them, has become more apparent. Threats to coral reefs and the ecologically-informed management strategies developed in response are vivid examples. Ecology provides a scientific basis for conservation action, pollution reduction and mitigation, and other environmentalist objectives. Indeed, conservation biology is sometimes conceptualized as a species of applied ecology, and concepts such as the 'balance of nature' have a central place in how biology students conceptualize environmental challenges (Hovardas and Korfiatis 2011; Ergazaki and Ampatzidis 2012). This marshaling of scientific resources to achieve ethical goals raises a multitude of philosophically rich issues.

One is the precise nature of the relationship between facts and values in such applied sciences. It often seems that facts and ethical values are very closely linked in the experimental and statistical methods these sciences employ (see also Gannett, this volume). For example, values seem to determine how uncertainty is managed, particularly whether the available data are sufficiently strong to overcome uncertainty and warrant accepting or rejecting hypotheses (Shrader-Frechette 1990). One of the most direct ways in which ethical and socio-political 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 non-epistemic, 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 ethical considerations. Numerous other examples could be cited. Some philosophers have recently argued this close connection between fact and value constitutes confluence, that facts and values are indelibly intertwined in such ethically-driven sciences (Putnam 2002); others believe this conclusion is overstated (Sober 2007).

A related issue concerns how the notion of "progress" should be conceptualized in sciences such as applied ecology. Innovations that constitute significant progress towards achieving the ethical goals some applied sciences are intended to help achieve—e.g. biodiversity conservation—often involve improvements in data acquisition, statistical analysis, or algorithm efficacy. That these clear advances do not resemble the kind of developments in theory paradigmatically considered scientific progress in other sciences does not mean they do not constitute genuine progress (*cf*. Linquist 2008). A different, broader notion of progress is therefore needed to recognize the role achieving ethical goals has in some applied sciences.

Although ecology underpins much of evolutionary theory and it seeks to understand vast portions of the biological world, the typical undergraduate exposure to biology often consists entirely of developmental biology and evolutionary theory, at the expense of ecological science. Similarly, philosophers of biology have paid relatively little attention to ecology. This inattention is due to disciplinary inertia rather than principled position, so it is ripe for change. This essay contributes to that change by describing some of the philosophically rich issues ecologists study.

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