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BOOK REVIEW

The diversities of biodiversity

James Maclaurin and Kim Sterelny: What is Biodiversity? The University of Chicago Press, Chicago, 2008, xii + 217 pp, US$ 24 PB

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A monograph-length analysis of biodiversity from two senior philosophers of biology reflects two things: the problematic complexity of the concept, and the interesting theoretical and methodological issues the sciences studying and endeavouring to protect it raise. The concept's significance is common currency within environmental ethics, but biodiversity has only recently garnered broader philosophical attention. Helping rectify this, Maclaurin and Sterelny make a novel and valuable contribution to the growing scientifically oriented philosophical literature on biodiversity.

For a thin book, its scope is ambitious. While other analyses of biodiversity focus primarily on ecological diversity, eight relatively short chapters (and brief conclusion) cover: disciplinary and legal circumstances in which the concept of biodiversity emerged (Chap. 1); taxonomic methodologies and their bearing on characterizing biodiversity (Chap. 1), especially different accounts of species (Chap. 2); differences and relationships between species richness and disparity (Chap. 3); morphological, developmental, and ecological diversity (Chaps. 4–6); and the problems in measuring and valuing biodiversity in conservation biology (Chaps. 7–8). Accessible prose and a wealth of well-chosen biological details are two superlative virtues of the analysis. Almost every page teems with scientifically informed, up-to-date examples illustrating the philosophical claims made.

Coined as a simple shorthand for 'biological diversity' in the mid-1980s, 'biodiversity' designates the diversity of biological systems at all organisational "levels", the population and community levels being the most common focus. How this diversity should be characterized depends upon how these systems are

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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 diversity may vary across these contexts as well. This underpins MacClaurin and Sterelny's expressly pluralistic approach throughout the book, as opposed to the view that biodiversity designates a *single* property of biological systems, an assumption implicit in some biologists' language and explicitly endorsed by some philosophers (e.g. Holmes Rolston).

After deftly reviewing species concepts and their underlying taxonomic philosophies, Chap. 2 recommends an evolutionary concept that recognizes the import of phenotypic differences, but also their evolutionary origin in different speciation mechanisms. This reflects a general concern to represent biodiversity as an effect *and cause* of ecological and evolutionary patterns and processes. The biodiversity concept provides no special insight into resolving these contentious taxonomic issues, in particular, how weaknesses of evolutionary species concepts are surmountable. But reviewing and being reminded of their fundamental role in characterizing biodiversity is illuminative and will be especially useful for environmentally minded readers interested in biodiversity but less familiar with theories of biological classification.

Differences between species obviously vary; humans and mockingbirds differ more than humans and bonobos but less than humans and nematodes. 'Disparity' designates the degree of such interspecific phenotypic variation. The difficult question is not whether disparity is a "genuine dimension" of biodiversity (p. 45)—it clearly is—but rather how it is measurable in a scientifically defensible way. Chapter 4 convincingly shows that morphospace distance can supply a principled measurement methodology, providing the disparity concept with the empirical and theoretical tractability science requires. Morphospaces are multidimensional spaces, each dimension representing a distinct morphological feature of actual, or merely possible, organisms; David Raup's 4-dimensional morphospace for mollusk shells is a well-known example (pp. 67–72). MacClaurin and Sterelny emphasize, however, that morphospace distance only characterizes disparity in terms of the phenotypic properties defining the space. Disparity is therefore only tractable with respect to specific, empirically well-motivated morphospaces, which are rarely available and typically only for clades of small size. No generalities emerge from the discussion, moreover, about when defensible morphospaces can be expected to emerge. The prospects accordingly appear dim for a general characterization of disparity across actual organismal morphologies, let alone possible ones. Chapter 3 initially motivates this view by arguing that Steven J. Gould's influential claim that Cambrian fauna were of much higher disparity than today requires a more expansive characterization of disparity than is currently scientifically justified.

After describing different forms of developmental plasticity and their likely significant role in maintaining biodiversity against environmental perturbation in Chapter 5, Chapter 6 defends a local, nonindividualistic conception of biological communities. Part of the view holds biological communities have *emergent* causal properties, i.e. ones that do not "simply reflect" properties of their constituent populations. A precise criterion for gauging this kind of emergence is not needed to agree that there are causally efficacious properties usually described at the community-level. Community stability, for instance, is often claimed to be responsible for and/or produced by diversity, also at the community-level. But a precise criterion would help in assessing whether specific conceptions of community stability support the emergence claim. On this issue, for instance, Maclaurin and Sterelny cite ecologist David Tilman, who characterizes community stability (labelling it 'temporal stability') in terms of mean population biomasses of different species, and their variances and covariances as measured during some time period ("The Ecological Consequences of Biodiversity: A Search for General Principles" *Ecology* 1999). Without further restrictions, however, presumably on the interspecific covariances, it seems individualistic communities as described could be at least as temporally stable as nonindividualistic ones: nothing about Tilman's specific measure prohibits or makes it unlikely that means, variances, and covariances of biomasses in individualistic communities would yield lower temporal stability. This conception of stability is thus a poor indicator of the kind of higher-level causal integration the emergence claim requires. This suggests that the proposed explanations of a positive correlation between temporal stability and diversity may not provide strong evidence of community-level emergent phenomena.

Chapter 6 contains the book's only apparent oversight, exceptional for a philosophical analysis so rich with scientific detail. Maclaurin and Sterelny claim that Robert May, in his influential study of the stability of mathematical models of biological communities (*Stability and Complexity in Model Ecosystems*, Princeton, 1973), identified diversity with species richness (p. 121). But May was concerned with relations between a particular type of stability (Lyapunov stability, which is very different from temporal stability) and what he called *complexity*, not species richness. For linear models of communities, complexity includes the frequency and mean strength of interspecific interaction besides species richness. In fact, given its focus on interspecific interactions, complexity is often distinguished from measures of ecological diversity, which typically focus instead on species richness and evenness: how individuals are distributed among community species (see Justus, J. "Complexity, Diversity, Stability" in Sarkar and Plutynski (eds) *A Companion to Philosophy of Biology*, Blackwell, 2008). Simpson's and Shannon's diversity indices are examples of these quantitative measures, which together with broader measures encompassing genetic and phylogenetic information and biodiversity surrogates, are the purview of Chap. 7.

After describing difficulties with these broader measures, specifically the methods developed for assessing genetic and phylogenetic diversity (e.g. the minimum spanning path method due to Dan Faith), Maclaurin and Sterelny consider the pervasive use of biodiversity surrogates in conservation biology. In real-world conservation planning, biodiversity is operationalised with surrogates: biotic and/or abiotic variables—such as the presence or absence of species, climatic, or geological factors—which are easily assayed for a region, for instance through relatively inexpensive surveys or remote sensing. Surrogates are then used to prioritize areas for conservation within that region. Information about *what surrogates are where* is the basis for these prioritizations, not surrogate *richness*. Biodiversity surrogates can be, and often are, sets of species, so this fact about areaprioritization reinforces the view emphasized throughout the book and widely held among conservation biologists that biodiversity is not adequately characterized as species richness. Maclaurin and Sterelny note that the choice of surrogates is partly conventional, depending on the interests of those studying biodiversity, but they also stress that the relationship between different sets of surrogates is an empirical, and largely unresolved issue. This illustrates the multifaceted nature of biodiversity and motivates their pluralistic approach, but one wonders whether a unique characterization of biodiversity could be formulated in some circumstances. If, for instance, information about a community is limited only to species richness and evenness (and no genetic, phylogenetic, or spatially referenced data on surrogate distributions is available), perhaps a single measure of its diversity is defensible. In such cases, the low representational specificity for the system being modelled might reduce the range of acceptable characterizations of its diversity. The discussion of morphospace diversity seems to countenance this possibility, and it would be worth exploring for the measurement of diversity in conservation biology. For example, one might defend a particular account of how species richness and evenness should be integrated into a unique quantitative index of community diversity (see Justus, J. "A Case Study in Concept Determination: Ecological Diversity" in Brown, de Laplante, and Peacock (eds) *Handbook of the Philosophy of Ecology*, Elsevier, 2010).

Chapter 8 concludes with a cogent examination of daunting problems with valuing biodiversity, illuminating the issues with theories of speciation and taxonomy considered earlier. In all the chapters, the analysis is scientifically informed and philosophically adept. This book, like the few others on biodiversity from a scientifically oriented philosophical perspective, will rightly help set the agenda for work in the philosophy of conservation biology, and environmental science in general.