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As natural as it gets

Natural Systems: The Organisation of Life, by Markus P. Eichhorn, 2016
Wiley-Blackwell, 392 pp. ISBN: 978-1-118-90588-3

Life, as a very special manifestation of the hierarchical organization of matter, can be studied at various levels, or simultaneously at multiple levels as evinced by the fast growing fields of molecular ecology, evo-devo, and eco-evo. The importance of these relatively new fields notwithstanding, recent developments in more traditional disciplines such as biogeography and community ecology are also exciting and can offer crucial insights into the way life manifests on our planet. Several textbooks offer nice accounts of findings in these fields (e.g., Morin 2011, Mittelbach 2012, Begon et al. 2014, Ricklefs and Relyea 2014), and one might think that there is no space left for a fresh textbook view on issues like ecological diversity, biotic communities, island biogeography, etc. Markus Eichhorn did not seem to agree, though, and came up with a book that justly attracts attention (Eichhorn 2016), not so much by its somewhat exceptional title – *Natural Systems: The Organisation of Life* – but mostly by its focus on important questions and a structure that combines the virtues of a compilation of self-sufficient chapters with a coherently unfolding volume. Each chapter starts with a ‘big question’ justifying its theme and ends with suggestions for future work plus a selection of the chapter’s references as recommended reading. It is certain that different authors might formulate the ‘big questions’ in a different way or even focus on different questions, but Eichhorn does not pretend to be ‘objective’ in any absolute sense. He explicitly offers his personal opinion in most debates explored, though without undermining the breadth of coverage and the quintessential authoritative character of a textbook. This alone is an admirable accomplishment; the insightful walk through the extensive and variable literature on each topic is another.

Basic concepts are introduced in the first chapter where the author straightforwardly dis-

credits the Clementian ‘super-organism’ view of ecological systems in a balanced nature, a view commonly held by non-experts. Next, Eichhorn goes on with an admittedly far from exhaustive critique of the species concept, mostly used to alert the reader that species should be considered as dynamic entities or even tentative hypotheses, always keeping in mind what they do and do not represent. The brief reference to the history of life that follows is mainly an introduction to the unevenness of diversity among lineages. Next, the author focuses on estimates of global species richness, pinpointing problems with simplistic methods and techniques that may lead to absurd estimations. As Eichhorn points out, evidently biased or downright inappropriate methods (I would also add their analogs in estimating ‘background extinction rates’) all too often find their way to highly ranked journals (see He and Hubbell 2011), obviously due solely to the ‘sexiness’ of their subject.

Chapters 5 to 9 are grouped as Part II dedicated to ‘Diversity’, and reasonably start with issues related to the measurement of diversity. Here Eichhorn introduces important concepts and tools, such as species accumulation curves, the lognormal distribution with its ‘veil line’, species turnover as pertaining to beta-diversity, and some common metrics of diversity. Chapter 5 is accompanied by an Appendix with a working example, enabling the reader to become familiar with metrics and concepts, playing with real data. This is a key chapter, of course, and the Appendix is well-structured and useful. Nevertheless, it might give a somewhat imbalanced nuance to the book, as similar quantitative exercises are lacking from other equally important chapters.

The chapter that follows will probably evoke strong responses from people working on ecological niches, since Eichhorn supports that a theoretical framework based on the ‘R* rule’ (or

'resource ratio hypothesis', Tilman 1982) offers a much more tenable alternative to traditional niche concepts. He introduces other niche theories briefly, in order to devote most pages to the description of this theory that supposedly bypasses problems faced by previous ones. The niche defined as the 'ZNGI [zero net growth isoclines] of an organism, combined with the impact vectors on the ZNGI in the multivariate space defined by the environmental factors' (see Chase and Leibold 2003), though, may not be able to provide a more tractable and meaningful solution to the niche problem. The selection of environmental factors that define the 'multivariate space', for instance, still remains subjective. The discussion of the niche problem by Looijen (1998) might be useful here, but to some disappointment, no reference to this work is made. Nevertheless, the chapter can stimulate a lot of thinking; the theory presented makes several interesting predictions that can be tested and explored further, and has many implications for our understanding of ecological systems.

An admirably comprehensive account of major spatial diversity patterns, such as the species-area relationship, elevation and depth gradients, mid-domain effects, local-regional richness patterns, etc., is given in Chapter 7. Several of these issues are discussed later on, so this is actually an introduction to Chapter 8, where the author explores drivers of diversity. Available energy, spatial and temporal heterogeneity, disturbance, and top-down control are considered and, along the way, density-dependence, Janzen-Connell and storage effects are introduced. Eichhorn favors the view that heterogeneity has positive effects on diversity and, in fact, uses the motto 'diversity begets diversity' in a title, but might be overly allured by 'humped curves'. In fact, he seems to concede to arguments by Allouche et al. (2012) regarding 'habitat heterogeneity gone wild' that predict a diminution of diversity in areas of high heterogeneity, without citing the ripostes by Hortal et al. (2013) and Carnicer et al. (2013). In the penultimate chapter of the book, though, he does present a more balanced account of the relevant dispute (Kadmon et al. 2007, Hor-

tal et al. 2009). The 'Diversity' part concludes with Chapter 9 posing another controversial question: does diversity matter? The author here, in contrast to his general attitude of skepticism, seems to be somewhat biased towards the noble 'diversity is good' worldview, despite the lack of decisive evidence from the real world.

Part III examines organization of living systems at the community scale, even though the distinction between 'community' and 'assemblage' remains a bit vague throughout this discussion (as is also the case in most ecological literature). In the first chapter of this part (Chapter 10), the author manages to move flexibly through a vast range of issues, from food chains to species abundance distributions, as well as the 'unified neutral theory' (Hubbell 2001) and the metabolic theory of ecology (Brown et al. 2004). Assumptions of the neutral theory are criticized, of course, but Eichhorn concludes that neutral theory can be very useful as it seems to work even in cases where it is clear that the assumptions are not met. This, of course, begs for a satisfactory mechanism; the recent suggestion by, *inter alia*, Stephen Hubbell (Chisholm et al. 2014), for bringing community ecology in line with the literature on population dynamics with *less emphasis on stability and neutrality* should be taken into account.

A more detailed examination of stability, succession and disturbance is provided in the next two chapters, using carefully selected examples that highlight crucial aspects of the respective discussions. Eichhorn also includes an, arguably superfluous, special reference to the Gaia hypothesis where he undermines its foundations. Some diffidence in the author's attitude towards the 'stability' concept is apparent here, though, as he argues that the planet moves between 'stable states' throughout its history. One might have expected a more consistent radical view questioning this concept at its core by asking, for example, how many components of a system should we find unchanged in time (or re-established after disturbance) in order to identify it as 'stable'. Or, more generally, which is the amount of 'acceptable' variation in any aspect of a stable

system (components or functions), and why should we consider it as mere variation and not as downright change.

The last chapter of the 'Communities' part (Chapter 13) deals with assembly rules, competitive exclusion, metacommunities and dispersal limitation. The traditionally considered role of competition in shaping patterns of coexistence among related species is debated in view of accumulating evidence from various sources. It may come as a surprise, though, that the relatively large literature on species 'co-occurrence' seems to be ignored, even though more recent findings are often in line with the views of the author (e.g., Gotelli and Ulrich 2010, Pitta et al. 2012).

The final part is dedicated to 'Biogeography'. It should be noted (with some satisfaction, to tell the truth) that Eichhorn does not use the term 'macroecology' anywhere in the book, obviously addressing 'macroecological' questions under more traditional titles. After a necessary chapter on biogeographic regions, biomes etc., several issues on regional species richness are briefly introduced and, then, the much debated topic of latitudinal gradients is discussed in more detail. All major explanatory hypotheses that have been proposed are presented in a balanced and critical way. Maybe the more perplexing and, in some respects, very intriguing chapter (Chapter 17) is the one on 'Earth history' that, rather unexpectedly, is inserted here. Of course, one should not expect a detailed account of the planet's complex geological past, a topic necessitating a separate book. Here, Eichhorn presents a brief overview that serves to introduce the ensuing discussion on the role of dispersal in shaping biotas. Assumed effects of the 'Ice Ages' are dealt with in length, always under the 'dispersal' framework. Nevertheless, the whole field of 'phylogeography', particularly pertinent to this whole approach, is almost neglected. We may overlook this shortfall, highlighting the chapter's concluding question, 'what do we mean when we call something a natural system?', a superficially semantic issue, but one that may have important consequences in our understanding of biodiversity, as suggested below. The discussion on disper-

sal continues in Chapter 18, delving more deeply into mechanisms and offering an account of two well worked-out examples on New Zealand and Madagascar.

No account of living systems could be complete, though, without a discussion on islands and island biogeography. This is attempted in chapters 19 and 20 which, in fact, can be considered as one. Topics like the 'island rule', endemism, disharmony etc., are introduced in a manner aiming to trigger further study by the reader. Of course, MacArthur and Wilson's (1967) Equilibrium Theory of Island Biogeography is also presented, albeit abbreviated as EMIB (a model) even though it is correctly called a theory (thus, ETIB) producing some epistemological confusion. The discussion emphasizes studies that have attempted to test aspects of the theory by subsequent authors, leading to a rather controversial critique, which leaves the false impression that issues like the target-area, rescue effects, effects related to habitat heterogeneity, or even the fact that islands occur in groups (!), pose major problems for the dynamic equilibrium theory. Additions and/or extensions of a theory do not undermine it (c.f. Darwinism) and, in fact, some of these issues were already considered in the original formulation of the theory (MacArthur and Wilson 1967). Findings supporting the 'core-satellite' pattern (Hanski 1982) that is often exhibited by species in island groups are also considered by Eichhorn as severe problems for ETIB, perceived as implying that islands are at a non-dynamic equilibrium that does not fit well with the theory. The existence of a core set of species not subject to turnover (at least in time scales we can address in our studies), though, cannot be considered as fatal for ETIB, since this 'core' rarely consists of the majority of the species (e.g., see Ulrich and Zalewski 2006); the examples of artificial *Spartina* islands (Rey 1985) corralled to illustrate a stable core are exceptional, not typical, of islands. Furthermore, there is strong evidence for intensive turnover of species on real islands and in other species assemblages (e.g., Panitsa et al. 2008, Dornelas et al. 2014, Morrison, in press). Overall, without getting into more details, the account of ETIB is a relative-

ly weak point in the book. The biogeography part ends with a discussion of how evolution might be introduced in island biogeography theory, culminating with an account of the advantages and limitations of the General Dynamic Model of Oceanic Island Biogeography (Whittaker et al. 2008, although this model is not explicitly mentioned by its name in the text).

The final chapter of the book is of a more metaphysical flavor, addressing the question of what is a natural system. The author clearly declares that the balance of nature is a myth, scale is all-important, ecological interactions are nested and cannot be understood by reducing them into separate components, and contingency is omnipresent making natural systems intrinsically unpredictable. Eichhorn, echoing Croizat on this, urges ecologists to focus more on processes than on system structure and properties, which he considers to be mere epiphenomena. A few more words along this line might be necessary.

The use of the adjective 'natural' to describe systems of living organisms can be regarded as a relic of a pre-Darwinian dualistic philosophy, distinguishing humans from the rest of the world. Alternatively, in view of the rapidly intensifying, extensive effects of humans on the biosphere, one may choose to use 'natural' as a value-judgment descriptor (presumably positively loaded) or to apply the distinction from 'anthropogenic' systems for purely practical reasons (e.g., conservation related). Eichhorn, making a good use of his deep knowledge of modern ecology, seems to lean toward the latter approach, but is not immune to value judgments, as all too often is the case with ecologists. This is maybe due to a tendency for researchers who have chosen to work in biodiversity-related fields to have done so because they already carried a deep concern and love, *a.k.a.* carried biased views, for biodiversity (but this could be the subject of another book). Eichhorn, for instance, often refers to the 'health' of natural systems and/or communities, as if disturbance (i.e., [relatively] rapid change of a system's status) is a 'bad' thing. He is not to be blamed for this, of course, since this language pervades almost all of ecology. Nevertheless, given

that throughout his book he challenges conventional approaches and puts under scrutiny almost all major concepts and traditional views, one might expect an even more radical treatment here too. This subtle ambivalence can be also found in the, often admittedly inevitable, use of concepts like 'species', 'stability' or even 'community', despite the explicit and thoughtful criticism on their vagueness he also presents in the book.

The time may have come for an unbiased post-Darwinian revision of our terminology and conceptualizations. Humans are an integral part of nature and continuous change at all temporal and spatial scales is the rule. Implicit value-judgments can and should be avoided, thus making ecology an even more robust and epistemologically consistent science. Eichhorn's book is a bold step towards this aim and shows the way ecology should be taught to students at all levels. At the same time, it presents an extensive overview of almost all important questions regarding biodiversity and the organization of living organisms at different levels that are currently under discourse. It would be impossible to be unable to identify a few weaknesses here and there, given the breadth of the book's scope and the vastness of the literature on almost all subjects dealt with. Eichhorn managed to keep these at a minimum, offering us a work that is at the same time comprehensive, informative, educational, stimulating and pleasant to read. The standards this book has set will not be easily met by future authors.

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