

The Problem of Biodiversity

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Abstract

After pointing out the severity of current biodiversity loss, I argue that the lack of an appropriate theory of biodiversity is one of the main obstacles standing in the way of an appropriate response. Reasons for this lack are investigated, followed by the discussion of a promising route towards building a theory of biodiversity.

1 The Great Collapse

Have you ever wondered what it would have been like to live during one of the great mass extinctions on earth? Well, just look around you. It is happening again. Right now [1].

According to the synthesis report on biodiversity by the Millennium Ecosystem Assessment [2], current extinction rates are 100 to 1000 times higher than they were throughout paleontological times, where extinctions and the creation of new species were in balance. Projections see this figure increase to about 10.000 to 100.000 over the next fifty years [2]. When looking at particular, well-studied groups of species and applying the IUCN-World Conservation Union criteria for threats of extinction, it is found that [2, 3] “some 12% of birds, 25% of mammals, and at least 32% of amphibians are threatened with extinction over the next century.” By another account [4], there are about 50-150 species lost every day. About one every fifteen minutes. Seriously.

The reasons for this catastrophic collapse of biodiversity (I shall here focus on diversity in terms of the number of species) are well known. Among the main environmental pressures are the loss of natural habitats to human use; the inability of native species to compete with invasive alien species introduced by humans or the complete re-organization of ecosystems by invasive species, anthropogenic climate change, and over-harvesting. It has been estimated that [3] “90% of the total weight of large predators of the ocean such as tuna, swordfish, and sharks has disappeared in modern times.[...] In some sea areas, the total weight of fish available to be captured is less than a hundredth of that caught before the onset of industrial fishing.” Further pressures on the world’s ecosystems result from the fact 40% to 50% of the fresh water running off the land is used by humans, who instead doubled the production of biologically usable nitrogen compared to natural levels, further upsetting the balance of nature [2].

2 So what?

While the Millennium Ecosystems Assessment does an excellent job in summarizing the difficult scientific work that has led to our current understanding of biodiversity loss and making it accessible to the public (and one would wish more people read it), it also reveals our poor understanding of the consequences of all this. Why should we worry?

The Assessment’s main line of the argument refers to the value of services provided by ecosystems to humans. These are services such as the provisions of clean air and water; regulation and stabilization of the environmental; production of food, fiber, and fuel; and recreational, aesthetic and ethic values. But do

we really need all of the estimated 5 million to 30 million species on earth to profit from these services? Ethical considerations aside, wouldn't we be just as well off with only half of the estimated eight million species of insects, centipedes and millipedes? Or only a thousands of them? It is well known that most species on earth are rare, having population densities of only a hundredth or a thousands of those few, dominant species that we are all familiar with (a phenomenon which is by itself not well understood [5]). It is not obvious what all the rare species are good for. In fact, while it is stressed that even on plain economic grounds more must be done to protect nature, the Assessment concedes that [2] "the total amount of biodiversity that would be conserved based strictly on utilitarian considerations is likely to be less than the amount present today (medium certainty)."

Yet, there are several ways in which each and every species could have its role in the working of nature and its value to us; and each of these has, to some extent, been demonstrated empirically. (1) Ecosystems seem to "function" the better the more species they contain [6]. The "function" most often considered in experiments, however, is simply production of biomass, and the effect seems to scale with the logarithm of the number of species, thus rapidly becoming weaker as the number of species increases. Furthermore, most systems investigated had a rather simple structure, consisting, for example, only of plants. (2) Rare species may serve as an "insurance" [7]. In the case that environmental conditions change such that one of the dominating species cannot maintain its population and its role in the system, one of the rare species could take over in a diverse system. (3) Rare species might be filling small ecological "niches" left open by the dominant species, and thus closing the ecosystems up against the invasion of alien species. [8] (4) Each species, rare or abundant, might carry in its genome or by its phenotype, some information useful for technical or medical applications.

The reason why we are currently unable to make a better case out of these considerations, in particular of (1) to (3), is the complexity of real ecosystems. The body of empirical results is not without contradictions. What is found for one system is not found for another one. Setting experiments up slightly differently or asking slightly different questions, one often gets different answers [6, 8].

3 A theory of biodiversity?

A theory that would organize the accumulated empirical data regarding the role of biodiversity, that would explain under which conditions what kind of outcome of impoverished biodiversity must be expected, is missing. We are therefore unable to extrapolate the empirical findings to the relevant scales of space, time and species number, and to the actual functional and trophic complexity of ecosystems, as would be necessary to assess their implications for us, humans. This lack of understanding of the role of biodiversity in nature is a direct consequence of our poor understanding of the *structure* of biodiversity. While there is plenty of data revealing consistent patterns in the relationships between the numbers of species and their abundances, their sizes, their phylogenetic groupings, their trophic levels, the size of areas studies and its geographic latitude, as well as dependencies on the size, age, and degree of isolation of the ecosystems they live in, a coherent theory that would make sense of much of this data is missing. Lack of such a theory of biodiversity, and the ensuing inability to put experiments on the role of biodiversity into context, are, I believe, at the core of the current problem of biodiversity.

Without a strong underlying theory, the debate on merits and necessity of biodiversity conservation will fall prey to selective readings and interpretations of disparate data by stakeholders, much as we have experienced it in the debate on global warming until recently. The question is, however, if such a theory can be found, and if it was found, if we would hear about it. Even 13 years after John Lawton's inspiring essay on the question of ecological theory [9] the WIWACS (World Is Infinitely Wonderful And Complex School), which holds that ecology is theory resistant, has still many followers. Even worse, it is by now standard to sell the observation of a correlation between two quantities as a "prediction" or "explanation", as if this was all we could hope for. Rightfully appalled by a tradition of theoretical ecology (allegedly going back to G. E. Hutchinson [10]) by which models may be unrealistically simple or even wrong, if only they are thought provoking, and by the habit of theorists to argue for their models by "plausibility" rather than their ability to reproduce observations, any ecological theory today is met with scepticism. Theoretical ecologists are regularly forced to hide the essence of their work, their models and derivations,

in appendices, of which some aren't even printed. As a result, it is unclear what exactly is said; concepts and predictions remain fuzzy, only adding to the confusion. If somebody came forward with a general theory of biodiversity today, which would necessarily be of some mathematical complexity, chances are slim that any ecological journal would publish it. Even with his comparatively simple neutral theory, S. P. Hubbell initially met stiff resistance, which he eventually evaded by publishing it as a book [11]. But how far are we really from understanding biodiversity at its basis?

4 Yes, we can (understand biodiversity)!

Selfishly, I may here advertise the Population Dynamical Matching Model—described in an online appendix [12]—as an example for the degree of realism that has now been reached in modeling biodiversity in complex, multitrophic communities. After some struggle with reviewers and editors, we were at least able to smuggle a detailed characterization of the model steady state into an article otherwise concerned with one particular model application [13].

The model describes the population dynamics and evolution of species interacting in a food web. Basically, each species is characterized by its total biomass, which is determined by population dynamics, and the mean body mass of individuals, which varies over 15 orders of magnitude, plus ten other abstract evolving traits, which together determine the trophic interaction structure. The set of species in a community evolves by invasions, speciations, and extinctions. Thus, we have a characterization of communities in terms of body sizes, biomasses (or abundances), and a trophic interaction structure. Jonsson et. al [14] suggested to break down the discussion of community structure by first considering each of these three aspects separately, then combinations in pairs, and finally considering the structure as a whole. To make a long story short: on each of these levels of description the model reaches semi-quantitative agreement with empirical data for pelagic aquatic communities [13].

Body sizes of species are distributed fairly evenly over 14 orders of magnitude, with somewhat more small than large species and the distribution dropping off sharply at about 10 kg. The distribution has a slight dip about 0.1 g, corresponding to the frequently observed gap in size distributions between fish and zooplankton. Only primary producers are unrealistically squeezed into a single size class. *Biomasses* of species—or abundances within a given size class—are distributed approximately log-normally, spreading over about three orders of magnitude, consistent with typical empirical data. *Food web topology* reproduces that of empirical data sets by 13 different measures. The *distribution of species over trophic levels*, with higher trophic levels becoming less sharp and less diverse, agrees with empirical data as well. The *exponent relating body size to abundance* is approximately -1 in agreement with observations. And, finally, the *ordering of species by trophic level* follows largely that by size and abundance (top predators are large and rare), but some deviations are found, as is the case in nature.

Thus, apart from aspects related to spatial distribution, the mapping of the structure of biodiversity onto a mechanistic model has here largely been successful. We are now working on an analysis of the mechanisms generating this structure by an inspection of the Population Dynamical Matching Model and simplified model variants. Since the model displays all structural features listed above at the same time, we can expect that the explanations found for each of these features will be consistent with each other, a point which is not generally clear for simpler models [5].

With a good understanding and further verification of model structure and dynamics, we will then be able to address, in a reliable form, specific questions regarding the role of biodiversity for ecosystem functioning and utility.

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