BOOK REVIEW: STEPHEN P. HUBBELL'S THE UNIFIED NEUTRAL THEORY OF BIODIVERSITY AND BIOGEOGRAPHY

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The tremendous increase in ecological publications over the last 50 years has made it impossible to keep up with all new ideas, concepts, reviews and syntheses. Diversification of ecological subdiciplines, cross-fertilisation with mathematics, chemistry, physics, geography and even economics have made ecology more relevant, but less understandable. Wide-ranging generic principles are as scarce as they have been 100 years ago. As is seems that only physical, chemical and evolutionary principles are accepted by all biologists (did I say "all"?), every higher ecological theory must be based on them. Stephen Hubbell's "Unified Neutral Theory of Biodiversity and Biogeography" is this type of rare and deep-rooted theory, and the book laying it out therefore has to be compared with other landmarks in ecological thinking, most obviously with Robert MacArthur & Ed Wilson's "Theory of Island Biogeography" (1967). To be able to judge this publication, a brief review of its content is appropriate. In ten chapters on 375 pages it comes as a thick book into our world of short attention spans, but once you started reading it, you will find it not a page too long.

The first three chapters set the stage by revisiting the theory of island biogeography (MacArthur & Wilson 1967) in the context of relative species abundance. As this theory uses species as the lowest explanatory level, no inference on the number of individuals per species can readily be made. Long before, and long after MacArthur & Wilson wrote their book, rank-abundance curves have intrigued ecologists, who consistently failed to explain them based on biological reasoning. Negative binomial distributions competed with lognormals, broken-stick-curves with logseries, but, as Hubbell illustrates, none of them fit the most accurate (and most recent) data very well (generally due to the fact that there are many more rare species than predicted). As an appetiser, Hubbell fits his "zero-sum multinomial" distribution with convincing precision. This model is one of a family of so-called "dynamic models of relative abundance of species", which he reviews in the third chapter. Most famous is the lottery model of Chesson & Warner, which is burdened by the problem of using frequency dependent birth rate to match expectations, but still does not fit the data satisfactorily. Hubbell starts his reasoning with the observation that landscapes are saturated with individuals rather than species. It thus follows that an individual must die to allow a new individual to enter the community. This will lead to constantly shifting abundances of species, which he calls "ecological drift", in analogue to genetic drift processes. While only presenting one graph to convince the reader of the correctness of his assumption, the logic is appealing. Even more so are the consequences, which are gradually introduced in chapters 4 and 5.

First, Hubbell focuses on one species in a local community with and without immigration. He finds "after six weeks of algebra" (p. 88) that dispersal from the "metacommunity", i.e. the pool of individuals around the local community under consideration, fully determines local species abundance. In the next chapter (5), he introduces speciation rate (as the probability of a new species per number of birth events) into the model. When calculating the probability of having only one species in a random sample of size n, he derives a formula featuring a small term which proves pivotal in the whole theory: $2Jm\nu$, which he calls Θ, the "fundamental biodiversity number" (where ν= speciation rate and Jm = size of metacommunity). Θ determines the shape of rank-abundance plots: small Θ generate steep and large Θ shallow curves. The model allows him to reconcile opposing ideas from Preston and Fisher, by showing them both right in specific cases. Overall, his "Unified Neutral Theory" (UNT) presents itself a an extension of the Theory of Island Biogeography, at the level of the individual. He goes on exploring its properties (dependence on immigration, size of local community and Θ) and fits it to real data with convincing success. It is able to generate observed pattern, such as that common species are commoner and rare species are rarer on islands, without any assumptions on differences between species (this is the "neutral" bit: *all* individuals have the same fecundity, birth, death, speciation and dispersal rate).

In most of the rest of the book, Hubbell investigates variation on and consequences of his UNT. He finds it to resemble a model that describes the random sampling of alleles from a genome as well as approaching Fisher's logseries for large local communities. Hubbell shows how high dispersal subsidises rare species in small communities and how regional diversity in archipelagos is decreased by high dispersal (while local diversity is increased). Having by now convinced the reader of his UNT, he takes on the fossil record, a benchmark for diversity and evolutionary theory. Most problematic in the fossil record are the apparently abrupt changes in speciation, with many new lineages appearing in some periods and seemingly no evolution in others ("punctuated equilibrium"). However, the UNT can explain it: the death of many individuals (caused by a natural catastrophe, a lethal virus etc) leads to many new births, as the community has now many "vacancies", and therefore also many more new species than normal. Hubbell shows that one does not have to invoke changes in speciation rate to explain the punctuated equilibrium of the fossil record: his theory remains neutral. Similarly, he investigates the lifespan of lineages, tries to correct the sample bias in the fossil record to generate more realistic speciation rates and so forth.

Before, in the final chapter, trying to reconcile his dispersal-assembly with the more classic niche-assembly theory, Hubbell gives an outline of how to calculate by simulation, and then runs through a variety of examples of fitting the UNT to rank-abundance data on forest, as well as animal communities: copepods, bats, bees, birds and fish. He also shows communities that are not fitted well and dwells on the reasons for that. But his final achievement is to convince the reader that the neutral theory actually is more accurate than the niche-assembly, because niche-assembly forces species into trade-offs that make their lifetime reproductive output equal, hence: especially niche-assembled communities consist of individuals with neutral characteristics!

Hubbell closes with comments on some criticism of his theory and leaves the reader both convinced and lost at sea: while the UNT has been so successful, we all know that species are different; while he assumes a landscape saturated in individuals, most communities clearly are not; while explaining an immense amount of the pattern that intrigue us, the UNT can hardly be used at the small scale.

So does the book live up to the standard of the "Monographs in Population Biology"-series, which has been the source of so many influential books since it published MacArthur & Wilson's book in 1967? Absolutely! It is a book rich about an idea that has the power to re-produce generic patterns and that will be in the back of your mind when you, again, try to make sense of the plethora of articles on species diversity, abundance and distribution.

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