Stephen Hubbell, or the paramount power of randomness.

Stephen Hubbell is the father of the “neutral theory” in ecology, which has already stimulated lots of empirical research and theoretical controversy among ecologists since the publication of his masterwork, The unified theory of biodiversity and biogeography in 2001 (UNTB hereafter).

In this book, Hubbell suggests a systematic explanation of many patterns of biodiversity to which ecologists are familiar, such as species richness in a community, species abundance distribution and species area curves; it is as simple as it is counterintuitive, and those two features constitute together its groundbreaking character. To figure this out, think of going into a forest – a tropical forest, which is a classical object of study for ecologists like Hubbell. You find thousand of species of different trees, and then you wonder: Why are there these species here? What accounts for the fact that those three or four species are very abundant, whether many of them are sparse and lots of them are very rare? A natural answer comes from our familiarity with Darwinian biology: some trees are good at exploiting wet soils, some are excellent in dry soils, some can flourish with few light while others need lots of light, etc. Hence each species is found in the places where it’s good at thriving, and the repartition of these places ultimately account for the distribution of the tree species. The key word here is “niche”: there are several qualitatively different niches, and each species lives in the one to which it is adapted. The accounting process for all that is the essential explanans of adaptation as Darwin taught us, namely natural selection.

Hubbell suggests that this intuitive answer is, if not wrong, at least not to be taken for granted. He built a sophisticated and wide-ranging theory showing that if you suppose that natural selection is not acting – i.e., that the effects of competition, namely the major dimension through which natural selection acts, cancel out at the scale of the community and beyond - then the distribution of tree species can be accurately predicted. In other word, assuming that fitnesses of all individuals are equivalent, namely that species have the same birth and death rate per capita, allows you to build a model (simulation, or analytic) that predicts patterns of diversity very close to the ones recorded, especially concerning the distribution of abundances. In a tropical forest such that the Barro Colorado Island in Panama, in which Hubbell gathered data for decades since the 70s, it does it better than the models developing the concepts of niche and competition, which became increasingly complicated at the times Hubbell published UNTB.

Hence the paradox: someone came up with a theory that is more simple – in terms of its parameters and assumptions – than the existing ones, and have at least an equal or better predictive accuracy. To some extent a supporter of this theory could compare it to major revolutions in science, such as Copernicus’ heliocentrism: a much more simple theory is invented, which overcomes the predictive power of the received view that, at the same time, started to be unbelievably complicated (in this case, multiplying epicycles). But that was not the unanimous reception, and in fact the controversy about the neutral theory has been intense, and raised deep philosophical issues about model testing, methodology, prediction, and more generally explanatory goals and validation criteria. Of course, this theory parallels Kimura’s neutral theory of evolution, and it shares with it the same concern for unifying theories, avoiding unnecessary assumptions, and experimental testing. But above all, UNTB raises the issue of how a simple and apparently unrealistic theory can be so accurate. Many answers have been given, often concerning the role of
scales and their articulation; I won’t discuss that in detail but we’ll touch upon it in scales and their articulation.

In this chapter, I’ll investigate the emergence and nature of the neutral theory of biodiversity. Neutral ecology is simple (besides its technical apparatus, which is very sophisticated); so simple that few ecologists could have dreamed of it, since the natural inclination was to complexify niche theories in order to fit the data and include many processes increasingly seeming to be relevant. It’s fair to say that achieving this dream revolutionized theoretical community ecology. How did Hubbell come to this theory, how did it meet in a radically novel manner the issues faced by ecologists, what were its ambitions, how was it received and then incorporated into the theory? This chapter asks those questions.

I’ll start by describing the background of community ecology in which Hubbell began his career: the major issues, the competing theories, the main assumptions. Then I will consider Hubbell’s elaboration of the neutral theory, first by telling his theoretical and academic trajectory, second by characterizing the main tenets of the theory in the book. A third section will situate the neutral theory in ecology, showing how it generalizes indeed some existing trends, but breaks up with other apparently similar theoretical views. The penultimate section relates the fate of the theory, in the current field of community ecology and biogeography. The late section considers some major features of Hubbell’s work epistemologically speaking – the role of simplicity and the quest for unification in his thinking.

1. The theoretical background: niches, competitive exclusion and limiting similarity.

Ecology has been called the “science of the struggle for existence” (Haeckel) or the “science of the relations between organisms and their environments” (Hutchinson & Deevey 1949, among others). This duality indicates that the emphasis on competition and selection can be more or less acute in the conception of ecology. Ecology includes subdisciplines that are not concerned by the same object, even though the concepts and models can overlap: population ecology deals with the relations between abundances of various species, for instance variation among prey and predator species abundances, often modeling them according to Lotka-Volterra equations. Community ecology is interested in accounting for the diversity of species composing the community, and its variation (especially, the conditions for its stability). Functional ecology considers relations between species in ecosystems from the viewpoint of the functional differences between species, and may include ecosystem ecology as the science of ecosystems (i.e. communities plus abiotic resources) considered as closed systems exchanging matter and energy with their environment. In the 60s, the latter as been revivified by the brothers Odum, while community ecology and biogeography have been deeply affected by the theoretical ambitions of Mc Arthur and Wilson’s Theory of island biogeography (1967). Together with Richard Levins or Richard Lewontin, those biologists and ecologists wanted to introduce into ecology mathematical rigor and systematic modeling. Many of these biologists were students of Georg Evelyn Hutchinson, who achieved in the 50s and the 60s a major synthesis of ecological thought. Ecology is also divided according to the scales one considers: biogeography considers regions, which are made of various communities, possibly exchanging species through dispersal.

A major issue raised by biogeography and community ecology concerns patterns of biodiversity. An important one, studied by biogeography, is the “species area curves”, which
relates area of a territory to the amount of species it includes. Mc Arthur and Wilson (1967) proposed an island–mainland model, which models according to few parameters the biodiversity dynamics yielding species area curves. Simply said, in an island-mainland model, species occupy a mainland, can colonize islands, and the amount of species to be found on each island depends upon its size, its distance to the island, the number of species on the mainland and other islands, and is given at the equilibrium between extinction and immigration. This simple model allows predicting the species area curve, their difference in continuous mainlands and in archipelagoes, as well as the evolutionary fate of some characters of those species (convergence or divergence).

In turn, traditional community ecology asks: how are species distributed according to their abundances? What processes account for these patterns? It’s known that many of the species-abundance distributions (SAD) are log-series, as indicated by Fisher; yet some are also log-normal curves, as advocated against him by Preston (1948), but mainly at a smaller scale. There is a regularity here that calls for explanations, as well as an explanation of the differences (Fig 1)

In this field the keywords are competition and niches. Gause in 1935 established the “competitive exclusion principle”: two species with exactly the same requirements can’t coexist; one will drive the other extinct because of competition. This set of requirements, represented according to Hutchinson (1959) as a subspace of the hyperspace of ecological parameters, is what is called “niche” (Pocheville 2015); it is proper to a species. From this “fundamental niche”, one should distinguish the “realized niche”, that is, the result of competition between two species whose fundamental niches overlap. Indeed, the better competitor will occupy its proper fundamental niche, whereas the lesser competitor will occupy the part of the niche that is not part of the fundamental niche of the better competitor. Competition therefore partitions the niche space into non-overlapping realized niches that correspond to the species, and this explains the

![Dominance-diversity curves for tree species in four closed-canopy forests, spanning a large latitudinal gradient. The four curves seem to represent a single family of mathematical functions, suggesting that a simple theory with few parameters might capture the essential metacommunity patterns of relative species abundance in closed-canopy forests. Redrawn from Hubbell (1979).](http://example.com/diagram.png)

Figure 1. Some Species abundance distributions in various ecological regions (From UNTB)

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coexistence of species at equilibrium. Such kind of explanation is called “limiting similarity” and attracted community ecologists for two decades after Hutchinson.

Yet Hutchinson was aware that this explanation does not entirely capture facts of biodiversity. As he famously argued in several papers if you consider plankton species, there are very few parameters along which the environment differs in ocean: light, pH, temperature… Therefore here should be few realized niches, and we expect few species; but in fact we find thousands phytoplankton species. Modeling realized niches is not enough to account for biodiversity here, which he famously coined the “paradox of the plankton”. Hutchinson had other explanations: for instance that the environmental parameters are quickly changing, so that the directions of competition constantly shift, and that the best competitor don’t have time to competitively exclude others. Another explanation would be that there are fine-grained environmental parameter differences that we don’t perceive and can’t take into account in our niche models.

Competition theory developed and gained in sophistication in order to account for facts and patterns of biodiversity as long as they were discovered through census in tropical forests, mangroves, coral reefs, natural parks. Under many theoretical aspects, community ecology revolved around this axiom: species coexistence should always be tracked down to niche differences, be they plain differences or tiny, periodical, chaotic, non-detectable differences. Hubbell proposed a radically new conception: against the axiom, explaining species coexistence and various diversity patterns does not in principle or a priori need to consider any difference between species biological requirements. Let’s see when and how he came to this view.

2. Stephen Hubbell and the elaboration of the neutral theory.

Like Darwin’s theory, the neutral theory in ecology appeared first as a book. Granted, Hubbell started his career in the late 70s; the book came out in 2001 and, instead of summarizing the teachings of already extant and discussed papers, it elaborated into a single theory those insights he forged from three decades of reflections upon community ecology theory and data gathering in the Barro Colorado Island, Panama.

Born in 1942, Hubbell, was the son of a statistician mother and a father entomologist and evolutionary biologist (director of the Museum of Zoology at the University of Michigan) who gave his son the taste for field trips by taking him with him. He wished to be an architect; a lack of gift for drawing turned him away and he interestingly came back to something closer to his parental background, i.e. biochemistry, after having graduated at Minnesota. As a grad student then in Berkeley he turned to ecology, with Baker as an advisor; his work was lab oriented, working on isopod crustaceans. (He now suggests that this could have been part of a general drive towards empirical science and application, initiated by the fear of the Sputnik as a major soviet technical achievement.) Then, a researcher at the University of Michigan, he was sent in Costa Rica to teach tropical ecology. This experience turned him towards his major topics, tropical plant ecology. He had to go back to University of Iowa, but remained attached to the tropical forest especially by getting involved in the Smithsonian program about tropical forests. Hubbell gathered data on Barro Colorado Island, Panama, since the late 70, and in 1980 together with Robin Foster he got in charge of a program of monitoring exhaustively a plot of 50ha in Barro Colorado, and then follow it year after year (noting the growth of propagules, their dispersion, the fate of trees of all species, etc.). That was the first project of this style; now 40 exist on Earth, and many are led by the Smithsonian Tropical Research Institute (of which Hubbell is a senior scientist, in addition to being at
the Biology Department at UCLA). All BCI data are on line: the growth, birth and death of trees of thousands of species have been monitored since the 80s. At the BCI center, hundreds of scientists have visited and undertook theoretical work in ecology and conservation: e.g. Theodore Schneirla studying for 35 years the ecology of ants have been resident at BCI, or Egbert Leigh who wrote about BCI two books about on community ecology (Leigh 1999).

The interest Hubbell took in establishing the BCI data attests also for the fact that he elaborated the neutral theory through a very tight intertwining between data gathering – i.e. fieldwork - and mathematical modeling. Hubbell’s activity seems to hold noteworthily those two things together to a large extent. Concern for tropical forests is a recurrent feature of his scientific activity, and he never stopped publishing about their specific features – mostly with coauthors Robin Foster and Condit, from the 70s to the most recent works that include a paper trying to evaluate the number of species in the tropical forest (Hubbell et al 2008). Some papers are about conservation (He and Hubbell 2011), others compare various plots now known, such as “A taxonomic comparison of local habitat niches of tropical trees” (Oecologia, 2013) – BCI is the oldest, but in south east Aisa Pasoh is a 50 ha plot that matches it (Condit et al. 1999). In 2012 he co-wrote a paper comparing all the plots worldwide, “The variation of tree beta diversity across a global network of forest plots (De Caceres et al. Global Ecology and Biogeography, 2013)

Before this exposition to tropical forest, Hubbell was comfortable with limiting similarity; however, in this environment he realized that such models don’t easily apply (pers. comm.). Because of the amount of species and the proximity, in fact the distance for competition is very small; species compete in general with their neighbors but in a tropical forest, given the vast amount of common species individuals, these to some extent don’t “see” their neighbors and finally don’t compete. Such realization underlied his dream of a neutral theory.

Hubbell’s first paper introducing ideas of the neutral theory was published in 1979, entitled “Tree Dispersion, Abundance, and Diversity in a Tropical Dry Forest”. It discusses the Janzen-Connell hypothesis, according to which dispersal and seed predation prevent any given species to be monodominant in a forest, since this lowers its probability of self-replacement. The paper tests such ideas about density dependence by confronting them to data about intergenerational turn-over in the BCI. But in the discussion of the paper Hubbell suggests a view of communities, which is the core of the neutral model to come.

However, the paper introduces this view as a side hypothesis, and it’s not developed extensively (the resulting distributions are calculated using Monte Carlo simulations). Actually, the neutral theory itself had to wait almost 20 years for the writing of the book published in 2001 to be constituted. That’s a long time, given that many core ideas were already formulated. Granted, many experimental evidences flourished since the BCI data accumulated during the period. In the meantime, Hubbell published three texts that sketched some of the core ideas – one in the journal Corals reff, another in a collective volume as a conference proceedings - which indicates that no publication in a major ecology or biology journal happened before UNTB came out. Those papers accompanied the writing of the book, whose publication he expected to come slightly before 2001; he calls neutral theory “the unified theory”, which indicates that the unifying ambition is a deep feature of the research program. Interestingly, only the last section of the Corals journal paper is about coral reefs; most of the paper explains a “unified theory” and refers to a forthcoming book whose theories are sketched – using tropical forest data. When the book came out, though, many community ecologists – especially tropical ecology, or coral ecology - were indeed acquainted with the message,
as ecologist Mark Mc Peek recalls (personal communication), though the neutral theory was not really visible as a major theoretical proposition before the book.

While at Princeton, Hubbell started to write this monograph on the neutral theory that he intended to provide a novel view of community ecology and biogeography, entitled *The unified theory of biodiversity and biogeography*. Even though many ideas have been laid before, it was both a systematic elaboration of a worldview, and a set of models likely to articulate it in a way that could be testable – as well as a series of empirical corroborations of the theory, including data from the BCI. The same year, Graham Bell, ecologist at Montréal, published a long paper in *Science* entitled “Macroeocology” where he presented roughly similar ideas about ecological equivalence, based on what he defended in *American naturalist* in 2000 about “neutral communities” (Bell 2000), and especially on a switch towards a scale larger than community ecology – also referring to Hubbell forthcoming book (Bell 2001). Bell was an initial supporter of the neutral theory. Knowing the manuscript of the book, he could propose his assessment of the scope of the theory at the moment where it was being proposed. The almost synchronous publication of Hubbell’s book and Bell’s paper sounds as a generalized attack of some community ecologists upon the whole discipline.

The book is divided in ten chapters – starting by a historical exposition of Island biogeography and of SADs in community ecology, then going through laying down the idea of neutral model, building a model at the scale of community then at the scale of metacommunity, then addressing the issue of species area curves, tackling the question of paleobiological diversity, and finally providing corroborations of neutral models across various ecological domains and discussing its robustness regarding assumptions violations. It finally concludes about the reasons why the theory is so accurate, and the later prospects of theoretical unification it brings. It is “one long argument”, and indeed, mutatis mutandis, echoes the construction of the *Origin of species*, for instance by devoting sections to the difficulties met by the theories. Let’s sketch the key ideas of the book first. Then I’ll show how the book moves forward the ideas exposed in the first paper, and situate this theory historically within 20th century ecology.

The **ecological equivalence assumption** is the main foundation of the models explored in the book: it states that the per capita birth and death rates and migrating or speciating probabilities for all species are equal.

That may be not true, or realistic, but Hubbell’s first question is: how does behave a model of biodiversity dynamics built upon this assumption – which obviously eliminates niche effects, or the effects of selection, since it states that the specific nature of an individual does not in principle affect its relative chances of birth and death. Then, species in the community – understood as “group of trophically similar, sympatric species that actually or potentially compete in a local area for the same or similar resources” (UNTB 5) undergo several processes: dispersal occurs as the appearance of an offspring at some distance from its parent individual; there is speciation, namely appearance of new species. In most of UNTB, speciation occurs instantaneously regarding the other species in the community (“point mutation”) – i.e. in a discrete time model, a novel species individual appears at time step n+1 – though chapter 8 explores “random fission”, another mode of speciation where a subpopulation is randomly sorted in a group of two (old and new) distinct species, a model that is closer to allopatric speciation. Finally there is “ecological drift”, meaning stochastic birth and death: individuals die randomly, and are randomly replaced. It corresponds exactly to the
process of frequency change of equal-fitness alleles in population genetics, named “random genetic drift” by Sewall Wright.

UNTB’s model is a “zero-sum game”: suppose that an individual of a given species in the community dies – then it’s replaced by an individual of a species randomly chosen. The assumption of zero-sum game is one way (explored in UNTB) to model ecological equivalence; empirically, zero-sum game is plausible to the extent that biotic communities are generally saturated (UNTB 53). Paradoxically, appealing to this resource limitation echoes the way Darwin relies on Malthusian considerations.

Ecological drift combines then with dispersal, namely, the fact that an individual dying in a community can also be replaced by an individual from another community, which hosts a different species pool. At each time step, randomly dying individuals are replaced by randomly chosen individuals, of the same or other species (Fig. 2) (Actually, refined models allow for replacement of n individuals at each time step). One can define transitions probabilities in the model: i.e. probabilities that a species of abundance $N_i$ loses an individual, earns an individual, or stays of equal abundance, which are easily defined as functions of the probabilities of death by time steps, size of the community and abundance $N_i$. UNTB’s first model then determines the time of fixation of one species by pure drift (exactly as population genetics models start by computing the time for fixation of one allele by drift alone).

![Figure 2. Simulation of the Markov process of a zero sum game in a community. (From UNTB)](image)

Then, embedding local communities in a regional set of communities is crucial. Hubbell calls this metacommunity. The term was forged on the basis of “metapopulation”, word introduced by Levins (1969) and developed among others by Hanski, who elaborated a “metapopulation ecology” (1986), that has been developed in the 90s especially, and is concerned by fragmentation of populations in distinct habitats. Populations are on habitats separated by some discontinuities. Similarly, metacommunity are pools of communities exchanging individuals through colonization but otherwise separated (hence non competing). The relation between community and metacommunity instantiates the relation between a local scale (explored by community ecologists interested in relative abundance patterns) and a regional scale (explored by TIB’s biogeography): UNTB first explores the neutral dynamics in communities, and then in metacommunity, while their relation defines the unity that’s aimed at by the theory (UNTB 111). Biodiversity patterns are result from this coupled dynamics.

In such model, because of drift in a community, species would get extinct except one, randomly picked up. In metacommunity, “because all species ultimately go extinct, diversity is maintained, in the last analysis, solely by the origination of new species in the
metacommunity” (UNTB 113), and this speciation process in metacommunity proves essential to understand the maintenance of diversity.

In the metacommunity, UNTB computes the unconditional probability, for a sampling, to sample $J$ individuals of the same species. On this basis, it can define the probabilities of various assemblages of species with distinct abundance in the metacommunity, and therefore derive relative abundance distributions. A crucial result is that across those equations emerges a dimensionless number, $J^*\nu$, which Hubbell called the fundamental biodiversity number. $\Theta$ occurs both in equations determining the amount of species and in those determining SAD, hence “$\Theta$ controls not only the equilibrium species richness but also the equilibrium relative species abundance in the metacommunity”.

A major feature of this theory is that species richness is derived from the model, as well as SAD — no need to assume the amount of species to derive SAD as was usually done in niche theories. Among unifying features of the theory, Hubbell shows that Preston’s lognormal curves and Fisher’s logseries could be both derived from the equations of the model, but the latter concerns metacommunities while the former concerns rather local communities. (UNTB134) – even though he more generally derives a distribution called “zero-sum multinomial”, which in practice is similar to logseries but mathematically different (it has a long tail of rare species).

Moreover, from UNTB models one can also derive species area curves in the metacommunity, which was the task of island biogeography. Given that metacommunity size is approximated by the product of area and density, $\Theta$ can be expressed as a function of area, and species-area curves in function of $\Theta$ can be derived. So, biogeography as a study of species area curves, and community ecology as a study of relative abundance can be both merged in a single mathematical theory centered on ecological equivalence, modeling metacommunities undergoing speciation, dispersal and drift – and governed by a single parameter, which in turn, can be estimated by abundance data from each single metacommunity. And at each step, Hubbell compares some data to the resulting patterns of the model – mainly BCI data – and show that they fit as well or better than predictions of niche theories.

Now, like any post-Darwinian biologist/ecologist, Hubbell knows that natural selection is powerful in shaping the traits of species, and in governing the dynamics of allele frequencies among populations. Why then the ecological equivalence? First, dispersal – especially here dispersal of seeds – may delay competitive exclusion, by minimizing the effects of competition upon close neighbors. In such a way, competitive exclusion is trumped, and individuals appear as having invariant fitnesses (Hurtt and Paccala 1995). Ecological equivalence, or near equivalence, can therefore be assumed even if individuals when considered for themselves will have varying fitnesses. For reasons pertaining to dispersal limitation ecological equivalence is therefore a very likely outcome of any evolutionary dynamics in ecosystems. Moreover, as UNTB develops in chapter 10, trade-offs between life history traits of individuals of various species will be increasingly numerous as species and traits are numerous, and this may result in equalizing fitnesses across species: “niche differentiation along life history trade-offs is the very mechanism by which per capita relative fitnesses are equalized among the coexisting species in a community.” (UNTB 325)

UNTBB undoubtedly presents a theory, rather than a hypothesis or a model: it provides a generator for models, based on a simple assumption with its justification, and an instantiation of it, in the form of a zero-sum game, with simulations that predict resulting
patterns, lots of figures discussed in the text, and finally, comparisons with some extended data, such as world avifauna, marine planktonic copepods or tropical trees (chap 9). This theory will be further developed by Hubbell and many other ecologists; it will also be discussed and criticized extensively. Before turning to its fate, let’s consider several of its major features.

3. Salient features of the neutral theory in its historical context.

Parallel with Neutral evolutionary genetics

First, as emphasized by Hubbell, the neutral theory in ecology parallels the neutral theory in evolutionary biology as advanced by Motoo Kimura (Crow 2008). Generally speaking, they have elaborated the same kind of model: assuming neutrality – i.e., fitness invariance for species, or relative fitness equality for alleles – they infer the diversity patterns exhibited by the varying alleles in the genome or species in the community. The parallel holds in a very detailed way: species (in ecology) correspond to alleles types (in genetics), population correspond to gene pool, speciation corresponds to mutation, dispersal corresponds to migration, niche effect corresponds to selection, and ecological drift corresponds to random genetic drift. Moreover, Hubbell found out a parameter \( \Theta \) governing biodiversity dynamics, where earlier Kimura has shown that, despite all the complexity of molecular interactions and evolutionary dynamics, a unique parameter called also \( \Theta \) by geneticists, and similarly made up by effective population size and mutation rate, governs neutral evolution. Interestingly, if both neutral theories are taken as true, a picture of ecology and evolution emerges in which stochasticity seems to rule the highest and the lowest levels of the hierarchy of biological domain: communities on the one hand, alleles on the other hand are mostly driven by stochastic dynamics,
whereas intermediary levels – organisms, groups, species – seem to be mostly governed by natural selection.

This evolution/ecology parallel was actually not there in Hubbell’s first formulations of his ideas. It has been introduced in the book, especially with the elaboration of the sampling formula in metacommunities, which appeared to be equivalent in the field of community ecology to Ewens sampling formula in molecular evolution, demonstrated by Warren Ewens in population genetics about sampling selectively neutral alleles in the infinite allele case (Ewens 1972) : sampling individuals from various species in an infinite metacommunity is the same formula. It was actually a case of serendipity: Hubbell admits not to have been very keen in studying population genetics at this time, and the latest technical developments of the neutral theory by evolutionary geneticists were not his major focus. Hence he derived by himself Ewens formula, and actually presented it at a conference in Brazil where by chance Ewens attended. The latter came to him after the talk and indicated that this formula reminded him something. Then Hubbell conceived of the parallel with neutral genetics more systematically and introduced it as a major element of the presentation of the theory. This important element distinguishes it from null models that have been discussed a decade earlier in ecology (see below). Caswell actually proposed a neutral view of ecology in 1976, including a parallel with neutral evolution (Caswell 1976), but Hubbell did not pay attention to it until he himself wrote UNTB, where he devotes part of chapter 2 to an assessment of Caswell models; actually, Caswell’s model were not discussed by ecologists in a comparable way. It’s fair to say that, notwithstanding those precedents, neutralism as a systematic body of ecological theory, and its subsequent development, was Hubbell’s endeavor.

One could philosophically argue against ecological neutral theory by emphasizing that in evolution, drift is not another process than selection (e.g. Beatty 1994, Walsh 2010): each time there is selection, there is also drift as sampling error proportional to the smallness of the population. Hubbell’s idea that ecological drift can occur in communities with no niche effects therefore contradicts this unity between selection and drift in evolutionary theory. However, the neutral theorist could answer two things:

First, drift in evolution covers two kinds of cases, (a) the fittest does not go to fixation, which indeed is always possible in a token population since fitness describes only probabilities possibly not actualized; (b) cases of equal fitness so that selection doesn’t occur, but random pick of the one that goes to fixation: Hubbell’s drift is equivalent to the latter only.

Second, actually, fitness invariance is itself yielded by the logics of niche differences: “niche differences obey life-history trade-off rules that maintain per capita fitness equivalence among the niche-differentiated species” (UNTB 327) So, as in evolution, in ecology the conditions for drift (i.e. ecological equivalence) are yielded by the fact of selection (i.e. by niche differentiation).

Novelties in UNTB

Neutral genetic evolution was not the only major development added to the 1979 paper insights. One major new concept in the formulation of the theory is the metacommunity, which is not cited in the 1979 formulations. By emphasizing the articulation between regional and local dynamics regarding biodiversity, Hubbell shares a general concern about the limits of community ecology: ecologists in the 2000s started to
doubt about the epistemic value of the community as a unit of analysis. Since the inception of the discipline, they've been concerned with rules for the constitution of the community (assemblage and succession), debates about the ontologically robust character of communities etc., as illustrated by the famous antinomy between Clementsian only oriented towards communities as superorganisms with cycles of life (Odum will pursue this project in ecosystem ecology) and Gleasonian ontology in which species are not participating to any holistic structure at the level of the whole. Yet around the 2000s, in the wake of studies of metacommunity and metapopulations, ecologists started to doubt about the value of a science centered on the dynamics of a community (e.g. Lawton 1999). A growing skepticism regarding the increasing sophistication of niche models of biodiversity, as presented above, may account for part of this suspicion. Ricklefs, who has been a fierce critique of the neutral theory (Ricklefs 2006 for example) - wrote a paper called the “Disintegration of the community” (Ricklefs 2008), in which he argues that focusing on the community misses the major determinants of the dynamics since what happens within it mostly hinges upon other communities around.

Actually, since the 70s, where major theories of limiting similarity, island biogeography, or diversity-stability were proposed (e.g. May 1974), the subdisciplines proliferated within ecology: after Odum’s ecosystem ecology, a focus on trophic network gave rise to functional ecology; community ecology was supplemented by landscape ecology, considering objects at larger time- and spatial scales; population biology gave rise to metapopulation biology; conservation biology and biogeography arose, which shared some of the tenets of theories in those fields but not all of them. This questioned the status of community ecology, which did not have any absolutely proper method or object.

In this sense, Hubbell’s UNTBB is already a response to the suspicion raised against the isolation of community ecology: in his own view, the dynamics of biodiversity at all scales (hence, biogeography, landscape ecology and community ecology) should be understood through the same theoretical framework, since the assumption of ecological equivalence was likely to be construed across all these scales. The concern for unification is therefore crucial in the neutral theory.

Another missing item in the first papers that the UNTB puts forth is speciation. Hubbell admits to have been driven to introduce speciation by a student in tropical ecology courses in Princeton who asked the question while considering materials of this initial paper (pers. comm.). He introduced it in UNTB as point speciation, which made indeed the parallel with neutral theory in genetic more salient. One of his latest challenges consists in considering a more realist view of speciation, namely, the fact that it takes some time, so that for several generations individuals from new species are not so highly distinguishable from individuals of the prior species. This “protracted” speciation models often yields fitter predictions than the classical neutral model (Rosindell et al. 2010), though not in all cases.

Speciation is crucial because its consideration allows Hubbell to embed insights of neutrality indicated in the 1979 paper – and in other attempts to build neutral theories – into the metacommunity dynamics, since it turns metacommunity into a reserve of potentially new species likely to bypass the absorbing character of the metacommunity under drift (whose composition ultimately should be monodominant). Then, “adding speciation unexpectedly resulted in a unification of the theories of island biogeography and relative species abundance-theories that heretofore have had almost completely
separate intellectual histories.” (UNTB 5). He shows in chapter 8 that if speciation is modeled differently (e.g. random fission), then SAD curves will be different; which is in turn a way to test for speciation modes in nature. Paleobiological data can be analyzed in this sense.

The heritage from island biogeography: niche vs. dispersal assembly

UNTB was intended as a major theoretical alternative proposition. As indicated, where ecologists were looking for niche differences as ultimate accountants, it started with ecological equivalence. Thus it was expected to meet some resistances, and in fact it triggered a debate that is not yet settled. Yet, as Hubbell indicates in the first chapter of UNTB, the neutral theory is in fact an extension of the TIB. In their theory, McArthur and Wilson started by considering only immigration and extinction, and therefore model island-mainland dynamics without including considerations about species fitness differences. Competition and fitness differences occur when they consider the fate of few species as colonizing an island, though the biogeographical question of the equilibrium number of species in islands as determined by immigration and extinction – is not addressed in the model through a focus on niches. To this extent, TIB is a “dispersal-assembly” model of communities, whereas prior community ecology was mostly favoring a niche-assembly model of biodiversity dynamics. Yet their ecological equivalence is precisely thought at the level of species, whereas Hubbell’s neutral equivalence is defined as individual equivalence. The latter therefore extends Mc Arthur and Wilson’s framework in a manner that allows him to model the variations of individuals’ frequencies within species, namely, the abundances of species.

To this extent, UNTB can not only predict species-area curves, like TIB, but also species relative abundances - a program proper to community ecology, which however assumes the amount of species in order to compute SADs. As Hubbell (1999) says, by shifting the level of equivalence this theory unifies “theory of island biogeography and relative species abundance”. But unification in the neutral theory means also the prospect of the last chapter of the book, namely a unification of niche- and dispersal-assembly views of diversity. Yet for Hubbell, the latter should be first fully elaborated – in the neutral theory – in order to consider any possible unification. What appears ultimately is that ecological equivalence may be yielded by niche differences in some complex way: “life-history trade-offs and fitness invariance rules potentially decouple niche differentiation from control of the species richness and relative species abundance of communities.” Niche-assembly therefore allows for setting ecological equivalence, which yields dispersal-assembly processes, and hence unifying perspectives is permitted. Yet, given that dispersal assembly studies have rather been pursued at large regional scales, and niche-assembly views at a community, local scale, the two kinds of unification overlap with each other.

One of the first reviews of UNTBB, by community ecologist Peter Abrams in Science, was entitled “a world without competition”; it indicates the shared feeling that Hubbell was shaking the key term of ecologists since decades – from Gause to the Marlboro group, through Hutchinson – “competition”. However, by some aspects Hubbell’s dream of an extensively equivalent nature was entrenched in potentialities that were already mainstream: neutral genetics, of course, outside ecology, and island biogeography within ecology. The radical novelty finally comes with extending such theory.

Yet two paradigm shifts characterize this dream. First, change occurs regarding the
paradigmatic ecological object: TBI had introduced the “island”, then finally ecological thinking came to detect islands everywhere (Losos 2011); Hubbell put the tropical forest at the center of the stage. Second, very deeply, what emerges with Hubbell is an ecology of non-equilibrium – which was already indicated as an empirical result in the 1979 paper: “the available circumstantial evidence suggests that the forest is in a nonequilibrium state.” Major theories in ecology were equilibrium theory: considering state of affairs from the viewpoint of equilibrium reached: competitive exclusion, equilibrium between immigration and extinction in TIB, optimal strategies reached by selection in behavioural ecology (e.g. Arthur and Pianka 1966). In many cases, natural selection brings about those equilibria, which entitles biologists to consider traits and phenotypes from the viewpoint of achieved selection. This is not available in UNTB; on the contrary, the zero-sum game models a system that is not oriented towards equilibrium (as would do fitness maximization). “Our most familiar theories in ecology all concern the population dynamics and community ecology of specific, named, or labeled species, each of which has an assigned dynamical equation or set of equations. However, because the dynamics of any given set of species in the metacommunity obey an absorbing process (all species eventually go extinct), no fixed, nontrivial equilibrium dominance-diversity distribution can exist for any set of named species in the metacommunity. Thus, the analysis of metacommunity dynamics is qualitatively different from most classical ecological theory” (UNTB 115). Since the “balance of nature” has been such a powerful metaphor in ecology (Pimm 1991, Simberloff 2014) the disruption Hubbell introduces was rightly seen as deeply provocative, notwithstanding the genuine filiation I just emphasized. This feature also explains that many physicists, especially from non-linear dynamics (out of equilibrium systems), have been interested by the neutral theory and suggested modeling advances (e.g. Azaele et al 2006, Houchmanzadeh and Vallade 2003).

4. Fate and developments.

The UNTB underwent a contrasted reception, even though most reviews acknowledged the novelty of the book. In a few years, it became a hot topic for ecologists. Sophisticated discussions pervaded ecology and general journals, mostly triggered by the obvious counterintuitive fact that an assumption as unrealistic as ecological equivalence sounded as good as the most refined niche models to account for known biodiversity patterns. Several aspects of the theory have been especially addressed in those discussion: first (a), the empirical attestations, the fit with the extant data; second (b), the legitimacy of the notion of ecological equivalence; third (c), the logical status of the theory itself. In 2006 a special issue of Ecology, journal of the Ecological Society of America (2006, 87 (6)) edited by Michel Loreau, Marcel Holyoak and Donald Strong, examined the neutral theory, as the “rigorous framework” that deserves stochasticity in ecological populations, acknowledged since the times of Gleason. A paper by Hubbell, another coauthored by Bell developed some of its implications, whereas papers by Ricklefs or others such as Mc Gill e al. doing an empirical evaluation were more critical. “Exploration of neutral theory has only just begun” concluded the editors.

Since UNTB, Hubbell himself made decisive advances on the two first points. As always, writing with lots of collaborators – papers about the BCI, as expectable, had often more than ten people involved – he applied the neutral theory to BCI data and other tropical forests plots; he also developed various other neutral models, and Volkov et al. (2003) formulated an analytic solution for species distributions under ecological equivalence, where UNTB was often doing simulations. As to (b), he suggested an evolution of the
ecological equivalence (Hubbell 2006) and recently elaborated the hypothesis that fungi-
trees parasitism relation was impacting competitive relations between trees in a way that
makes ecological equivalence plausible (Barberan et al. 2015).

The current work on the neutral theory is much concerned by what Hubbell (2006)
indeed highlighted namely the fact that a whole bunch of processes, often niche
processes, may lead to neutral patterns. Therefore, instead of trying to falsify the neutral
theory, another way of research is about integrating niches into the neutral theory (Adler
et al. 2007, Holt 2006, Mc Gill 2010), in a framework where the effect of niches
difference should be progressively added to a baseline neutral model (see also Vellend
2010). Another research directions consists in considering near-ecological equivalence,
which may not satisfy strict per capita equality, but still across the metacommunity carries
similar consequences regarding biodiversity dynamics: this parallels the shift in neutral
molecular evolution towards “nearly neutral theories” (Ohta 1992), and was sketched in
UNTB (chapter 10), “incorporating modest fitness differences does not result in the
rapid competitive exclusion and extinction of disadvantaged species in the
metacommunity” (337). Whatever the next developments, it seems fair to assert that, as
in the case of neutral evolution, an idea that originally sounded so disruptive regarding
the almost century long teachings of ecology have proved to be part of the theoretical
apparatus of the science, and clearly fuels empirical research programs, and requiring
more data gathering – even though its core was a shift in mathematical modeling.

Other authors, after the publication of UNTB and subsequent neutralist papers,
criticized the widespread validity of the theory (e.g. for coral reefs). Yet a major issue
raised about the status of the theory was the place for null hypotheses. Some ecologists
indeed consider that the neutral theory is a null hypothesis (Mc Gill et al. 2006,
Doncaster 2005), to which any hypothesis about species coexistence or SAD should be
measured, but not a hypothesis by itself.

Null models.

Yet in ecology the notion of null hypothesis or null model had a rich and tormented
history. In 1977 started what some people call the null models war. Jared Diamond
argued that when ecosystems display a checkerboard distribution of species, for instance
in a archipelago, species being present on an island only when another is absent locally
and reciprocally, then it’s the result of competition. Ecologists Daniel Simberloff and
John Connor, in response argued that this pattern means nothing since, first, one should
randomly shuffle the data (presence-absence matrixes of all species in all islands),
producing all patterns that could happen randomly, and then compute among them the
probability of the checkerboard distribution. This probability being high they concluded
that nothing could be said regarding the effects of competition from a checkerboard-like
attested pattern (Simberloff and Connor 1982, Connor and Simberloff 2014). It was a
rude controversy, all the harsher that the object was tied to conservation practices – the
conclusion regarding wildlife management were absolutely different if Diamond, or
Simberloff, were right. The side of Simberloff, apparently more technically refined, was
accused of being oblivious to actual biology (and conservation needs). The war
culminated in an issue of American Naturalist devoted to “A Round Table on Research in
Ecology and Evolutionary Biology” (Vol. 122, No. 5, Nov., 1983), and publishing some
of these authors. In it, Jonathan Roughgarden (1980) for instance says: “No biological
processes are exhibited that produce the distributions predicted by the null models.
Hence we do not learn anything by falsifying these hypotheses.” And he adds: “the
neutrality hypothesis is about real processes.” Ironically, the methodological attitude he
sketches suits Hubbell’s very well since UNTB presents a neutral hypothesis with the 3 processes - drift, random dispersal and random speciation. After his first paper hinting at neutral dynamics, Hubbell didn’t publish almost anything on neutrality, in part because he did not want to get involved in those speculations (pers. comm.), or also because of the possible hostility the use of neutral or null models in ecology could trigger at those times among some field ecologists. Publishing UNTB had to wait for the null models war to calm down a bit.

Granted, UNTB can appear as a null model (McGill et al. 2006): testing whether niches determine species coexistence seems to require that it’s not already the case by chance (see also Gotelli and McGill 2006, arguing that null is not neutral). However even if viewed as a null model, Hubbell’s neutral theory does not correspond to Simberloff’s or later on Gotelli and Graves (1996) null models: it is not built by randomly reshuffling the extant data, but by starting with some processes – migration, speciation, dispersal, ecological drift - , and then considering the outcomes, before comparing it to what would happen through niche effects10.

Yet the times when ecologists designed null models correspond exactly to the emergence of neutral models in another field – paleobiology. As a major event in the advent of this new discipline, one counts the MBL model by Gould, Raup, Schopf and Simberloff (himself involved in the null models controversy in ecology), simulating shape of clades at a very long timescale (Raup et al. 1973, Huss 2004). Biologists’ interest for neutral modeling was obvious in this period; a volume edited by Nitecki entitled Neutral models in biology (1981) includes sections about neutral models in paleobiology, another about ecology, and one on genetics (written by Jim Crow). UNTB appears to have maturated in such an atmosphere of neutrality-friendly biology, but then emerged genuinely when it was over; possibly, the null model wars in ecology made people more acquainted with neutral models and less reluctant to selection-free models. Paleobiology was not expectedly an influence for Hubbell, though UNTB centered the speciation chapter on paleobiology, making hypotheses about neutral processes underlying marine fossil diversity, and one of his recent papers compares the neutral theory with Gould’s views (Hubbell 2009). Here, he recalls that he shares with Gould and then fellow paleobiologists the notion of “symmetry” – another name for equivalence between processes or individuals. He develops the idea, indicated in UNTB (ch 9) that Raup et al. (1977) neutral models did not show that the shapes of clades result from drift because, like TIB, they define neutrality at the level above individual (TIB: species, Raup et al. : lineage), which prevents them to capture the real process. In UNTB, Hubbell analyses a paper by Levinton (1979) which builds a neutral paleobiogical model explaining diversity steady states in the fossil record without invoking niche assembly rules – a view closer to UNTB than the MBL model since it focuses on individual level. In the 2009 paper, Hubbell indicates that paleobiology, with all the data regarding the phylogenies of biodiversity, may provide a set of evidences even more reliable for the neutral theory than ecological data. In fact, a fundamental level of unification lurks behind the overall theory, namely unification between ecology and evolution, that have been always sought since Hutchinson11, but never reached. Indeed, metacommunity drift dynamics, governed by a parameter $\Theta$ which is very large, proves very slow (common species tend to dominate for a very long time), so that “ecological and evolutionary rates of change will become commensurate on large landscape scales” (UNTB 149). To this extent, neutral ecology directly pertains to macroevolution, hence to paleobiology.
5. Epistemic status of the theory

If UNTB is not one more null hypothesis, at least according to Hubbell, then what is it? And, to conclude, what kind of epistemological attitude did allow its elaboration by Hubbell?

In 1999 ecologist John Lawton published a paper (cited above) entitled “are there laws in ecology” and answered “no” – there is a handful of generalizations, different across ecosystems, and that’s it. This very skeptical paper – at such point that its author left research afterwards – has been widely read among ecologists. Hubbell confessed to find it depressing to read (while he was working on the book), and to some extent this is very understandable: it says that ecology is a gerrymandered patchwork of generalizations at all scales. This plainly contrasts with Hubbell’s unifying intent.

Moreover Hubbell’s attitude is exactly opposite: not about finding one generality here, one generality there and then look for an overlapping law, but exactly what Vellend (2010) defines here: “starting first from principles and then asking what patterns in nature we expect to see based on the action of elementary processes”. Hubbell starts with generality and then (biological) differences may or may not emerge as explanation. On the basis of simple assumption, construct a model and then reflect upon the plausibility of the assumptions. Neutral theory is to some extent the parsimonious hypothesis: parameters such as niches differences are set to 0, and then one builds the model and compute outcomes – and compare them to data. Where this parsimonious theory fails, it shows that biological difference (niches and competition abilities) should play an explanatory role – and not before, otherwise the model will face testability problems.

In contrast, niche theory in the 80s elaborated a very sophisticated variant called R* (“resource-ratio”) theory; stemming from Mc Arthur and Levins (1964) paper on patchy environments and the competition between species foraging a finite set of identical resources heterogeneously distributed. Developed later on by Tilman (1982) it asserts that “when resources are heterogeneously distributed, the number of species can be larger than the number of limiting resources, thereby resolving Hutchinson’s paradox of the plankton. R* theory is a conceptual advance over previous phenomenological-competition theories, such as the Lotka-Volterra predator–prey model, because it predicts the outcome of competition experiments before they are performed.” (Marquet et al 2009). However, it includes a high amount of free parameters, whereas the neutral theory in fact has only three or four depending upon the models (Θ, m, J). Considering that they yield the same predictions, one should then favor the neutral theory for parsimony reasons. Moreover, the epistemic cost of the sophistications of the R* theory is that it’s very hard to falsify it, since one can set the parameters in the correct way to yield the expected results. Inversely, estimating the value of parameters is highly difficult, given their amount, which is an advantage of the neutral theory, because calibrating models is easy since it has only three parameters.

Neutral theory in ecology appears as an attempt to systematize the simplest explanatory framework for pervasive pattern generalities in ecology: log-series or log-normal shapes of SAD, species area curves such as Arrhenius law, which proves very robust. Hubbell’s gambit is that a single theory can account those seemingly universal patterns – and that this theory should minimize its amount of parameters. Especially, it should rather derive key parameter values from a few parameters such as m (migration rate), J (metacommunity size) and Θ, rather than assume them. Extinction rates were assumed in
TIB, but derived in UNTB; community ecology assumes species richness in order to investigate SAD, and biogeography also assumes it to explain species area curves; and in general, niche theories assume the set of niches, in order to apply competitive exclusion principles. In contrast, the neutral theory derives SAD and species area curves, as well as the amount of species, from its basic parameters. If the predictions fit the data, then it has a legitimate pretension to be taken seriously.

Simplicity and testability are therefore key epistemic values advanced by Hubbell, added to simplicity, unifying character and parsimony. The second one sounds Popperian; indeed Hubbell says that as a student he has been impressed by a paper published by biologist Joseph Platt in *Science*, “Strong inference”, which advocated a strong stance on testability. This hypothetico-deductive model of science favoring predictions and mathematical simplicity was a first inspiration for his methodology, and a continuous one, whereas few philosophers of science have been explicitly his references.

More generally, Hubbell advocated from the start an attitude inspired by physicists, especially with regard to their use of mathematics, which impressed him when he took classes besides biology in these disciplines (pers comm.), and the way they start with simple theories, check with experiments, change parameters, etc. He is critical of this “loop” between mathematical models and experiments among ecologists, arguing that they too often want to derive from statistical analyses of data their theories, and is still very skeptical about the way the use of so-called “big data” strengthen such inclination.

Borrowing a word physicists like, Hubbell explicitly says his preference for what he calls “efficient theories” (Marquet et al. 2014), that is, theories likely to use general mathematical framework, few parameters, and can predict and therefore be tested. Yet being efficient is also important in an ordinary sense, namely for practical matters like conservation: if models rely on hundreds of parameters whose estimation is not feasible, then they can’t be of any use for prediction, and therefore for conservation.

His latest topic is a joint work with Patricia Gowaty, his wife, who is a prominent expert in evolutionary biology of mating behavior and sexual selection. Interestingly, a same approach guides the research here: instead of multiplying the fixed sex differences, and assuming the male and female stereotypical behaviors as given parameters in the problem (i.e. “promiscuous males” and “coy females”), they built a model in which a few parameters regarding the environment determine an equation – the “Switch point theorem” - which for a given individual decides in fine what will be its mating strategy (Gowaty and Hubbell 2009). No strategy is therefore embedded within a male or female individual, and even if the model often concurs with ordinary types of sexual and mating behavior, it lets the difference between individuals emerge from environmental parameter values. Sex differences don’t originally make a difference, exactly as in the UNTB where species differences don’t make a difference from the start.

**Conclusion.**

The neutral theory today belongs to the corpus of theoretical ecology; Morin’s community ecology textbook, 8 years after the publication of UNTB, includes a section on the neutral theory (Morin 2009). Even though the controversy on the scope, meaning and accuracy of the neutral theory is going on, ecology has already integrated such approach as something that has to be taken into account by future ecologists (a fact echoed by the prestigious awards received by Hubbell since 2006). To some extent the
fate of this theory parallels its predecessor and analogon within evolutionary biology. Especially, while Kimura triggered new questions, not only about the extent of neutrality but also about new objects such as the molecular clock, UNTB rose a new problem for ecologists, namely the extent of ecological equivalence, the detection of equivalence-ecology/neutrality patterns in extant ecosystems, and the estimation of biodiversity number.

Neutral views in ecology have preceded Hubbell: the abovementioned papers by Caswell and Levinton in the 70s were obvious forerunners of the idea of individual ecological equivalence as a base for model building. The historical question is therefore: “why did the neutral theory, as such, emerge in 2001 with Hubbell?” The answer of course should pinpoint Hubbell’s proper trajectory and intellectual interests, as well as his epistemic stance towards systematicity and generality; but it’s also about the embedding of the theory within a thorough fieldwork about censing and monitoring trees in tropical forest, which provided a source for data that continuously fueled mathematical modeling and provided patterns to be fit by predictions. Finally, the fading of the neutral models wars possibly left some room for such a generalized theory to be not only dreamt, but also systematically built. At this condition, one of Hubbell’s initial goal, namely "dispel the pervasive resistance of ecologists to neutral theory by demonstrating its considerable predictive power" (UNTB 11) was attainable, and the book reached it.

Granted, Hubbell’s neutral theory was entrenched within earlier theories, especially TIB – exactly like Kimura’s theory developed well-established conceptions about random drift and extended them. Yet it extend them through a major concern for parsimony and a thorough mathematical treatment, to a point where they could make manifest the paramount power of randomness regarding ecological diversity – in a way which does not exactly contradict the ‘paramount power of selection’ as demonstrated by Darwin, but provides us with new tools to understand the levels, scales and situations where it can be overwhelming.

References.


Hubbell and Gowaty 2009

Hubbell S. et al. (2008) “How many tree species are there in the Amazon and how many of them will go extinct?” *PNAS*, 105, 1: 11498–11504


*Science*, 204:335-336


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1 See Odenbaugh (2013).

2 “Some are steeper, and some are shallower, but all of the distributions basically exhibit an S-shaped form, bending up at the left end and down at the right end. Is there a general theoretical explanation for all of these curves?” (UNTb 4).


5 “Suppose that forests are saturated with trees, each of which individually controls a unit of canopy space in the forest and resists invasion by other trees until it is damaged or killed. Let the forest be saturated when it has \( K \) individual trees, regardless of species. Now suppose that the forest is disturbed by a wind, storm, landslide, or the like, and some trees are killed. Let \( D \) trees be killed, and assume that this mortality is randomly distributed across species, with the expectation that the losses of each species are strictly proportional to its current relative abundance. Next let \( D \) new trees grow up, exactly replacing the \( D \) "vacancies" in the canopy created by the disturbance, so that the community is restored to its predisturbance saturation until the next disturbance comes along. Let the expected proportion of the replacement trees contributed by each species be given by the proportional abundance of the species in the community after the disturbance.

Finally, repeat this cycle of disturbance and resaturation over and over again. In the absence of immigration of new species into the community, or of the re-colonization of species formerly present but lost through local extinction, this simple stochastic model leads in the long run to complete dominance by one species. In the short run, however, the model leads to lognormal relative abundance patterns, and to geometric patterns in the intermediate run.”

6 A major driver of fragmentation is human activities, hence metapopulation ecology directly connects to conservation biology.

7 Even though as Elliot 2009 pointed out, this view is widely misleading historically.

8 Because Hubbell had no time to get involved in the analytic treatment before handling the manuscript to the publisher, even though he wanted ultimately an analytic solution because this provides an indubitable result about the model (pers. comm.)

9 “Simberloff”, in Outliers

10 As Bell indicates: “the weak version recognizes that the neutral theory is capable of generating patterns that resemble those arising from survey data, without acknowledging that it correctly identifies the underlying mechanism responsible for generating these patterns. The role of the neutral theory is then restricted to providing the appropriate null hypothesis when evaluating patterns of abundance and diversity. (...) statistical null hypotheses based on randomization are not appropriate for evaluating ecological patterns that stem from species distributions, because local dispersal readily gives rise to spatial patterns.” (Bell 2001).

11 Author of the *Ecological theater and evolutionary play*, a title that indicates both the need and difficulty of unification between both

12 Compare with TBI: “From these a priori mathematical considerations, a biological portrait of the superior colonist is drawn, and matched against an empirical description of superior colonising species made by previous biogeographers”.

13 “Exactly when and how a good formal neutral theory fails should be as interesting, if not more so, as when and how it succeeds.” (UNTb 311)

14 Notwithstanding the fact that epistemological considerations have been vindicated by him and coauthors in the 2014 paper, and also that controversies around UNTB have been quickly revolving around deep epistemic issues: model testing, statistics, parameter estimations, null hypotheses, etc.