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The Unified Neutral Theory of Biodiversity and Biogeography Revisited

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Abstract
The central question in this review is whether the global and local patterns of biodiversity and abundance distribution dynamics are only subject to general statistical laws, such as these predicted by the Central Limit Theorem (CLT) and Unified Neutral Theory of Biodiversity (UNTB), or whether ecological mechanisms are important too for structuring the biodiversity of our planet. The mathematical foundations of the UNTB appear to rely on some principle of gate-keeping of biological data. An important role of the gate-keeping principle is detected in various biodiversity estimates. Besides, the question has risen whether the ecological dimension of the world's ecosystems can be adequately described in terms of mathematical distributions and whether alternative abundance distributions are better suited to fit the experimental data.

Outline:

1. *Introduction: common species and specialists*
2. *Long distance similarities, Gate-keeping and Biodiversity*
3. *Statistics for species abundance distributions*
4. *Pros and Cons of Hubbell's Unified Neutral Theory of Biodiversity (UNTB)*
5. *Alternative prospects: towards a (fractal) Global Ecosystem Approach (GEA)*

Keywords: Biodiversity, Unified Neutral Theory of Biodiversity and Biogeography (UNTB), Metacommunities, Gate-keeping principle, Species Abundance distributions, Fractal Global Ecosystem Approach (fGEA).

Introduction: common species and specialists

It is well known from taxonomic and biogeographical surveys that certain species inhabit a vast geographical distribution area, for instance because they are omnipresent in lowland areas or follow human cultivated or urban areas (e.g. several members of the *Muridae*, like Norway rat, *Rattus norvegicus*, Black rat, *R. rattus*, House mouse, *Mus musculus*). Also in many cases, their distribution is widespread because they are so-called exotic species with a global distribution (in the temperate climate zones), some of them introduced in modern times (like Muskrat, *Ondatra zibethica*; Raccoon, *Procyon lotor*; et cetera). Several seabirds as well as migrating birds hibernating in subarctic regions, also have a global distribution in the (Northern) hemisphere at both sides of the Atlantic; the oceanic environment in fact facilitates their global distribution. The vast geographical distribution doesn't necessarily mean that they are abundantly present in all habitats (e.g. sandy or rocky island shores for breeding), or present during all seasons. Common examples are found among the Gulls and Terns (*Laridae*), Alcids and Guillemots (*Alcidae*), such as the Razorbill (*Alca torda*) and the Common murre (*Uria aalge*). Inhabitants of both Old and New World are also found among

the Sea ducks and Mergansers (*Anatidae*), like the Common eider (*Somateria mollissima*), the Common merganser (*Mergus merganser*) and the Smew (Mergus albellus), but also some song birds like the Winter wren (*Troglodytes troglodytes*) are present on both continents (Fig. 1). On the other hand, a multiple of this number of vertebrate species show only a limited geographical distribution or show taxonomically related species in similar habitats. Due to an evolutionary speciation process, they became distinct, non-interbreeding species. When considering European reptiles and amphibians, for instance, common species with a continental distribution area are:

1. several frog species of the Ranidae, some possibly interbreeding, like the *Pelophylax* (*Rana*) *lessonae* & P. (*Rana*) *klepton esculentus* species cluster,
2. to some degree also *R. temporaria and R. arvalis*, as well as
3. several lizards (*Lacerta agilis, L. viridis, L. vivipara, et cetera*) and
4. some common snakes and vipers (*Natrix natrix, Vipera berus*) (Fig. 2) [1]. In the Mediterranean coastal regions, islands and peninsulas however, a multiple of distinct

reptile species occur, probably also as a result of the geographical isolation that subsists speciation.

Figure. 1.A.

Figure. 1.B.

Figure 1(A,B) : Two examples of common bird species that are widespread in Old and New World: the Winter Wren (*Troglodytes troglodytes)* (A, top) and Common Merganser (*Mergus merganser*) (*B, below*). In contrast to these species and a number of others, most bird species are confined to either the Old World or the New World (Photographs by Biological Publishing, A&O).

Provided the taxonomic and biogeographical considerations given above, it seems logic and conceivable that the abundance similarities of common species at large distance have a much larger impact, than the specialist species with a limited areal distribution (see-2. Long distance similarities, Gate-keeping and Biodiversity).

The observation that in many taxonomic groups, communities and habitats, a variety of very common species, rather uncommon species and also very rare species (may) occur, has provided a strong motive to infer a mathematical model for describing and predicting the dynamics of species abundance and biodiversity [2-5]. The relationship between the relative species abundance and the species rank in abundance, i.e. the species ordered according to their rank in abundance (from commonest at the left to rarest on the right) (Fig. 3), according to Stephen P. Hubbell, is best represented using a lognormal (-like) distribution [5]. This distribution not only

follows the logic of a strict mathematical deduction (see - 3. Statistics for species abundance distributions). The central theorem of Hubbell's work is that "relative species abundances are lognormal-like if community dynamics obey a zero-sum random drift process" (p. 57). In his view, this theorem is corroborated by the observation that "large landscapes are always biotically saturated with individuals" and "the total number of individuals increases linearly with the area" (first noted by Preston, 1948) [6]. Hubbell's theory however, also builds upon assumptions regarding the nature of biodiversity and the absence of a role of ecological niches and trophic levels in driving biodiversity dynamics. Hubbell uses the term 'biodiversity' as synonymous to 'species richness' and 'relative species abundance (in space and time)' (Hubbell, p. 3), and not the more inclusive definition of biodiversity (like ecological 'performance' or interactiveness) as "it is commomly used in policy circles" (*ibidem*) [7]. In particular, Hubbell considers metacommunities as a group of "trophically similar, sympatric species" that "actually or potentially compete in a local area for the same or similar resources" (Hubbell, p. 5). Therefore, in Hubbell's theory, "most biodiversity resides within rather than between trophic levels (because there are more species than trophic levels)" (*ibidem*). When interactions between trophic levels and influence of niche-interactions would be taken into account, a very different kind of biodiversity theory would have resulted (see - 4. Pros and Cons of Hubbell's Unified Neutral Theory of Biodiversity).
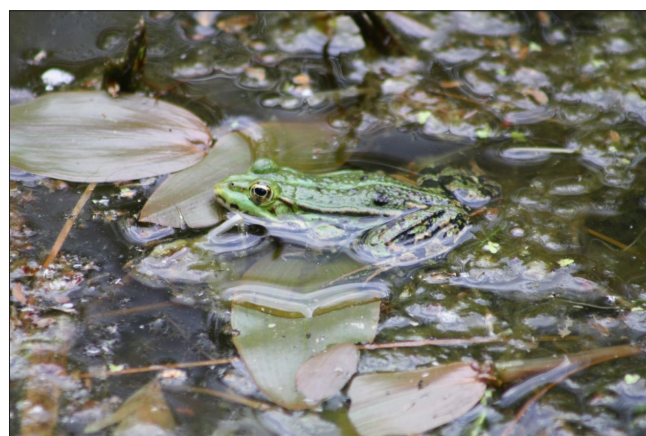

Figure:2.A.

Figure. 2.B.

Figure.2.C.

Figure. 2.D.

Figure 2 : Four common species that show a wide distribution area in Europe: A. The Pool Frog (*Pelophylax [Rana] lessonae & klepton esculentus*); B. Common Frog (*Rana temporaria*); C. Common Slowworm (*Anguis fragilis*); D. Common European Viper (*Vipera berus*). Beside these common, dominant, 'continental' species, many other amphibians and reptiles in the eastern hemisphere have only a limited or regional distribution (Photographs by Biological Publishing, A&O).
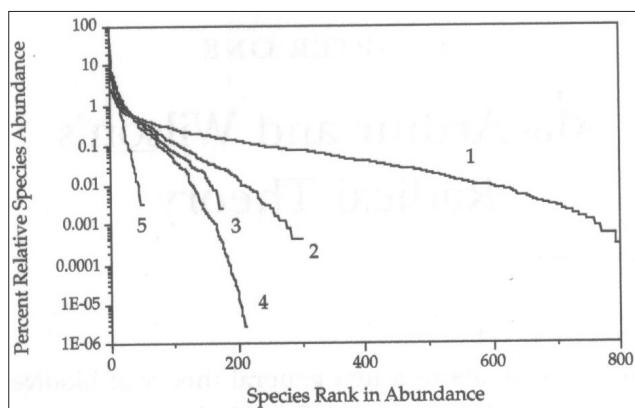

Figure 3: Relationship between species rank in abundance (*horizontal axis*) and percent relative species abundance (*vertical axis*) in 5 different ecological 'metacommunities' (courtesy of prof.dr. Stephen P. Hubbell, 2001). The rank in abundance goes from the commonest species (*at the left*), to the rarest species (*on the right*). Surprisingly all ecosystems

display a similar pattern (at least when metacommunities are confined to the same or 'similar' trophic levels):

1. Tropical wet forest in Amazonia;
2. Tropical dry decidual forest in Costa Rica;
3. Marine planktonic copepod community from the North Pacific Gyre;
4. Terrestrial breeding birds of Britain;
5. Tropical bat community from Panama.

Recently, a lot of evidence has been gathered showing that not only specialist species occupy a very specific niche in habitats to which they are adapted. Obviously, specialists also interact with the other species, generalists or specialists, that occur in the same habitat (e.g. the insectivorous birds living on the back of large mammals and reptiles, or between skin-sucking remoras and sharks). Also it has been well-documented following years of ecological and mycological research, both in Europe and the Far East, that many bark beetles and saproxylic beetles are preferentially associated with certain tree species and also exert some form of commensalism on these trees with specific fungal species [8]. Moreover, many other forms of species-specific commensalism are found in the taxonomic groups of *Lichens* and in the *Algae* and coral communities in coral reefs.

The coral reef diversity, however, was found to refute the neutral theory of biodiversity, a theory first formulated in Hubbell's book [5,9]. The results of Dornelas et al. were shown to deviate from the neutral model in "a direction opposite to that predicted in previous critiques of the neutral theory" [3,10,11]. Other studies reported to corroborate 'neutral biodiversity' patterns, for instance in fish communities within the North-American Mississippi-Missouri river basin [12]. In the following paragraphs, we'll explain how the *Unified Neutral Theory of Biodiversity and Biogeography* (UNTB) builds upon general statistical principles and distributions, like the *Central Limit Theorem* (CLT), and how these statistical principles may (or may not) eventually explain ecological mechanisms.

The species named in this study are mostly derived from the Northern hemisphere (with some exceptions), for several reasons, such as the larger percentage covered with continents at the Northern hemisphere and the greater impact of climate change and human activity on speciation and extinction.

Long distance similarities, Gate-keeping and Biodiversity
Long distance similarities in species abundance are the result of several mechanisms such as seasonal migration mechanisms, areal expansion – e.g. following introduction through human activities, like several groups of eutherian mammals (*Placentalia*), being introduced in Australia and New Zealand - or as a result of species extinction in parts of a larger pre-existing distribution area. Here we confine ourselves to the dynamic long-distance migration patterns and their influence on biodiversity.

One of the possible ways of representing the similarity between remote areas is the *Jaccard Similarity Index* (JSI), as calculated for a pair of so-called *Direct Tributary Areas* (DTAs), defined

as the geographical region directly draining to a group of streams (and, therefore, not including areas upstream of it) [12]. This definition especially holds for river beds and is not appropriate for describing migration patterns that are not river-borne. However, the JSI represented by the following formula may find a broader range of applications:

$$JSI_{ij} \approx S_{ij}\big/(S_i + S_j - S_{ij})$$

where S_{ij} is the number of species present in two (comparable) distinct areas, separated by some distance, S_i is the total number of species in i, et cetera [12].

The seasonal migration of for instance many bird species, may be drawn as geodetic lines that in time may constitute a complex harmonic pattern. Their amplitudes may depend on fluctuations of the weather conditions, the number of individuals (larger groups may need longer passage times) and specific landmarks recognized by the species. Well-characterized migration routes are known for many bird groups, with conspicuous migration features like that of the Storks (*Ciconiidae*), Flamingos (*Phoenicopteridae*), Cranes (*Gruidae*), Geese and ducks (*Anatidae*). Less well-known are the migration routes followed by smaller bird species, that often travel at night or at high altitude, or that accompany the seasonal migration of larger bird species.

A general expression of the harmonic migration pattern of the time-averaged group center of a number of species could be represented by:

$$M_N(N_i,t,l) = \sum_i N_i A_i(l) \sin\left(\frac{2\pi}{T_{i.mig}} t + \sigma_i\right)$$

with N_i the number of individuals in species i, A_i a factor representing the species-dependent amplitude of the seasonal migration, l the latitude (e.g. for migration from and to the subarctic/temperate vs. subtropical/tropical climate zones), $T_{i,mig}$ the duration of the migration season of species i and σ^2_i, a species-dependent finite variance term.

Presented like the above formula, the global migration pattern is the sum of a finite number of harmonic functions (Fig. 4), that also can be represented as a finite multiple of infinite exponential series $e^x = 1 + \frac{x}{1!} + \frac{x^2}{2!} + \frac{x^3}{3!} + ...$, which happens to converge for every x.
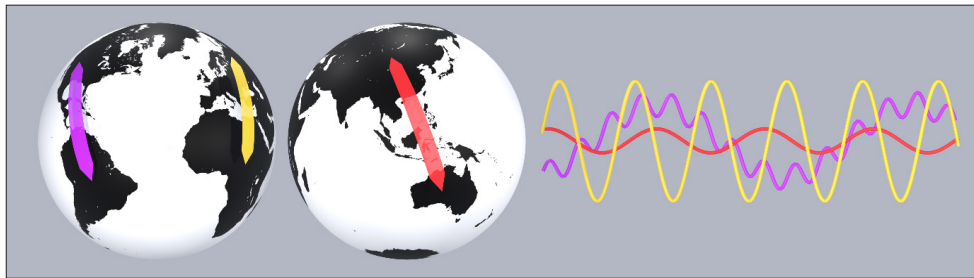

Figure 4: Long-distance (distribution) similarities, biodiversity and seasonal migration patterns. The global migration results in a finite number of harmonic functions, that can be decomposed as a sum of variations of the seasonal and latitude-dependent abundance numbers.

The sum of these multiple (infinite) series remains a series of exponentials. In theory this approach is similar to the mathematical theory of Fourier series and Fourier transformation, as proven to be useful in many biological disciplines [13]. In the following paragraph (3), the usefulness of this approach is evaluated in the perspective of the statistics of species abundance distributions. An important question hereby is whether an observed Poisson- or normal distribution may uncontestably point towards a specific ecological mechanism, or whether that distinct processes may yield similar statistical distributions.

Of course, periodic fluctuations in abundance numbers are also well known in non-flying animals, like in several mammals: for instance in the Brown Lemming (*Lemmus trimucronatus*) or in the European Field Vole (*Microtus arvalis*). From prey analysis in pellets from the Barn Owl (*Tyto alba*) and other owls (Fig. 5), it is well known that in periods with low numbers of Field Voles (*Microtus arvalis*), the Barn Owl may replenish their diet with shrews, especially the Eurasian Shrew (*Sorex araneus*) (Fig. 5. A) [14]. Other owl species, like the Long-eared Owl (*Asio otus*) predate very rarely on shrews or other Insectivora, and will rather replenish their Field Vole diet with

Wood Mice (*Apodemus sylvaticus*) (Fig. 5. B) [15,16]. This however doesn't mean that the periodic fluctuations in Field Vole numbers are also reflected in fluctuations in the abundance numbers of Wood Mice or Shrews. At least the Common Shrew appeared to have a rather stable population density in the periods studied [14-16]. When pellets of the more forestial Tawny Owl (*Strix aluco*) are analysed, a greater variety of prey animals is found, including occasional numbers of Dormice (*Gliridae*), including the Edible Dormouse (*Glis glis*), at least until these mammals became very rare in the area (after 1933) (Fig. 5. C) [15,16]. The complementarity in frequency distribution between Field Vole and Insectivora (*in Tyto alba*) (Fig. 5. A) or between Field Vole and Wood Mice (*in Asio otus*) (Fig. 5. B), thus rather reflects the limiting capacity of predation by the owls inhabiting the area. When the total numbers of prey animals are compared with the number of offspring, it is clear that too low numbers of prey animals – as well as increased human interference with the foraging or sheltering locations – occasionally result in the absence of offspring or removal of the owl family [14]. The complementarity therefore must be considered as a reflection of a 'gate-keeping' principle, here operated by the predator species. In the forestial *Strix aluco*, the observed biodiversity (in prey animals) is bigger (Fig. 5.C),

demonstrating that also more foraging strategies are used and/or more niches are frequented by this predator. When testing the influence of sample size on prey animal diversity (*in Tyto alba*), a rather constant picture emerges (Fig. 5. D) [17]. However, a far greater incidence of less common prey species (including the rare *Glis glis*) is observed when comparing pellets from *Strix aluco* with pellets from *Tyto alba* [17].
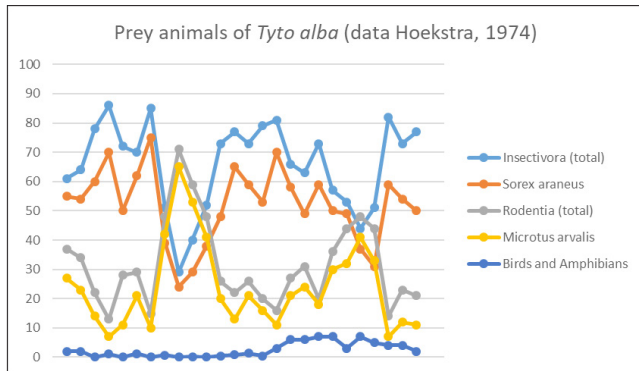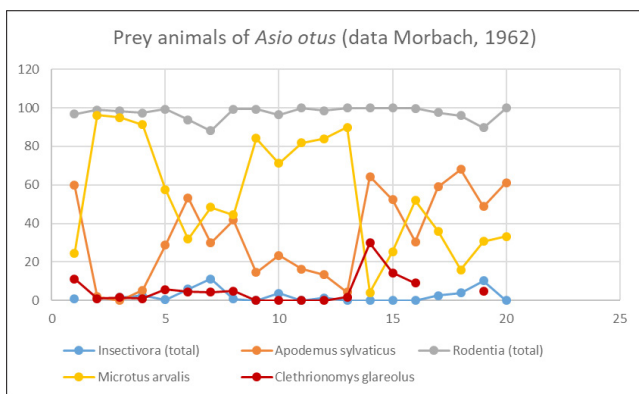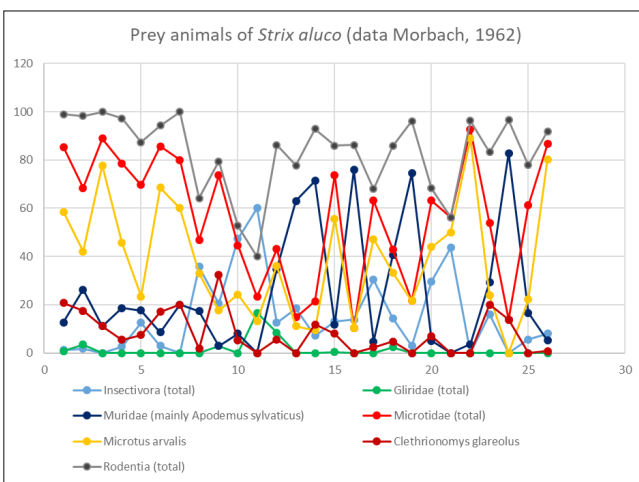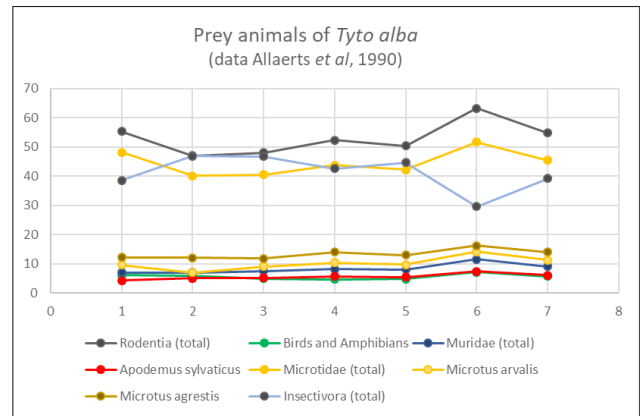

Figure 5(A)

Figure 5(B)

Figure 5(C)

Figure 5(D)

Figure 5: Complementarity of relative prey species abundance in pellets from Northern and/or European owls: A. prey animals of the Barn Owl (*Tyto alba*), collected in the Netherlands between 1953 – 1959, data from Hoekstra (1974); B, C: prey animals of Long-eared Owl (*Asio otus*) (B) and Tawny Owl (*Strix aluco*) (C), collected in Grand Duchy of Luxembourg between 1930-1947, data from Morbach (1962), reviewed in Minkenberg *et al*., 1987); D. influence of sample size on prey abundance in pellets from Barn Owl (*Tyto alba*), collected in 1986 in Belgium, Gaume region, data from Allaerts *et al.* (1990).

In the next paragraphs, it will appear that 'gate-keeping' principles do also occur in other sampling approaches or biodiversity estimates, if not in all.

Statistics for species abundance distributions

The distribution of biological species is generally characterized by the frequent occurrence of 'common' species – i.e. common for a given climate zone, for a specific trophic level or community of species - and a large number of more or less 'rare' species, that are mostly found at very low incidence numbers (frequencies) (see also 1. Common species and specialists) [4].

The statistical distribution that best describes the combination of very rare as well as quite common events in large samples is the Poisson distribution, after the French mathematician Siméon M. Poisson (1781-1840) [18]. For instance, the binomial distribution derived from a sample size k=1000 for a probability space of only two very different probabilities $\{p,q\}$, namely p=0.001 (rare) and q=0.999 (common), yields the expression $(0.001 + 0.999)^{k=1000}$, which is rather cumbersome to calculate. Therefore, one may become more interested in finding an expression for one tail of the distribution, in particular for the rare events:

$$p^0q^k, C(k,1)p^1q^{k-1}, C(k,2)p^2q^{k-2}, C(k,3)p^3q^{k-3}, ... \quad [19]$$

The Poisson series offers a discrete frequency distribution that is especially useful for the estimation of the frequency of rare events. With μ the parametric mean of the distribution (a constant for a given problem, here for instance a given species), this Poisson series becomes:

$$\frac{1}{e^{\mu}}, \frac{\mu}{1!e^{\mu}}, \frac{\mu^2}{2!e^{\mu}}, \frac{\mu^3}{3!e^{\mu}}, \ldots \frac{\mu^r}{r!e^{\mu}}$$

which are the (discrete) successive counts of the rare event (Y). The expression above equals the terms of the infinite series expansion of e^{μ} (see 2., above), when each term is divided by e^{μ} (given that the parametric mean $\underline{\mu}$ is known). In recursive form, it may be re-written as $\hat{f}_i = \hat{f}_{i-1}(\overline{Y}/i)$ for $i = 1, 2, 3, \ldots$ where $\hat{f}_0 = e^{-\overline{Y}} = 1/e^{\overline{Y}}$ [19]. Because the parametric mean μ of the Poisson distribution is not known in general, the sample mean $\overline{Y}$ is taken to replace it, which in the limit gives a similar frequency distribution.

According to the *Central Limit Theory* (CLT), when identically distributed, independent random variables are added, their normalized sum converges toward the normal distribution, even if the original variables themselves are not normally distributed. In the formulation of the CLT by J.W. Lindeberg (1922), only finite variances but not strictly identical distributions are required [20]. Therefore, the CLT is applicable to many biological distribution problems. Strictly speaking, when the *probability density functions* (PDF) are used instead of probability distributions, the density of the sum of two or more variables is the convolution of their densities (probabilities integrated within a range of values). The logarithm of these convolution products is simply the sum of the logarithms of the factors. Therefore, when random variables with only positive values (that approach a normal distribution) are multiplied, the product of different random factors necessarily follows a lognormal distribution.

According to Hubbell (1995), the term 'lognormal-like' (or *zero-sum multinomial*) should be preferred, because "the theoretical distribution of relative species abundance predicted to occur in local communities by the unified theory is not a lognormal" (Hubbell, 2001, p. 58) [21]. Also, when density or frequency-dependent mechanisms are at stake, the lognormal-like distributions are not found.

For Hubbell the critical factor is that when all individuals (Ni) of all species i are taken together (called the number $J = \sum N_i$), then the fluctuations of all these species collectively must obey the zero-sum rule. To our opinion, this rule represents a 'gate-keeping' principle simple and pure (see - 3. Long-distance similarities, Gate-keeping and Biodiversity). The zero-sum rule is like the postulate that for a zoological garden, as a metaphor for the earth's biodiversity, the total number of all individual animals kept in the zoo, must remain constant (e.g. in order to maintain the zoo's economic profitability). Of course, this is a poor metaphor, but it is important to have a clear view on the impact of uncanny premises on the ecological theories they procreate, and sometimes also poor metaphors can be helpful. Briefly, Hubbel's zero-sum rule is that "if density (ρ) of individuals in an area is a constant, then any increase in one species must be accompanied by a matching decrease in the collective number of all other species in the community" (p. 54). One could also call this the tilers-rule (Fig. 6): if a tiler has to cover a wall of fixed size, with a fixed number of equal-sized tiles, then, if he would decide to put a number of some nice Dutch delft blue tiles instead of the ordinary tiles, the number of ordinary tiles would decrease accordingly. In mathematical terms, this tiler's rule yields the following formulas, respectively for the probabilities that species i will decrease, stay constant or increase by one individual:

$$P\{N_i - 1 \mid N_i\} = \mu N_i (J - N_i)/J(J-1)$$
$$P\{N_i \mid N_i\} = 1 - 2\mu N_i (J - N_i)/J(J-1)$$
$$P\{N_i + 1 \mid N_i\} = \mu N_i (J - N_i)/J(J-1) \quad \text{(Hubbell, 2001, p. 56)}$$

with μ the probability that an individual dies per unit time. (Note the symmetry in the formulas yielding the same expression for increasing or decreasing the number of individuals of any species *i*). As a result, the sum of these three probabilities, corresponding to all possible dynamic changes of all species *i*, equals unity, or the total number of individuals (*J*) remains constant (which was an *a priori* condition). Hubbell refers to his earlier work on closed-canopy forests and the work of Hughes on benthic marine invertebrate systems (e.g. in ocean plankton, see below) to provide empirical data supporting his viewpoint [22,23].

Figure 6: 2D-Space-filling Tiles and the Forest Canopy perspective of counting Biodiversity: Front cover picture of S.P. Hubbell's monograph, demonstrating the limiting factor of surface area for the number of trees in a (deciduous) forest canopy.

For the *metacommunity*, a notion used by Hubbell either to denote "all trophically similar individuals and species in a regional collection of local communities", or, a notion used "when applying the theory to biodiversity questions on large, biogeographical spatial scales and evolutionary timescales" (Hubbell, *ibidem*, p. 5), a similar approach is followed. Then, when "sampling with replacement" is found a good approximation, a multinomial probability function can be formulated that, in principle (!), describes "a specifiable Markovian process for the multinomial zero-sum random walk (for all the species in the metacommunity)" (ibidem, p. 119):

$$P\{n_1^{t+1}, n_2^{t+1}, ..., x_1, x_2, ..., n_1^t, n_2^t, ...\} = \frac{J_M!}{\prod_i n_i^{t+1}! \prod_k x_k!} \prod_i \left[\frac{n_i^t(1-\nu)}{J_M} \right]^{n_i^{t+1}} \cdot \prod_k \nu^{x_k}$$

(Hubbell, p. 119)

with J_M the (total!) size of the metacommunity, ν the 'speciation rate', and n_i^t the abundance of species i in generation t. (With the symbol n_i^{t+1}, Hubbell denotes the "abundance of the ith previously extant species in generation $t+1$", whereas x_k is the abundance of the kth newly arisen species). We will hereafter discuss the role of timescales and speciation rates in Hubbell's theory (see also next paragraph: **4. Pros and Cons of Hubbell's UNTB**).

From the rather unmanageable formula above, Hubbell derives the following expression for "F_2^{t+1}, the probability of drawing two individuals of the same species in generation $t+1$", namely:

$$F_2 = \frac{(1-\nu)^2}{J_M - (1-\nu)^2(J_M-1)} \cong \frac{1}{1+2J_M\nu}$$

(Hubbell, ibidem, p. 121).

This result follows from a number of assumptions, like the assumption that a dominance-diversity equilibrium is reached in the metacommunity (see above), meaning that "no changes occur in the probabilities from one generation to another", or $F_2^{t+1} = F_2^t = F_2$, as well as from the well-validated ignoring of higher order terms, since the speciation rate ν is a very small number (e.g. $\nu \ll 10^{-10}$). From this expression, the important 'composite' parameter $\theta = 2J_{M\nu}$ is derived, called a 'fundamental biodiversity number' (θ), which notion obtained significant follow-up in subsequent ecological literature [24]. We should bear in mind that this θ parameter, the product of a very large number J_M (the total number of individuals of all species in a metacommunity) with ν, a very small number (the average speciation rate from one generation to another), yields a manageable "number of intermediate value" (*ibidem*, p. 121). However, it necessarily forms a hypothetical construct, based on several assumptions. For instance, the equilibrium conditions described are similar to dynamical chemical equilibria, where the concentrations of reacting molecules remain constant at equilibrium. Needless to say that this metaphor is lost, a solar system away from what is currently observed in ecological dynamics. Unfortunately, these assumptions have little bearing on the global biodiversity decline mechanisms occurring in the contemporary world.

Hubbell's calls the mechanism underlying his UNTB theory a *zero-sum ecological drift* (*ibidem*, p. 57). His basic assumption is that "community change arises **only** through ecological drift, stochastic but **limited** dispersal, and random speciation" (*ibidem*, p. 7). The term 'ecological drift' recalls an analogy with the notion of 'genetic drift' in population genetics (following the principle of Hardy and Weinberg, formulated around 1908), stating that allele and genotype frequencies in a population (for instance the frequencies represented by the allele pair $\{p,q\}$) remain constant in the absence of other evolutionary influences [25]. Or, following the mathematical rule stating that the binomial distribution for a pair selected from the set $\{p,q\}$ results from the equation $(p+q)^2 = p^2 + 2pq + q^2$. In biological terms, this means that the frequency distribution of homozygotes and heterozygotes for each allele pair is entirely determined by purely mathematical principles, yielding a tautology so-to-speak, at least when other biological influences are ruled out. Hubbell, however, stresses his viewpoint that 'neutrality' is defined at the *individual* level (not at the population level) (*ibidem*, p. 6), although demographic stochasticity plays a role too in shaping the community (see above). This discussion, according to Hubbell, is analogous to the long-standing discussion in population genetics whether "most change in gene frequencies results from random, neutral evolution or from natural selection" (*ibidem*, p. 8). Natural selection, following the logic of Darwinism, indeed occurs at the individual level, whereas the mechanisms of speciation and persistence of species is obviously a group phenomenon (of populations or clusters of populations that constitute a species). Also in this debate, the notion of timescales and the distinction between effects at the individual versus population levels, are equally important (see below).

Pros and Cons of Hubbell's Unified Neutral Theory of Biodiversity (UNTB)

A number of important challenges to Hubbell's *Unified Theory of Biodiversity* (UNTB) have been presented, following meticulous statistical analysis of empirical data, in particular Gilbert's and Lechowicz' data on dispersal and niche-dependent distribution of (small) vascular plants in a temperate forest understory vegetation [11]. The choice of these authors for small vascular plants - and not for the canopy-constituting trees - makes a 'gate-keeping' principle influencing the biodiversity estimates less likely (see 2). The evidence provided by their test, whether the distribution and abundance of species follows a neutral versus a niche-based expectation pattern, strongly supported the niche-structuring hypothesis and found little support for neutral predictions [11]. Moreover, they concluded that the contamination of environmental factors that covariate with geographic distance, may even provide "misleading support for neutral spatial processes" [11]. Also McGill tried to test whether several empirical data supported a zero-sum polynomial (like presented by Hubbell, 2001) better than a lognormal distribution [24]. However, it did not, for instance when data of the North American Breeding Bird Survey (BBS) or the Barro Colorado Island (BCI) tree data sets were used [24].

Hubbell's UNTB, however, remains very valuable in many cases, like it seems to explain biodiversity in fish communities in river beds [12]. The continuity of a wide range of geographical regions, connected through one river basin, and principles like 'large-mouthed (animals) eat small-mouthed (animals)' (alternative reading of 'one size fits them all'), may be in favor for a niche-independent neutral dispersal mechanism. The similarity with the previously mentioned 'gate-keeping' principle is obvious. The same rule may hold for the benthic invertebrate communities in our oceans [23]. Also in the data of Gilbert and Lechowicz , a neutral decrease of similarity with distance may be observed in the distribution

of tree seedlings (not when fully grown to constitute the forest canopy), although "this effect explained only one percent of the total variation in tree seedling distribution" (p. 7653) [11].

Hubbell's interpretation of the relative unimportance of ecological niche, the conviction that "niche differences are not essential to coexistence" (Hubbell, 2001, p. 10), or the designation of niche as a result of an evolutionary speciation process, is indeed a dangerously misleading concept when viewed in the light of the anthropogenic, fast and huge industrial-scale devastations of the planet's ecosystems. The association of species coexistence and niche-dependency with persistence or extinction "measured in millions to tens of millions of years" (Hubbell, *ibidem*), with an actual, empirically based statistical-mechanical approach of biodiversity change in our post-modern, anthropogenic world, may cause a perfect horror for nature conservation aspirations. For Hubbell, however, the "incorporation of speciation (into the theory of island biogeography) is that (which) enables the unified theory to predict relative species abundance from local to global biogeographical scales" (*ibidem*, p. 11-12). Hubbell is referring to the island theory of biogeography, namely that of MacArthur and Wilson, indeed describing the immigration and extinction rates of species at a timescale that could be witnessed by human intervention [26]. The biggest misconception underlying this conflicting viewpoints thus follows the mingling of anthropocentric and evolutionary timescales (see also 3).

Further, it is obvious that setting aside the "obligate mutualisms and host-parasite relationships", because they (almost) necessarily occur between species of different trophic levels and, therefore, are excluded from the domain of Hubbell's UNTB, creates the perfect conditions for his premise that species abundances are independent from one another (*ibidem*, p. 15). Also in Gilbert's and Lechowicz' data, for reasons of study design, only part of the sessile, vascular plant community is concerned (the so-called understory vegetation), but a large number of ecological niche-dependent, biological, biochemical and biophysical factors explain environmental dissimilarities [11]. An important, still unanswered question therefore is whether a global theory of biodiversity dynamics like UNTB, would be possible when multiple trophic levels are integrated, as for instance based on a fractal topology of natural ecosystems [27].

The breakthrough of a dynamical approach in modeling biodiversity change, as proposed by Hubbell's UNTB, remains to be established in a fractal, multi-trophic ecosystem. One other advantage of modeling based on the CLT (see above), is that also a measure of calculating the entropy of the characteristic function Z_n of a number of independent (and identically distributed) random variables can be defined: namely the entropy of Z_n appears to increase monotonically to that of the normal distribution [28]. If the second law of thermodynamics indeed may be applicable to complex biological networks like ecosystems, a structural deviation from the normal distribution may be regarded as a state of the system with a lowered entropy value. The practical usefulness of this entropy notion in dynamical modeling of biological or ecological systems, however, needs to be further explored [27].

Alternative prospects: towards a (fractal) Global Ecosystem Approach (fGEA)

Given the powerful tools of statistical mechanics and big data analysis, it may seem rashly ambitious to develop an alternative global theory of biodiversity, that much in contrast to Hubbell's UNTB, does take multi-trophic interactions and niche-dependent ecological relationships into account. The question also is: do we need an alternative? On the other hand, the most powerful instrument in empiricism is Nature itself. What are the lessons learned from global biodiversity decline? And if a global theory of biodiversity would work, build on fractal self-similarity relations between different trophic levels or not, what are the tools that can help to contain the damage or help to repair from man-made destruction? [27]

It appears that the most conspicuous signs of global biodiversity loss are the mass disappearances and surplus numbers of one species or a group of a specific taxonomic group within one trophic level compared to and at the cost of other taxonomic groups. Examples are the mass extinctions of prey birds as revealed by Rachel Carson in 1962 (due to the extensive use of pesticides and insecticides in agriculture, during the fifties and sixties), the concomitant rise in several species of the *Corvidae* (at least in parts of Europe) [29]. Other examples are the gradual disappearance of insectivorous farmland bird species in the new millennium, the huge (> 75 %) decline in flying insect biomass, the use of soil fumigation with dichloropropene and metam-sodium as nematocides (killing the *Nematoda* or round worms) and their effect on soil-inhabiting insects, et cetera. In all these examples, it is exactly the interaction between trophic levels that results in general or in species-specific distortions of the food chain [30-32]. The global climate warming is another important cause for biodiversity loss, which already has resulted in mass extinction of several bird species (Fig. 7) [33]. In many cases, it was shown that the global climate and local average temperature changes caused local distortions of the food chain, resulting in mass extinction. It has been made abundantly clear by several world wildlife organizations, that the speed of speciation during the previous eons of evolution are largely surpassed by the speed of species extinction in the Anthropocene era.

At a much smaller scale, the overcrowded, enclosed reserve areas populated with huge herds of red deer (*Cervus elaphus*) and other big ungulates in Dutch natural reserves, in the absence of large carnivores, resulted in the severe demolition of plant communities and disappearance of many other trophic levels [34]. A better demonstration that a neutral theory of biodiversity dynamics doesn't work in enclosed, man-made domains, when dispersal is impeded, is hard to imagine. Therefore, a stepping stone approach, revealing the breakdown of the chain of intertrophic-level interactions, rather than the homeostatic within trophic-level approach, seems more adequate to describe these gross losses in biodiversity. Also the

successful introduction of extinct predator species may have beneficial effects on the restoration of the biodiversity pyramid, provided the food chain resulting from the lower trophic levels and other niche-defining parameters aren't distorted.
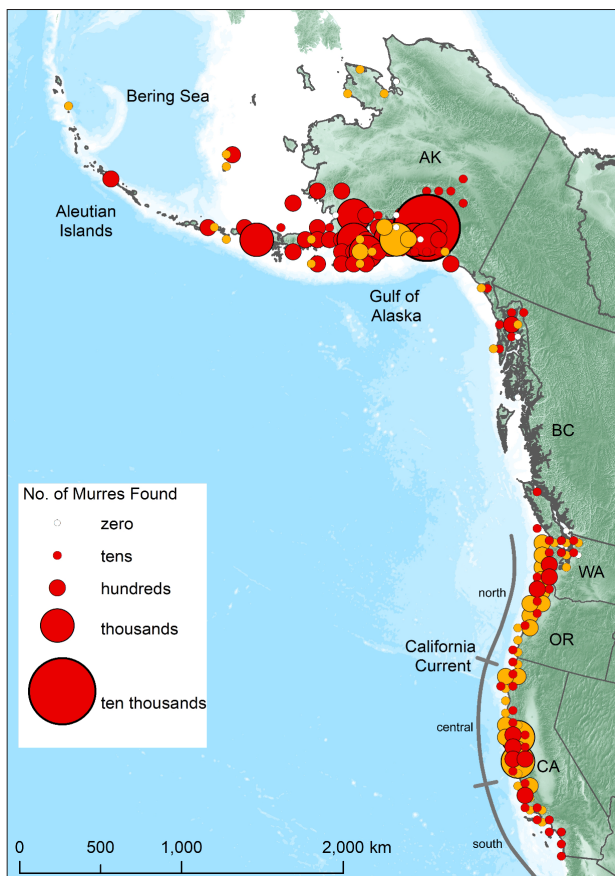

Figure 7: Mass extinction of the Common Murre (*Uria aalge*) resulting from the northeast Pacific marine heatwave of 2014-2016, probably due to a major distortion of the marine food web *(Courtesy of dr. John F. Piatt, Seabird and Forage Fish Ecology Program, Ecosystems Research Office, USGS Alaska Science Center, Anchorage Alaska; published in PLOS One 15 (1), January 2020, e0226087; https://doi.org/10.1371/journal. pone.0226087)*

In order to develop a global theory of biodiversity that doesn't exclude inter-trophic interactions, we previously stressed the importance of the notion of a critical dimensionality of a hierarchical cluster [27]. This fractal approach of biodiversity was derived from percolation theory, as beautifully demonstrated in the work of B.B. Mandelbrot [35]. Up to now, several attempts have been formulated to define the critical percolation threshold in ecological systems, either of an ecosystem with multiple trophic levels, or in an area distribution network of a single species (necessarily within one trophic level) [27,36]. Further research will be needed to extend this percolation dimensionality concept to local hierarchical clusters, in order to develop a fractal Global Ecosystem Approach (fGEA) that is indeed 'gobal' as well as 'ecosystem'-based.

Finally, a serious criticism of Hubbell's UNTB may be reduced to the criticism of Hubbell's definition of 'biodiversity'

(see 1). The highest biodiversity doesn't coincide with the highest number of species. E.g. in (sub) arctic regions and mountain ranges at alpine zones, biodiversity would never become comparable to what is found in pristine rain forests. Also the global latitude does matter, because 'alpine' altitudes (>2.500 m) of the moderate climate zones do not at all correspond with rain forests found at these altitudes in equatorial latitudes. In the definition of sir David Attenborough, biodiversity appears on the most harsh places of our planet – when regarded from a anthropocentric perspective – where "biodiversity becomes an answer to the difficult conditions of life on our planet" [37]. Biodiversity thus appears as an opposite answer of nature to the more comfortable spaces and conditions mankind has created for his own purpose. These harsh places may be found in the arctic or alpine climate zones as well as in the inland forests of Borneo (Kalimantan) [37]. A completely different approach of biodiversity may be found in the representation of biodiversity as an array of song-bird vocal registrations, like in the musical compositions by Olivier Messiaen (1908 - 1992) [38]. The enormous diversity of song-bird territorial singing and vocalizations to communicate are not only a reflection of their huge diversity, it also forms an inspiration for the artist and for those that get inspired by their beauty. However, "the very problem with biodiversity loss, is not that we can't measure it, or that we can't register it, but it is our incessant endeavor to convert ignorance (negentropy) into value" [39]. This is probably the main reason why eco-tourism is forming a relatively new treat for the persistence of already endangered species in our natural reserves. Given the only-for-profit premises of our anthropogenic, neo-liberal society, this problem may constitute a major obstacle and challenge for future conservation programs, like in the follow-up of Europe's *Natura* 2000 program, presented as *Nature, People & Economy* (Brussels, June 2017) [7,40].

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