

# The unified theory of biodiversity - the neutral way out

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**Abstract.** The unified theory of biodiversity is a simple mathematical model for explaining the diversity and relative abundance of species in ‘neutral’ ecological communities. Here neutrality refers to the assumption of per capita ecological equivalence among all individuals of a species, and thus it stands in striking contrast to the believe of many ecologists that different species behave in different ways from one another. Notwithstanding neutral theories have been applied successful to describe empirical patterns in diverse ecosystems, giving rise to a controversial debate of ‘neutrality vs the niche’ in modern ecology.

This lecture will provide a gentle introduction into neutral models. Starting from Hubble’s first formulation we will discuss the calculation of species abundance distributions, the comparison to field data and several modern developments of the theory.

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## 1 Introduction

For decades ecologists have been wondering about the huge diversity of life, the factors and natural laws that determine whether a species can survive or goes extinct and, in particular, about the puzzling patterns of diversity exhibited in natural ecosystems [1]. On the one hand there is a striking variation of diversity among sites across the globe, from species rich systems, such as tropical forests and coral reefs, to species poor regions. On the other hand, even within a single site abundances of different species are characterized by huge variations: in a typical ecological community there exists a huge proportion of rare species, contrasted by a minor fraction of highly abundant species. These linked themes of diversity, abundance and distribution form the core of community ecology and still remain one of the central problems of modern ecology.

This central problem of gaining insight into the distribution of abundance among interacting species bears many formal similarities to classic many-body problems from physics. However in ecology the complex forces of the interactions between species are not known a priori. Traditionally, most theories of biodiversity were concerned with the concept of ecological niches [2]. This concept takes into account that ecological species differ in their traits and responses to the environment, which allows them to coexist in a common habitat. In other words, every species should have its niche, which defines the specie's ecological function and determines where it can persist. This can be summarized by the rule that a system cannot have more species than underlying niches. If more species compete for a restricted number of niches, only a subset of the species can persist, while the remaining, least-fit species are out-competed and go extinct. However, niche theory did not go without critics, most importantly due to some inherent difficulties of niche theory to adequately describe the large diversity that is empirically observed in systems with only few essential resources or niches.

As an attempt to overcome these conceptual problems, recently an alternative theory of species abundance was formulated. This theory originated from an attempt by Stephen Hubbel to understand abundance patterns of tropical forest trees in Barro Colorado Island of Panama, and it is now commonly referred to as the *The unified neutral theory of biodiversity and biogeography*, following his seminal book [3]. This unified neutral theory in its simplicity and basic assumptions forms a striking contrast to previous elaborate niche theories of coexistence and assumes that the effective interactions among species are weak, so that abundance patterns are determined by random, stochastic forces alone. Thereby, the distribution of species is described simply as a balance of random birth, death, speciation and dispersal events, which means that in the neutral theory all well-established differences between species (i.e., trade-offs, competitive abilities) have no functional significance. To the huge surprise of the whole ecological science community, this extreme simplification of the complex ecological processes is capable to give a successful prediction of empirical patterns of species abundance in real natural communities [4-7].

The unified theory of biodiversity not only started a big controversial debate in ecology, but also initiated remarkable research efforts. In the last couple of years a

huge number of scientific studies on this topic have been published [8]. Beside the original formulation of the theory by Hubbel [3] and Graham Bell [9], there are many excellent introductions [10–13].

## 2 Description of the theory

The unified neutral theory describes the abundances  $n_i$  of species in a community of  $S$  species. Here  $n_i$  is the number of individuals (or the population size) of species  $i = 1, \dots, S$ . The total number of individuals in the community (or the community size) equals  $J = \sum_{i=1}^S n_i$ . The crucial quantity to be predicted by the theory is the species abundance distribution, which describes the frequency  $\phi_n$  of species in the community containing exact  $n$  individuals.

To achieve these aims the unified neutral theory builds on the two basic principles of neutrality and zero-sum dynamics [3]:

*Neutrality* refers to the per-capita ecological equivalence of all species as described above. In this viewpoint ecological traits, such as competitive advantages, are simply neglected and all species are regarded to be ecologically equivalent. Hubbel termed his theory as ‘neutral’ in direct analogy to neutral models in population genetics, which state that the molecular evolution of neutral genes is dominated by random genetic drift and not natural selection [14]. Similar to this neutral genetic drift, in Hubbel’s theory of biodiversity ecological drift is assumed to be neutral in the sense that all individuals of a species experience the same ecological processes.

*Zero-sum dynamics* contributes to the empirically well established rule, that in equilibrium the total number of individuals in a community of trophically equivalent species is typically a conserved quantity. This implies a saturation effect, where birth of a new individual of a certain species is only possible after the death of another individual.

The theory does not attempt to describe all possible ecological communities, but is restricted to communities of species which are ecologically similar and occupy the same trophic position. For example, communities with complex foodwebs with predator-prey or mutualistic interactions are not described by the theory. Further the theory is concerned with stationary states and mainly treats species rich communities, such as tropical forests and coral reefs.

One has to keep in mind that there is not a single unified neutral theory. Instead neutral theories come in different flavours. The most popular variant is the two-scale theory [3] which describes the abundance distributions in two different types of communities: (i) a *metacommunity*, which represents the full biological diversity in a large region, and (ii) a *local community* representing a small sub-sample of the metacommunity. While the local community is variable, the metacommunity has a fixed number of species and individuals, and acts like a heat bath to the local community. The reason for such a two-scale theory is that the dynamics of the full metacommunity, due to its sheer size, are in general not observable. Only smaller, local communities are accessible to field measurements. Therefore one must clearly distinguish between the actual distribution of species abundances in the whole (meta-)community and the

observed abundance distribution in smaller samples. In principle, the distribution in such a local community can rigorously be obtained by finite sampling from the metacommunity, a problem that is addressed by sampling theory [15, 16]. However such statistical intricacies can be avoided by distinguishing in the model between a local and a regional (= the metacommunity) community, which are coupled through migration processes. To clearly separate between local and meta-community, properties of the metacommunity usually obtain a subscript  $M$ . For example, the size of the metacommunity is denoted as  $J_M$ , whereas the size of the local community is  $J$ .

In practice the model is simulated as an urn model, where each individual is represented as a ball with a color that is characterizing the species. New balls are placed and taken out of the urn at discrete time steps according certain rules, but the total number of balls in the urn remains constant after each simulation step (zero-sum dynamics). Such a theory is neutral in the sense that all ball colors are treated as equivalent.

- The regional urn model for the metacommunity of fixed size  $J_M$  works as follows:
  1. at each time step with probability  $1 - \nu$  two individuals from the urn are randomly selected. If they belong to the same species nothing happens, otherwise with equal probability one of the individuals is replaced by a copy of the other (representing death and birth events)
  2. with probability  $\nu$  a single individual is taken at random and replaced by another individual of a new color (i.e. a new species, representing a speciation event).
- The urn model for the local community works in a similar fashion. Now strictly speaking there are two urns, one for the local and one for the metacommunity, both of which have fixed size, but the metacommunity-urn remains unchanged:
  1. at each time step with probability  $1 - m$  two individuals from the local urn are randomly selected. If they belong to the same species nothing happens, otherwise with equal probability one of the individuals is replaced by a copy of the other (representing death and birth events)
  2. with probability  $m$  a single individual from the local urn is taken at random and replaced by a copy of another individual, which is randomly taken from the metacommunity (immigration).

These rules are straightforward to implement numerically. If the dispersal parameter  $m = 0$ , the local community is isolated from the metacommunity and all species but one will eventually go extinct. On the other hand, if  $m = 1$  the local community is just a sample from the metacommunity, without local dynamics. In the intermediate non-trivial case,  $0 < m < 1$ , the local community is characterized by a broad uni-modal distribution.

### 3 Analytical calculation

We now perform some analytical calculations of the model (here we closely follow the analysis in [10]). The dynamics of the population of a single species is given as a Markov process [17] with generalized birth and death events, including speciation (i.e., the emerging of a new species), emmigration and immigration. Denote the one-step transition rates for generalized birth or death in the  $k$ th species with  $n$  individuals as

$$b_{n,k} = T_k(n+1|n) \quad \text{and} \quad d_{n,k} = T_k(n-1|n), \quad (1)$$

with  $b_{-1,k} = d_{0,k} = 0$ . We are interested in the probability  $P_{n,k}(t)$  that the  $k$ th species contains  $n$  individuals at time  $t$ . The evolution of the probabilities  $P_{n,k}(t)$  can be described by the master equation [17]

$$\frac{dP_{n,k}(t)}{dt} = P_{n+1,k}(t) d_{n+1,k} + P_{n-1,k}(t) b_{n-1,k} - P_{n,k}(t) (b_{n,k} + d_{n,k}) \quad (2)$$

with a steady-state solution

$$P_{n,k} = P_{0,k} \prod_{i=0}^{n-1} \frac{b_{i,k}}{d_{i+1,k}} \quad (3)$$

for  $n > 0$ .  $P_{0,k}$  follows from the normalization  $\sum_n P_{n,k} = 1$ . The goal then will be to calculate the average number of species containing exactly  $n$  individuals

$$\langle \phi_n \rangle = \sum_{k=1}^S P_{n,k}. \quad (4)$$

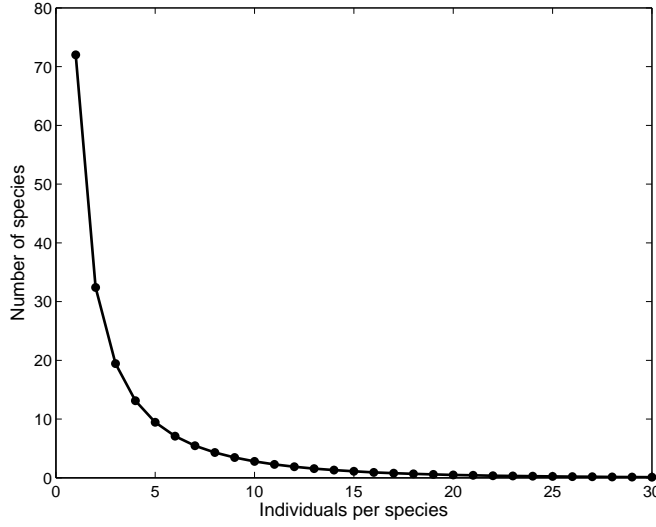
#### 3.1 Abundance patterns in the metacommunity

We first consider the equilibrium configuration of the metacommunity. A natural assumption for the birth and death rates is given by

$$b_{n,k} = b n, \quad d_{n,k} = d n. \quad (5)$$

Here we first assume neutral ecological equivalence, which means that the species are demographically identical and the birth and death rates are independent of  $k$ , ( $b_{n,k} = b n$ ,  $d_{n,k} = d n$ ). Second, we consider that in the metacommunity the probability for an individual of a species to die or to give birth are independent of the population size of that species (density independence), which means that for  $n > 0$  we have  $b_n = b n$  and  $d_n = d n$ . Finally, speciation can be taken into account by assuming a non-zero probability for the emergence of an individual of a new species, by  $b_0 = \nu$ .

We are interested in the average number of species with  $n$  individuals in the metacommunity  $\langle \phi_n^M \rangle$  (here the index  $M$  stands for ‘‘metacommunity’’). As birth and death rates are independent of the species label  $k$ , the subscript  $k$  in the probabilities can be discarded  $P_{n,k} = P_n$ . From Eq. (4)  $\langle \phi_n^M \rangle$  is simply proportional to  $P_n$ , so that



**Figure 1:** Illustration of the logseries. Plotted is the expected number of species as a function of the population  $n$  size according to the log-series Eq. (7). This distribution is a decaying function of  $n$  with a large number of species with few individuals and a small number of species with large size.

$\langle \phi_n^M \rangle = S_M P_n$  (with  $S_M$  being the total number of species in the metacommunity). Substituting the rates Eq. (5) into Eq. (3) we obtain

$$\langle \phi_n^M \rangle = S_M P_n = S_M P_0 \frac{b_0 b_1 \dots b_{n-1}}{d_1 d_2 \dots d_n}. \quad (6)$$

This can be written in the compact form

$$\langle \phi_n^M \rangle = \theta \frac{x^n}{n} \quad (7)$$

using the abbreviations  $x = b/d$  for the ratio of the per-capita birth and death rates and the Hubbel biodiversity number  $\theta = S_M P_0 \nu / b$ . Eq. (7) describes the species abundance in the metacommunity and is known as the Fisher log series [18] (see Fig. 1). In this context, the biodiversity number  $\theta$  is called Fisher's  $\alpha$ .

In the limiting case of  $\nu = 0$  we obtain  $\theta = 0$  and in equilibrium there are no individuals in the metacommunity. This makes sense since in the absence of speciation the state  $n = 0$  is absorbing. On the other hand, if speciation events are possible,  $\nu > 0$ , the birth-to-death ratio  $x$  must be less than 1 in order to maintain a finite metacommunity of size

$$J_M = \sum_{n=1}^{\infty} n \langle \phi_n^M \rangle = \sum_{n=1}^{\infty} \theta x^n = \theta \frac{x}{1-x} \quad (8)$$

and total number of species

$$S_M = \sum_{n=1}^{\infty} \langle \phi_n^M \rangle = \theta [-\ln(1-x)] . \quad (9)$$

### 3.2 Abundance patterns in the local community

To describe the equilibrium state in the local community, we have to rephrase the one-step transition rates as follows,

$$b_{n,k} = (1-m) \frac{n}{J} \frac{J-n}{J-1} + m \frac{\mu_k}{J_M} \left(1 - \frac{n}{J}\right) \quad (10)$$

and

$$d_{n,k} = (1-m) \frac{n}{J} \frac{J-n}{J-1} + m \left(1 - \frac{\mu_k}{J_M}\right) \frac{n}{J} . \quad (11)$$

Here now  $n_i$  is the abundance of species  $i$  in the local community, whereas  $\mu_k$  denotes the abundance of the  $k$ th species in the metacommunity and  $J_M$  is the total number of individuals in the metacommunity. In these two equations in each case the left hand term of the sum corresponds to the first rule of the model, with a birth (or death) in the  $k$ th species with probability  $1-m$ , followed by a death (or birth) somewhere else in the community. The right hand terms describe the effects of immigration (or emmigration) into (or out of) the local population of species  $k$  with probability  $m$ . Note that the probability of migration scales with the relative abundance  $\mu_k/J_M$  of species  $k$  in the metacommunity. Further we want to stress that here, in contrast to the transition rates in the metacommunity Eq. (5), birth and death rates depend on the species  $k$  and also are not any more simply proportional to the abundance  $n$ .

Substituting the birth and death rates into Eq. (3) yields the steady state solution

$$P_{n,k} = \frac{J!}{n!(J-n)!} \frac{\Gamma(n+\lambda_k)}{\Gamma(\lambda_k)} \frac{\Gamma(\vartheta_k-n)}{\Gamma(\vartheta_k-J)} \frac{\Gamma(\lambda_k+\vartheta_k-J)}{\Gamma(\lambda_k+\vartheta_k)} \quad (12)$$

with

$$\lambda_k = \frac{m}{(1-m)} (J-1) \frac{\mu_k}{J_M} \quad (13)$$

and

$$\vartheta_k = J + \frac{m}{(1-m)} (J-1) \left(1 - \frac{\mu_k}{J_M}\right) . \quad (14)$$

Here  $\Gamma(z) = \int_0^{\infty} t^{z-1} e^{-t} dt$  is the Gamma function with  $\Gamma(z) = (z-1)!$  for integer  $z$ . In this expression, the  $k$  dependence enters only through the species abundances  $\mu_k$  in the metacommunity,  $P_{n,k} = P_n(\mu_k)$ . This and assuming an infinite metacommunity allows to write the average (Eq. 4) as

$$\langle \phi_n \rangle = \sum_{k=1}^{S_M} P_{n,k} = S_M \langle P_n(\mu_k) \rangle = S_M \int d\mu \tilde{\rho}(\mu) P_n(\mu) , \quad (15)$$

where  $\tilde{\rho}(\mu) d\mu$  denotes the probability distribution of mean abundance levels in the metacommunity. From Eq. (7) this distribution is given by the Fisher log series, which can be represented in a singularity-free way as a continuous gamma density distribution with parameters  $\epsilon$  and  $\delta = x/(1-x)$  [18]

$$\tilde{\rho}(\mu) = \frac{1}{\Gamma(\epsilon)\delta^\epsilon} \exp(-\mu/\delta) \mu^{\epsilon-1}. \quad (16)$$

After substitution of Eq. (16) into the average Eq. (15), and taking the limits  $S_M \rightarrow \infty$  and  $\epsilon \rightarrow 0$  with  $\theta = S_M \epsilon$ ,  $\gamma = \frac{m(J-1)}{1-m}$  and  $y = \mu\gamma/\delta\theta$  one obtains the central result [10]

$$\langle \phi_n \rangle = \theta \frac{J!}{n!(J-n)!} \frac{\Gamma(\gamma)}{\Gamma(J+\gamma)} \int_0^\gamma \frac{\Gamma(n+y)}{\Gamma(1+y)} \frac{\Gamma(J-n+\gamma-y)}{\Gamma(\gamma-y)} \exp(-y\theta/\gamma) dy. \quad (17)$$

Even though Eq. (17) looks complicated, one can use this equation in a straightforward way to numerically calculate the expected number of species with a certain abundance in the local community,  $\langle \phi_n \rangle$  for any parameter combination of  $J$ ,  $\theta$  and  $m$ . For example, one can easily show that  $\langle \phi_n \rangle = 0$  if  $n > J$ . The abundance patterns resulting from Eq. (17) can also be shown to match direct numerical simulations of the two-scale model of birth, death, speciation and immigration processes (see Sec. 2).

Eq. (17) summarizes the description of the neutral theory for real field-data abundance patterns. As in any real-case example the local community size  $J$  and the total number of species of the local community  $S_L = \sum_{k=1}^J \langle \phi_k \rangle$  are known, the formula contains only one free parameter, which can be used to fit the distribution to empirical data.

## 4 Concluding remarks

In the last decade huge research efforts were spent to either confirm or falsify the unified neutral theory with empirical data [4–7, 19–22]. As a rule it was found that the unified neutral theory can describe field data with high accuracy. Thus, despite its enormous simplicity the neutral theory of biodiversity leads to analytical and computational results that are in excellent agreement to empirical species-abundance patterns. However ultimately it has turned out that species abundance curves taken alone are not sufficient to discriminate one theory in favour from another. This is also reflected in many new developments of the theory, which aim to reconcile niche and neutrality as two complementary approaches that form two ends from a continuum of possible theories [23–28].

In summary, the unified neutral theory of biodiversity and in particular the principle of ecological equivalence gave rise to a highly controversial debate of ‘neutrality vs the niche’ among ecologists. Obviously this assumption of neutrality, or non-interacting species, does not imply that ecological species do not interact at all. Instead, the theory merely states that these interactions do not play a decisive role for determining diversity patterns. However, independent from the question of whether or not neutral theories give a ‘true’ description of the processes ongoing in ecological

communities, one major offspring of these theories is an enormous enrichment of the arsenal of ecological theory and concepts. In future every theory of species abundance will have to be measured against the simple rules of neutral dynamics, which will serve as a first null-hypothesis or benchmark. In this sense the ultimate question about the role of niches in determining species abundance is still not resolved and remains one of the most central and heavily discussed topics of contemporary ecology.

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