Species Abundances Distribution in Neutral Community Models

Zoltán Néda* and Mária Ravasz
Babeș-Bolyai University, Department of Theoretical Physics
str. Kogălniceanu 1, RO-400084 Cluj-Napoca, Romania
* E-mail: zneda@phys.ubbcluj.ro

Abstract

An analytical approximation is derived for the Zero Sum Multinomial distribution which gives the Species Abundance Distribution in Neutral Community Models. The obtained distribution function describes well computer simulation results on the model, and leads to an interesting relation between the total number of individuals, total number of species and the size of the most abundant species of the considered metacommunity. Computer simulations on neutral community models, proves also the validity of this scaling relation.
I. INTRODUCTION

Communities of ecologically similar species that compete with each other solely for resources are often described by neutral community models (NCM) [1–4]. These models proved to be successful and useful in describing many of the basic patterns of biodiversity such as the distribution of abundance, distribution of range, the range-abundance relation and the species-area relation [2,3]. The neutral theory is considered by many ecologists as a radical shift from established niche theories and generated considerable controversy [5–9]. The relevance of NCM for describing the dynamics and statistics of real communities is still much debated and criticized [10].

Nowadays NCM are studied mostly by Monte Carlo type computer simulations [3,2,11], and apparently there are no analytical results. One of the key issues that macro-ecologist are often investigating is the species abundances distribution (SAD), introduced for characterizing the frequency of species with a given abundance [12–14]. In case of NCM, SAD is generated numerically and it is called the Zero Sum Multinomial (ZSM) distribution [11,15]. The aim of the present paper is to give an analytical mean-field type approximation for ZSM. By using the invariance of the system against the intrinsic fluctuations characteristic for NCM, we derive an analytic solution that describes the results of computer simulations. The derived analytical form of SAD leads also an interesting relation between the total number of individuals, total number of species and the size of the most abundant species of the considered meta-community. This novel scaling relation is confirmed by computer simulations on neutral models.

II. NEUTRAL COMMUNITY MODELS

NCM are usually defined on lattice sites, on which a given number of $S_{max}$ species can coexist [1,2,11] and compete for resources. Each lattice site can be occupied by many individuals belonging to different species, however the total number of individuals for each lattice site is limited to a fixed $N_{max}$ value. This limiting value models the finite amount of available resources in a given territory. As time passes individuals in the system can give birth to individuals belonging to the same species, can die or can migrate to a nearby site. The neutrality of the model implies that all individuals (regardless of the species they belong) are considered to be equally fit for the given ecosystem, and have thus the same $b$ multiplication, $d$ death and $q$ diffusion rate. The system is considered also in contact with a reservoir, from where with a small $w << 1$ probability per unit time an individual from a randomly chosen species can be assigned to a randomly chosen lattice site. This effect models the random fluctuations that can happen in the abundances of species. The dynamics of the considered community is than as follows:

- A given number of individuals from randomly chosen species are assigned on randomly chosen lattice sites.

- With the initially fixed probabilities we allow each individual to give birth to another individual of the same species, to die or to migrate on a nearby site.
We constantly verify the saturation condition on each site. Once the number of individuals on a site exceeds the $N_{\text{max}}$ value, a randomly chosen individual is removed from that site.

- We apply the random fluctuations resulting from the reservoir.

After on each lattice site saturation is achieved a dynamical equilibrium sets in, and one can study the statistical properties of several relevant quantities. Computer simulations usually focus on generating SAD and on studying several scaling relations like species-area and range-abundance relations.

III. ANALYTICAL APPROXIMATION FOR SAD

Let us consider a fixed area in a NCM (a delimited region in the lattice) on which we study SAD. In the selected area we denote by $S(x,t)$ the number of species with size $x$ at the time-moment $t$. ($x$ is a discrete variable $x = 1, 2, ..., k...$). $S(x,t)$ divided by the total number of species yields the mathematically rigorously defined SAD (Species Abundances Distribution). We mention here that in most of the papers dealing with SAD, instead of this rigorously defined distribution function a histogram on intervals increasing as a power of 2 is constructed [12–14]. On a log-normal scale this histogram usually has a Gaussian shape, and thus SAD is called a log-normal distribution. Without arguing on the relevance of this histogram (a nice treatment on this subject is given by May [13]) for the sake of mathematical simplicity we will not use this representation, and calculate instead the mathematically rigorous distribution function. It is of course anytime possible to re-plot the obtained distribution function in the form that is usually used by ecologists, using instead of the $x$ variable the $z = \log_2(x)$ variable.

In the framework of the considered model the time evolution of $S(x,t)$ for an infinitesimally short $dt$ time can be approximated by the following master-equation:

$$S(x, t + dt) = S(x, t) + [W_+(x - 1)S(x - 1, t) + W_-(x + 1)S(x + 1, t) - W_+(x)S(x, t) - W_-(x)S(x, t)]dt$$

(1)

In the equation from above $W_+(x)$ denotes the probability that one species with size $x$ increases its size to $x + 1$ in unit time and $W_-(x)$ denotes the probability that one species with size $x$ decreases it’s size to $x - 1$ in unit time. We neglected here the possibility that in the small $dt$ time-interval one species increases or decreases it’s size by more than one individual. The value of $dt$ can be always taken as small, as needed so that this starting assumption should hold. It worth also mentioning that this master equation is not applicable in the neighborhood of the limiting values of $x$ since here either $x - 1$ or $x + 1$ is not existing. We expect thus that the shape of SAD determined from (1) can have problems for very low and very high values of $x$.

We assume now that SAD reaches a steady-state in time. All computer simulations on neutral models shows that this is true. This means that $S(x,t)$ should be time invariant in respect of the fluctuation governed by equation (1). Under this stationarity assumption we get the equation:
\[ W_+(x-1)S(x-1,t) + W_-(x+1)S(x+1,t) - W_+(x)S(x,t) - W_-(x)S(x,t) = 0 \] (2)

We have to approximate now the \( W_+(x) \) and \( W_-(x) \) probabilities. We will work with the assumptions of the NCM, and consider all species having the same birth, death and migration rate. Let us denote by \( P_+ \) the probability that one individual multiplies itself in unit time (we assume \( P_+ \) is the same for all individuals and species). Let us denote by \( P_- \) the probability that one individual disappears from the considered territory in unit time (again the same for all individuals and species). Further we assume that:

\[
\begin{align*}
P_+ &<< 1 \\
P_- &<< 1
\end{align*}
\] (3)

By simple probability theory we get:

\[ W_+(x) = xP_+[1 - (P_+ + P_-)]^{x-1} \] (4)

The above equation tells us, that the increase by unity of the size of one species can be realized if any of the \( x \) individuals from a selected species multiplies itself, while the other individuals remain unchanged. (Of course there are many other possibilities involving the birth and death of more than one individual. However, since we considered the (3) assumption all other possibilities will be with orders of magnitude smaller). It is also worth mentioning that for the selected local community the effect of migration and the stochastic contribution from the reservoir can be taken into account through the birth and death processes, changing slightly the values of this probabilities. Migration inside the considered area is equivalent with a birth process, while migration outside from the considered territory is equivalent with death of individuals.

Using the assumptions (3) we can make now the following approximations:

\[ W_+(x) = xP_+[1 - (P_+ + P_-)]^{x-1} = xP_+[1 - (P_+ + P_-)]^{[1/(P_++P_-)](P_++P_-)(x-1)} \approx \]

\[ \approx xP_+e^{-(P_++P_-)(x-1)} \] (5)

In the same manner, one can write:

\[ W_-(x) = xP_-[1 - (P_+ + P_-)]^{x-1} \approx xP_-e^{-(P_++P_-)(x-1)} \] (6)

Instead of \( P_+ \) and \( P_- \) we introduce now two new notations:

\[
\begin{align*}
s & = P_+ + P_- \\
q & = P_+ - P_- \end{align*}
\] (7)

(8)

from where:

\[
\begin{align*}
P_+ &= \frac{s + q}{2} \\
P_- &= \frac{s - q}{2}
\end{align*}
\] (9)

(10)

From the assumptions (3) it is clear that it also holds:
Let us assume now that
\[ |P_+| = |P_-| \rightarrow q = 0, \quad (13) \]
which would mean that the probability of multiplication and death is the same, so there is a constant number of individuals in the considered local community. In other words this means that the territory is saturated, and although the size of different species fluctuates, the total number \( N_t \) of population is constant.

The probability density for the species abundances distribution (SAD) is given than as:
\[ \rho(x, t) = \frac{S(x, t)}{S_t}. \quad (14) \]

Instead of \( x \) let us introduce now a new variable \( y = x/N_t \ll 1 \) \( (N_t \gg 1 \) is the total number of individuals in the system).

For \( \rho(y, t) \) we have the (2) equation:
\[ W_+(yN_t - 1)\rho(y - \frac{1}{N_t}, t) + W_-(yN_t + 1)\rho(y + \frac{1}{N_t}, t) - W_+(yN_t)\rho(y, t) - W_-(yN_t)\rho(y, t) = 0 \quad (15) \]

Since \( \rho(y, t) \) is a limiting distribution (not depending on \( t \) anymore) we will simply denote is as \( \rho(y) \).

\[ W_+(yN_t - 1)\rho(y - \frac{1}{N_t}) + W_-(yN_t + 1)\rho(y + \frac{1}{N_t}) - W_+(yN_t)\rho(y) - W_-(yN_t)\rho(y) = 0 \quad (16) \]

We can use now Taylor series expansion to get \( \rho(y - \frac{1}{N_t}) \) and \( \rho(y + \frac{1}{N_t}) \):
\[ \rho(y - \frac{1}{N_t}) = \rho(y) - \frac{1}{N_t}\rho'(y) + \frac{1}{2N_t^2}\rho''(y) \quad (17) \]
\[ \rho(y + \frac{1}{N_t}) = \rho(y) + \frac{1}{N_t}\rho'(y) + \frac{1}{2N_t^2}\rho''(y) \quad (18) \]

We denoted here by \( \rho'(y) \) and \( \rho''(y) \) the first and second order derivatives of the \( \rho(y) \) function, respectively. Taking account of \( q = 0 \), the values of \( W_\pm(y) \) are given by (5, 6) as follows:
\[ W_+(yN_t - 1) = \frac{(yN_t - 1)s}{2} exp[-(yN_t - 2)s] \quad (19) \]
\[ W_-(yN_t + 1) = \frac{(yN_t + 1)s}{2} exp[-yN_ts] \quad (20) \]
\[ W_+(yN_t) = \frac{yN_ts}{2} exp[-(yN_t - 1)s] \quad (21) \]
\[ W_-(yN_t) = \frac{yN_ts}{2} exp[-(yN_t - 1)s] \quad (22) \]
Plugging all these in equation (16):

\[
\frac{(yN_t - 1)s}{2} \exp[-(yN_t - 2)s][\rho(y) - \frac{1}{N_t}\rho'(y) + \frac{1}{2N_t^2}\rho''(y)] + \\
\frac{N_t + 1}{2} \exp[-yN_t s][\rho(y) + \frac{1}{N_t}\rho'(y) + \frac{1}{2N_t^2}\rho''(y)] = \frac{yN_t s}{2} \exp[-(yN_t - 1)s] s(yN_t) 
\]  

Simplifying both sides with \( s \cdot \exp[-yN_t s] \), some immediate algebra yields the following second order differential equation for \( \rho(y) \):

\[
\rho(y)\left[\frac{yN_t}{2}(e^{2s} - 2e^{s} + 1) - \frac{1}{2}(e^{2s} - 1)\right] + \rho'(y)\left[\frac{yN_t}{2}(1 - e^{2s}) + \frac{1}{2}(1 - e^{2s})\right] + \\
+ \rho''(y)\left[\frac{yN_t}{2}(e^{2s} + 1) + \frac{1}{2}(1 - e^{2s})\right] = 0 
\]  

Since \( s \ll 1 \) the following approximations are justified

\[
e^{2s} \approx 1 + 2s
\]

\[
e^{s} \approx 1 + s
\]

and the differential equation becomes:

\[
- \rho(y)s + \rho'(y)\left[\frac{1}{N_t}[s + 1 - yN_t s]\right] + \rho''(y)\left[\frac{1}{2N_t^2}[yN_t + yN_t s - s]\right] = 0 
\]  

For solving this differential equation, in the **first approximation** we neglect all term that are proportional with the \( 1/N_t \rightarrow 0 \) quantity. This yields a first order differential equation:

\[
s\rho(y) = -ys\rho'(y) 
\]  

This equation has the immediate solution

\[
\rho_I(y) = \frac{1}{y}C_1/
\]

with \( C_1 \) an integration constant.

The histogram \( \sigma(z) \) that is usually used for SAD can be immediately determined from (29), writing the \( \rho_I(y) \) distribution as a function of the \( z = \log_2(x) = \log_2(yN_t) \) variable. It is immediate to realize that this would yield a constant distribution \( (\sigma_I(z) = C) \).

A **better approximation** can be achieved by keeping the terms proportional with \( 1/N_t \) and neglecting the second orderly small \( 1/N_t^2 \) and \( s/N_t \) terms. This yields the differential equation. Going back now to the \( x = yN_t \) variable

\[
-s\rho(x) + \rho'(x)[1 - xs] + \rho''(x)\frac{x}{2} = 0, 
\]
we get the general solution
\[ \rho_{II}(x) = \frac{C_1}{x} + \frac{e^{2sx}C_2}{x}, \tag{32} \]

where \( C_1 \) and \( C_2 \) are two integration constants.

By visually comparing with the experimental and simulated SAD curves we can conclude that we need \( C_1 > 0 \) and \( C_2 < 0 \) to get the right shape. The general solution for SAD, should write thus
\[ \rho_{II}(x) = \frac{K_1}{x} (K_2 - e^{2sx}), \tag{33} \]
with \( K_1 \) and \( K_2 \) two real, positive constants.

It is immediate to observe that the obtained distribution for SAD, has a cutoff, i.e. there is a maximum value of \( x \) until \( \rho(x) \) is acceptable (remains positive). This results, is not surprising, since due to the finite number of individuals in the system and the finite value of the number of species one would naturally expect a cutoff in the distribution.

There are three fitting parameters in the mathematical expression of \( \rho_{II}(x) \) (\( K_1, K_2 \) and \( s \)). Since \( \rho_{II}(x) \) has to be normalized, we can determine \( K_1 \) as a function of \( K_2 \) and \( s \). The normalization of this distribution function is not easy and cannot be done analytically, since there is no primitive function for \( \exp(\alpha x)/x \).

However, if we can use the \( sx << 1 \) assumption and consider a Taylor expansion in the exponential we obtain the more simple
\[ \rho_{II}(x) \approx F_n \frac{F_1 - x}{x}, \tag{34} \]
(\( F_n \) and \( F_1 \) are again two positive real constants) distribution, which has a cutoff for \( x = F_1 \). This distribution function is exactly the same as the one proposed by Dewdney using totally different arguments [16], and named *logistic-J distribution*. As argued in [16] it describes well the SAD for many real communities.

The normalization condition for this distribution function is:
\[ \int_{1}^{F_1} F_n \frac{F_1 - x}{x} dx = 1, \tag{35} \]
and an immediate calculus gives:
\[ F_n = \frac{1}{F_1 \ln(F_1) - F_1 + 1}. \tag{36} \]

The approximated normalized distribution function for SAD is then:
\[ \rho_{II}(x) \approx \frac{1}{F_1 \ln(F_1) - F_1 + 1} \frac{F_1 - x}{x}. \tag{37} \]

We can consider thus the above simple one-parameter fit to approximate the results for SAD on NCM.

The shape of \( \sigma(z) \) can be again quickly obtained from \( \rho_{II}(x) \), by changing the variable in this distribution function to \( z = \log_2(x) \). A simple calculation yields the form
\( \sigma_{II}(z) = C \ast (F_1 - 2^z), \)  

(38)

where \( \sigma \) is another normalization constant. It is important to realize, that \( \sigma(z) \) given by the above approximation does not show the generally observed bell shaped curve, and for small values of \( z \) it is a constant. We must remember however that the shape of SAD given by our approximation can not be trusted for small \( z \) values, since in this limit the starting master equation (1) is not valid.

IV. SAD FROM COMPUTER SIMULATIONS

In order to check the validity of our analytical approximation for SAD we performed computer simulations on the model presented in Section 2. We considered a lattice of size \( 20 \times 20 \), \( S_t = 400 \) species, and \( N_{max} = 1000 \) for each lattice site. We studied a local community on a square of \( 9 \times 9 \) lattice sites, and we fixed several values for the dynamical parameters \( d/b \) and \( q/b \). We used periodic boundary conditions, and the efficient kinetic or resident time Monte Carlo algorithm was implemented. The simulations were made on a Pentium\(^{(TM)}\) 4 cluster. As a general results, we obtained that the analytical form given by (37) describes well the simulation data for SAD. On Figure 1 we present a characteristic fit for the simulation data. The parameters used in the simulation were \( d/b = 0.3 \) and \( q/b = 0.2 \). The obtained best fit parameter for equation (37) was \( F_1 = 14500 \). The rigorously defined \( \rho(x) \) distribution function suggest that in NCM SAD has a scale-invariant nature. The finite size of the system introduces a natural cutoff in this scale-invariant behavior.

Computer simulations on NCM proves thus the applicability of our analytical approximations for the form of the ZSM distribution.

V. SCALING LAWS RESULTING FROM SAD

Starting from the analytical approximation (37) for the form of SAD, we can derive an interesting relation between the size of the most abundant species \( (N_s) \), the total number of individuals \( (N_t) \) and the number of detected species \( (S_t) \) in the considered meta-community. The distribution function (37) has a cutoff at \( x = F_1 \), from where it results that \( F_1 \approx N_s \). It is also immediate to realize that from the definition of \( \rho(x) \) it results

\[
\begin{align*}
N_t &= \int_1^{N_s} C x \frac{\rho(x)}{F_n} \, dx = C \int_1^{N_s} x \frac{N_s - x}{x} \, dx, \\
S_t &= \int_1^{N_s} C \frac{\rho(x)}{F_n} \, dx = C \int_1^{N_s} \frac{N_s - x}{x} \, dx,
\end{align*}
\]

(39)

where \( C \) is a normalization constant, which normalizes \( \rho(x) \) to the total number of species in the local community. The above two integrals are easily calculated and leads to the following two coupled differential equations:

\[
\begin{align*}
N_t &= C N_s (N_s - 1) - \frac{C}{2} (N_s^2 - 1) \\
S_t &= C N_s \ln(N_s) - C(N_s - 1)
\end{align*}
\]

(40)

(41)

(42)
Working on relatively large habitats, one can use the $N_s >> 1$ assumption, and the coupled equation system from above can be simplified:

$$N_t \approx \frac{C}{2} N_s^2$$

(43)

$$S_t \approx C N_s [\ln(N_s) - 1]$$

(44)

Eliminating from this system the normalization constant $C$ we obtain the important relation:

$$\frac{S_t N_s}{N_t [\ln(N_s) - 1]} = 2$$

(45)

Computer simulation results on NCM supports again the validity of the magic formula from above. (The simulations were made on a $20 \times 20$ lattice, and we choose $S_t = 400$, $N_{max} = 1000$, $d/b = 0.3$ and $q/b = 0.2$). On Figure 2 we plotted the simulation results for different local community sizes, and the plot shows that equation (45) works well, however the constant on the right side of the equation seems to be slightly different from 2. We think that this slight difference is the result of our crude approximation: $F_1 \approx N_s$, and in reality we should have $F_1$ slightly bigger than $N_s$. The simulation data from Figure 2 was obtained after averaging on several local communities of size $A$.

Increasing the size $A$ of the considered habitat one would naturally expect $N_t \sim A$. Using equation (45) one would immediately get thus the interesting scaling-law:

$$\frac{S_t N_s}{\ln(N_s) - 1} \sim A$$

(46)

The (46) scaling relation can be also immediately verified in computer simulations on NCM. Results for a $20 \times 20$ lattice, $S_t = 400$, $N_{max} = 1000$, $d/b = 0.3$ and $q/b = 0.2$ are shown on Figure 3. On the figure with a dashed line we indicated the power-law with exponent 1. As seen from the figure, the simulation data supports the scaling-law given by our analytical approach.

VI. CONCLUSIONS

We have given here an mean-field type analytical approximation for the species abundances distribution function for neutral community models. By using the invariance of this distribution regarding the internal fluctuations characteristic for the model, we derived an analytical approximation for the distribution function which describes well the simulation data obtained on NCM. The derived distribution function has a natural cutoff, governed by the finite extent of the system, and leads to an interesting relation between the total number of individuals, total number of species and the size of the most abundant species, found in the considered habitat. Computer simulations on neutral models confirms the validity of this scaling relation.

VII. ACKNOWLEDGMENTS

The present study was supported by the Sapientia KPI foundation for interdisciplinary research. We are grateful for Dr. N. Stollenwerk for helpful suggestions and discussions.
We also thank Dr. A. Balogh and Dr. V. Markó for introducing us in this fascinating interdisciplinary field, and for providing us a lot of interesting bibliography on the subject.
REFERENCES

[1] S.P. Hubbel, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, Princeton, New Jersey, 2001)
[2] G. Bell, Neutral Macroecology, *Science*, 293, 2413-2418 (2001)
[3] J. Chave, Neutral theory and community ecology, *Ecology Letters*, 7, 241-253 (2004)
[4] S. Norris, Neutral Theory: A New, Unified Model for Ecology, *BioScience*, 53 124-129 (2003)
[5] J.M. Levine, Species diversity and relative abundance in metacommunities, *Trends Ecol. Evol.* 17, 99-100 (2002)
[6] B.J. Enquist, J. Sanderson and M.D. Weisser, Modeling macroscopic patterns in ecology, *Science* 295, 1835-1837 (2002)
[7] P.A. Abrams, A world without competition, *Nature* 412, 858-859 (2001)
[8] A. Clark, Macroecology comes of age, *Trends Ecol. Evol.* 17, 352-353 (2002)
[9] J.Chave, H. C. Muller-Landau and S.A. Levine, *The American Naturalist* 159, 1-23 (2002)
[10] S. Nee and G. Stone, *Trends Ecol. Evol.* 18, 433-434 (2003)
[11] B.J. McGill, A test of the unified neutral theory of biodiversity, *Nature*, 442, 881-885 (2003)
[12] F.W. Preston, The commonness and rarity of species, *Ecology* 29, 254-283 (1948)
[13] R.M. May, Patterns of Species Abundance and Diversity, in *Ecology and Evolution of Communities* eds. M.L. Cody and J.M. Diamond (the Belknap Press of Harvard University Press, Cambridge, Massachusets and London, 1976)
[14] E.C. Pielou, Mathematical Ecology, chapter 18 Species Abundances Relations (Wiley-Interscience, New-York 1977)
[15] R. Condit et. al, Beta diversity in tropical forest trees, *Science*, 295 666-669 (2003)
[16] A.K. Dewdney, A dynamical model of communities and a new Species-Abundance Distribution, *Biol. Bull.* 198 pp. 152-165 (2000)
FIG. 1. Characteristic fit (continuous line) with equation (37) for the simulation results (circles) on Species Abundances Distribution in Neutral Community Models. Simulations done on a 20 × 20 lattice, \( S_t = 400 \), \( N_{max} = 1000 \), \( d/b = 0.3 \) and \( q/b = 0.2 \). The best fit parameter for SAD yield \( F_1 = 14500 \).

FIG. 2. Validity of the (45) equation. Circles are simulation data and the dashed line indicates the expected value of 2. Parameters of the simulation are the same as in Figure 1.
FIG. 3. Validity of the (46) scaling law. Circles are simulation data and the dashed line indicates a power-law with exponent 1. Parameters of the simulation are the same as in Figure 1.