MODELLING ECOLOGICAL SYSTEMS
A NICHE THEORY

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• An ecological system $D$ is composed by different interacting communities as a set of species in a determinated environment $E$. Our idea is to consider the ecological niches as a basins where some species go in and others go out and they can modify the environment.

• **Phenotypically** an ecological system can be represented by a subset $G$ of $N$ – dimensional Euclidean space, where $N$ is the maximum possible number of phenotypical characters ($\neq 0$) related to the individuals which belong to $D$.

• $D$ is characterized to have a number of ecological niches $\beta_j$ where several species live together.
Definition of ecological niche

- In *Ecology*, a **niche** is a set of specific environmental conditions under which a set of species live and fit (distribution of **resources** and competitors).

- According to **A.T.Peterson et al. (2011a)**: "The type and number of variables comprising the dimensions of an environmental niche vary from one species to another [and] the relative importance of particular environmental variables for a species may vary according to the geographic and biotic contexts".

- According to **G.E.Hutchinson (1957)** in order to analyze the dynamics and the ecological transformations into and out a niche, one uses mathematics and statistics i.e. to try to explain how species coexist within a given community. She sees the niche as an "**n-dimensional** hypervolume", where the dimensions are environmental conditions and **resources**.

- Alteration of an ecological niche by its inhabitants is the topic of **niche construction** (see A.T.Peterson et al. (2011b))
• The idea of an ecological system $D$ and in particular of the niche $\beta_j$ is based on the mutual influence between the environment $E$ and the organisms or individuals of different species which live in $E$. According to Richard Lewontin (2000), “the organisms propose, but the environment decides”. But actually the individuals modify the $E$ (see *exploitive system*, Conrad H.Waddington (1959))

• The relationship between the genotype and $E$ concerns only the selection by $E$ on the phenotypes which the first controls.

• The organism adaptation to $E$ includes also the alterations of $E$ through the organisms. Hence also $E$ evolves, independently of the reproductive process.

• Interventation of the organisms on the environment: aeries, nests, dens, barriers, etc.
Examples of ecological niches
Packing and stratification through different species levels in an ecological niche

Meccanismi di coesistenza

Nicchia ecologica: “Impacchettamento” di specie

Stratificazione di piante specializzate e di nicchie animali a vari livelli di una foresta tropicale pluviale (da Miller 1997).

Questa nicchie specializzate permettono alle specie di evitare o minimizzare la competizione per le risorse con le altre e permettono la coabitazione di una grande varietà di specie.

La specializzazione della nicchia è regolata dall’adattamento delle piante a livelli diversi di luce disponibile negli strati della foresta e da centinaia di migliaia di anni di evoluzione in un clima abbastanza costante.
Beaver construction and alteration of the niche
• A general schema of a niche

• A niche $\beta_j$ has a heart $\alpha_j$ where the different species are consolidated. But it is possible that by means of the interferences and the modifications of the environment change the values of the genotypes and phenotypes. In its turn the individuals of species $\Lambda$ modify the environment, that is they go out in another part $\beta_j - \alpha_j$ of $\beta_j$. In $\beta_j - \alpha_j$ the ecological situation is more fragile.

Viceversa, the ecological situation can change and the individuals of a species are inclined to go in $\alpha_j$ where the characters of the species becomes more robust.
• In the case a) the species A, B, C are lumped in $\beta_j - \alpha_j \neq \emptyset$ and $\alpha_j = \emptyset$. In this ecological situation the functions $x_i$ prevail and the niche becomes very fragile.

• In the case b) of the nearby schema exemple, the species A, B, C are lumped in $\alpha_j \subset \beta_j$. In this case $\beta_j - \alpha_j = \emptyset$, and $\alpha_j \neq \emptyset$. In this ecological situation the functions $y_u$ prevail and the niche becomes very robust.
• From this preamble, the evolutionary dynamics into the niche is given schematically and in general by the following system of equations:

\[
\begin{align*}
\frac{d\omega}{dt} &= f(\omega, E) \\
\frac{dE}{dt} &= g(\omega, E)
\end{align*}
\]

where \( \omega(t) \) expresses a generic organism which varies during the time \( t \). \( f \) and \( g \) are suitable functions, \( E(t) \) represents the environmental agents or factors which vary during the time. If \( z_i(t) \) denotes a phenotype of a generic individual of a species \( A \) then the previous system can be written so:

\[
\begin{align*}
\frac{dz_i}{dt} &= f(z_i, E) \\
\frac{dE}{dt} &= g(z_i, E)
\end{align*}
\]
Fundamental aspects on niche description

• By virtue of the literature for a niche $\beta_j$ we have the following structure:

$$\beta_j \equiv \langle G(t), E(t) \rangle$$

where $G(t)$ represents the genotypical and phenotypical aspects and their dynamics of the species which stay in $\beta_j$, while $E(t)$ denotes the related environment of $\beta_j$ and its dynamics.
• Now we will consider a sole value, that is the phenotype \( z_i \) for every individual \( a_i \) of a species \( A \), instead of taking an \( n \)-tuple \( A_i^n \in G \) of phenotypical characters. Hence for every species \( A \) we have a set of phenotypes \( F_A \).

• Everyone of these phenotypes is related to everyone individual of \( A \). Therefore \( A \) is individualized by its \( F_A \). And we denote by \( G^* \) the set of all \( z_i \) and, of course, \( F_A \subset G^* \).
Mathematical modelling of $G(t)$

- **1st case**, when in $\alpha_j$ or in $\beta_j - \alpha_j$ a species $A$ has some generations. Let be

  \[ N : \text{population size of a species } A \]
  \[ z_i : \text{phenotype of an individual } i \quad (0 < i \leq N) \]
  \[ \bar{z} : \text{mean phenotype in the population} \]
  \[ \delta_{ij} : \text{difference between phenotype of the } j^{th} \text{ descendant of individual } i \text{ and } i' \text{ s phenotype} \]
  \[ W_i : \text{number of descendant of individual } i \text{ that is its fitness} \]
  \[ \bar{z}' : \text{mean phenotype of the descendant} \]

Price’s Theorem

$$\bar{z}' = \frac{\sum_{i=1}^{N} \sum_{j=1}^{W_i} (z_i - \delta_{ij})}{\sum_{i=1}^{N} W_i}$$
Price’s (1972) theorem (or equation)

- For every species $A_r$ in the niche $\beta_j$ we have:

$$\Delta \bar{z}_{A_r} = \frac{1}{\bar{W}_{A_r}} \left[ \text{cov}(W_i, z_i) + E(W_i \bar{\delta}_i) \right]$$

- where:

$\bar{W}_{A_r}$ : mean number of descendants (mean fitness of population $A_r$)

$\bar{\delta}_i$ : difference between the mean value of $z$ among $i$'s descendants and $z_i$
Price’s components

• We must remark

- The part \( \frac{1}{W_A} \text{cov}(W_i, z_i) \) represents the change due to differential survival and reproduction (selection and genetic drift)

- The part \( \frac{1}{W_A} E(W_i \delta_i) \) is an accuracy measure of the transmission of phenotype \( z_i \)
Mathematical descriptions of $E(t)$

- The mathematical descriptions of $E(t)$ is very complex, as well as of the environtmental transformations of $E$ by its inhabitants. We propose this definition which depends on the time $t$

$$E(t) = \langle \nu(t), r(t), T(t), p(t), \eta(t) \rangle$$

where:

- $\nu(t)$ is the density of individuals of the various species in $E(t)$ during $(t_i - t_0)$
- $r(t)$ expresses the (alimentary etc.) resources during $(t_i - t_0)$
- $T(t)$ expresses the mean climate situation during $(t_i - t_0)$
- $p(t)$ represents the pollution factors during $(t_i - t_0)$
- $\eta(t)$ is the total water rate in $E(t)$ during $(t_i - t_0)$
Definition of an environment (of a niche)

- Two elements which define $E(t)$ can be individualized, for instance, by the solutions of the following equations (simple deterministic case):

$r(t): \quad \dot{r} = \lambda - kr$

$p(t): \quad \dot{p} = Ap (1 - p)$

and $T$ by

$$T = \frac{4\sqrt{(1-a)S}}{4\varepsilon \sigma}$$

The stochastic description would be more interesting.
Mathematical modelling of $G(t)$

- **2\textsuperscript{d} case**, without generation, that is alteration of the phenotype through migration inside the niche $\beta_j$ as effect of the environment action (i.e., in virtue of the wind or the water or the insects etc.). In this case we have the so-called ecological transformations which are determined by the following kind of functions.

- Let be $F_{A(t)}$ the set of phenotypes at the time $t_i$ of the individuals of $A$ in $\alpha_j$ and $F'_{A(t)}$ the altered phenotypes at the time $t_j$ of the individuals of $A$ in $\beta_j - \alpha_j$, we will have:

$$
\begin{align*}
    x_i(t) : F_{A(t)} &\rightarrow T' \subset F'_{A(t)} \text{ go out} \\
    y_u(t) : F'_{A(t)} &\rightarrow T \subset F_{A(t)} \text{ go in}
\end{align*}
$$
• Topological scheme (two possible different situations) of a niche $\beta_j$.
• One has in both cases: $\alpha_j \neq \emptyset$ and $\beta_j - \alpha_j \neq \emptyset$
• Now we introduce the notion of *out-in balance of a phenotype* $z$, so:

\[
\sum_{i=1}^{n_1} x_i - \sum_{j=1}^{n_2} y_j
\]
• In general, it is possible to establish the following dynamics. 

We will consider a general case of degree 2 of paroxysm according the Cherruault model, where \( \forall i \ x_i + y_i = m \) constant.

\[
\begin{align*}
\dot{x}_1 &= a_{11} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right) + a_{12} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right)^2 \\
\quad \text{....} \\
\dot{x}_n &= a_{n1} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right) + a_{n2} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right)^2 \\
\dot{y}_1 &= b_{11} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right) + b_{12} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right)^2 \\
\quad \text{....} \\
\dot{y}_n &= b_{n1} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right) + b_{n2} \left( \sum_{i=1}^{n} x_i - \sum_{i=1}^{n} y_i \right)^2
\end{align*}
\]
• If in the previous system we subtract member to member, we have:

\[
\sum_{i=1}^{n}(\dot{x}_i - \dot{y}_i) = \sum_{i=1}^{n}(a_{i1} - b_{i1}) \sum_{i=1}^{n}(x_i - y_i) + \sum_{i=1}^{n}(a_{i2} - b_{i2}) \sum_{i=1}^{n}(x_i - y_i)^2
\]

If we put

\[
\sum_{i=1}^{n}(\dot{x}_i - \dot{y}_i) = \dot{z}_b
\]

\[
\sum_{i=1}^{n}(a_{ij} - b_{ij}) = c_j
\]

\[
\sum_{i=1}^{n}(x_i - y_i) = z_b
\]
• We obtain:

\[
\dot{z}_b = \sum_{i=1}^{2} c_i z_b^i
\]

\(\text{(\$\$)}\)

• If we put

\[
V(z_b, t) = -\sum_{i=2}^{2} c_{i-1} z_b^i
\]

which we call \textit{out-in potential}. Hence the previous equation becomes

\[
\dot{z}_b = -\frac{\partial V(z_b, t)}{\partial z_b}
\]

• The condition in order to have a basin (i.e. the center of an ecological niche) is to have local \textit{minima} of the potential \(V(z, t)\).
The ($$\text{&}$$) becomes

\begin{align*}
(\&) \quad \dot{z}_b &= z_b + \lambda z_b^2
\end{align*}

- In particular when the initial condition $z(0) > 0$ the solution diverges in a finite time (upper curve) whereas when and $z(0) < 0$ we have a negative asymptotic value for $t \to \infty$. We have asymmetric situation when the parameter $\lambda$ is negative.
- The solutions of (\&) are:

$$z_{b_1} = -\frac{1}{\lambda} \quad \text{and} \quad z_{b_2} = \frac{ce^t}{\lambda(1-ce^t)}$$
Struggle for life into the niche

• For the description of the dynamics in the niche it is necessary also of a mathematica representation of the: *Struggle for life* (evolutionary dynamics): general Lotka-Volterra equations

\[
\frac{dN_r}{dt} = \left( \varepsilon_r + \frac{1}{\beta_r} \sum_{s=1}^{n} a_{sr} N_s \right) N_r \quad \text{with } r = 1, 2, \ldots, n
\]
The Most Frequent Distribution Abundance Curve of the Species in a Niche
From previous considerations we have:

- **Prop. 1**: $E(t)$ can be represented through a suitable manifold in $\mathbb{R}^{5+1}$ (cfr. G.E. Hutchinson (1957))

Because a species $A$ is individualized by its $F_A$ and $F_A \subset \mathbb{R}^+$ we have:

- **Prop. 2**: Phenotypical form of Lotka-Volterra equations

\[
\frac{dF_{A_r}}{dt} = \left( \varepsilon_r + \frac{1}{\beta_r} \sum_{s=1}^{n} a_{sr} F_{A_s} \right) F_{A_r} \quad \text{with } r = 1, 2, \ldots, n
\]

- **Prop. 3**: The set of the functions (4) $x_i(t)$ and $y_u(t)$ determines a suitable *functional space*.

Because every species is well characterized and it does not change its fundamental features in the whole of the niche $\beta_j$, both in $\alpha_j$ and $\beta_j - \alpha_j$, we have:

- **Prop. 4**: The Lotka-Volterra *laws* are invariant for the *ecological transformations* $x_i(t)$ and $y_u(t)$ in $\beta_j$.
Other propositions

From the solutions of (&) and from ($) we have:

- **Prop. 5**: If we know at the time $t_r$ the value of the difference between the summations on the right of ($) then we can determine the equation (&), that is the value of $\lambda$.

- **Hypothesis**: If one establishes the value of $\lambda$, obtained at time $t_r \in [t_0, t_s]$ as the result of *ecological transformations*, then $\forall t \in [t_0, t_s]$ it is possible to know the value of one of the summations on the right of ($$)

One can show that

$$\lambda = \frac{1}{\sum_{j=1}^{n_2} y_j - \sum_{i=1}^{n_1} x_i}$$
An example

- Now we consider three species $A_1, A_2, A_3$ (*cattail* etc.) of plants which can live neighbouring to a lake (zone $\alpha_j \subset \beta_j$). Let be $A_4, A_5$ two other species (*Pickerehweed* etc.) which live in periphery of $\beta_j$. I.e. the wind has brought their pollens farther away (zone $\beta_j - \alpha_j$ or respectively zone $\alpha_j$).

- Case $y_i$ : ($l_i$ is the length of the central stem [phenotype] of a generic plant of $A_r$)

\[
F_{A_1} \Rightarrow \overline{l}_1(t_0) \xrightarrow{y_1(t)} \overline{l}_1 + 2cm = (18+2)cm = \overline{l}_1'(t_1) \in F_{A_1}'.
\]

\[
F_{A_2} \Rightarrow \overline{l}_2(t_0) \xrightarrow{y_2(t)} \overline{l}_2 + \sqrt{2}cm = (20+1.41)cm = \overline{l}_2'(t_1) \in F_{A_2}'.
\]

\[
F_{A_3} \Rightarrow \overline{l}_3(t_0) \xrightarrow{y_3(t)} \overline{l}_3 + 1cm = (15+1)cm = \overline{l}_3'(t_1) \in F_{A_3}'.
\]

\[
\sum_{i=1}^{3} y_i(t_1) = \sum_{i=1}^{3} \overline{l}_i'(t_1) = 53 + 4.41 = 57.41
\]
• Ecological niche related to our example
An example

- Case $x_i$ : ($p_i$ is the length of the central stem [phenotype] of a generic plant of $A_s$)

\[
F_{A_4} \Rightarrow p_4(t_0) - x_4(t) - p_4 - \frac{2}{3}cm = (24 - 1.73) = 2257 = p_4'(t_1) \in F_{A_4}
\]

\[
F_{A_5} \Rightarrow p_5(t_0) - x_5(t) - p_5 - 2cm = (27 - 2) = 25 = p_5'(t_1) \in F_{A_5}
\]

\[
\sum_{i=4}^{5} x_i(t_i) = \sum_{i=4}^{5} p_i'(t_i) = 51 - 3.73 = 47.27
\]

Hence:

\[
\sum_{i=4}^{5} x_i(t_1) - \sum_{i=1}^{3} y_i(t_1) = 47.27 - 57.41 = -10.14
\]

\[
\hat{\lambda} = \frac{1}{10.14} = 0.098
\]

\[
\hat{z}_b = z_b + 0.098z^2
\]
Set of niches in a network landscape (ecosystem) – Landscape Potential

Let be $z^*_i$ a local minimum in $V_i = -V(z^*_i)$ which is associated to an ecological niche. The population of the niches is the result of random walk which can be represented through suitable network in the landscape.
The dynamics of our ecological niche is labeled by the behaviour of $z_b$ also with the addition of a stochastic dynamics component, so (equation of Smoluchowski):

$$\dot{z}_b = -\frac{\partial V(z_b, t)}{\partial z_b} + \sqrt{2T}\xi(t)$$

where $T$ is a temperature of the ecological system that measures the stability of the different species and $\xi(t)$ is a white noise.

Without loss of generality we set $V(z_b, t) \leq 0$ in the region of a basin. So that the quantity

$$V_s = -\frac{V(z_s, t)}{T}$$

is the deepness of the potential well (of $z_s$) using $T$ as potential unit.
• Without the noise effect (i.e. $T = 0$) any individual trajectory of the member of the $j$-community is attracted by the critical point $z_s$, that is the individual stay in $\beta_j - \alpha_j$ or in $\alpha_j$, but it does not go out from $\beta_j$.

• On the contrary, for $T > 0$ each trajectory has the possibility to jump between potential wells, that is niches, modelling an interactions between the corresponding communities.

• We define *success of the $j$-community $n^*_j$* the number of individuals of the different species that populate the corresponding niche.

• **Remark 1**: According to our interpretation of the model, the success of the $j$-community is directly proportional to the probability of finding a representative individual (standard representative individual) in the neighborhood of $\beta_j$. 
• **Remark 2**: One can associate a stationary distribution probability \( P_{st}(z_b) \) to the stochastic dynamics (\(^\wedge\)) according to:
\[
P_{st}(z_b) = A \exp (- V(z_b, t)/T)
\]

• **Remark 3**: In the stationary state the success \( n^*_j \) of the \( j \)-community is given by the deepness of the *potential well* (Maxwell-Boltzmann distribution)
\[
n^*_j \propto \exp (V_j)
\]
and the relation
\[
\sum_{j=1,...,N} n^*_j = N_T
\]
give the total number of the individuals in the ecosystem.
• **Remark 4:** On can prove that the *escape rate* from the \( j \)-potential well is proportional to (Arrhenius’ law)

\[
P_{\text{esc}, j}(z_b) \propto \exp(-V_j)
\]

• **Remark 5:** A possible definition of the *interaction rate* \( \pi_{ij} \) of the community \( j \) with the community \( i \) depends on the related potential wells, so:

\[
\pi_{ij} = \frac{1}{N} \exp(V_i - V_j) = \frac{1}{N} \frac{n_i^*}{n_j^*}
\]

where \( N \) is the number of different communities.
Maxwell Boltzmann Distribution

We expect a stationary distribution of the form

\[ n_i \propto d_i \exp(-V_i) \]

where \( d_i \) is the connectivity of the niche. The equilibrium solution is the result of an interaction dynamics

\[ \pi_{ij} = \frac{c_{ij}}{d_j} \exp(V_i - V_j) \]

c_{ij} is the \textit{connectivity matrix} and

\[ d_i = \sum_j c_{ij} \]
Now we propose a Lotka-Volterra model for the population dynamics related to the landscape-ecosystem

\[
\dot{n}_i = n_i \left[ g(n_i^* - n_i) + \sum_{j=1}^{N} (\pi_{ij} - \delta_{ij}) n_j \right] \quad i = 1, \ldots, N
\]

\(g\) is the generation rate and \(n^*\) denotes the equilibrium solutions

**Problem:** How to derive the *interaction matrix* \(\pi_{ij}\) from the populations
• The Lotka-Volterra equations describe, in an effective way, the average dynamics of the community success $n^i(t)$. We impose the existence of stationary equilibrium $n^*_i$ and we introduce a birth rate $g$ (which represents the reproduction mechanism). The condition $g > 0$ implies the stability for the stationary solution $n^*_i$ and $g$ is directly proportional to the exponential of the fitness. Because we consider $N$ communities, the Lotka-Volterra equation becomes a system of equations. Hence the matrix

$$
\begin{pmatrix}
\pi_{ij} - \delta_{ij} = \\
\pi_1 & \ldots & \pi_{1N} \\
\ldots & \ldots & \ldots \\
\pi_{1N} & \ldots & \pi_{NN}
\end{pmatrix}
- 
\begin{pmatrix}
1 & \ldots & 0 \\
0 & \ldots & 0 \\
0 & \ldots & 1
\end{pmatrix}
$$

with $i = 1, \ldots, N$, represents a cooperative interaction among the communities.
Therefore we write the Lotka-Volterra dynamics of the communities as

\[ \dot{n}_i = n_i \left[ g(n_i^* - n_i) + \sum_{j=1}^{N} (\pi_{ij} - \delta_{ij})n_j \right] \quad i = 1, \ldots, N \]

We are interested in the dynamics near the stationary state \( n_i \sim n_i^* \)

\[ \frac{\dot{n}_i}{n_i^*} = n_i^* g + n_i^* \left( \frac{1}{N} \sum_{j=1}^{N} \frac{n_j}{n_j^*} - (g + 1) \frac{n_i}{n_i^*} \right) \]
Linearized Equations

We linearize the system near the equilibrium state

\[ \dot{n}_i \approx n_i^* \sum_{j=1}^{N} [\pi_{i,j} - (g + 1)\delta_{ij}] (n_j - n_j^*) \]

\[ = (n_i^*)^2 g + n_i^* \sum_{j=1}^{N} [\pi_{i,j} - (g + 1)\delta_{ij}] n_j \]

\( \pi_{ij} \) has eigenvalues \( \leq 1 \) and the solution is stable for \( g > 0 \). Studying eigenvalue distribution of \( \pi_{ij} \) is possible for \( N \) large.
By using the variable $z_i = n_i / n_i^*$

\[
\dot{z}_i = n_i^* z_i + n_i^* \left( \sum_j \frac{c_{ij}}{d_i} z_j - (g + 1) z_i \right)
\]

We associate a *Master Equation* to consider the finite size effects
Master Equation

$P(m, t)$ is the probability that the normalized populations have $m$ individuals

$$
\dot{P}(m, t) = \sum_{i=1}^{N} n_i^* (E_i^+ - 1) \left[ (g + 1)m_i P(m, t) - E_i^- \left( g + \sum_{j=1}^{N} \frac{c_{ij}}{d_i} m_j \right) P(m, t) \right]
$$

where $E^\pm$ are the Van Kampen operators

$$
E_i^\pm P(m) = P(m_1, \ldots, m_i \pm 1, \ldots, m_N)
$$
Solution in the Detailed Balance

**Idea:** To study the stationary solution of the Master Equation to relate the fluctuations properties to the interaction matrix.

We consider an easy case when then Detailed Balance condition holds

\[ J_i(m, t) = n_i^* \left( g + \frac{1}{N} \sum_{j=1}^{N} m_j \right) P(m, t) - n_i^* E_i^+ (g + 1) m_i P(m, t) \]

The stationary solution satisfies

\[ E_i^+ P_s(m) = \frac{N g + \sum_{j=1}^{N} m_j}{N(g + 1)(m_i + 1)} P_s(m) \quad \forall \ i \]
Analytical solution

It is possible to get an analytical form for the solution (multinominal negative distribution)

\[
P (m_1, \ldots, m_N) = \Gamma(Ng + M) \frac{p_0^{Ng} p_1^{m_1} \cdots p_N^{m_N}}{\Gamma(Ng)m_1! \cdots m_N!}
\]

where the probabilities are

\[
p_i = \frac{n_i^*}{N(g + 1)} \quad i = 1, \ldots, N \quad p_0 = 1 - \frac{1}{g + 1} = \frac{g}{g + 1}
\]
Fluctuations properties

We compute the moments of the distribution

\[ \langle n_i \rangle = n_i^* \]

\[ \langle n_i n_j - \langle n_i \rangle \langle n_j \rangle \rangle = n_i^* \left( \frac{n_j^*}{Ng} + \delta_{ij} \right) \]

The correlation scales with the connectivity
RSA distribution: two species

Bazzani, A; Sala, C; Giampieri, E; Castellani, G, Master Equation and Relative Species Abundance Distribution for Lotka-Volterra Models of Interacting Ecological Communities, «THEORETICAL BIOLOGY FORUM», 2017, 11, pp. 37 - 47
Marginal distribution

Neutral hypothesis by Hubbell of non-interacting species with an external source from the surrounding environment
Experimental application example has been realized

- in WILDLIFE RESERVE (WWF) of Burano lake and related all around (Capalbio, GR, Italy)
• We have taken in account the following works:
• A. Townsend Peterson; Jorge Soberôn; RG Pearson; Roger P Anderson; Enrique Martínez-Meyer; Miguel Nakamura; Miguel Bastos Araújo (2011). "Species-environment relationships". Ecological Niches and Geographic Distributions (MPB-49). Princeton University Press. p. 82. See also Chapter 2: “Concepts of niches”, pp. 7


Thanks for the attention

Perspectives: new results using measures on the fluctuations of the populations in a network of ecological niches (ecosystem)

Bazzani, A; Sala, C; Giampieri, E; Castellani, G, Master Equation and Relative Species Abundance Distribution for Lotka-Volterra Models of Interacting Ecological Communities, «THEORETICAL BIOLOGY FORUM», 2017, 11, pp. 37 - 47