Neutral and niche theories
in tropical forest communities

Nordforsk PhD Summer School
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Smithsonian Tropical Research Institute
Neutral and niche theories in tropical forest communities
Importance of the neutral theory is not neutrality

Stochastic & individual-based community theory:

- stochastic individual demography
- species input (an open community)
Stochastic community theory

(the Hubbell approach)
A stochastic community theory

Biology of individuals:
- Mortality
- Reproduction
- Growth
- Dispersal

Community patterns:
- Competition
- Diversity
- Abundance
- Spatial patterns
- Species-area relationship
- Extinction
A stochastic community theory

Biology of individuals:
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Traits easily measured in real organisms
A stochastic community theory

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Traits easily measured in real organisms

Not easily measured or associated with real organisms
A stochastic community theory

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Community properties of broad interest emerge from the model without any direct assumptions.
A stochastic community theory

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Community patterns:
- Competition
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Community properties of broad interest emerge from the model without any direct assumptions

(ie, no assumption about diversity required to produce diversity, etc.)
A stochastic niche theory:

Biology of individuals:

- Mortality
- Reproduction
- Growth
- Dispersal
- Speciation

Individuals of different species differ in ways that affects community structure.
A stochastic niche theory:

Biology of individuals:

- Mortality
- Reproduction
- Growth
- Dispersal
- Speciation

* Individuals of different species differ in ways that affects community structure

* I.e., species differ in these individual-level traits
A stochastic niche theory:

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation

Individuals of different species differ in ways that affects community structure

Niche theories generally do not follow the stochastic and individual approach to communities
A stochastic neutral theory:

Biology of individuals:

- Mortality
- Reproduction
- Growth
- Dispersal
- Speciation

Individuals of different species are identical
Background of the stochastic community model


The stochastic community model

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The stochastic community model

depth

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The stochastic community model

dispersal
The stochastic community model

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Torus wrapping
The stochastic community model

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(= the Hubbell model)
The stochastic community model

Dispersal

(= the 2D Voter model)
Basic results
Basic results

Stochastic model without speciation leads to a monodominant community (Gause’s principal)
Stochastic model without speciation leads to a monodominant community (Gause’s principal)

In 3D model, not so!
Basic results

Stochastic model without speciation leads to a monodominant community (Gause’s principal)

In 3D model, not so!

Diversity is maintained despite no niche differences, as long as there is speciation
Hubbell proved that with speciation, the neutral community reaches an equilibrium diversity and abundance distribution.
Recent advances in theory


Abundance distributions
The species abundance distribution (SAD)
Stochastic community demonstration

votersimulation()
z=voter.model(gridsize=10,start=NULL,v=.05,chartdispersal=F,printiter=5,printit="hist",generations=200,walkthrough=TRUE)
distributionbook(data=T)
z=voter.model(gridsize=50,start=NULL,v=.05,chartdispersal=F,printiter=10,printit="loghist",generations=100)
The master equation in theories of abundance

\[ \frac{dP_k}{dt} = \sum_i T_{ik} P_i \]

- $P_k$: probability of occupying state $k$
- $T_{ik}$: transition probability from state $i$ to state $k$
Life table theory is based on a master equation

<table>
<thead>
<tr>
<th>size</th>
<th>time 0</th>
<th>time 1</th>
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</thead>
<tbody>
<tr>
<td>seedlings</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>saplings</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>poles</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>canopy trees</td>
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- 4 size classes are 4 states
- growth from one class to another is a transition probability
- reproduction is transition from adult to offspring states

\[ \Delta N_3(time\ 1) = T_{13} N_1(time\ 0) + T_{23} N_2(time\ 0) - T_{34} N_3(time\ 0) \]
Life table theory is based on a master equation

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Life table theory is based on a master equation

<table>
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<th>Probabilities!</th>
<th>size</th>
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<tr>
<td></td>
<td></td>
<td>time 0</td>
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<td>seedlings</td>
<td>1</td>
<td>0.40</td>
</tr>
<tr>
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- at equilibrium

\[
P_3 = T_{13}P_1 + T_{23}P_2 - T_{34}P_3 + T_{33}P_3
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A master equation for species abundances

<table>
<thead>
<tr>
<th>species abund</th>
<th>1982</th>
<th>1985</th>
<th>1990</th>
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<td>21</td>
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- the state refers to the number of individuals in a species
- frequency is the number of species in each state
- species shift from one state to another via births and deaths
- species input (speciation) is shift from state 0 to state 1
A master equation for species abundances

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\[ S_3 = T_{23} S_2 + T_{43} P_4 - T_{32} P_3 - T_{34} P_4 + T_{33} S_3 \]
A master equation for species abundances

Define transition probability for 1 step of model: exactly 1 birth and exactly 1 death

\[ b = \text{birth probability} \]
\[ d = \text{death probability} \]

\[ S_3 = b_2 (1 - d_2) S_2 + d_4 (1 - b_4) S_4 + (1 - b_3) (1 - d_3) S_3 \]
\[ -d_3 (1 - b_3) S_3 - b_3 (1 - d_3) S_3 \]
A master equation for species abundances

\( \text{birth probability} \)

\( \text{death probability} \)

\[ P_3 = b_2 (1 - d_2) P_2 + d_4 (1 - b_4) P_4 \]

\[ + (1 - b_3)(1 - d_3) P_3 \]

\[ - d_3 (1 - b_3) P_3 - b_3 (1 - d_3) P_3 \]

\[ P_n = k \prod_{i=0}^{n-1} \frac{b_i}{d_{i+1}} \]

neutral assumption: for all \( i \) and \( j \) \( b_i = b_j, \quad d_i = d_j \)
A master equation for species abundances

\[ b = \text{birth probability} \]

\[ d = \text{death probability} \]

\[ P_n = k \prod_{i=0}^{n-1} \frac{b_i}{d_{i+1}} \]

neutral assumption: \[ P_N = k \left( \frac{b}{d} \right)^n = k x^n \quad (x \text{ just } < 1) \]

the log-series as proposed by Fisher et al. (1943)

Niche theory
Chesson's niche theory

- Species coexistence hinges on stabilizing factors
- Neutrality $\rightarrow$ equalizing (not stabilizing)
- Stochastic demography is ignored (but doesn't have to be)

Chesson's niche theory

Lotka-Volterra equation for 2-species competition:

\[
\frac{dN_i}{dt} = N_i r_i (1 - \alpha_{ii} N_i - \alpha_{ij} N_j)
\]

\(\alpha_{ii}\) intraspecific competition coefficient

(impact of species \(i\) on itself)

\(\alpha_{ij}\) interspecific competition coefficient

(impact of species \(j\) on species \(i\))
Chesson's niche theory

Lotka-Volterra equation for 2-species competition:

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Chesson's niche theory

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\frac{dN_i}{dt} = N_i r_i \left( 1 - \alpha_{ii} N_i - \alpha_{ij} N_j \right)
\]

species \( j \) can invade species \( i \) when \( \alpha_{ii} > \alpha_{ji} \)

assume equal fitness at low density \( r_i \approx r_j \)
Competition between species $I$ and species $J$.

$J$ is rare.
Chesson's niche theory

Lotka-Volterra equation for 2-species competition:

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\frac{dN_i}{dt} = N_i r_i (1 - \alpha_{ii} N_i - \alpha_{ij} N_j)
\]

species \(j\) can invade species \(i\) when \(\alpha_{ii} > \alpha_{ji}\)
Chesson's niche theory

Lotka-Volterra equation when $j$ is rare:

$$\frac{dN_i}{dt} = N_i r_i (1 - \alpha_{ii} N_i - \alpha_{ij} N_j)$$
Chesson's niche theory

Lotka-Volterra equation when $j$ is rare:

$$\frac{dN_j}{dt} = N_j r_j (1 - \alpha_{jj} N_j - \alpha_{ji} N_i)$$
A range of niche theories

- Environmental niches
- Regeneration niches
- Demographic niches
- Predator niches

All can be subsumed into Chesson's framework

- Every species benefits when it falls below its own carrying capacity
- Intraspecific competition > interspecific competition
- Rare species advantage
Korup 50 ha plot (Cameroon)
494 species, 329000 individuals in full census ≥1 cm dbh

D. Thomas, D. Kenfack, G. Chuyong, R. Condit
Tropical tree species abundances vary four orders of magnitude

<table>
<thead>
<tr>
<th>Panama: BCI plot 1990 (50 ha)</th>
<th>N</th>
<th>Congo: Ituri plot 1995 (20 ha)</th>
<th>N</th>
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<td>Hampea appendiculata</td>
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<td>Rothmannia whitfieldii</td>
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<td>Sorindeia multifoliolata</td>
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<td>Hybanthus prunifolius</td>
<td>36060</td>
<td>Sorindeia nitidula</td>
<td>10</td>
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<tr>
<td>Hieronyma alchorneoides</td>
<td>88</td>
<td>Spathodea campanulata</td>
<td>0</td>
</tr>
</tbody>
</table>

306 species, with 17 singletons
361 species, with 36 singletons
choose tree to die at random

accept choice with prob=$m$, where $m=f(elev)$

if rejected, choose again
Korup plot

- *Anthonotha lamprophylla*
Simulated species distributions with niche differences
plus speciation

Community has 140 species, one with 17484 individuals ... 45 singletons

44 unique niche responses, 10 most abundant species all have one of these 4
Summary: Abundances and the neutral theory

Neutral theory predicts abundance distribution correctly...

... but it's not neutrality, it's species input & stochastic demography

Nevertheless, species differences may sometimes be irrelevant in understanding abundances because of dominating influence of species turnover
Korup plot

- *Belonophora wernhamii*
Korup plot

Pleiocarpa rostrata
Resource competition

- Species coexist by differing in resource use
- Provides details of what differences are necessary
- Falls under Chesson's general framework

\[ \hat{r}_i = b_i (k_i - \rho k_s) \]

\[ \hat{r}_i = b_i (k_i - k_s) + b_i (1 - \rho) k_s \]

equalizing stabilizing

- \( k \) average fitness, \( i \) invader and \( s \) resident
- \( \rho \) resource overlap
Neutral simulation

Preston binning

Linear bins