Neutral and niche theories

in tropical forest communities

Nordforsk PhD Summer School
31 July 2008

Richard Condit
Smithsonian Tropical Research Institute

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course material: ctfs.si.edu/localdata

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:

Community patterns:

A stochastic community theory

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation

Community patterns:

Competition
Diversity
Abundance
Spatial patterns
Species-area relationship
Extinction

A stochastic community theory

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation

→ Traits easily measured in real organisms

A stochastic community theory

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation

Traits easily measured in real organisms

Not easily measured or associated with real organisms

A stochastic community theory

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation

Community patterns:

Competition
Diversity
Abundance
Spatial patterns
Species-area relationship
Extinction

A stochastic community theory

Biology of individuals:

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Community patterns:

Competition
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Extinction

Community properties of broad interest emerge from the model without any direct assumptions

A stochastic community theory

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation

Community patterns:

Competition
Diversity
Abundance
Spatial patterns
Species-area relationship
Extinction

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

* Ie, 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

Kimura, M., and Weiss, G.H. 1964. The stepping stone model of population genetic structure and the decrease of genetic correlation with distance. Genetics 49:561-576.

Caswell, H. 1976. Community structure: a neutral model analysis. Ecological Monographs, 46: 327-354.

Liggett, T.M. 1985. *Interacting partical systems*. Springer.

Dewdney, A.K. 2000. A dynamical model of communities and a new species-abundance distribution. Biological Bulletin, 198: 152-165.

Hubbell, S.P. 2001.*The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ, Princeton University Press.

Leigh, E.G. 2007. Neutral theory: an historical perspective. Evolutionary Biology, doi:10.1111/j.1420-9101.2007.01410.x




The stochastic community model

1	2	1	2	1
1	1	1	4	1
1	3	1	1	2
4	1	1	3	1
1	1	2	1	1

The stochastic community model

1	2	1	2	1
1	1	1	4	1
1	3	~~1~~	1	2
4	1	1	3	1
1	1	2	1	1

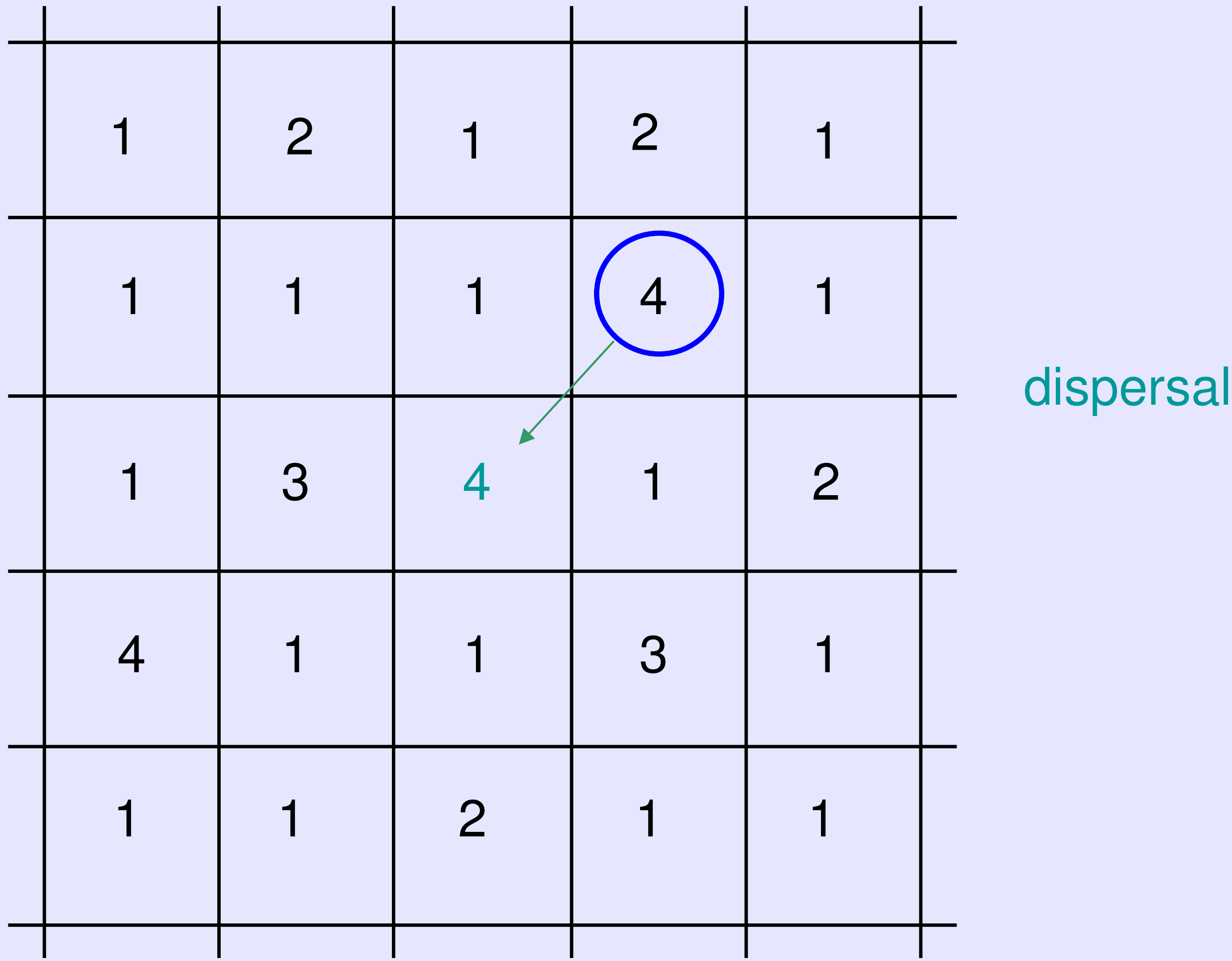
death

The stochastic community model

1	2	1	2	1
1	1	1	4	1
1	3		1	2
4	1	1	3	1
1	1	2	1	1

birth

The stochastic community model



The stochastic community model

1	2	1	2	1
1	1	1	4	1
1	3	6	1	2
4	1	1	3	1
1	1	2	1	1

Torus wrapping

The stochastic community model

1	2	1	2	1
1	1	1	4	1
1	3	4	1	2
4	1	1	3	1
1	1	2	1	1

dispersal

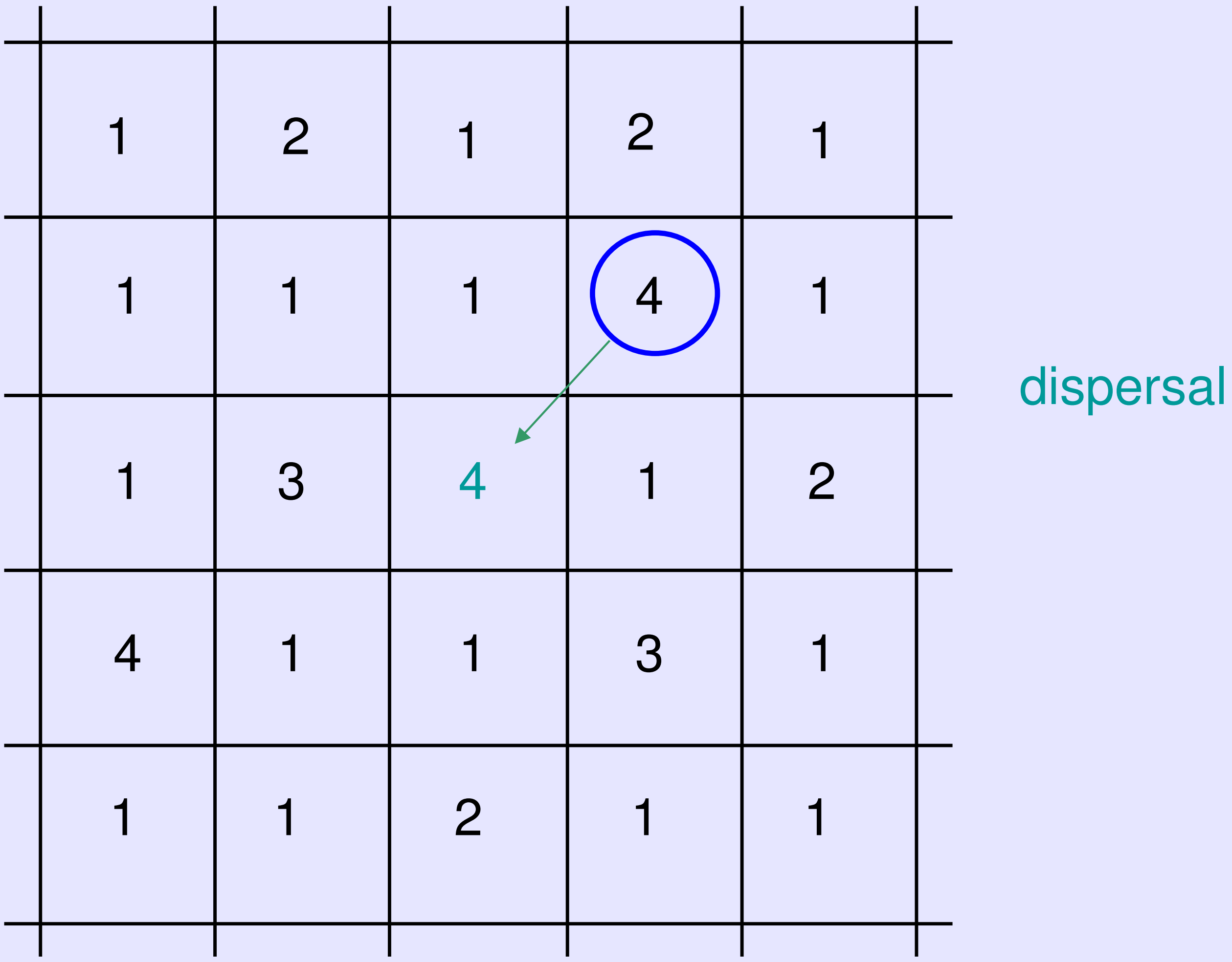
The stochastic community model

1	2	1	2	1
1	1	1	4	1
1	3	6	1	2
4	1	1	3	1
1	1	2	1	1

speciation
or
immigration

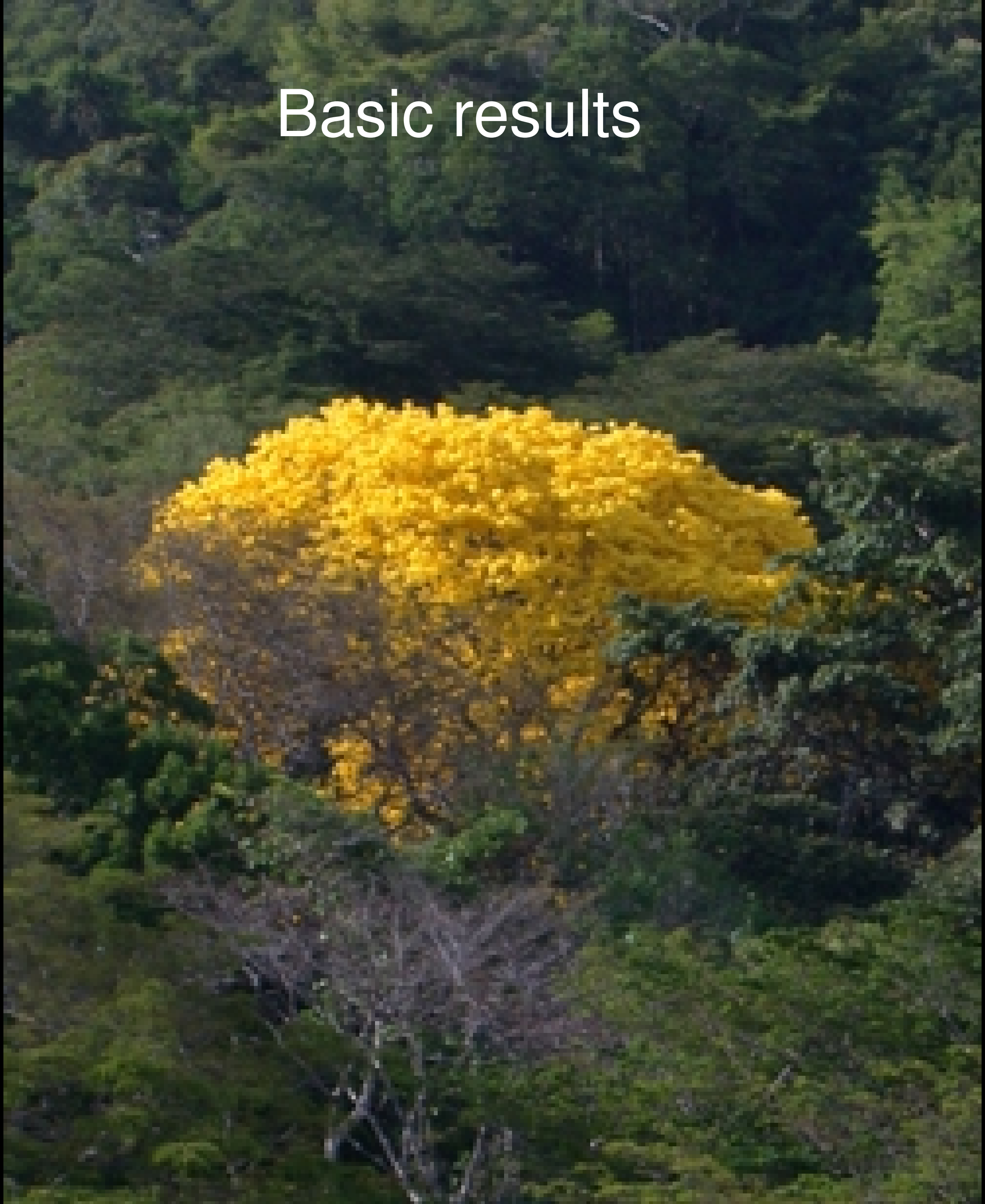
(= the Hubbell model)

The stochastic community model



(= the 2D Voter model)

Basic results



Basic results

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

Basic results

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

In 3D model, not so!

Basic results

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

In 3D model, not so!

Diversity is maintained despite no niche differences, as long as there is speciation

Equilibrium species abundance distribution

Hubbell proved that with speciation, the neutral community reaches an equilibrium diversity and abundance distribution.

Recent advances in theory

Volkov, I., et al. 2003. Neutral theory and relative species abundance in ecology. Nature 424: 1035-1037.

Volkov, I. et al. 2005. Density dependence explains tree species abundance and diversity in tropical forests. Nature 438: 658-661.

Etienne. R. 2005. A new sample formula for neutral biodiversity. Ecology Letters, 8: 253-260.

Zillio, T., and Condit, R. 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. Oikos, doi: 10.1111/j.2007.0030-1299.15662.x

Abundance distributions

The species abundance distribution (SAD)

/home/condit/meetings_workshops/Lammi/Lammi1_NeutralNicheVert.odp#Slide 1

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

	size	Population time 0	time 1
seedlings	1	10	
saplings	2	8	
poles	3	5	
canopy trees	4	2	

- 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

	size	Population time 0	time 1
seedlings	1	10	
saplings	2	8	
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$$N_3(time\,1) = T_{13} N_1(time\,0) + T_{23} N_2(time\,0) - T_{34} N_3(time\,0) + T_{33} N_3(time\,0)$$

Life table theory is based on a master equation

Probabilities!

	size	Proportion time 0	Proportion time 1
seedlings	1	0.40	
saplings	2	0.32	
poles	3	0.20	
canopy trees	4	0.08	

- 4 size classes are 4 states
- growth from one class to another is a transition probability
- reproduction is transition from adult to offspring states

$$P_3(time\,1) = T_{13}P_1(time\,0) + T_{23}P_2(time\,0) - T_{34}P_3(time\,0) + T_{33}P_3(time\,0)$$

Life table theory is based on a master equation

Probabilities!

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- 4 size classes are 4 states
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$$P_3(time\,1) = T_{13}P_1(time\,0) + T_{23}P_2(time\,0) - T_{34}P_3(time\,0) + T_{33}P_3(time\,0)$$

- at equilibrium

$$P_3 = T_{13}P_1 + T_{23}P_2 - T_{34}P_3 + T_{33}P_3$$

A master equation for species abundances

	frequency BCI plot		
species abund	1982	1985	1990
1	22	21	17
2	8	11	10
3	7	6	11
4	4	7	7
5	4	4	2

- 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

	frequency BCI plot		
species abund	1982	1985	1990
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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

$$S_3 = T_{23} S_2 + T_{43} P_4 - T_{32} P_3 - T_{34} P_4 + T_{33} S_3$$

A master equation for species abundances

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

b = birth probability
d = 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

b = birth probability
d = 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 $\quad b_i = b_j, d_i = d_j$

A master equation for species abundances

b = birth probability
d = death probability

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

neutral assumption: $P_N = k\left(\frac{b}{d}\right)^n = k\,x^n$ (x just < 1)

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

Fisher, R.A., Corbet, A.S. and Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**: 42-58.


Niche theory

Chesson's niche theory

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

MacArthur, R.H. 1970. Species-packing and competitive equilibrium for many species. Theoretical Population Biology, 1:1-11.

Tilman, D. 1982. Resource *Competition and Community Structure*. Monographs in Population Biology, Princeton University Press. 296 pp.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343-366.

Chesson's niche theory

Lotka-Volterra equation for 2-species competition:

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

α_{ii} intraspecific competition coefficient (impact of species *i* on itself)

α_{ij} interspecific competition coefficient (impact of species *j* on species *i*)

Chesson's niche theory

Lotka-Volterra equation for 2-species competition:

exponential growth

competition

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

α_{ii} intraspecific competition coefficient (impact of species *i* on itself)

α_{ij} interspecific competition coefficient (impact of species *j* on species *i*)

Chesson's niche theory

Lotka-Volterra equation for 2-species competition:

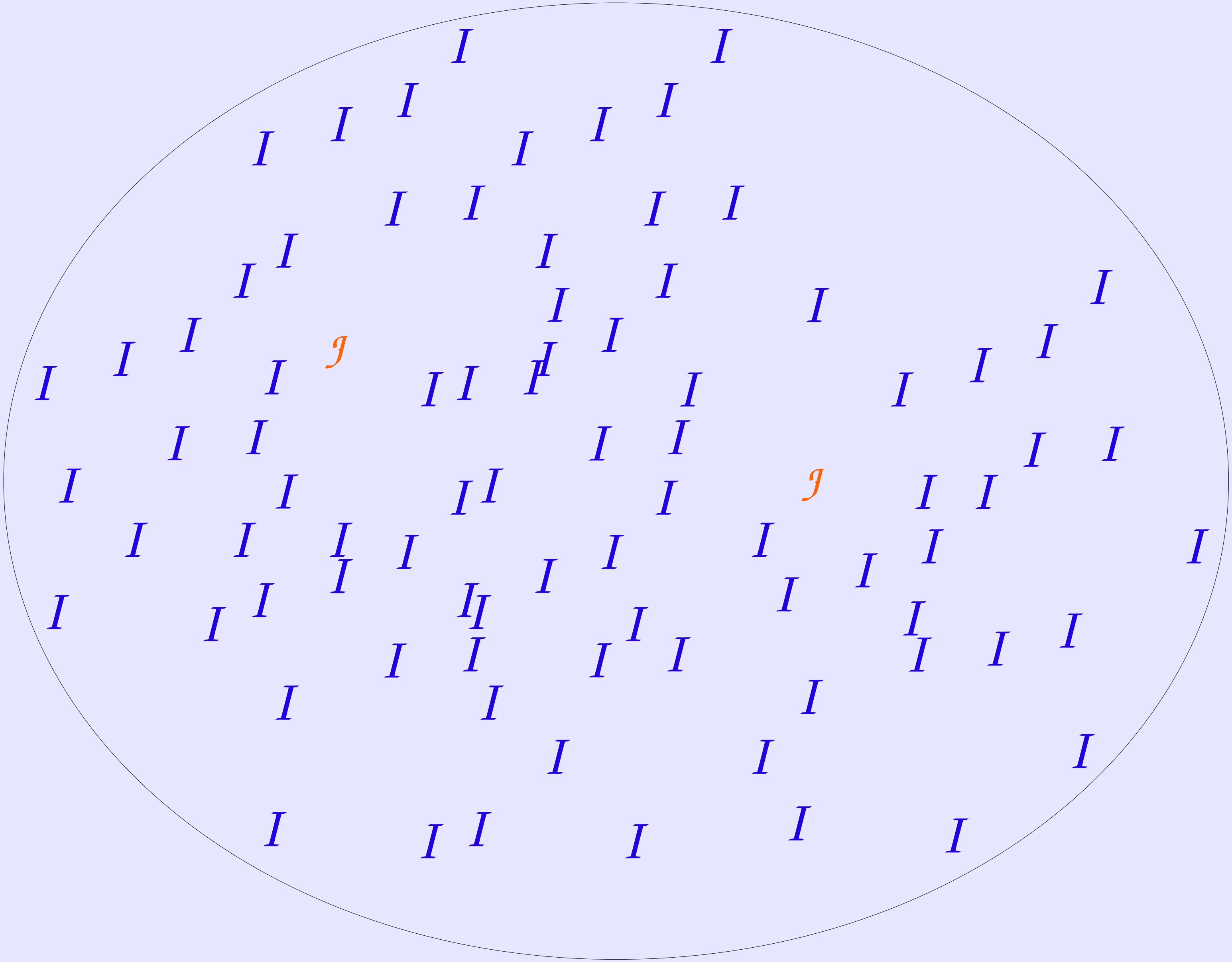
$$\frac{dN_i}{dt} = N_i r_i (1 - \alpha_{ii} N_i - \alpha_{ij} N_j)$$

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:

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

species *j* can invade species *i* when $\alpha_{ii} > \alpha_{ji}$

Chesson's niche theory

Lotka-Volterra equation when *j* is rare:

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

Chesson's niche theory

Lotka-Volterra equation when *j* is rare:

$$\frac{dN_j}{dt} = N_j r_j \left(1 \cancel{- \alpha_{jj} N_j} - \alpha_{ji} N_i\right)$$

A range of niche theories

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

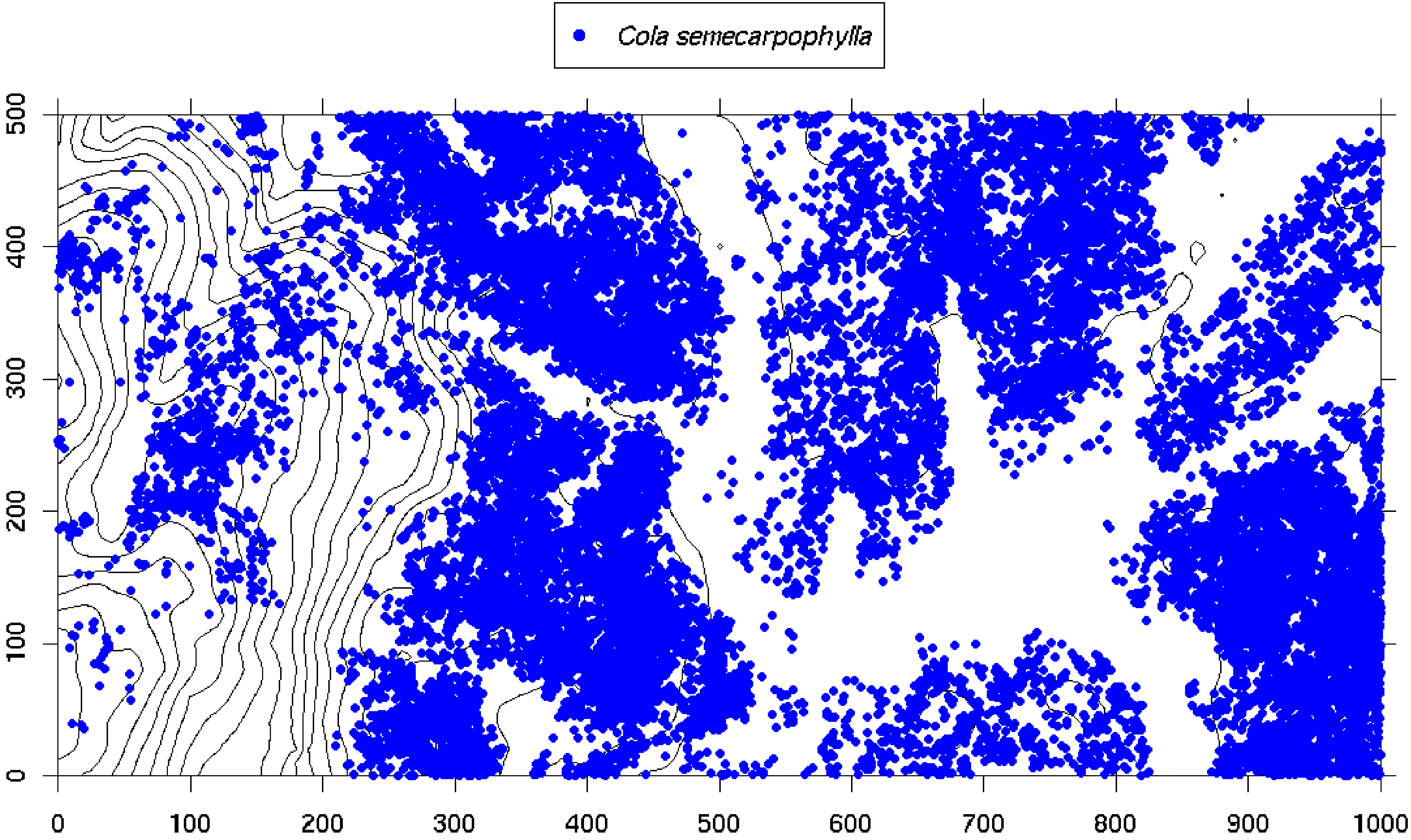
All can be subsumed into Chesson's framework

- Every species benefits when it falls below its own carrying capacity
- Intraspecific competition > interspecific competition
- Rare species advantage

Africa
Morocco
Tunisia
Mediterranean Sea
ASIA
nary Is.
estern Sahara rocco)
Algeria
Libya
Egypt
Nile R.
Red Sea
Mauritania
Mali
Niger
Eritrea
Arabian Sea
Burkina Faso
Chad
Sudan
Djibouti
Guinea
Benin
one
Ghana
Nigeria
Ethiopia
Liberia
C.A.R.
Cameroon
Togo
Somalia
te d'Ivoire
Eq. Guinea
Democratic Rep. of the Congo
Uganda
Sao Tome & Principe
Gabon
Kenya
INDIAN OCEAN
Rep. of the Congo
Rwanda
Burundi
Cabinda (Angola)
Tanzania
Seychelles
Malawi
Comoros
TIC OCEAN
Angola
Zambia
Korup
Mozambique
Mauritius
Namibia
Zimbabwe
Madagascar
Botswana
800 Miles
Réunion (France)
Swaziland
800 Kilometers
South Africa
Lesotho
20° W
0°
20° E
40° E
60° E

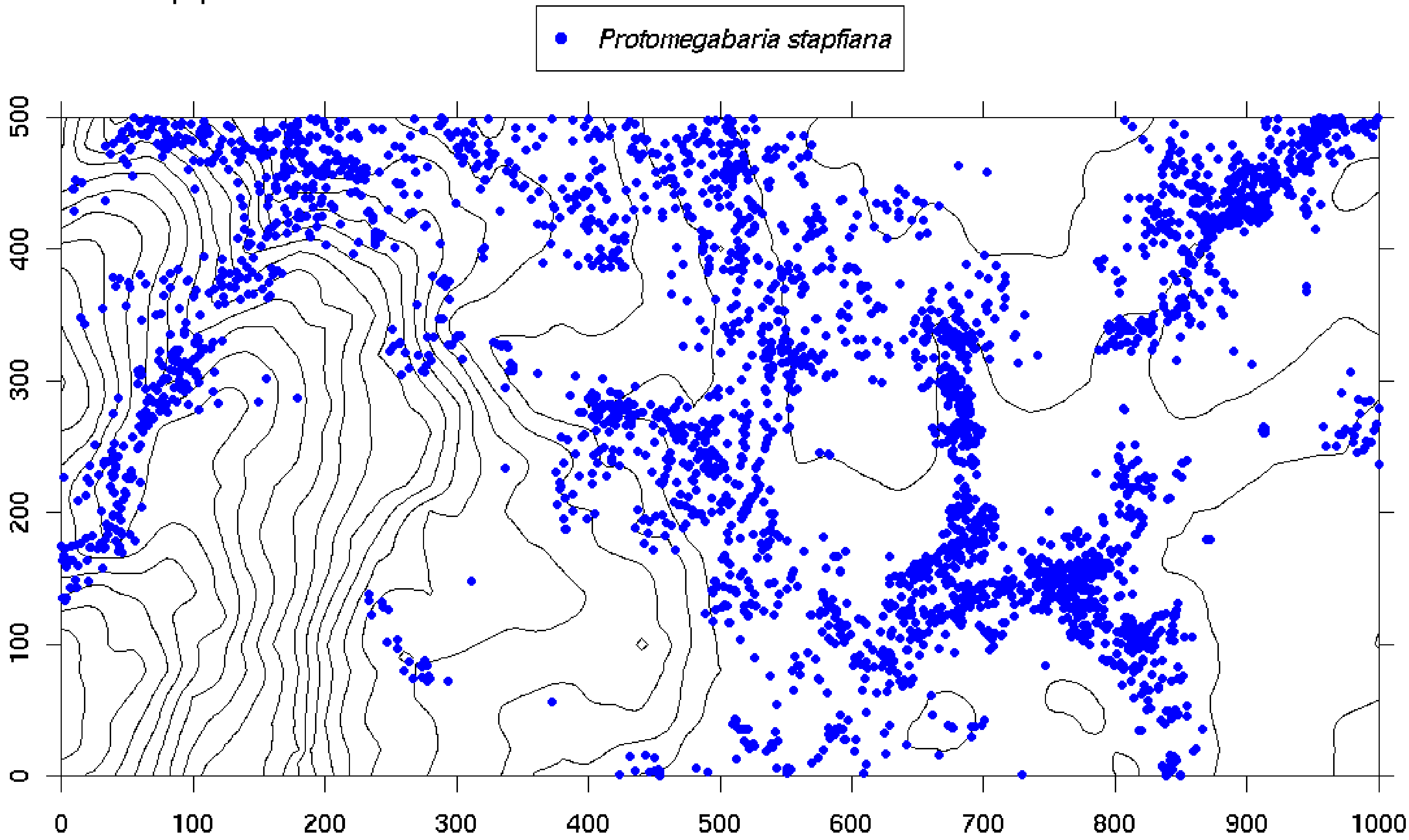
Korup 50 ha plot (Cameroon)

494 species,329000 individuals in full census ≥1 cm dbh



D. Thomas, D. Kenfack, G. Chuyong, R. Condit

Korup plot


Protomegabaria stapfiana
0
100
200
300
400
500
0
100
200
300
400
500
600
700
800
900
1000


460 100

Africa
Morocco
Tunisia
Mediterranean Sea
ASIA
nary Is.
estern Sahara rocco)
Algeria
Libya
Egypt
Nile R.
Red Sea
Mauritania
Mali
Niger
Chad
Sudan
Eritrea
Arabian Sea
Burkina Faso
Djibouti
Guinea
Benin
one
Ghana
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Ethiopia
Liberia
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Cameroon
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Somalia
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Gabon
Kenya
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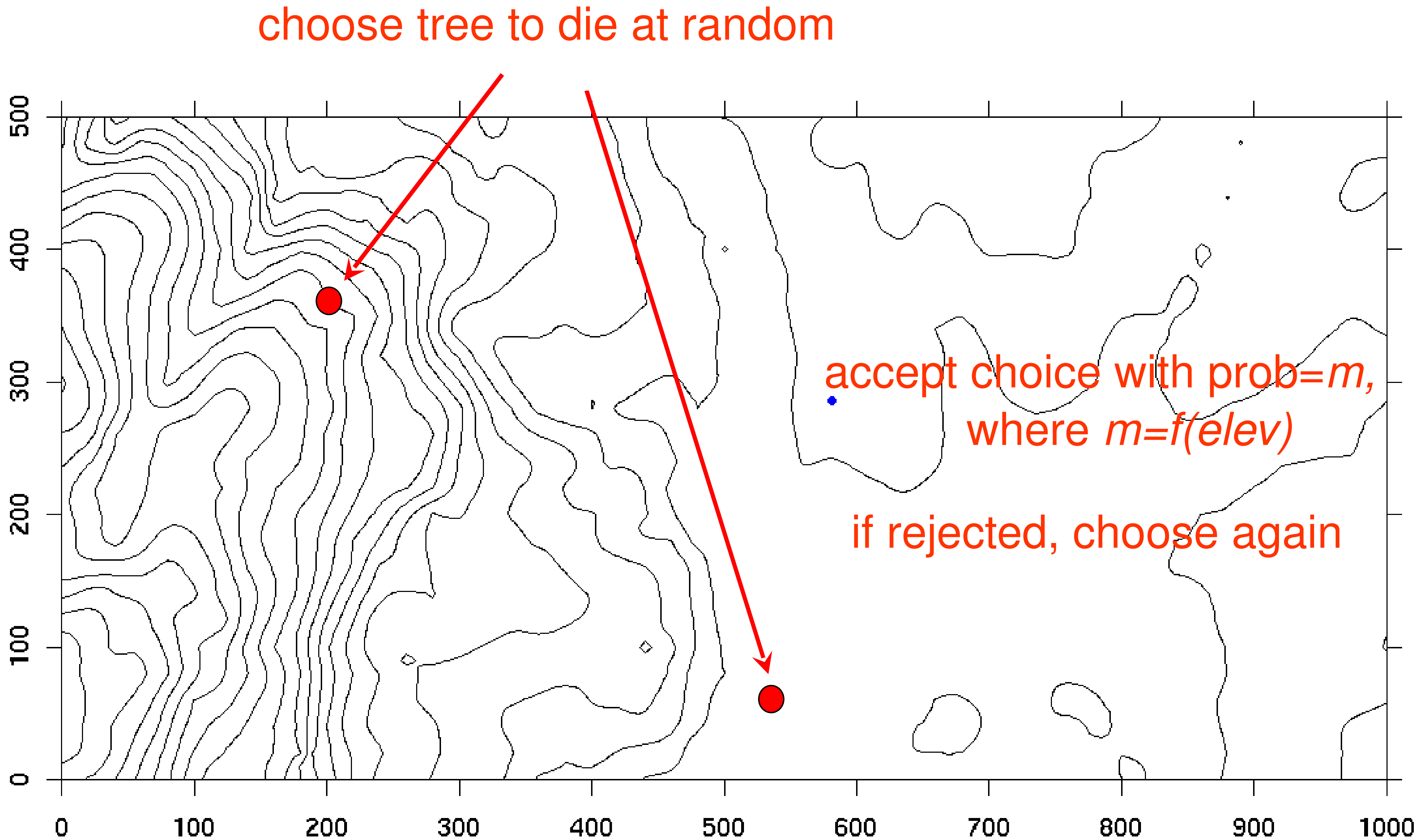
Rep. of the Congo
Rwanda
Burundi
Cabinda (Angola)
Tanzania
Seychelles
Malawi
Comoros
TIC OCEAN
Angola
Zambia
Ituri
Mozambique
Mauritius
Zimbabwe
Namibia
Madagascar
Botswana
800 Miles
Réunion (France)
Swaziland
800 Kilometers
South Africa
Lesotho
20° W
0°
20° E
40° E
60° E

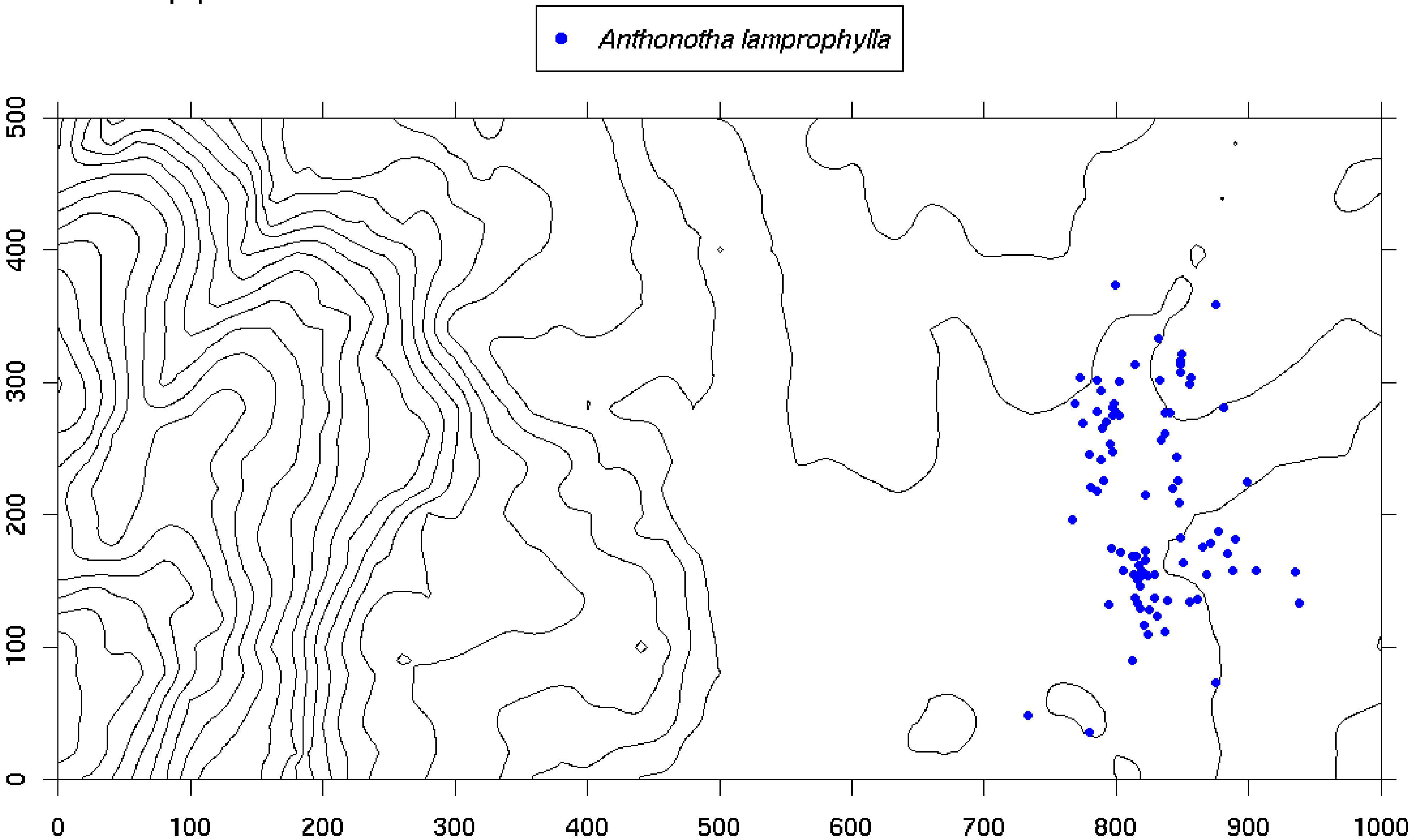
Tropical tree species abundances vary four orders of magnitude

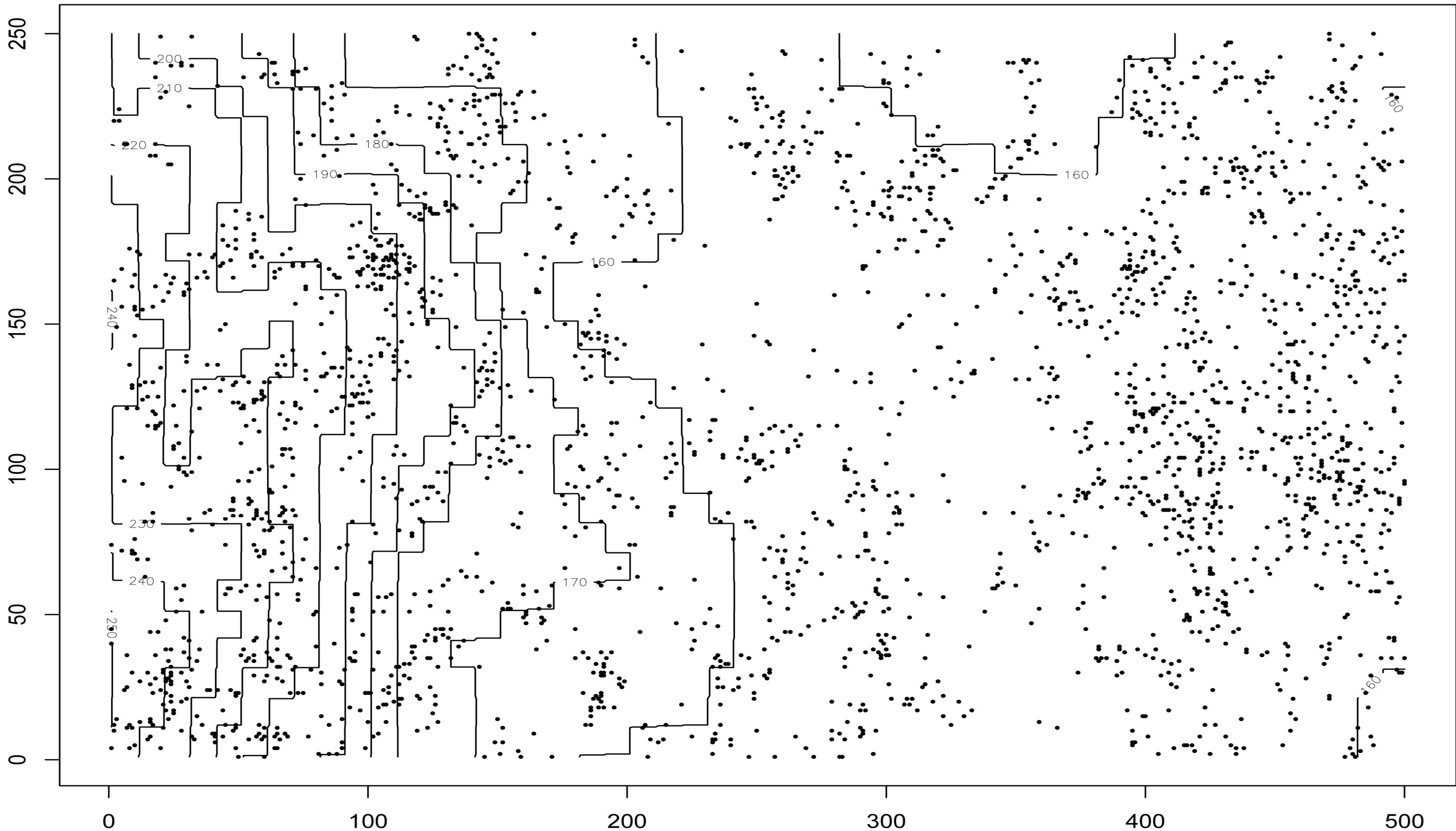
Panama:		Congo:	
BCI plot 1990 (50 ha)	N	Ituri plot 1995 (20 ha)	N
↑		↑	
Hamelia patens	1	*Rothmannia urcelliformis*	3
Hampea appendiculata	22	*Rothmannia whitfieldii*	262
Hasseltia floribunda	686	*Rungia grandis*	1
Heisteria acuminata	108	*Rytigynia dubiosa*	6
Heisteria concinna	973	*Sarcocephalus pobeguinii*	58
Herrania purpurea	528	*Scaphopetalum dewevrei*	60212
Hirtella americana	40	*Schumanniophyton magnificum*	72
Hirtella triandra	5044	*Scottellia klaineana*	412
Hura crepitans	112	*Sorindeia multifoliolata*	27
Hybanthus prunifolius	36060	*Sorindeia nitidula*	10
Hieronyma alchorneoides	88	*Spathodea campanulata*	0
↓		↓	
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
0
100
200
300
400
500
600
700
800
900
1000

Korup plot

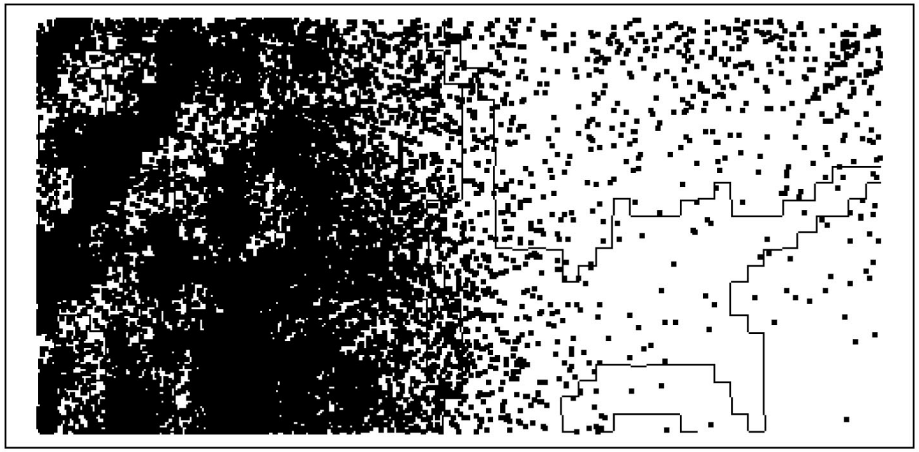

Anthonotha lamprophylla
500
400
300
200
100
0
0
100
200
300
400
500
600
700
800
900
1000



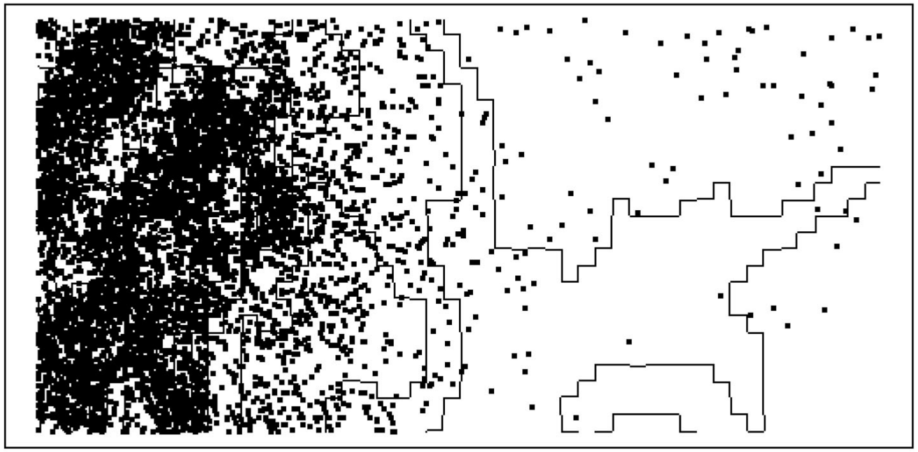
250
200
150
100
50
0
0
100
200
300
400
500
200
210
220
180
190
160
160
160
240
230
240
250
170
160

Simulated species distributions with niche differences
plus speciation

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

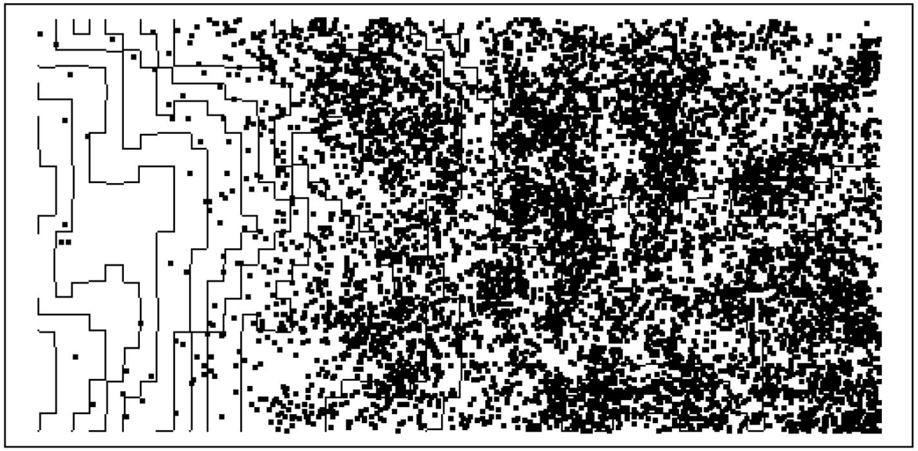


x1



x2

44 unique niche responses, 10 most abundant species all have one of these 4



x3

x4

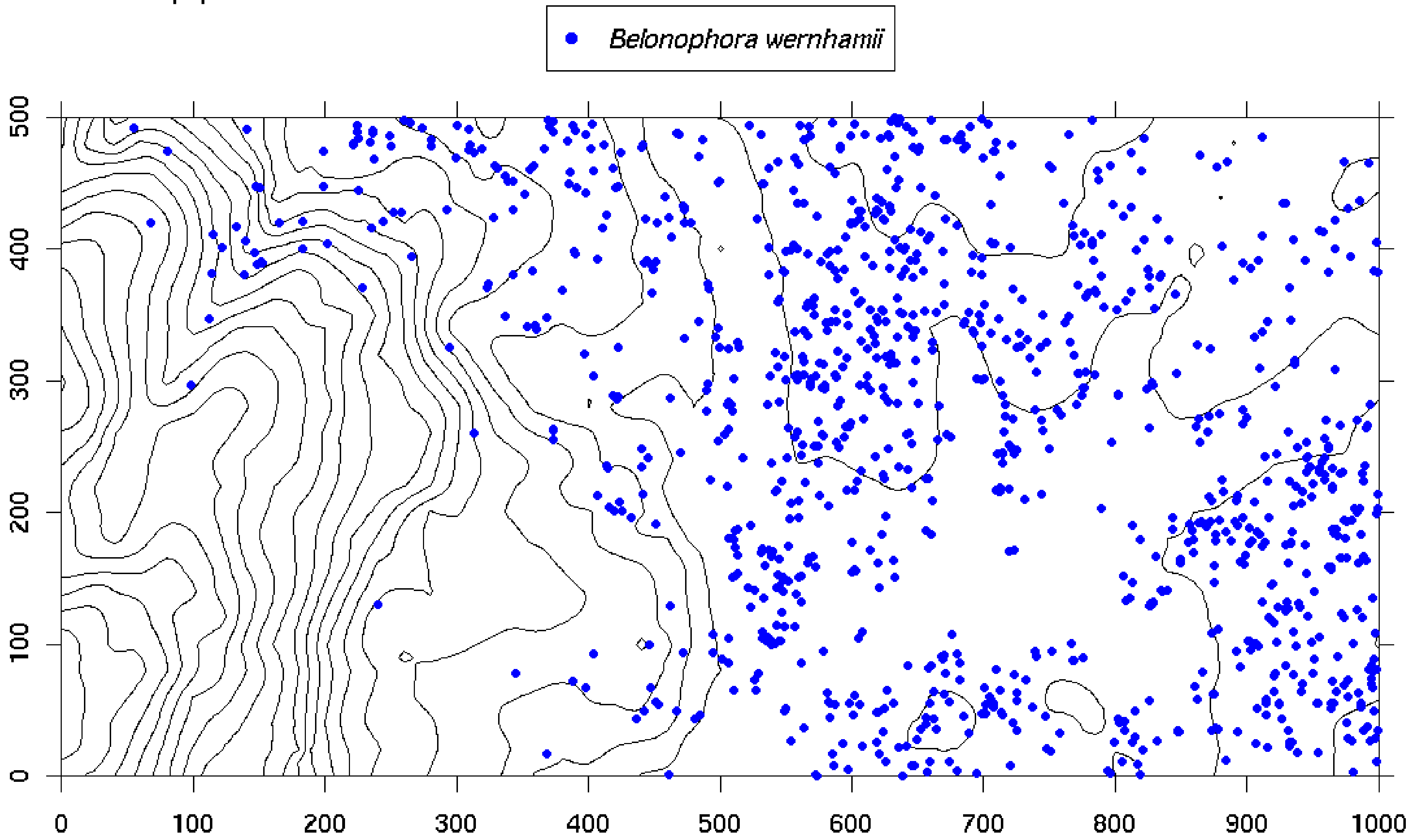
Summary: Abundances and the neutral theory

Neutral theory predicts abundance distribution correctly ...

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

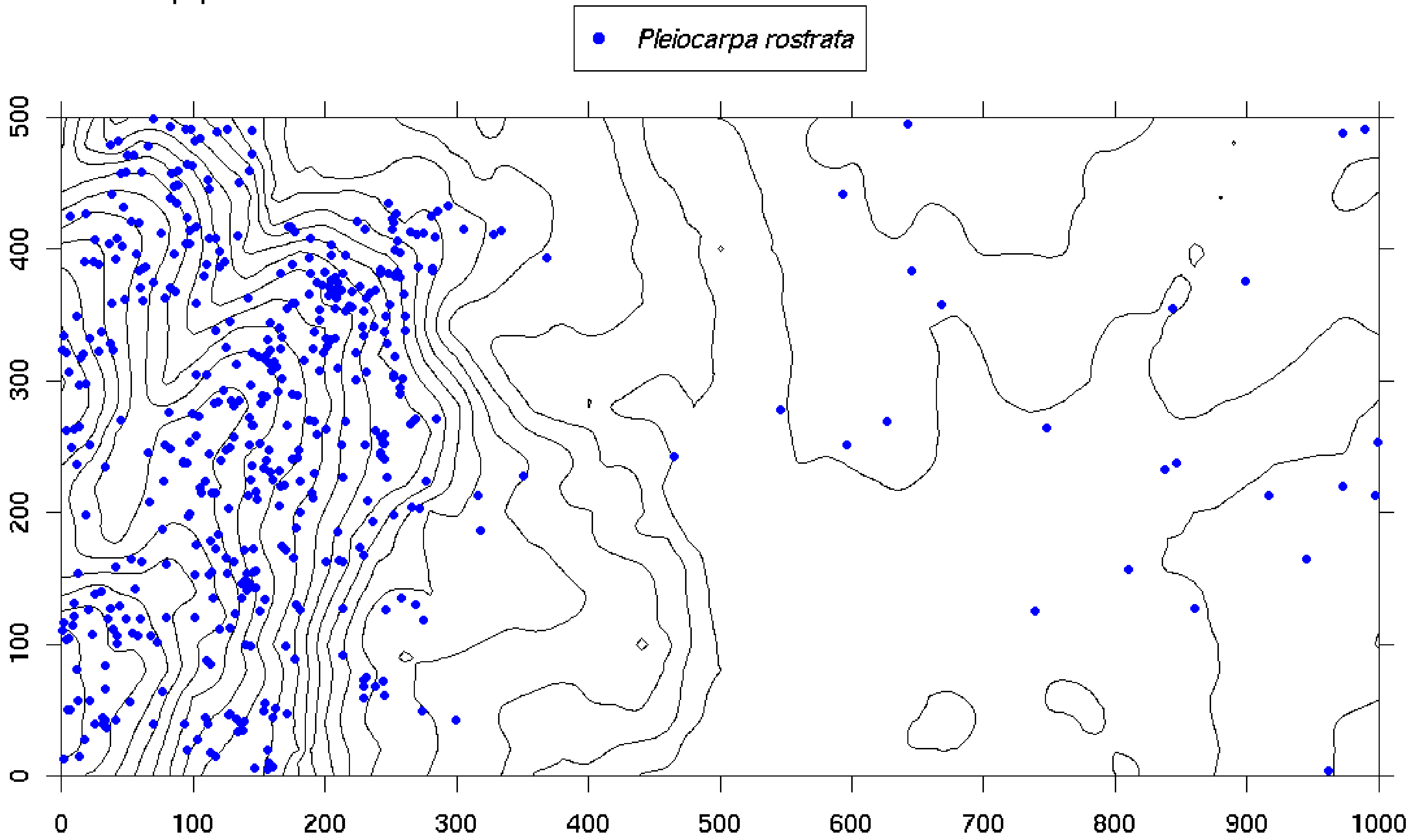
Nevertheless, species differences may sometimes be irrelevant in understanding abundances because of dominating influence of species turnover

Korup plot



Belonophora wernhamii
0
100
200
300
400
500
600
700
800
900
1000

Korup plot



Pleiocarpa rostrata
500
400
300
200
100
0
0
100
200
300
400
500
600
700
800
900
1000

Resource competition

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

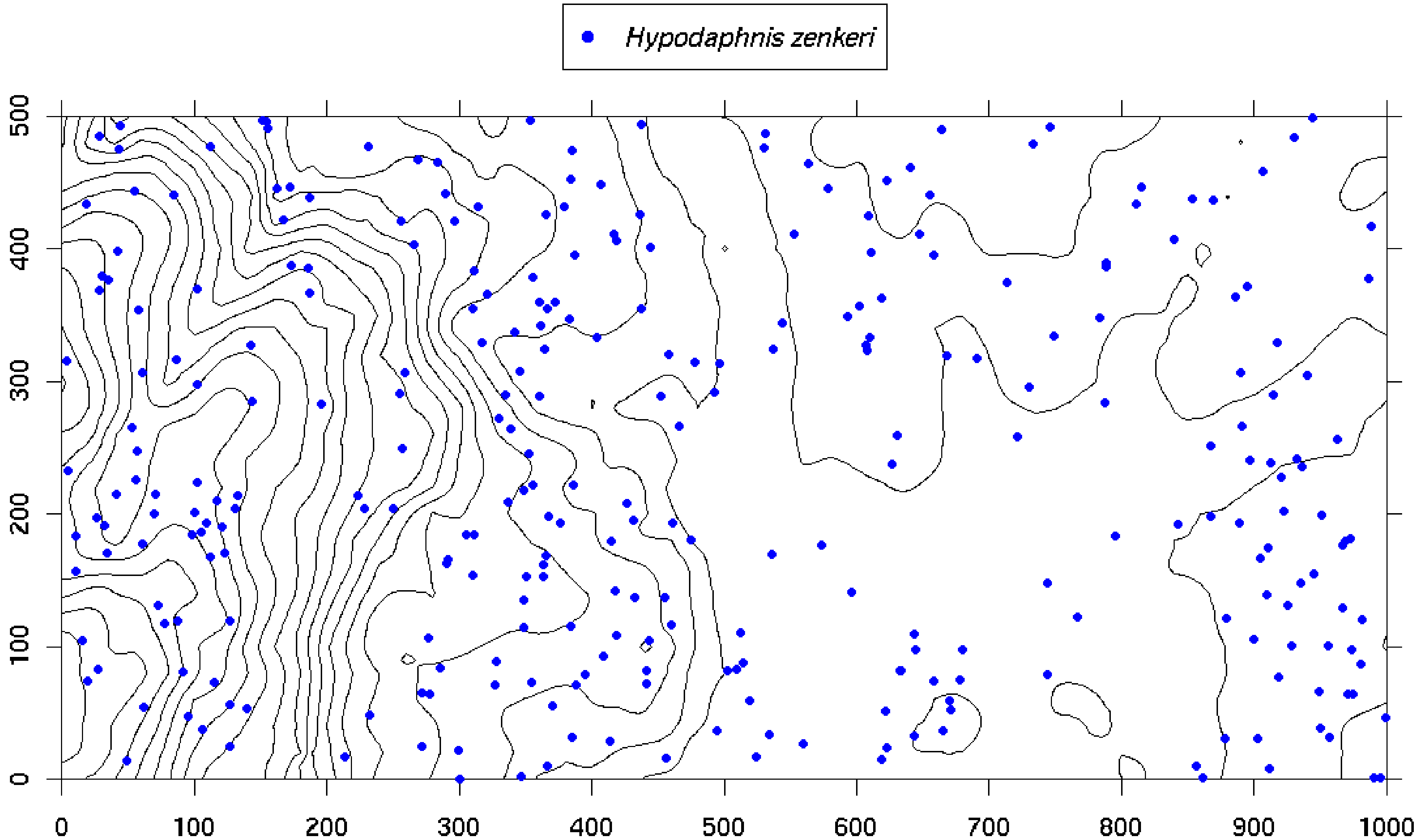
$$\hat{r}_i = b_i(k_i - \rho k_s)$$

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

equalizing stabilizing

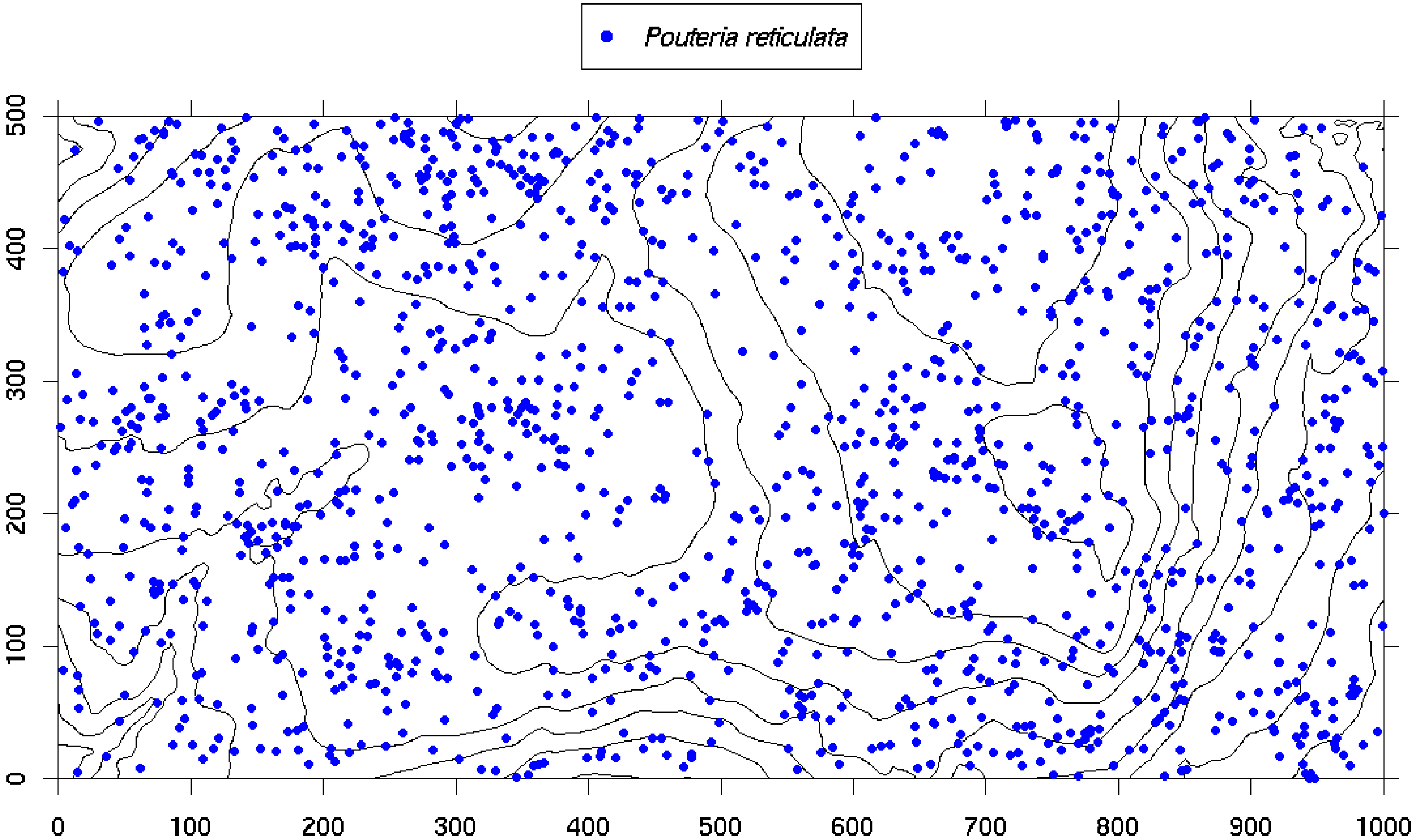
k average fitness, *i* invader and *s* resident

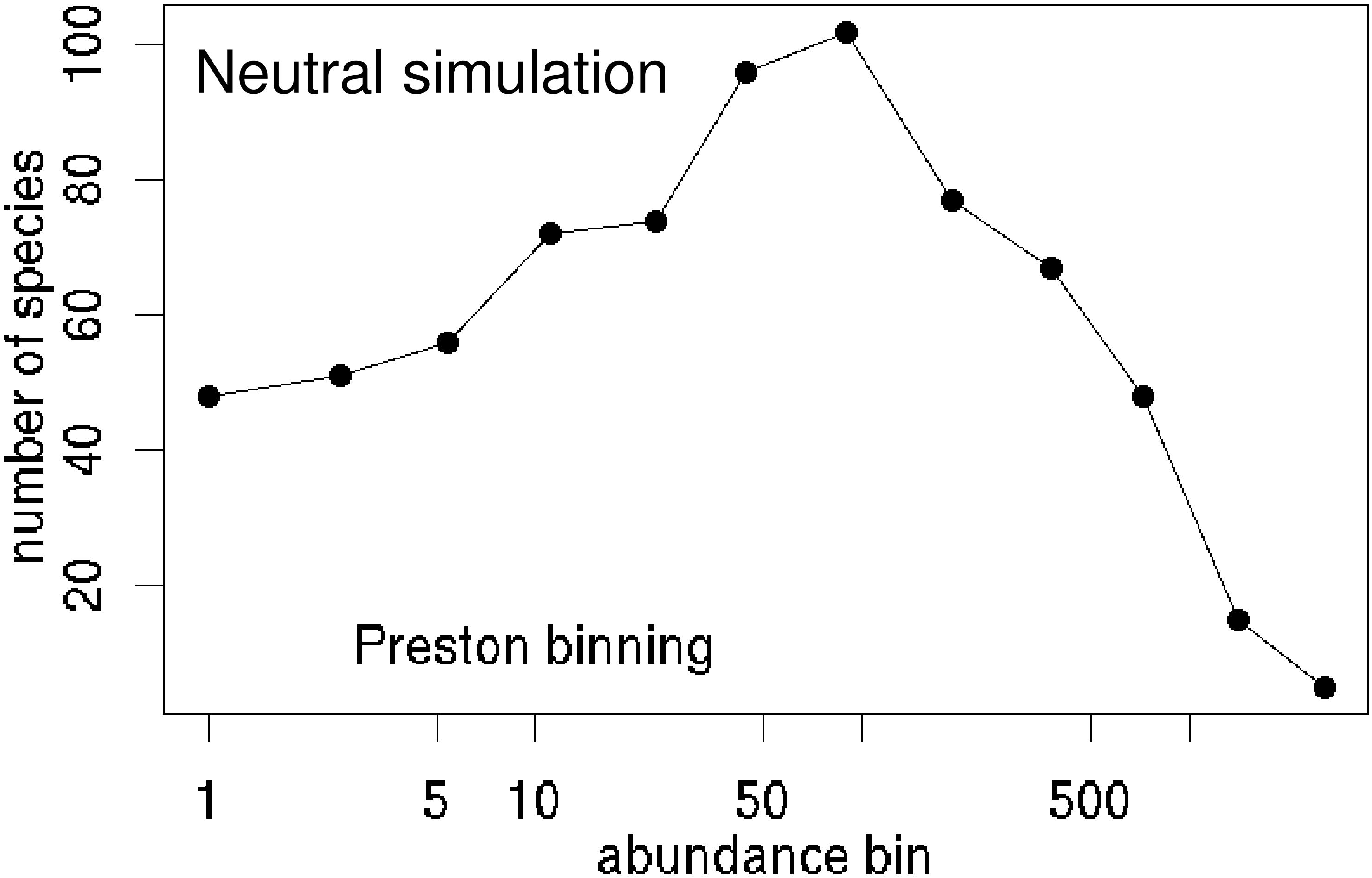
ρ resource overlap

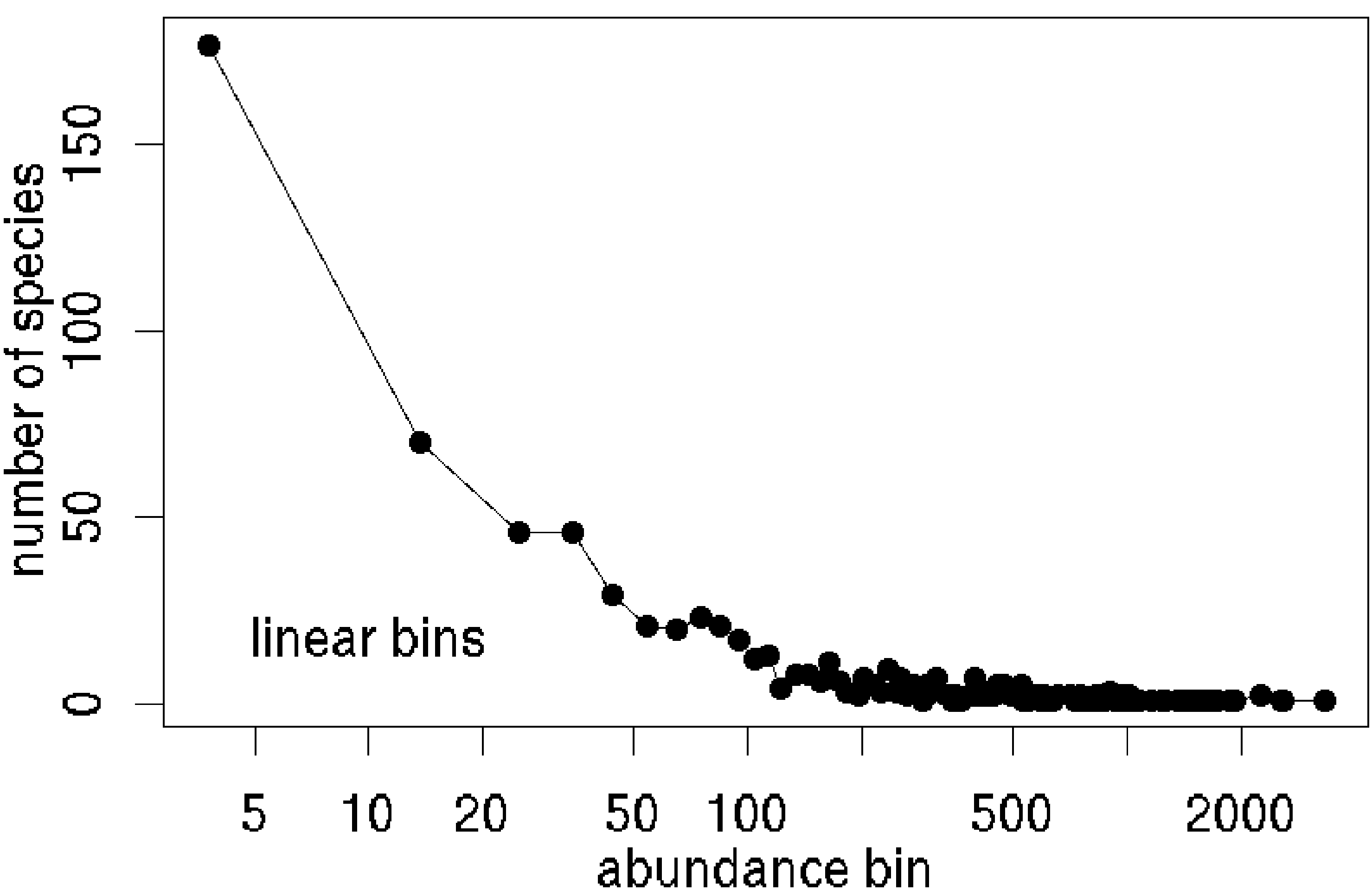


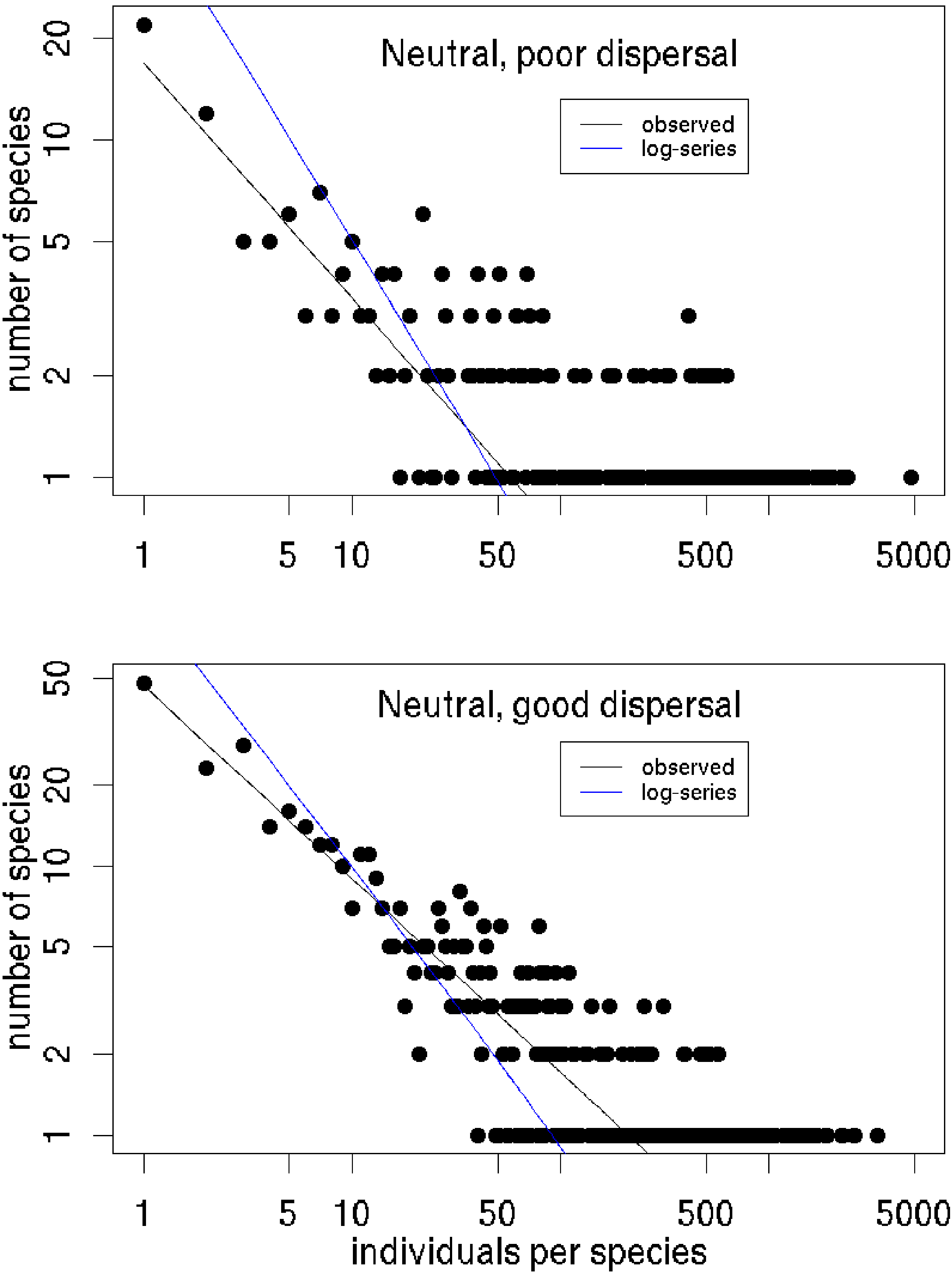
Hypodaphnis zenkeri
500
400
300
200
100
0
0
100
200
300
400
500
600
700
800
900
1000

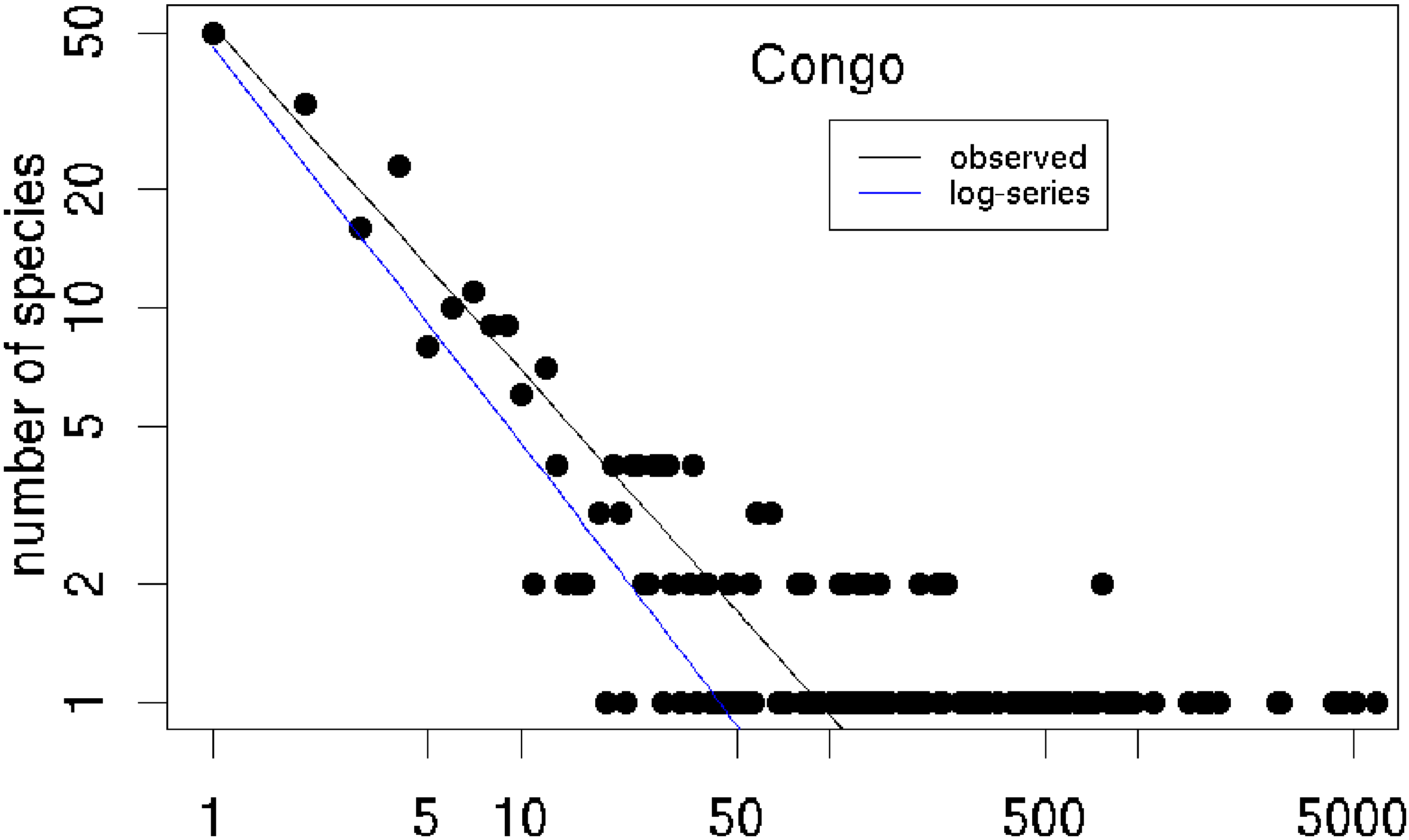
Barro Colorado plot

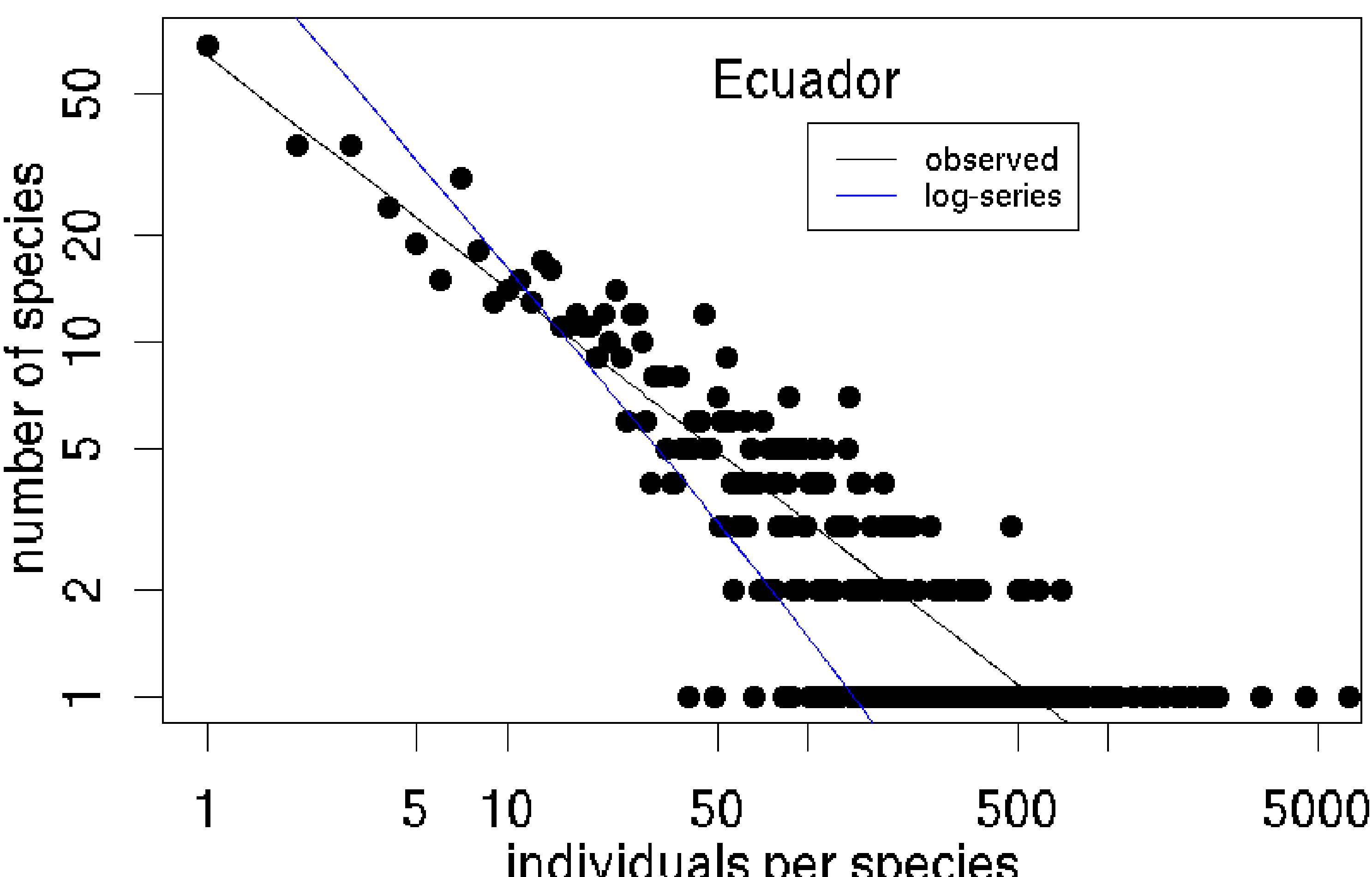


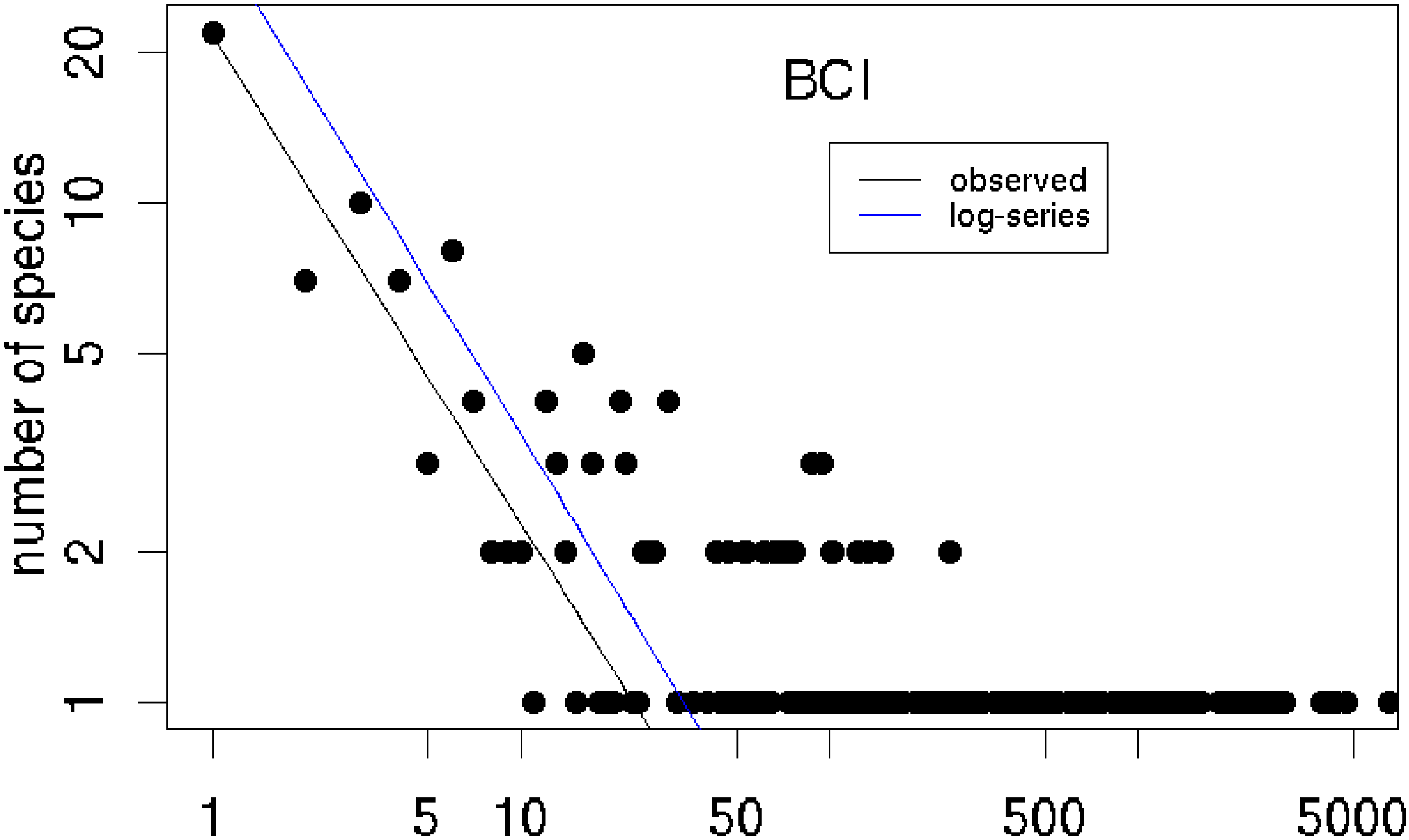

Neutral simulation
Preston binning
number of species
abundance bin
20
40
60
80
100
1
5
10
50
500

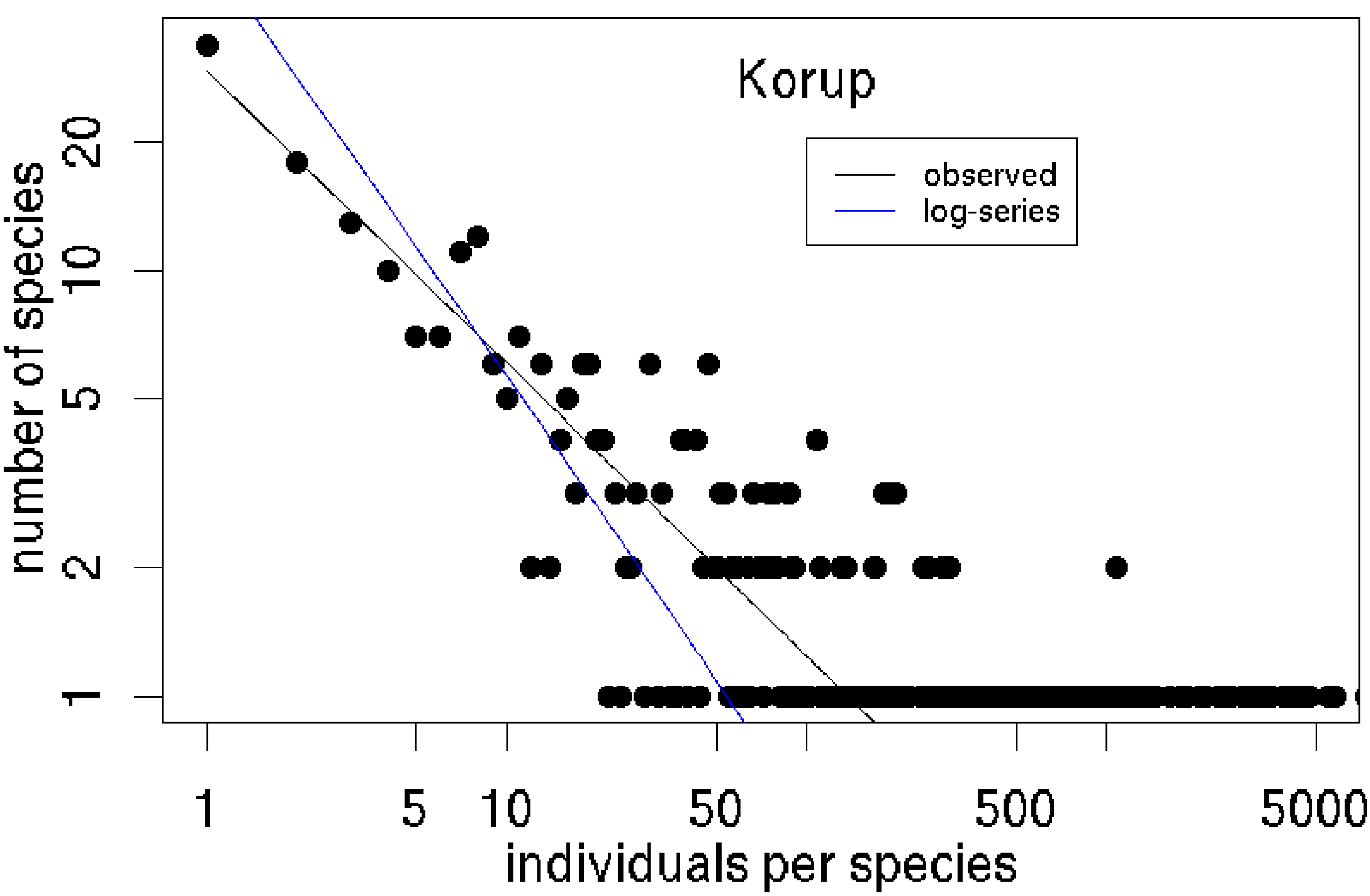

linear bins
number of species
abundance bin
0
50
100
150
5
10
20
50
100
500
2000

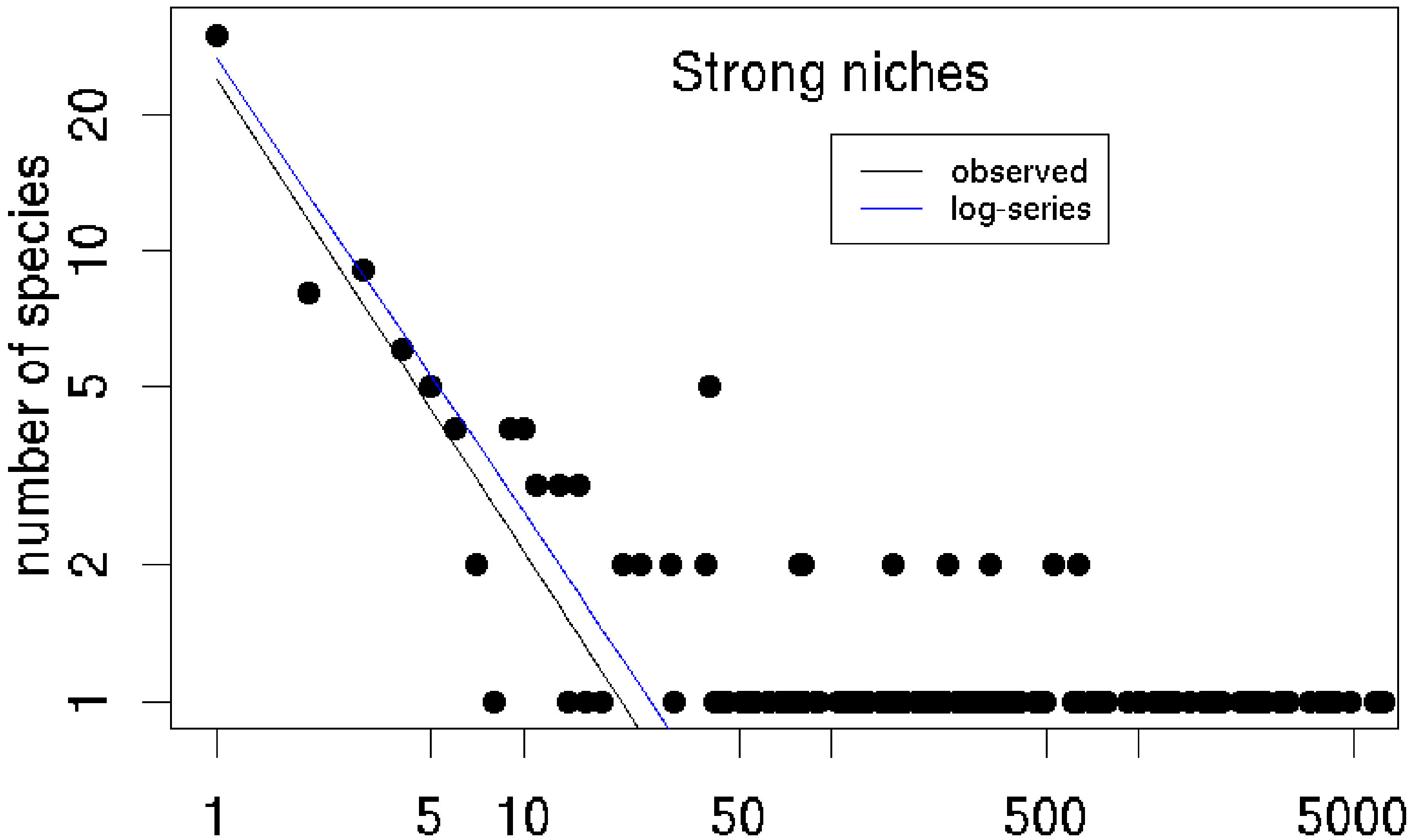

Neutral, poor dispersal
observed
log-series
number of species
20
10
5
2
1
1
5
10
50
500
5000
Neutral, good dispersal
observed
log-series
number of species
50
20
10
5
2
1
1
5
10
50
500
5000
individuals per species


Congo
observed
log-series
number of species
50
20
10
5
2
1
1
5
10
50
500
5000

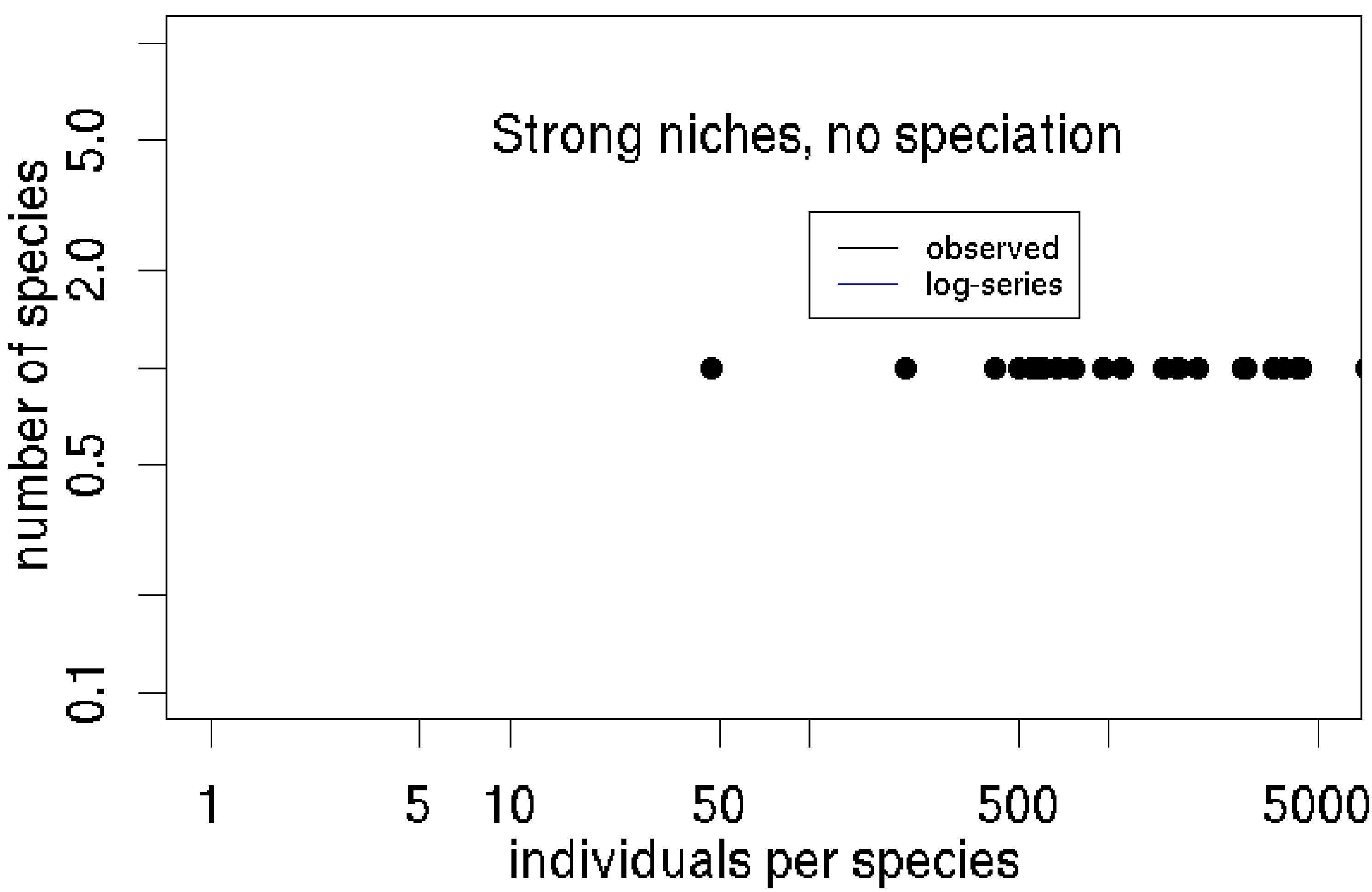

Ecuador
observed
log-series
number of species
50
20
10
5
2
1
1
5
10
50
500
5000
individuals per species


BCI
observed
log-series
number of species
20
10
5
2
1
1
5
10
50
500
5000

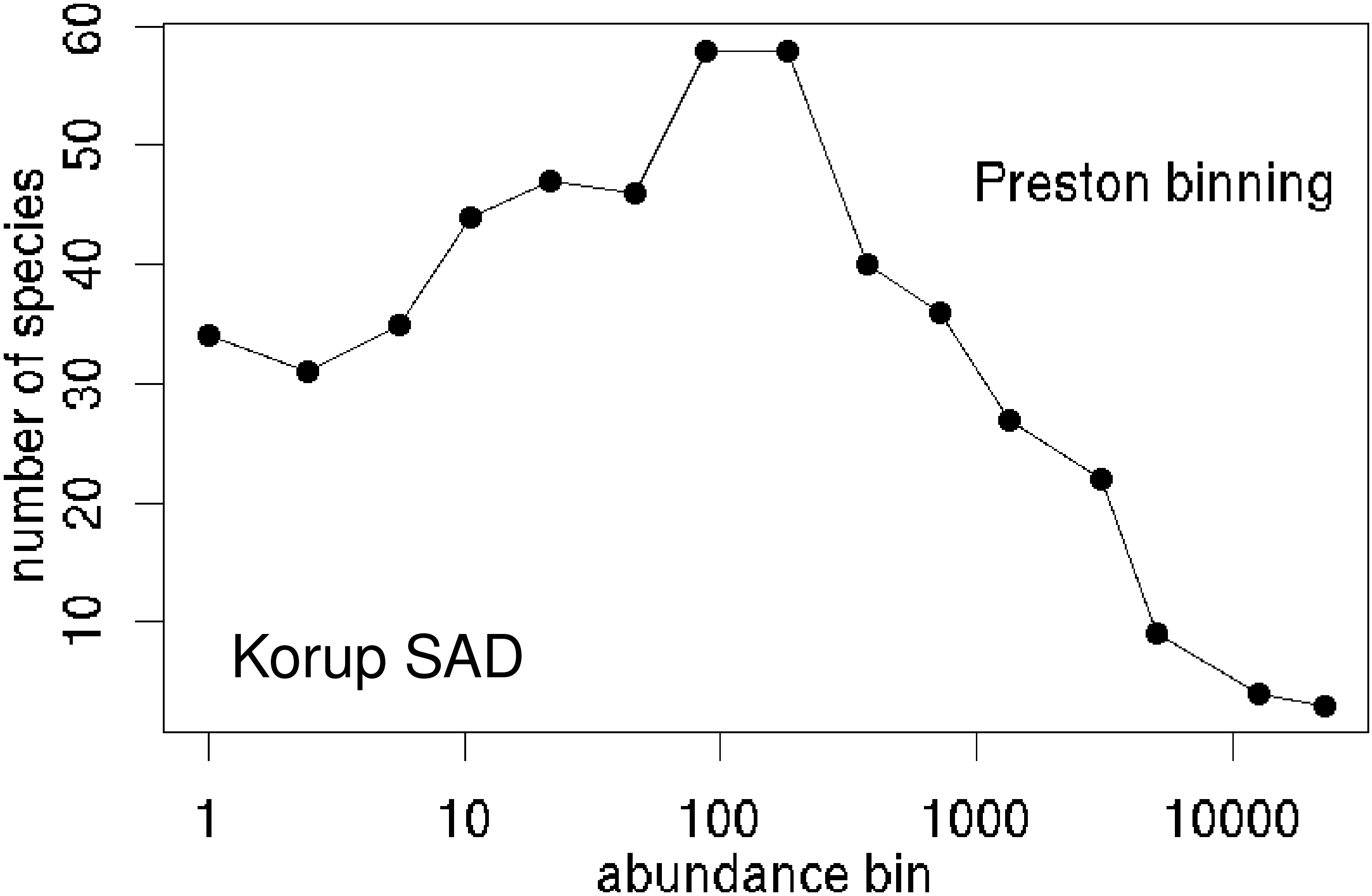

Korup
observed
log-series
number of species
20
10
5
2
1
1
5
10
50
500
5000
individuals per species

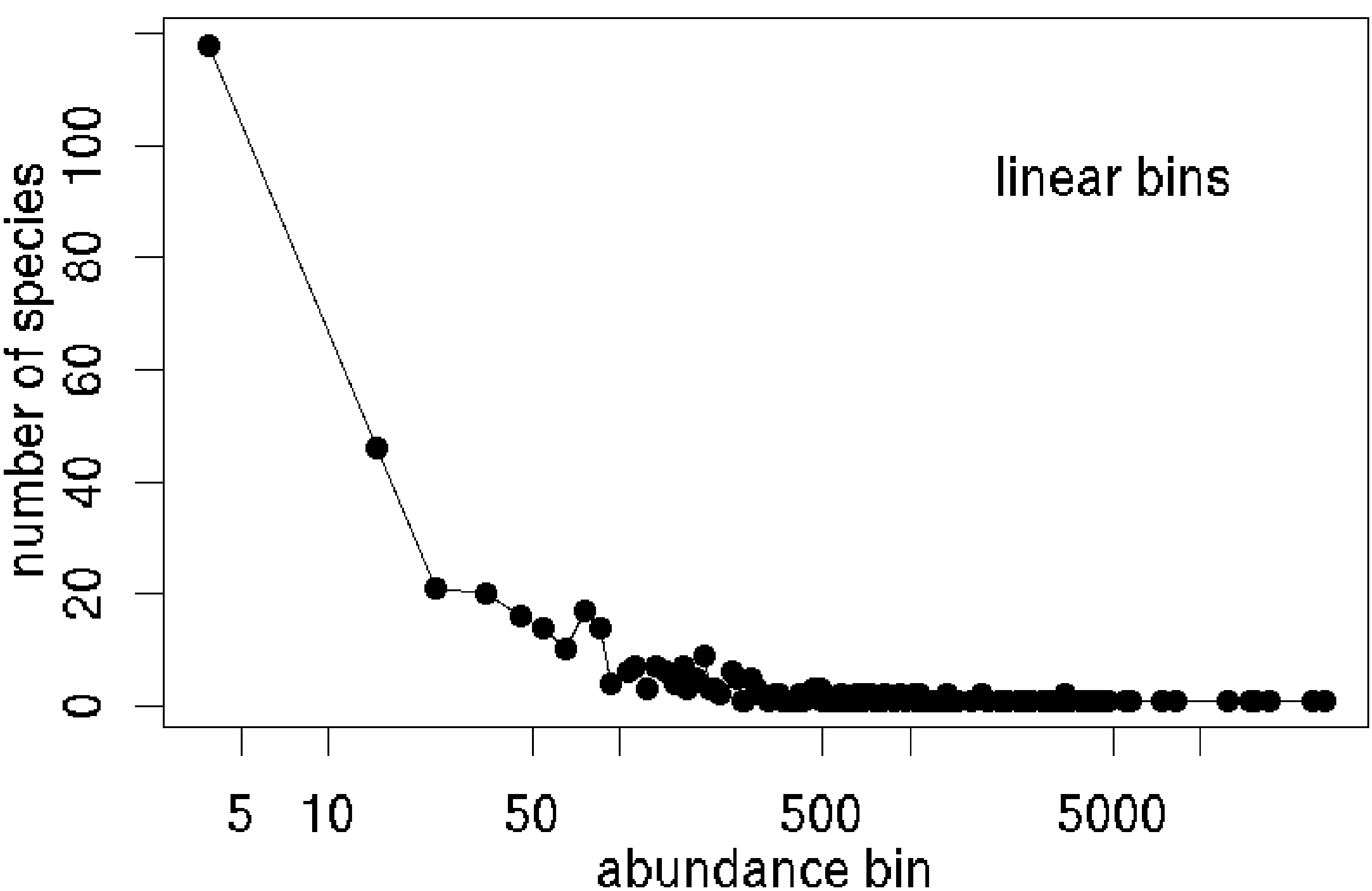


Strong niches
observed
log-series
number of species
1
2
5
10
20
1
5
10
50
500
5000



Strong niches, no speciation
observed
log-series
number of species
0.1
0.5
2.0
5.0
1
5
10
50
500
5000
individuals per species


Preston binning
Korup SAD
number of species
abundance bin
0
10
20
30
40
50
60
1
10
100
1000
10000


linear bins
number of species
abundance bin
0
20
40
60
80
100
5
10
50
500
5000