

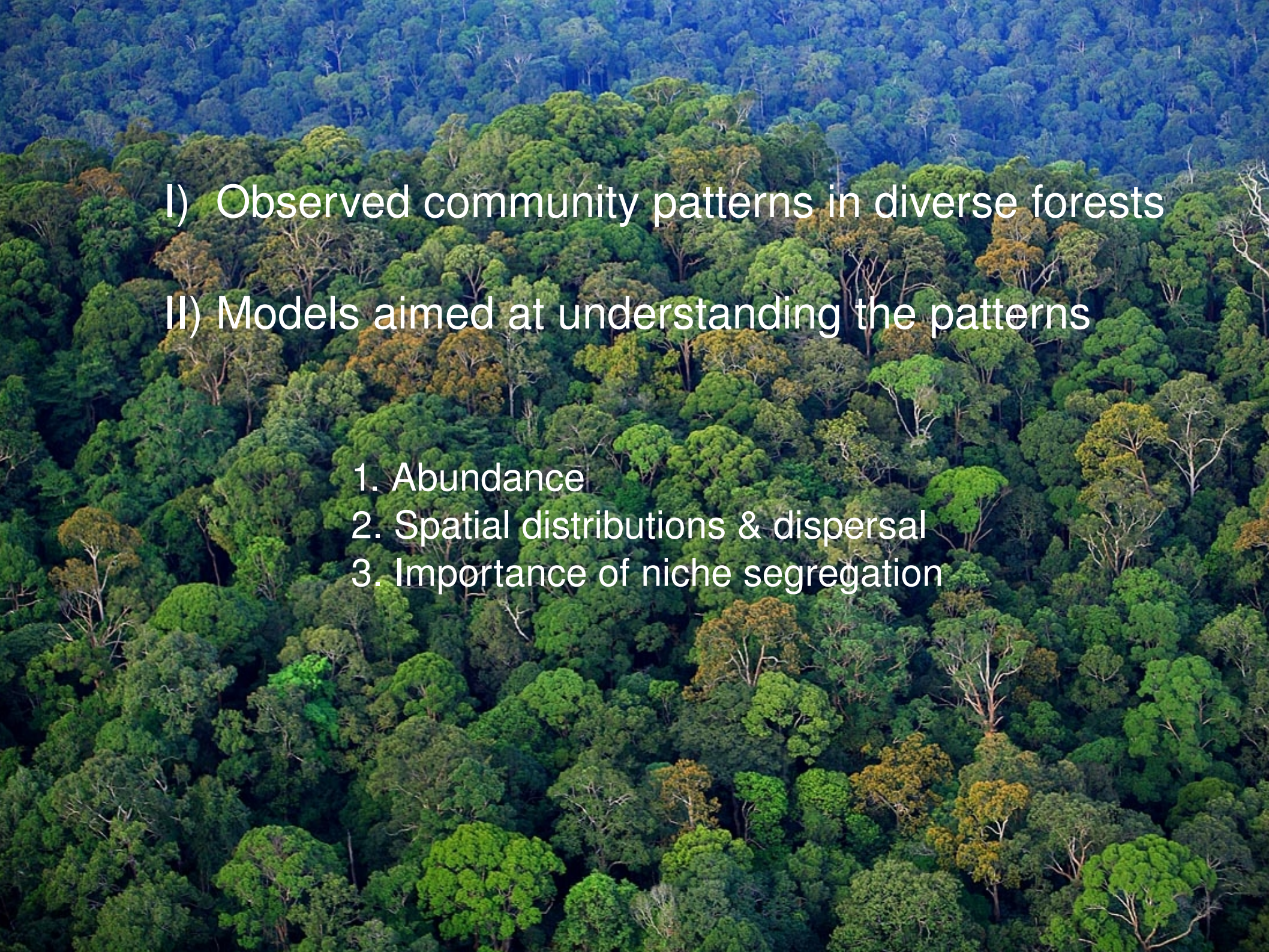
Distribution, abundance, and coexistence in stochastic communities

Modeling abundances and distributions in diverse communities
based on individual biology: birth, death, dispersal

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Panama

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Ecology, Evolution, Behavior
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- 
- An aerial photograph of a vast, dense tropical rainforest. The canopy is thick and multi-layered, with a variety of green shades from deep forest green to bright, sunlit yellow-green. Some taller trees with lighter-colored trunks are visible, rising above the main canopy. The overall impression is one of immense biodiversity and scale.
- I) Observed community patterns in diverse forests
 - II) Models aimed at understanding the patterns



I) Observed community patterns in diverse forests

II) Models aimed at understanding the patterns

1. Abundance

2. Spatial distributions & dispersal

3. Importance of niche segregation

Global Forest Observatory Network (GFON)

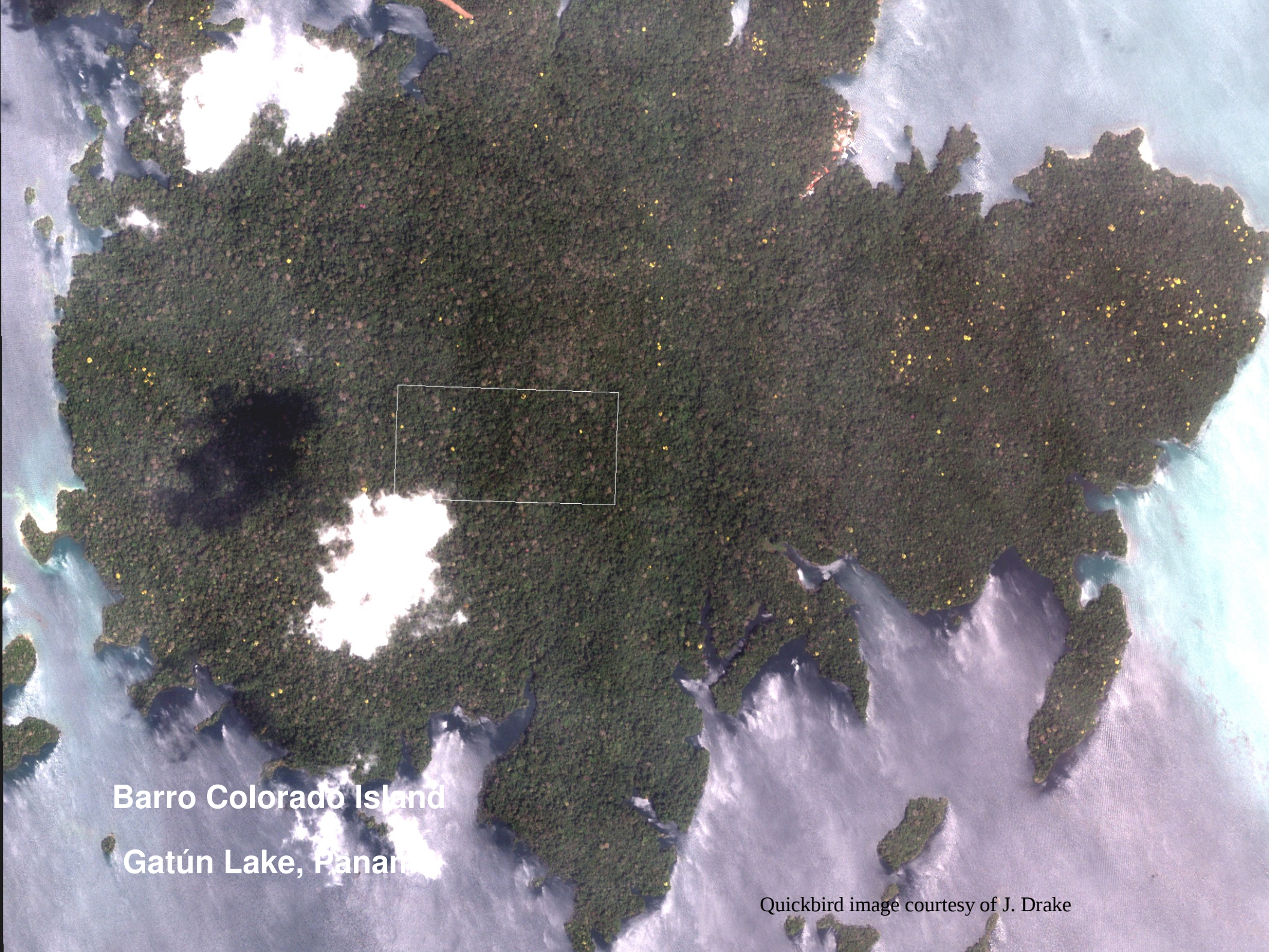
~8,000 species
3.323 million trees monitored currently



Species diversity

	species ≥ 1 cm dbh	annual rainfall (mm)	dry season (months)
Panama, BCI	274	2500	4
Ecuador, Yasuni	1104	3000	0
Colombia, La Planada	241	3500	0
Puerto Rico, Luquillo *	120	3500	0
India, Mudumalai	66	1200	6
Thailand, HKK	206	1450	6
Thailand, Kao Chong	660	1600	2
Malaysia, Pasoh	785	1800	0
Malaysia, Lambir	1111	2700	0
Sri Lanka, Sinharaja	205	4400	0
China, Xishuangbanna *	470	2500	0
China, Changbaishan	52	1000	(winter)
Cameroon, Korup	482	5000	2
D.R. Congo, Ituri			
--monodominant *	403	1700	2
--mixed *	409	1700	2

* species in exactly 25 hectares unless noted with asterisk (16-20 ha)



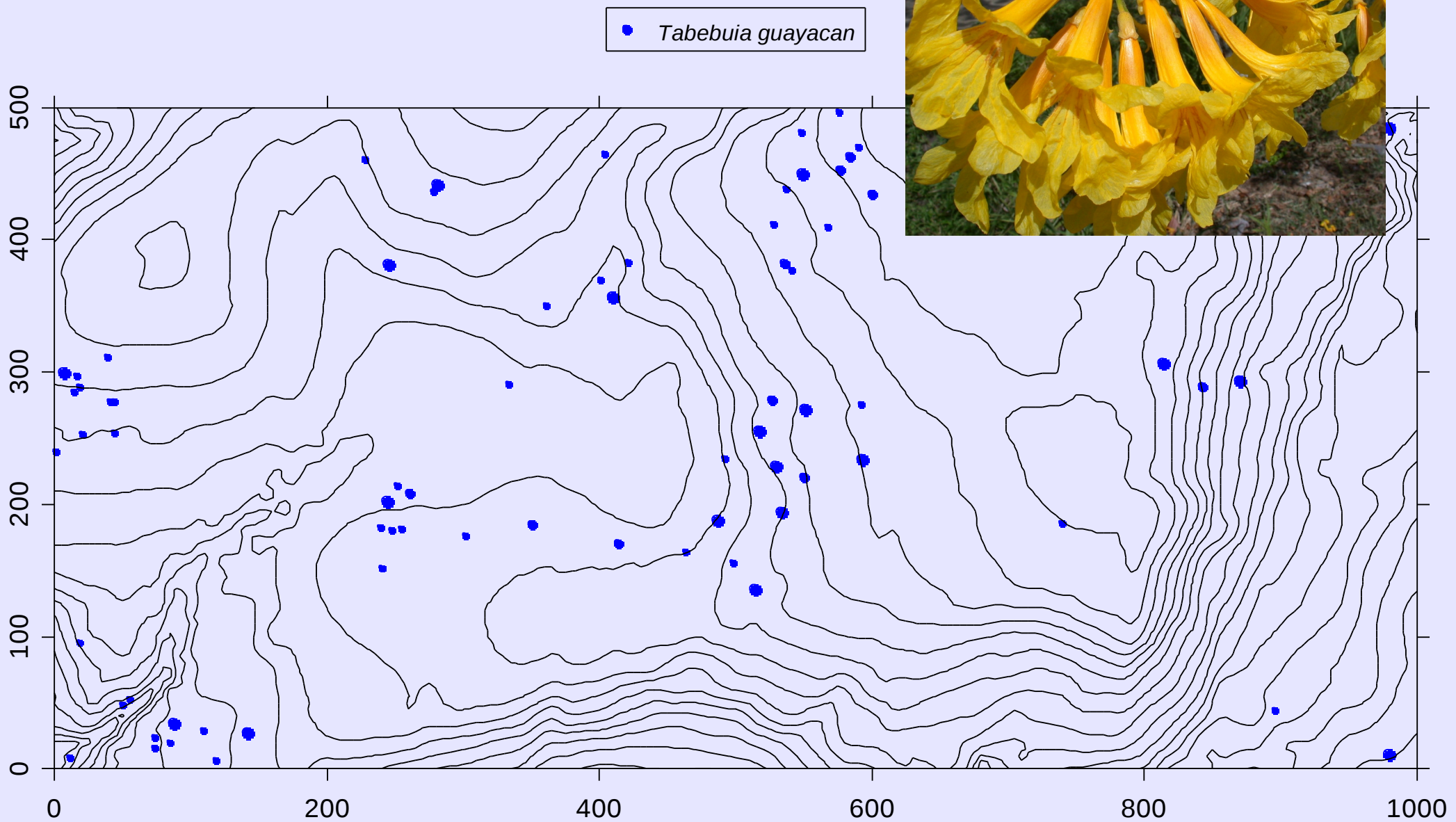
Barro Colorado Island

Gatún Lake, Panama

Quickbird image courtesy of J. Drake

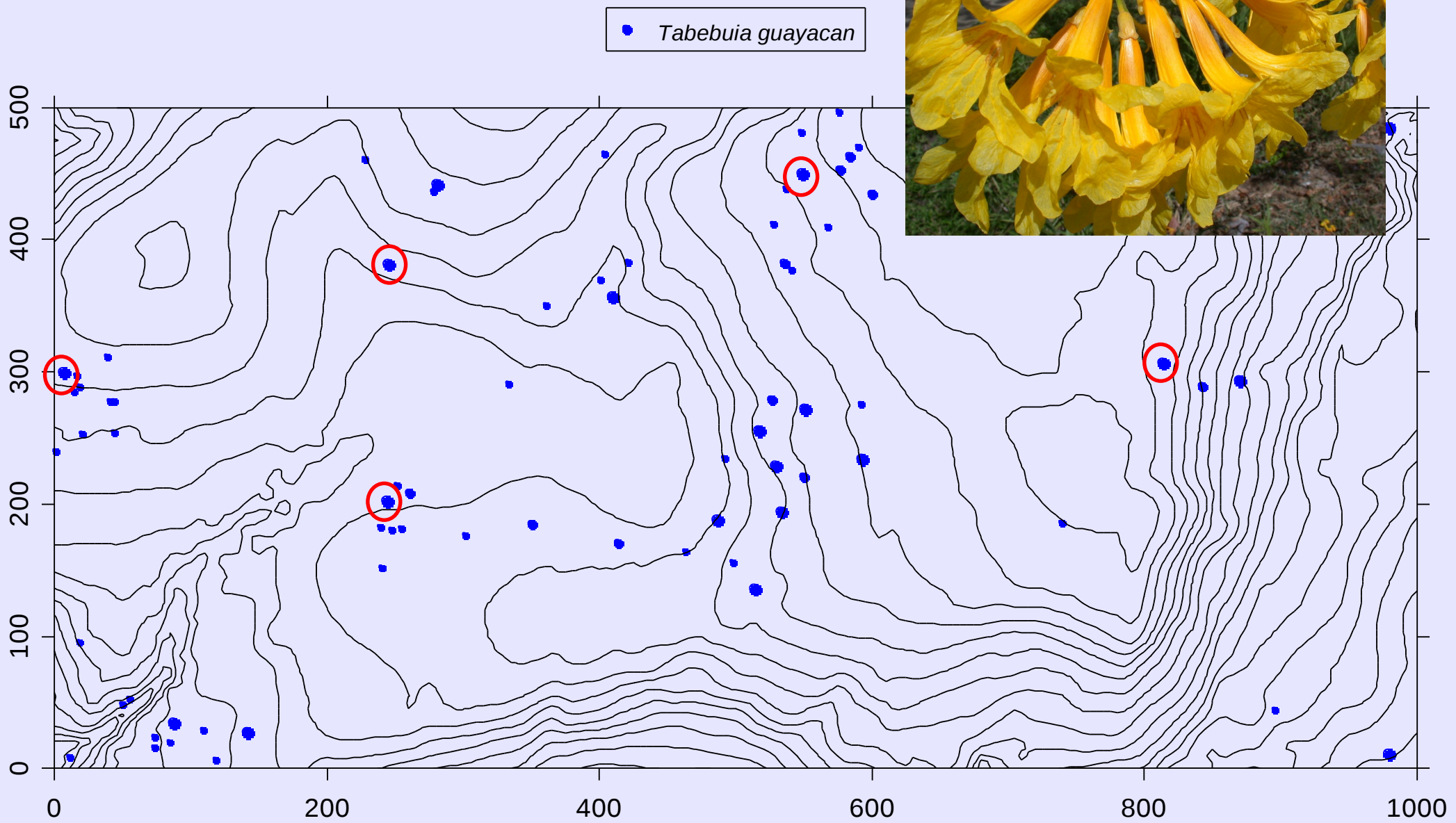
Barro Colorado 50 ha plot (Panama)

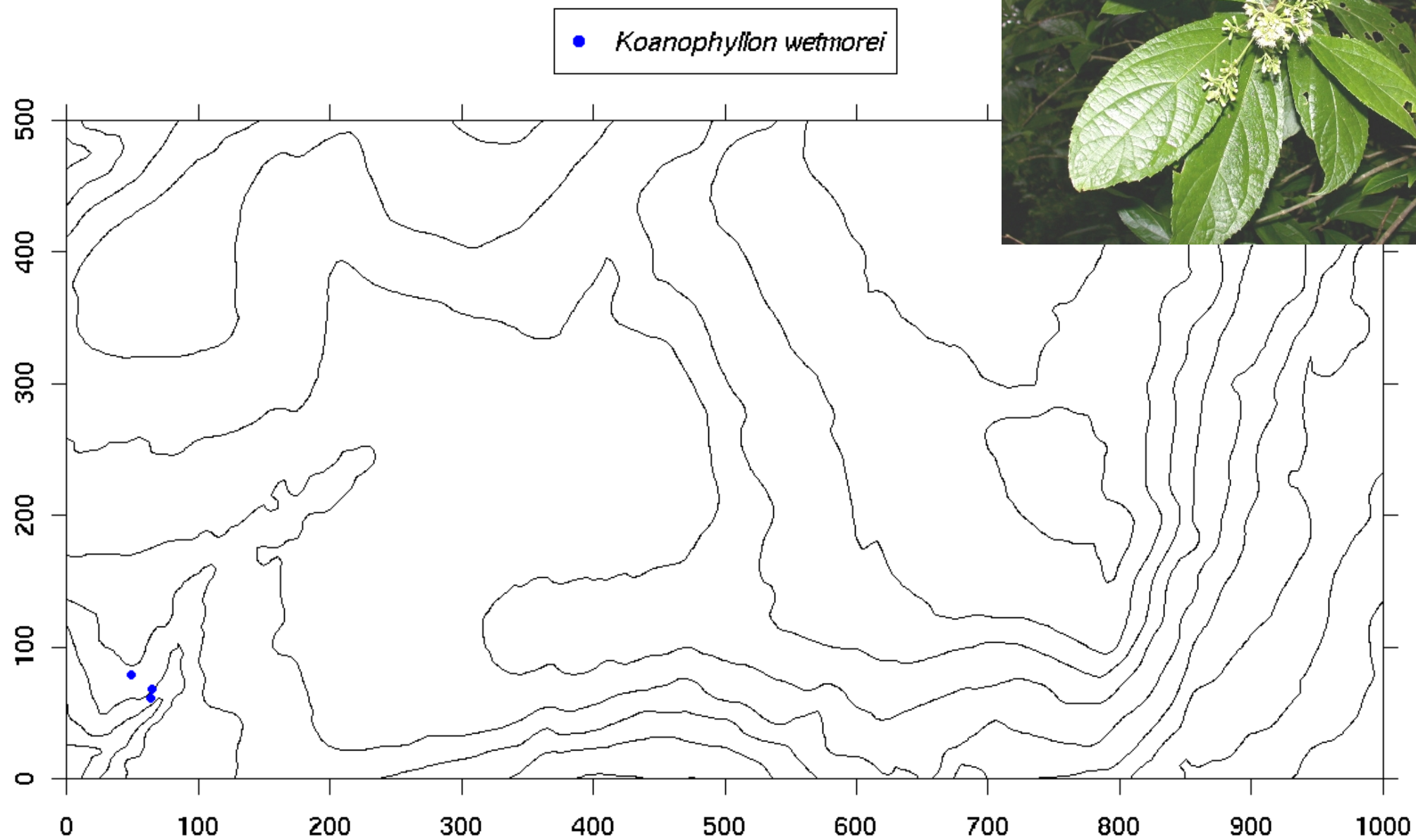
301 species, 213000 individuals in full census ≥ 1 cm dbh

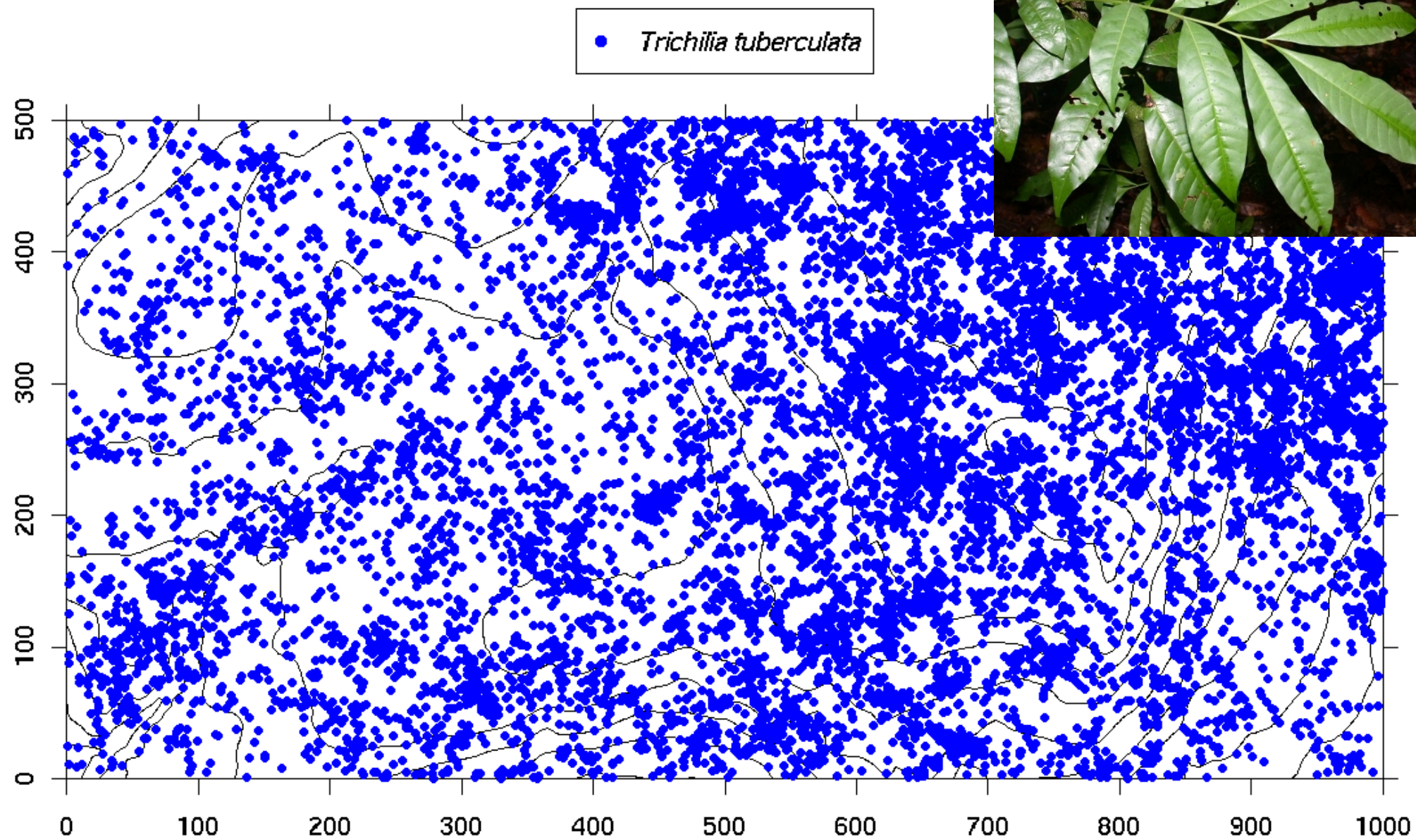


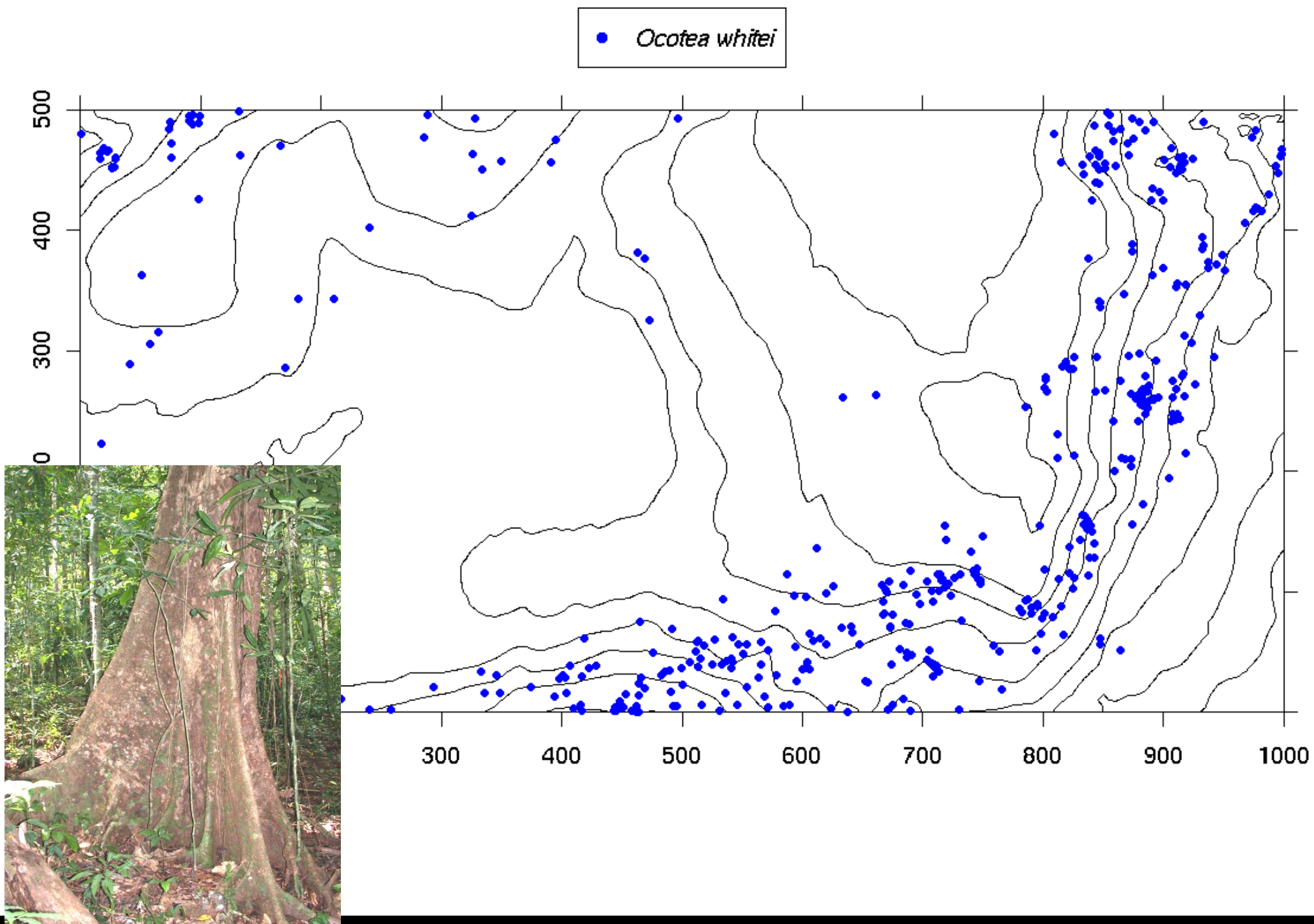
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301 species, 213000 individuals in full census ≥ 1 cm dbh

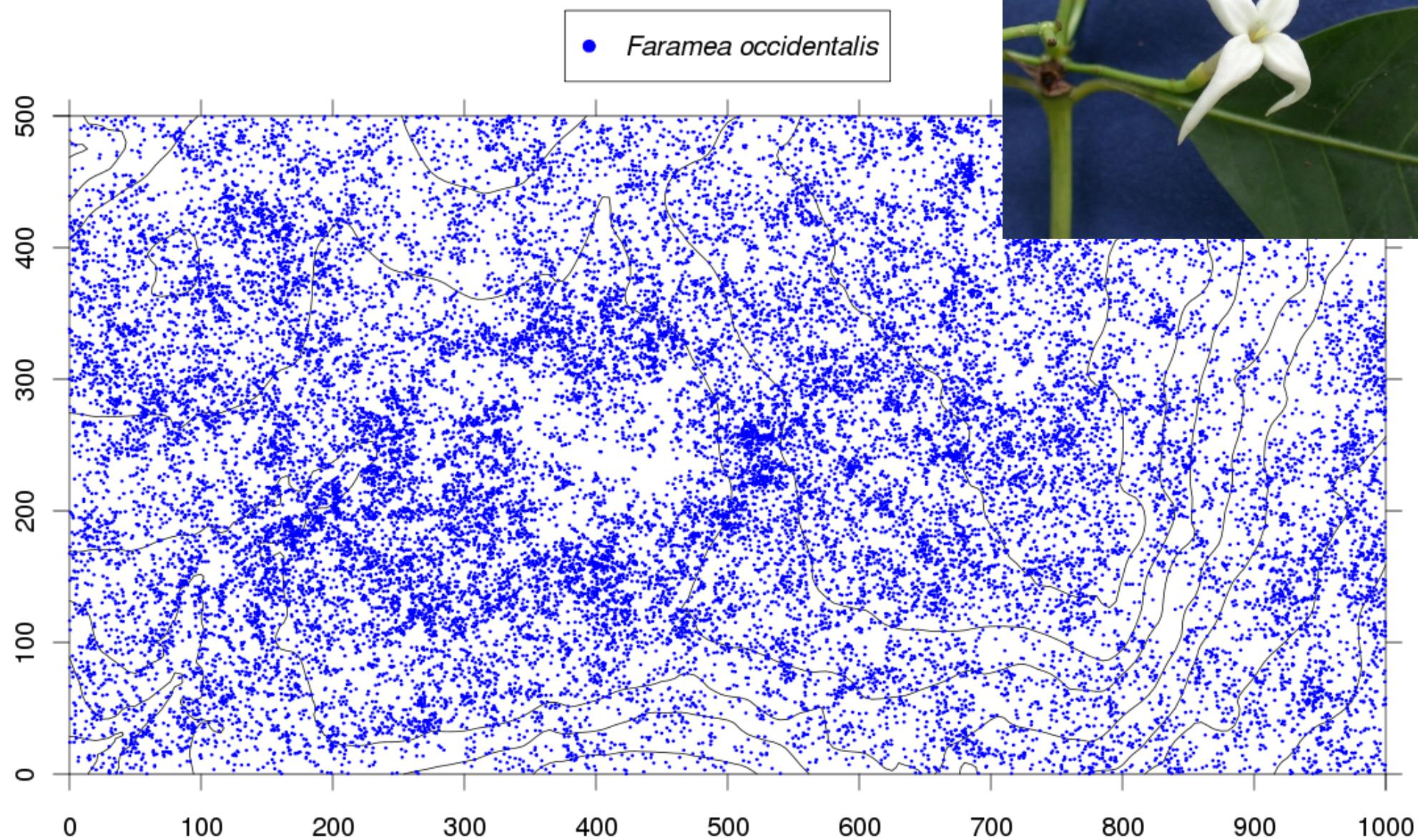




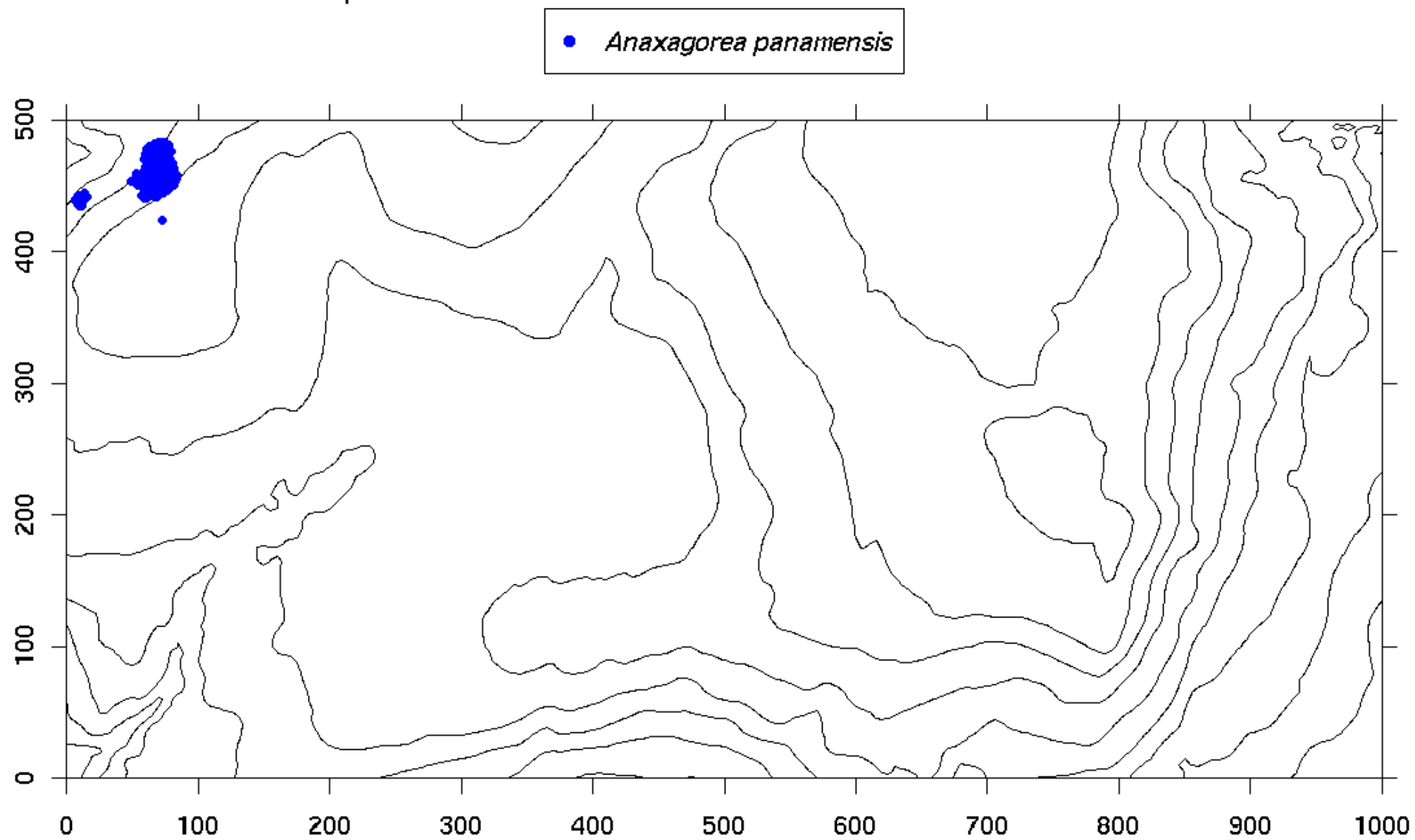




Barro Colorado plot



Barro Colorado plot

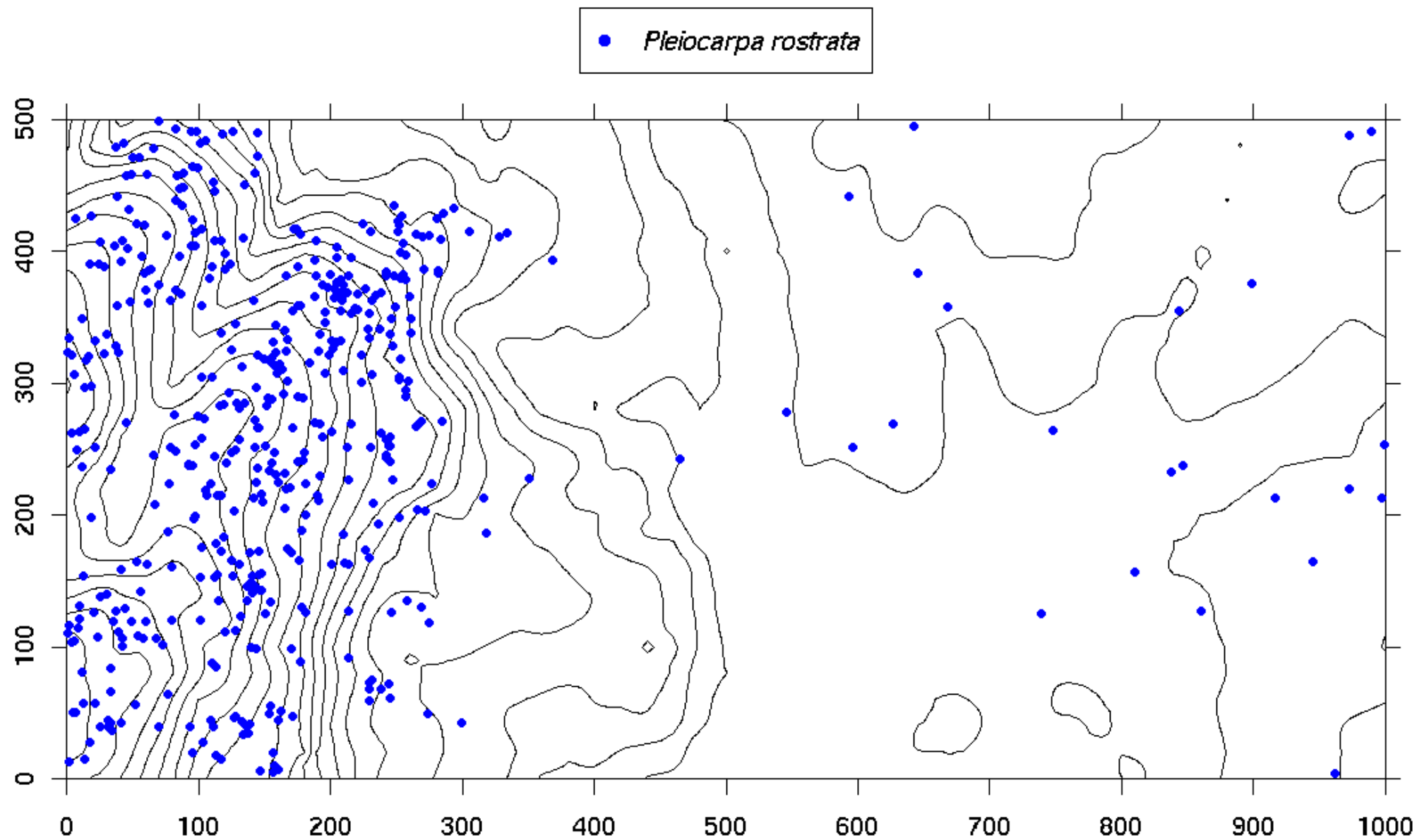


Africa

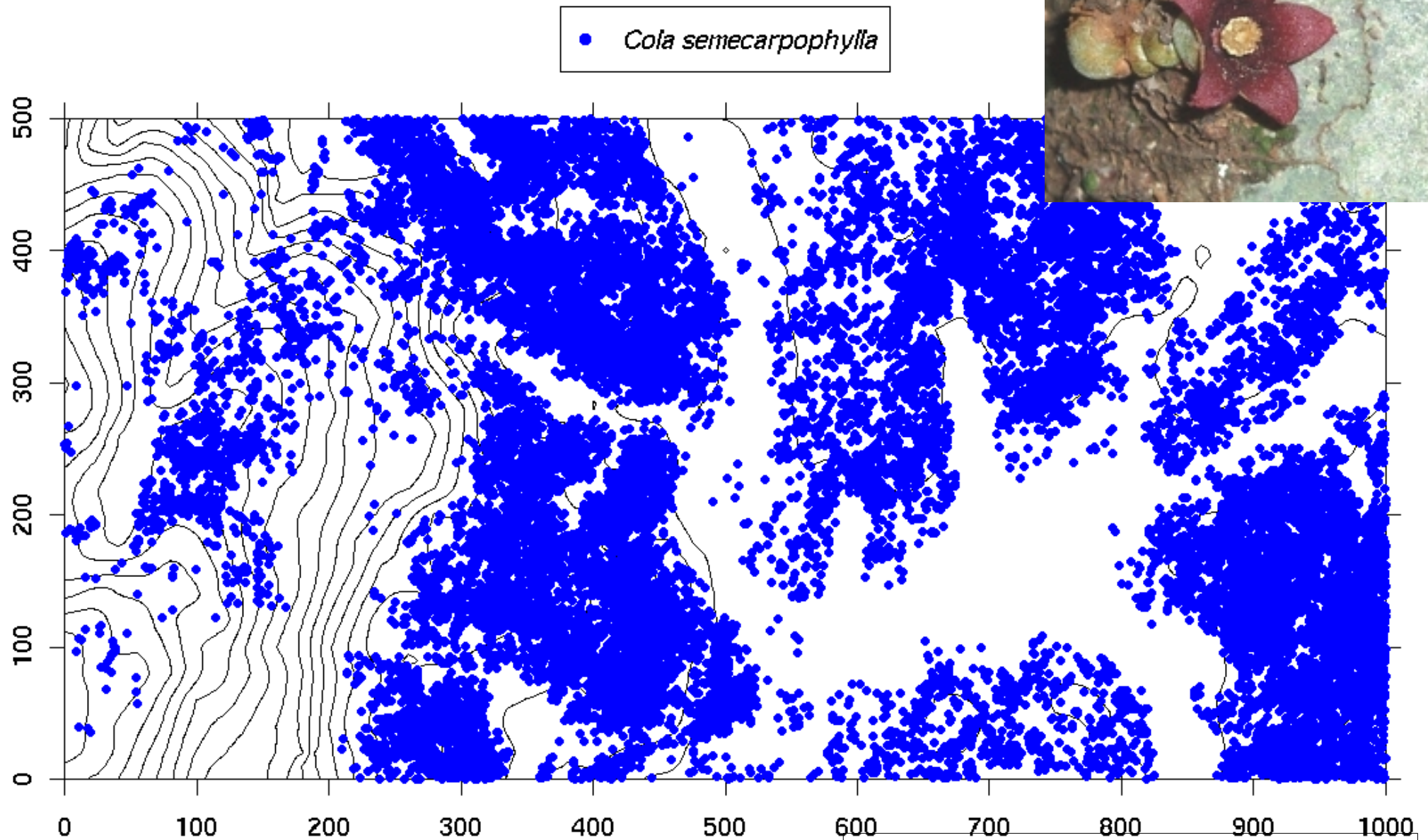


Korup 50 ha plot (Cameroon)

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

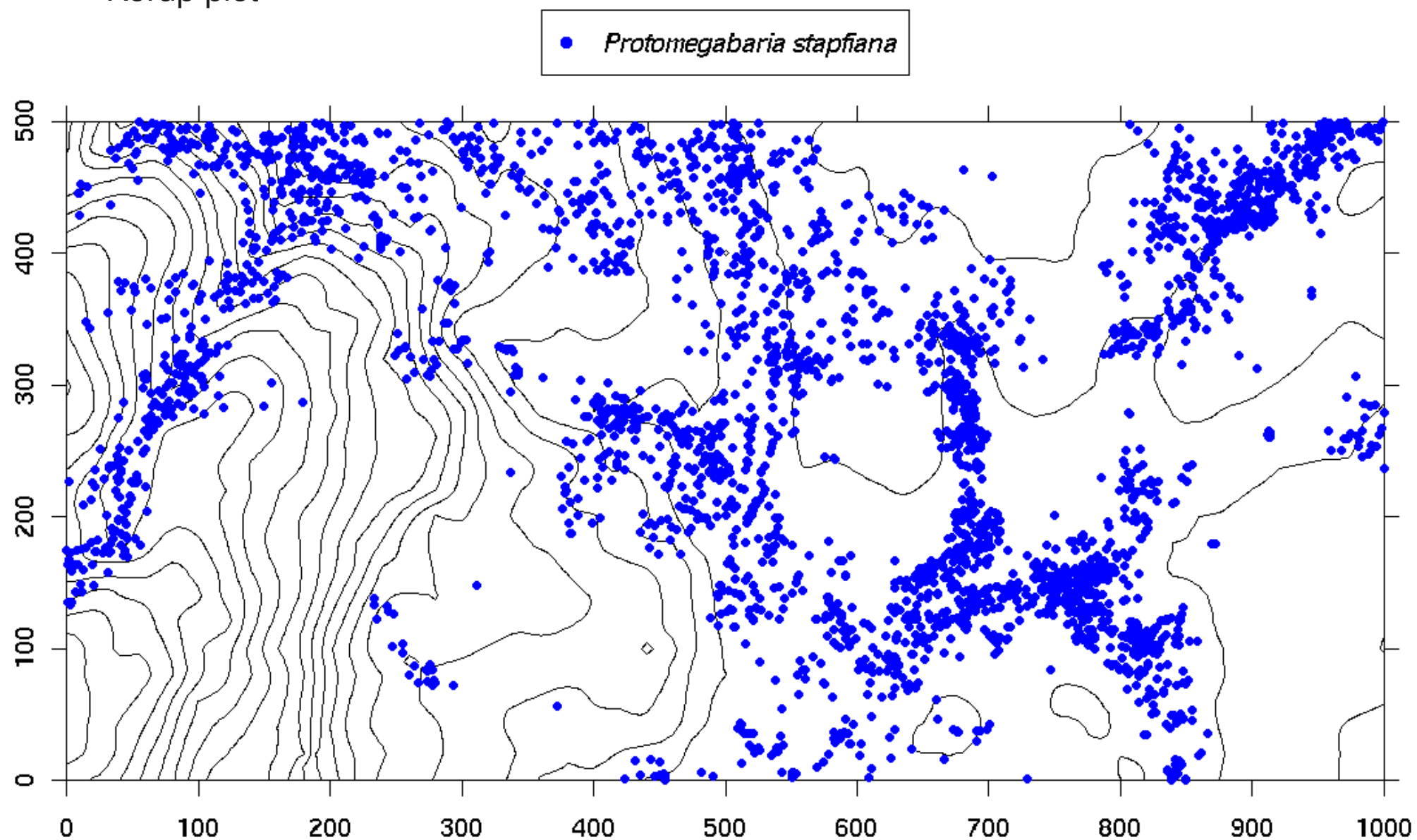


Korup 50 ha plot (Cameroon)

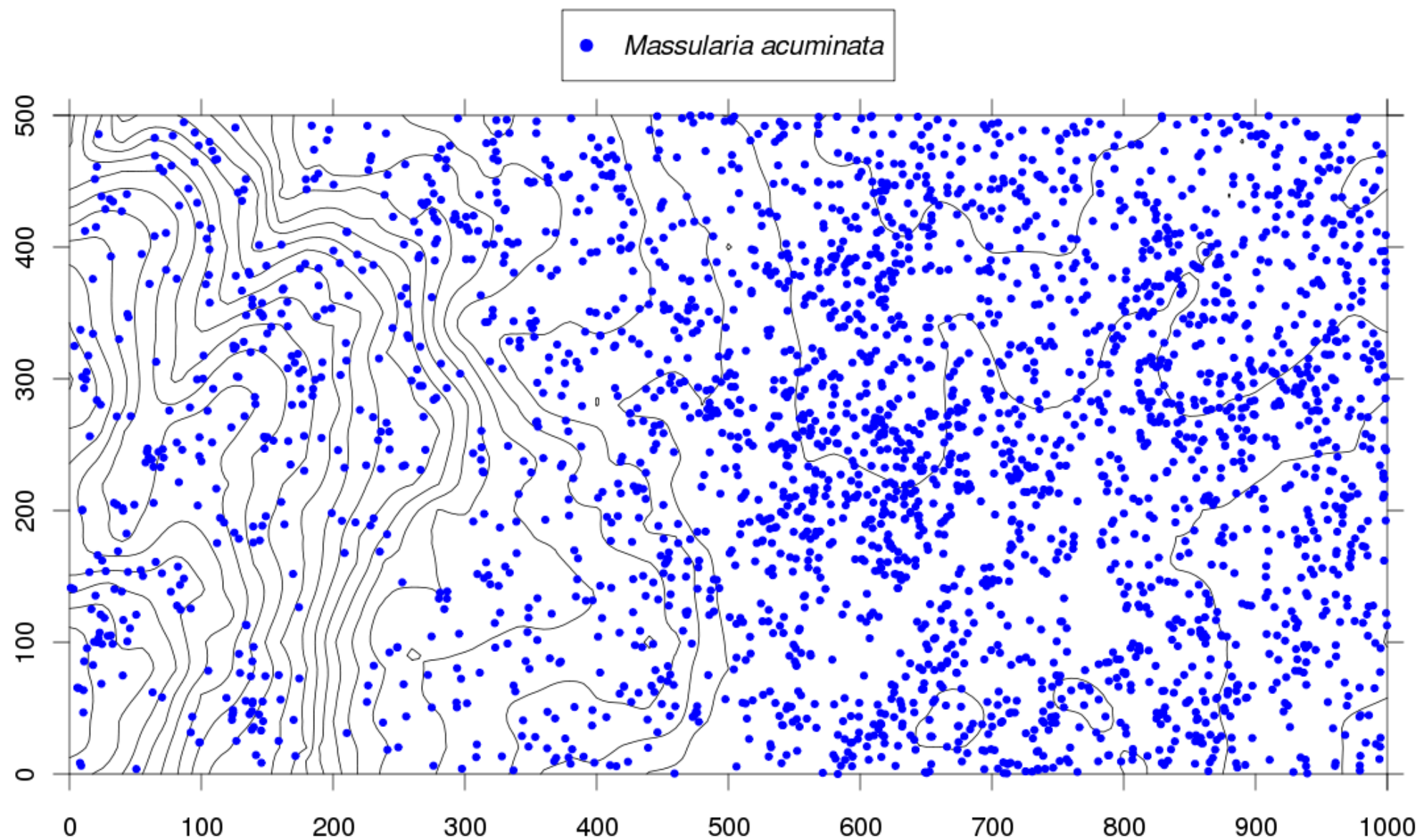


- ◆ IUCN risk (lowest)
- ◆ Range ~50,000 km²
- ◆ 10,200 reprod. trees in 50 ha

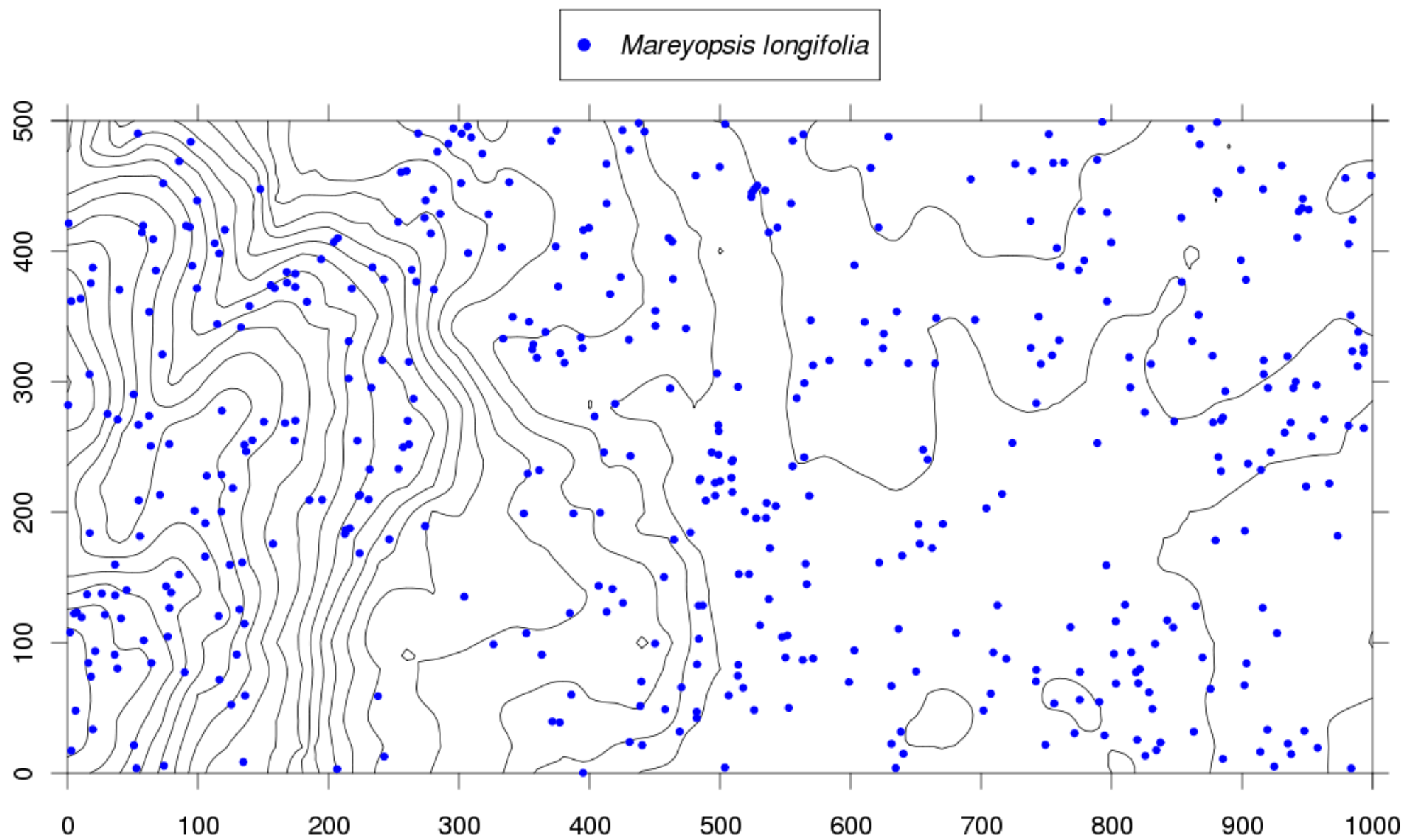
Korup plot



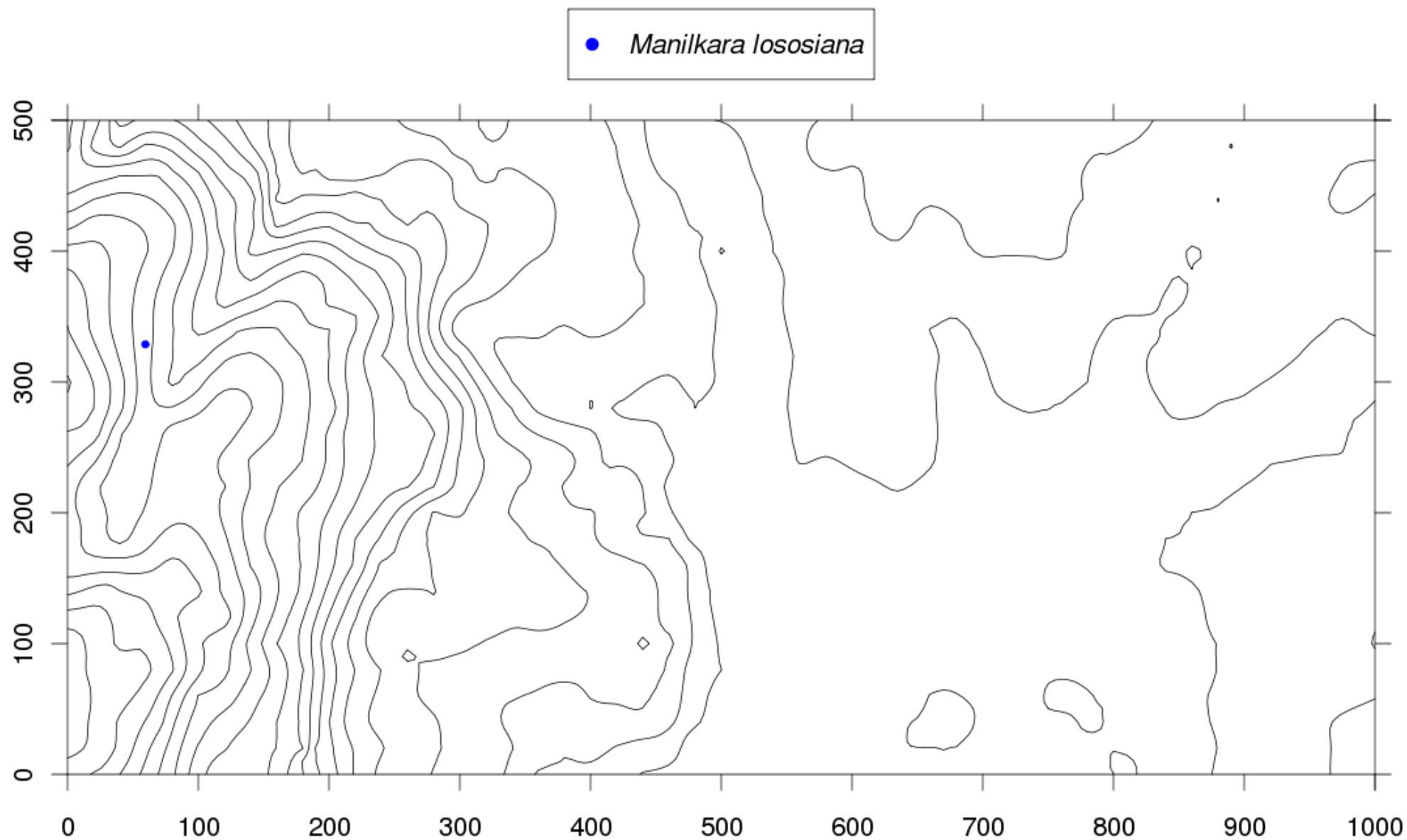
Korup plot



Korup plot



Korup plot



Newly described from this tree (Kenfack & Thomas)

I) Observed community patterns in diverse forests

1. Abundance variation



Turnera panamensis

I) Observed community patterns in diverse forests

1. Abundance variation
2. Spatial distribution



Turnera panamensis

I) Observed community patterns in diverse forests

1. Abundance variation
2. Spatial distribution
3. Niche segregation



Turnera panamensis

I) Observed community patterns in diverse forests

II) Theory aimed at understanding the patterns

1. Abundance variation
2. Spatial distribution
3. Niche segregation



Turnera panamensis

A stochastic community theory

Biology of individuals:

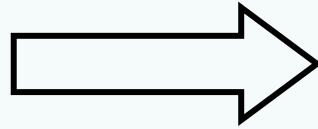
Community patterns:



A stochastic community theory

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation



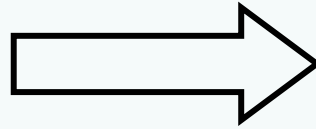
Community patterns:

Competition
Diversity
Abundance
Spatial patterns
Species-area relationship
Extinction

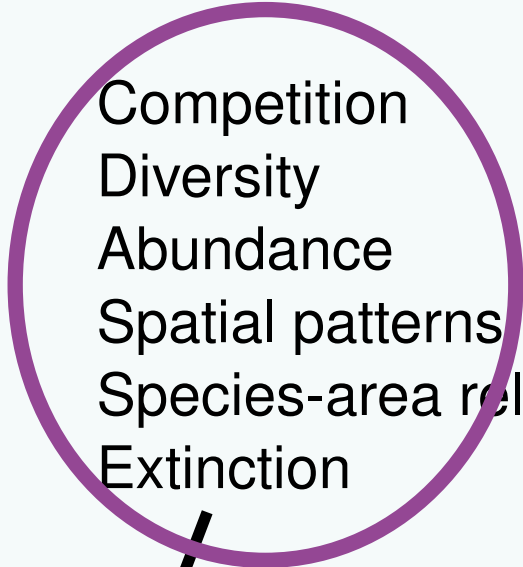
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Biology of individuals:

Mortality
Reproduction
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Community patterns:



Competition
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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.)

Importance of the neutral theory is not neutrality

Stochastic & individual-based community theory:

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

Importance of the neutral theory is not neutrality

Stochastic & individual-based community theory:

- stochastic individual demography
- species input (an open community)*

* The weakest feature in terms of biological realism

The Voter Model



Stochastic Community Demography

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 Voter Model

Caswell (1976), Liggett (1985), Dewdney (2000), Hubbell (2001)

Stochastic Community Demography

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

Stochastic Community Demography

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

birth &
dispersal

Stochastic Community Demography

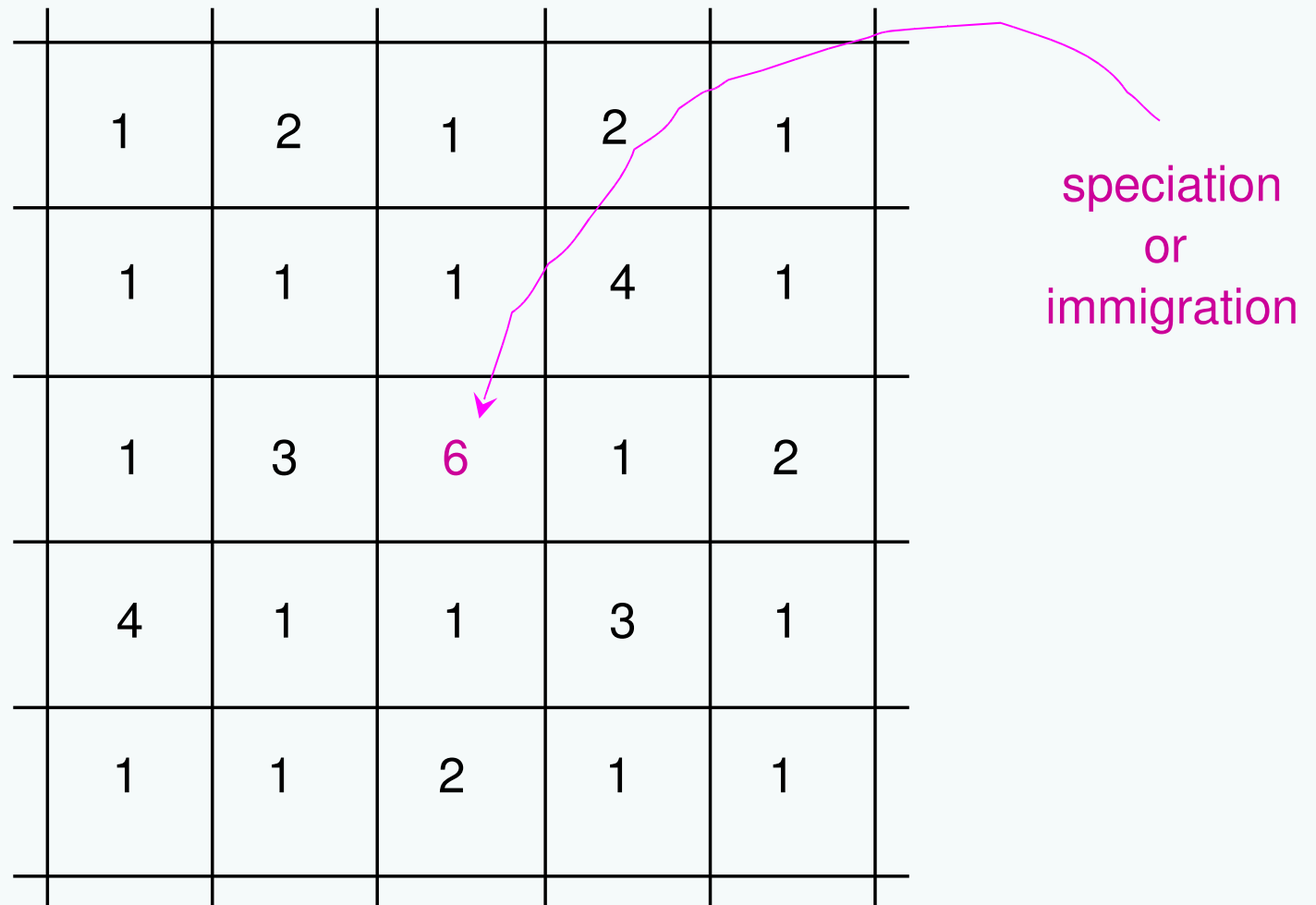
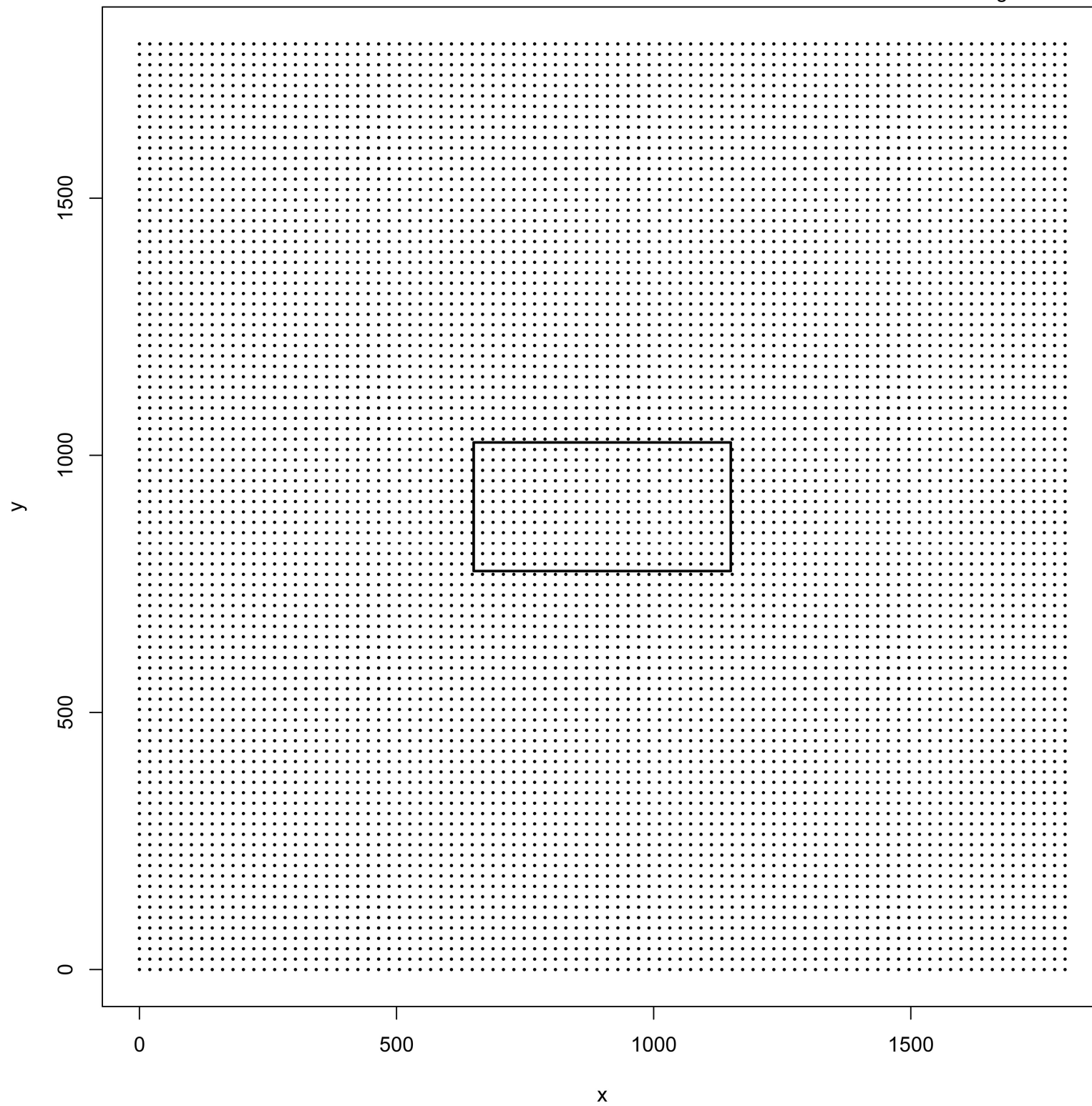


Fig. 6.1



Forestry models

- Individual trees
- Map positions
- Growth & resources
- Neighborhood competition
- Mortality
- Dispersal
- Distinct species
- Thousands of species
- Millions of years
- Speciation

Diversity models

- Individual trees
- Map positions
- Growth & resources
- Neighborhood competition
- Mortality
- Dispersal
- Distinct species
- Thousands of species
- Millions of years
- Speciation

Basic results

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

Diversity is maintained despite no niche differences, as long as there is species input

Equilibrium species abundance distribution

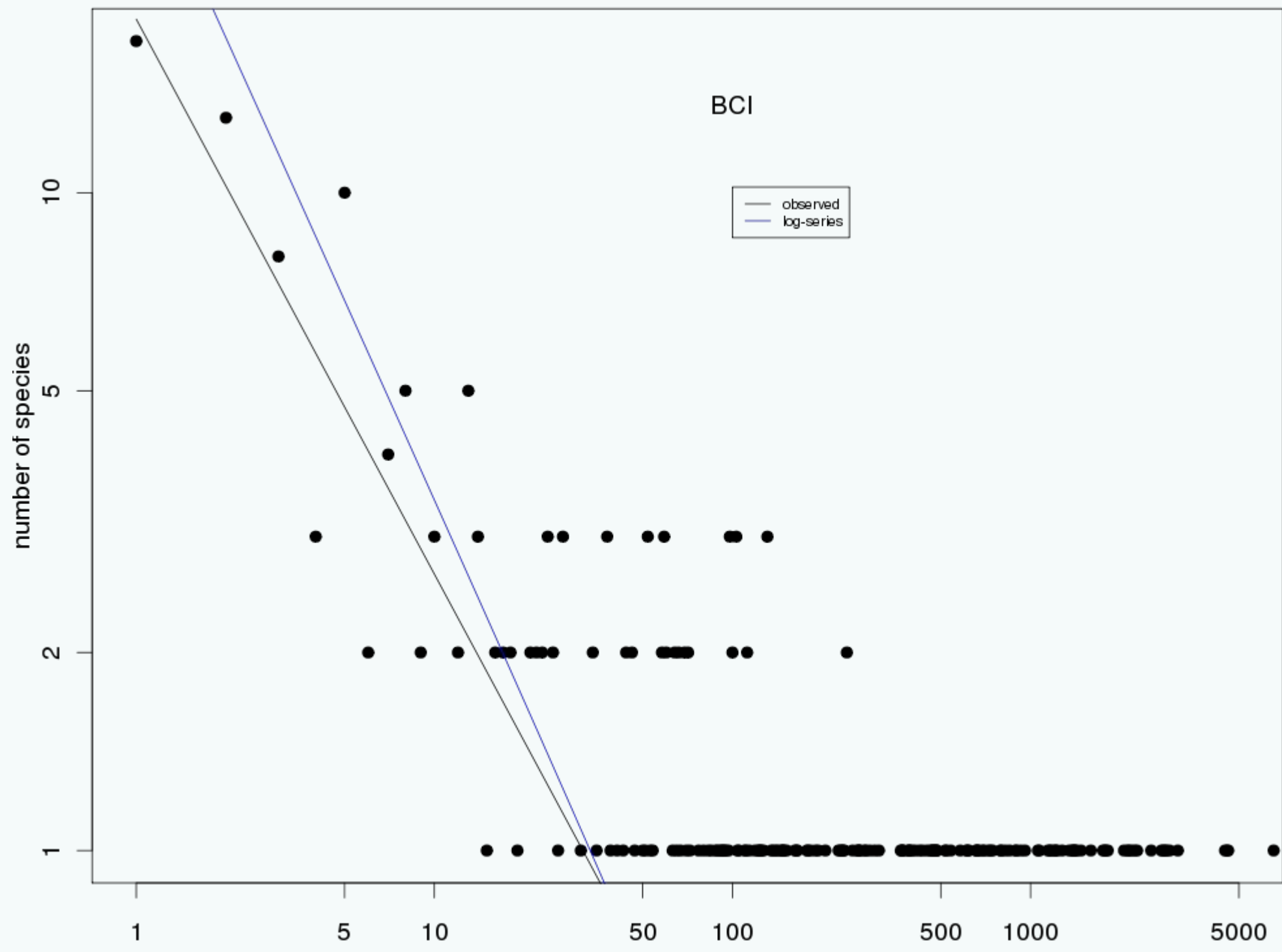
The neutral stochastic model with speciation leads to a log-series abundance distribution

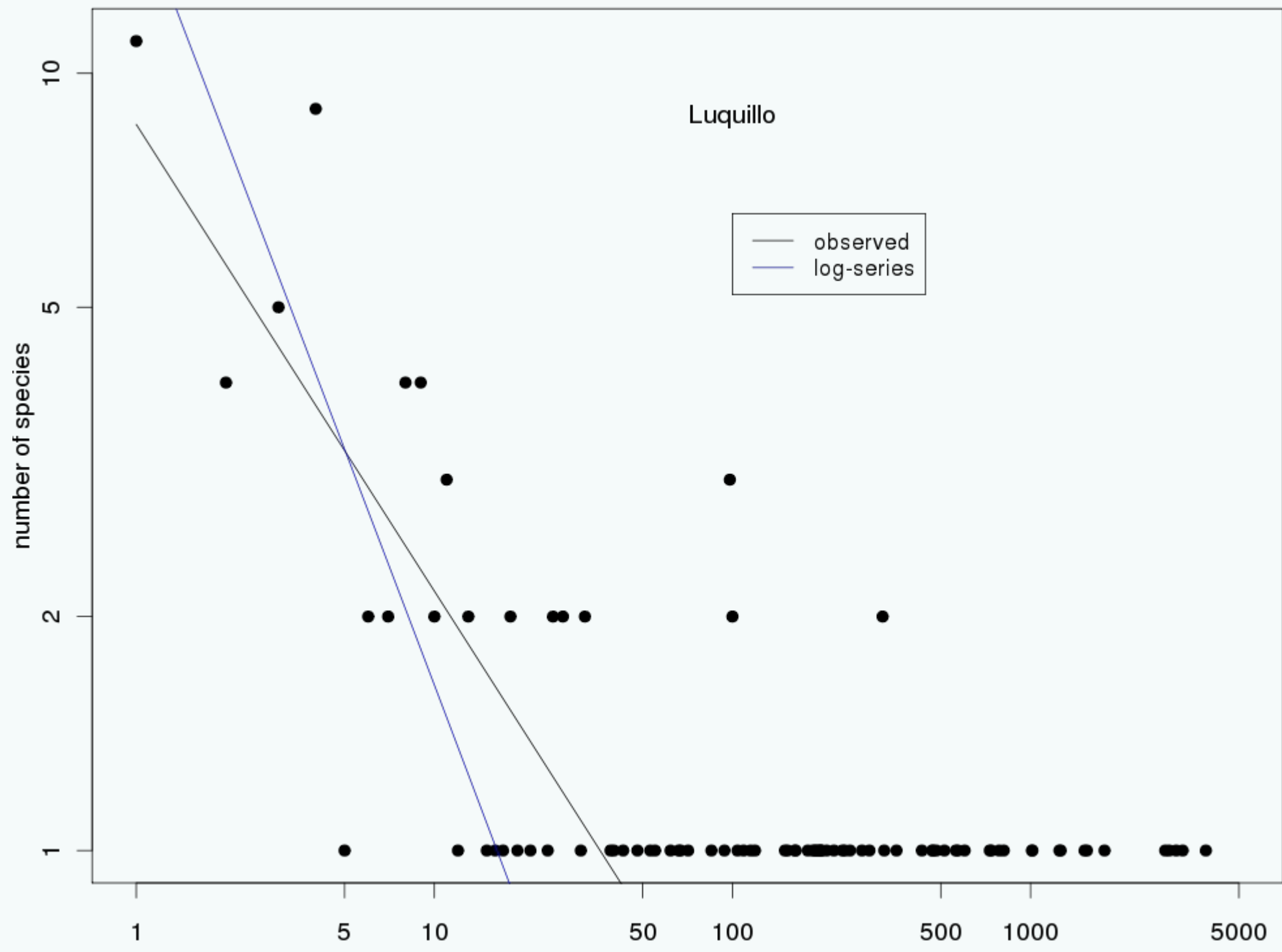
The log-series has a rare tail, with singletons always the most frequent category

The dominance of singletons is driven by speciation

many recent advances:

Volkov et al.(2005), Pueyo et al. (2007), Zillio et al. (2007), Harte et al. (2008)





Summary I: Abundances in a stochastic community

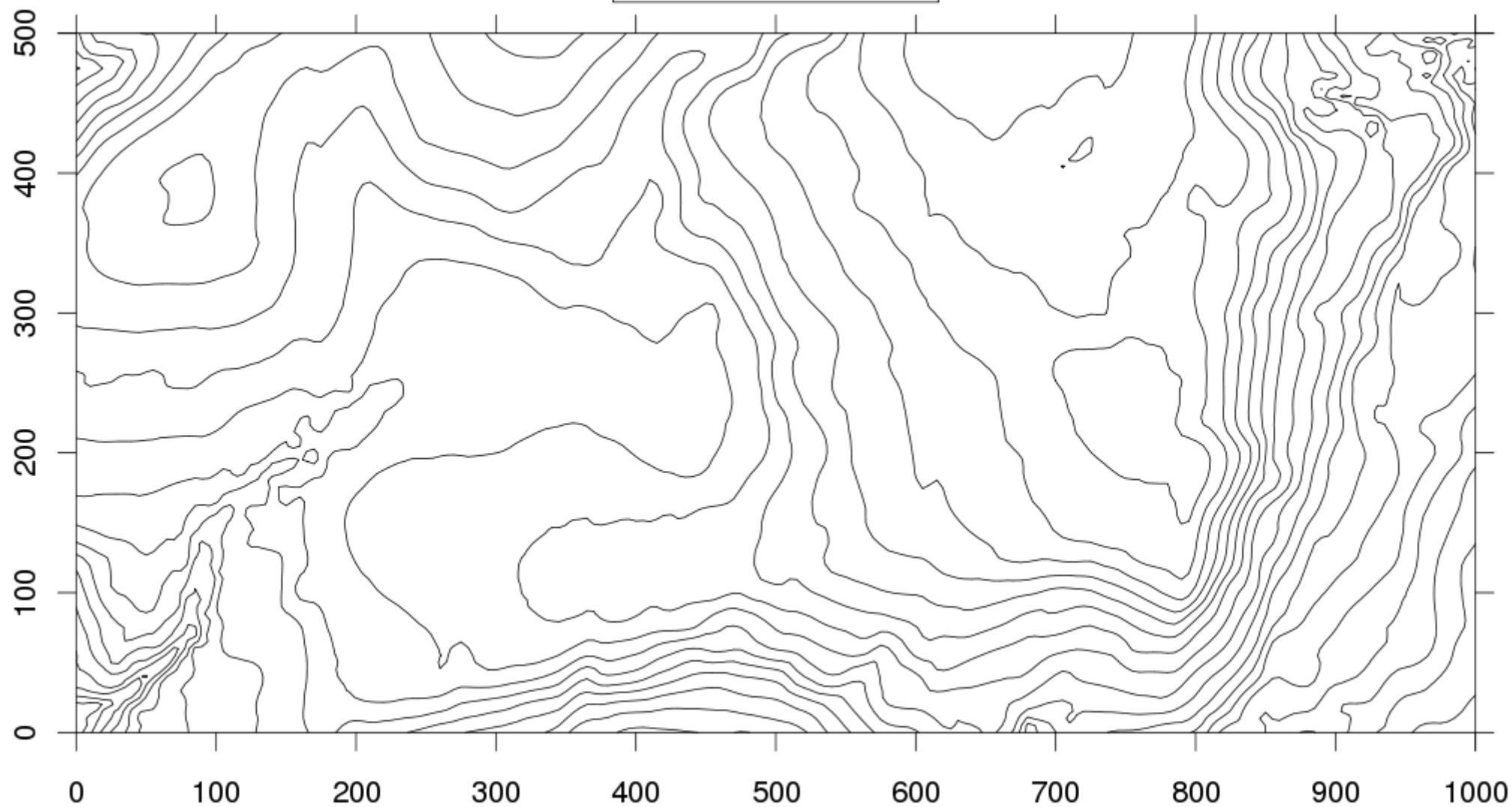
Neutral theory predicts abundance distribution correctly and on first principles ...

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

Is turnover observed in 50 ha plots?

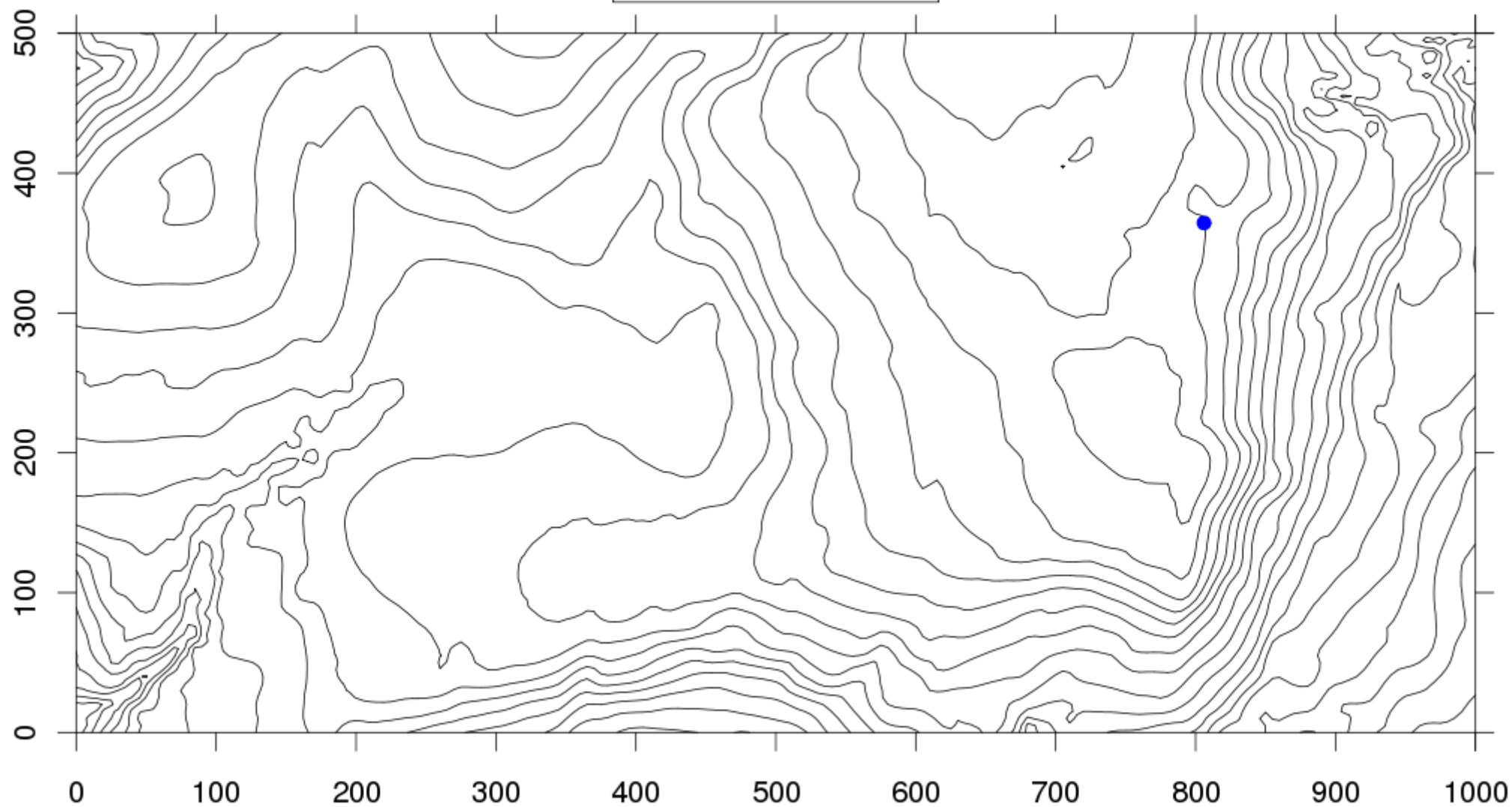
● *Rauvolfia littoralis*

1990



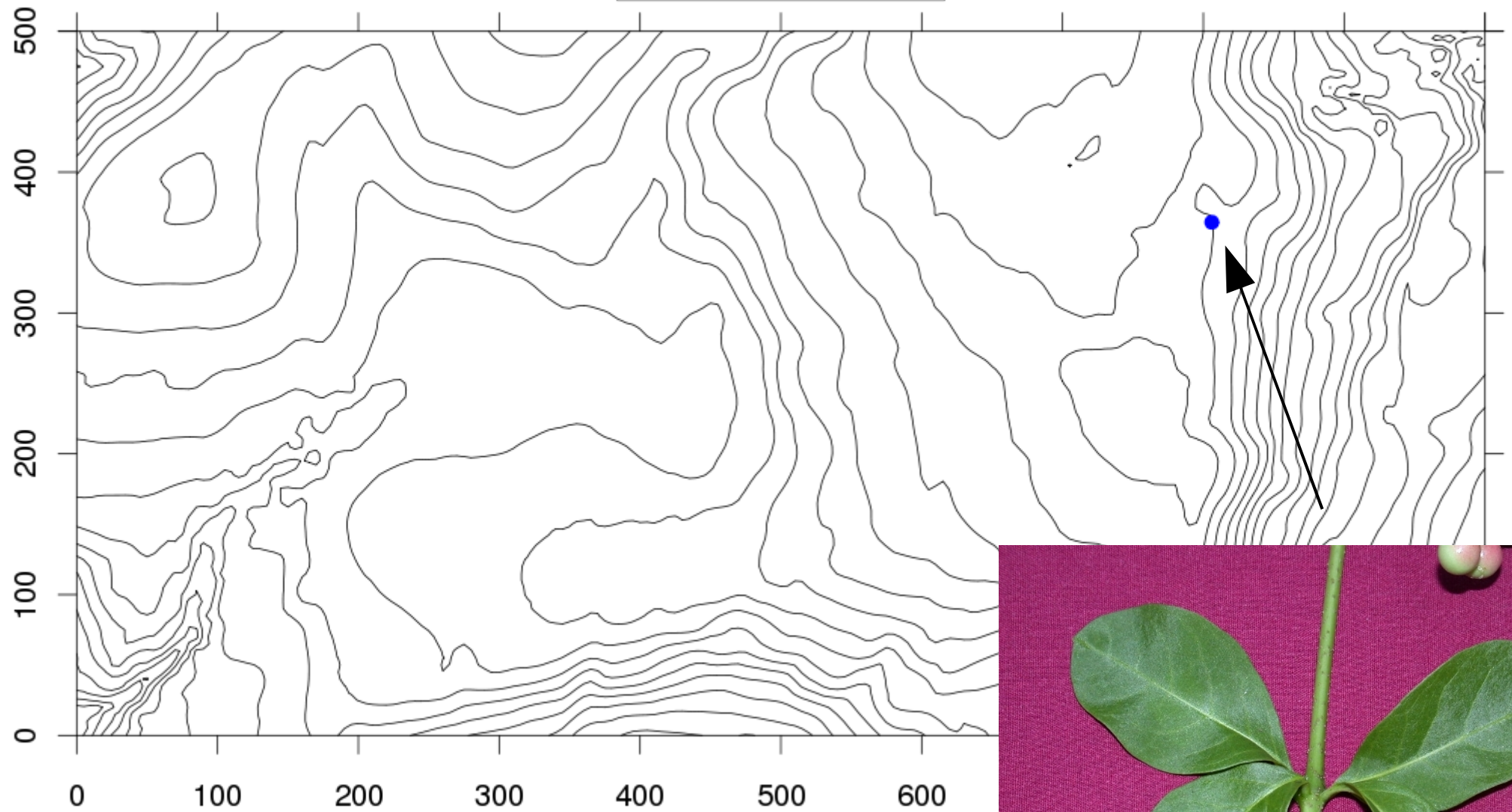
● *Rauvolfia littoralis*

1990 . . . 1995



● *Rauvolfia littoralis*

1990 . . . 1995



Rates of species invasion in tropical forest plots

Luquillo 1996-2001: 5 new species among 25090 recruits

$$\text{rate} = 2.0 \times 10^{-4}$$

(*Mimosa pudilla*, *Phytolacca rivinoides*, *Piper pellatata*, *Neuroleana lobata*, *Rauvolfia nitida*)

BCI 1990-1995: 4 new species among 21727 recruits

$$\text{rate} = 1.8 \times 10^{-4}$$

(*Cecropia longipes*, *Psychotria psychotriifolia*, *Rauvolfia littoralis*, *Vismia macrophylla*)

BCI 1995-2000: 4 new species among 21473 recruits

$$\text{rate} = 1.9 \times 10^{-4}$$

(*Clidemia septuplinervia*, *Leandra dichotoma*, *Miconia dorsiloba*, *Verbesina gigantea*)

Theory on dispersal and range size

- ◆ Patchiness predicted from dispersal
- ◆ Conditions under which range size can be dispersal-limited



Cavanillesia platanifolia

Theory on dispersal and range size

- ◆ Patchiness predicted from dispersal
- ◆ Conditions under which range size can be dispersal-limited
- ◆ Conclusions about forest trees...



Cavanillesia platanifolia

Summary II

Spatial patterns in a neutral stochastic community change to highlight second point

Poor dispersal creates very patchy distribution ...
... the degree of patchiness is simply related to dispersal distance

Most tree species are widely distributed across 50 hectares ...
... and match simulations with ~ 200 m or better dispersal distances

Dispersal has minor impact on abundances

Niche segregation in a stochastic community



Niche segregation in a stochastic community

Coexistence where species input and dispersal are important

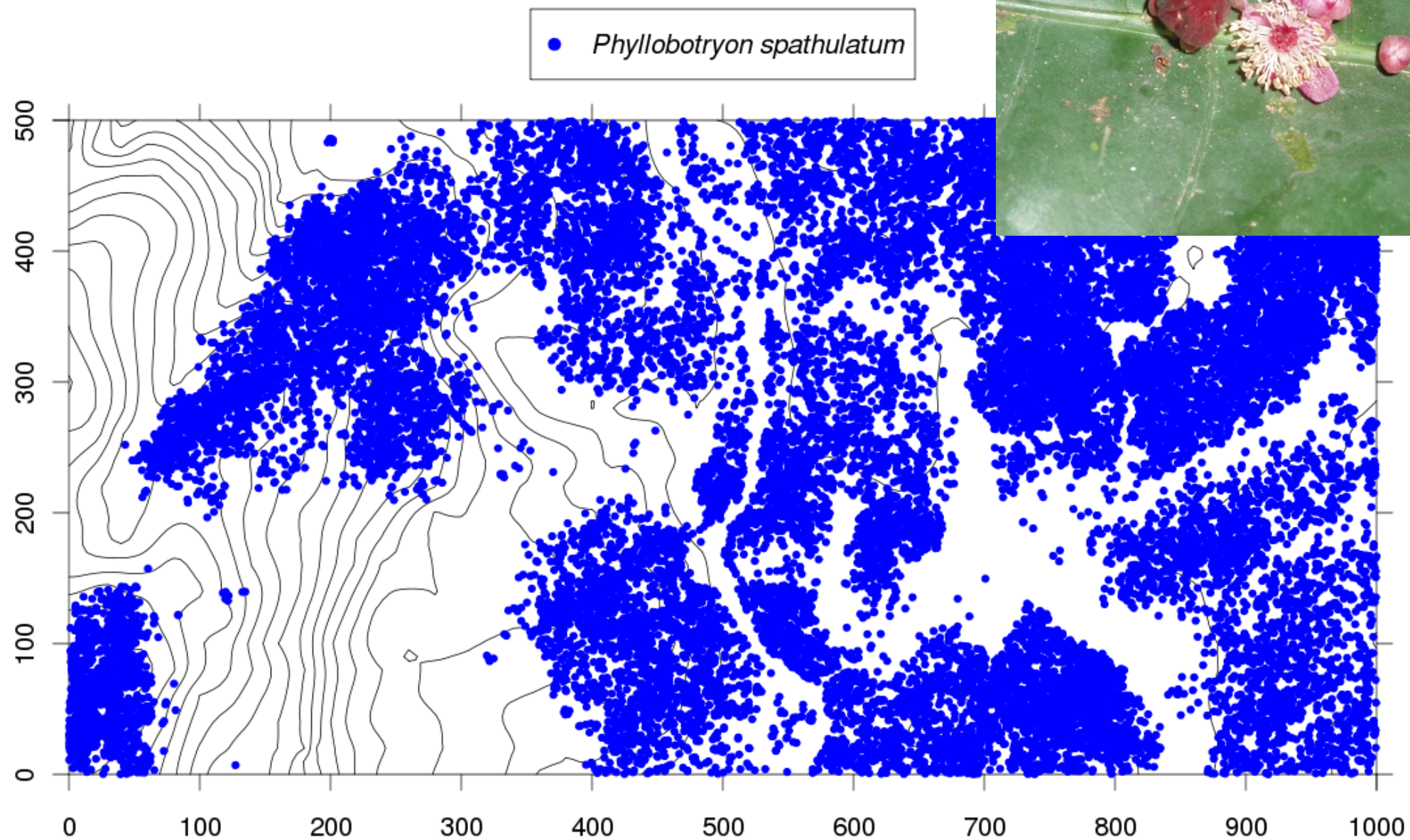


Niche segregation in a stochastic community

Coexistence where species input and dispersal are important

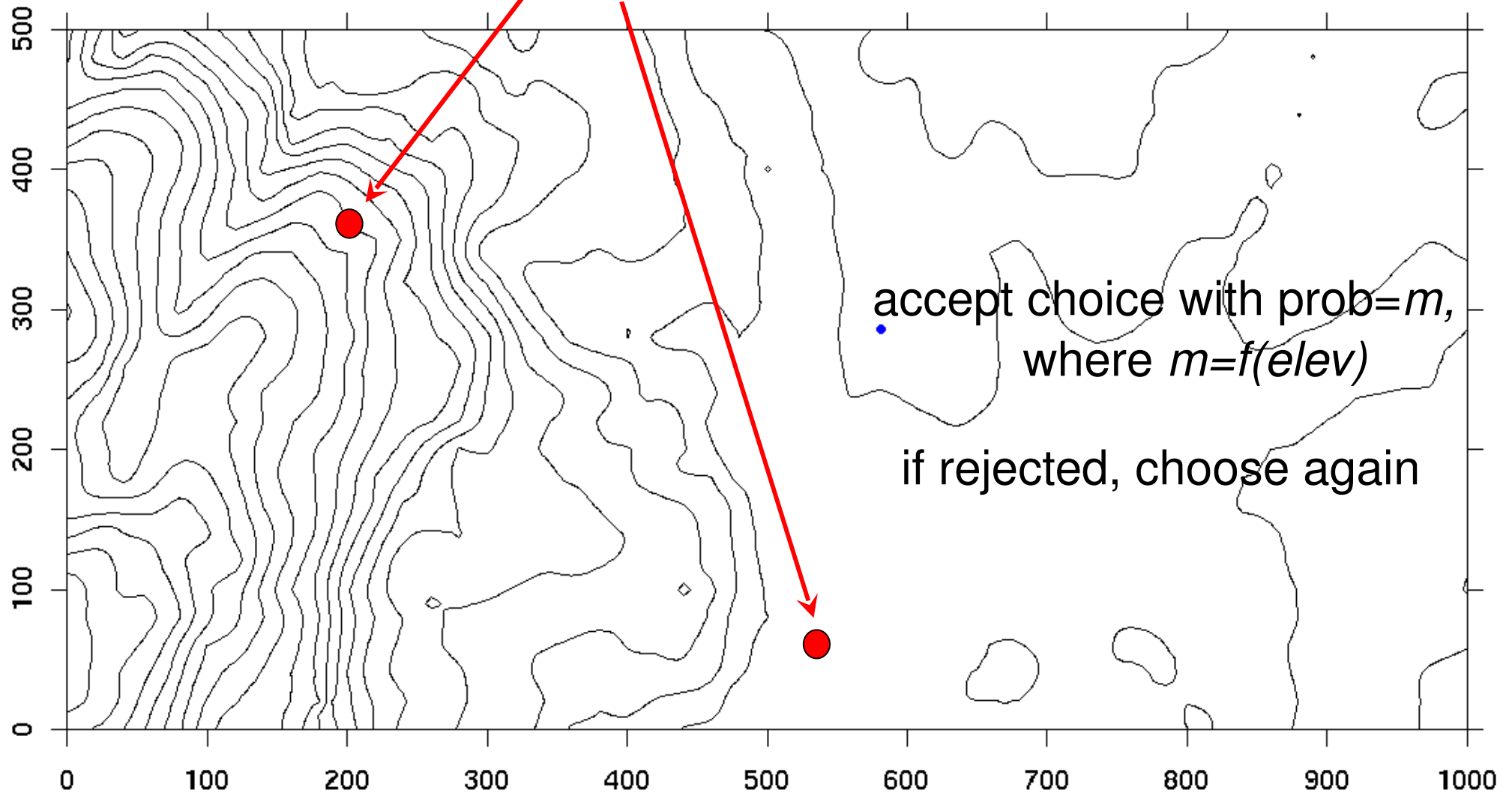
(Tilman 1994, Zobel 2001, Mouquet & Loreau 2003, McRae et al. 2008)

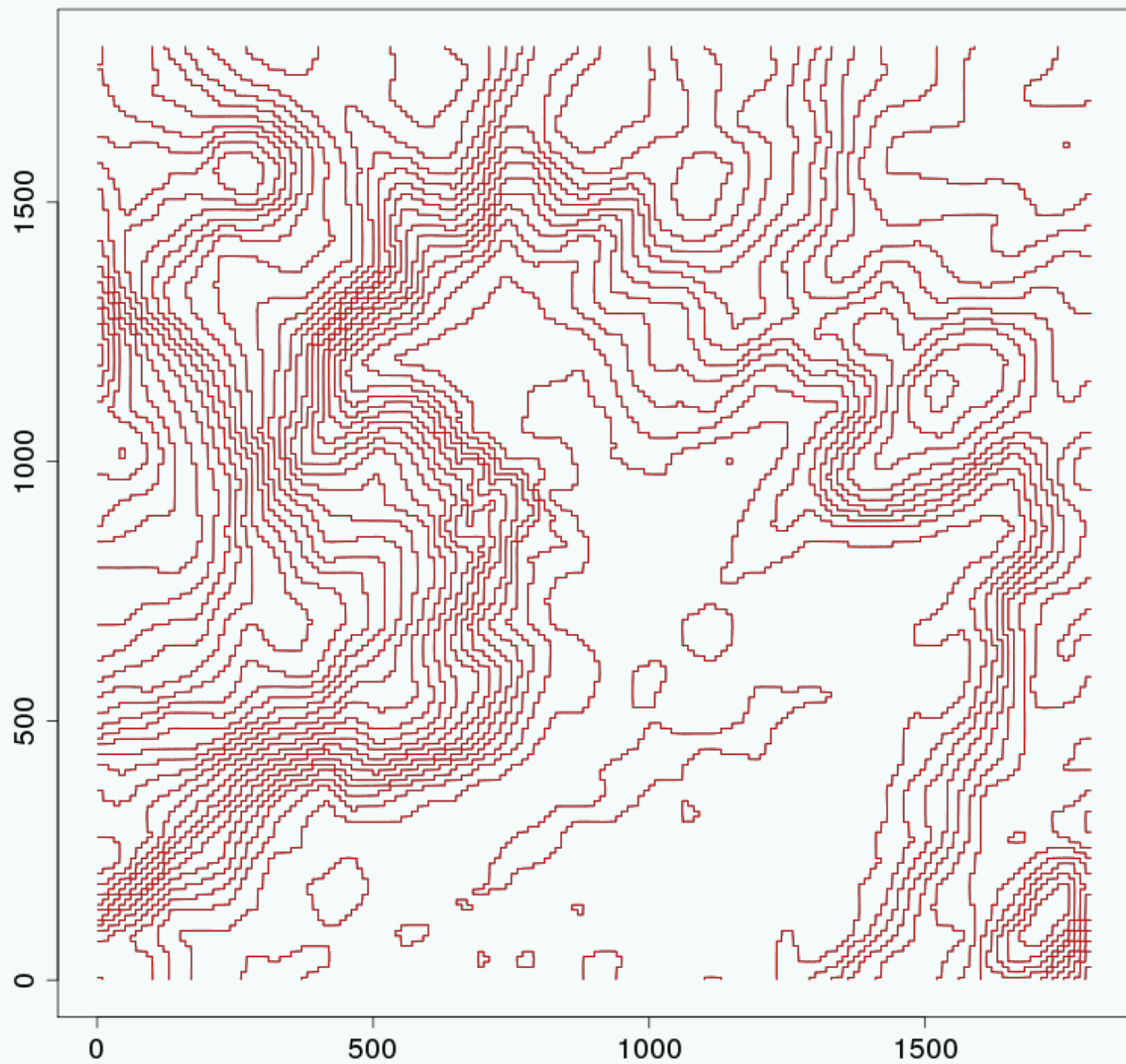
Korup 50 ha plot (Cameroon)

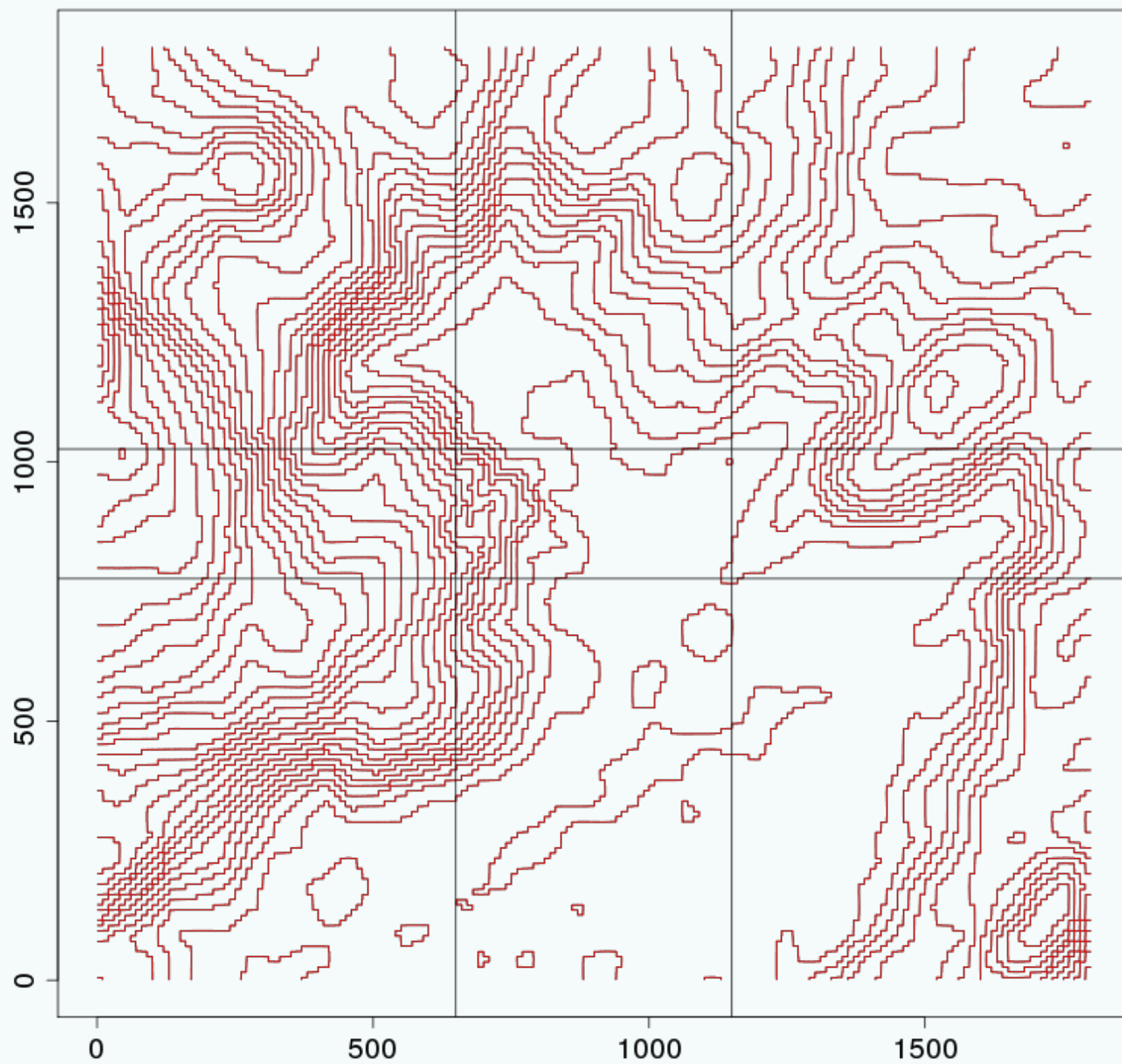


Incorporating niche differences into the stochastic model

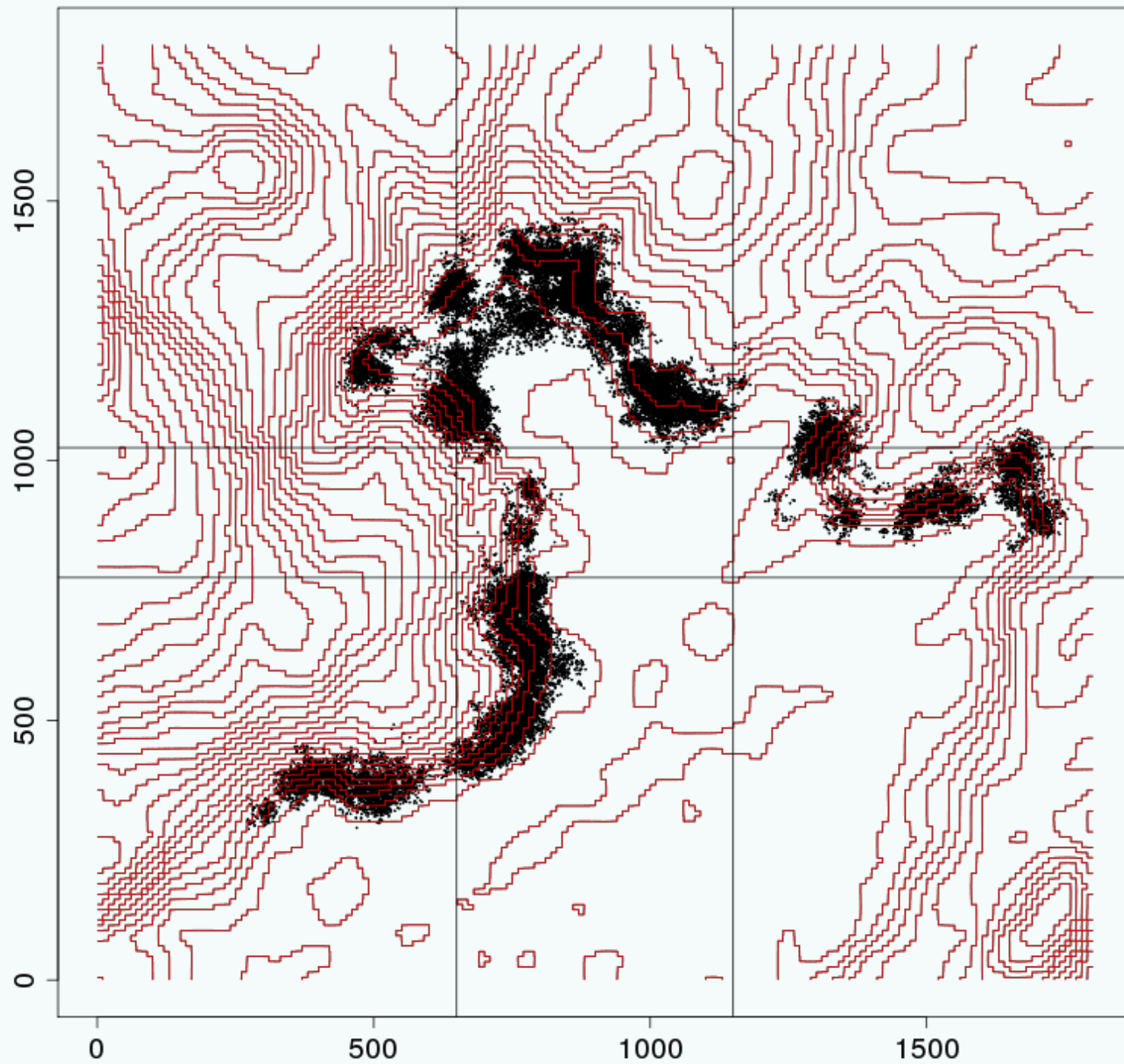
choose tree to die at random



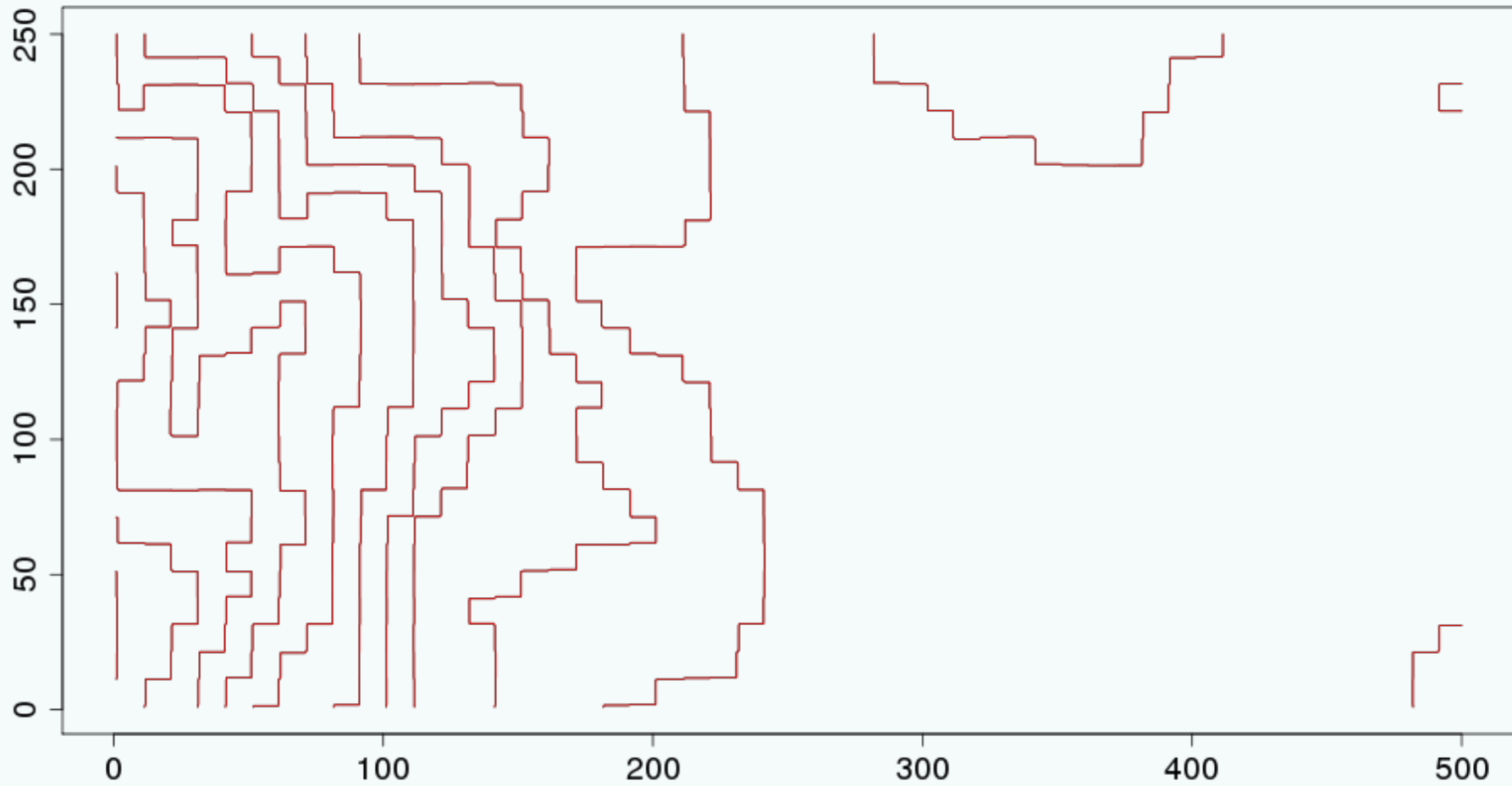




moderate Gaussian niches: 4 m elevation bands

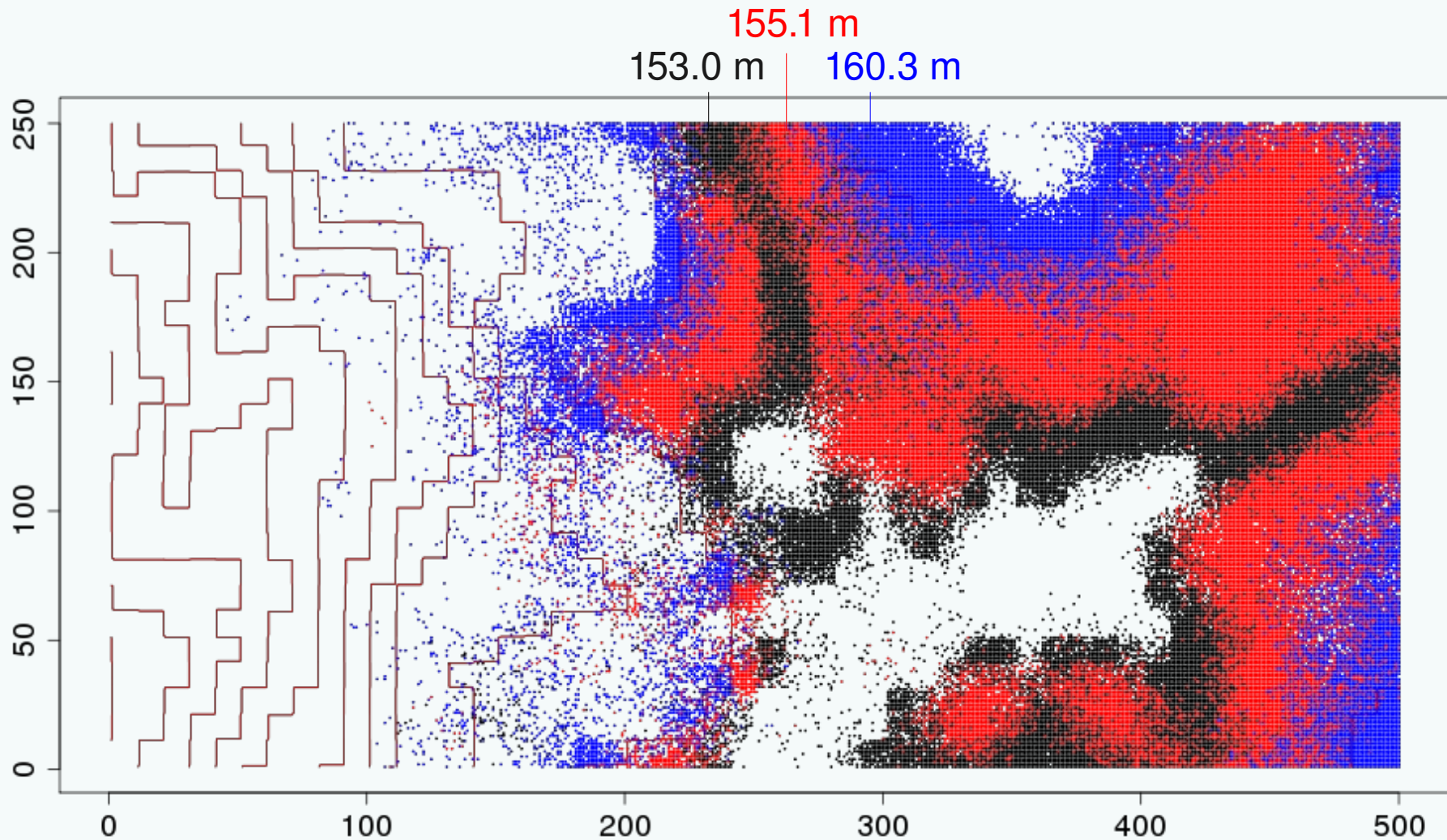


Elevation of simulated 50 ha plot
(real contours of the Korup plot)



Elevation of simulated 50 ha plot
(real contours of the Korup plot)

simulated species #18, #13, #3

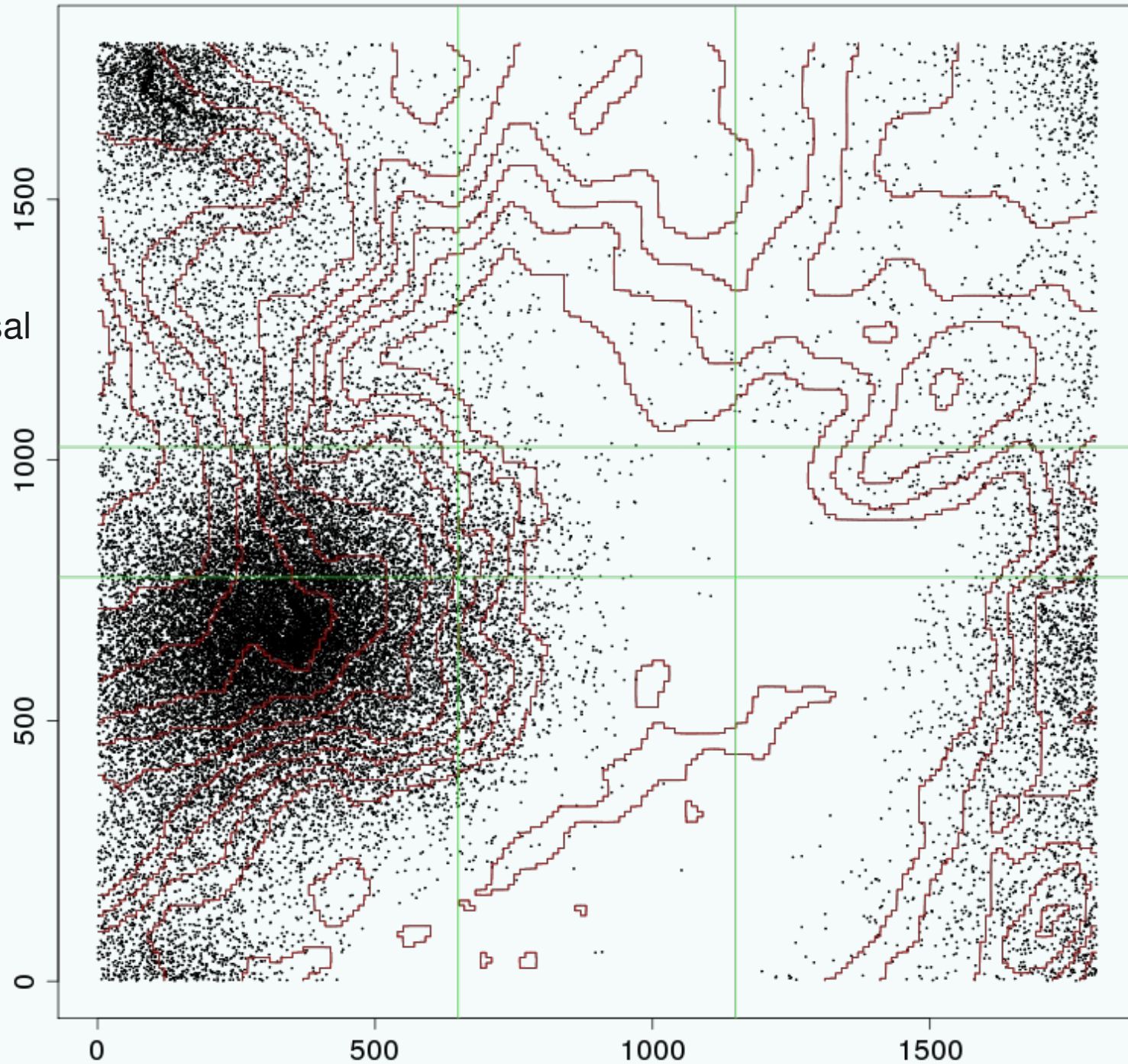


narrow Gaussian niches
precise tradeoffs in performance

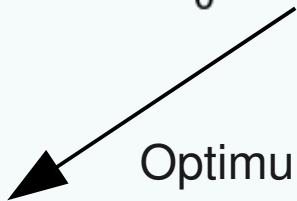
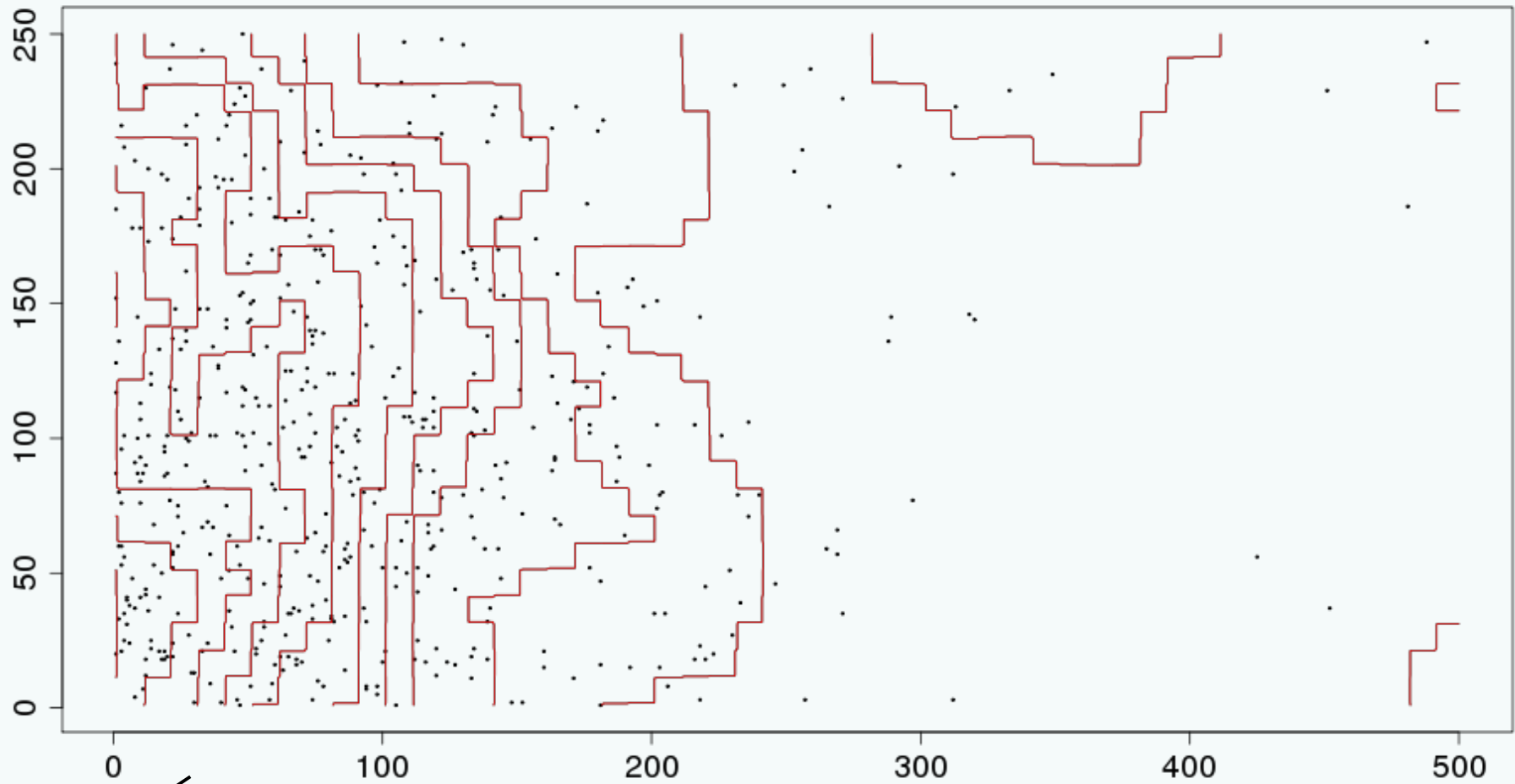
poor dispersal (10 m limit)

Species 29 has its niche optimum outside the 50 ha plot

good dispersal
(100 m limit)



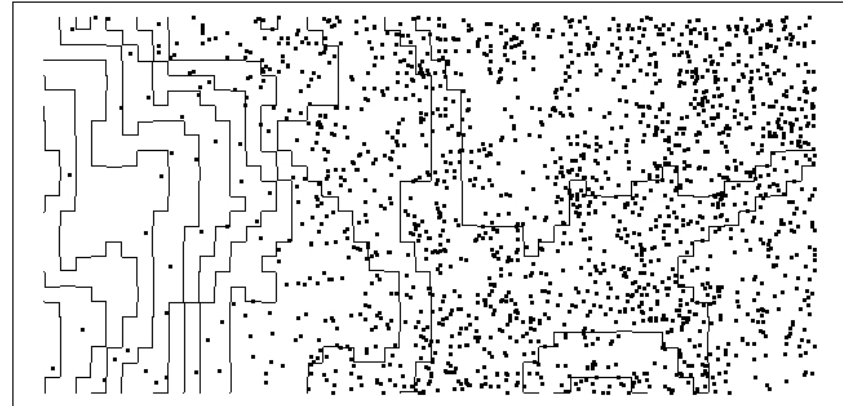
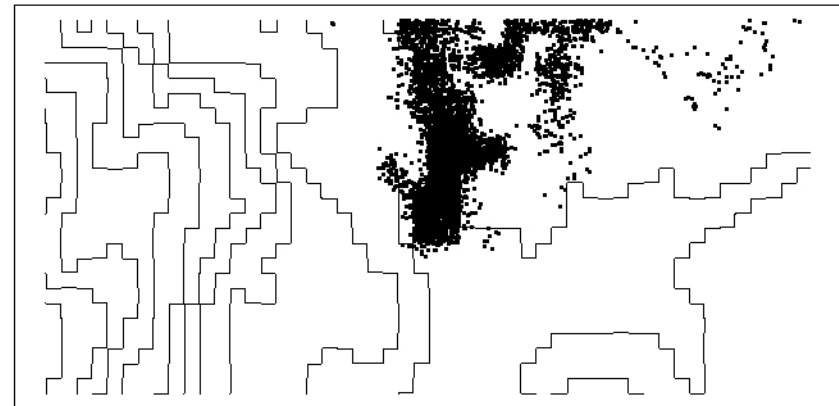
Species 29



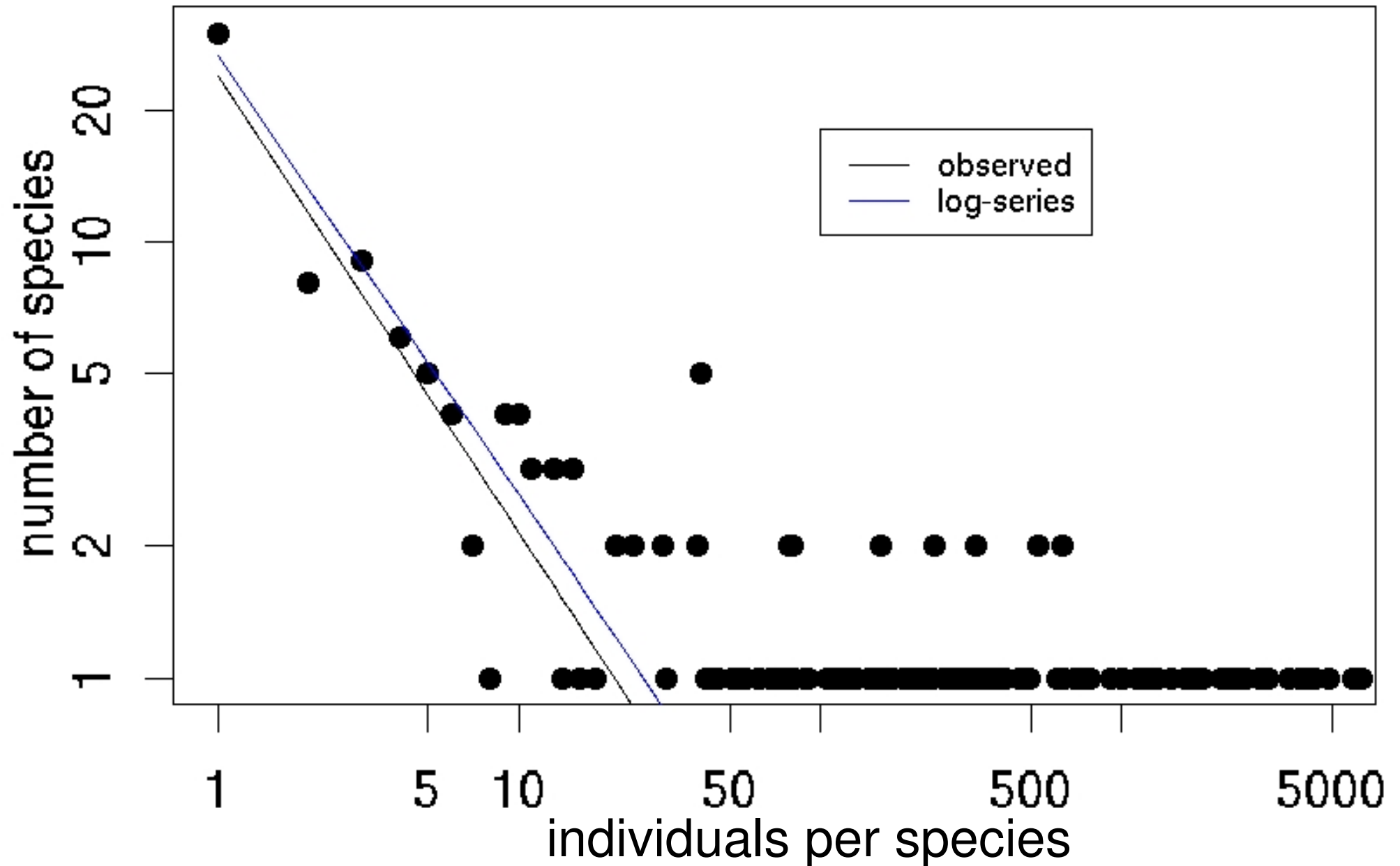
Optimum is 500 m
outside the plot

A stochastic community with niche partitioning and high species input (rate 10^{-5})

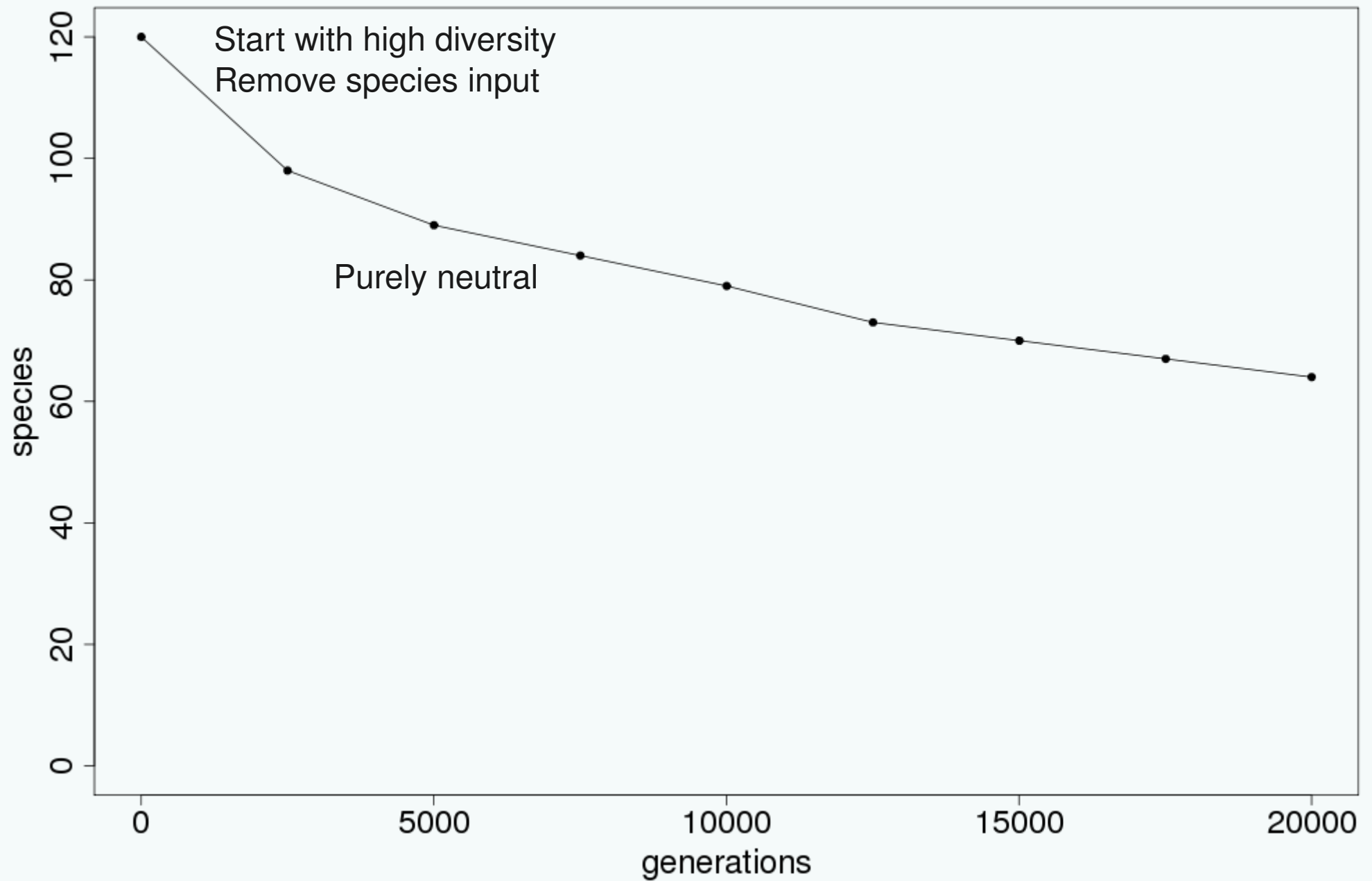
- Community has 140 species
- One species has 17484 individuals
- 45 species are singletons
- Many share identical niches:



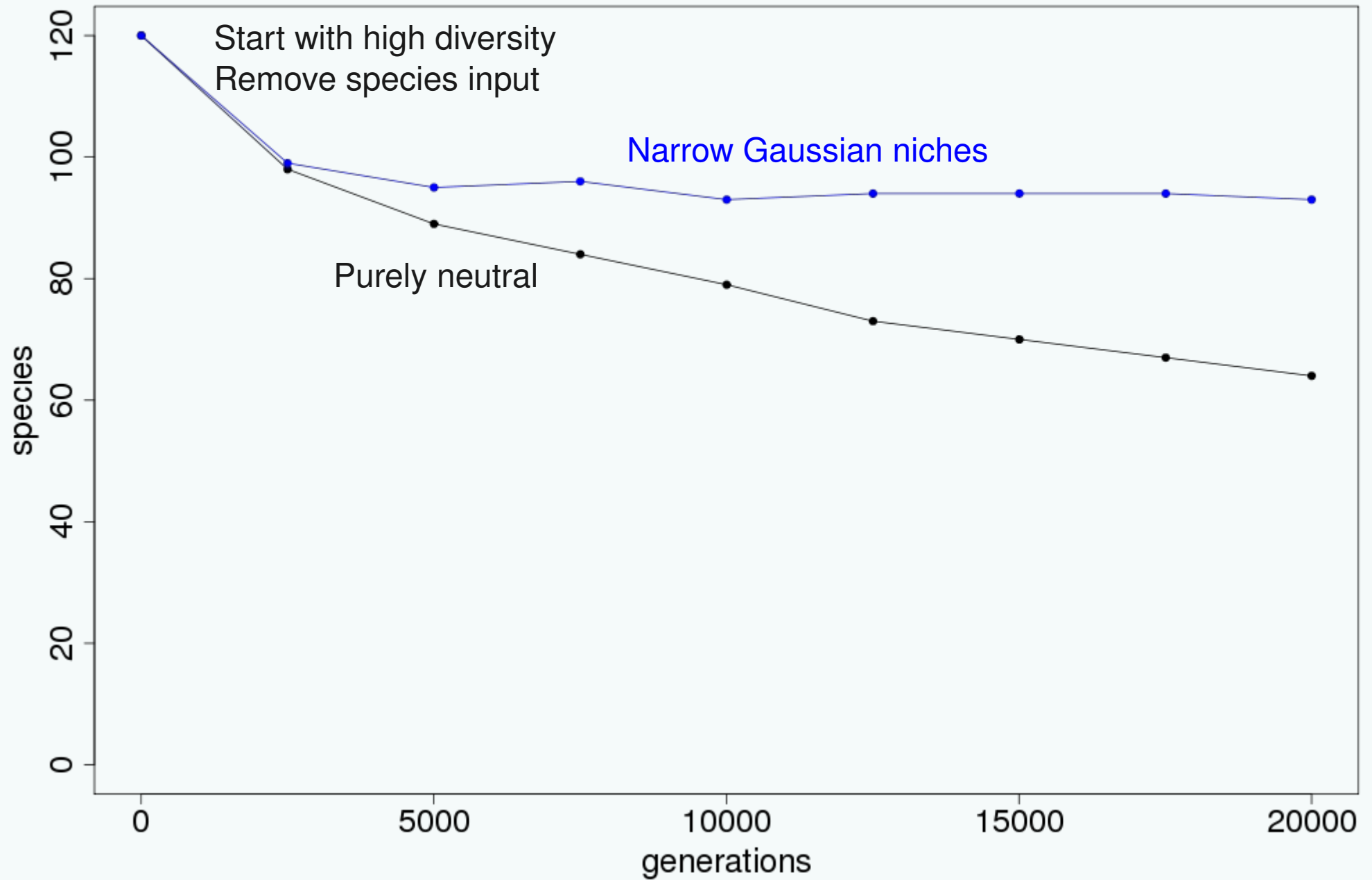
Species abundance distribution
Moderate Gaussian niches
High species input (10^{-5})



Change of species richness through time in stochastic models

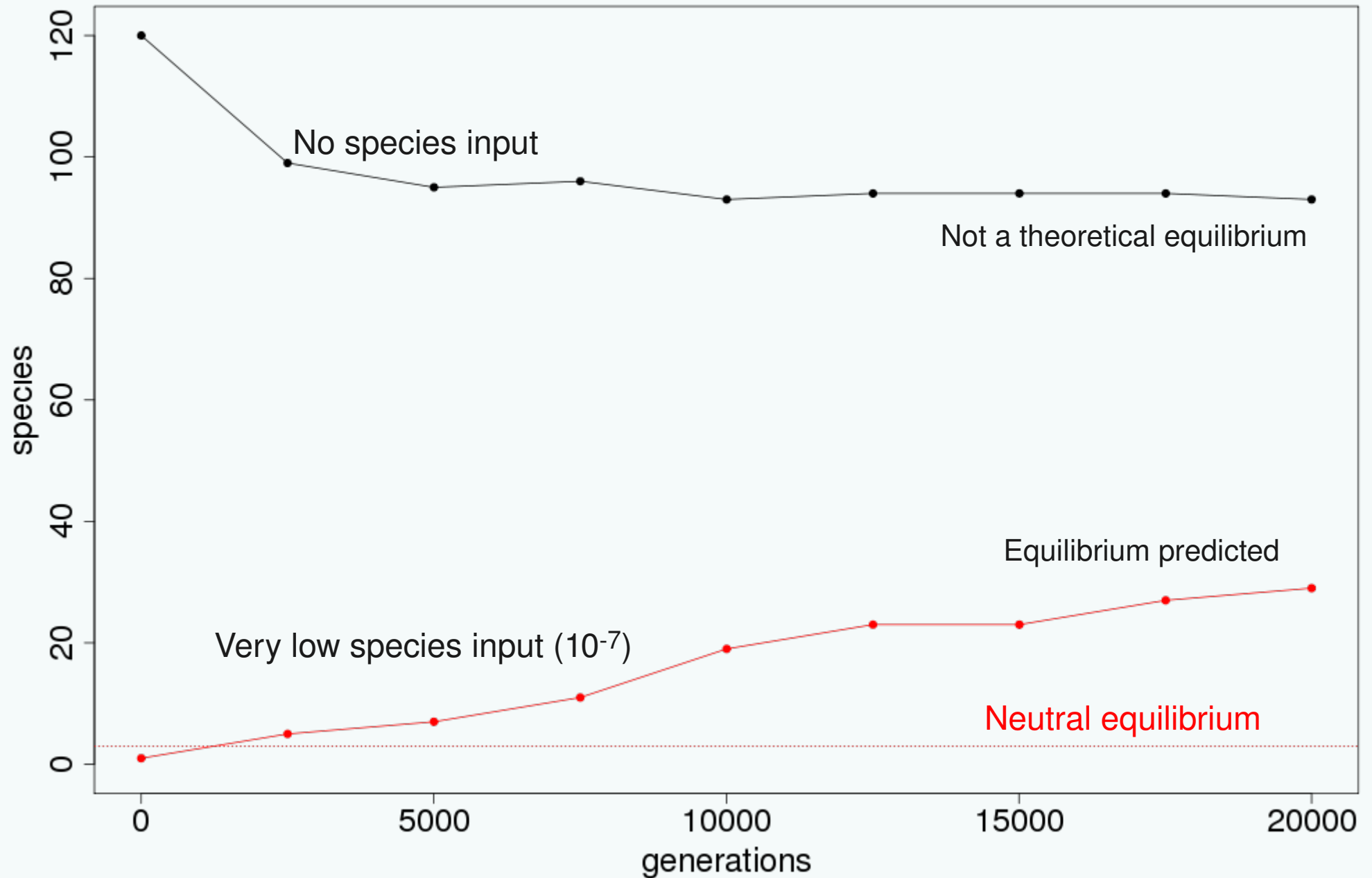


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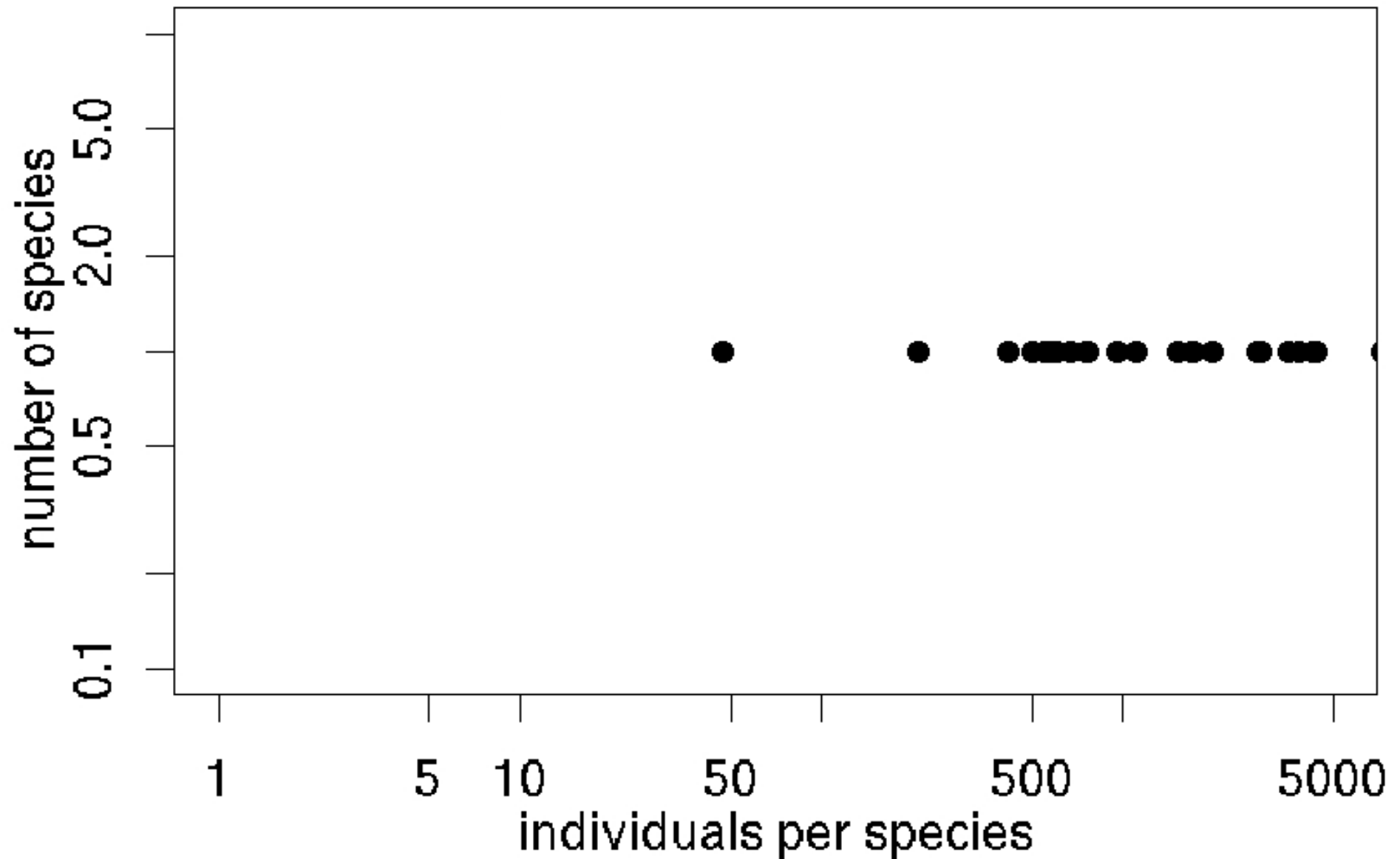


Change of species richness through time in stochastic models

Narrow Gaussian niches



Species abundance distribution
Moderate Gaussian niches
No species input (rate=0)

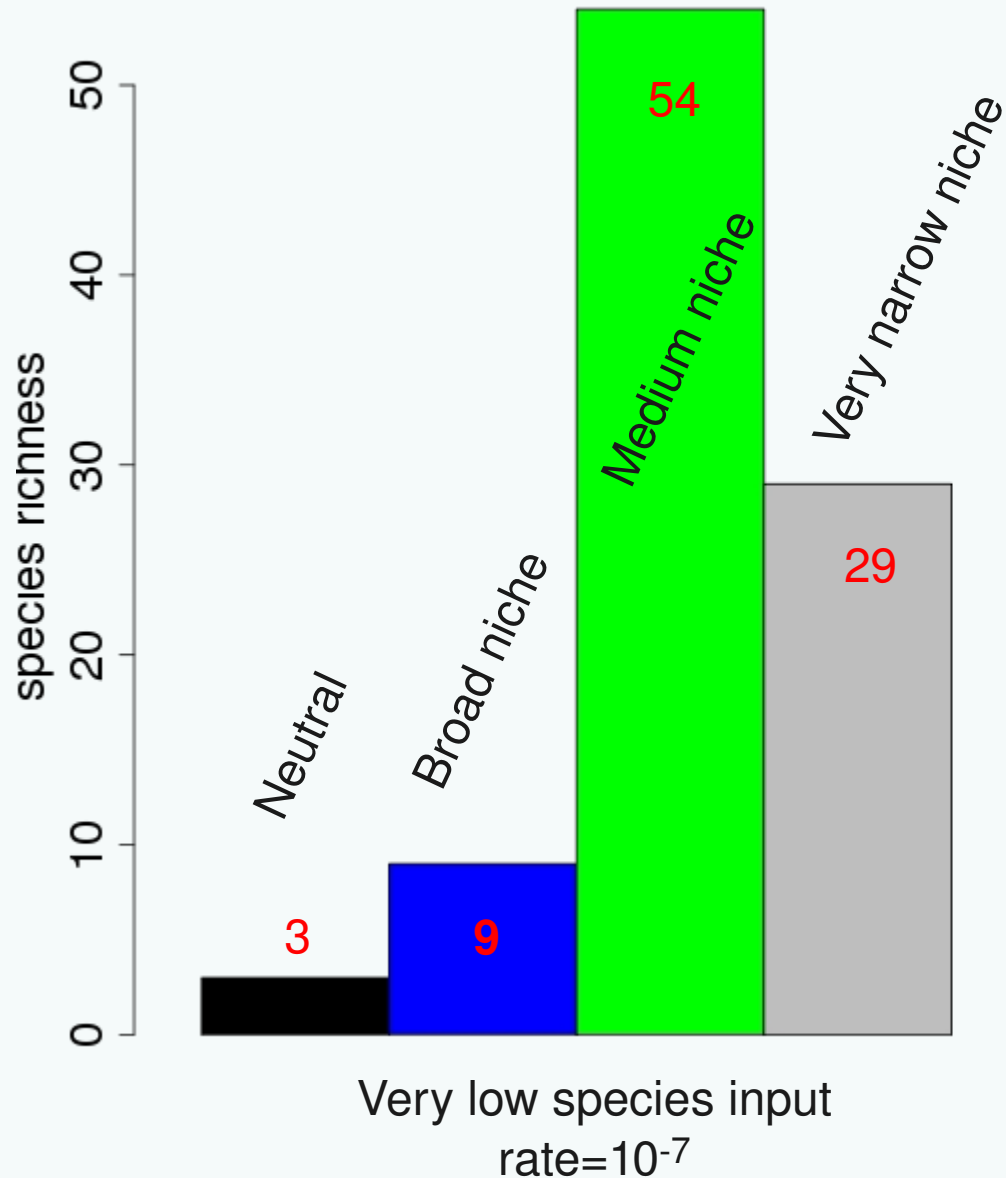


Species input vs. niche segregation

Diversity maintained by species input

Diversity maintained by niche segregation

Species richness in a simulated 50-ha plot --niche breadth

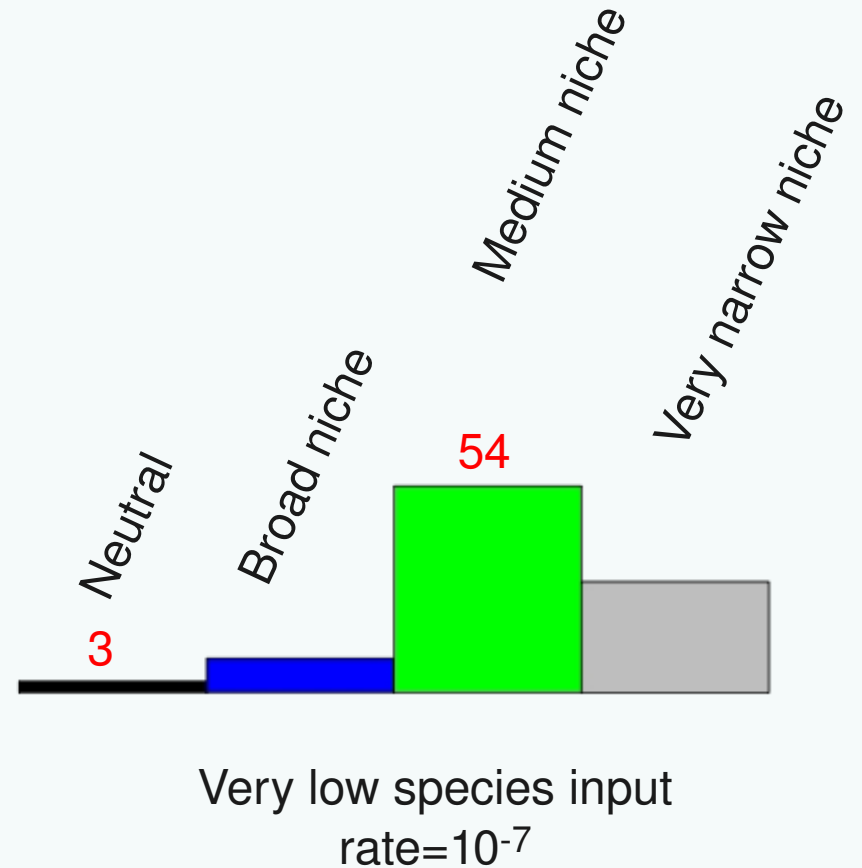
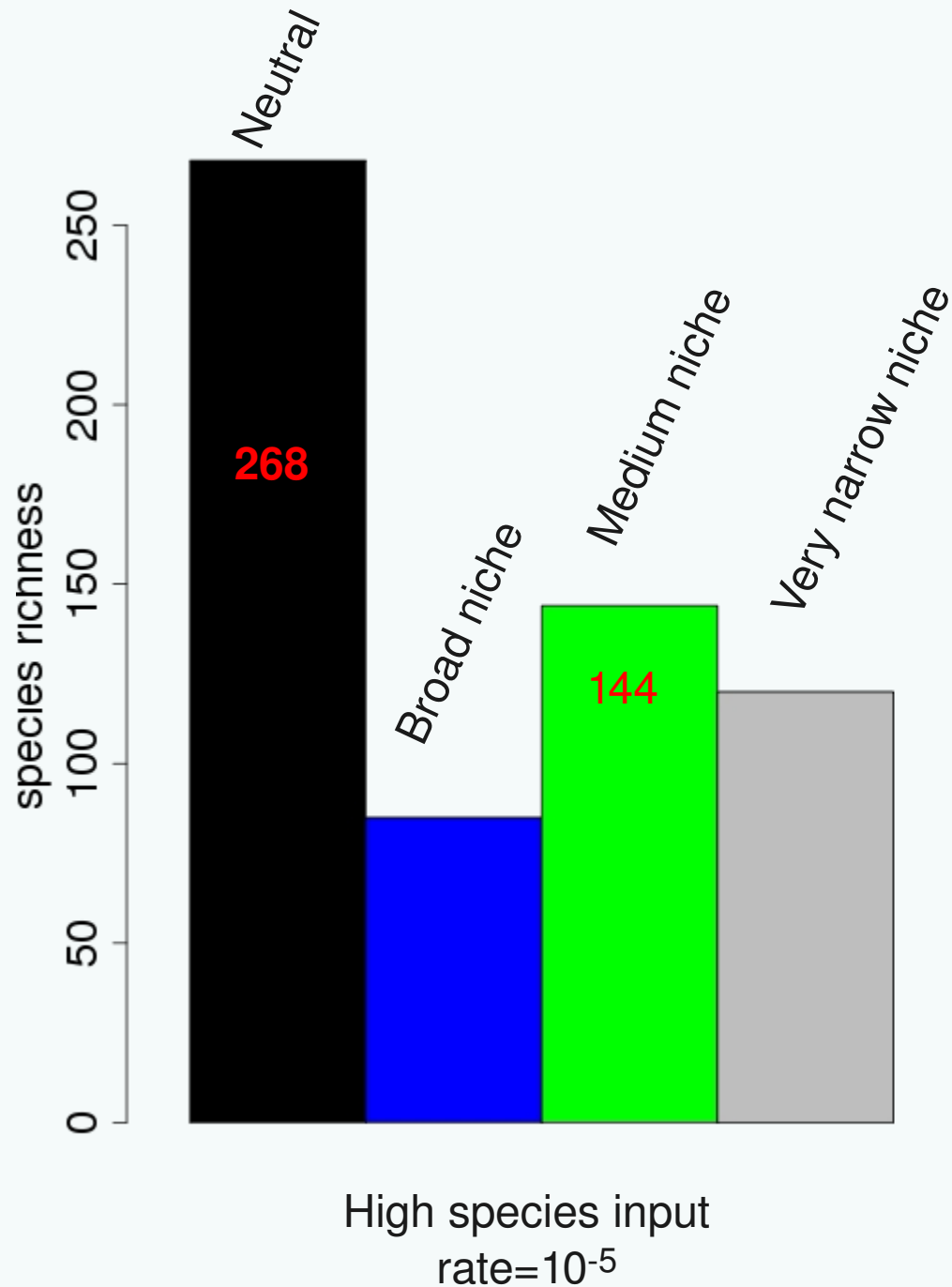


Observed after 20,000 generations
Not equilibria?

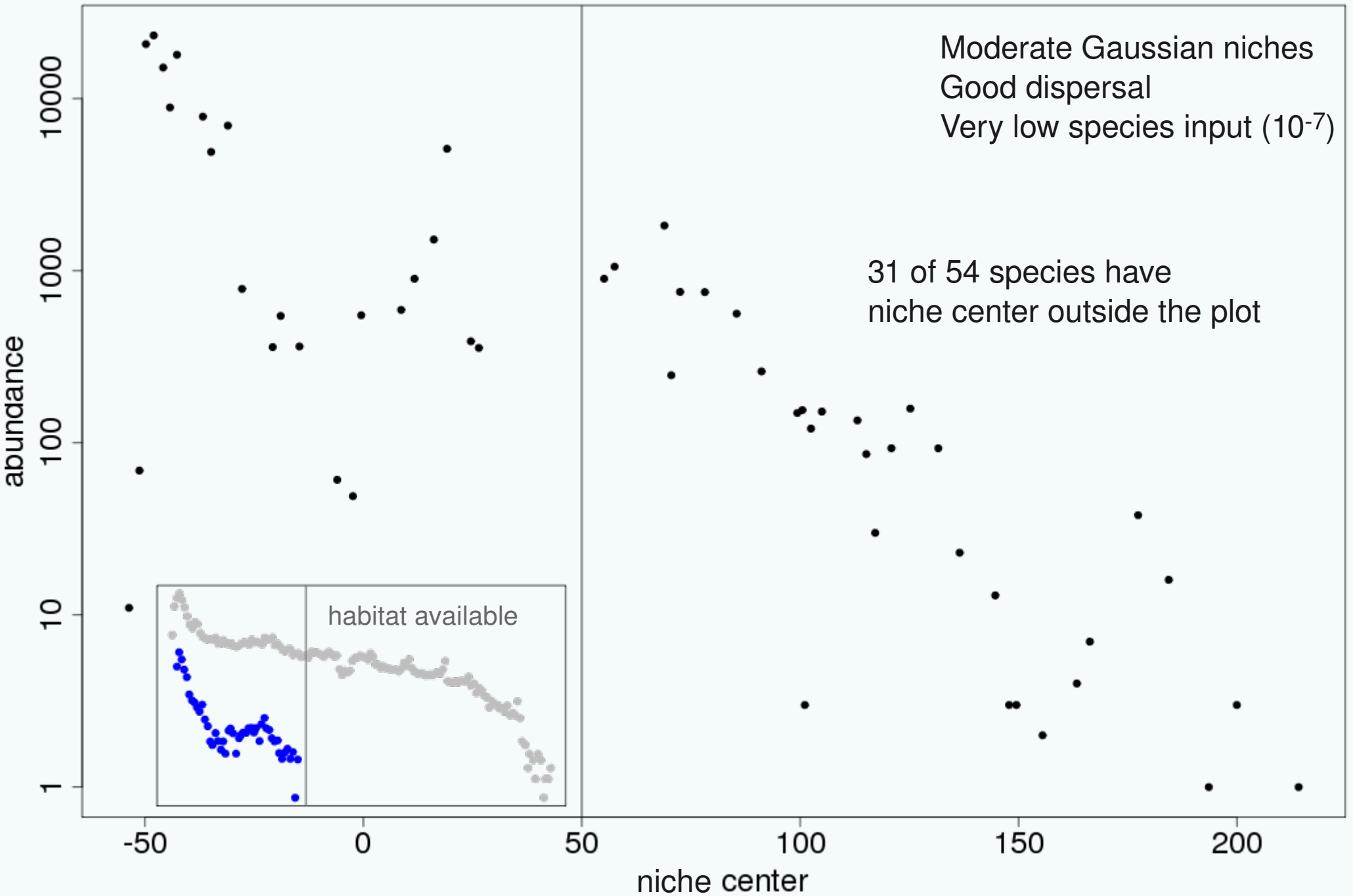
Species richness in a simulated 50-ha plot

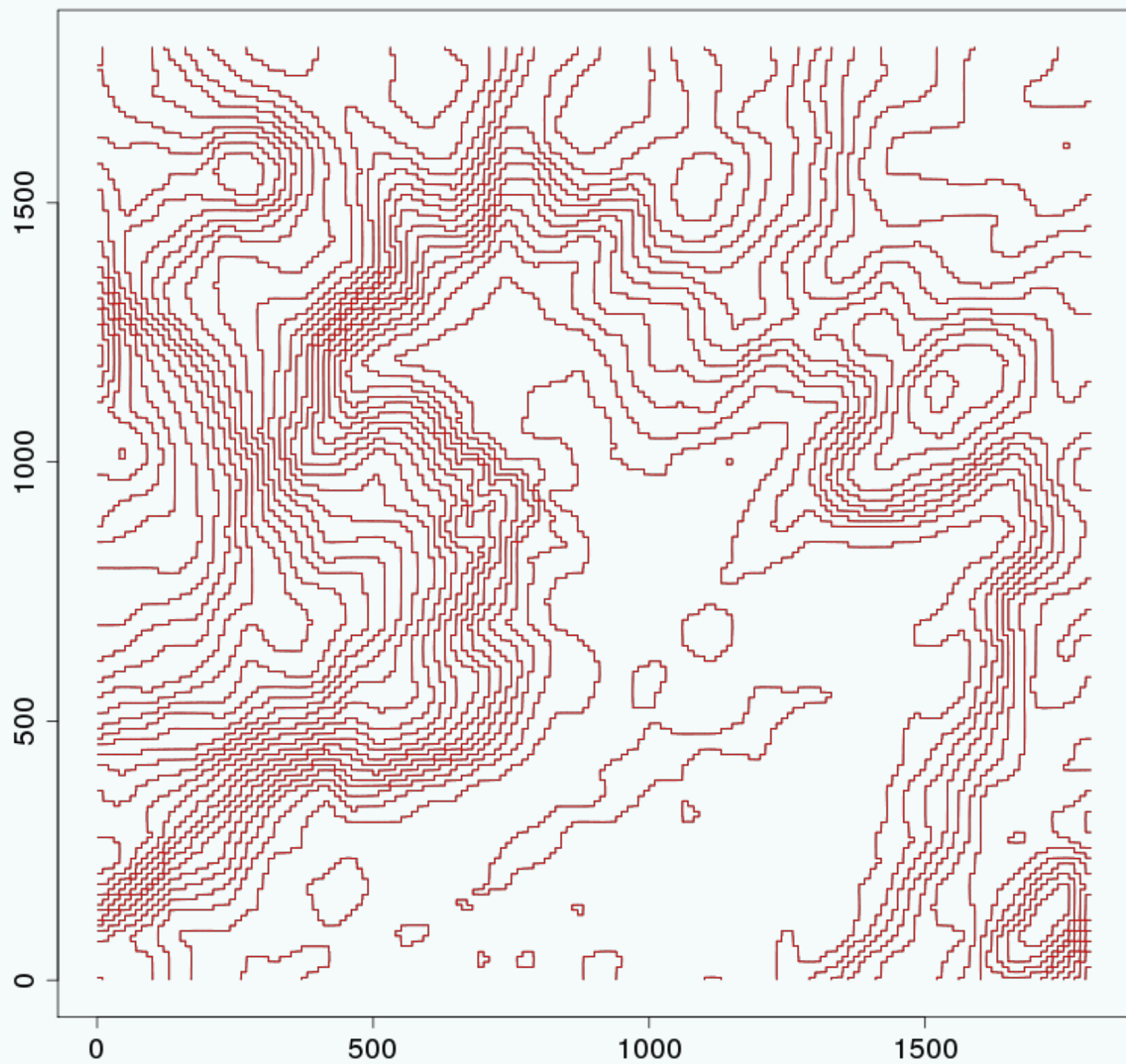
--species input

--niche breadth

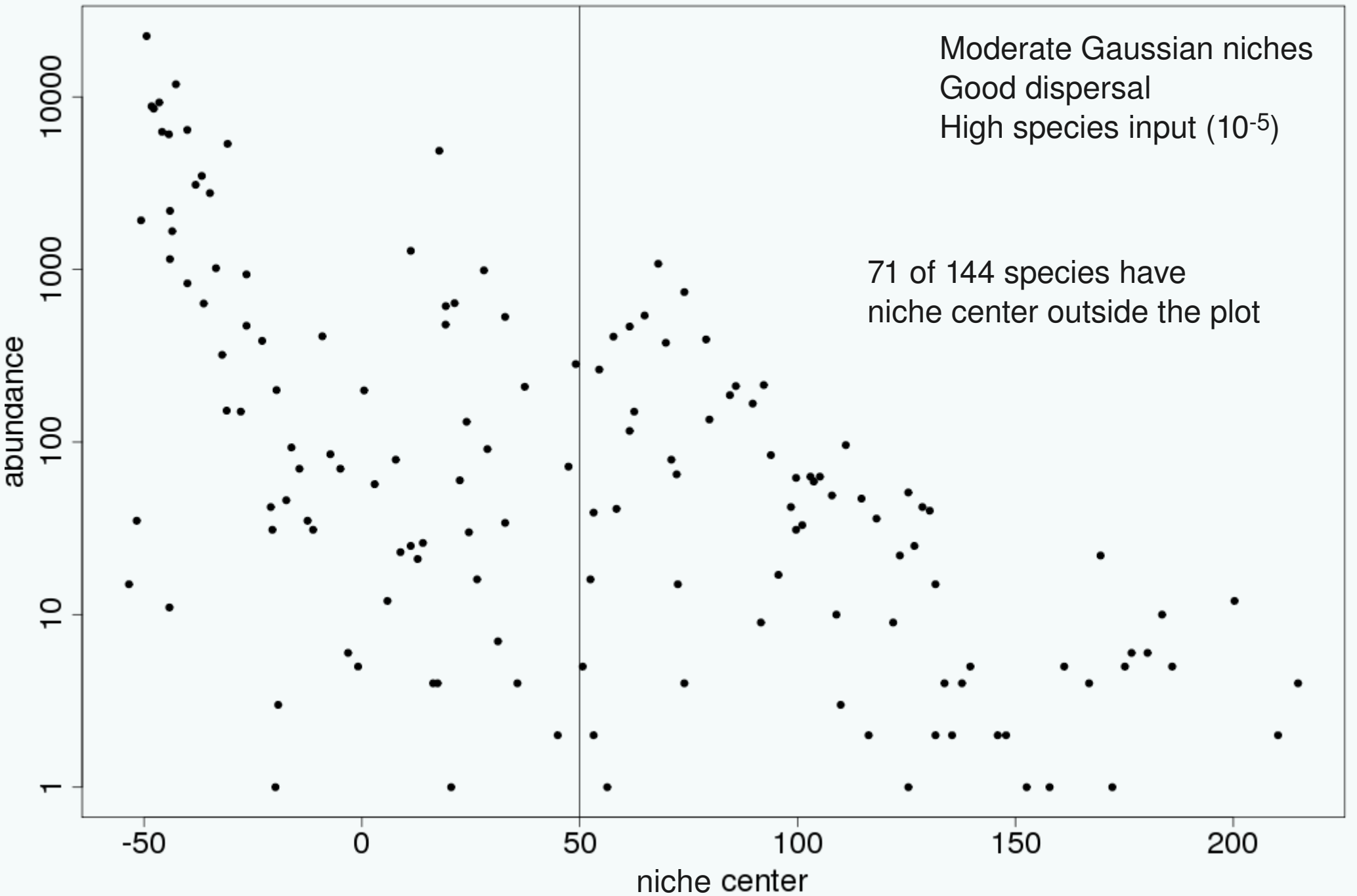


Abundance vs. species traits





Abundance vs. species traits



Species input vs. niche segregation

Diversity maintained by species input

- Diversity can be very high
- Many rare species
- Species traits weakly related to abundance
- Species differences are unimportant to diversity
- Community appears neutral



Diversity maintained by niche segregation

- At local scale, diversity is at best moderate
- Few rare species
- Species traits strongly related to abundance
- Coexistence theories matter and should predict diversity



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Dispersal and coexistence

- Immigrants compete with locally well-adapted species
- Substantial proportion of community may be sink populations
- Provides a mechanism by which neutral (or even sub-neutral) species can persist



Parmentiera cereifera

Summary III: Niches in a stochastic community

Dispersal and species input may be important to diversity, abundances, niche structure

Several features of diverse forests suggest species input from outside is the driving force

A full theory would predict rate of input needed to override local differences

A full theory must account for diversity 'outside'

Community size $\sim 10^{12}$ to 10^{20} individuals?

Rate of true speciation? 10^{-8} or 10^{-12} ??

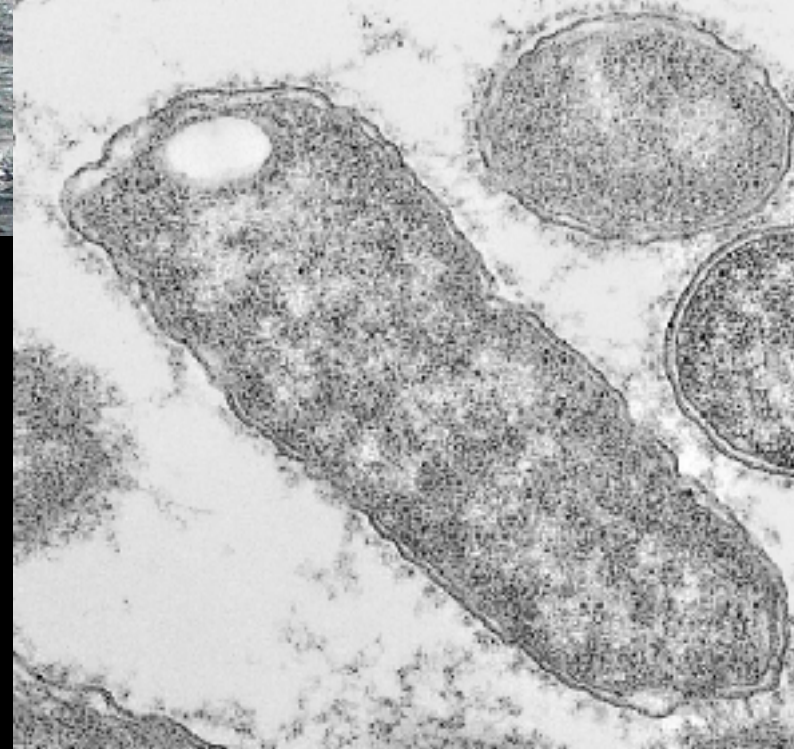
Niche segregation over $\sim 10^7$ km² ??

Past research

marine mammals



bacterial plasmids



birds



Current research:
(collaborators)

Global study of range size using published herbarium and plot databases

(B. Enquist, Ariz

B. Boyle, Ariz

R. Peet, UNCC

S. Dolins, Bradley

M. Schildauer, NCEAS

B. Thiers, NYBG

J. Cavender-Bares, UMinn

etc.)

CTFS Databases

(S. Dolins, Bradley & CTFS working group)



Current research:
(collaborators)

Demography individual tree species with Bayesian methods
(N. Ruger, M. Metz, post-docs; N. Kraft, student)

Models with density dependence
(T. Zillio, post-doc)

Range limits and climate across isthmus of Panama
(B. Engelbrecht, SFSU; B. Turner, STRI)

Seal demography
(R. Zeno, student)

Elephant seals



... the CTFS Working Group

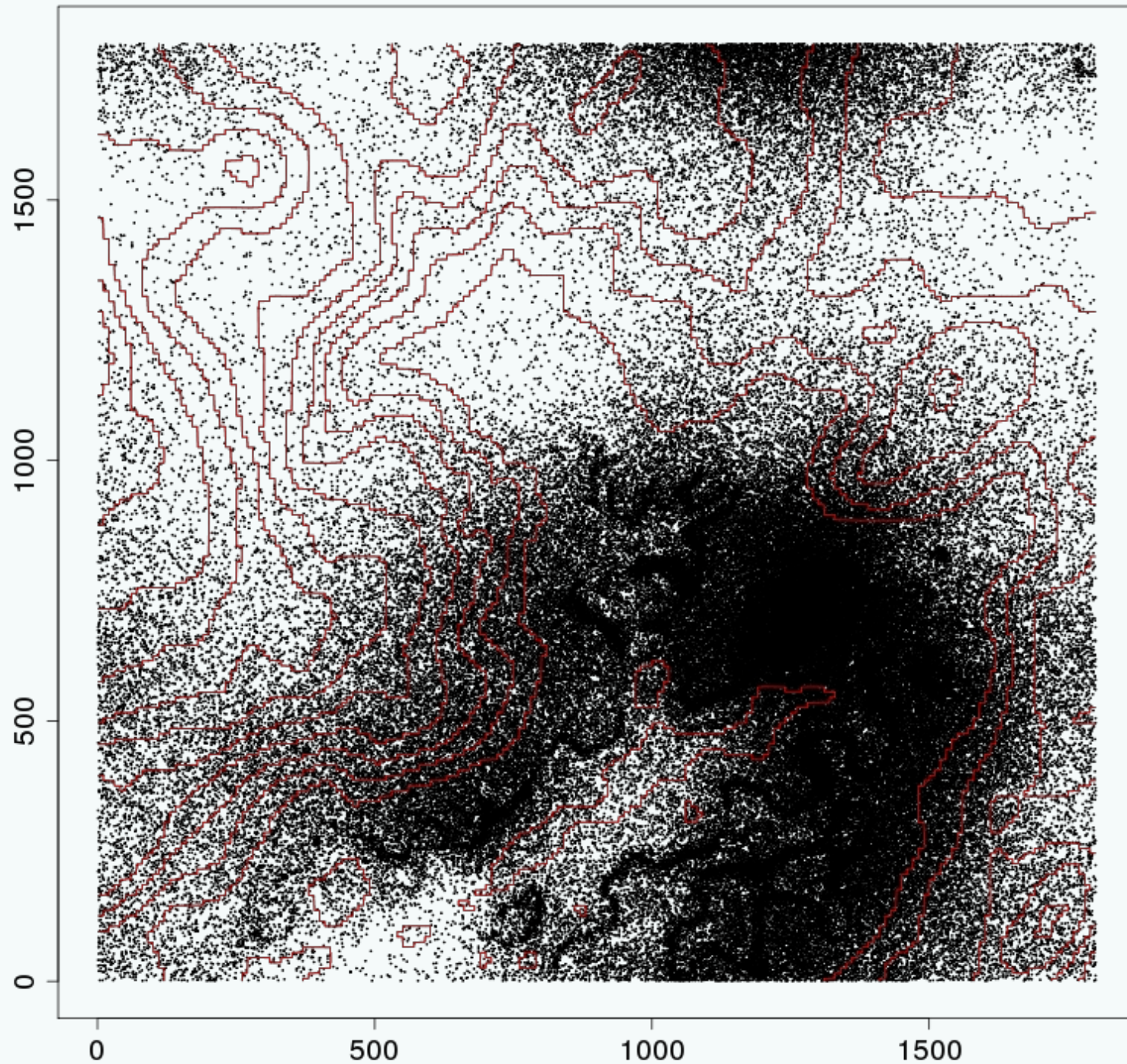


Center for Tropical Forest Science (CTFS)

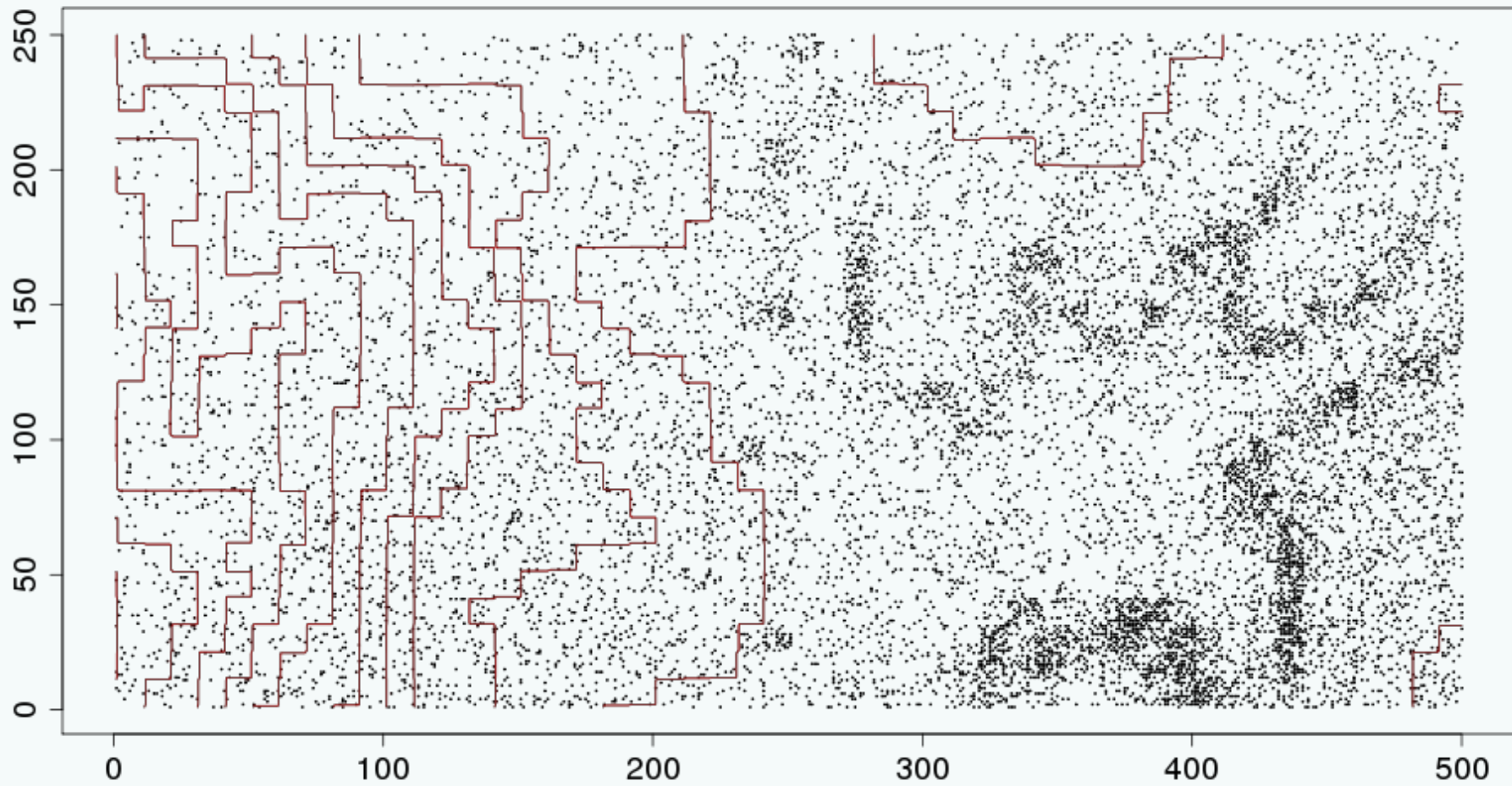


With good dispersal, species spread far from their niche optimum

species 69



species 69



Comparing observed patterns with models

Log-series abundance distribution with many rare species and high diversity
==> *only matched by simulations with high species input, rare species turnover*

Nearly all species have distributions spanning most of 50 ha
==> *only matched by simulations with dispersal > 100 m*

Many species show niche preferences around topography

Some with abrupt boundaries (little spillover)
==> *consistent with poor dispersal, or very high mortality difference*

Others with hazy boundaries (much spillover)
==> *consistent with good dispersal and moderate mortality difference*

But some species are generalists
==> *mixing of specialists and generalists offers more intrigue*

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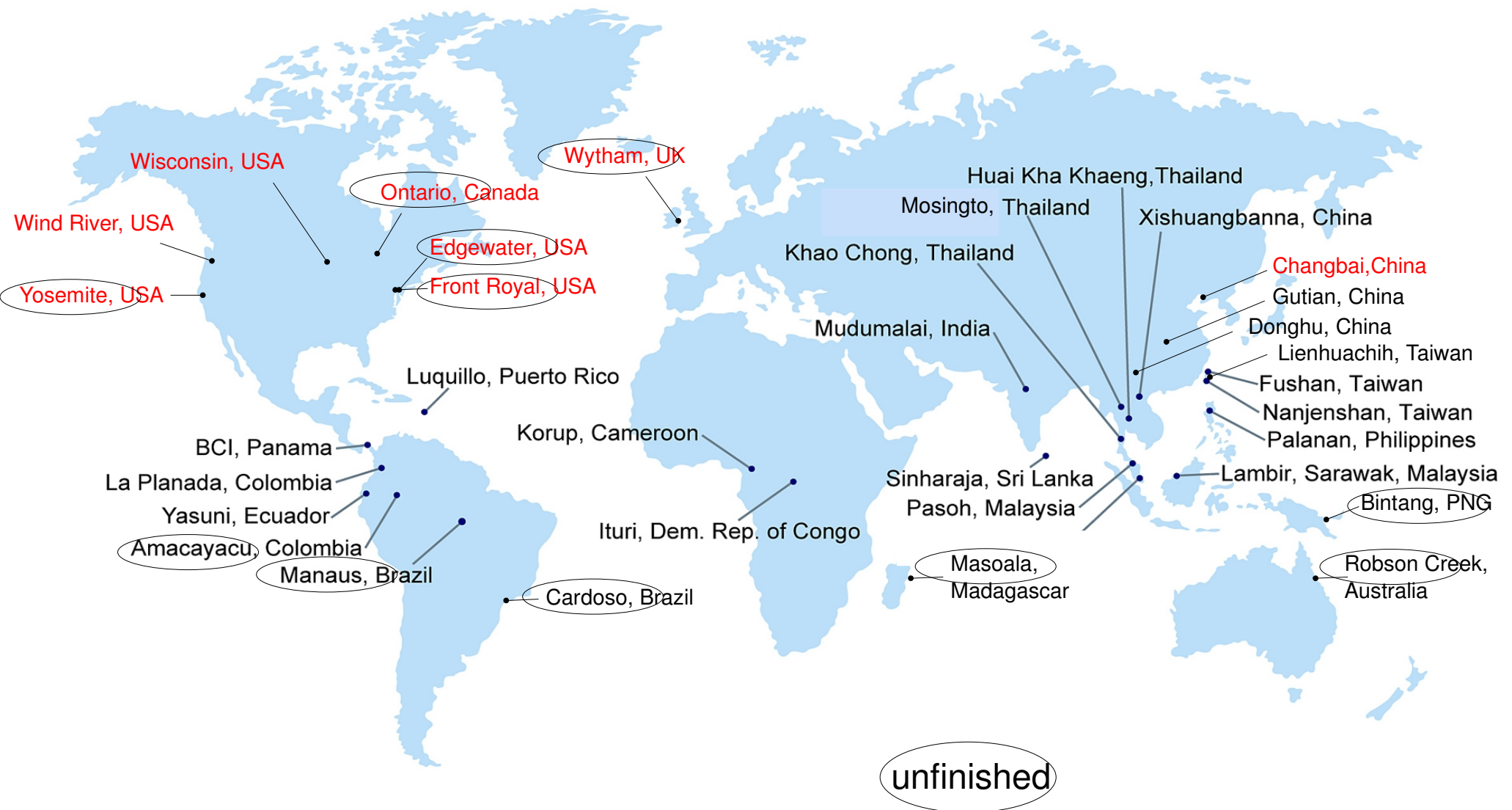
Some with abrupt boundaries (little spillover)
==> *consistent with poor dispersal, or very high mortality difference*

Others with hazy boundaries (much spillover)
==> *consistent with good dispersal and moderate mortality difference*

But some species are generalists
==> *mixing of specialists and generalists offers more intrigue*

Global Forest Observatory Network (GFON)

~8,000 species
3.323 million trees monitored currently



... the CTFS Working Group



Center for Tropical Forest Science (CTFS)

What would Peter Chesson say?

What would David Tilman say?

Peter Grubb's question

Neutral theory

- Local scale fits: abundance, diversity

- Wide scale and long-term seem not to fit

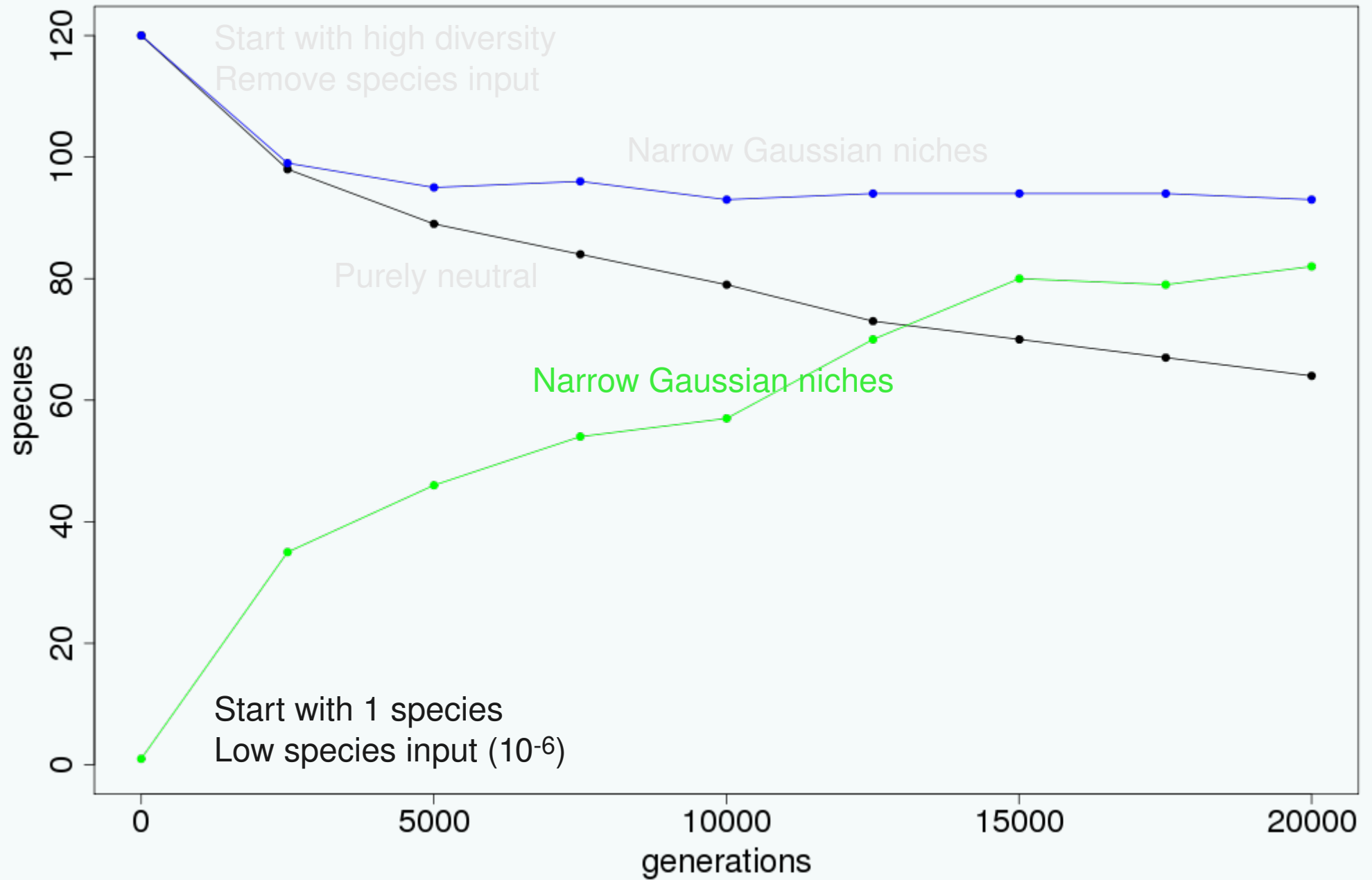
- Reconciling:

 - => species are different, but at much wider scales

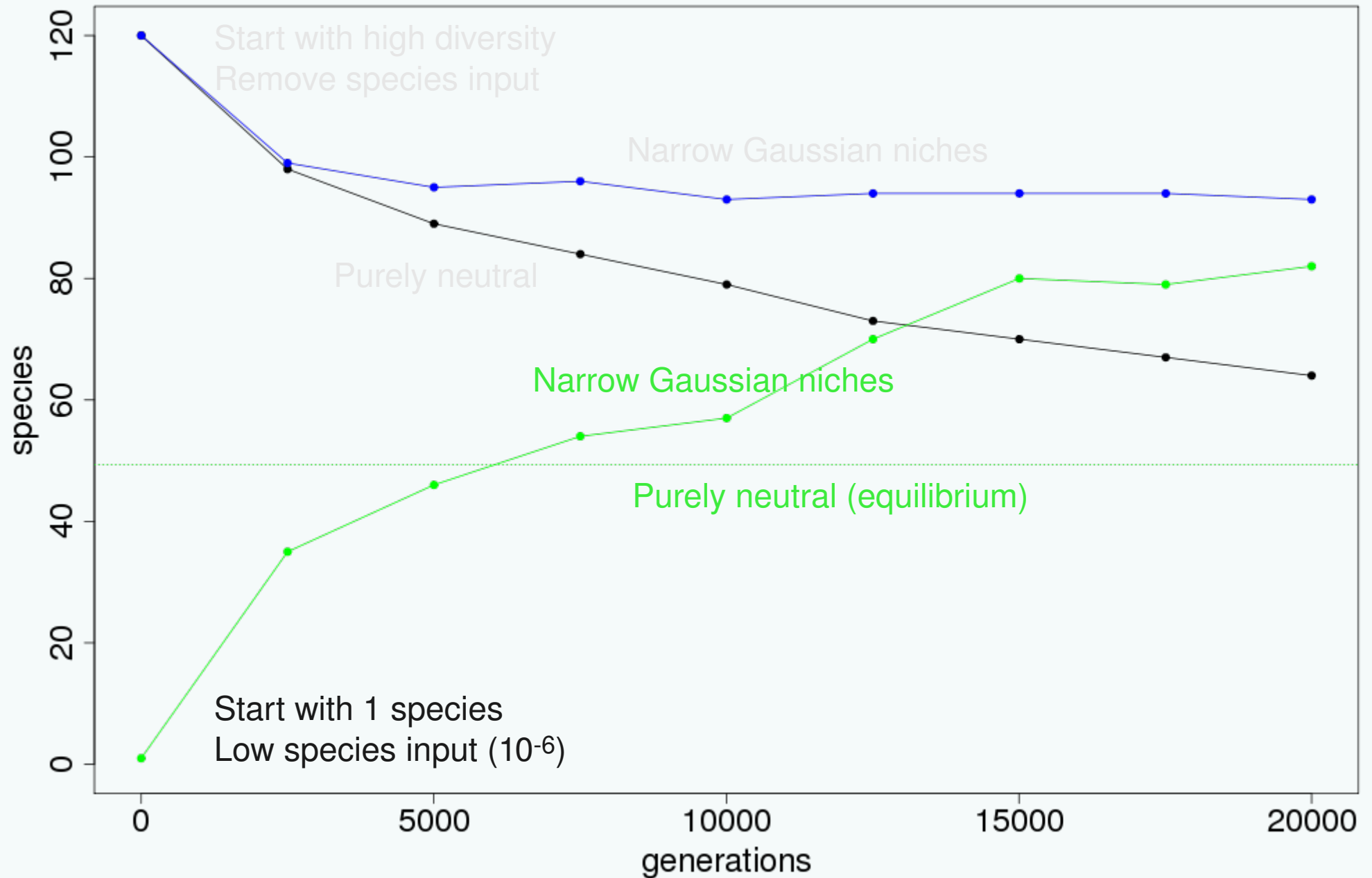
 - => locally, many species persist due to immigration

"Hubbell et al. (1990) presented data suggesting that rare tree species in neotropical forests may generally occur as sink-populations." (Eriksson et al 1996)

Change of species richness through time in stochastic models



Change of species richness through time in stochastic models



Country	Plot	Censuses	Species	Trees	Measurements
Colombia	Amacayacu	1	707	6324	6324
Panama	bci	6	319	368069	1593994
Panama	sherman	3	238	24428	76083
Panama	cocoli	3	176	9464	31278
Singapore	Bukit Timah Big Trees	1	414	10242	11019
Singapore	Bukit Timah Primary	5	378	18245	69807
Singapore	Bukit Timah Secondary	2	206	4648	13154
Brasil, Brazil	restinga	1	116	15301	18036
China	CBS	1	53	45394	65602
United States	CRC	1	39	2154	2261
Taiwan	Fushan	1	110	114508	166591
Malaysia	Pasoh	5	937	413443	1635447