

Causes of tree distribution patterns

simulating spatial patterns from individual biology:
birth, death, dispersal

BES Symposium
Tropical Forest Spatial Patterns
September 2006

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Smithsonian Tropical Research Institute

The Hubbell approach

Biology of individuals:

Mortality
Reproduction
Growth
Dispersal
Speciation



Community patterns:

Diversity
Abundance
Spatial patterns
Species-area relationship

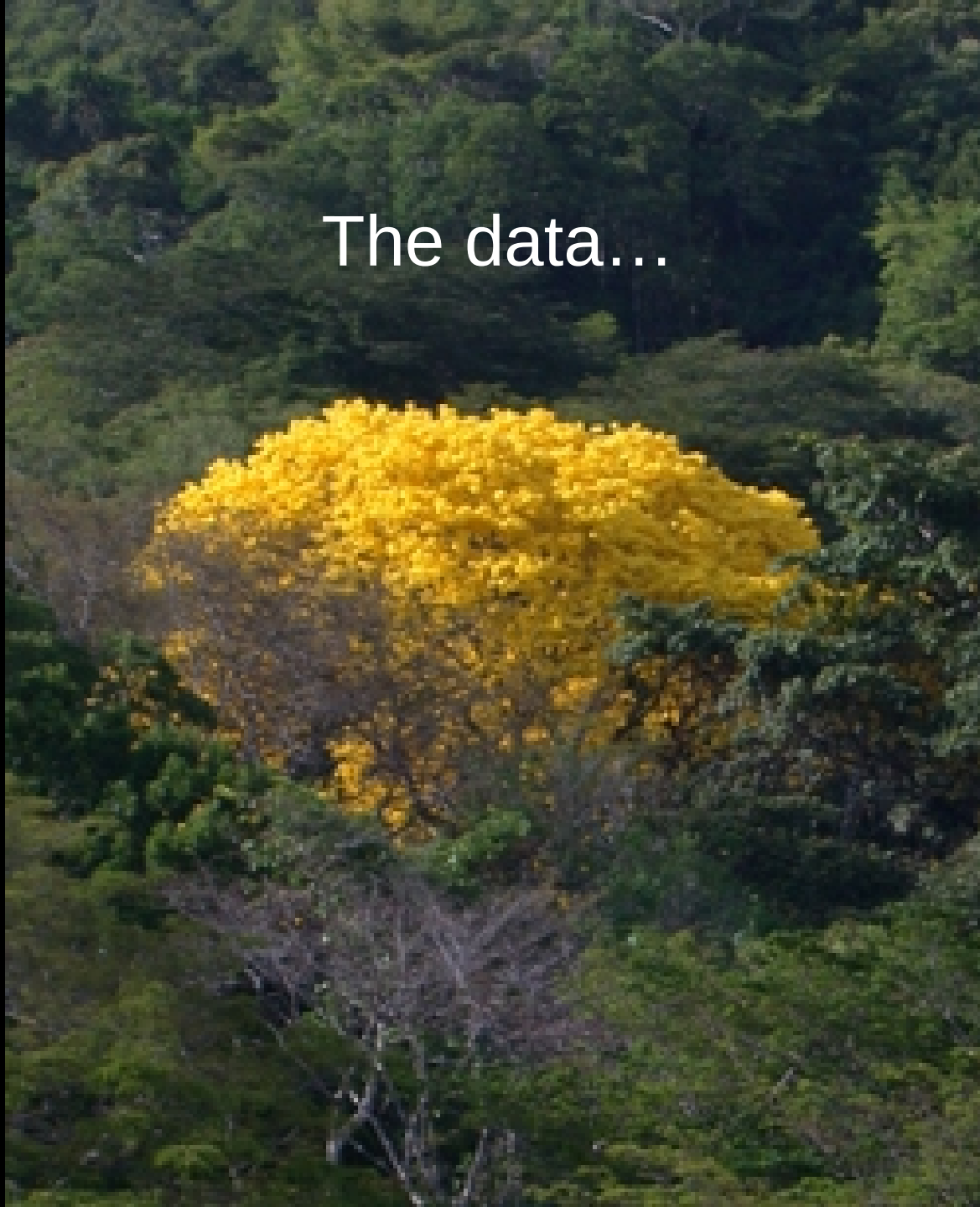
remove emphasis on neutrality

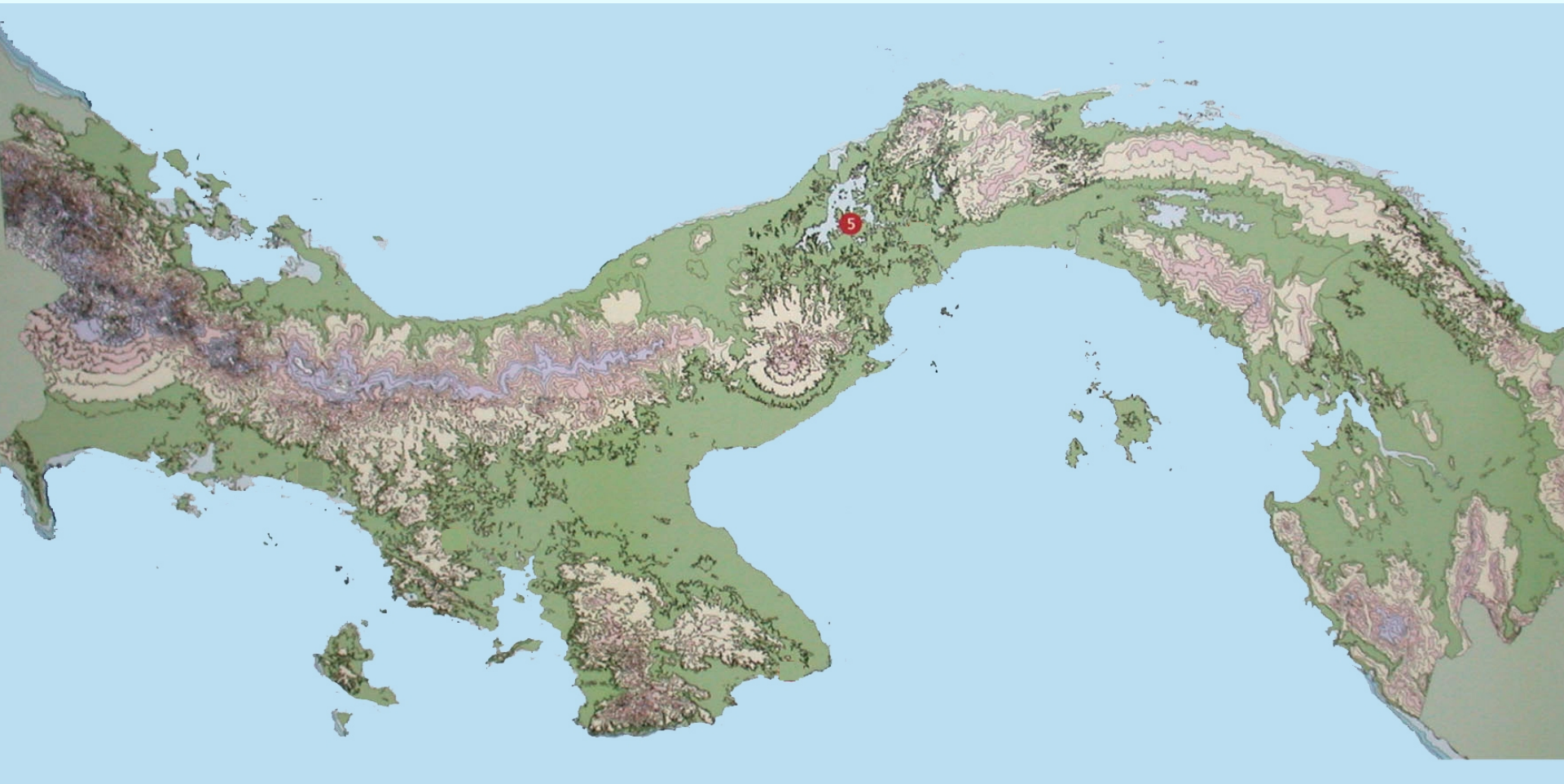
The goal

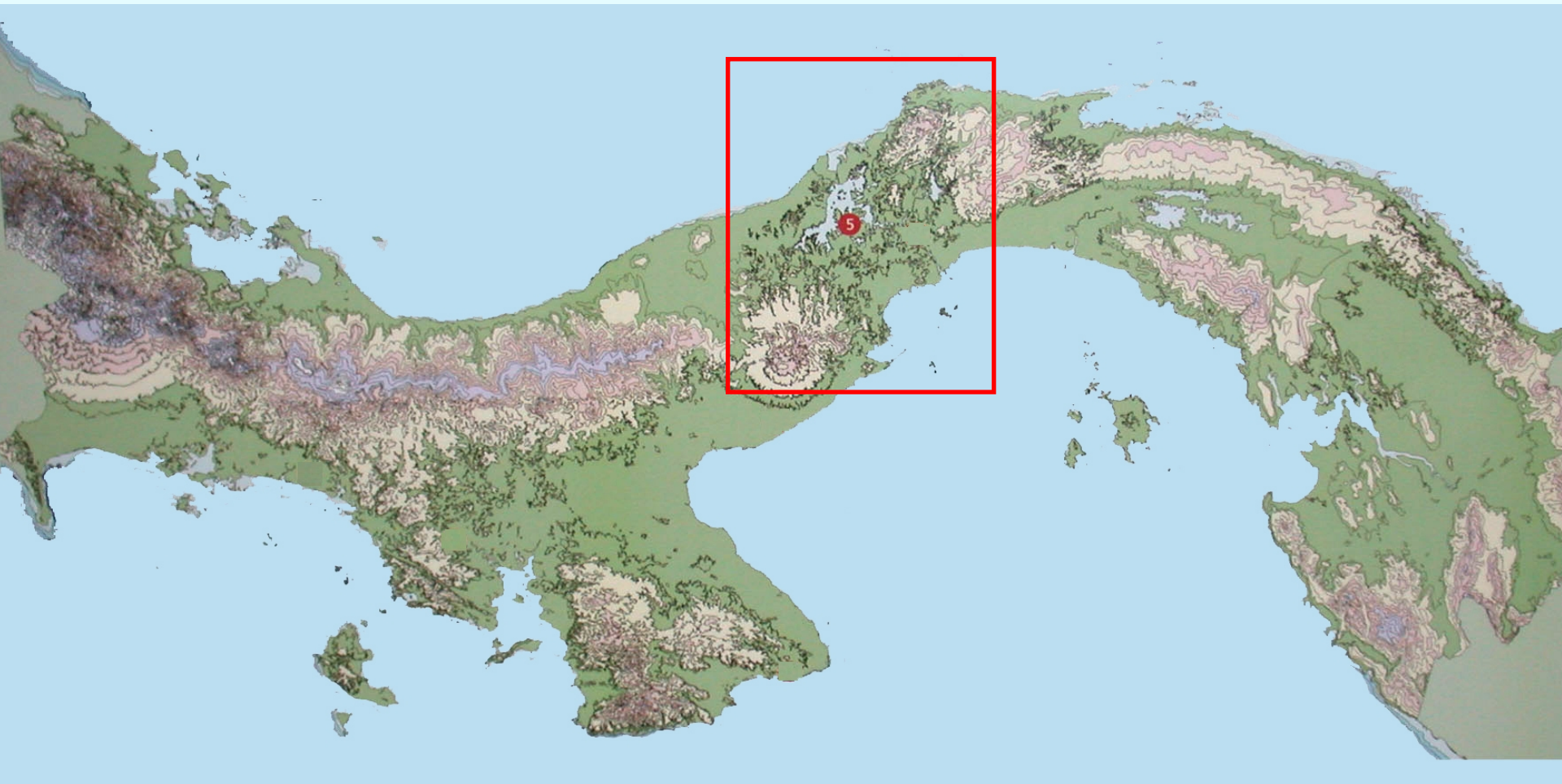
- Simulate dispersal and mortality
- Generate spatial patterns
- Compare to observed

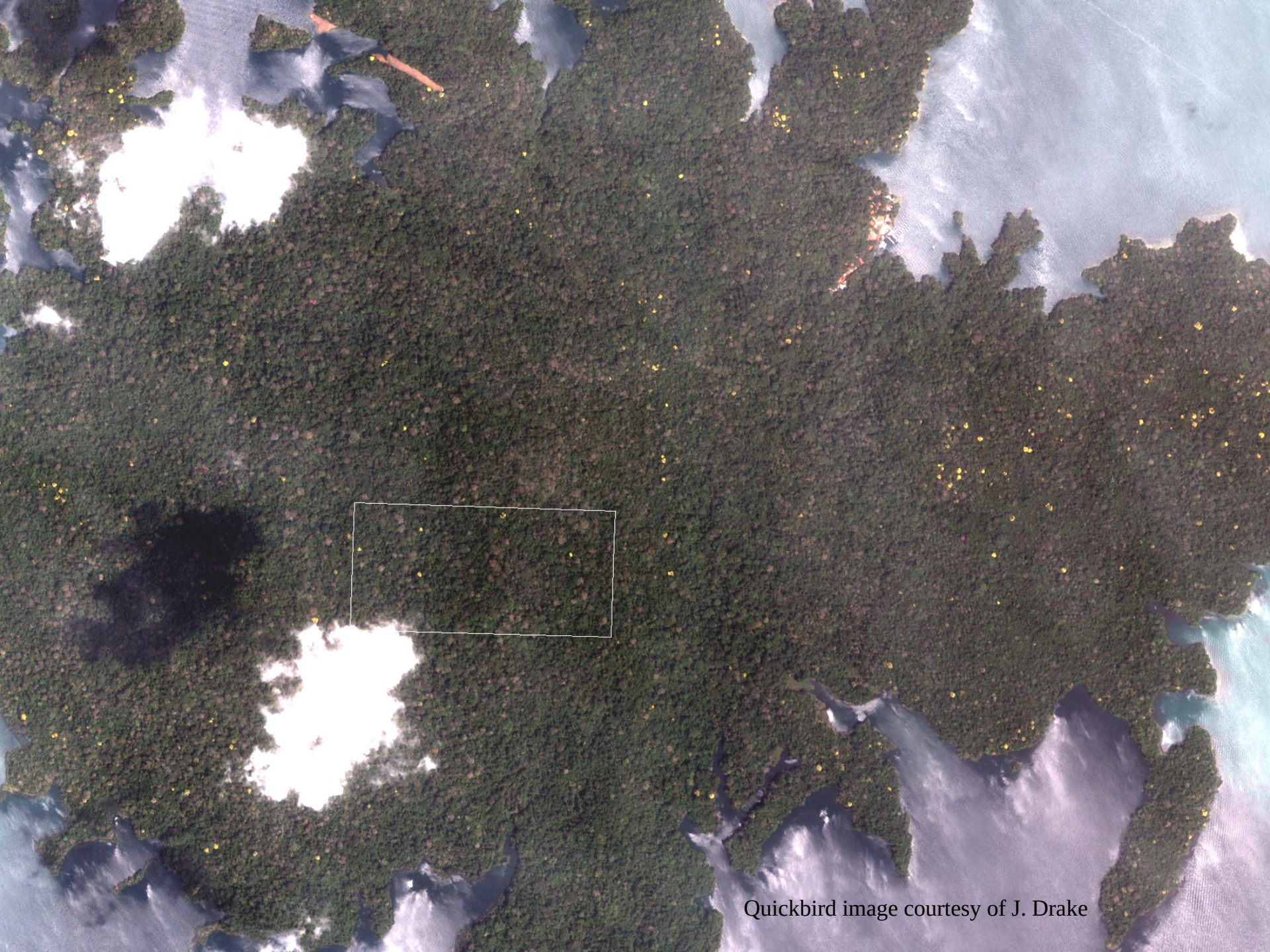


The data...







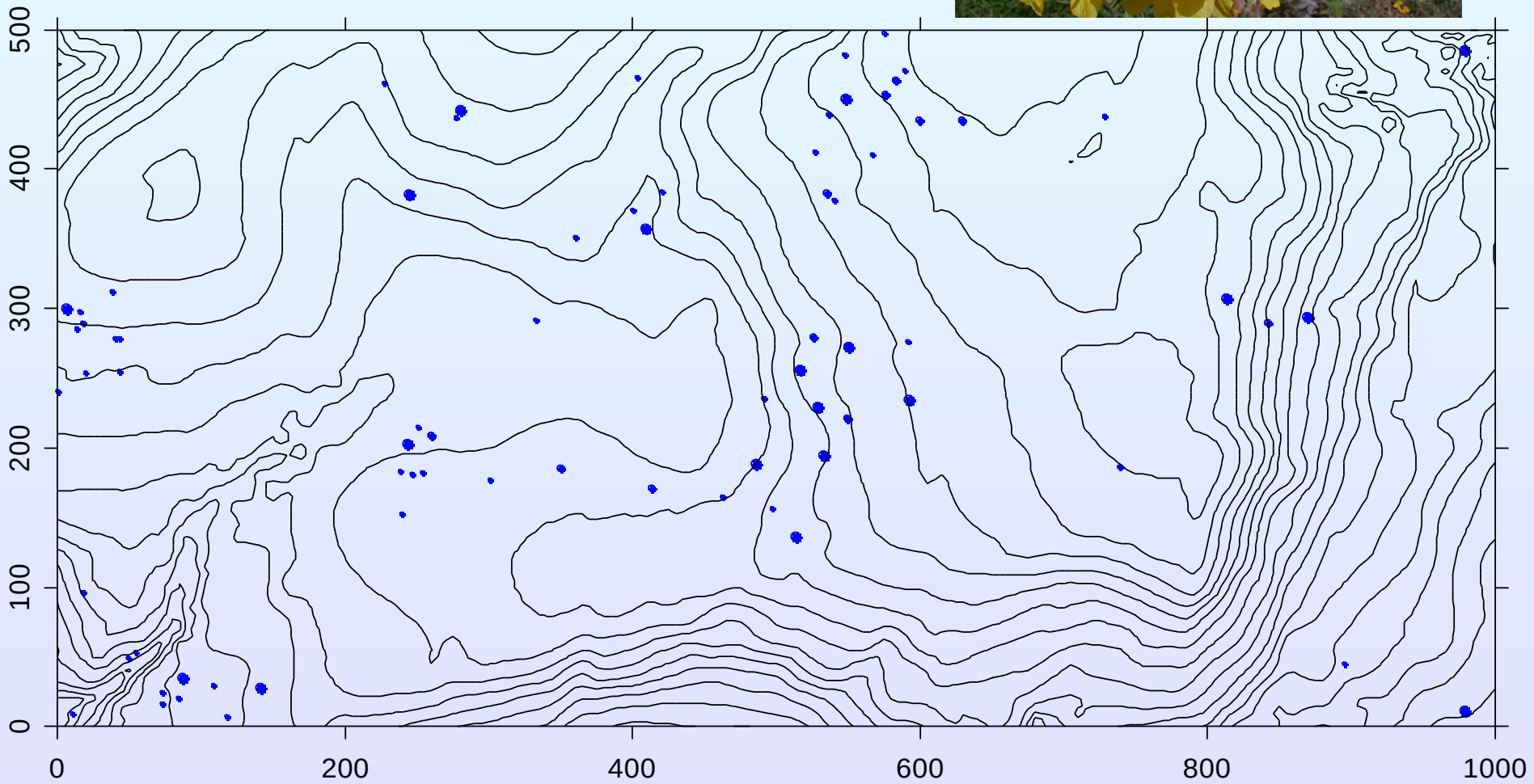


Quickbird image courtesy of J. Drake

Barro Colorado 50 ha plot (Panama)

S. Hubbell
R. Foster
R. Condit
R. Perez
S. Lao

• *Tabebuia guayacan*





Yasuni

WCMC vegetation map

Yasuni 25 ha plot, Ecuador

full census ≥ 1 cm dbh

1150 species

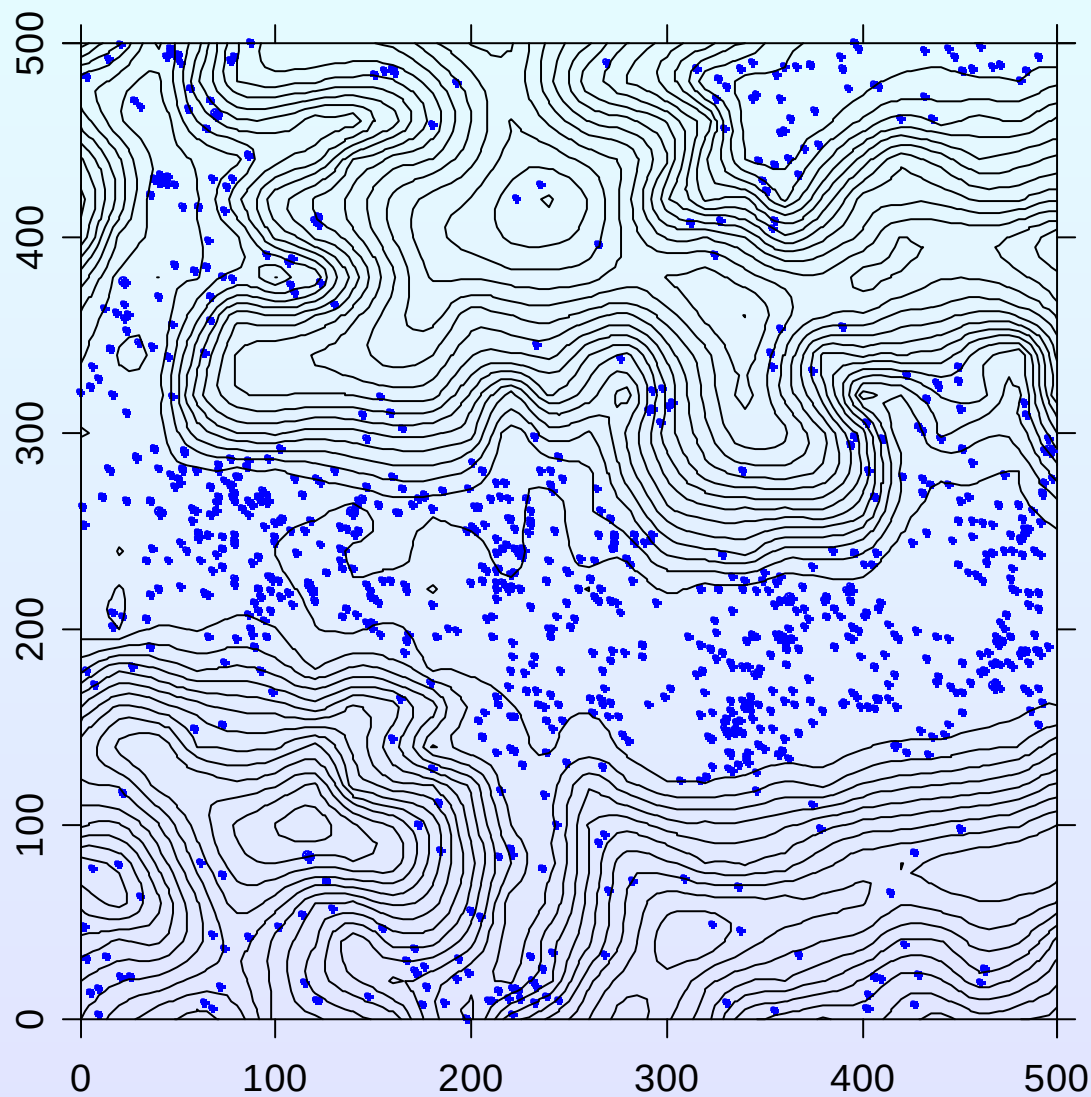
152000 trees

R. Valencia

R. Foster

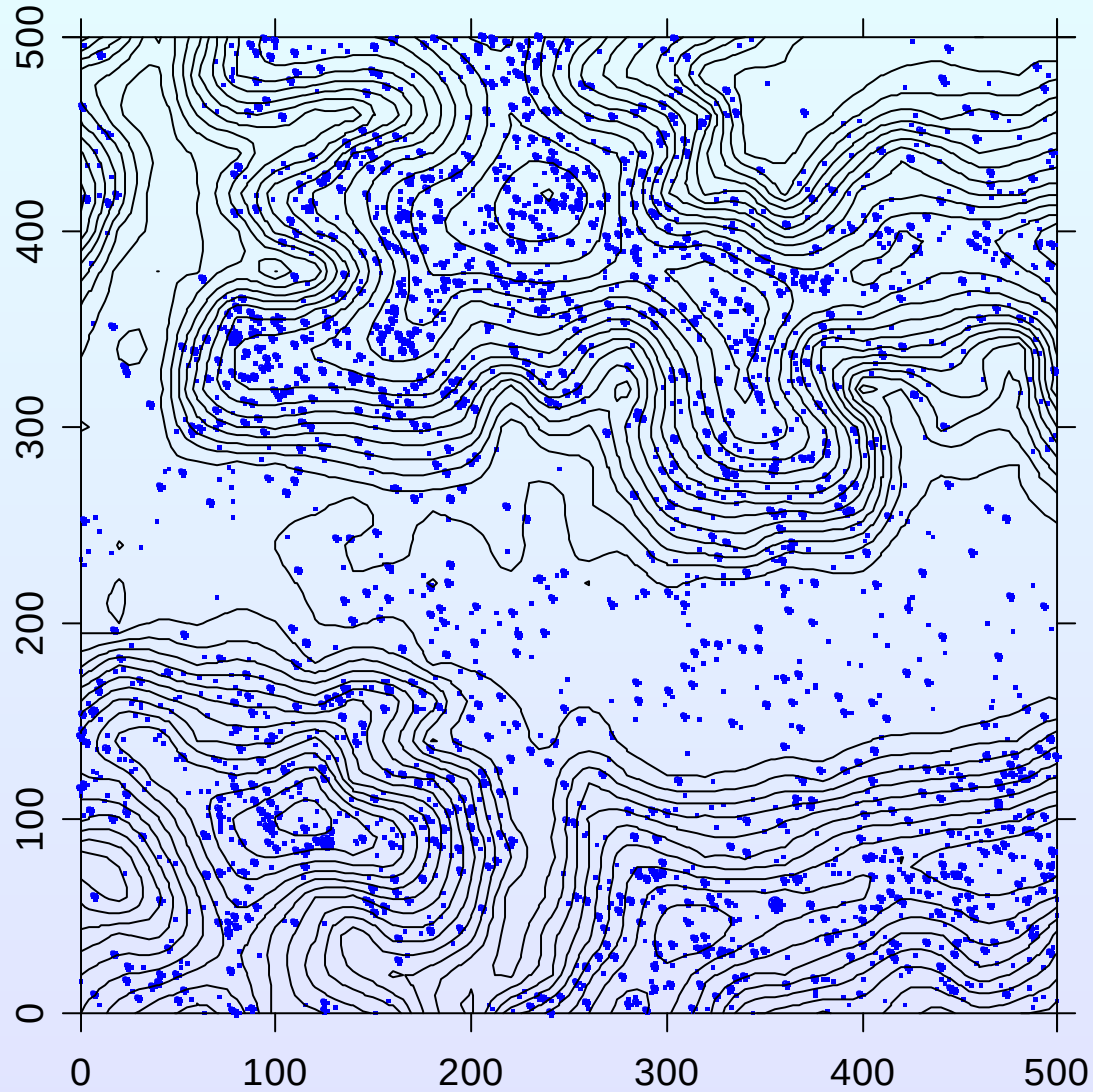
G. Villa

Neea 'bajio'
Nyctaginaceae



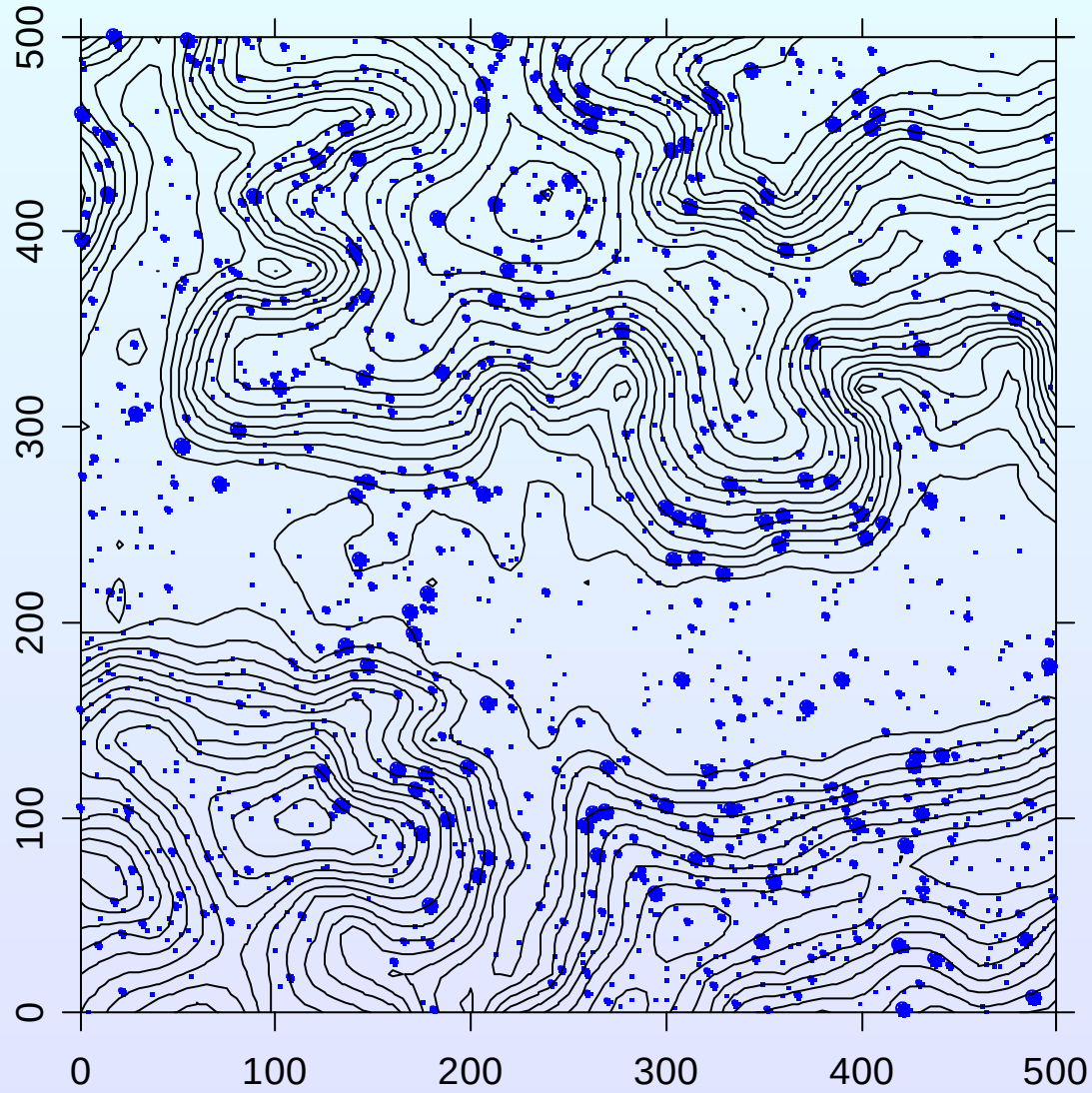
Yasuni 25 ha plot
Ecuador

Matisia malacocalyx
Malvaceae



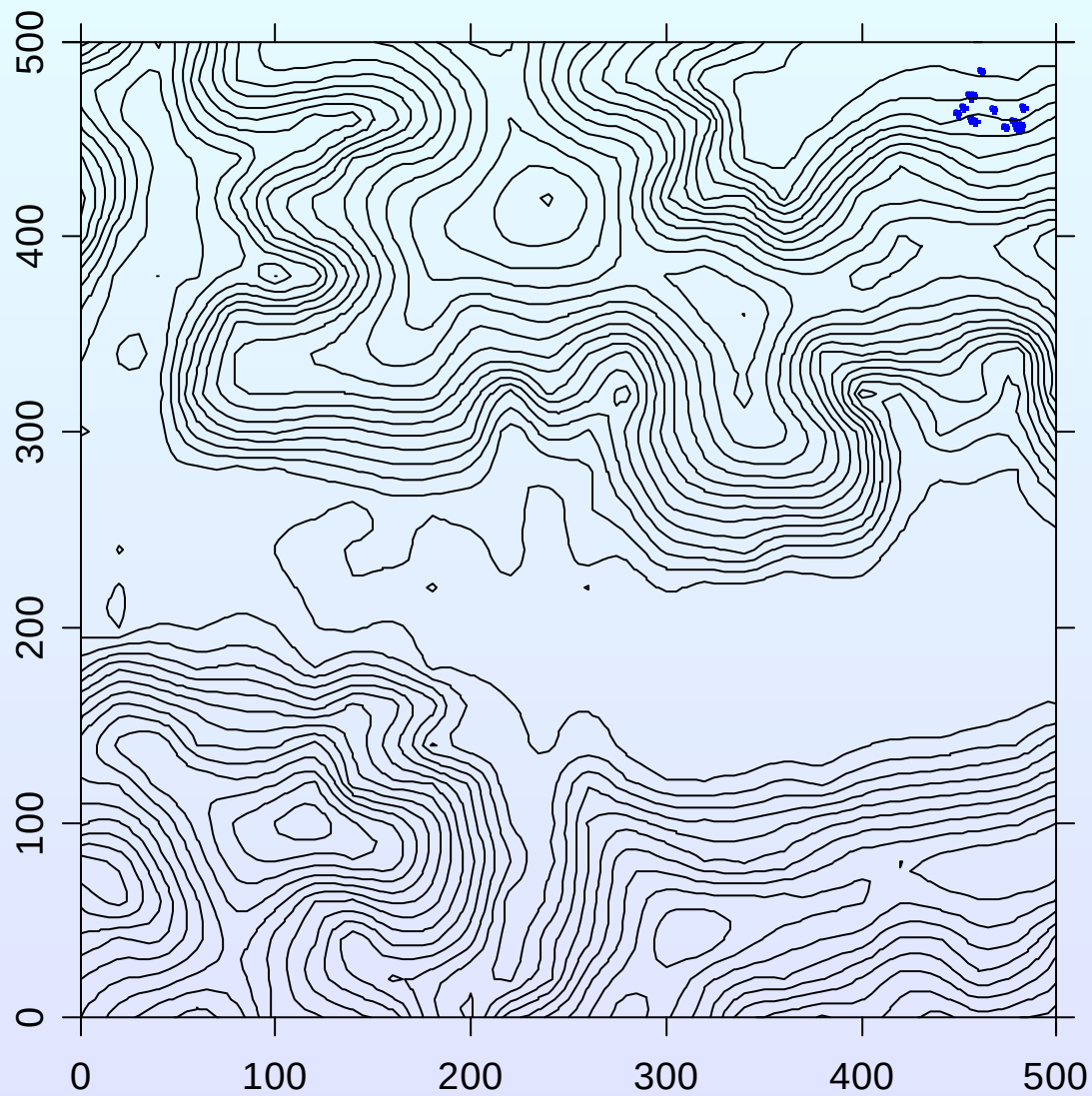
Yasuni 25 ha plot
Ecuador

Eschweilera coriacea
Lecythidaceae



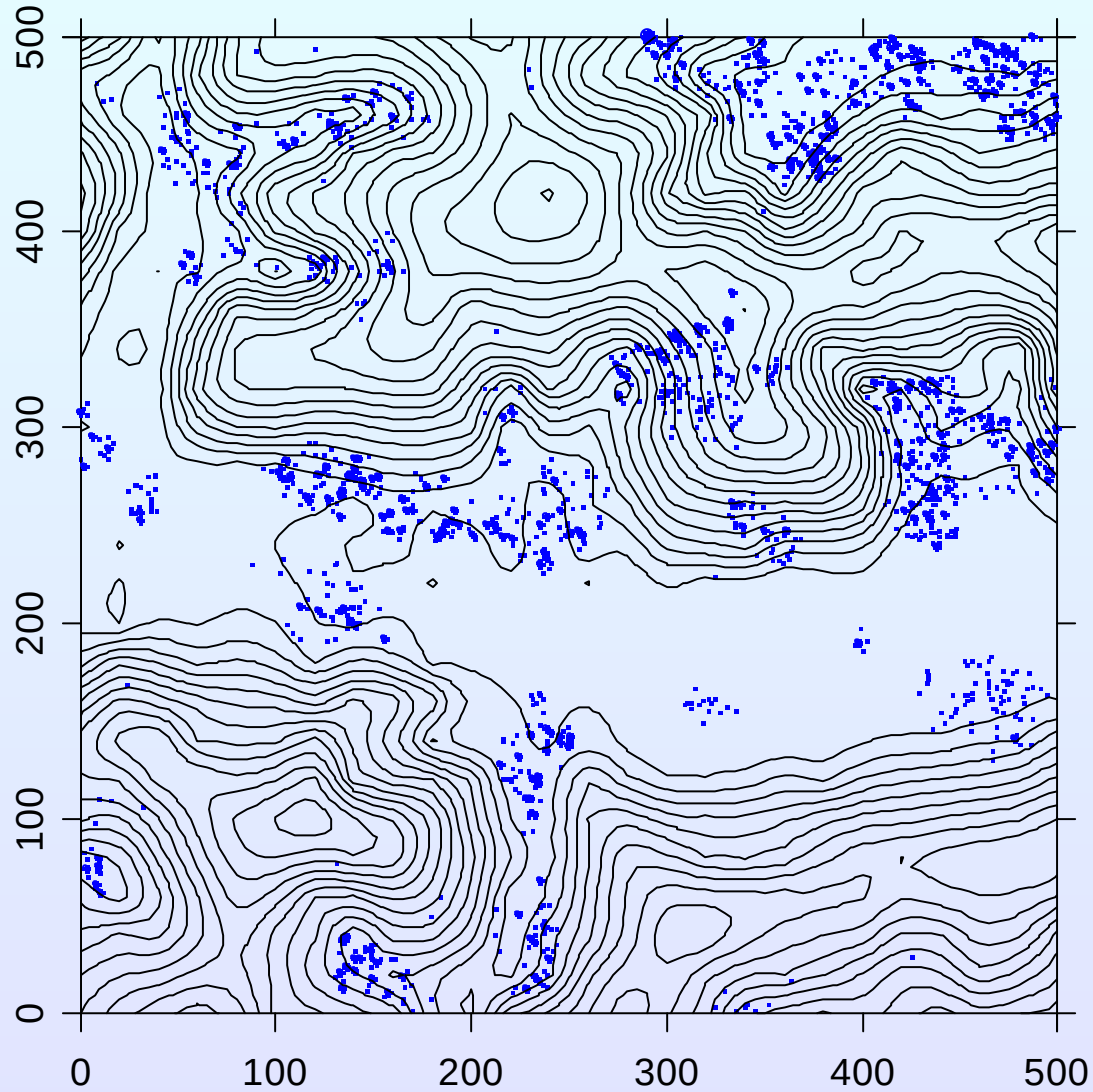
Yasuni 25 ha plot
Ecuador

Esenbeckia 'lisa'
Rutaceae



Yasuni 25 ha plot
Ecuador

Rinorea viridifolia
Violaceae



The entire genus has no dispersal mechanism

The theory (model)...



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

The Voter 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 Voter Model

death

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

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 Voter 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 Voter 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 Voter Model

(generalized)

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 Voter Model

(generalized)

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

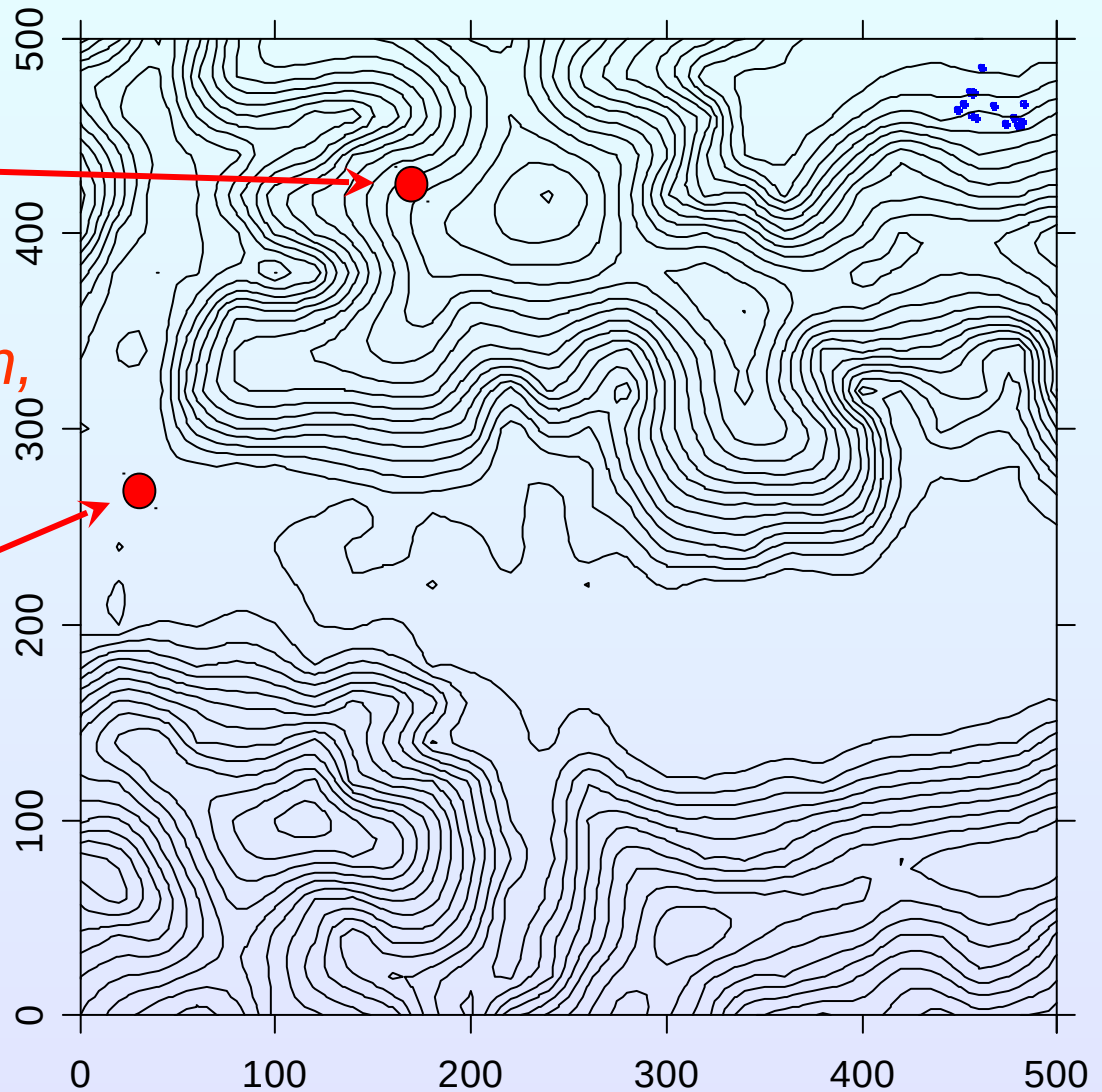
speciation
or
immigration

Habitat association in the Voter Model

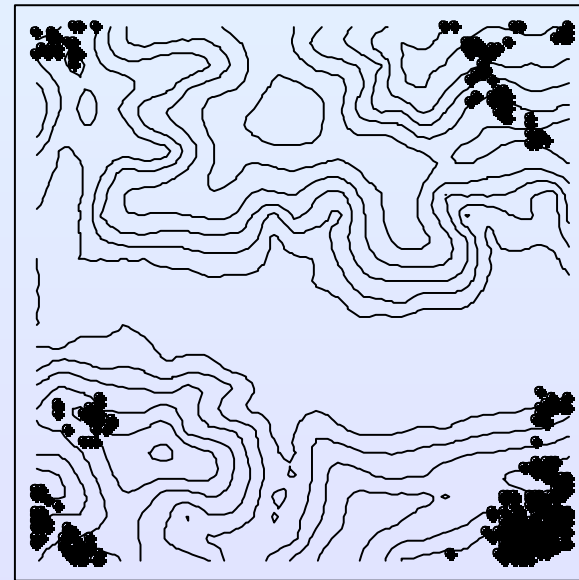
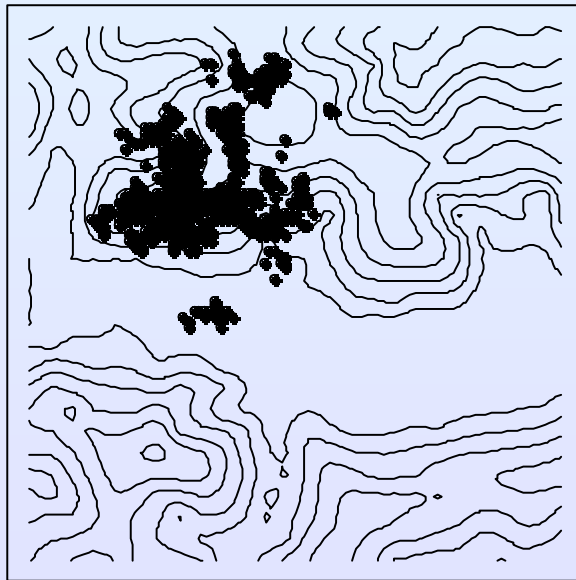
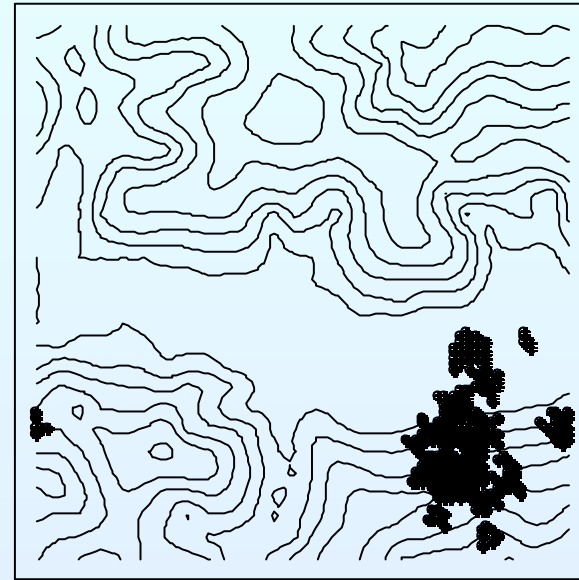
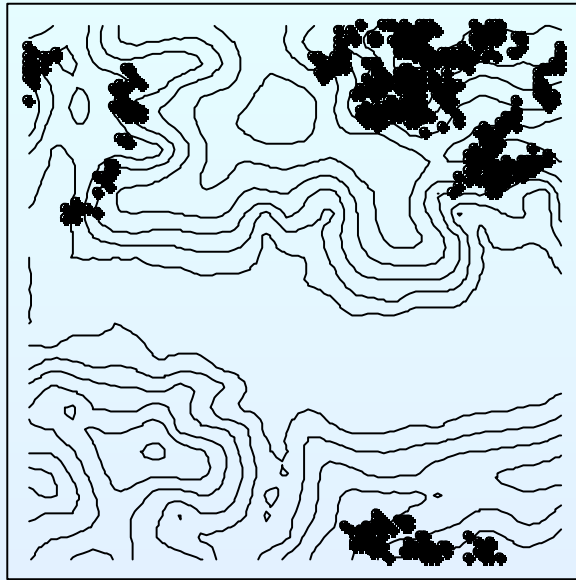
choose tree at random
to die

accept choice with prob= m ,
where $m=f(\text{elev})$

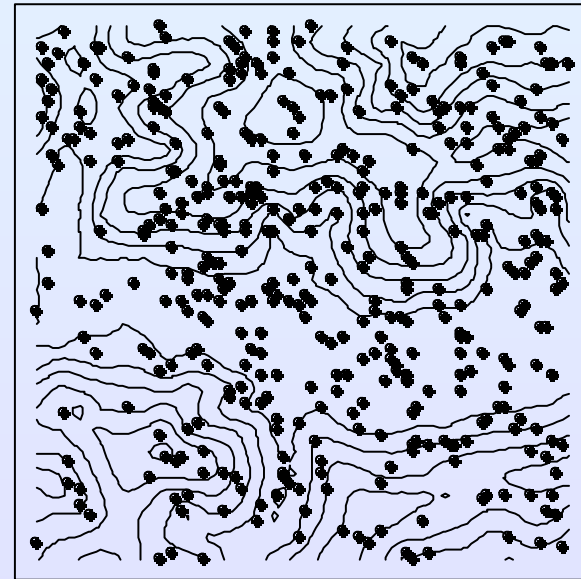
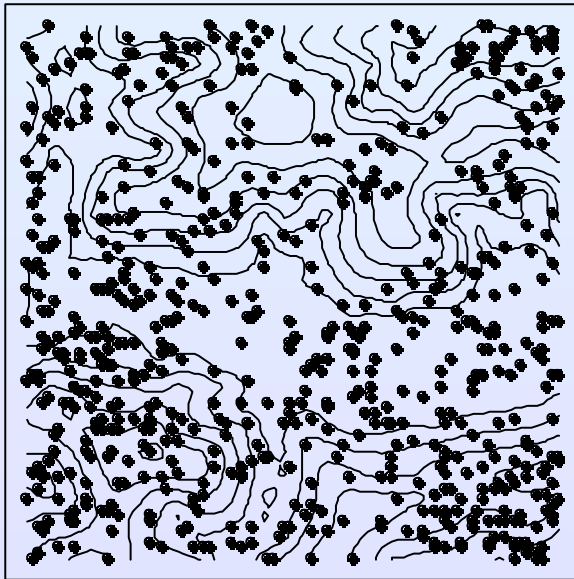
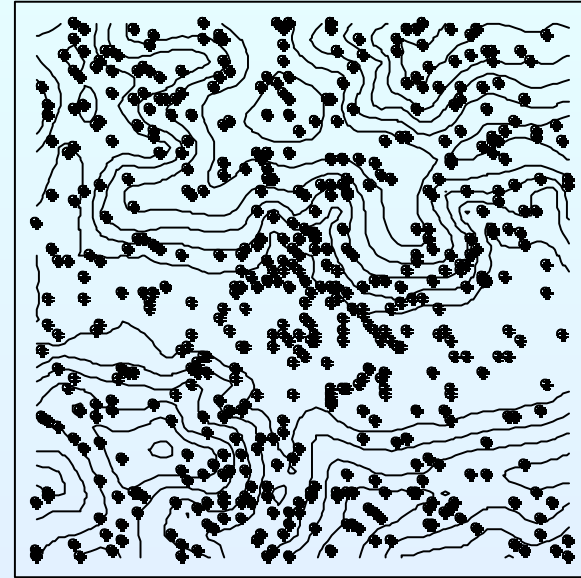
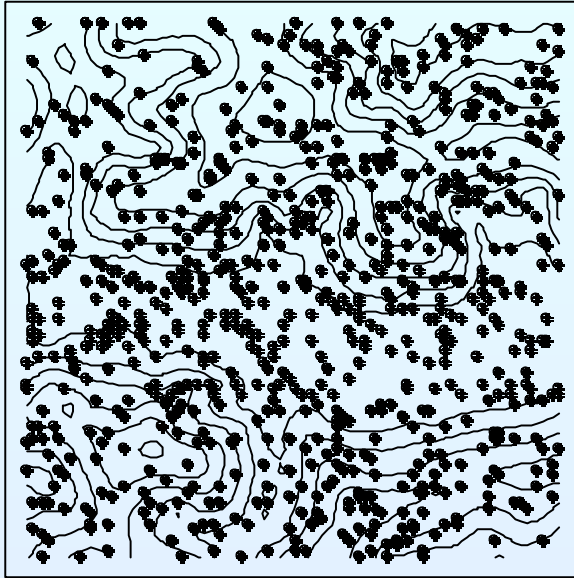
if rejected, choose again



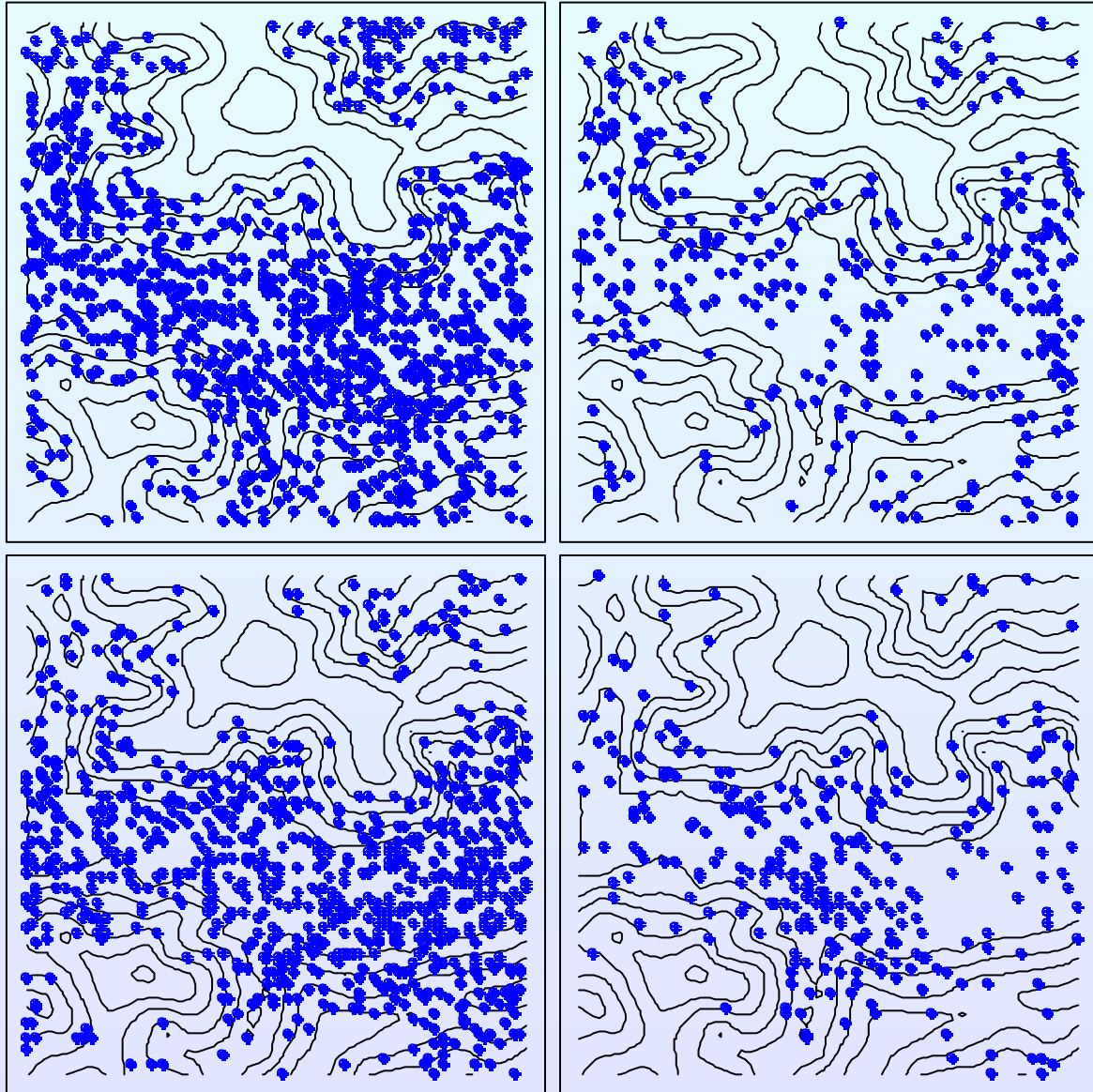
Common species are very clumped with 5-m dispersal



But allow 75-m dispersal (15 grid cells)



Strong valley preference, dispersal = 75 m



A digression about dispersal...



Dispersal distances BCI plot

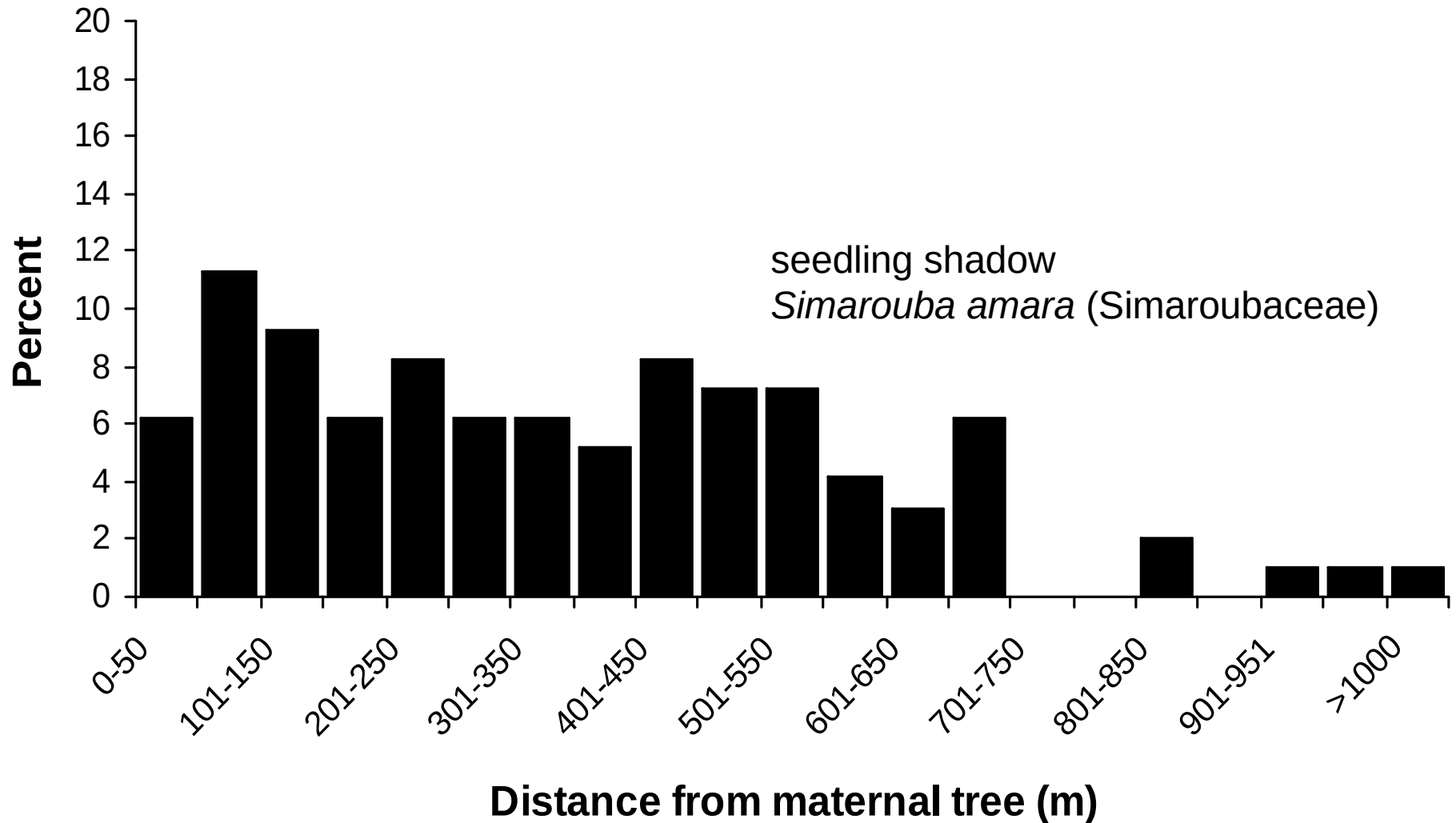
Seedlings

maternity analysis via DNA microsatellites
(D. Hardesty, S. Hubbell)

Seeds

Seed traps

(H. Muller-Landau, J. Wright, O. Calderon)



Dispersal distances BCI plot

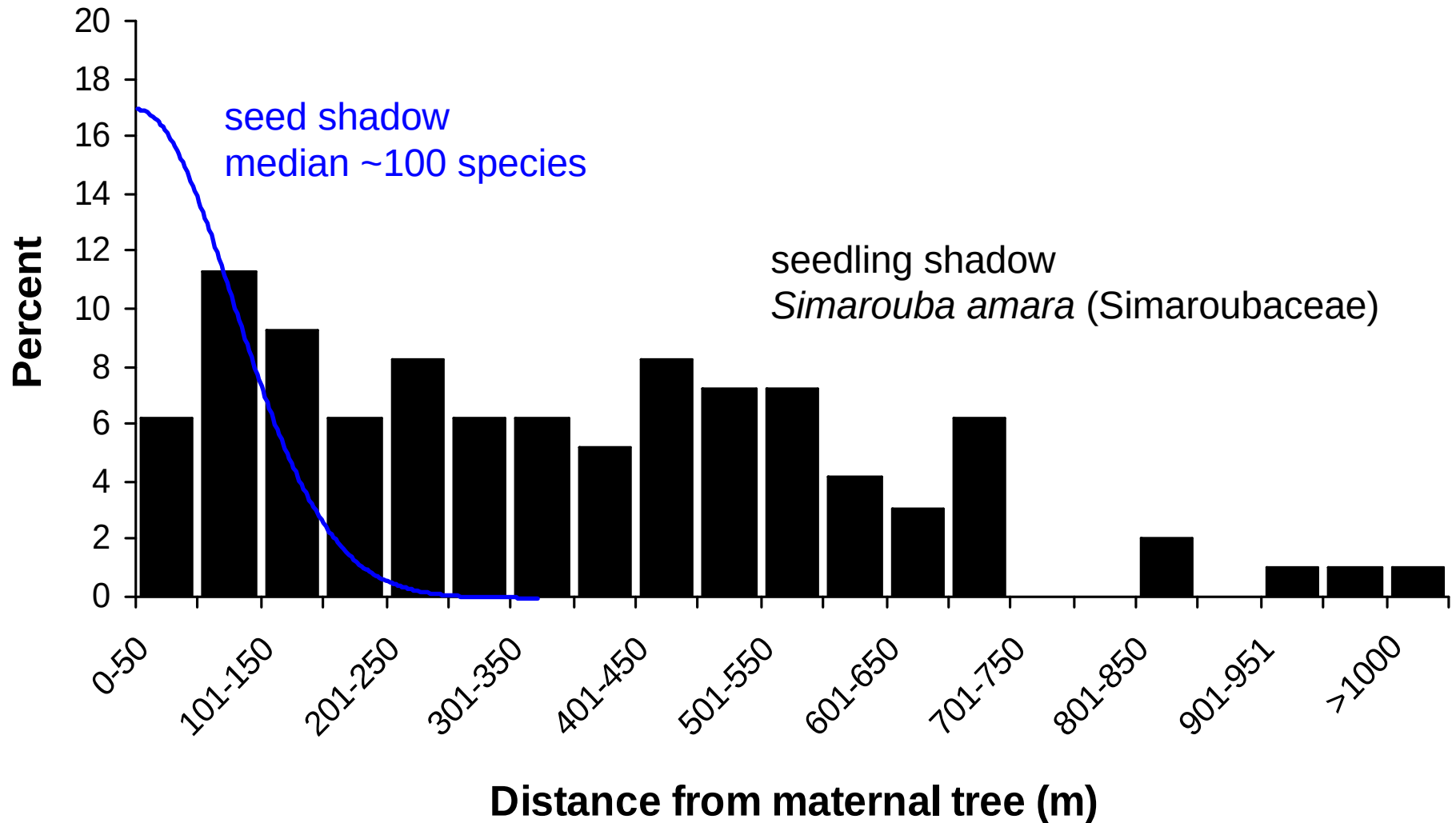
Seedlings

maternity analysis via DNA microsatellites
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Seeds

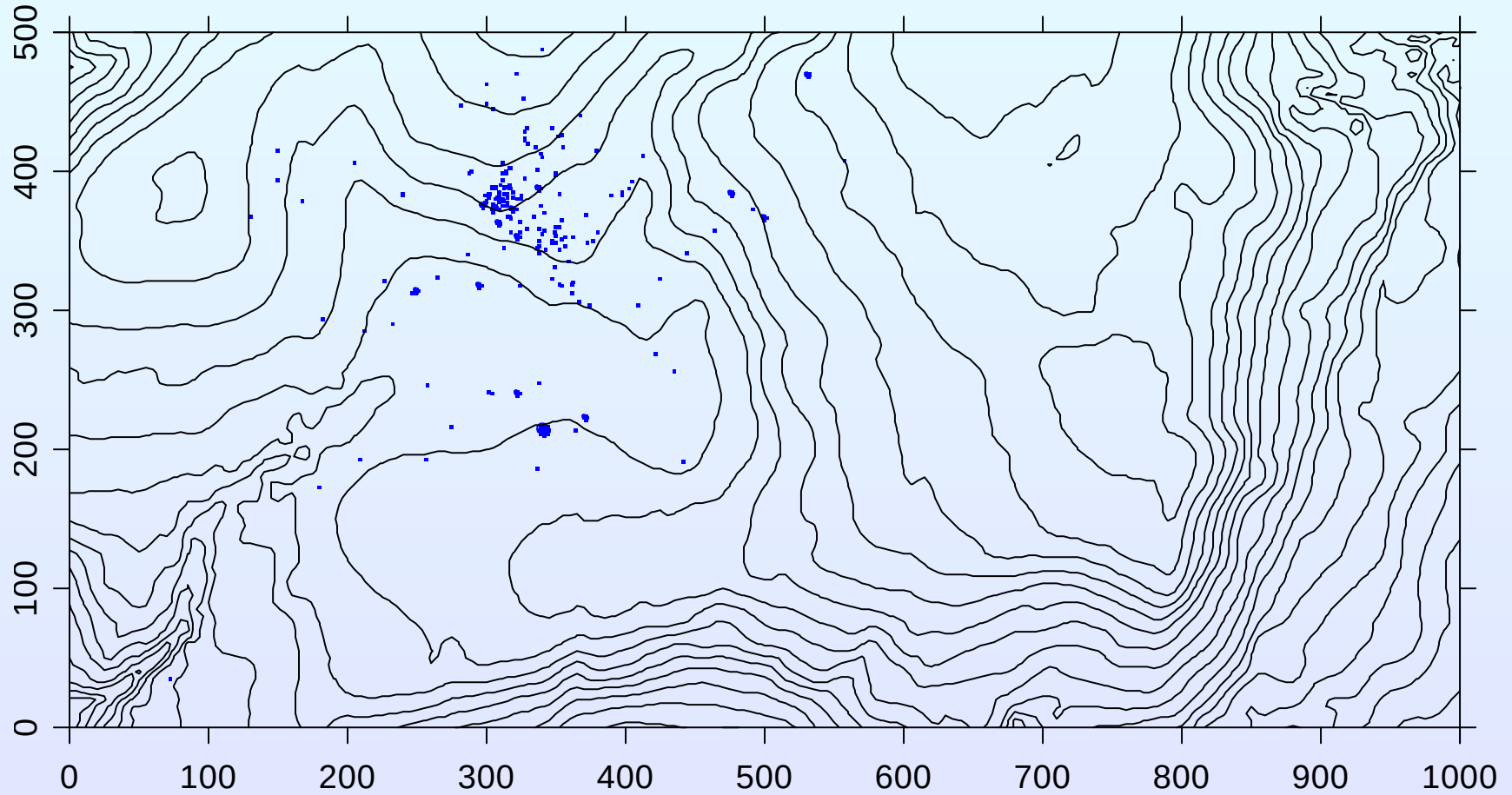
Seed traps

(H. Muller-Landau, J. Wright, O. Calderon)



BCI 50 ha plot, Panama
full census > 1 cm dbh
213000 trees
301 species

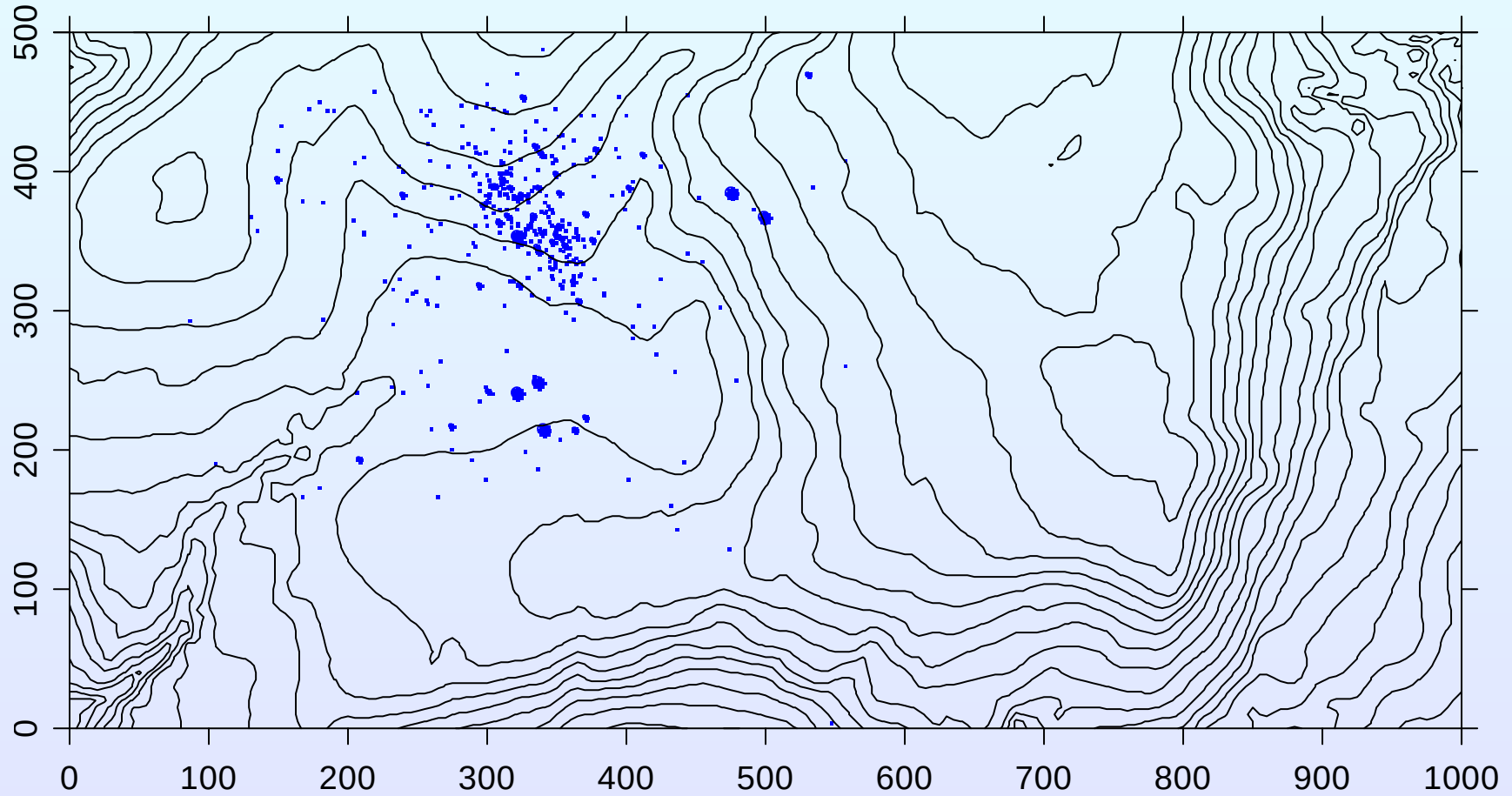
Chamguava schippii
Myrtaceae
1982



S. Hubbell, R. Foster

BCI 50 ha plot, Panama
full census > 1 cm dbh
213000 trees
301 species

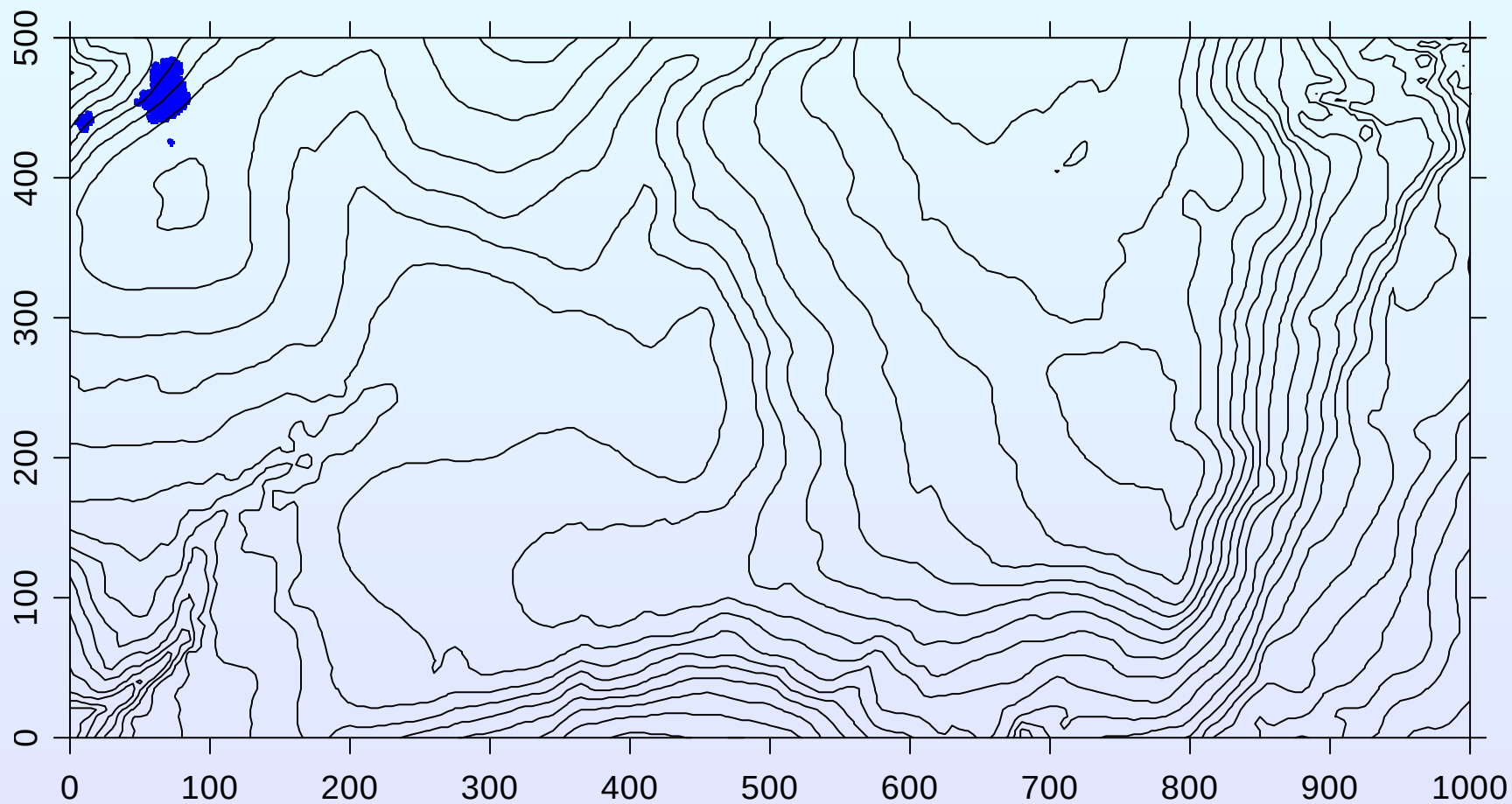
Chamguava schippii
Myrtaceae
2000



S. Hubbell, R. Foster

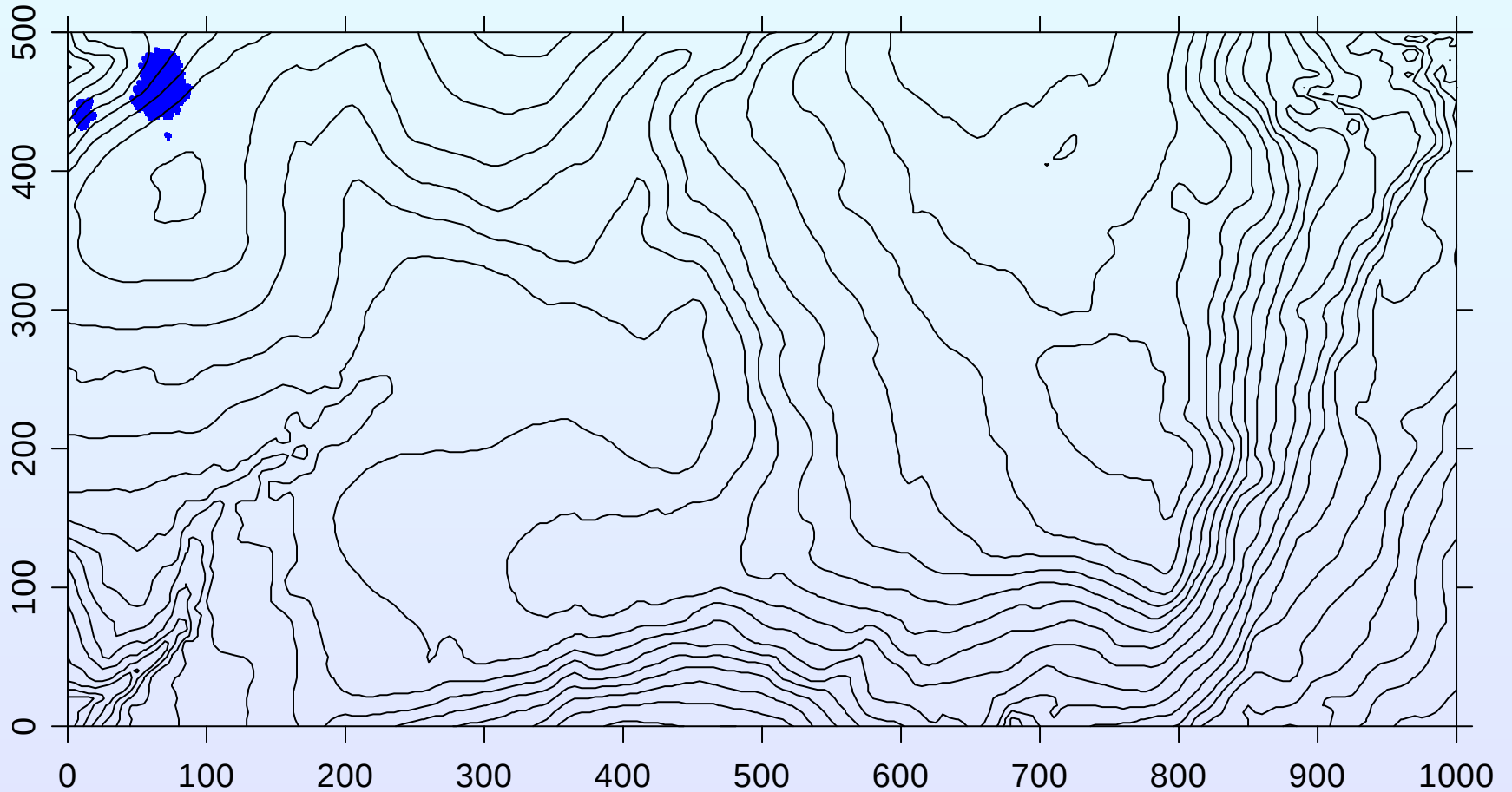
BCI 50 ha plot
Panama

Anaxagorea panamensis
Annonaceae
1982



BCI 50 ha plot
Panama

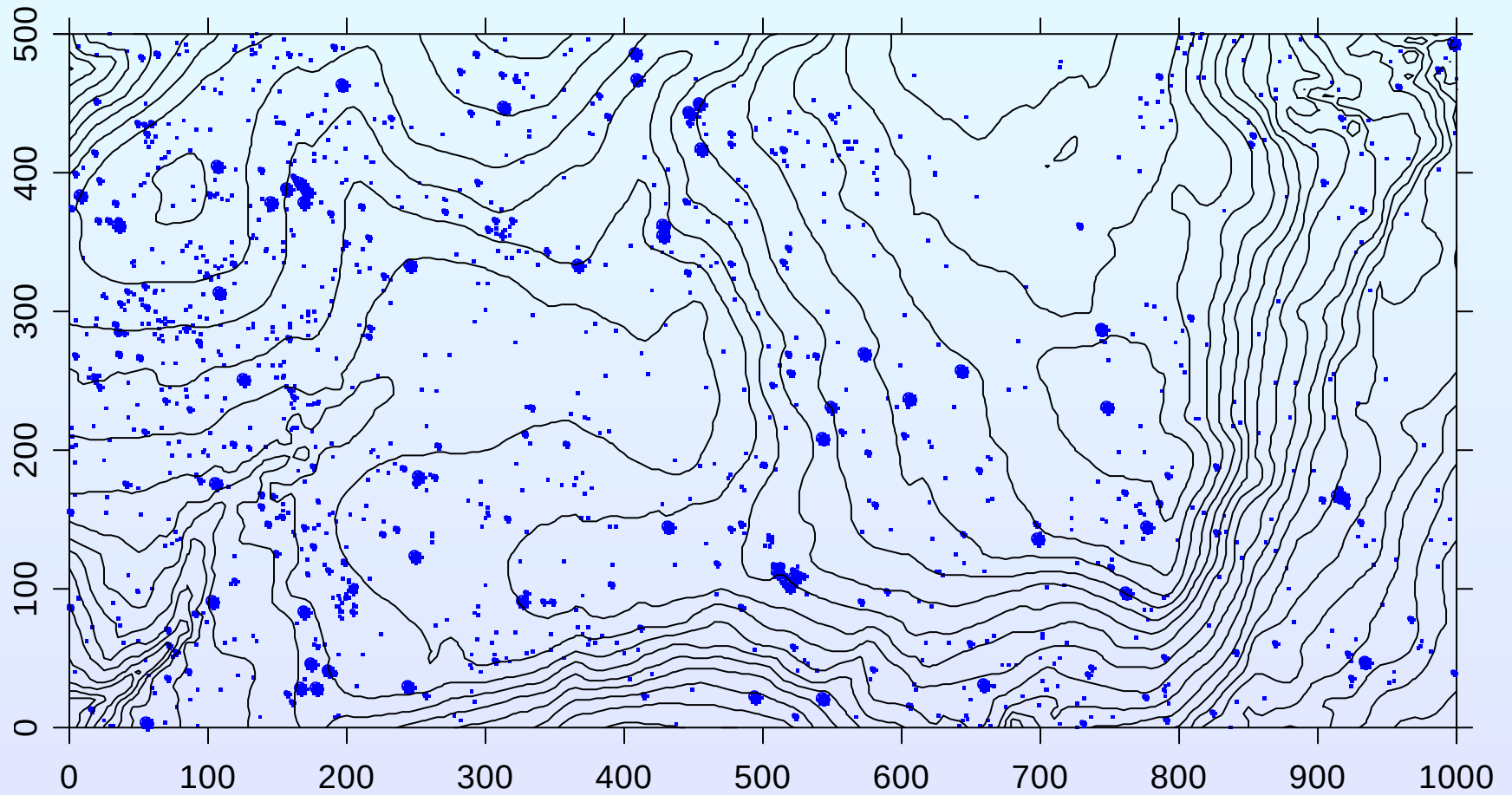
Anaxagorea panamensis
Annonaceae
2000



No dispersal mechanism in *Anaxagorea*

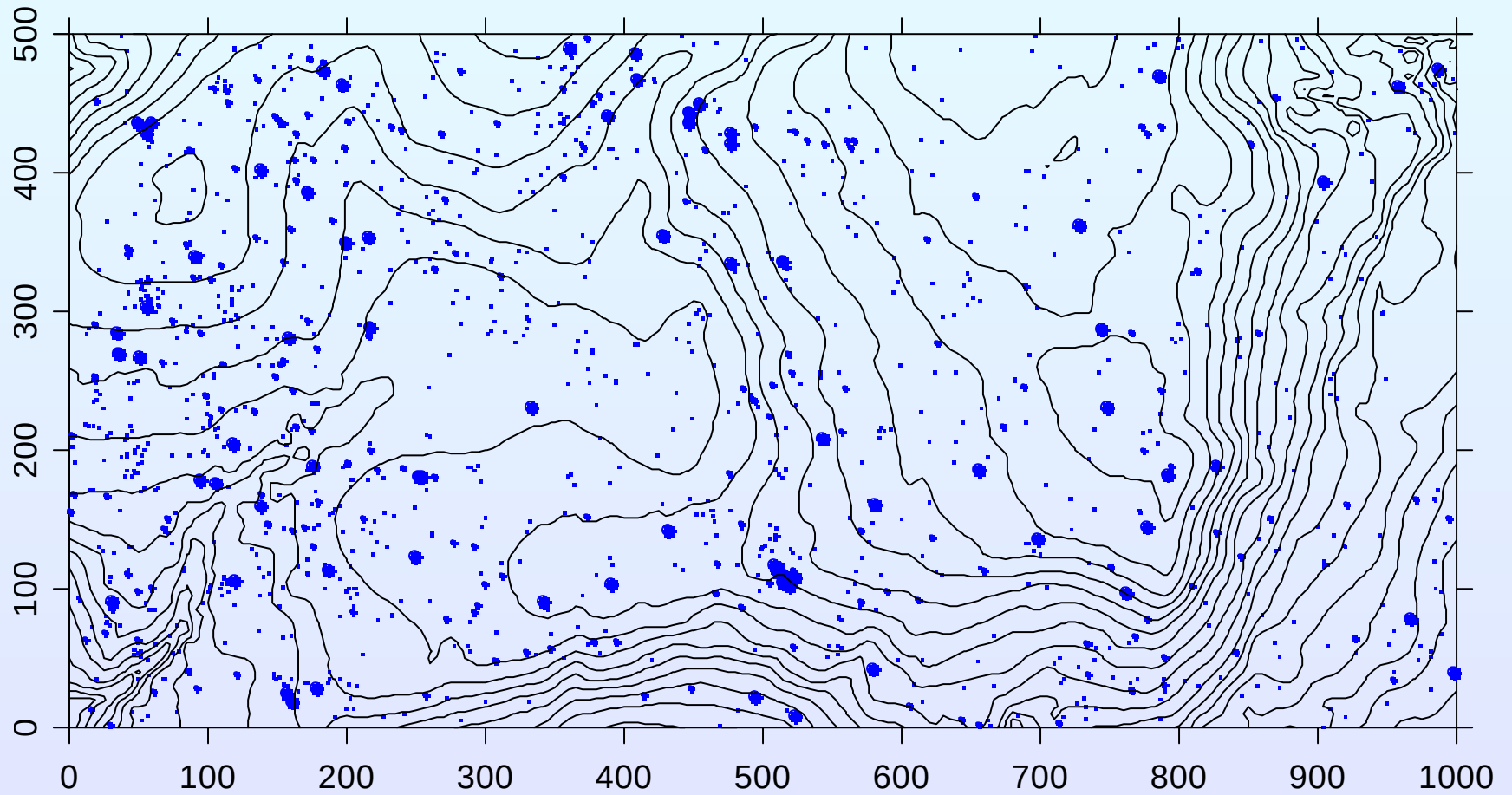
BCI 50 ha plot
Panama

Simarouba amara
1982



BCI 50 ha plot
Panama

Simarouba amara
2000



Neutral theory for diversity

Neutrality is *anti*-diversifying
Speciation maintains diversity



Review: basic results from theory

➤ XXX

➤ XXX



Basic results

- Voter model without dispersal limitation but with speciation is Hubbell's neutral model
- Voter model without speciation leads to a monodominant community (Gause's principal)

Abundance distribution

- Precisely predicted in simple neutral model
- Slope of -1 on log-log scale
- Driven by speciation
- Unaffected by dispersal or niche differences

Abundance distribution

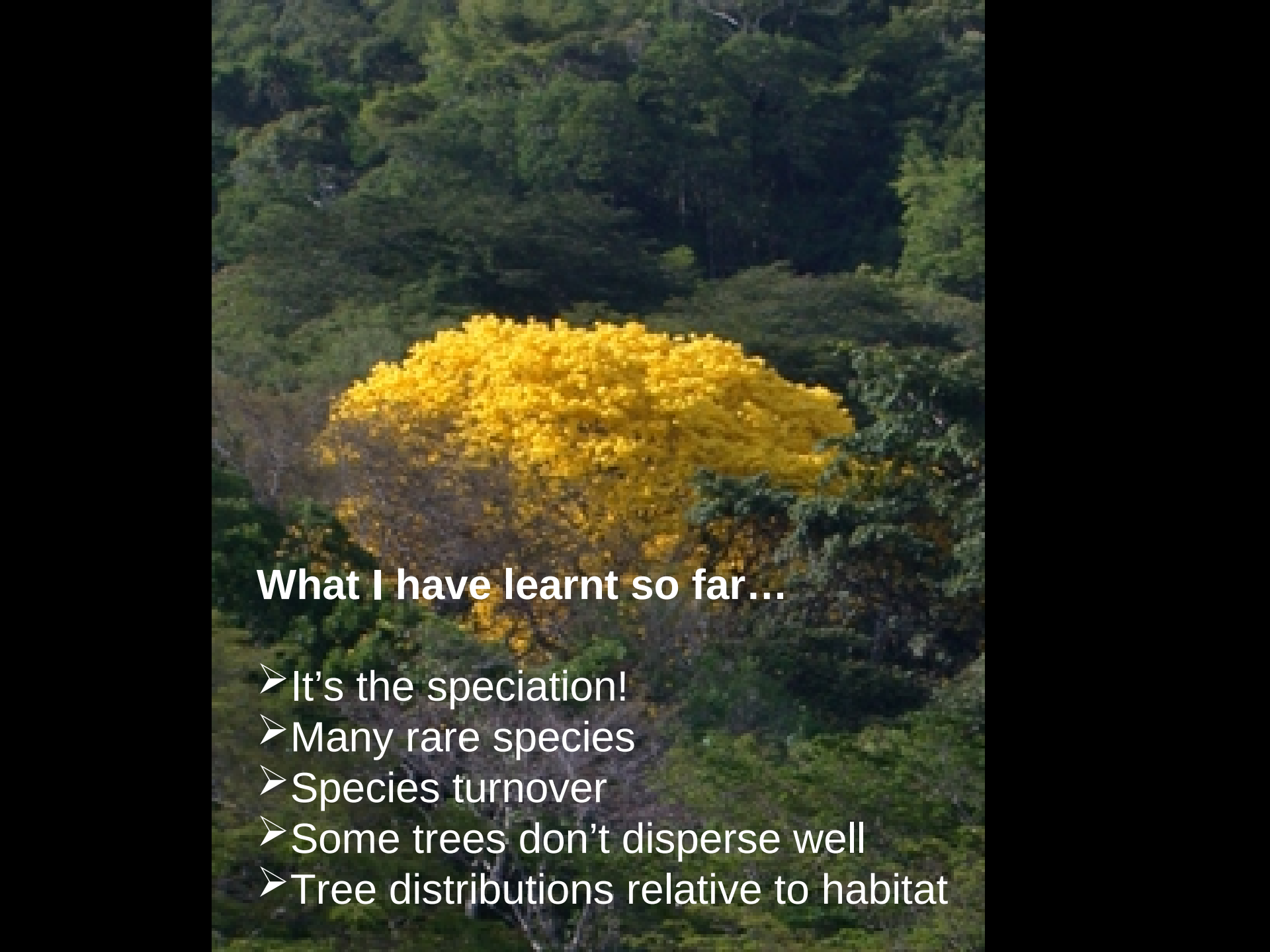
- Precisely predicted in simple neutral model
- Slope of -1 on log-log scale
- Driven by speciation
- Unaffected by dispersal or niche differences

Diversity

- Precisely predicted in simple neutral model
- Driven by speciation
- Unaffected by dispersal or niche differences

Make graph of abundance distribution under neutrality

And with niche differences, density-dependence

A photograph of a forest landscape. In the center, a large tree with a dense, rounded canopy of bright yellow leaves stands out prominently. The surrounding forest is composed of many other trees with green foliage, creating a textured background. The lighting suggests a sunny day, with the yellow leaves appearing very vibrant.

What I have learnt so far...

- It's the speciation!
- Many rare species
- Species turnover
- Some trees don't disperse well
- Tree distributions relative to habitat

Models

Speciation-driven communities:

- Narrow, circular patches if dispersal is poor
- Abundant species widespread
- Many rare species
- Abundance distribution closely matches observed



XXX

➤ XXX

➤ XXX



XXX

➤ XXX

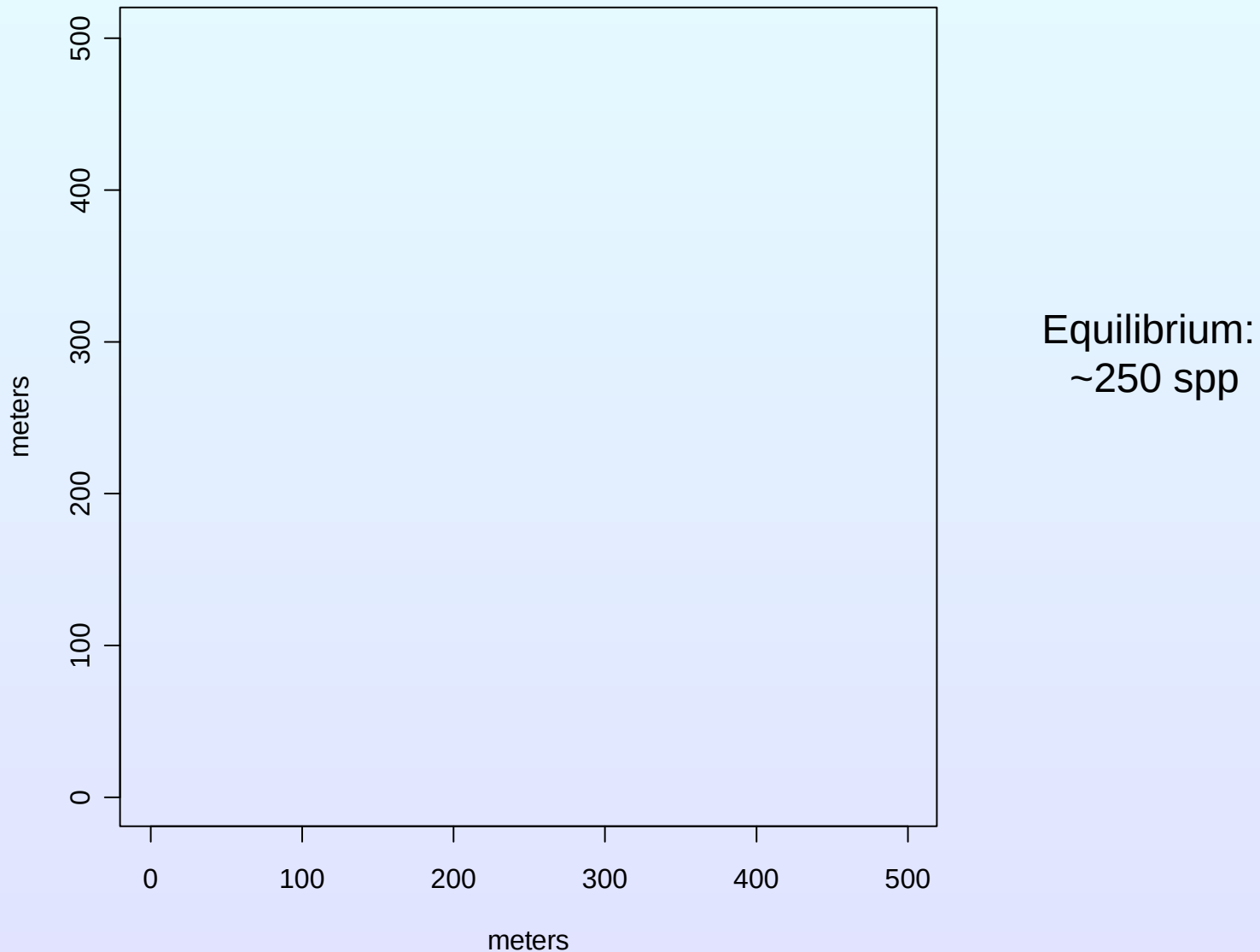
➤ XXX



range size, aggregation patterns
have not been analyzed in a general
dispersal model

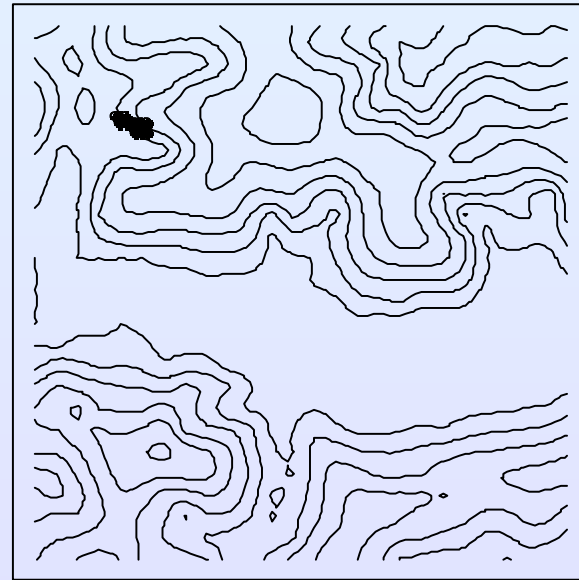
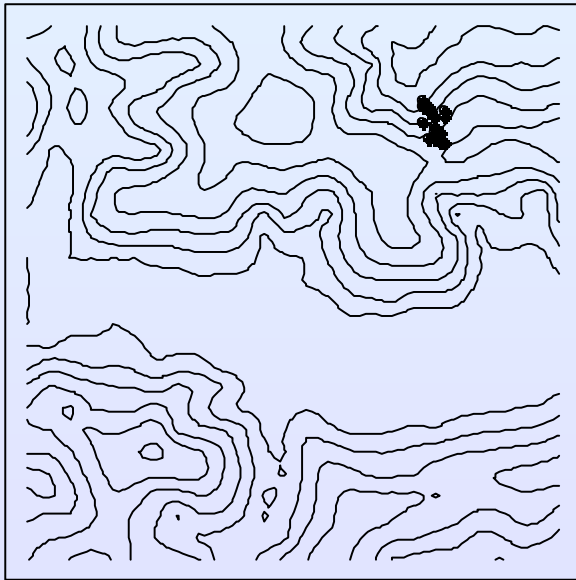
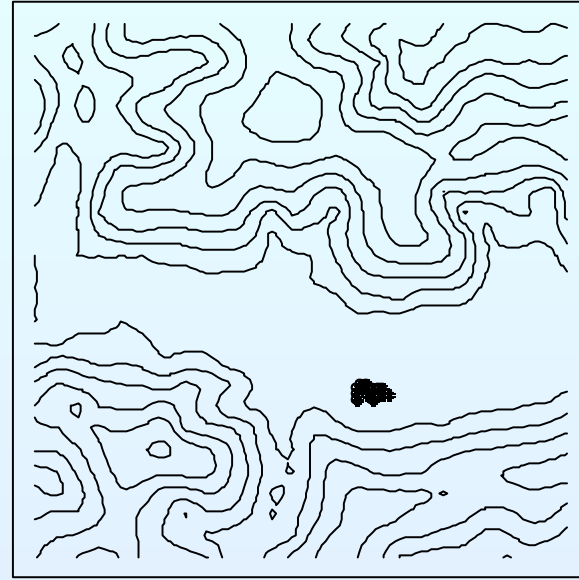
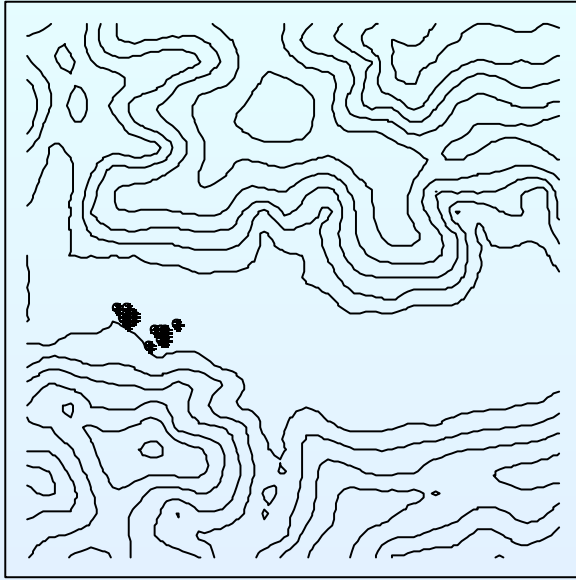
adding habitat variation...

dispersal model with 'realistic' distances
1 step (1 grid cell) = 5 meters, 1 tree per 5 meters

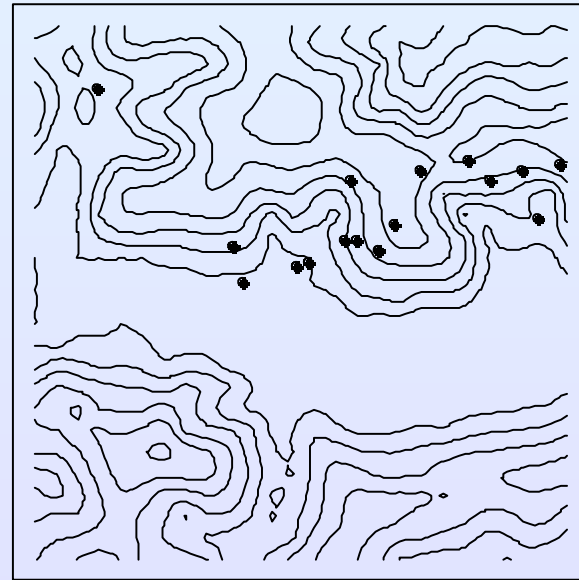
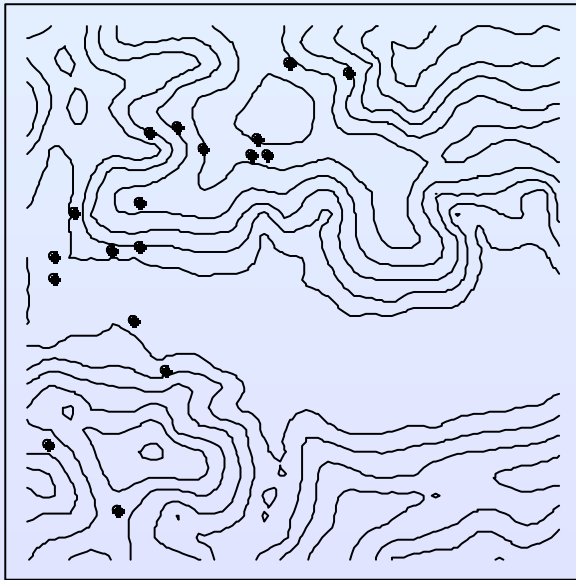
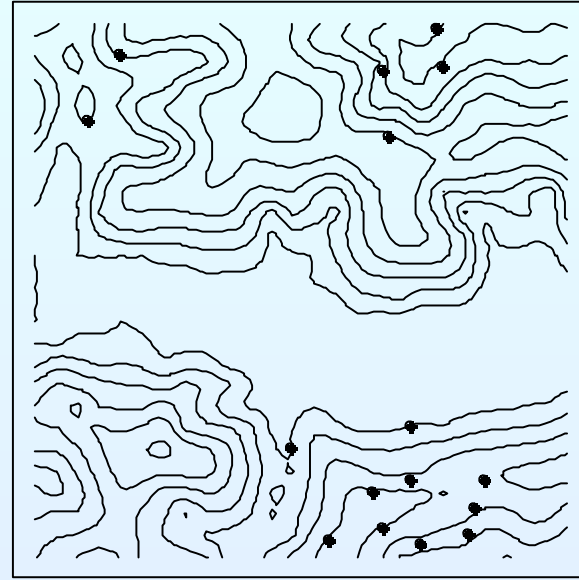
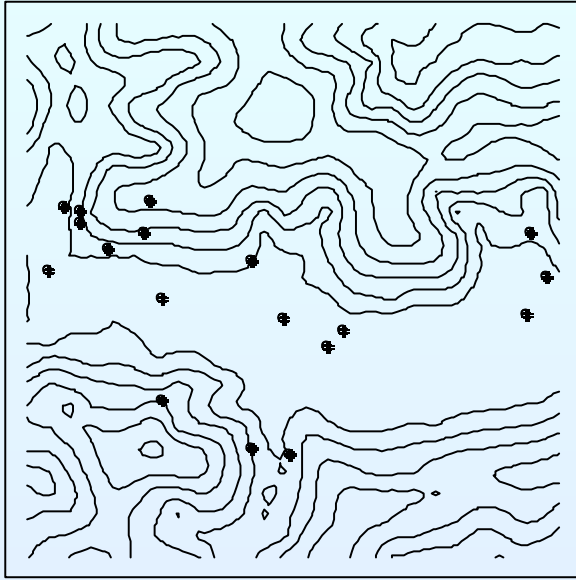


1e4 individuals, 1e9 deaths (1e7 years), speciation rate $v=0.005$

... rare species even more so



... rare species too



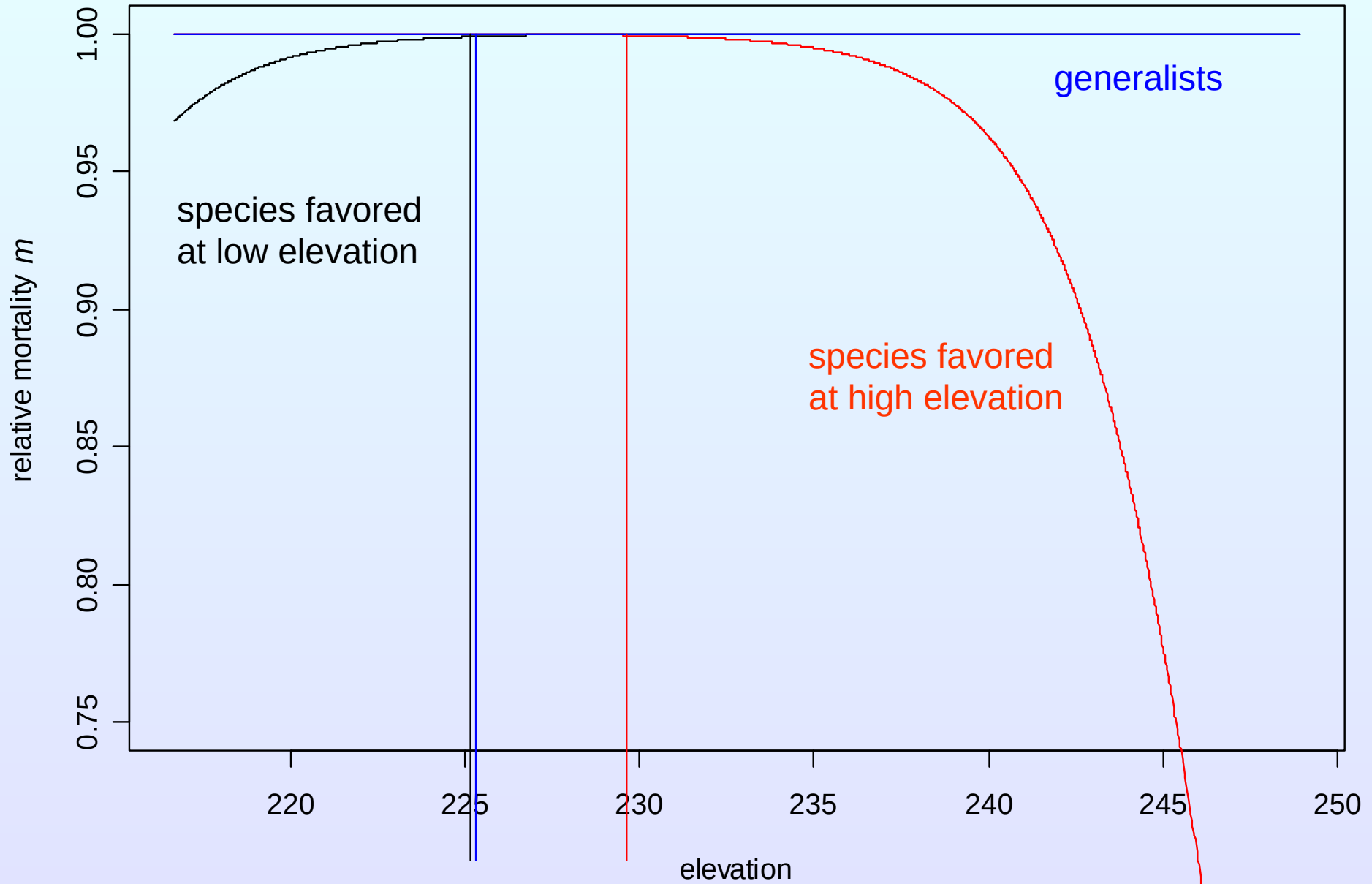
Why aggregation?

key elements of a neutral community

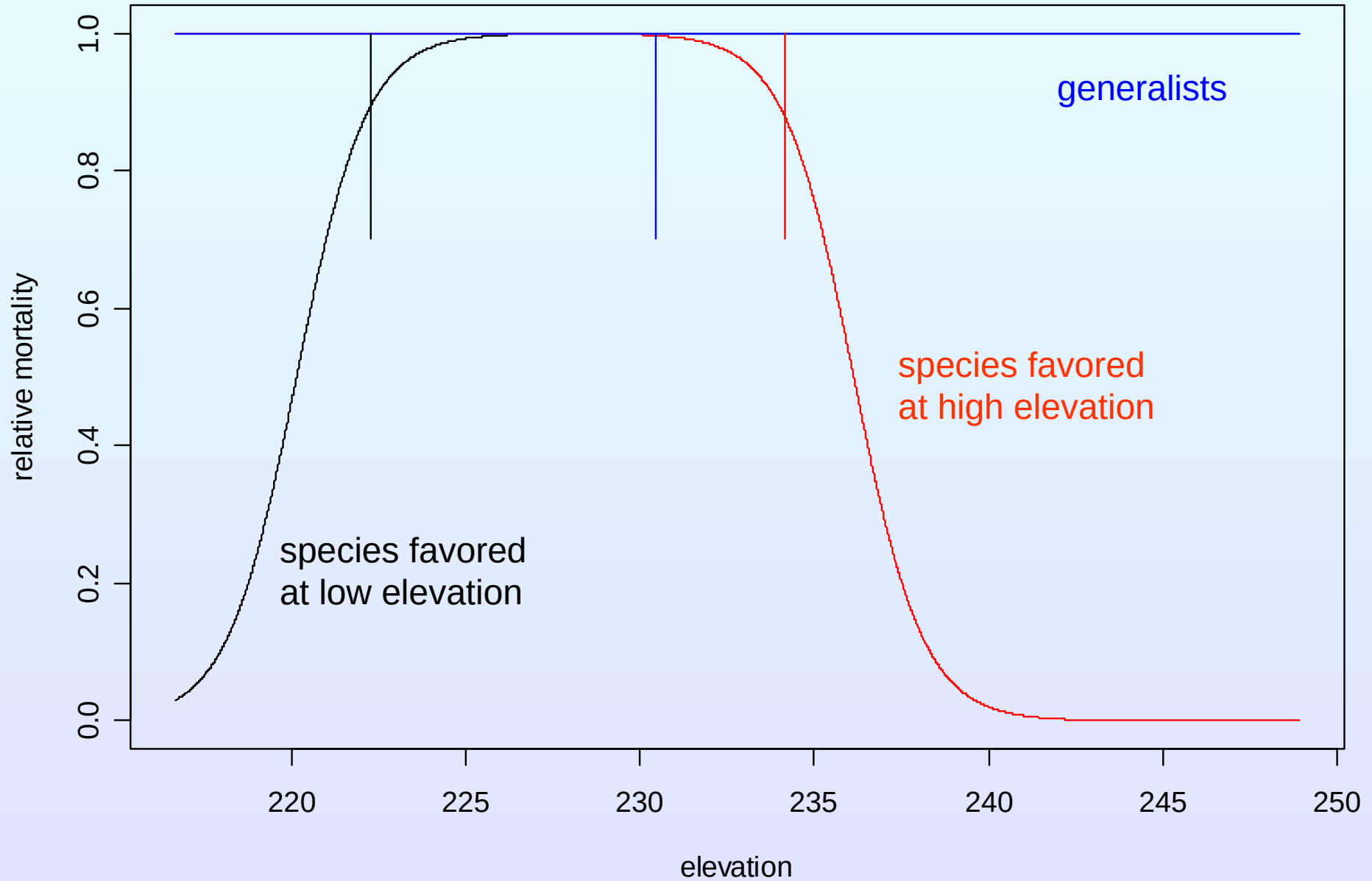
- Poor dispersal
- High speciation (immigration),
meaning species are young

Rare species advantage might produce a different pattern
(species could be old)

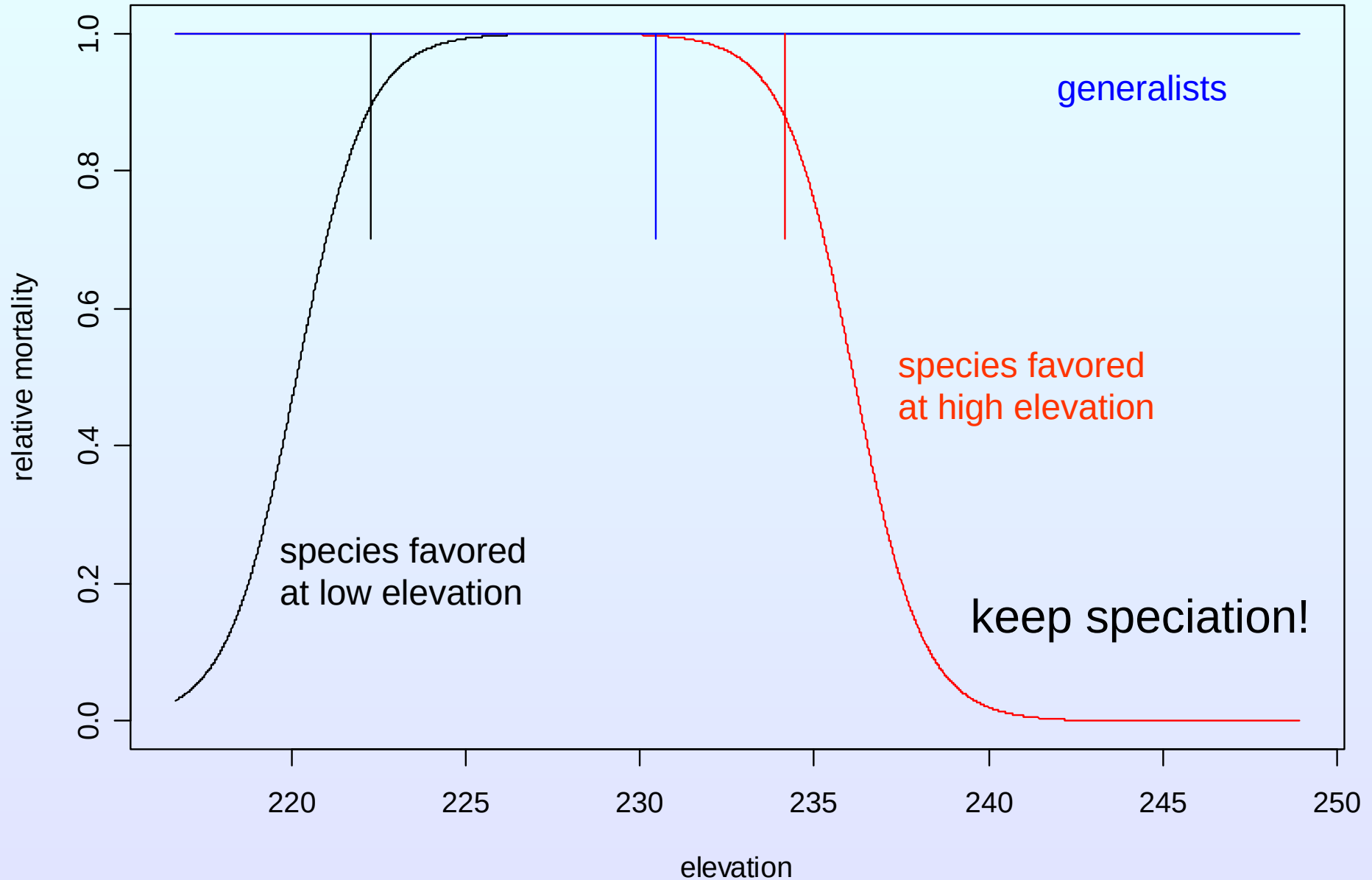
Elevation effects mortality rate slightly



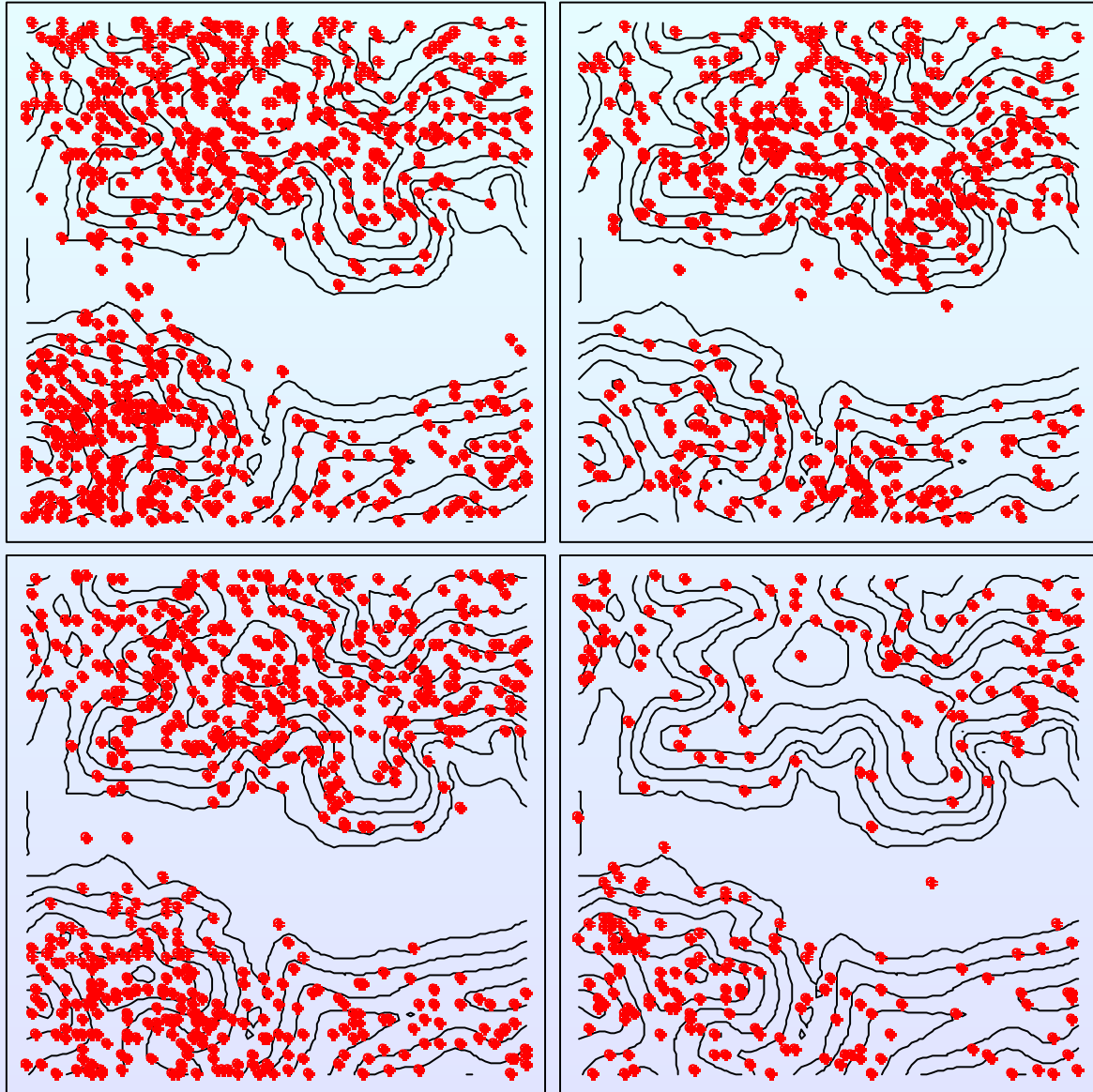
Elevation effects mortality rate severely



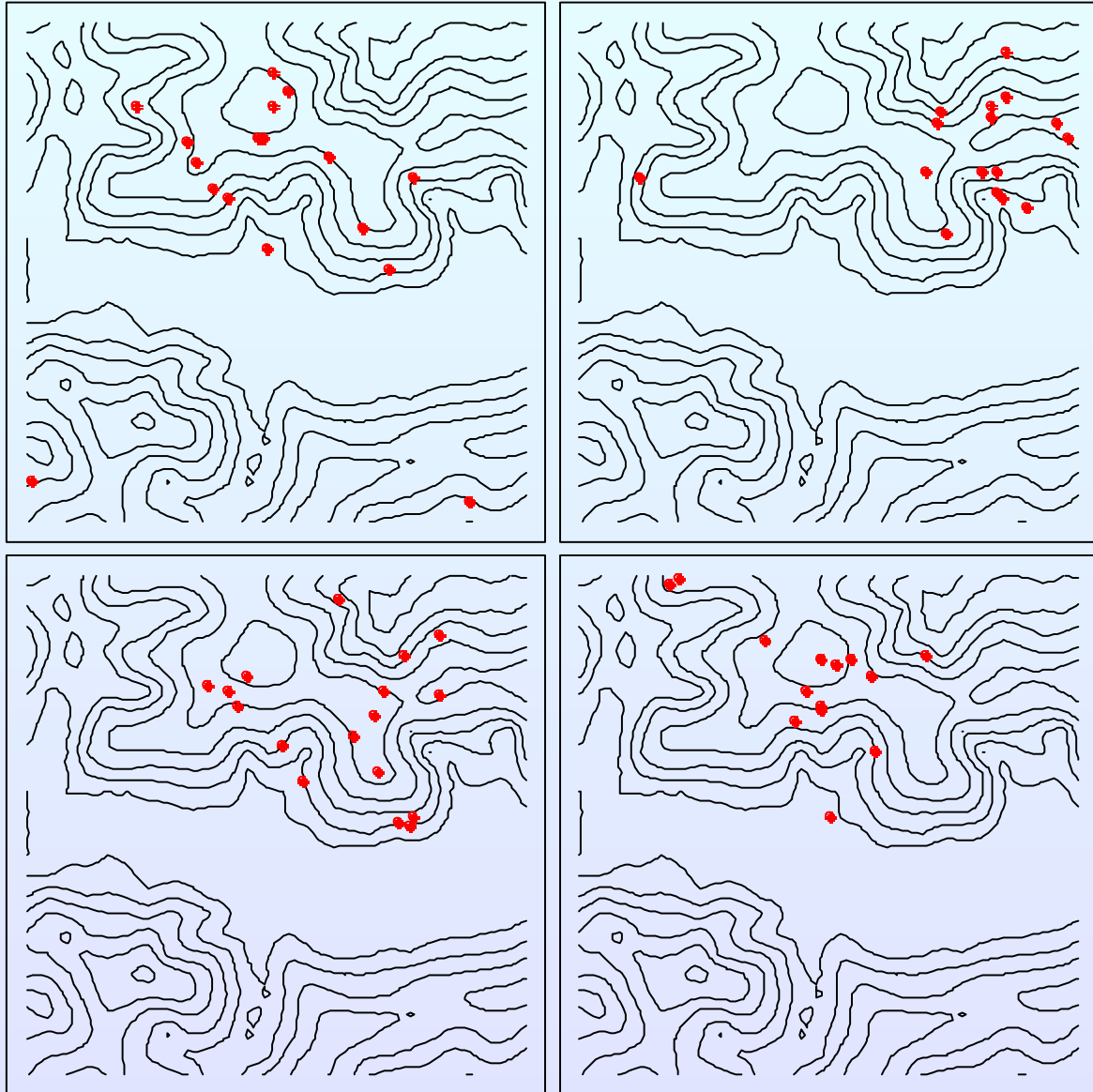
Elevation effects mortality rate severely



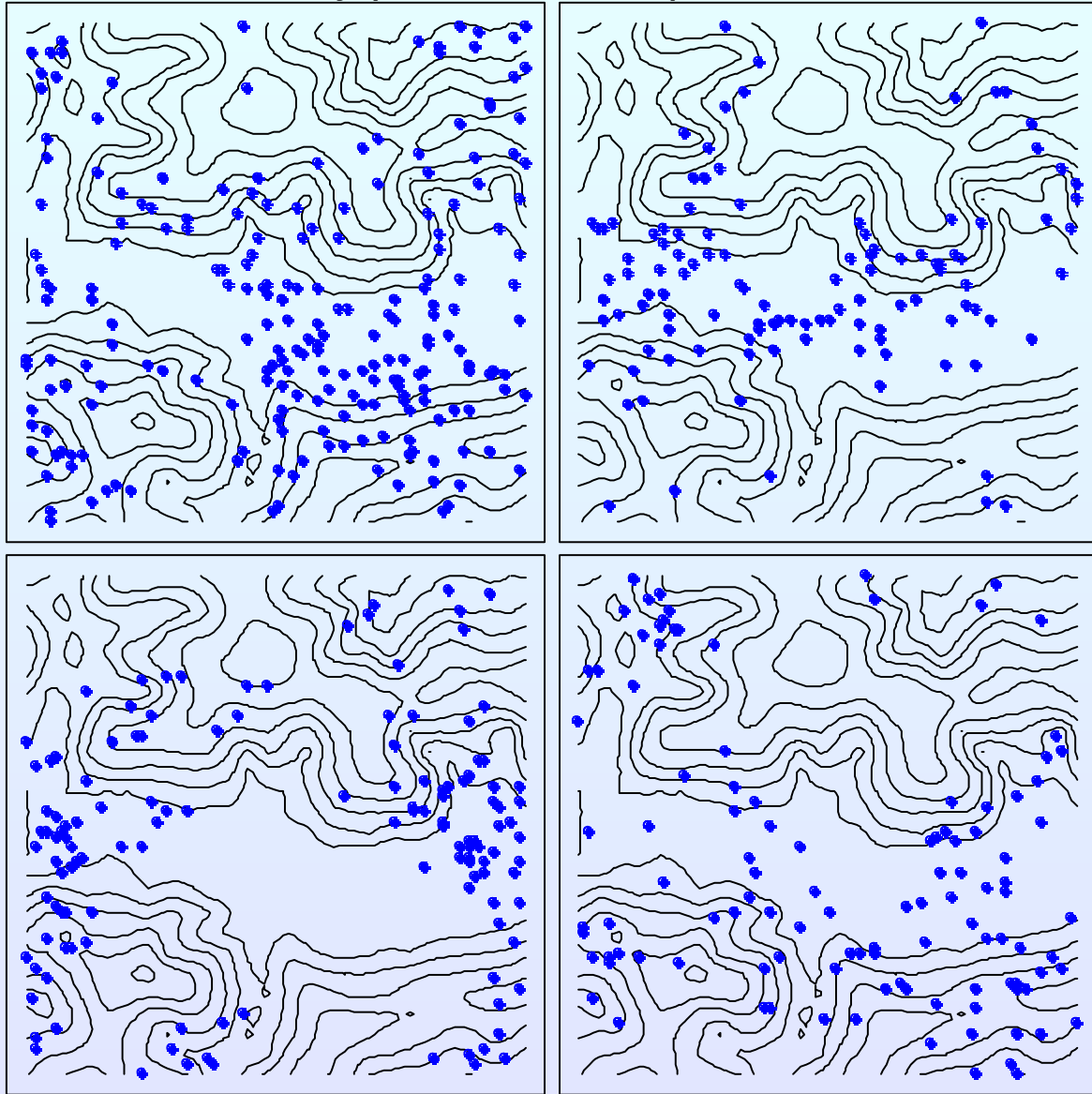
Strong ridge preference, dispersal = 75 m



Strong ridge preference, dispersal = 75 m, rare species

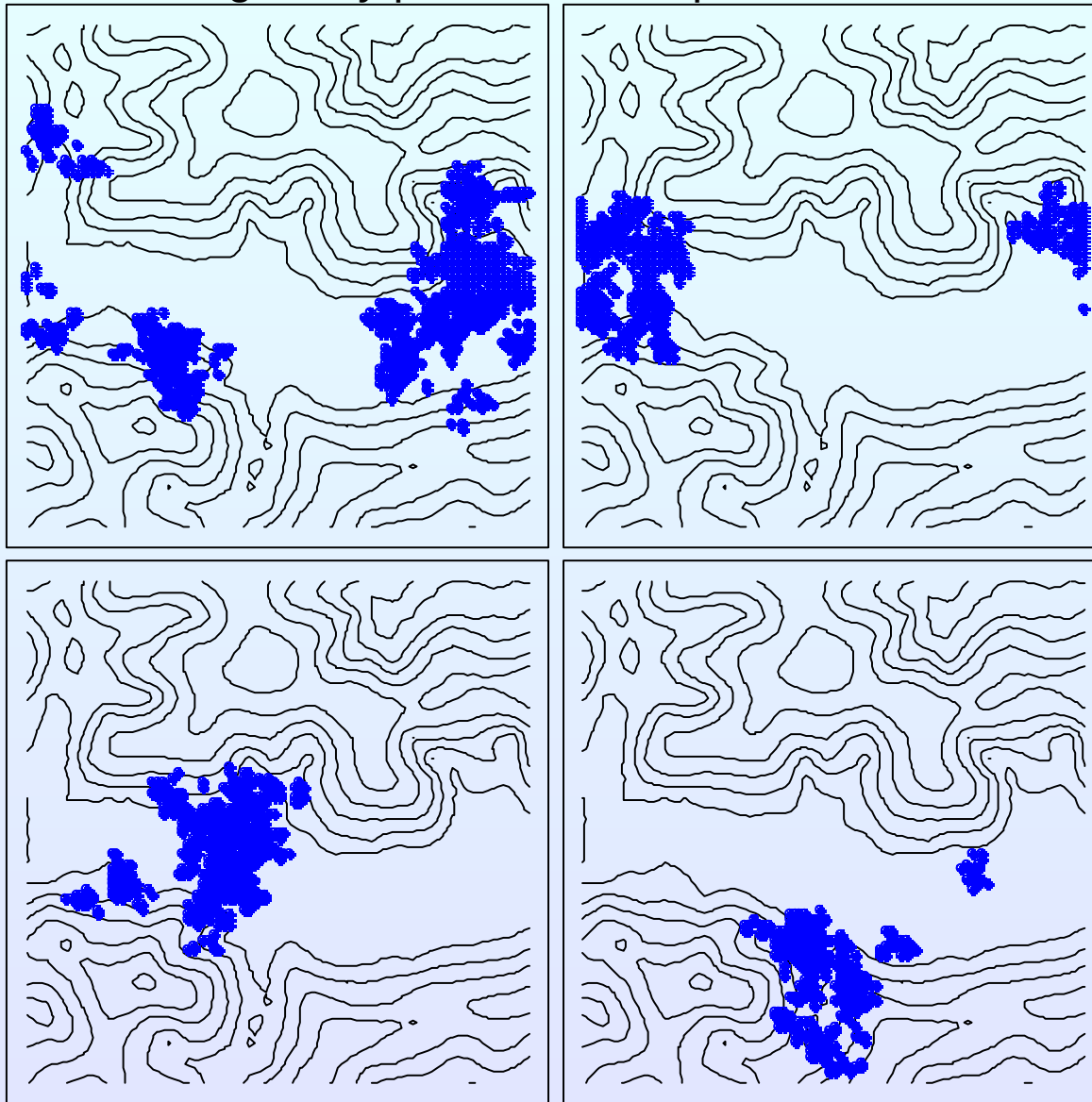


Weak valley preference, dispersal = 50 m

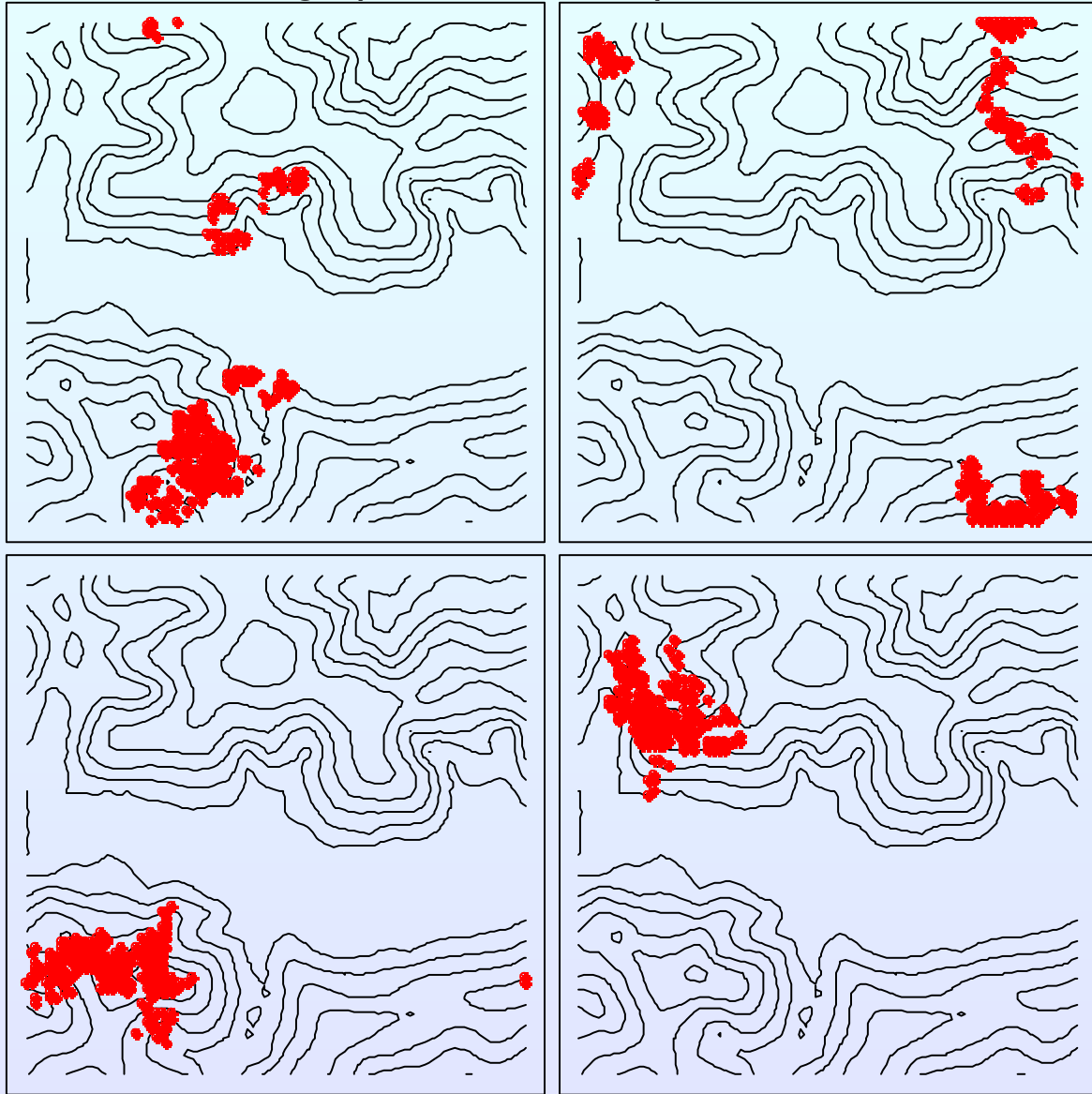


good dispersal can conceal weak habitat preference

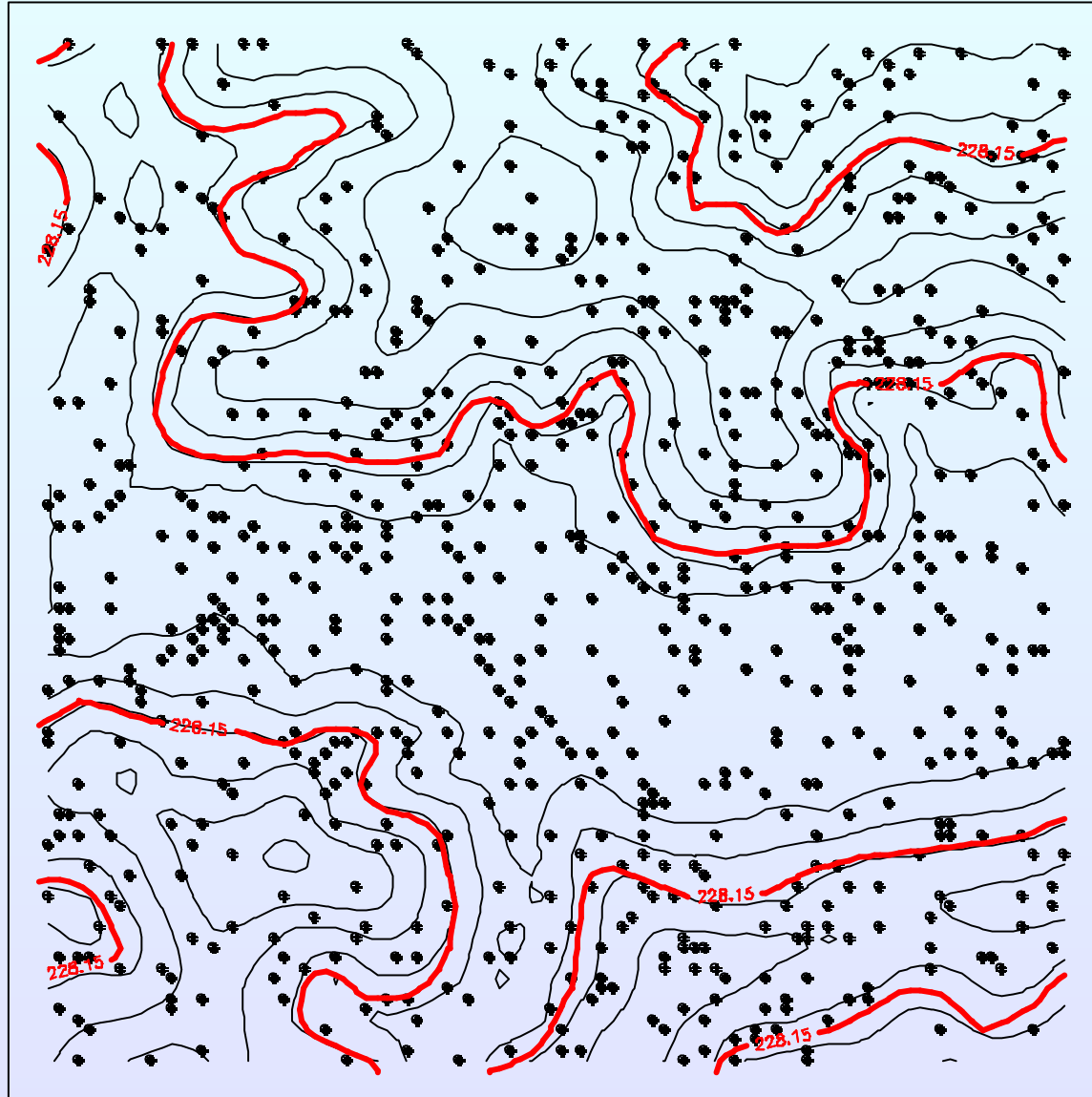
Strong valley preference, dispersal = 5 m



Weak ridge preference, dispersal = 5 m

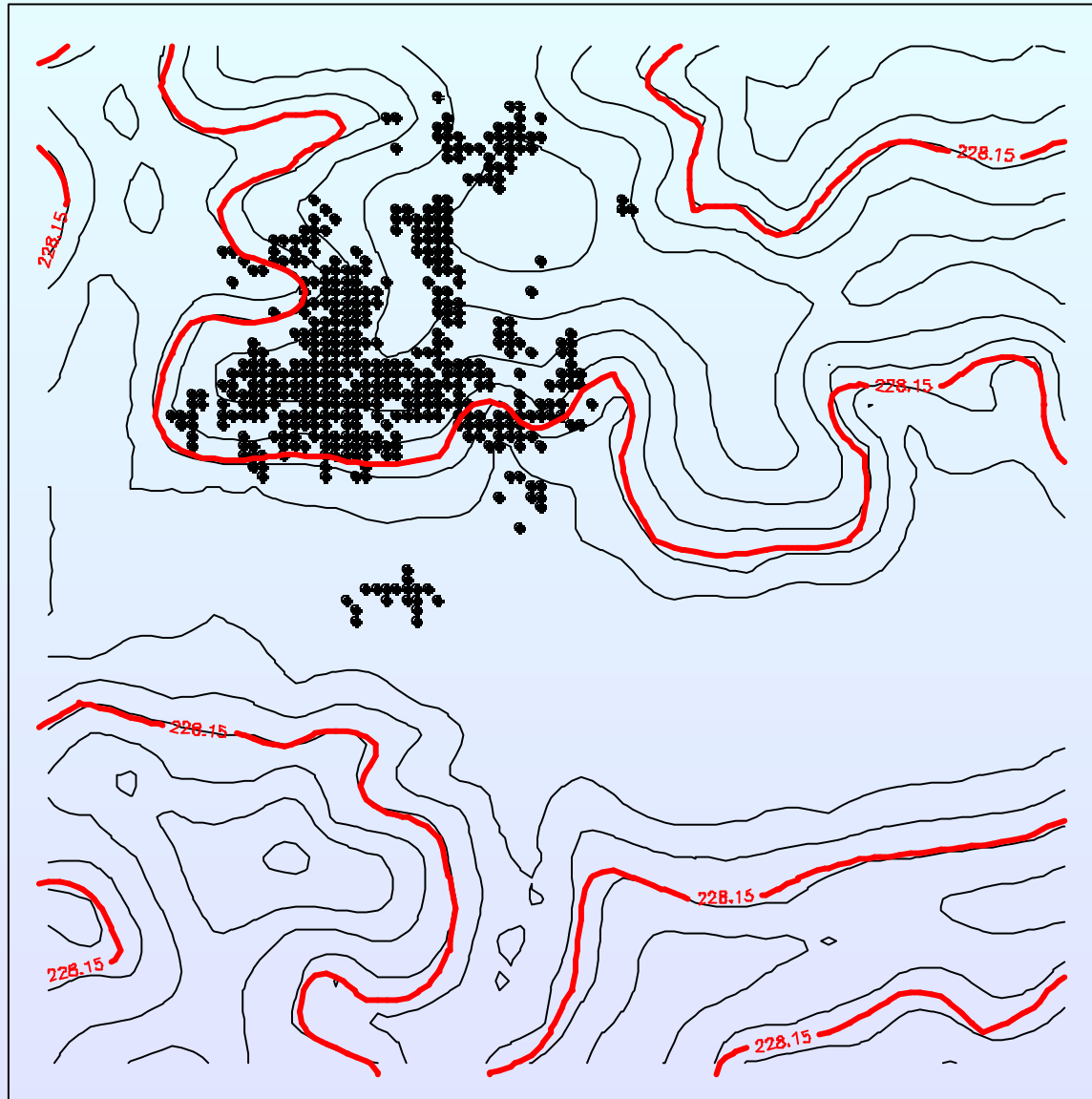


Habitat preference index: density low elevation/overall density
No habitat preference, dispersal = 75 m

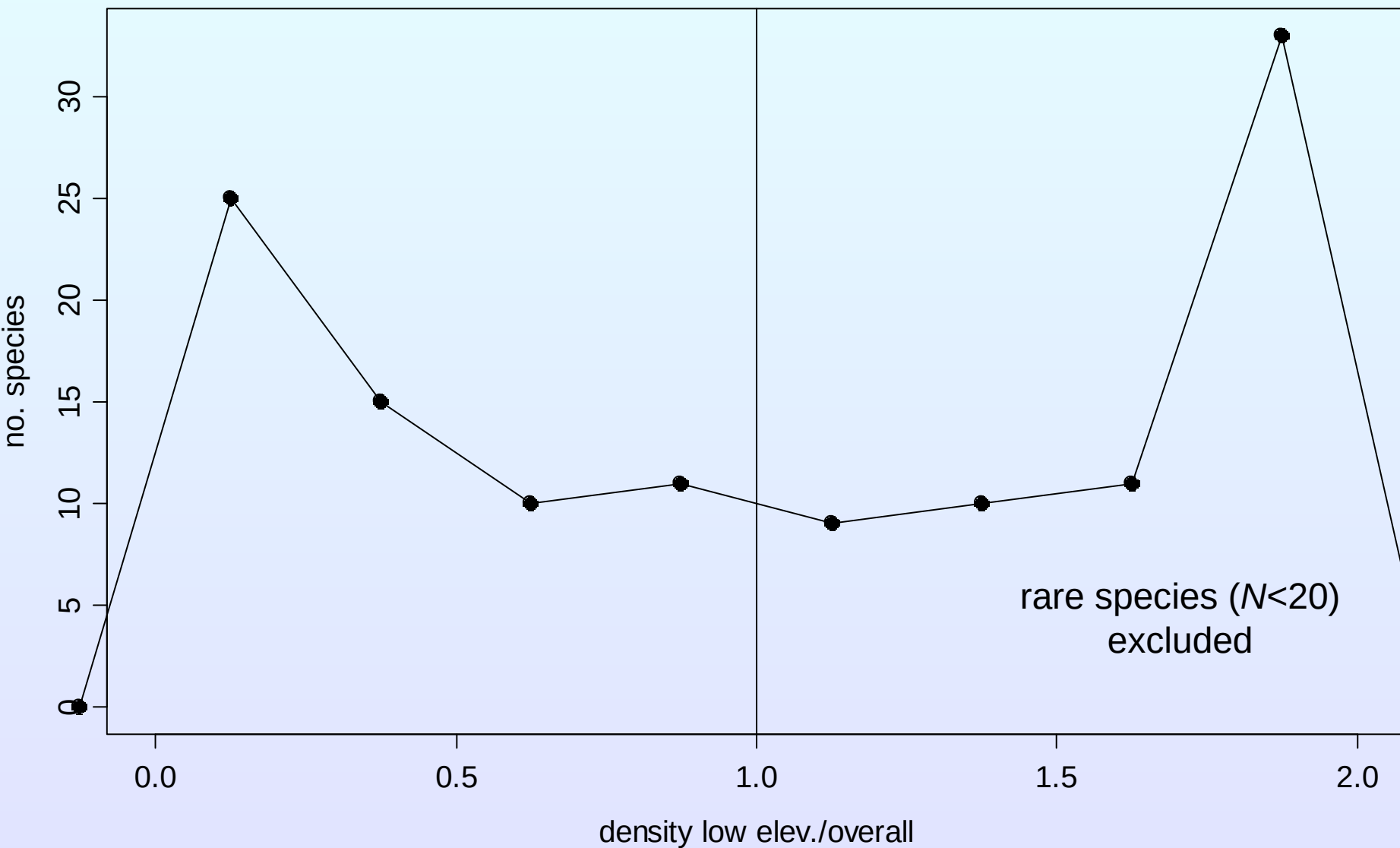


Habitat preference index: density low elevation/overall density

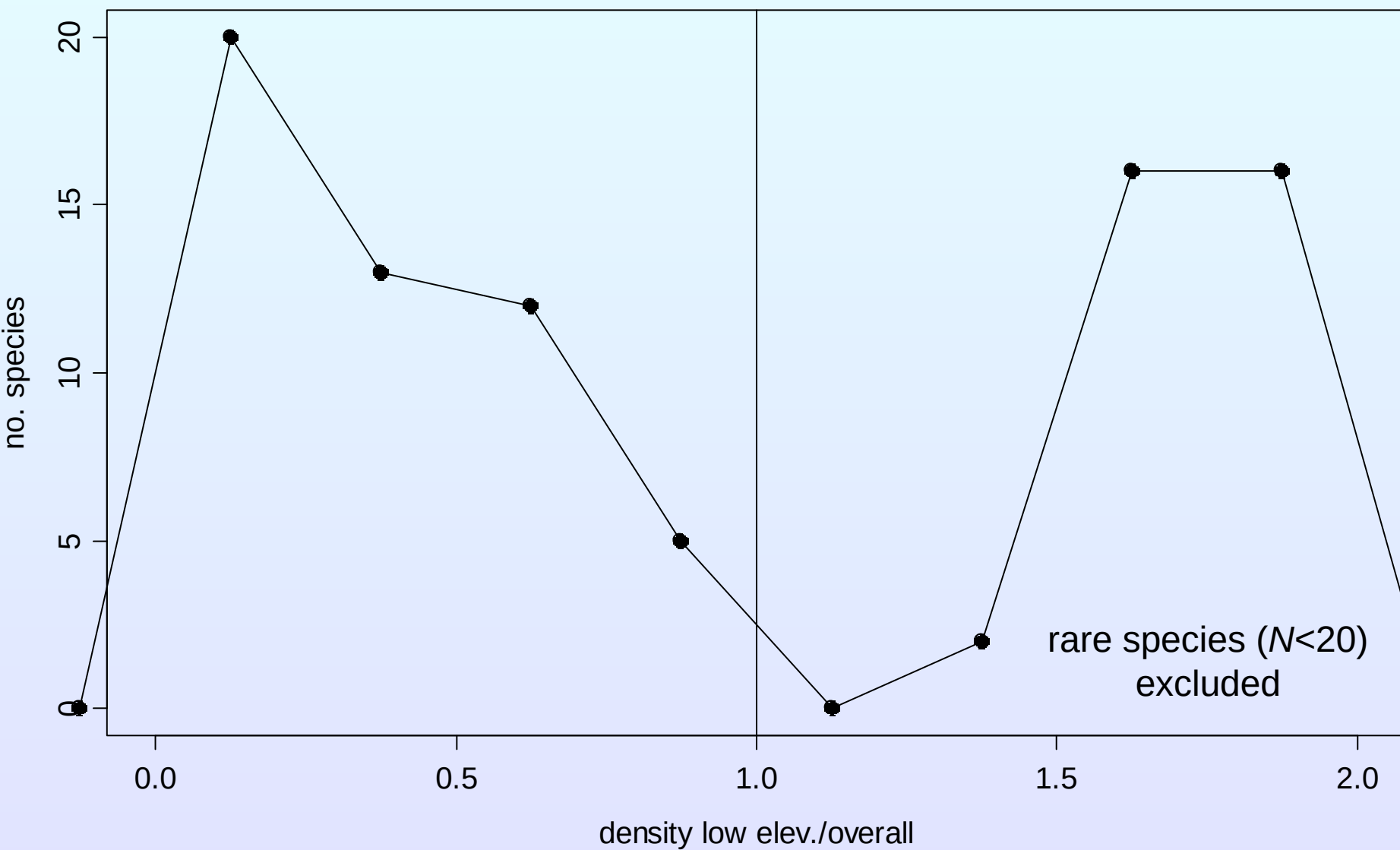
No habitat preference, dispersal = 5 m



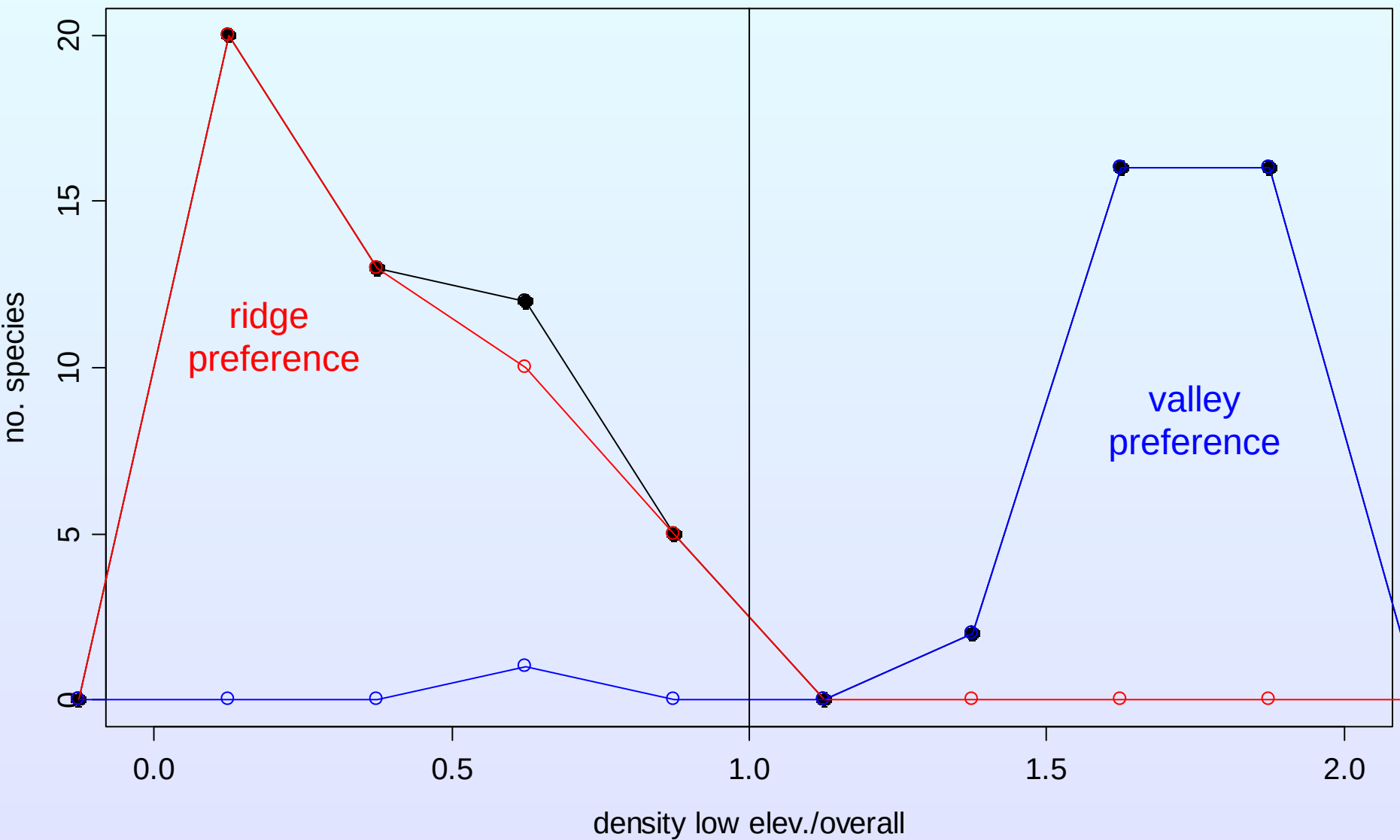
Habitat preference index (favor low elevation)
no habitat preference, dispersal = 5 m



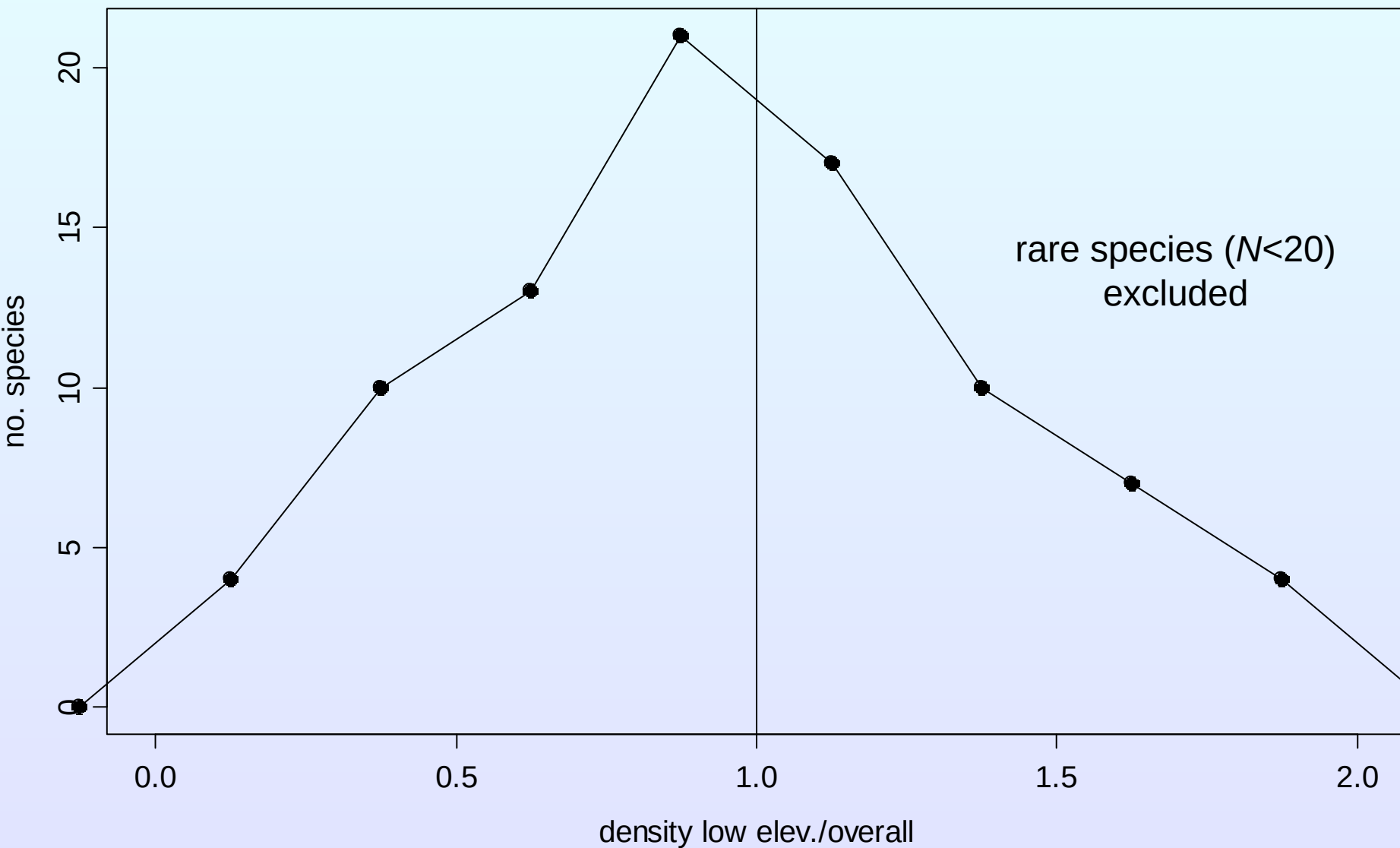
Strong habitat preference, dispersal = 5 m



Strong habitat preference, dispersal = 5 m

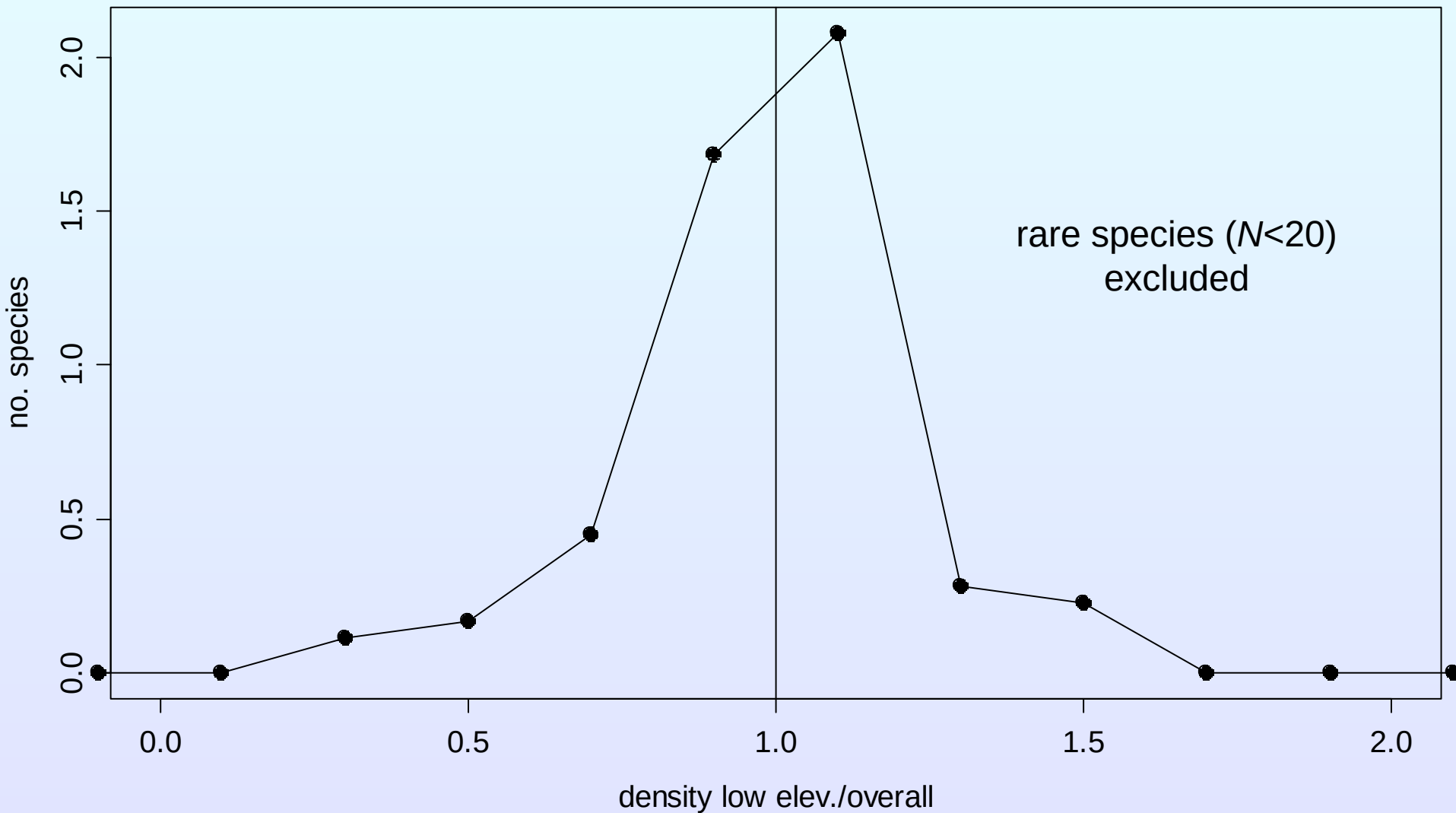


Habitat preference index (favor low elevation)
no habitat preference, dispersal = 25 m



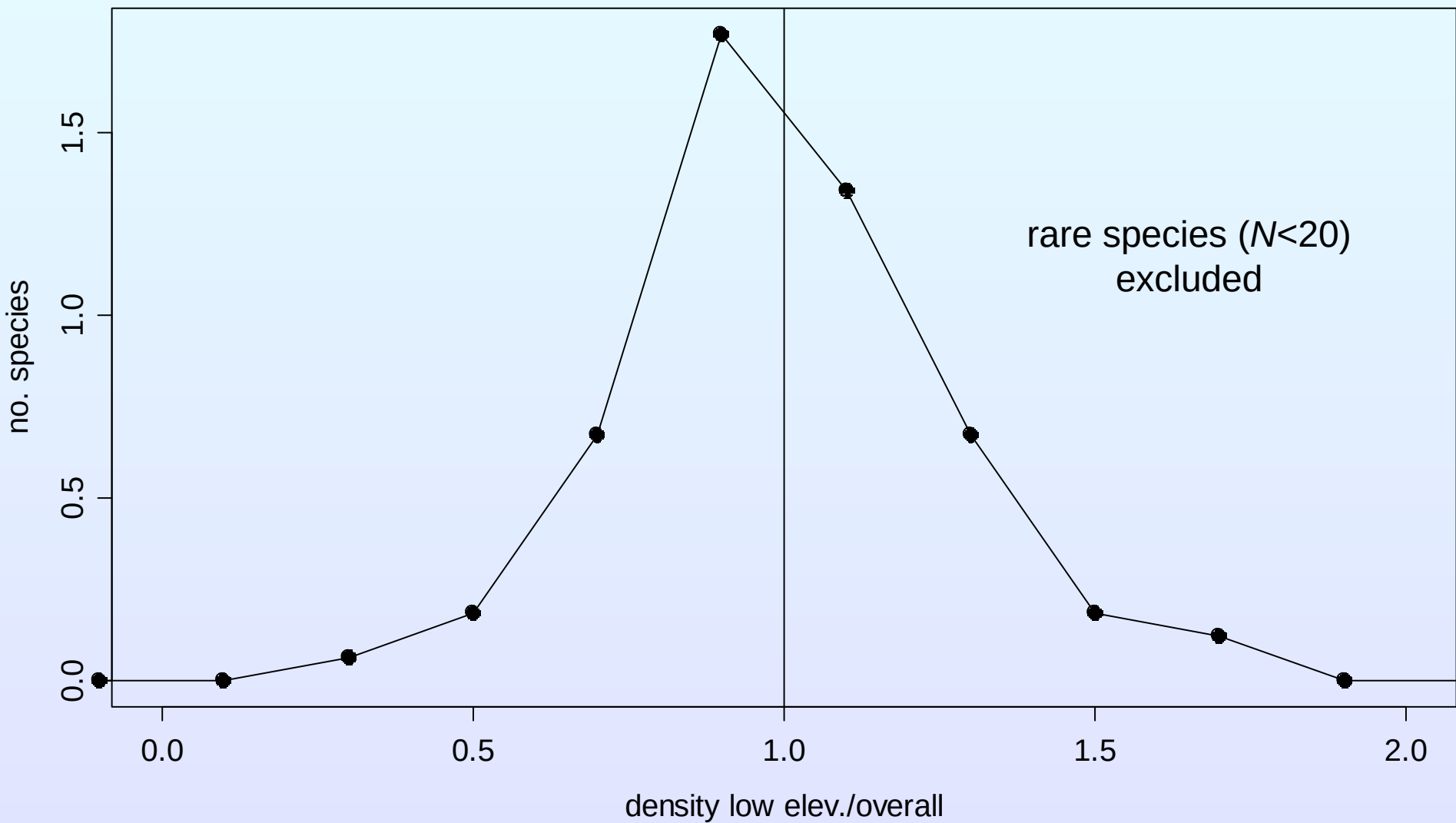
Habitat association index

No habitat preference, dispersal = 75 m



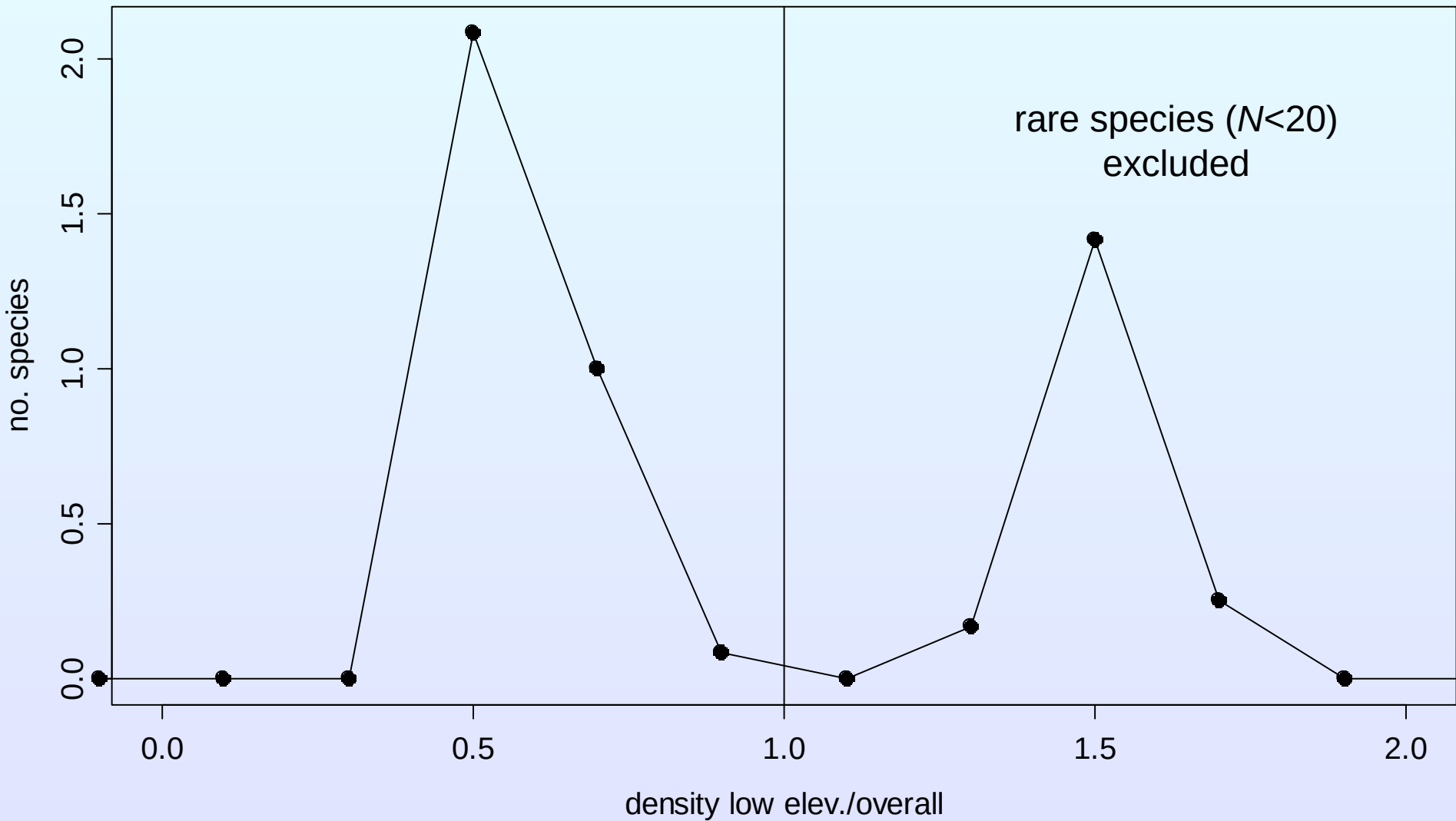
Habitat association index

Weak habitat preference, dispersal = 75 m



Habitat association index

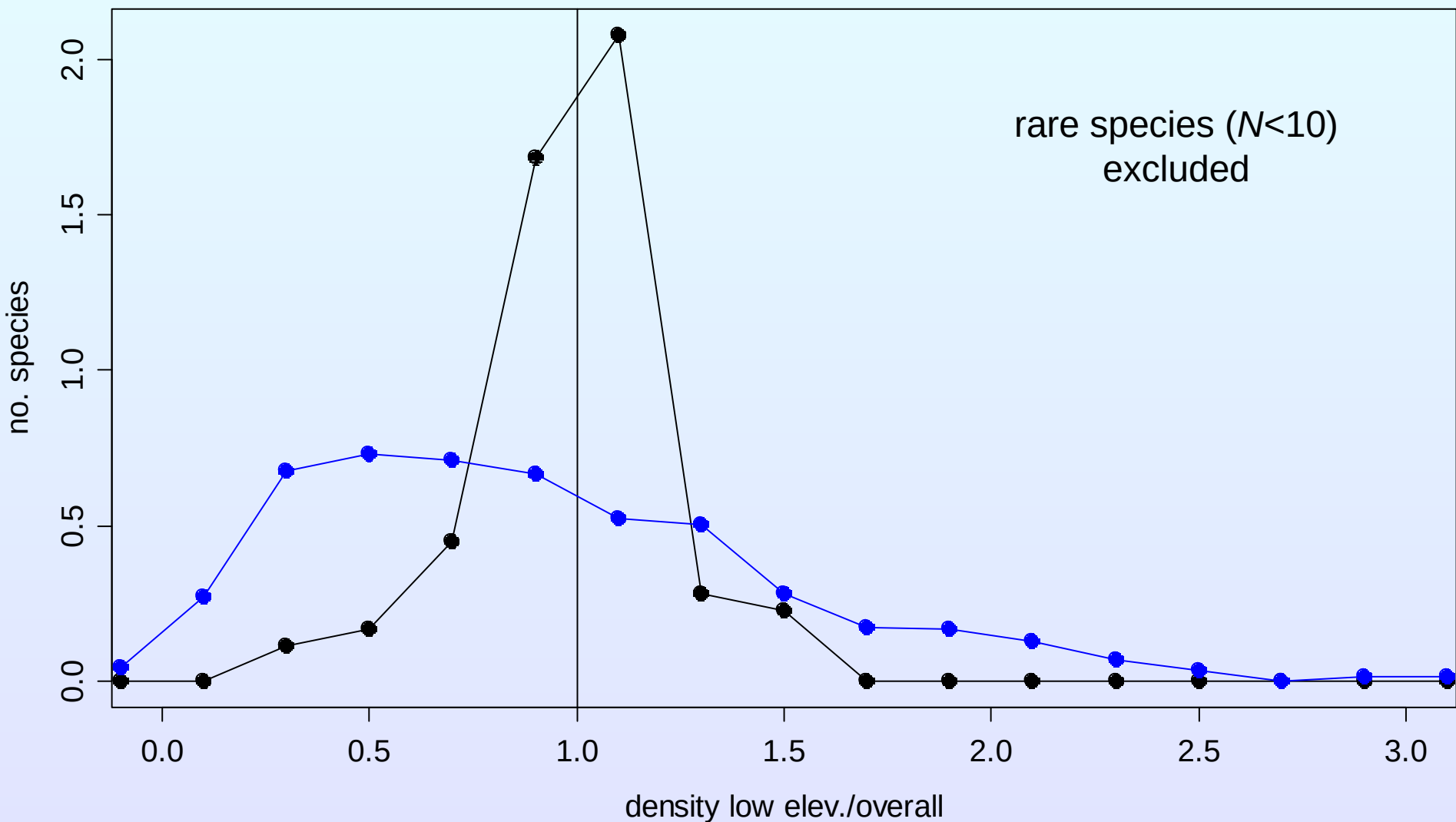
Strong habitat preference, dispersal = 75 m



Habitat association index

Simulation: no habitat preference, dispersal = 75 m

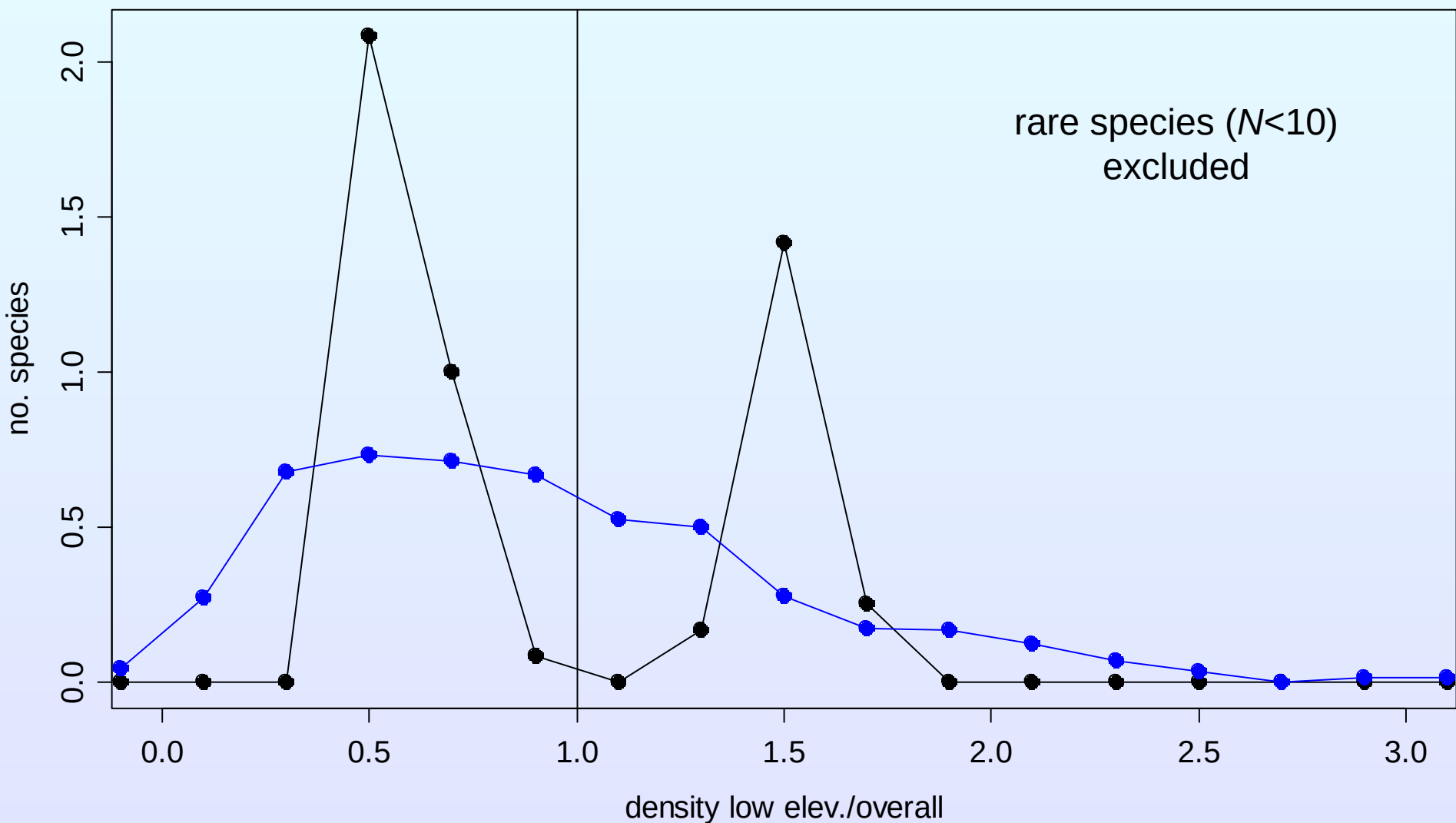
Real forest: Yasuni plot



Habitat association index

Simulation: strong habitat preference, dispersal = 75 m

Real forest: Yasuni plot



Real forest: Yasuni plot

Not consistent with:

- Every species highly dispersal limited (~5 m dispersal)
- Every species strongly effected by habitat

Real forest: Yasuni plot

Consistent with:

- No habitat specialization,
with some poorly dispersed species
- All species well-dispersed,
some strong habitat associations
- A mixture of habitat specializations
and dispersal limitations

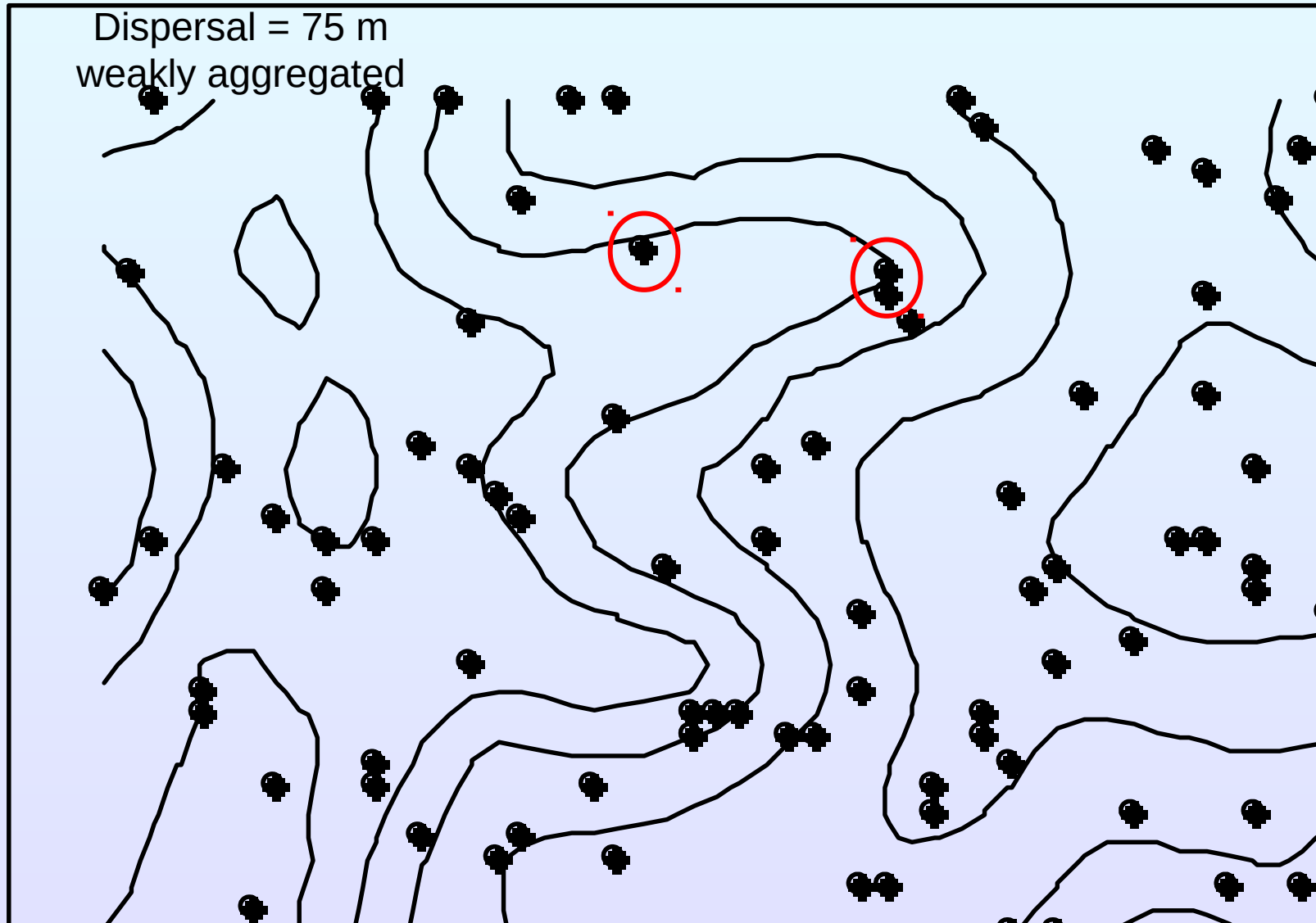
Interpreting the maps

By themselves (ie without dispersal information),
habitat correlations provide no information

What more information is there in the maps?

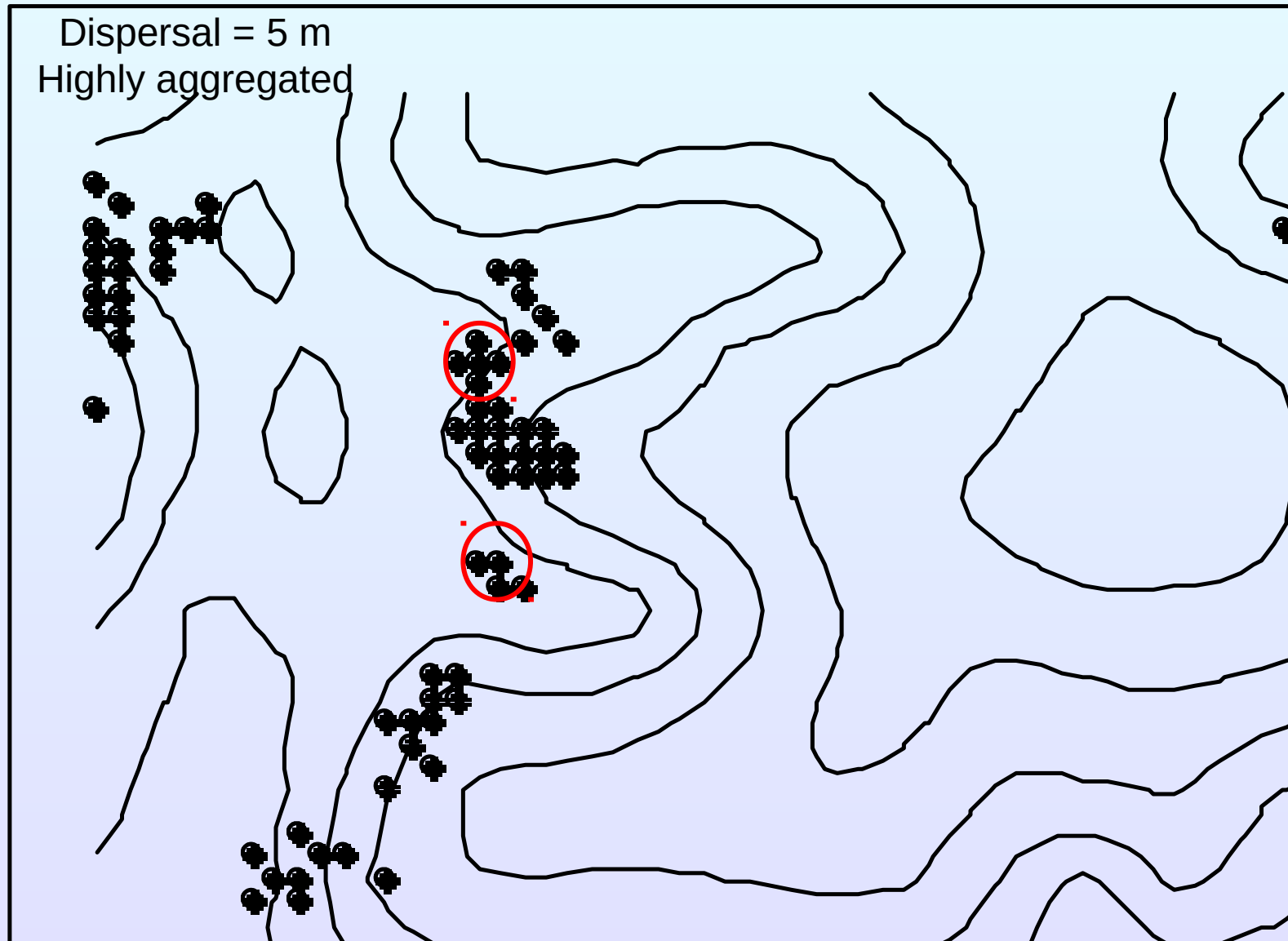
Aggregation index

mean no. conspecific neighbors within 5 m [= Ripley's $K(5)$]...



Aggregation index

...divided by overall density per 10 m circle



Aggregation index

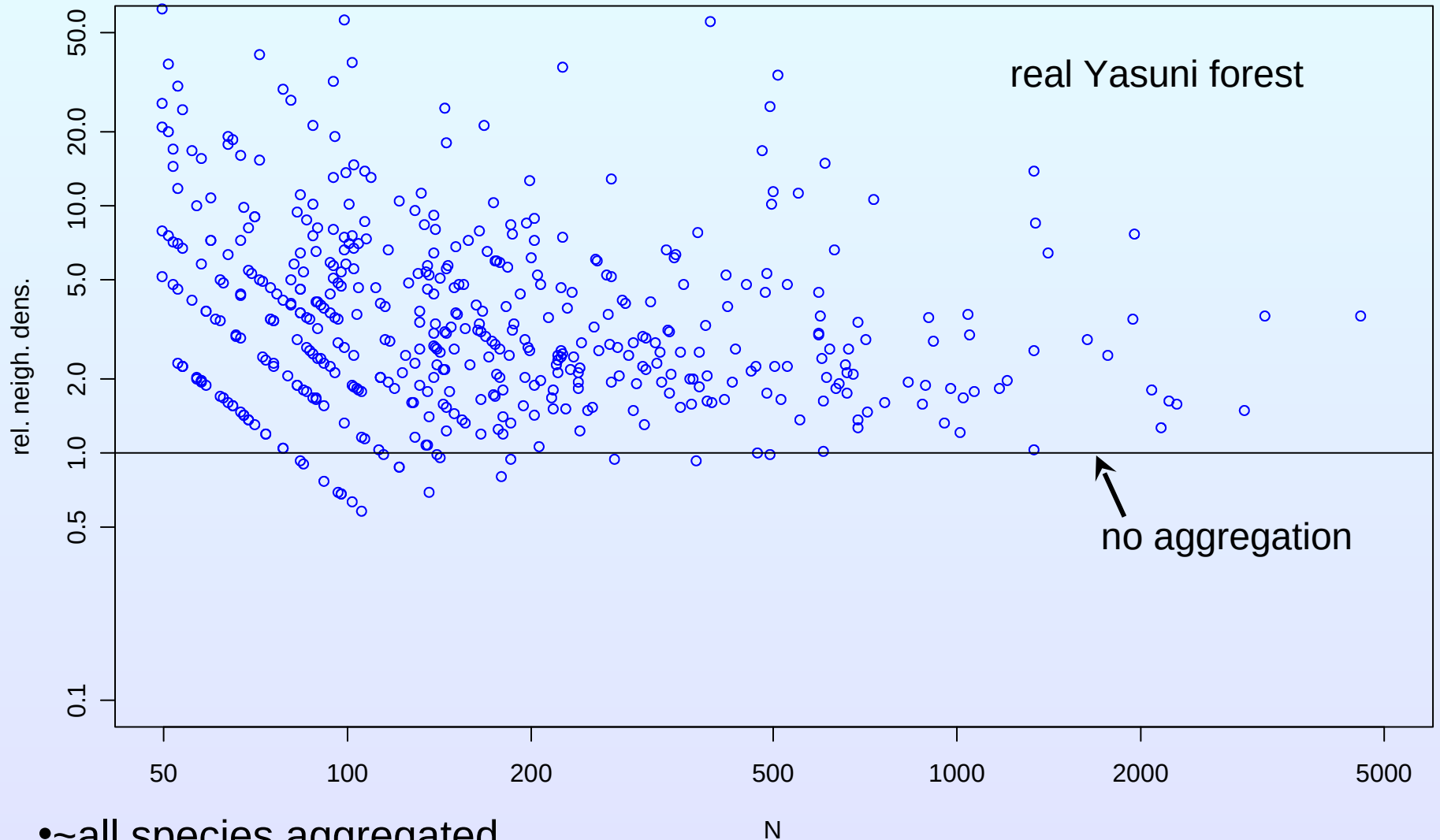
relative neighborhood density at 0-5 m

$$\Omega(5) = \frac{K(5)}{\lambda}$$

K = Ripley's K

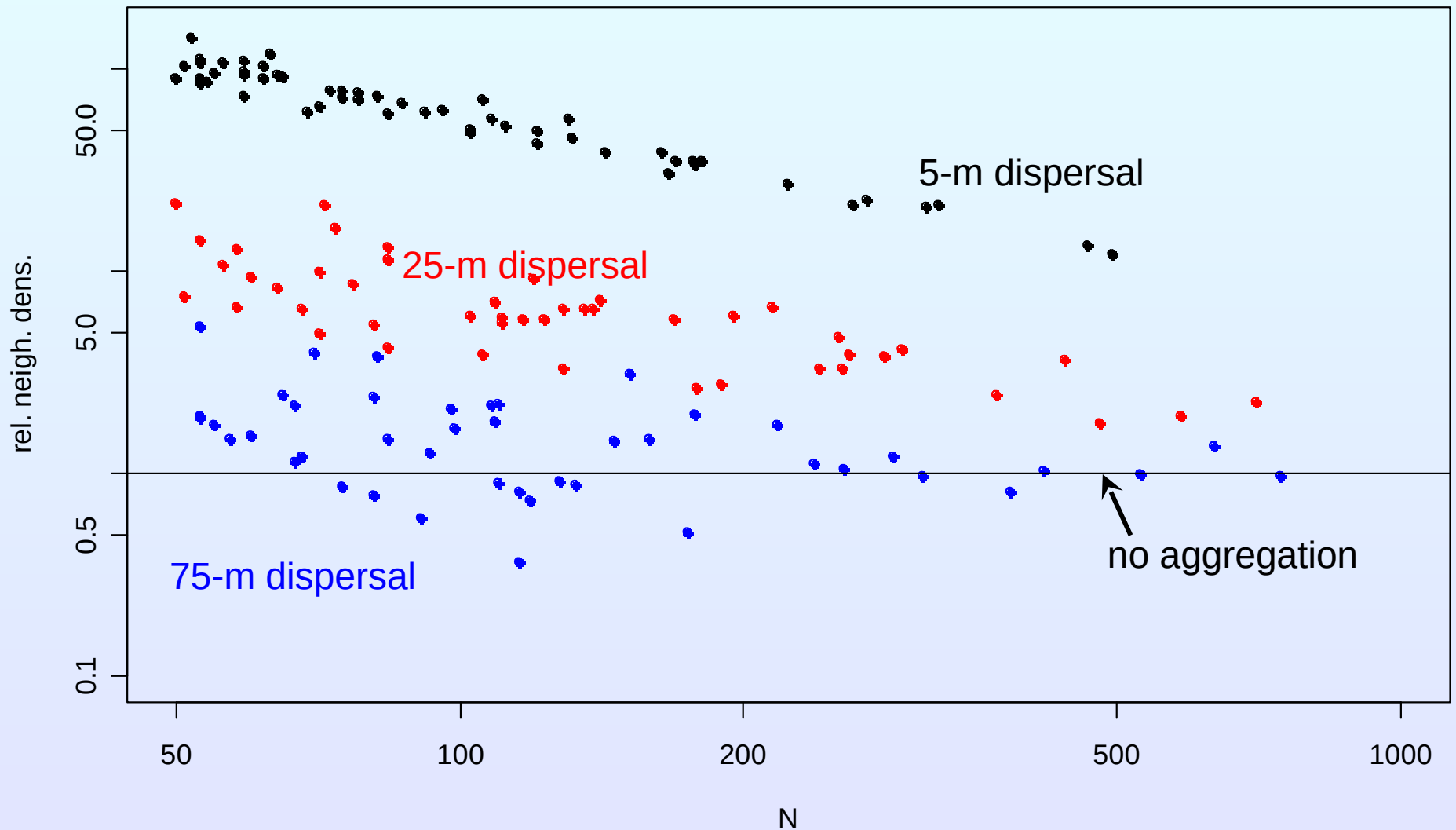
λ = mean density per 10-m radius circle

Aggregation parameter (relative neighborhood density)



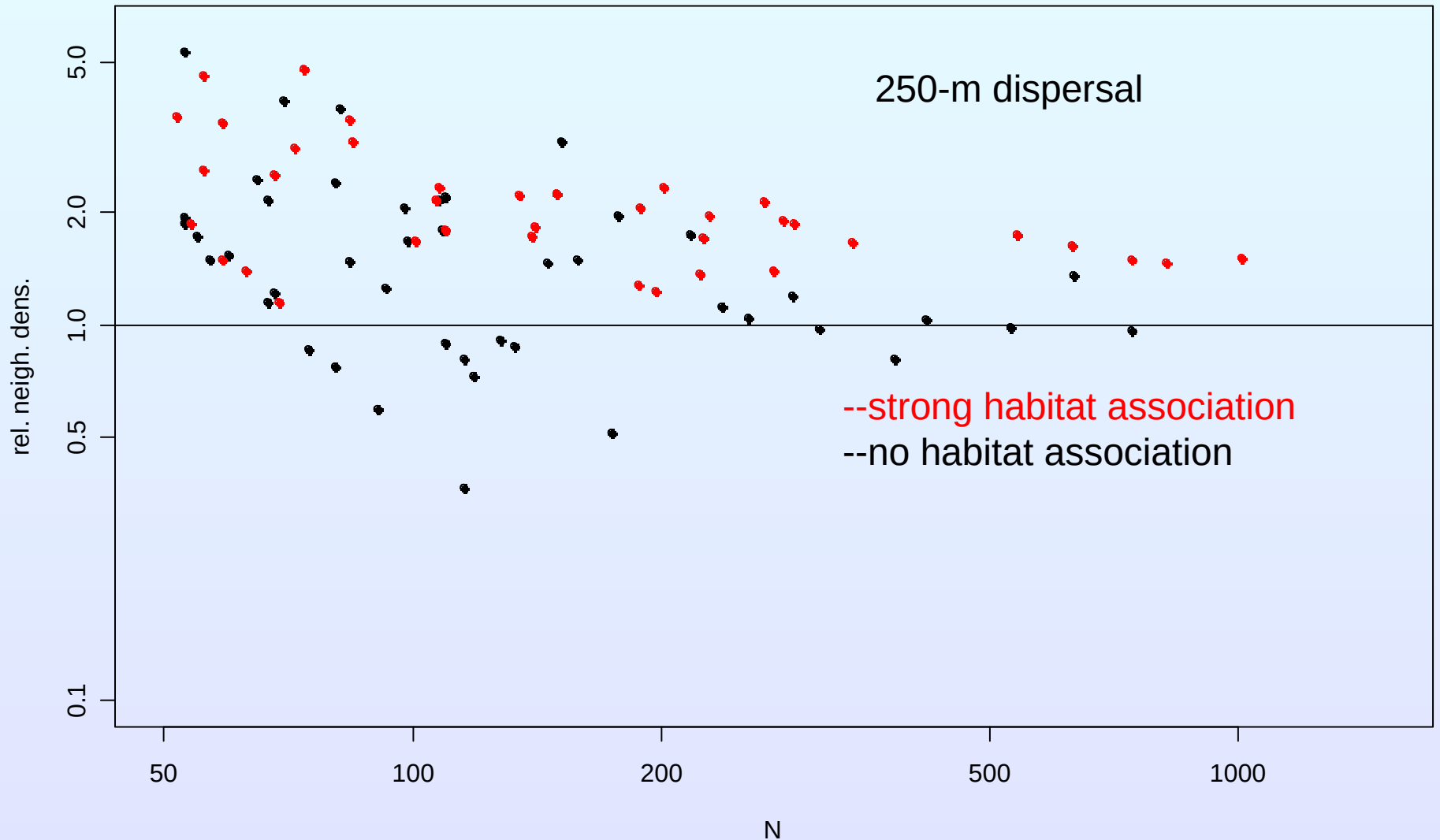
- ~all species aggregated
- rare species moreso

Aggregation parameter (relative neighborhood density) simulation



- large decrease with better dispersal
- decrease with abundance

Aggregation parameter with habitat specialization



small but consistent impact of habitat association



Conclusions

Small proportion (10%?) of species are highly dispersal-limited (5-10 m dispersal)

Many (half?) moderate- to well-dispersed species are habitat generalists

Magnitude of survival variation in habitat specialists...

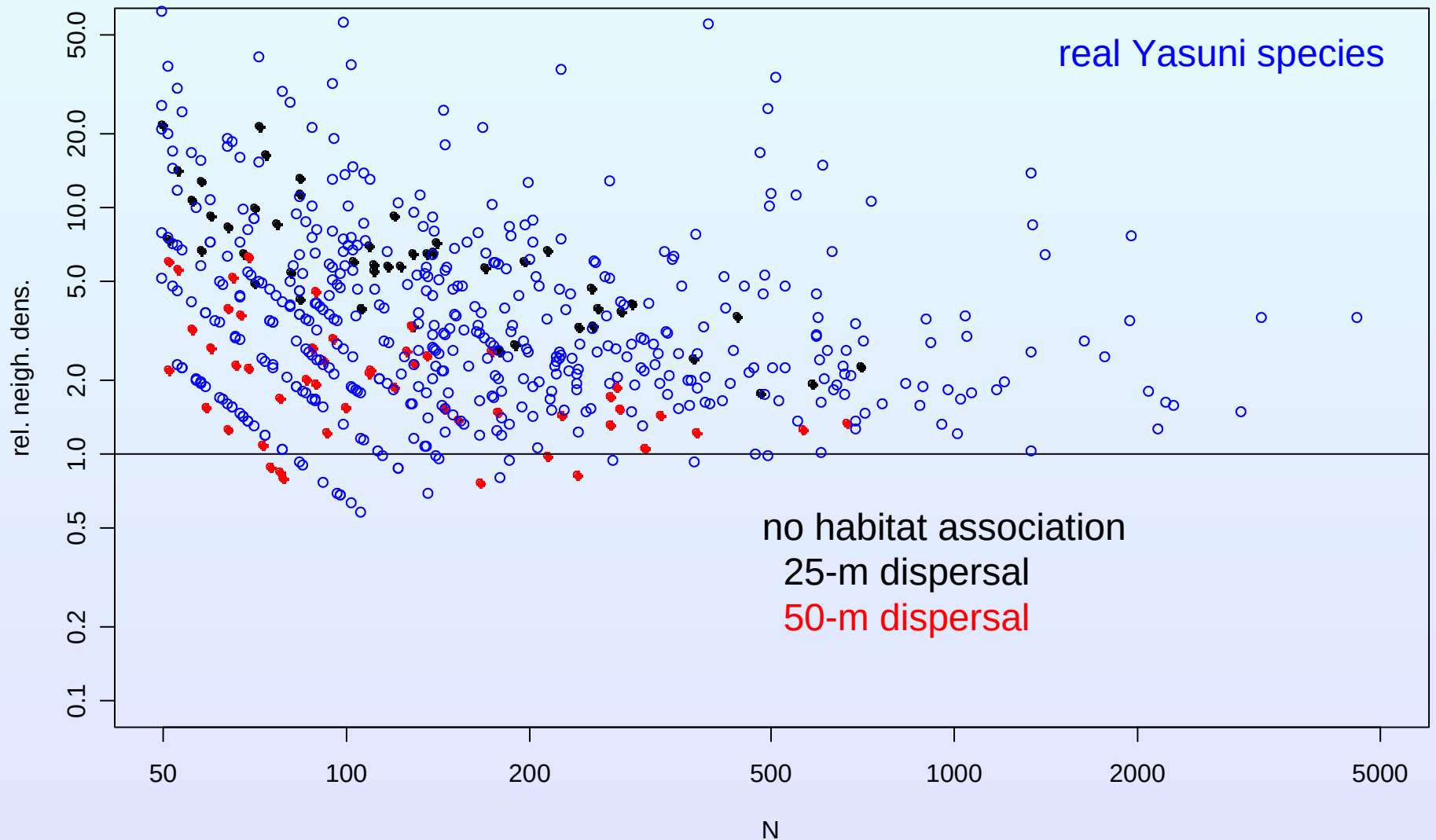
Other factors to be modeled

Density-dependence maintaining rare species

Variation among adults in reproductive output

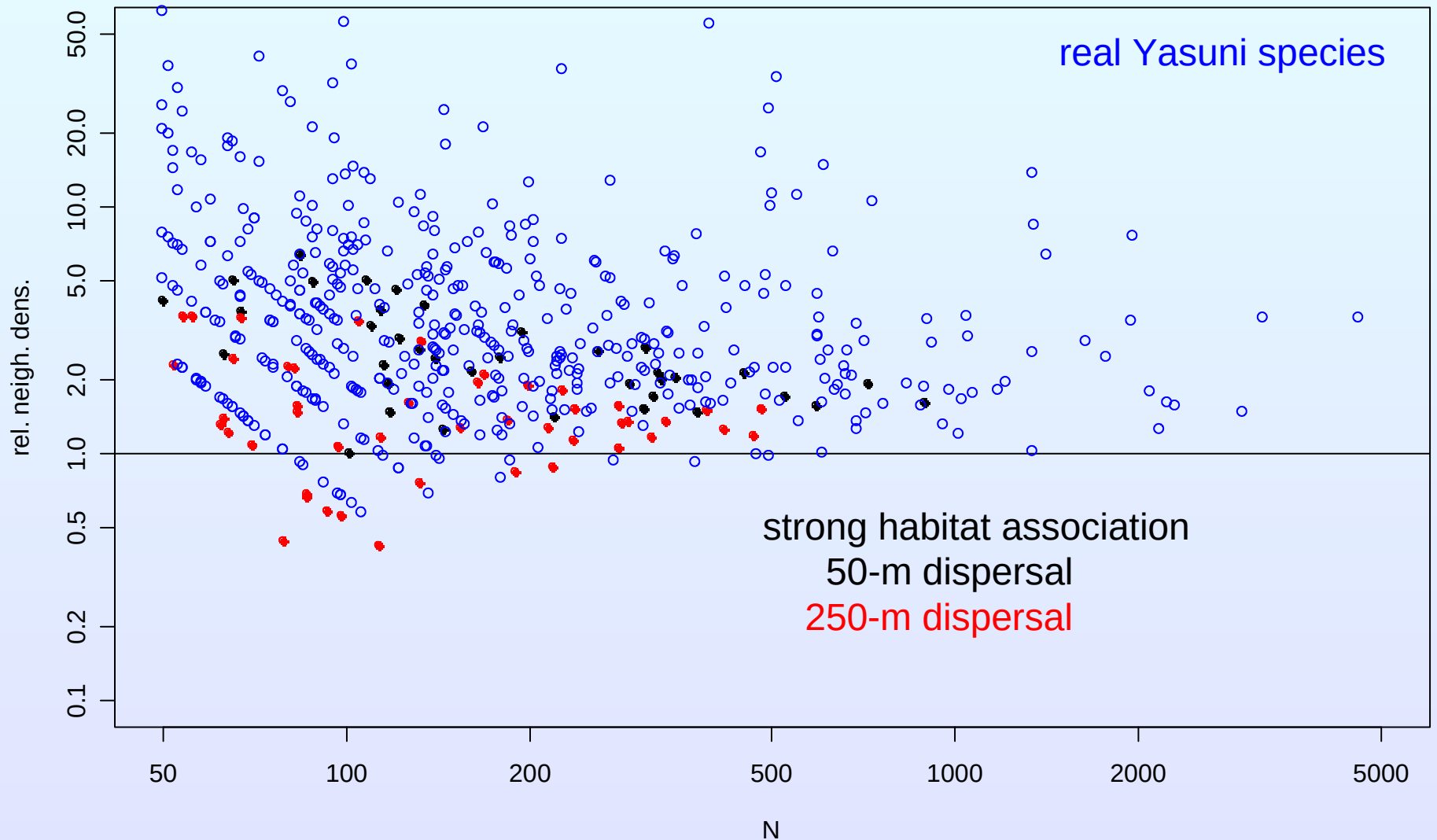
Long lifetime of trees, delay between seed dispersal and adulthood

Aggregation parameter Yasuni plot



resembles model with ~40-m dispersal and no habitat specialization, or...

Aggregation parameter Yasuni plot

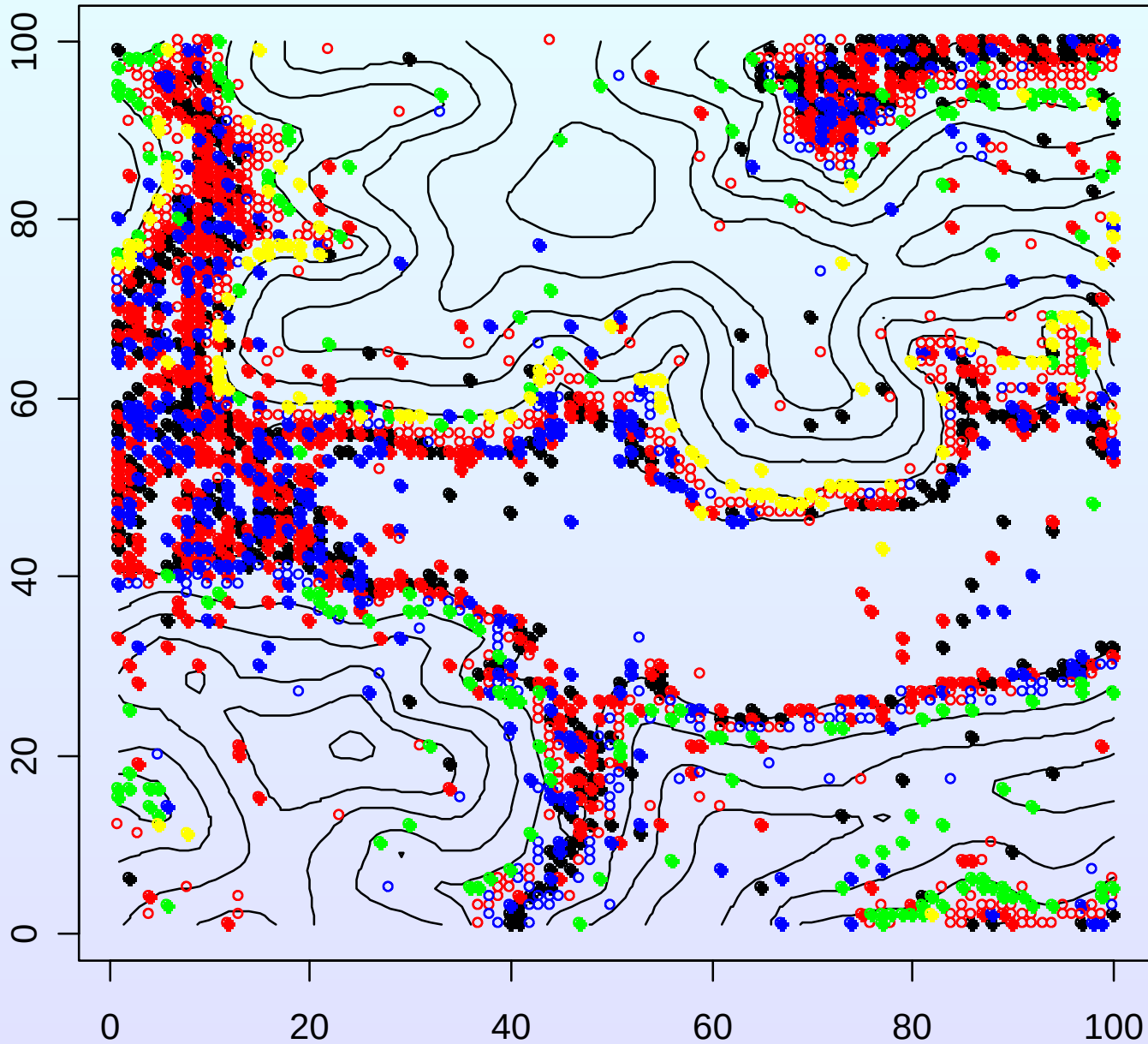


resembles model with 50-m dispersal and strong habitat specialization

Calculate aggregation index in model with narrow habitat categories

Calculate range spans likewise

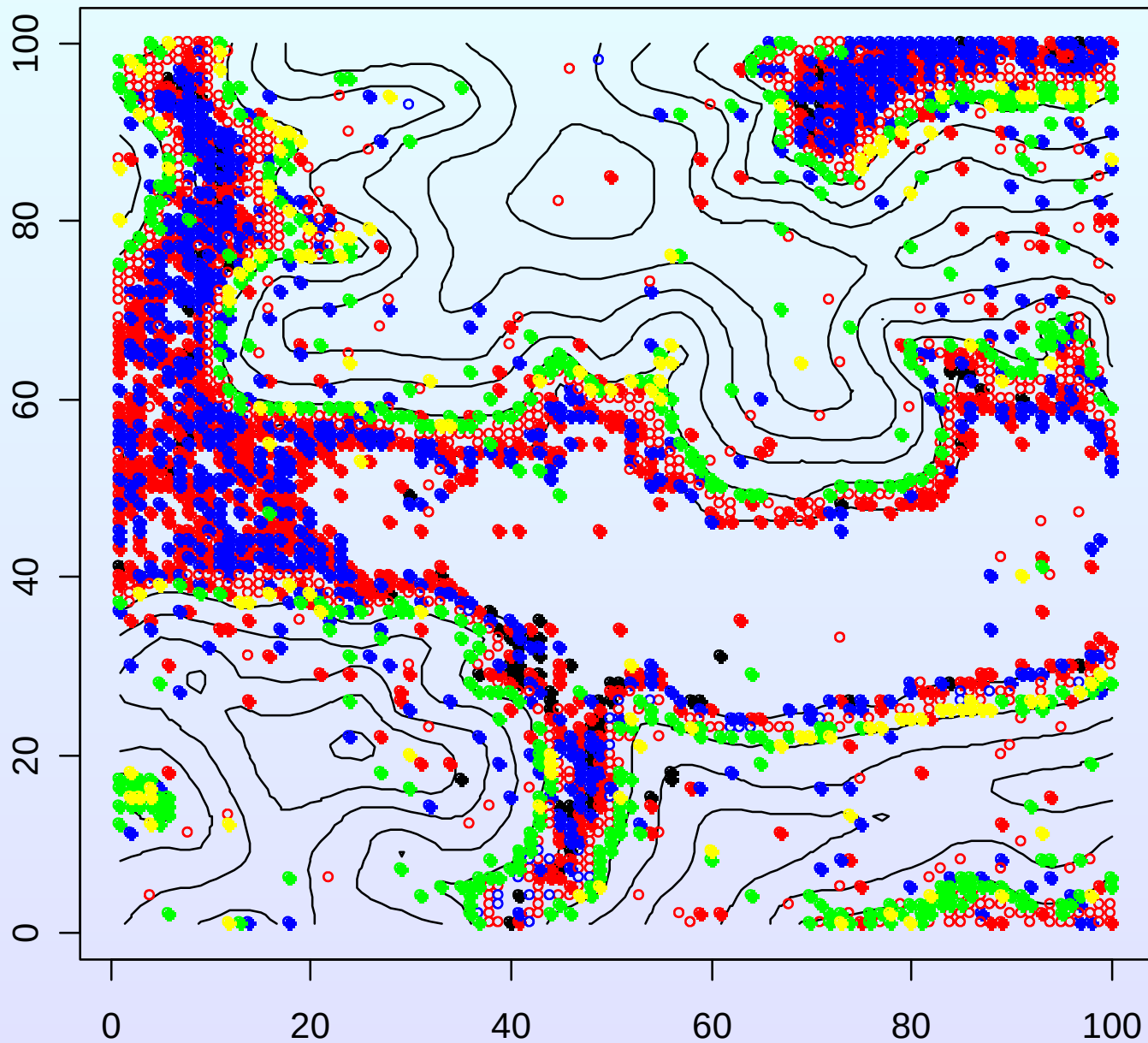
Strong (narrow) habitat preference
75-m dispersal, speciation = 0.005



181 species at 1e7 yr
16 distinct habitats
2-19 spp share each

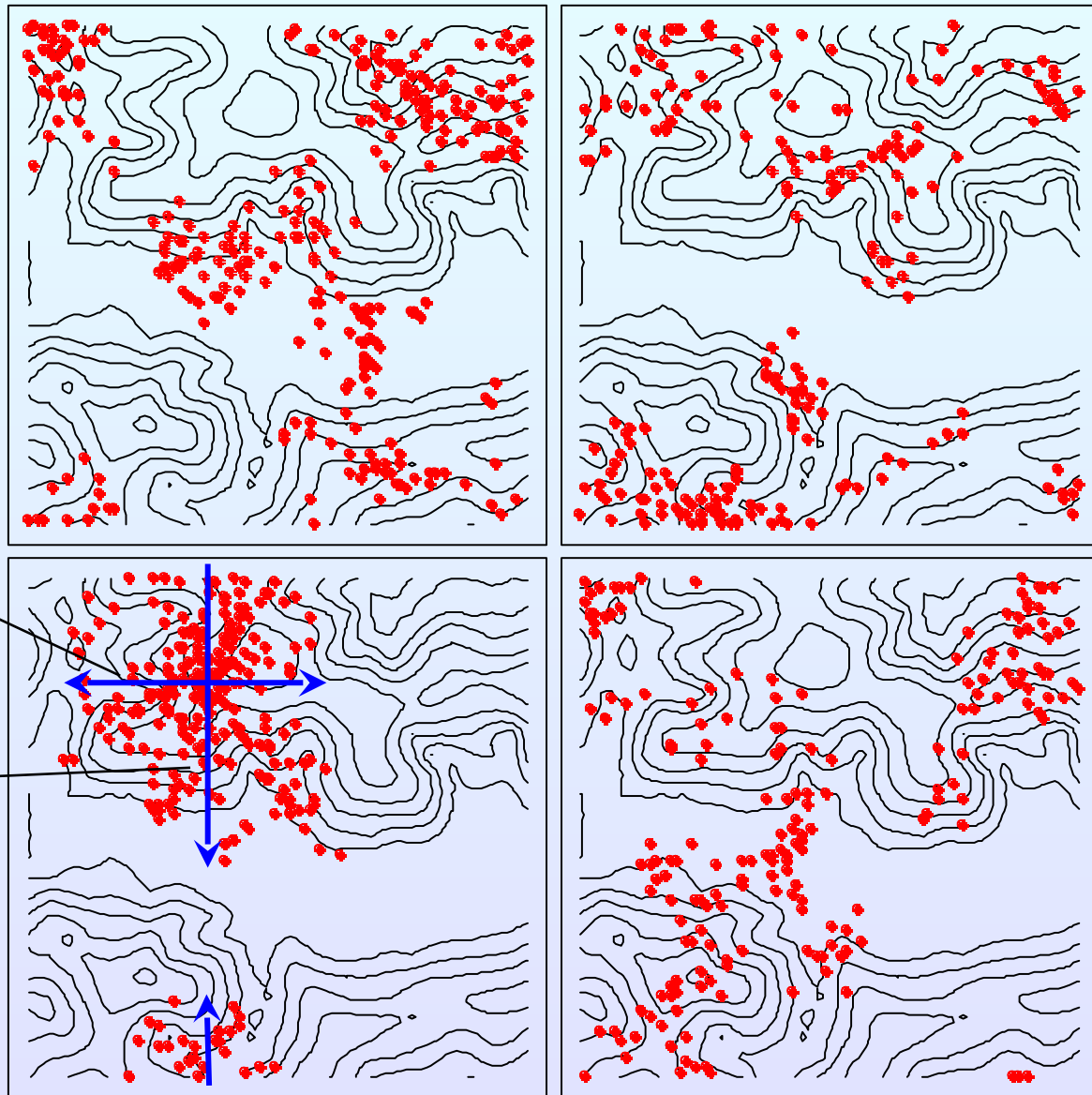
Same model:
no habitat preference
258 species at equil.

Strong (narrow) habitat preference
75-m dispersal, no speciation

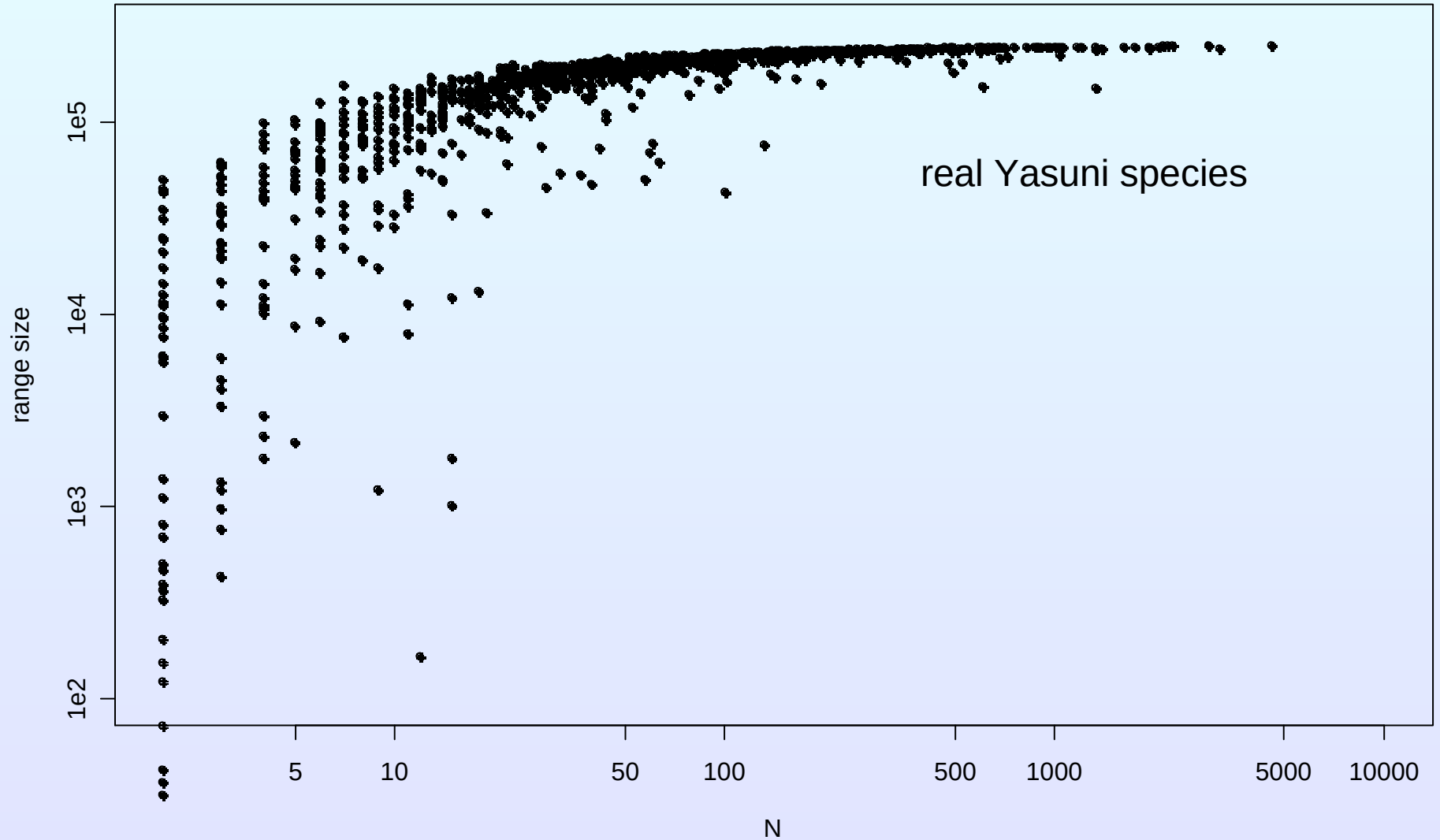


26 species at 1e7 yr
16 distinct habitats
1-3 spp share each

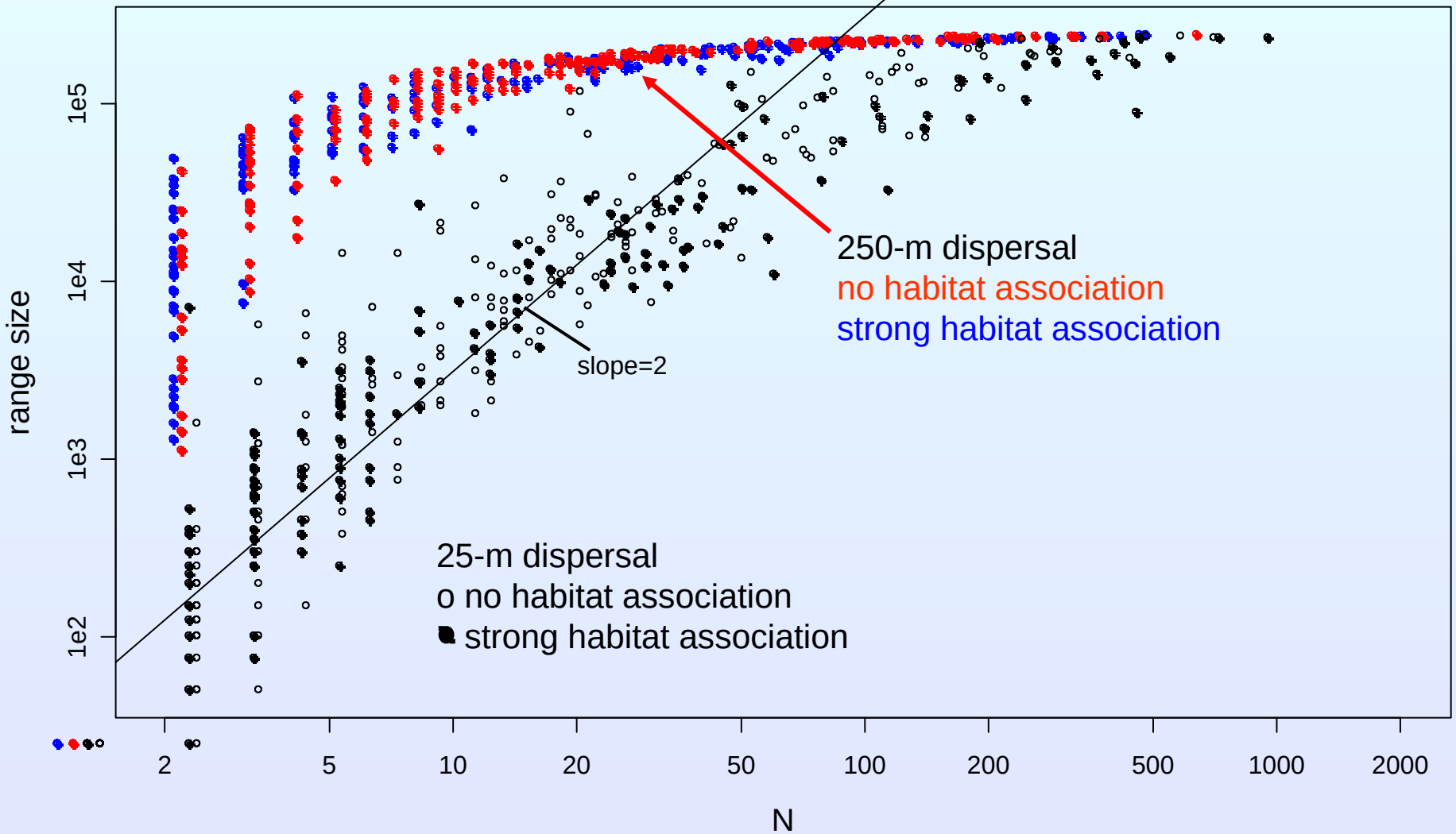
span of 'geographic' range



range size vs. abundance

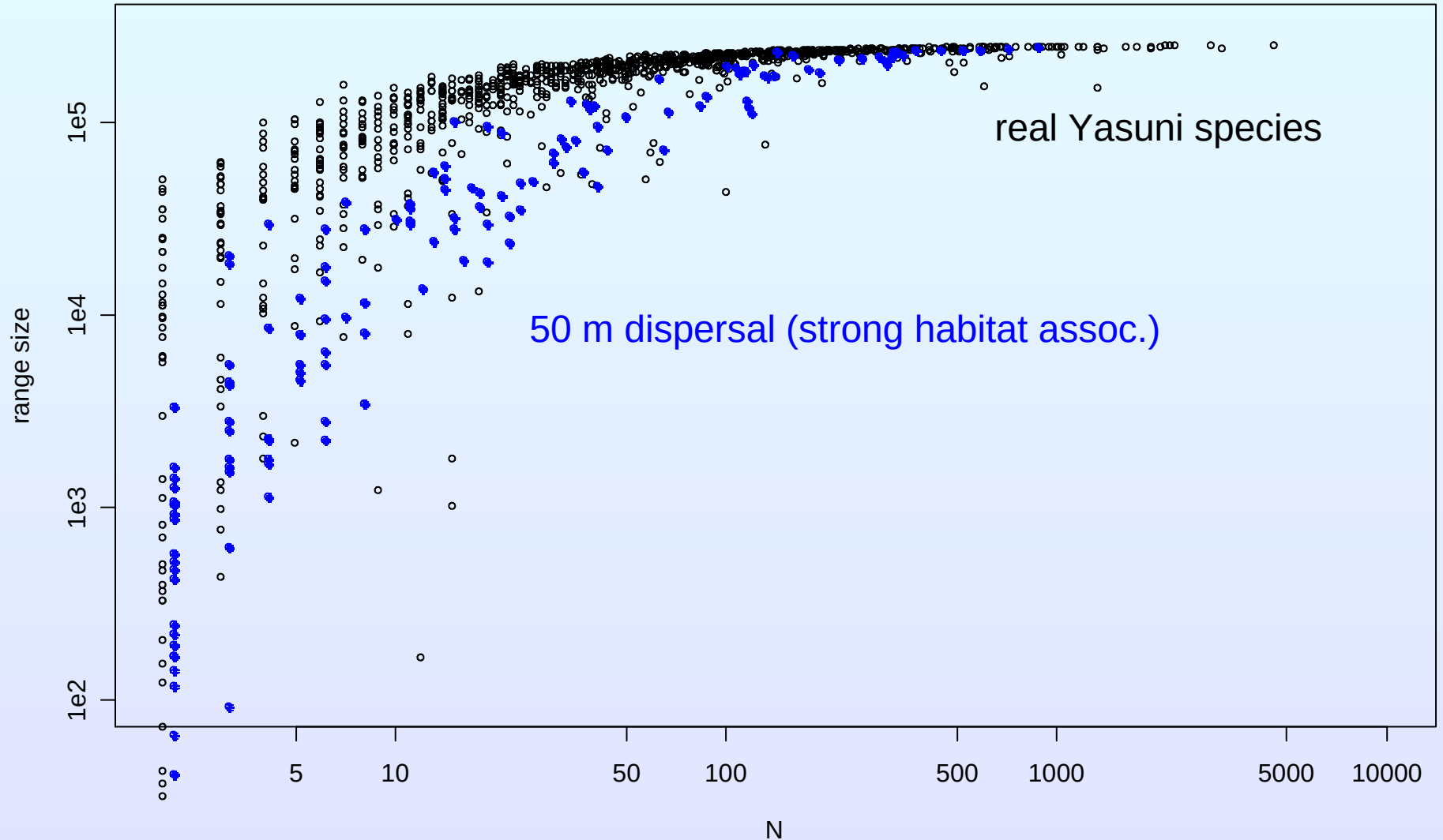


range size in simulation

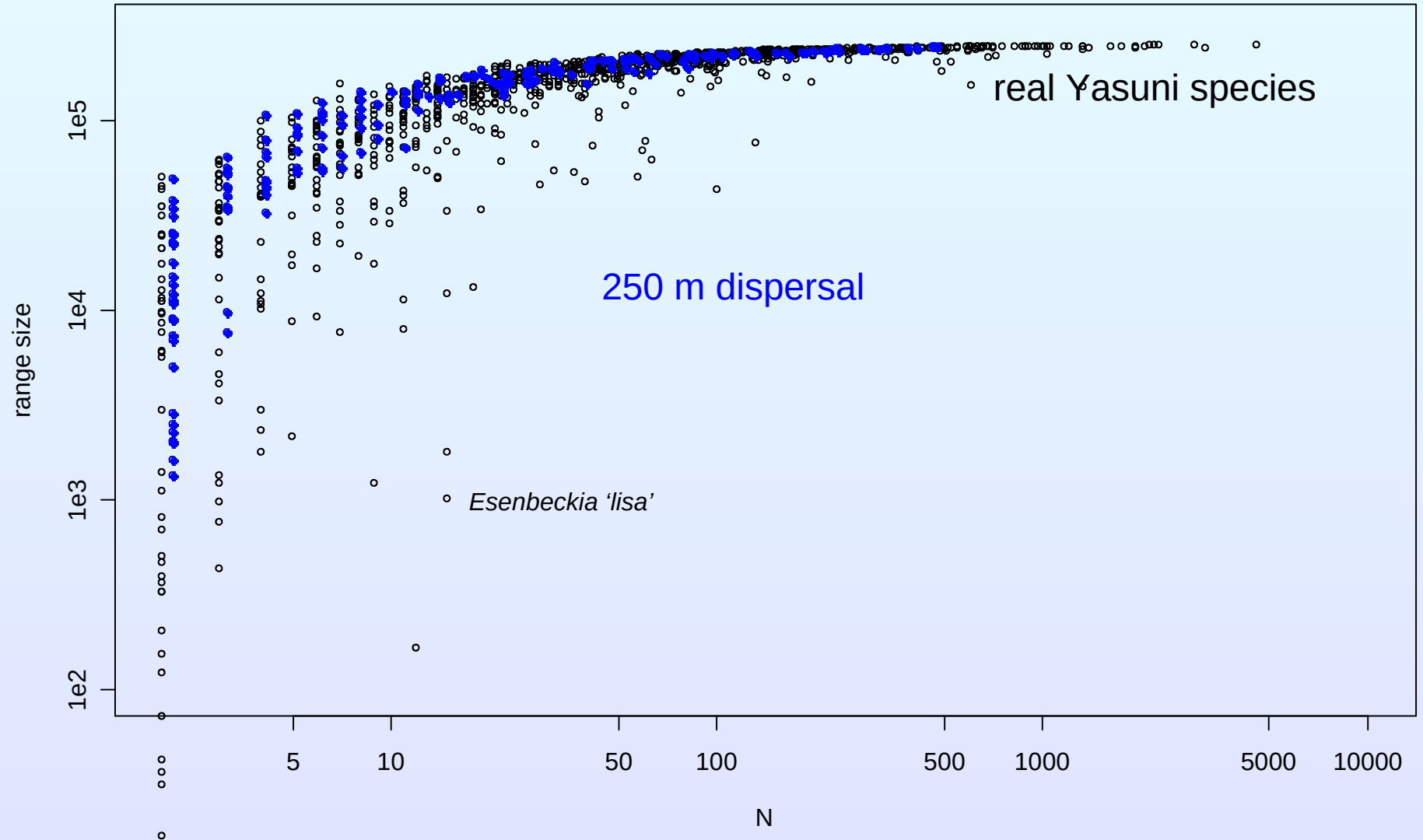


habitat association not relevant
limited dispersal, limited range

range size simulated vs. observed



range size simulated vs. observed



A view of how tree communities work

At local scale, speciation (invasion) is an important driving force

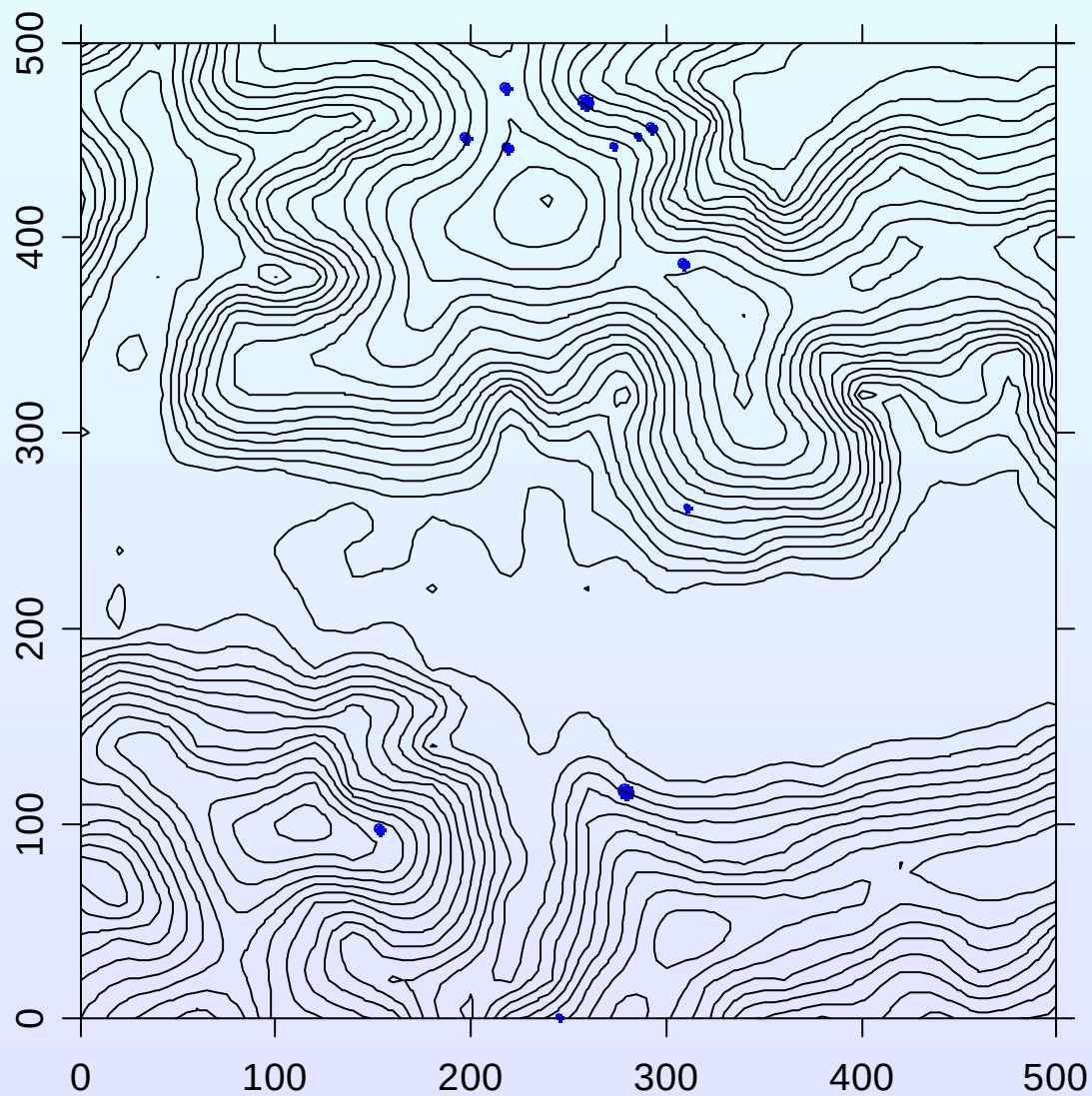
- High diversity due to species input
- Many species are rare
- Populations are too low to persist, even with equilibrating forces or habitat differences
- Rare species are turning over
- Resembles a neutral community

but at wider scale...



Yasuni 25 ha plot
Ecuador

Laxoplumeria tessmannii
Apocynaceae



Atlas of United States Trees

by Elbert L. Little, Jr.

<http://climchange.cr.usgs.gov/data/atlas/little/>

Leitneria floridana
(Simaroubaceae)
corkwood



Macroecology

dispersal

species abundance

β -diversity

habitat turnover

species-area

geographic ranges

no general relationship among these

Macroecology

dispersal

species abundance

β -diversity

habitat turnover

species-area

geographic ranges

speciation (species immigration)

Macroecology

dispersal

species abundance

β -diversity

habitat turnover

species-area

geographic ranges

speciation (species immigration)

Neutrality and the Hubbell model

Neutrality is only the third most important feature:

- First, stochasticity
- Second, the Hubbell model



Neutrality and the Hubbell model

Neutrality is only the third most important feature:

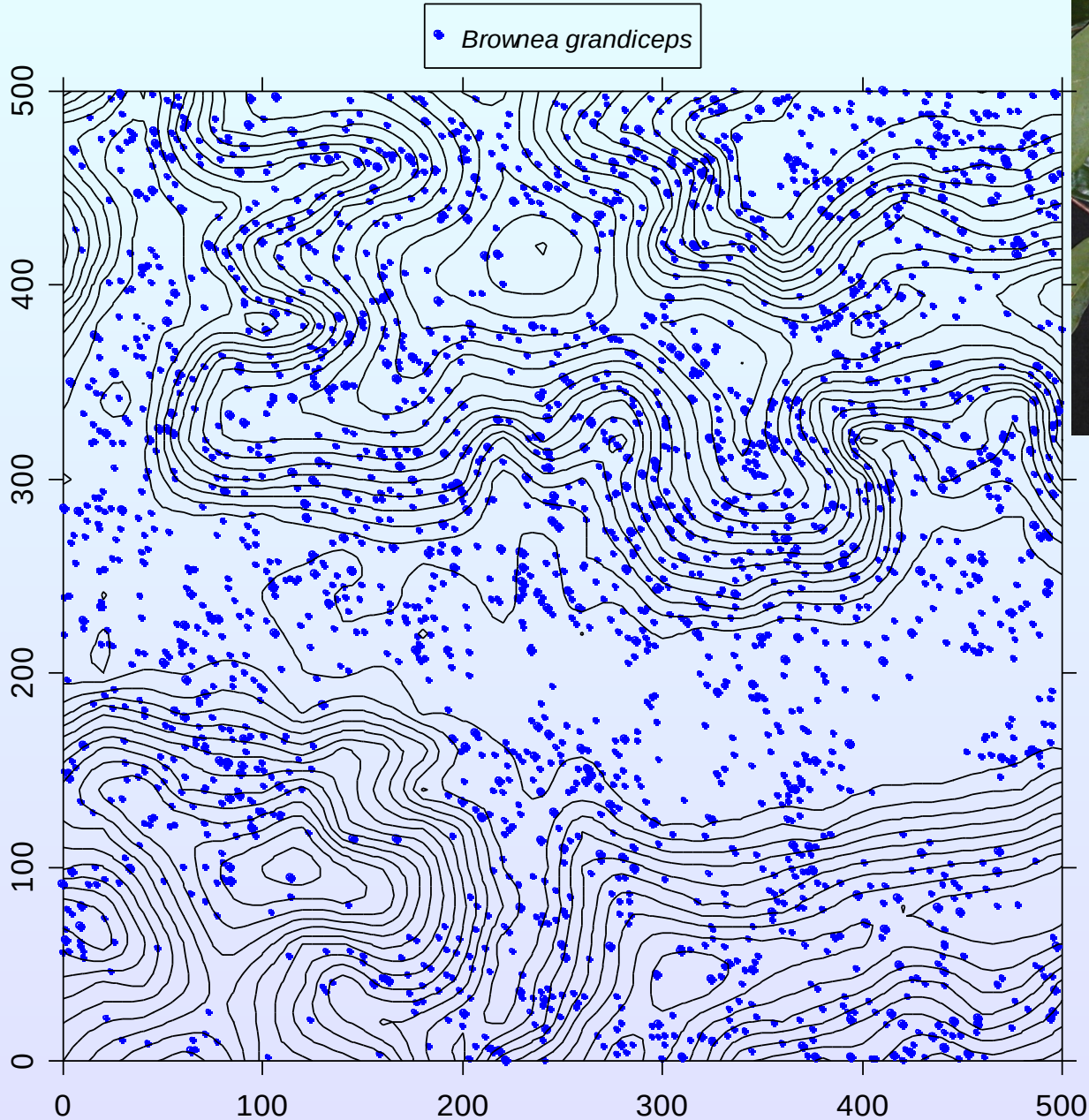
- First, stochastic biology of individuals
- Second, the speciation pump

Neutrality and the Hubbell model

Neutrality is only the third most important feature:

- First, stochastic biology of individuals
- Second, the speciation pump

Yasuni 25 ha plot (Ecuador)



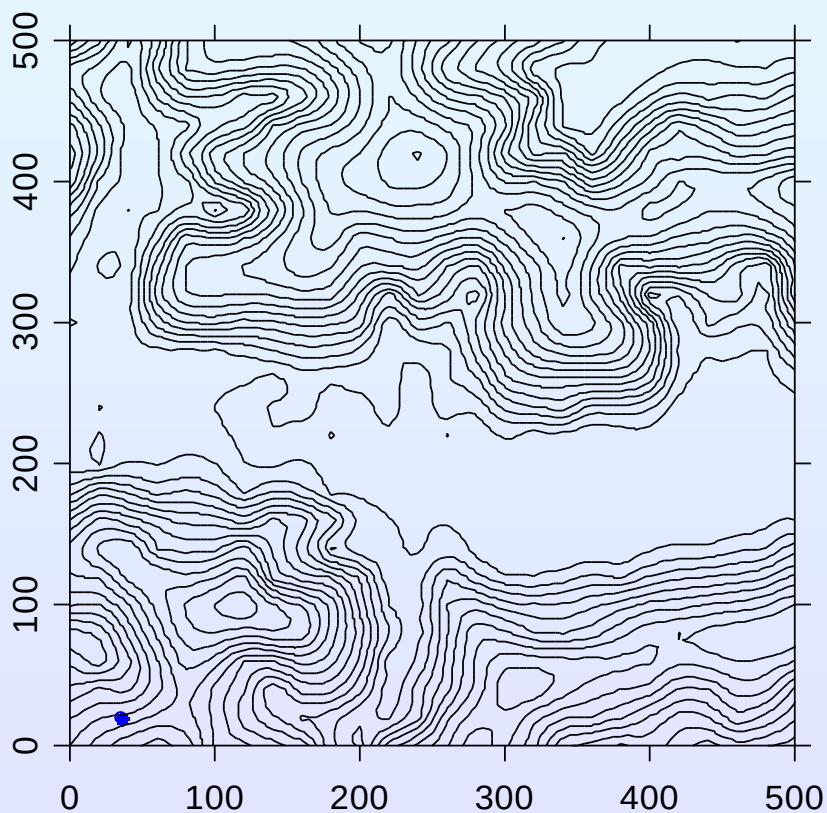
152000 trees ≥ 1 cm dbh
1132 species
--732 known
--400 morphospecies

R. Foster
G. Villa
R. Condit
R. Valencia
C. Hernandez
S. Lao
E. Losos
H. Balslev

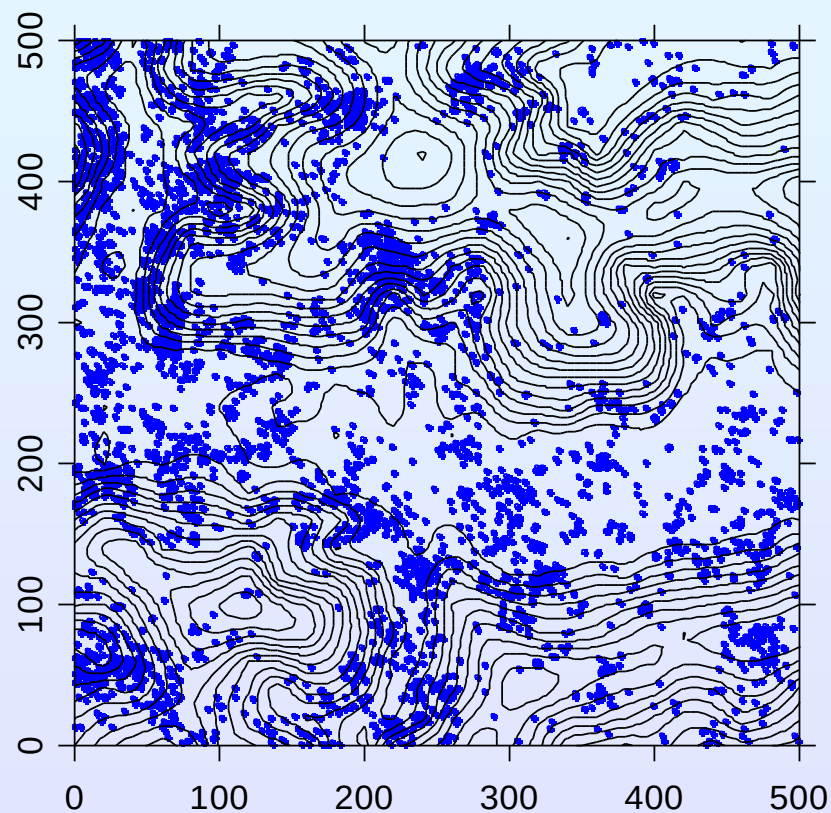
Tree abundances vary several orders of magnitude

Yasuni, Ecuador (25 ha plot)

Quiina amazonica, N=1



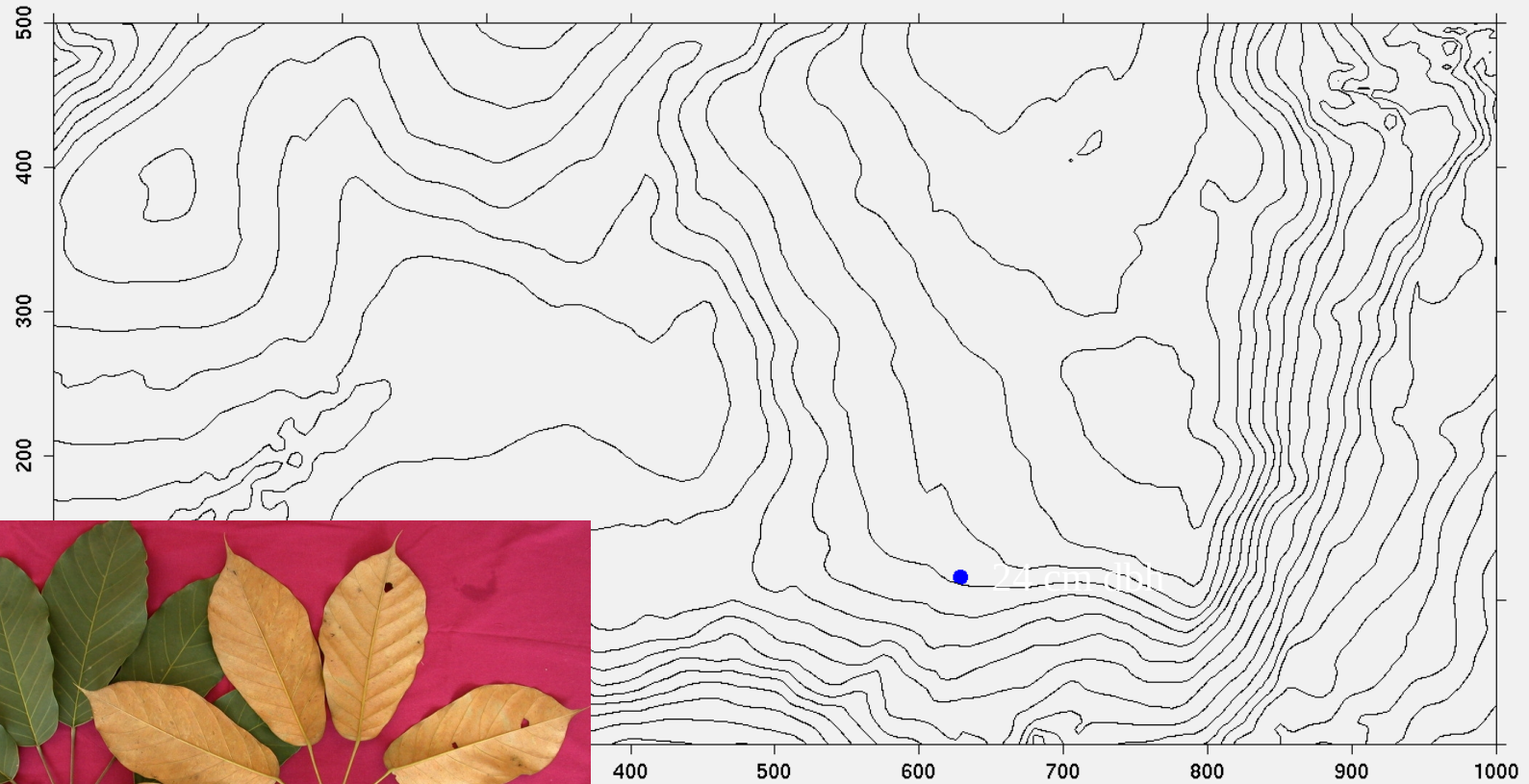
Matisia oblongifolia, N=4622



68 species have a single individual

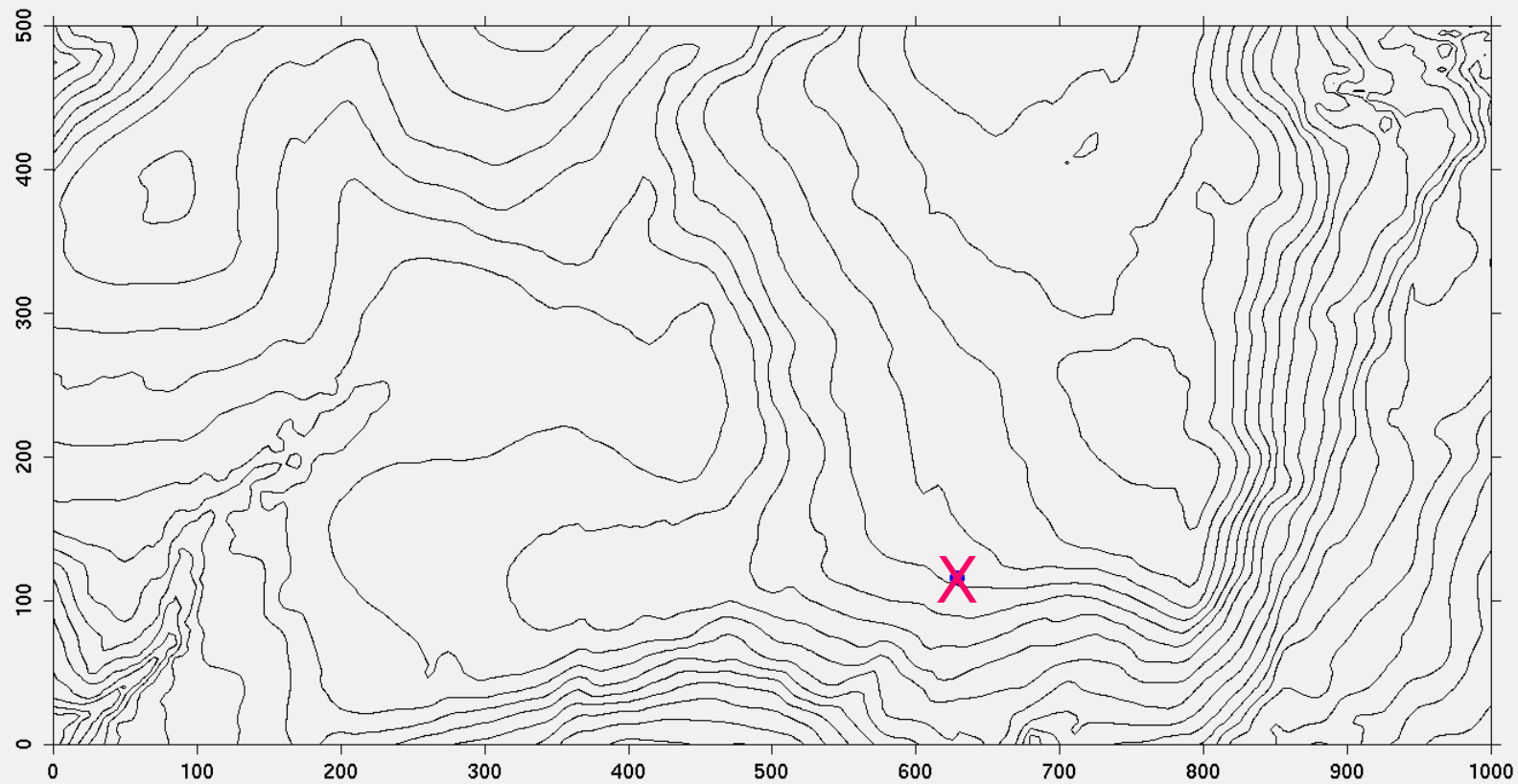
BCI 50-ha plot

Schefflera morototoni 1982-1985

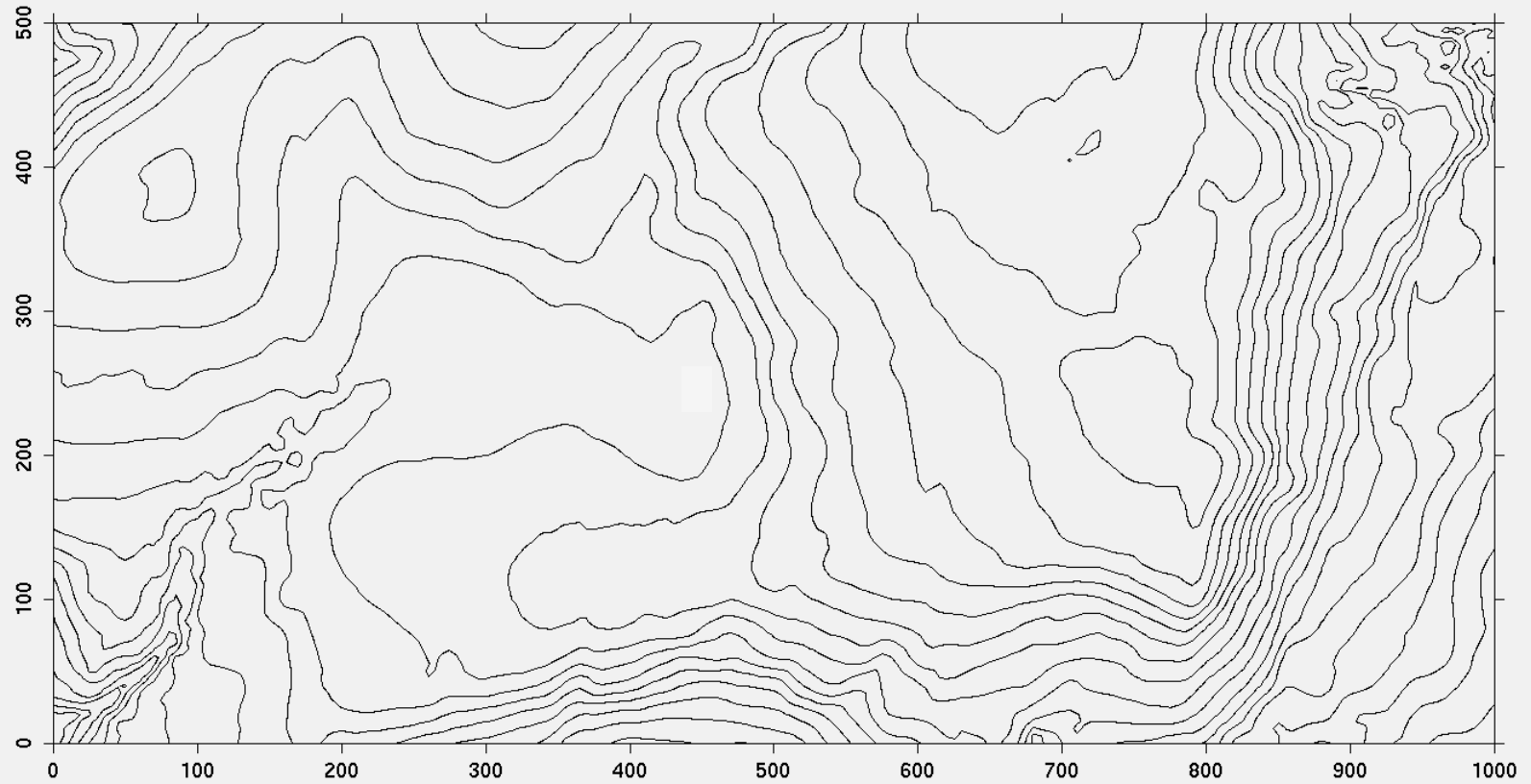


BCI 50-ha plot

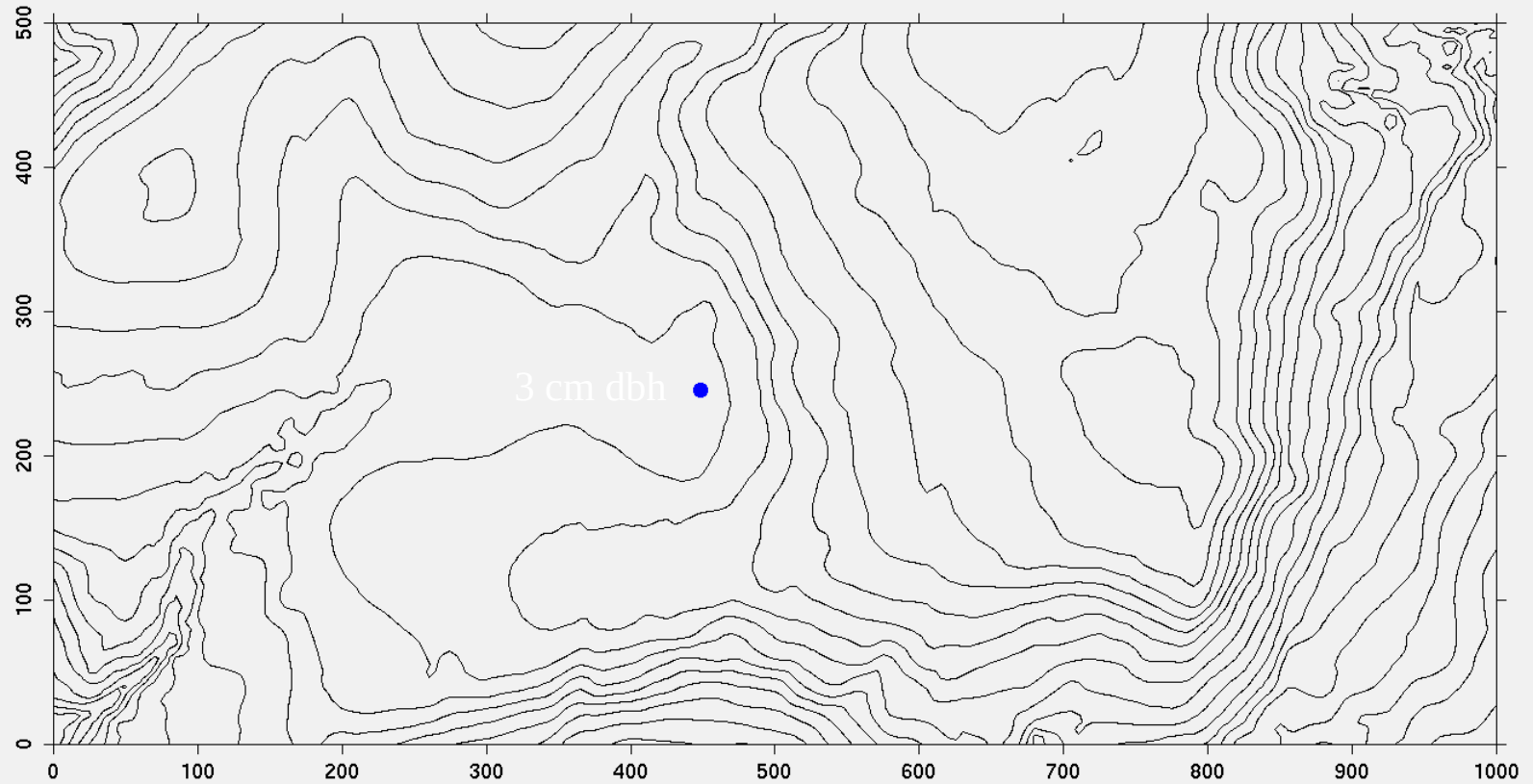
Schefflera morototoni 1990



Schefflera morototoni 1995-2000



Schefflera morototoni 2005



Equilibrium abundance distribution solved analytically using Pauli's master equation approach from statistical physics (Volkov et al., *Nature*, 2003, 2005)

Neutral:

$$P(n) = P(1) \left(\frac{v}{D_1} \right) \prod_i \frac{B_i}{D_{i+1}}$$

Density dependence:

$$P(n) = \theta \frac{\left(\frac{B}{D} \right)^n}{B_1 + n}$$

$P(n)$ = proportion of species with n individuals

B = birth rate (constant, or as a function of abundance i)

D = death rate (constant, or as a function of abundance i)

No dispersal limitation

θ , $P(1)$ are normalizing constants

Real forest: Yasuni plot

Not consistent with:

- Every species highly dispersal limited (~5 m dispersal)
- Every species strongly effected by habitat

Real forest: Yasuni plot

Consistent with:

- No habitat specialization,
with some poorly dispersed species
- All species well-dispersed,
some strong habitat associations
- A mixture of habitat specializations
and dispersal limitations

Aggregation and range

Local aggregation consistent with moderate dispersal (50-75 m)

Ranges across plot are consistent with higher Dispersal (250 m)

Model is missing...

- Other forces maintaining diversity
- Inappropriate growth simulation