Theories of species ranges in tropical forest tree

R. Condit
NCEAS Ecolunch
20 March 2008

Species response to the environment

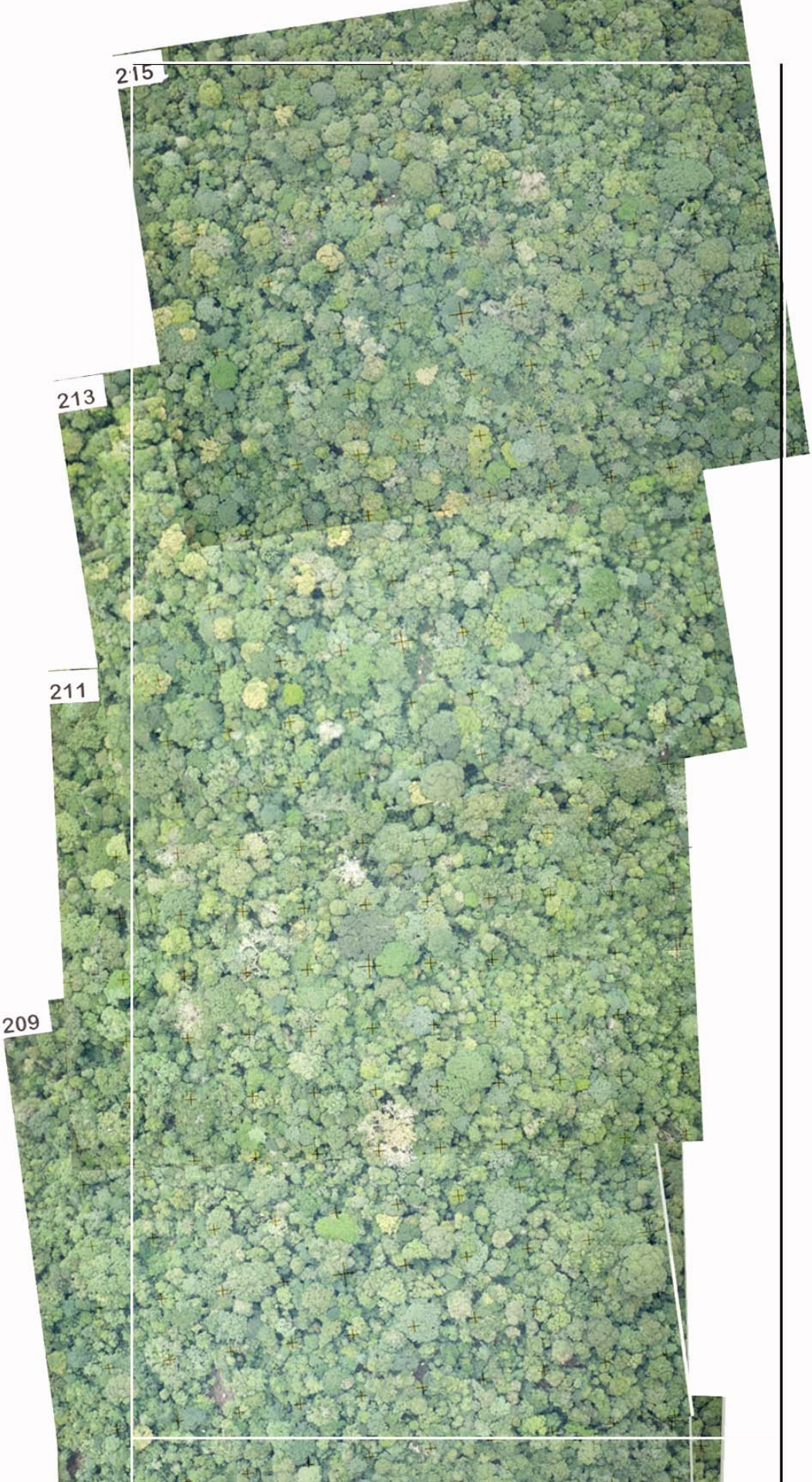
Environment => demography

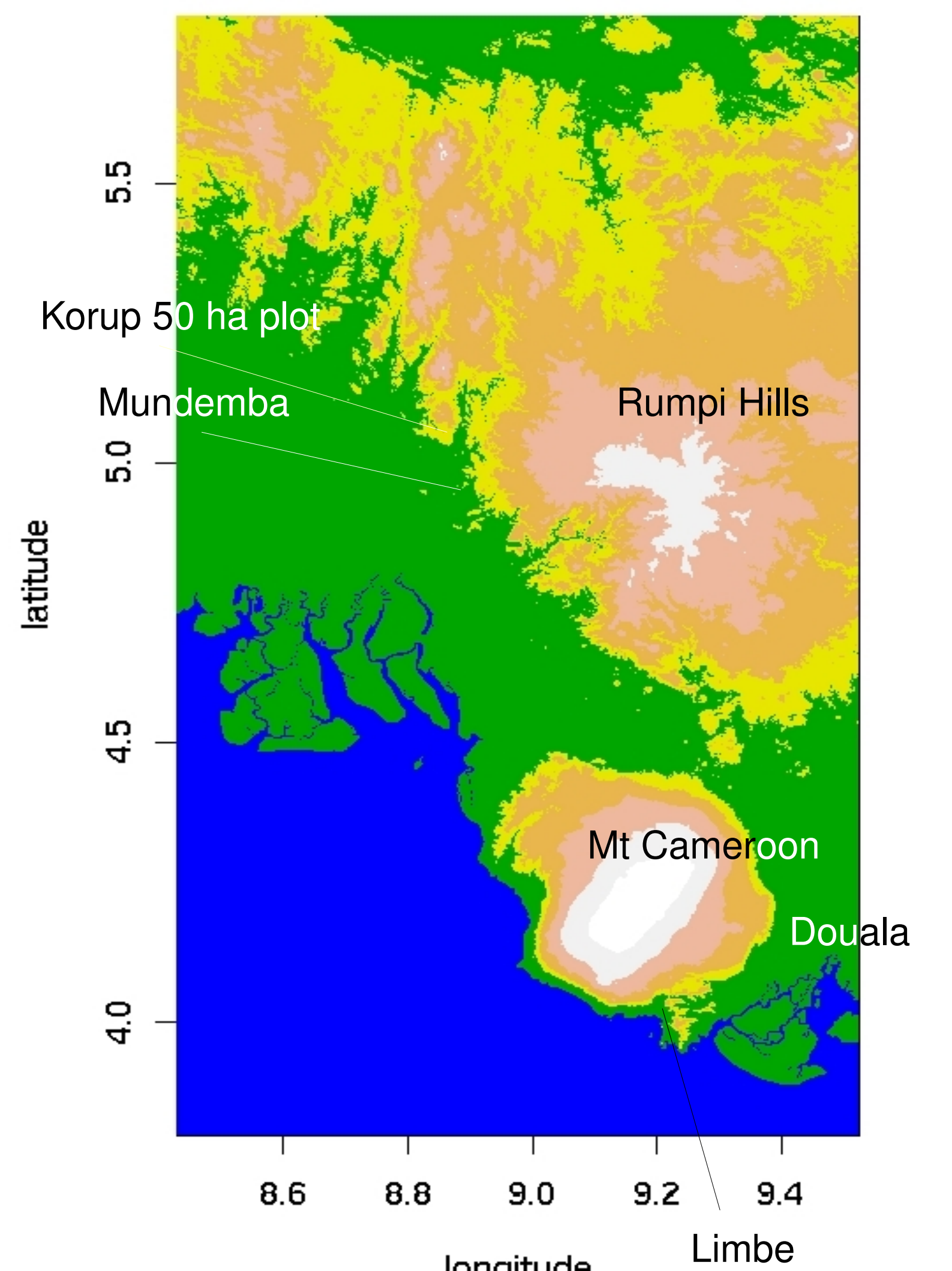
Environment => distribution

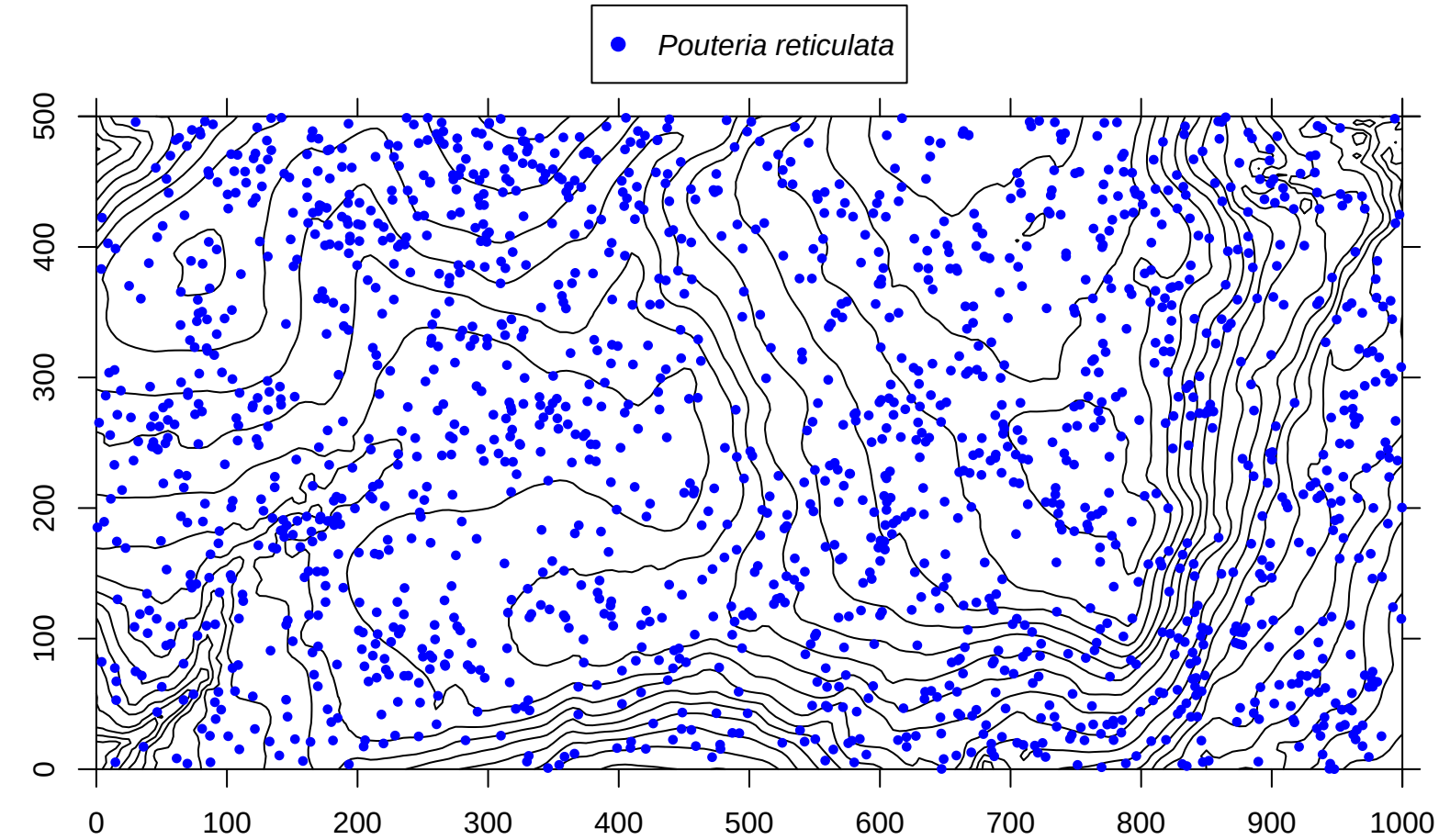
Species response to the environment

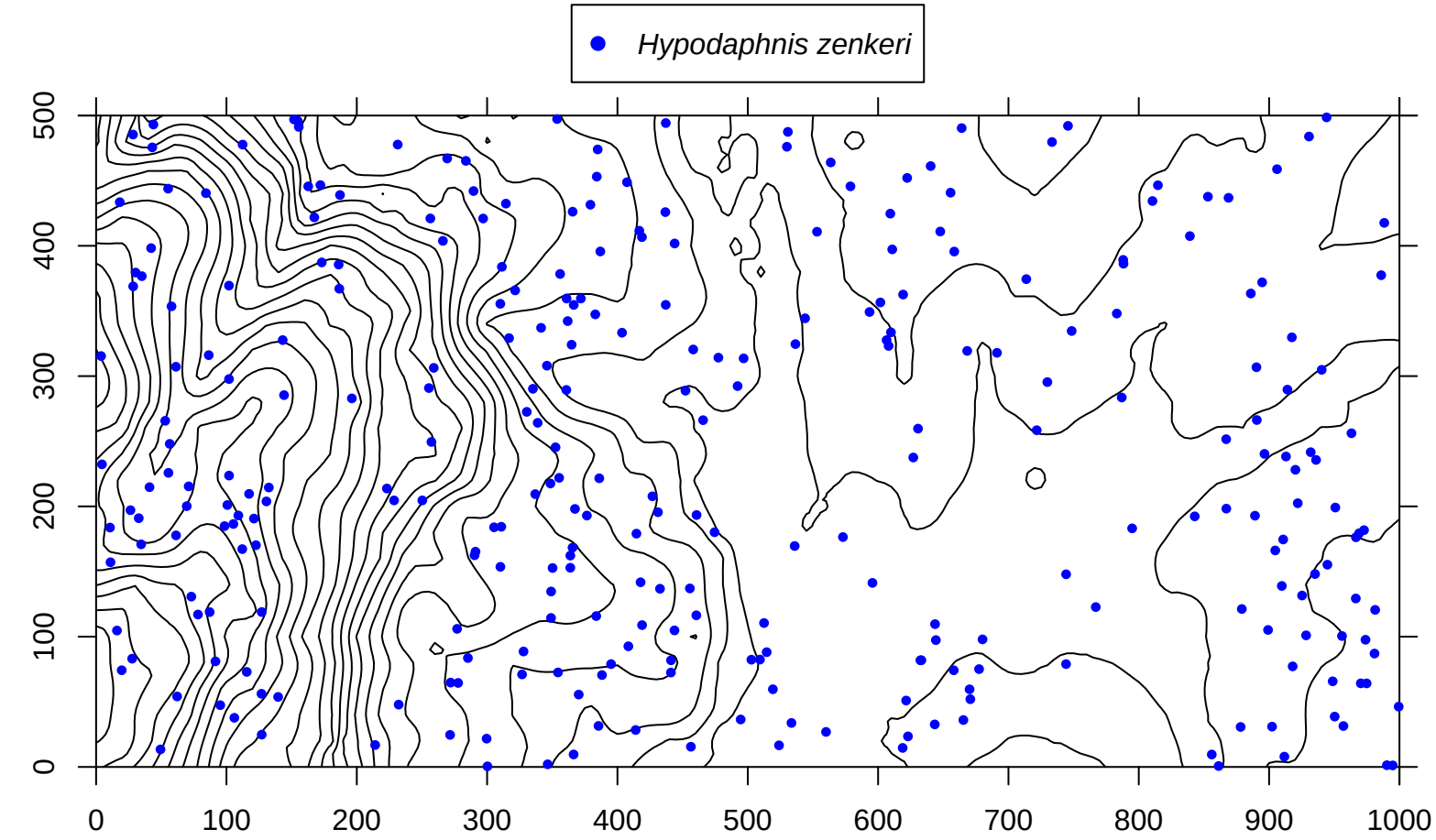
Environment => demography
(fundamental niche)

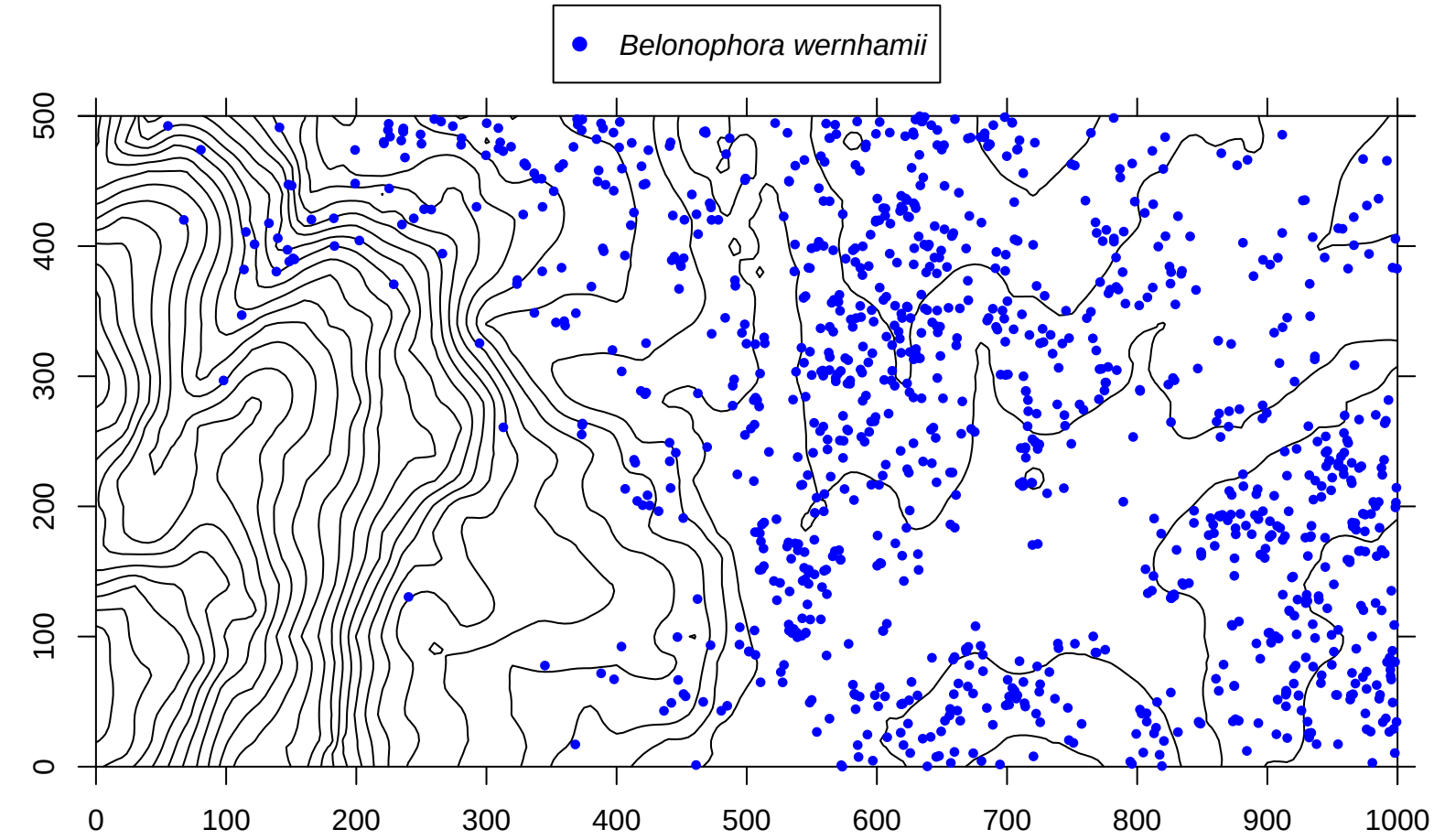
Environment => distribution
(realized niche)

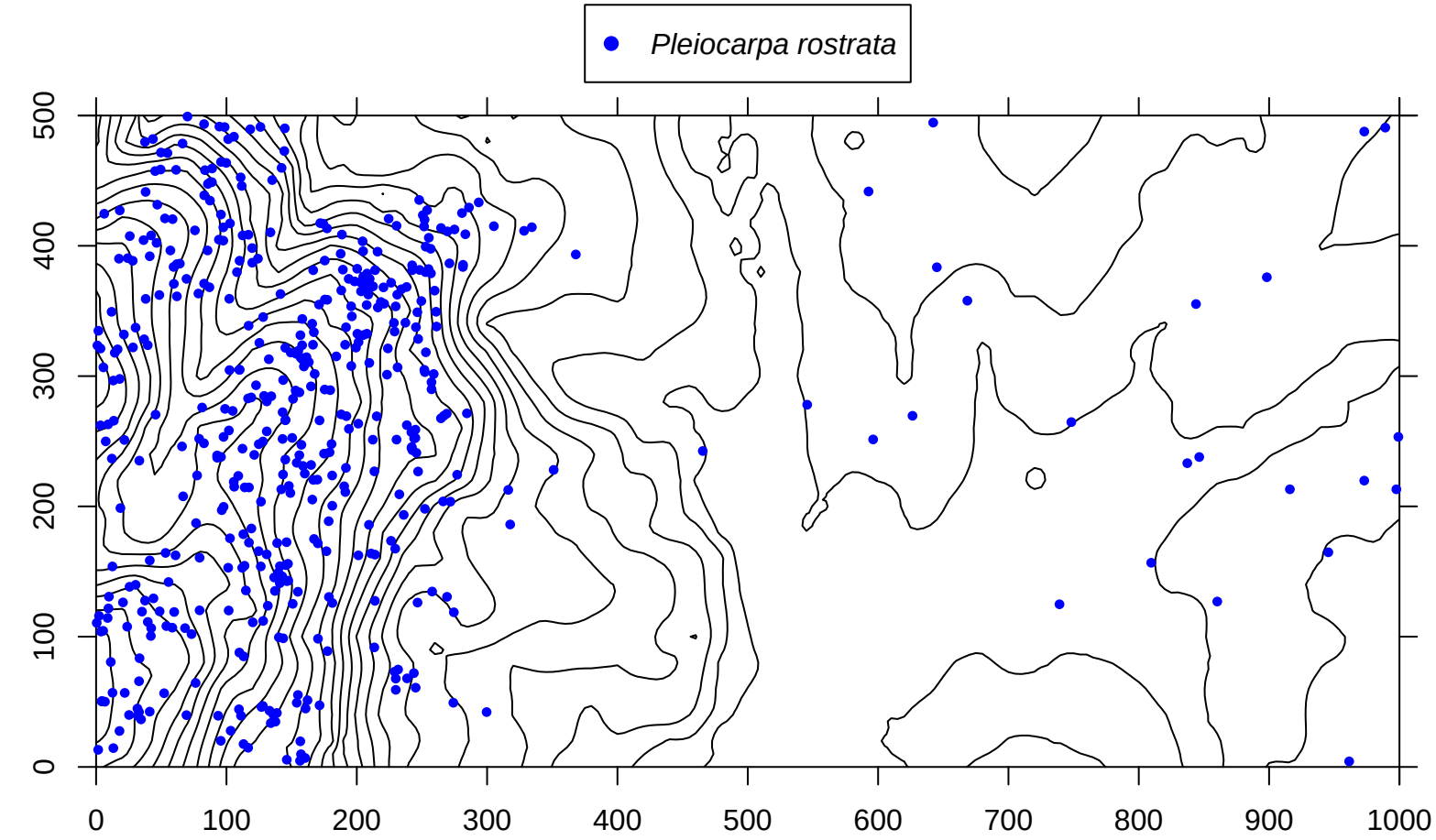

215
213
211
209

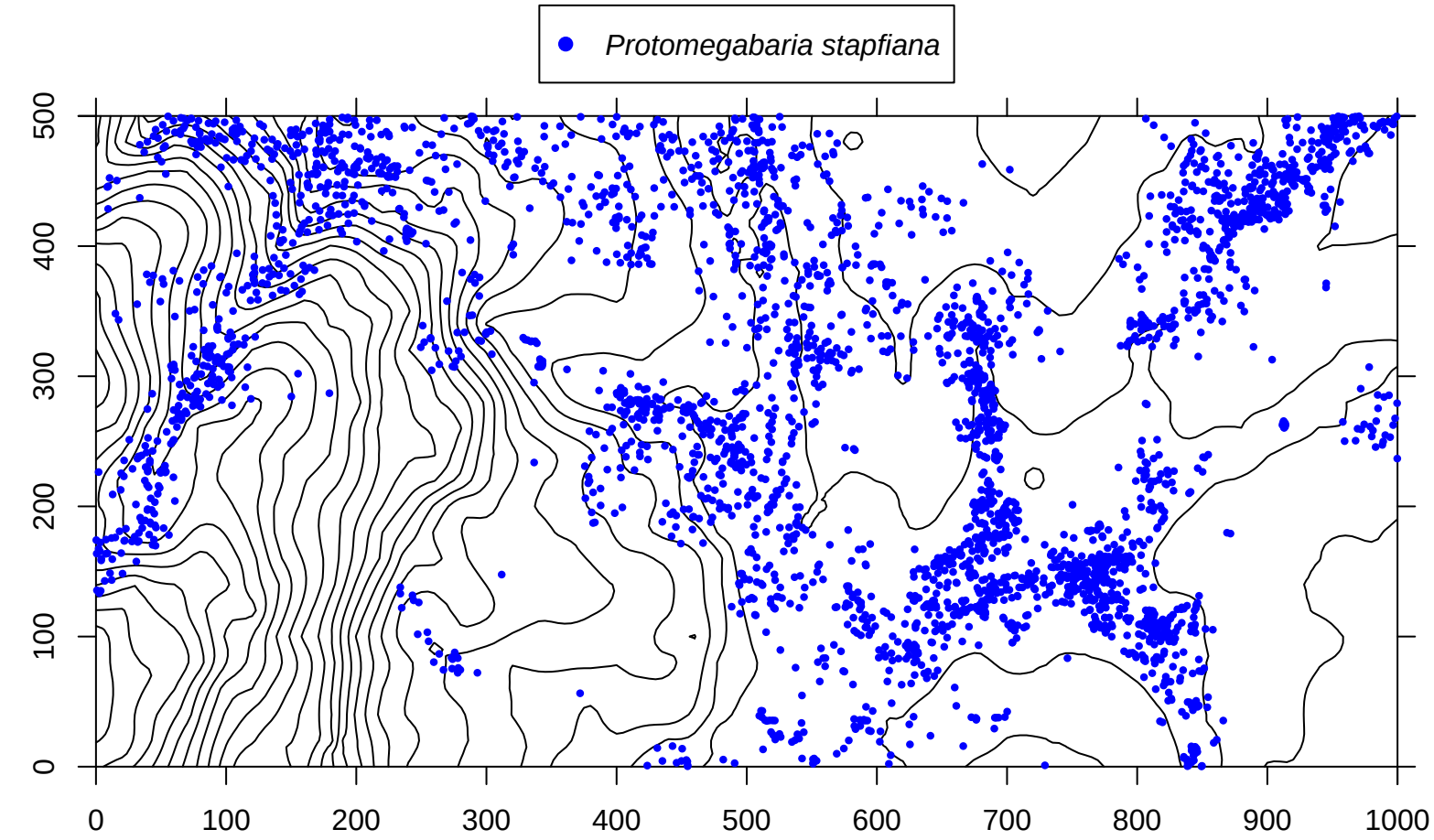

Korup 50 ha plot
Mundemba
Rumpi Hills
Mt Cameroon
Douala
Limbe
latitude
longitude
5.5
5.0
4.5
4.0
8.6
8.8
9.0
9.2
9.4

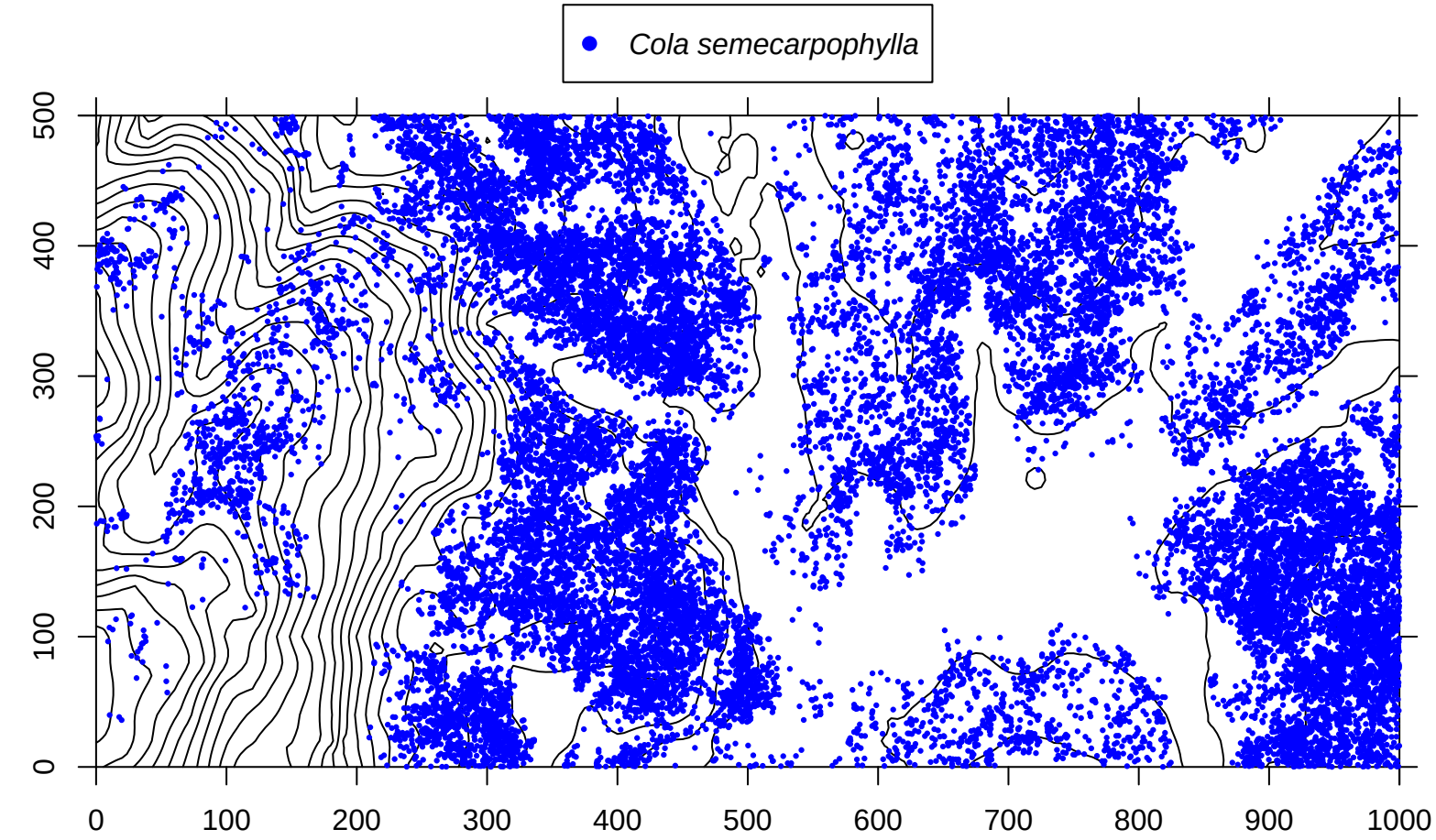

Pouteria reticulata
0
100
200
300
400
500
600
700
800
900
1000

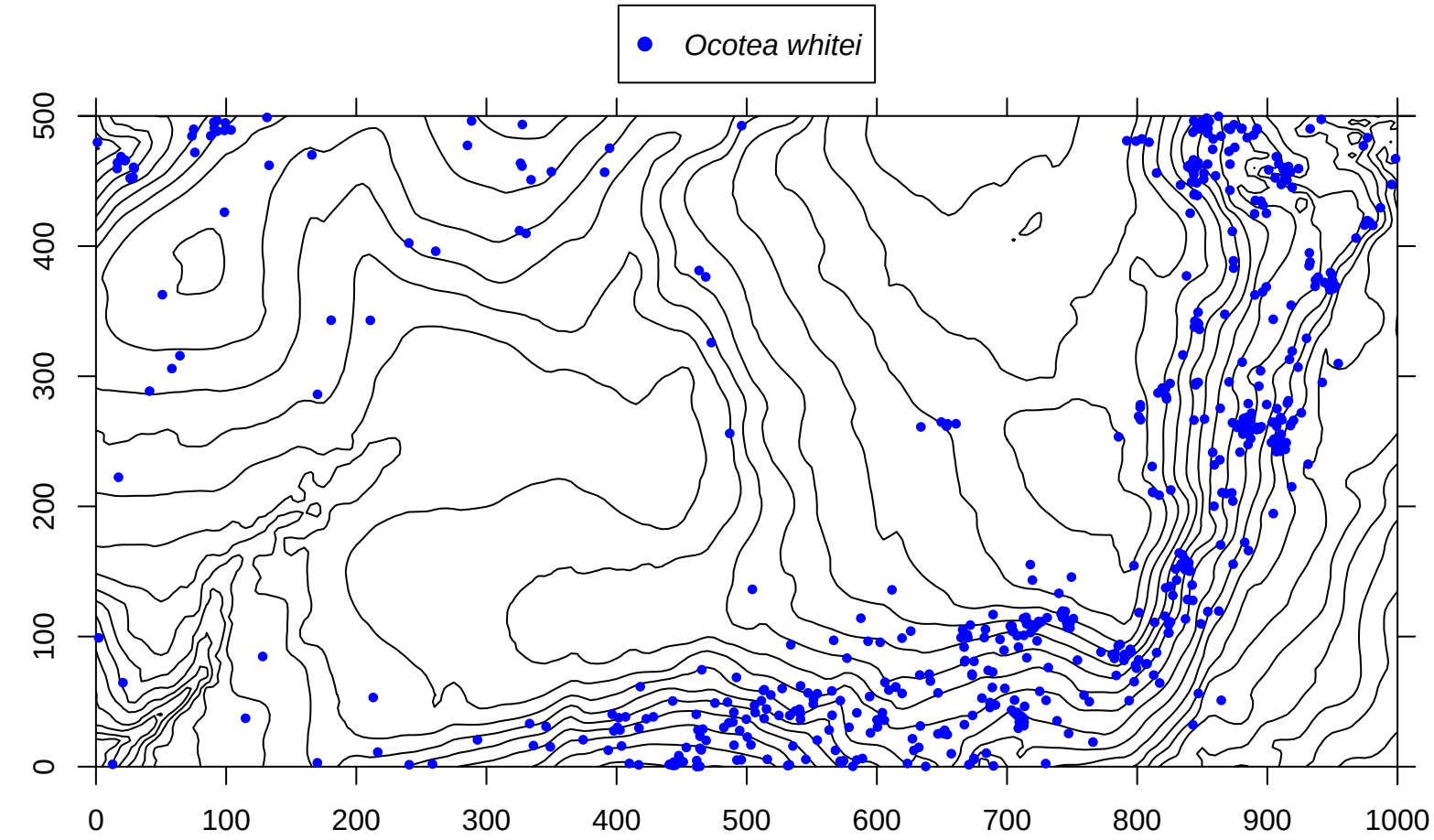

Hypodaphnis zenkeri
0
100
200
300
400
500
600
700
800
900
1000

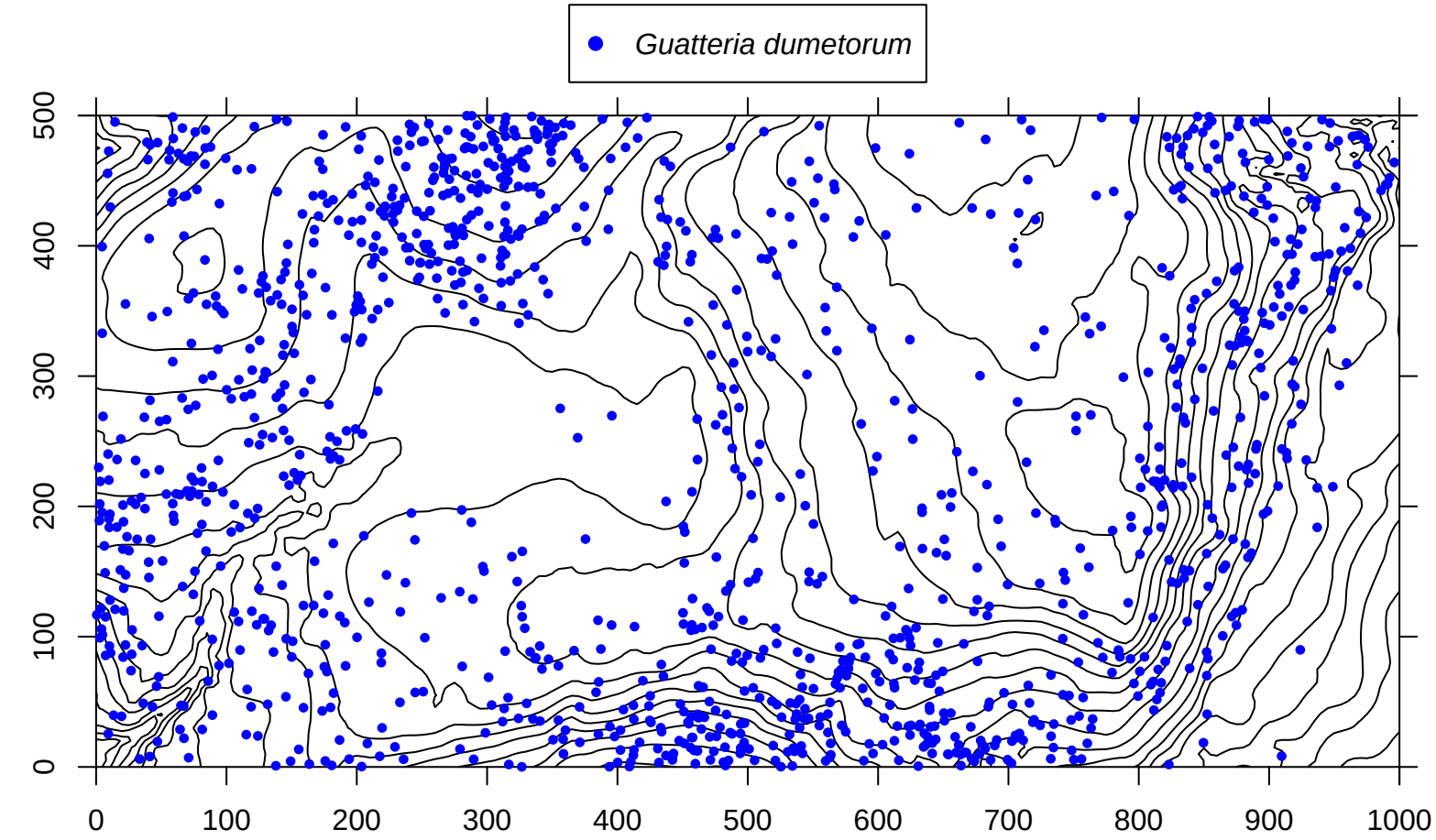

Belonophora wernhamii
0
100
200
300
400
500
600
700
800
900
1000

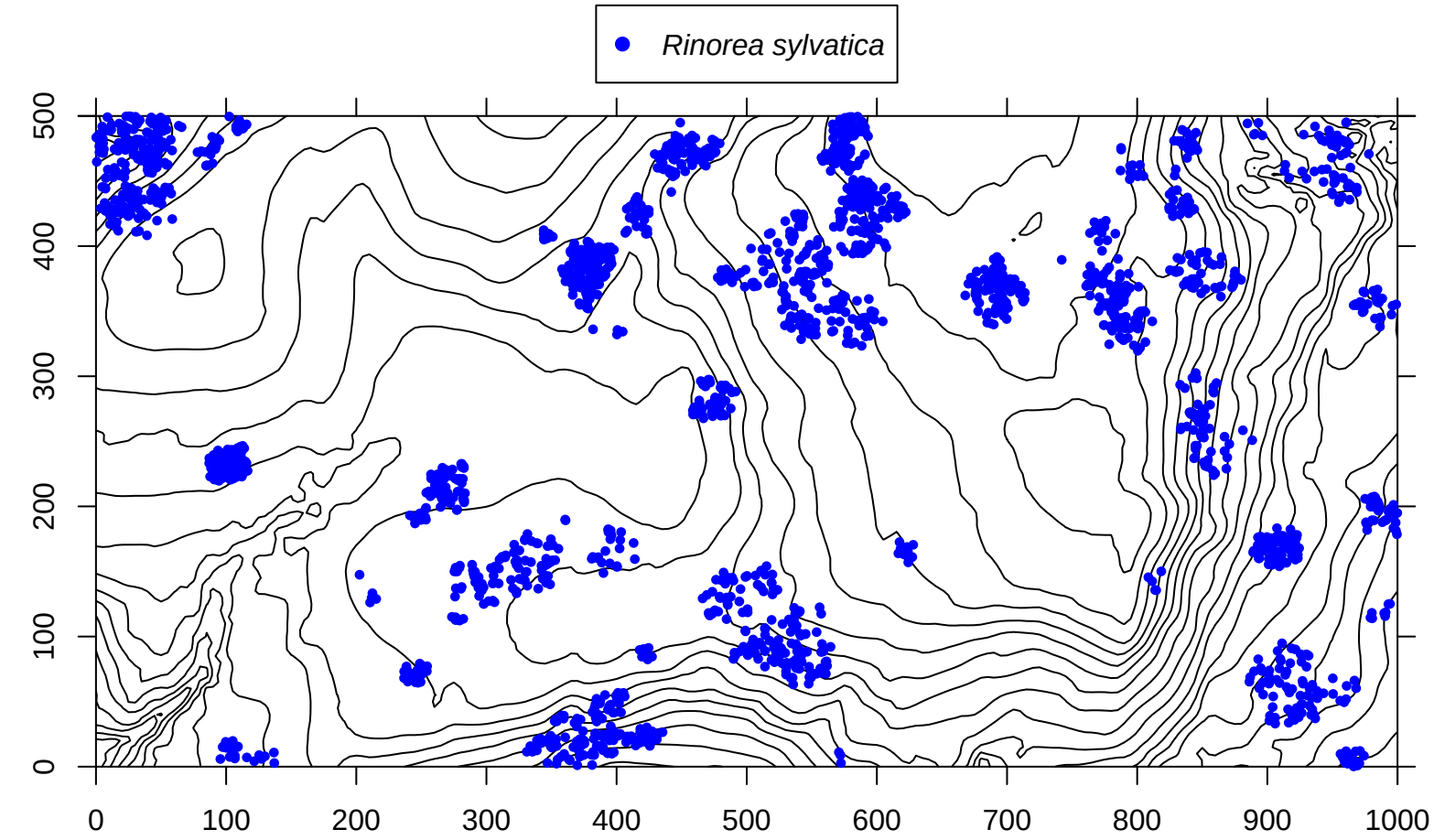

Pleiocarpa rostrata
0
100
200
300
400
500
600
700
800
900
1000

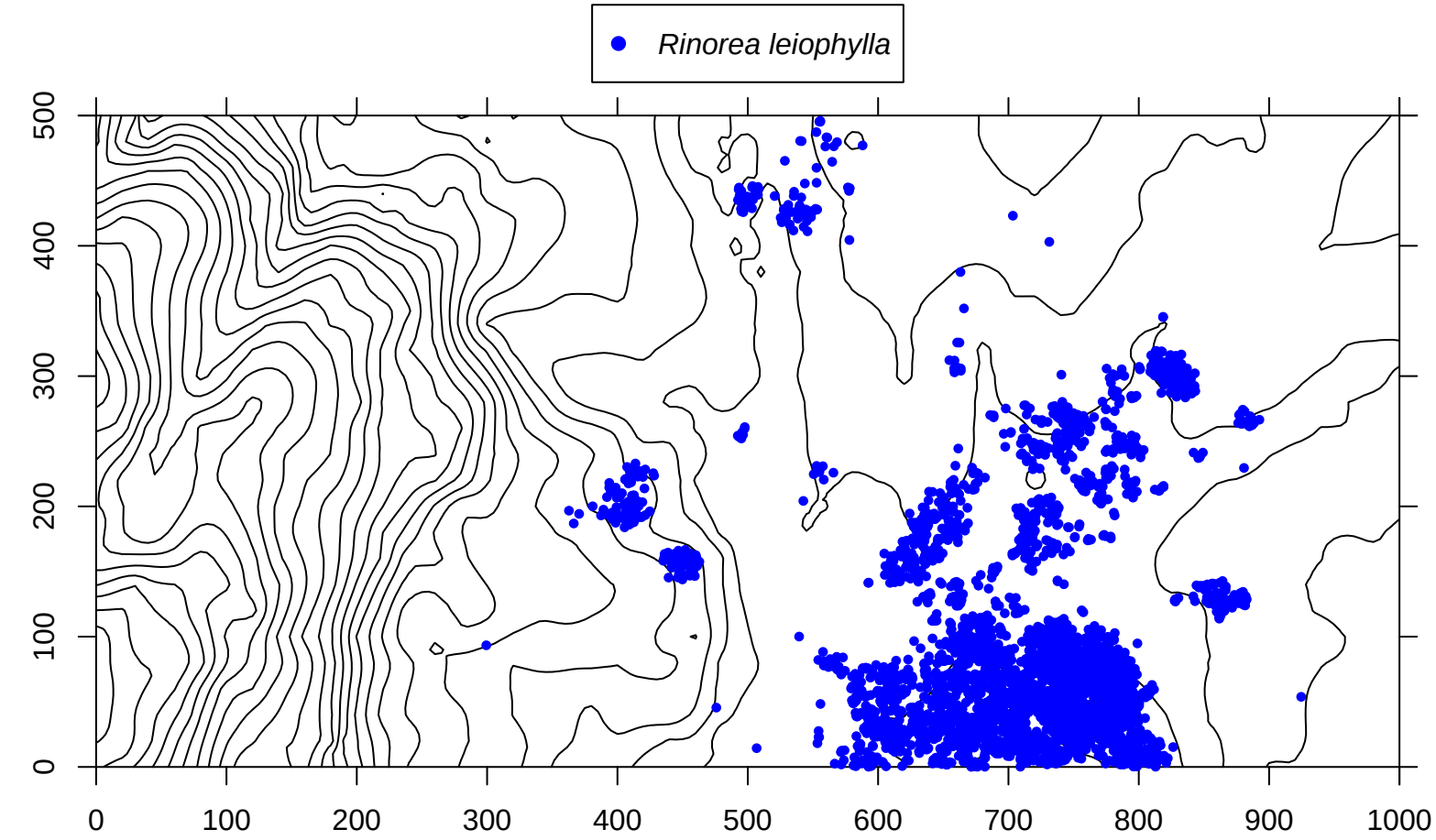

Protomegabaria stapfiana
0
100
200
300
400
500
600
700
800
900
1000

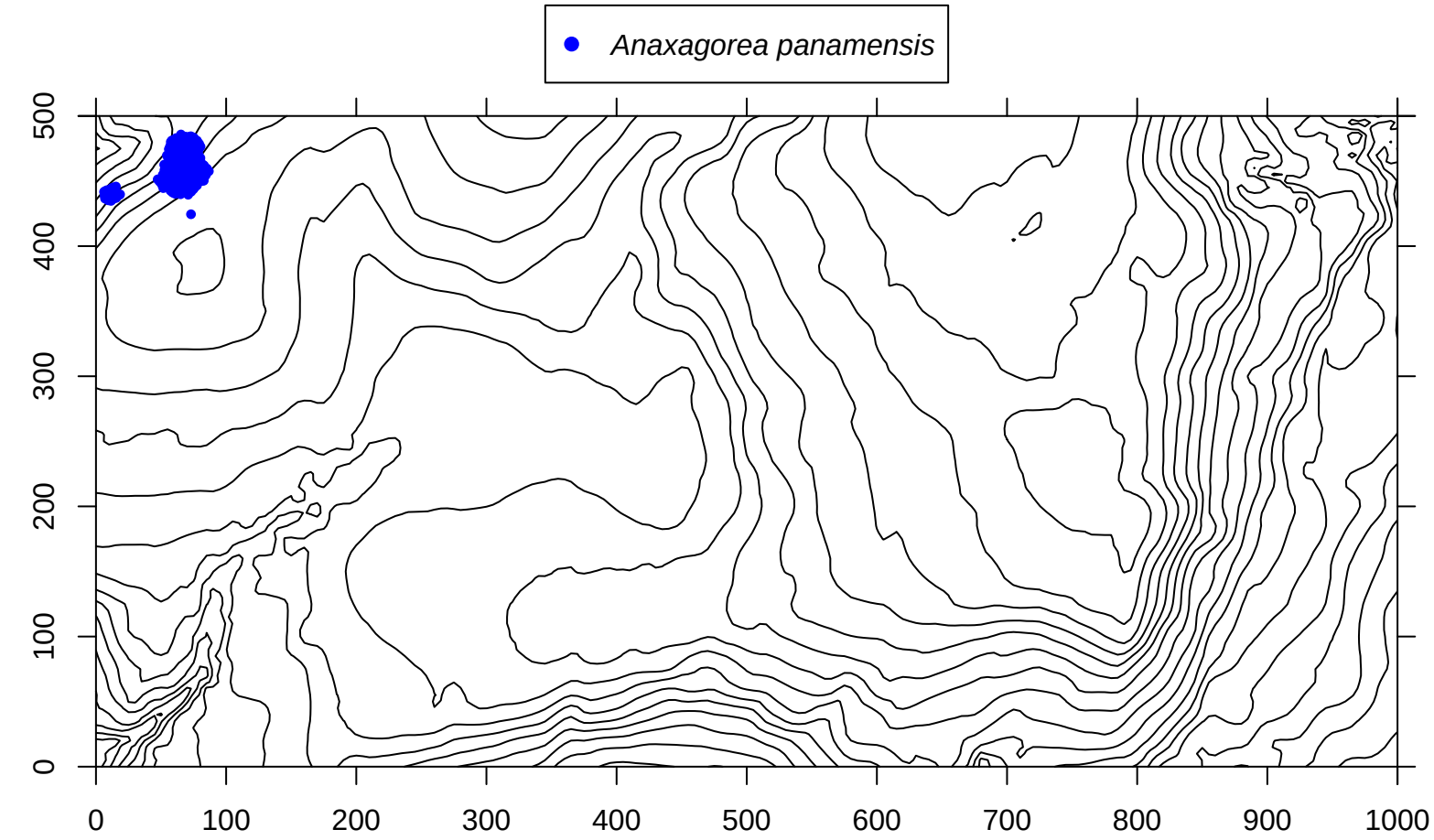

Cola semecarpophylla
0
100
200
300
400
500
600
700
800
900
1000

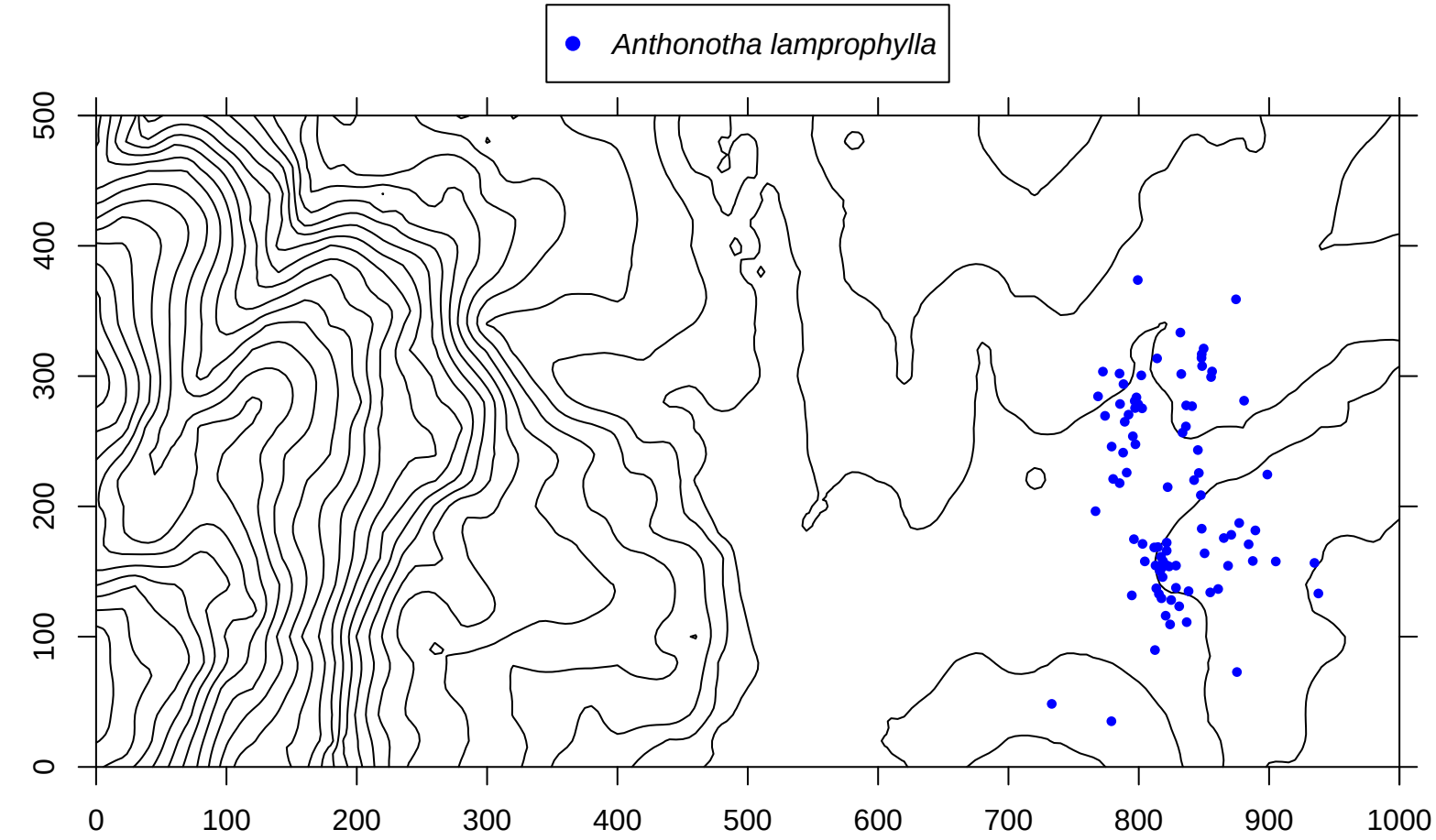

Ocotea whitei
0
100
200
300
400
500
600
700
800
900
1000

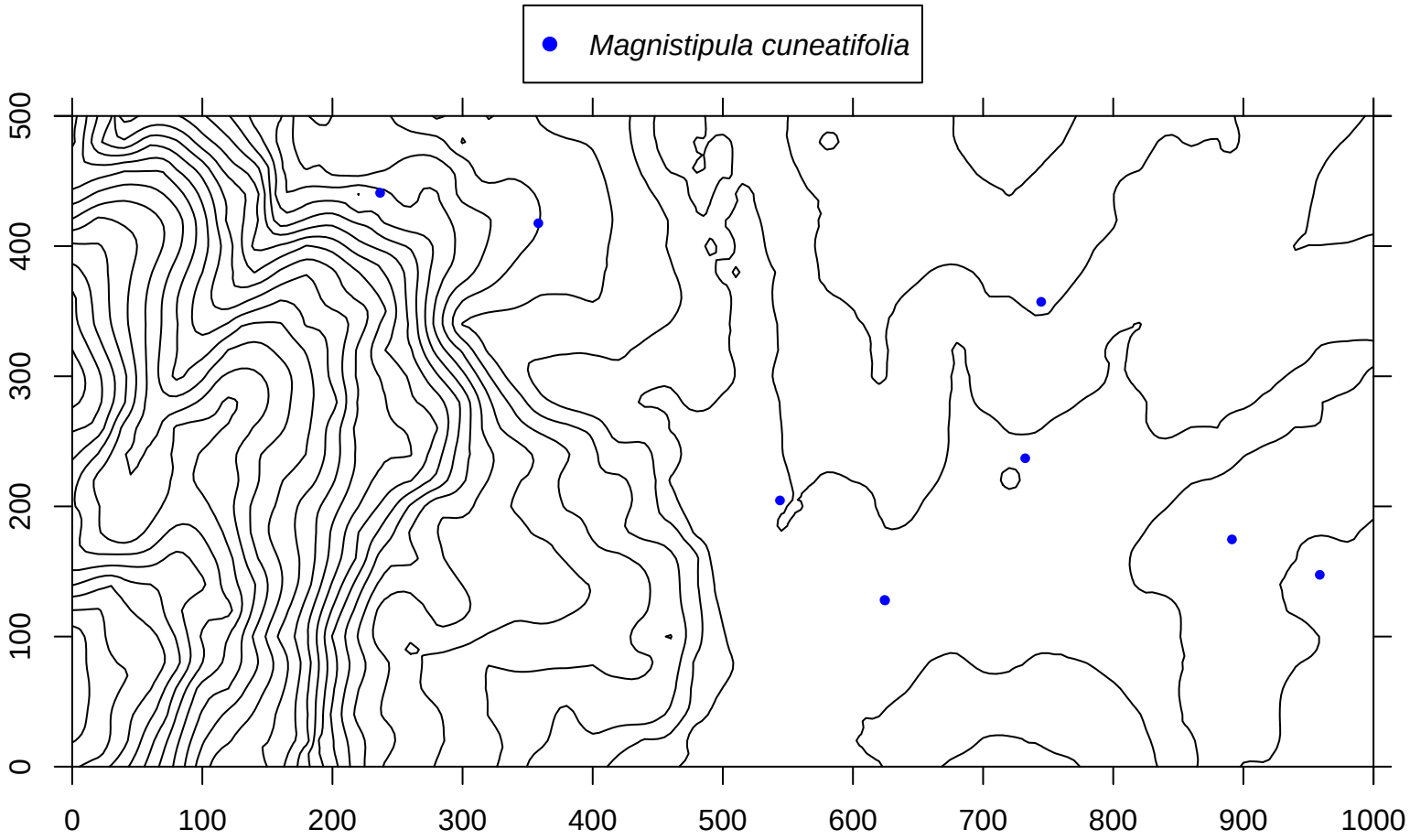

Guatteria dumetorum
0
100
200
300
400
500
600
700
800
900
1000

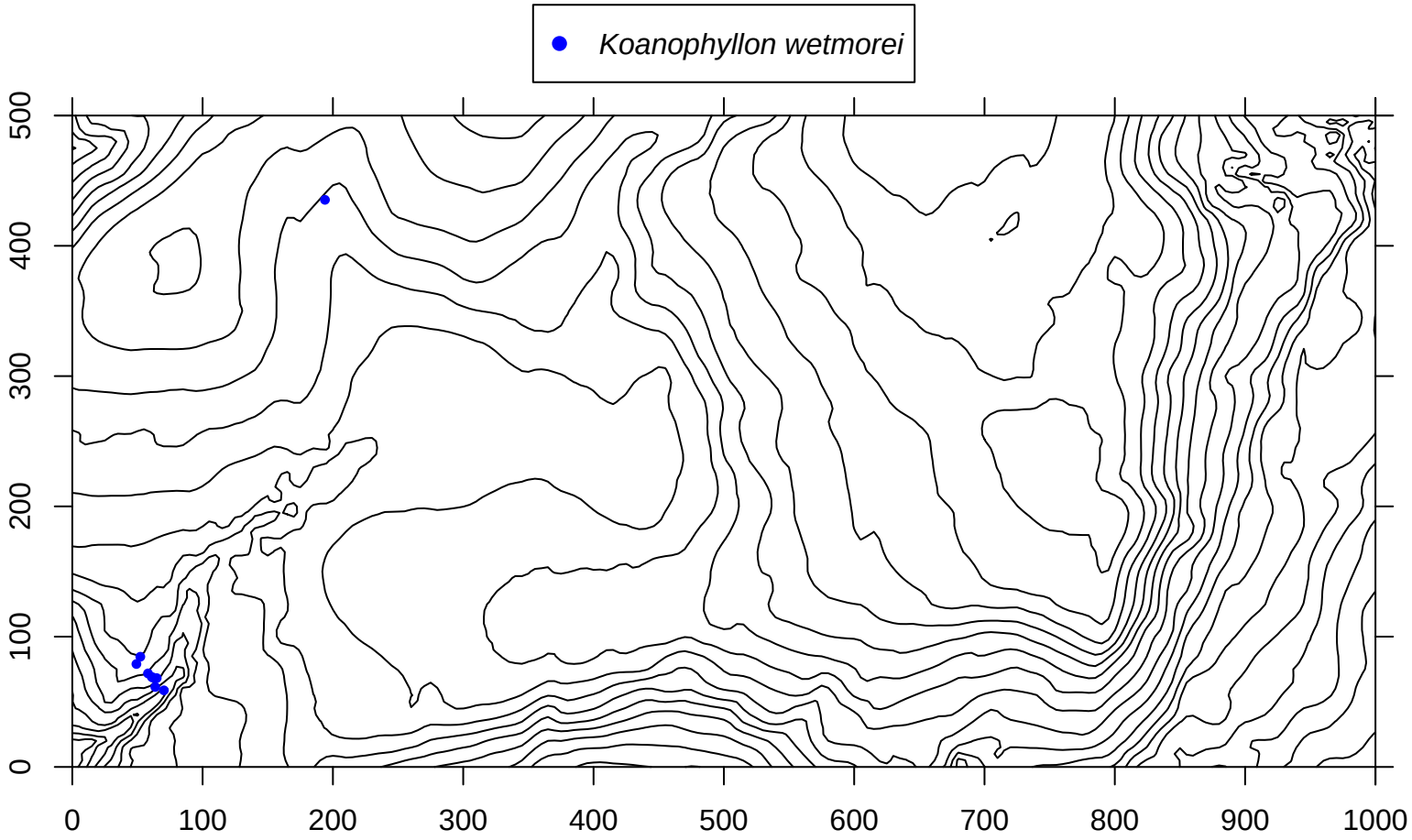

Rinorea sylvatica
0
100
200
300
400
500
600
700
800
900
1000

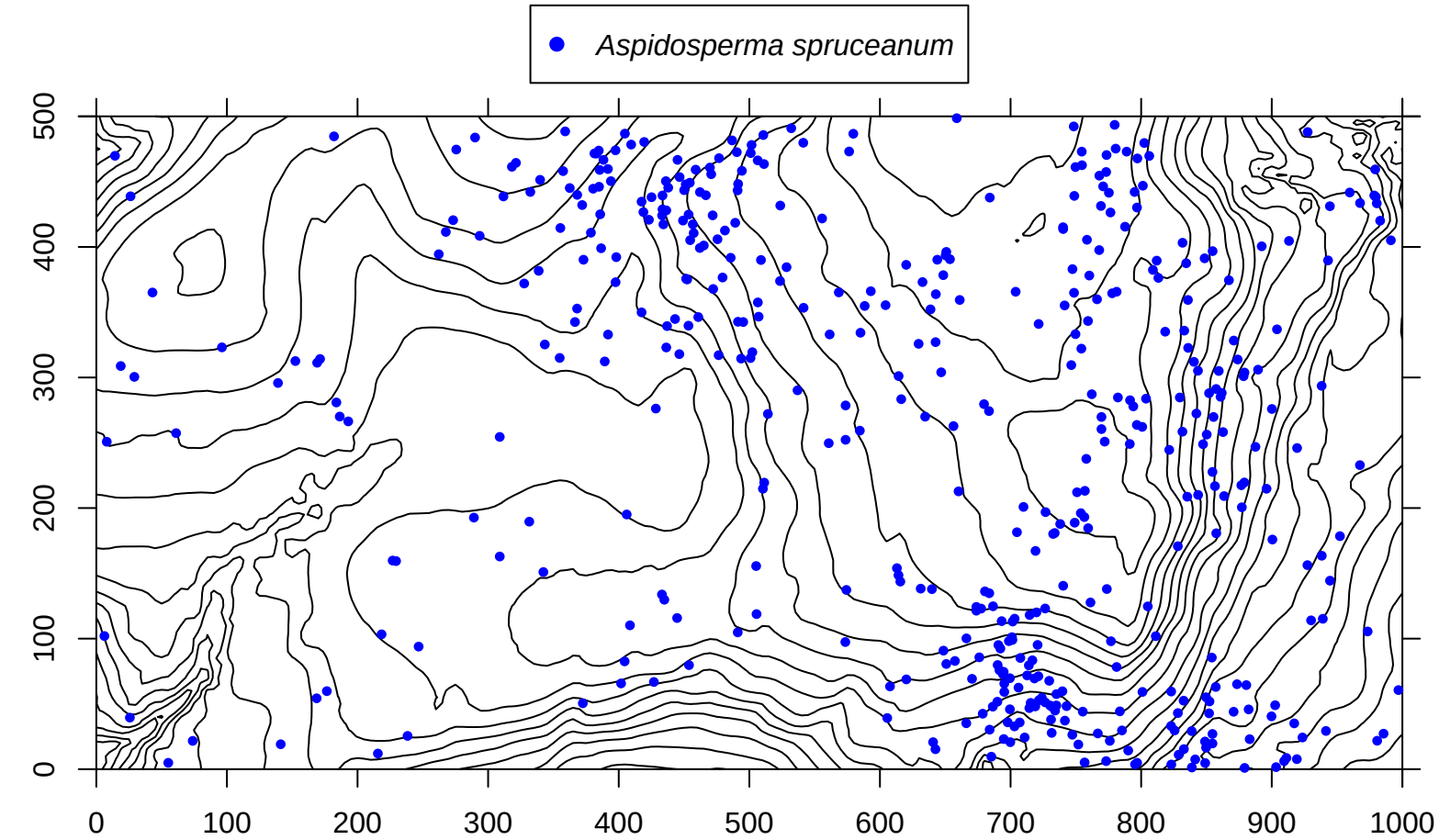

Rinorea leiophylla
0
100
200
300
400
500
600
700
800
900
1000

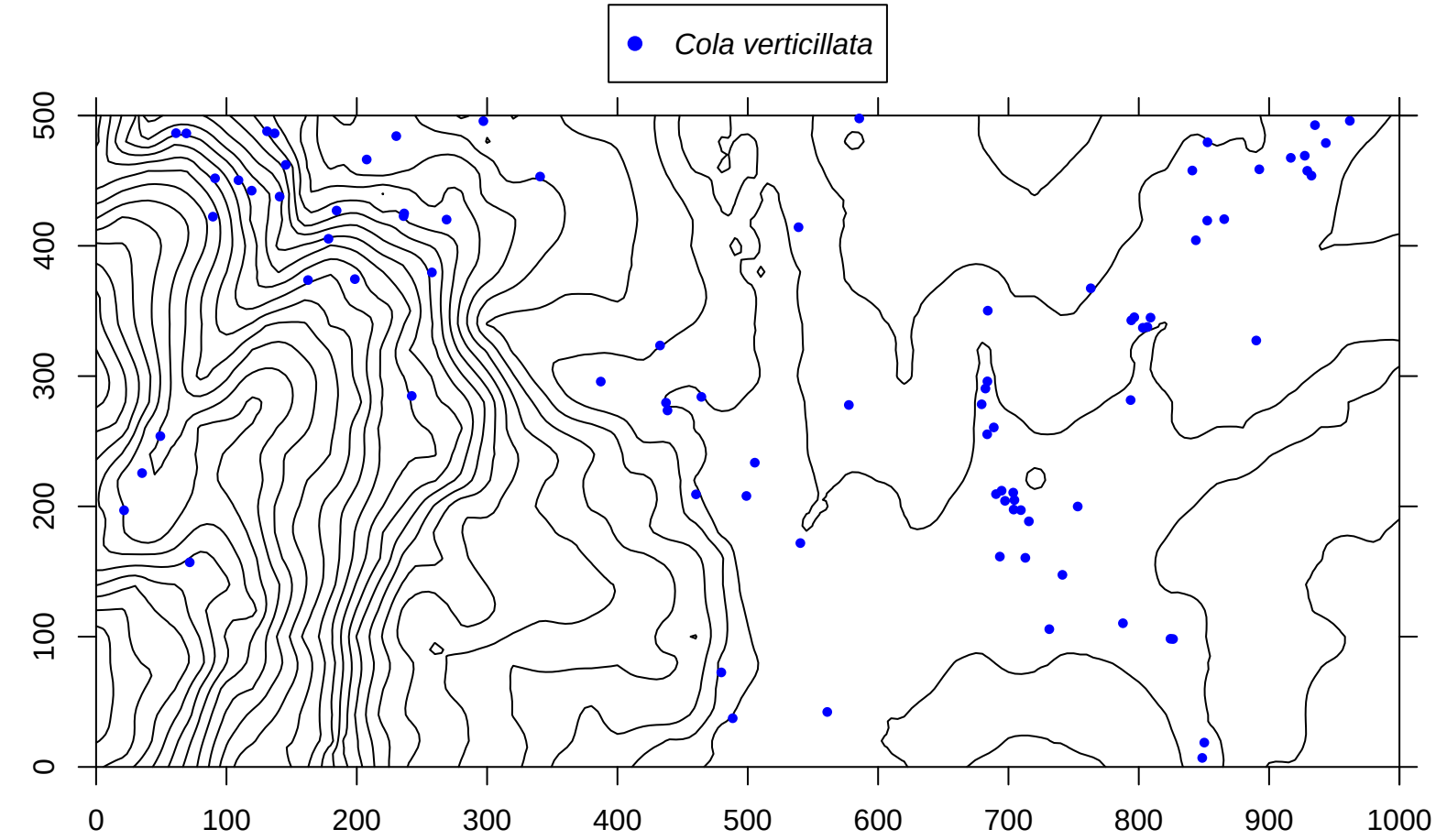

Anaxagorea panamensis
0
100
200
300
400
500
600
700
800
900
1000


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


Magnistipula cuneatifolia
0
100
200
300
400
500
600
700
800
900
1000


Koanophyllon wetmorei
0
100
200
300
400
500
600
700
800
900
1000


Aspidosperma spruceanum
0
100
200
300
400
500
600
700
800
900
1000


Cola verticillata
0
100
200
300
400
500
600
700
800
900
1000

Species response to the environment

Demographic response + dispersal (+ competitors) = realized niche

My NCEAS goal

1) Use models (simulations) to create communities whose species have known demography and dispersal

2) Examine how spatial distributions compare to real forests

i.e. How do spatial patterns reflect the demographic processes?

The theory (model)…

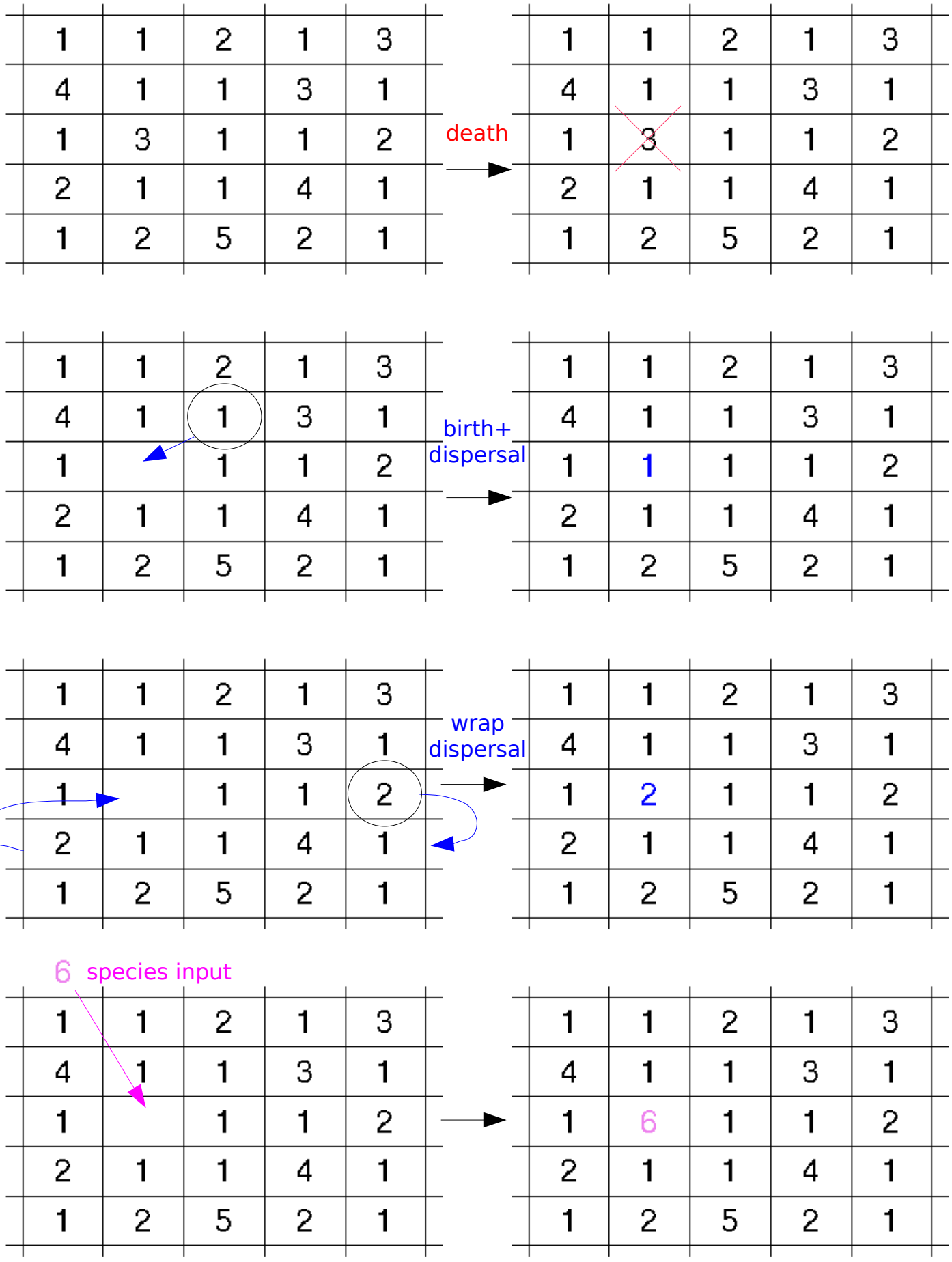
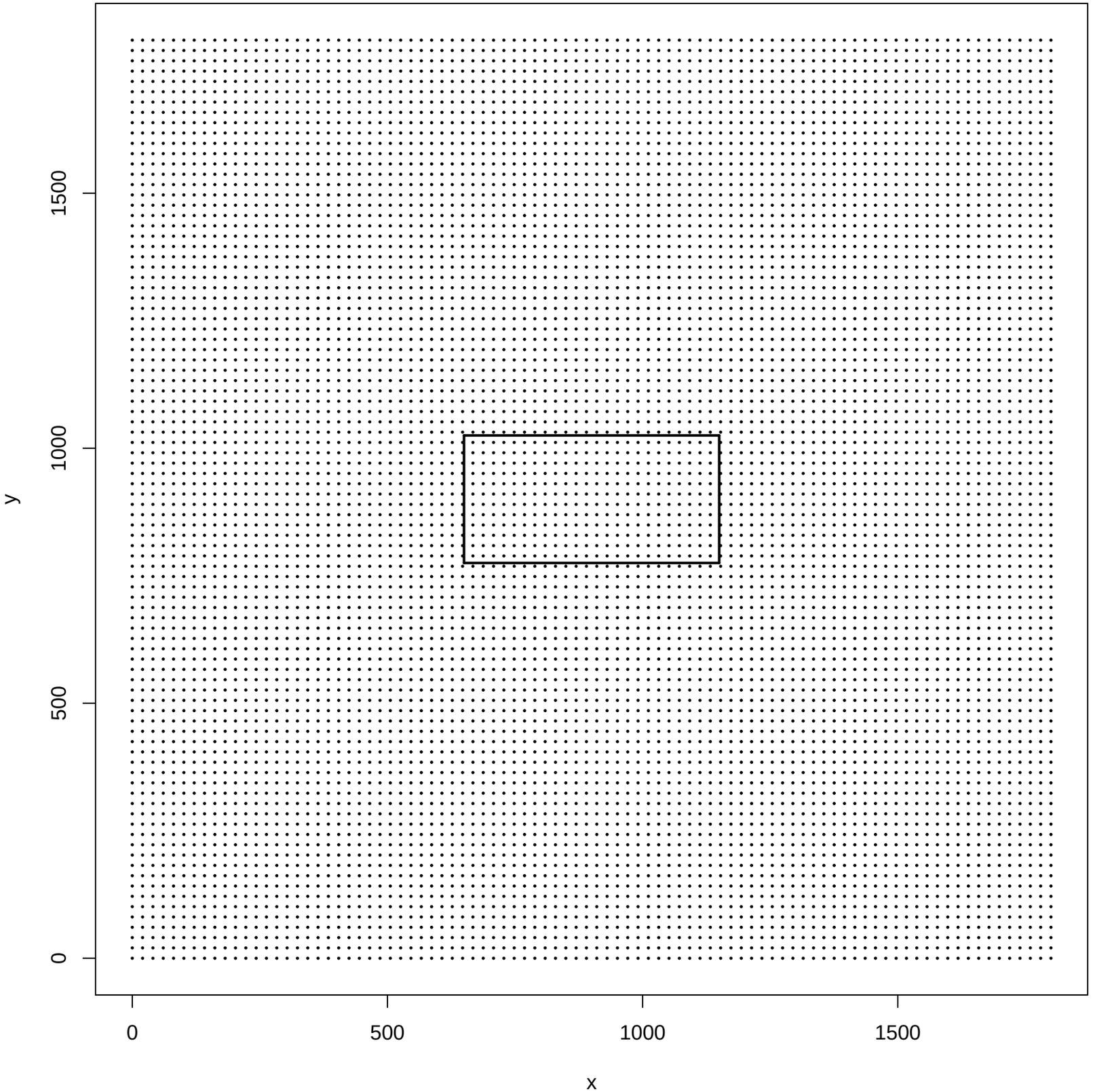

1 1 2 1 3
4 1 1 3 1
1 3 1 1 2
2 1 1 4 1
1 2 5 2 1
death
1 1 2 1 3
4 1 1 3 1
1 3 1 1 2
2 1 1 4 1
1 2 5 2 1
1 1 2 1 3
4 1 1 3 1
1 1 1 2
2 1 1 4 1
1 2 5 2 1
birth+
dispersal
1 1 2 1 3
4 1 1 3 1
1 1 1 1 2
2 1 1 4 1
1 2 5 2 1
1 1 2 1 3
4 1 1 3 1
1 2 1 1 2
2 1 1 4 1
1 2 5 2 1
wrap
dispersal
6 species input
1 1 2 1 3
4 1 1 3 1
1 1 1 2
2 1 1 4 1
1 2 5 2 1
1 1 2 1 3
4 1 1 3 1
1 6 1 1 2
2 1 1 4 1
1 2 5 2 1

Fig. 6.1



Stochastic model of individuals in a community

Strengths

Abundance, extinction, diversity, ranges are emergent traits

--Spin off 1000s of simulated species whose abundance and distribution emerge from demographic traits

--Long time scales include species turnover

--No assumption about number of species needed

Weaknesses

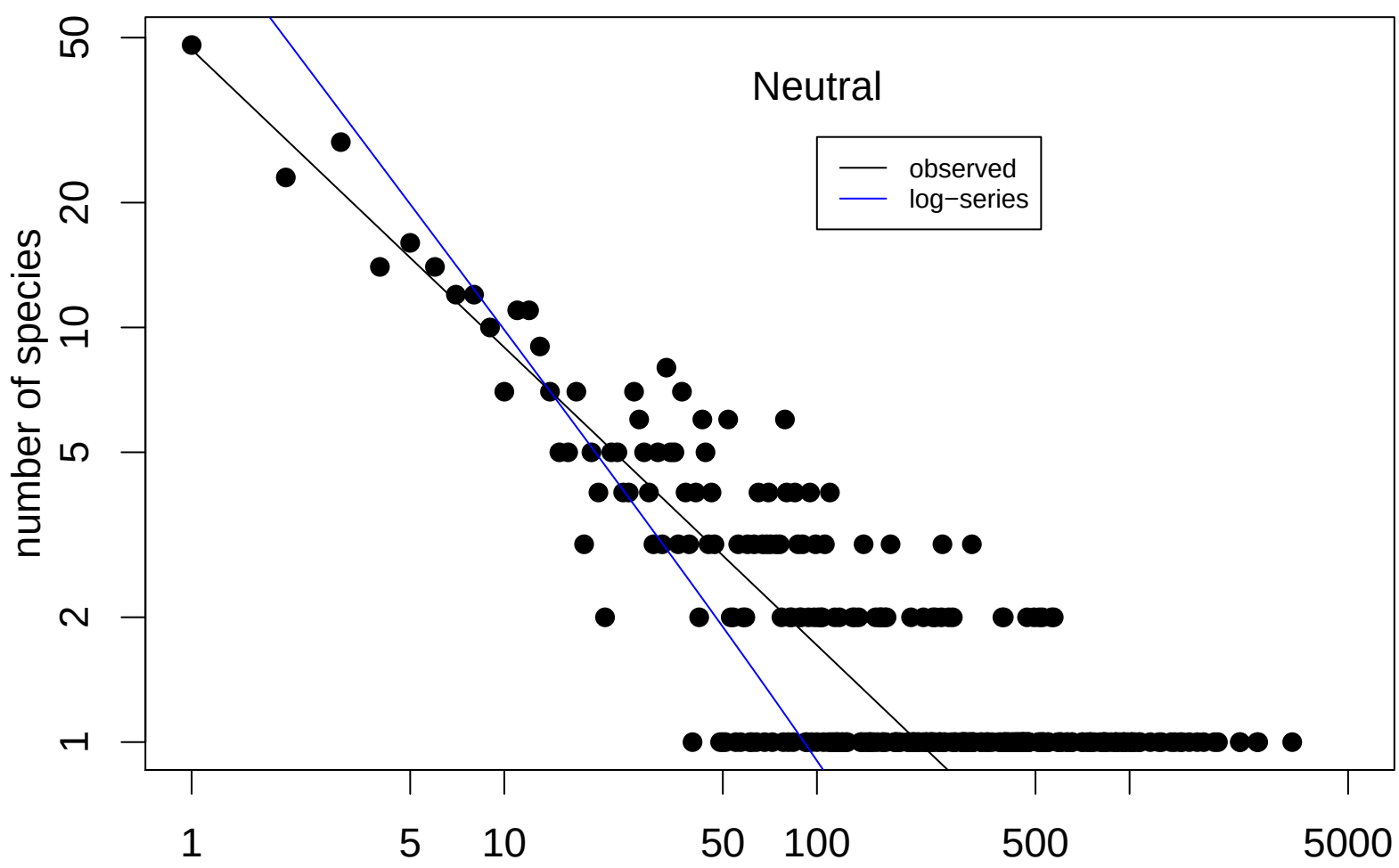
--Species input must be assumed (but see Carlos Melían)

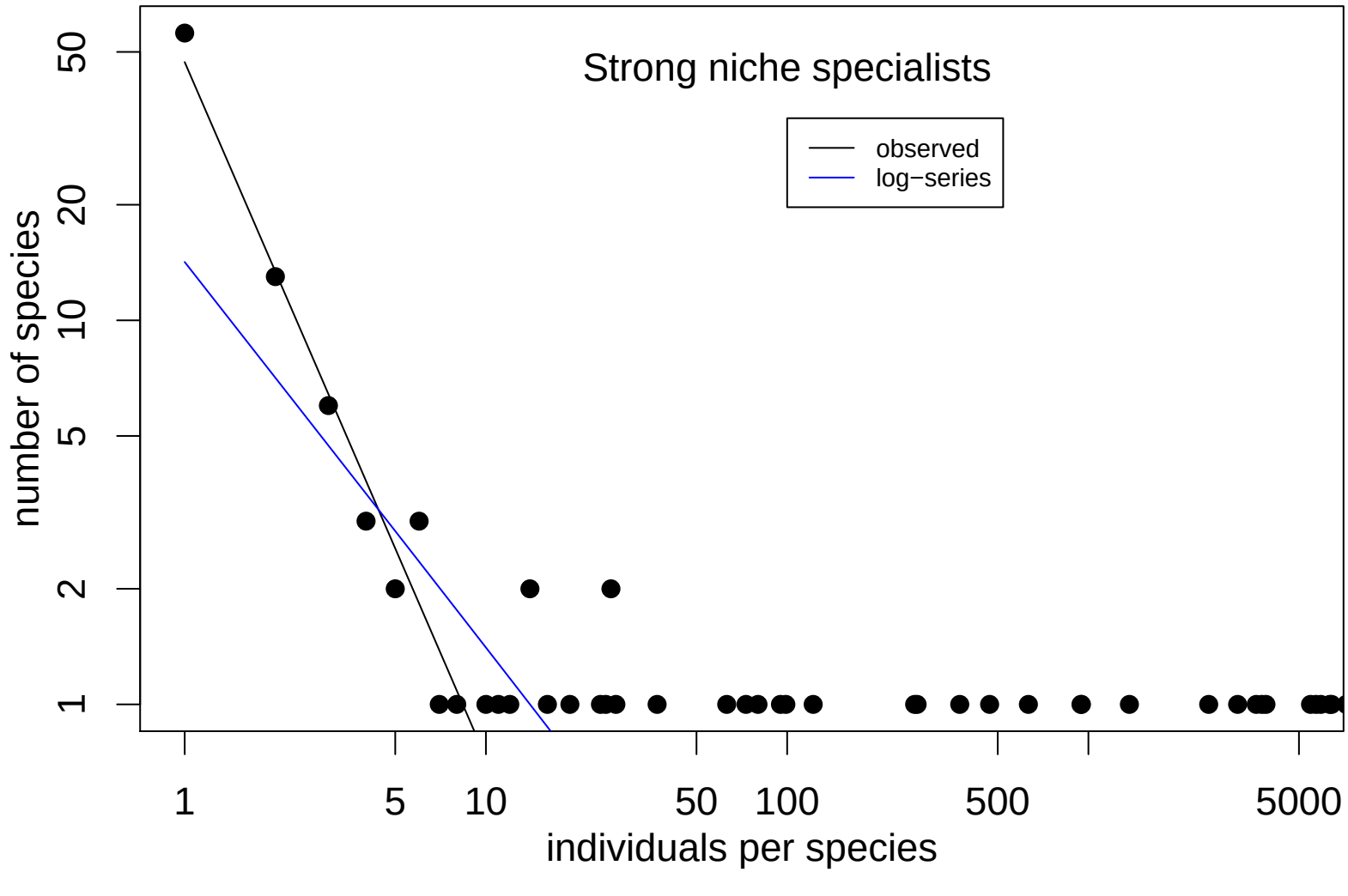
--No details of growth or development (instant adulthood)

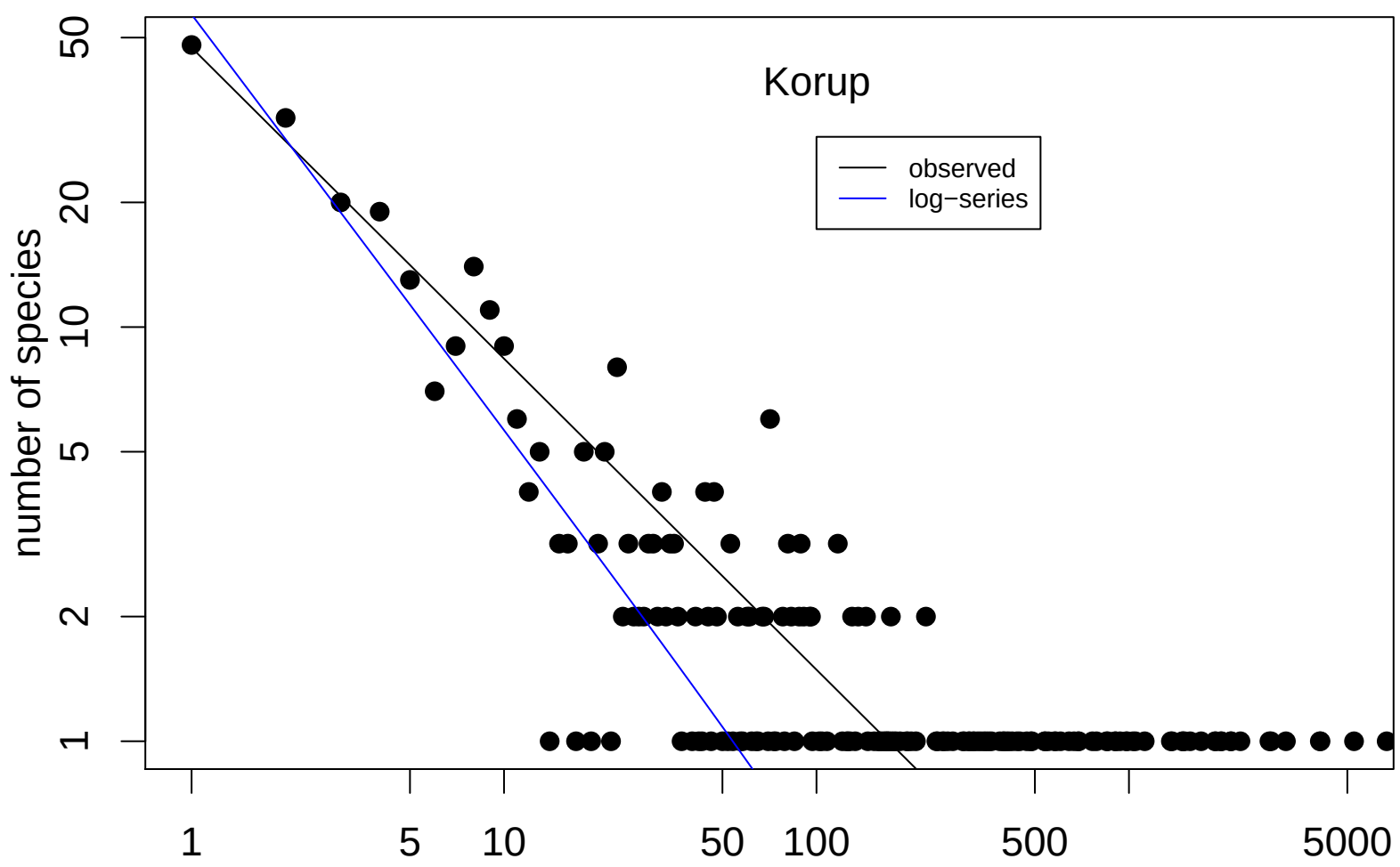
Review of main results of the stochastic model

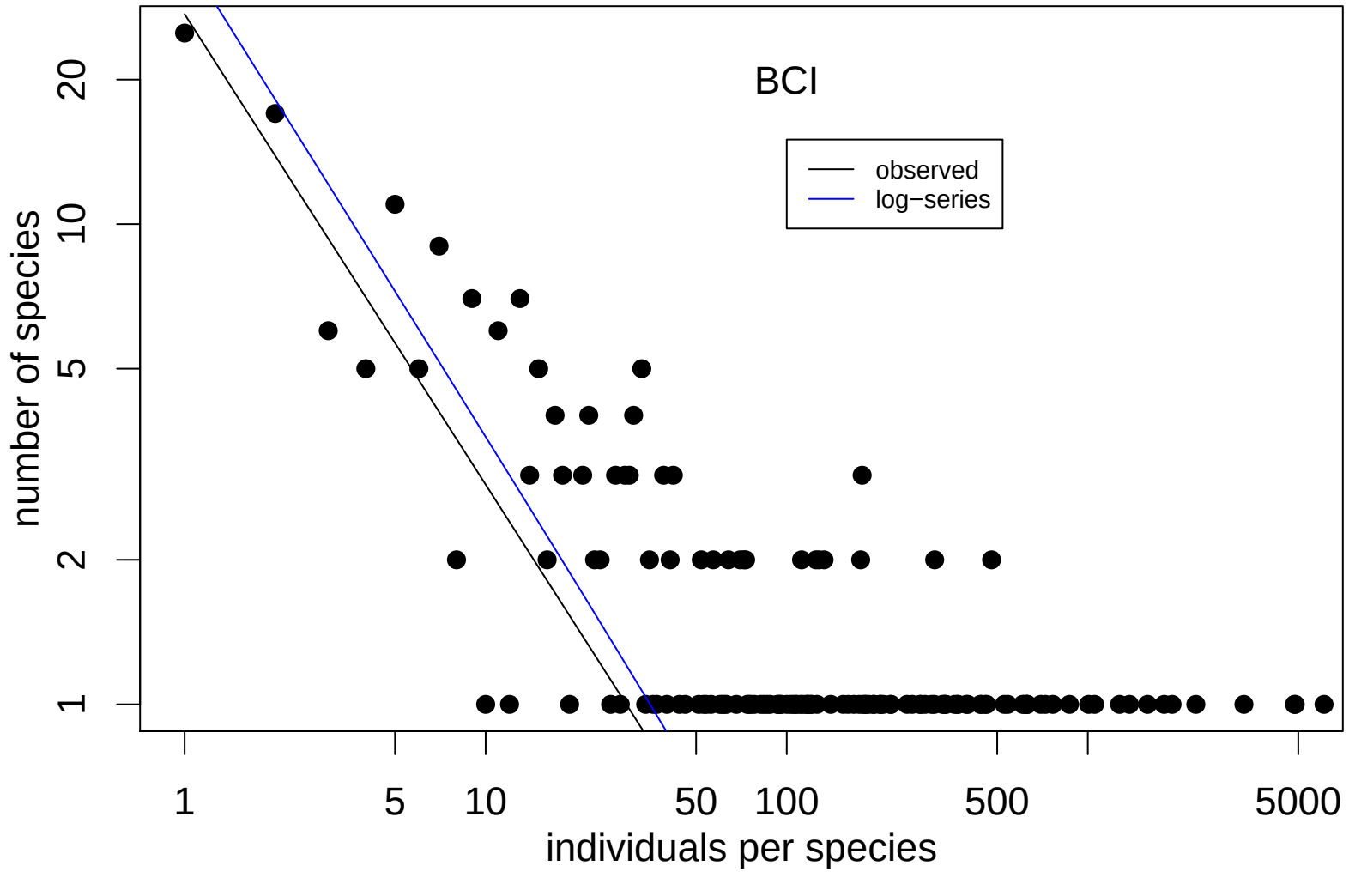
- Diversity can be high with no species differences
- Abundances follow log-series (also derived from maxent)
- Species input drives diversity and abundances
- Niches tied to terrain have small on impact on diversity nor abundances

  Zillio, T., Condit, R. 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. Oikos. 116.: 931-940
- Environmental stochasticity (see Drew Allen)


Neutral
observed
log−series
number of species
1
2
5
10
20
50
1
5
10
50
100
500
5000


Strong niche specialists
observed
log−series
number of species
1
2
5
10
20
50
1
5
10
50
100
500
5000
individuals per species


Korup
observed
log−series
number of species
1
2
5
10
20
50
1
5
10
50
100
500
5000


BCI
observed
log−series
number of species
1
2
5
10
20
1
5
10
50
100
500
5000
individuals per species

Neutral theory

Theory of equal fitness:

Community dynamics for species with equal fitness
(ie, no stabilizing mechanisms)

Neutral theory is not

Community dynamics when all species are identical

Community dynamics when all species have equal fitness

Neutral thinking

Equal fitness easily accommodates diversity (maintenance)

Two species fitness equally fit at one site (time) may differ at other sites (times)

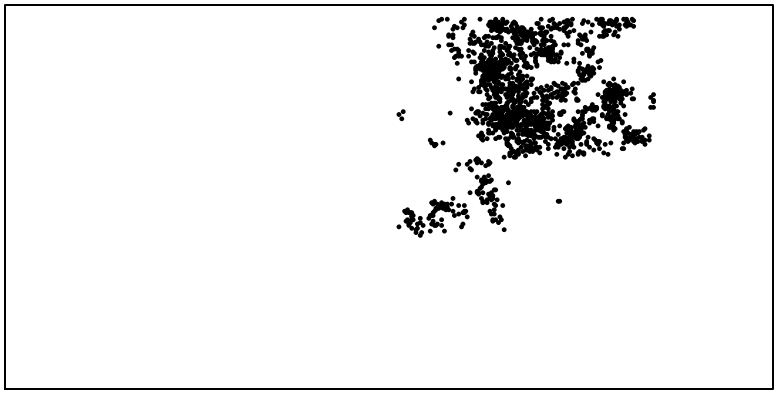
Origin of diversity requires fitness advantages??

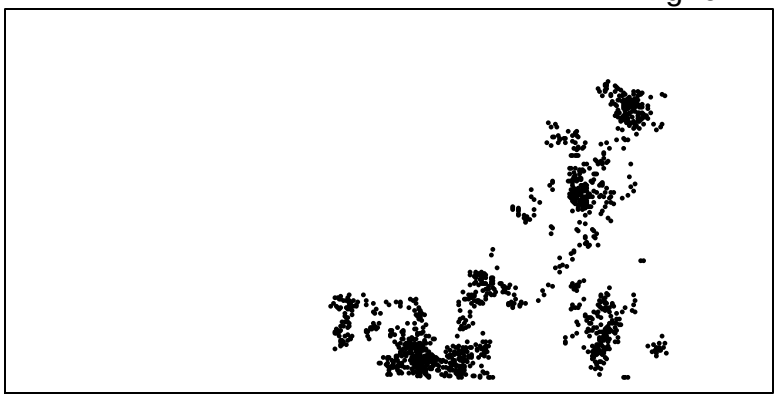
How does dispersal* impact spatial distributions?

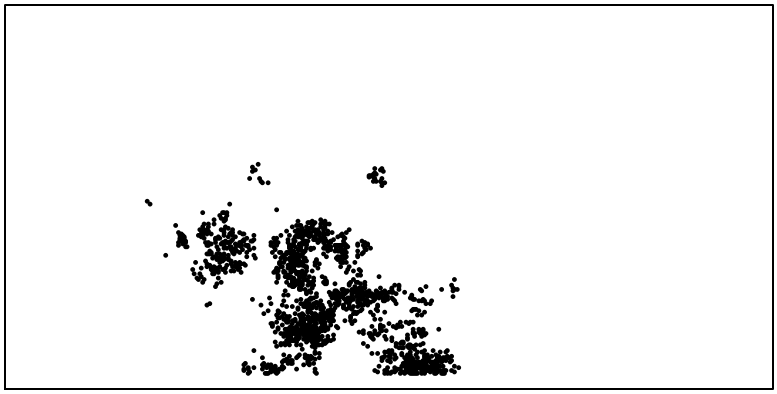
the models predictions...

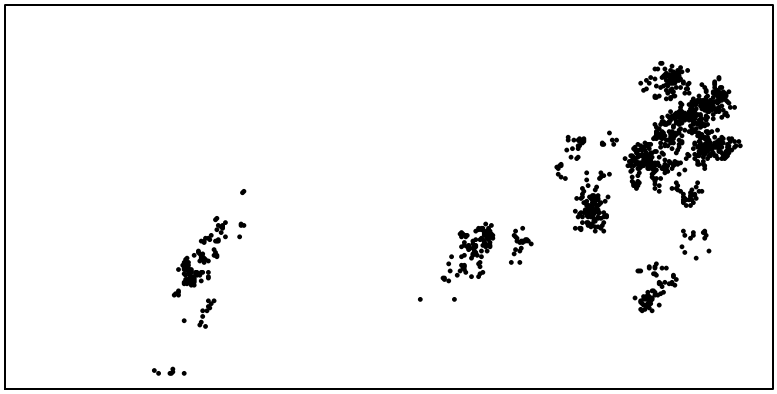
* parent-offspring distance

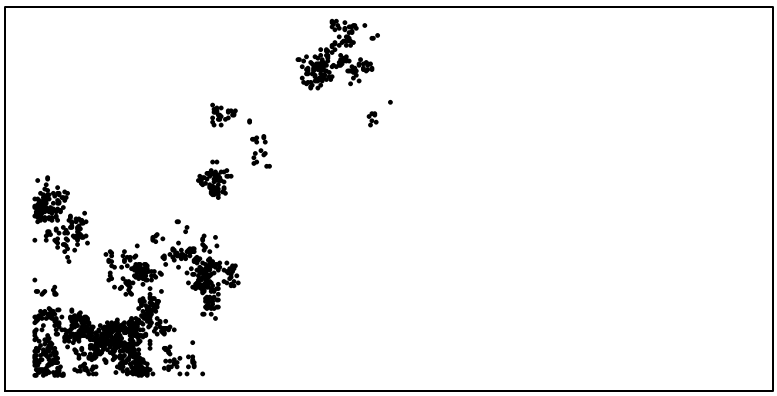
Fig. 6.2

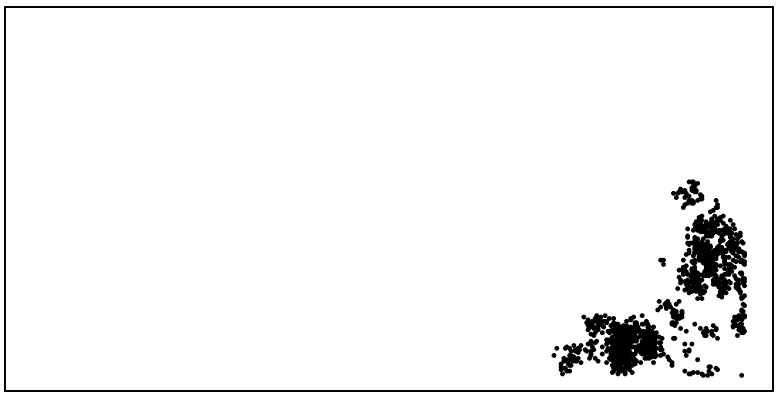


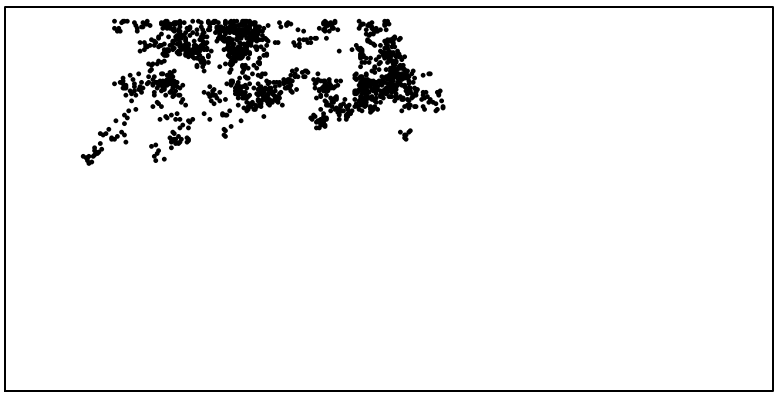












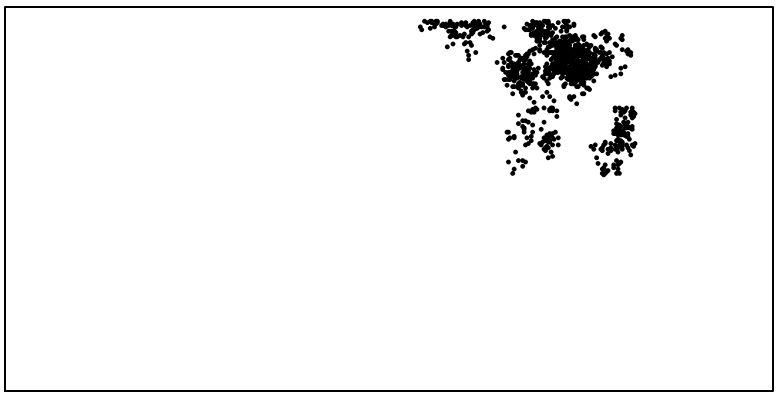
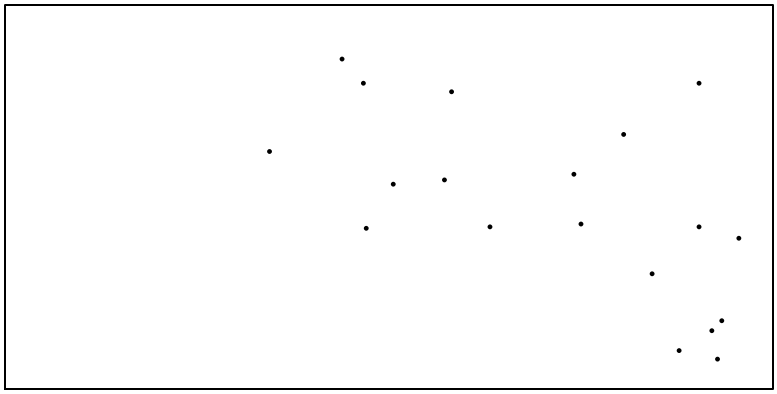
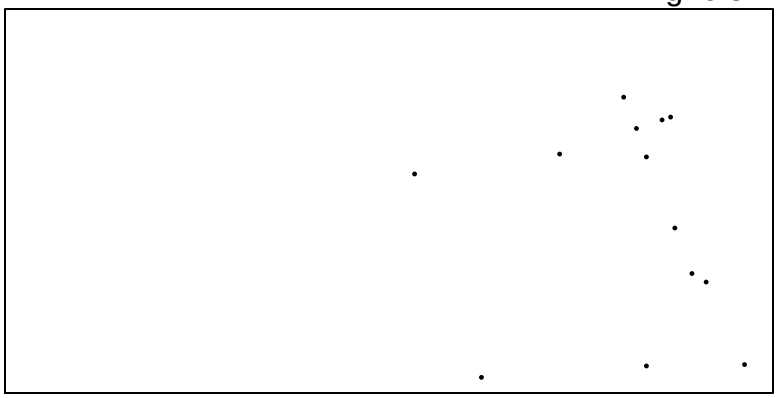
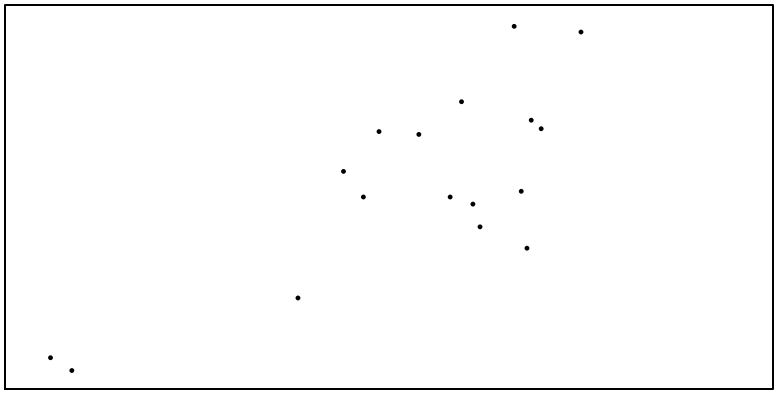
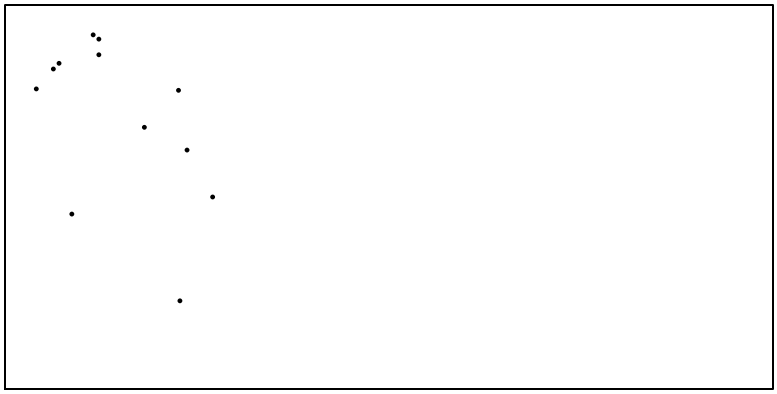


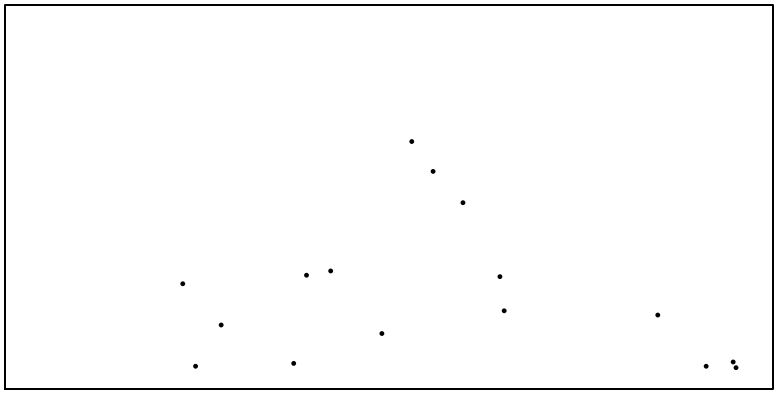
Fig. 6.5

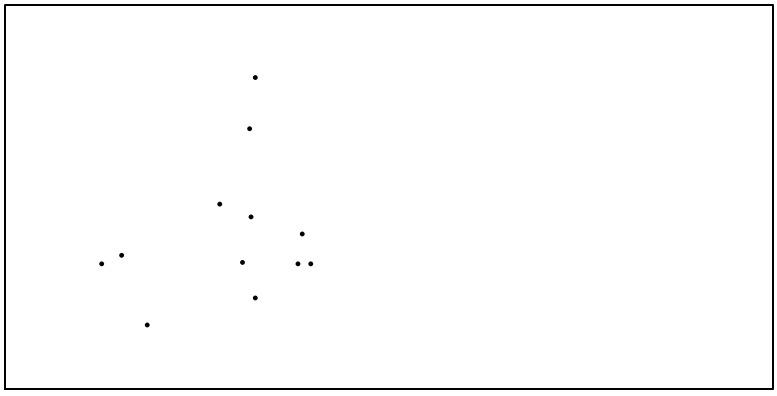


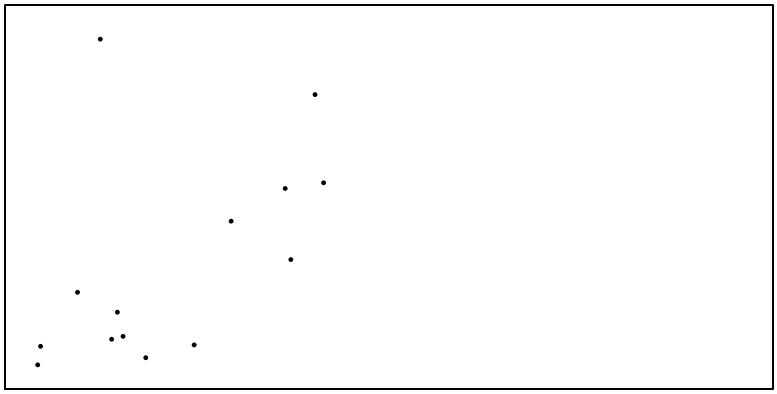












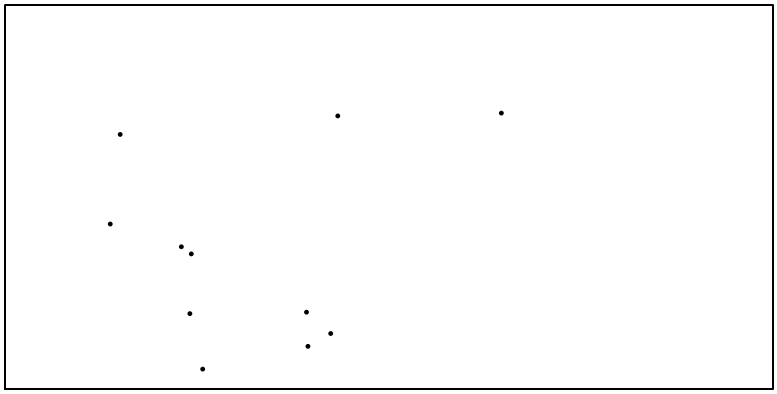
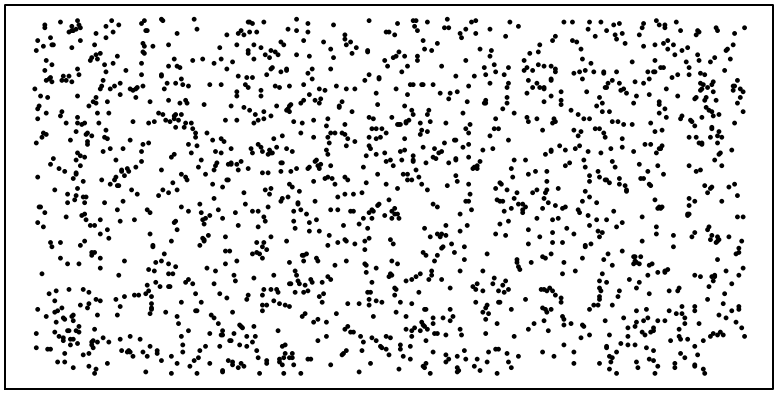
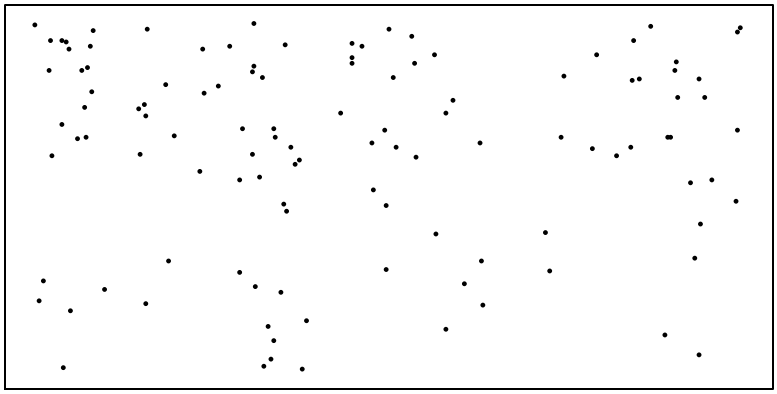
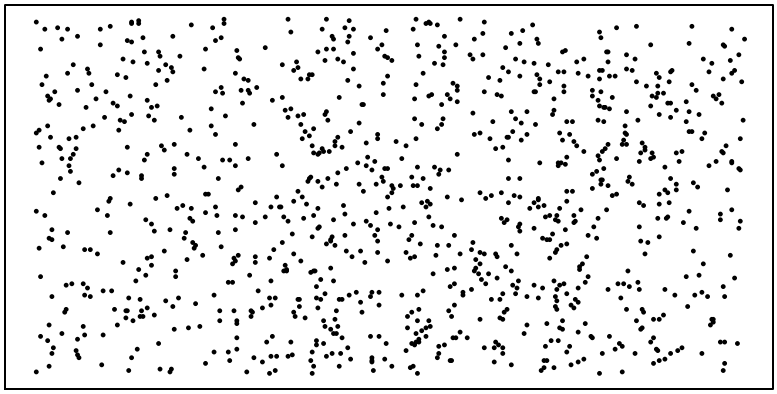
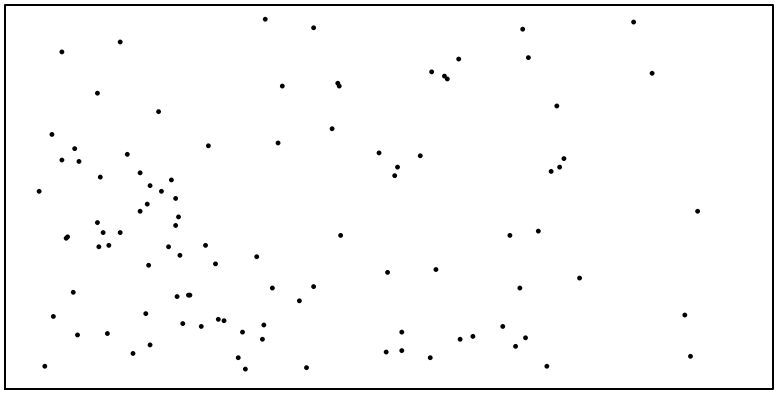


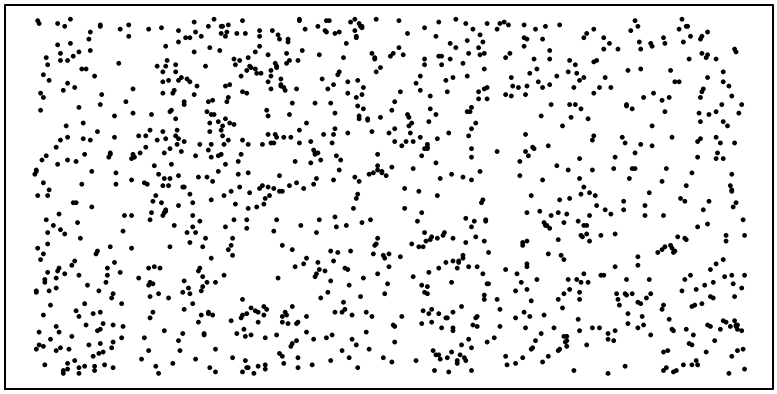
Fig. 6.4

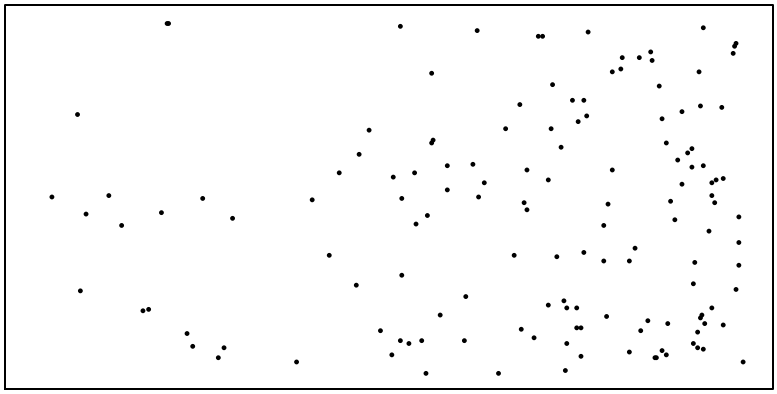


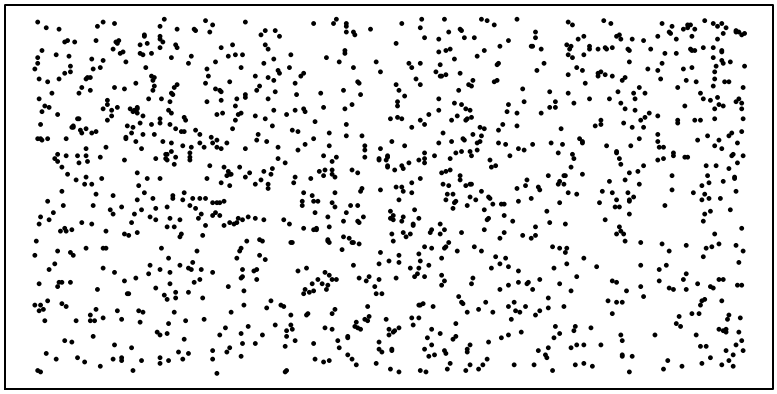












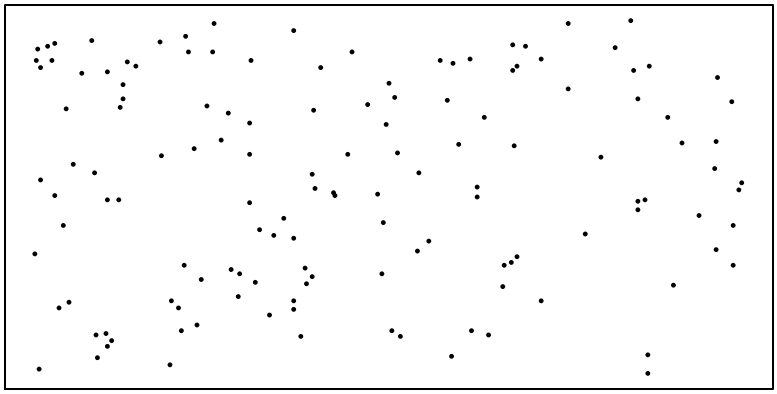
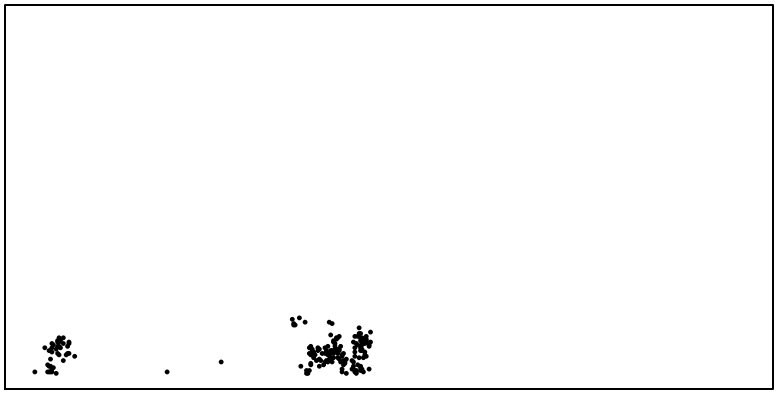
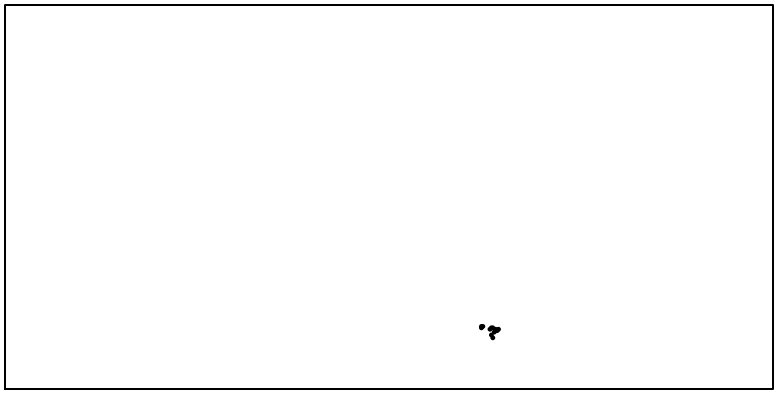
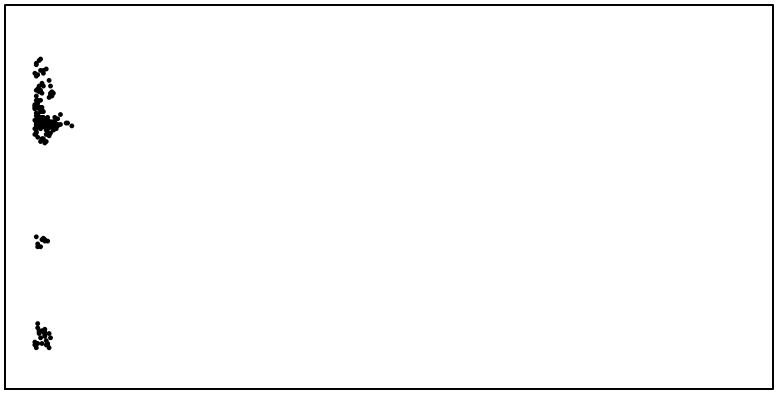
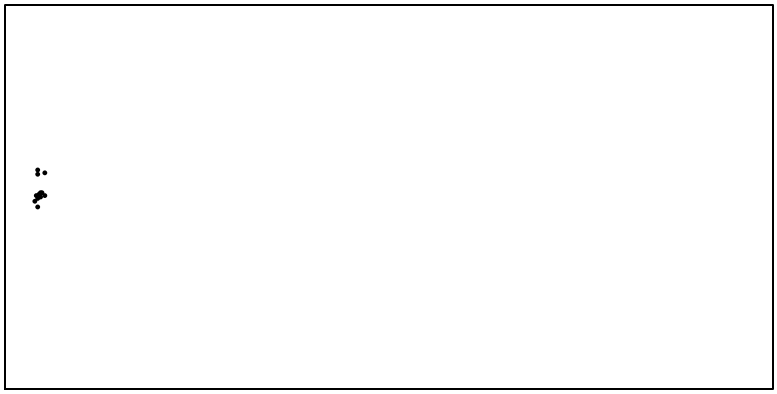


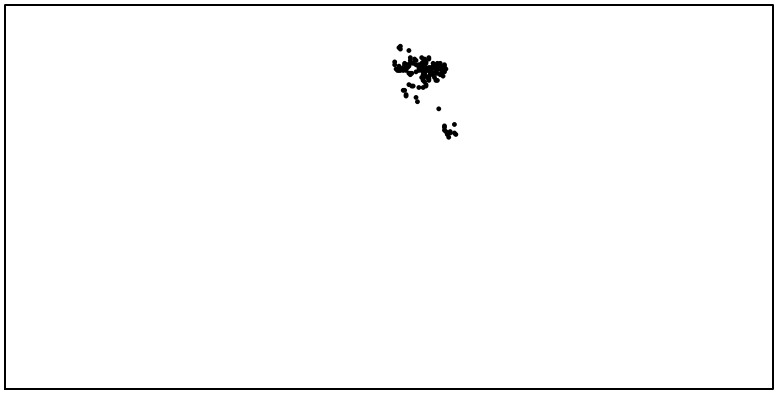
Fig. 6.3

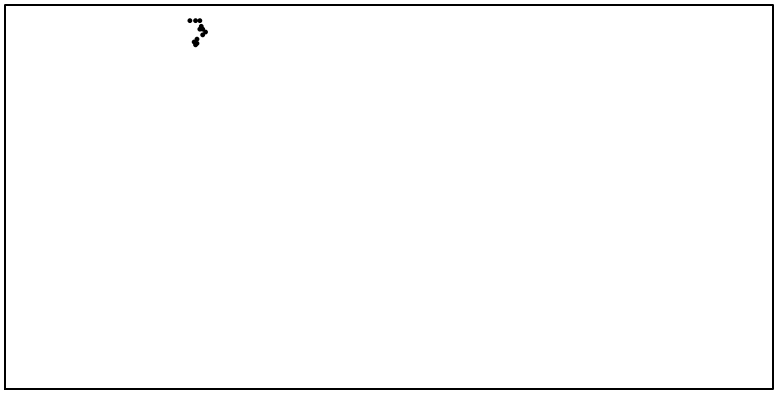


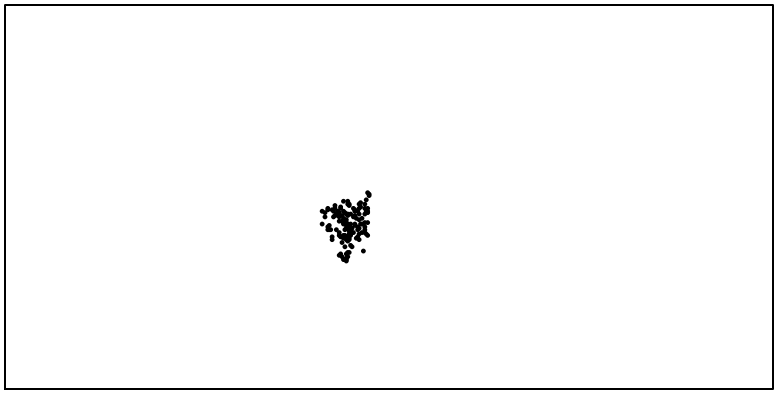












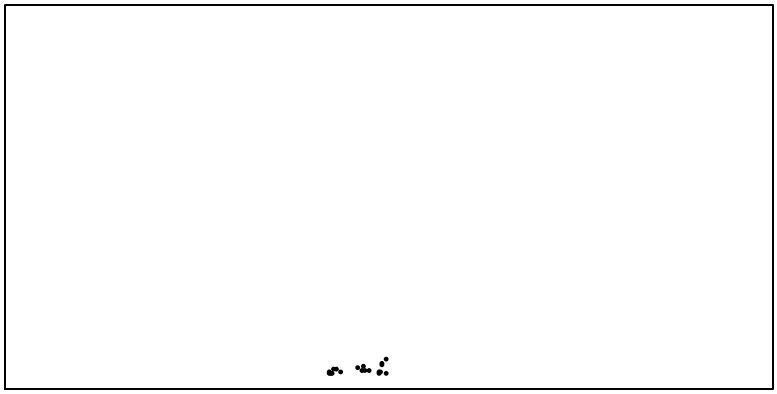
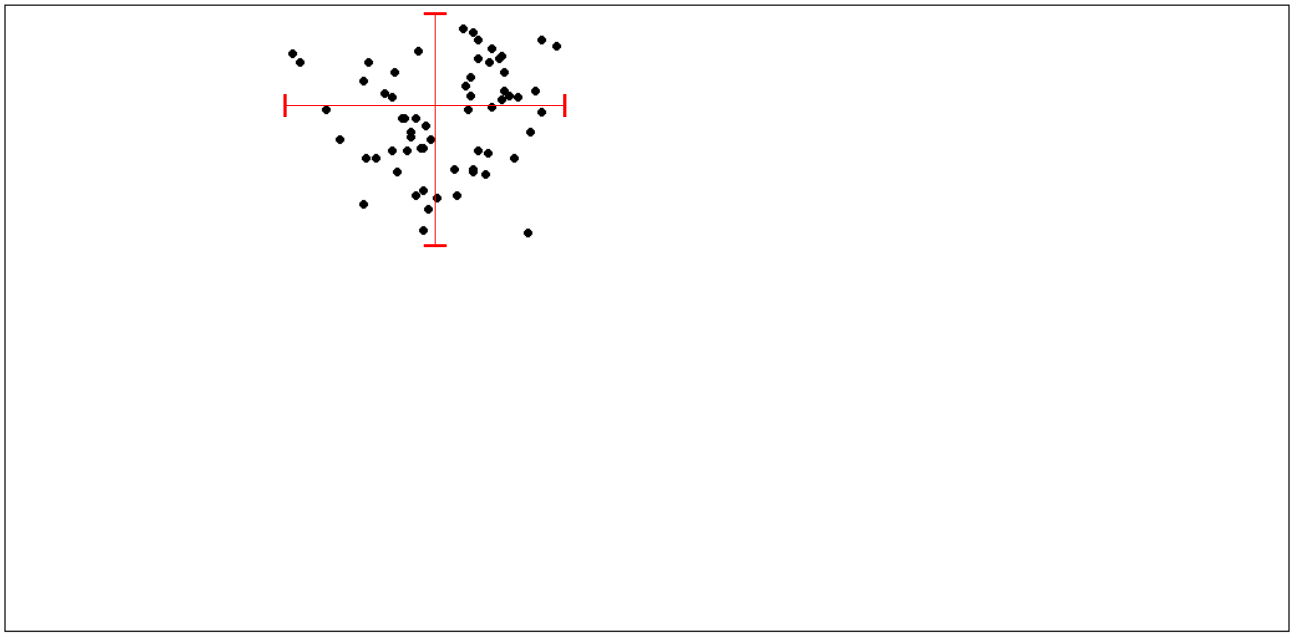


Fig. 6.6



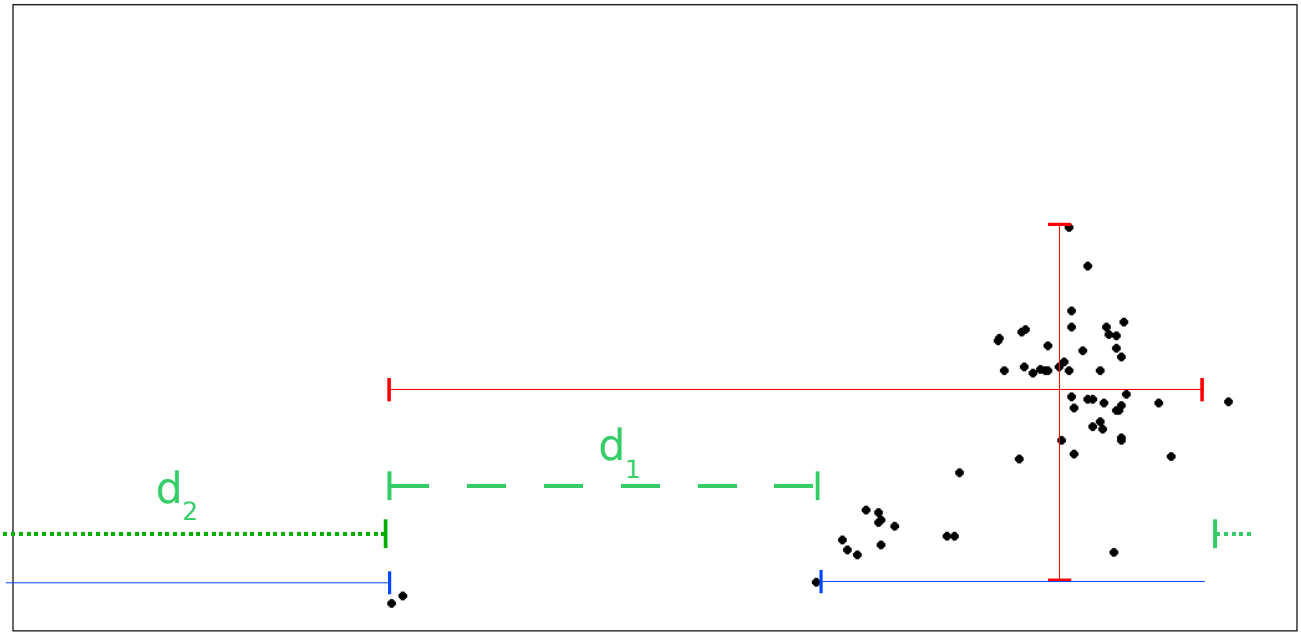
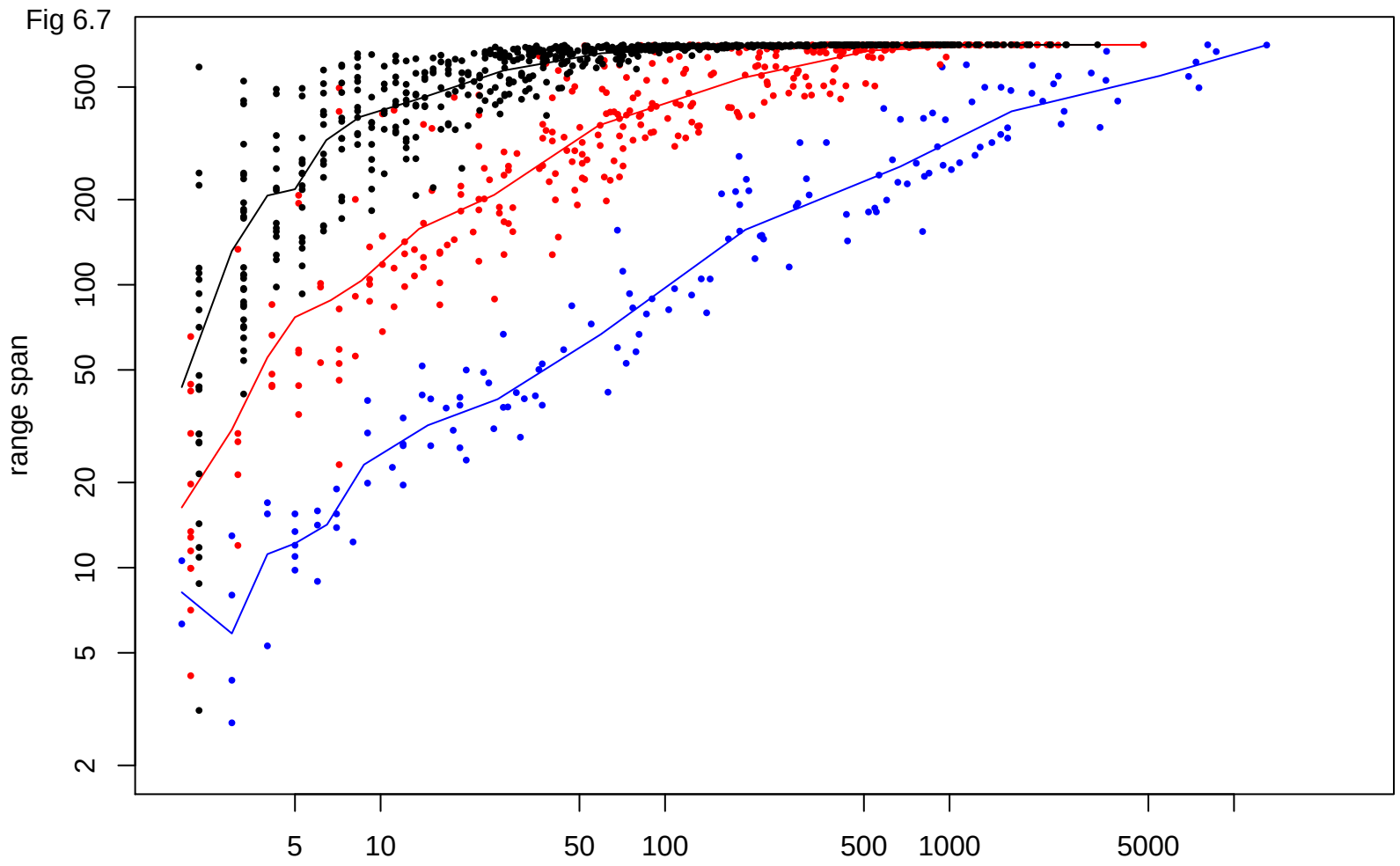


Fig 6.7


range span
2
5
10
20
50
100
200
500
5
10
50
100
500
1000
5000

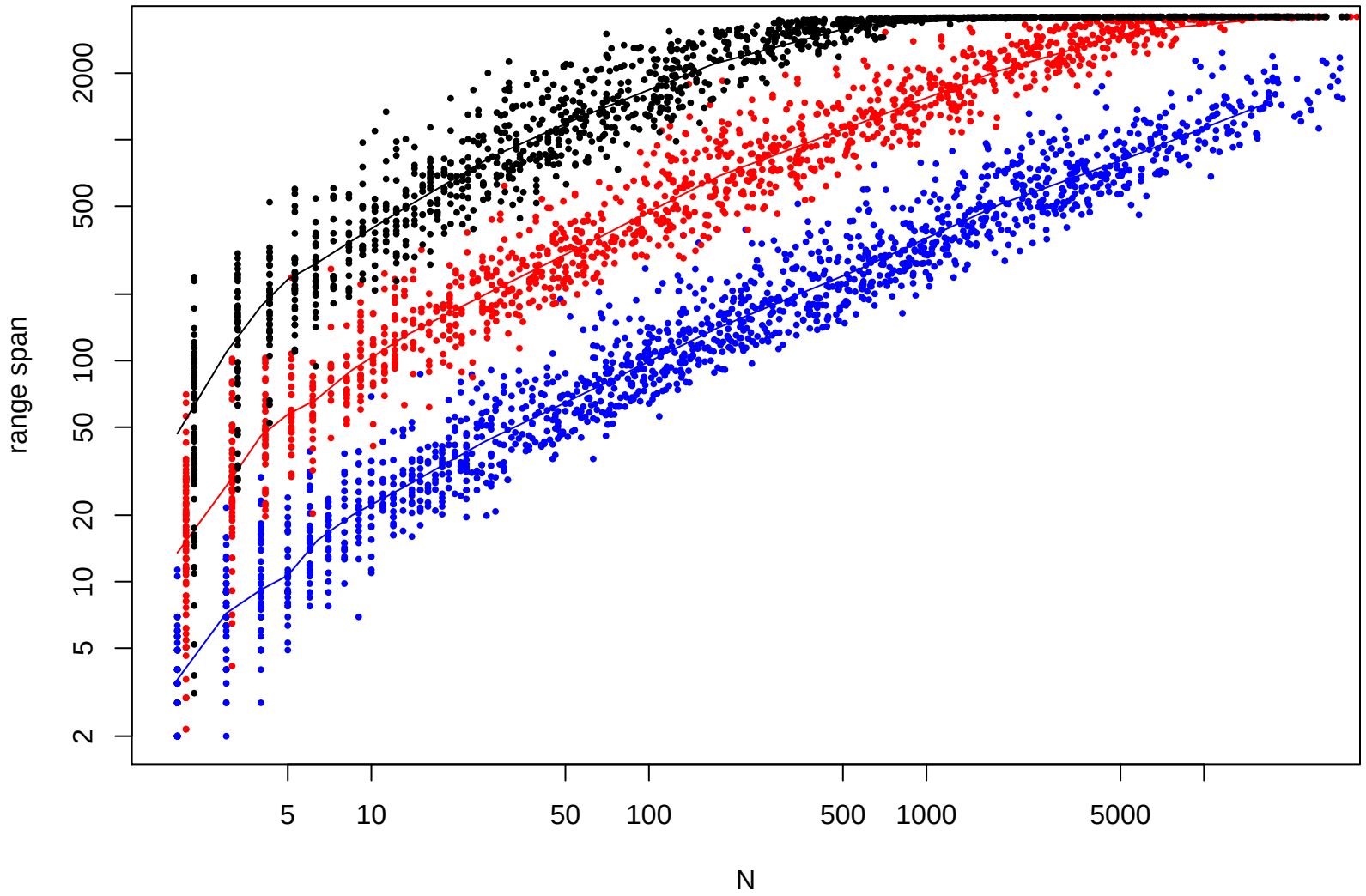
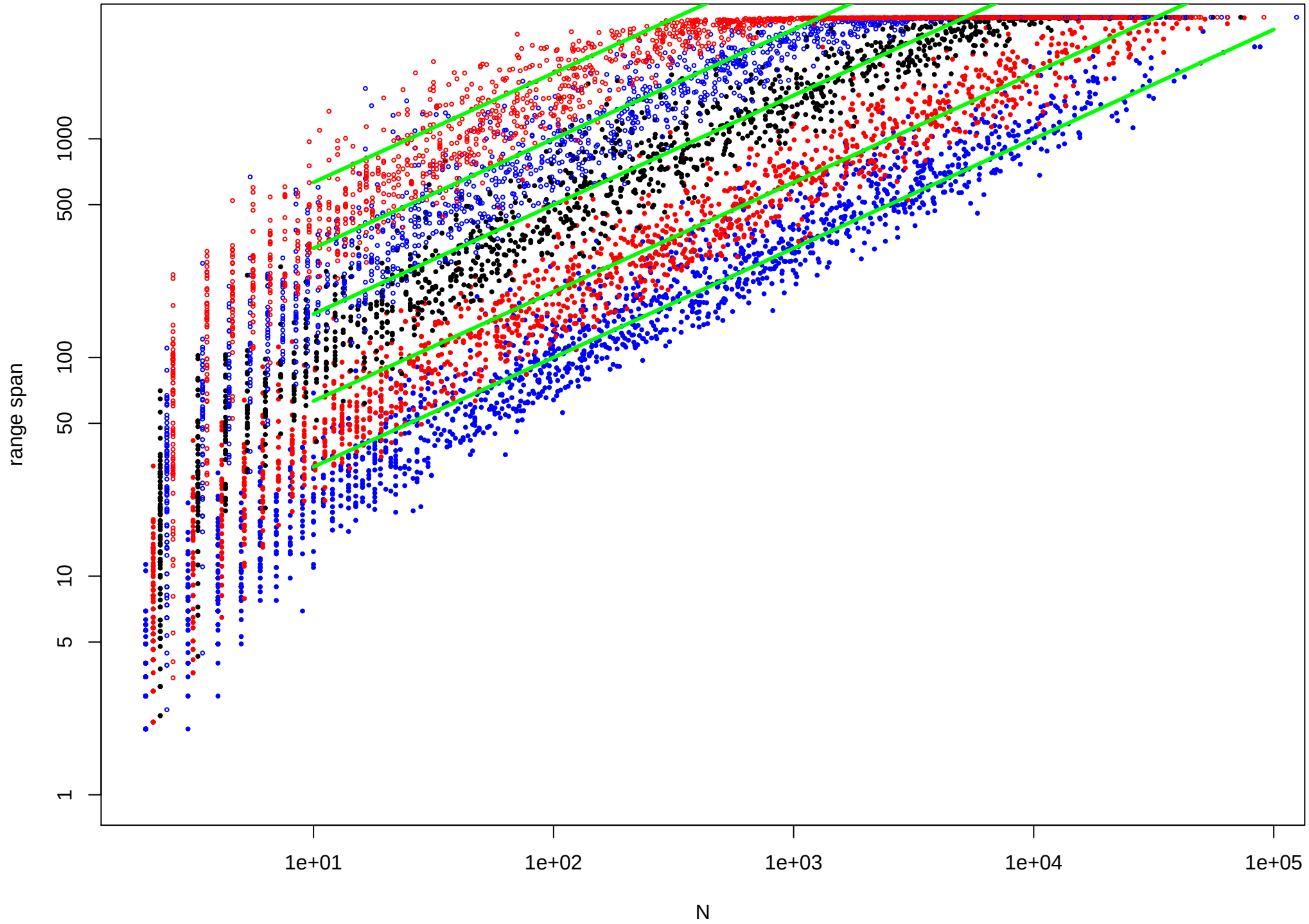

range span
2
5
10
20
50
100
500
2000
5
10
50
100
500
1000
5000
N

Fig. 6.9



A theory of dispersal limiting range size

$$R \approx 2D\sqrt{(N)}$$

N = population size

R = linear span of range

D = maximum dispersal distance

Model results vs. real forests…

quantitative

Fig. 6.10

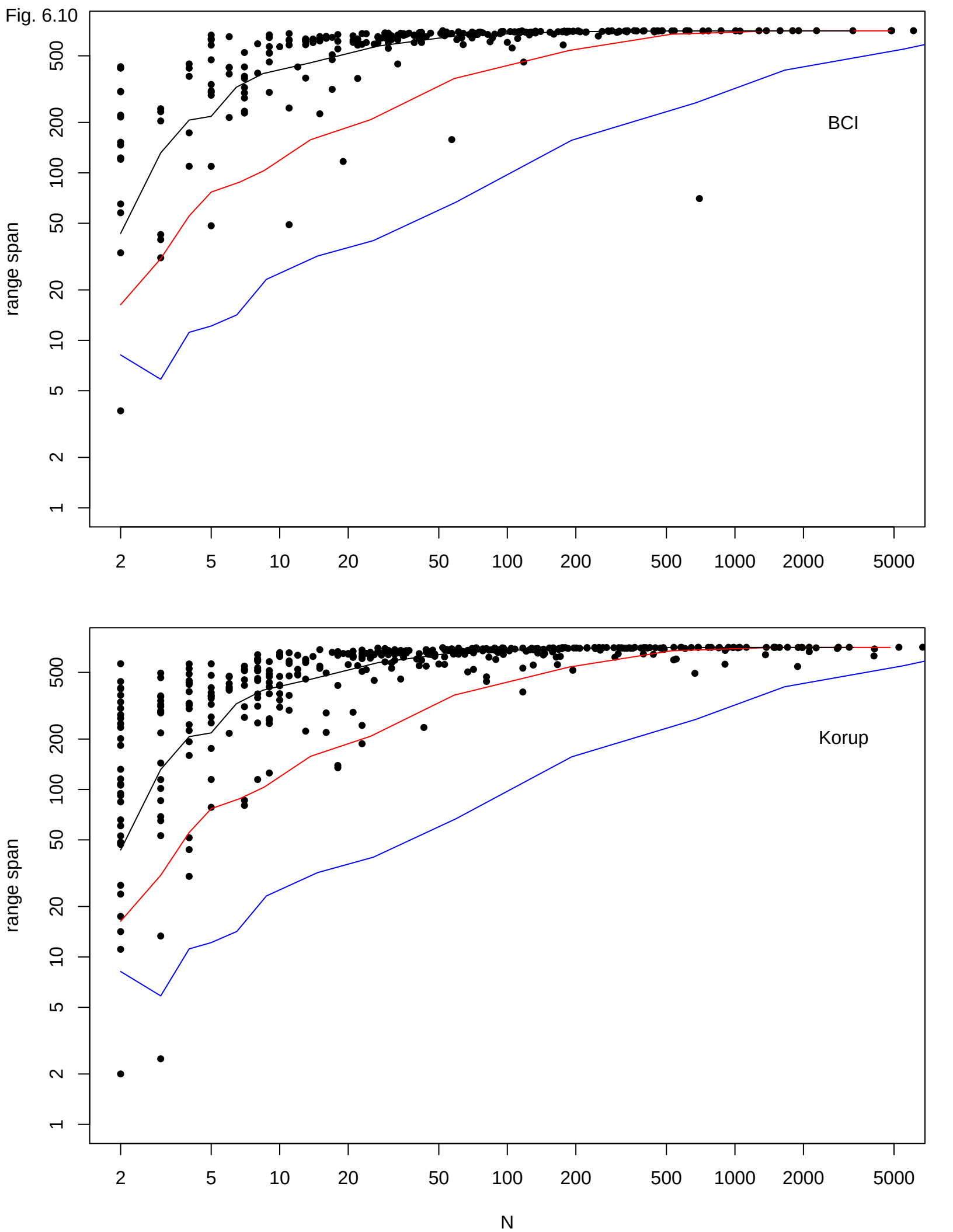
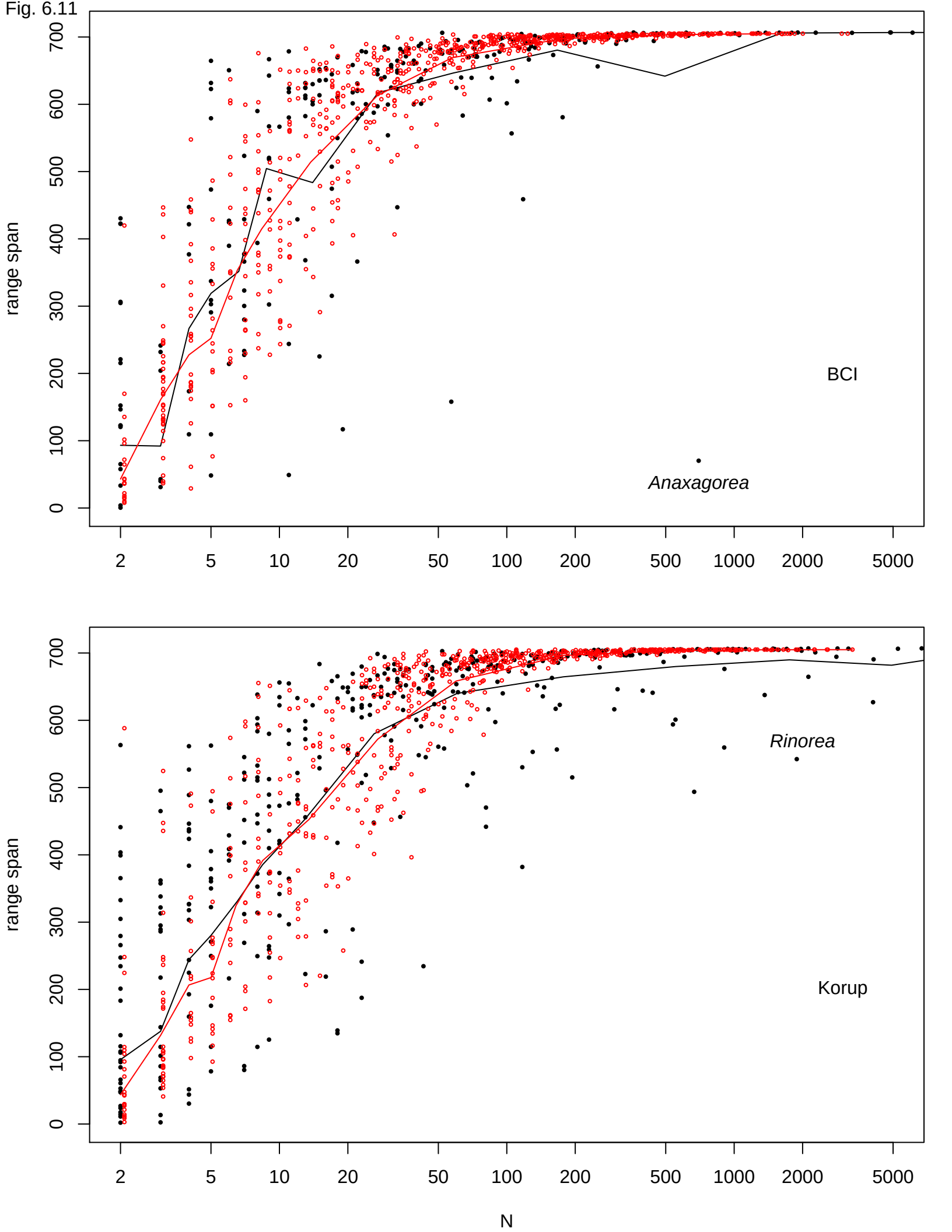
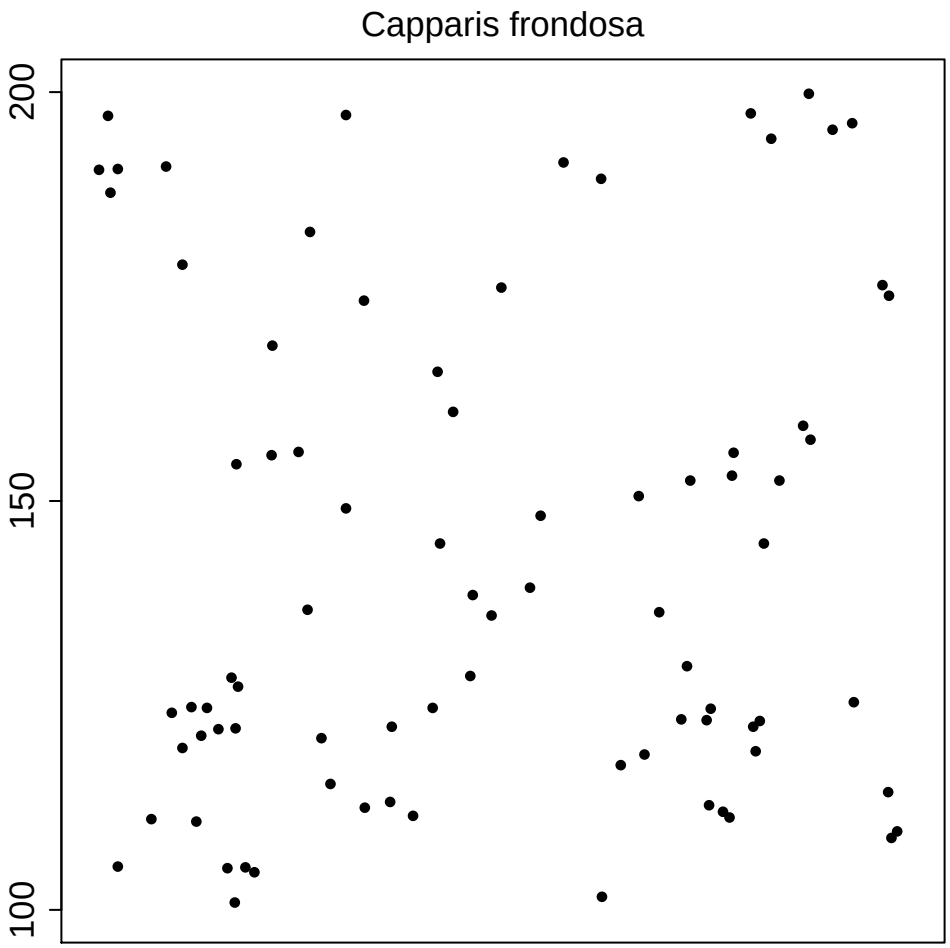
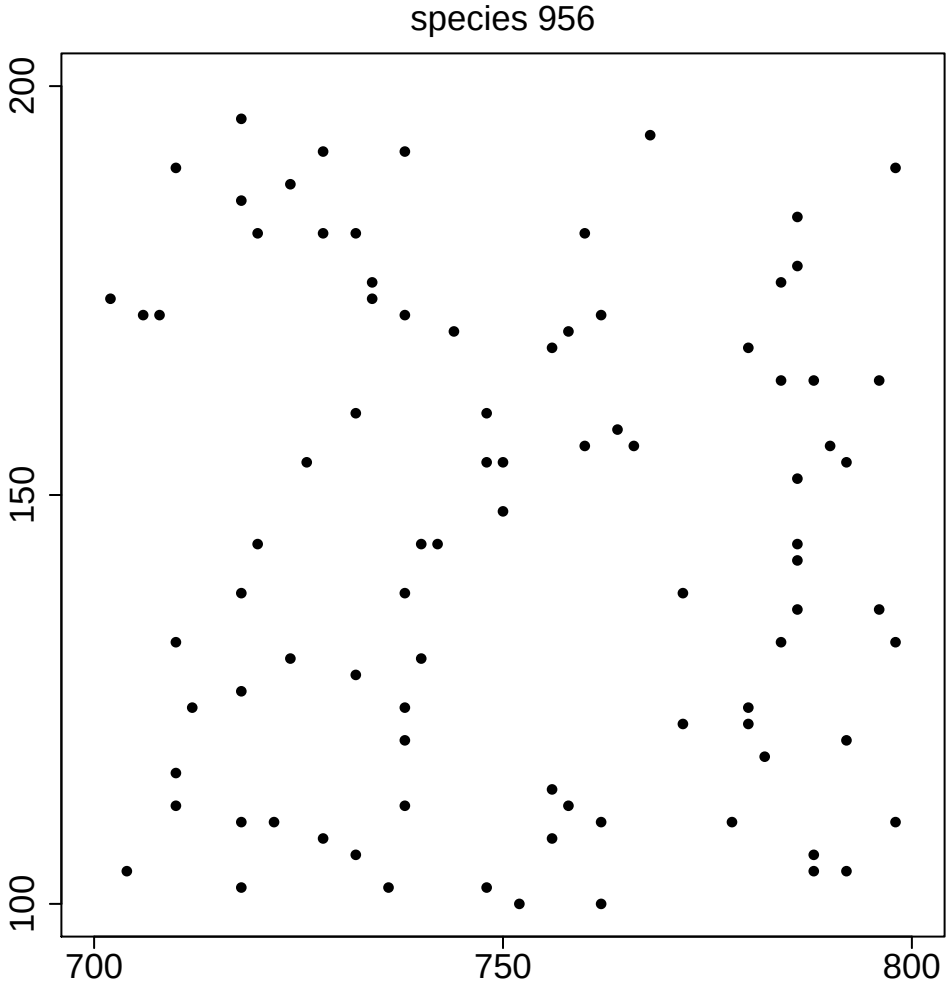
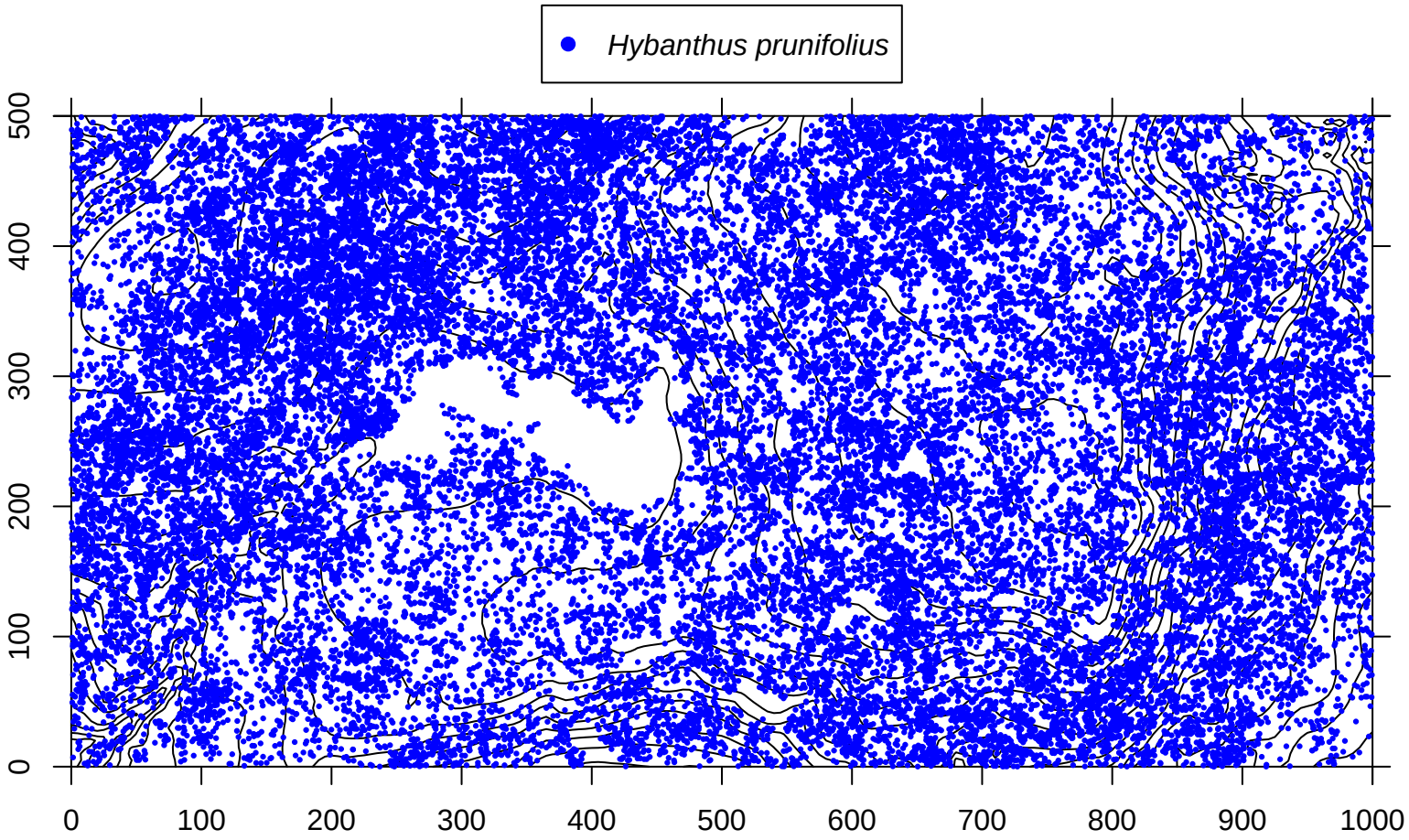

range span
1
2
5
10
20
50
100
200
500
2
5
10
20
50
100
200
500
1000
2000
5000
BCI
Korup
N

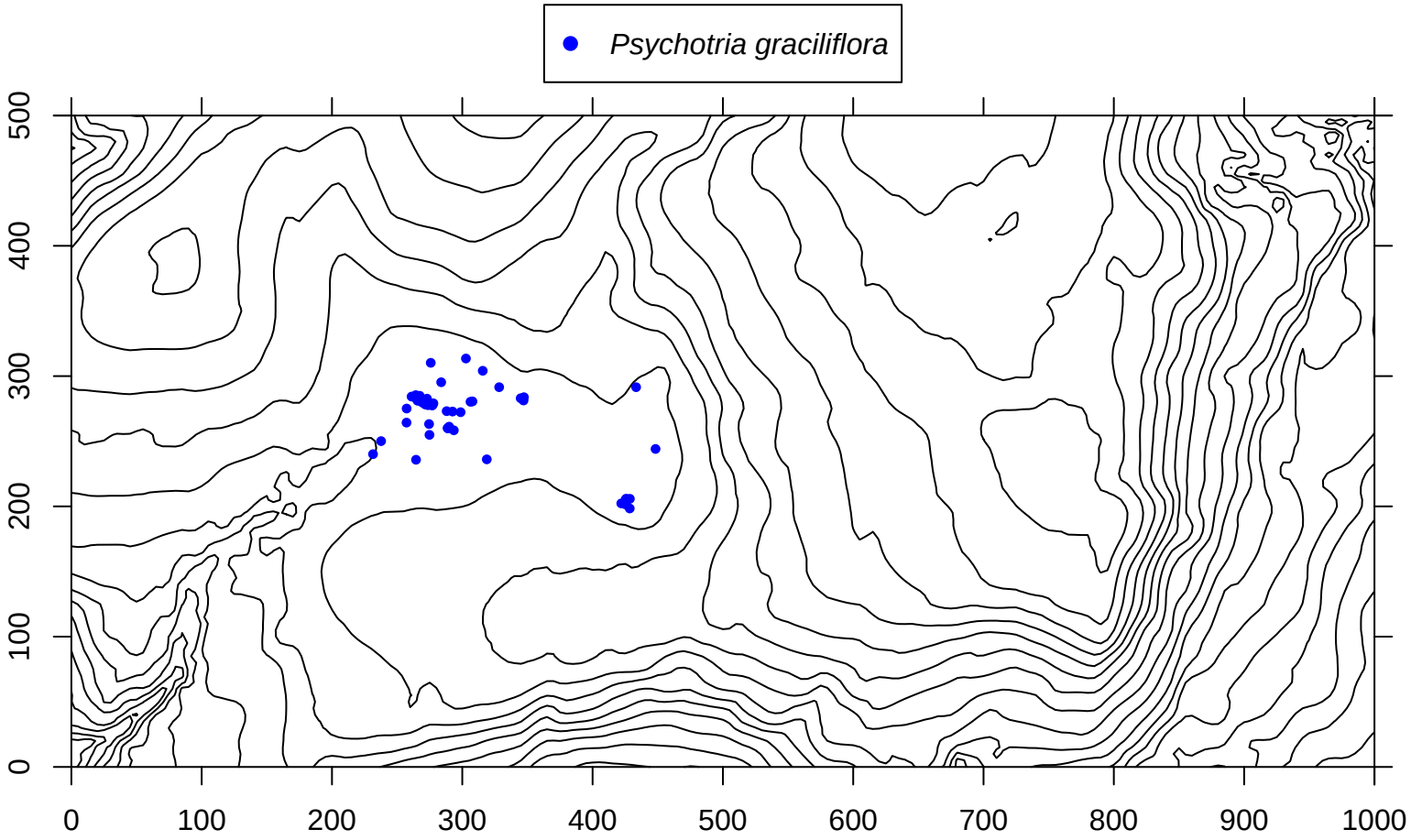
Fig. 6.11


range span
0
100
200
300
400
500
600
700
2
5
10
20
50
100
200
500
1000
2000
5000
BCI
Anaxagorea
Rinorea
Korup
N


Capparis frondosa
200
150
100

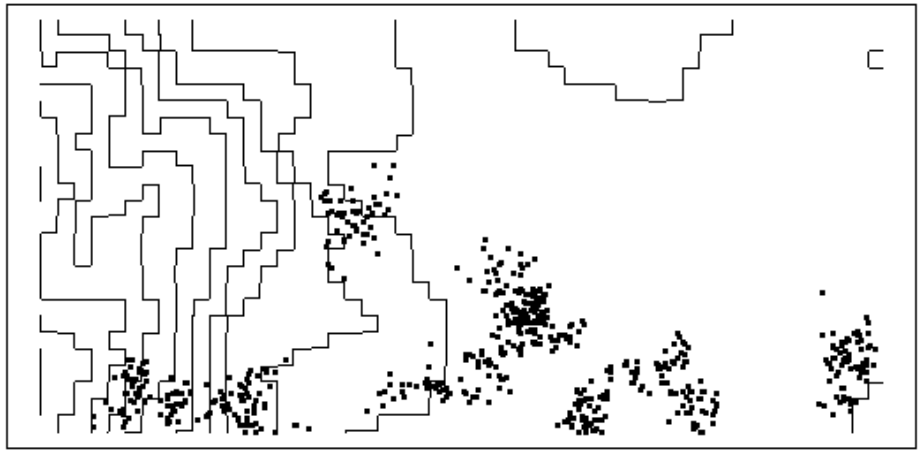

species 956
200
150
100
700
750
800

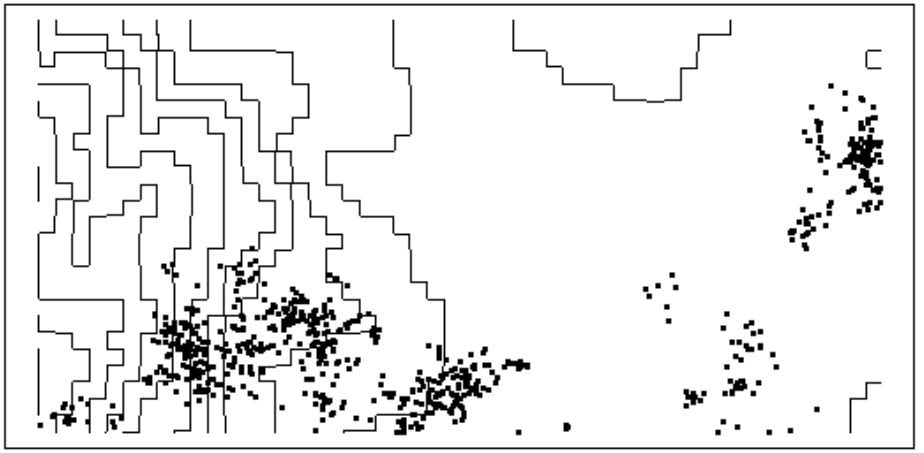

Hybanthus prunifolius
0
100
200
300
400
500
600
700
800
900
1000


Psychotria graciliflora
0
100
200
300
400
500
600
700
800
900
1000

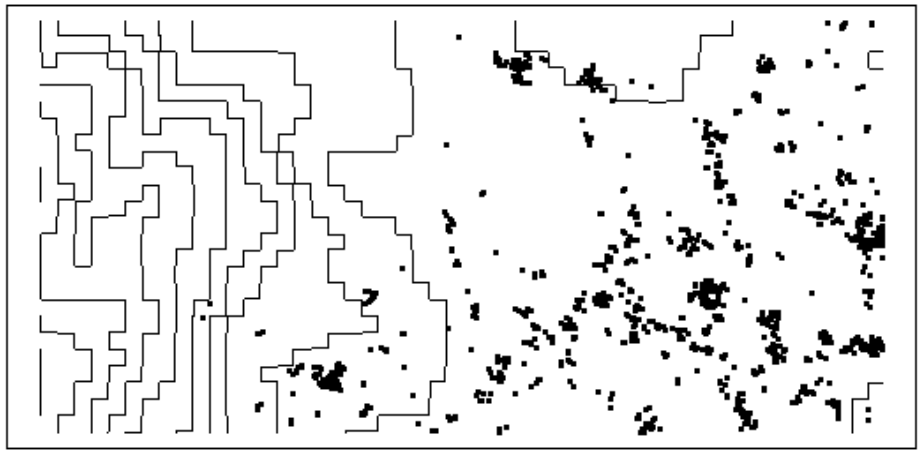
Rare long-distance dispersal and range

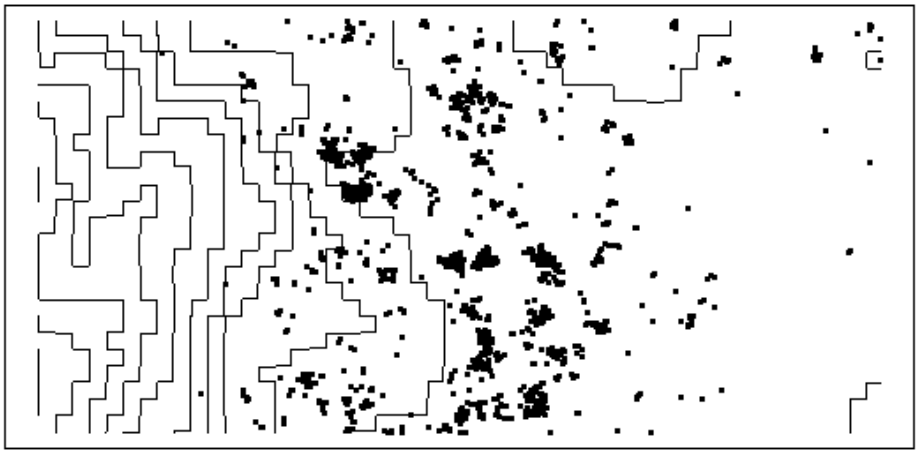
10-m dispersal (plus 1 in 1000 100-m dispersal)

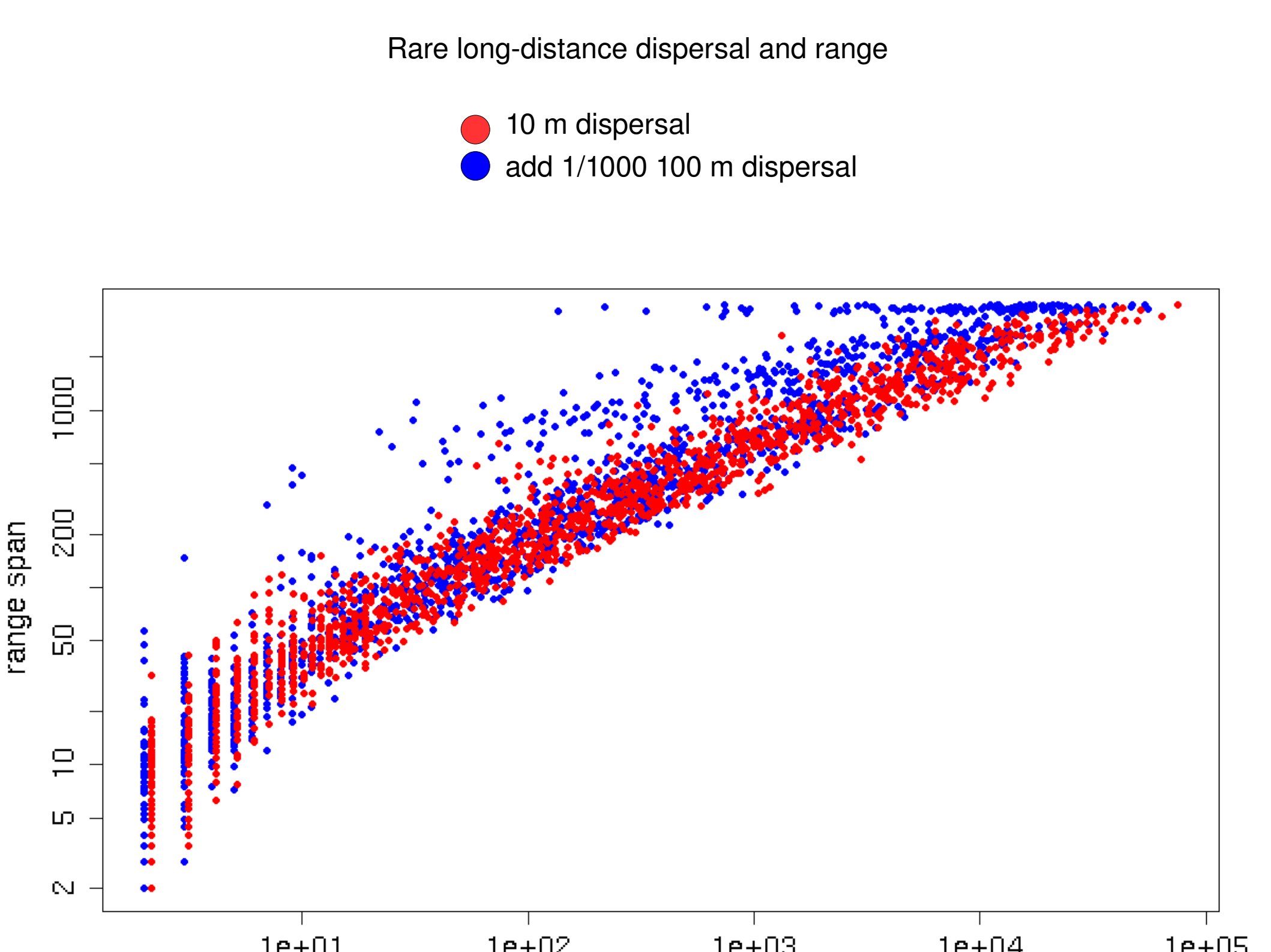




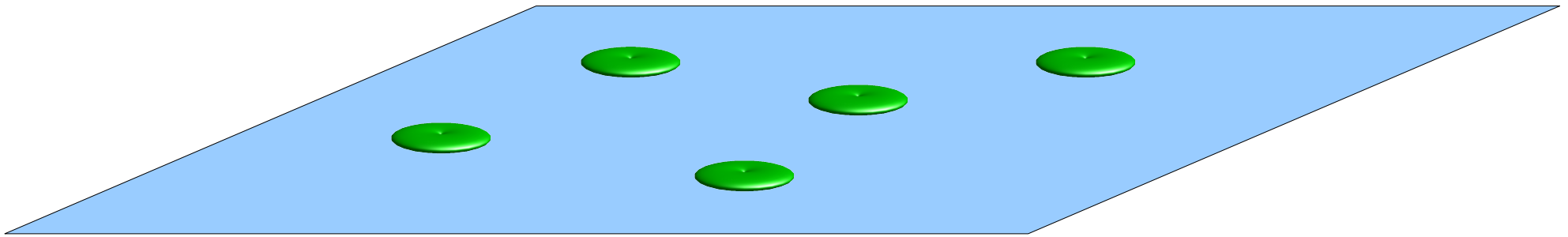
6-m dispersal (plus 1 in 10 100-m dispersal)





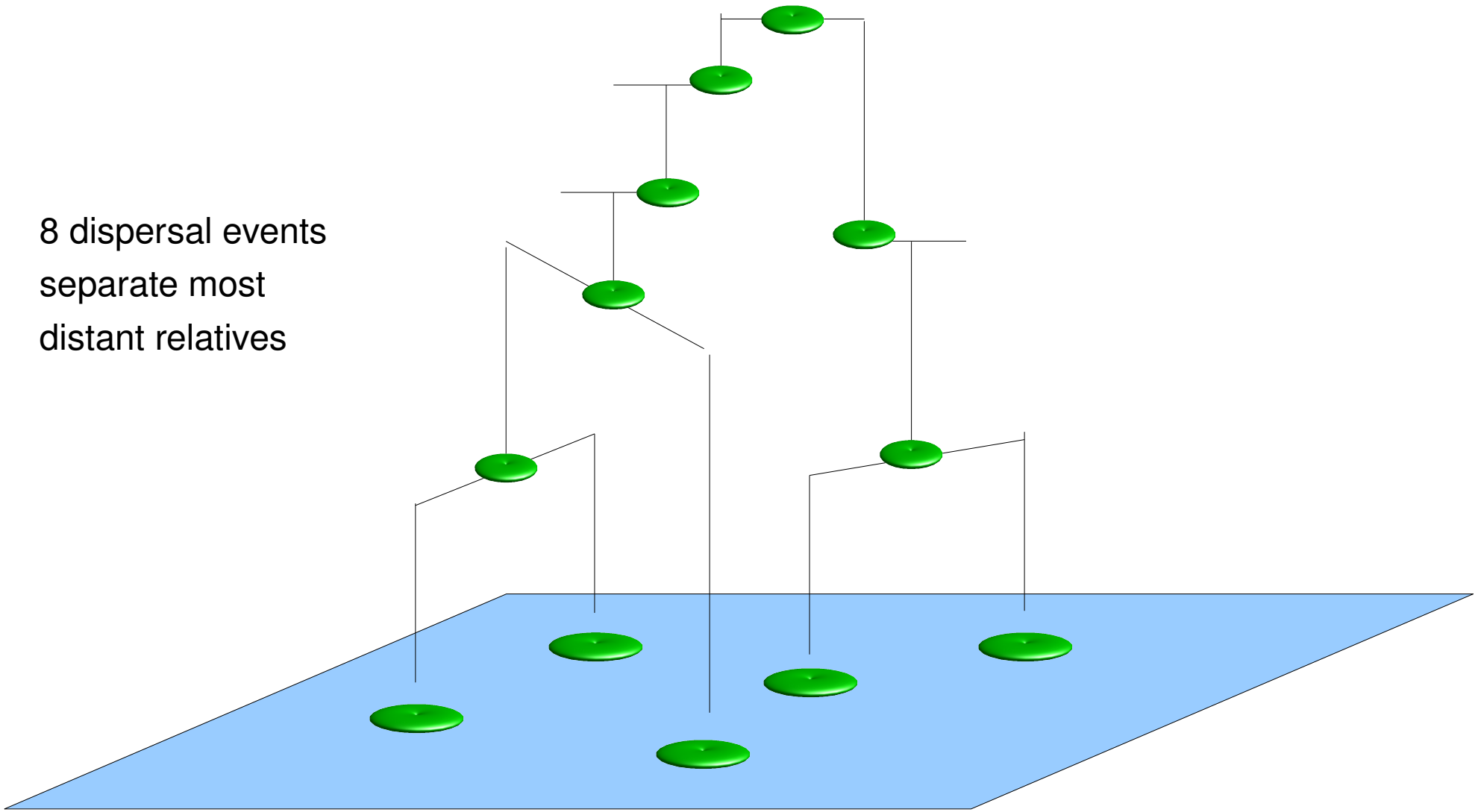

Rare long-distance dispersal and range
10 m dispersal
add 1/1000 100 m dispersal
range span
2
5
10
50
200
1000
1e+01
1e+02
1e+03
1e+04
1e+05

dispersal & range



Pedigree + dispersal = range

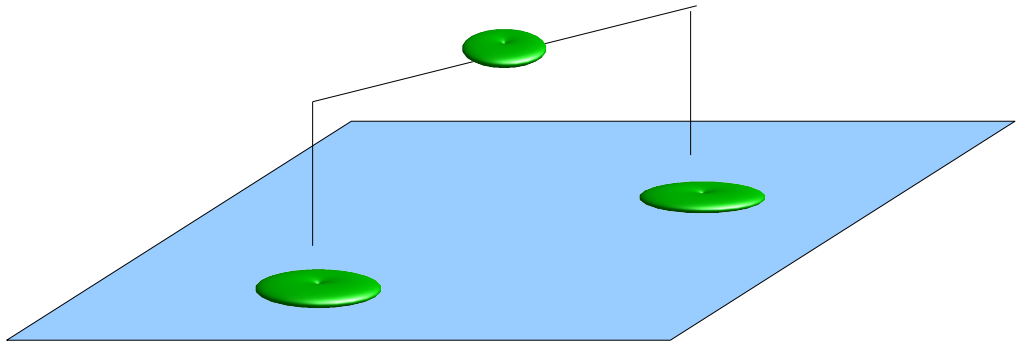
8 dispersal events separate most distant relatives

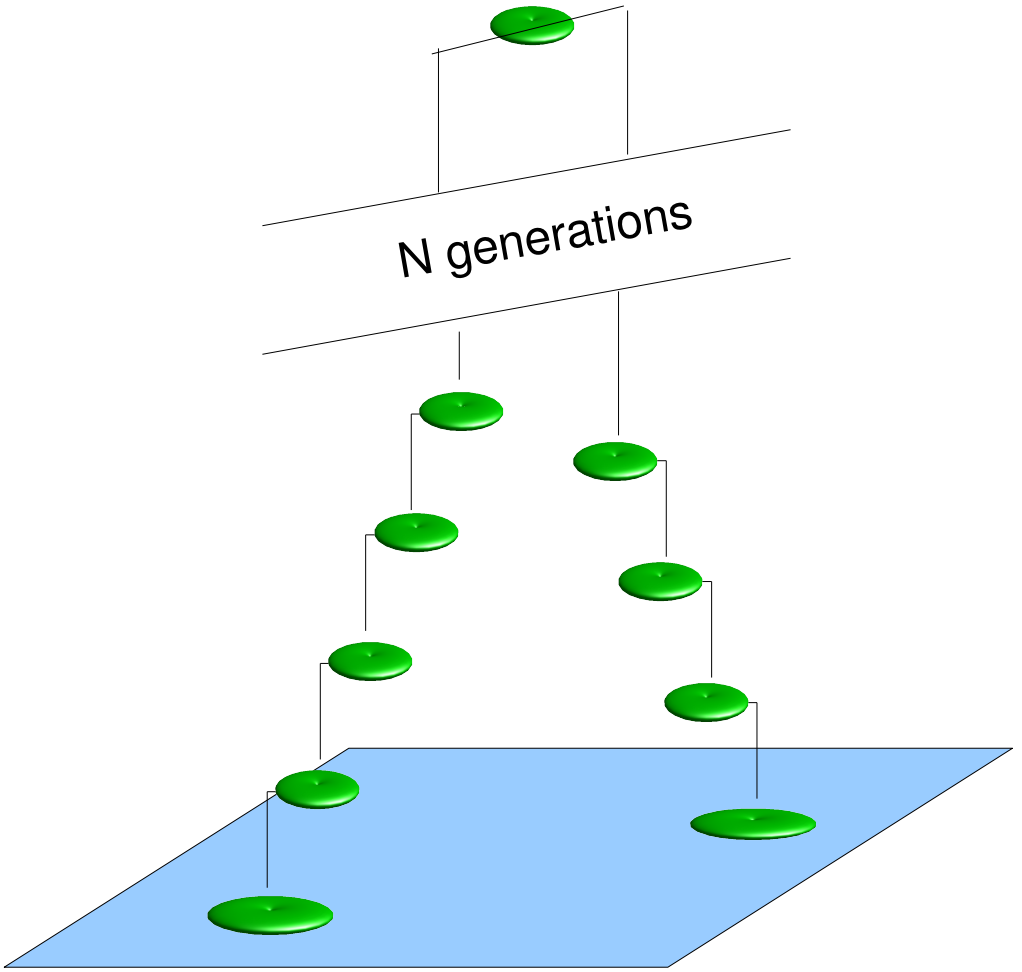


Two-individuals in population

Long pedigree=
widely separated

Short pedigree=
neighbors

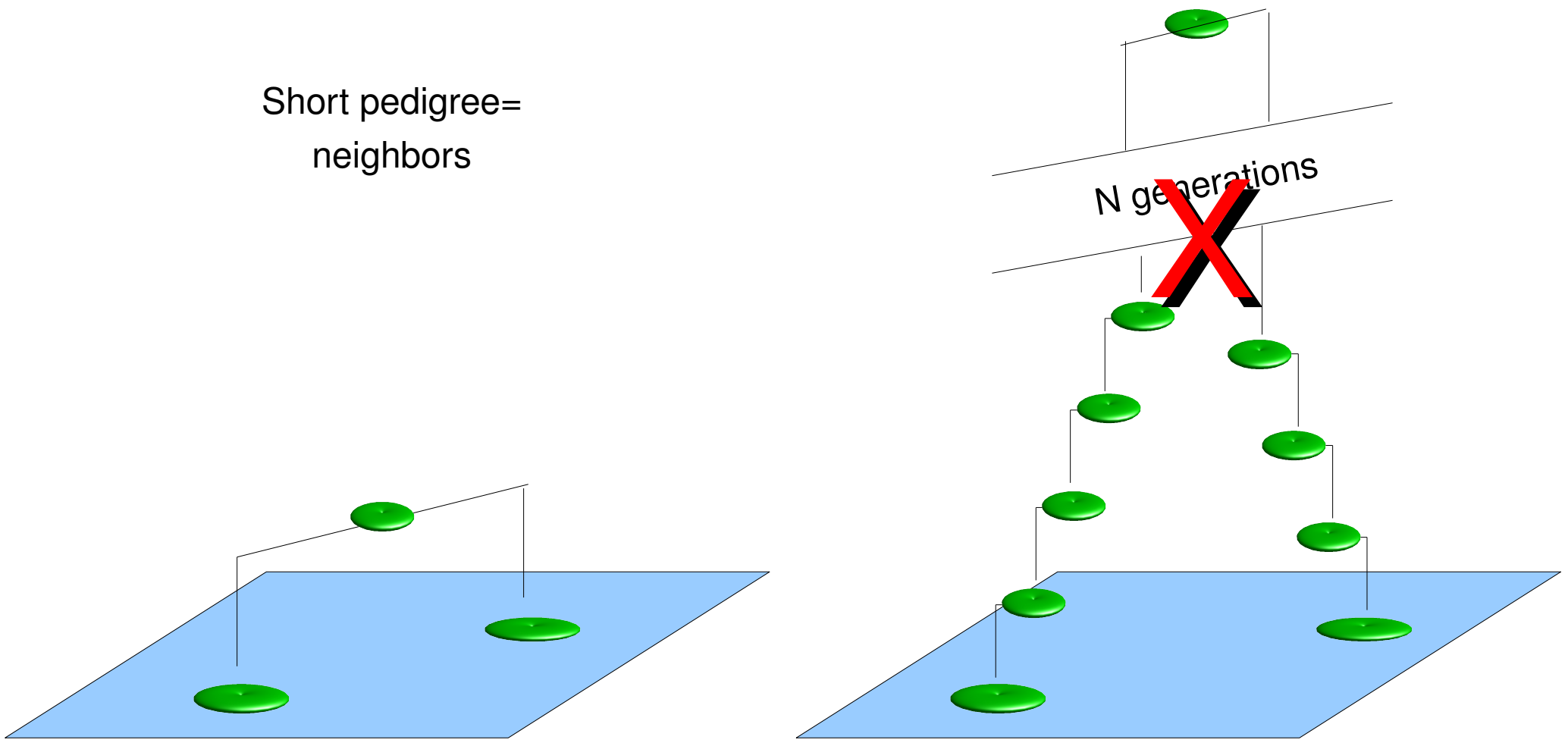




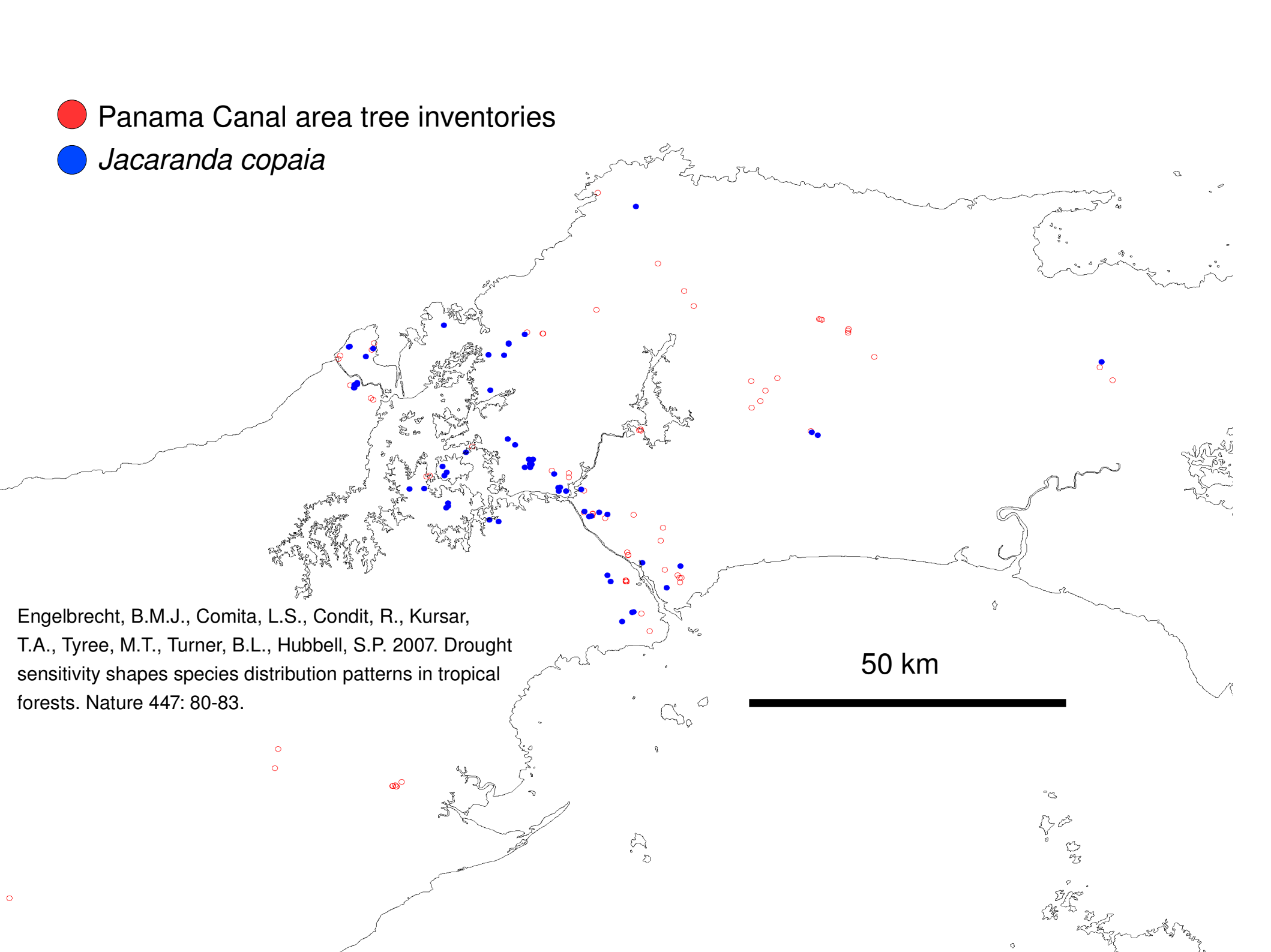
Two-individuals in population

Long pedigree=
widely separated

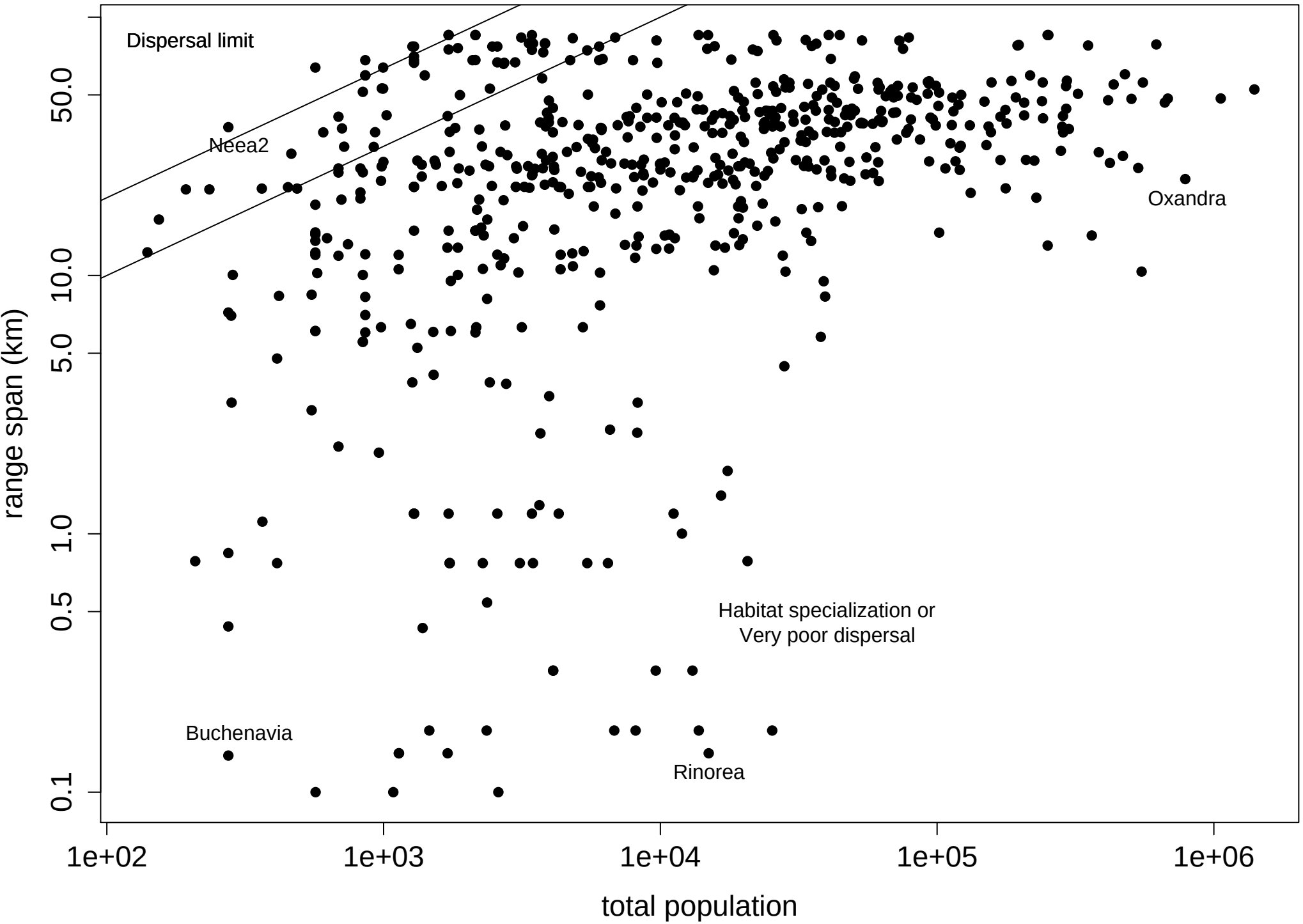
Short pedigree=
neighbors



what scenarios might allow long pedigrees?



Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., Hubbell, S.P. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80-83.


Dispersal limit
Neea2
Oxandra
Habitat specialization or
Very poor dispersal
Buchenavia
Rinorea
range span (km)
0.1
0.5
1.0
5.0
10.0
50.0
1e+02
1e+03
1e+04
1e+05
1e+06
total population

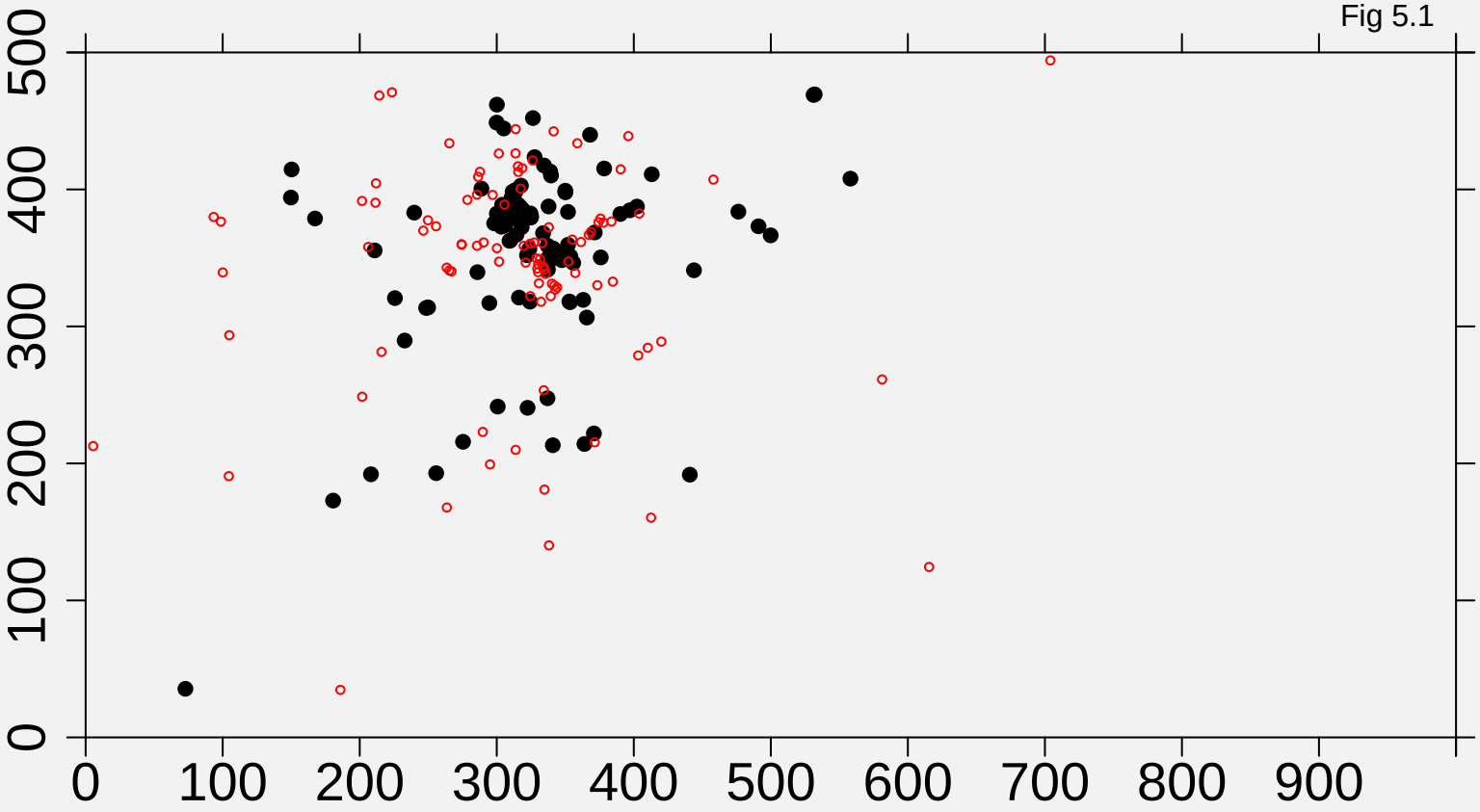
Oxandra longipetala

Rinorea lindeniana

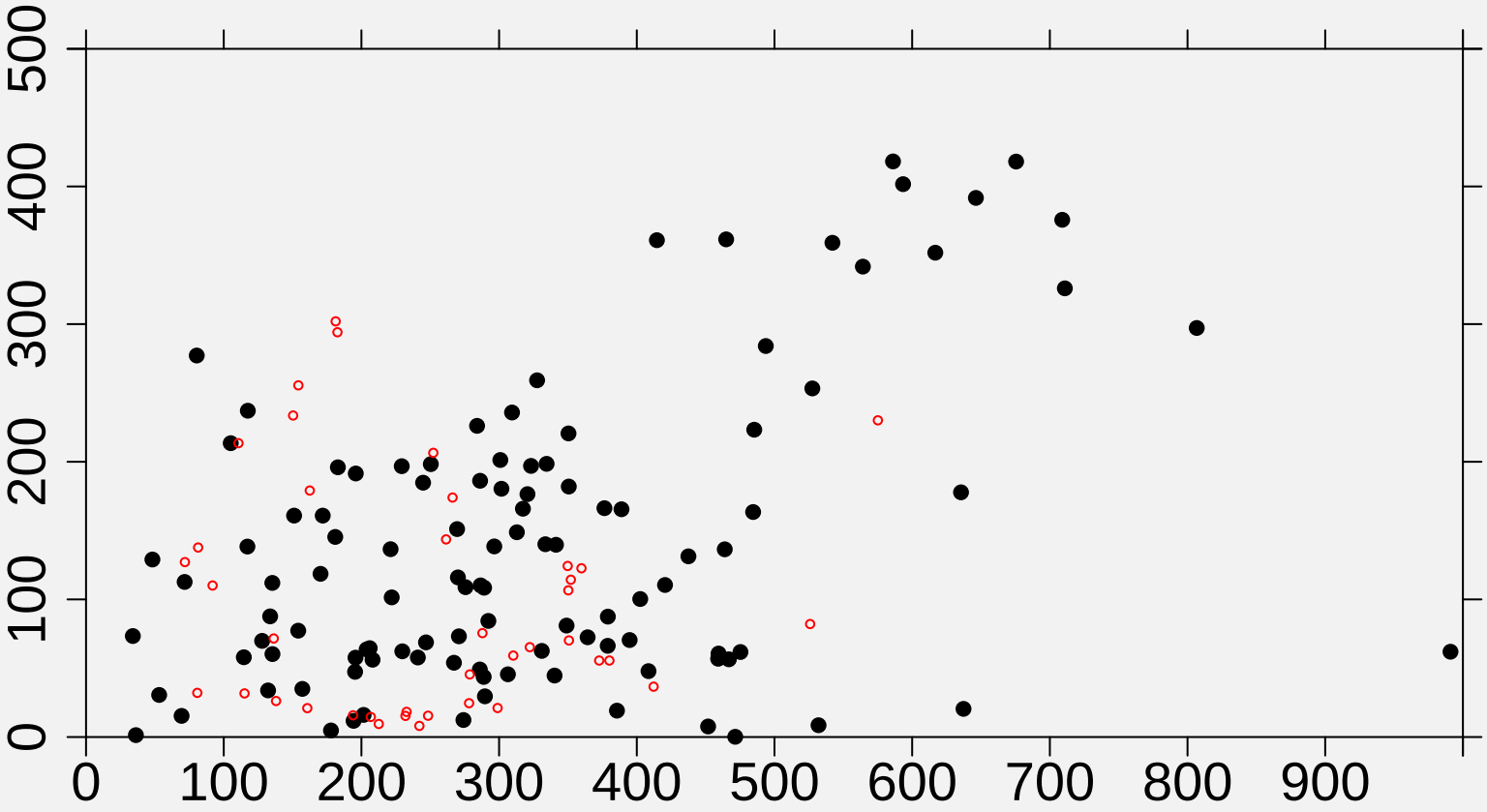
A digression about dispersal…

Chamguava

Fig 5.1

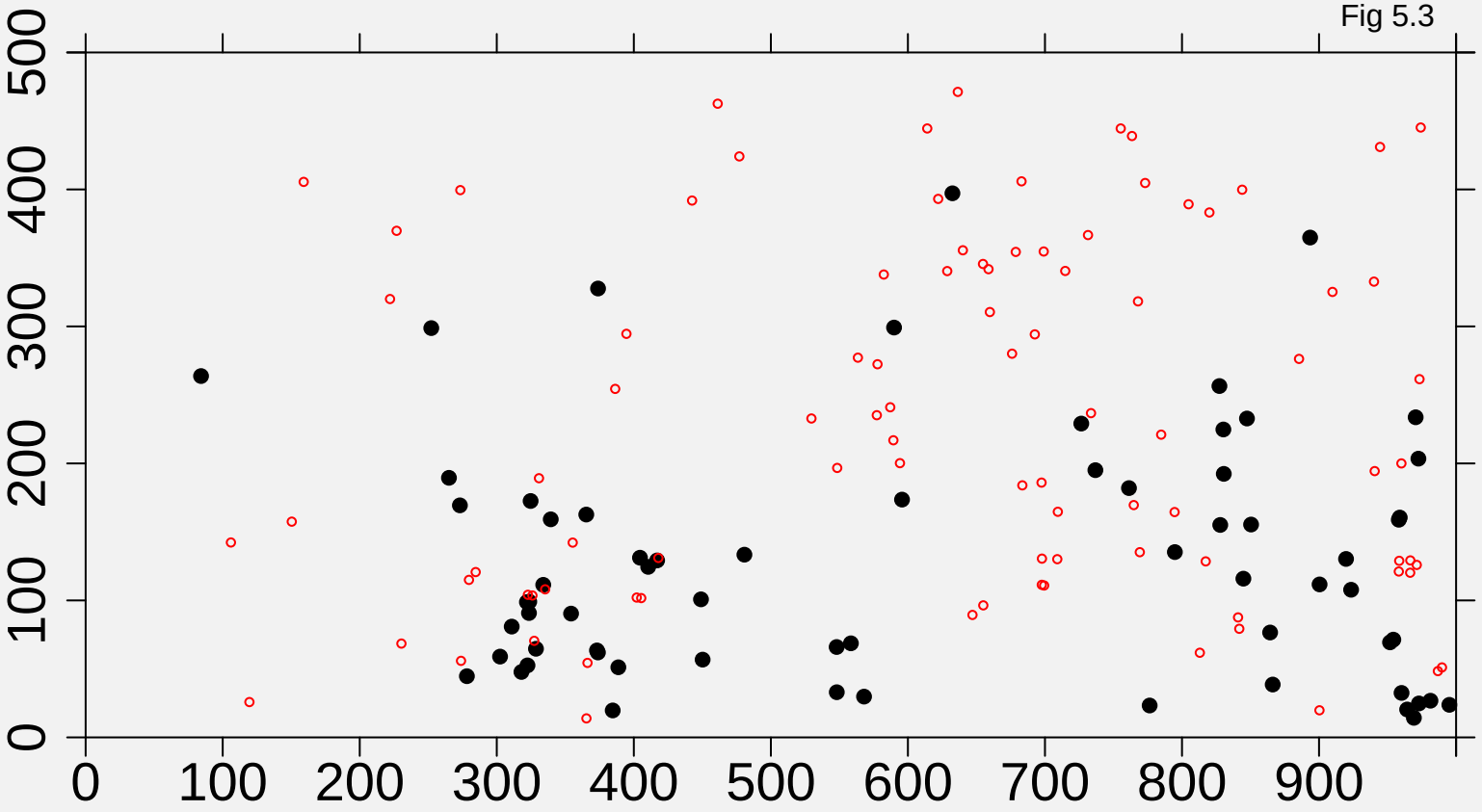


Prioria

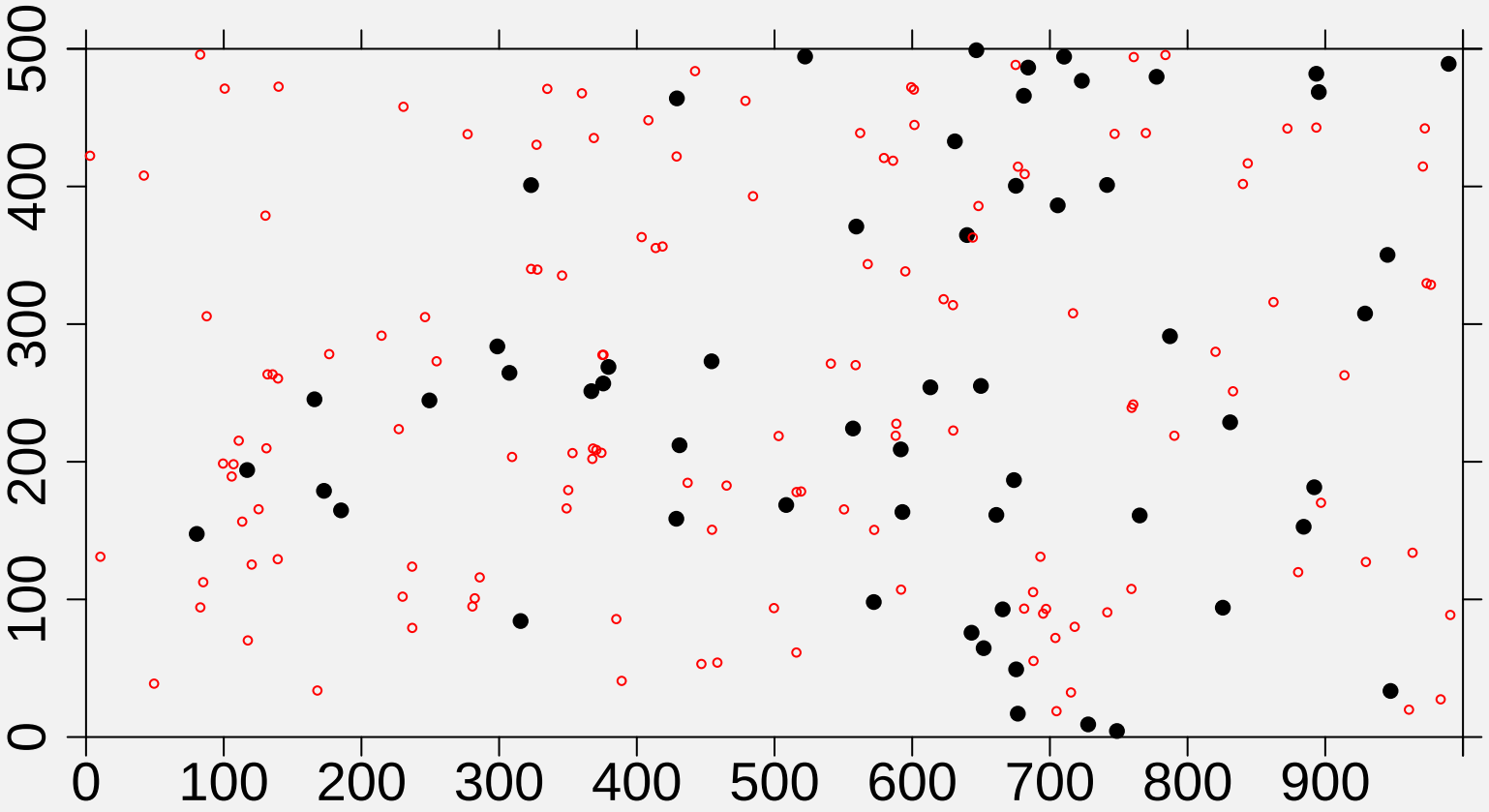


Inga

Fig 5.3



Pterocarpus



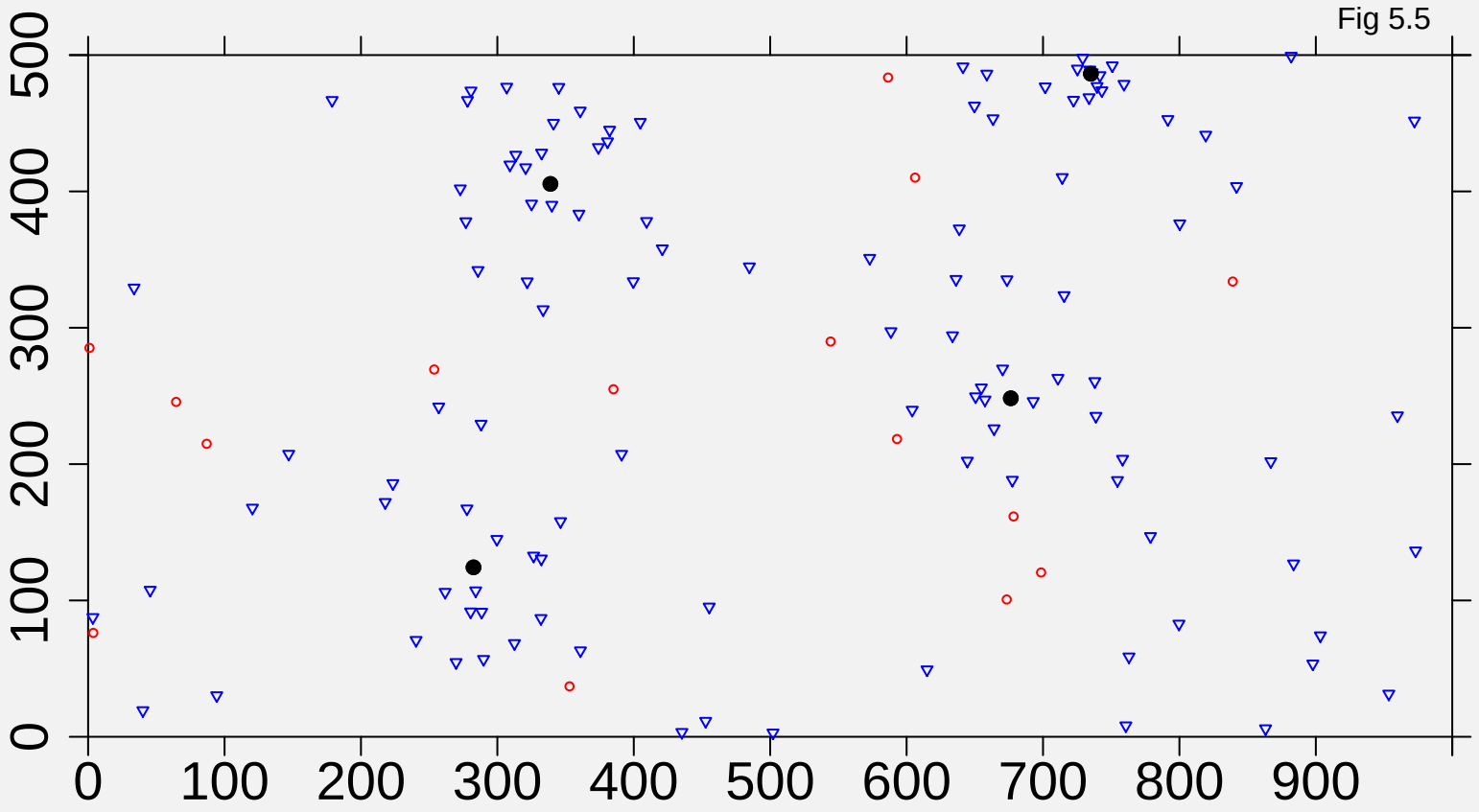


Fig 5.5
0
100
200
300
400
500
600
700
800
900

Proportion of recruits dispersing various distances from their parents

species	**< 30 m**	**> 100 m**
Chamguava schippii	**0.383**	**0.224**
Prioria copaifera	**0.287**	**0.242**
Cecropia obtusifolia	**0.186**	**0.237**
Eugenia coloradoensis	**0.256**	**0.591**
sTalisia princeps	**0.045**	**0.494**
Inga marginata	**0.132**	**0.645**
Chrysophyllum argenteum	**0.041**	**0.712**
Pterocarpus rohrii	**0.034**	**0.770**
Hampea appendiculata	**0.089**	**0.714**
Calophyllum longifolium	**0.006**	**0.842**
Inga acuminata	**0.023**	**0.848**
Nectandra lineata	**0.027**	**0.861**

How do demographic habitat response and dispersal interact to create spatial distributions?

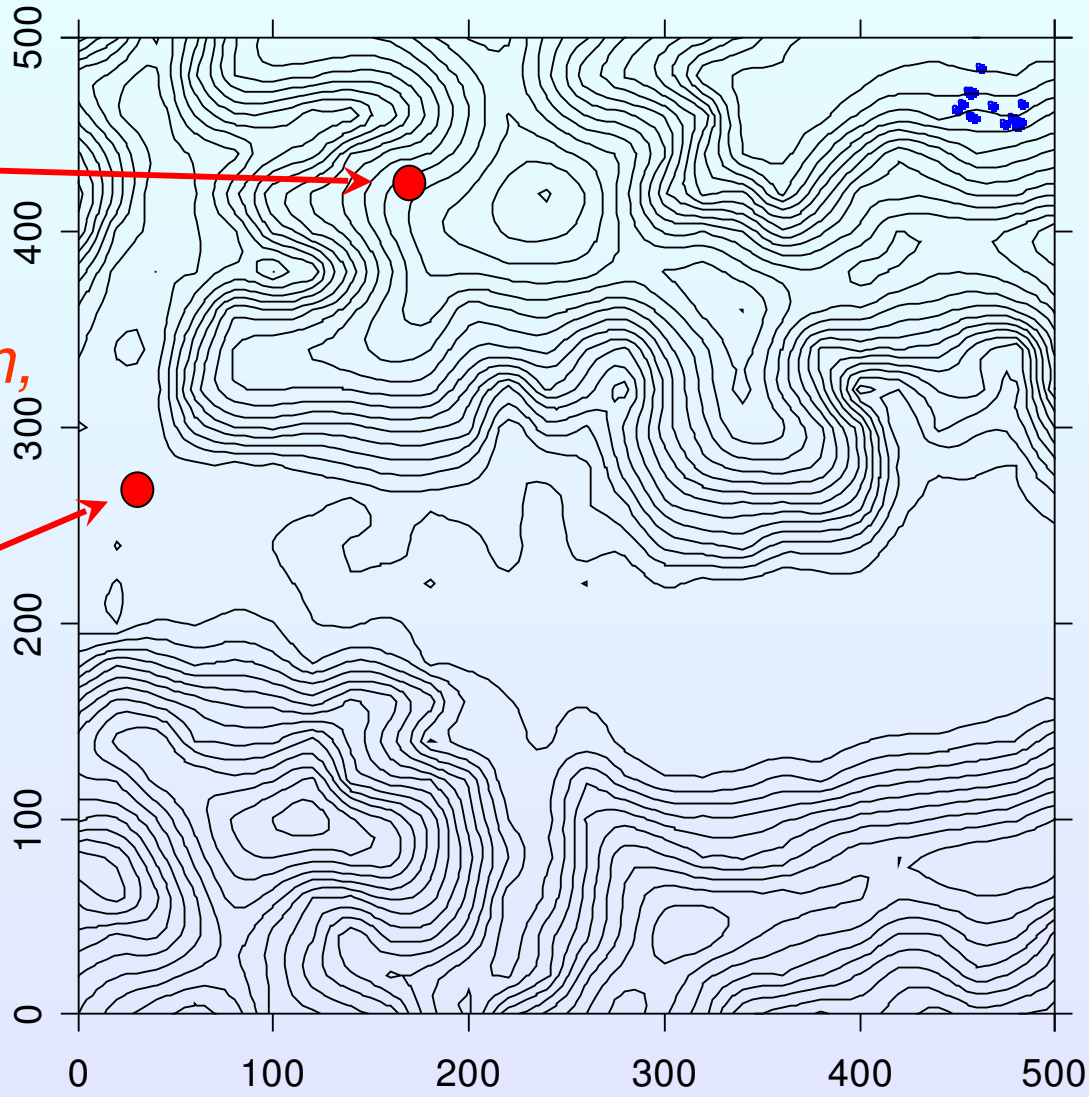
the models predictions...

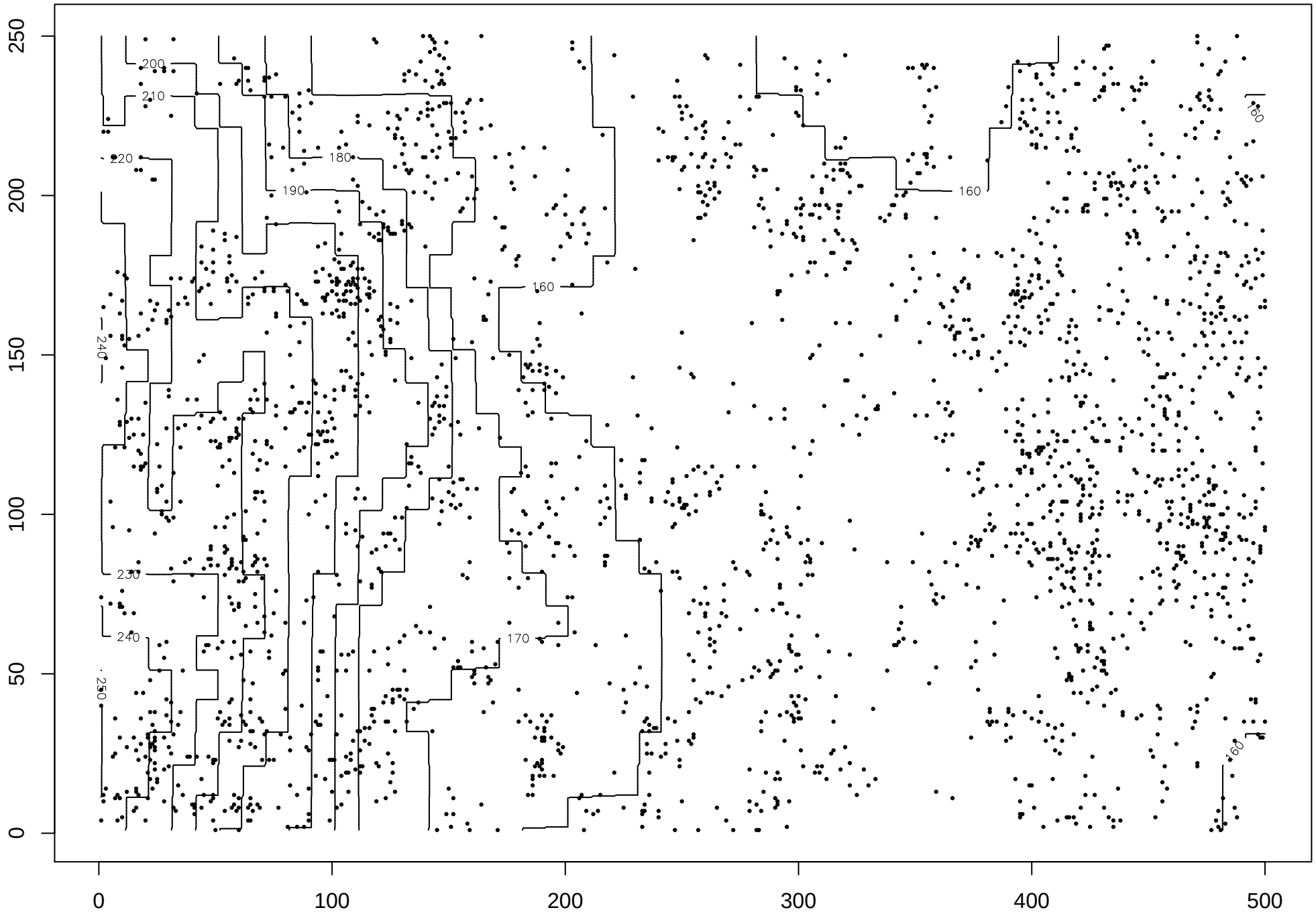
Habitat association in the Voter Model

choose tree at random to die

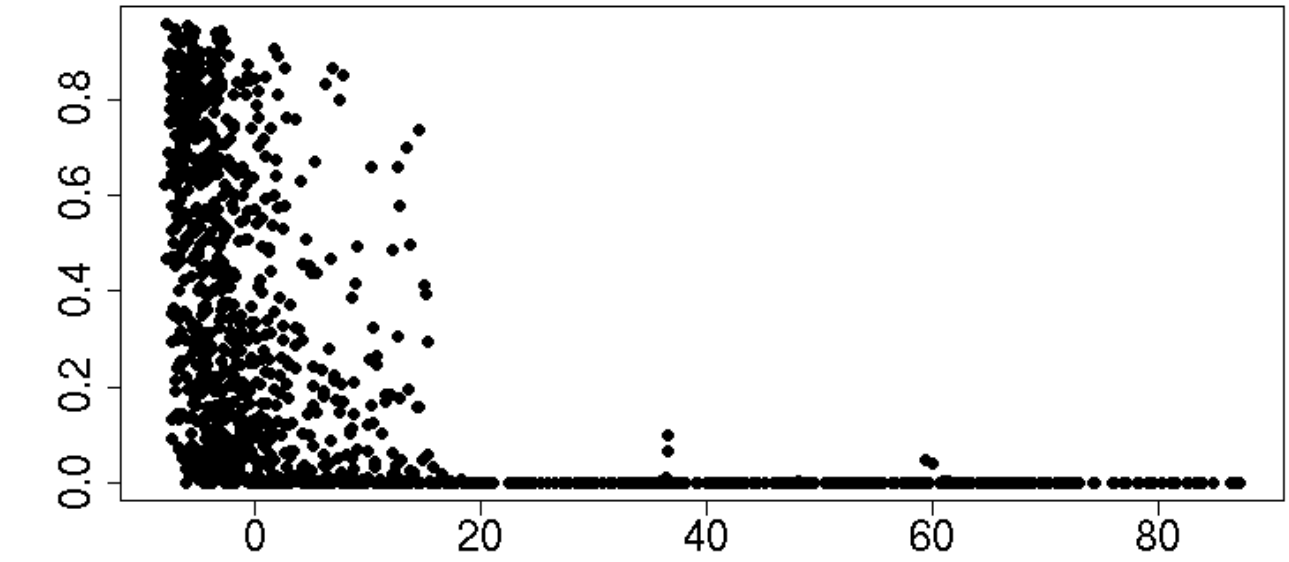
accept choice with prob=*m*, where *m=f(elev)*

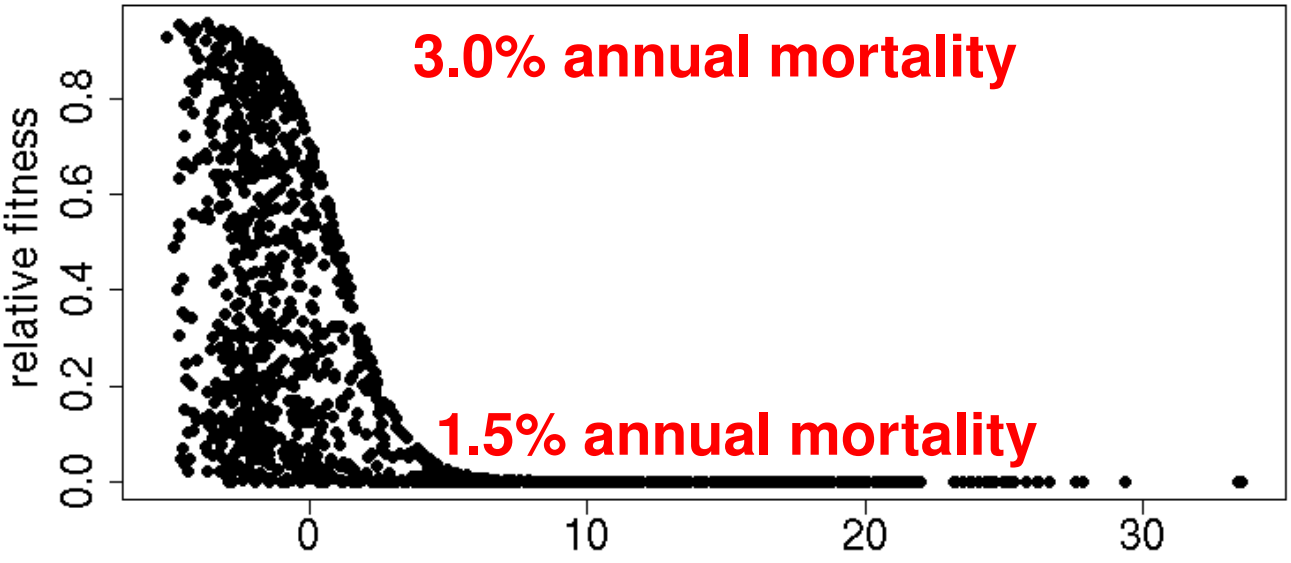
if rejected, choose again

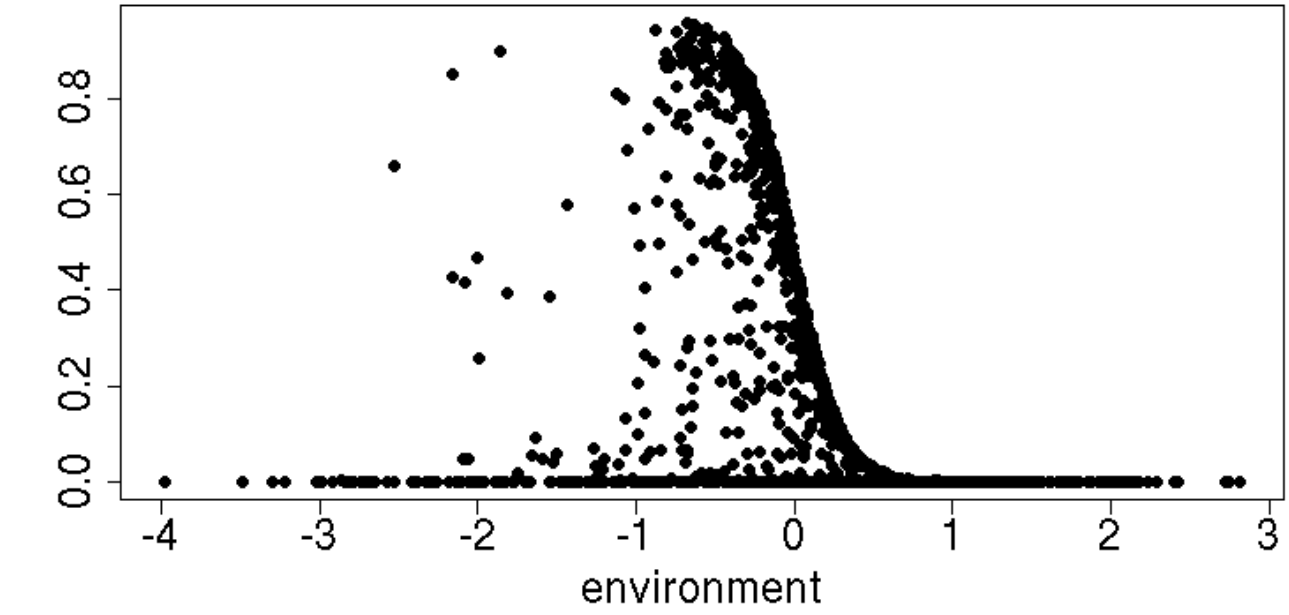



0
50
100
150
200
250
0
100
200
300
400
500
200
210
220
180
190
160
160
240
230
240
250
170
160
160

Simulated fitness (survival) response to 3 environments

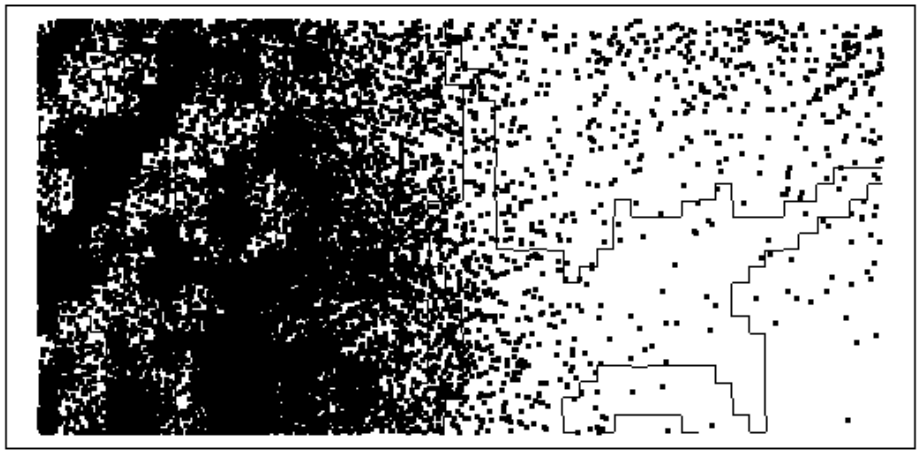




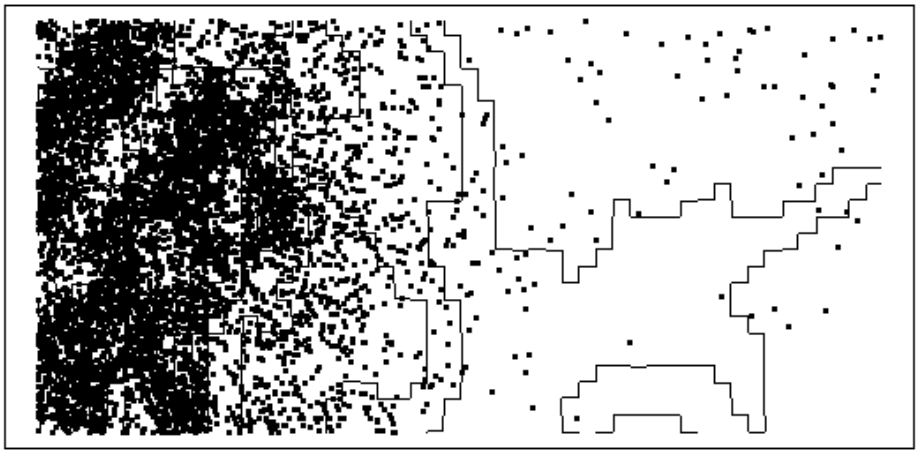


Simulated species distributions with niche differences

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

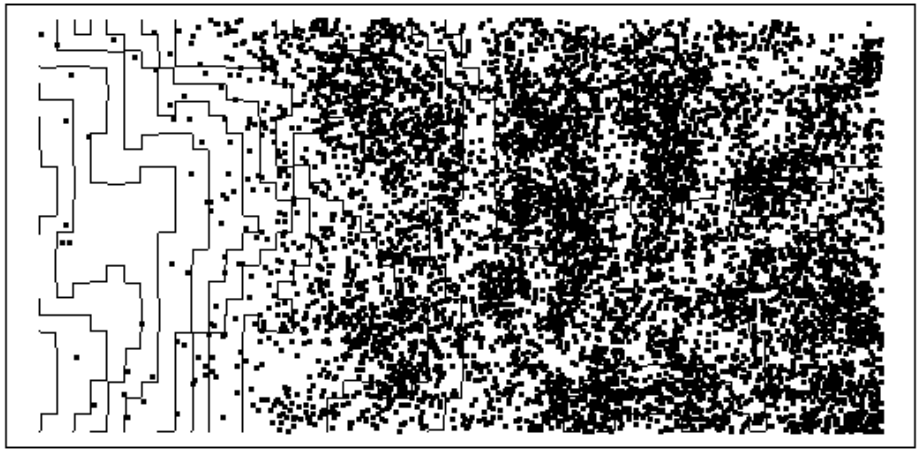


x1



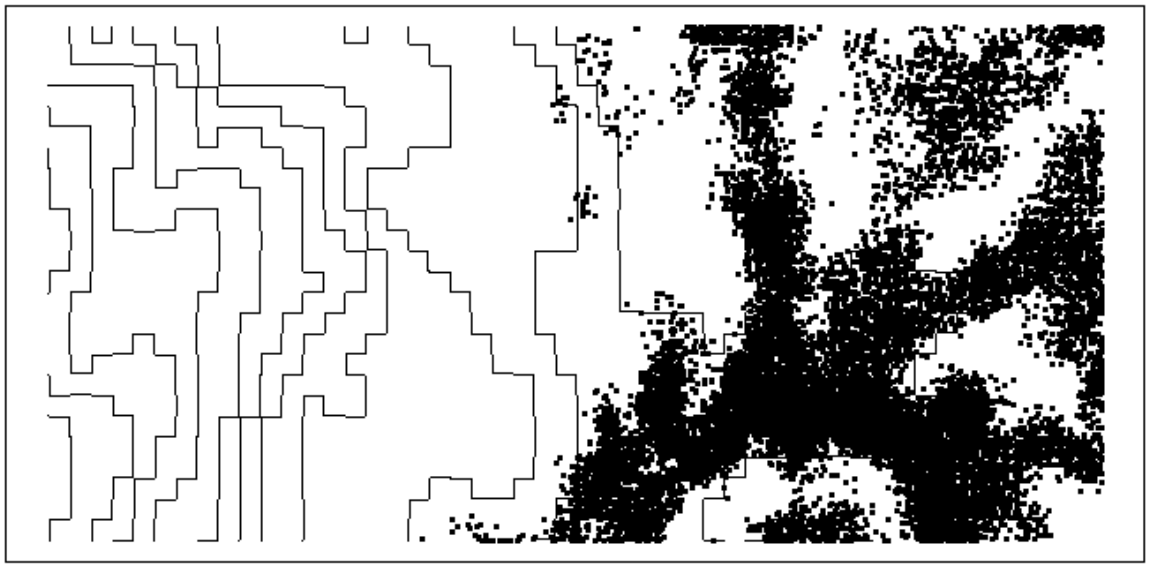
x2

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

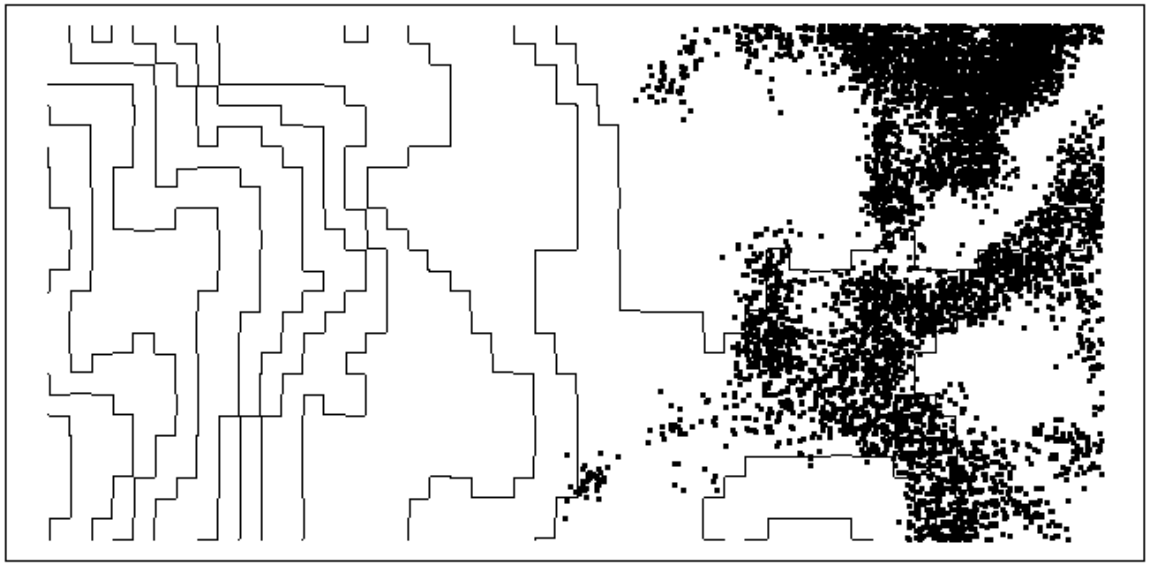


x3

x4

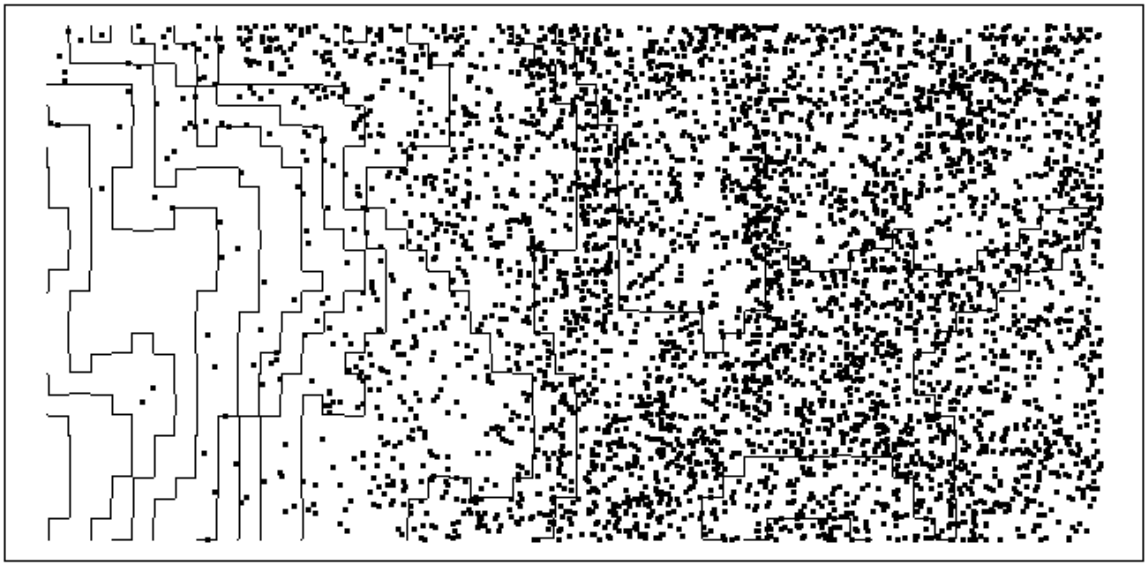


20-m dispersal, strong mortality effect of environment

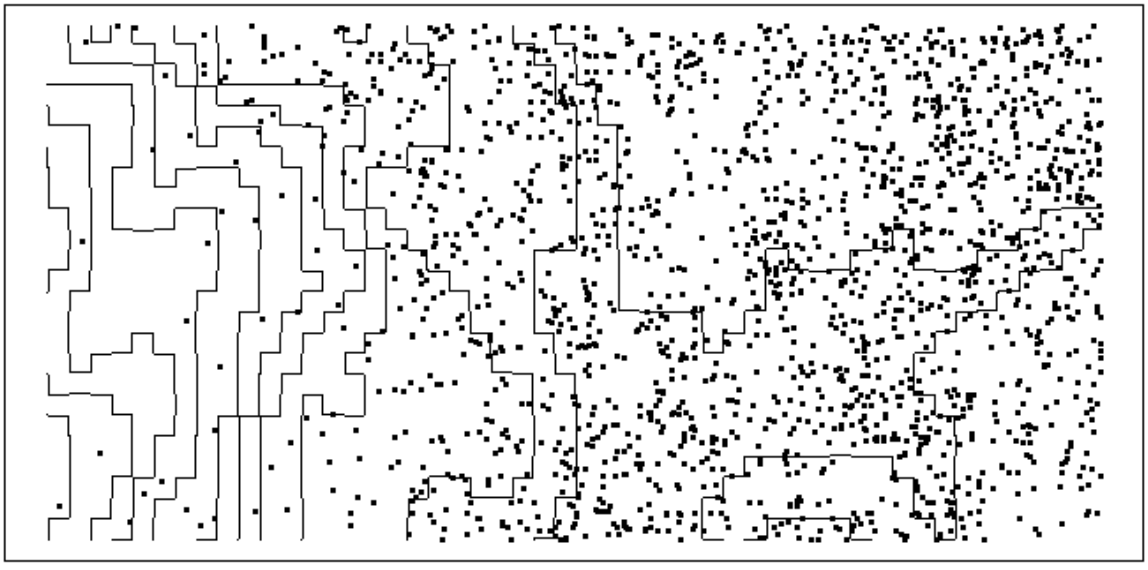


3 coexisting species with identical environmental response

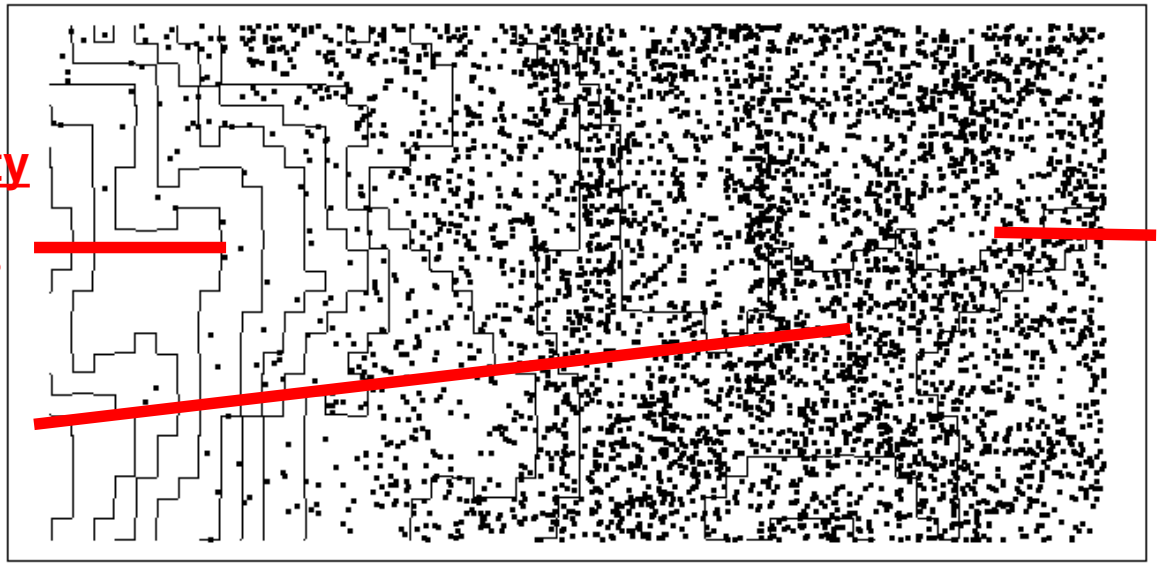
200-m dispersal, strong mortality effect of environment



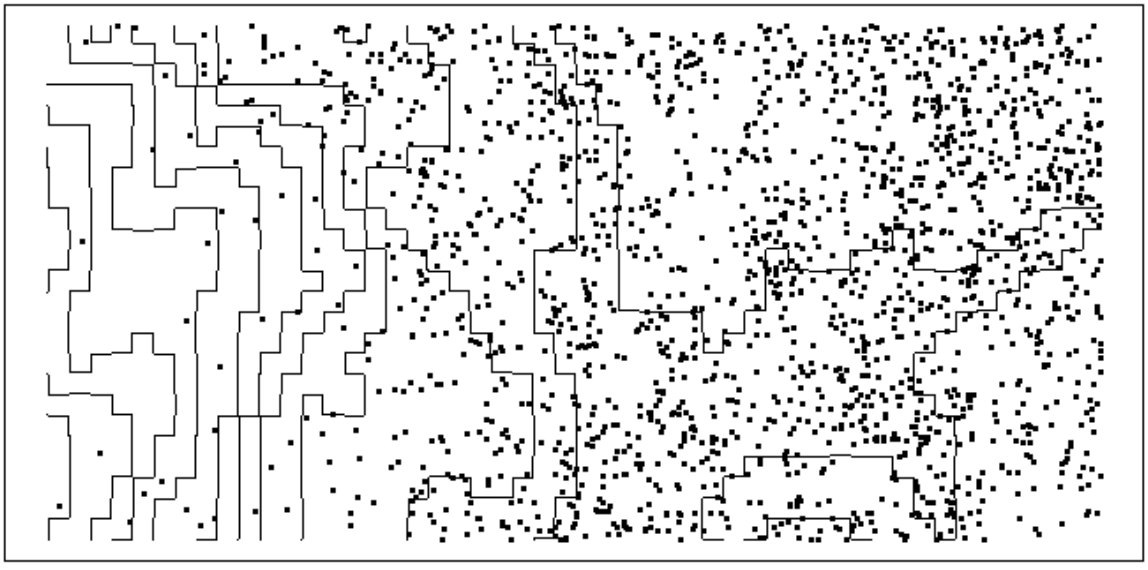
3 coexisting species with identical environmental response



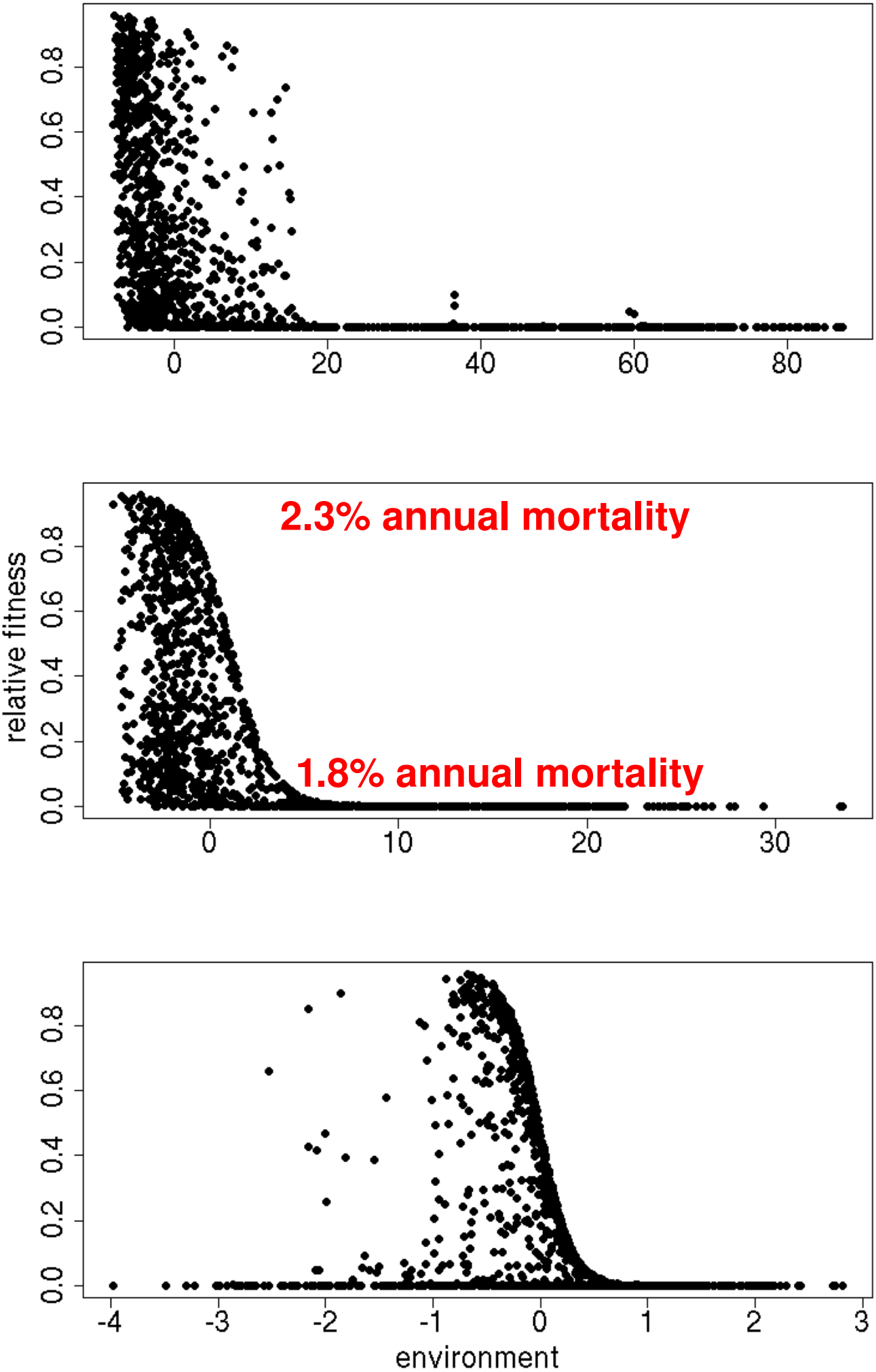
200-m dispersal, strong mortality effect of environment

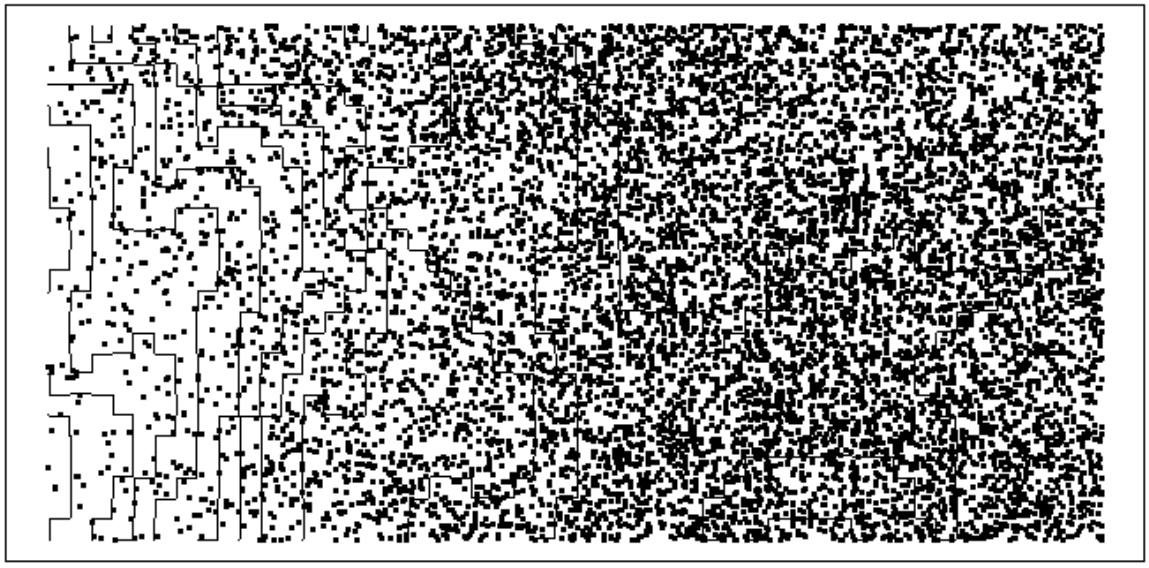


3 coexisting species with identical environmental response



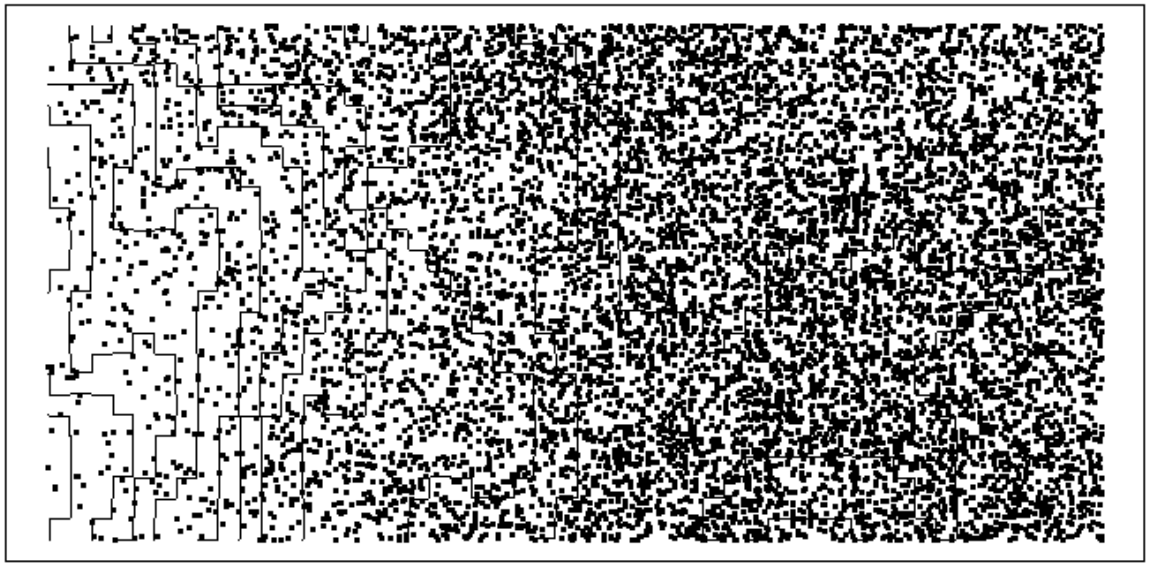
Simulated fitness (survival) response to 3 environments



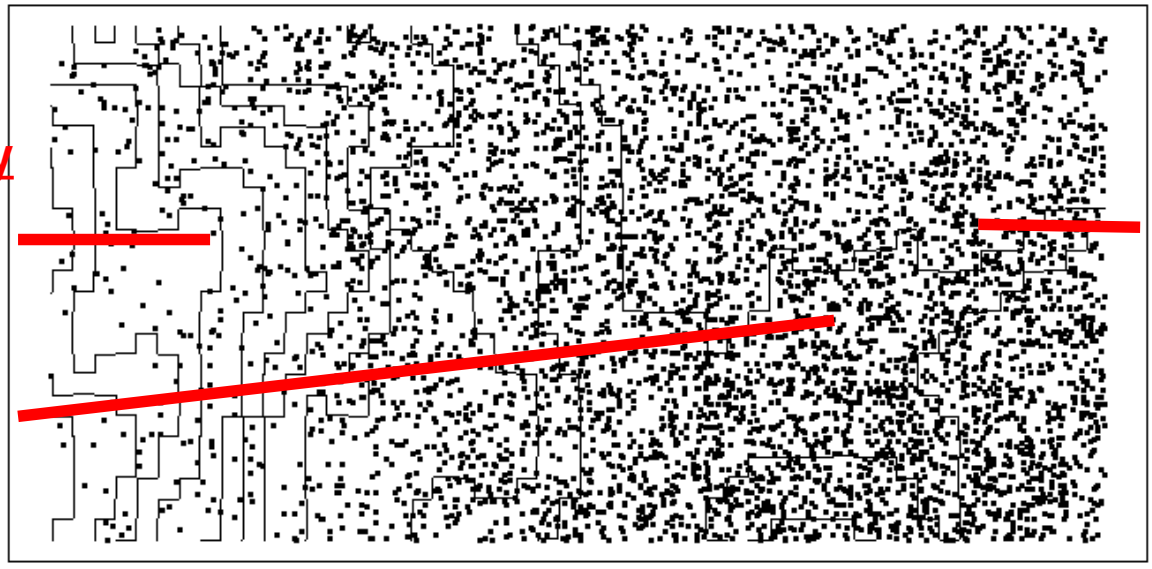


200-m dispersal, weak mortality effect of environment

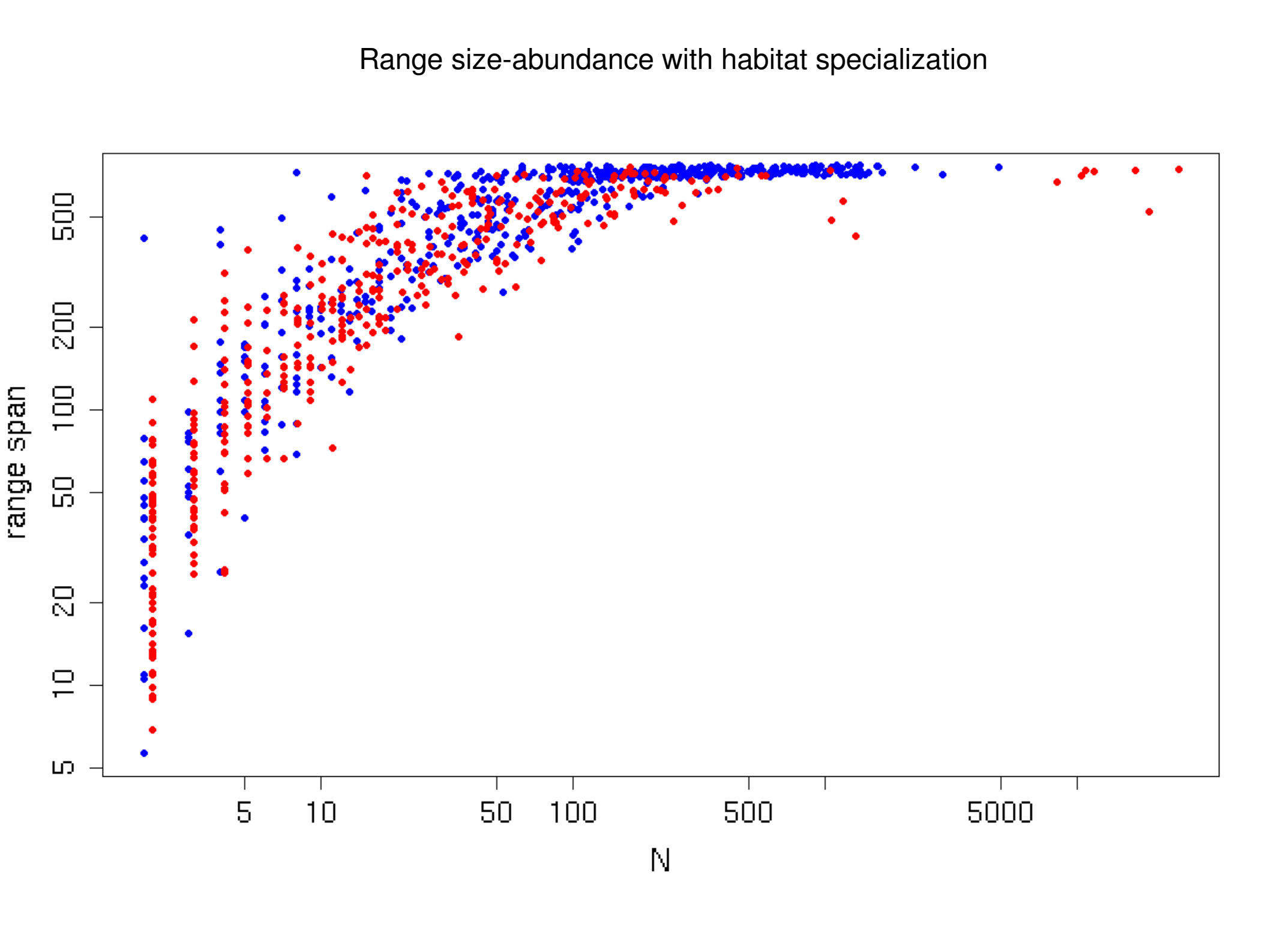
3 coexisting species with identical environmental response



200-m dispersal, weak mortality effect of environment



3 coexisting species with identical environmental response


Range size-abundance with habitat specialization
range span
5
10
20
50
100
200
500
5
10
50
100
500
5000
N

Summary

1) Neutral models produce a simple relationship between dispersal and range size, and it may hold widely under many non-neutral assumptions: $R = 2D\sqrt{(N)}$

2) Forest tree species are mostly well-dispersed at the scale of 50 hectares (~200 m), reflected by wide spatial ranges of rare species and direct adult-recruit distances

3) Spatial distribution often clearly reflects demographic differences, but...

-- With poor dispersal, species routinely fail to occupy their habitat

-- With good dispersal can easily spread to adjacent habitat

-- Within 50 ha, dispersal is good enough for trees to fill their niches, but mortality differences are weak enough for spillover

Thanks...

NCEAS

Nick Brand & Thomas Hetmank

Rick Reeves

Jim Regetz

Stephanie Hampton, Jim Reichmann, Bill Murdoch

Joan, Marlene, Gail, Leslie, Erin, Eduardo, Patty

Cameroon

David Kenfack, Duncan Thomas, George Chuyong & many field workers

BCI

Steve Hubbell, Robin Foster, Roland Pérez, Suzanne Lao & many field workers

Princeton

Sam Elworthy, Robert Kirk, Henry Horn, Si Levin