Stability and turnover of tropical forest communities

Change in species abundances

Climate and forest change

Nordforsk PhD Summer School
July-August 2008

Richard Condit and …

… the CTFS Working Group

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A tendency for species to increase when rare, then, would constitute evidence for niche theory and against neutral theory.

GREGORY M. MIKKELSON, *Biology and Philosophy* (2004)

A review of Jonathan M. Chase, J. M. and Mathew A. Leibold, *Ecological Niches: Linking Classical and Contemporary Approaches*, University of Chicago Press, Chicago, IL, 2003, 212 pp.

The data:

10 large-scale forest plots

- Sinharaja wet forest (Sri Lanka)
- Lambir wet dipterocarp forest (Borneo)
- Pasoh wet dipterocarp forest (Malaya)
- Mudumalai dry deciduous forest (SW India)
- Huai Khae Khaeng dryish evergreen forest (Thailand)
- Ituri monodominant caesalp forest (Congo)
- La Planada wet montane (Colombia)
- Yasuni wet Amazonian forest (Ecuador)
- Barro Colorado seasonal moist forest (Panama)

Counts of all individuals of all species (1 cm dbh)

- 1,808,024 individuals and 4990 species-records

Two or more censuses at 3-8 year intervals

Forest Dynamics Plots

	species ≥ 1 cm dbh	annual rainfall (mm)	dry season (months)
Panama, BCI	274	2500	4
Ecuador, Yasuni	1104	3000	0
Colombia, La Planada	280	3500	0
Puerto Rico, Luquillo *	120	3500	0
India, Mudumalai	66	1200	6
Thailand, HKK	206	1450	6
Malaysia, Pasoh	785	1800	0
Malaysia, Lambir	1111	2700	0
Sri Lanka, Sinharaja	205	4400	0
Cameroon, Korup	482	5000	2
D.R. Congo, Ituri			
--monodominant *	403	1700	2
--mixed *	409	1700	2

Species in 25 ha unless marked with *

Barro Colorado Island

Gatún Lake, Panama

Barro Colorado 50 ha plot (Panama)

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R. Foster
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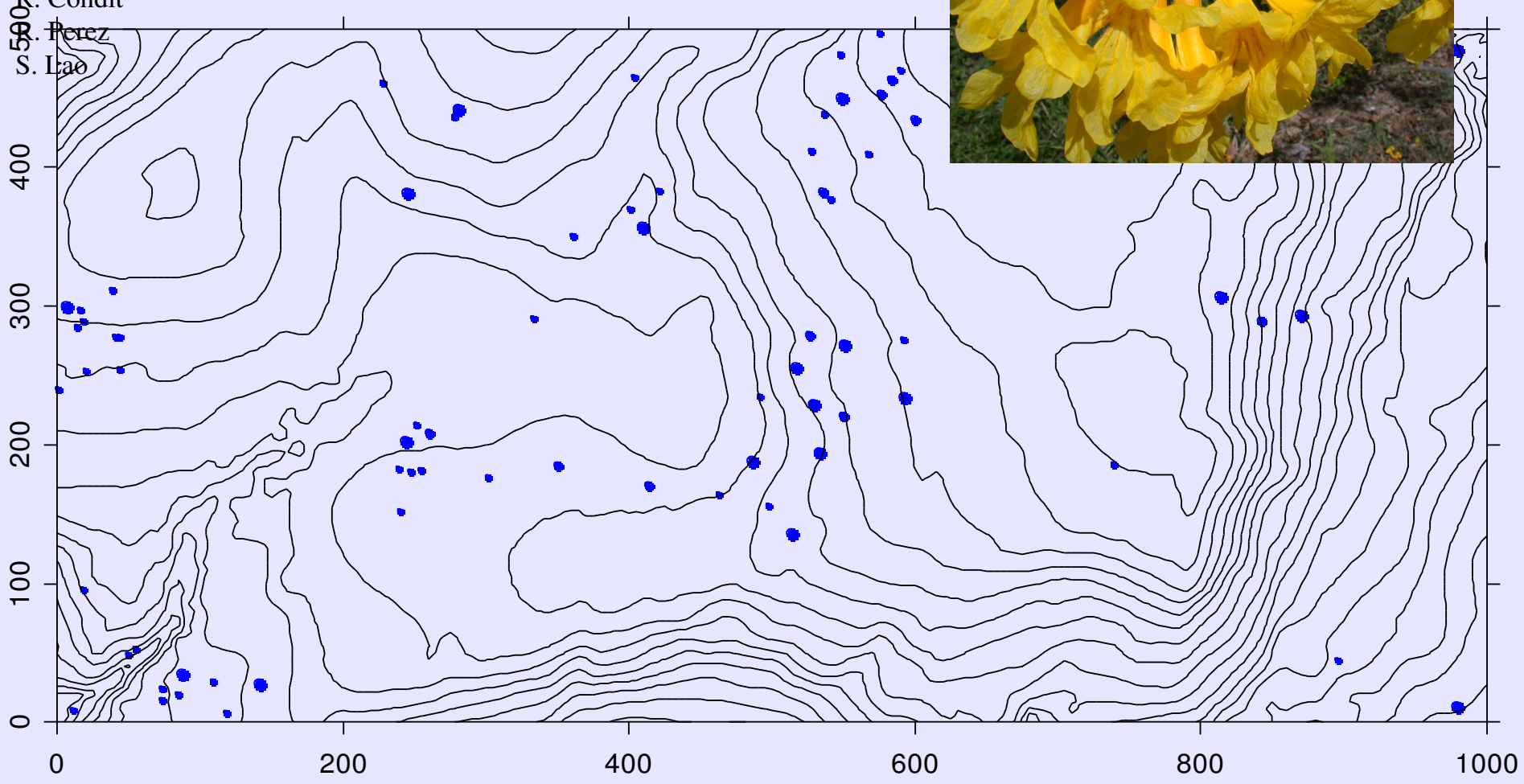
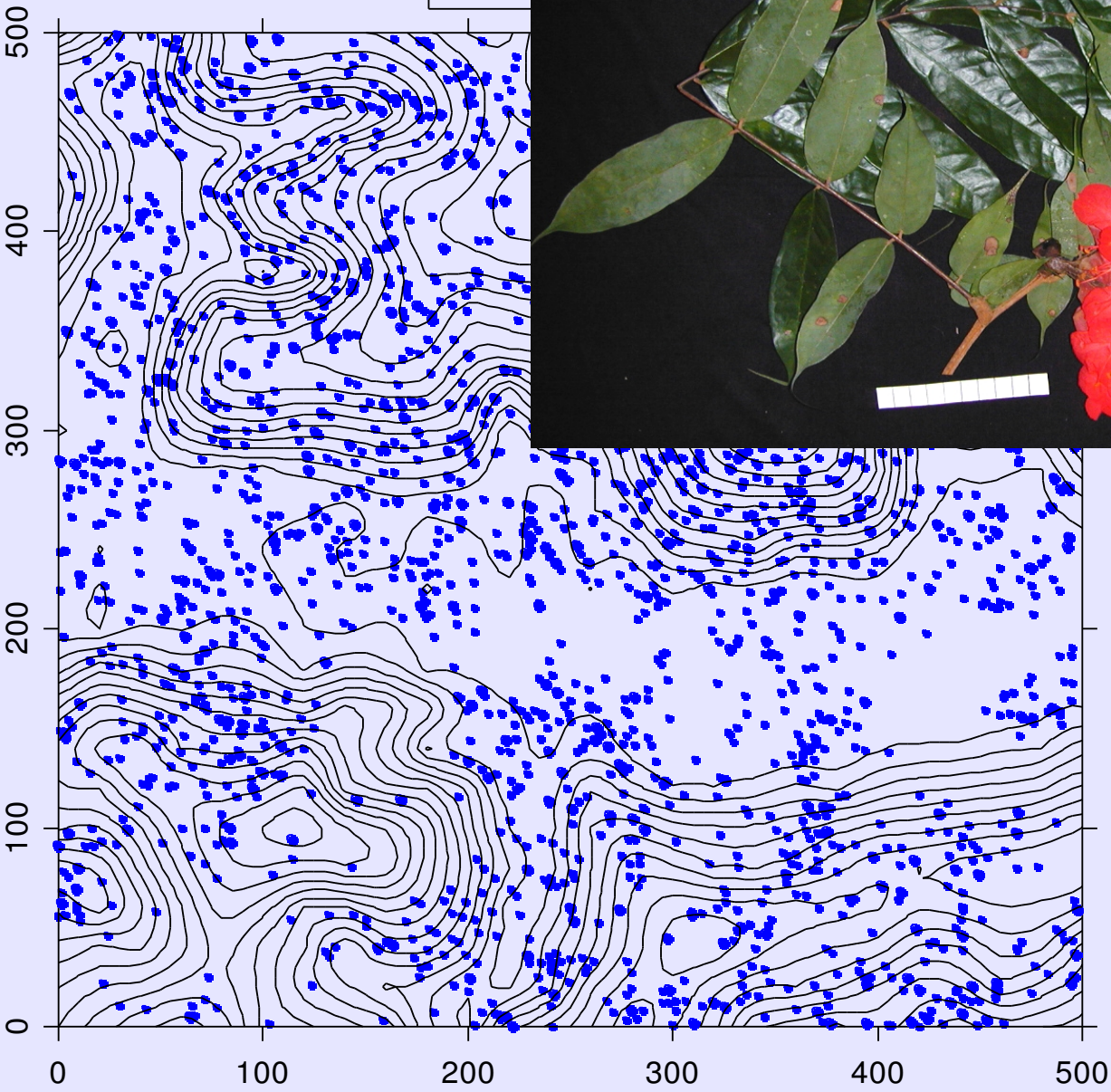


Yasuni 25 ha plot (Ecuador)



R. Foster
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C. Hernandez
S. Lao
E. Losos
H. Balslev

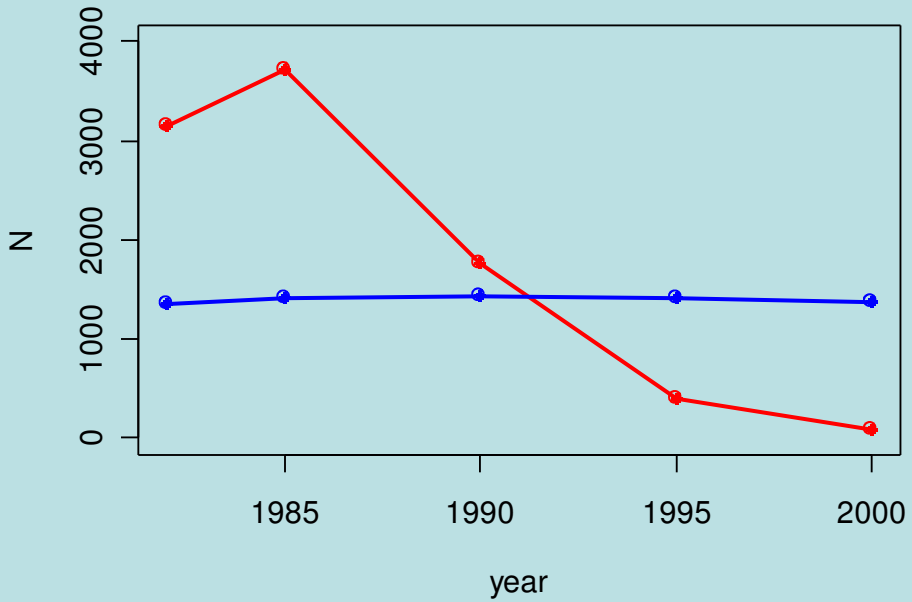
Are tree populations stable through time?

--Determine how much a population would change under random drift (random mortality and recruitment)

--Estimate a community-wide distribution of rates of population change as a measure of forest stability (correcting for random change)

--Compare stability of different forests

--Compare stability of rare and common species



Prioria copaifera, BCI

$\lambda = 1.001$

Piper cordulatum, BCI

$\lambda = 0.819$

Variance in population size through time

--Stochastic variance: random drift (random mortality and recruitment)

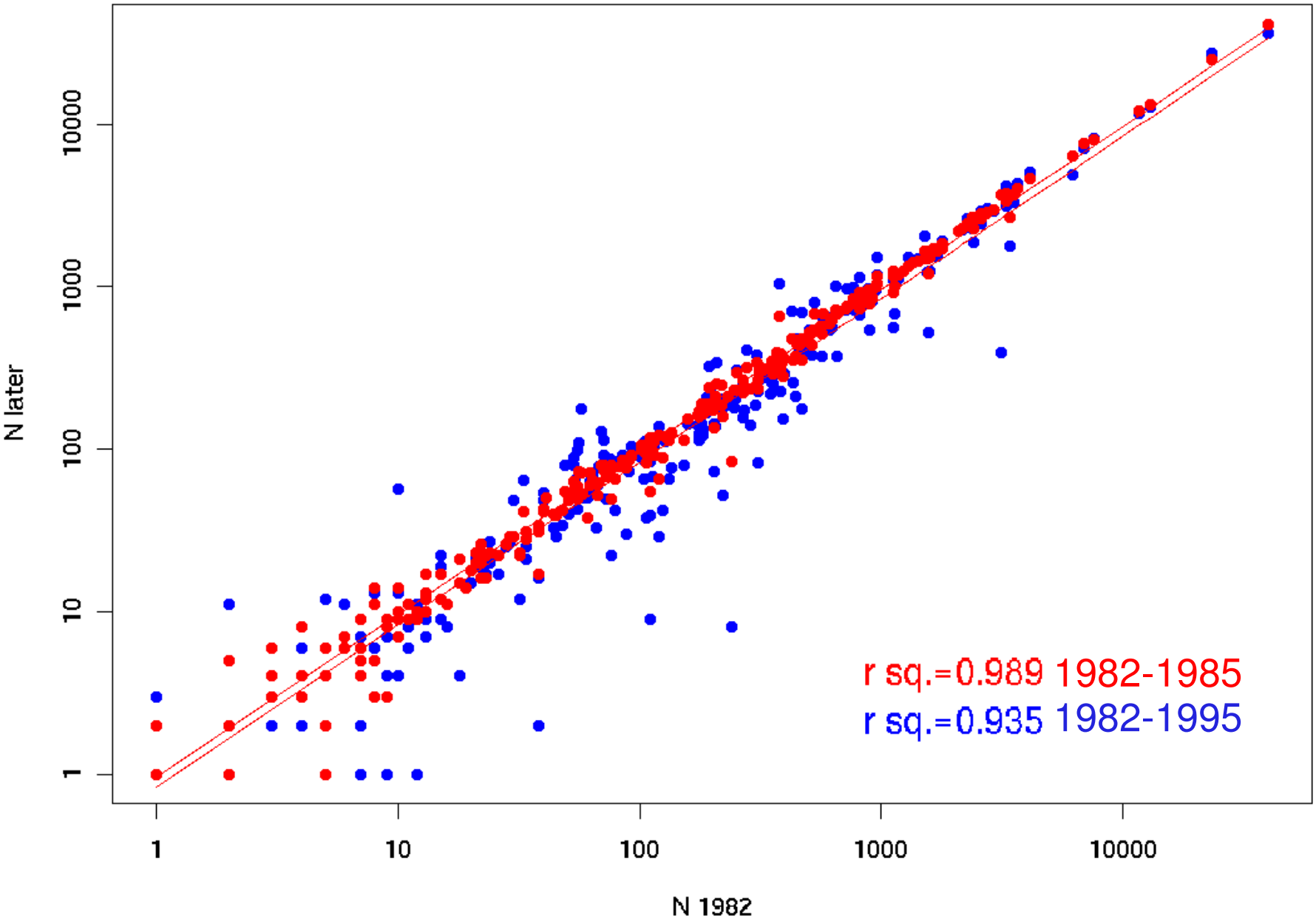
--Environmental variance: external forces affecting population

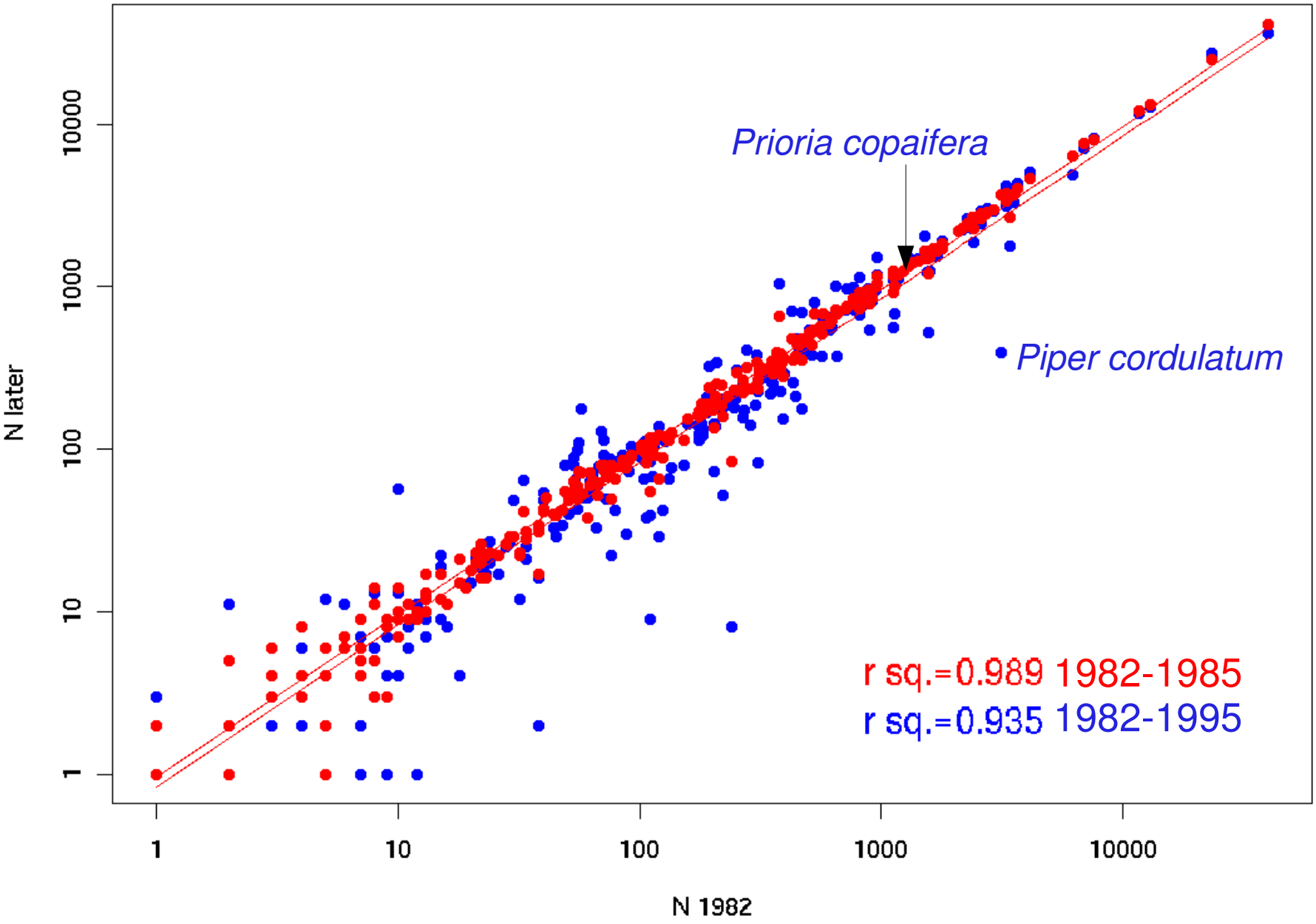
Lande, R., Engen, S., and Saether, B.-E. 2000. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford.

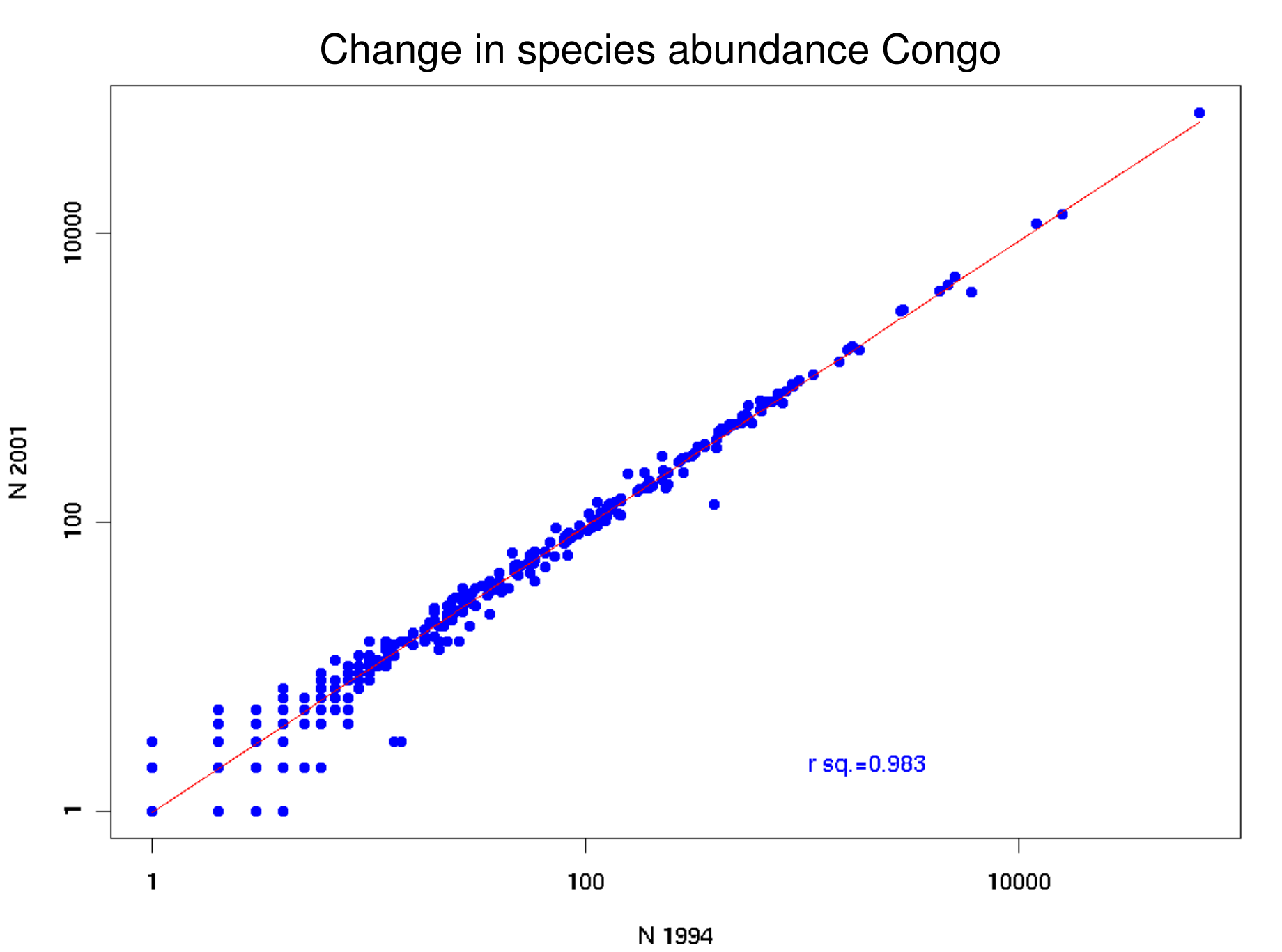
Allen, Andrew P.; Savage, Van M.2007. Setting the absolute tempo of biodiversity dynamics. Ecology Letters 10: 637-646.

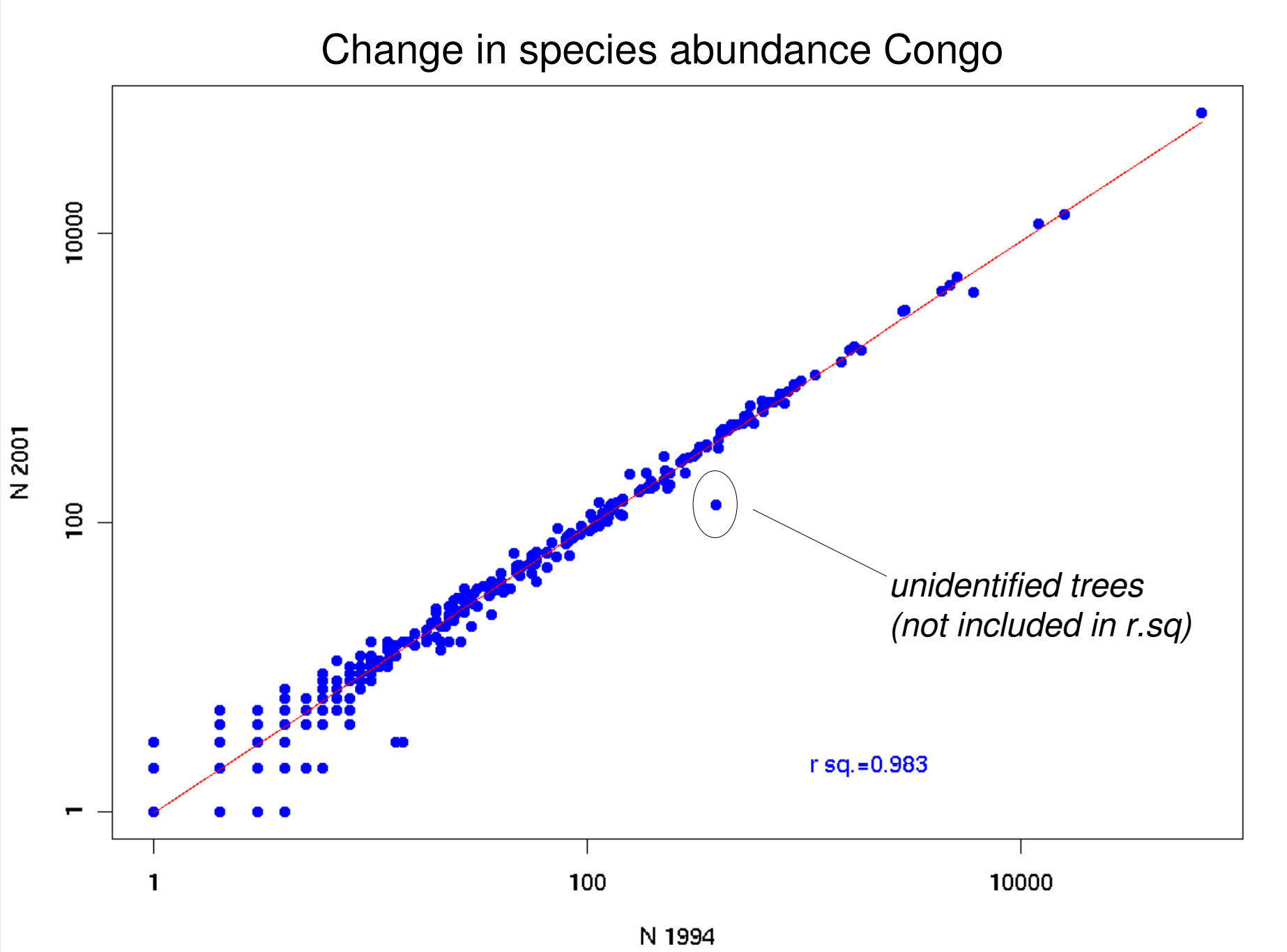
abundance data from Ituri 20 ha plot (Congo)

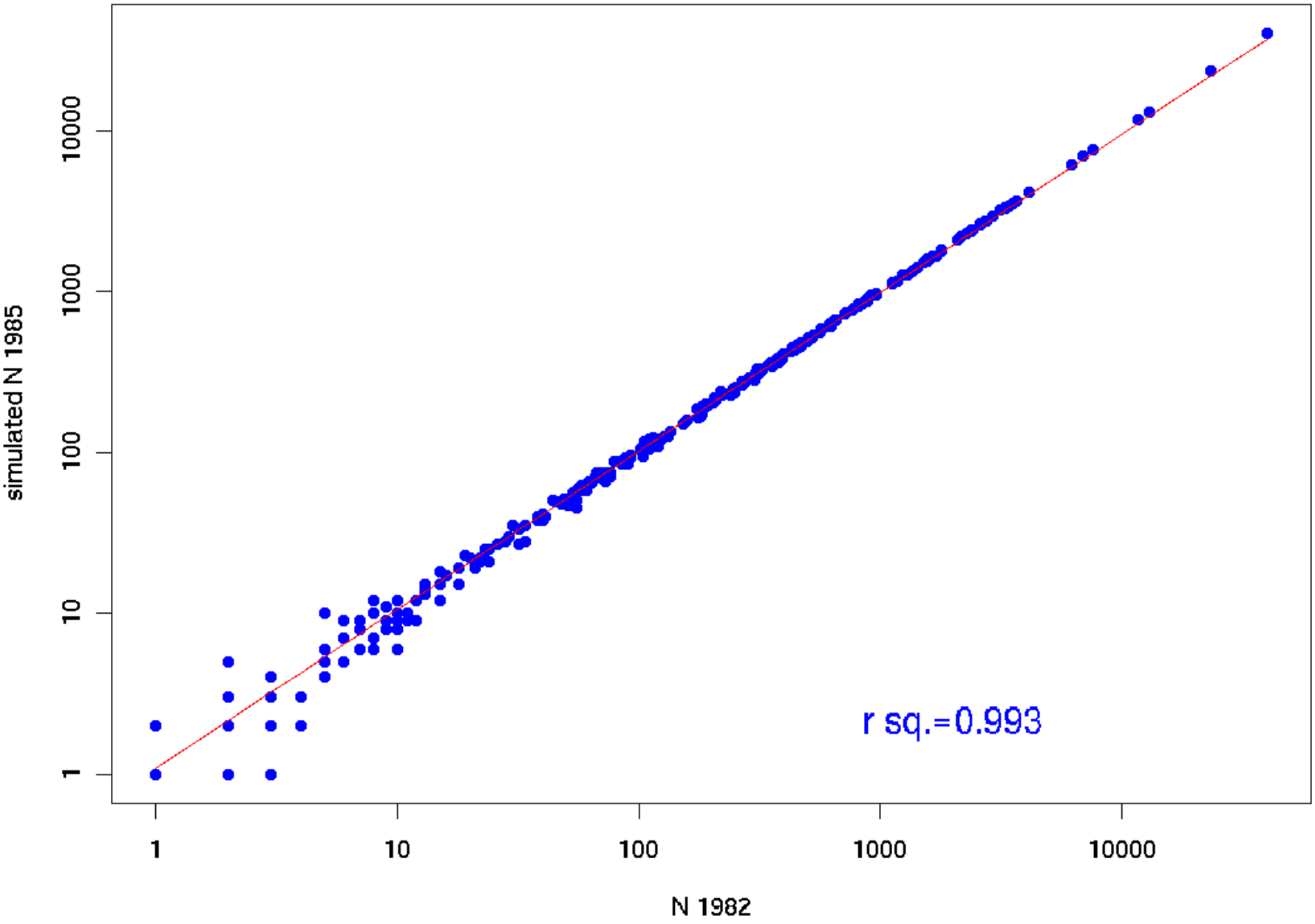
species	N1	N2	interval (yr)	lambda
Afrostyrax lepidophyllus	3	3	6.35	1.000
Afzelia bipindensis	8	8	6.05	1.000
Aidia micrantha	638	694	6.25	1.014
Albizia ealaensis	0	1	6.37	Inf
Albizia gumifera	125	109	6.36	0.979
Albizia leptophylla	2	1	5.85	0.888
Albizia zygia	3	3	6.16	1.000
Alchornea floribunda	5999	3896	6.03	0.931
Allanblackia floribunda	5	6	6.61	1.028
Allophylus africanus	124	101	6.17	0.967
Allophylus longicuneatus	20	24	6.32	1.029
Allophylus schweinfurthii	4	6	6.54	1.064
Alstonia boonei	65	49	6.08	0.955
Amphimas ferrugineus	4	4	6.35	1.000


Change in species abundance at BCI
N later
N 1982
1
10
100
1000
10000
r sq.=0.989 1982-1985
r sq.=0.935 1982-1995

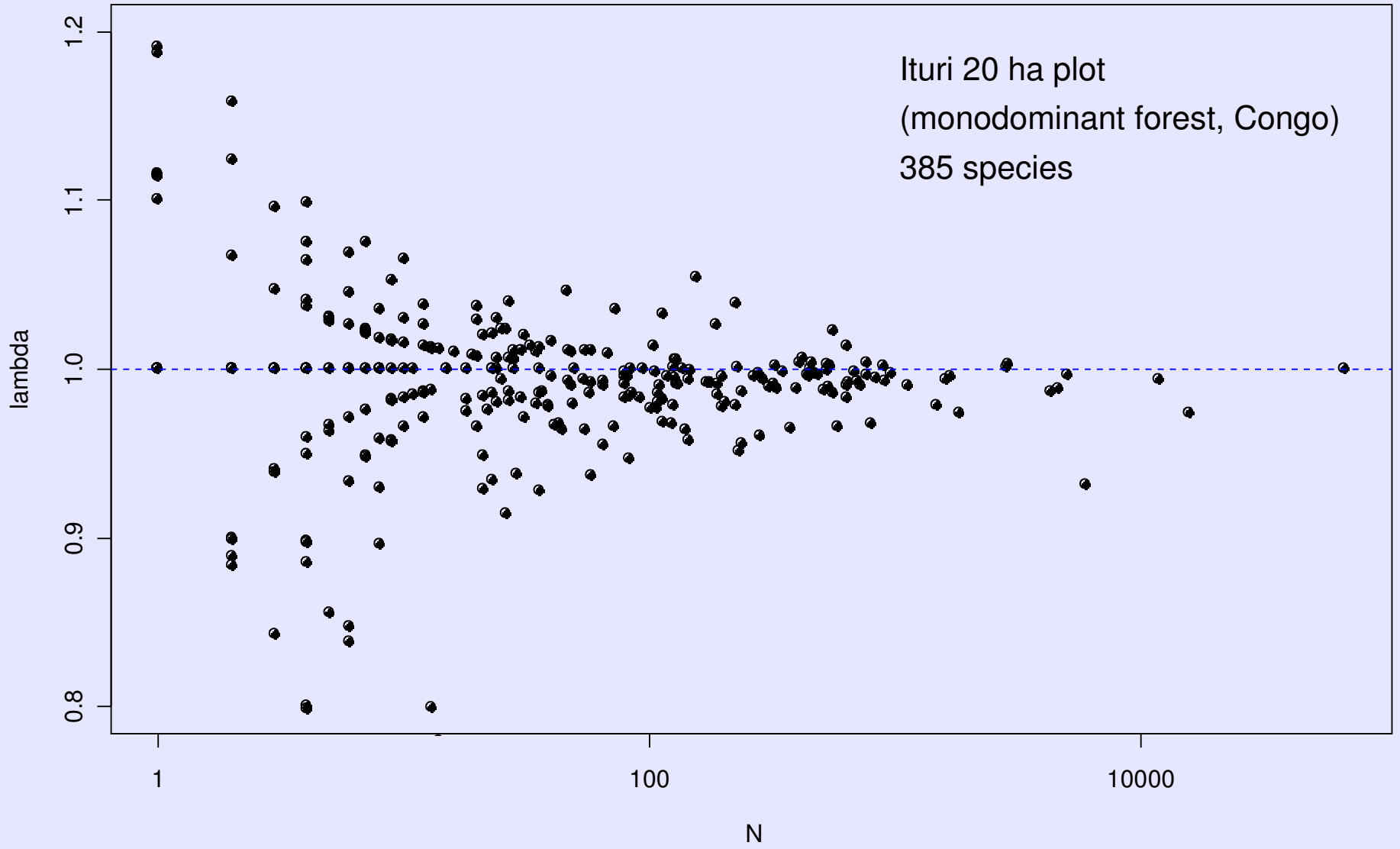

Change in species abundance at BCI
Prioria copaifera
Piper cordulatum
r sq.=0.989 1982-1985
r sq.=0.935 1982-1995
N later
N 1982
1
10
100
1000
10000


Change in species abundance Congo
N 2001
10000
100
1
1
100
10000
N 1994
r sq.=0.983

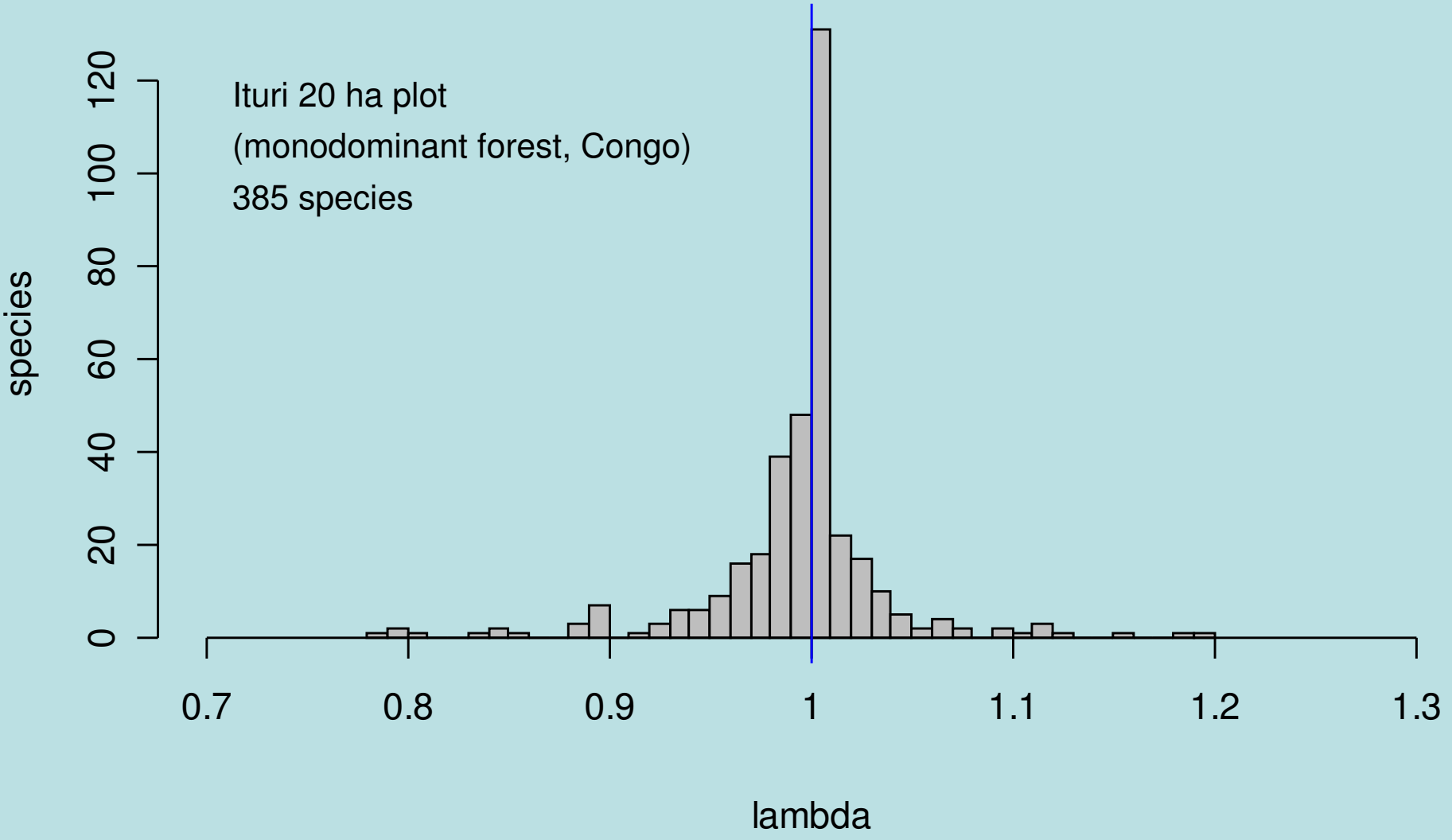

Change in species abundance Congo
N 2001
10000
100
1
1
100
10000
N 1994
unidentified trees
(not included in r.sq)
r sq.=0.983


simulated N 1985
1
10
100
1000
10000
N 1982
1
10
100
1000
10000
r sq.=0.993

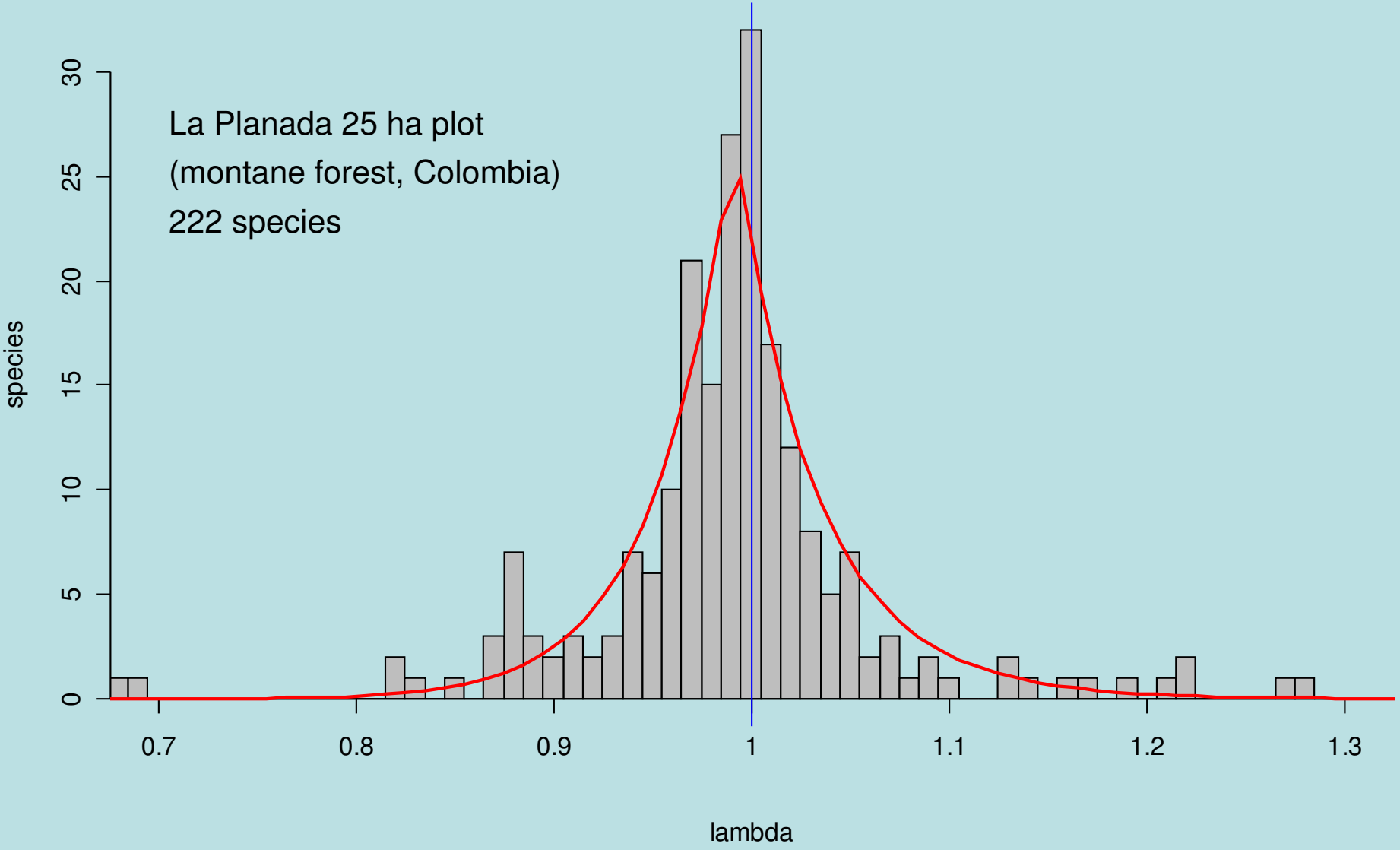
λ varies more in rare species: sampling error

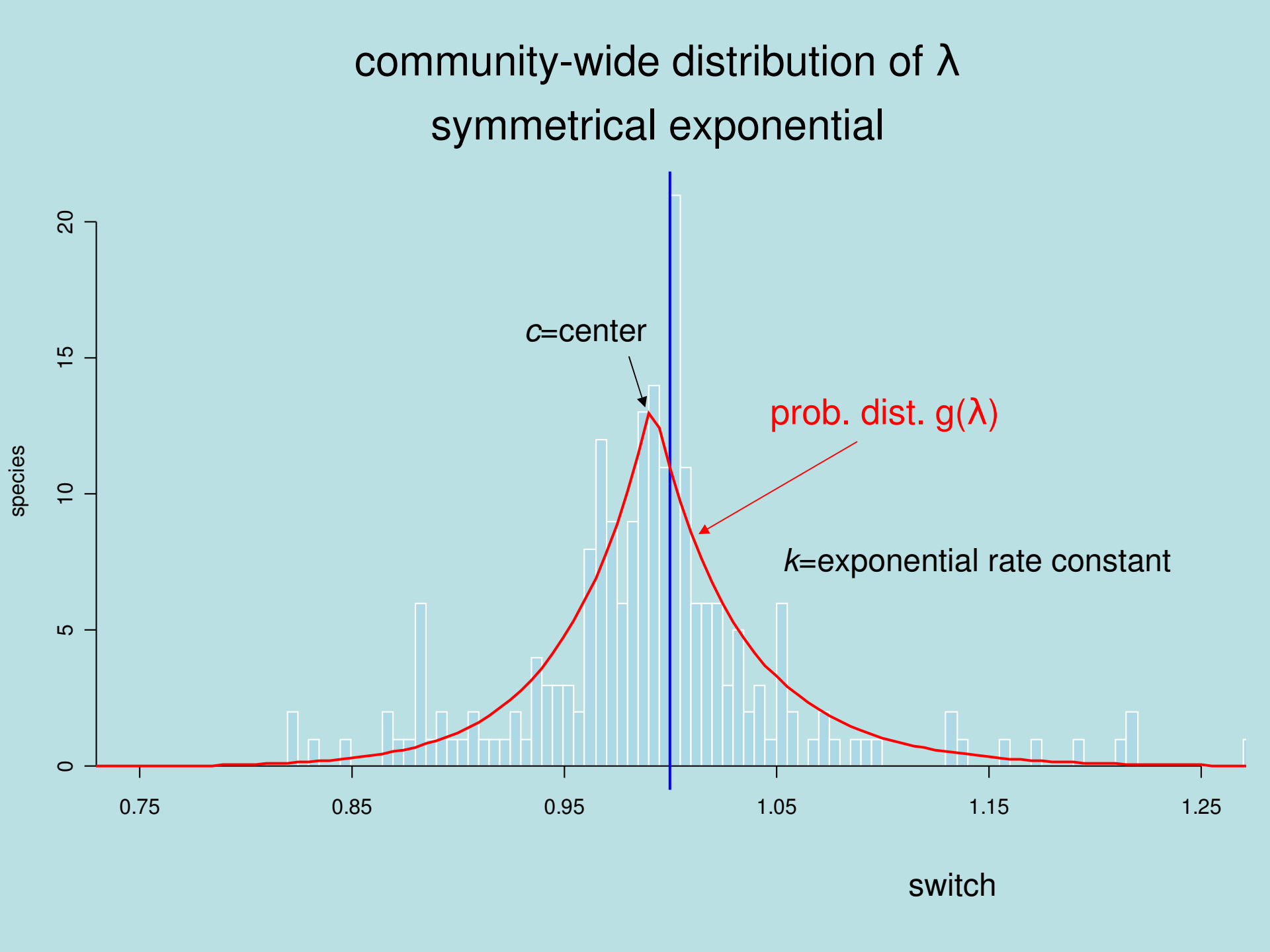


The variance of the distribution of λ reflects the stability of the community



Mission: fit the ‘hyperdistribution’ of lambda accounting for abundance and stochasticity




community-wide distribution of λ
symmetrical exponential
c=center
prob. dist. g(λ)
k=exponential rate constant
species
0
5
10
15
20
0.75
0.85
0.95
1.05
1.15
1.25
switch

Calculating the likelihood of observations for all species in a forest

1) Probability of observing growth rate $r=\log(\lambda)$

$$prob(r) = g(r) \sim symExponential(c, k)$$

2) Probability of observing population change, given survival θ and population growth rate λ (time adjusted)

$$prob(N_1 | \lambda, N_0, \theta) = f(N_1 | \lambda, N_0, \theta) \sim Normal(\lambda, \lambda - \theta^2)$$

3) Likelihood of observations N and θ for species i

$$L(i) = \int f(N_1 | r) g(r) dr$$

4) Probability of observations for all species in a forest

$$L_T = \sum_i \log\left(L(i)\right)$$

Easier to read in R …

L[i] = integrate(dnorm(mean= λ,sd= $\lambda + \theta$) * dsymexp(c,k))

1) Probability of observing growth rate $r=\log(\lambda)$

$$prob(r) = g(r) \sim symExponential(c, k)$$

2) Probability of observing population change, given survival θ and population growth rate λ (time adjusted)

$$prob(N_1 | \lambda, N_0, \theta) = f(N_1 | \lambda, N_0, \theta) \sim Normal(\lambda, \lambda - \theta^2)$$

3) Likelihood of observations N and θ for species i

$$L(i) = \int f(N_1 | r) g(r) dr$$

Calculating the likelihood of observations for all species in a forest

1) Probability of observing any growth rate $r=\log(\lambda)$

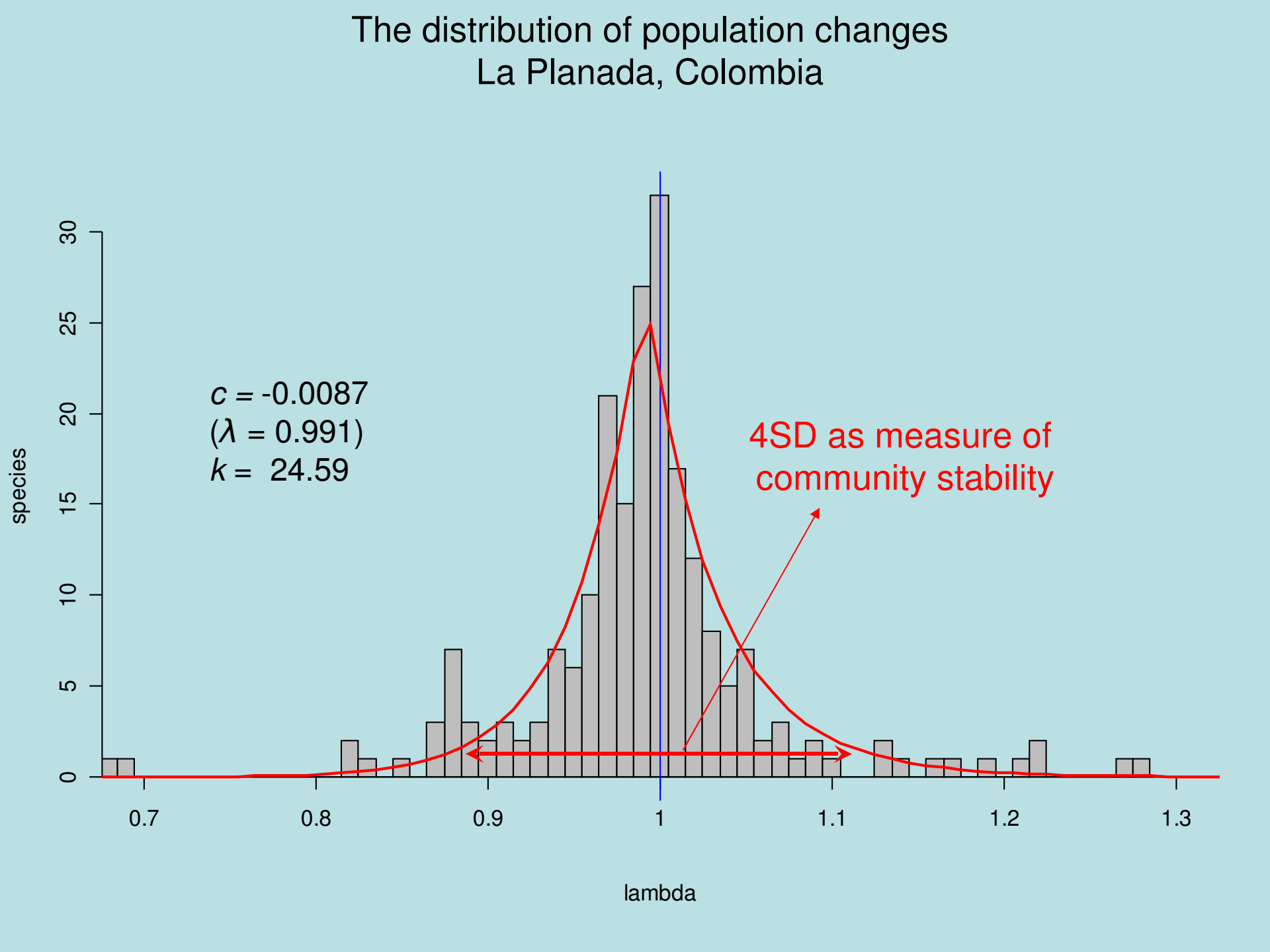
$$prob(r)=g(r)\sim symExponential(c,k)$$

.....

4) Probability of observations for all species in a forest

$$L_T=\sum_i \log\left(L(i)\right)$$

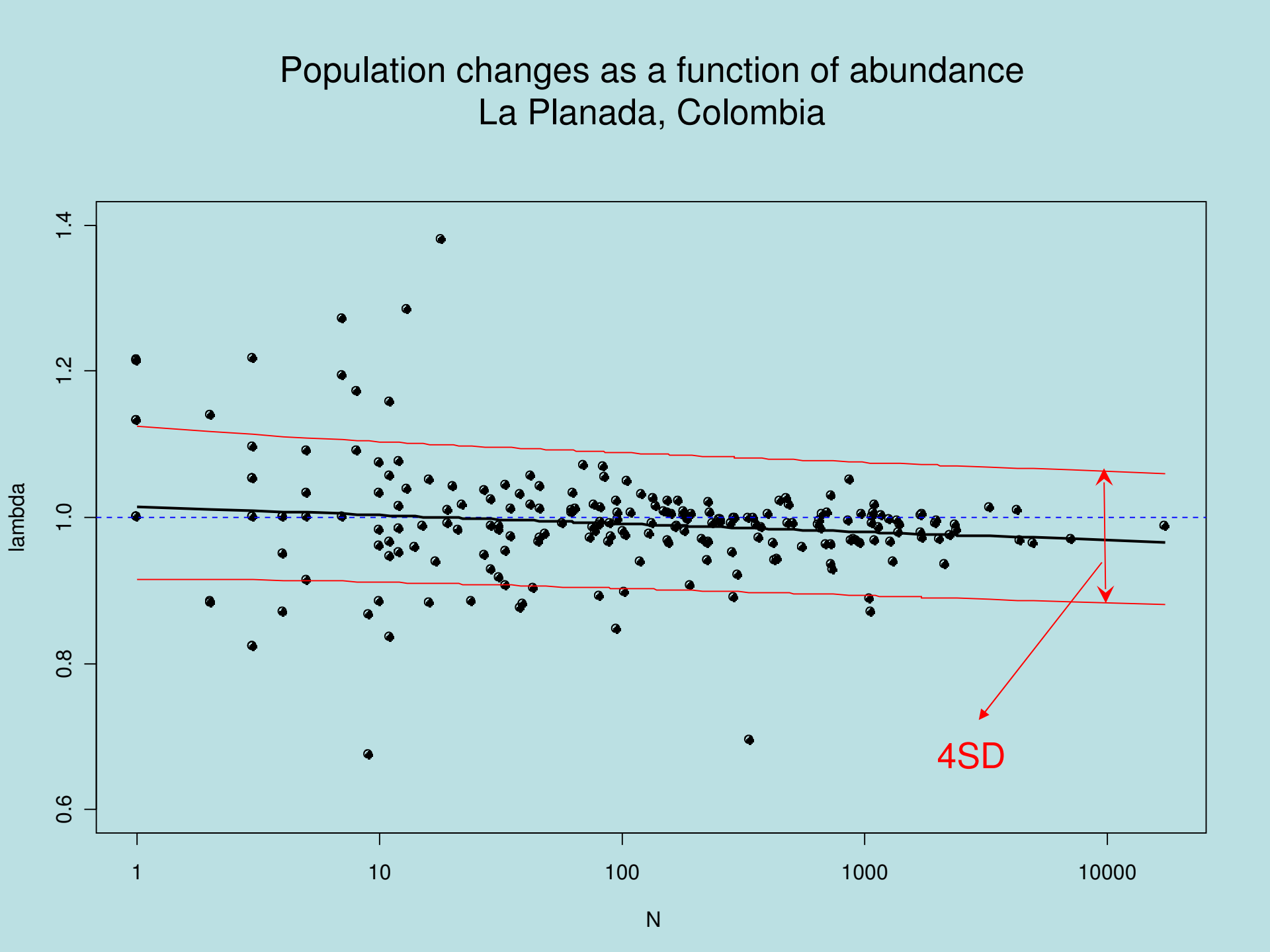
L_T is a function of c, k only – find c, k to maximize L


The distribution of population changes
La Planada, Colombia
c = -0.0087
(λ = 0.991)
k = 24.59
4SD as measure of
community stability
species
lambda
0
5
10
15
20
25
30
0.7
0.8
0.9
1
1.1
1.2
1.3

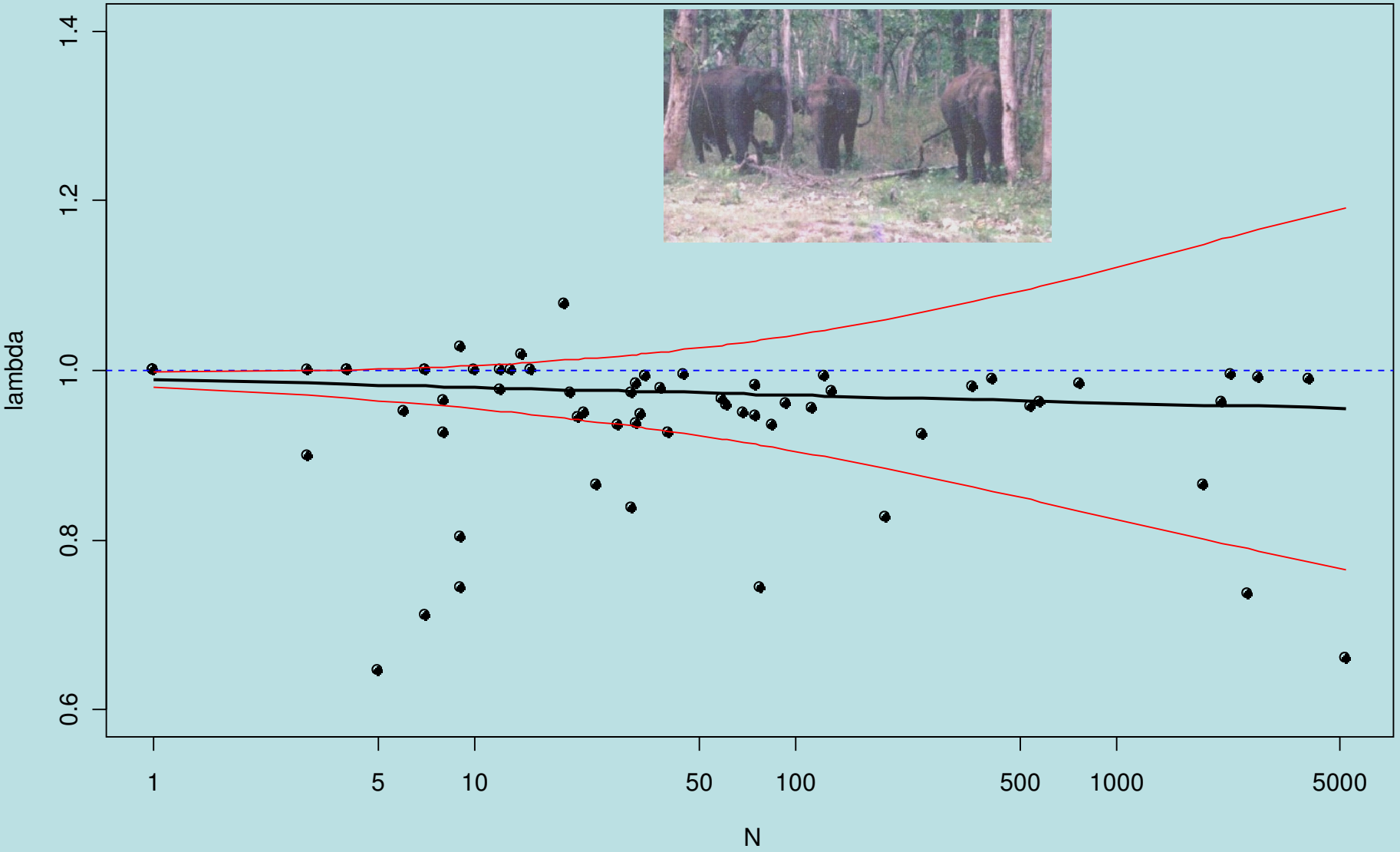
Testing difference in rate species
4-parameter model

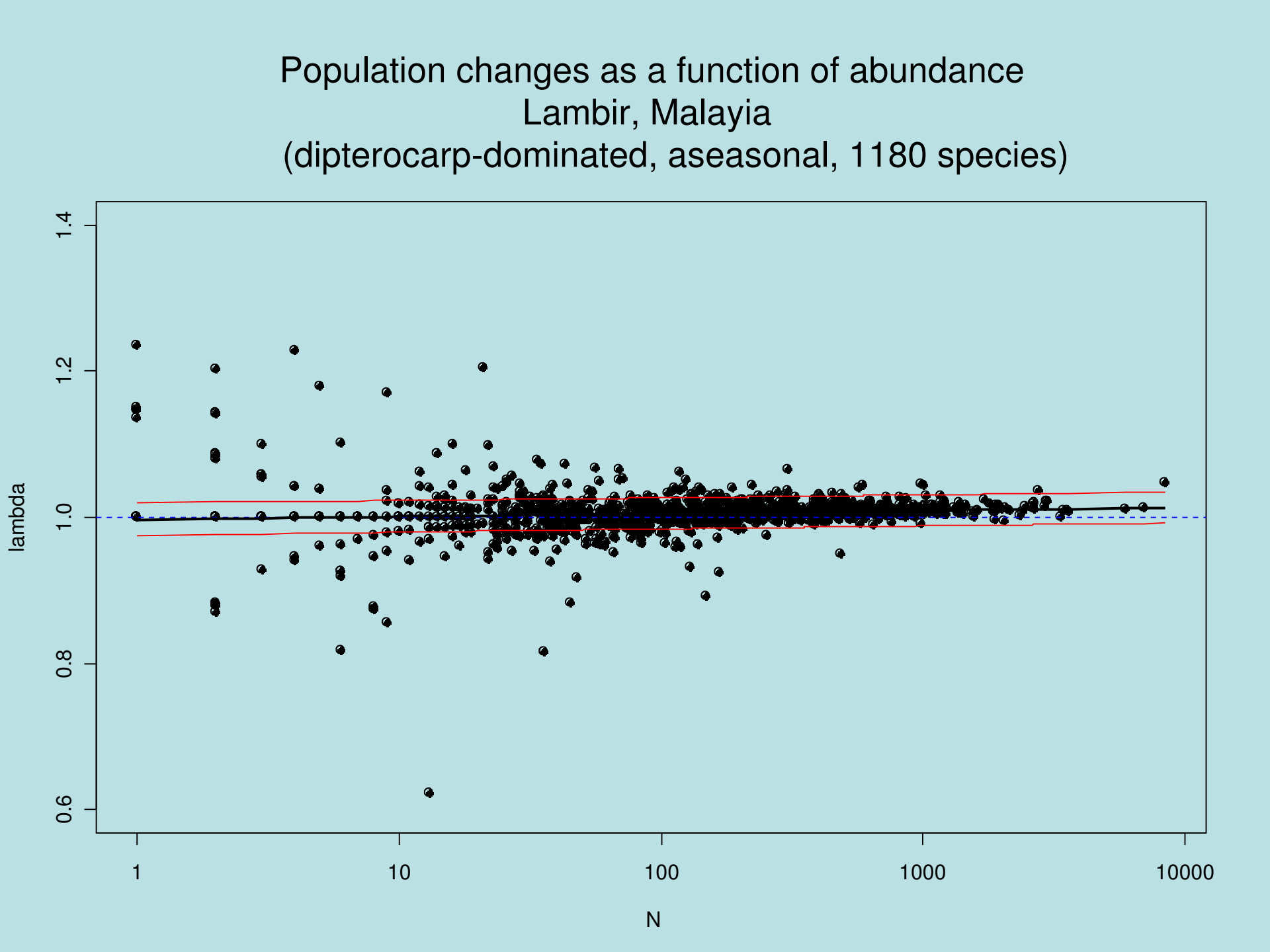
distribution of r=log(λ) allowing variation with abundance

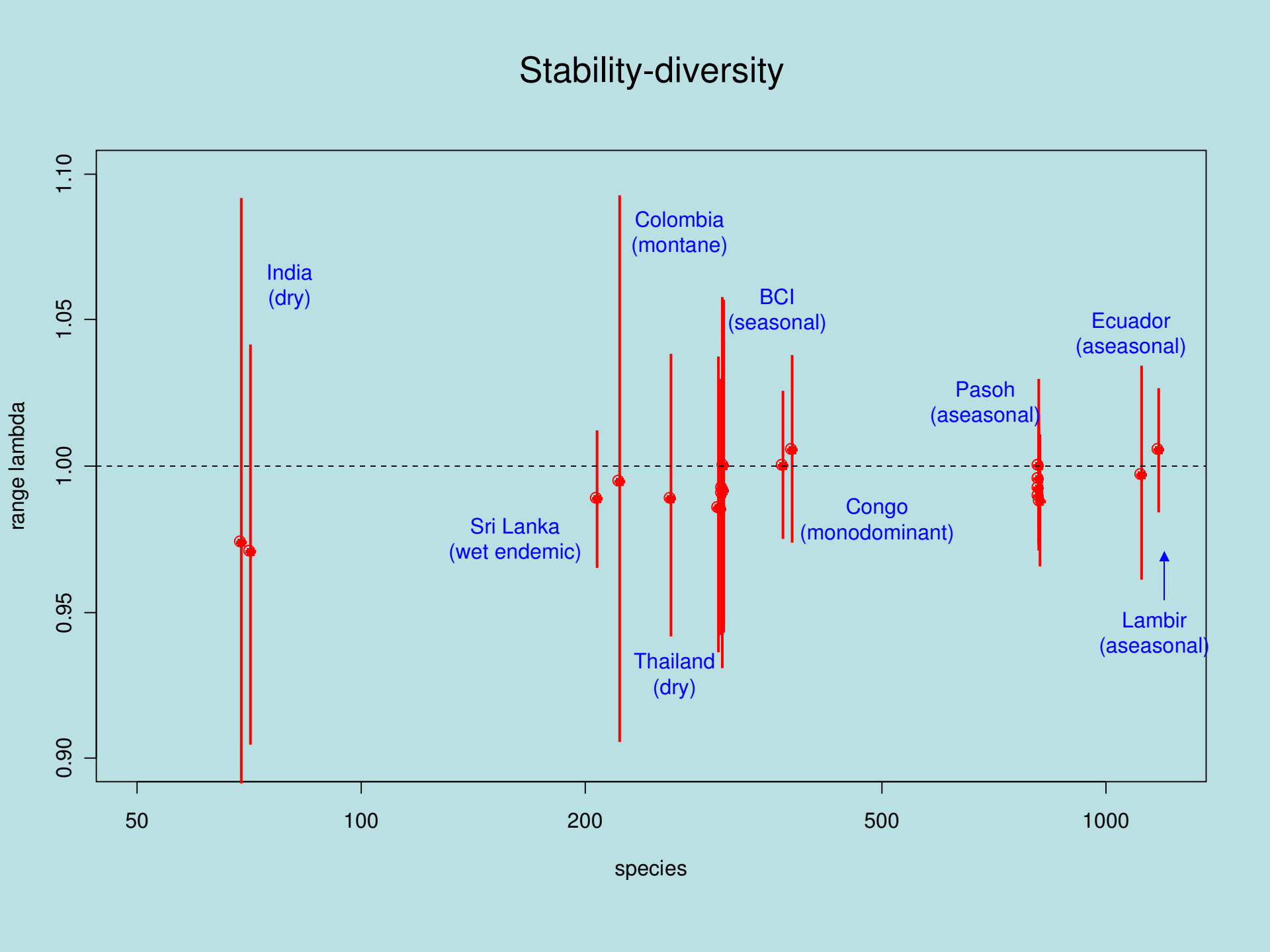
$$g(r) \sim symExponential\left[c_o + c\ln(N_0), k_o + \frac{k}{N_0^2}\right]$$

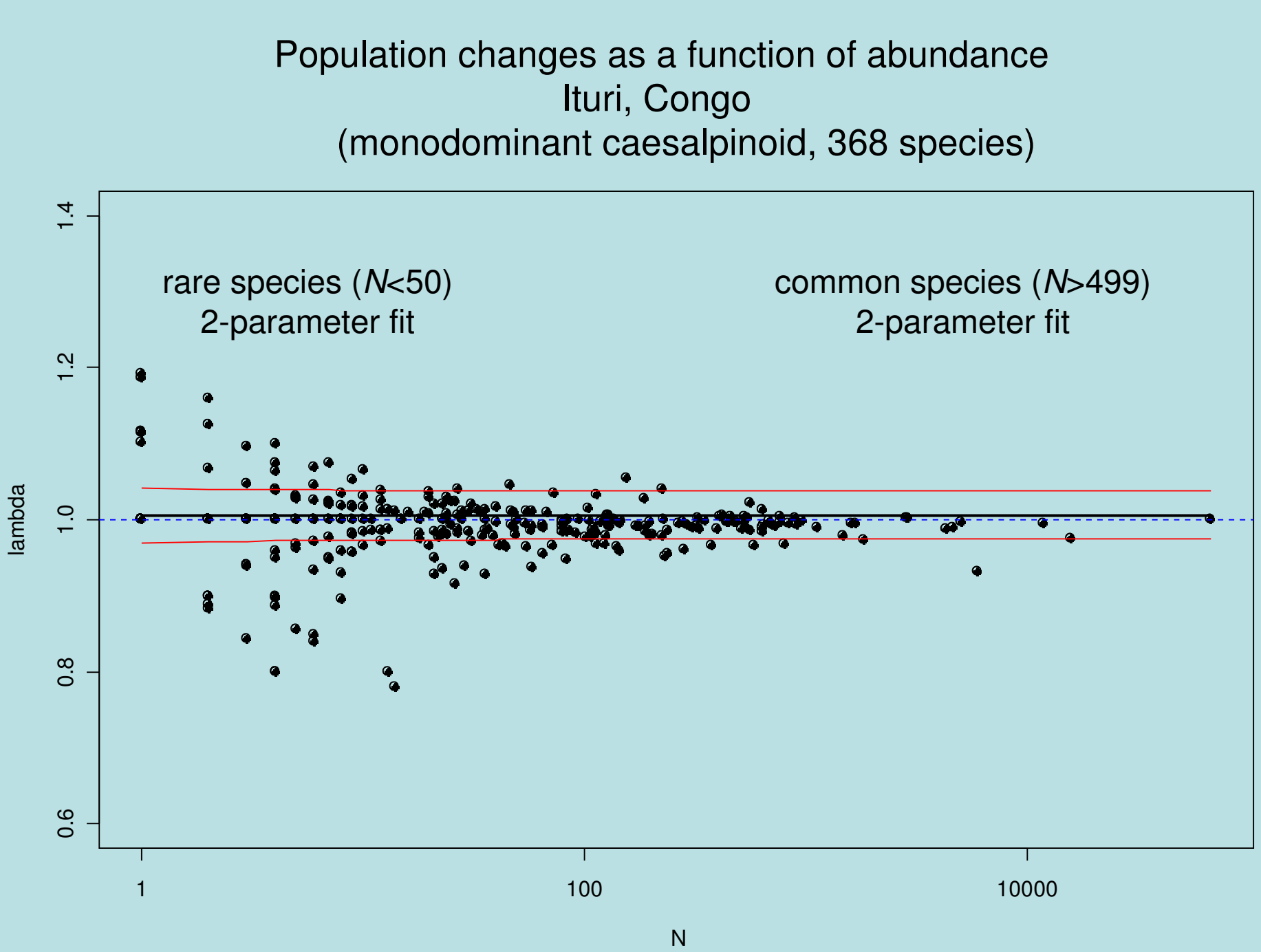

Population changes as a function of abundance
La Planada, Colombia
lambda
1.4
1.2
1.0
0.8
0.6
1
10
100
1000
10000
N
4SD

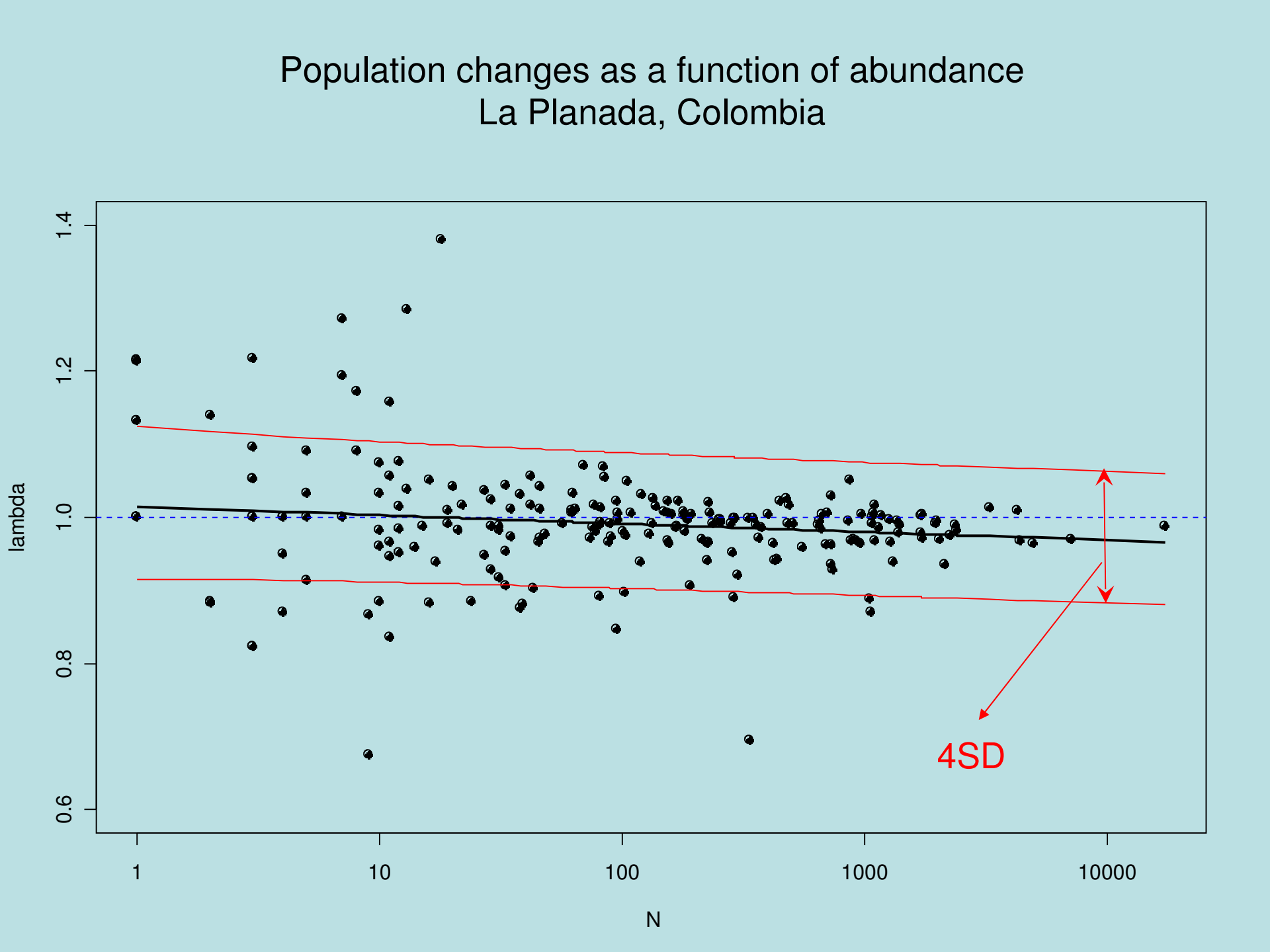
Population changes as a function of abundance
Mudumalai, India
(dry deciduous, elephant-dominated, 71 species)

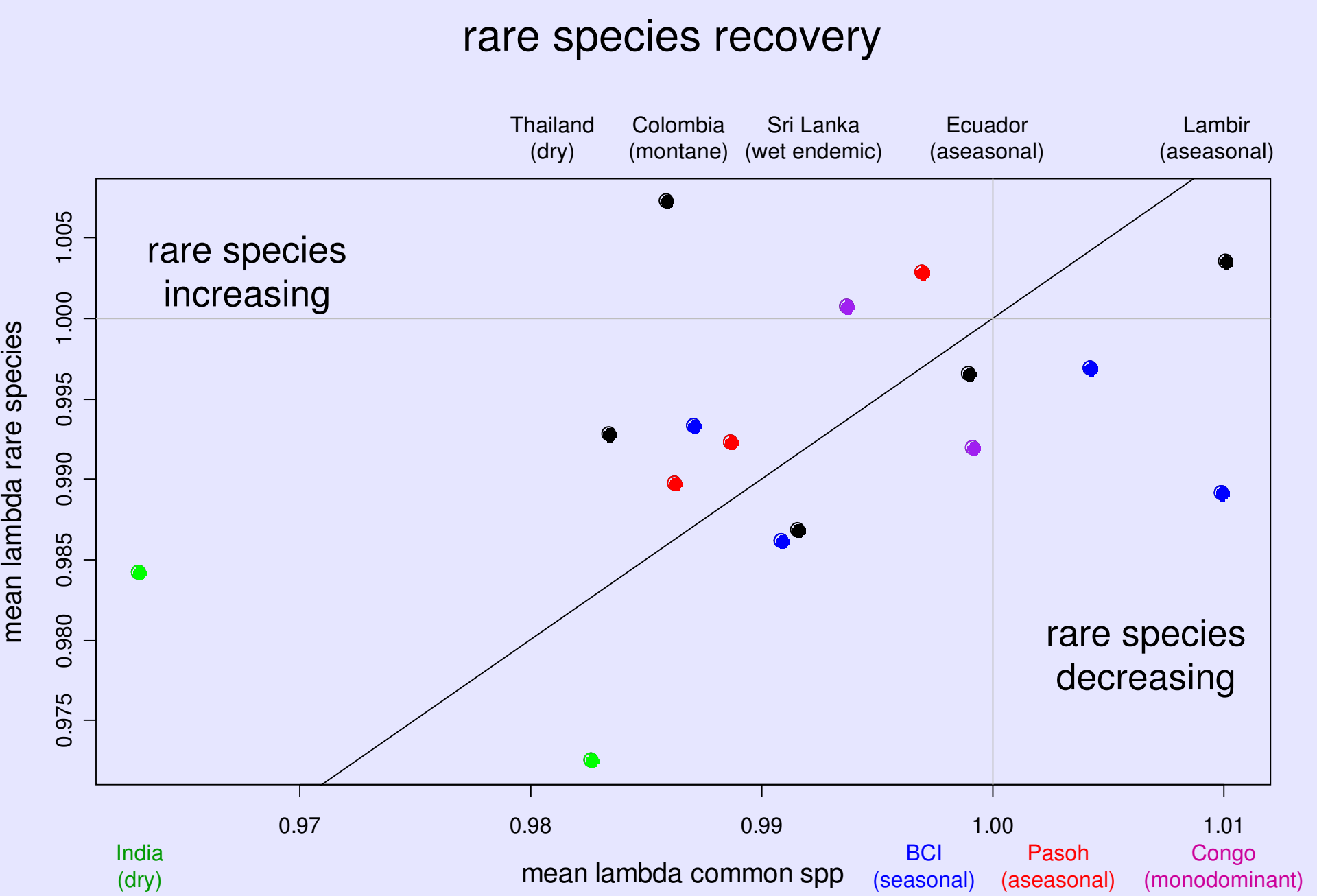



Population changes as a function of abundance
Lambir, Malayia
(dipterocarp-dominated, aseasonal, 1180 species)
lambda
1.4
1.2
1.0
0.8
0.6
1
10
100
1000
10000
N

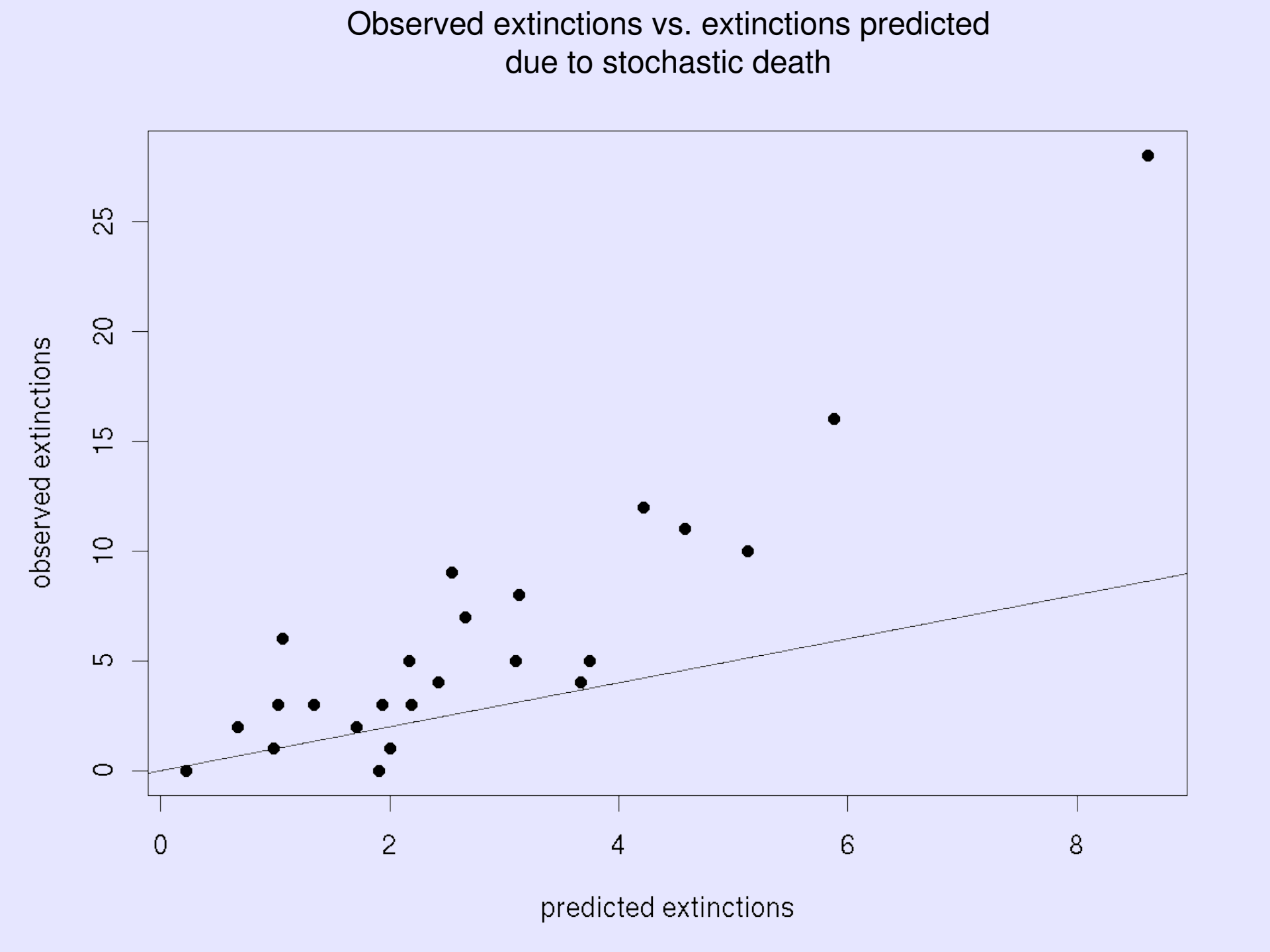

Stability-diversity
range lambda
1.10
1.05
1.00
0.95
0.90
50
100
200
500
1000
species
India
(dry)
Colombia
(montane)
BCI
(seasonal)
Ecuador
(aseasonal)
Pasoh
(aseasonal)
Sri Lanka
(wet endemic)
Congo
(monodominant)
Thailand
(dry)
Lambir
(aseasonal)


Population changes as a function of abundance
Ituri, Congo
(monodominant caesalpinoid, 368 species)
rare species (N<50)
2-parameter fit
common species (N>499)
2-parameter fit
lambda
1.4
1.2
1.0
0.8
0.6
1
100
10000
N


Population changes as a function of abundance
La Planada, Colombia
lambda
1.4
1.2
1.0
0.8
0.6
1
10
100
1000
10000
N
4SD


rare species recovery
Thailand (dry)
Colombia (montane)
Sri Lanka (wet endemic)
Ecuador (aseasonal)
Lambir (aseasonal)
rare species increasing
rare species decreasing
mean lambda rare species
0.975
0.980
0.985
0.990
0.995
1.000
1.005
0.97
0.98
0.99
1.00
1.01
mean lambda common spp
India (dry)
BCI (seasonal)
Pasoh (aseasonal)
Congo (monodominant)

site	N۰	deaths	births	species	extinct	input	singleton
BCI	۲۳۴۲۶۱	۲۵۹۴۵	۳۳۰۲۹	۳۰۰	۲	۱	۲۲
	۲۴۱۳۴۵	۳۷۰۹۷	۳۹۲۹۷	۳۰۱	۶	۹	۲۱
	۲۴۳۵۴۵	۳۶۶۱۰	۲۱۶۹۵	۲۹۸	۴	۵	۱۷
	۲۲۸۶۳۰	۳۶۵۷۷	۲۱۴۱۸	۲۹۷	۴	۵	۲۳
	۲۱۳۴۷۱	۳۱۳۴۴	۲۵۹۴۰	۲۹۶	۵	۷	۲۲
Pasoh	۳۳۵۳۵۲	۱۴۲۶۴	۵۷۰۹	۸۱۴	۱	۱	۲۴
	۳۲۶۷۹۷	۲۷۵۵۲	۳۹۰۱۷	۸۱۴	۷	۳	۲۷
	۳۳۸۲۶۲	۳۵۱۹۳	۱۳۷۰۱	۸۱۸	۰	۲	۱۸
Mudumalai	۲۵۵۵۴	۸۳۶۸	۴۶۰	۷۲	۱	۳	۸
	۱۷۶۴۶	۳۰۲۶	۶۹۰	۷۰	۱	۶	۷
	۱۵۳۱۰	۱۱۶۱	۳۹۶۰	۶۵	۵	۰	۴
Lambir	۳۳۰۱۰۴	۲۱۲۹۱	۳۸۷۰۷	۱۱۷۹	۶	۳	۲۴
HKK	۷۸۴۴۸	۲۳۰۲۷	۱۶۸۴۱	۲۹۰	۷	۱۰	۲۵
Sinharaja	۲۰۵۱۰۵	۲۱۸۲۴	۹۶۹۶	۲۰۶	۰	۲	۷
Yasuni	۱۴۴۹۳۹	۲۲۵۵۸	۲۰۶۱۸	۱۱۱۴	۴۵	۲۸	۶۹
La Planada	۱۱۲۲۹۳	۳۰۰۲۰	۲۳۰۷۳	۲۲۰	۲۰	۰	۱۰
Edoro	۱۶۱۸۱۸	۱۶۴۷۰	۸۹۶۶	۳۷۳	۱۴	۱۱	۵۰
Lenda	۱۳۶۲۳۵	۱۳۴۴۲	۱۰۴۵۳	۳۶۰	۱۰	۸	۳۶


Observed extinctions vs. extinctions predicted
due to stochastic death
observed extinctions
0
5
10
15
20
25
0
2
4
6
8
predicted extinctions

In sum

All forests are changing more than neutral expectation:
--communities are not stable

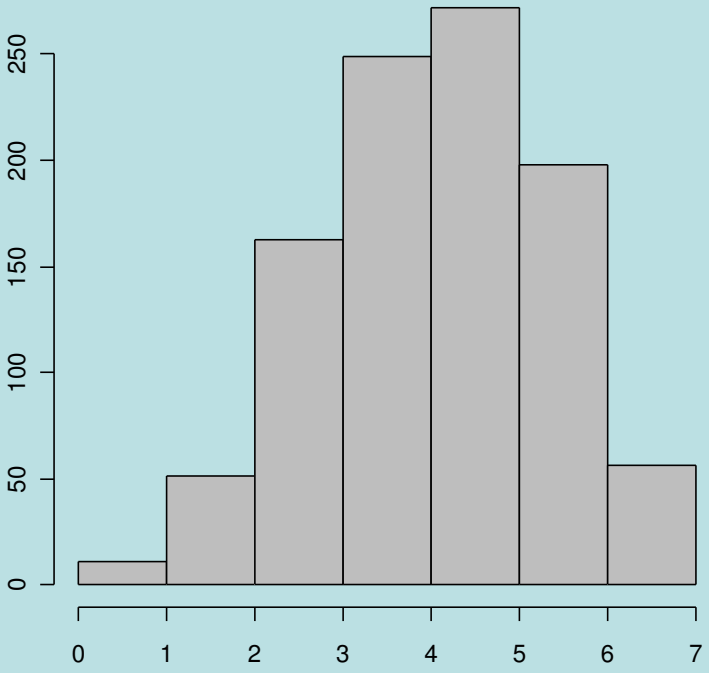
In some forests, there are considerable changes:
--a few species are declining dramatically

Rare species show no tendency to increase

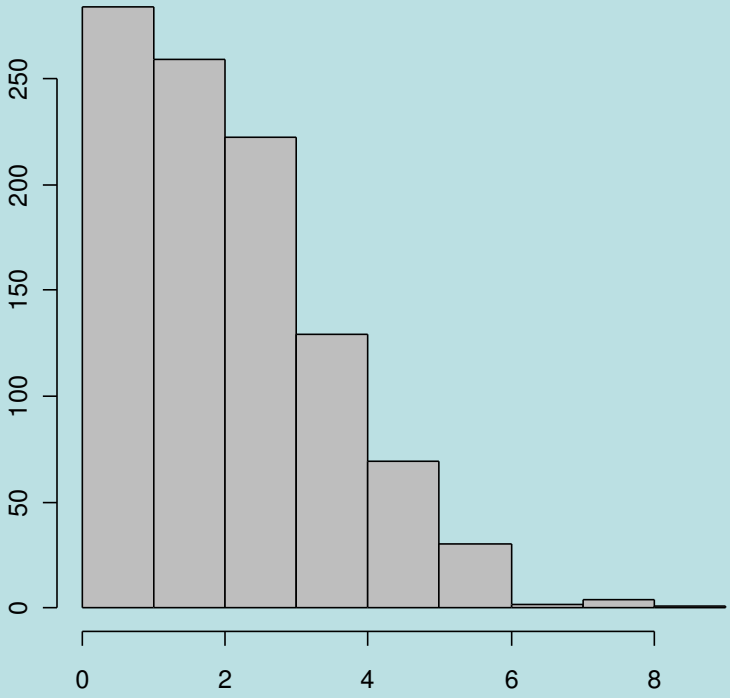
Rare Example: *Aphelandra sinclairiana*

7 individuals in year 0
5-year survival θ=0.71

1000 Random draws on 5-year survival:



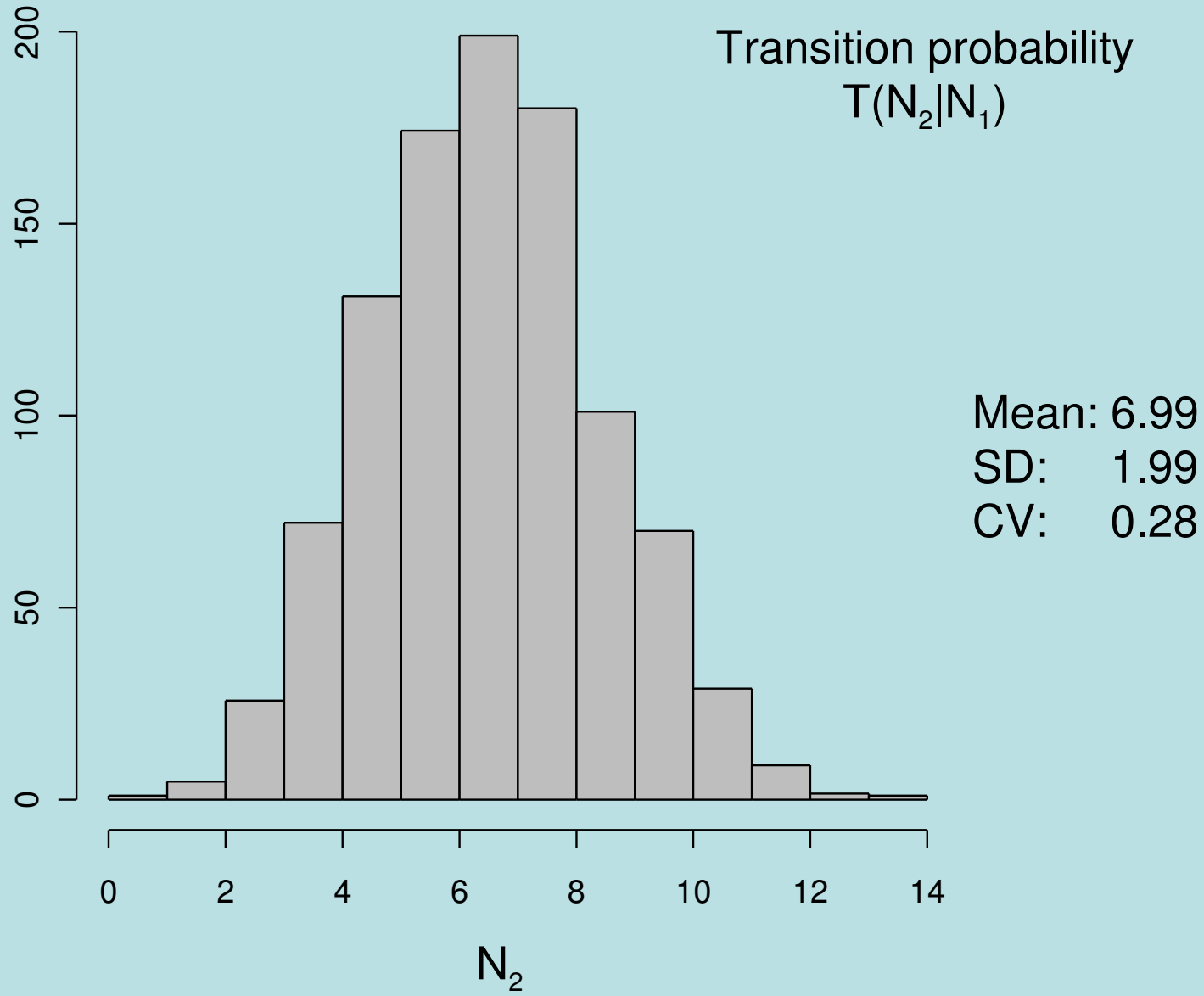
1000 Random draws on 5-year recruitment:



Rare Example: *Aphelandra sinclairiana* (cont)

N_1=7 individuals in year 0

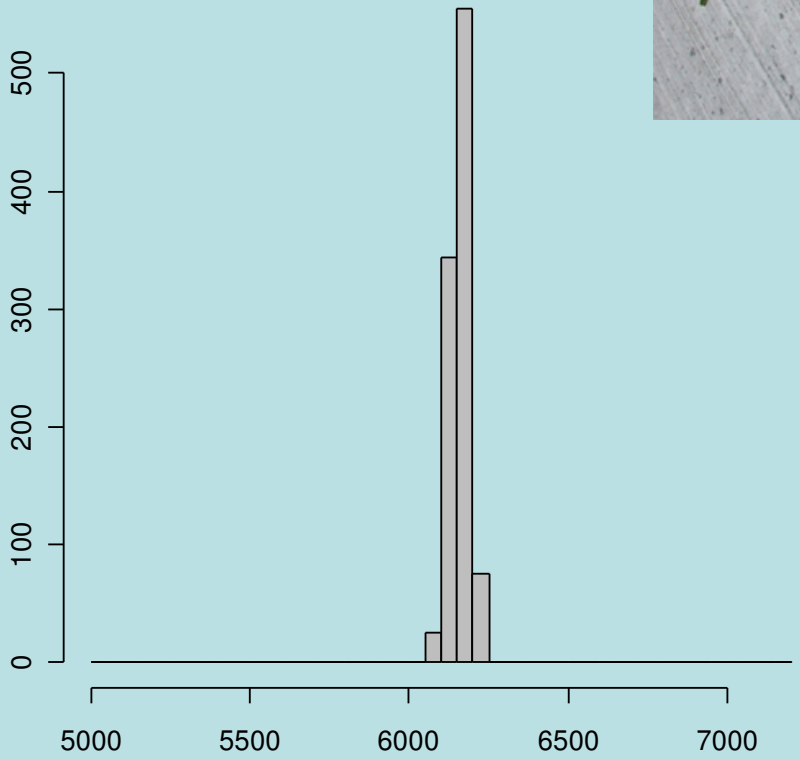
survival + recruitment produces:
1000 Random draws on 5-year population change:



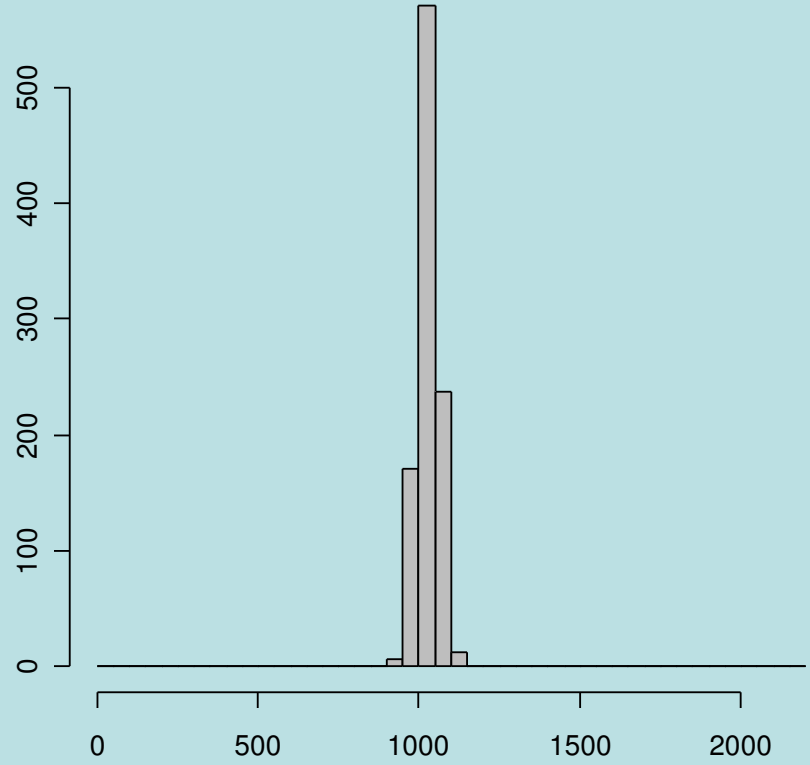
Abundant example: *Alseis blackiana*

7190 individuals in year 0
estimated survival θ=0.820

1000 Random draws on 5-year survival:



1000 Random draws on 5-year recruitment:

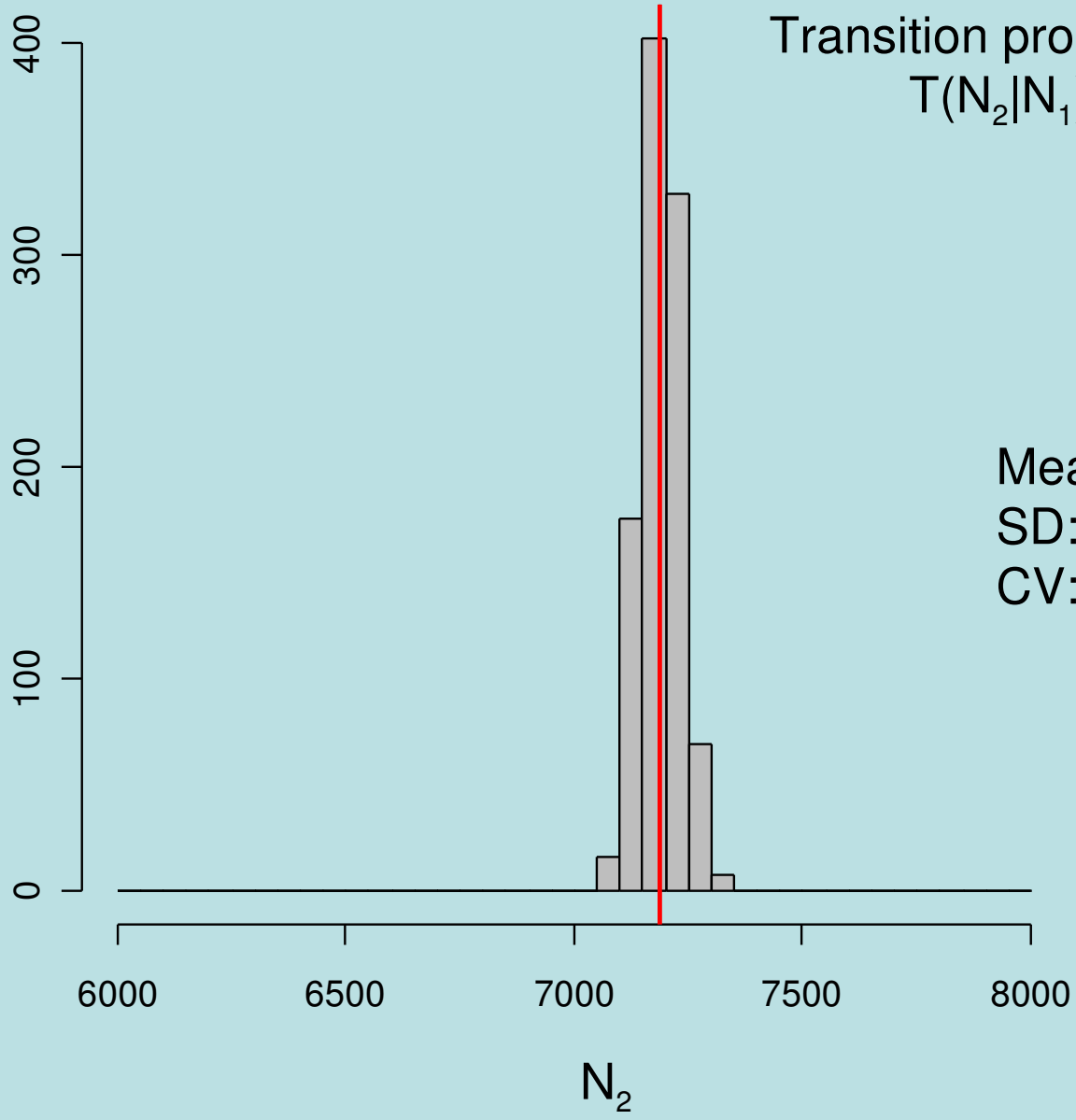


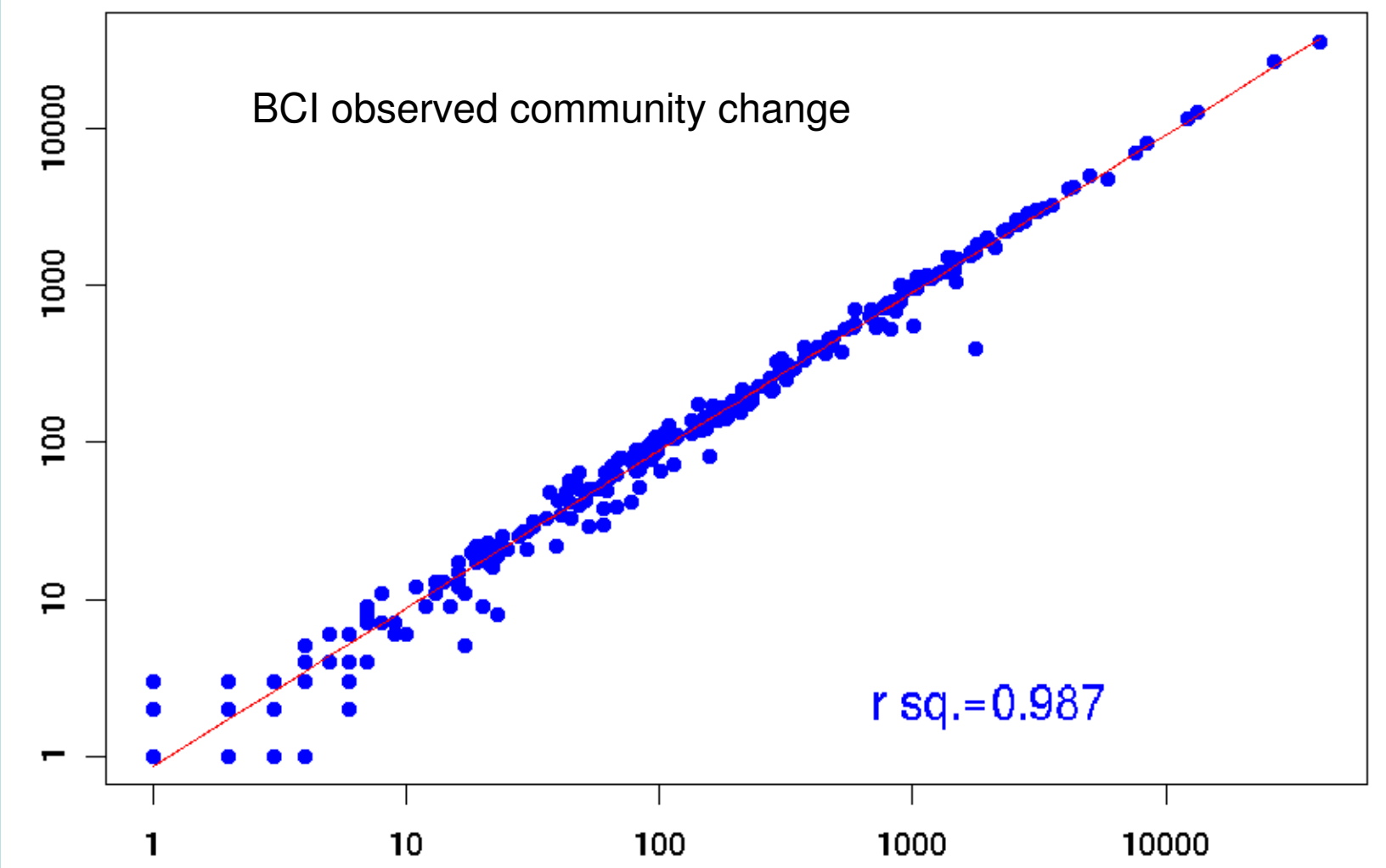
Abundant example: *Alseis blackiana*

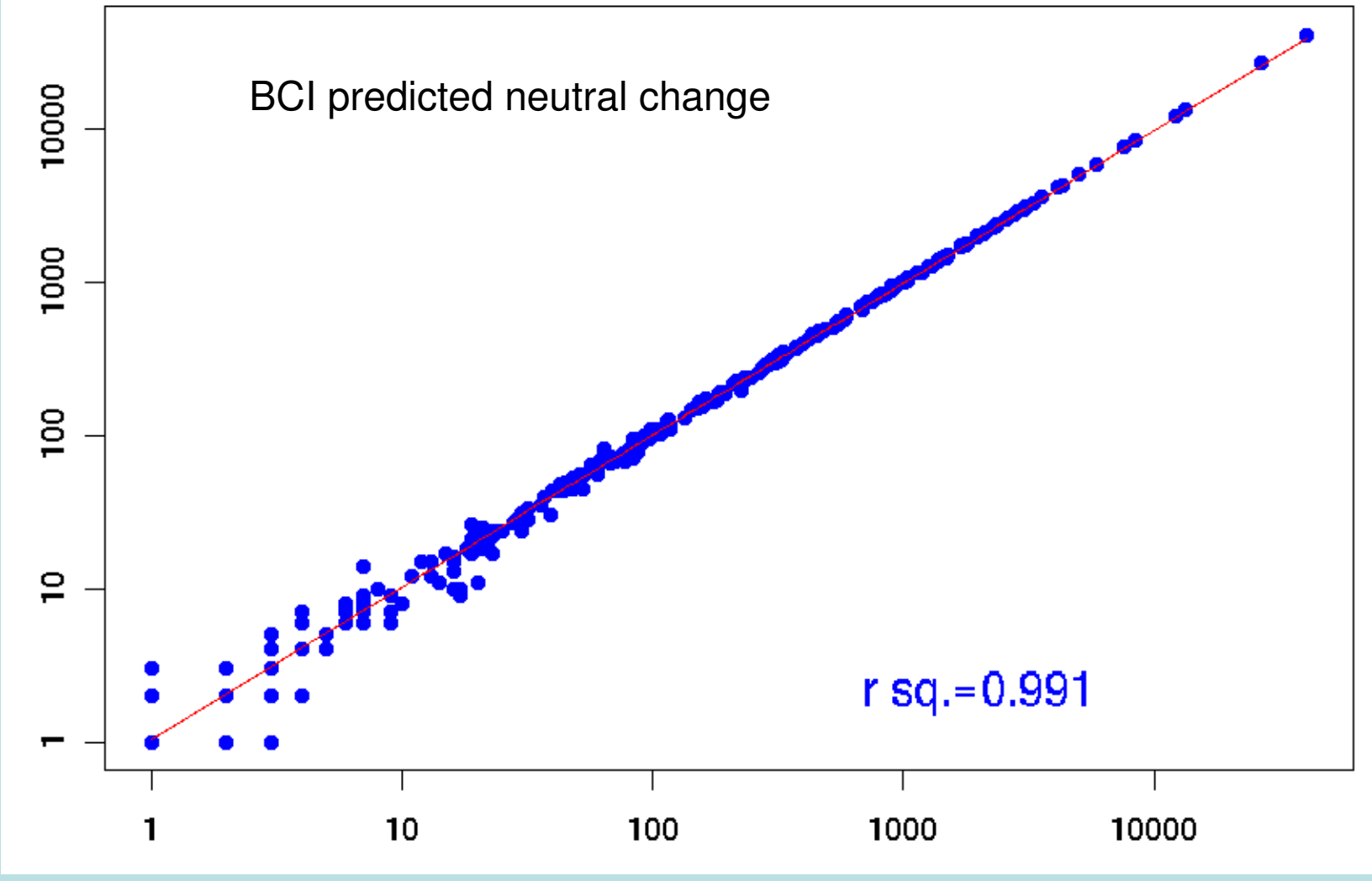
7190 individuals in year 0

survival + recruitment produces:

1000 Random draws on 5-year population change:



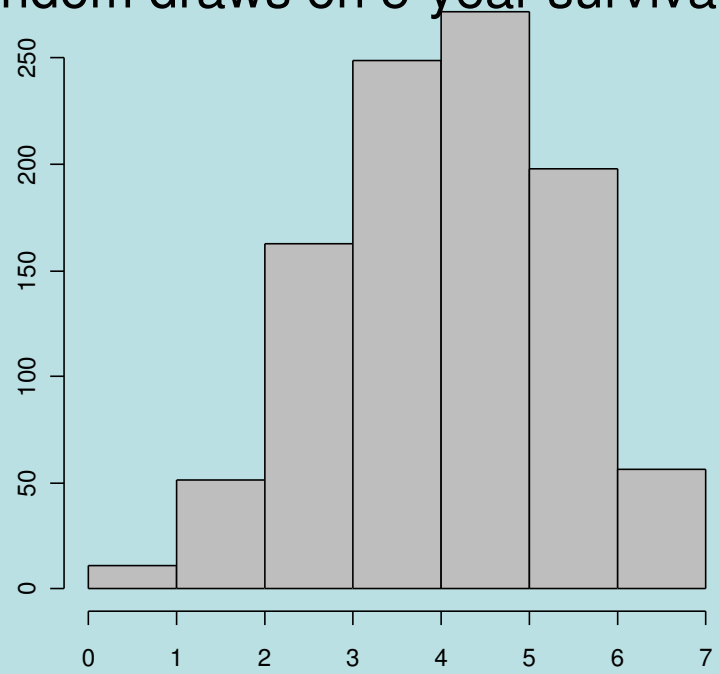

BCI observed community change
r sq.=0.987
1
10
100
1000
10000


BCI predicted neutral change
r sq.=0.991
1
10
100
1000
10000

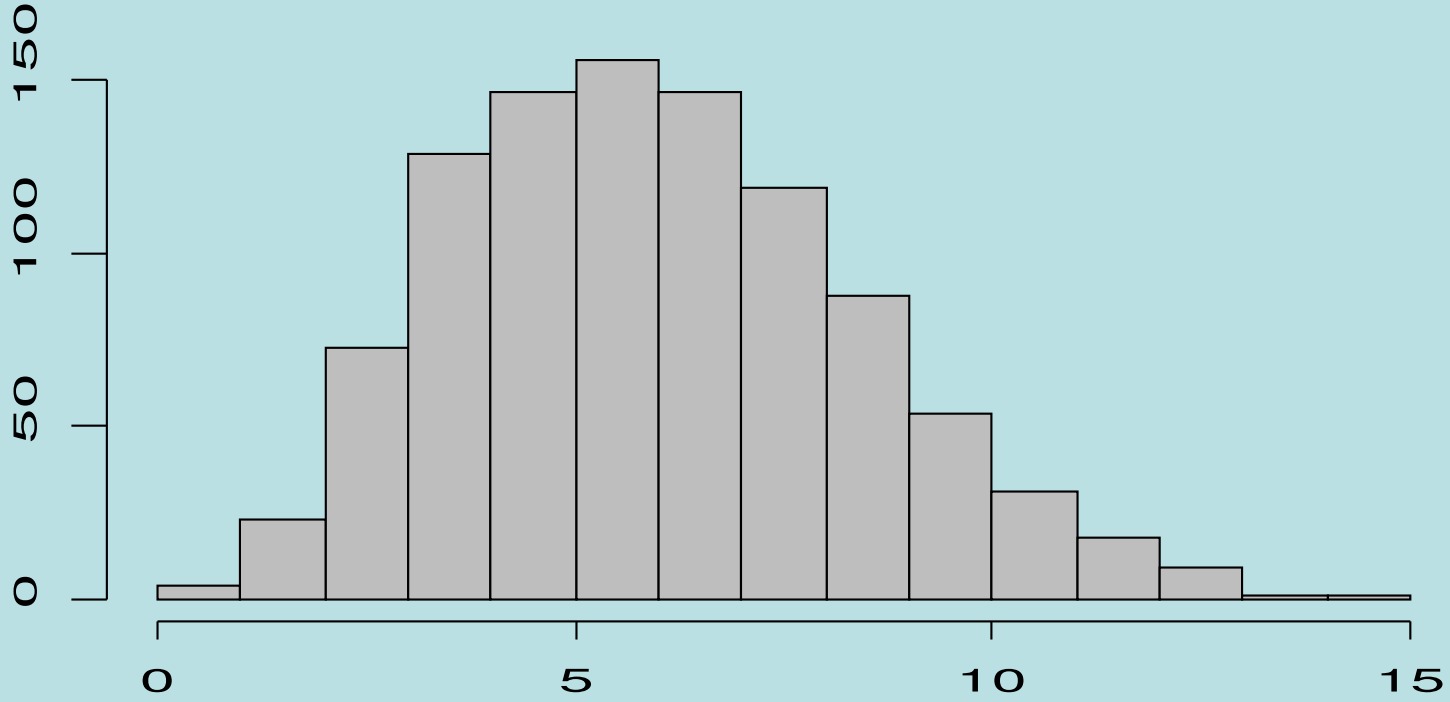
Rare example: *Aphelandra sinclairiana*
But now set λ=1.4

7 individuals in year 0, 10 in year 5

1000 Random draws on 5-year survival:



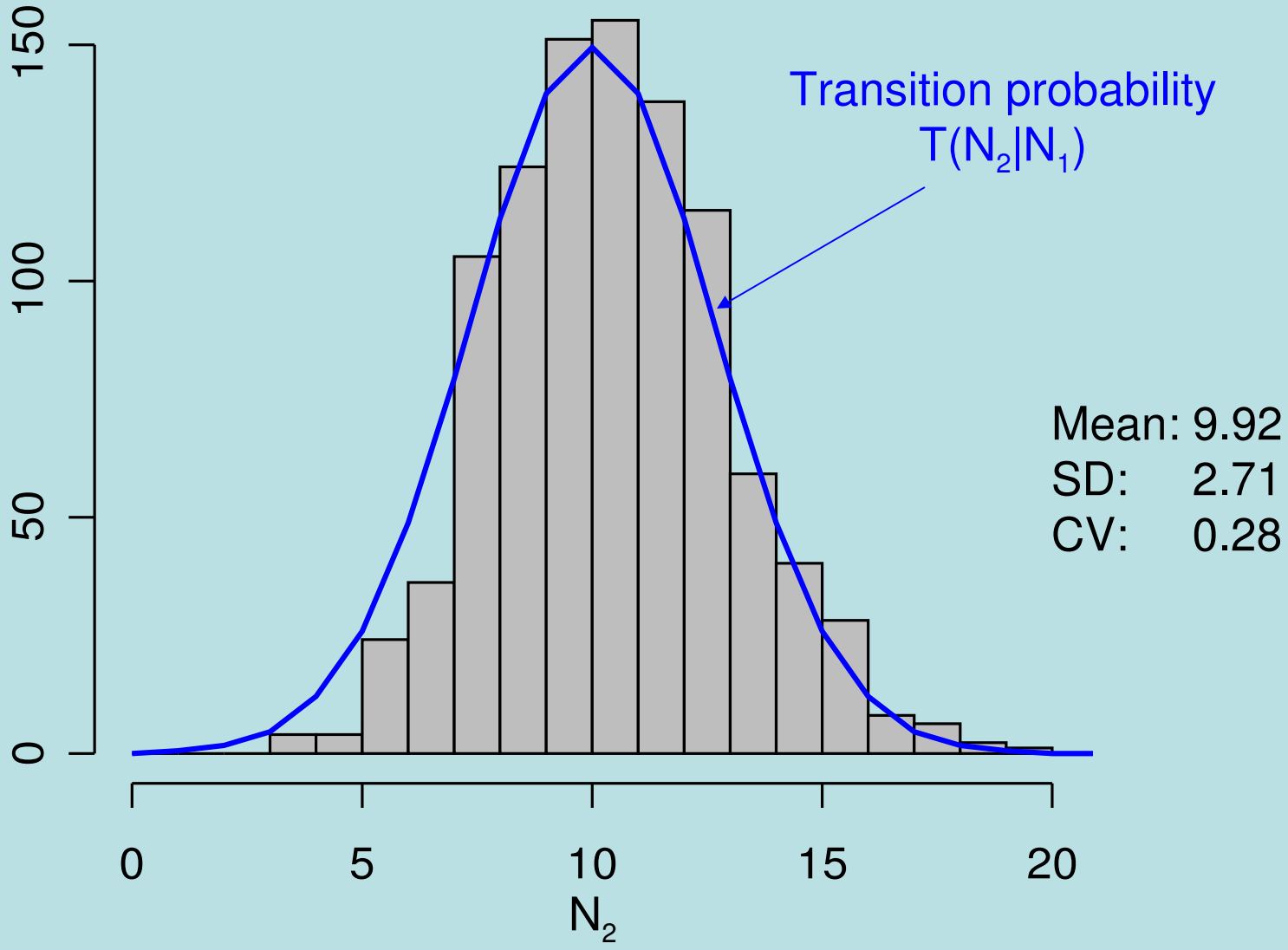
1000 Random draws on 5-year recruitment:



Rare Example: *Aphelandra sinclairiana* (cont)
with λ=1.4

N_1=7 individuals in year 0
estimated survival θ=0.71

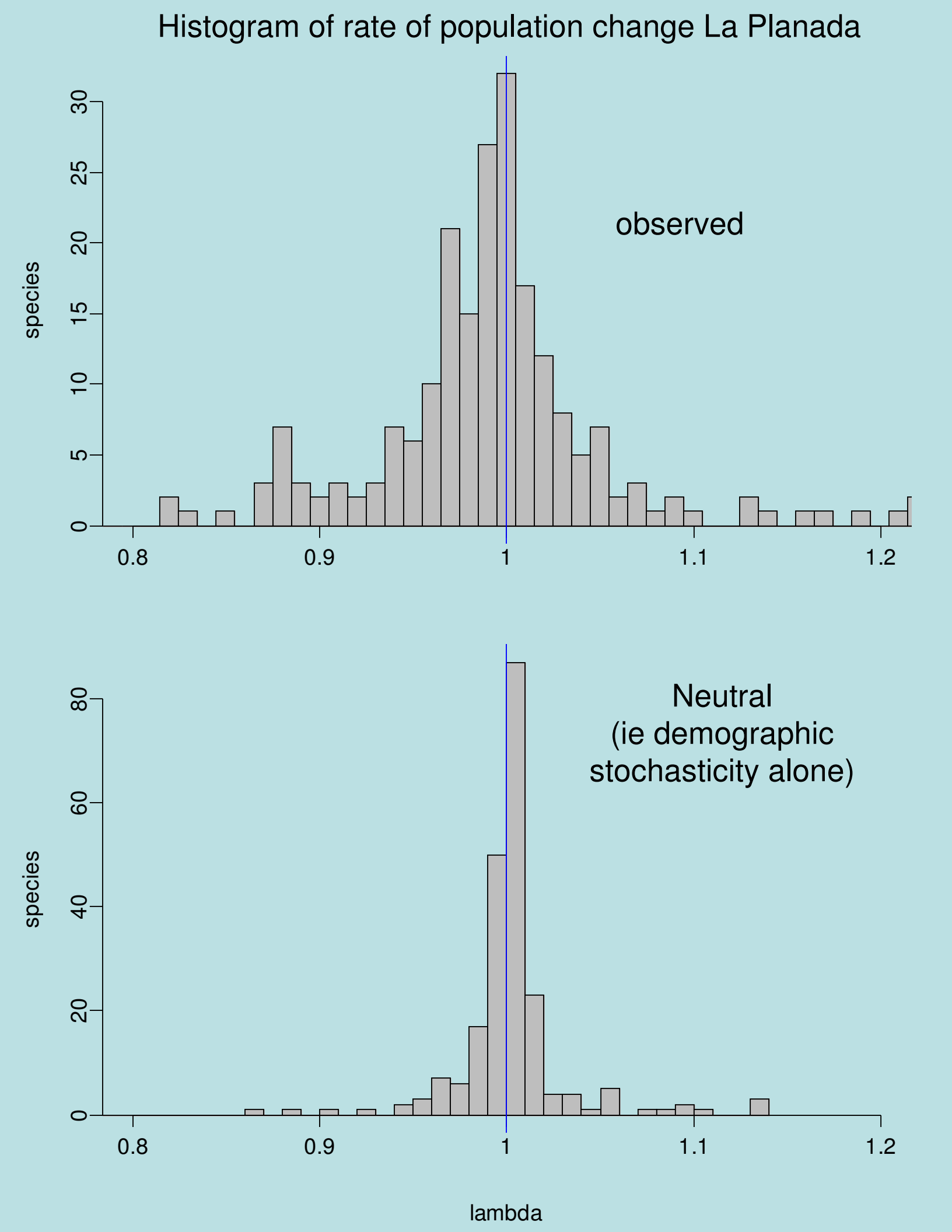
survival + recruitment produces:
1000 Random draws on 5-year population change:

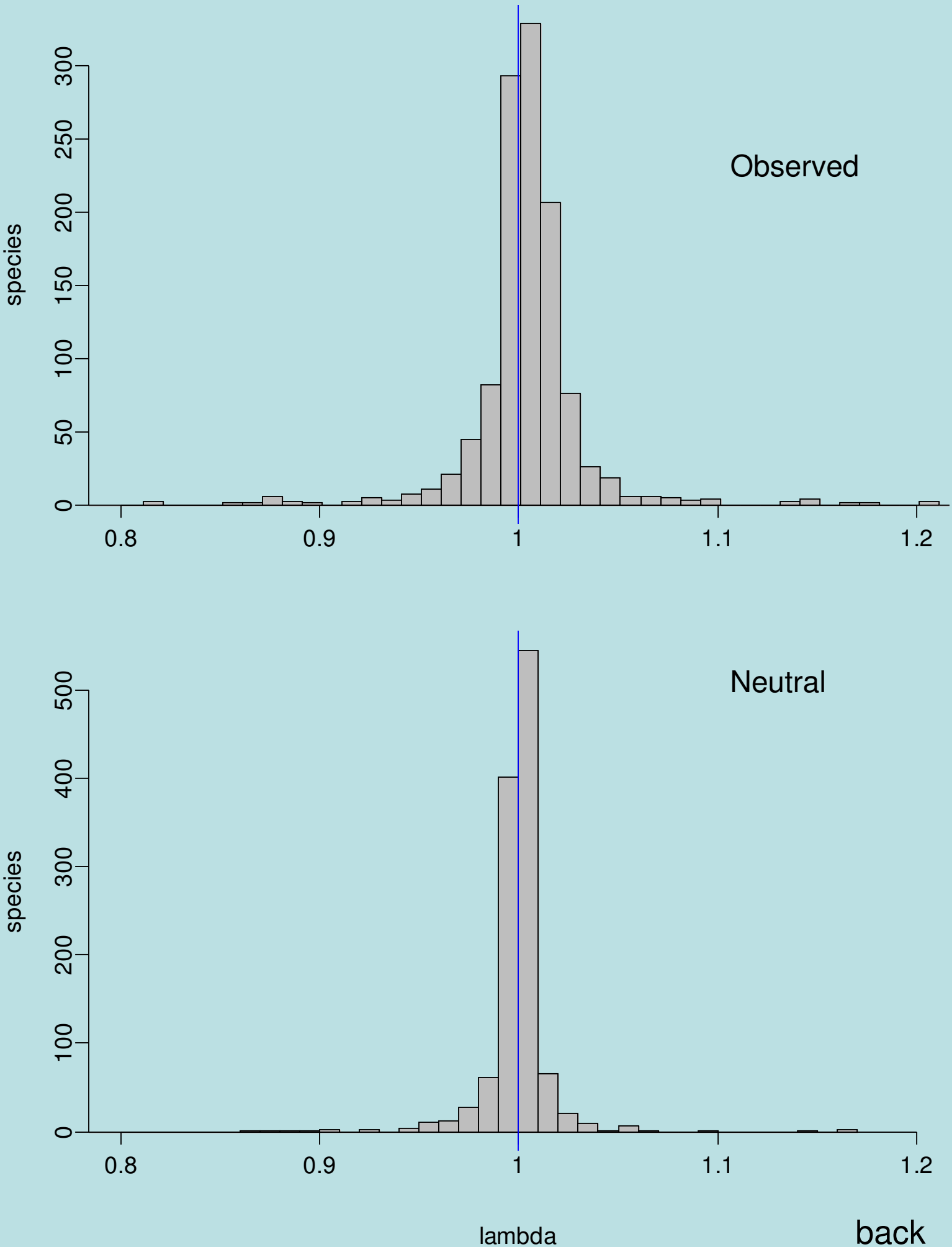


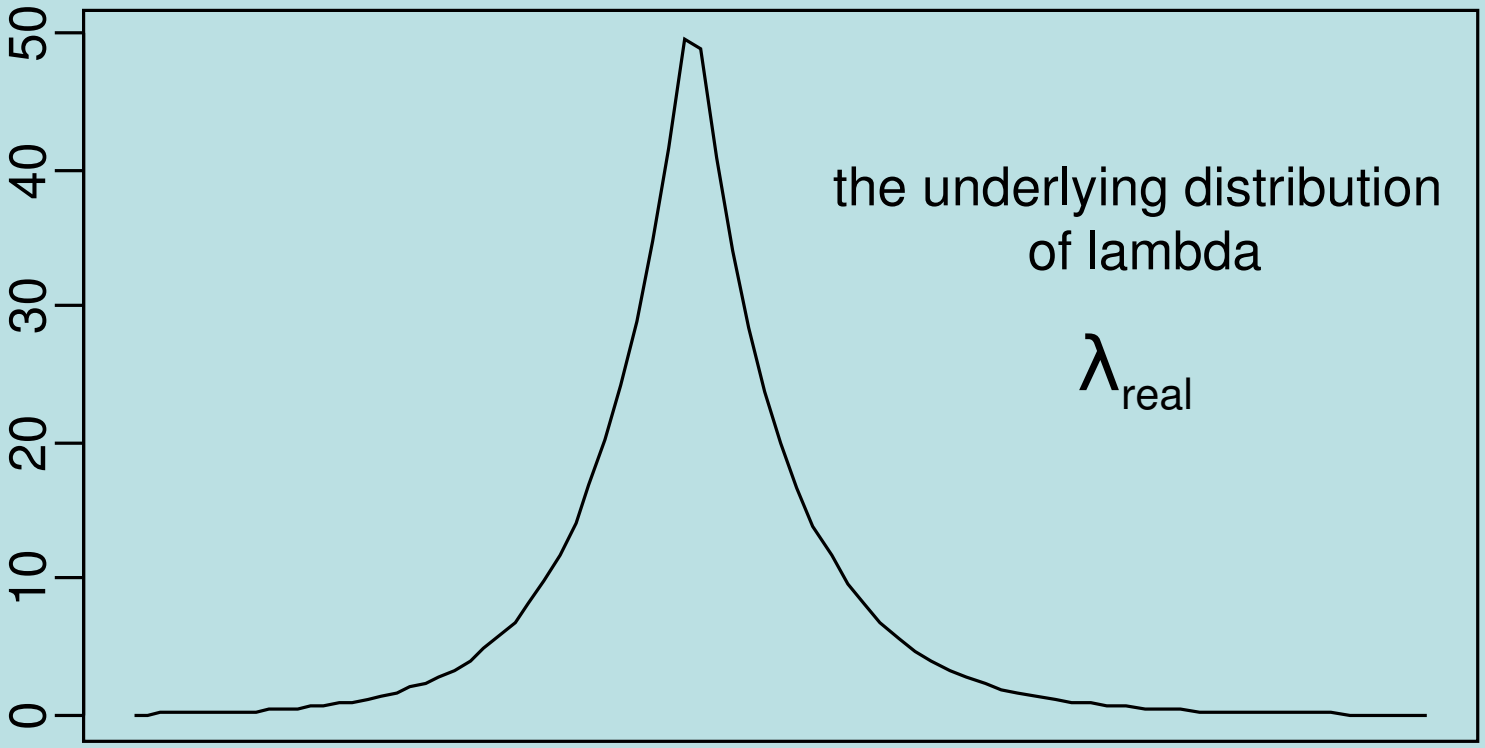
The probability distribution of N_t is approx. normal,

$$\text{mean} = N_0\lambda$$

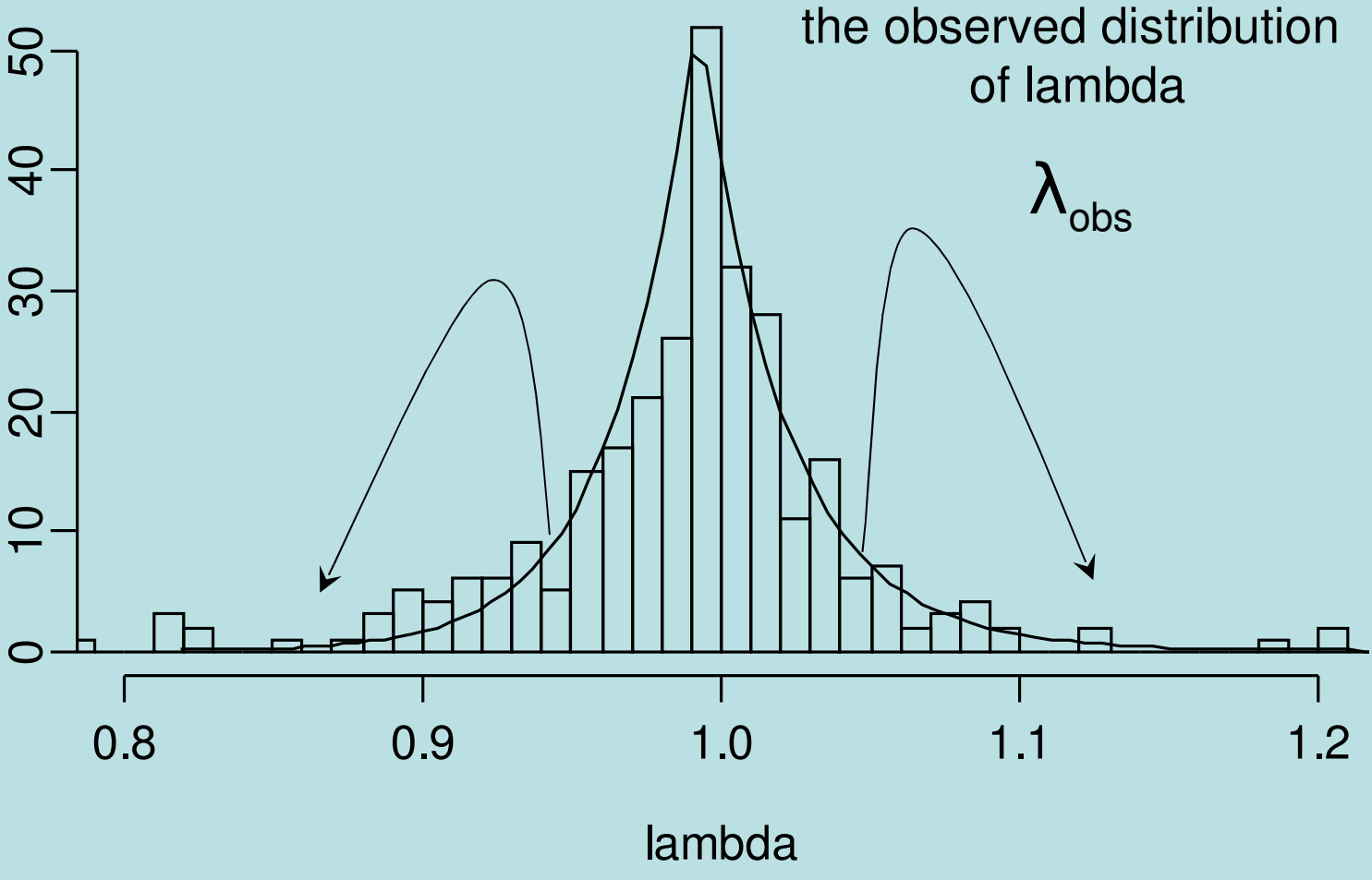
$$\text{var} = N_0(\lambda - \theta^2)$$


Histogram of rate of population change La Planada
observed
species
0
5
10
15
20
25
30
0.8
0.9
1
1.1
1.2
Neutral
(ie demographic
stochasticity alone)
species
0
20
40
60
80
0.8
0.9
1
1.1
1.2
lambda


Histogram of rate of population change Lambir
Observed
species
0
50
100
150
200
250
300
0.8
0.9
1
1.1
1.2
Neutral
species
0
100
200
300
400
500
0.8
0.9
1
1.1
1.2
lambda
back


0
10
20
30
40
50
the underlying distribution
of lambda
λ_{real}

add noise…


0
10
20
30
40
50
the observed distribution
of lambda
λ_{obs}
0.8
0.9
1.0
1.1
1.2
lambda

Substracting the noise

Simulate demographic stochasticity (a neutral community):

-- Mortality rates vary across species

-- Recruitment=mortality

-- Mortality is binomial process

-- Recruitment is poisson process