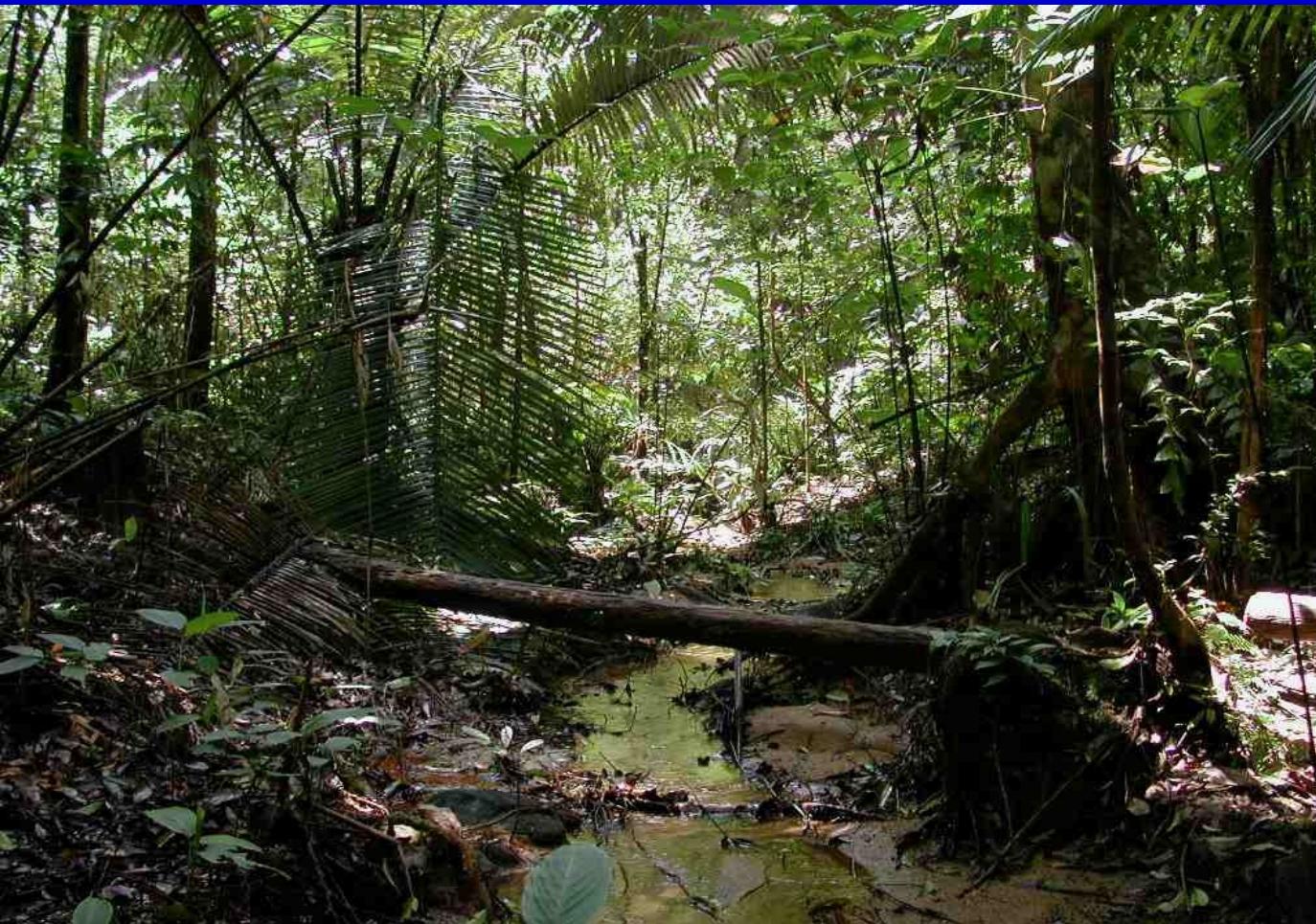


# Stability and turnover of tropical forest communities



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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Center for Tropical Forest Science (CTFS)

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

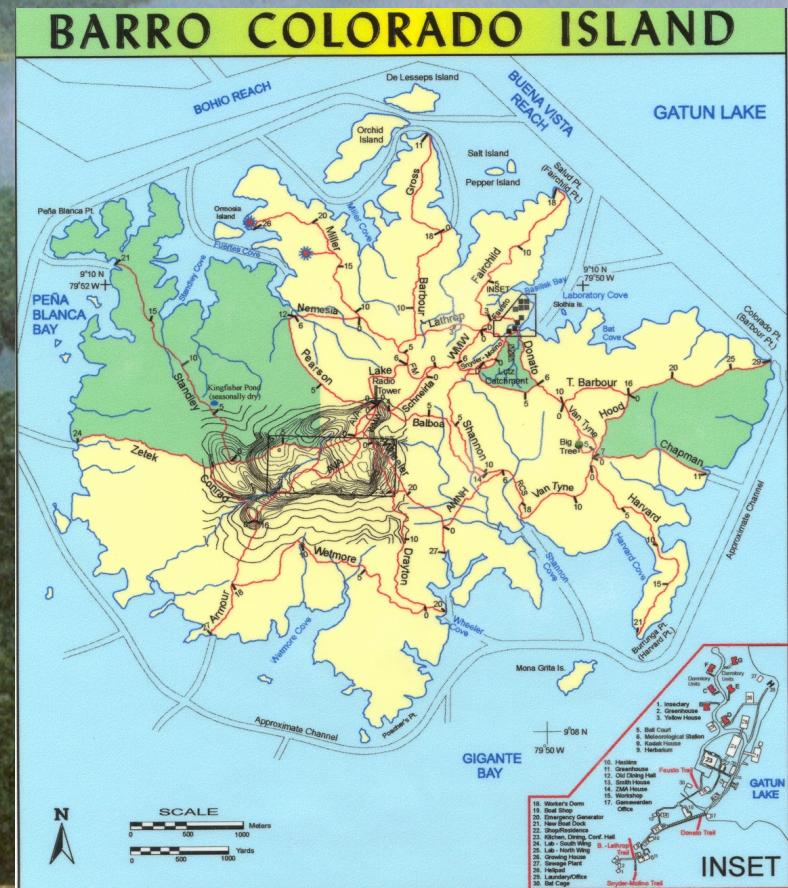
	species ≥ 1 cm dbh	annual rainfall (mm)	dry season (months)
Panama, BCI	274	2500	4
Ecuador, Yasuni	1104	3000	0
Colombia, La Planada	280	3500	0
Puerto Rico, Luquillo *	120	3500	0
India, Mudumalai	66	1200	6
Thailand, HKK	206	1450	6
Malaysia, Pasoh	785	1800	0
Malaysia, Lambir	1111	2700	0
Sri Lanka, Sinharaja	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

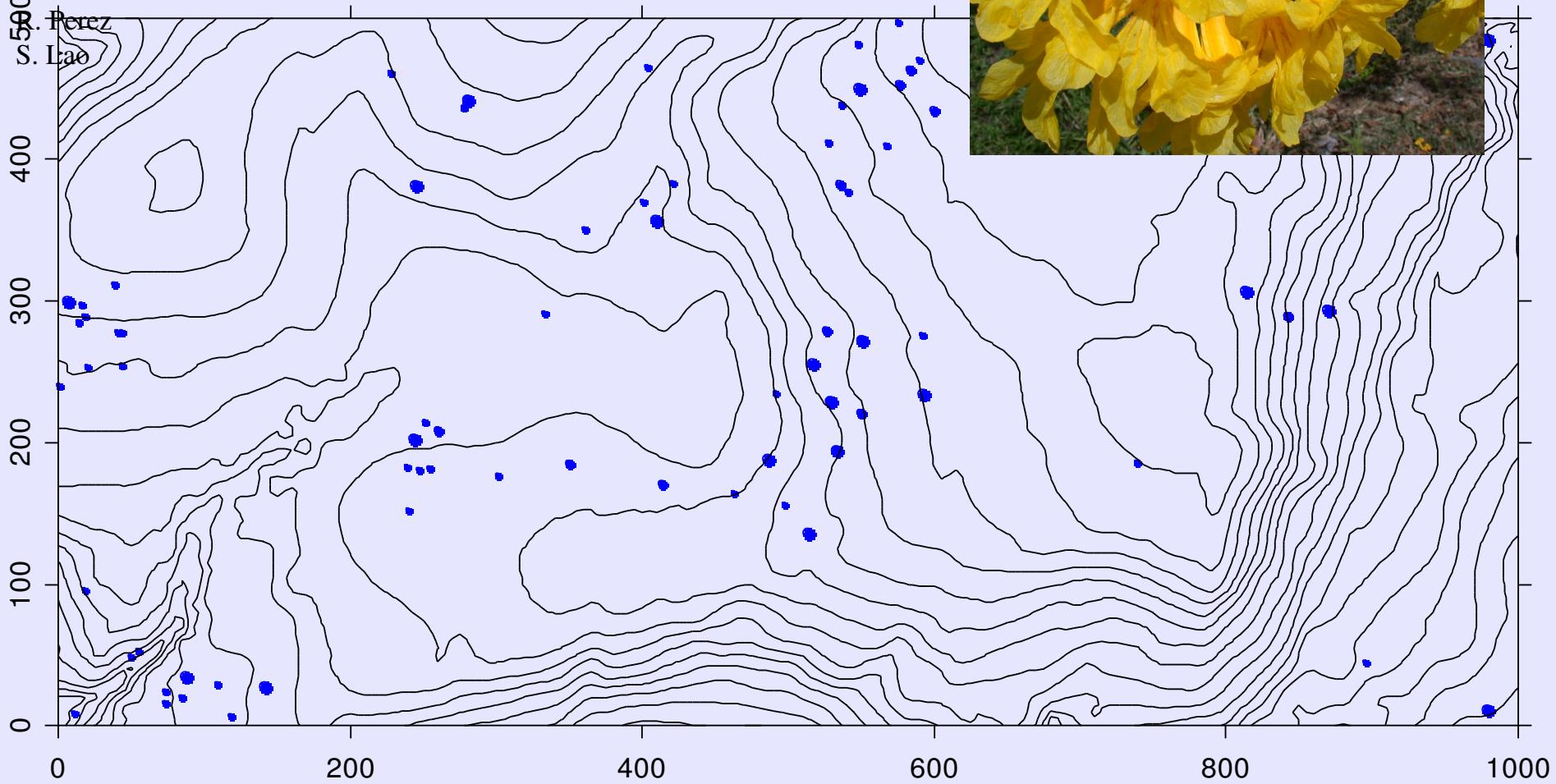
## Gatún Lake, Panama



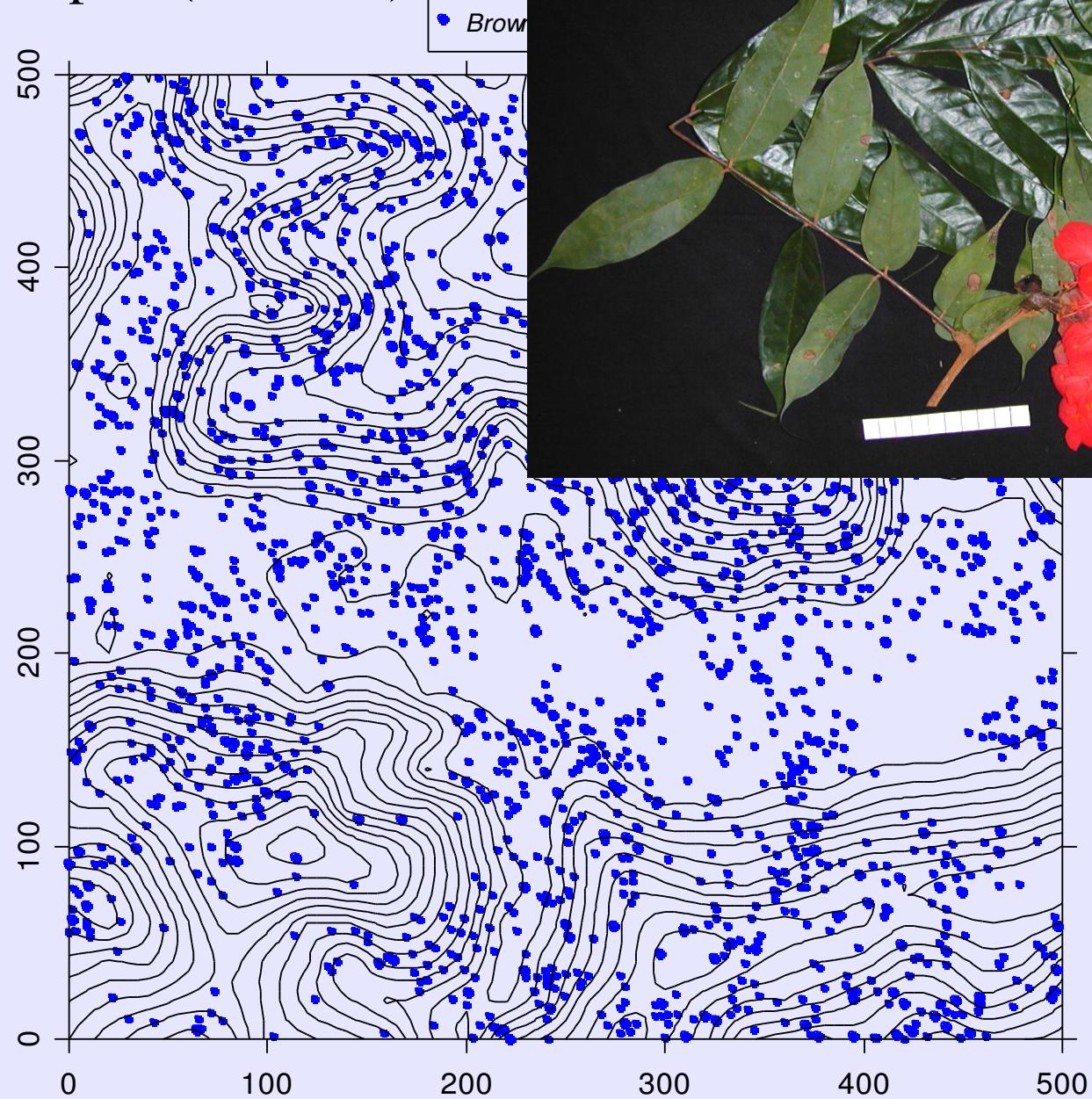
# Barro Colorado 50 ha plot (Panama)

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

• *Tabebuia guayacan*



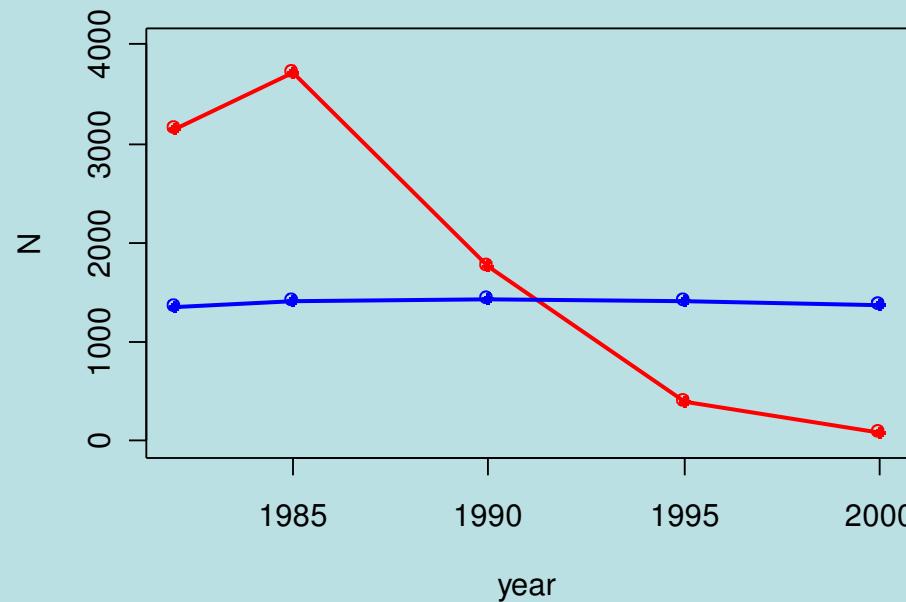
# Yasuni 25 ha plot (Ecuador)



R. Foster  
G. Villa  
R. Condit  
R. Valencia  
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

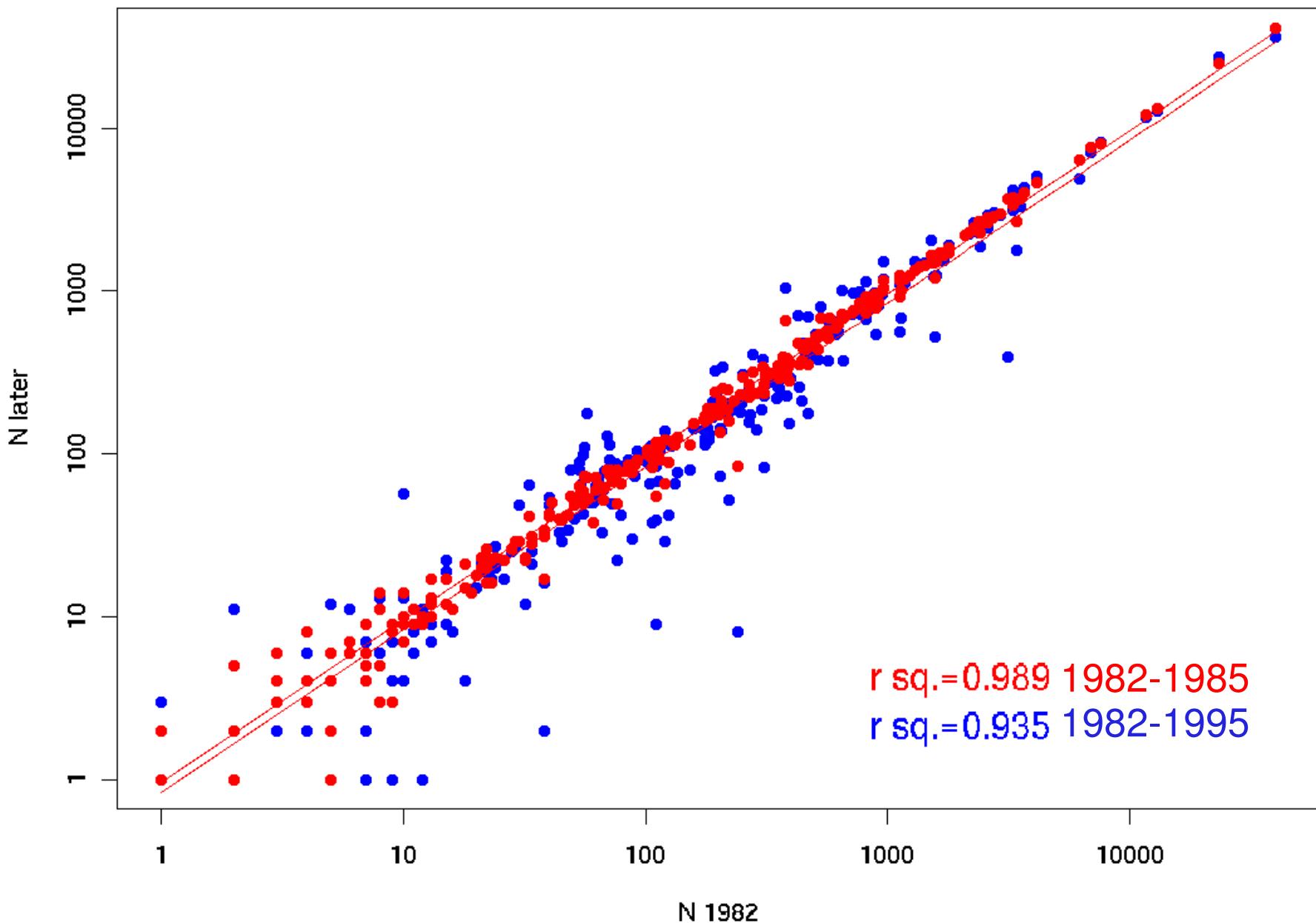
Lande, R., Engen, S., and Saether, B.-E. 2000. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford.

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

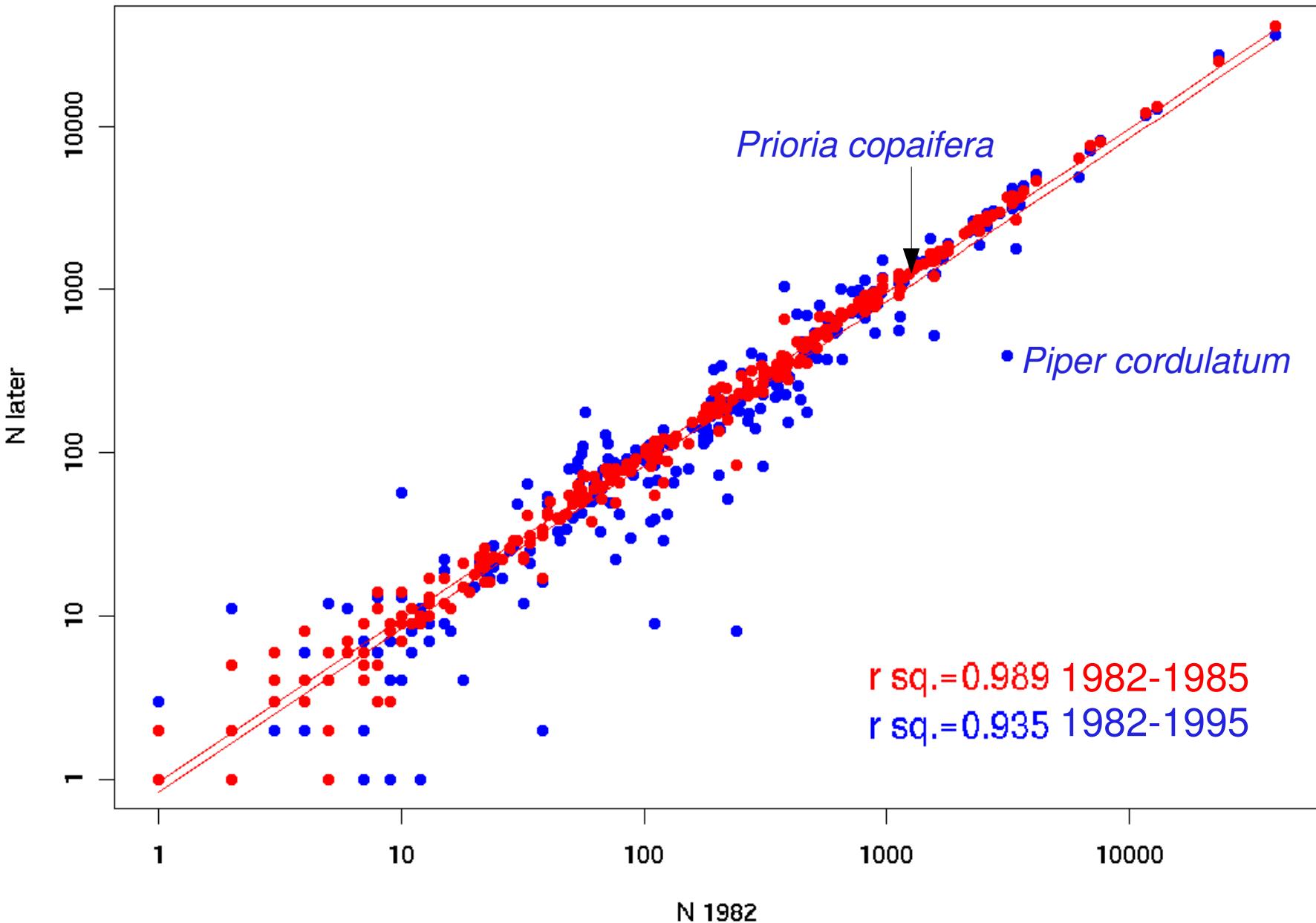
## abundance data from Ituri 20 ha plot (Congo)

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

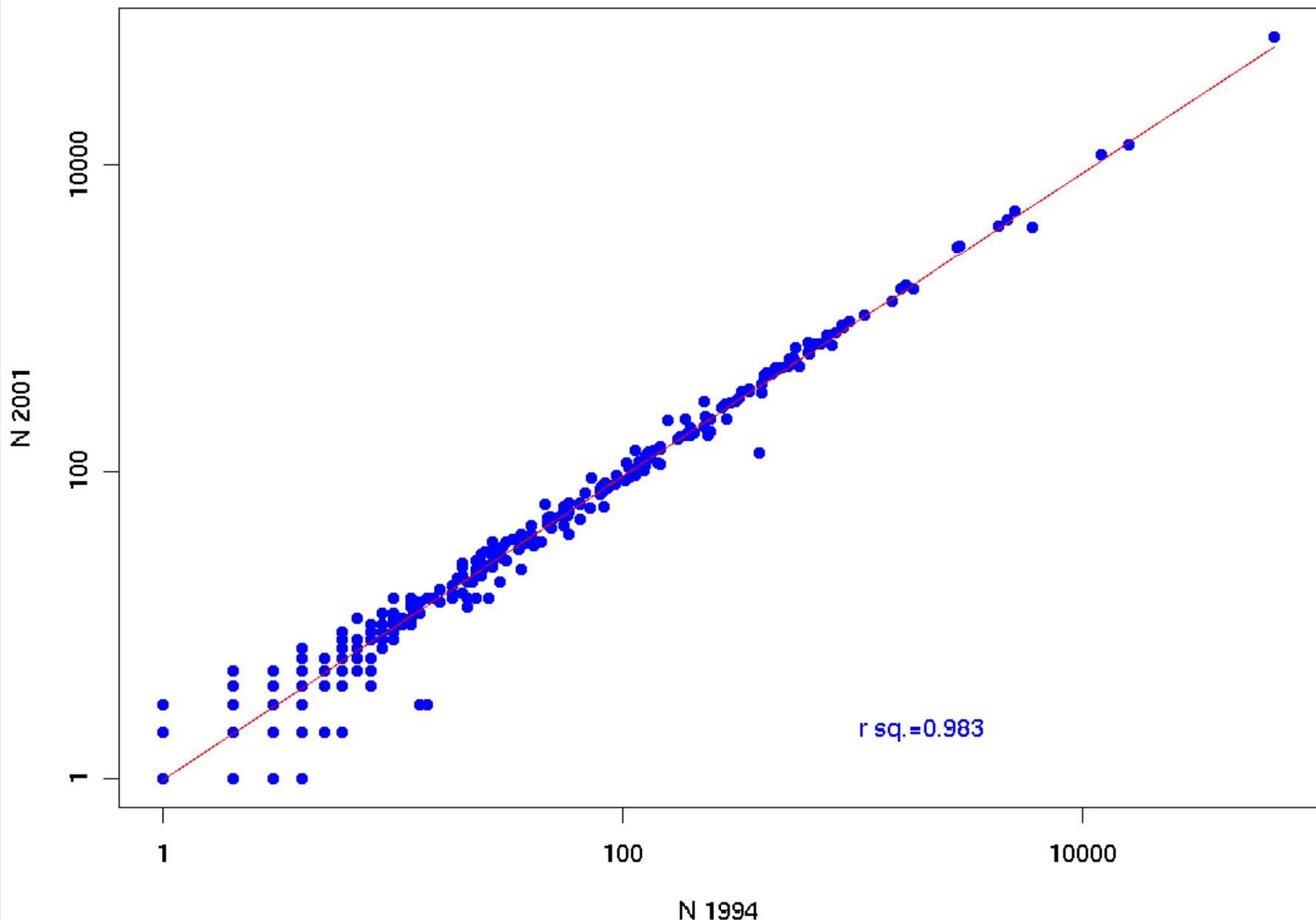
# Change in species abundance at BCI



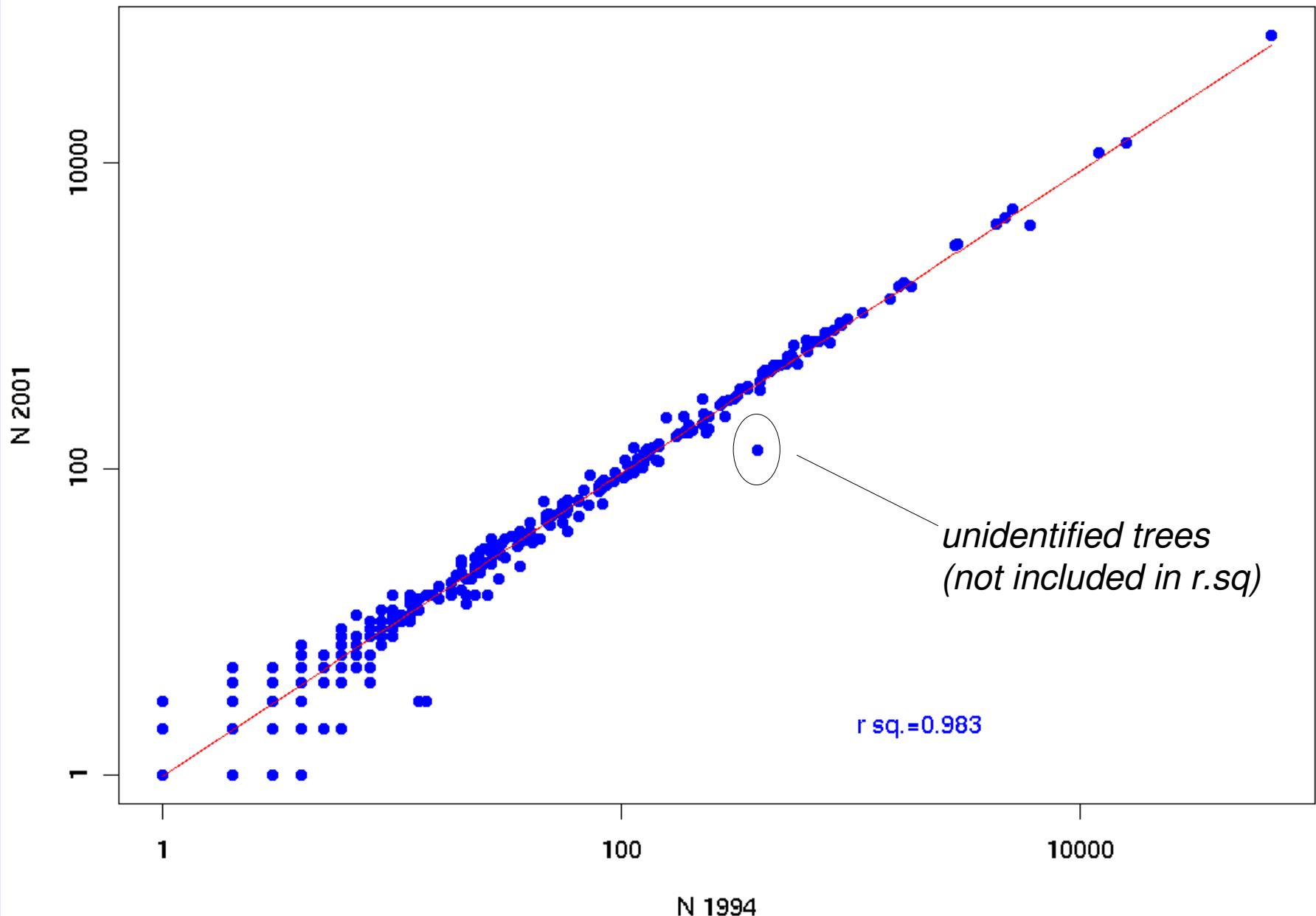
# Change in species abundance at BCI

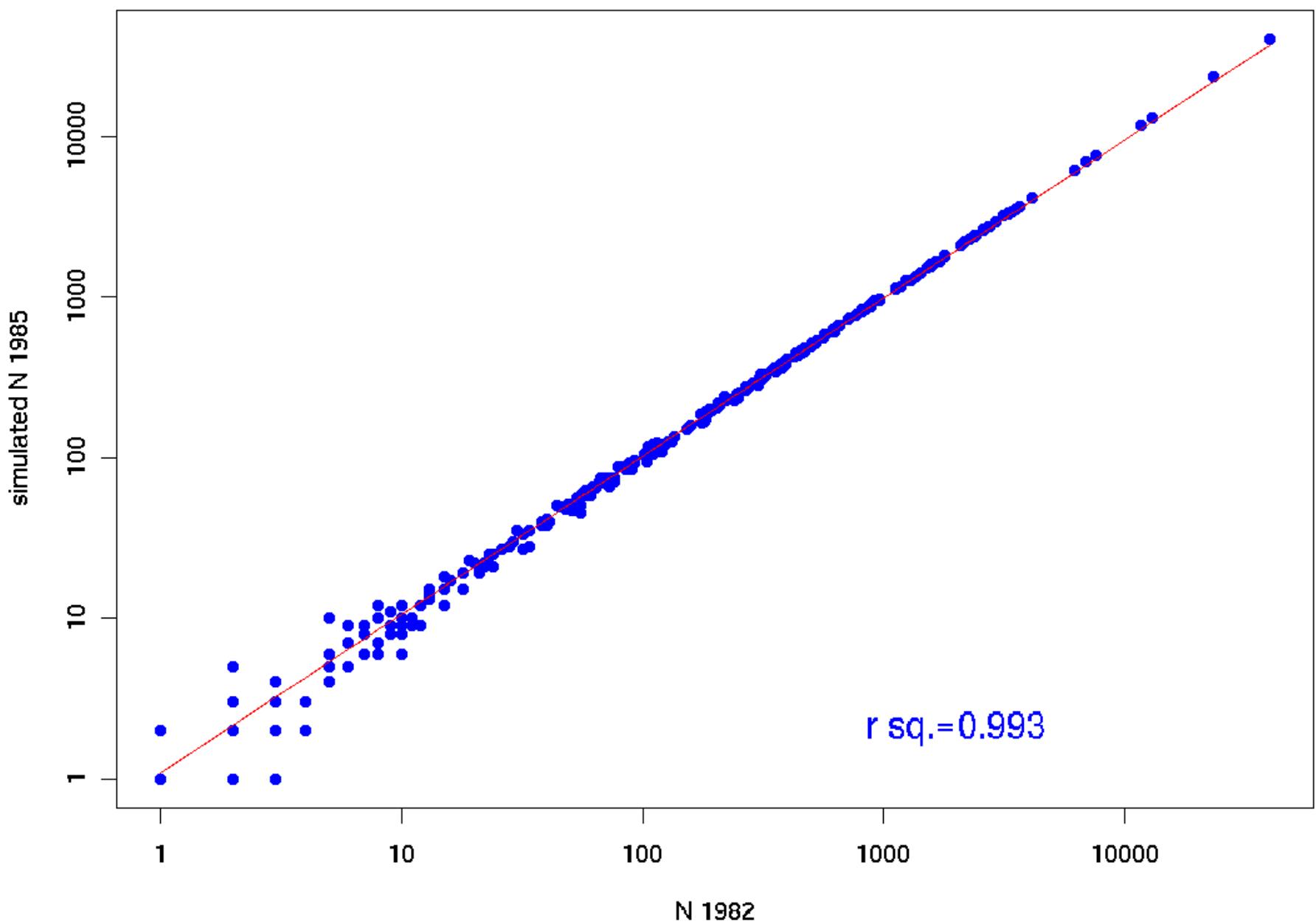


# Change in species abundance Congo



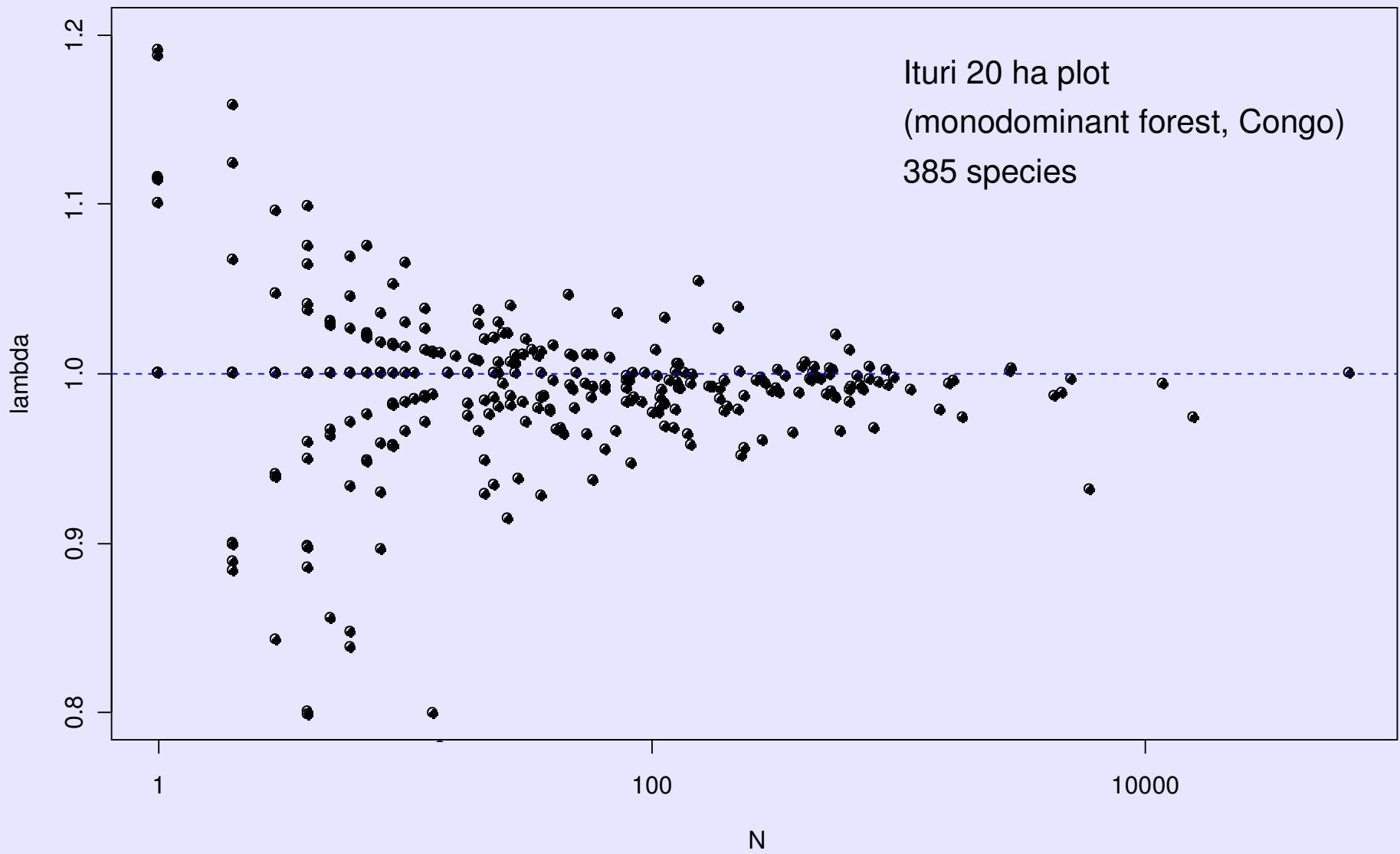
# Change in species abundance Congo



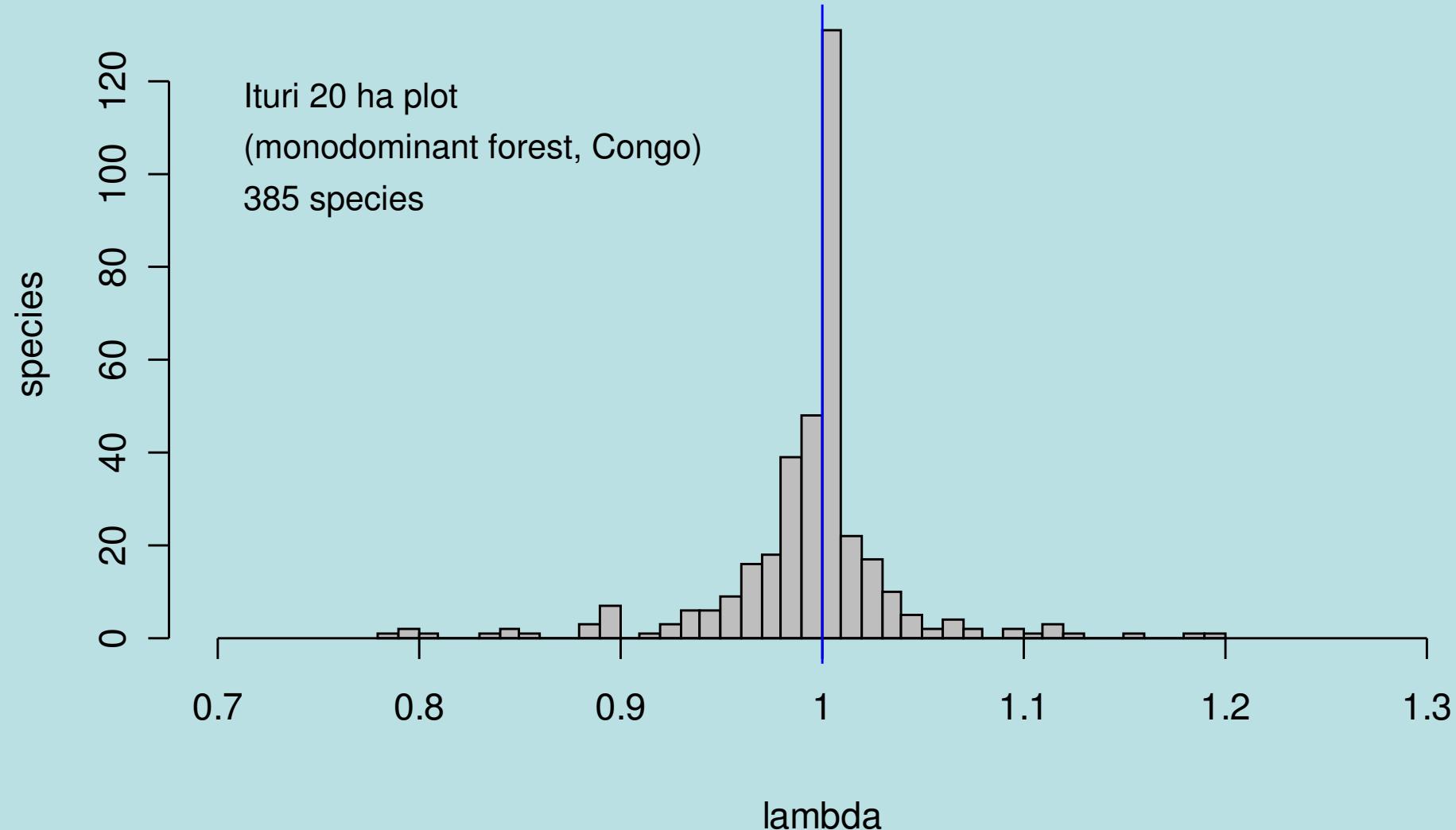




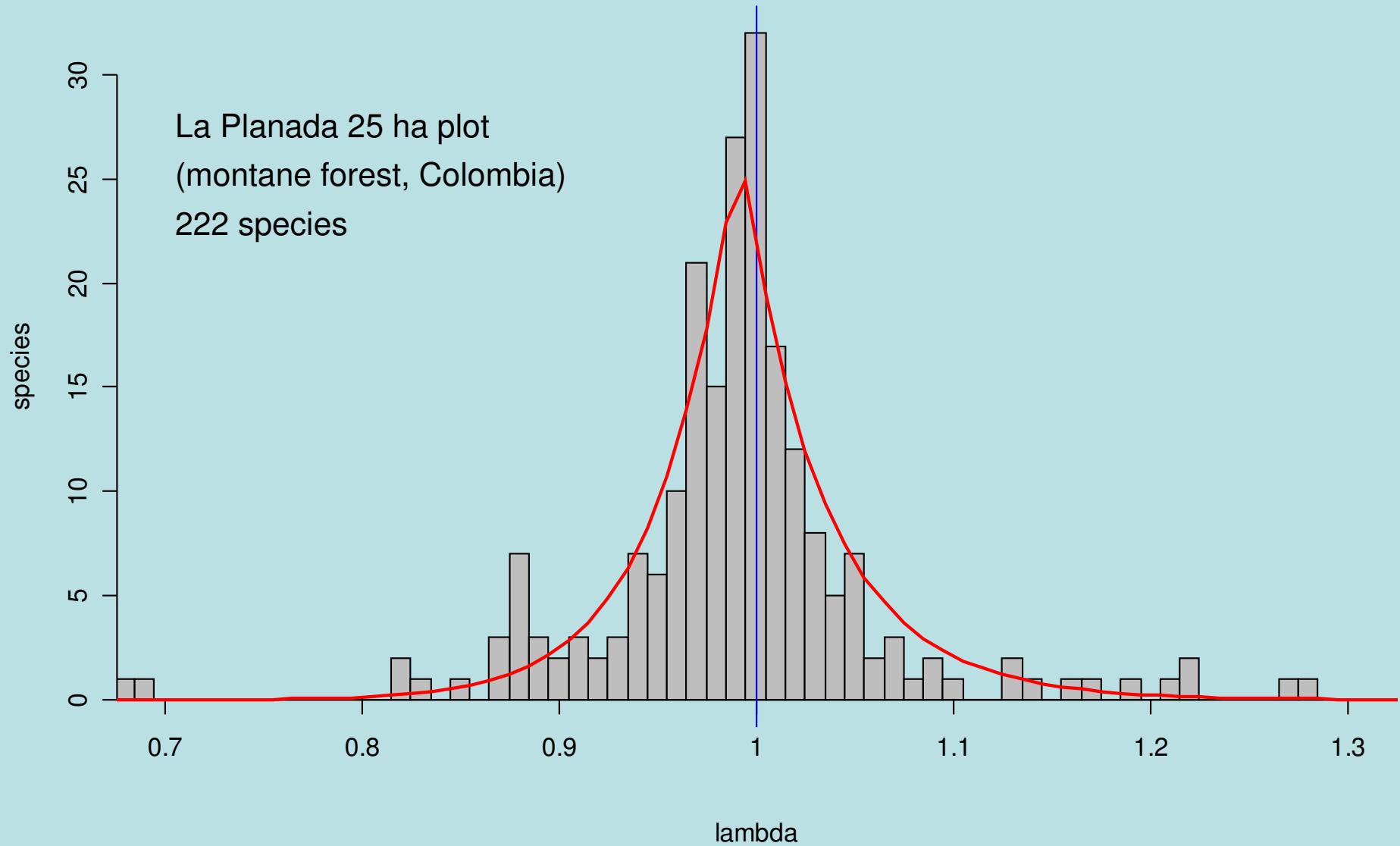
# $\lambda$ varies more in rare species: sampling error



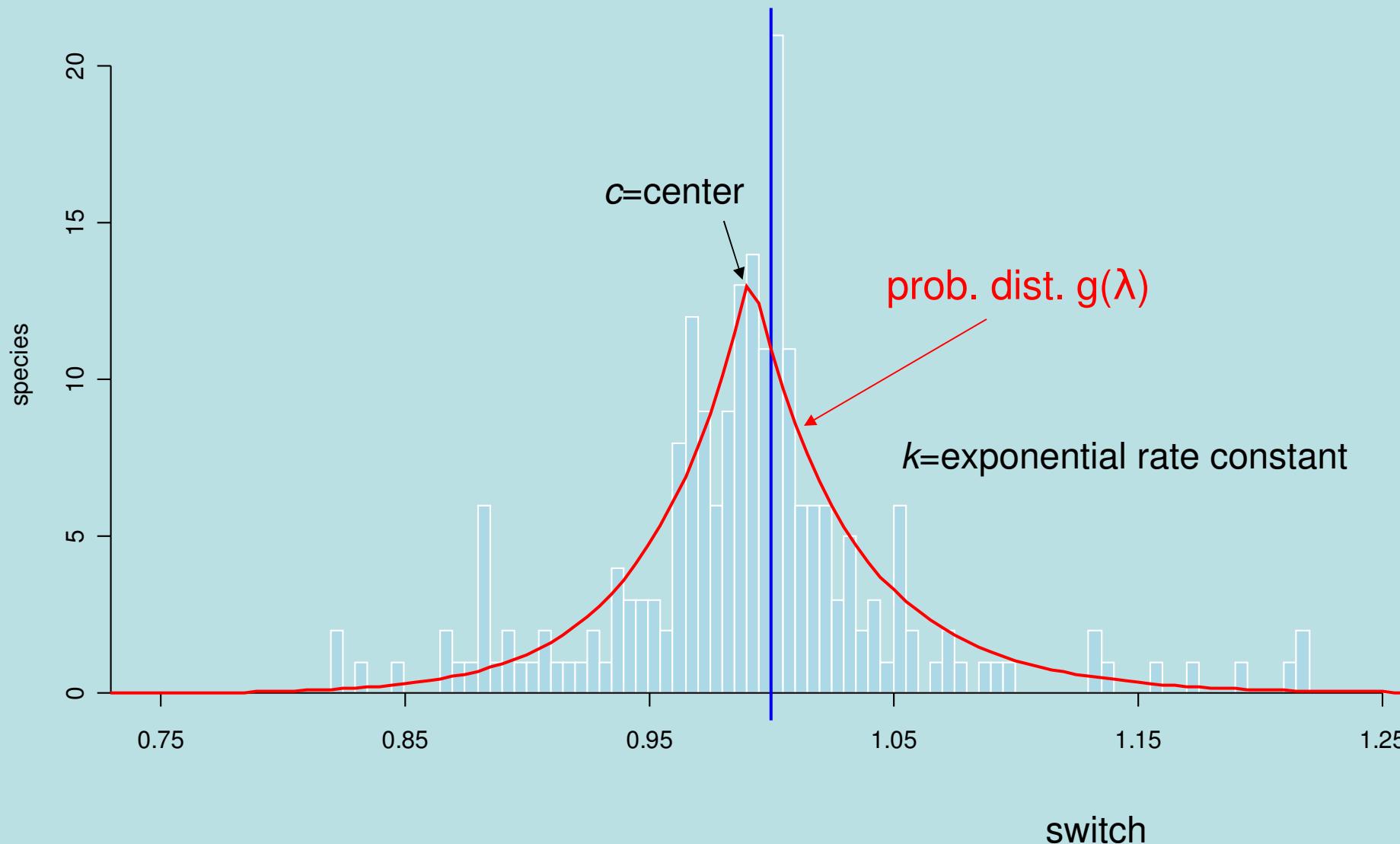
The variance of the distribution of  $\lambda$  reflects the stability of the community



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



# community-wide distribution of $\lambda$ symmetrical exponential



# Calculating the likelihood of observations for all species in a forest

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

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

- 2) Probability of observing population change, given survival  $\theta$  and population growth rate  $\lambda$  (time adjusted)

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

- 3) Likelihood of observations  $N$  and  $\theta$  for species  $i$

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

- 4) Probability of observations for all species in a forest

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

Easier to read in R ...

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

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

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

- 2) Probability of observing population change, given survival  $\theta$  and population growth rate  $\lambda$  (time adjusted)

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

- 3) Likelihood of observations  $N$  and  $\theta$  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  $r = \log(\lambda)$

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

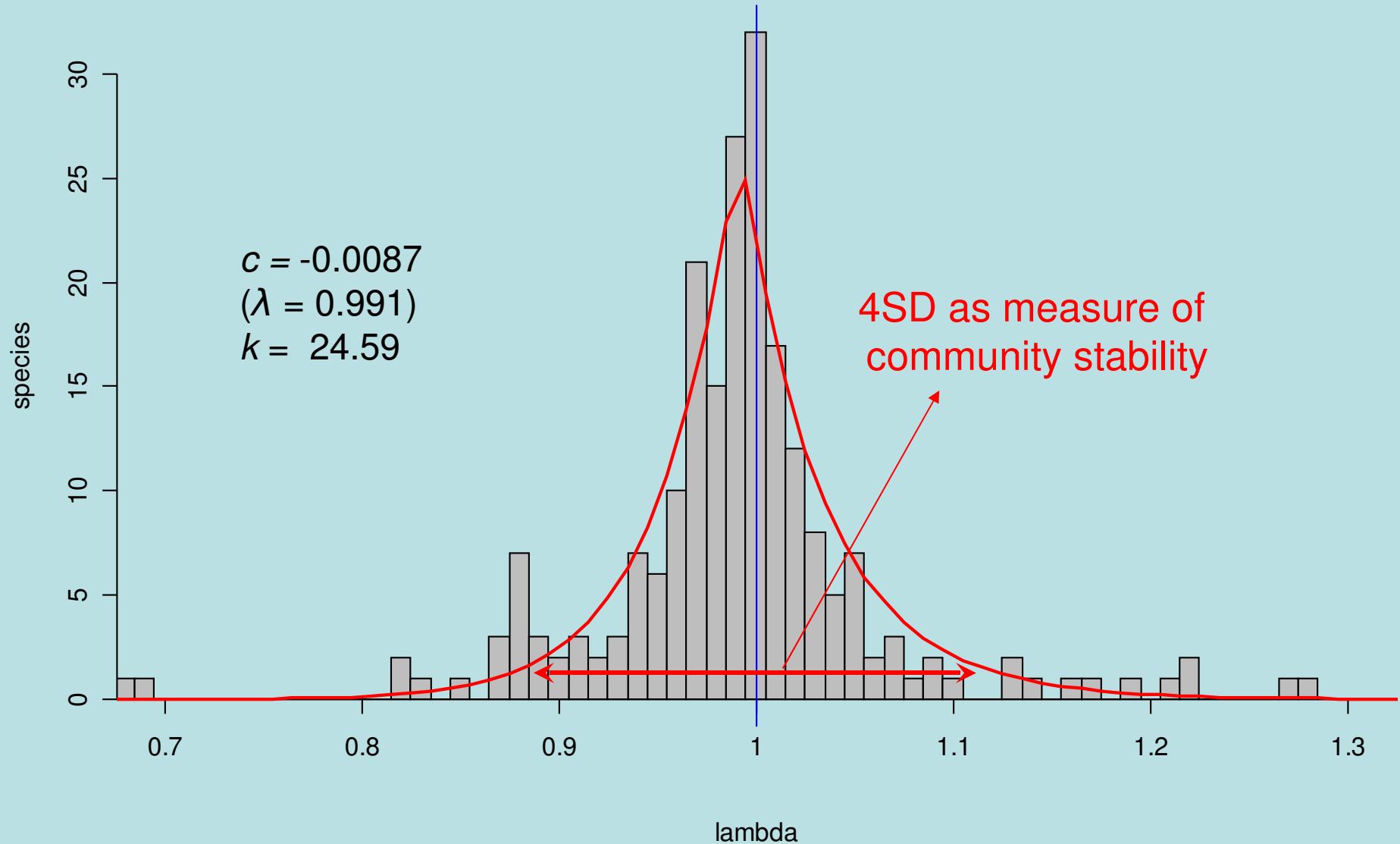
.....

- 4) Probability of observations for all species in a forest

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

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

# The distribution of population changes La Planada, Colombia



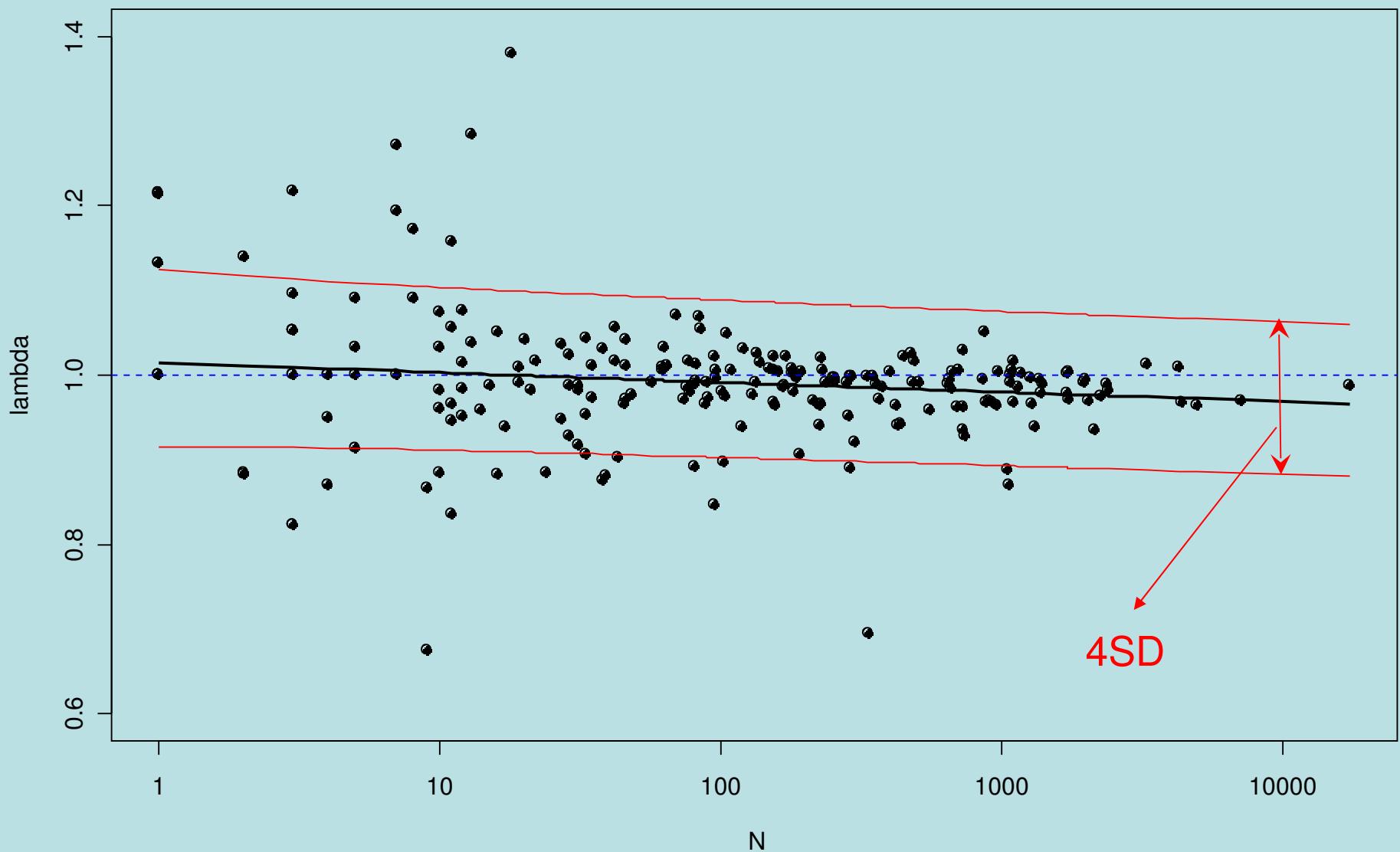
## Testing difference in rate species 4-parameter model

distribution of  $r=\log(\lambda)$  allowing variation with abundance

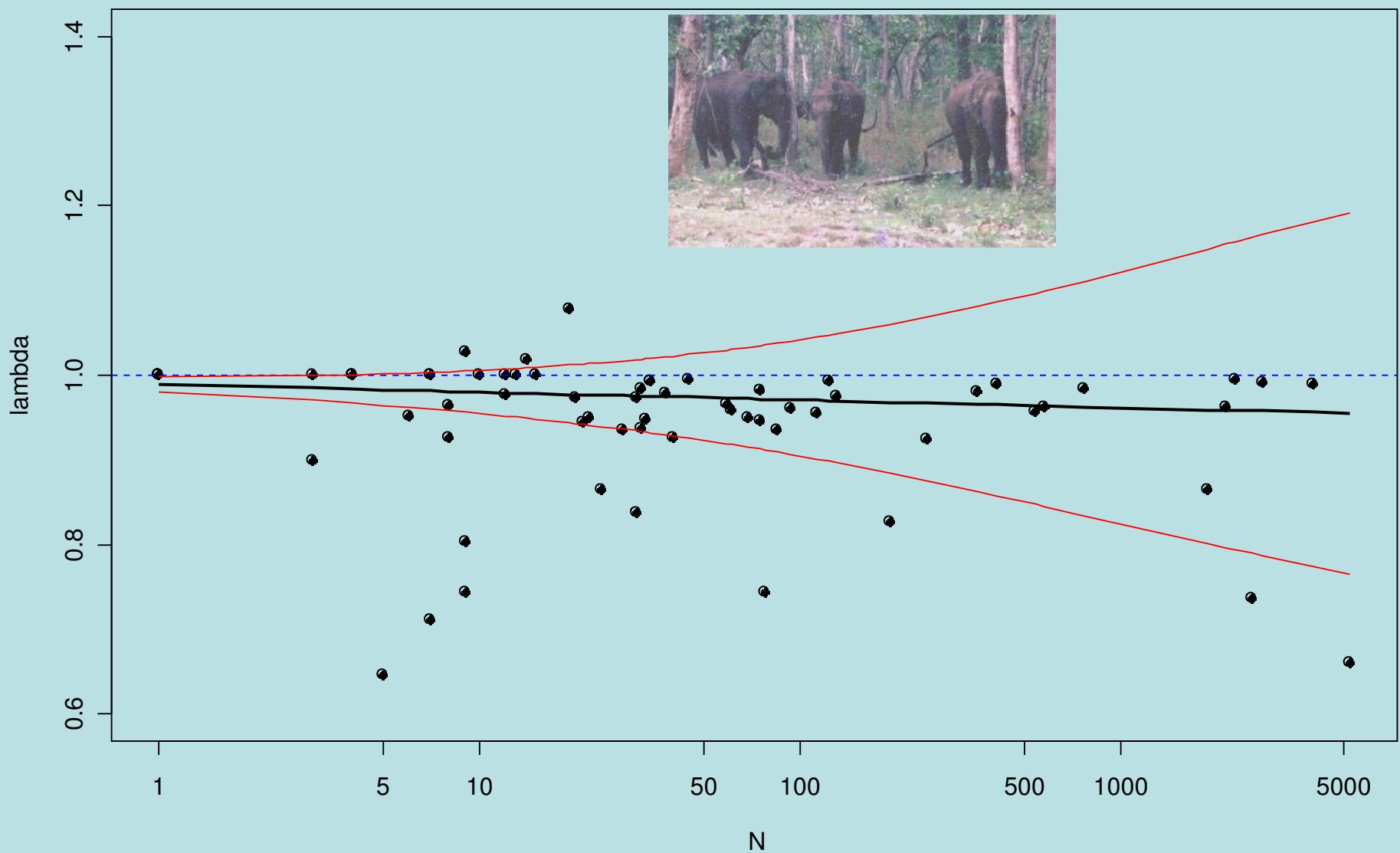
$$g(r) \sim \text{symExponential} \left[ c_o + c \ln(N_0), k_o + \frac{k}{N_0^2} \right]$$

# Population changes as a function of abundance

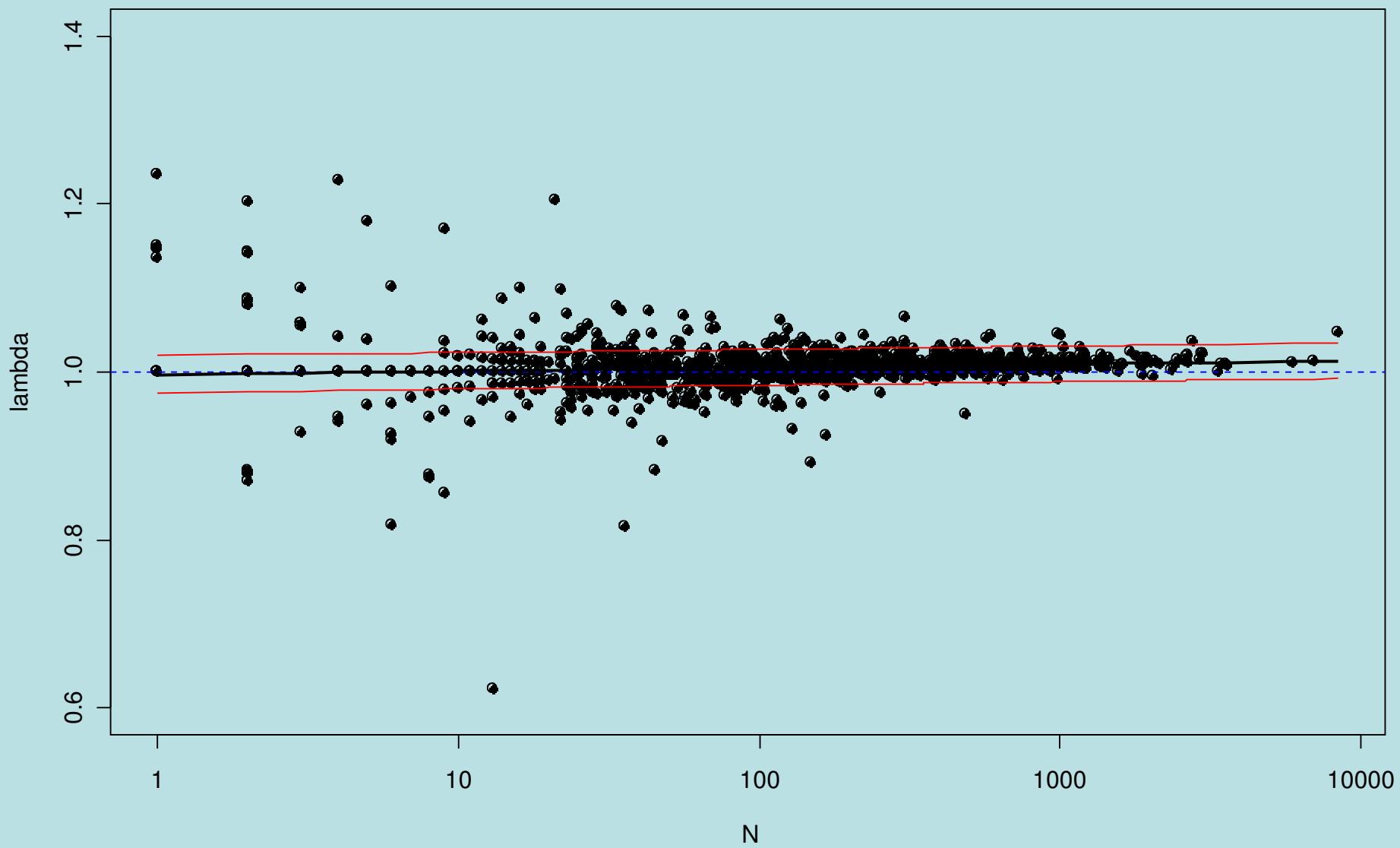
## La Planada, Colombia



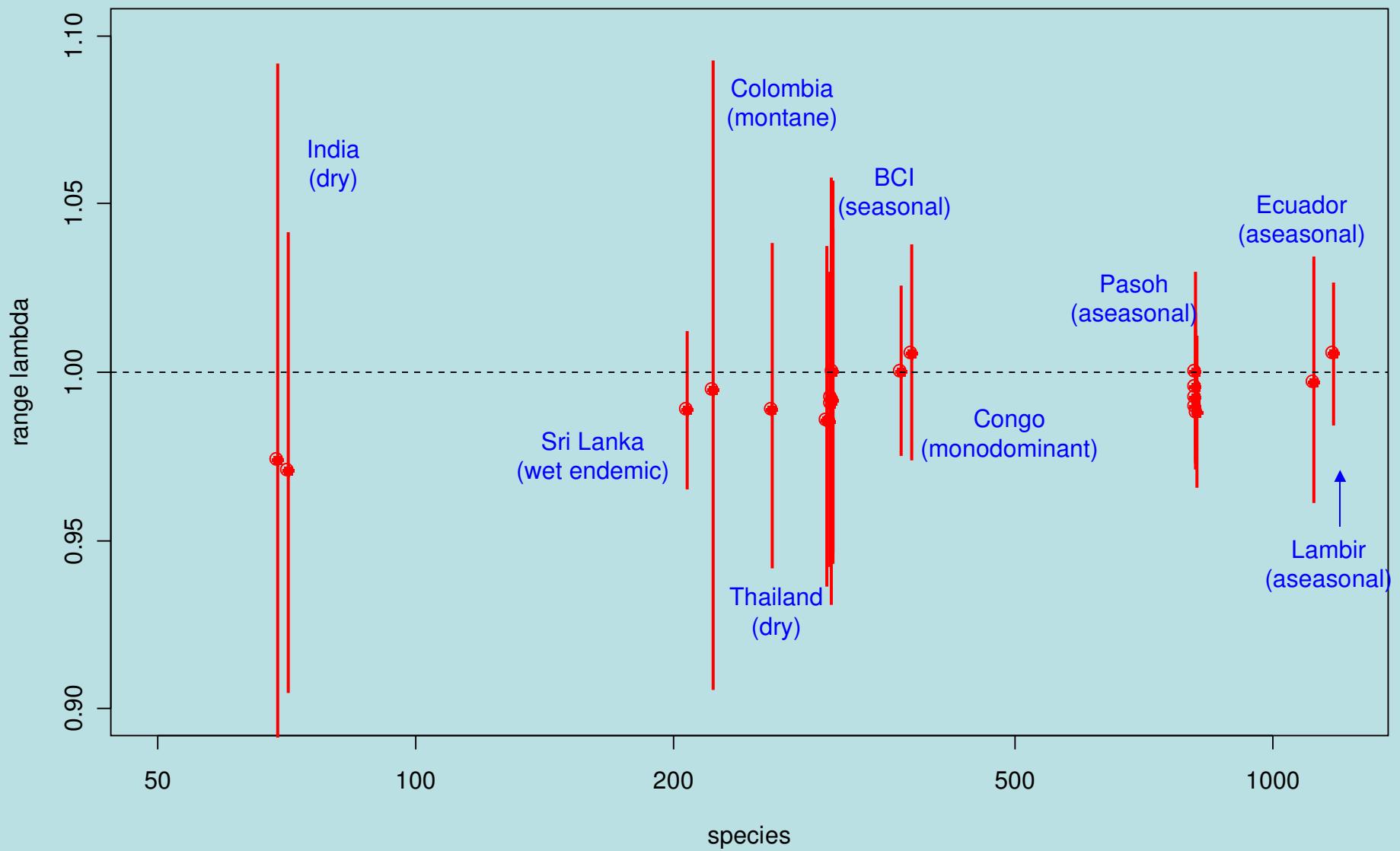
Population changes as a function of abundance  
Mudumalai, India  
(dry deciduous, elephant-dominated, 71 species )



Population changes as a function of abundance  
Lambir, Malayia  
(dipterocarp-dominated, aseasonal, 1180 species)



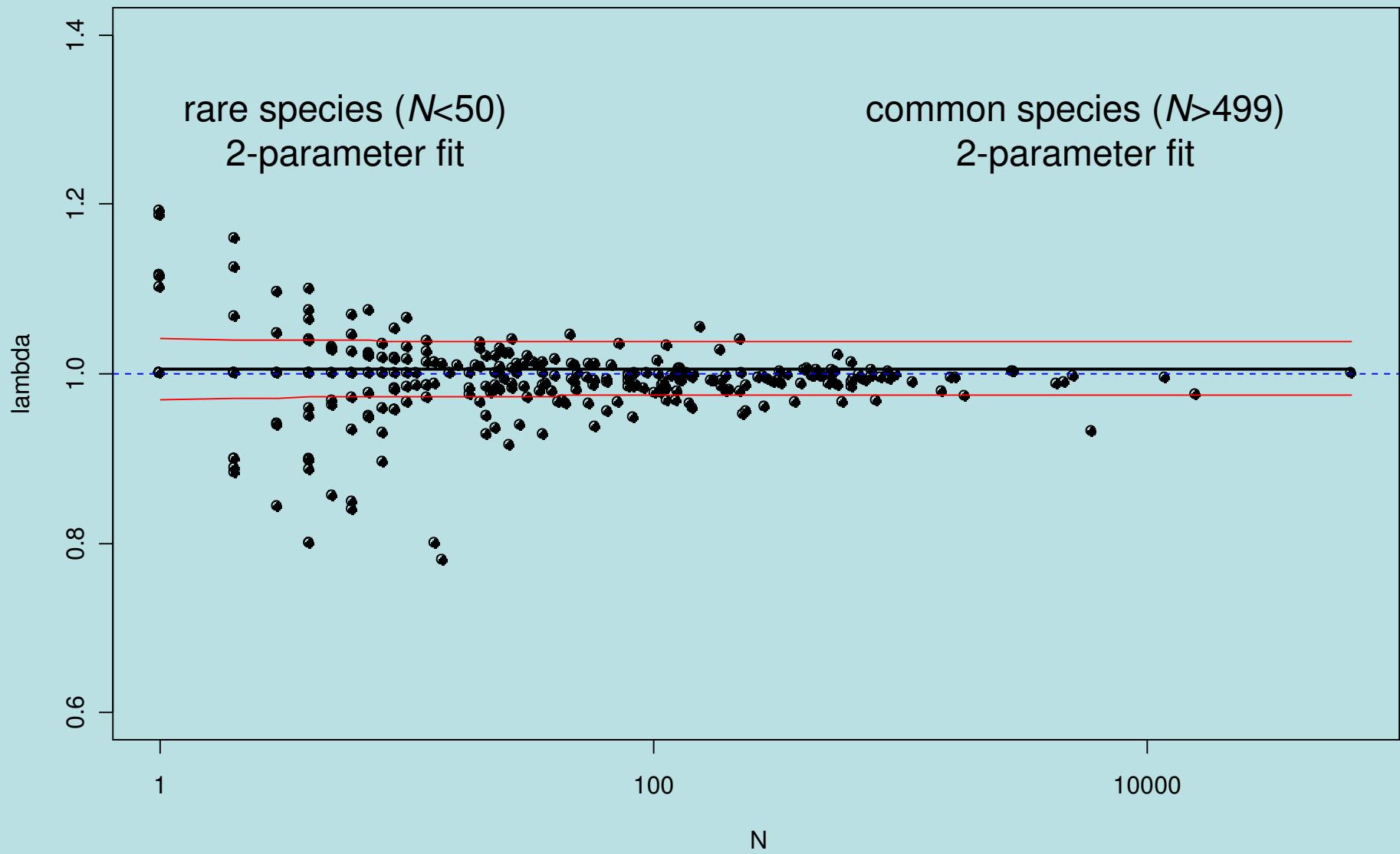
# Stability-diversity



# Population changes as a function of abundance

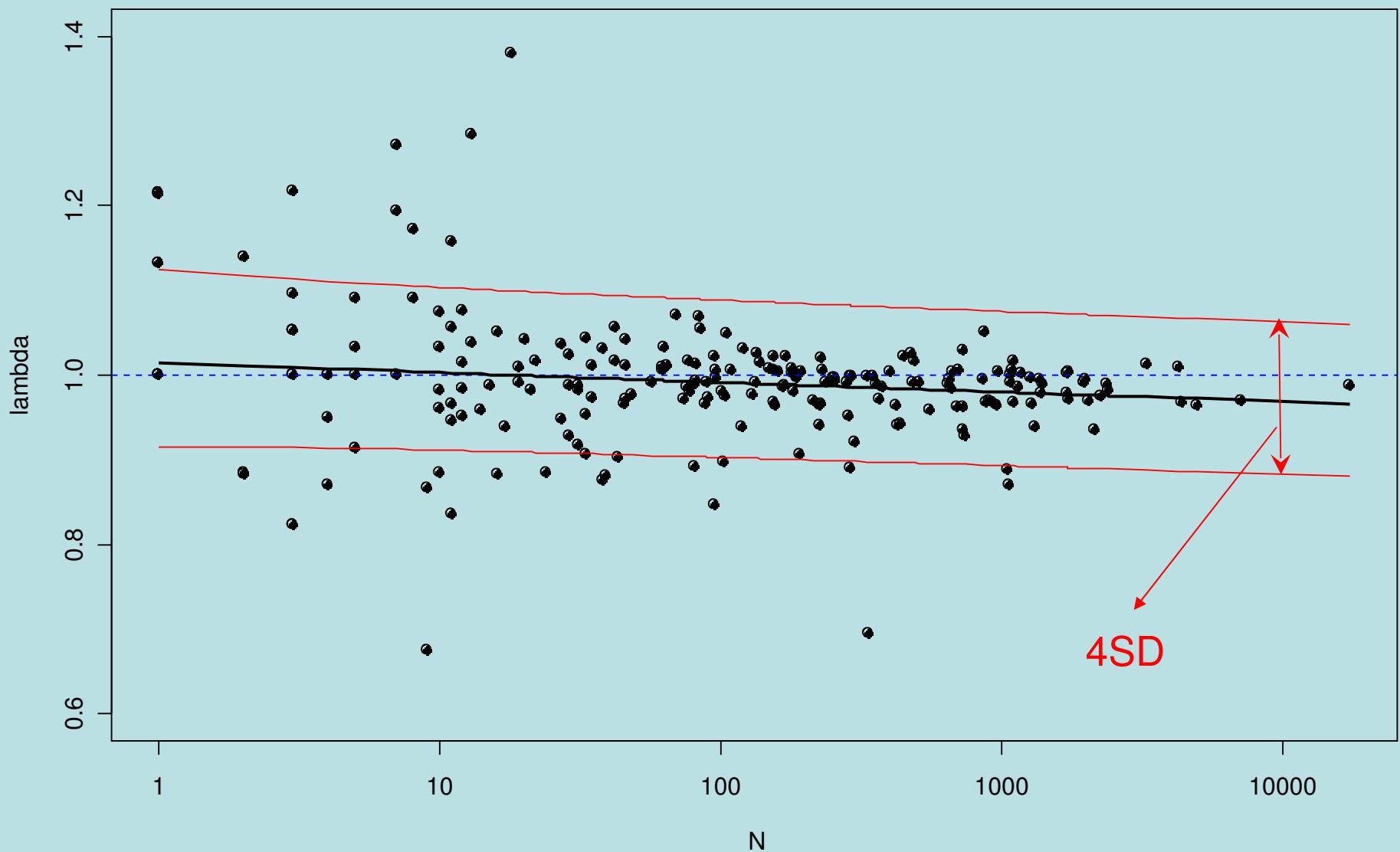
Ituri, Congo

(monodominant caesalpinoid, 368 species)

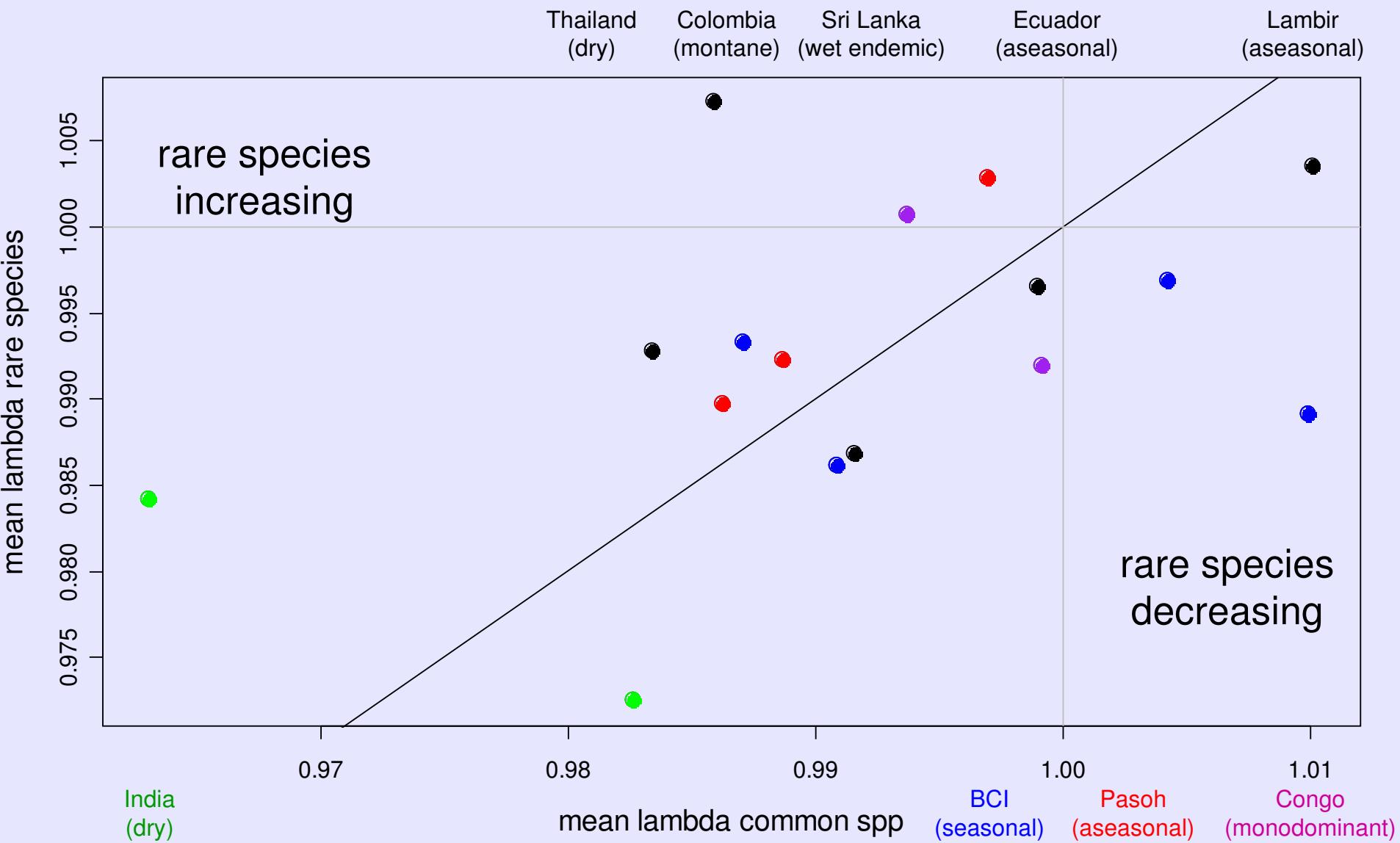


# Population changes as a function of abundance

## La Planada, Colombia

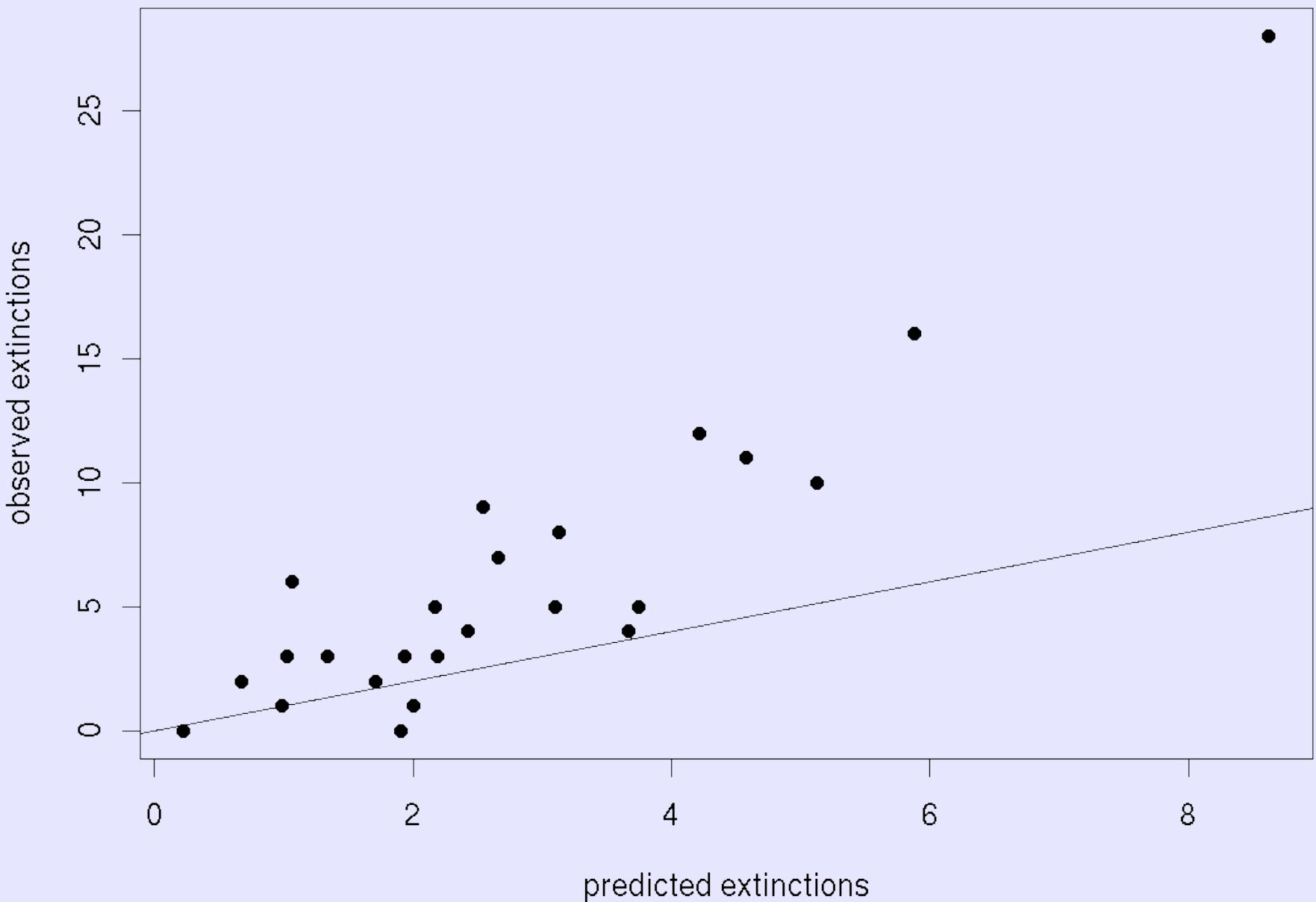


# rare species recovery



site	N°	deaths	births	species	extinct	input	singleton
BCI	234261	20945	33029	300	2	1	22
	241345	37097	39297	301	6	9	21
	243555	36610	21695	298	4	5	17
	228630	36077	21418	297	4	5	23
	213471	31344	20940	296	5	7	22
Pasoh	330352	14264	5709	814	1	1	24
	326797	27052	39017	814	7	3	27
	338262	30193	13701	818	0	2	18
Mudumalai	255554	1368	460	72	1	3	8
	17646	3026	690	70	1	6	7
	15310	1161	3960	65	5	0	4
Lambir	330104	21291	38707	1179	6	3	24
HKK	78448	23027	16841	290	7	10	25
Sinharaja	205105	21824	9696	206	0	2	7
Yasuni	144939	22558	20618	1114	45	28	69
La Planada	112293	30020	23073	220	20	0	10
Edoro	161818	16470	8966	373	14	11	50
Lenda	136235	13442	10453	360	10	8	36

Observed extinctions vs. extinctions predicted  
due to stochastic death



## 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

