Mechanisms maintaining high species diversity in tropical rainforests

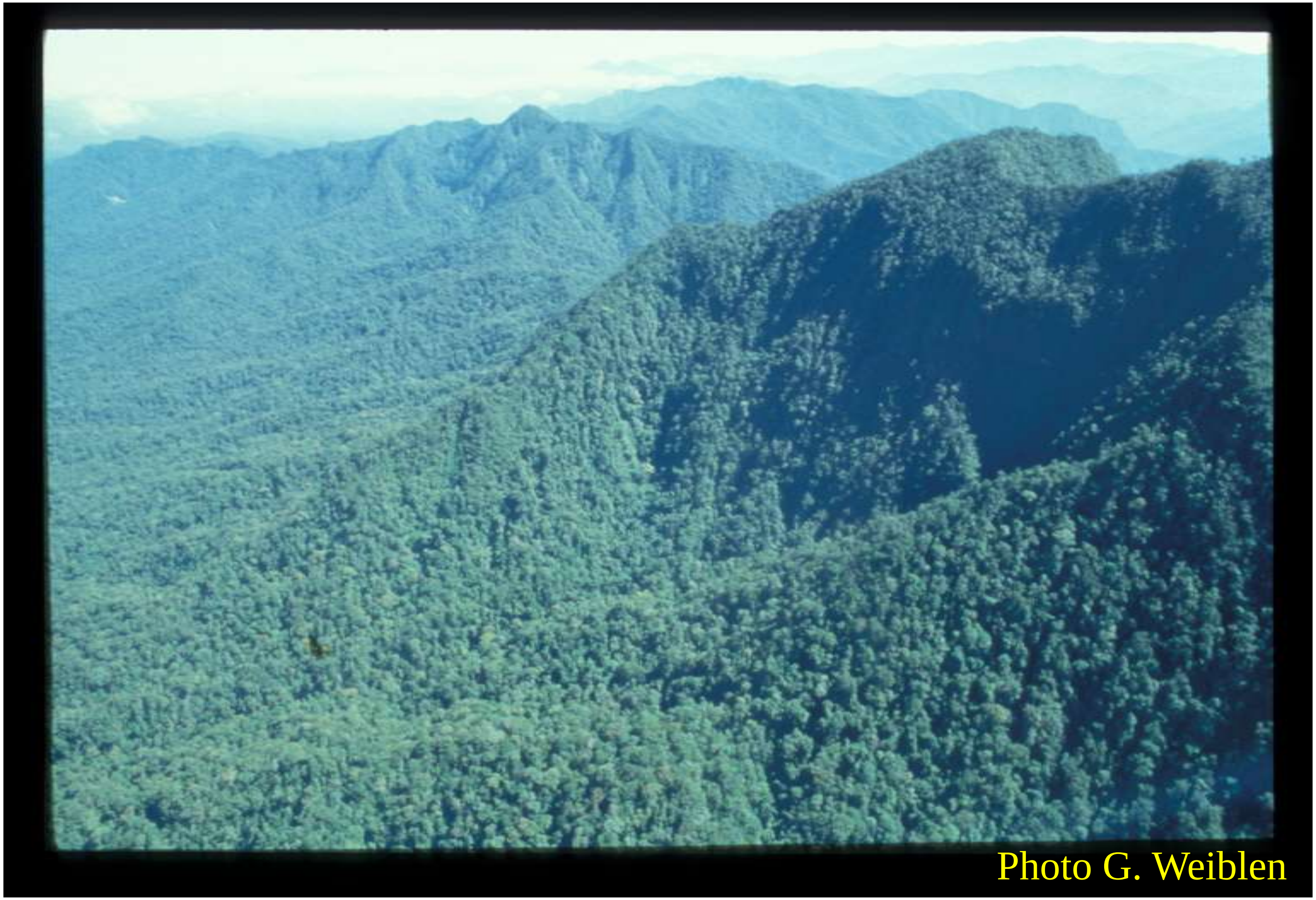
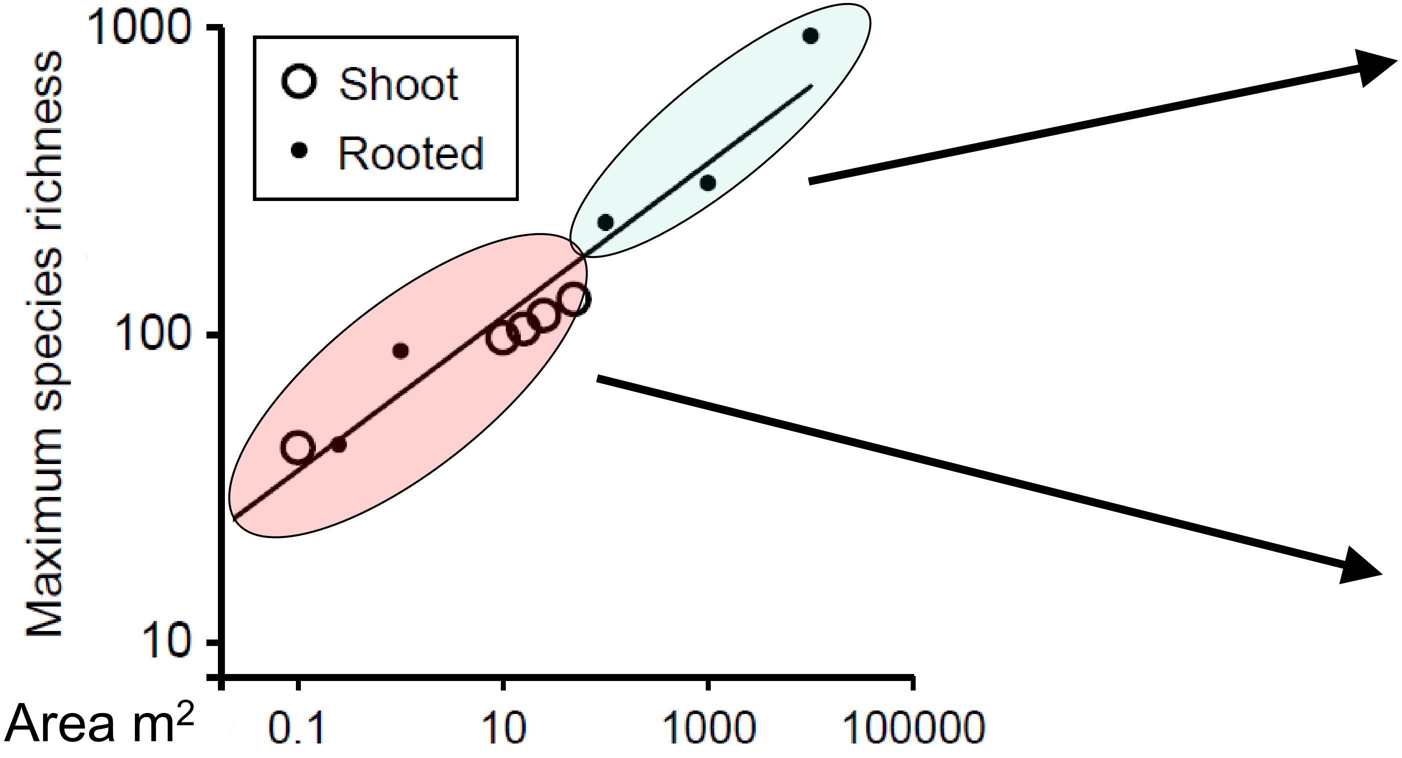


Photo G. Weiblen

Quiz question: where is the global maximum of vascular plant diversity?

Global diversity maxima for vascular plants



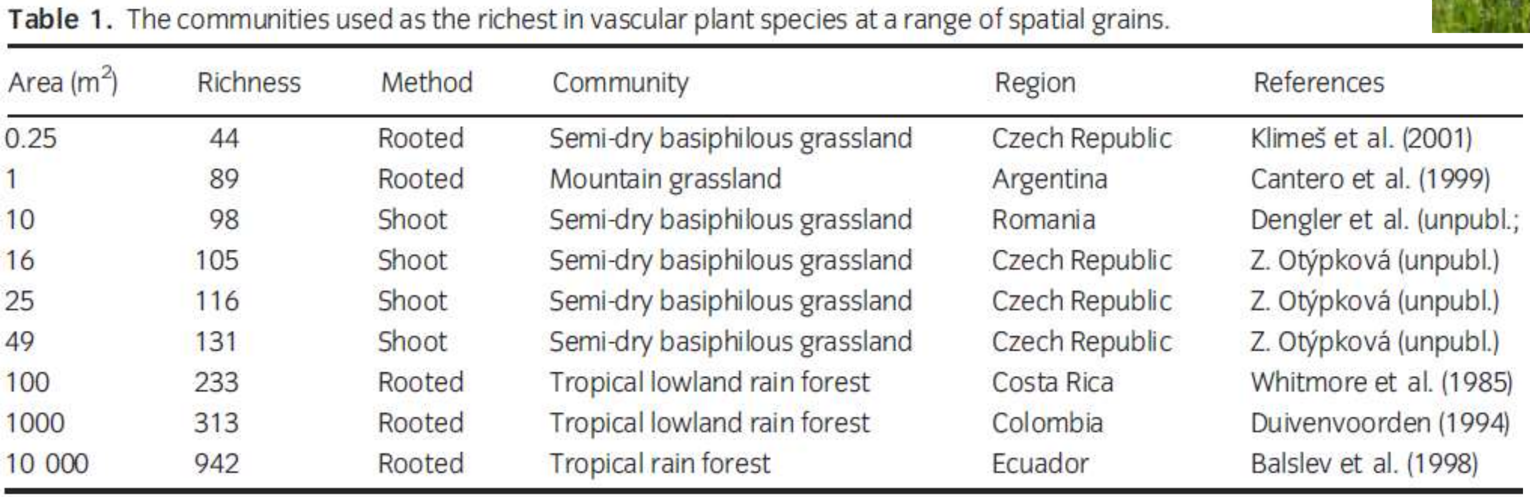


Table 1. The communities used as the richest in vascular plant species at a range of spatial grains.

Area (m^2)	Richness	Method	Community	Region	References
0.25	44	Rooted	Semi-dry basiphilous grassland	Czech Republic	Klimeš et al. (2001)
1	89	Rooted	Mountain grassland	Argentina	Cantero et al. (1999)
10	98	Shoot	Semi-dry basiphilous grassland	Romania	Dengler et al. (unpubl.;
16	105	Shoot	Semi-dry basiphilous grassland	Czech Republic	Z. Otýpková (unpubl.)
25	116	Shoot	Semi-dry basiphilous grassland	Czech Republic	Z. Otýpková (unpubl.)
49	131	Shoot	Semi-dry basiphilous grassland	Czech Republic	Z. Otýpková (unpubl.)
100	233	Rooted	Tropical lowland rain forest	Costa Rica	Whitmore et al. (1985)
1000	313	Rooted	Tropical lowland rain forest	Colombia	Duivenvoorden (1994)
10 000	942	Rooted	Tropical rain forest	Ecuador	Balslev et al. (1998)

J. Veg. Sci. 23 (2012)
796–802
Plant species richness:
the world records
Wilson JB et al

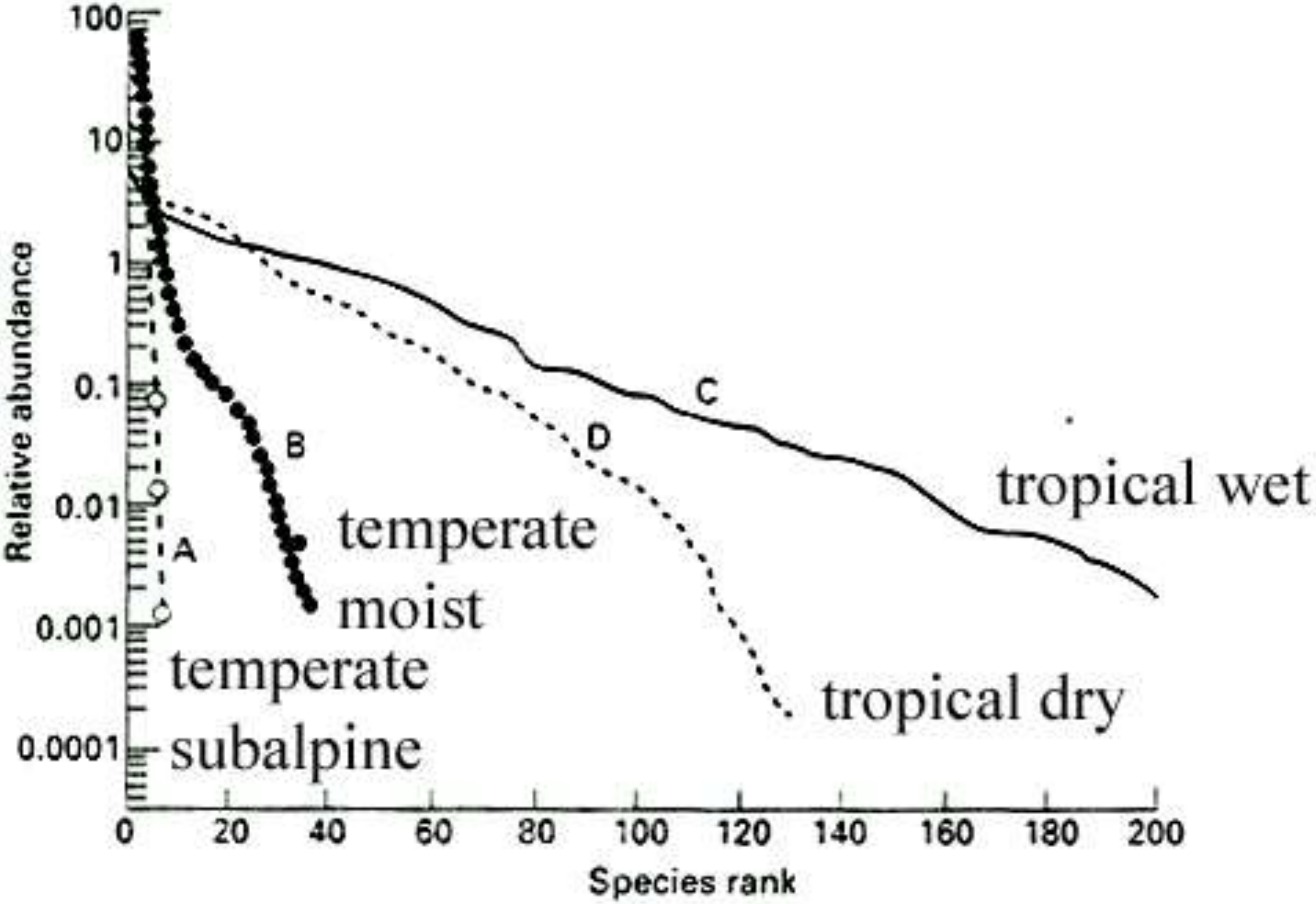
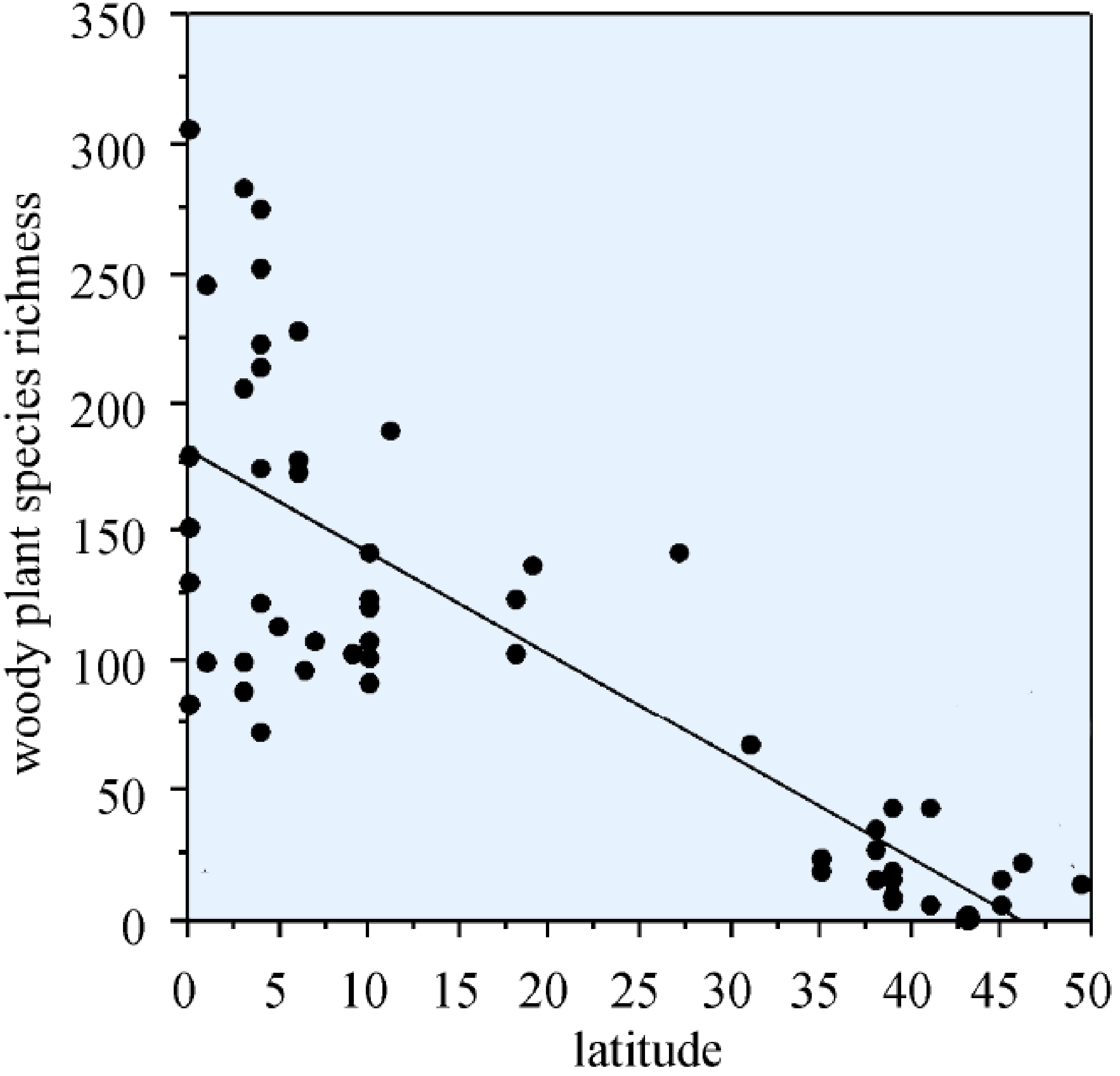


Fig. 7.16 Rank–abundance patterns of tropical and temperate forests: A, temperate montane (subalpine) forest (Smoky Mountains, Tennessee); B, temperate moist forest (Smoky Mountains, Tennessee); C, tropical wet forest (Manaus, Brazil); D, tropical dry forest (Guanacaste, Costa Rica). (After Hubbell 1979.)

Latitudinal gradient in species diversity
woody plants with DBH>10cm in 1 ha forest plots



Novotny et al. 2006, Science

1 ha of lowland rainforest = 150-300 tree species with DBH>10cm

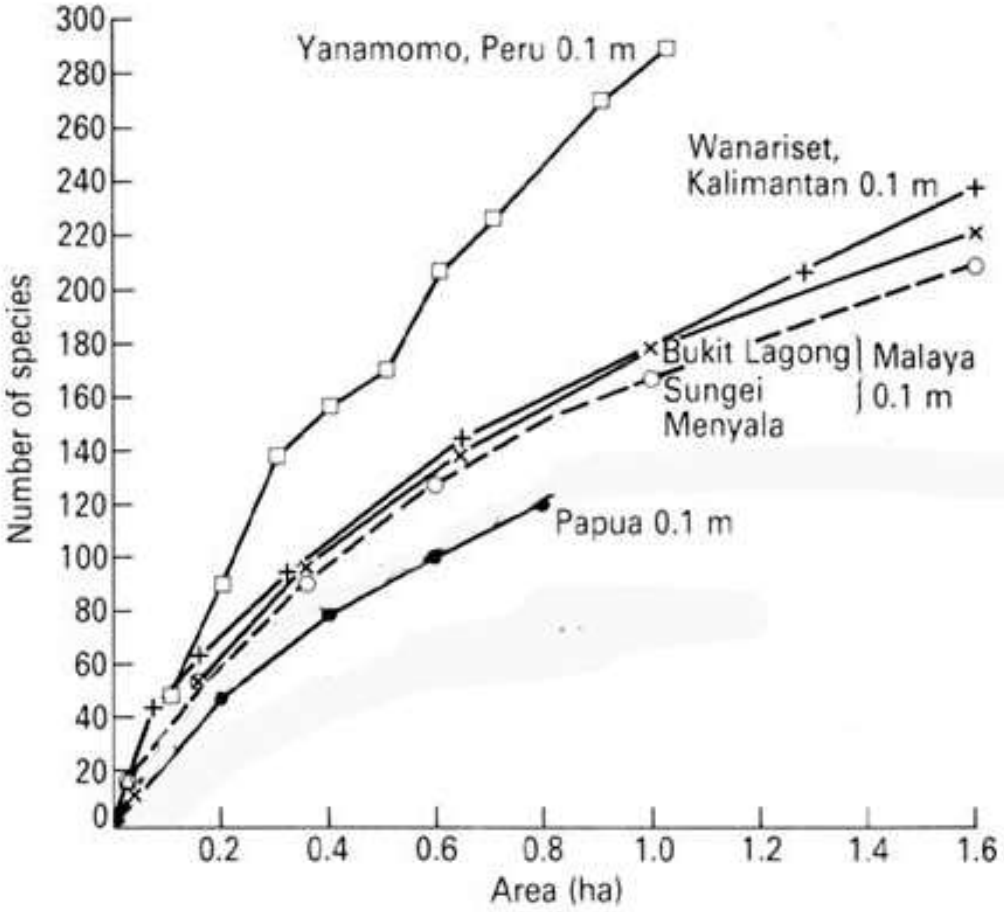
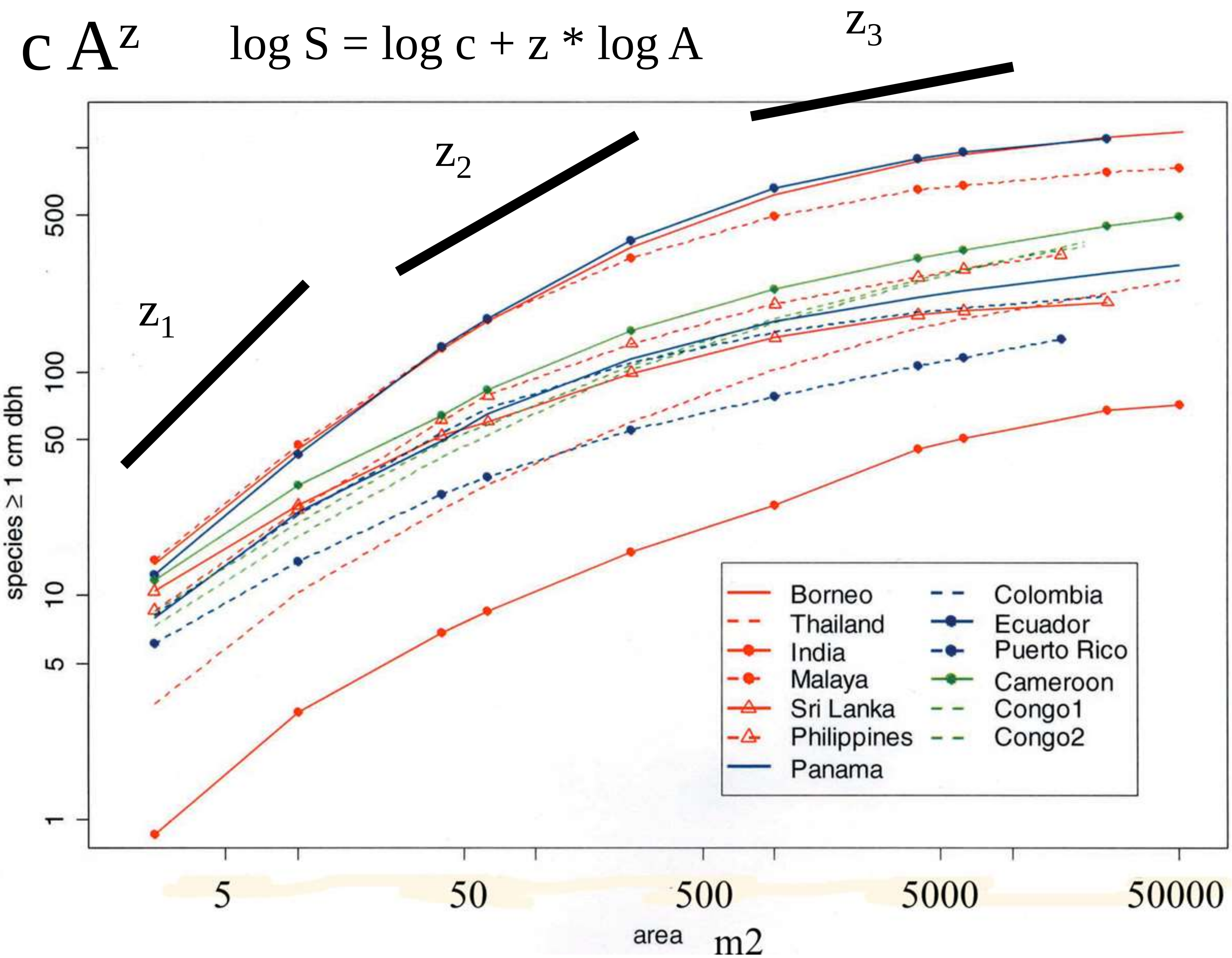


Fig. 2.28. Species area curves for tropical lowland evergreen rain forests. (After Whitmore 1984*a* and Genry 1988*b*).

$S = c A^z$ $\log S = \log c + z * \log A$



CONDIT, R., et al. (2005). "Tropical tree alfa-diversity: Results from a worldwide network of large plots." *Biol. Skr.* **55**: 565-582.

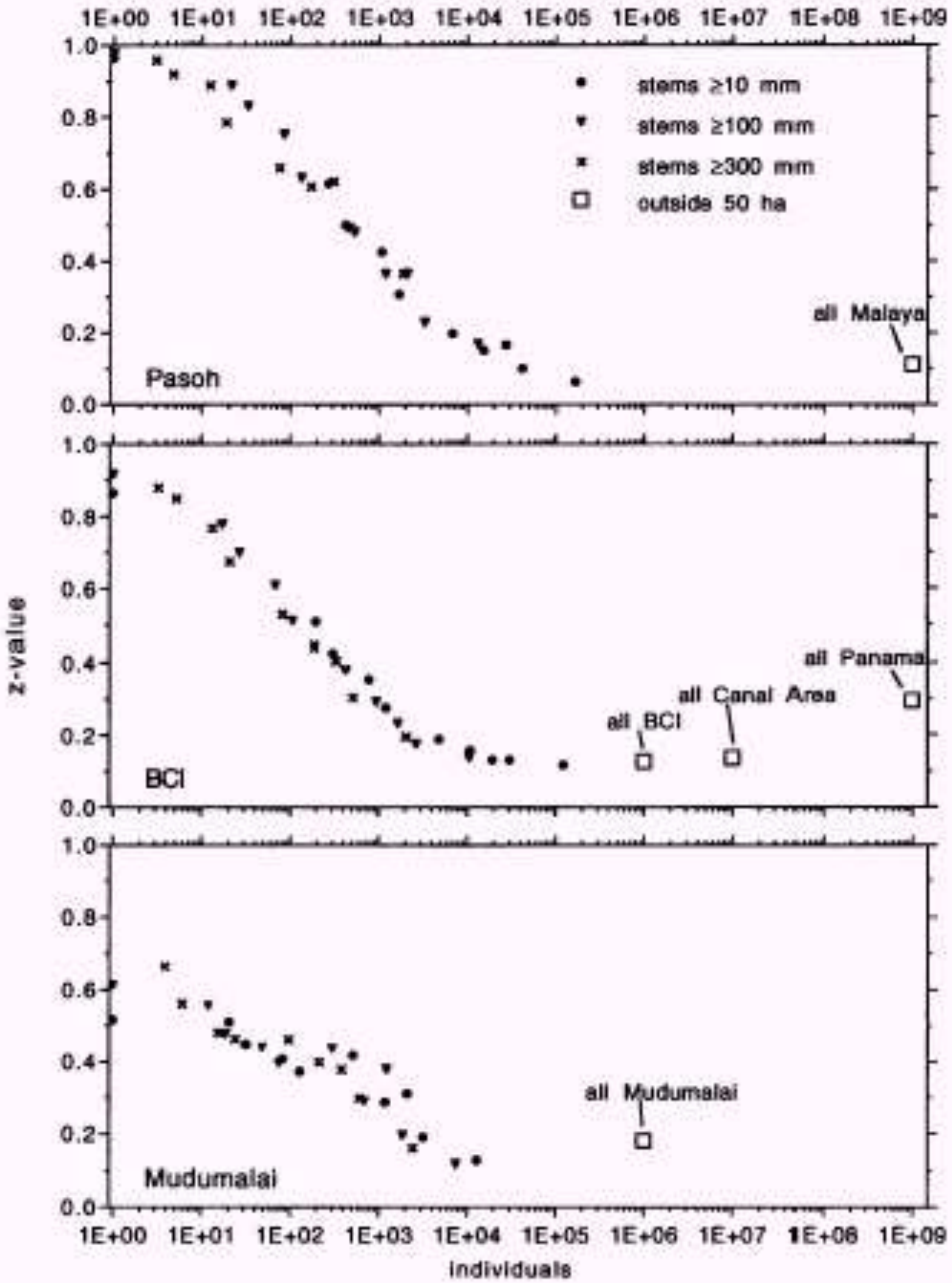
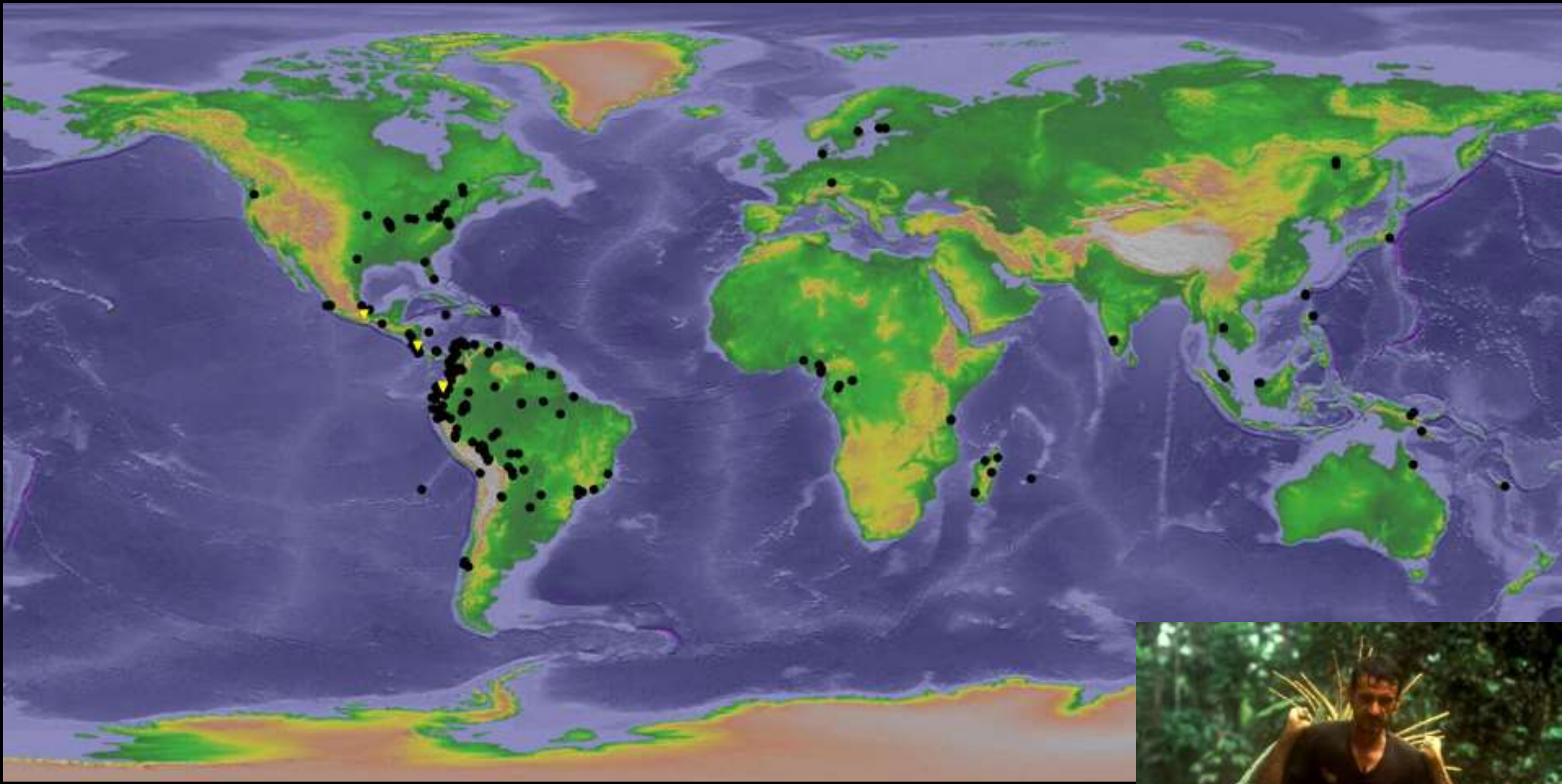


Fig. 4 Slope of log–log species–individual curves (*z*-values) for three 50-ha plots and from 50-ha plots to larger regions.

Slope of log-log species accumulation curves depends on spatial scale

Condit, R. et al. 1996. *Journal of Ecology*, 84: 5

Alwyn Gentry's plots: 2 x 50 m = 0.1 ha DBH>2.5cm, 226 plots

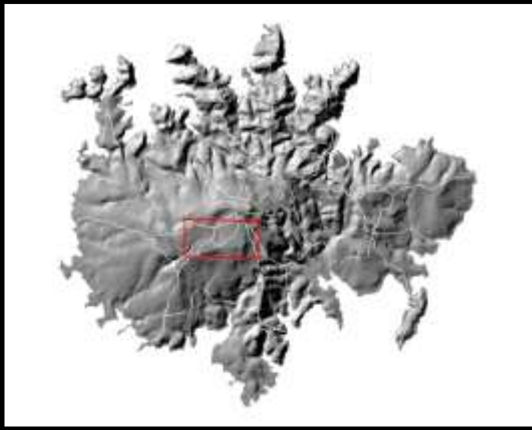


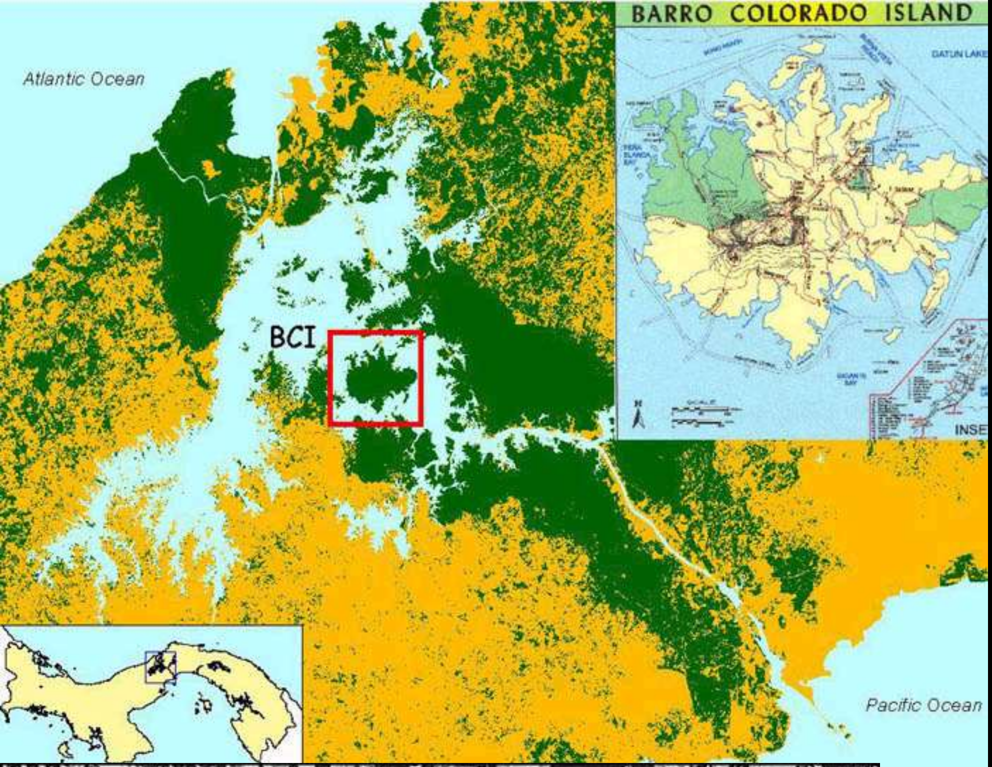
Start of the most successful ecological research in tropical botany: in 1980, Stephen Hubbell and Robin Foster had a good inventory

1 ha stems with DBH>5cm
~1,000 stems

→

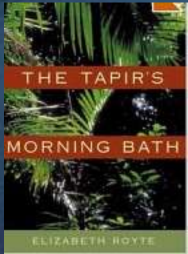
50 ha stems with DBH>1cm
~300,000 stems



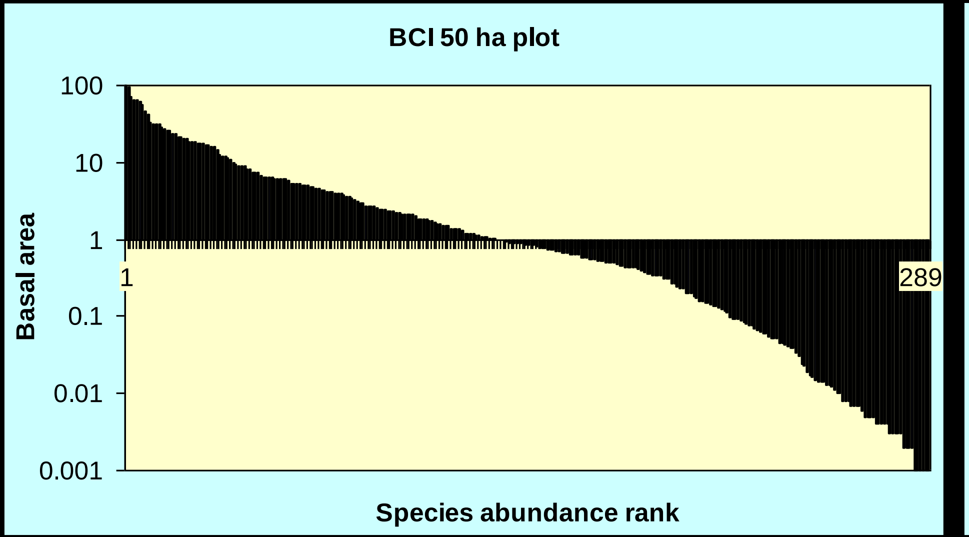


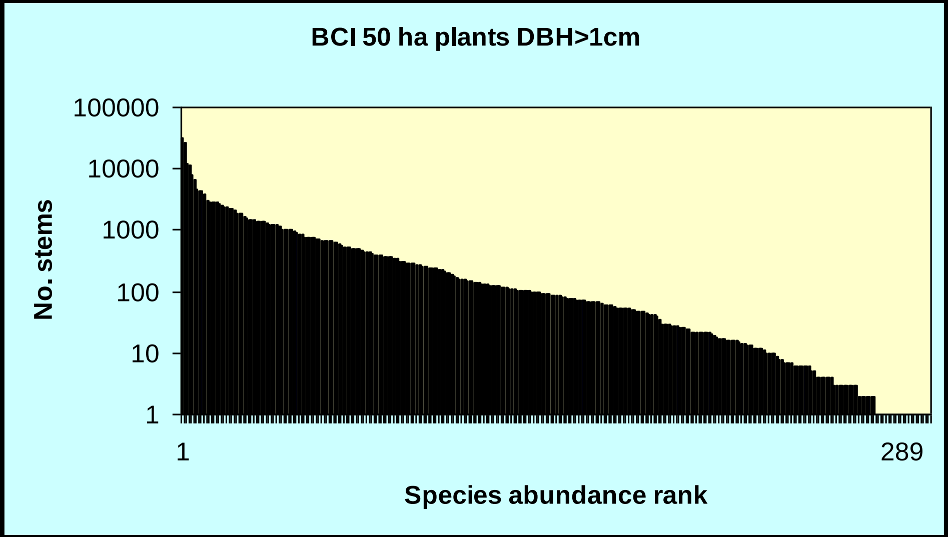
Mecca of tropical ecology: the Barro Colorado Island

1924 BCI lab opens



Barro Colorado Island: the first 50-ha plot





Forest Dynamics Plots

- Large scale (16-52 ha)

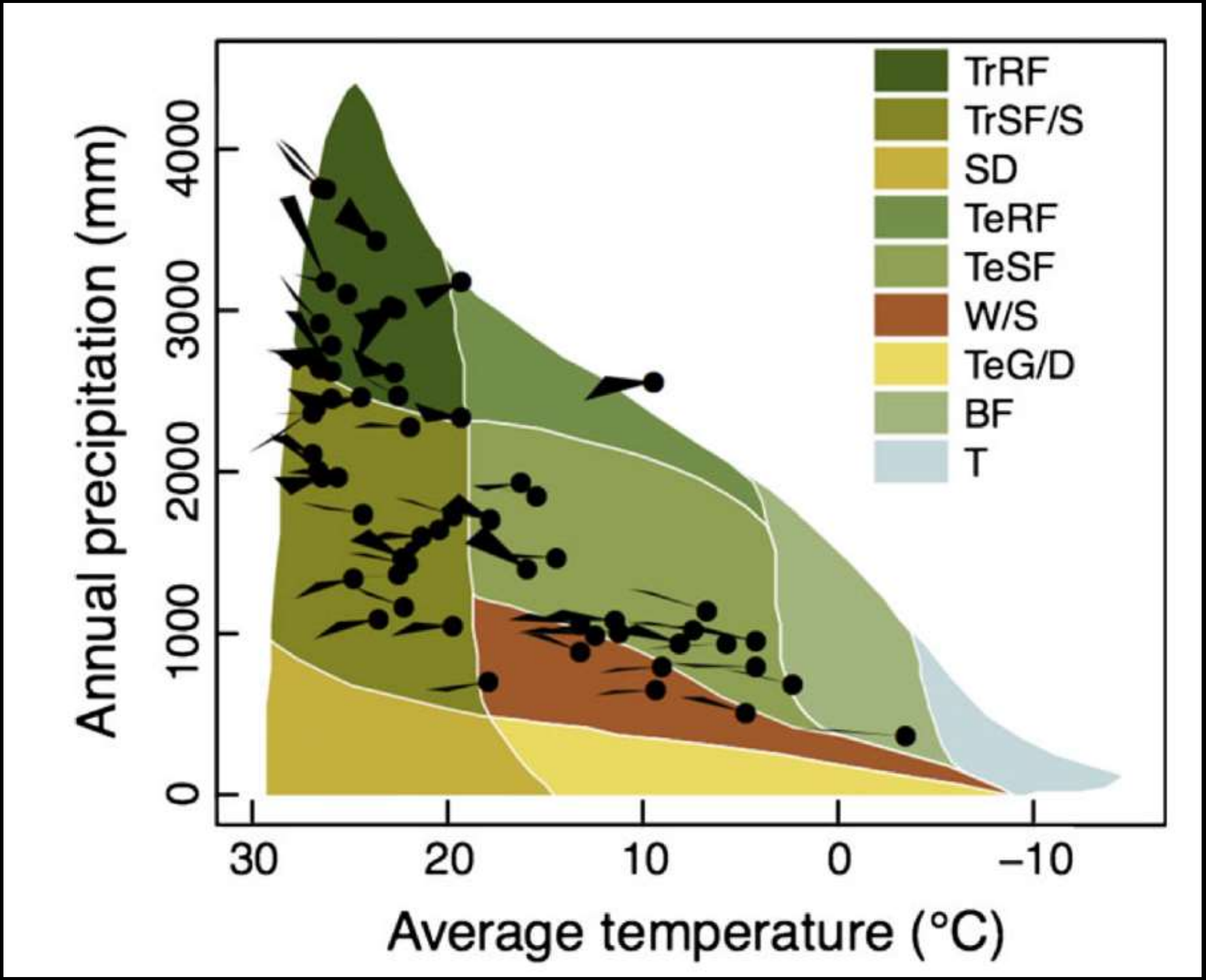
- All stems ≥1 cm mapped, measured, tagged, and identified to species

- Entire plot recensused every 5 years

- Standardized method used by all CTFS research sites

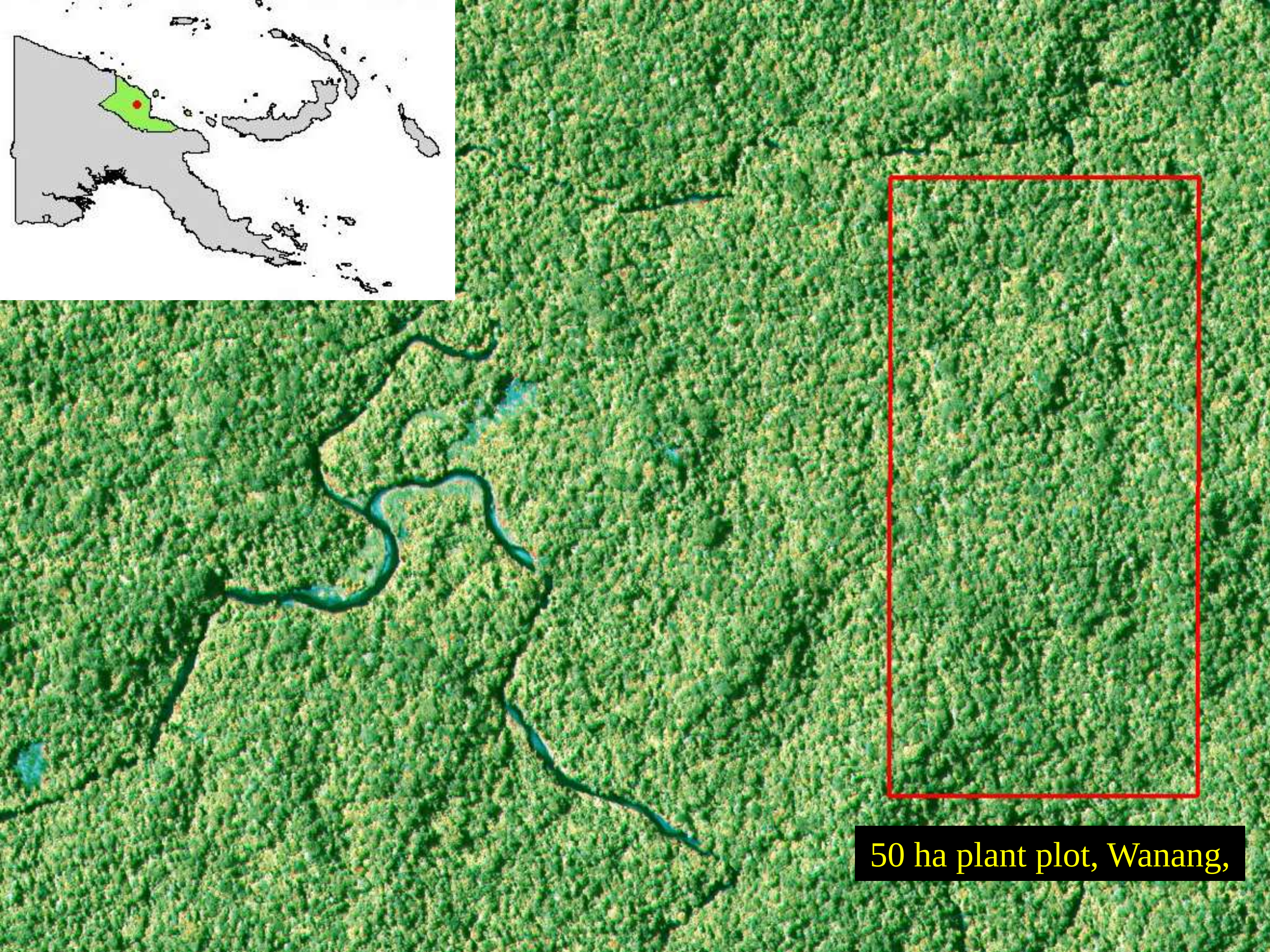
The Center for Tropical Forest Science network

Current and projected future (2050) mean annual temperature and precipitation of CTFS plots



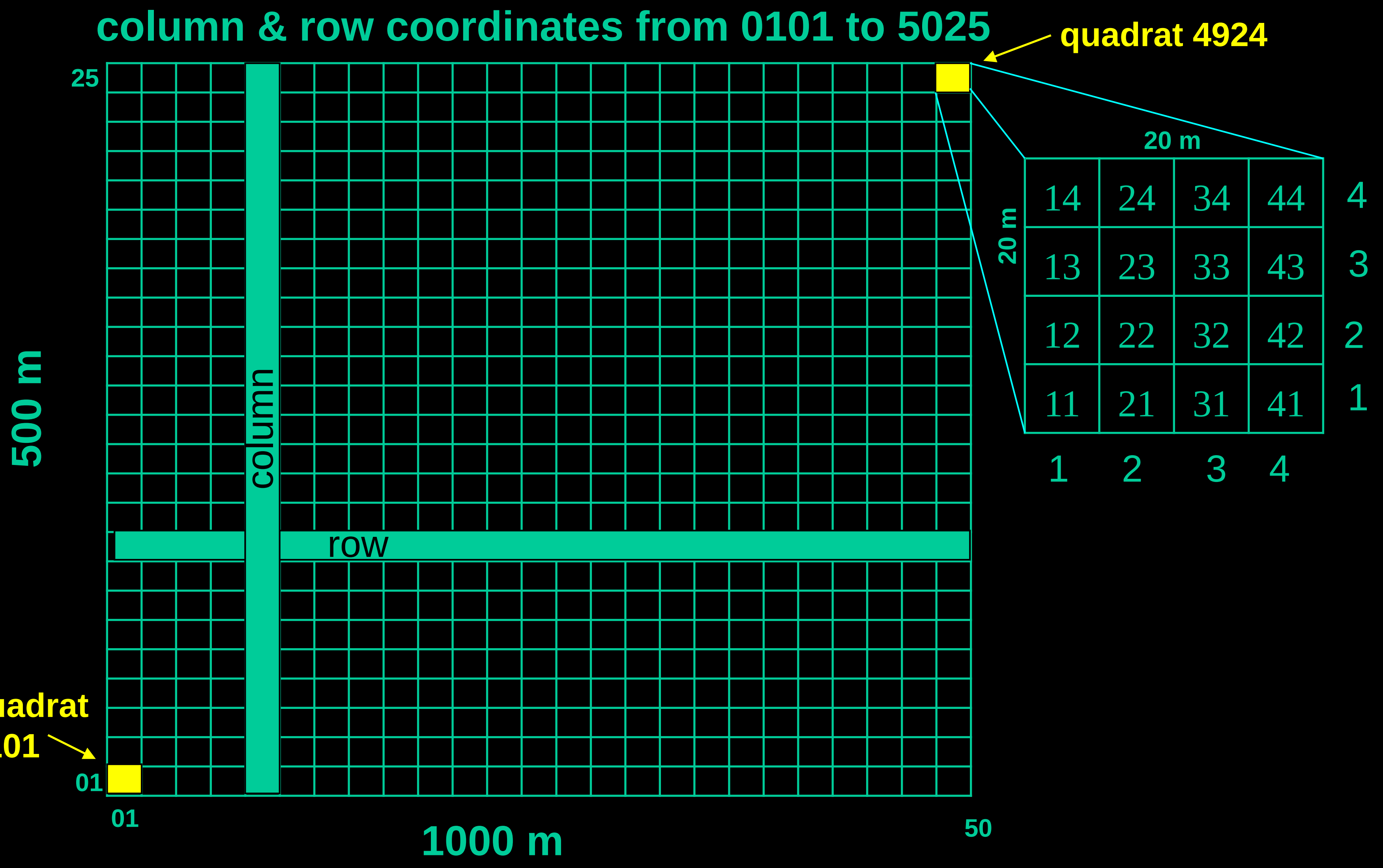
TrRF, tropical rain forest; TrSF/S, tropical seasonal forest/savanna; SD, subtropical desert; TeRF, temperate rain forest; TeSF, temperate seasonal forest; W/S, woodland/shrubland; TeG/D, temperate grassland/desert; BF, boreal forest; T, tundra

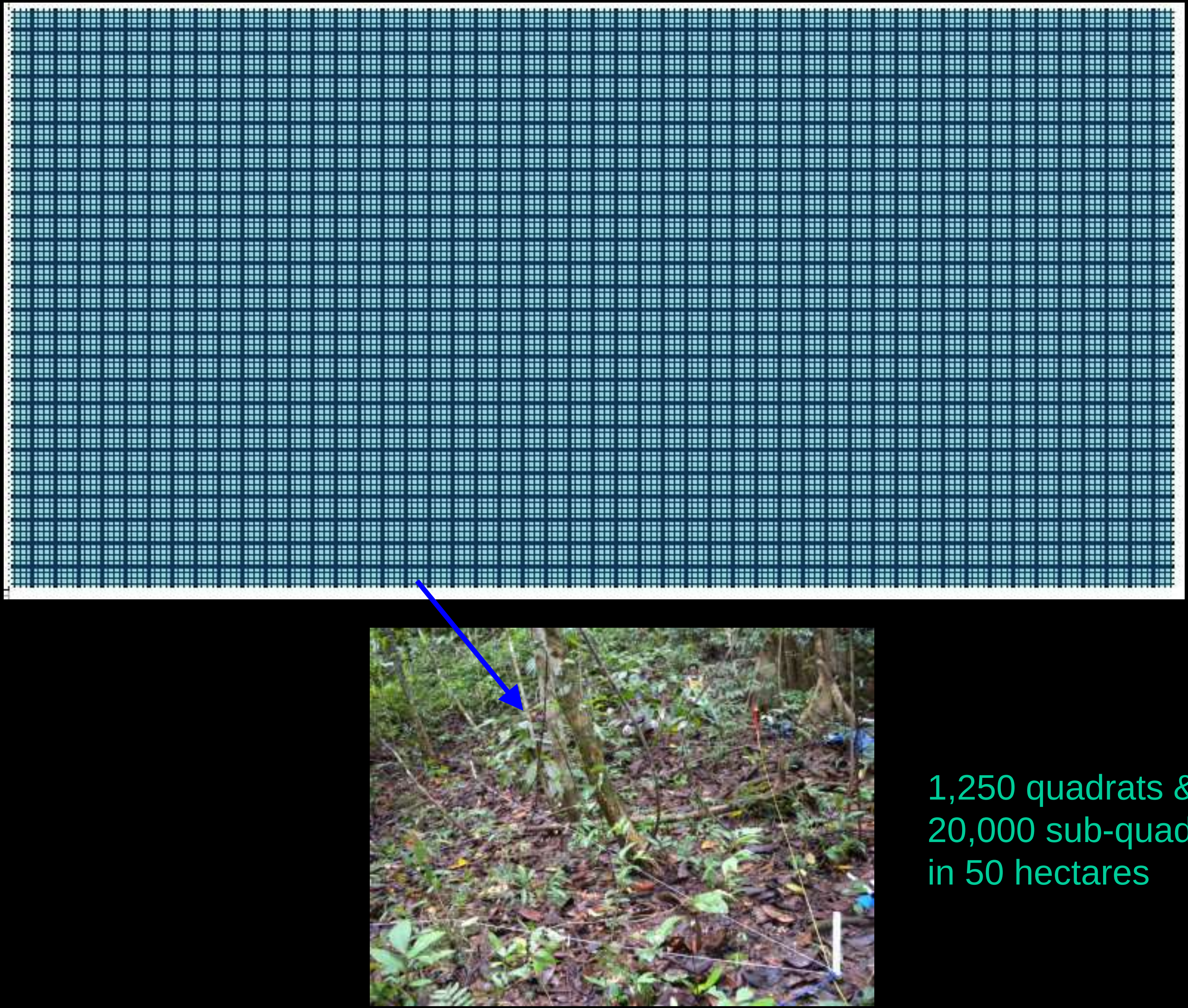
Teixeira et al., Global Change Biology (2014), doi: 10.1111/gcb.12712



50 ha plant plot, Wanang,

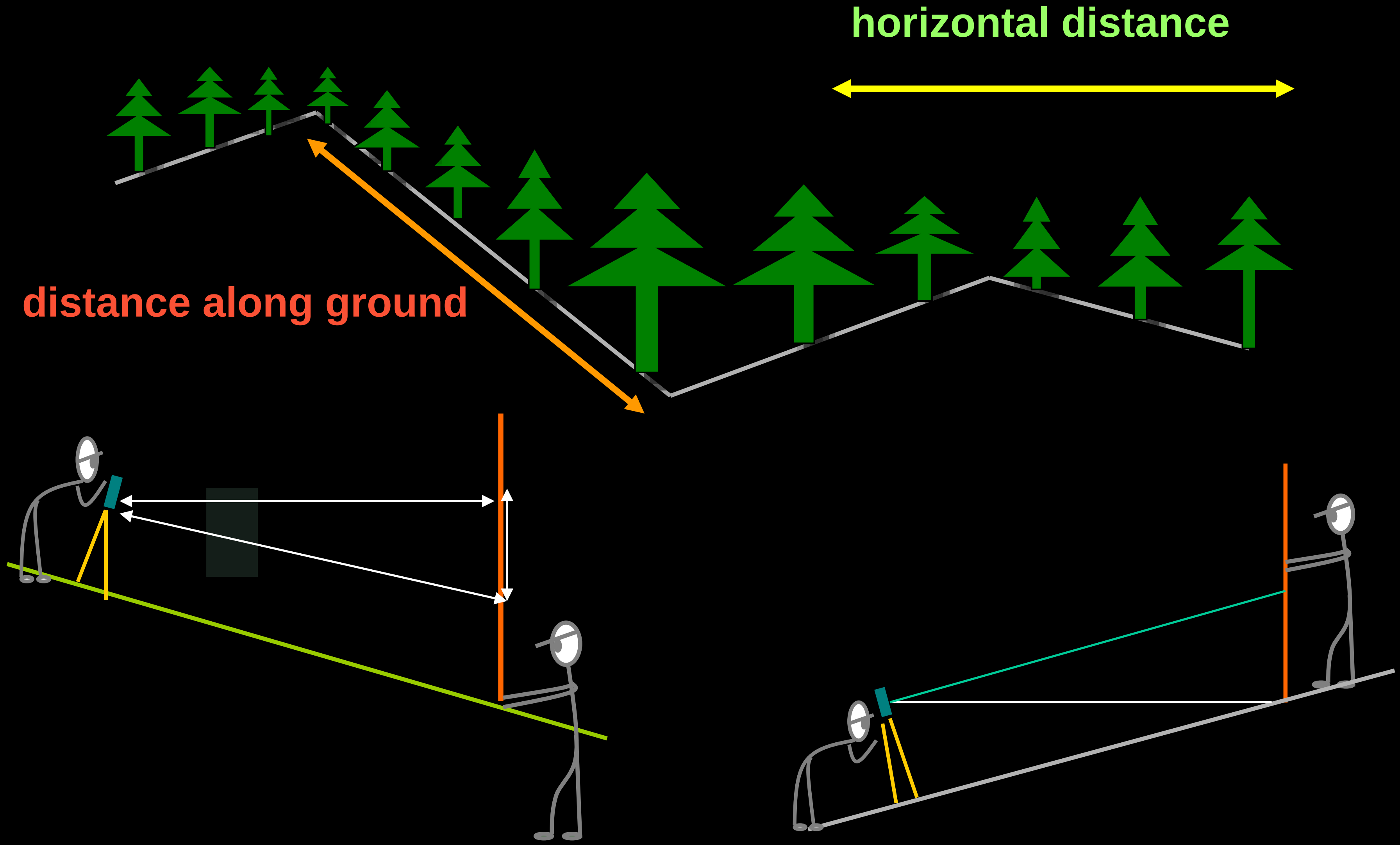
Quadrats (20 mx 20 m)
& Subquadrats (5 m x 5 m)



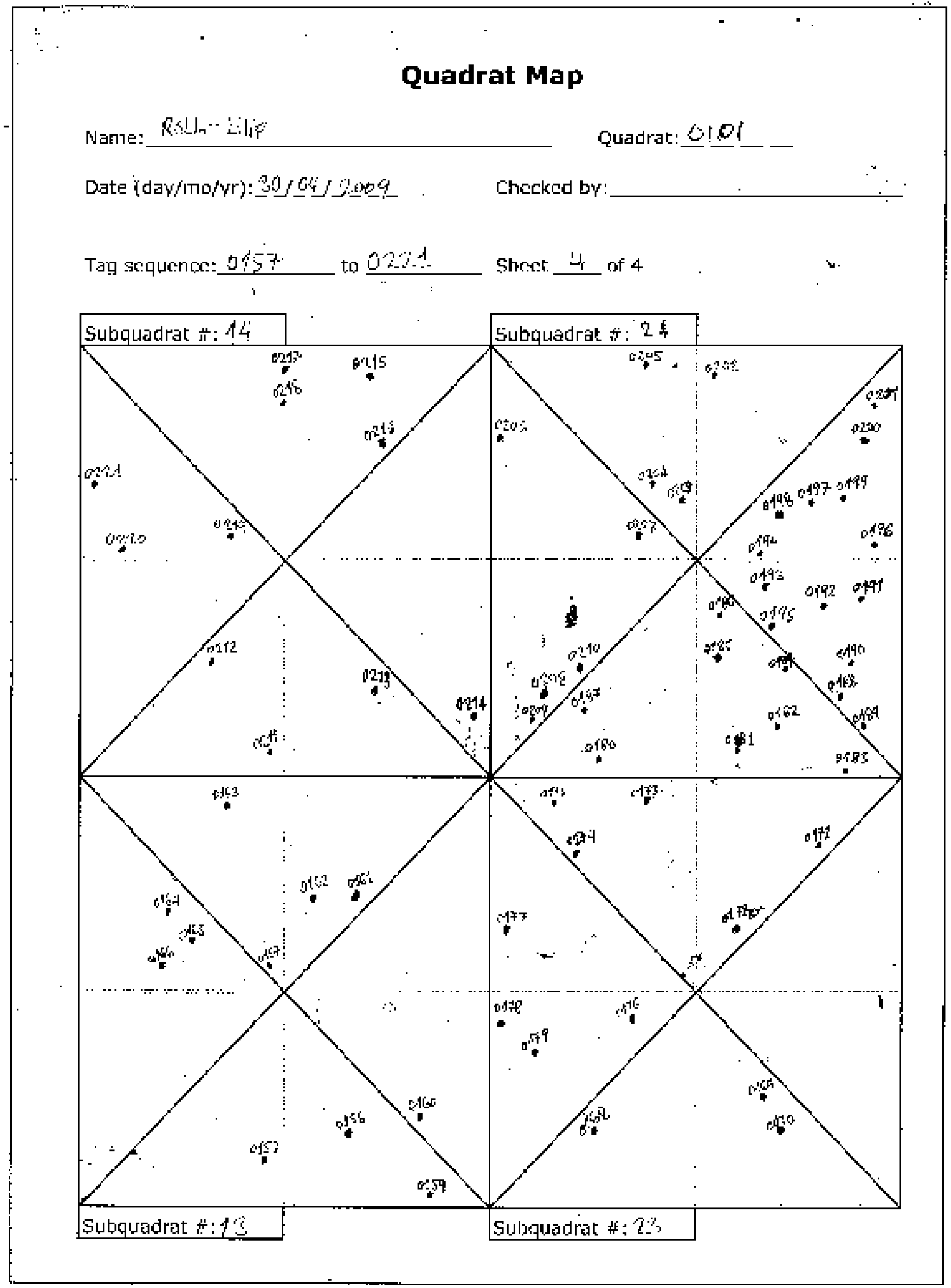


1,250 quadrats &
20,000 sub-quadrats
in 50 hectares

20 x 20 survey principals




SOUTH
CE



Quadrat Map

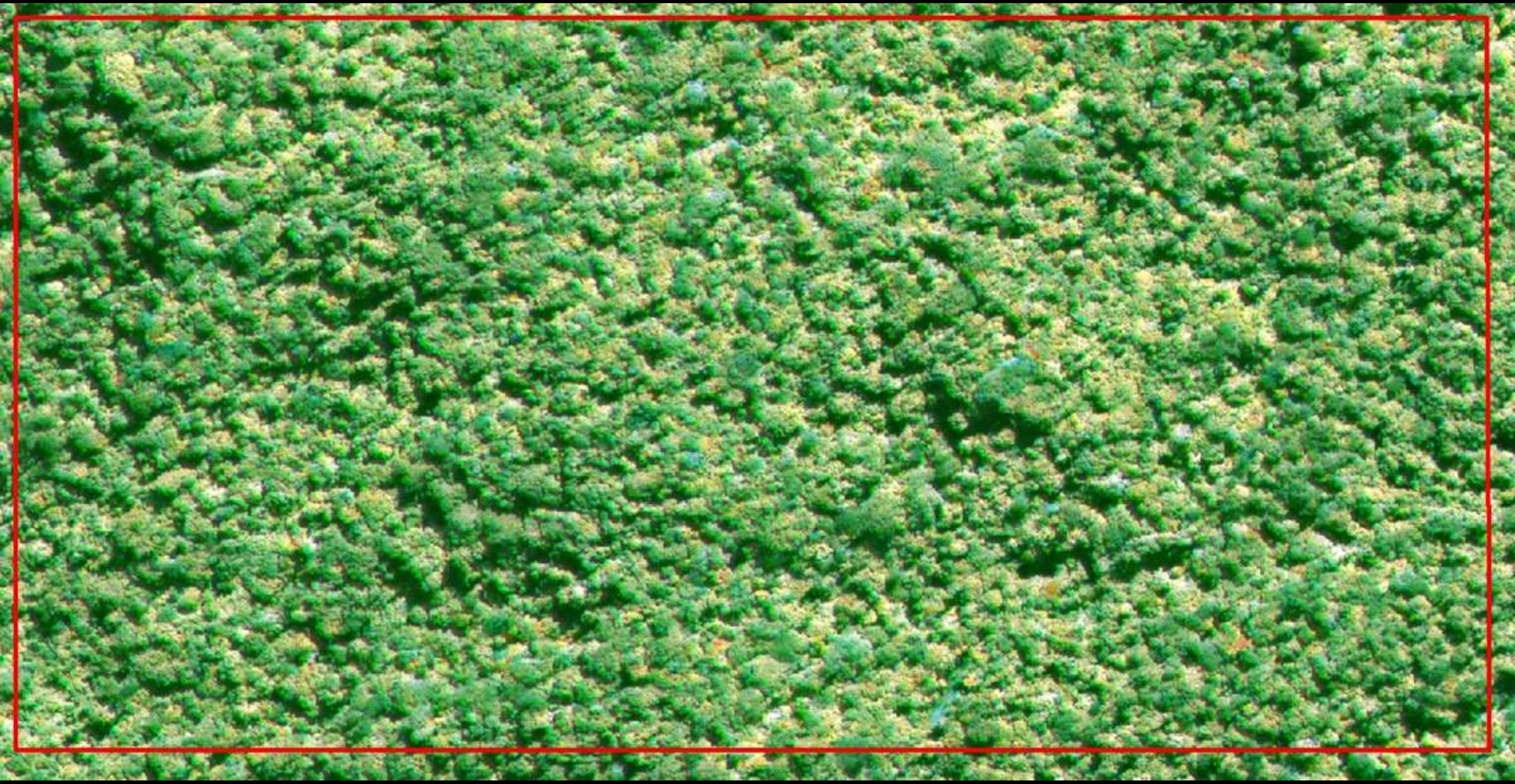
Name: RsUh Elip
Quadrat: 0101
Date (day/mo/yr): 30/04/2009
Checked by:
Tag sequence: 0157 to 0221
Sheet 4 of 4

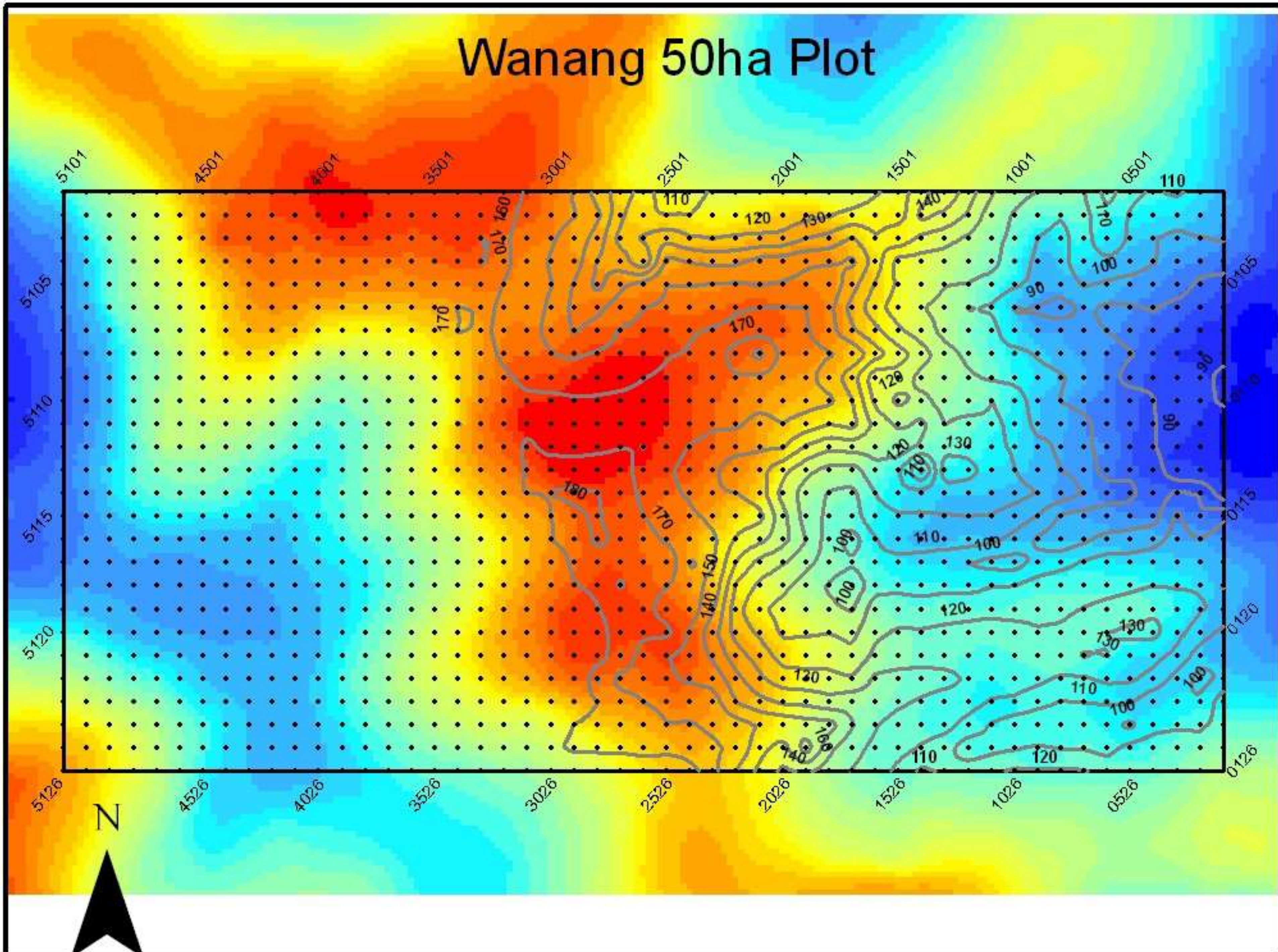
Subquadrat #: 14
Subquadrat #: 24
Subquadrat #: 13
Subquadrat #: 23

288,204 plant stems
with DBH>1 cm,
536 species

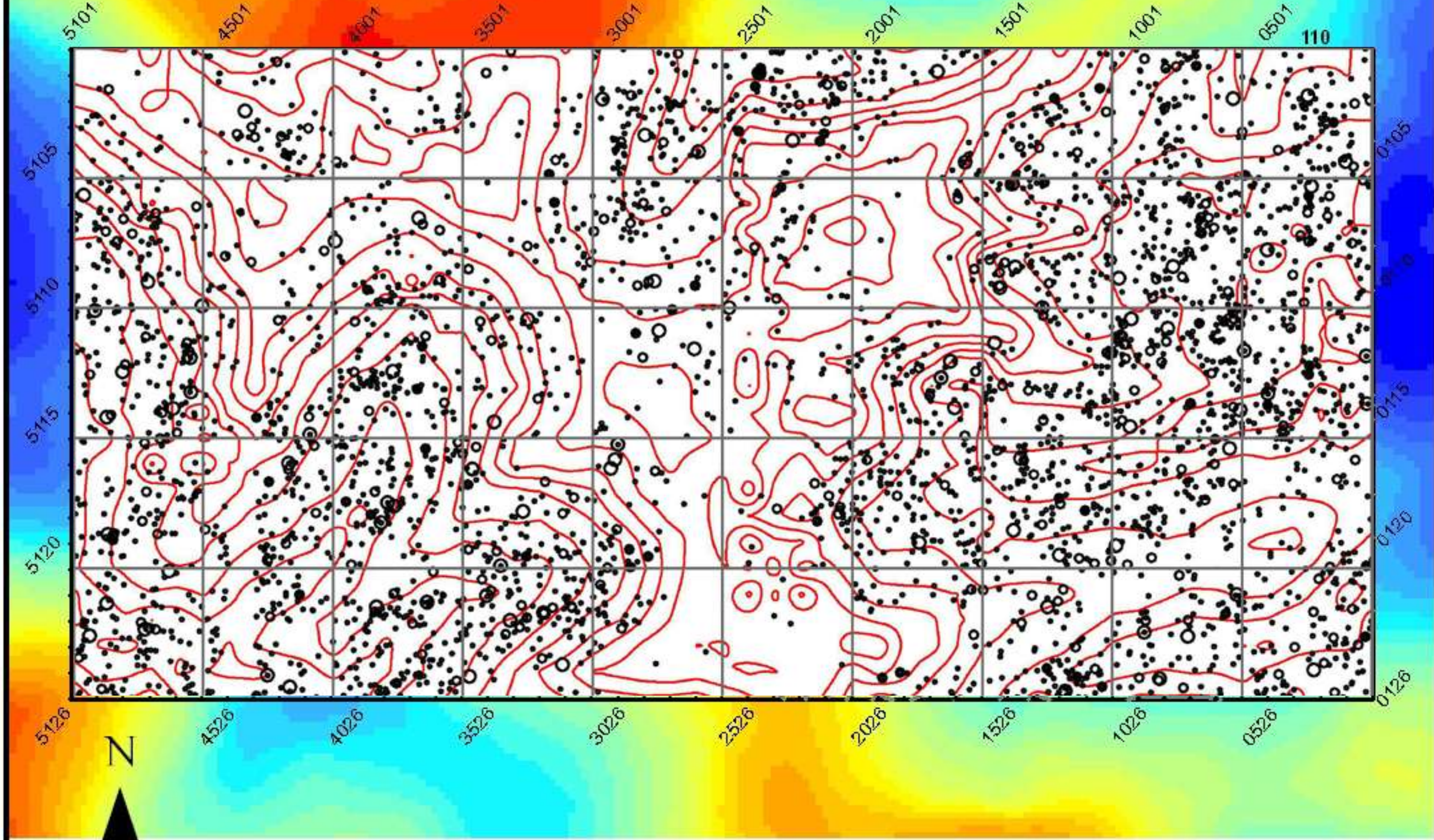
500 kg of aluminium tags,
50 km of copper wire

Landsat satellite image of 50 ha plot in Wanang Papua New Guinea

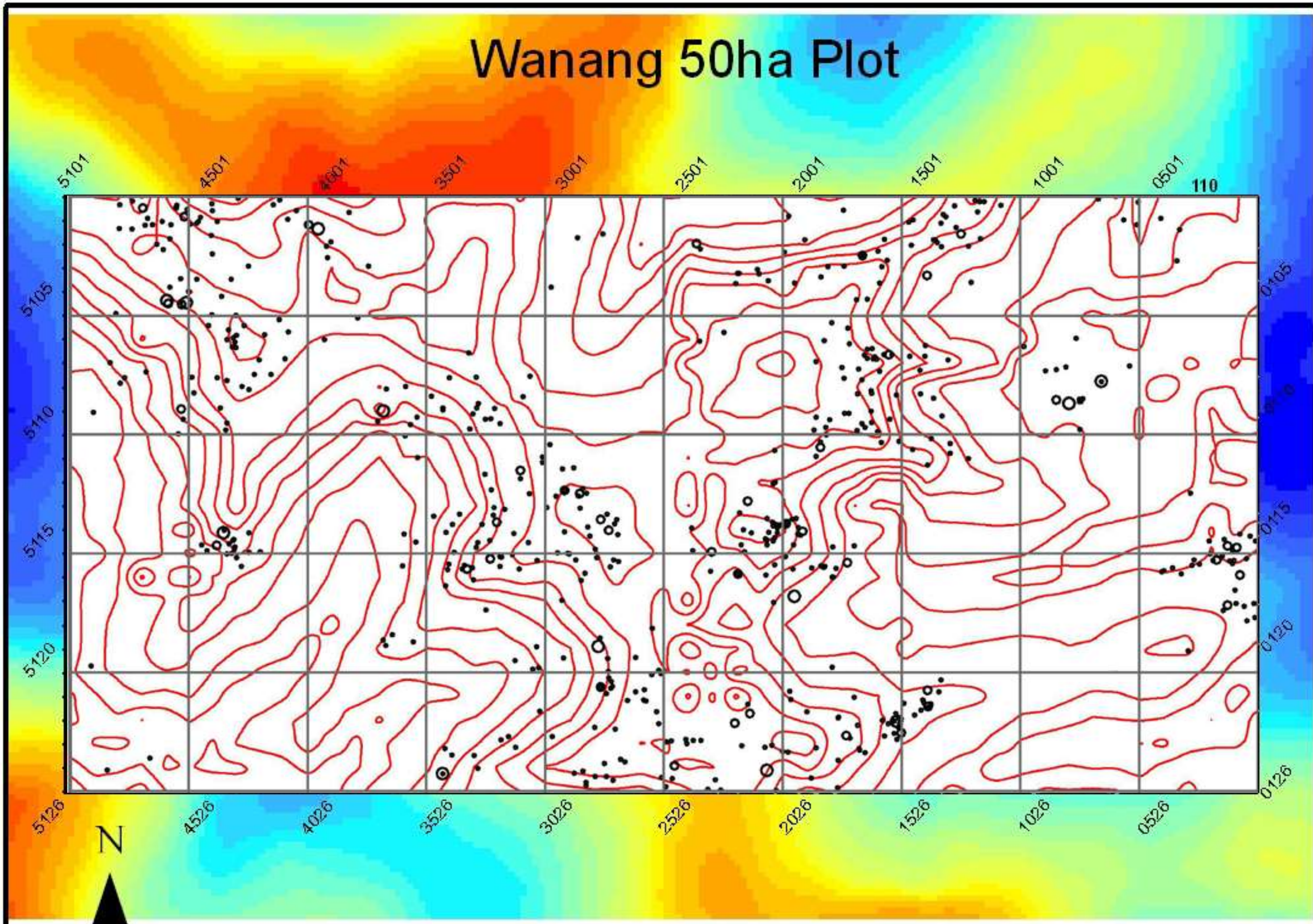



Wanang 50ha Plot
5101
4501
4001
3501
3001
2501
2001
1501
1001
0501
5105
5110
5115
5120
5126
4526
4026
3526
3026
2526
2026
1526
1026
0526
0126
0120
0115
0110
0105
110
120
130
140
160
170
180
150
100
90
N

Wanang 50ha Plot

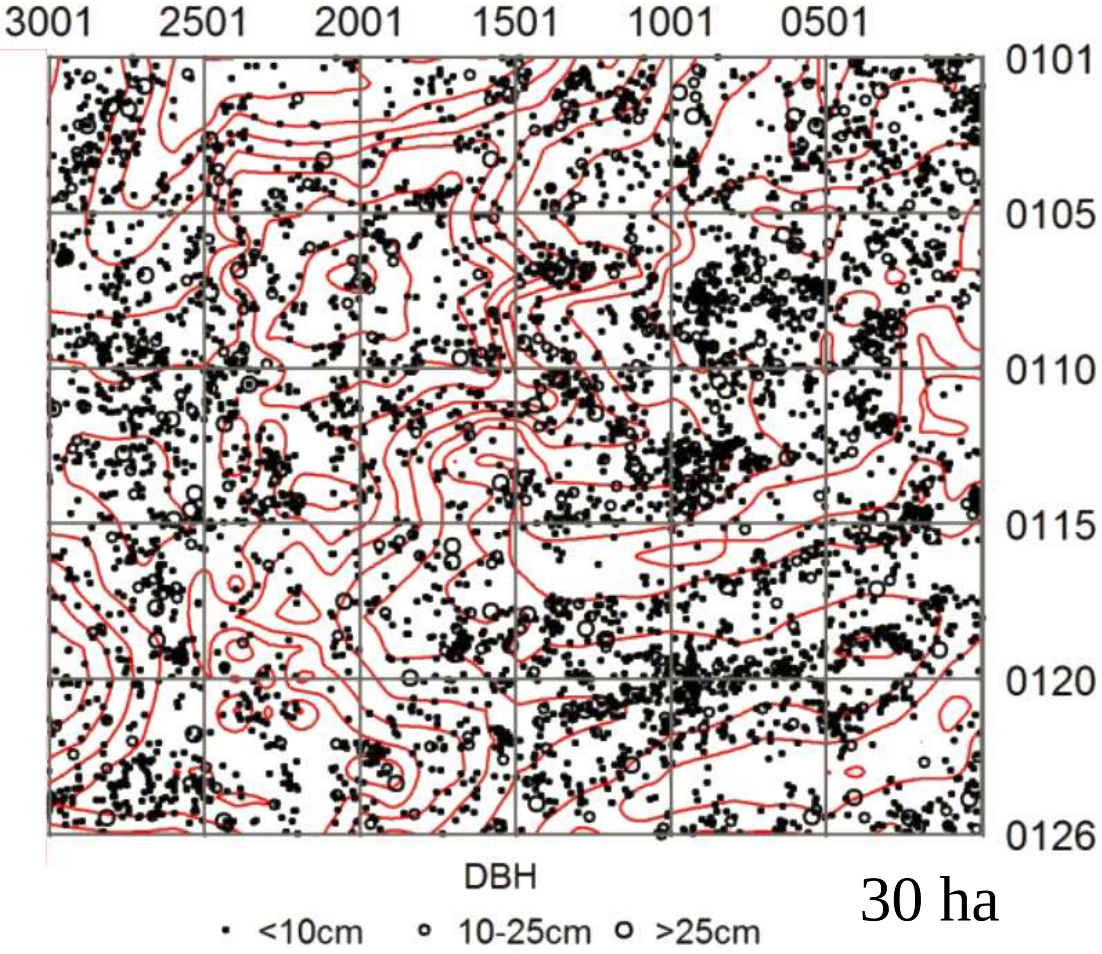


Pometia pinata

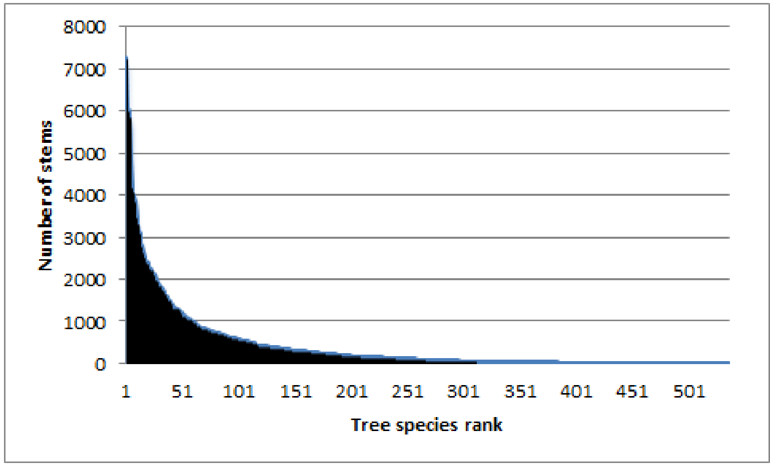


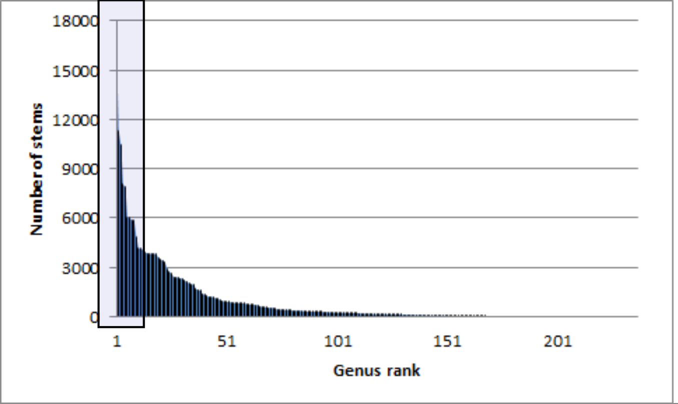
Intsia bijuga

Celtis latifolia
3.4% of all stems

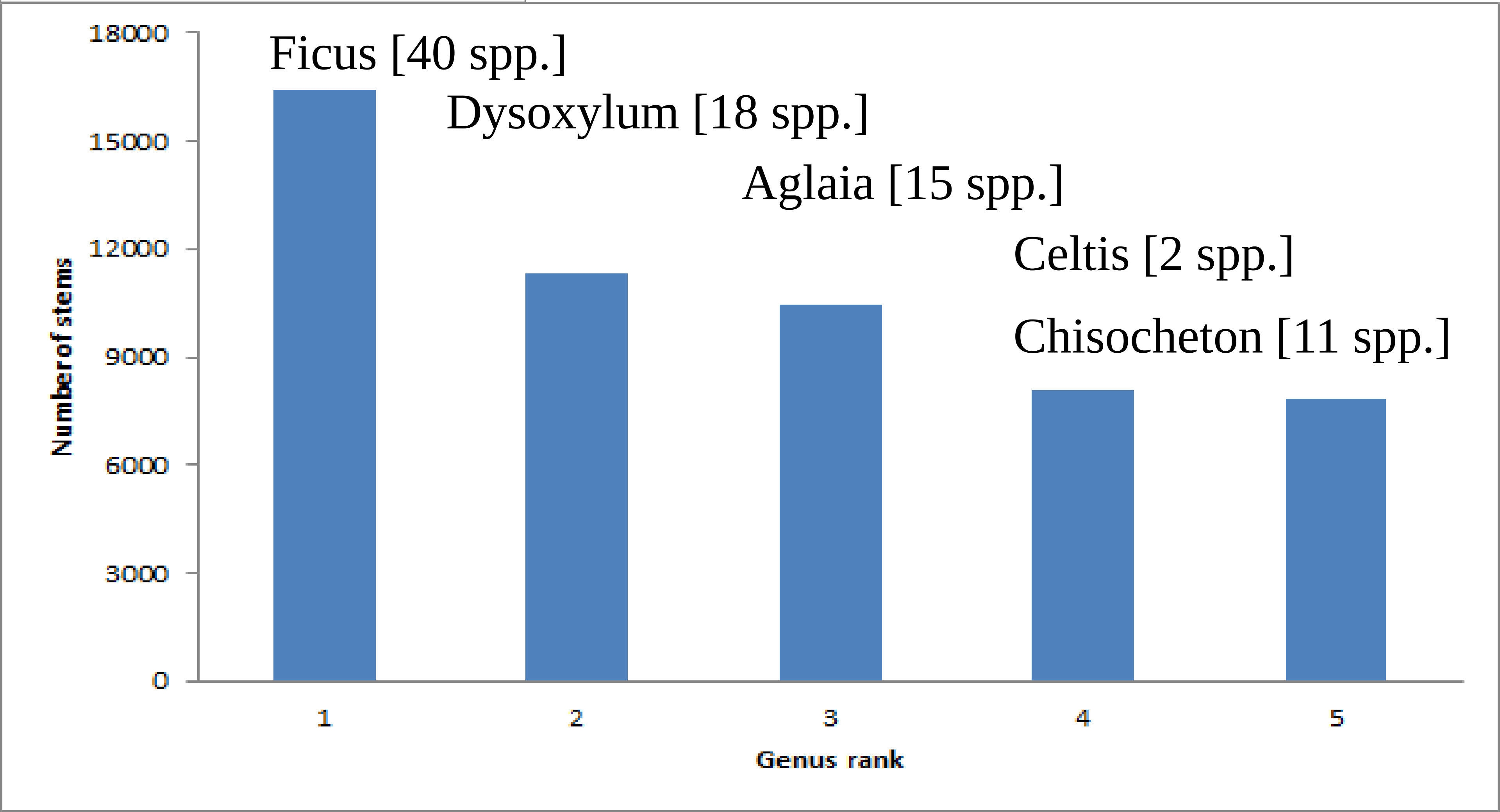


30 ha





Ficus
7.7% of all stems



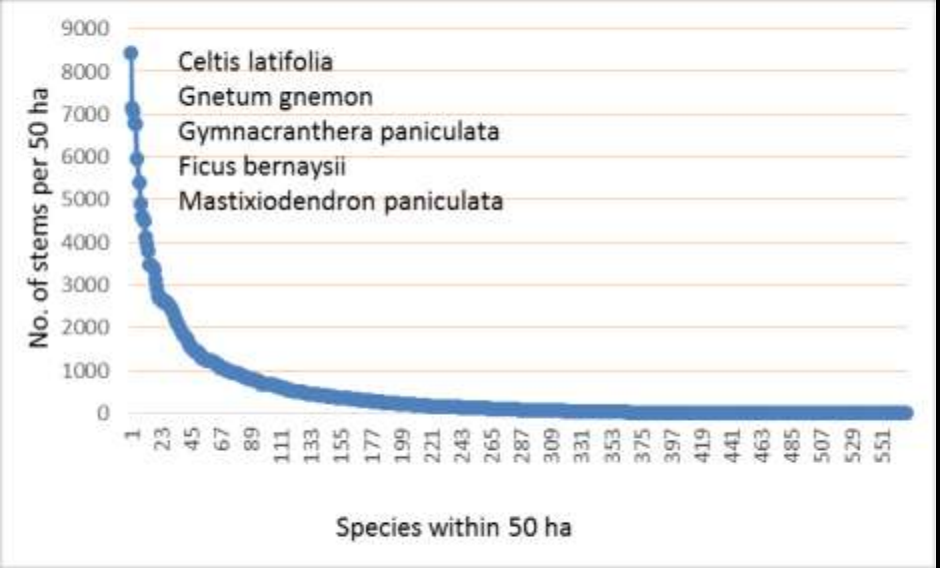
Ficus [40 spp.]

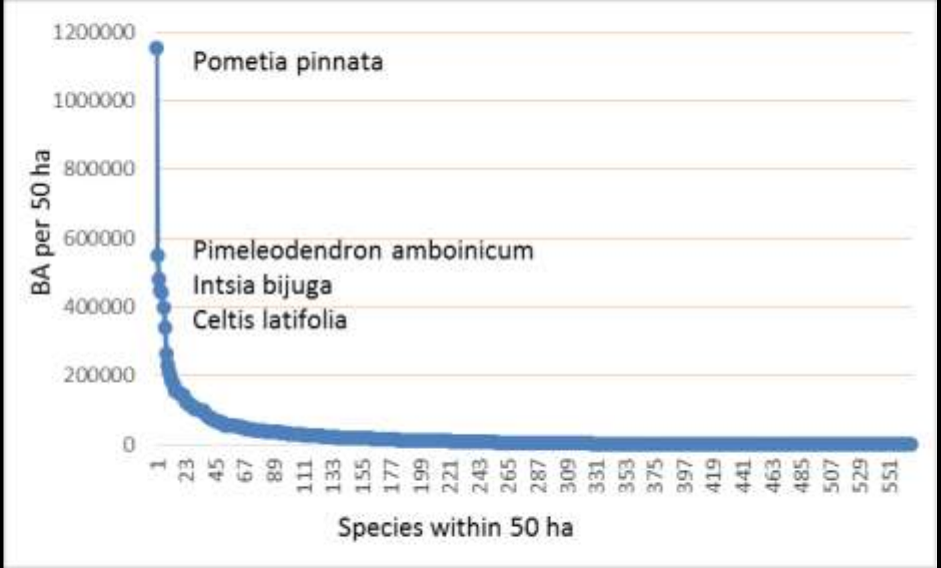
Dysoxylum [18 spp.]

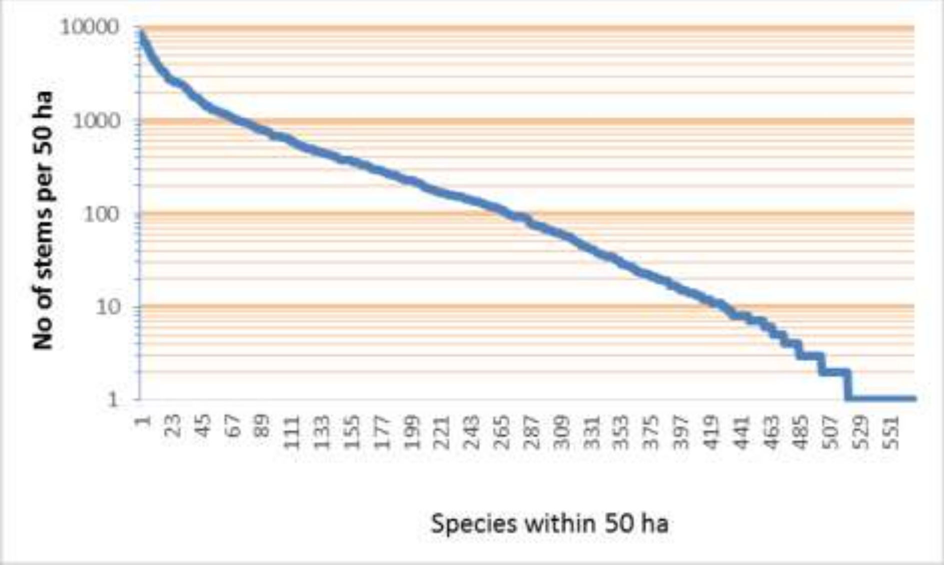
Aglaia [15 spp.]

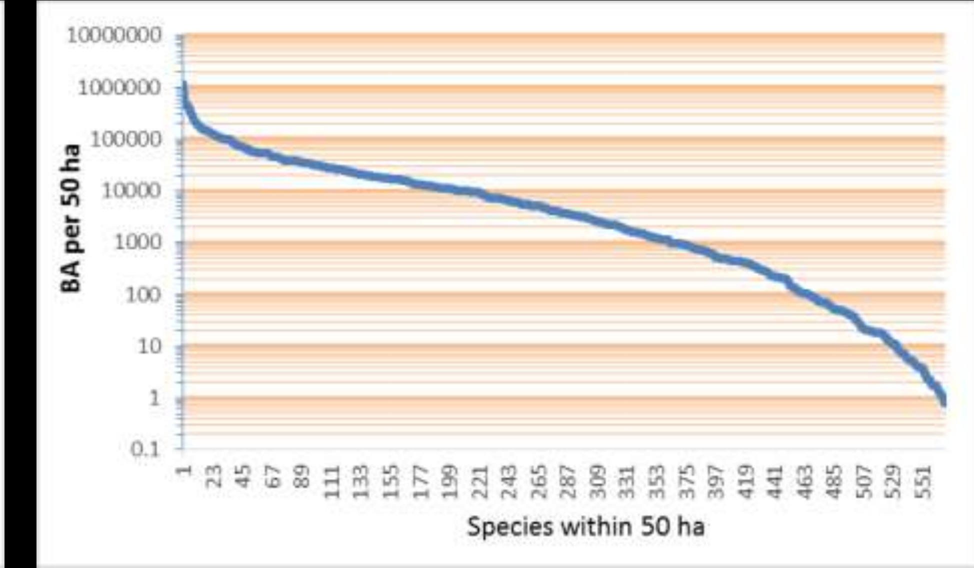
Celtis [2 spp.]

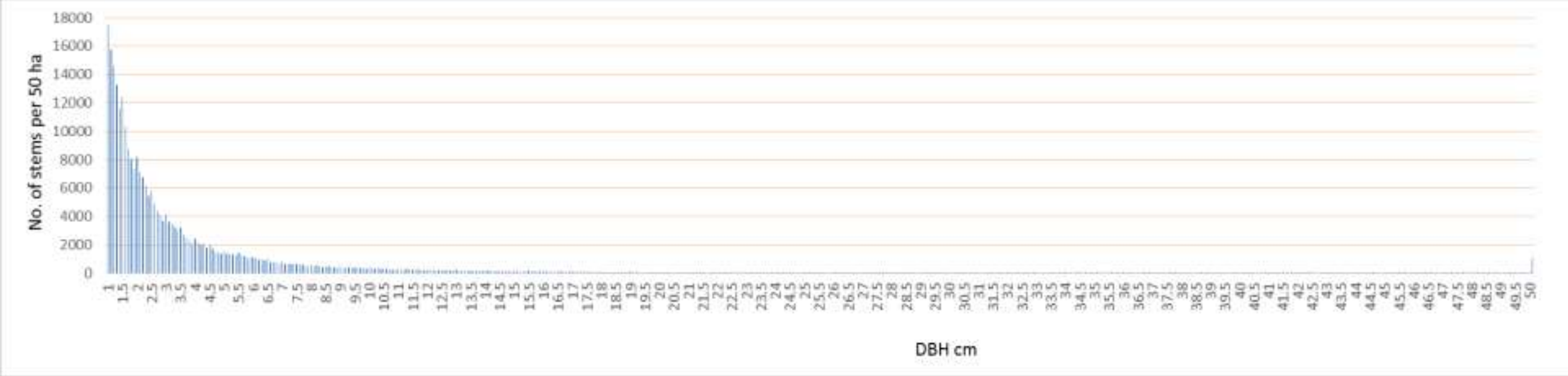
Chisocheton [11 spp.]

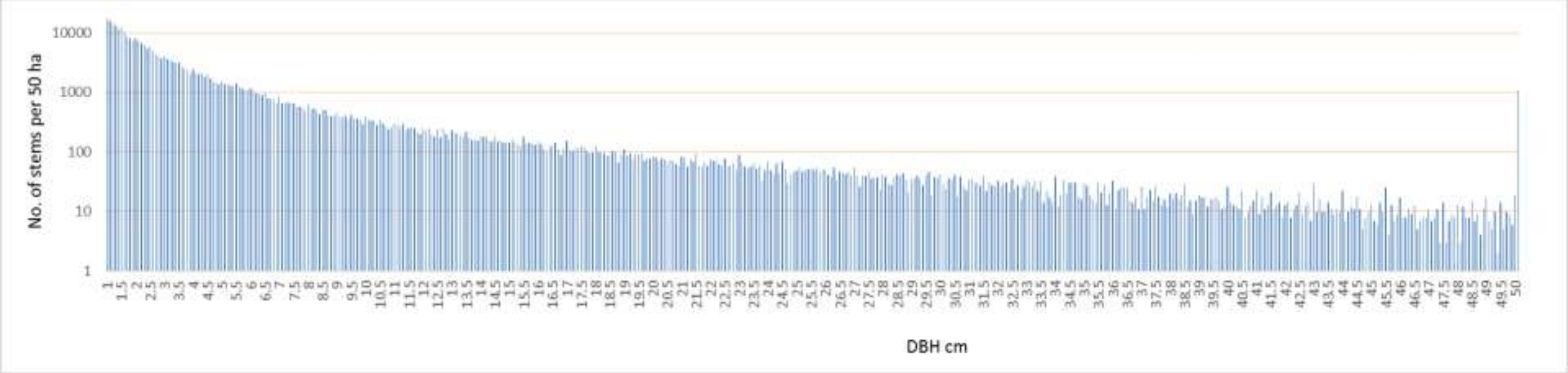

No. of stems per 50 ha
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
Celtis latifolia
Gnetum gnemon
Gymnacranthera paniculata
Ficus bernaysii
Mastixiodendron paniculata
1
23
45
67
89
111
133
155
177
199
221
243
265
287
309
331
353
375
397
419
441
463
485
507
529
551
Species within 50 ha

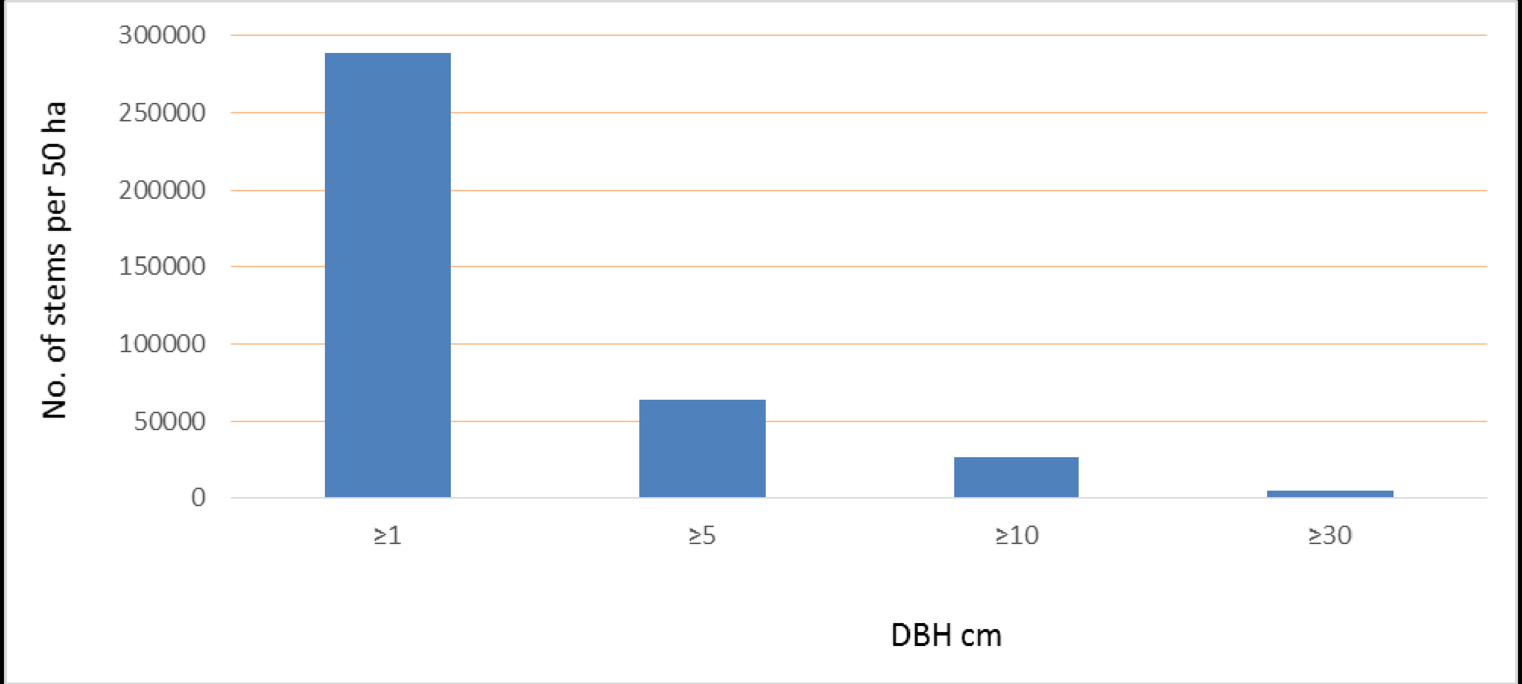

BA per 50 ha
1200000
1000000
800000
600000
400000
200000
0
Pometia pinnata
Pimeleodendron amboinicum
Intsia bijuga
Celtis latifolia
1
23
45
67
89
111
133
155
177
199
221
243
265
287
309
331
353
375
397
419
441
463
485
507
529
551
Species within 50 ha

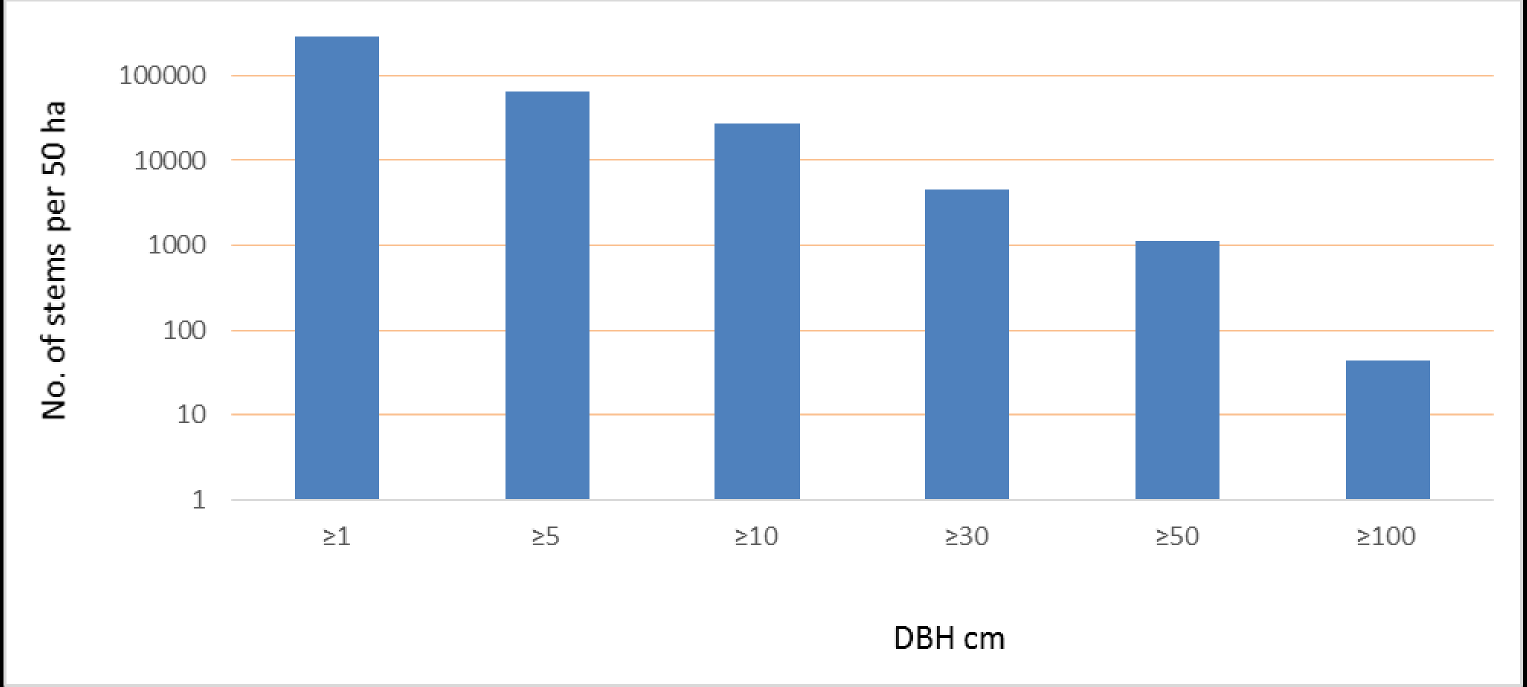

No of stems per 50 ha
10000
1000
100
10
1
1
23
45
67
89
111
133
155
177
199
221
243
265
287
309
331
353
375
397
419
441
463
485
507
529
551
Species within 50 ha

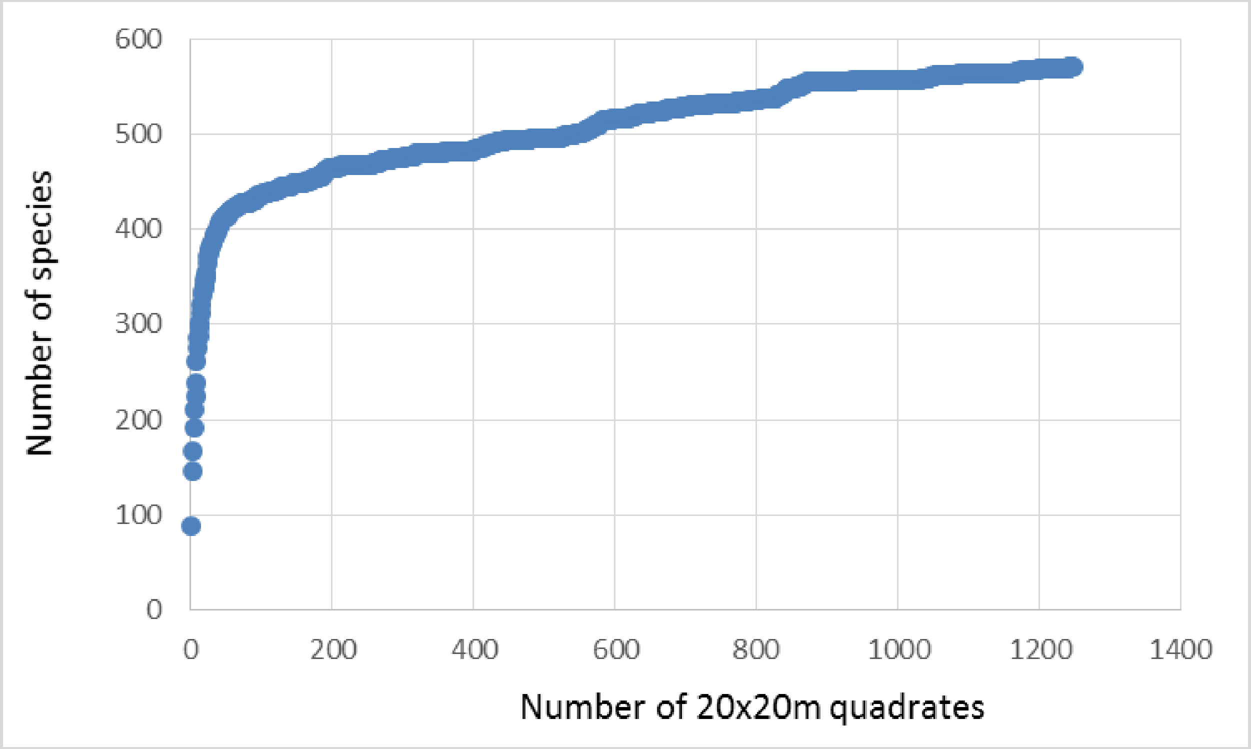

BA per 50 ha
10000000
1000000
100000
10000
1000
100
10
1
0.1
1
23
45
67
89
111
133
155
177
199
221
243
265
287
309
331
353
375
397
419
441
463
485
507
529
551
Species within 50 ha

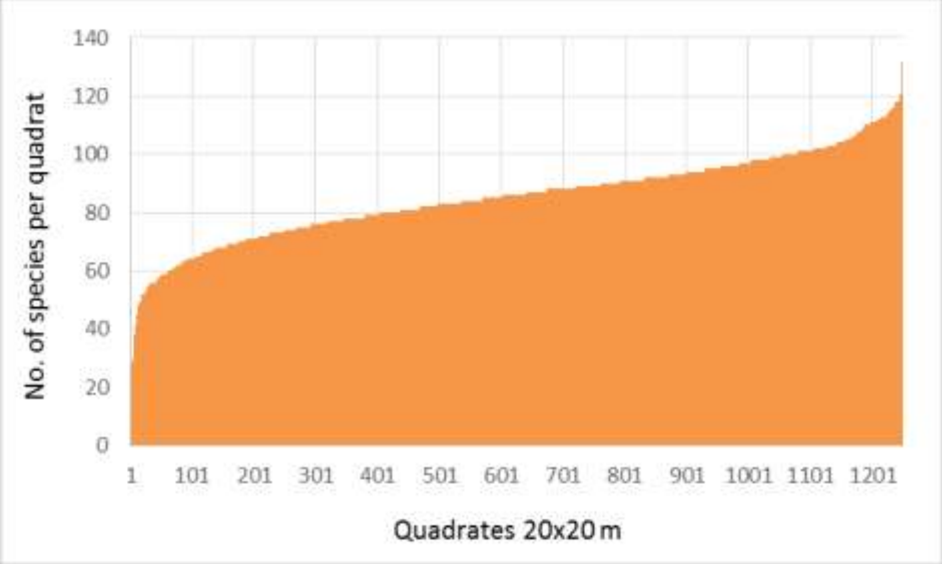

No. of stems per 50 ha
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
1 1.5 2 2.5 3 3.5 4 4.5 5 5.5 6 6.5 7 7.5 8 8.5 9 9.5 10 10.5 11 11.5 12 12.5 13 13.5 14 14.5 15 15.5 16 16.5 17 17.5 18 18.5 19 19.5 20 20.5 21 21.5 22 22.5 23 23.5 24 24.5 25 25.5 26 26.5 27 27.5 28 28.5 29 29.5 30 30.5 31 31.5 32 32.5 33 33.5 34 34.5 35 35.5 36 36.5 37 37.5 38 38.5 39 39.5 40 40.5 41 41.5 42 42.5 43 43.5 44 44.5 45 45.5 46 46.5 47 47.5 48 48.5 49 49.5 50
DBH cm

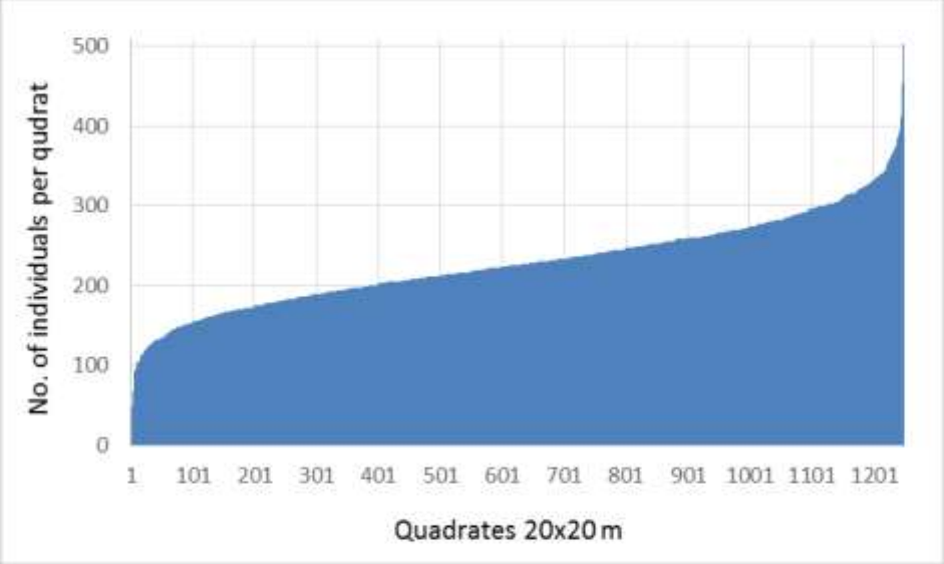

No. of stems per 50 ha
10000
1000
100
10
1
1 1.5 2 2.5 3 3.5 4 4.5 5 5.5 6 6.5 7 7.5 8 8.5 9 9.5 10 10.5 11 11.5 12 12.5 13 13.5 14 14.5 15 15.5 16 16.5 17 17.5 18 18.5 19 19.5 20 20.5 21 21.5 22 22.5 23 23.5 24 24.5 25 25.5 26 26.5 27 27.5 28 28.5 29 29.5 30 30.5 31 31.5 32 32.5 33 33.5 34 34.5 35 35.5 36 36.5 37 37.5 38 38.5 39 39.5 40 40.5 41 41.5 42 42.5 43 43.5 44 44.5 45 45.5 46 46.5 47 47.5 48 48.5 49 49.5 50
DBH cm

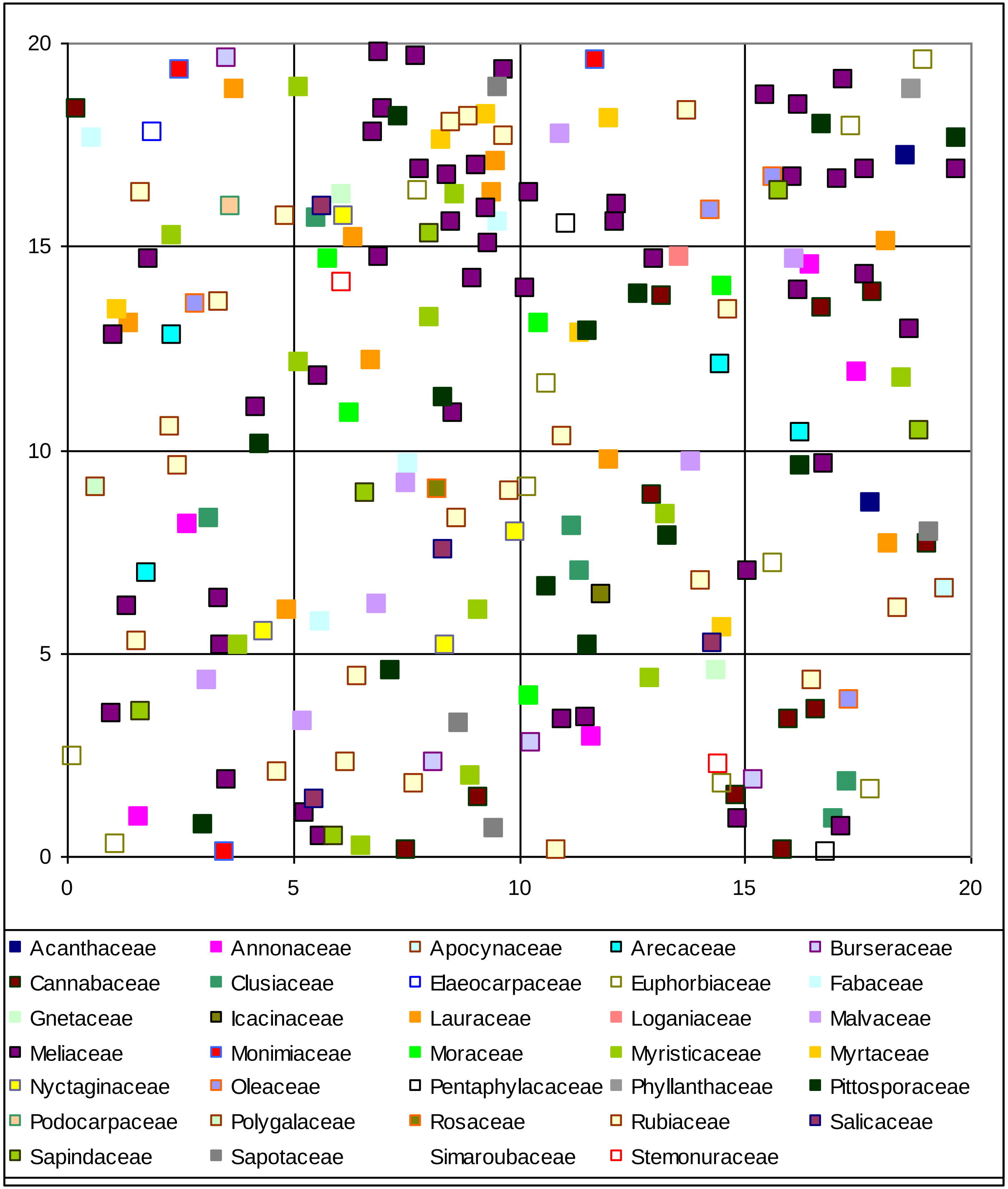

300000
250000
200000
150000
100000
50000
0
No. of stems per 50 ha
≥1
≥5
≥10
≥30
DBH cm


100000
10000
1000
100
10
1
No. of stems per 50 ha
≥1
≥5
≥10
≥30
≥50
≥100
DBH cm

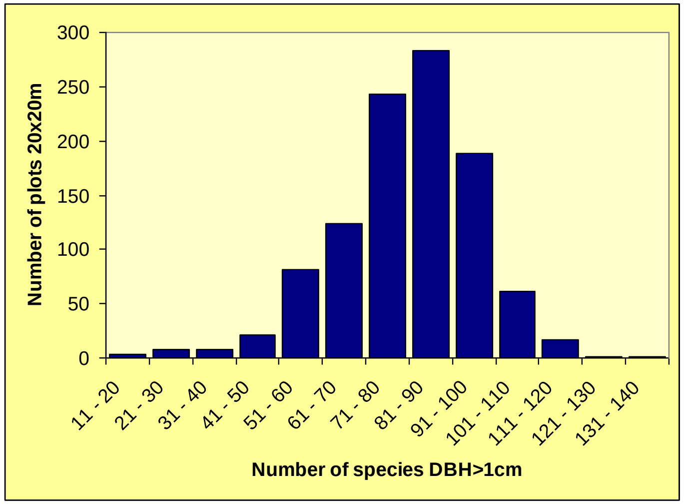

Number of species
600
500
400
300
200
100
0
0
200
400
600
800
1000
1200
1400
Number of 20x20m quadrates


No. of species per quadrat
140
120
100
80
60
40
20
0
1
101
201
301
401
501
601
701
801
901
1001
1101
1201
Quadrates 20x20 m


No. of individuals per qudrat
500
400
300
200
100
0
1
101
201
301
401
501
601
701
801
901
1001
1101
1201
Quadrates 20x20 m



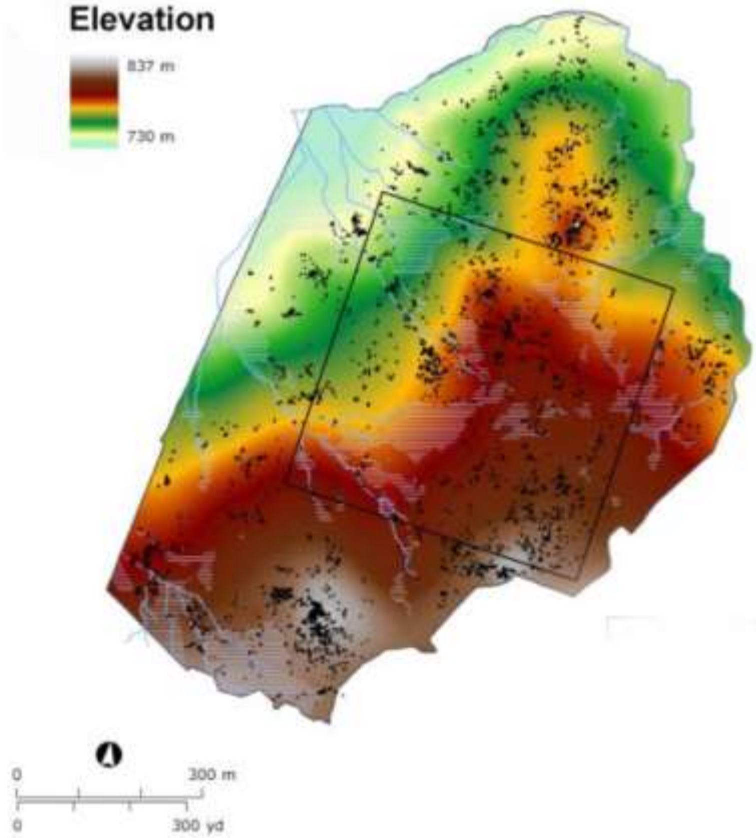
Wanang:
20 x 20 m plot
DBH > 1 cm
34 plant families

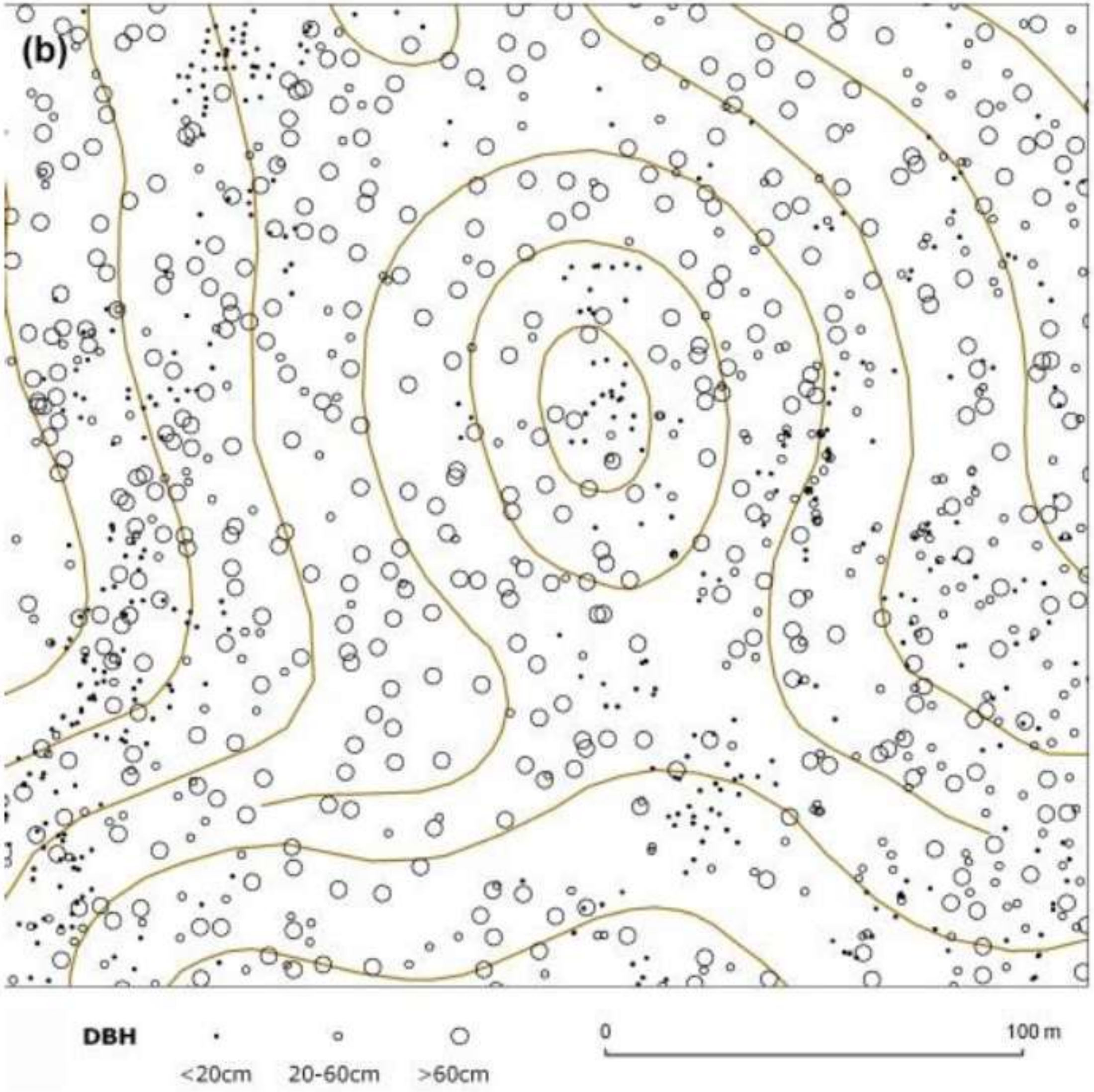


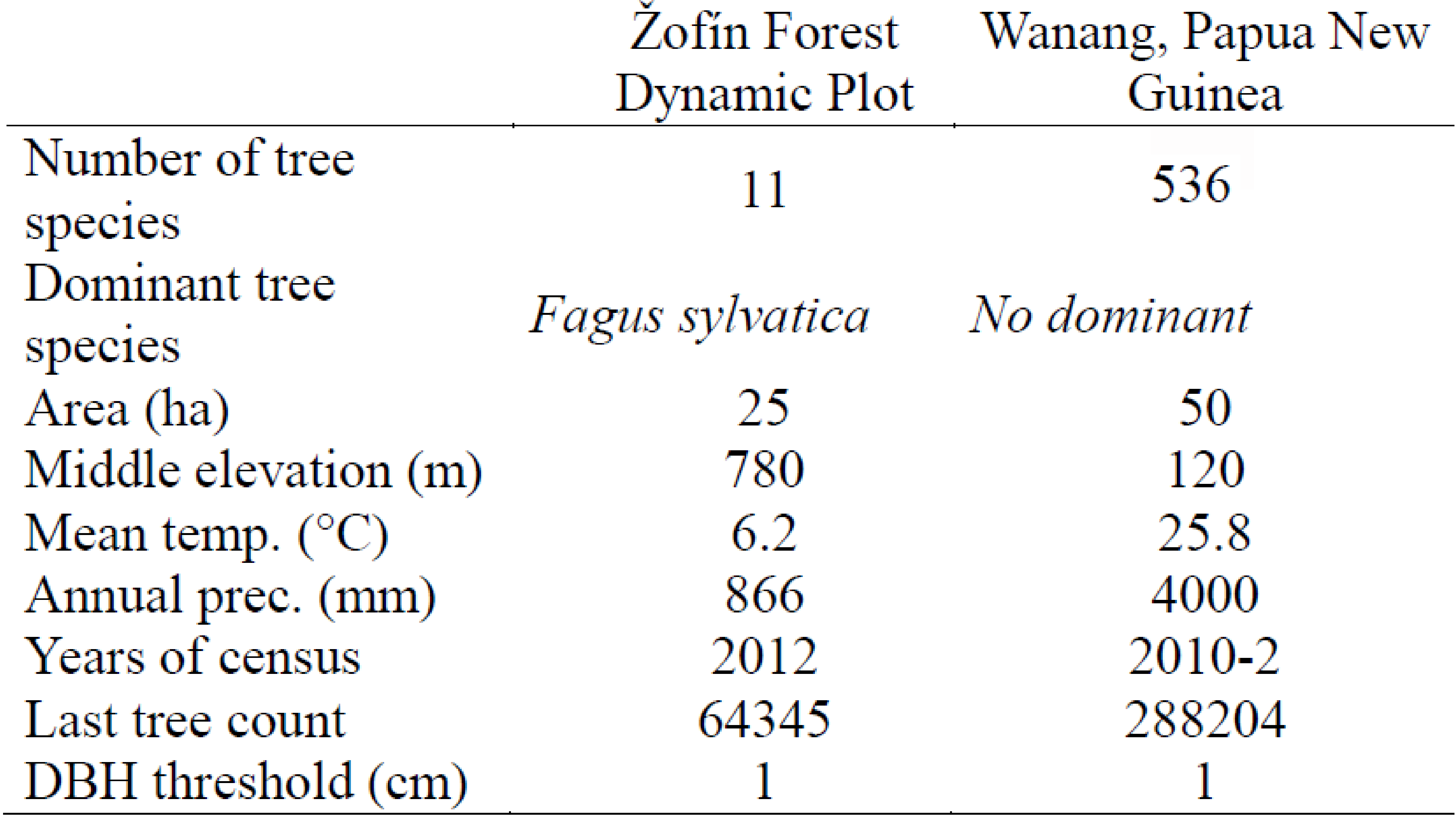
modus
81 – 90 species
per 20x20 m plot
DBH > 1 cm

ŽOFÍNSKÝ PRALES
ZALOŽEN 28.8.1838
VÝMĚRA 98.10 ha
ŽOFIN, 28.8.1988
LZ NOVÉ HRADY
ČSVTS LZ NOVÉ HRAD

Fagus sylvatica distribution

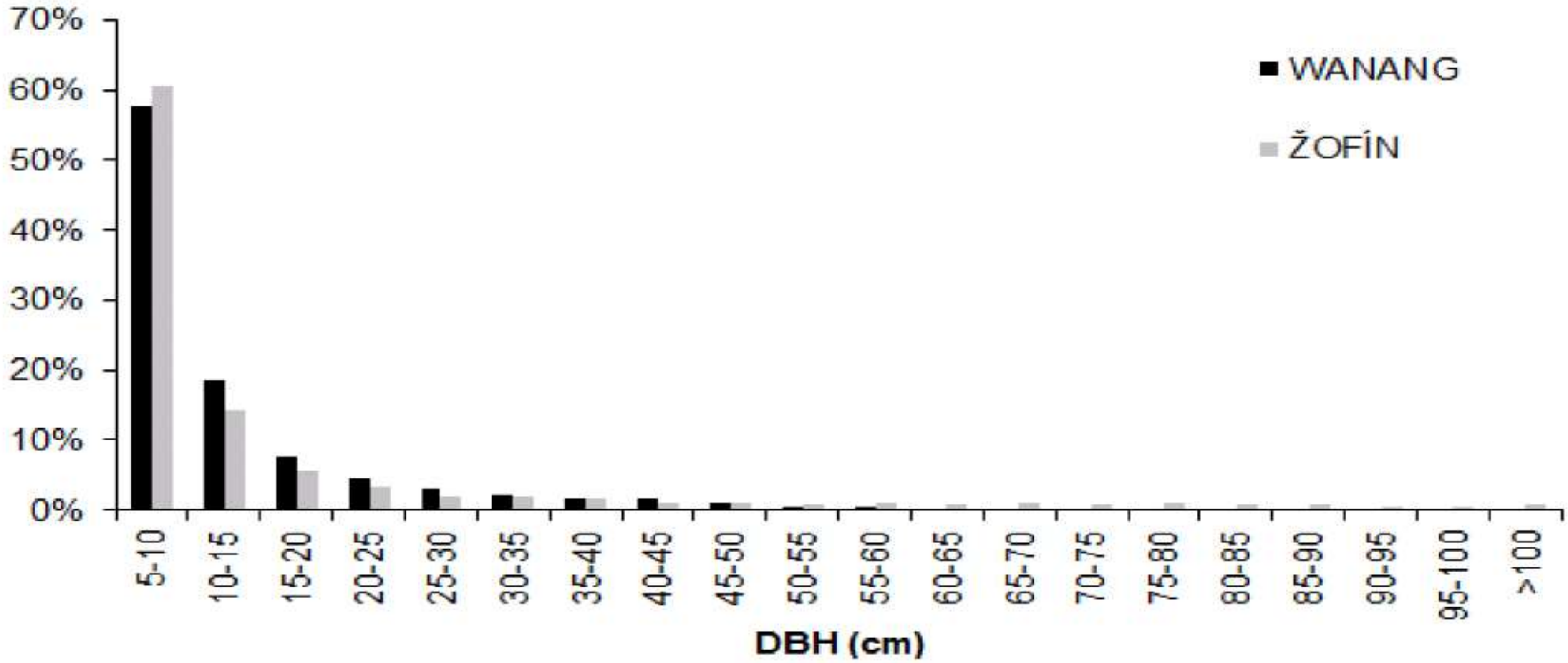






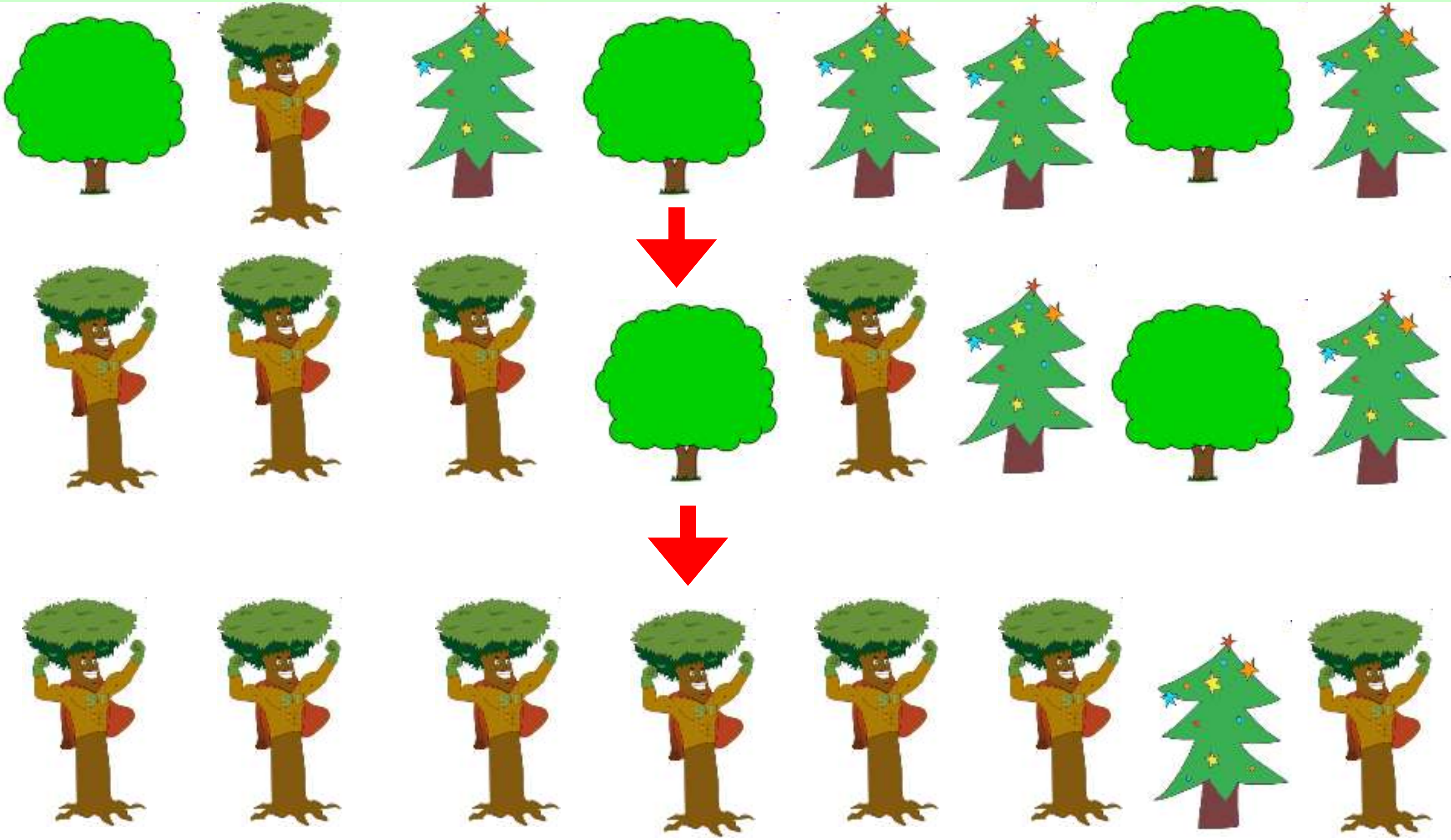
	Žofín Forest Dynamic Plot	Wanang, Papua New Guinea
Number of tree species	11	536
Dominant tree species	*Fagus sylvatica*	*No dominant*
Area (ha)	25	50
Middle elevation (m)	780	120
Mean temp. (°C)	6.2	25.8
Annual prec. (mm)	866	4000
Years of census	2012	2010-2
Last tree count	64345	288204
DBH threshold (cm)	1	1

Tree density: stems per ha	2,574	5,764



70%
60%
50%
40%
30%
20%
10%
0%
■ WANANG
■ ŽOFÍN
5-10
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
60-65
65-70
70-75
75-80
80-85
85-90
90-95
95-100
>100
DBH (cm)

How can there be be hundreds of tree species coexisting in tropical forests when they all compete for the same solar energy and nutrients?



What prevents a single "superman" tree species, best adapted to local conditions, from out-competing others and prevailing in the rainforest?

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Immigration prevents competitive exclusion
[non-equilibrium community composition]

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[recruitment limitation]

Rare species are demographically favoured
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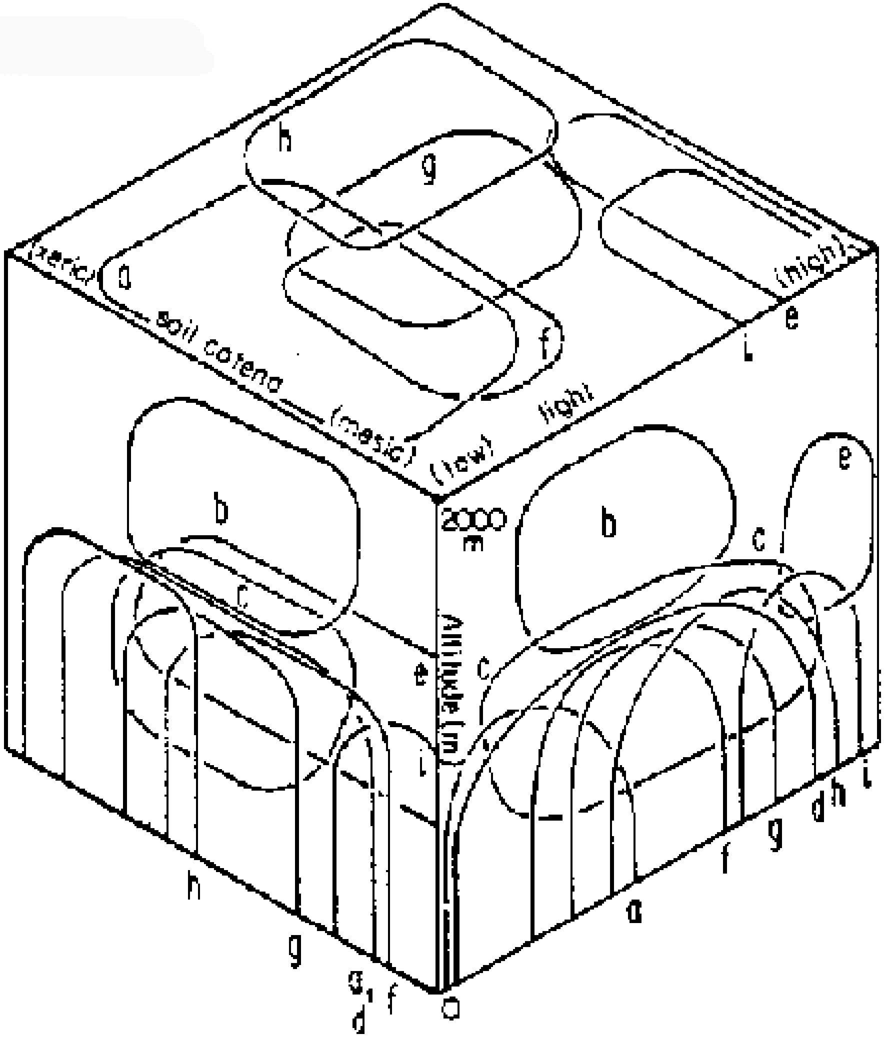
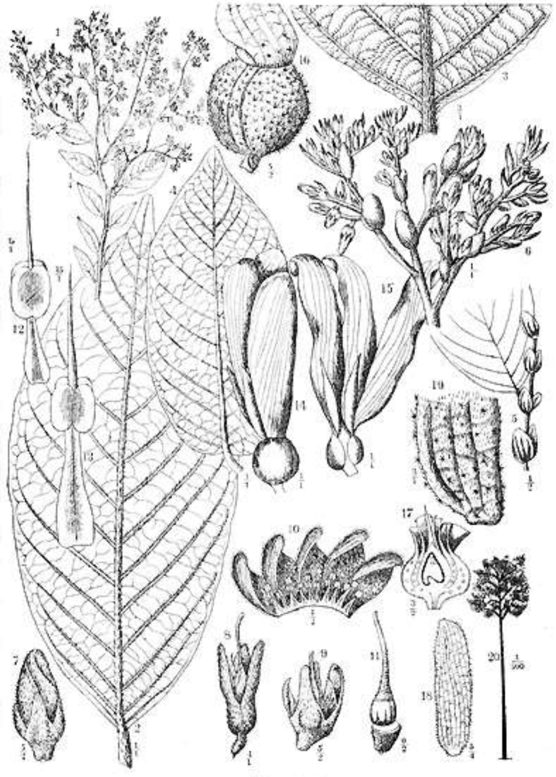


ire 2 Schematic ecological range, in the wet zone forests of Sri Lanka, of the species of *ea.* section *Doona*. Key: **a.** *Shorea cordifolia* **b.** *S. gardneri* **c.** *S. zeylanica* **d.** *S. iis* **e.** *S. trapezifolia* **f.** *S. megistophylla* **g.** *S. disticha* **h.** *S. worthingtonii* **i.** *S. con- iflora*

SHOREA

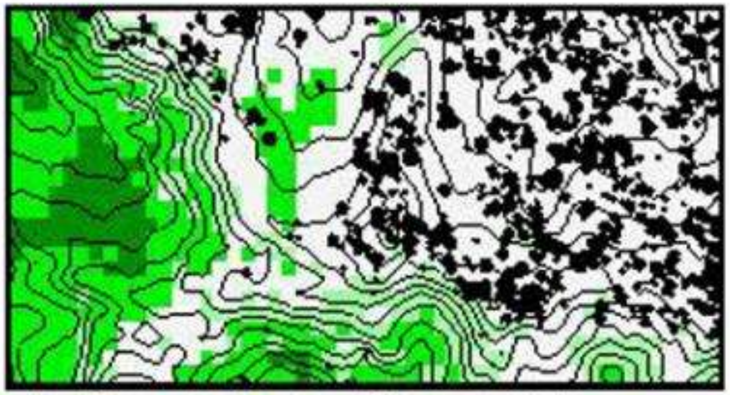
Icones Bogorienses IV. Tab. LXXX.



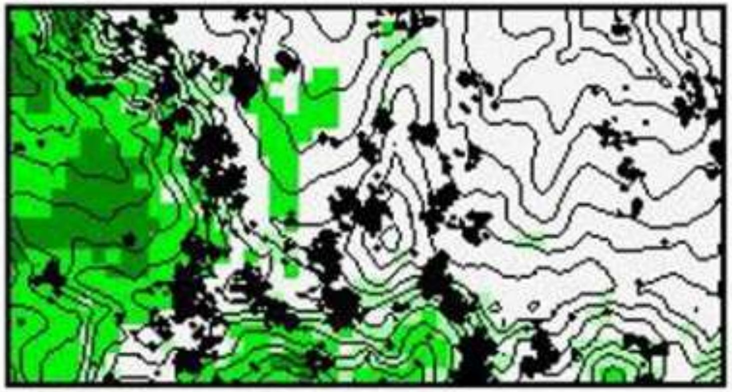
Shorea Koordersii Brandis.

Niche differences and environmental heterogeneity

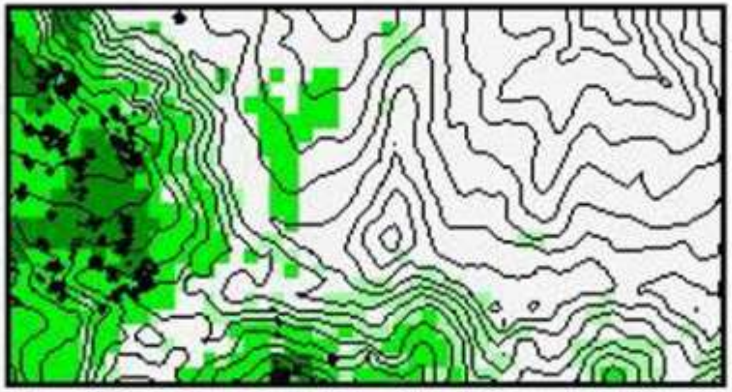
Shorea
in Lambir Hills



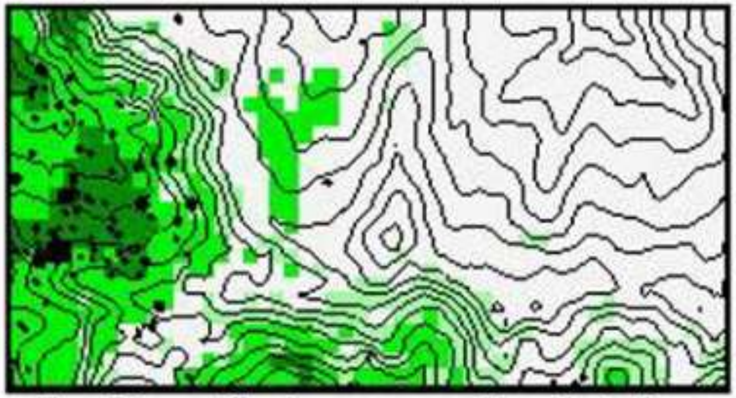
A. Sandy loam (S. acuta)



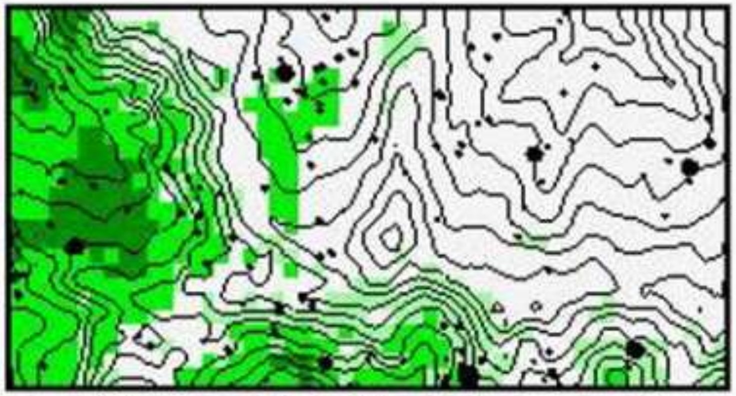
B. (S. amplexicaulis)



C. Fine loam (S. xanthophylla)



D. Clay (S. inappendiculata)



E. Generalist (S. ochraceae)

increasing fertility and moisture:
white, sandy loam
light green, loam
green, fine loam
dark green, clay

Russo, S. E., S. J. Davies,
D. A. King, and S. Tan.
2005. Journal of Ecology
93:879-889.

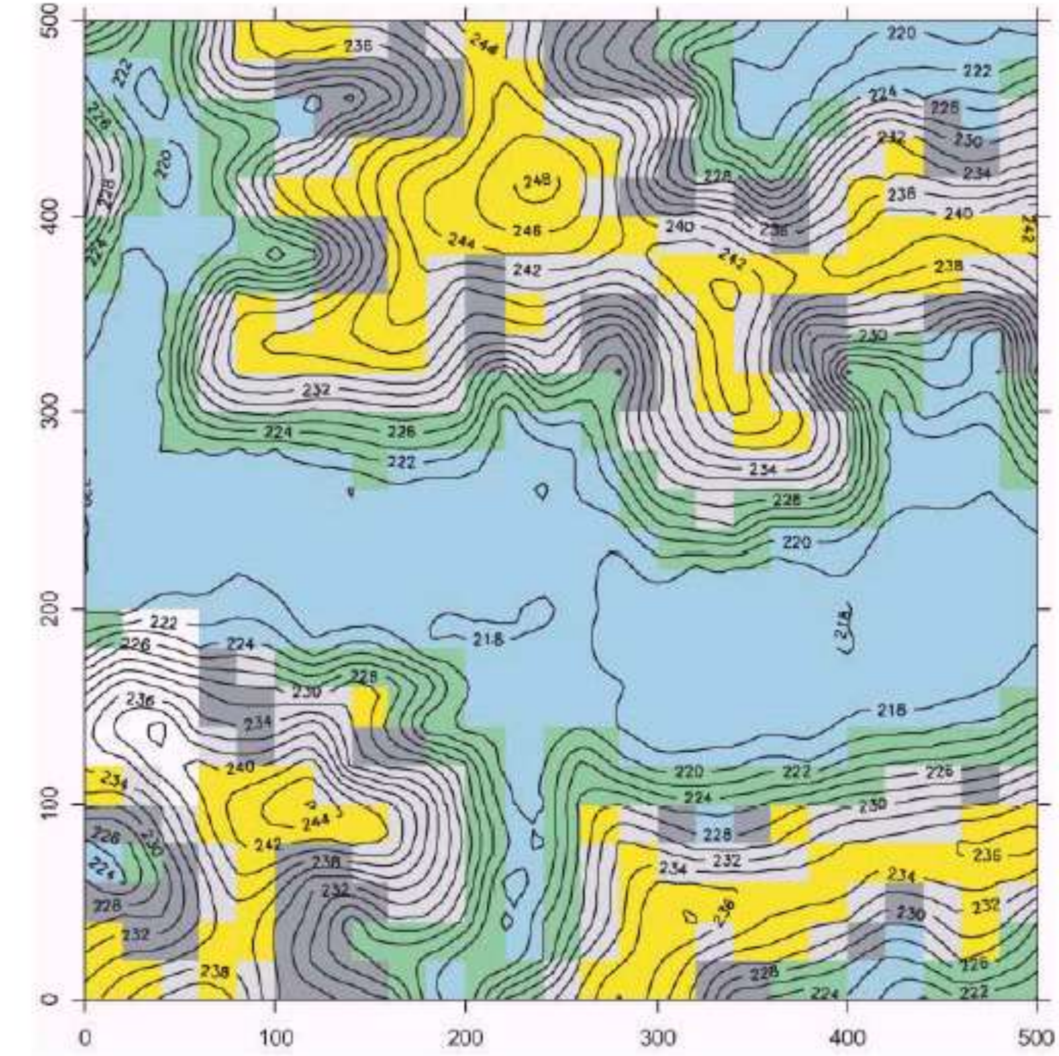
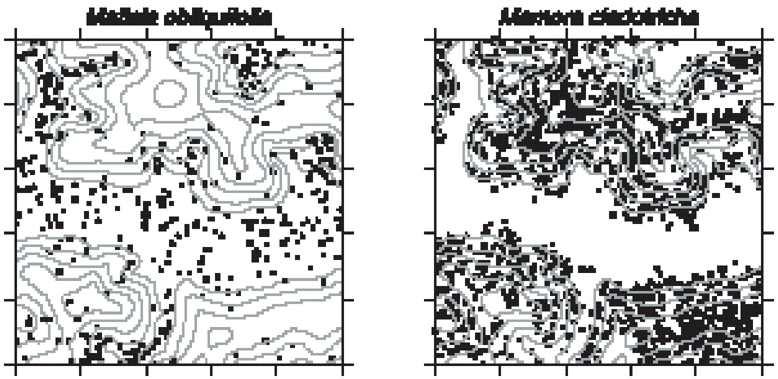


Fig. 2 Topographic map of the 25-ha plot, with 2-m contour intervals. Numbers marking each line are metres above sea level. Six habitats are indicated: valley (blue), low-slope (green), high-gully (dark grey), upper-slope (light grey), ridge-top (yellow), and secondary forest (white). Axes are marked in metres; north is up.

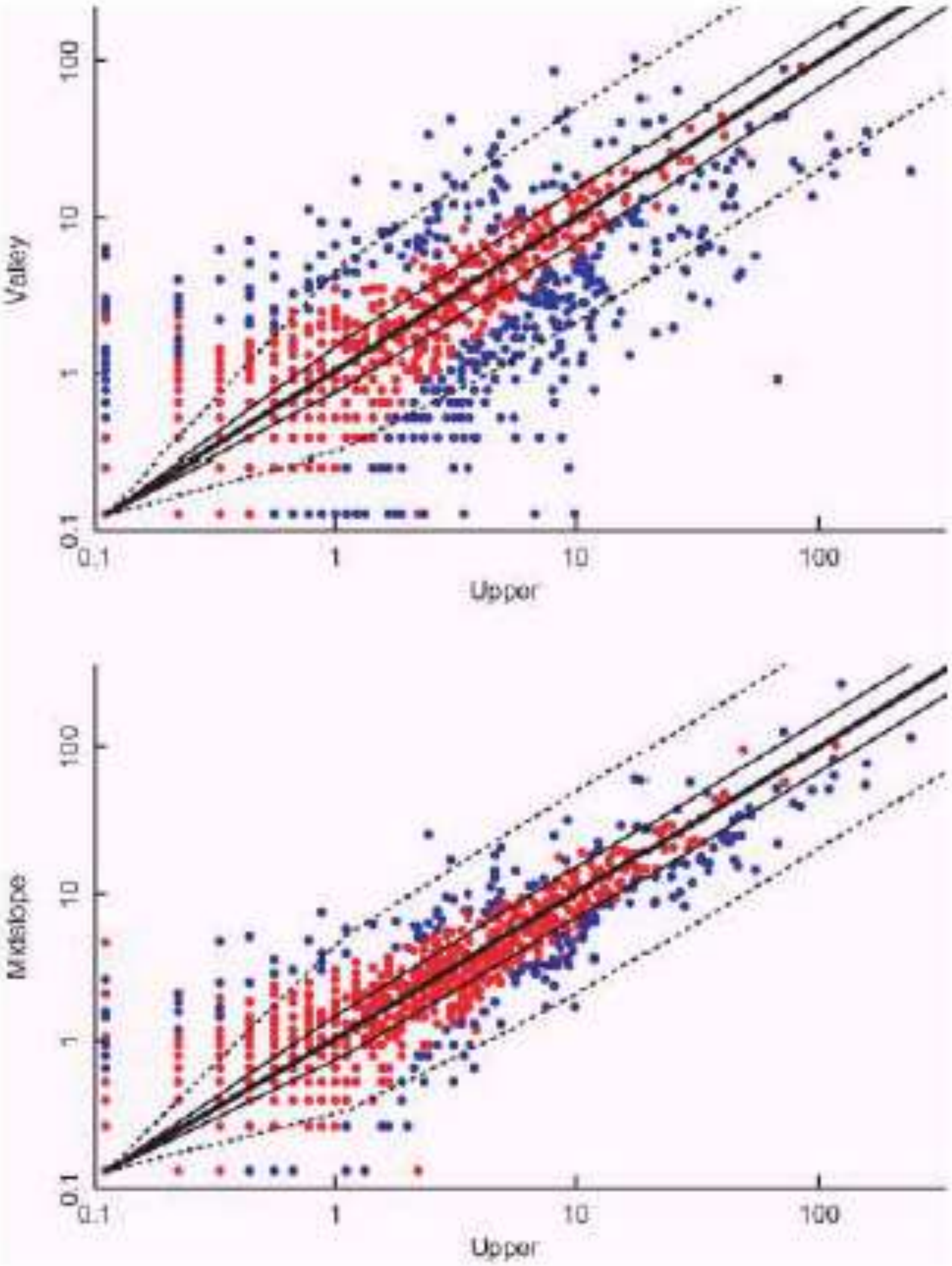


blue: valley
green: low slope
dark grey: high gully
light grey: upper slope
yellow: ridge top
white: disturbance

Distribution of plants with respect to topography and habitats

Lowland rainforest, Yasuni National Park, Peru

Valencia, R. et al. 2004. *Journal of Ecology*, 92,



Habitat preference
of tree species:
blue - significant
red - not significant

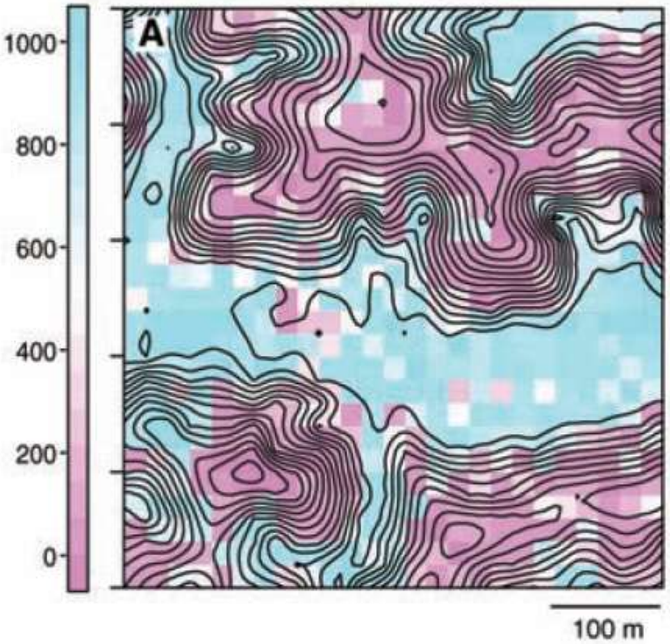
A: valley x upper slope

B: mid-slope x valley

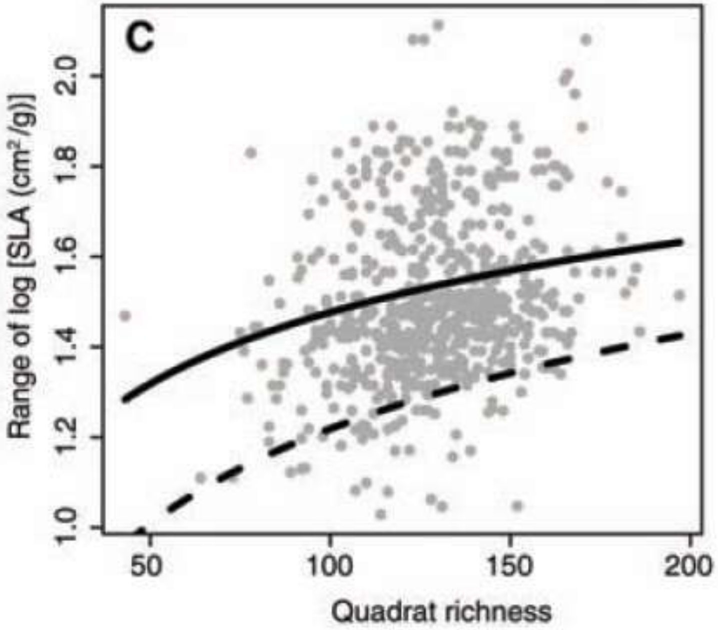
t vs.
tats)
gure
lines
xes,
cate

Valencia, R. et al. 2004. *Journal of Ecology*, 92, 214

Tropical forests: do ecologically similar species occur together, or avoid each other?

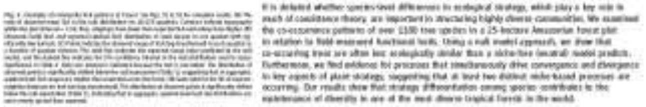


Habitat filtering:
should select for particular trait values
trees with low SLA (specific leaf area) grow on ridge tops, while valleys have species with high SLA within 25 ha forest plot in Yasuni. Each habitat has smaller range of SLA values than expected for random distribution of species.



Coexistence of dissimilar species:

should select for variability in trait values
Within each habitat, tree species co-occurring within a 20x20 m quadrat had wider range of SLA than expected under random distribution of trees among quadrats.



Kraft et al. 2008 Science 322: 580

What prevents a single "superman" tree species, best adapted to local conditions, from out-competing others and prevailing in the rainforest?

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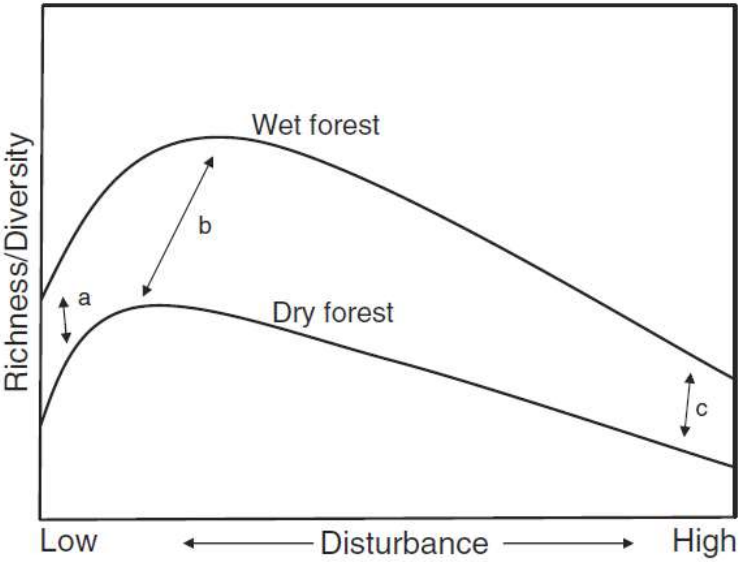
Wright, S. J. 2002. Plant diversity in tropical forests: A review of mechanisms of species coexistence. Oecologia 130: 1–14.

Intermediate Disturbance Hypothesis

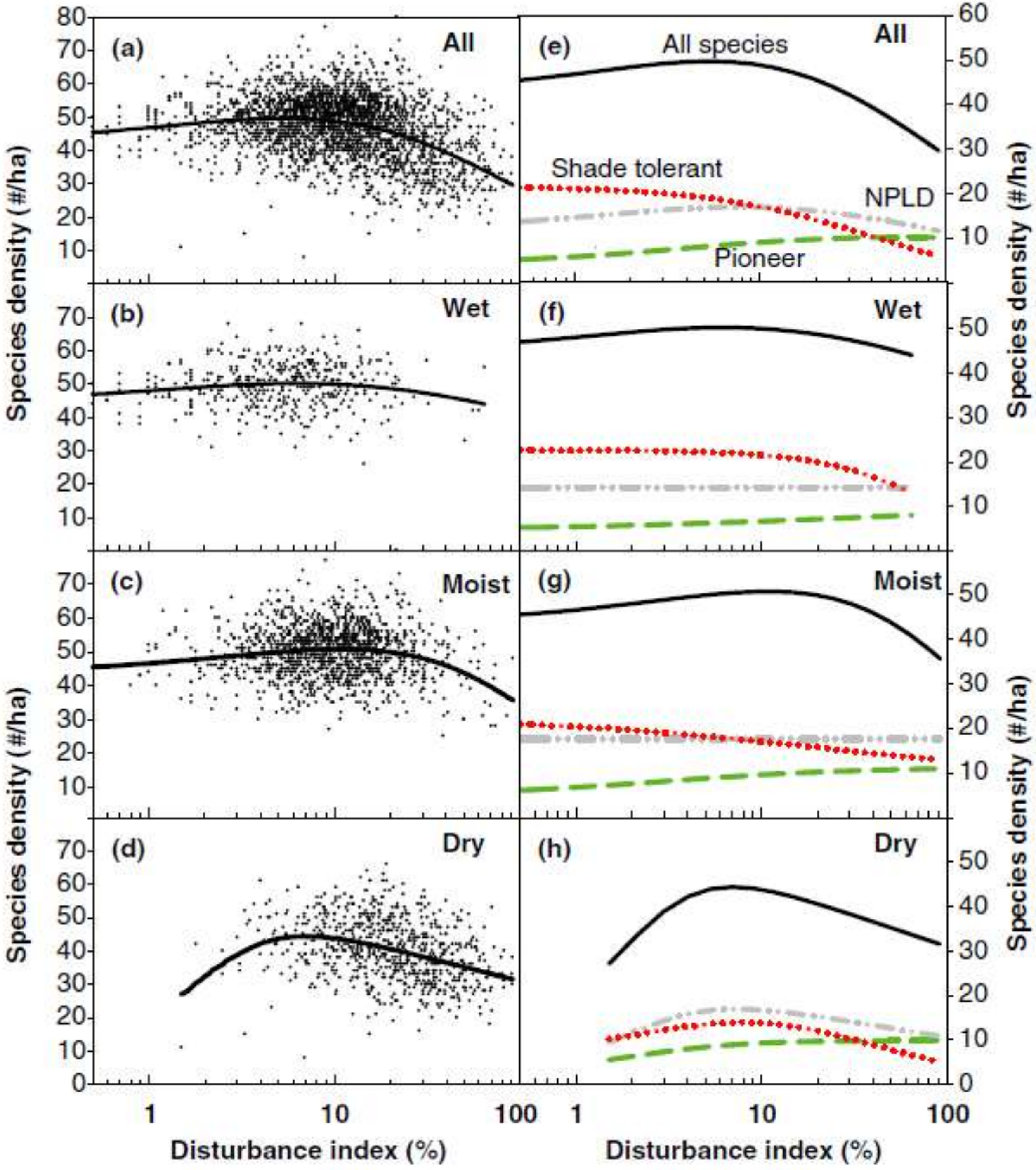
Two possible mechanisms:
disturbance

- removes dominant species opening thus an opportunity for others

- creates new habitat [for pioneer spp.]



Bongers et al. 2009: The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecology Letters,12: 798–805



Diversity peaks at intermediate disturbance levels but little variation is explained outside dry forests

points = 1ha tropical forest plots [2504 plots],
NPLD = non-pioneer light demanding spp.
Disturbance index = % of trees that belong to the pioneer species

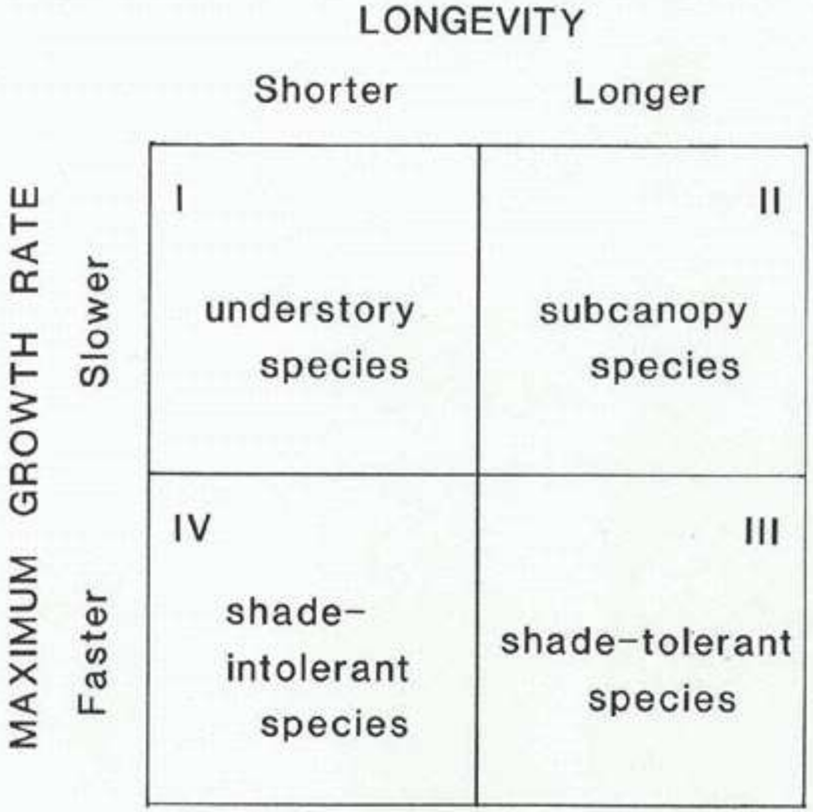


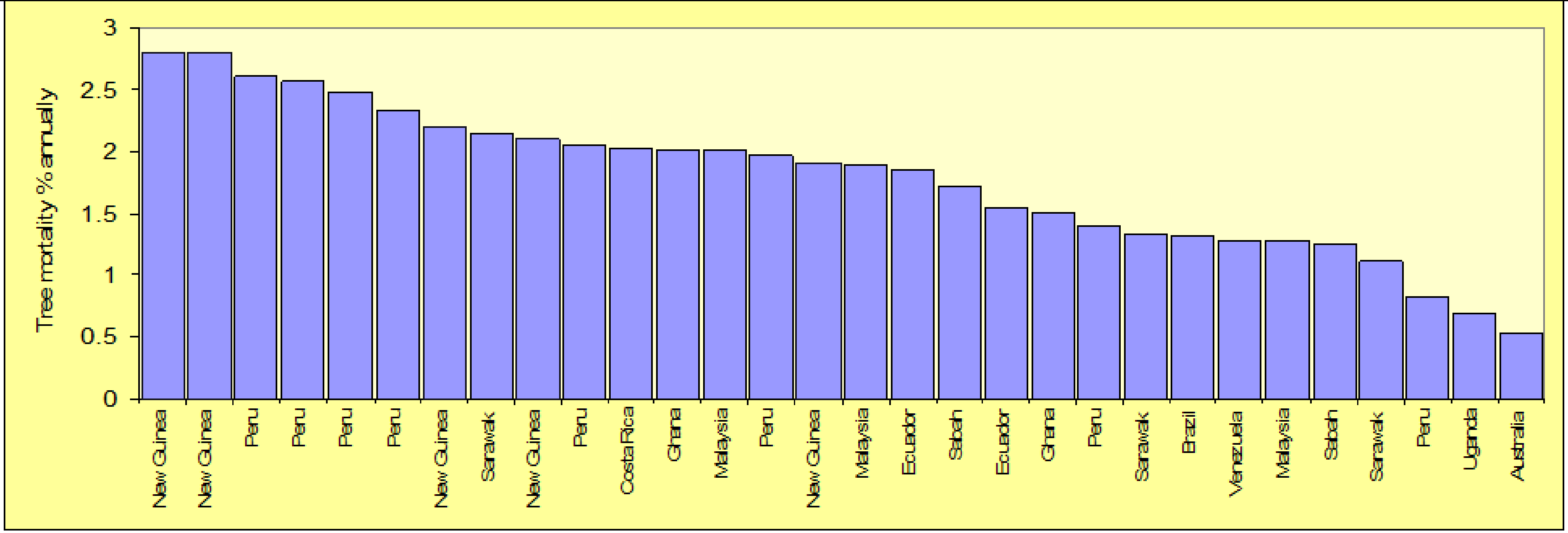
FIGURE 25.2. Diagrammatic classification of tree species according to maximum growth rate (slow v. fast) and projected lifespan (short v. long). *Group I*: understory species, *Group II*: slow-growing subcanopy species, *Group III*: fast-growing, shade-tolerant canopy and subcanopy species that respond opportunistically to increased light levels; *Group IV*: putative shade-intolerant canopy and subcanopy species.

Problem:

pioneer trees always represent only small % of the total diversity

Rainforests are dynamic

Annual mortality of trees with DBH>10cm : 0.5 – 2.7%



Mortality of forest trees (DBH>10cm) New Guinea: Wright, Mack & Supuma unpubl. Continental: Phillips et al. 1994 PNAS

Dynamic forests are more diverse: the mean mortality matters

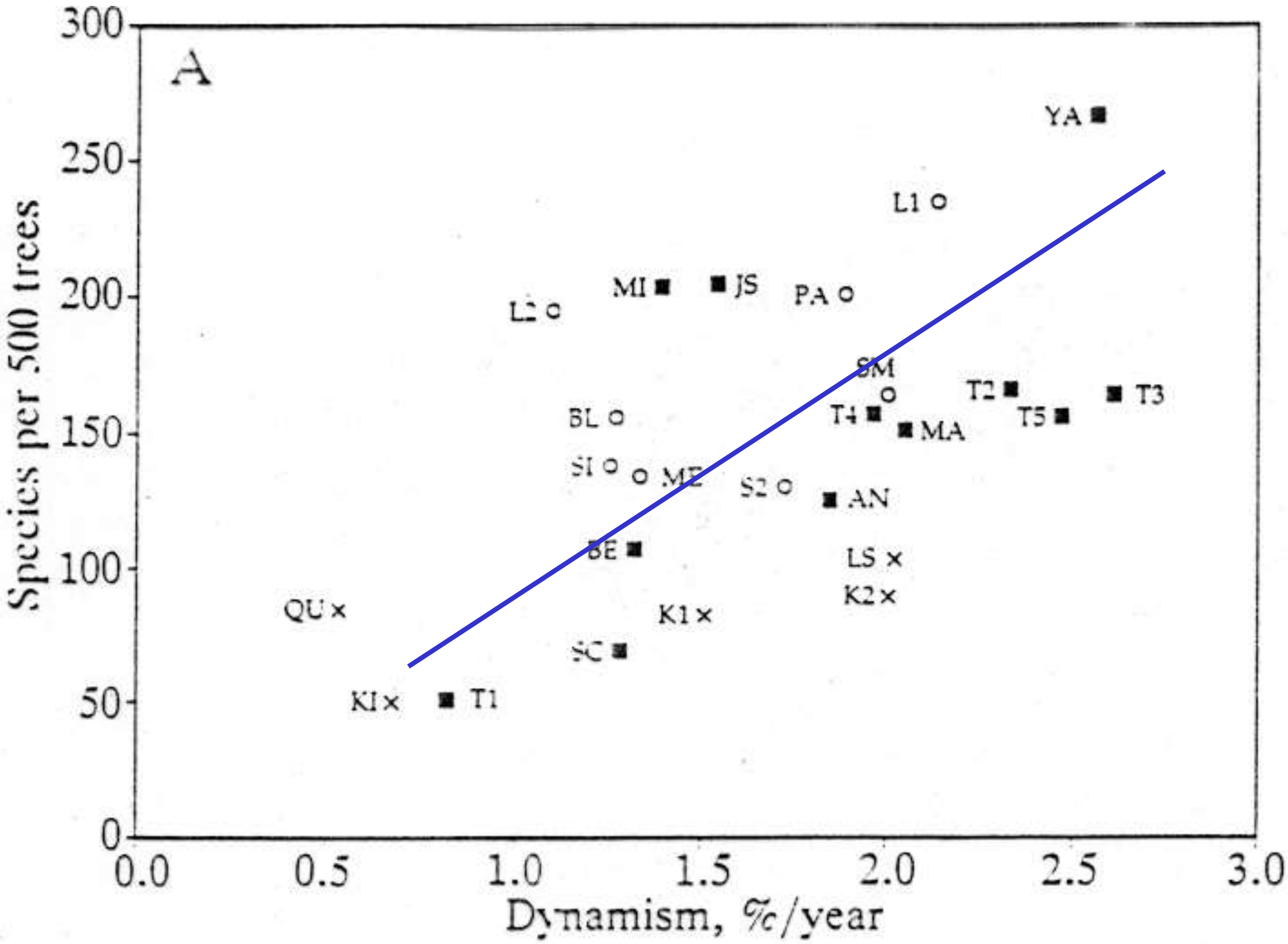
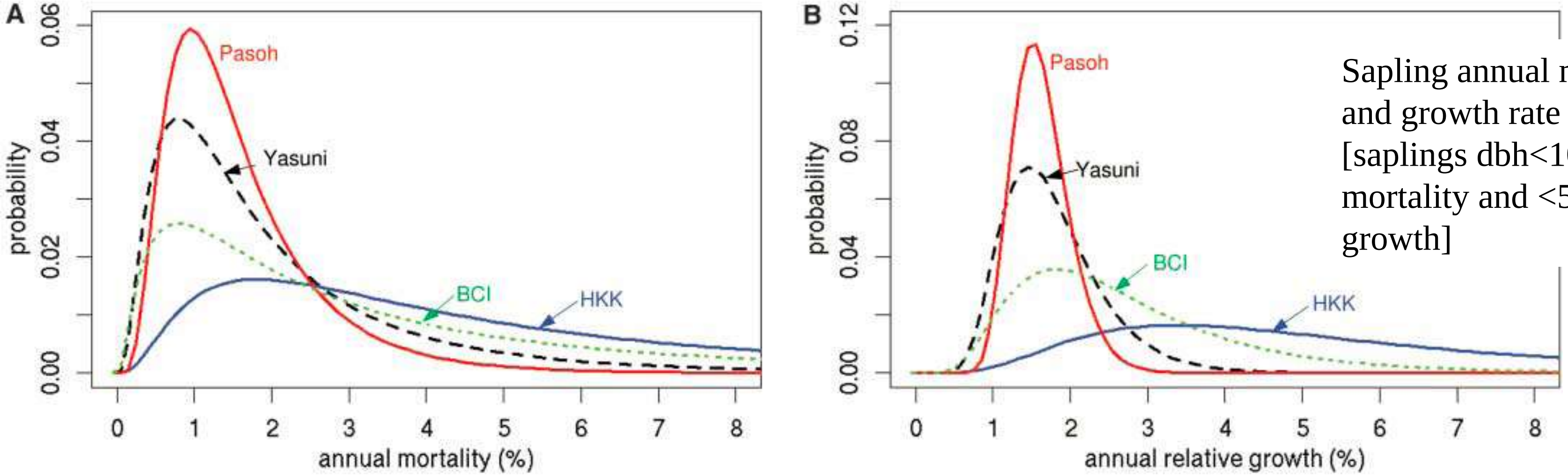
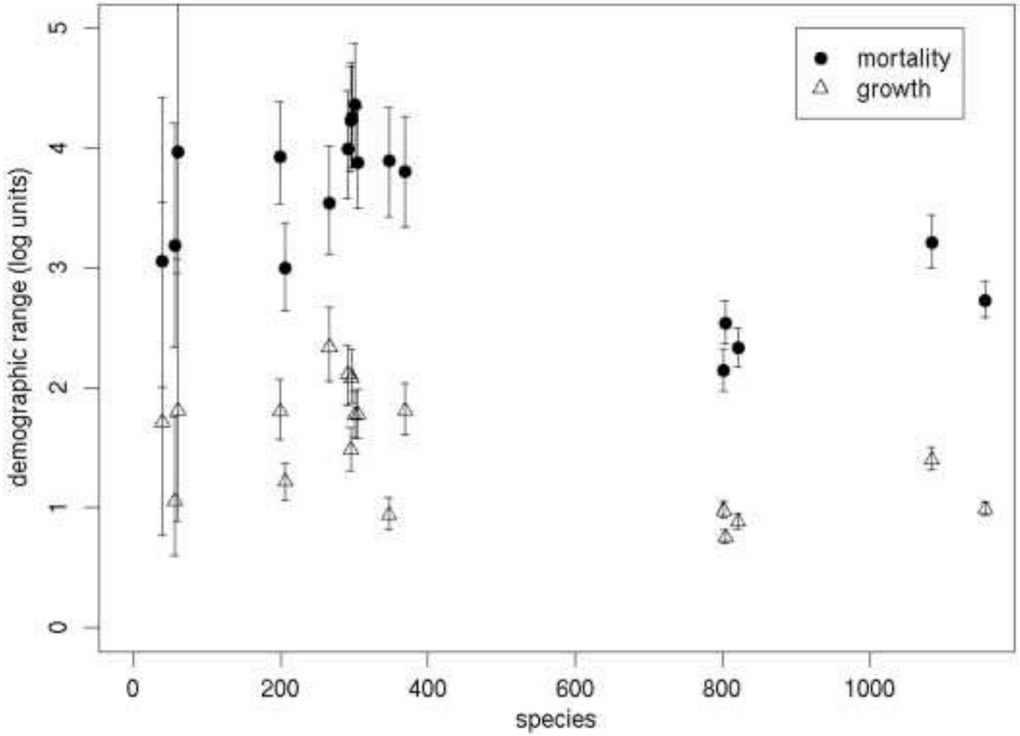


FIG. 1. (*A*) Tree species richness vs. dynamism (mean of annual mortality and recruitment). (*B*) Tree species richness predicted by multivariate regression model vs. observed tree species richness. ○, Sites in South-East Asia; ■, sites in Amazonia; X, sites in "Other" phytogeographical regions (Africa, Australia, and Central America). See Table 1 for complete site descriptions, Table 4 for multivariate model.

Demographic differences facilitate species richness: more species would coexist in plots with higher variability in growth and mortality among species – not confirmed in 50-ha plots



Sapling annual mortality and growth rate in 4 forests [saplings dbh<10cm for mortality and <5cm for growth]



Range of sapling demographic rates (mortality, growth) for tree species within a community versus the number of species at the site. The range is the logarithm of the ratio between the 97.5 and 2.5 percentiles of the fitted distributions

Variability in mortality & growth does not matter

Condit, R et al. (2006). **The Importance of Demographic Niches to Tree Diversity**." Science **313**: 98.

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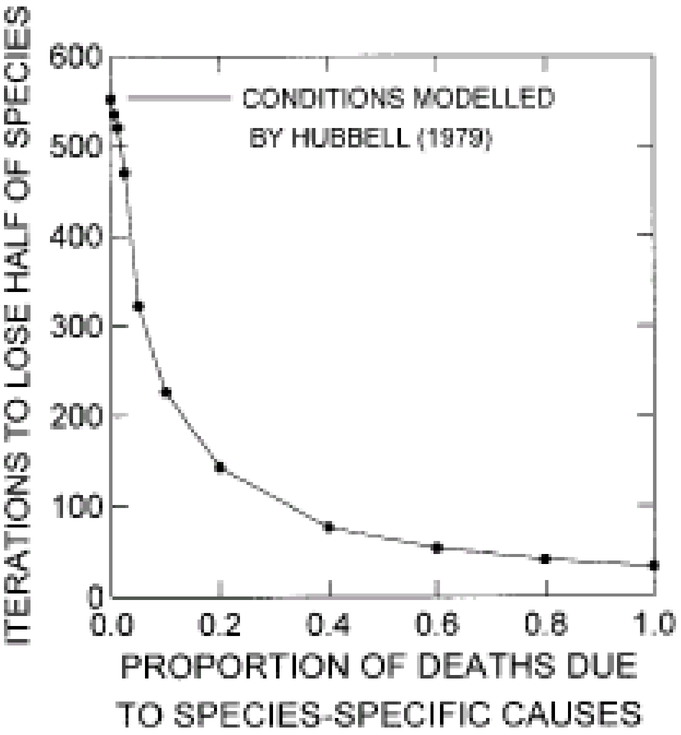

Fig. 4 The transitory maintenance of community diversity by chance (*vertical axis*) decays rapidly as the proportion of deaths determined by chance declines and the proportion determined by species-specific causes increases (*horizontal axis*). Hubbell (1979) simulated the indicated conditions. In contrast, Yu et al. (1998) simulated conditions similar to those at the opposite extreme along the horizontal axis. I used annual probabilities of mortality observed for different tree species on BCI (Condit et al. 1995) for species-specific deaths and equal probabilities for every individual regardless of species for chance deaths and for all births. Following Hubbell (1979), the simulated community included 1,600 trees initially divided among 40 equally abundant species with 160 tree deaths per model iteration

Wright 2001. Oecologia 130:1

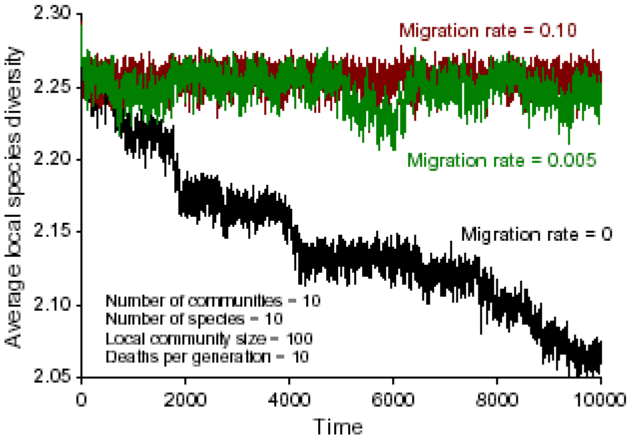

Figure 1. Decline in Shannon–Wiener species diversity in simulated neutral communities composed of ecologically equivalent species. Simulations were run for 10,000 time steps, where 10 death/replacement events constituted a single time step. Initial abundances of species were identical within each of ten local communities. Species diversity was calculated at each time step for each community and then averaged across communities. Higher migration rates slow the decline in species diversity.

Mass effect (immigration) slows down loss of species from the community due to competition

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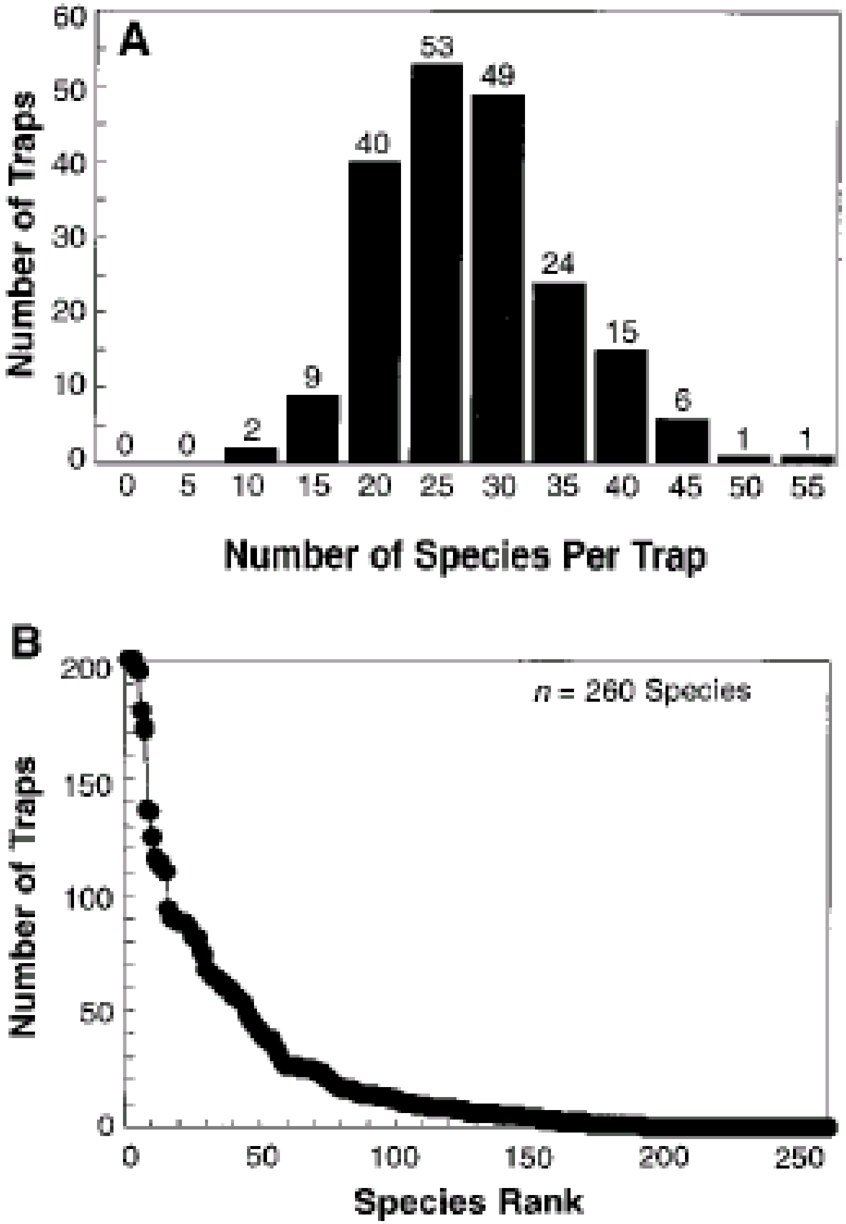


Seed traps at BCI:

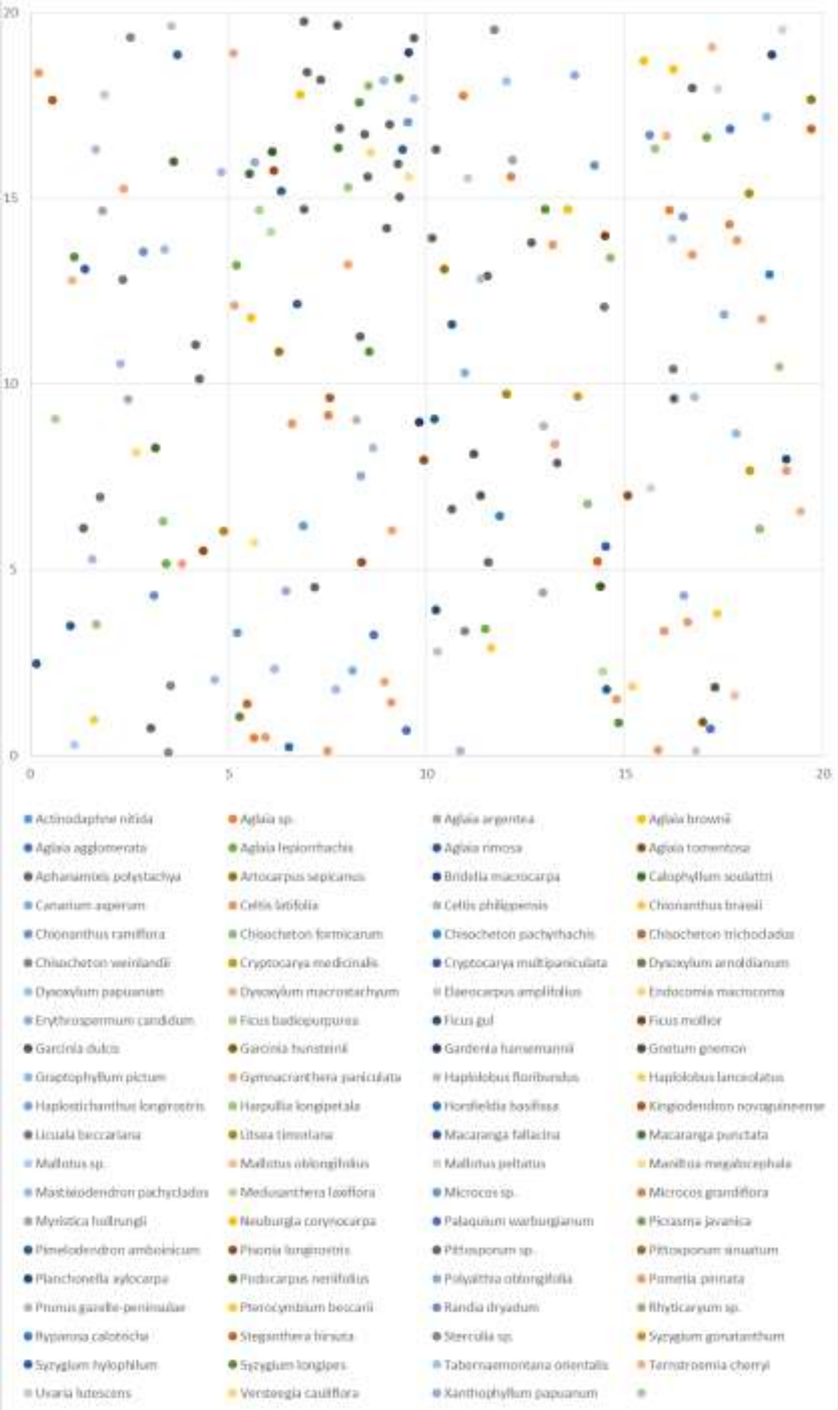
evidence for dispersal limitation,

or most of the tree species does not get to most of the places most of the time

Fig. 4. Evidence for dispersal limitation in BCI trees from a 10-year seed trap study using 200 traps in the 50-ha plot. Seeds of a total of 260 species of the 314 species in the plot census were collected at least once. (**A**) Frequency distribution of the number of species captured per trap during the 10-year trapping period (1987–96). The average number of species per trap was 30.8 ± 7.5 SD. (**B**) The total number of traps into which each species dispersed at least one seed during the 10-year trapping period.

. We also thank O. Calderón for counting and identifying $>10^6$ seeds in the seed traps over the years.

Hubbell et al. 1999. Science 284:554



20x20m plot in Wanang
DBH>1cm

220 stems
85 species
40 singletons

Most common species:
16 stems (7.3%)
Aphanamixis polystachia

85 spp from the species pool of 536 spp (15.9%)

3,570 locally possible pair-wise interactions from the total of 143,380 (2.5%)

Aphanamixis polystachia

(Meliaceae): the most common tree sp.

Nearest neighbours:
4 conspecific trees and 9 other spp

Aphanamixis polystachia	4
Cryptocarya multipaniculata	2
Maniltoa megalocephala	2
Pittosporum sp.	2
Actinodaphne nitida	1
Articarpus sepicanus	1
Harpulia longipetala	1
Macaranga punctata	1
Mastixiodendron pachycladus	1
Planchonella xylocarpa	1

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Negative density-dependency: four mechanisms

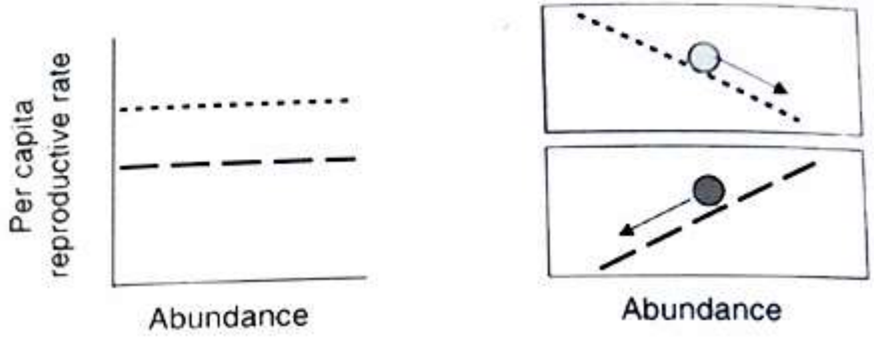
- Intra-specific self-thinning
- Inter-specific competition
- Mortality due to density-responsive pests/pathogens
- Mortality due to distance-responsive pests/pathogens

Yoda’s power law

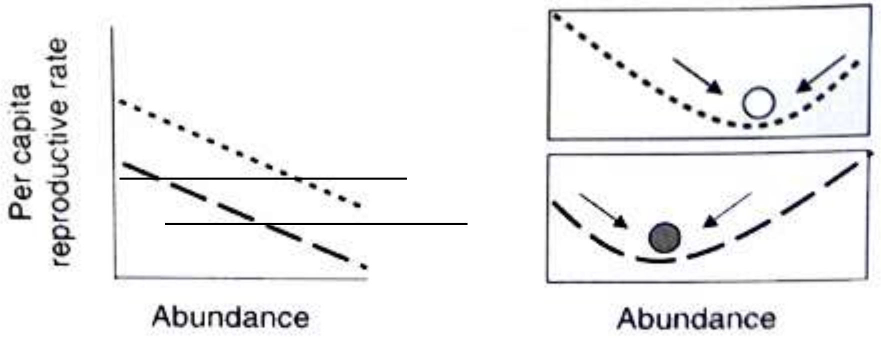
mean plant biomass = c * density$^{-3/2}$

$W^{2/3}*N\ ^{=}$ constant

Density-dependence of reproductive rate [r] and species coexistence



two species differ in their r, which is density independent
species with higher r competitively excludes the other species

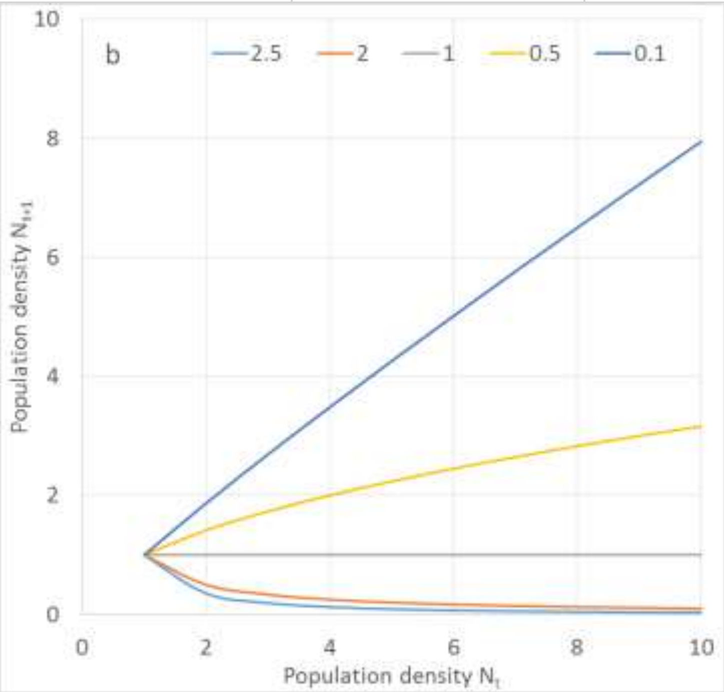


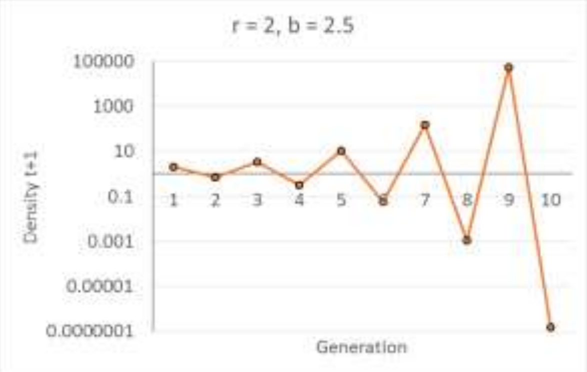
two species differ in their r, which is density dependent
two species coexist at densities where they have identical value of r

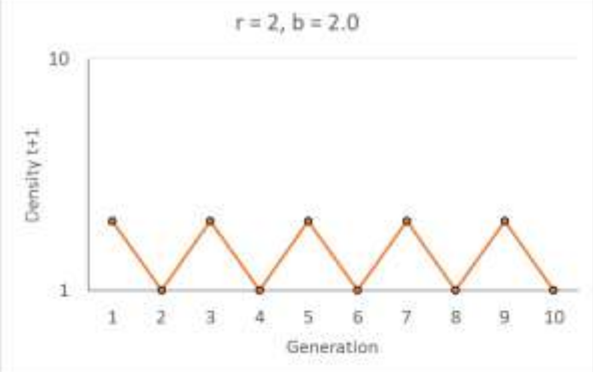
Muller-Landau 2008 in Carson & Schnitzer: Tropical Forest Community Ecology

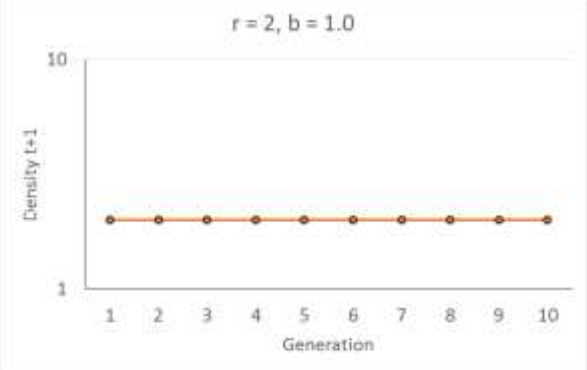
$$N_{t+1} = r*N_t^{(1-b)}$$

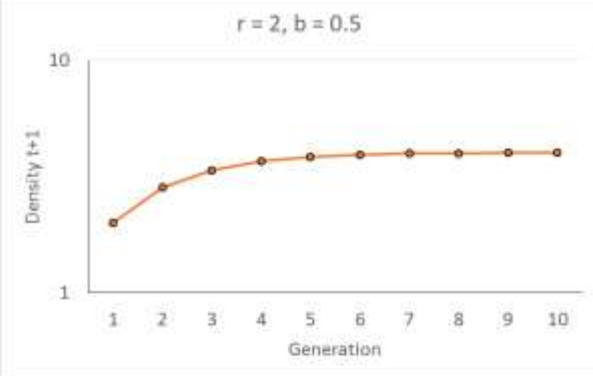
N_{t+1}	population density next generation
N_t	population density initial [0,1]
r	growth rate
b	density dependent limit on growth
$2>b>0$	stable population

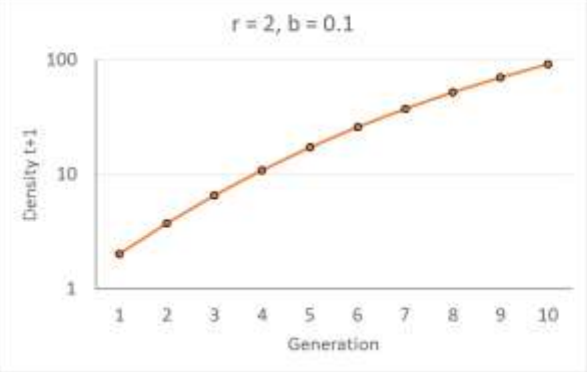



r = 2, b = 2.5


r = 2, b = 2.0


r = 2, b = 1.0

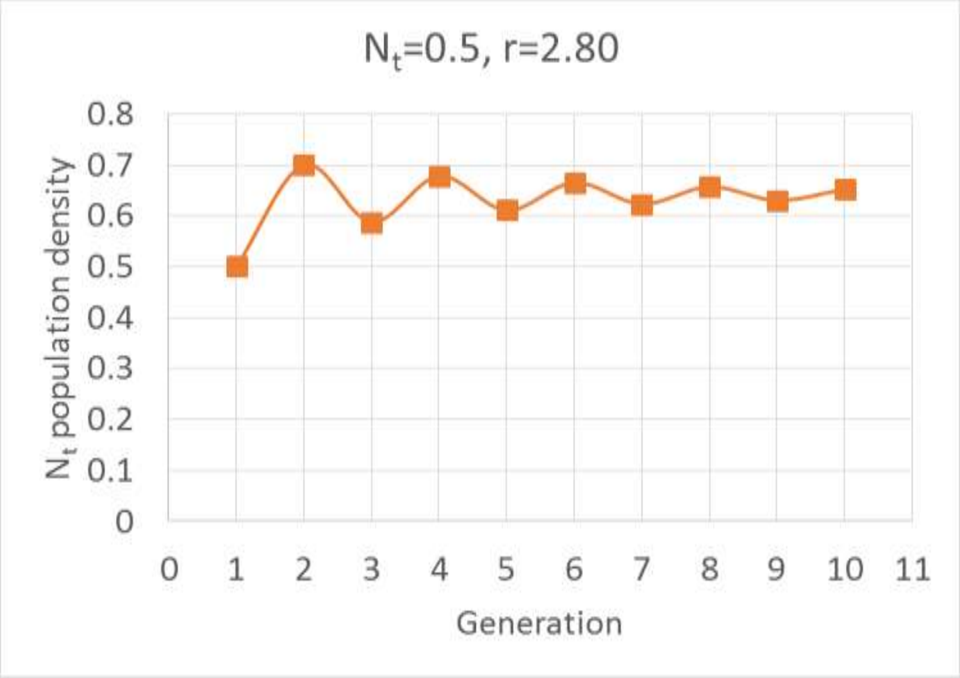

r = 2, b = 0.5

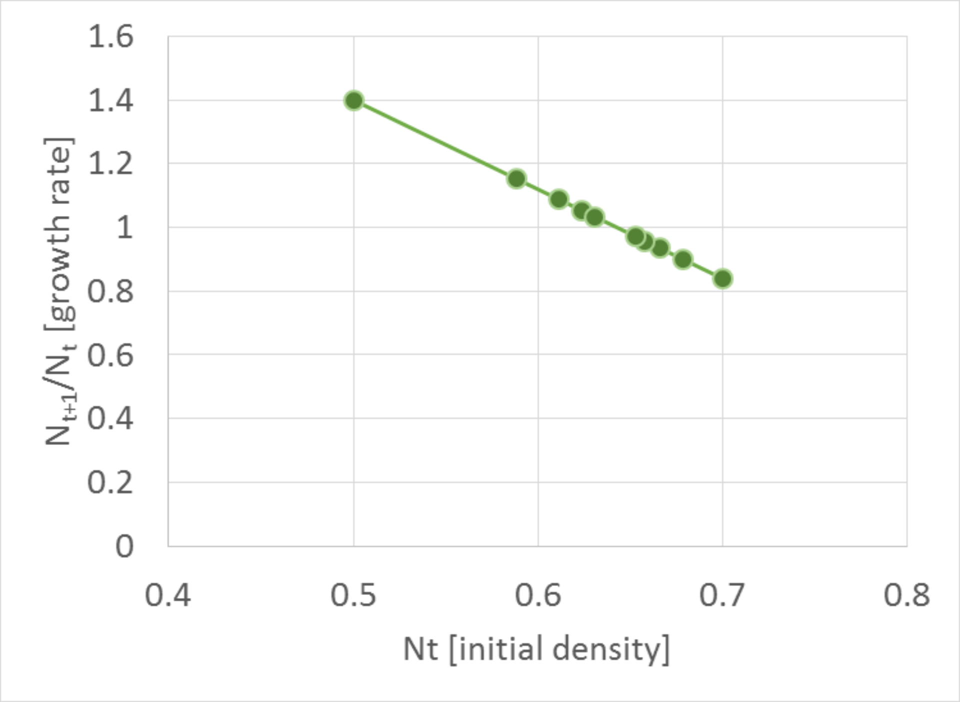

r = 2, b = 0.1

$$N_{t+1} = rN_t - rN_t^2$$

$$N_{t+1} = r*N_t*(1 - N_t)$$

N_{t+1}	population density next generation
N_t	population density initial [0,1]
r	growth rate
rN_t	exponential growth
$-rN_t^2$	density dependent limit on growth



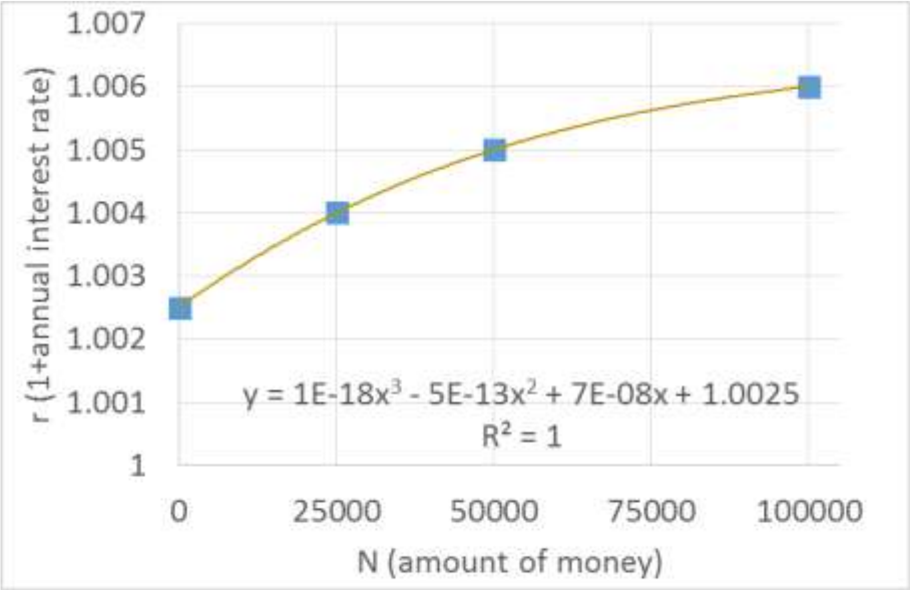


The roots of social inequality problem: the dynamics of money is positively density dependent

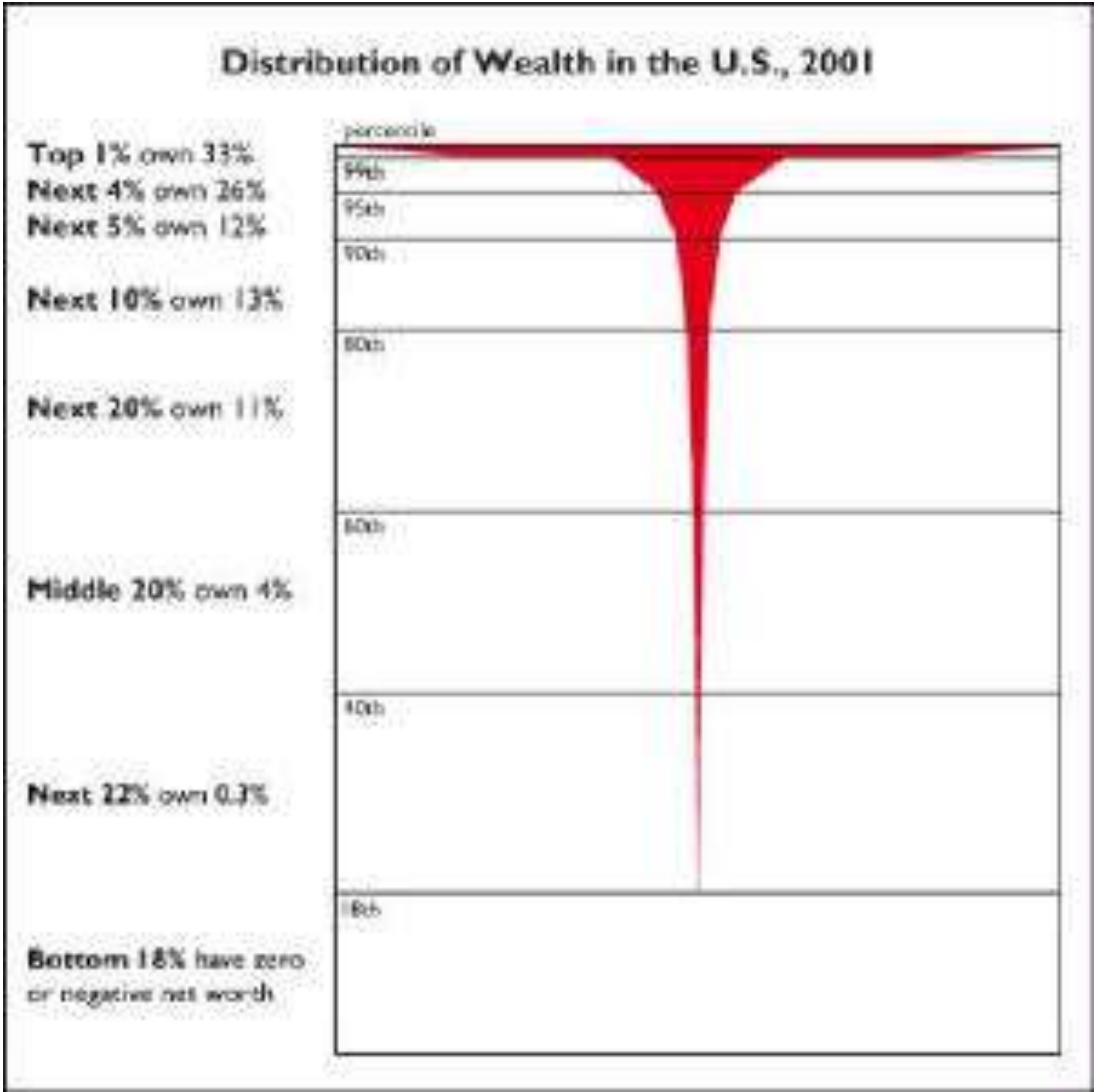
BARCLAYS

Current interest rates

Balance	Gross pa%
£1 - £24,999	0.25
£25,000 - £49,999	0.40
£50,000 - £99,999	0.50
£100,000 +	0.60



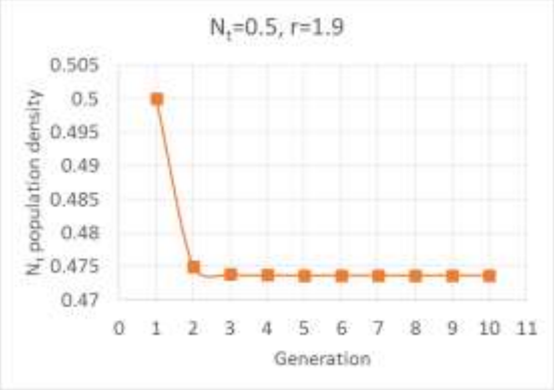
$$N_{t+1} = N_t * (r_1 + 10^{-18}*N^3 - 5*10^{-13}*N^2 + 7*10^{-8}*N)$$

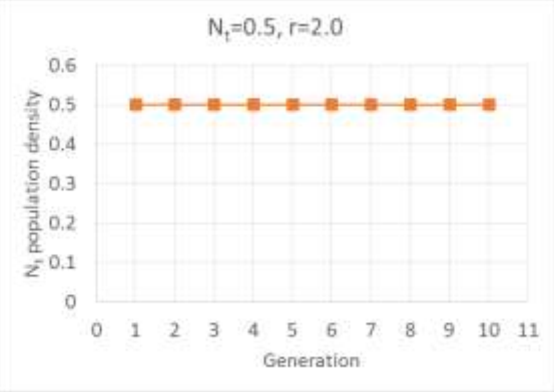


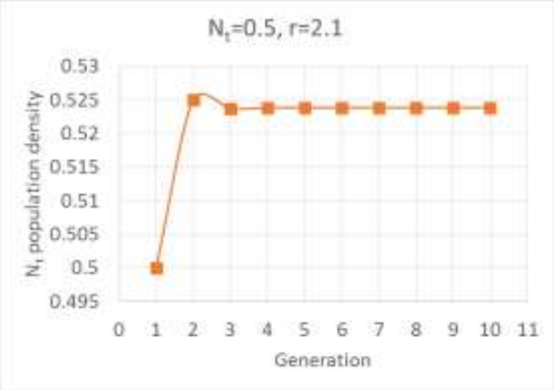
Distribution of Wealth in the U.S., 2001

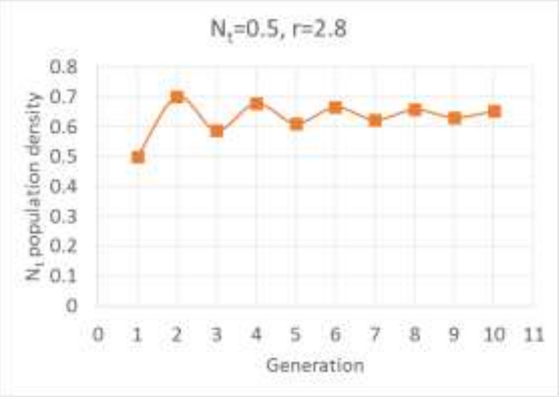
$$N_{t+1} = rN_t - rN_t^2$$

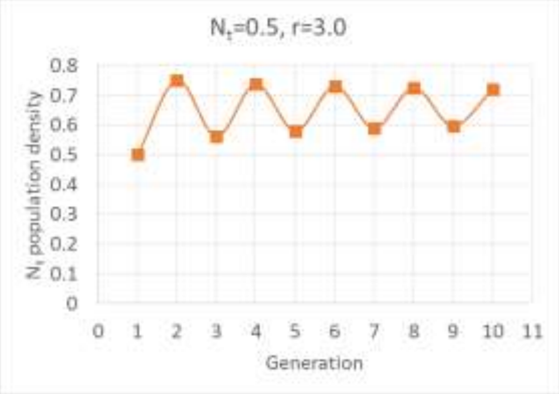
$$N_{t+1} = r*N_t*(1 - N_t)$$


N_t=0.5, r=1.9


N_t=0.5, r=2.0


N_t=0.5, r=2.1


N_t=0.5, r=2.8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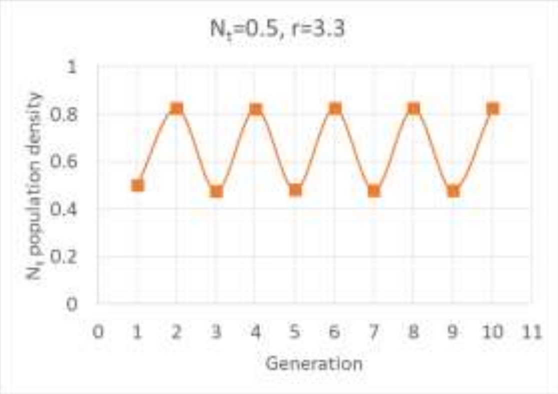
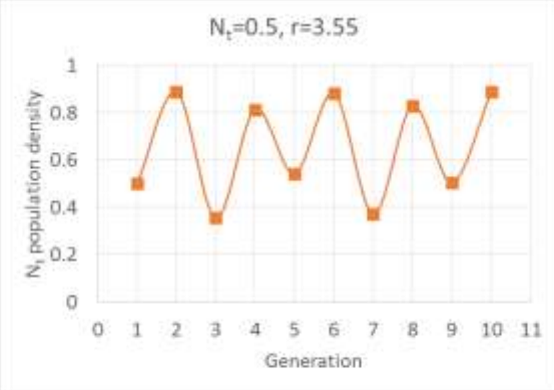
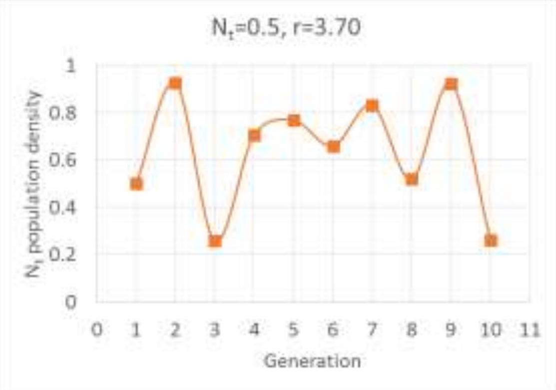
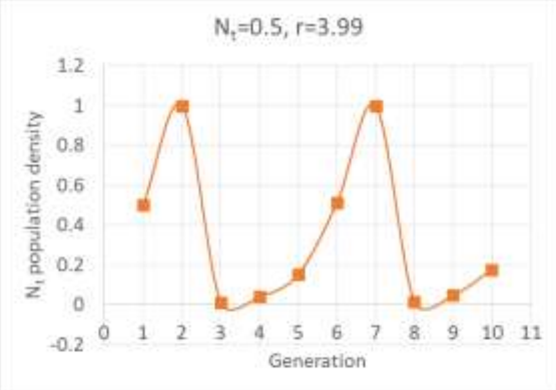

N_t=0.5, r=3.3


N_t=0.5, r=3.55


N_t=0.5, r=3.70

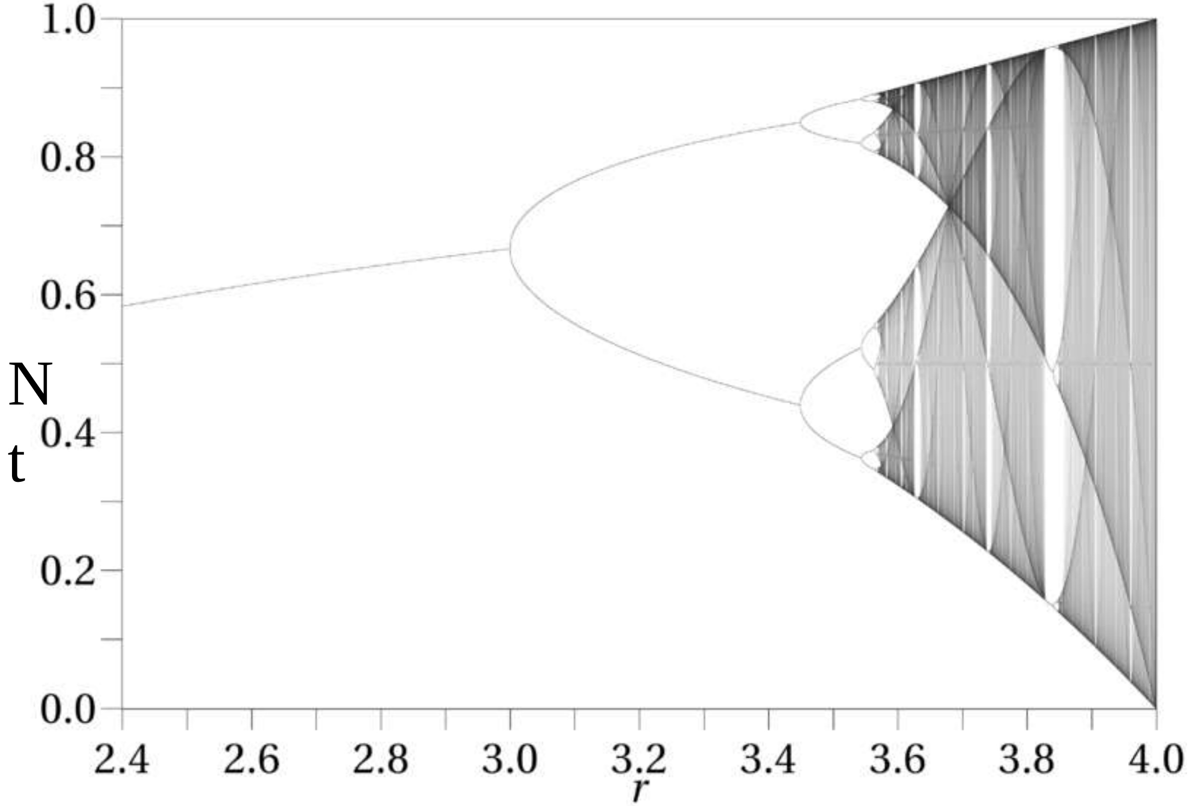

N_t=0.5, r=3.99

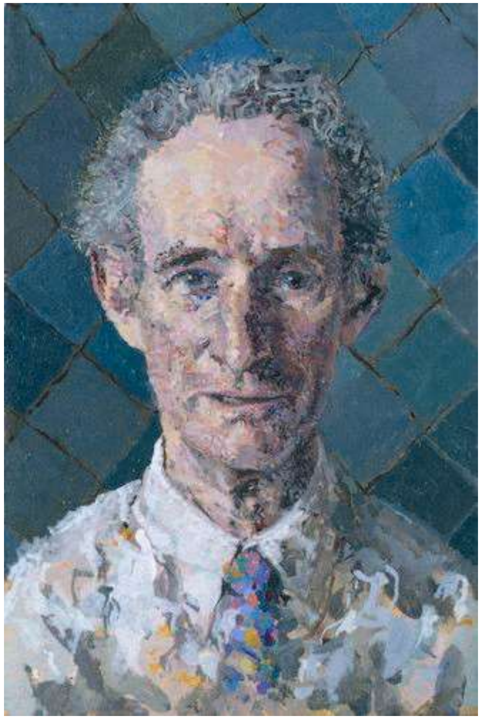
$$N_{t+1} = rN_t - rN_t^2$$

$$N_{t+1} = r*N_t*(1 - N_t)$$

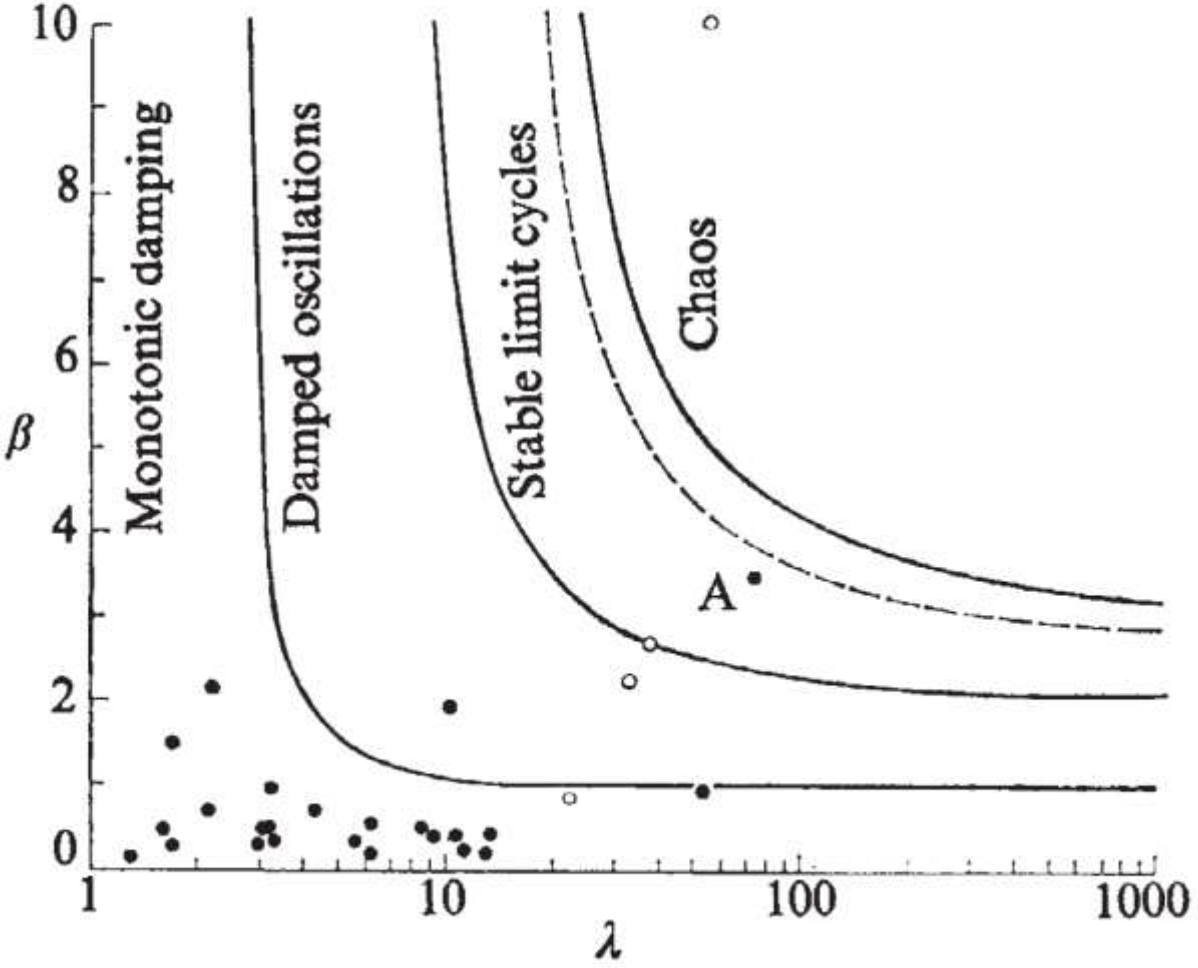
N_{t+1}	population density next generation
N_t	population density initial [0,1]
r	growth rate
rN_t	exponential growth
$-rN_t^2$	density dependent limit on growth

Simple mathematical models with very complicated dynamics
RM May Nature 261 (5560), 459-467



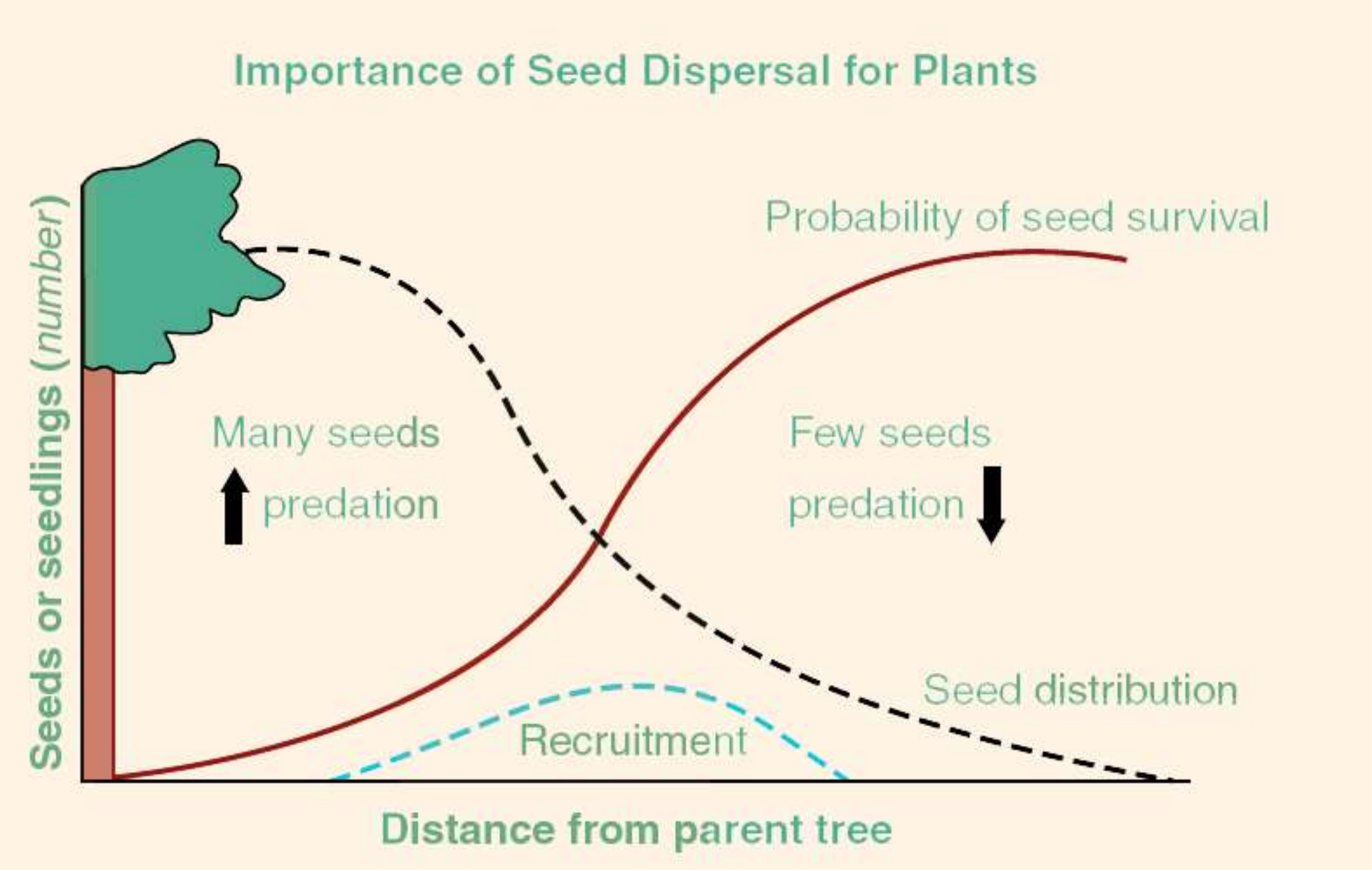


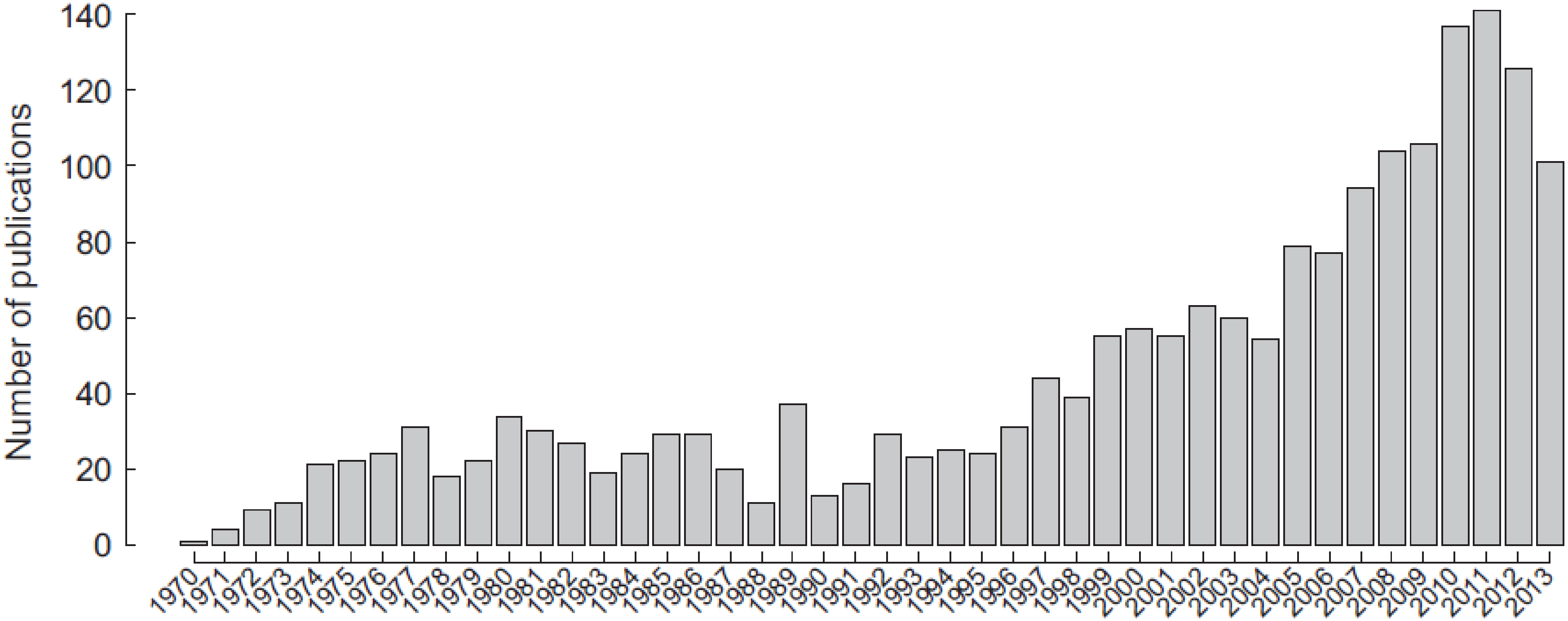
$$X_{t+1} = \lambda X_t (1 + X_t)^{-\beta}$$



Rare species are favoured demographically

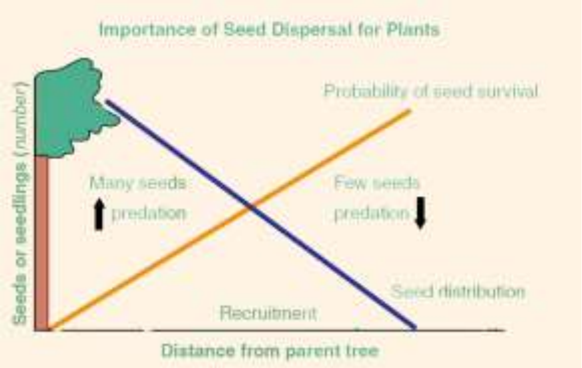
The Janzen-Connell hypothesis: seedlings are more likely to be dispersed near their parent, but more likely to survive far from their parent.





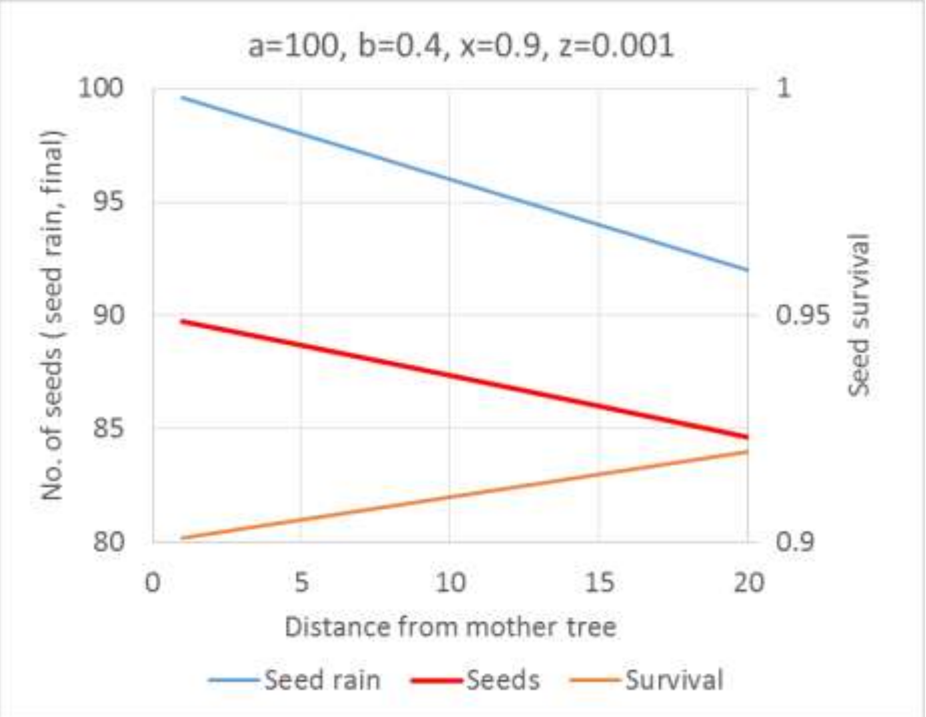
Number of articles citing Janzen (1970) or Connell (1971) between 1970 and 2013 (total = 1976).

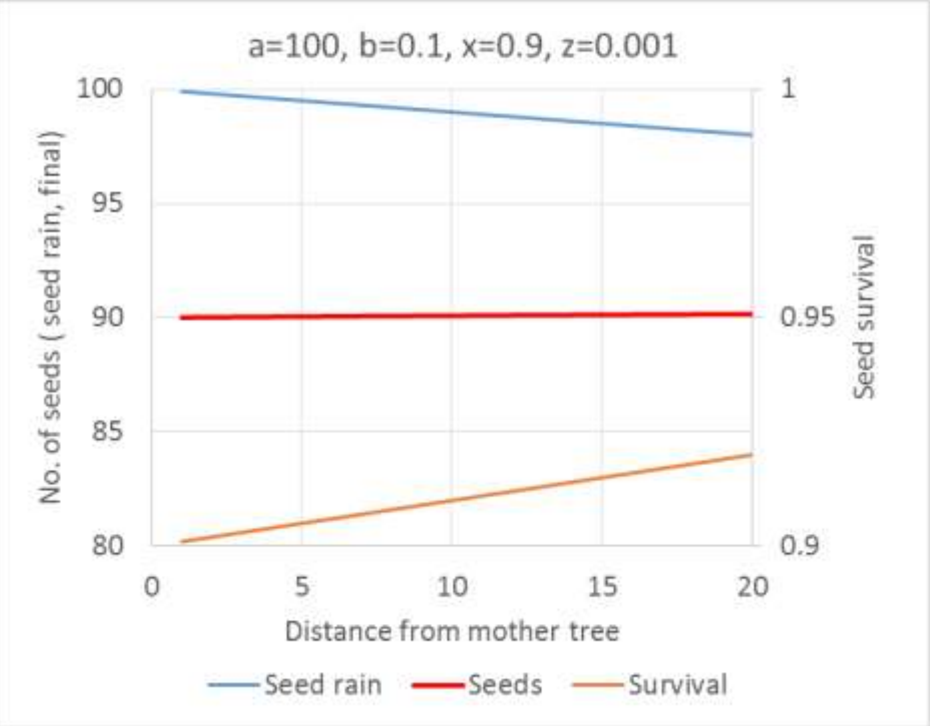
Comita et al. 2014, Journal of Ecology, 102, 845–856

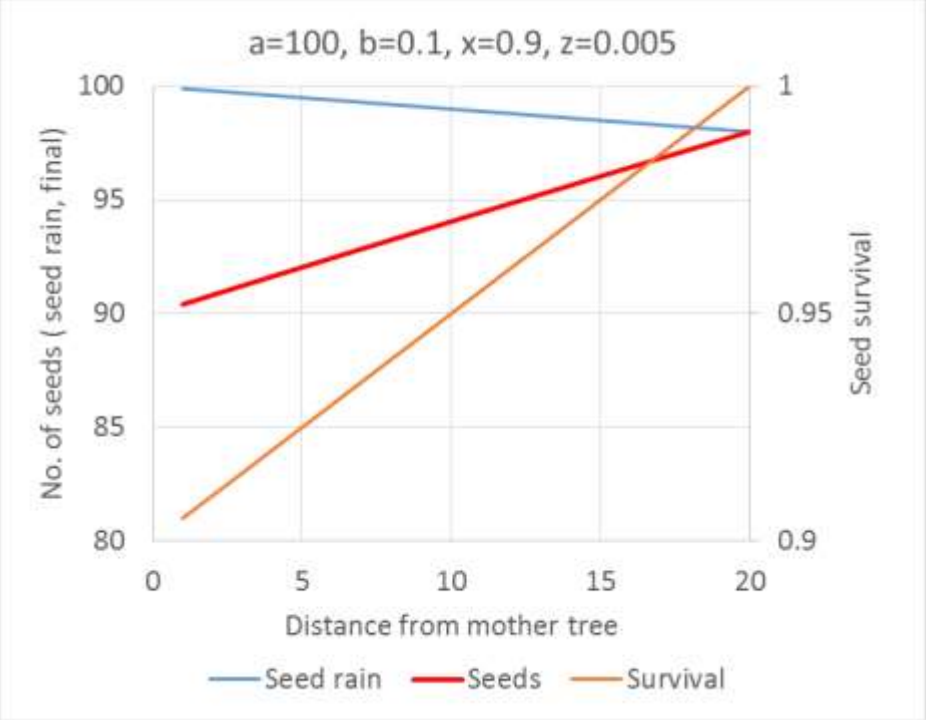


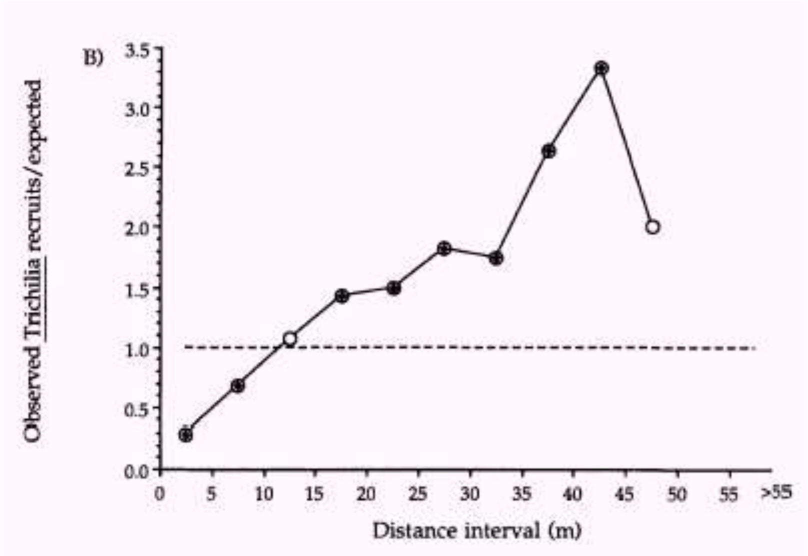
seed rain = a - b*distance

survival = x + z*distance


a=100, b=0.4, x=0.9, z=0.001

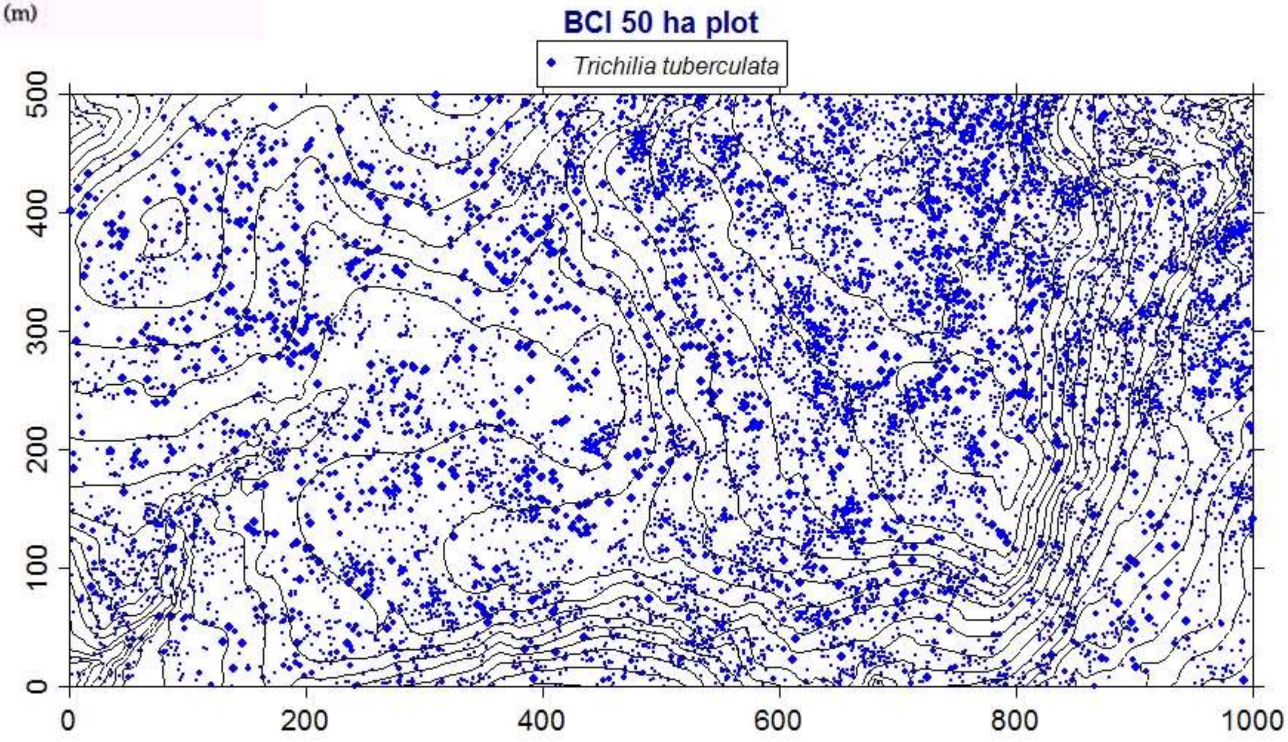

a=100, b=0.1, x=0.9, z=0.001


a=100, b=0.1, x=0.9, z=0.005

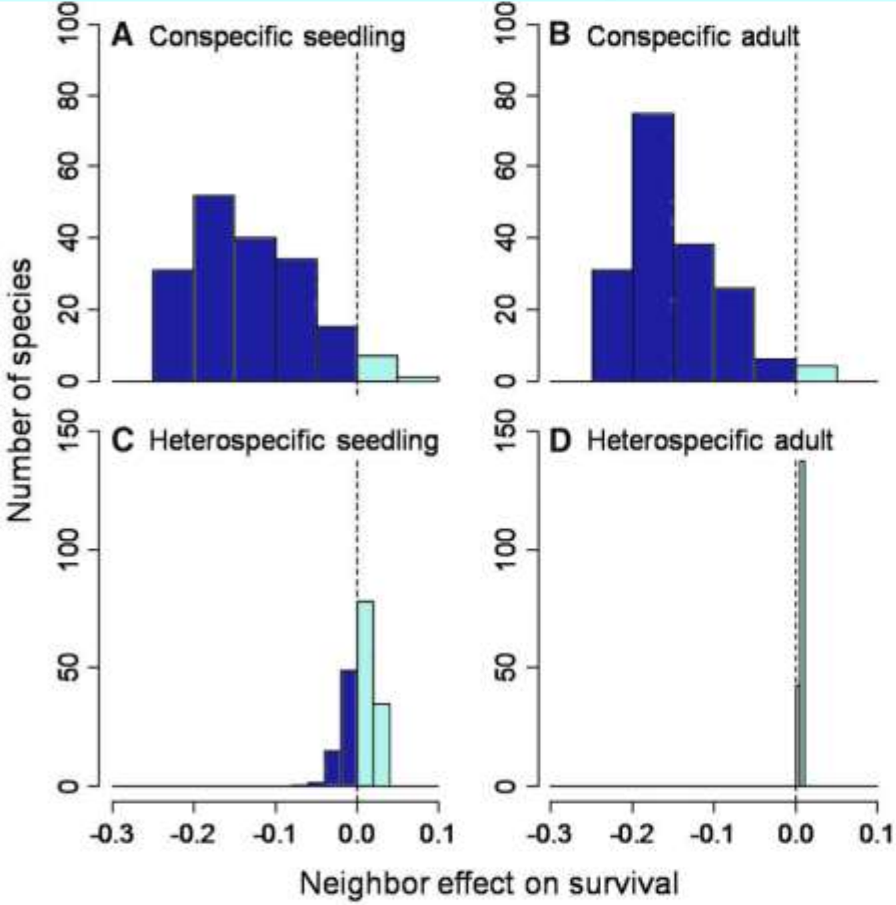


Density dependency: recruitment increases with distance from mother tree

Trichilia tuberculata



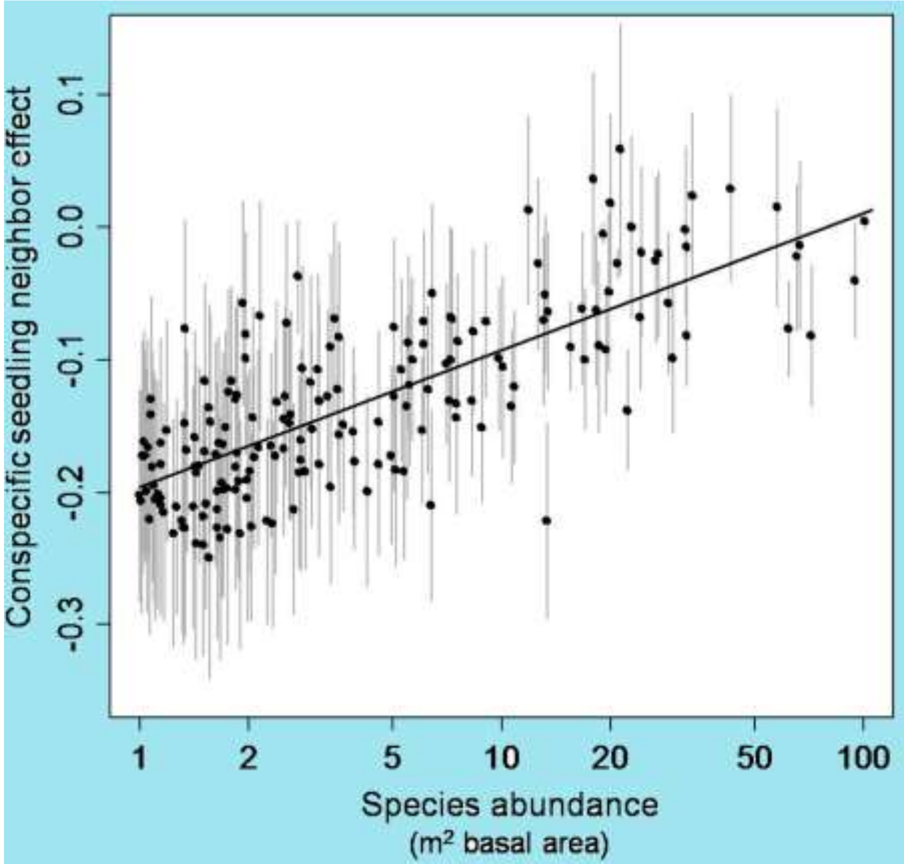
The effect of a conspecific neighbour on seedling survival is **negative** and **varies among species according to their abundance:** rare species suffer more their conspecific neighbours than common species [which may explain their rarity]



Effects of conspecific and heterospecific neighbors on seedling survival. [BCI in Panama]. Bars to the left of the dashed zero line indicate species whose survival is reduced by increasing density of neighbors.

Liza S. Comita, et al. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science 329:330, 2010

Neighbour effect on survival by conspecific seedling for tree species on BCI is correlated with their abundance



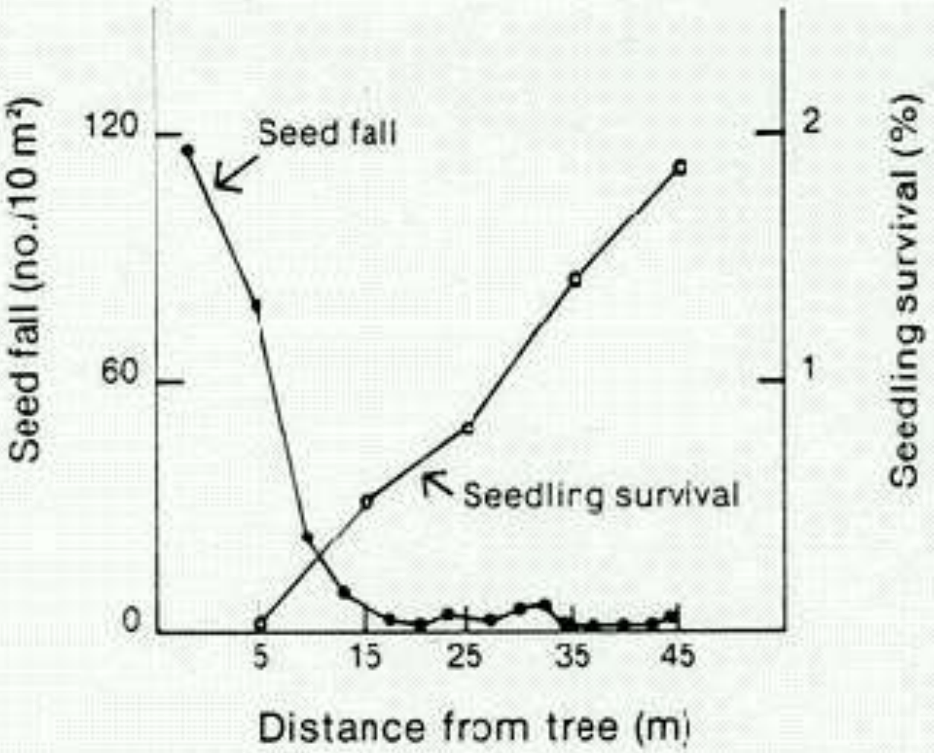
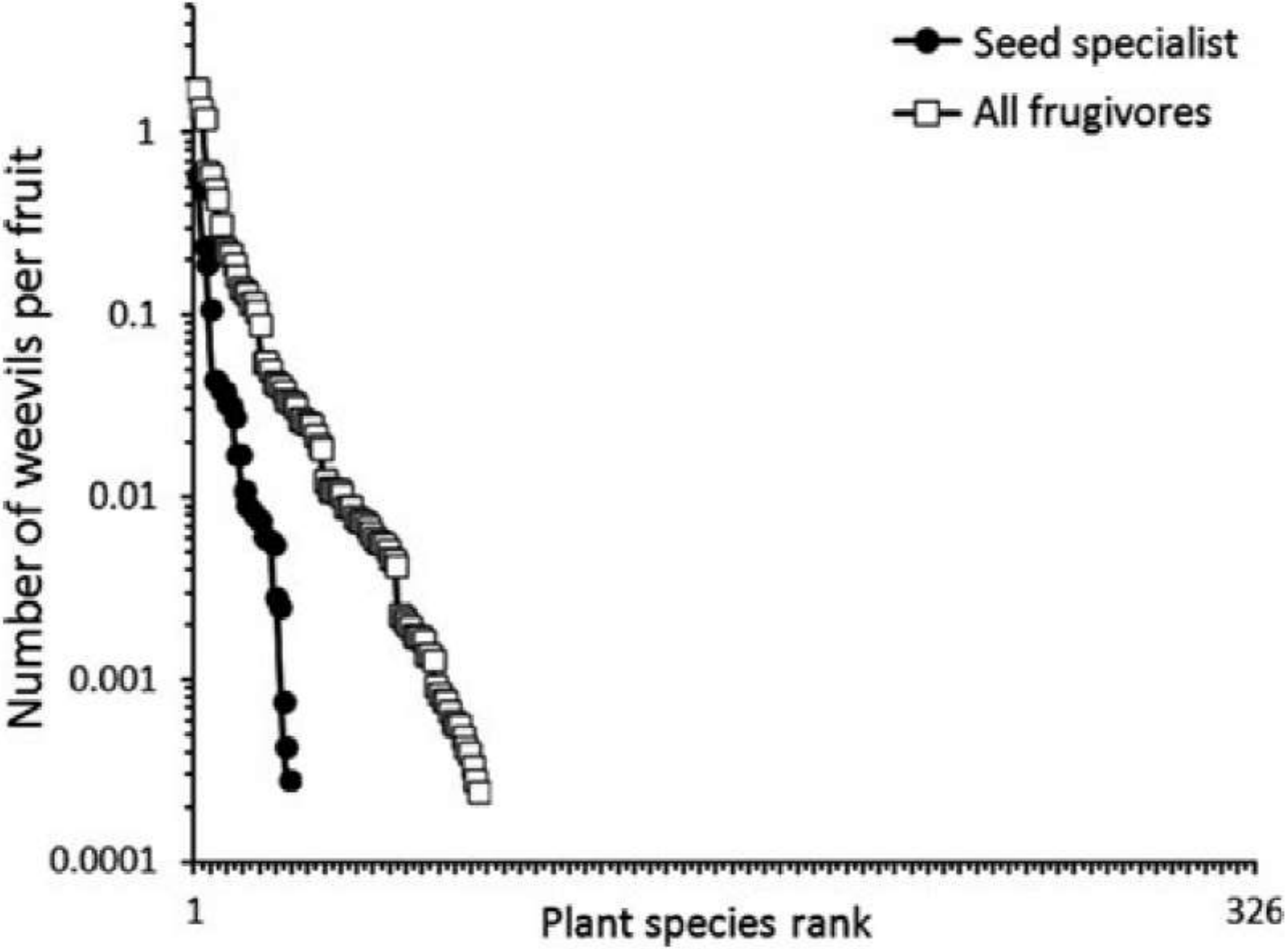
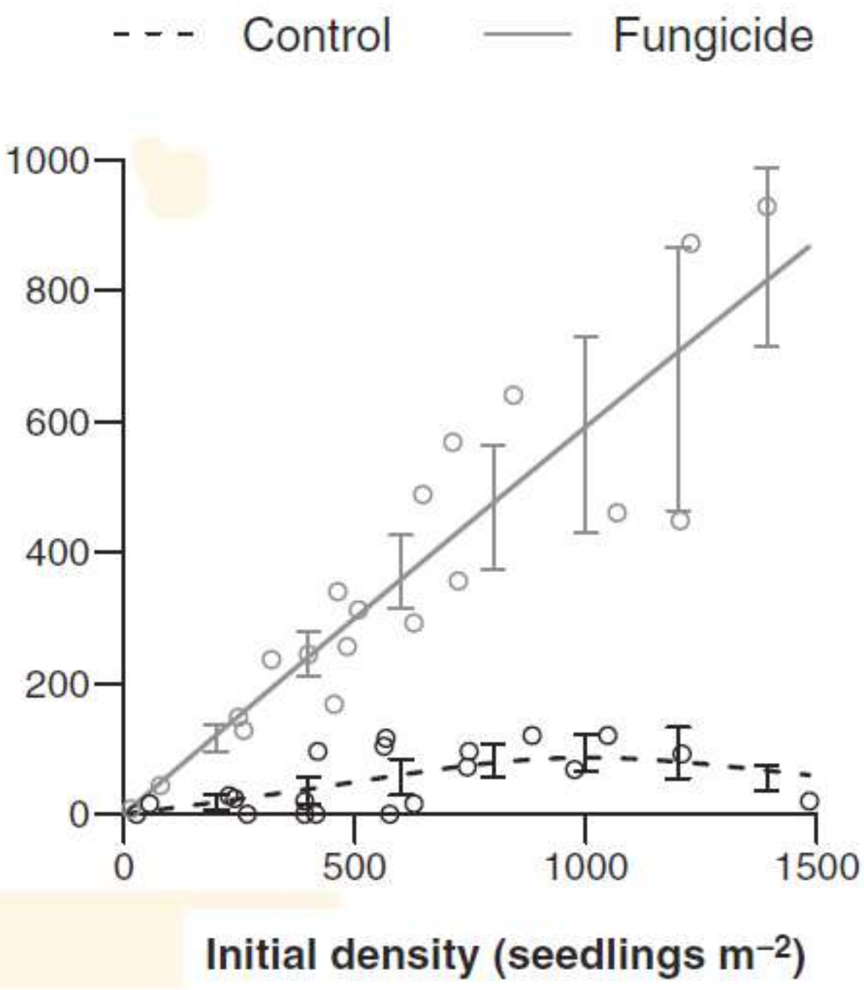


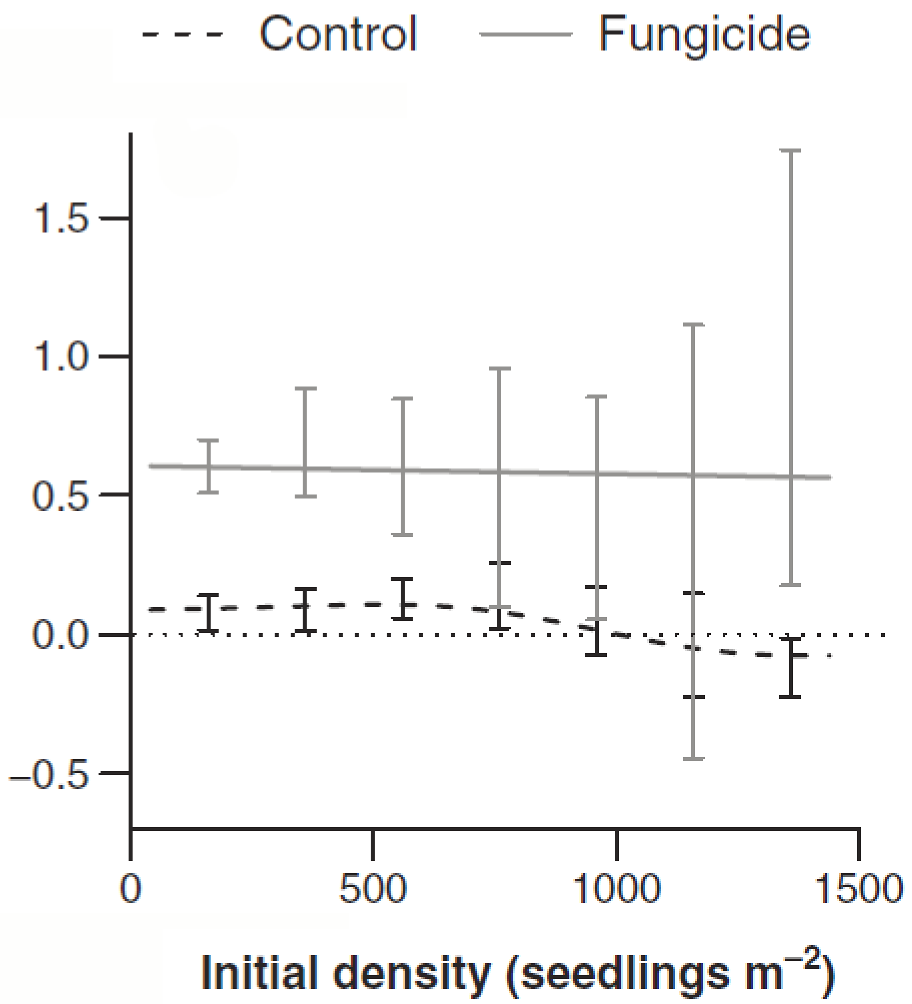
Fig. 7-16 Actual patterns of seed fall and seed and seedling survival three months after fruit drop in the toucan dispersed tree, *Virola surinamensis*, in Panama. Seed and seedling mortalty due to *Conotrachelus* weevil infestations are so heavy under the crown that the seed fall and seedling survival curves cross at the crown edge, 10–15 m from the tree base. Not surprisingly, adults of this species are clumped, with an average nearest neighbor distance of 18 m. Overall, there is a 40-fold advantage to seed dispersal only 45 m from fruiting *Virola* rees. Data from Howe et al. (1985).


Seed specialist
All frugivores
Number of weevils per fruit
1
0.1
0.01
0.001
0.0001
1
Plant species rank
326

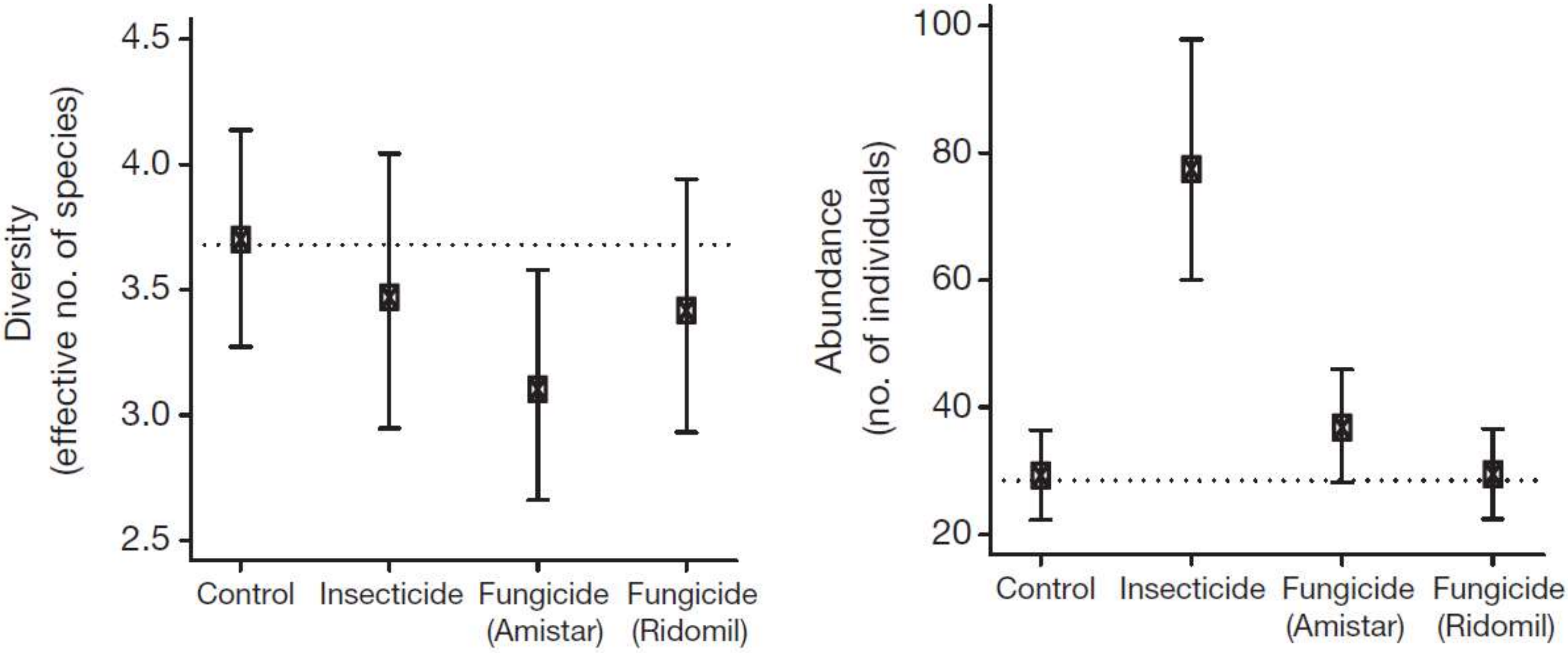
Fungal infection may have Janzen-Connell effect

Negative relationships between dNt/dN0 and initial density indicate NDD. Overcompensation when dNt/dN0 < 0.



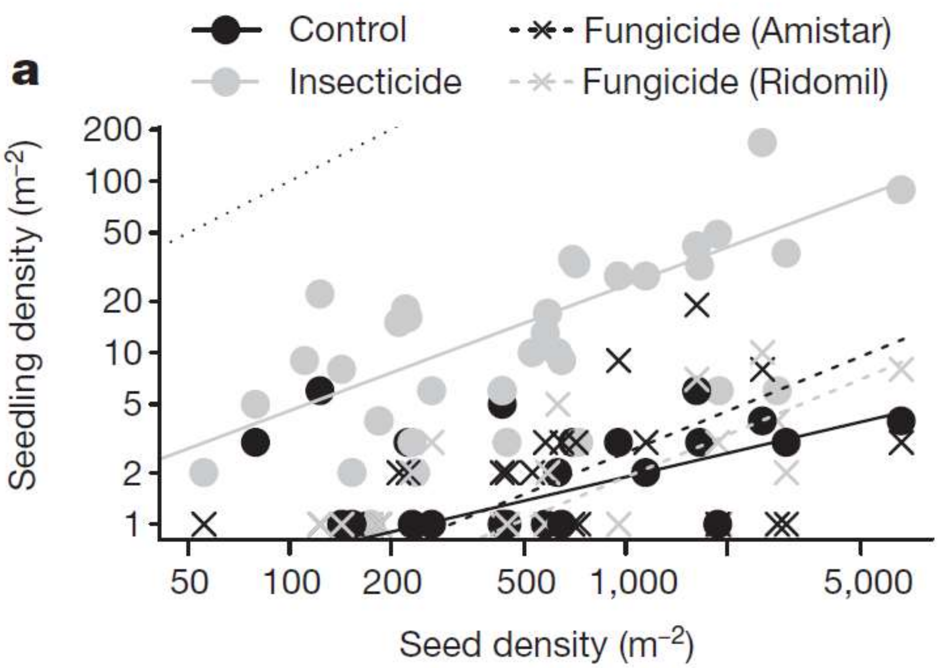


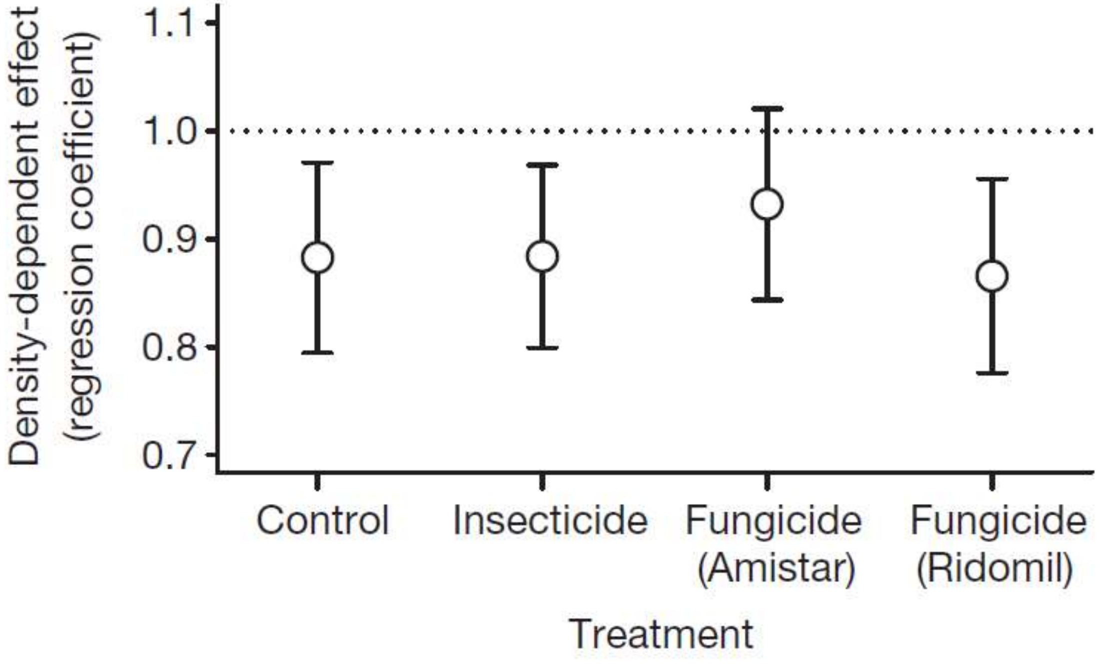
Bagchi, R et al. (2010). Ecology Letters **13**: 1262-1269.



Pathogens and insect herbivores drive rainforest plant diversity and composition

Robert Bagchi[1,2], Rachel E. Gallery[1,3], Sofia Gripenberg[1,4], Sarah J. Gurr[5,6], Lakshmi Narayan[1], Claire E. Addis[1],
Robert P. Freckleton[7] & Owen T. Lewis[1]





Pathogens and insect herbivores drive rainforest plant diversity and composition

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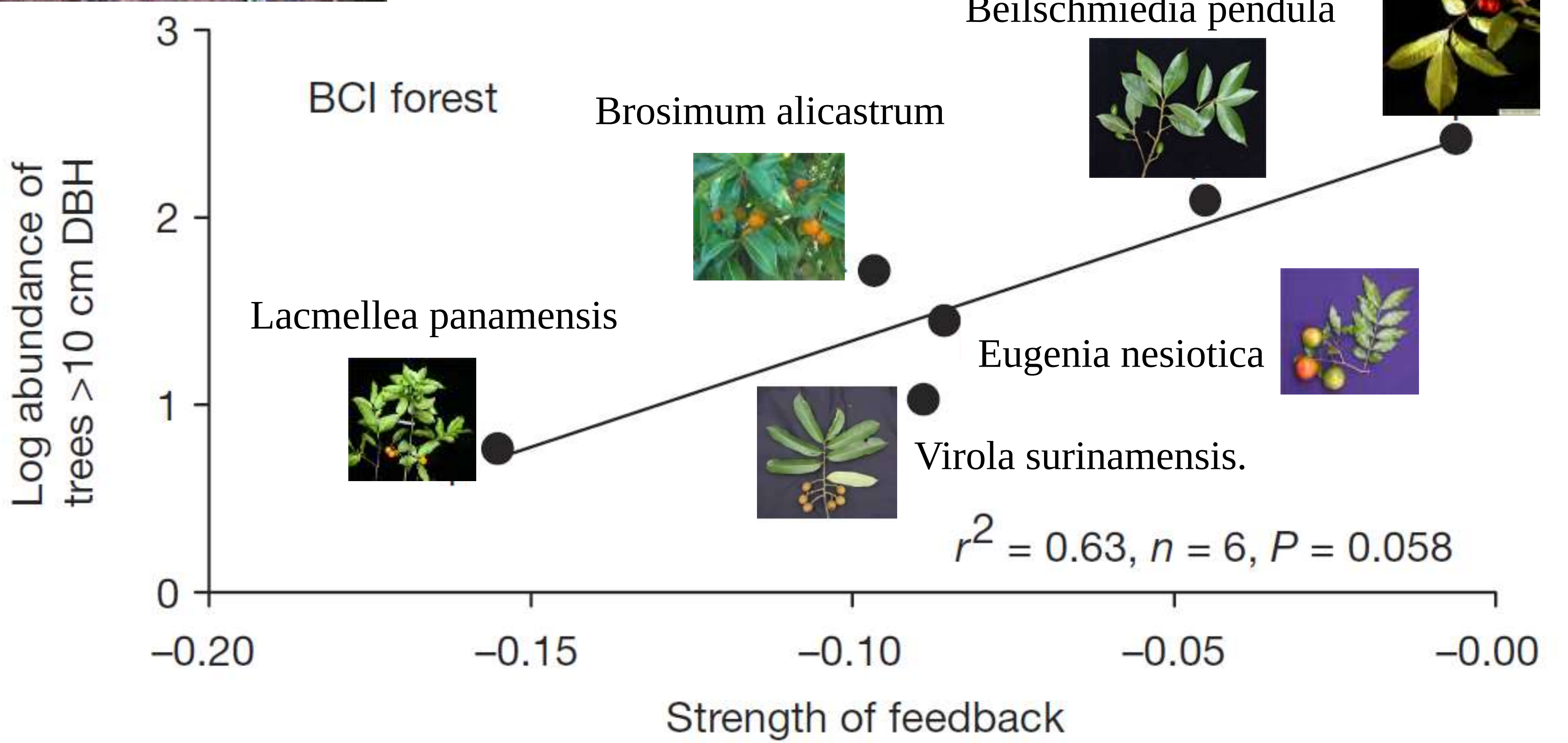
Robert P. Freckleton[7] & Owen T. Lewis[1]

Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest

Seedling biomass after 5 months in experiments in soil from conspecific -heterospecific trees



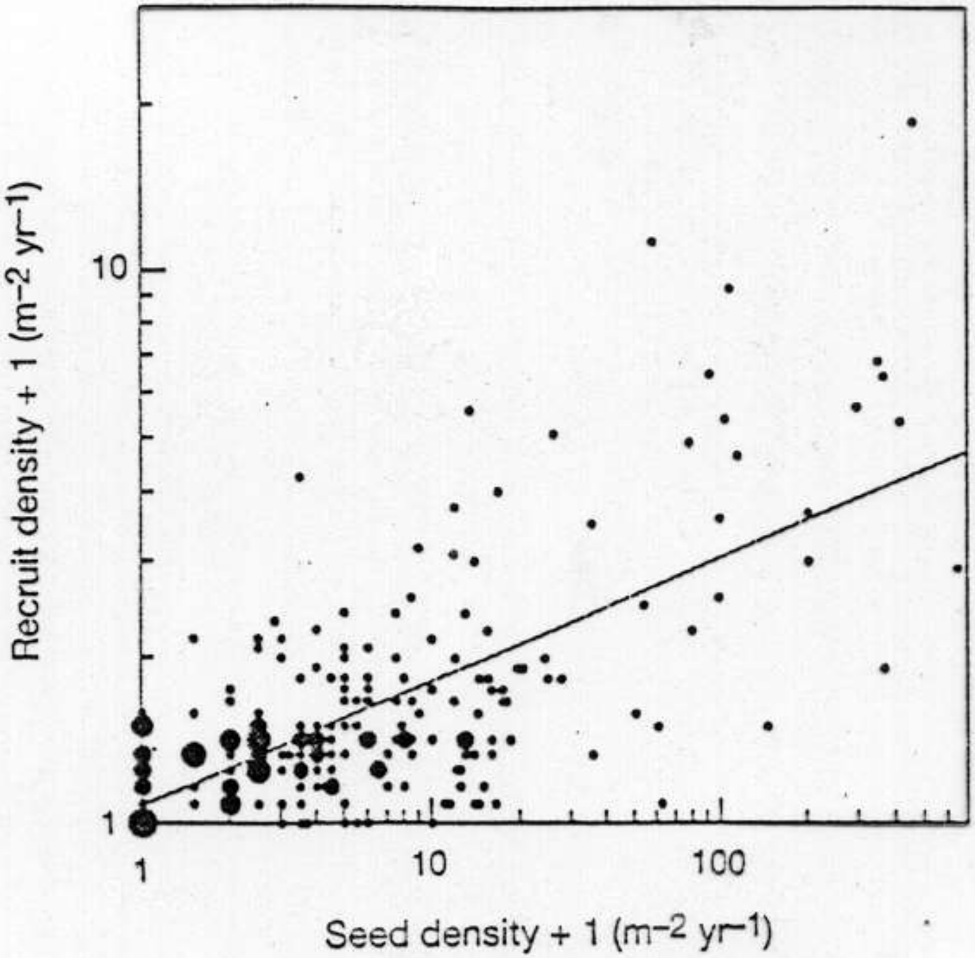


Figure 1 The relationship between the seed density and recruit seedling density for *Trichilia tuberculata* (Meliaceae). The slope of the log–log relationship is less than 1, indicating that recruitment is negatively density dependent. Nonetheless, recruit density increases with seed density. Each symbol represents a census station(s) consisting of one 0.5-m^2 seed trap and three 1-m^2 seedling plots. Symbol size is proportional to the number of stations (ranging from one to six) with identical counts of seeds and recruits.

Seed traps at BCI

slope <1 → density-dependent recruitment

Hubbell et al. 1999. Science 284:554

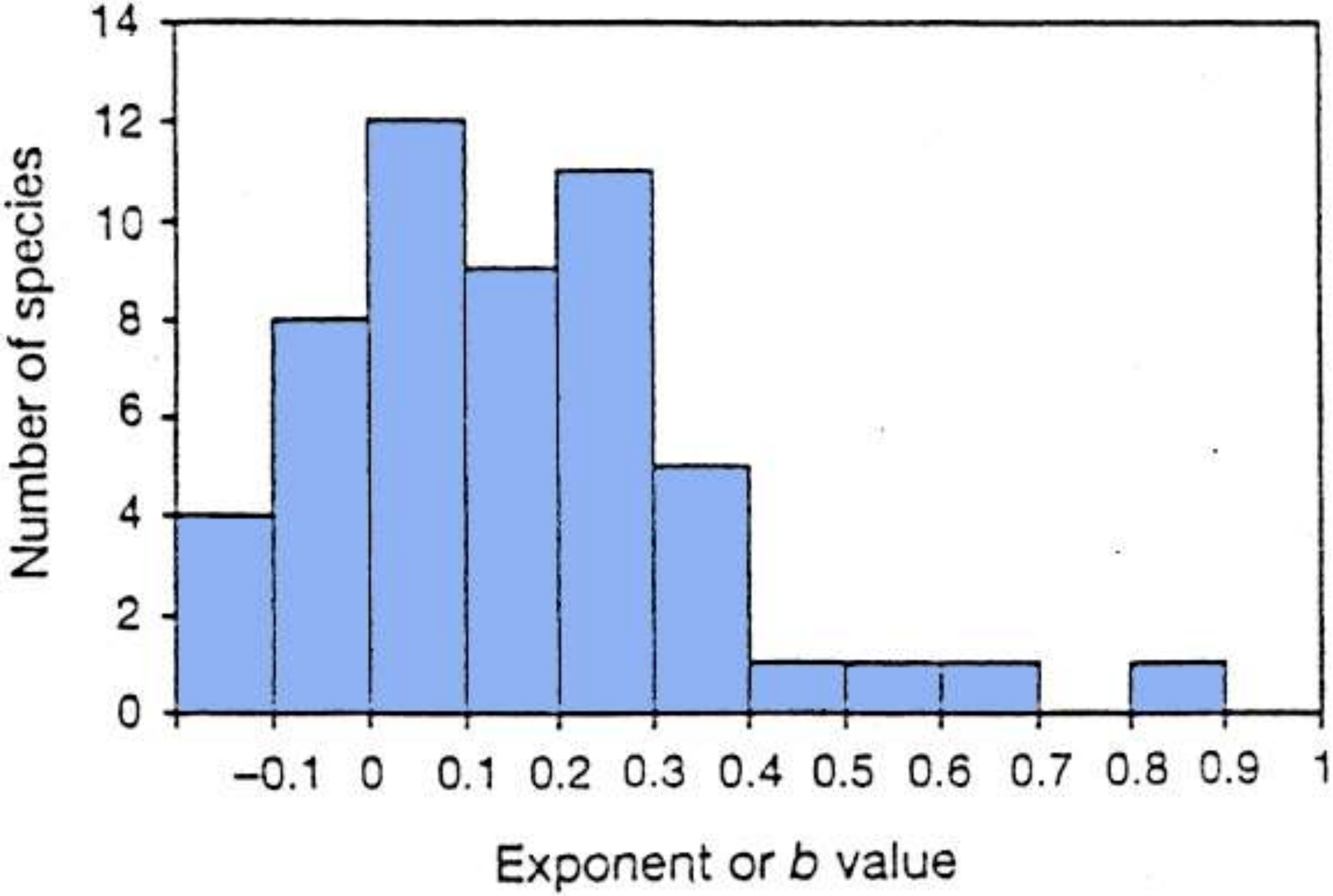
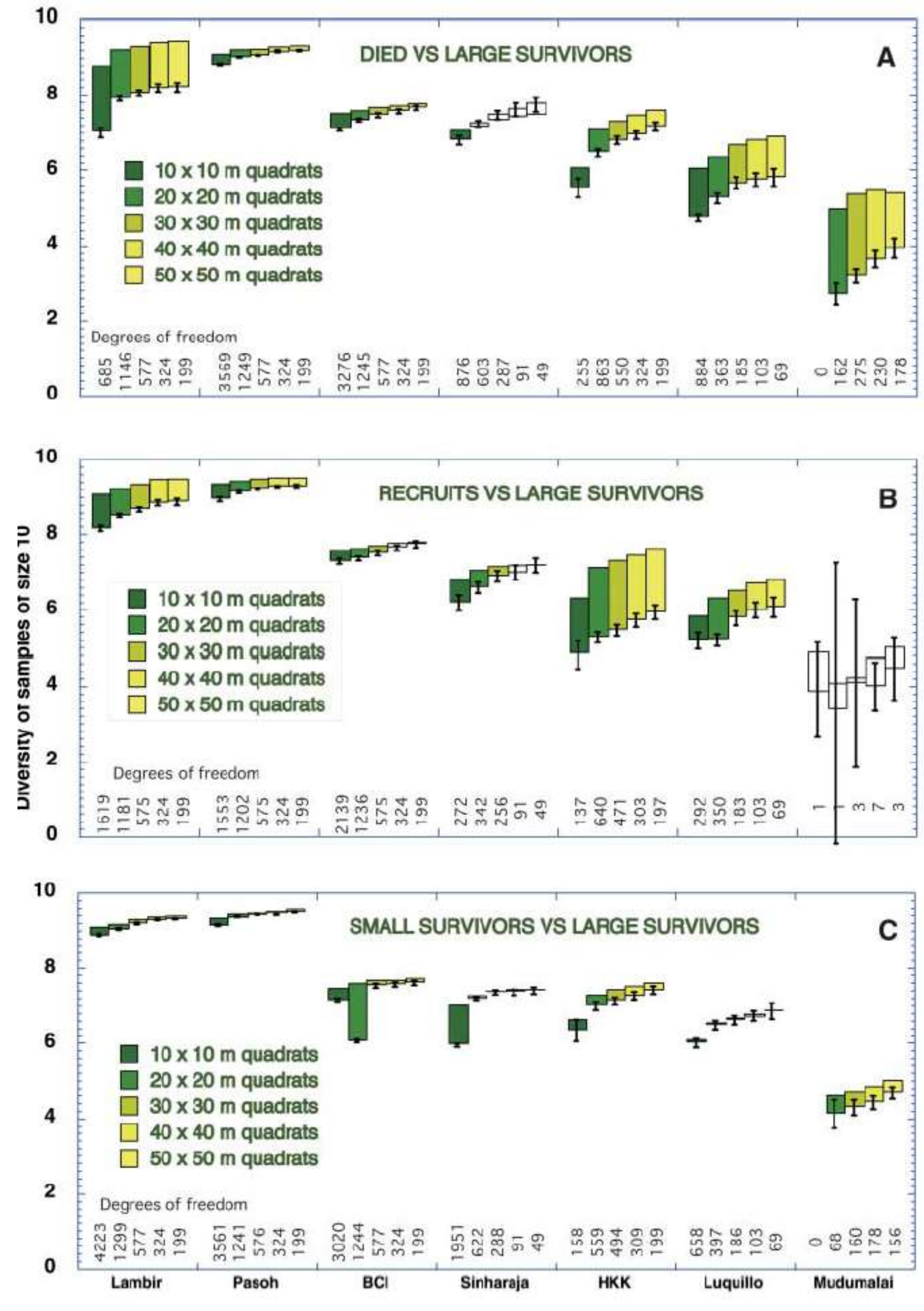


Figure 2 The frequency distribution of the exponent of the relationship between recruit density and seed density for 53 species of shrubs, trees and lianas. All exponents were less than 1 and the median was 0.23, suggesting that strong negative density dependence characterizes seedling recruitment.



Tree mortality increases species diversity

No. of species per 10 randomly selected trees: comparison between
A - those which died and survived
B - recruits and large survivors
C - small and large survivors

In all cases the latter group was more diverse, which means the forest diversity increases over time as dying trees are less diverse than those surviving, and this trend continues as survivors grow in size

Nonrandom Processes Maintain Diversity in Tropical Forests

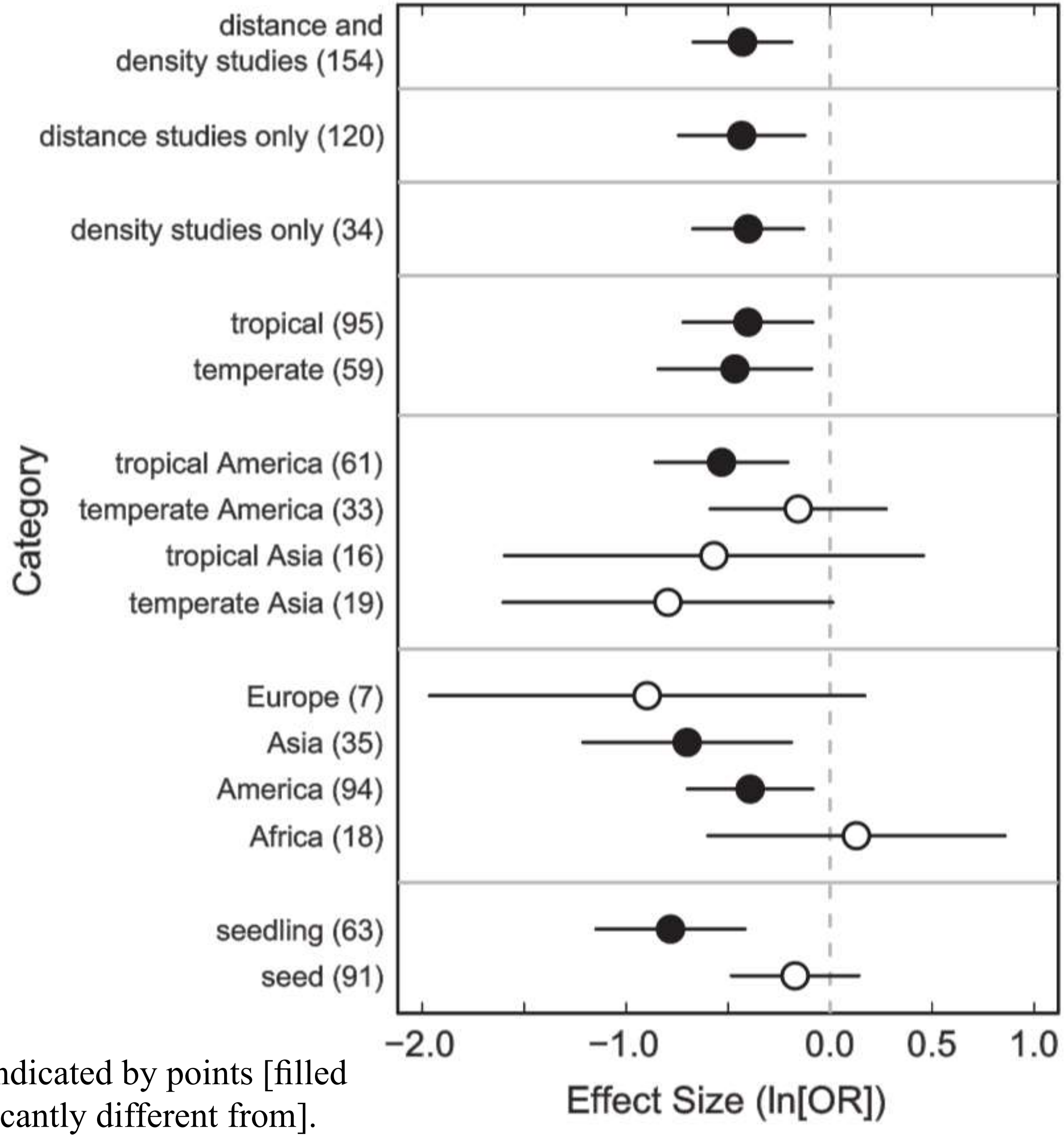
Journal of Ecology

SPECIAL FEATURE – STANDARD PAPER
META-ANALYSIS IN PLANT ECOLOGY

Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival

Liza S. Comita[1,2*], Simon A. Queenborough[1], Stephen J. Murphy[1], Jenalle L. Eck[1], Kaiyang Xu[1], Meghna Krishnadas[1], Noelle Beckman[3] and Yan Zhu[4]

distance- and density-dependent mortality occurs in plant communities world-wide. natural enemies are frequently the cause of such patterns, consistent with the Janzen–Connell hypothesis

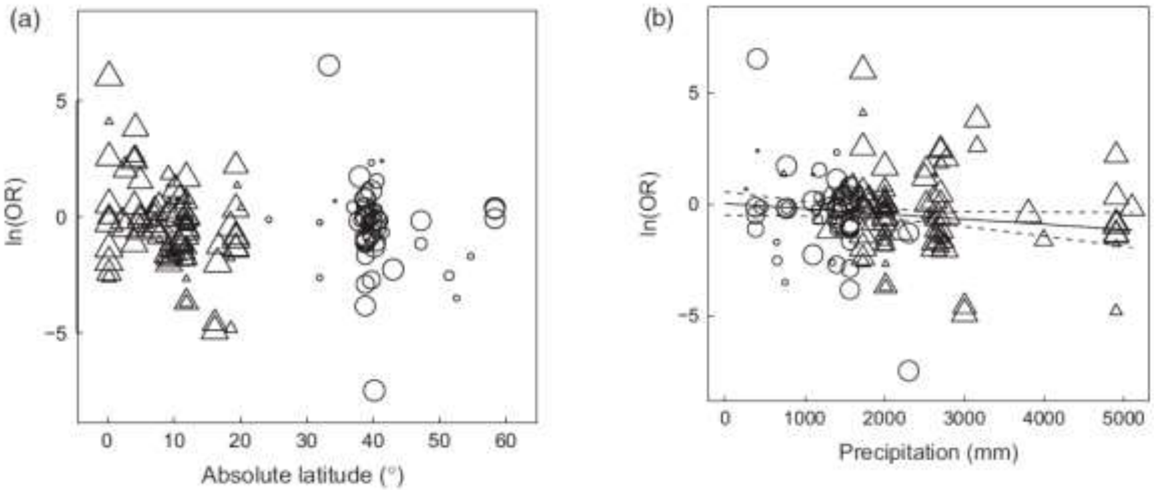


Effect sizes are indicated by points [filled circles are significantly different from].

significant support for both the distance- and density-dependent predictions.
survival rates reduced near conspecifics compared to far from conspecifics, and in areas with high densities of conspecifics compared to areas with low conspecific densities.

unrelated to latitude, and there was no significant effect of study region.
stronger distance and density dependence in wetter sites
effects were significantly stronger at the seedling stage compared to the seed stage.

natural enemies are frequently the cause of such patterns, consistent with the Janzen–Connell hypothesis, but additional studies are needed to rule out other mechanisms (e.g. intraspecific competition).



The effect of (a) absolute latitude, (b) precipitation and (c) study duration on the log odds ratio of survival of seeds and seedlings in a meta-analysis of experimental tests of density and distance dependence. The size of each point is proportional to the precision of the estimate. In panels (a) and (b), tropical (circles) and temperate (triangles) studies are indicated.

So, what are the most promising theories to explain high species richness in tropical forests?

- niche differences
- infrequent competition in rare species
- Janzen-Connell effects, particularly for pathogens
- negative density dependence for abundant species
- mass effects and dispersal limitation
- disturbance

But no single effect is strong enough to provide overall explanation

BIOTROPICA 36(4): 447–473 2004

Why Do Some Tropical Forests Have So Many Species of Trees?[1]

Egbert Giles Leigh Jr.
Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, U.S.A.
Priya Davidar
Salim Ali School of Ecology and Environmental Science, Pondicherry University, Kalapet, 605014 Pondicherry, India
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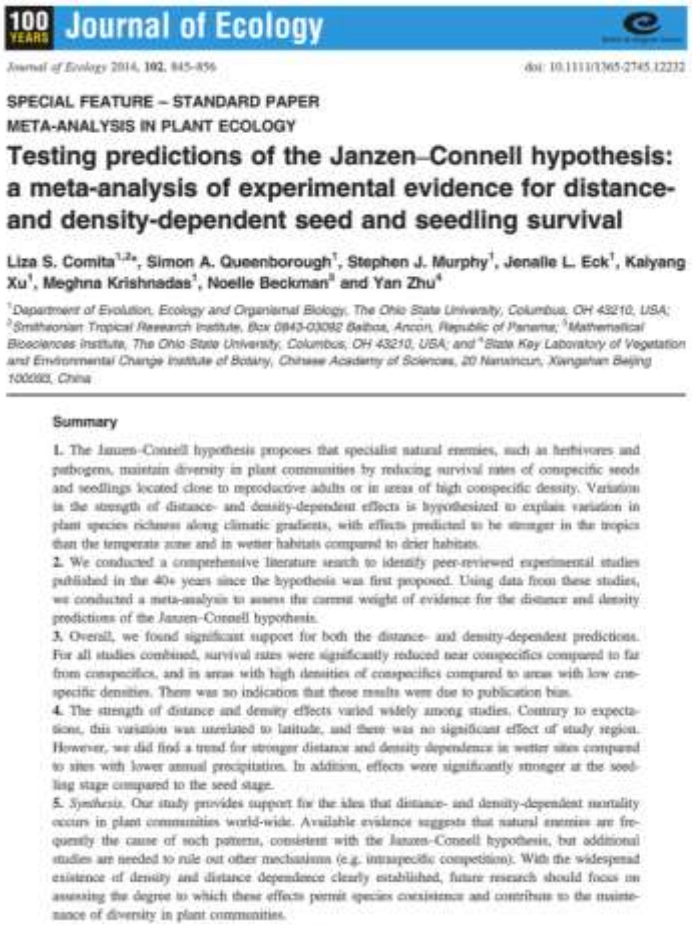
Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, U.S.A.

ABSTRACT

Understanding why there are so many kinds of tropical trees requires learning, not only how tree species coexist, but what factors drive tree speciation and what governs a tree clade's diversification rate. Many report that hybrid sterility evolves very slowly between separated tree populations. If so, tree species rarely originate by splitting of large populations. Instead, they begin with few trees. The few studies available suggest that reproductive isolation between plant populations usually results from selection driven by lowered fitness of hybrids: speciation is usually a response to a "niche opportunity." Using Hubbell's neutral theory of forest dynamics as a null hypothesis, we show that if new tree species begin as small populations, species that are now common must have spread more quickly than chance allows. Therefore, most tree species have some setting in which they can increase when rare. Trees face trade-offs in suitability for different microhabitats, different-sized clearings, different soils and climates, and resistance to different pests. These trade-offs underlie the mechanisms maintaining α-diversity and species turnover. Disturbance and microhabitat specialization appear insufficient to maintain α-diversity of tropical trees, although they may maintain tree diversity north of Mexico or in northern Europe. Many studies show that where trees grow readily, tree diversity is higher and temperature and rainfall are less seasonal. The few data available suggest that pest pressure is higher, maintaining higher tree diversity, where winter is absent. Tree α-diversity is also higher in regions with more tree species, which tend to be larger, free for a longer time from major shifts of climate, or in the tropics, where there are more opportunities for local coexistence.



100 YEARS Journal of Ecology

Journal of Ecology 2014, **102**, 845–856 doi: 10.1111/1365-2745.12232

SPECIAL FEATURE – STANDARD PAPER
META-ANALYSIS IN PLANT ECOLOGY

Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival

Liza S. Comita[1,2]*, Simon A. Queenborough[1], Stephen J. Murphy[1], Jenalle L. Eck[1], Kalyang Xu[1], Meghna Krishnadas[1], Noelle Beckman[3] and Yan Zhu[4]

[1]Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43210, USA; [2]Smithsonian Tropical Research Institute, Box 0843-03092 Balboa, Ancon, Republic of Panama; [3]Mathematical Biosciences Institute, The Ohio State University, Columbus, OH 43210, USA; and [4]State Key Laboratory of Vegetation and Environmental Change Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan Beijing 100093, China

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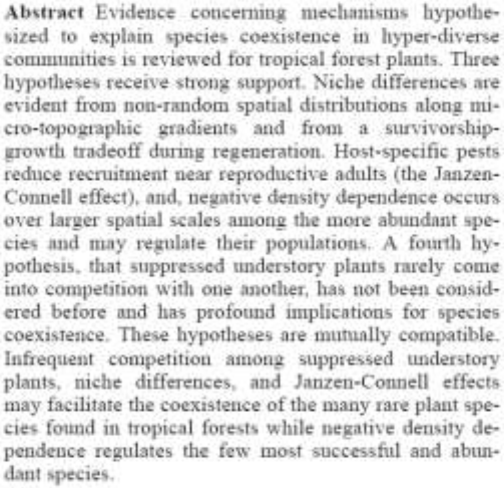
Summary

1. The Janzen–Connell hypothesis proposes that specialist natural enemies, such as herbivores and pathogens, maintain diversity in plant communities by reducing survival rates of conspecific seeds and seedlings located close to reproductive adults or in areas of high conspecific density. Variation in the strength of distance- and density-dependent effects is hypothesized to explain variation in plant species richness along climatic gradients, with effects predicted to be stronger in the tropics than the temperate zone and in wetter habitats compared to drier habitats.
2. We conducted a comprehensive literature search to identify peer-reviewed experimental studies published in the 40+ years since the hypothesis was first proposed. Using data from these studies, we conducted a meta-analysis to assess the current weight of evidence for the distance and density predictions of the Janzen–Connell hypothesis.
3. Overall, we found significant support for both the distance- and density-dependent predictions. For all studies combined, survival rates were significantly reduced near conspecifics compared to far from conspecifics, and in areas with high densities of conspecifics compared to areas with low conspecific densities. There was no indication that these results were due to publication bias.
4. The strength of distance and density effects varied widely among studies. Contrary to expectations, this variation was unrelated to latitude, and there was no significant effect of study region. However, we did find a trend for stronger distance and density dependence in wetter sites compared to sites with lower annual precipitation. In addition, effects were significantly stronger at the seedling stage compared to the seed stage.
5. *Synthesis*. Our study provides support for the idea that distance- and density-dependent mortality occurs in plant communities world-wide. Available evidence suggests that natural enemies are frequently the cause of such patterns, consistent with the Janzen–Connell hypothesis, but additional studies are needed to rule out other mechanisms (e.g. intraspecific competition). With the widespread existence of density and distance dependence clearly established, future research should focus on assessing the degree to which these effects permit species coexistence and contribute to the maintenance of diversity in plant communities.

Oecologia (2002) 130:1–14
DOI 10.1007/s004420100809

S. Joseph Wright

Plant diversity in tropical forests: a review of mechanisms of species coexistence



Abstract Evidence concerning mechanisms hypothesized to explain species coexistence in hyper-diverse communities is reviewed for tropical forest plants. Three hypotheses receive strong support. Niche differences are evident from non-random spatial distributions along micro-topographic gradients and from a survivorship-growth tradeoff during regeneration. Host-specific pests reduce recruitment near reproductive adults (the Janzen-Connell effect), and, negative density dependence occurs over larger spatial scales among the more abundant species and may regulate their populations. A fourth hypothesis, that suppressed understory plants rarely come into competition with one another, has not been considered before and has profound implications for species coexistence. These hypotheses are mutually compatible. Infrequent competition among suppressed understory plants, niche differences, and Janzen-Connell effects may facilitate the coexistence of the many rare plant species found in tropical forests while negative density dependence regulates the few most successful and abundant species.

Recommended additional reading for interested students