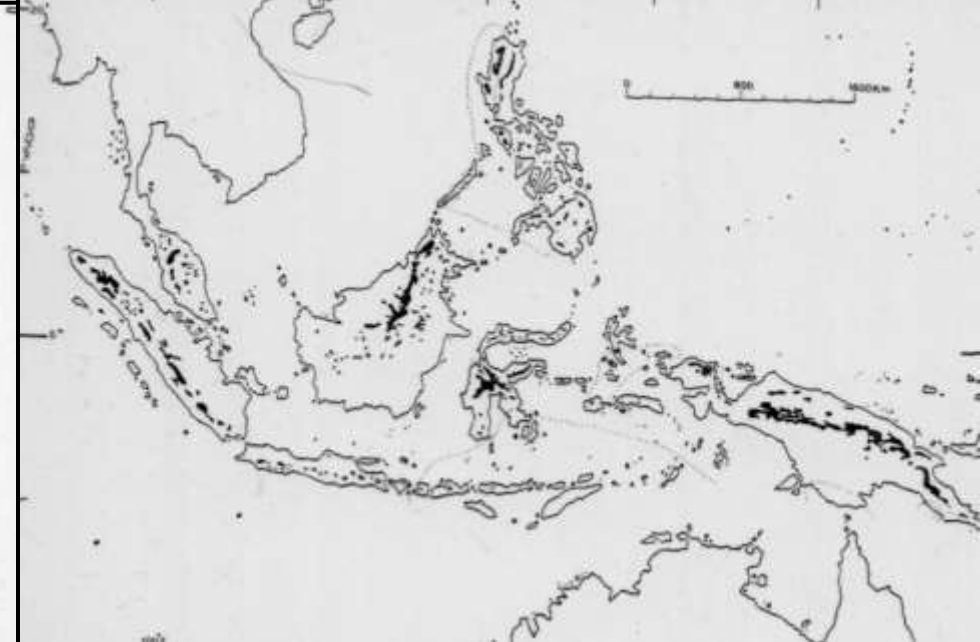
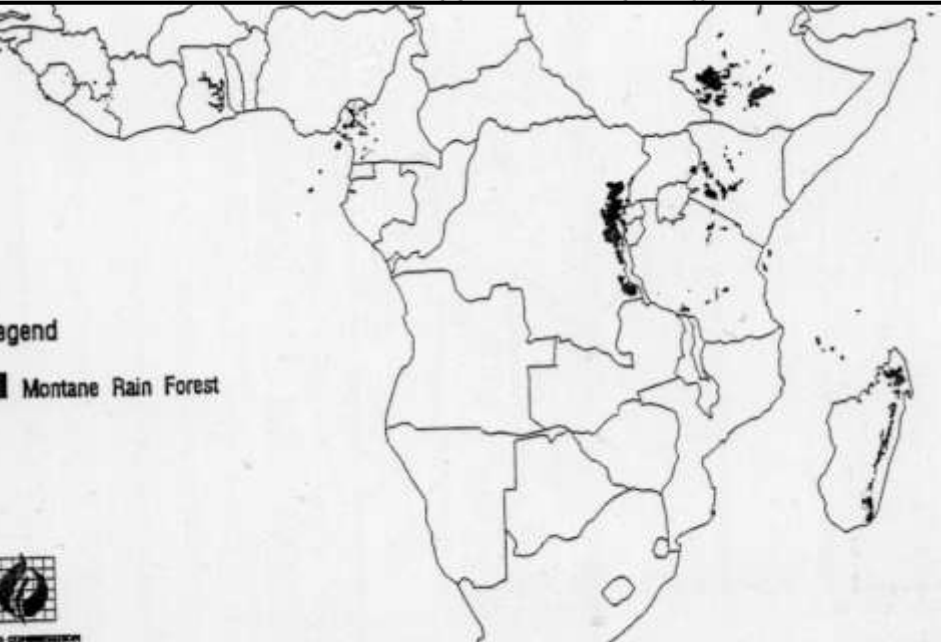


# Altitudinal gradients



# Montane forests in the tropics



Temperature at the forest limit in altitude in tropical, subtropical and temperate mountains

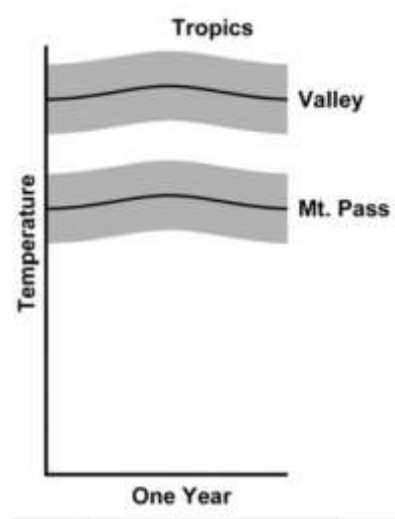
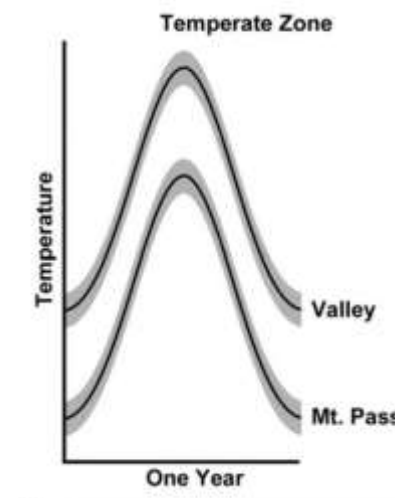
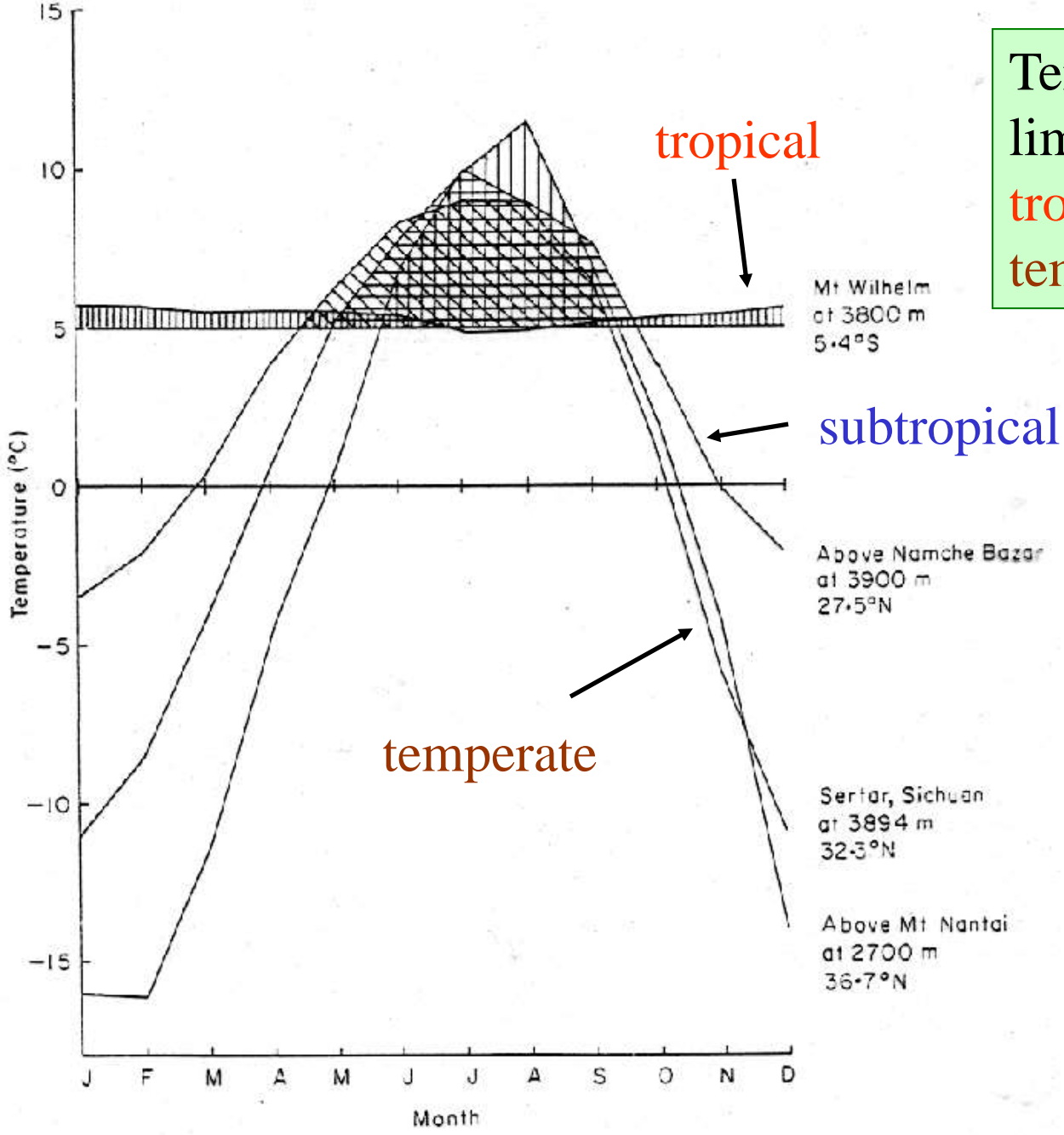
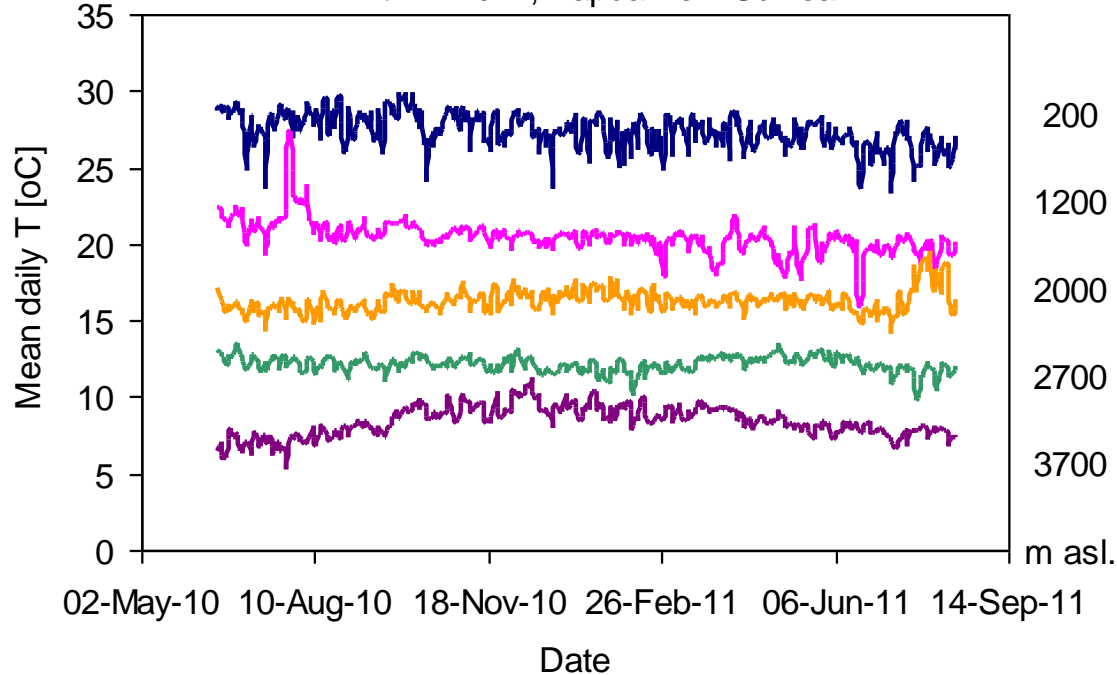


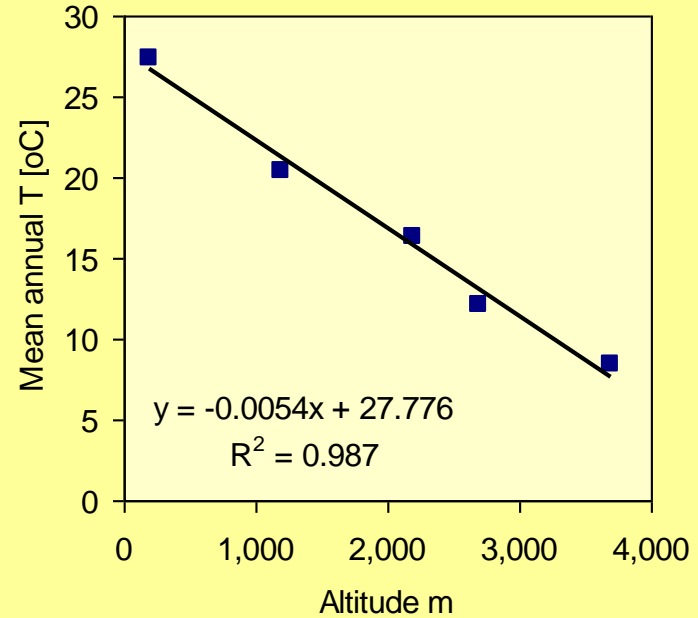
FIG. 3. Annual course of mean monthly temperature at the forest limit in East and South Asian mountains. Hatched areas denote the temperature sum (above 5 °C) for each temperature curve.

# Decrease in temperature with altitude: 5-6°C per 1000 m

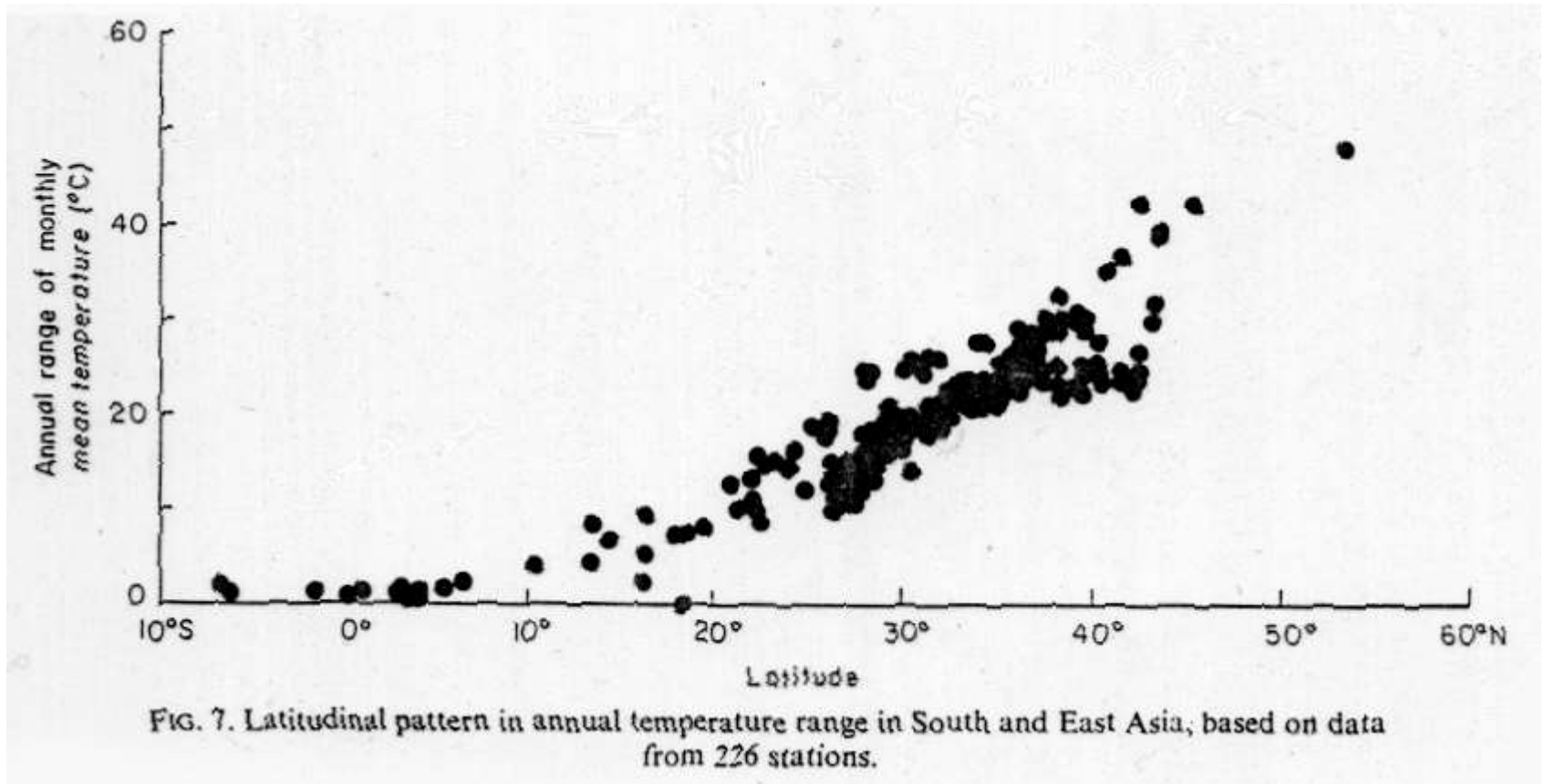
Mt. Wilhelm, Papua New Guinea



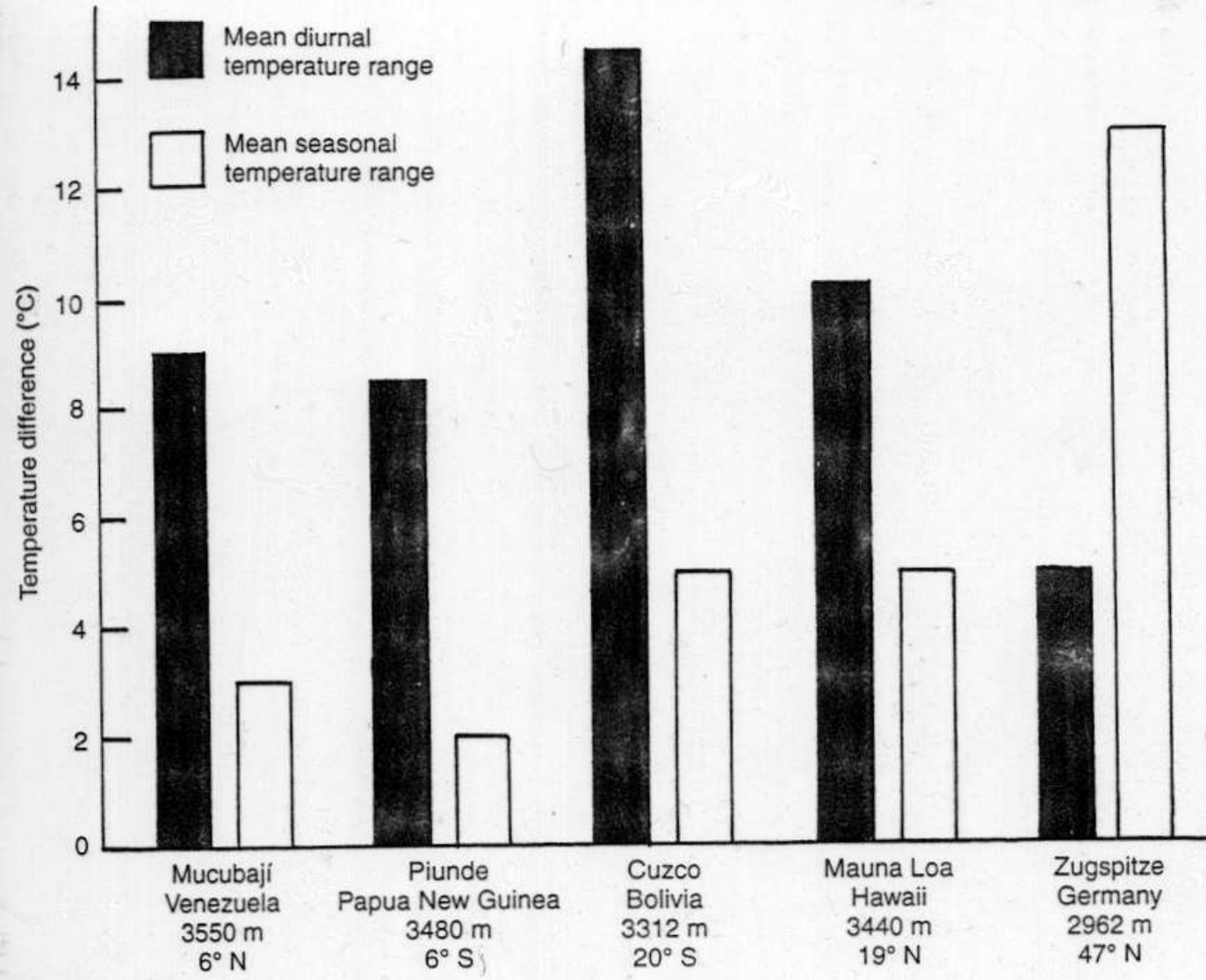
Mt Wilhelm: 5.4 °C per 1000 m elevation



Annual range of monthly mean temperature:  
an altitudinal gradient



Diurnal  
and annual  
temperature  
range in high  
mountains

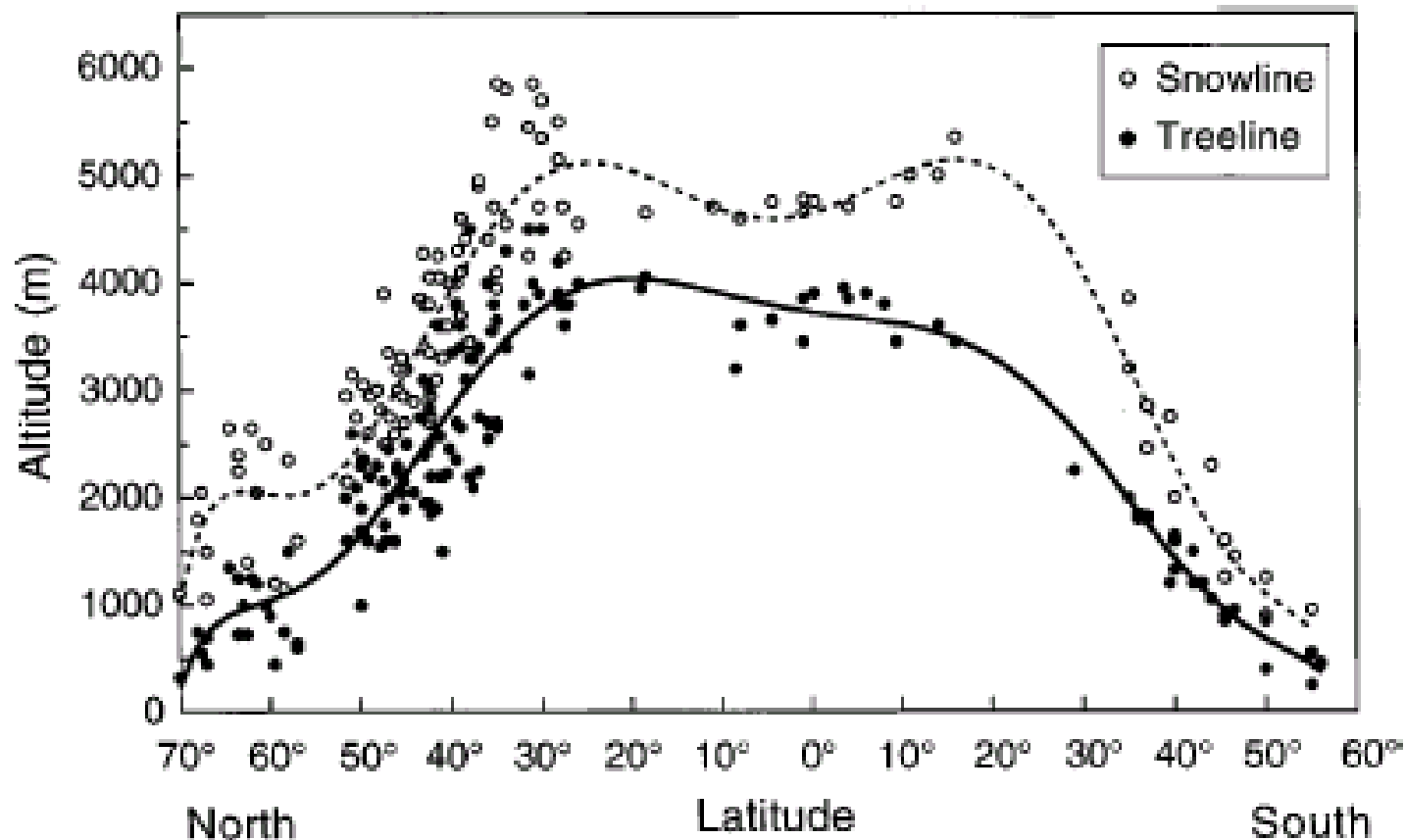


tropical

-

temperate

# Altitude of treeline and snowline at different latitudes



**Fig. 1** The latitudinal position of treeline and snowline taken from a worldwide survey by Hermes (1955), supplemented by data from various other sources

# Altitudes and tree species at the forest limit in humid Asian mts.

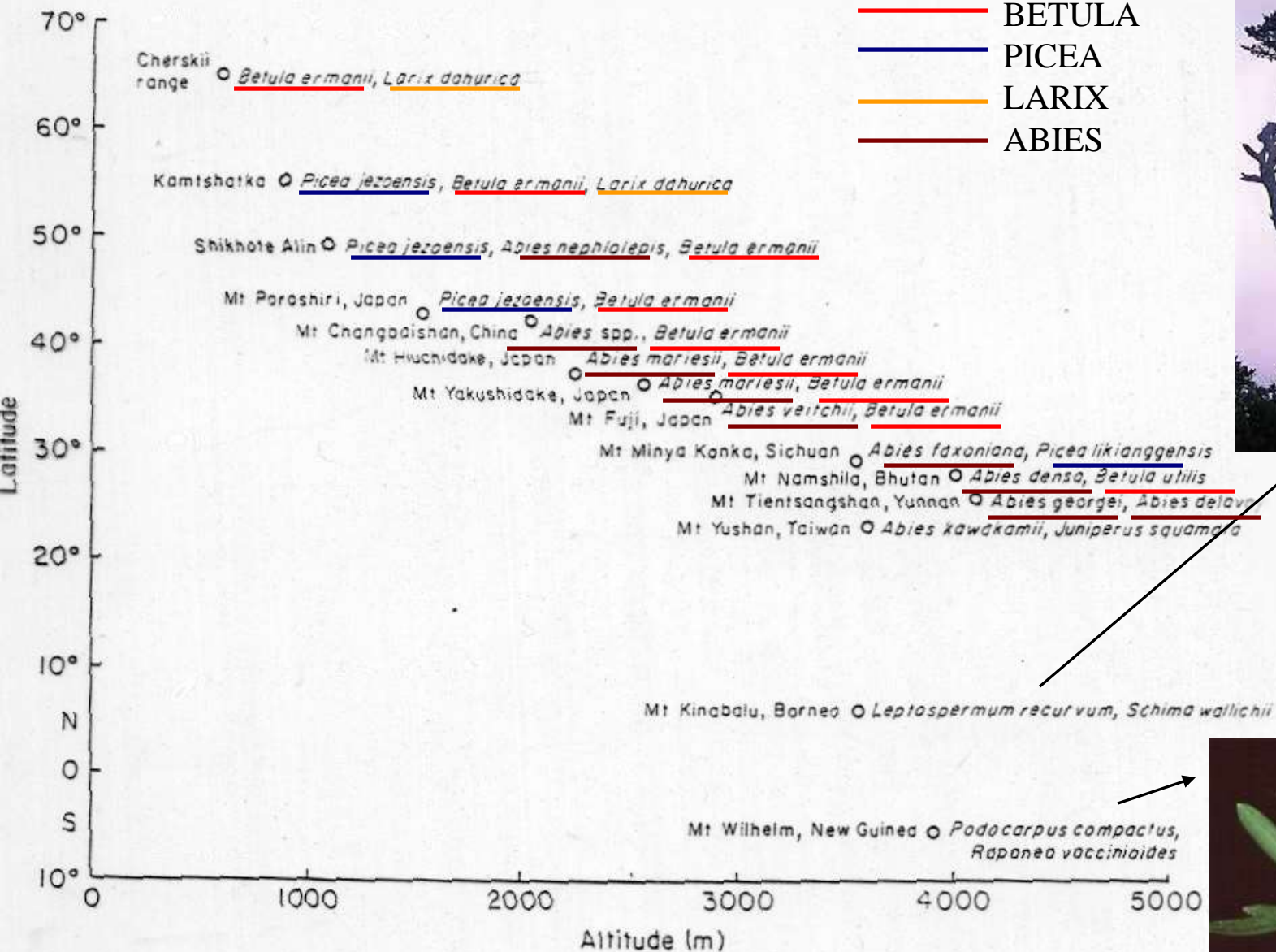
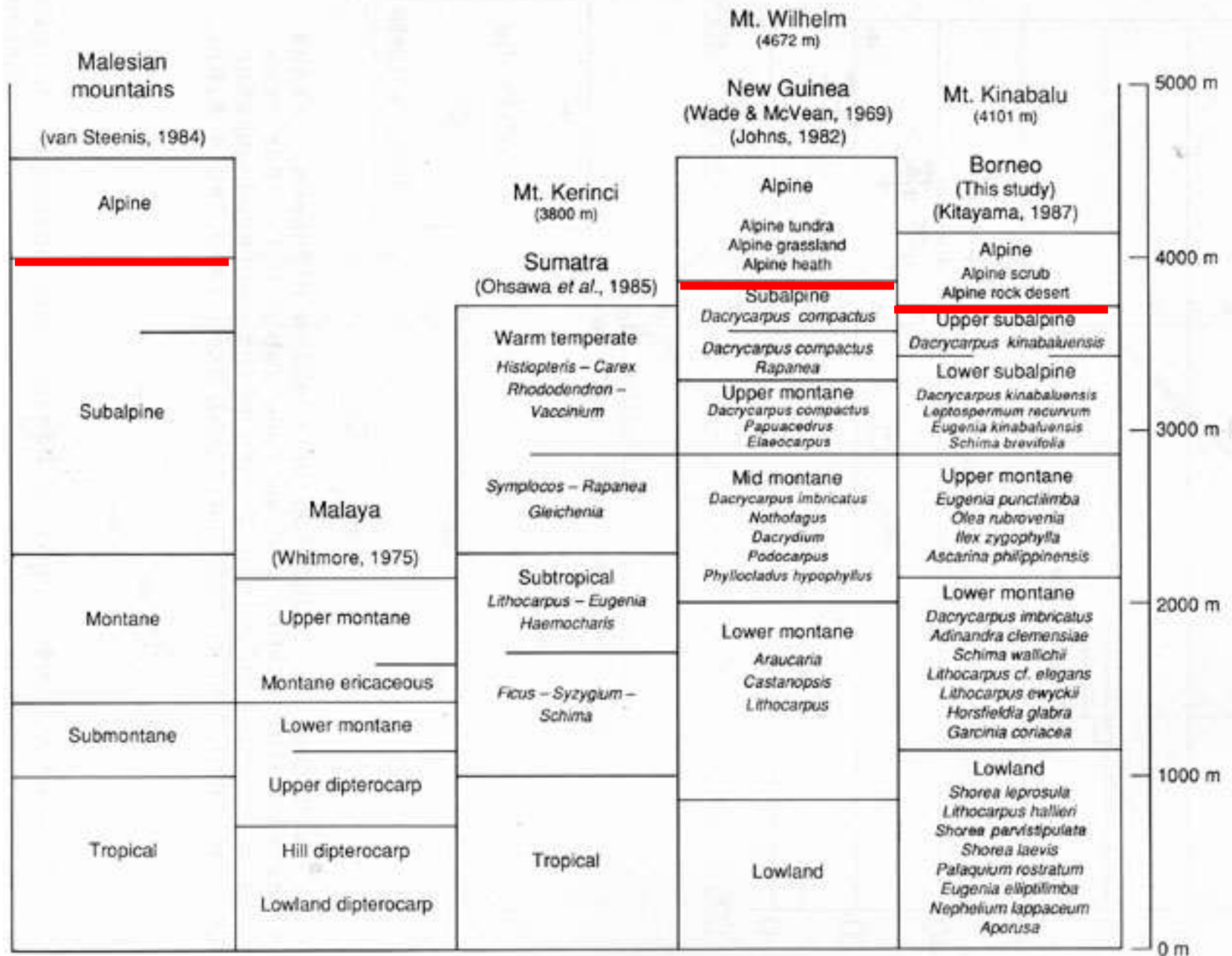


FIG. 1. Altitudes and tree species at the forest limit in humid Asian mountains.





Forest altitudinal zonation in Malesia

# Altitudinal zonation on some tropical mountains

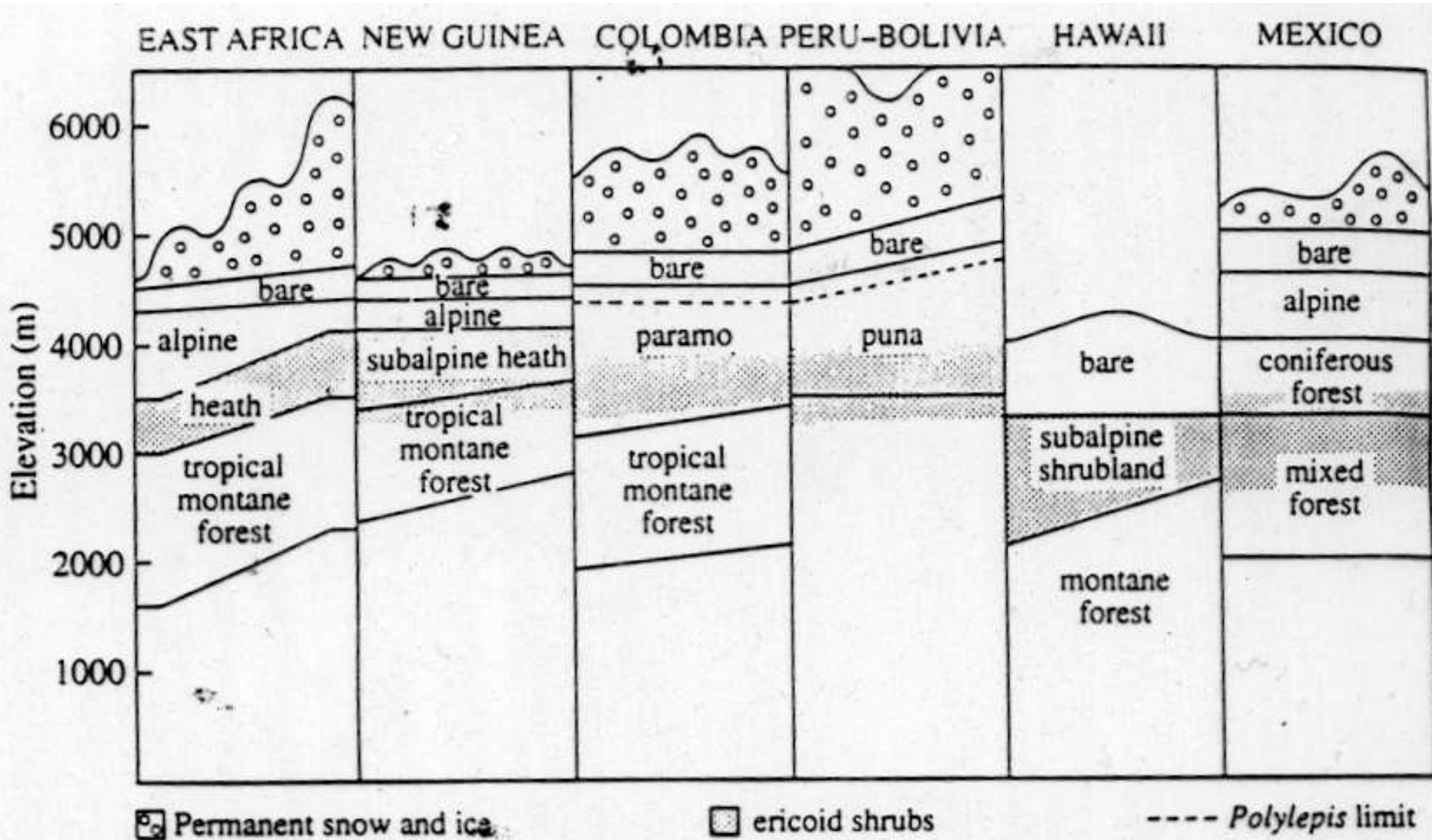


Figure 1.1. A diagrammatic summary of vegetation distribution on some New and Old World mountains. (Adapted from Troll 1968, Figure 16.)

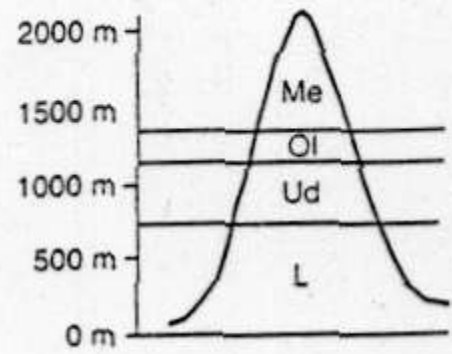
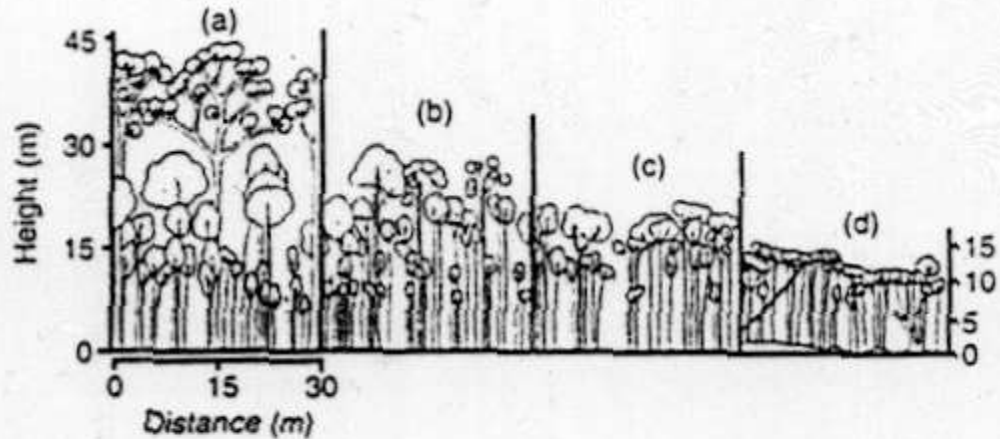


Figure 2.32 Altitudinal forest formation series in Malay Peninsula: (a) lowland evergreen rain forest, 150 m asl; (b) lower montane rain forest 'upper dipterocarp', 780 m; (c) lower montane rain forest, 'oak-laurel' 1500 m asl; (d) upper montane rain forest, 'montane ericaceous'. (From Robbins and Wyatt-Smith, 1964;

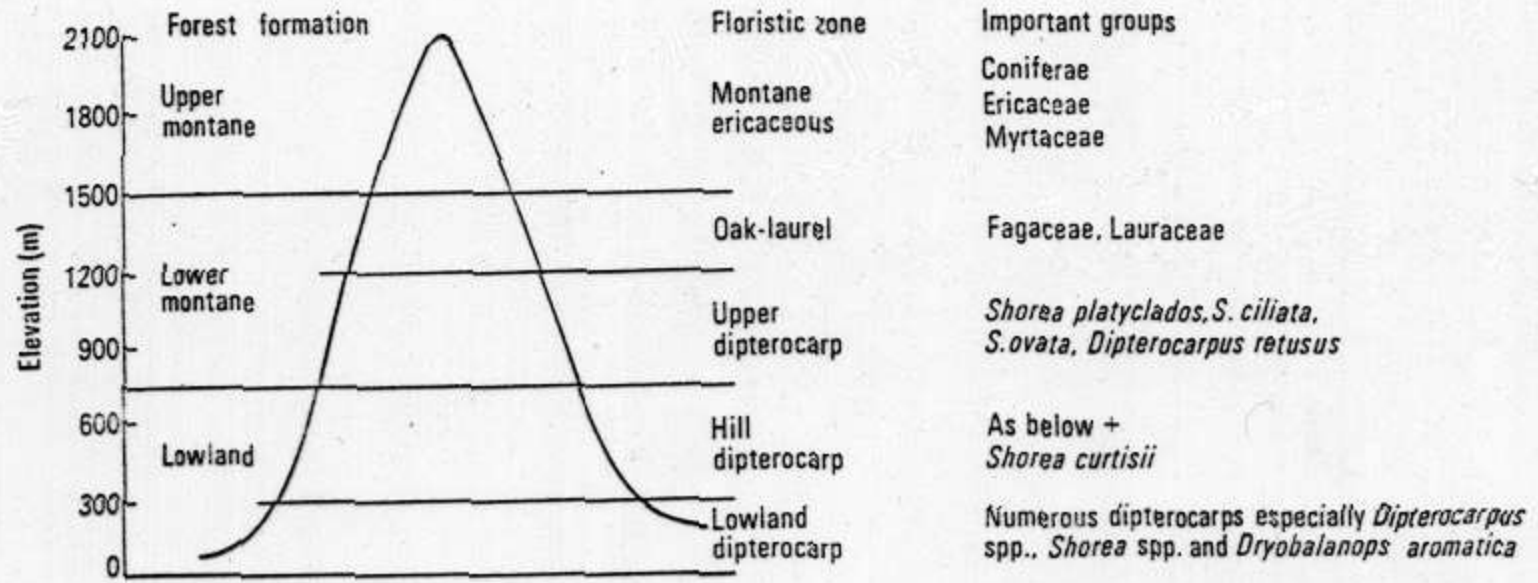
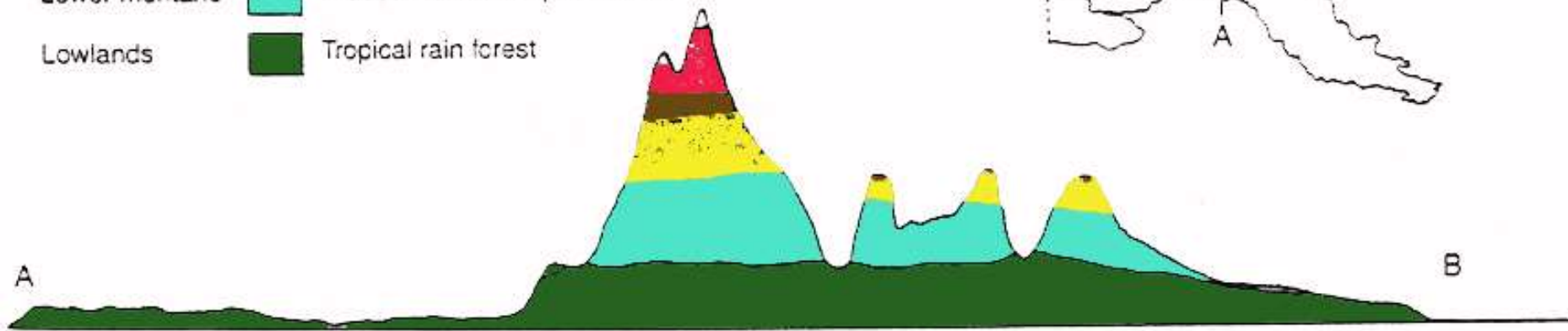


Fig. 2.7. Forest zones on the main mountains of Malaya. (Whitmore 1984a, fig. 18.1.)

Malay Peninsula

# Altitudinal zonation in New Guinea

- Alpine  Short grassland
- Sub-alpine  Grassland with shrubs
- Upper montane  Moss forest
- Mid montane  *Nothofagus, Podocarpus* forest
- Lower montane  *Araucaria, Lithocarpus* forest
- Lowlands  Tropical rain forest

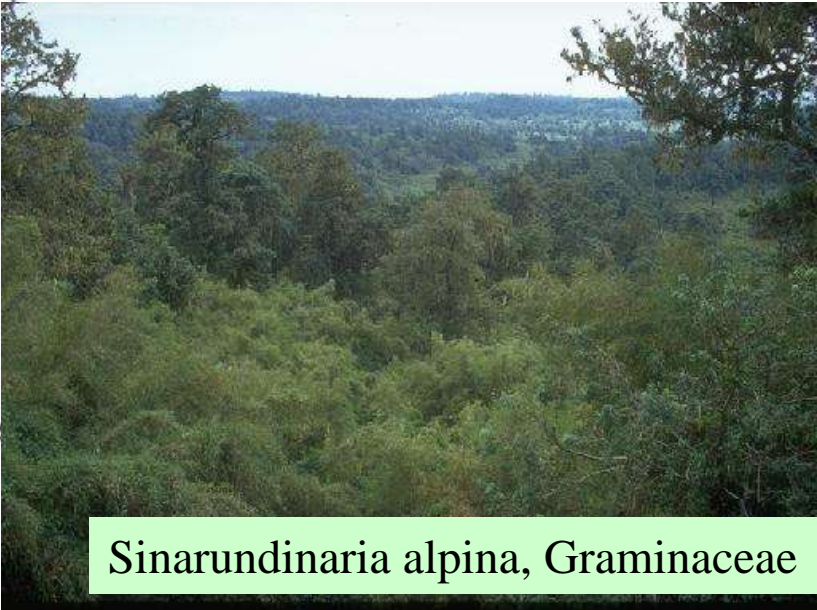
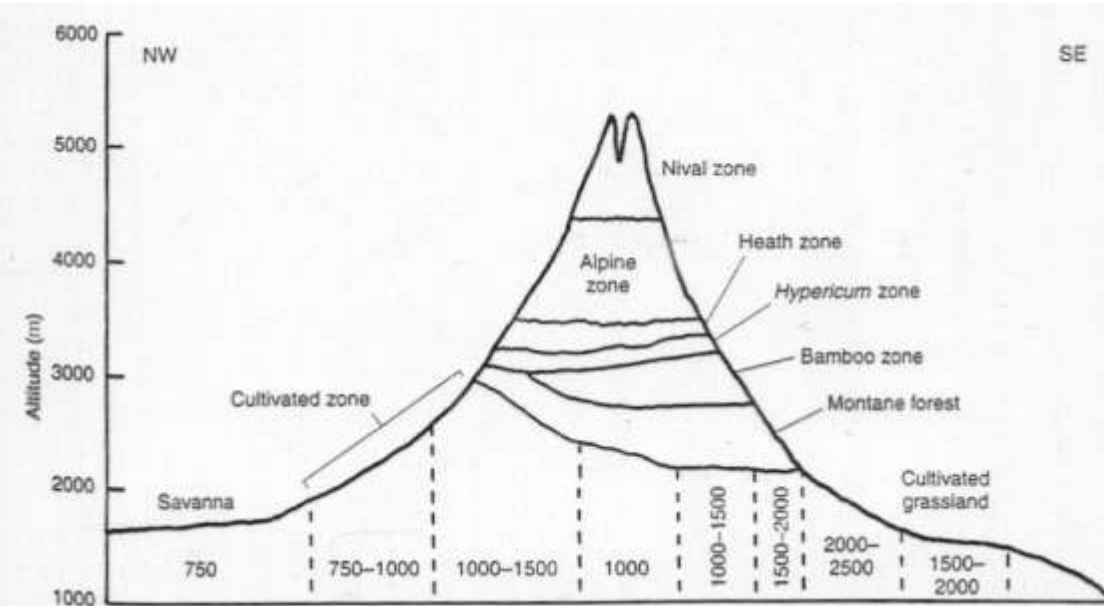




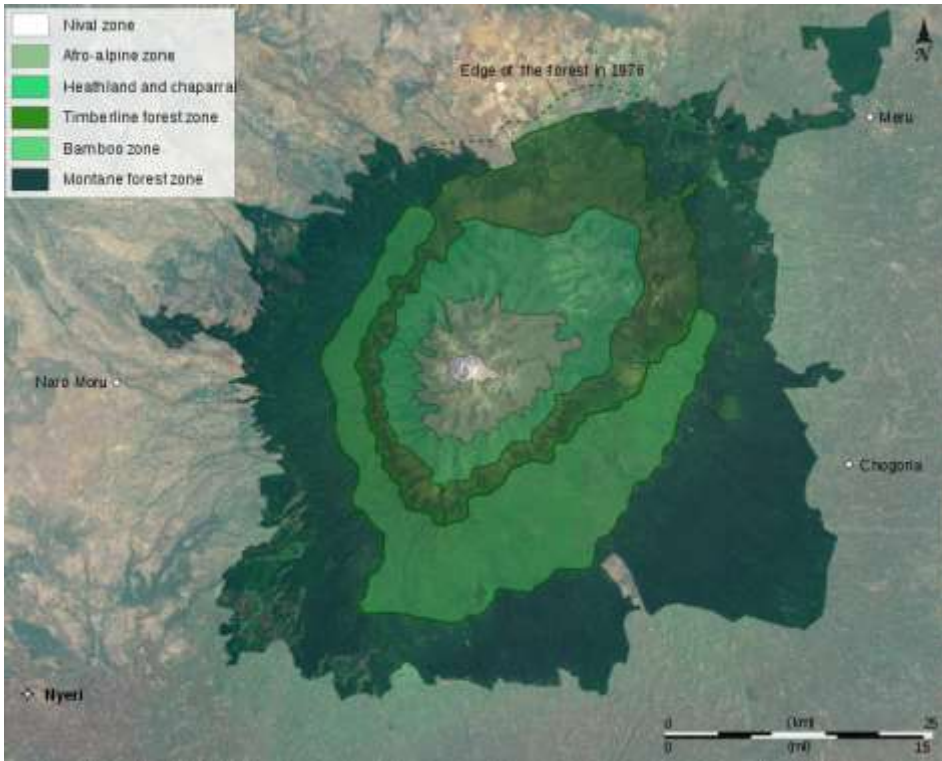
Mt. Wilhem, New Guinea  
forest limit at 3,600 m asl



# Mt. Kenya



*Sinarundinaria alpina*, Graminaceae





a)

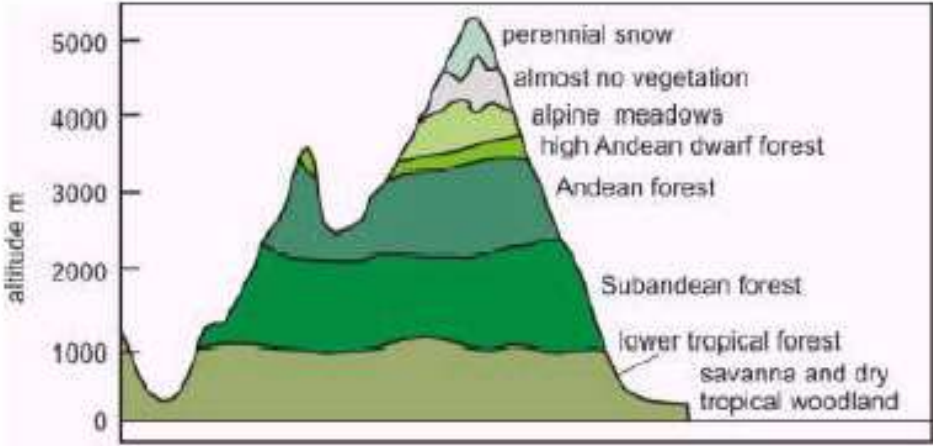
b)

c)

a) tree and shrub savannah area, up to 2.200 m;

b) mixed forest belt up to 3300m : the blue line represents a Bamboo dominant area, the yellow line defines a Hagenya-Hypericum zone;

c) alpine zone: composed mainly of Ericaceae and grass thickets.



# Tropical alpine grasslands: Paramo

- wettest northern high-Andean vegetation called "paramo" (containing thick-stemmed grasses)





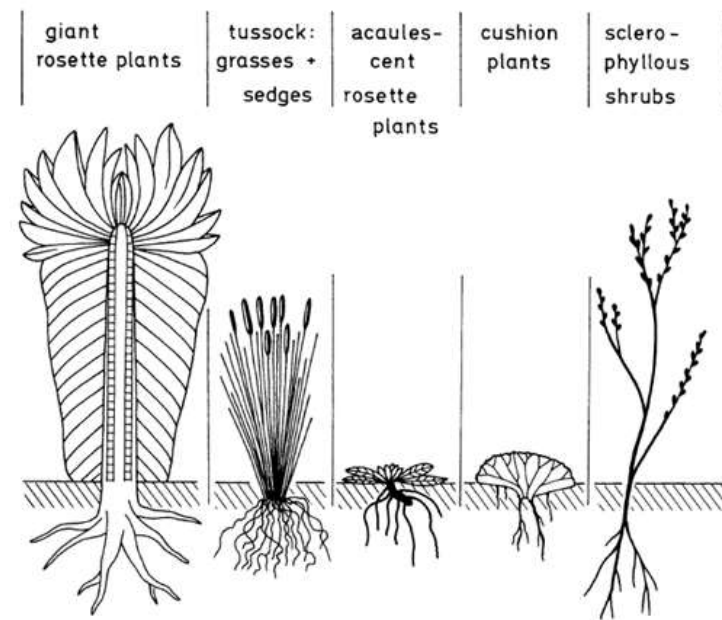
- southern high Andes is drier and contains grass-dominated vegetation called "puna"



Tropical alpine  
grasslands: Puna



Alpine tropical plants:  
meristems isolated  
against cold by rosettes,  
hairs, dry leaves...



Lobelia telekii (Africa)

Senecio (Africa)

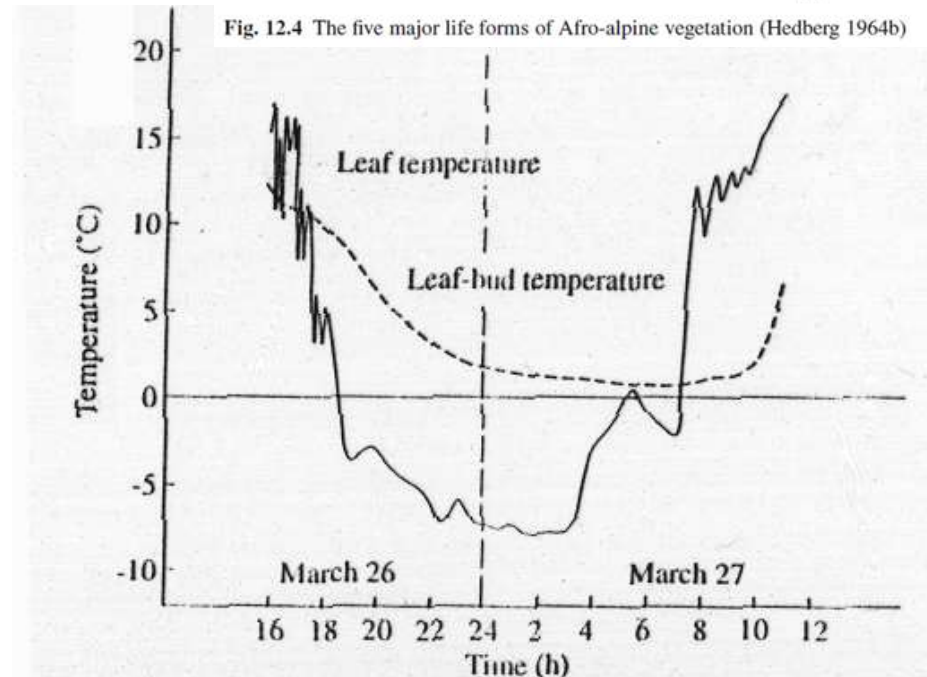
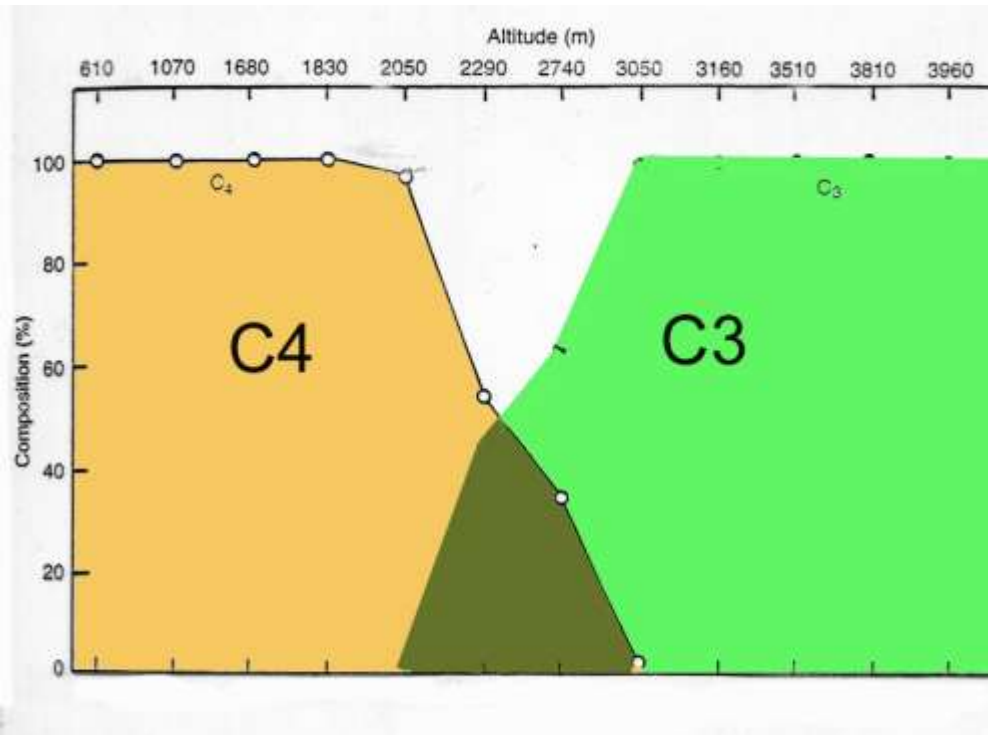
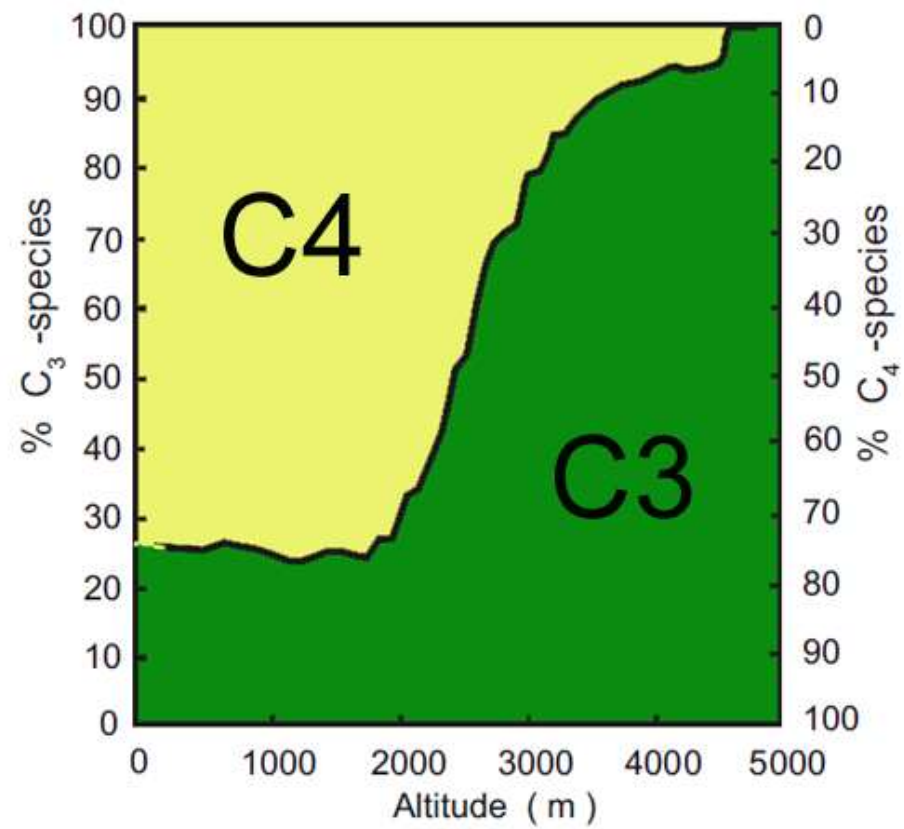


Figure 5.1. *Senecio keniensis* (Mount Kenya, 4150 m elevation): comparison of the temperature course of an adult (outer) rosette leaf with that measured inside the cone-shaped leaf bud. Reference air temperatures are shown in the top panel (from Beck *et al.* 1982).

# C3 replace C4 grasses along an altitudinal gradient

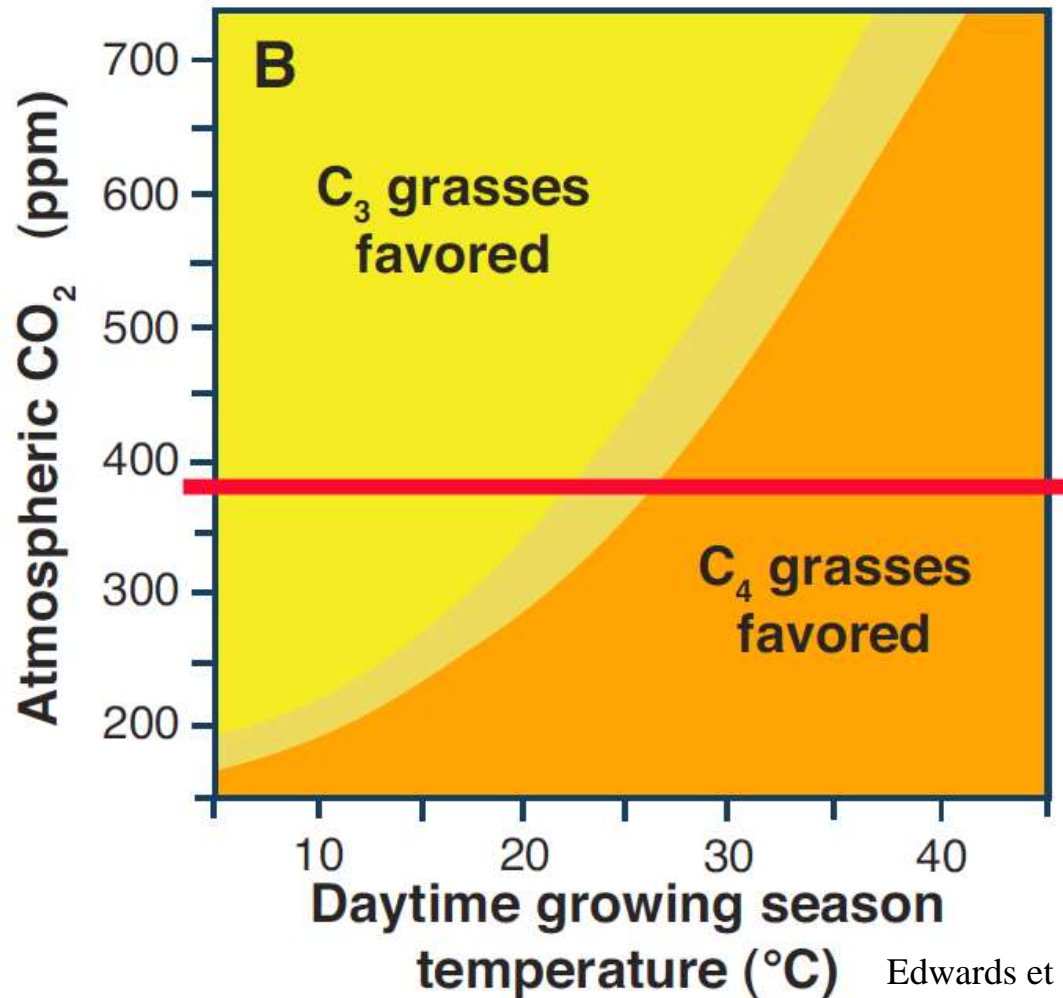


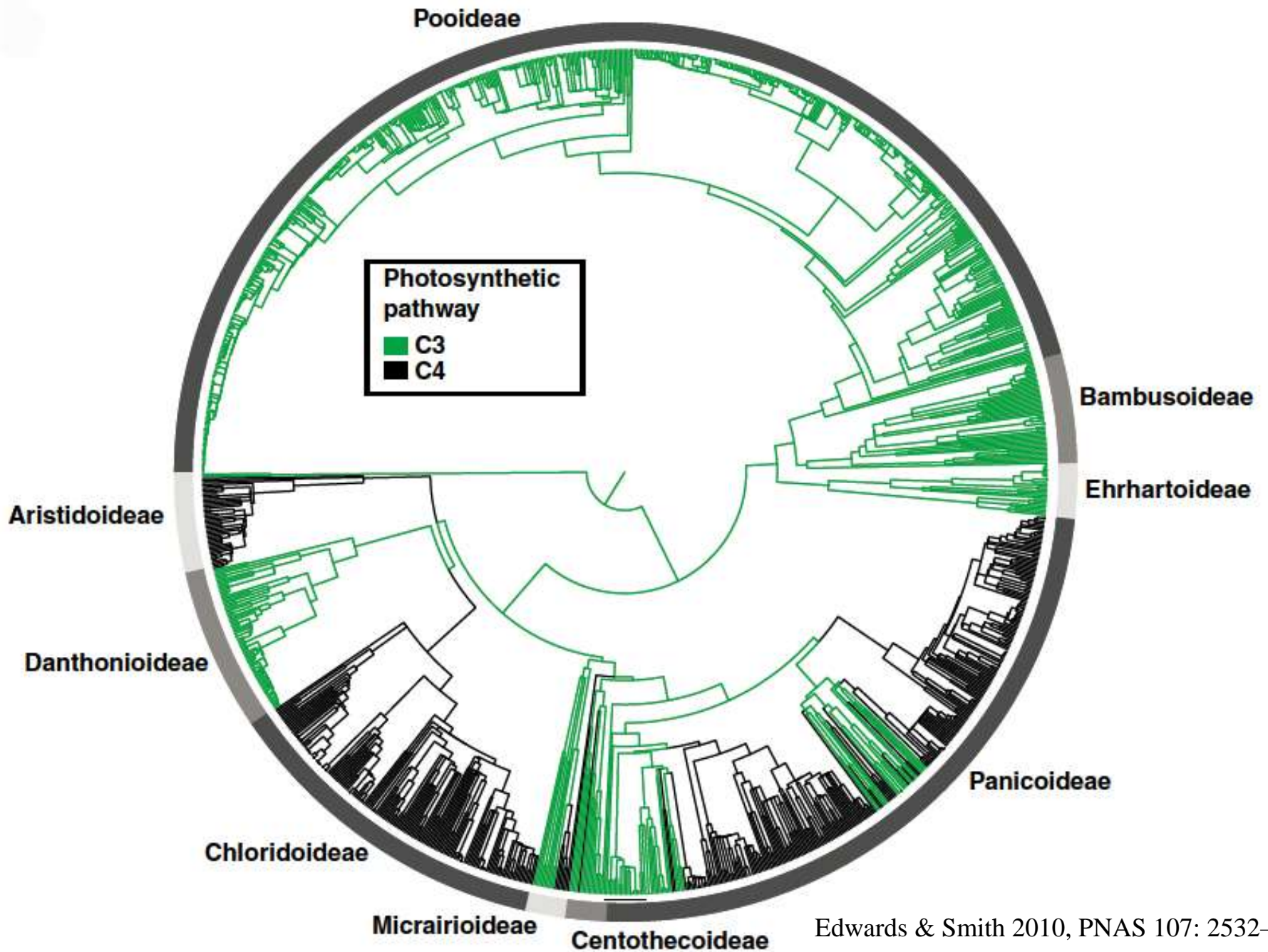
Kenya



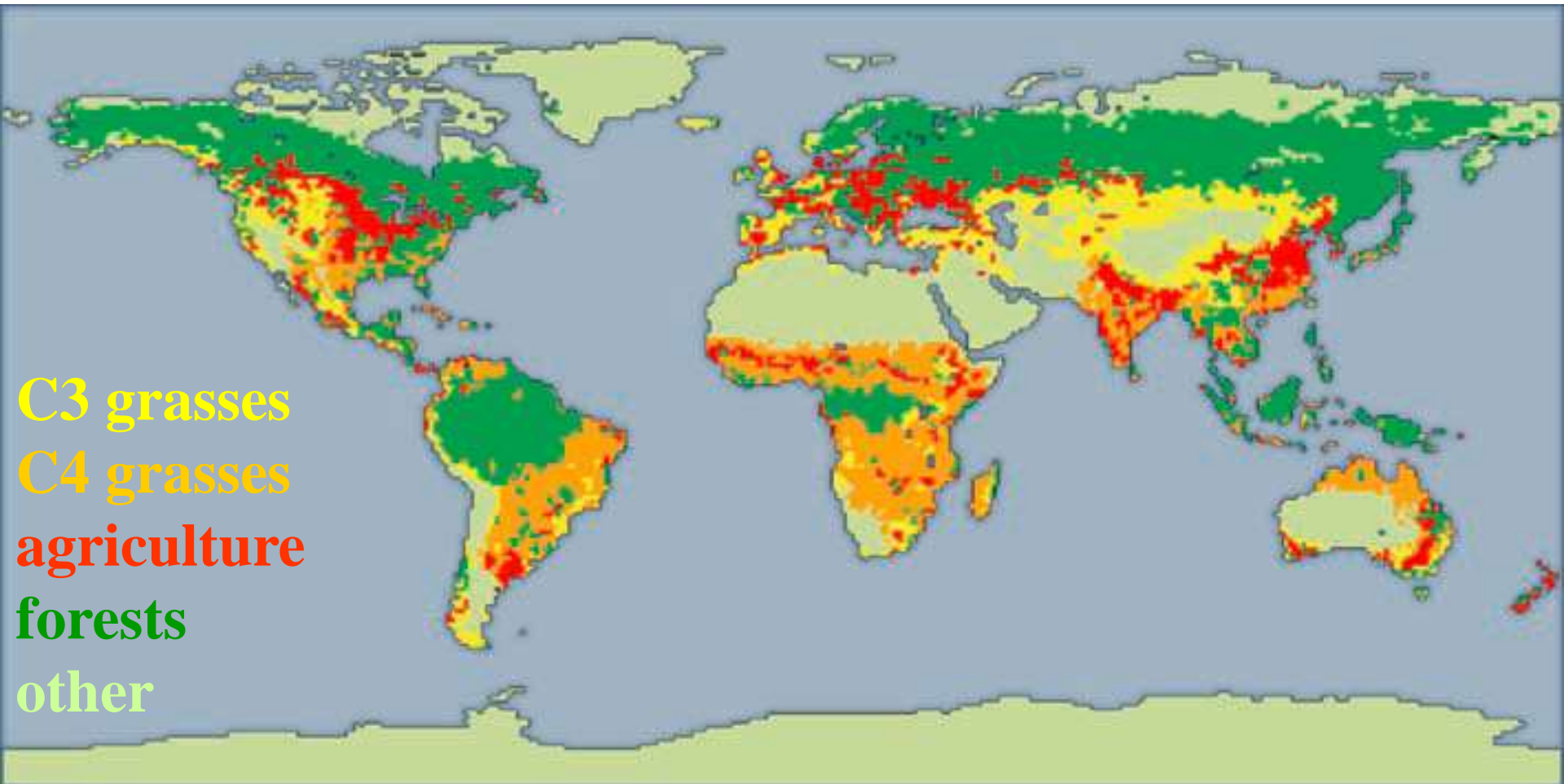
Ecuador [based on 220 species]

At high temperatures and low CO<sub>2</sub>, the C<sub>3</sub> photosynthetic enzyme rubisco fails to completely distinguish CO<sub>2</sub> and O<sub>2</sub>. This leads to photorespiration, resulting in losses of photosynthetic carbon. C<sub>4</sub> photosynthesis suppresses photorespiration by concentrating CO<sub>2</sub> internally, but this comes with an energetic cost, which exceeds the photorespiratory costs of C<sub>3</sub> photosynthesis at high CO<sub>2</sub> and low temperatures.





# C4 grasses dominate in the tropics





# Montane forests

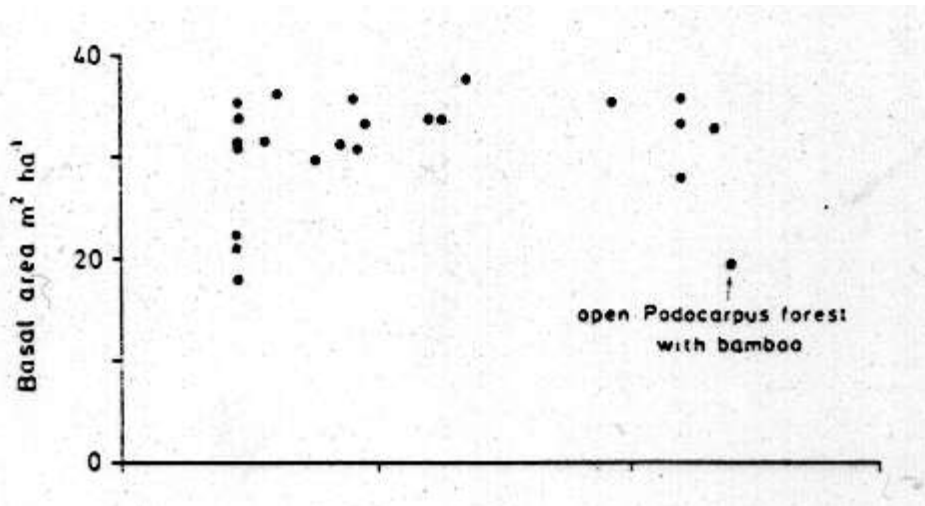
# New Guinea, montane forest at 2,200 m asl





# Altitudinal trends - trees >20 cm DBH in Africa

basal area  $\text{m}^2/\text{ha}$



no. of species /ha

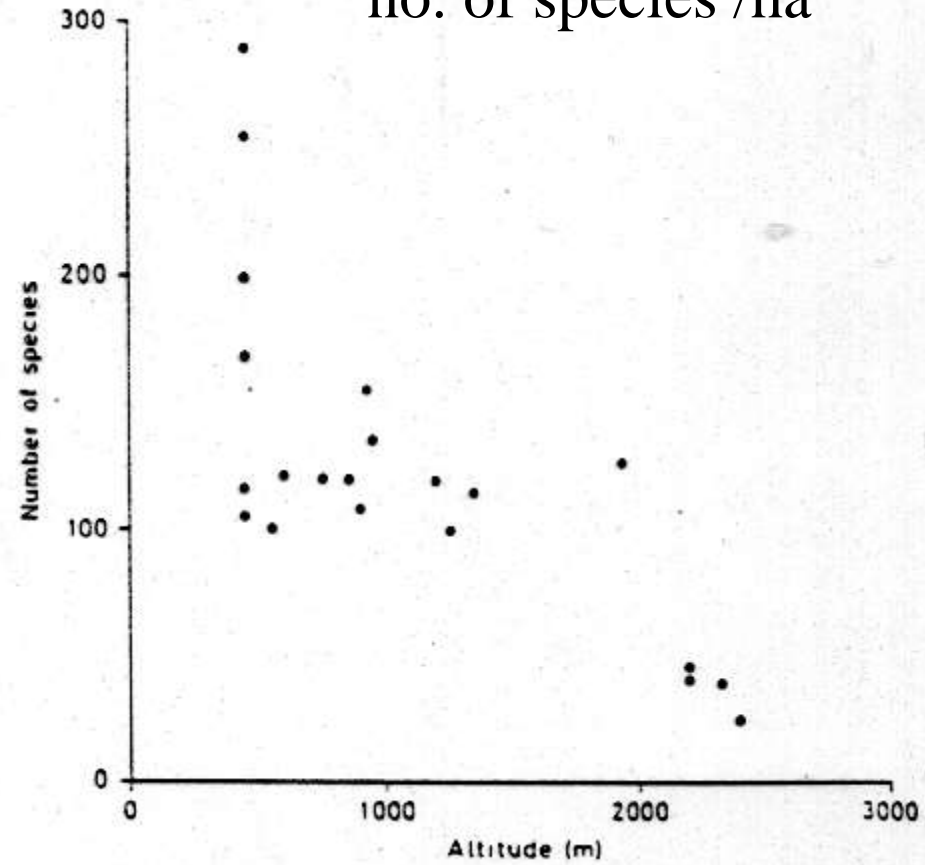


Fig. 8.9. Basal area, tree density and species diversity plotted against altitude for central African forests, mainly in Kivu (Zaire). Only individuals over 20 cm circumference at a height of 1.5 m above the ground are included. (Constructed from data in Pierlot, 1966.)

# Altitudinal trends in the main forest characteristics

Characteristics	Lowland rainforest	Lower montane	Mid montane	Upper montane
Mean height:				
canopy	25–45 m	30–40 m	20–30 m	18–20 m
emergents	60–80 m	70–80 m	to 30 m	to 25 m
Stratification	3–4 layers	Diffuse	Diffuse	1 or 2 layers
Buttress roots	Frequent and large	Common	Rare	Absent
Surface roots	Rare	Rare to common	Common	Abundant
Stilt roots	Rare	Absent to rare	Common to abundant	Absent to rare
Cauliflory	Frequent	Rare	Rare	Absent
Drip tips on leaves	Frequent	Occasional to frequent	Rare	Absent
Lianas	Frequent	Common	Rare	Absent
Lichens, mosses	Rare	Rare	Abundant	Abundant
Tree ferns	Absent	Present	Occasional to common	Abundant
Palms	Abundant	Common	Absent	Absent
<b>Pinnate leaves</b>	<b>Frequent</b>	<b>Rare</b>		<b>Very rare</b>
<b>Leaf size</b>	<b>Mesophyll</b>	<b>Mesophyll</b>		<b>Microphyll</b>

# Elfin forest Costa Rica



Botanical Society of America  
(photo by Alan Rebertus)



## Elfin x lowland forests

trees DBH>10cm:	Elfin forest Puerto Rico	Lowland forest Malaysia
No. trees/ha	4000	500
Basal area m <sup>2</sup> /ha	44	30
LAI	2.2	7.4
wood support efficiency kg wood/m <sup>2</sup> foliage * m height	1.1 [90 t of wood to support 2 ha leaves 4 m above ground]	0.2 [420 t of wood to support 7.4 ha leaves 30 m above ground]

# Biomass and water interception in a mossy elfin forest Tanzania (2140 m asl)

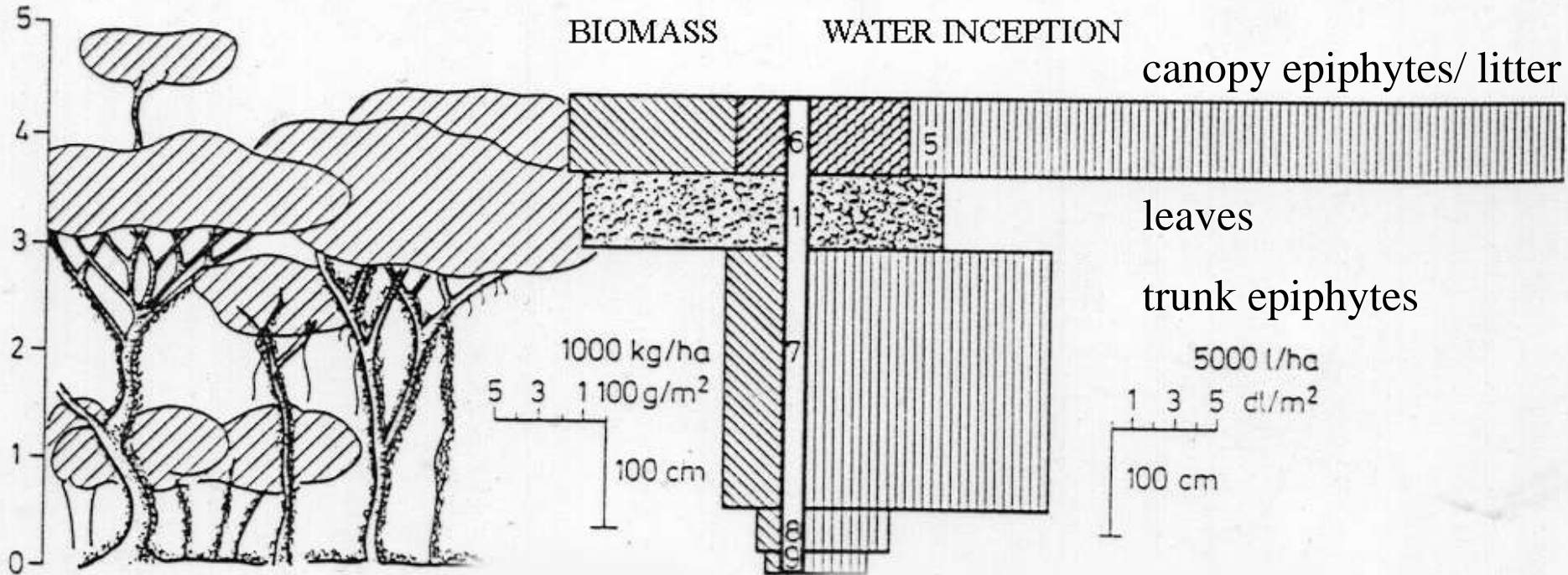


Fig. 16.5. The biomass and water interception of epiphytes and phorophyte leaves in a mossy elfin forest in Tanzania, Uluguru Mts. at 2140 m alt. (after Pócs, 1980). On the left side the dry weight of different layers in  $1000 \text{ kg ha}^{-1}$ . On the right side the water interception capacity in  $\text{l ha}^{-1}$  according to the different layers, as: 1. Leaves of phorophyte trees forming the canopy; 5, humus and detritus among the canopy epiphytes (the darker part); 6, canopy microepiphytes including small orchids; 7, microepiphytes (bryophytes and filmy ferns) on the trunk; 8, microepiphytes (bryophytes) on the roots; 9, bryophyte cover on the ground.

# Bryophytes along tropical altitudinal gradient

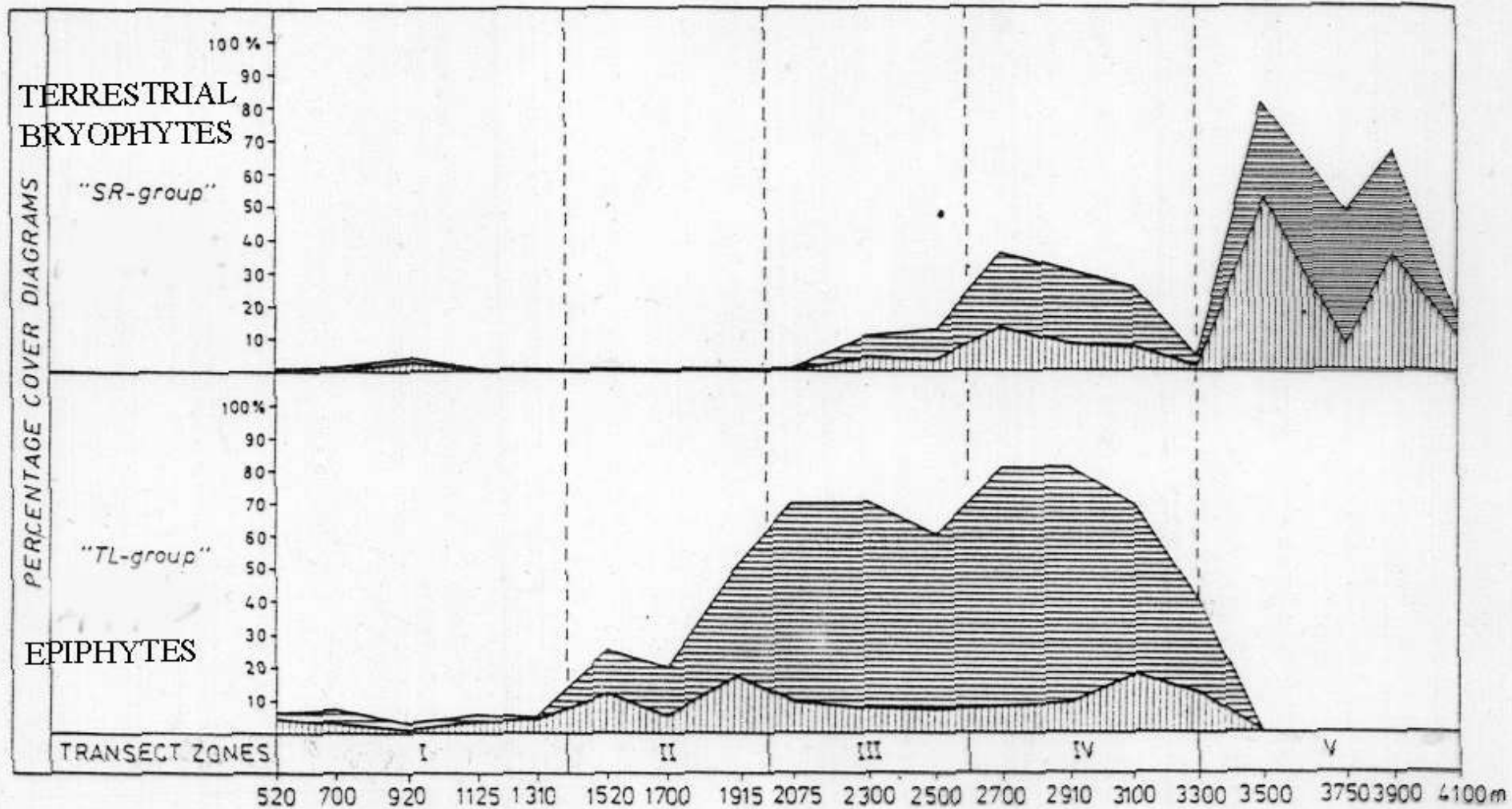
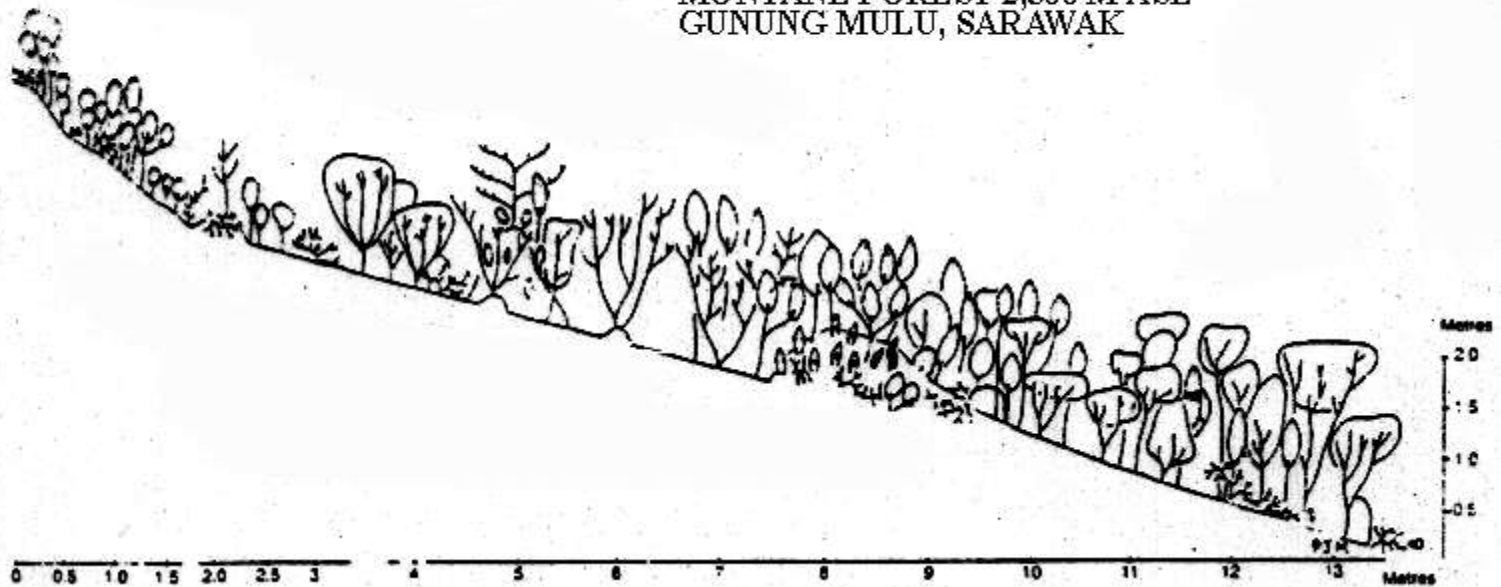
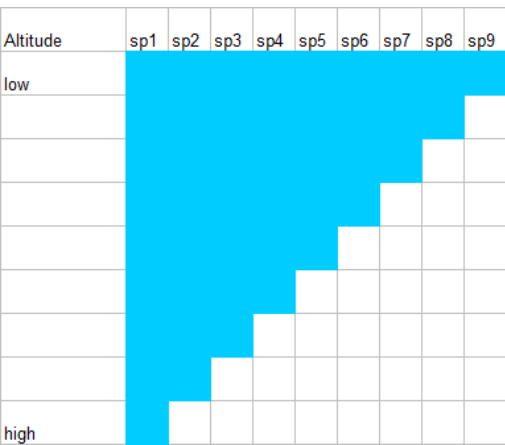
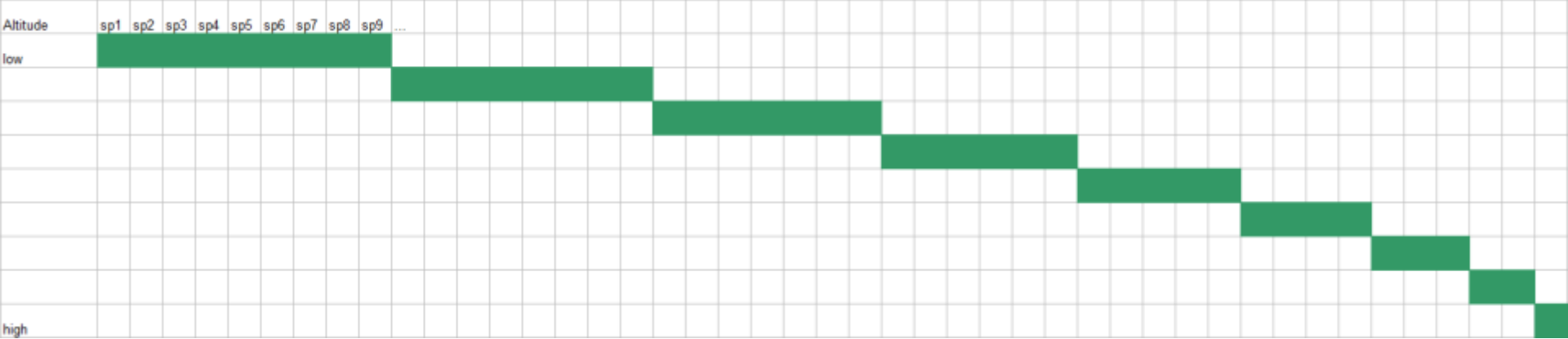


Fig. 16.4. Bryophyte cover values in relation to altitude in the Sierra Nevada de Santa Marta, Colombia (after Van Reenen and Gradstein, 1983). Zone I: lowland rain forest; zone II: submontane rain forest; zone III: lower montane rain forest; zone IV: upper montane rain forest (condensation zone); zone V: paramo. TL group: epiphytes; SR group: terrestrial and saxicolous species. Vertical lines: mosses; horizontal lines: liverworts.

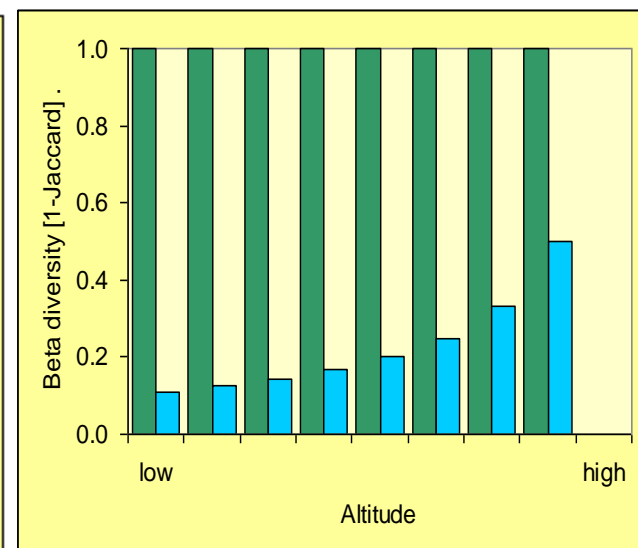
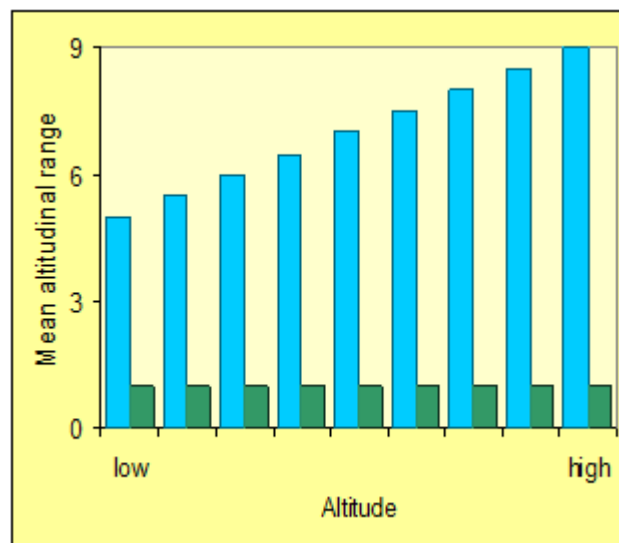
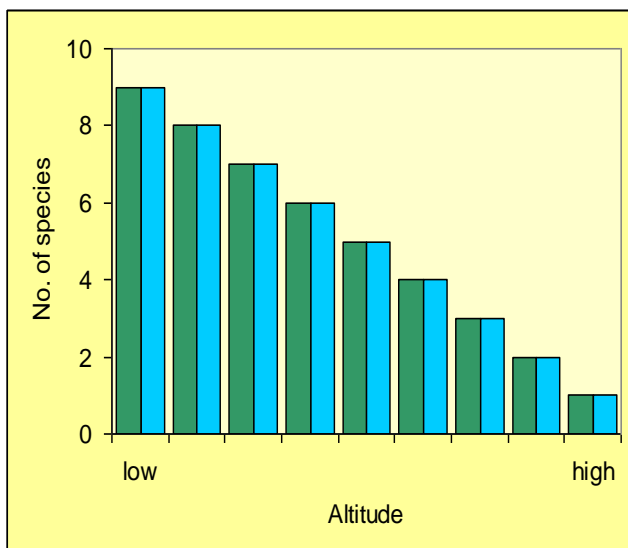
MONTANE FOREST 2,300 M ASL  
GUNUNG MULU, SARAWAK





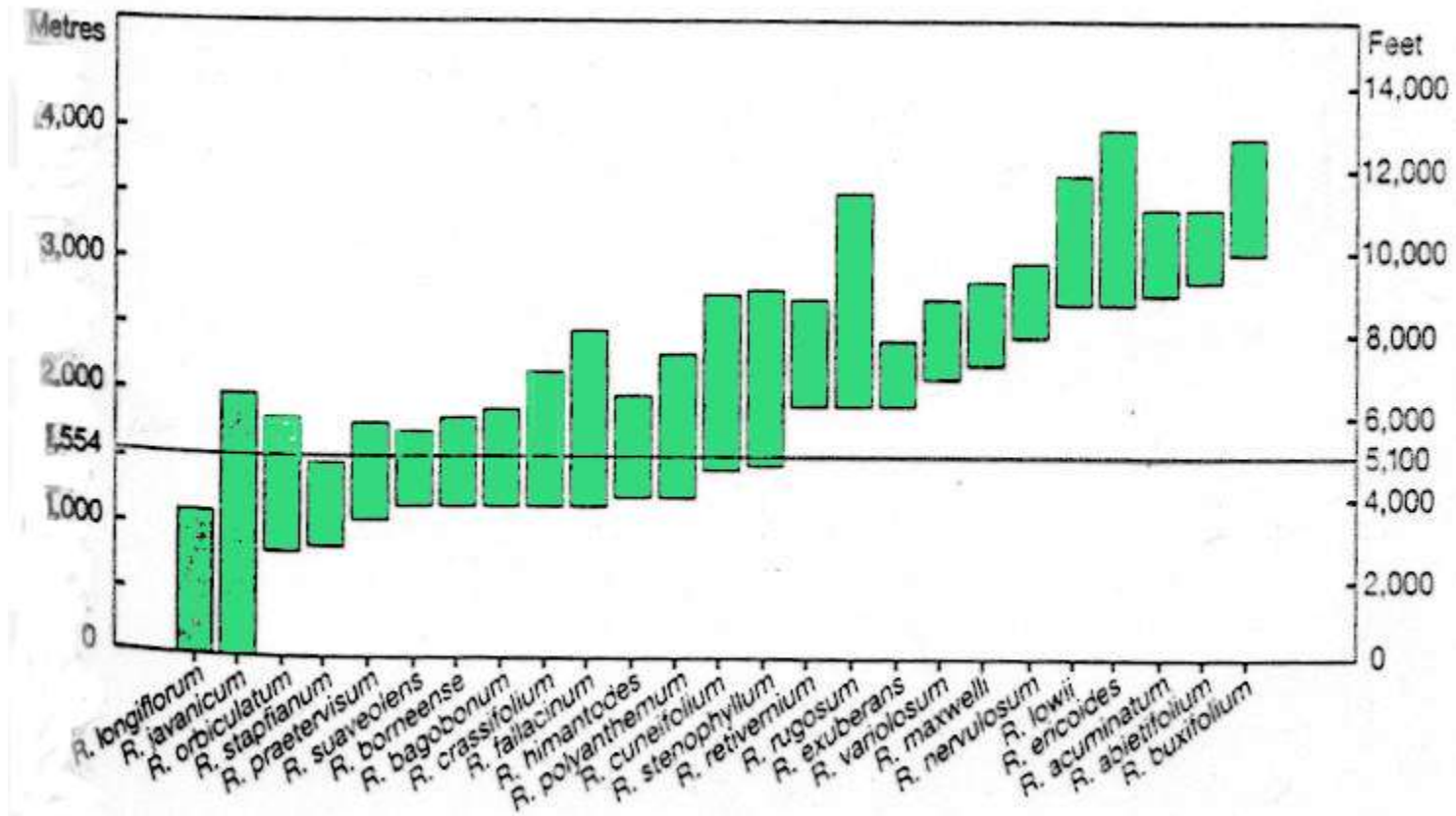
## Two modes of altitudinal species turnover: with **complete nestedness** and **zero nestedness**

Identical altitudinal trends in species richness mean different trends in mean altitudinal range of species and beta diversity between adjacent altitudes





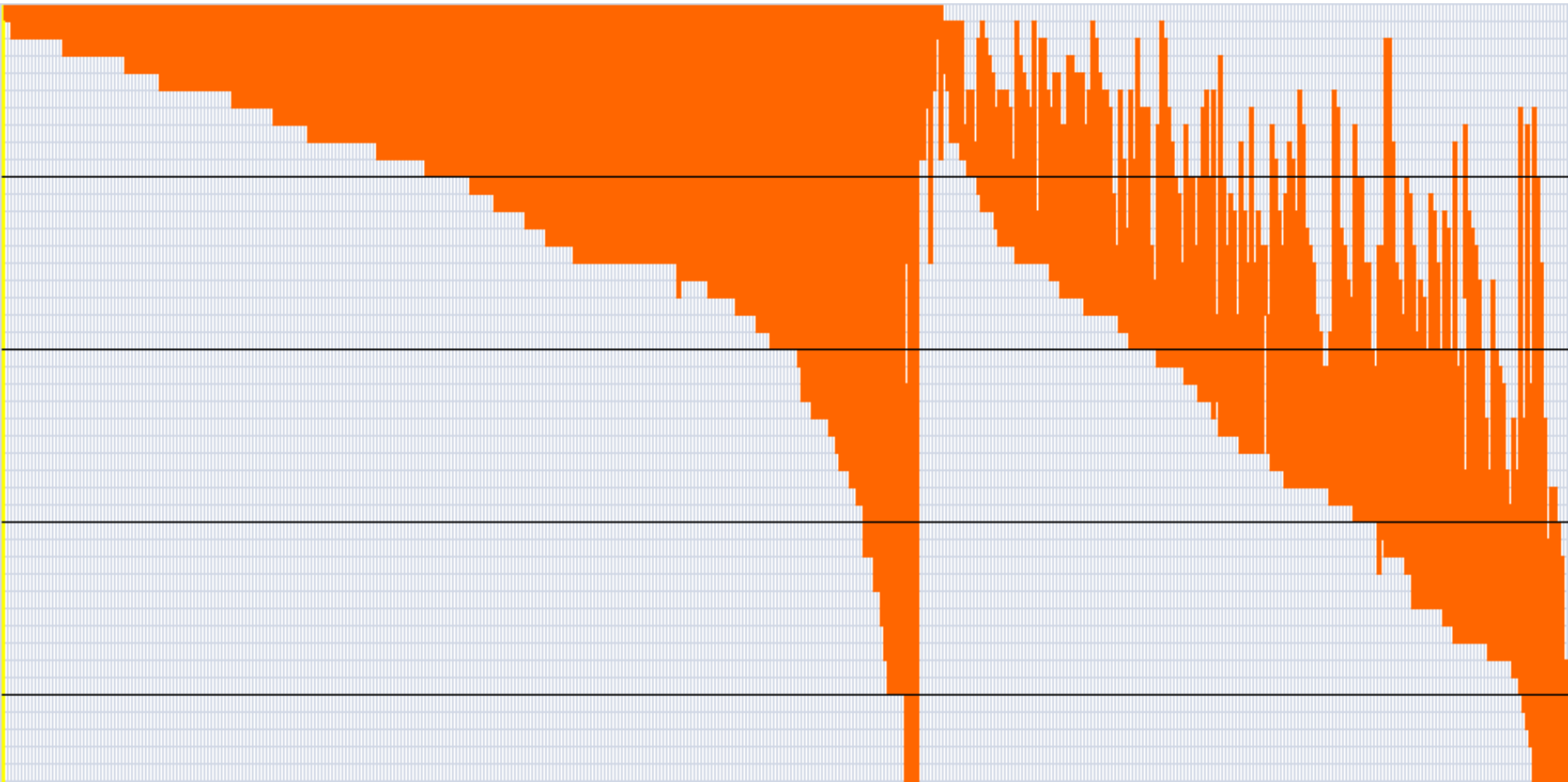
# Species turnover along altitudinal gradients: *Rhododendron* spp. on Mt. Kinabalu



**Rhododendrones:** 900 spp. worldwide, 300 spp. in SE Asia, 50 spp. in Borneo, 25 spp. on Mt. Kinabalu, incl. 5 endemic spp.

# Altitudinal distribution of 454 bird species in Papua New Guinea

0 m asl.

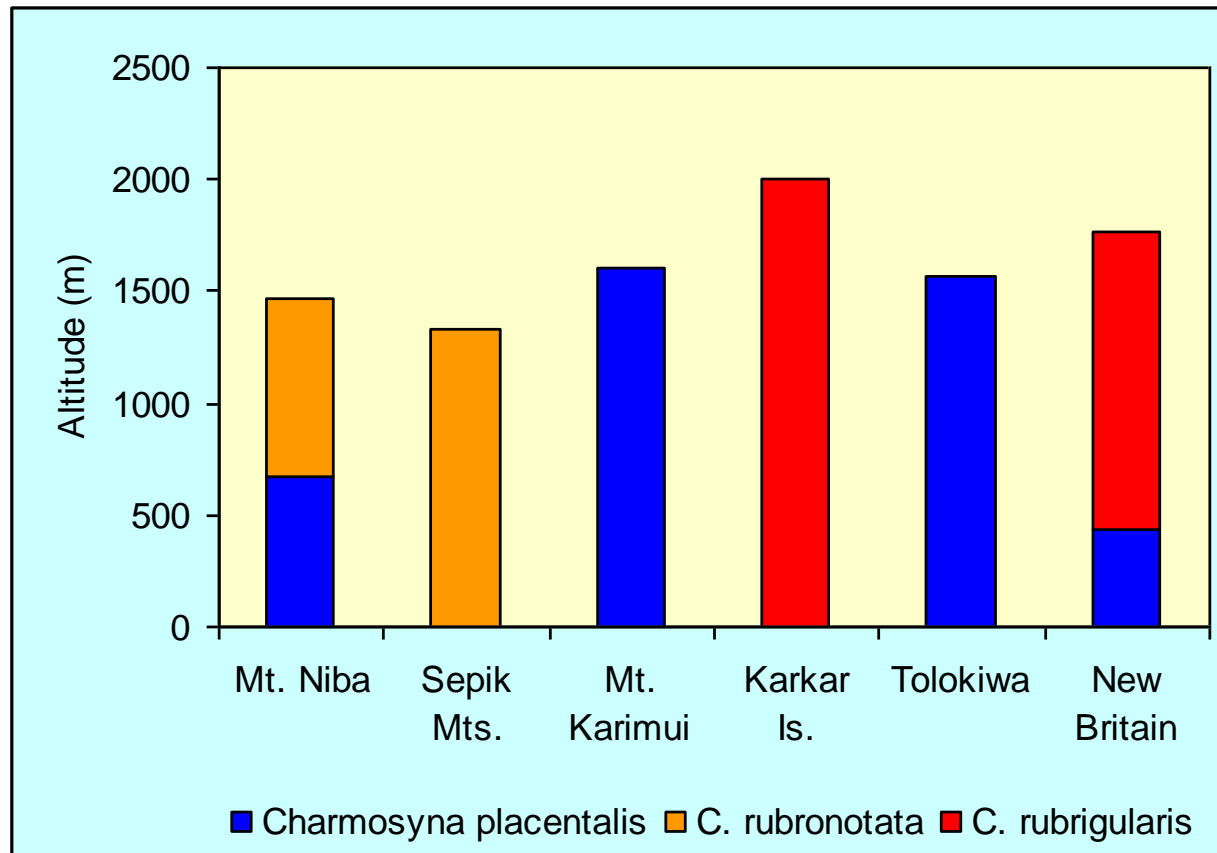


4500 m asl.

each row is 100 m elevation belt, each column a bird species

# Checkerboard distribution along an altitudinal gradient

Altitudinal segregation of competing parrots in New Guinea:



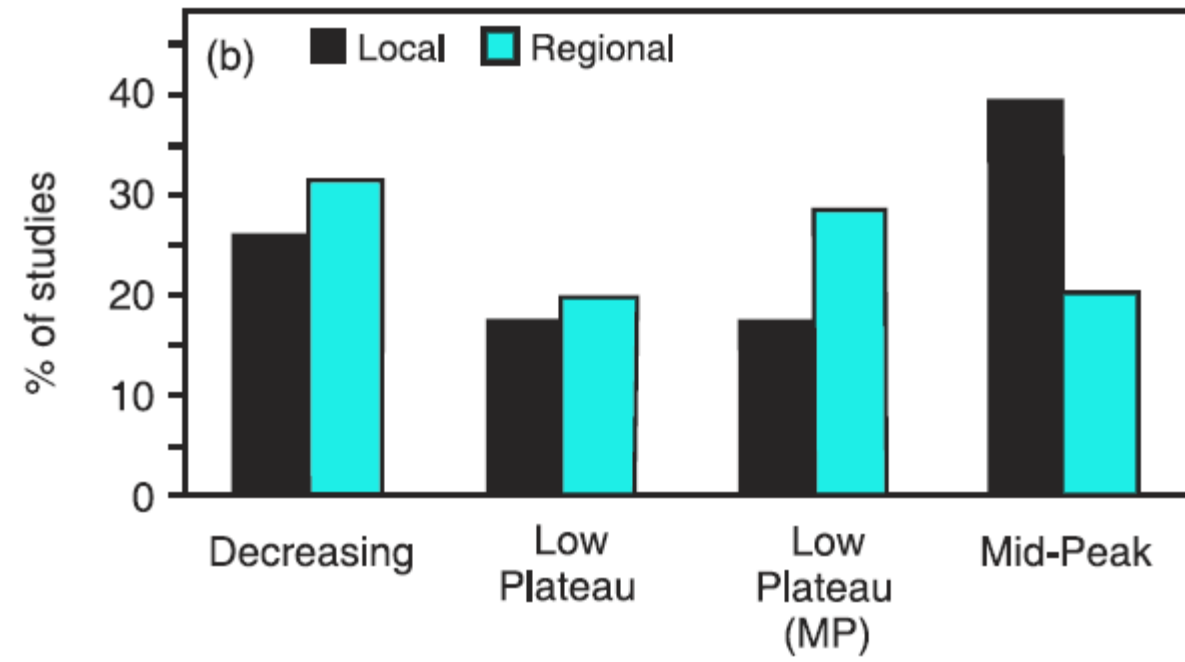
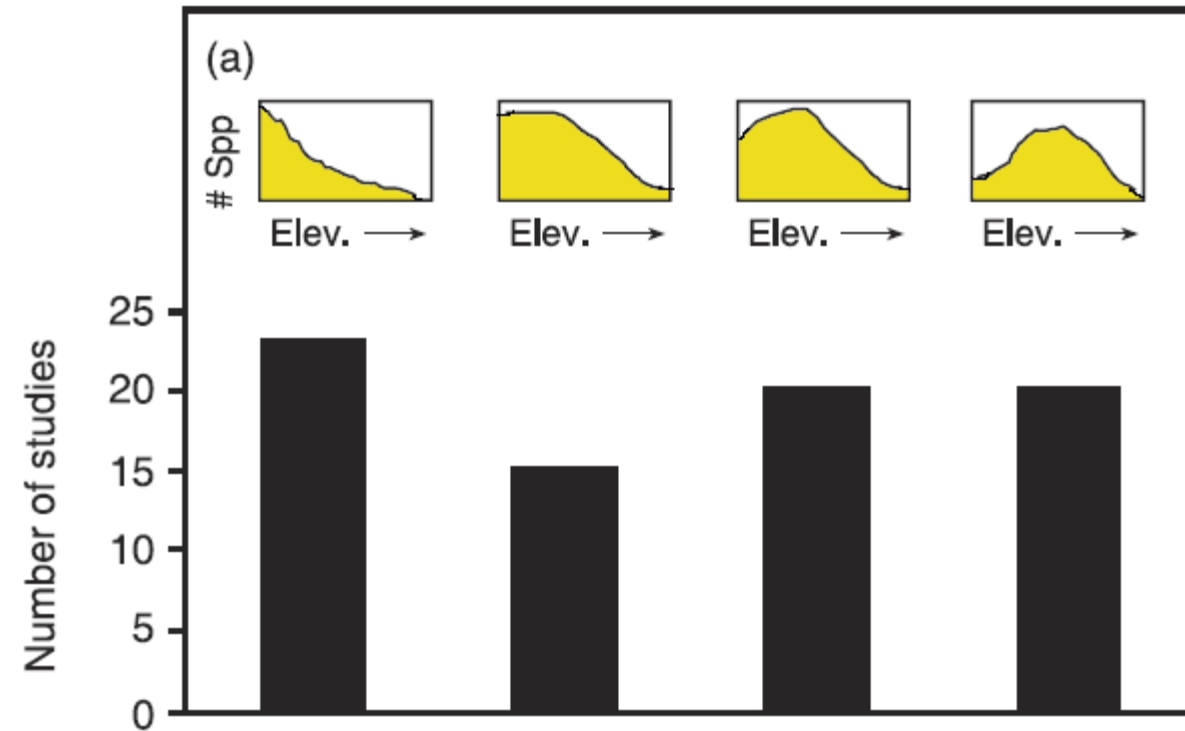
Global elevation patterns of bird diversity decreasing diversity

low-elevation plateaus

low-elevation plateaus with mid-peaks

unimodal midelevational peaks

*McCain, Global Ecology and Biogeography, (2009) 18, 346–360*



## Species richness along altitudinal gradients:

- monotonous decrease from the lowland maximum
- OR
- peak at mid-elevations?

## Factors causing decreasing species richness with altitude:

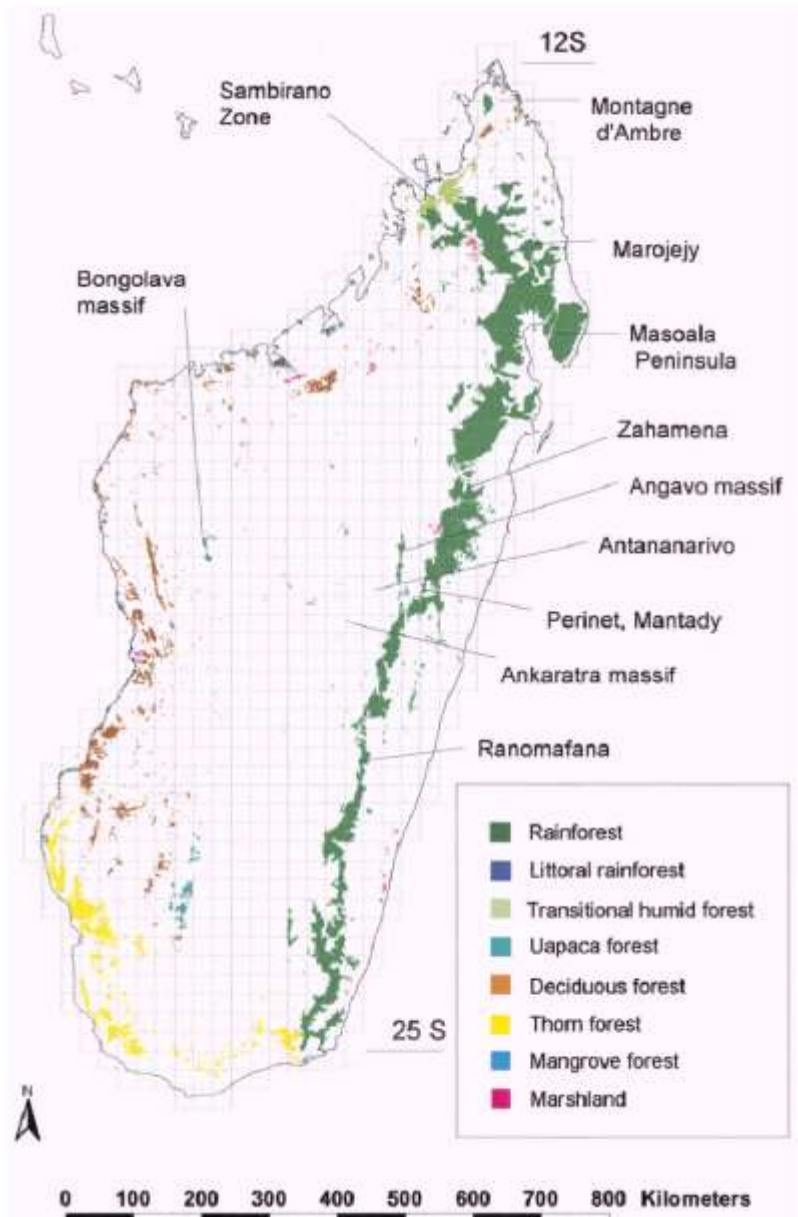
- harsh environmental conditions (temperature)
- diminishing habitat area with altitude

## Mid-elevation peak:

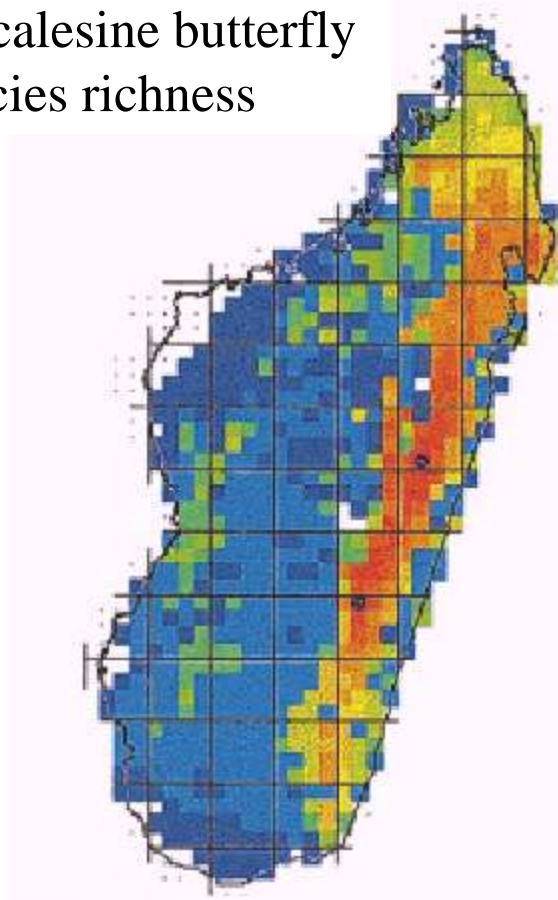
- possibly as a result of geometric constraints:

both lowland and high-montane species can overlap to the mid-elevation

# Geometric constraints: Madagascar study of mycalesine butterflies

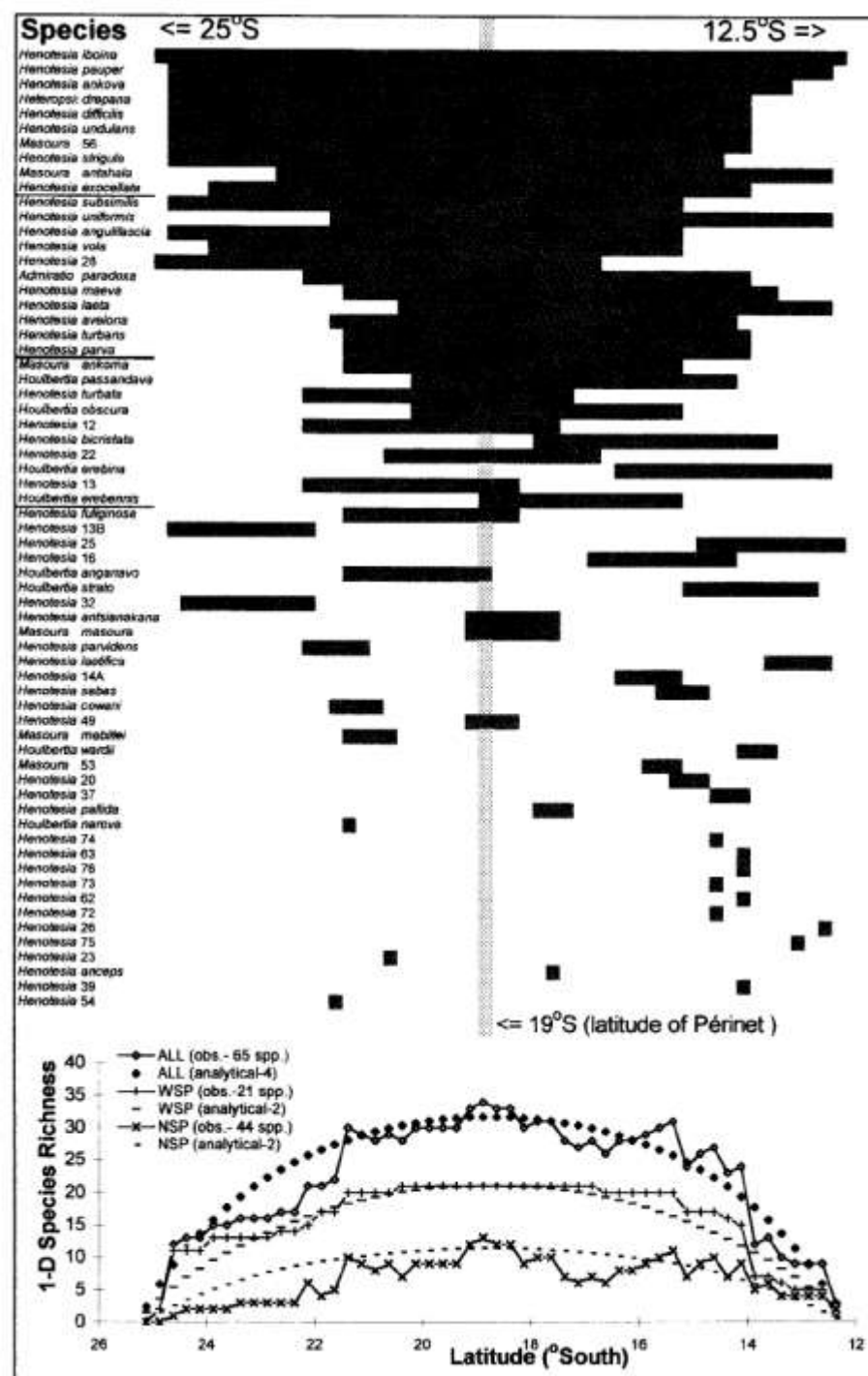
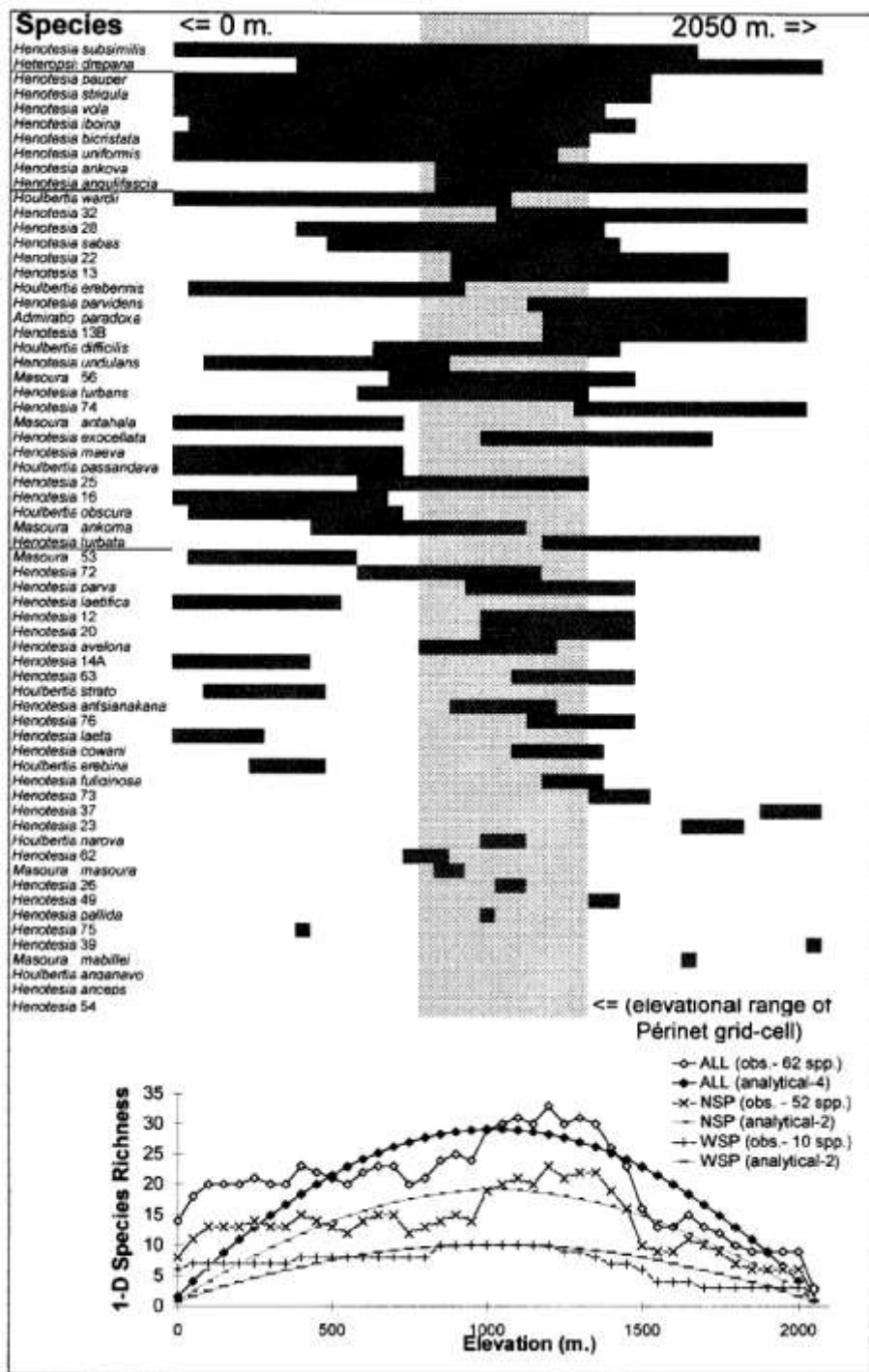


## Mycalesine butterfly species richness

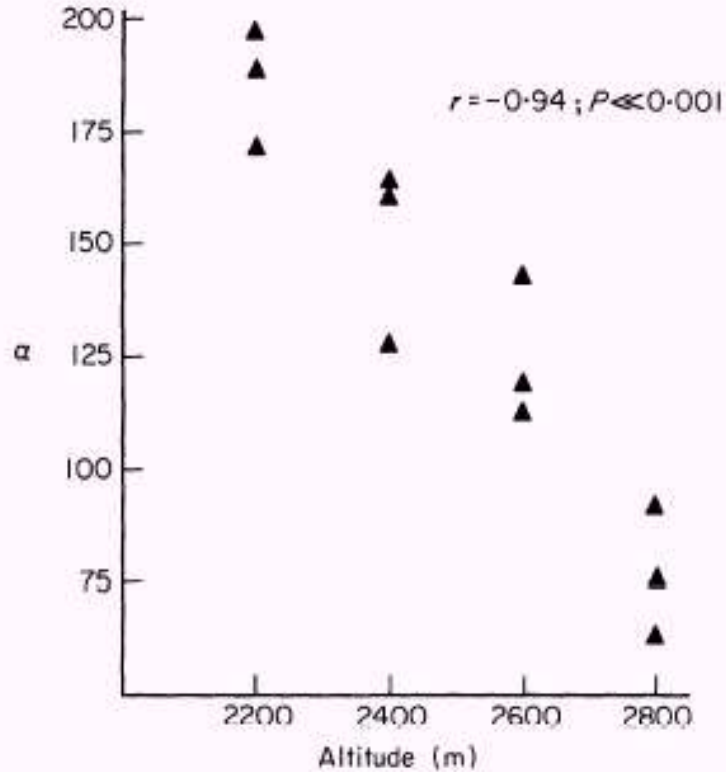


*Henotesia fraterna*

Lees et al. 1999. Biol. J. Linn. Soc. 67:529

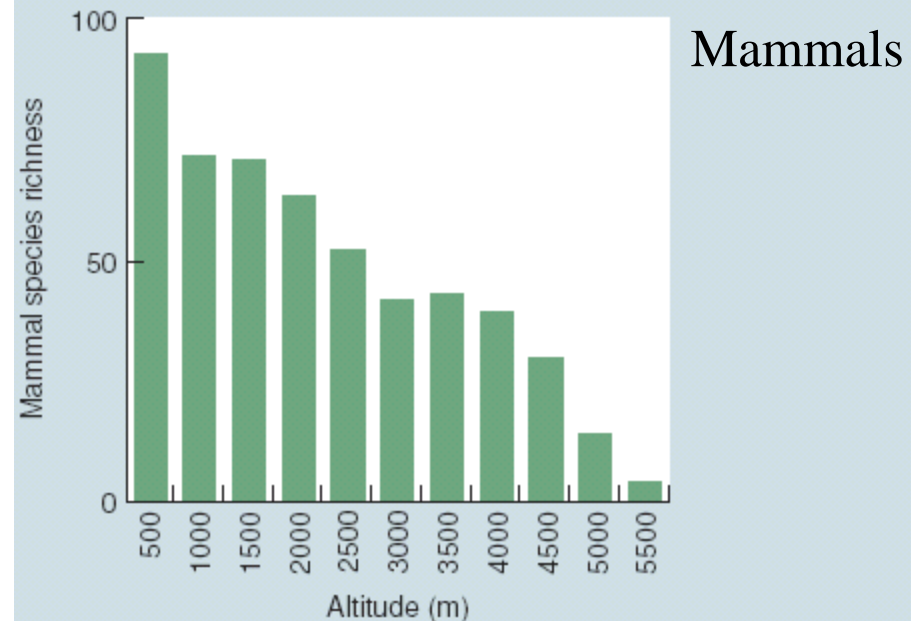
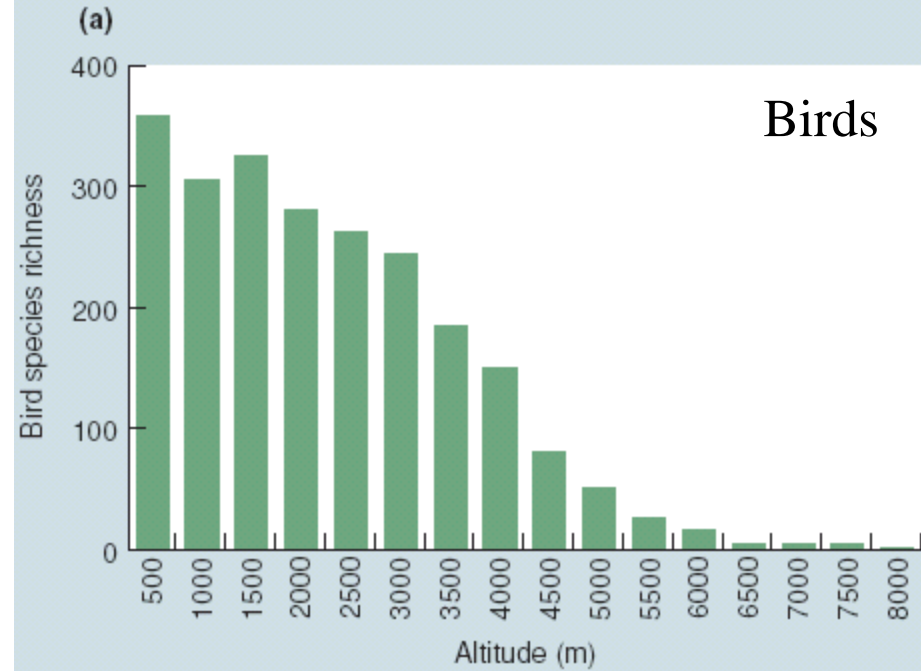


# Himalayas



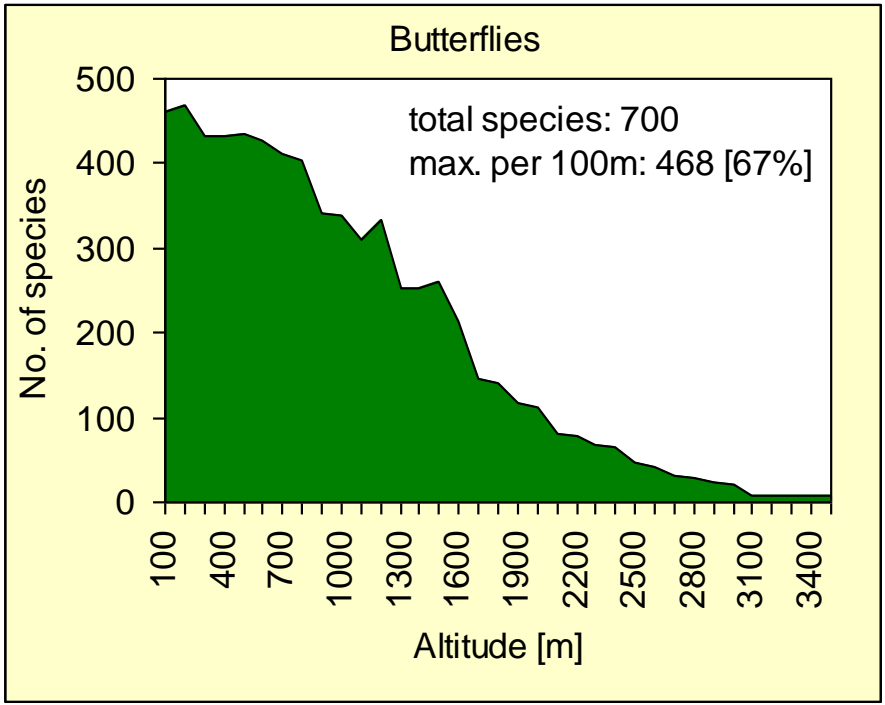
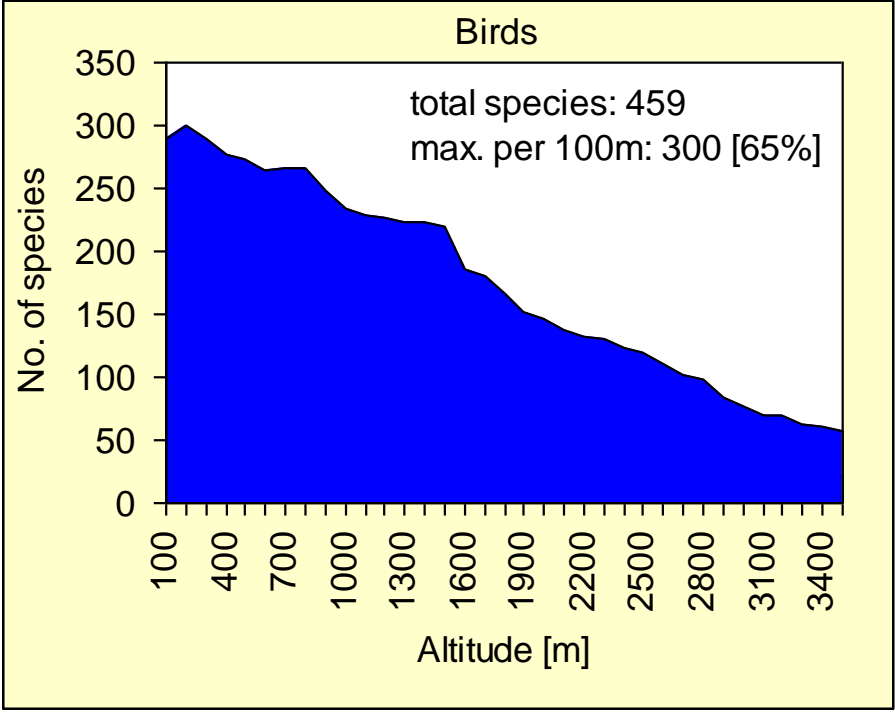
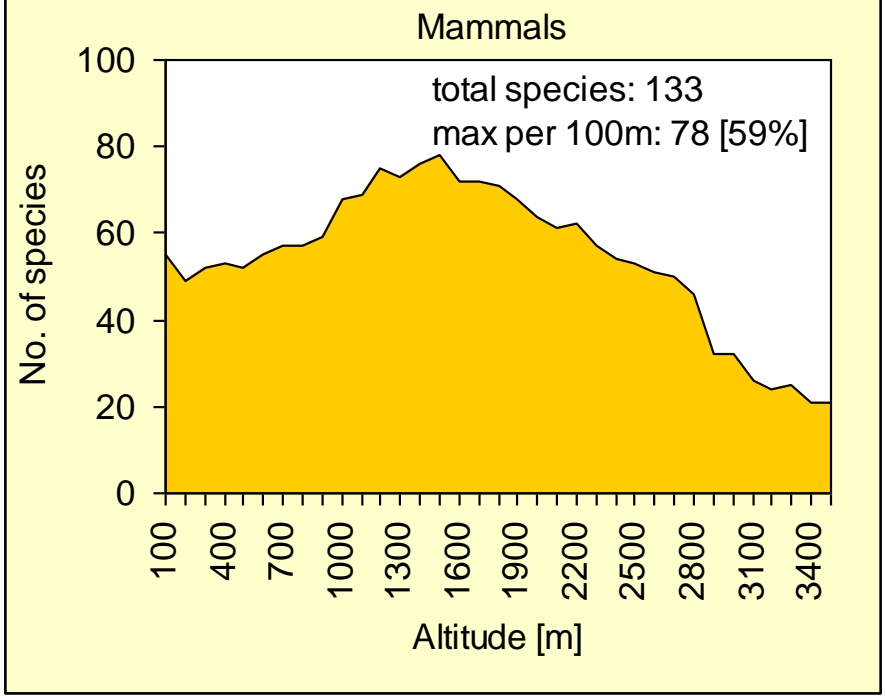
Lepidoptera, Mt Wilhelm, New Guinea

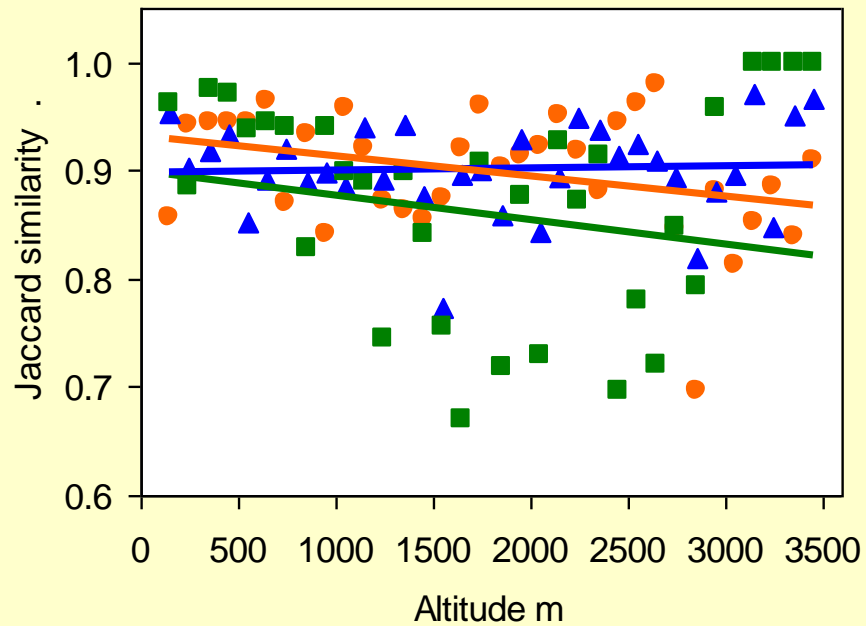
Ants: decreasing abundance and species richness with altitude, practically absent above 1,800 m



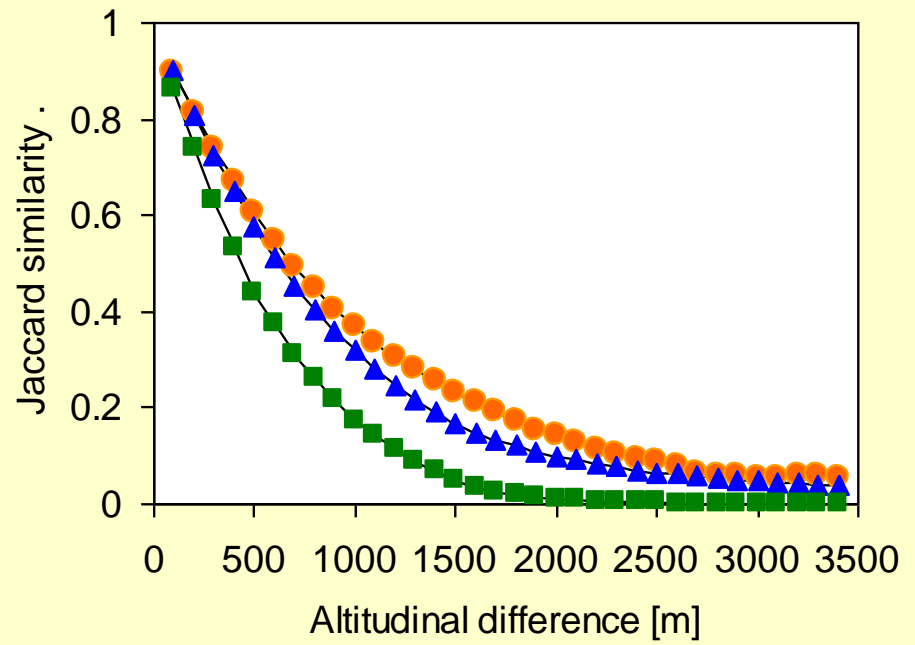


# Altitudinal gradients in New Guinea

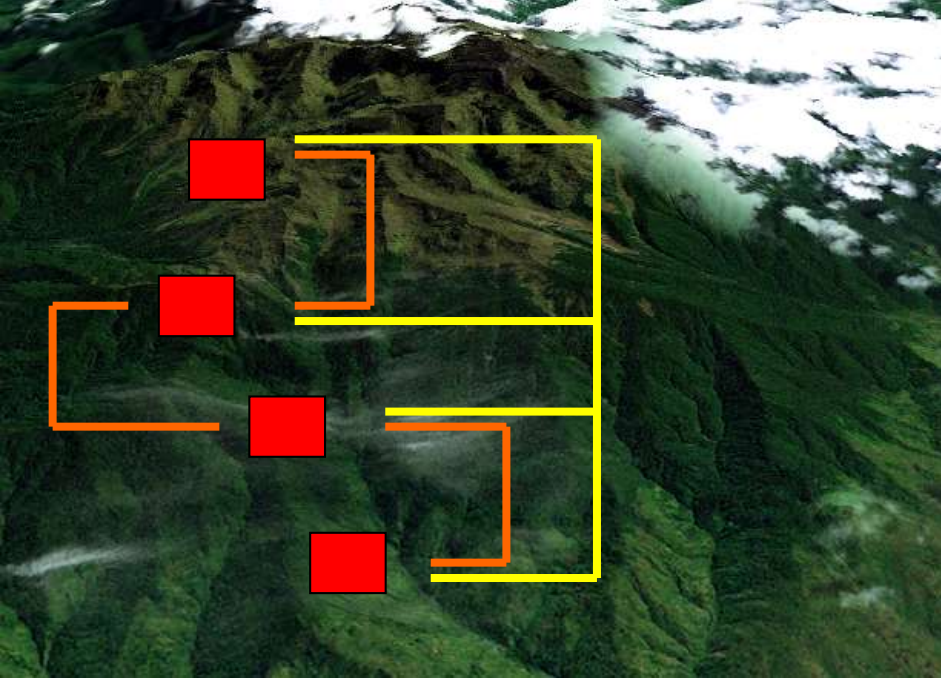




● Mammals      ▲ Birds      ■ Butterflies  
— Linear (Butterflies)    — Linear (Birds)    — Linear (Mammals)



—●— Mammals      —▲— Birds      —■— Butterflies



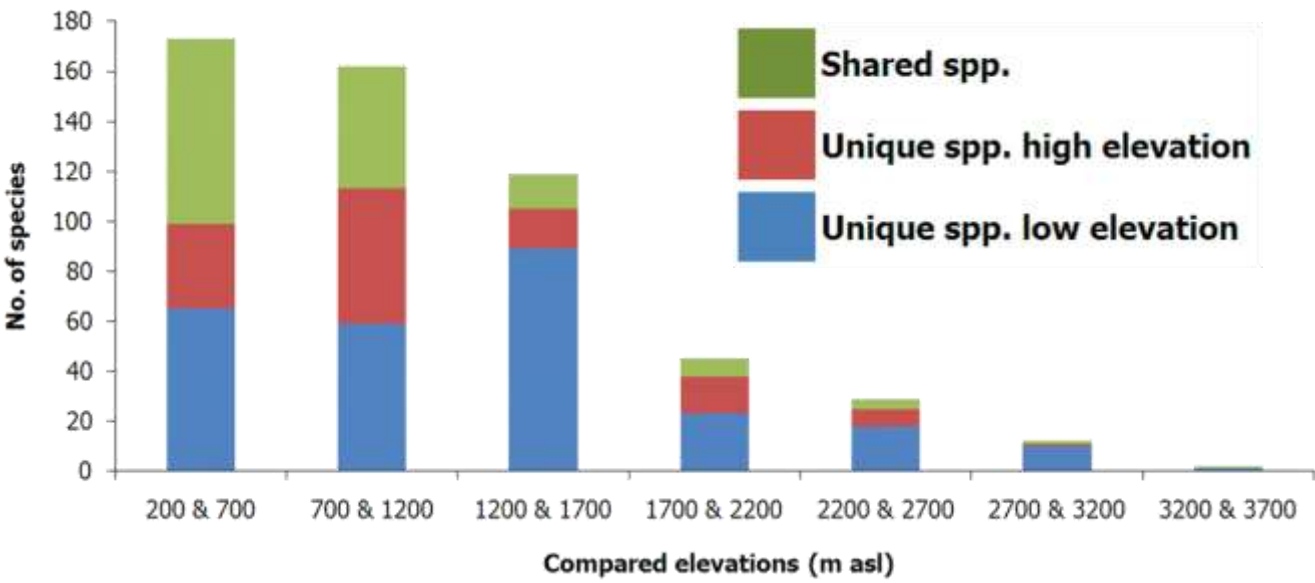
## Species turnover:

- between neighbouring 100m altitudinal zones
- with increasing altitudinal distance

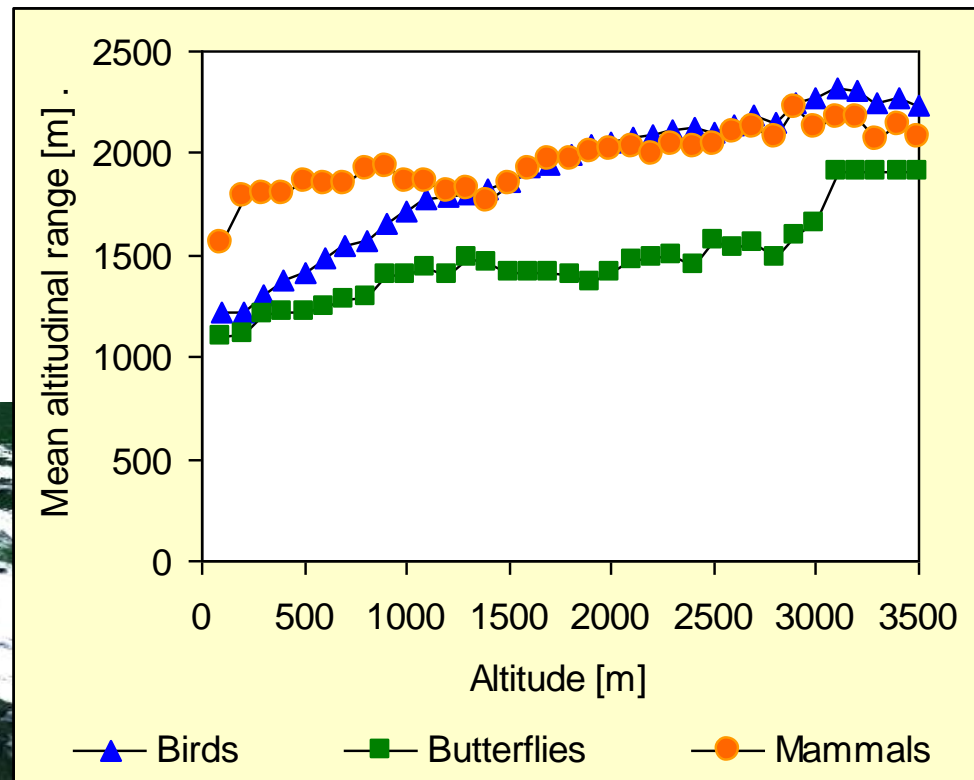
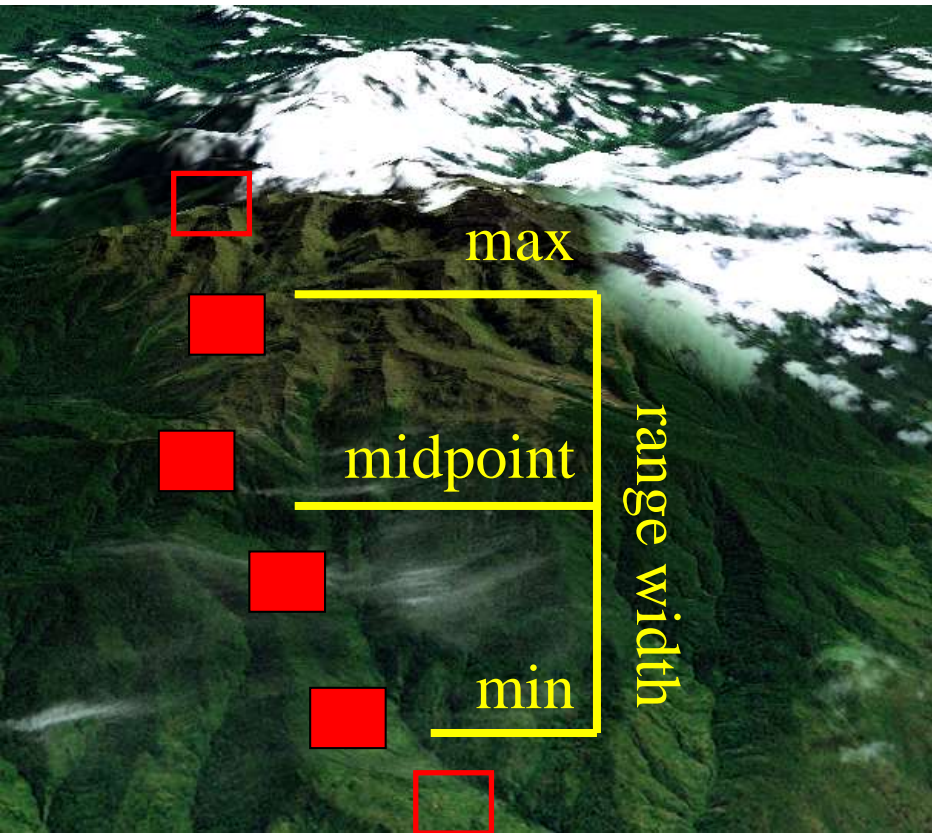


Butterflies along altitudinal transect at Mt Wilhelm:

are lowland species just disappearing with altitude, or are only new montane species appearing, or both at the same time?



Rapoport's rule:  
do montane species have wider altitudinal ranges?

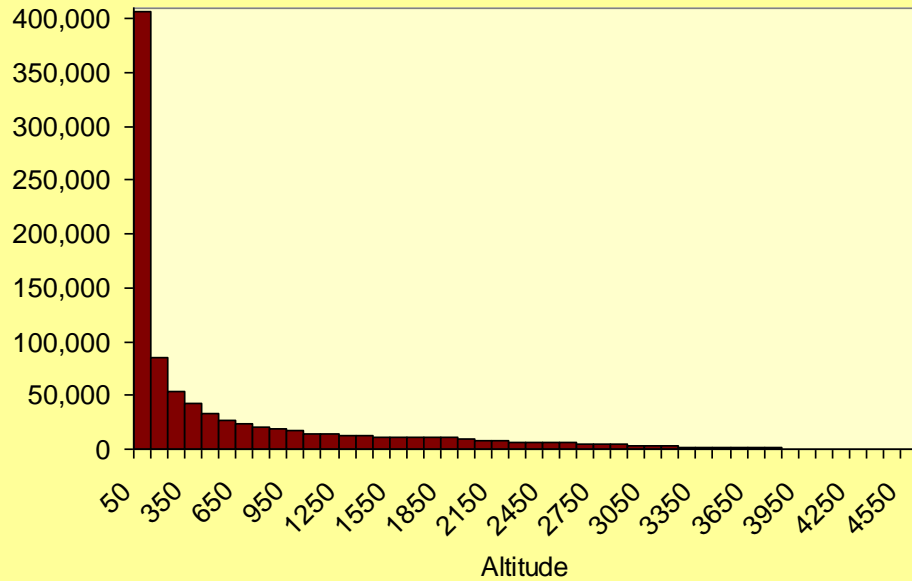




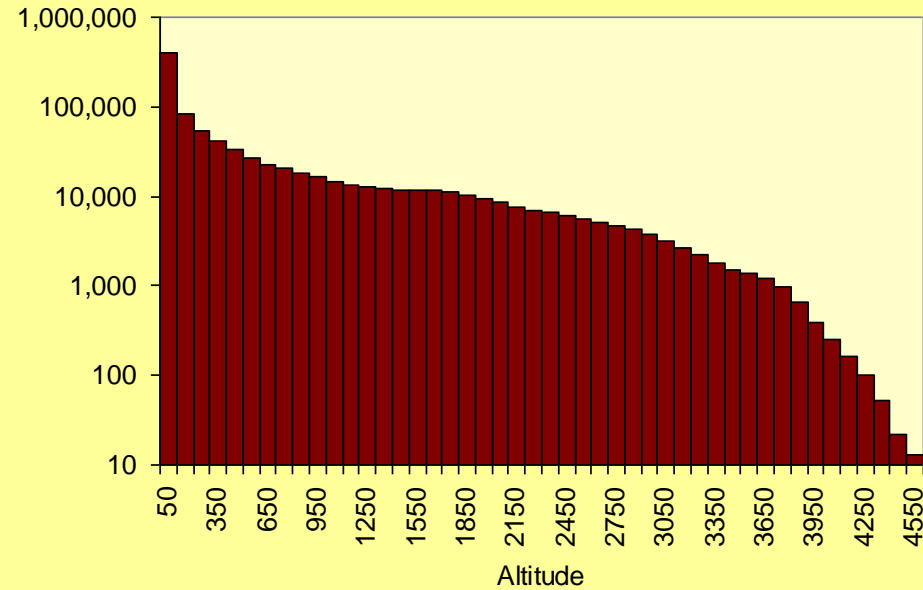
Land area decreases enormously with altitude:

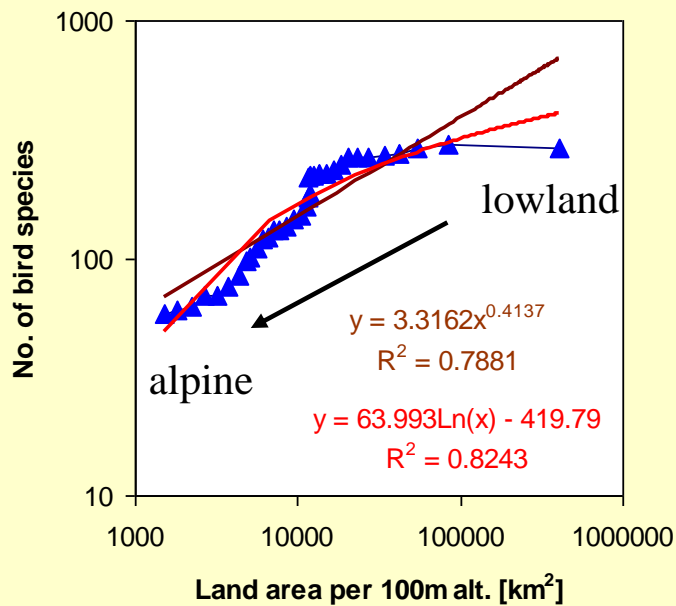
we need to consider species-area effect in all altitudinal patterns

New Guinea: Surface Area km<sup>2</sup>



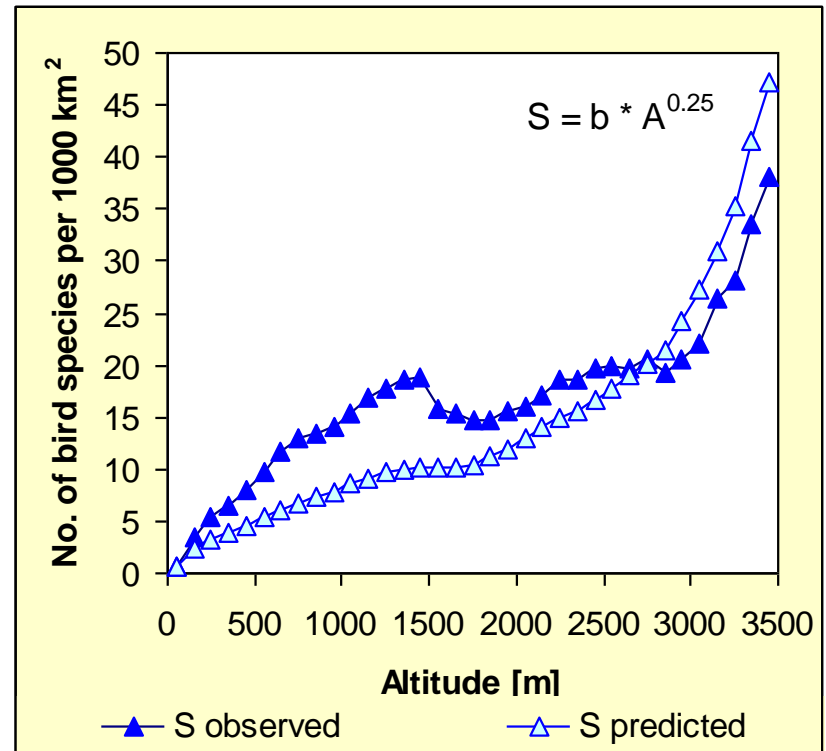
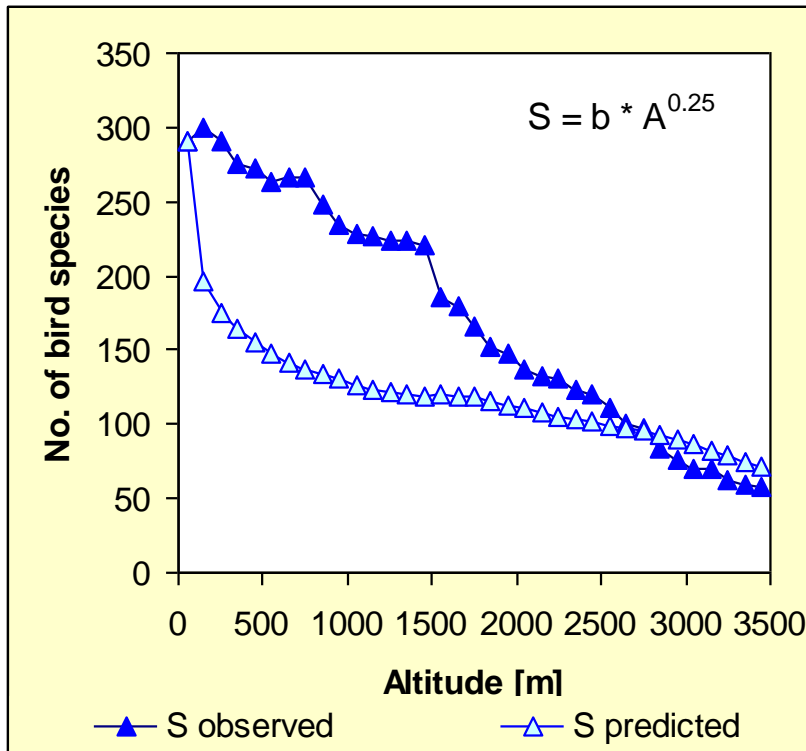
New Guinea: Surface Area km<sup>2</sup>





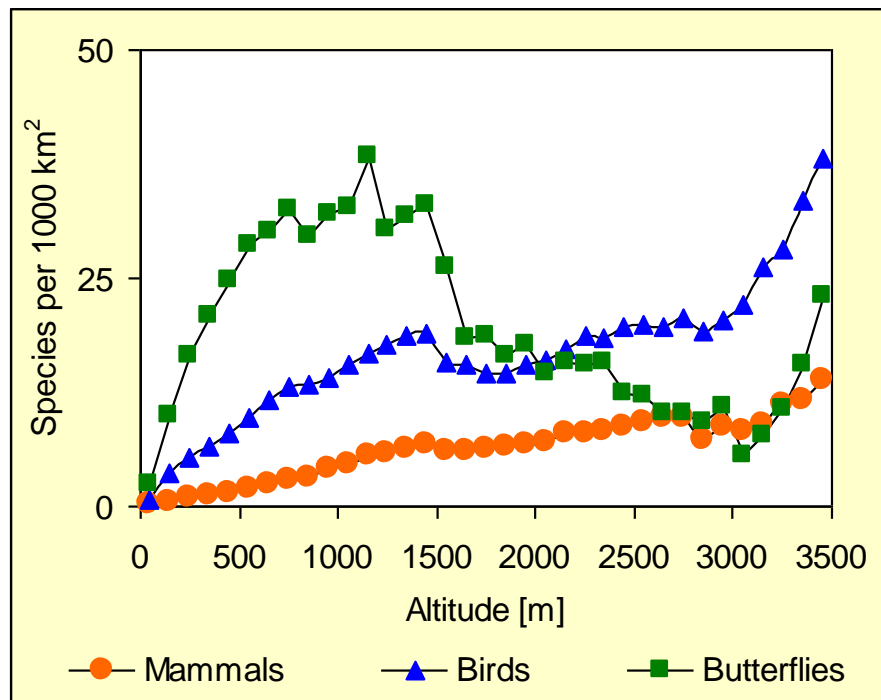
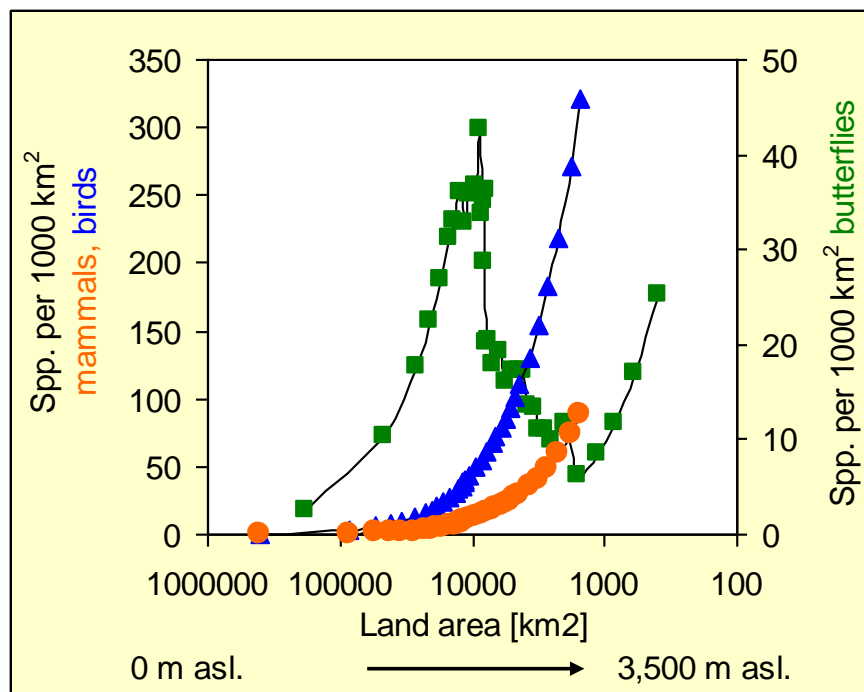
Species-area curves [power and logarithmic] fitted in altitudinal richness gradient: area alone predicts a strong diversity trend

Species-area curve  $S=b \cdot A^z$  with  $z=0.25$  and  $b$  estimated from lowland data used to predict altitudinal trends in species richness and density in birds



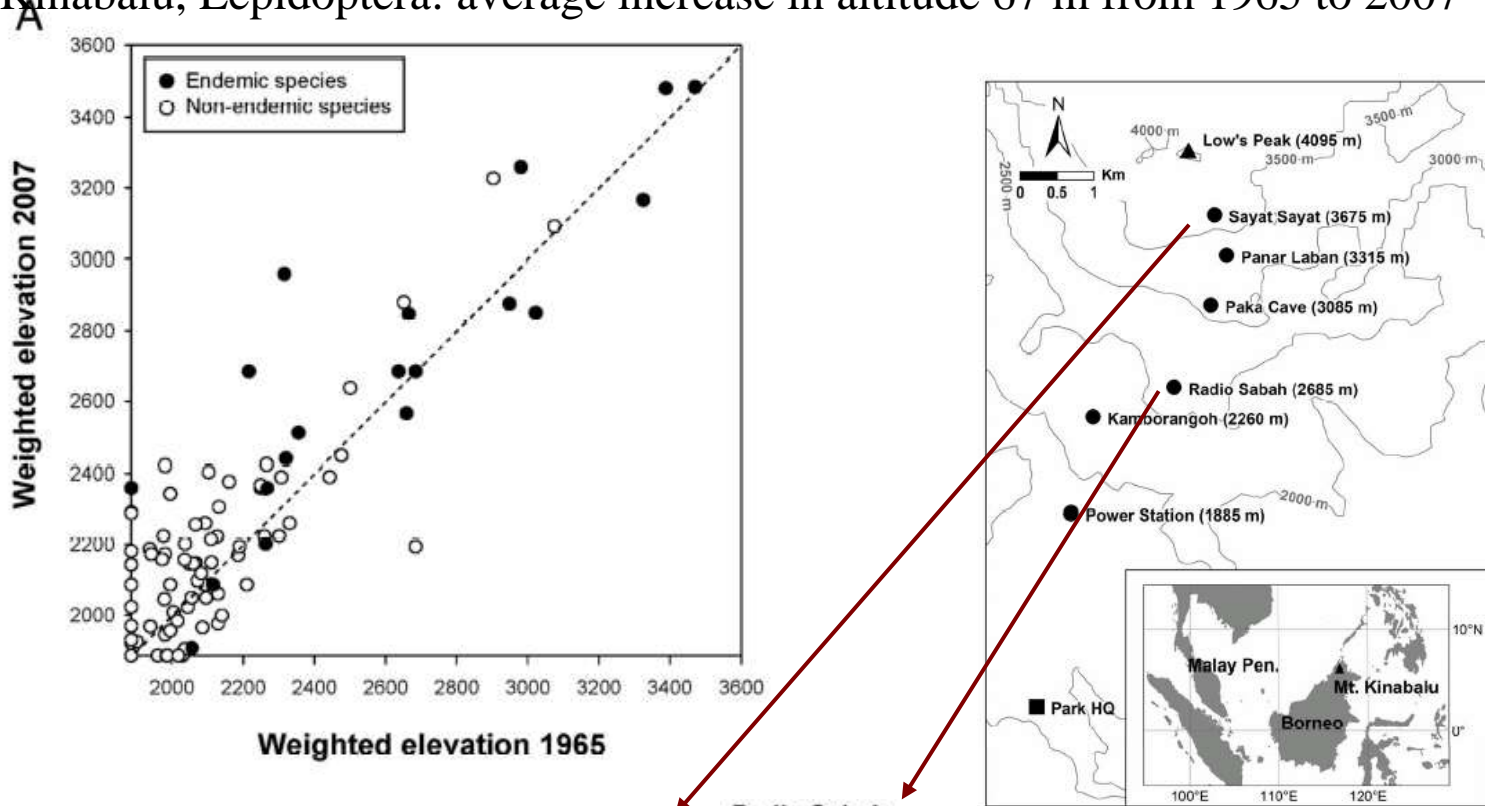
Species density:

typically [but not always] increases with altitude, as expected from a power species area relationship



# Climate change: species climbing up montane slopes

Mt. Kinabalu, Lepidoptera: average increase in altitude 67 m from 1965 to 2007



Sayat Sayat



1965



2007

Radio Sabah



1965

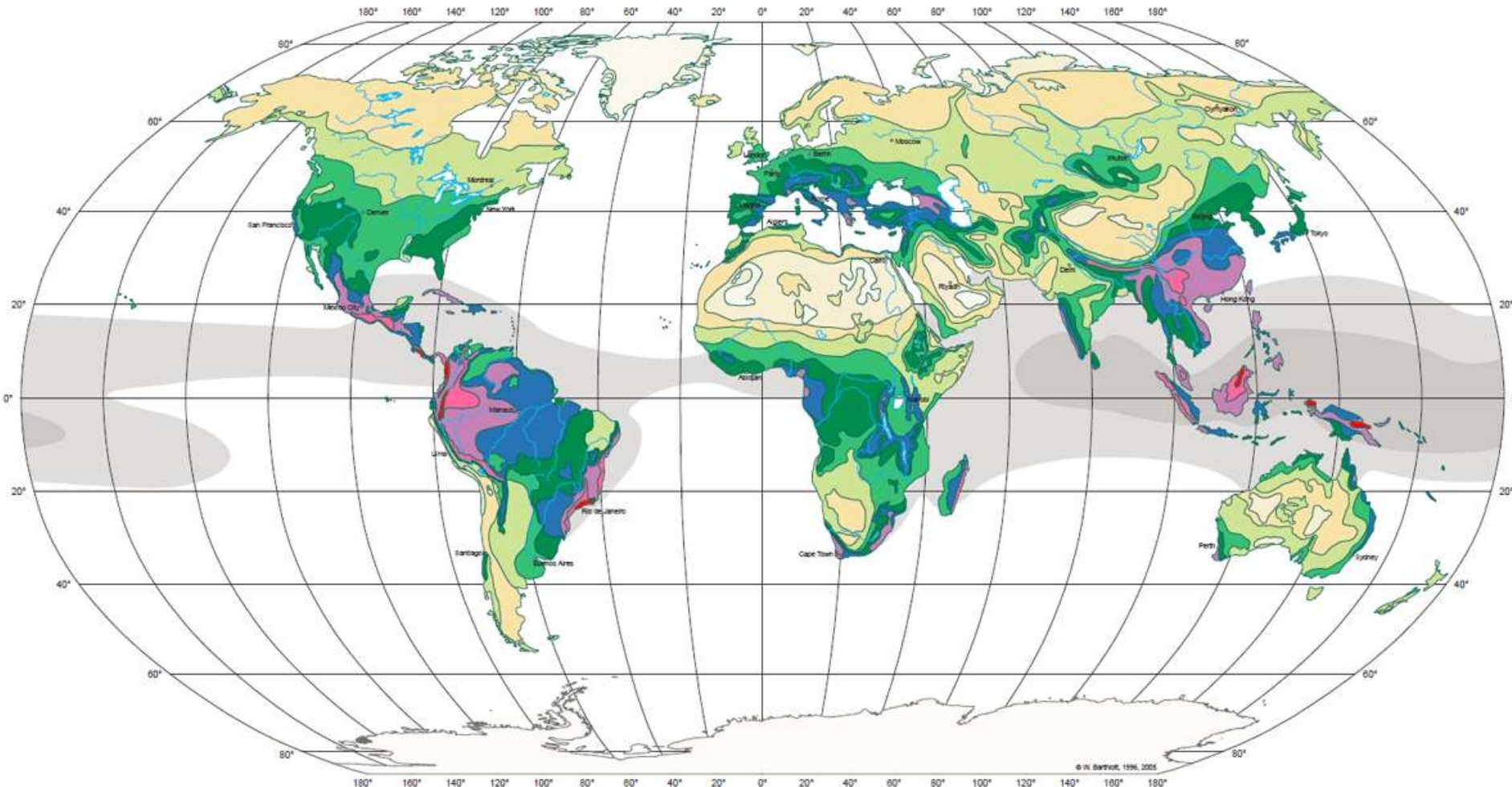


2007













# Altitudinal gradient: the mother of all environmental gradients



## GLOBAL BIODIVERSITY: SPECIES NUMBER OF VASCULAR PLANTS



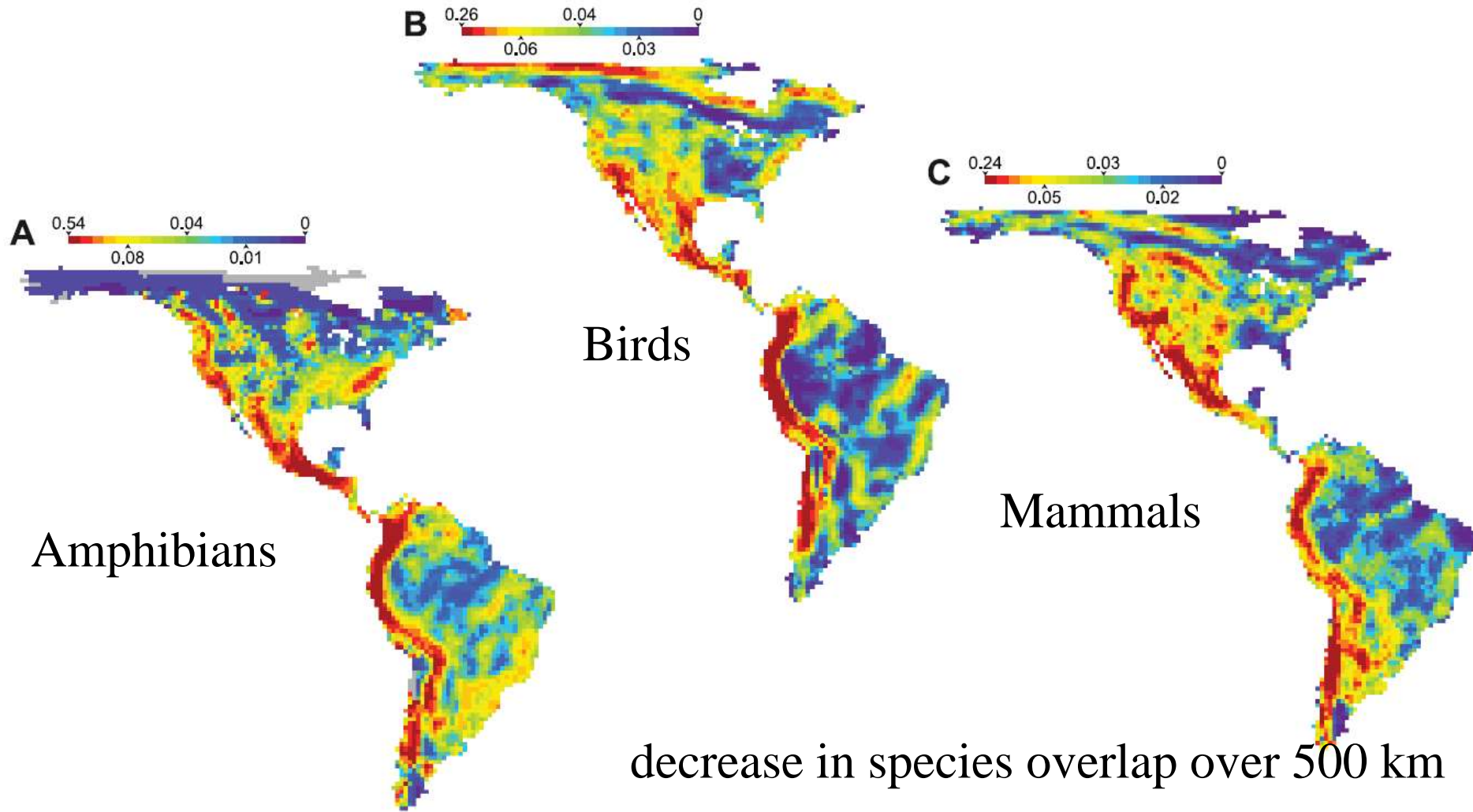
Diversity Zones (DZ): Number of species per 10 000 km<sup>2</sup>

 DZ 1 (<100)	 DZ 5 (1000 - 1500)	 DZ 9 (4000 - 5000)
 DZ 2 (100 - 200)	 DZ 6 (1500 - 2000)	 DZ 10 (>5000)
 DZ 3 (200 - 500)	 DZ 7 (2000 - 3000)	
 DZ 4 (500 - 1000)	 DZ 8 (3000 - 3500)	

sea surface temperature

	> 27°C
	> 29°C

# Altitudinal gradient: the mother of all environmental gradients



$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)}$$

**Figure 1.** Beta-Diversity of Amphibians, Birds, and Mammals Mapped Continuously across the Continental Western Hemisphere  
Beta-diversity ( $\beta_{sim-d}$ ) values for each taxon are divided into 20 quantiles, represented by warm (higher  $\beta_{sim-d}$ ) to cool (lower  $\beta_{sim-d}$ ) colors.