TROPICAL ECOLOGY

WBNZ-849

Tropical biodiversity:

Latitudinal Diversity Gradient

Krzysztof Wiąckowski

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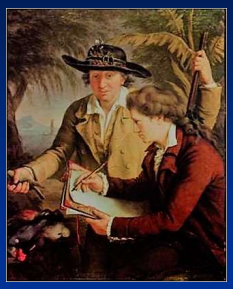
The first scientific description of the Latitudinal Diversity Gradient:



Johan Reinhold Forster a naturalist on James Cook's voyage around the world (1772 – 1775)

Johan R. Forster with his son Georg during Cook's expedition

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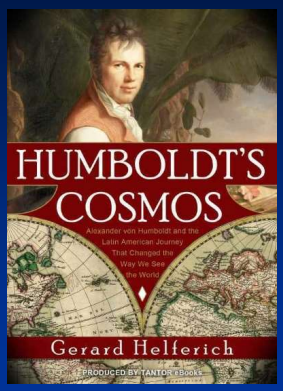

Kindle edition

The first extensive scientific exploration of tropical America (1799-1804) by Alexander von Humboldt and Aimé Bonpland

Wikipedia: By Alexrk translated by Cäsium137 (T.)

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Alexander von Humboldt in South America

His first impression after landing in the tropics illustrates well the difference between temperate and tropical diversity

A fragment of a letter Humboldt sent to his brother after landing in Cumaná, Venezuela:

"We are here in a divine country," Humboldt wrote his brother. "Wonderful plants; electric eels, jaguars, armadillos, monkeys, parrots; and many, many, real, half-savage Indians, a handsome and interesting race . . . What trees! . . . and what colours in birds, fish, even crayfish (sky-blue and yellow!). We rush around like the demented; in the first three days we were quite unable to classify anything; we pick up one object to throw it away for the next. Bonpland keeps telling me that he will go mad if the wonders do not cease soon."

Helferich, Gerard. Humboldt's Cosmos Tantor eBooks. Kindle Edition.

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Examples of amazing tree diversity in tropical rain forests

Source: Edward O. Wilson 2010. The Diversity of Life.

Peter Ashton discovered over 1,000 species on ten selected 1-hectare plots in Borneo — 700 native species are known from all of the US and Canada, in all major habitats .....

Alwyn Gentry found about 300 tree species in each of two 1-hectare plots in the rainforest near Iquitos, Peru — a world record for tree diversity at one site …

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Examples of insect diversity in tropical rain forests

Source: Edward O. Wilson 2010. The Diversity of Life.

429 butterfly species were recorded within twelve hours at one site in Brazil (the site has since been cleared for agriculture) — there are only about 440 species in all of eastern North America and 380 in Europe and the Mediterranean coast of North Africa combined.

43 ant species, belonging to 26 genera, were identified from a single tree at the Tambopata Reserve (Upper Peru) — This number approximately equals the entire ant fauna of the British Isles.

Erwin estimated that over 18,000 species of beetles occurred in 1 hectare of a Panamanian rainforest (most species previously unknown).
— To date, only 24,000 beetle species are known from all of the United States and Canada (and 290,000 from the entire world).

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BIRDS OF POLAND:
227 breeding species
(Tomiałojć and Stawarczyk 2003)

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Birds of Kenia (Zimmerman et al., 1999)
1089 species (almost 5 x more)

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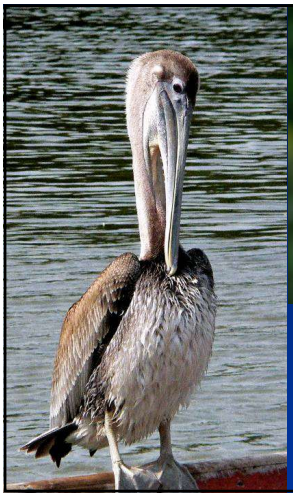

Birds of Venezuela (Hilty, 2003)
1382 species (more than 6 x more)

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A fragment of northern hemispheric gradient: number of breeding bird species in land areas of roughly similar sizes:

Greenland	56
Labrador	81
Newfoundland	118
New York State	195
Guatemala	469
Colombia	1 525

Edward O. Wilson 2010. The Diversity of Life. Penguin Books Ltd. Kindle Edition.

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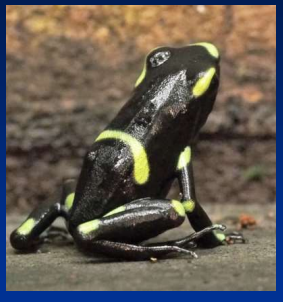

	Number of species	
	Amphibians	Reptiles
Poland	18	10
Costa Rica	190	228

Surface of Poland > 6 x larger

This applies almost without exception to all larger taxa

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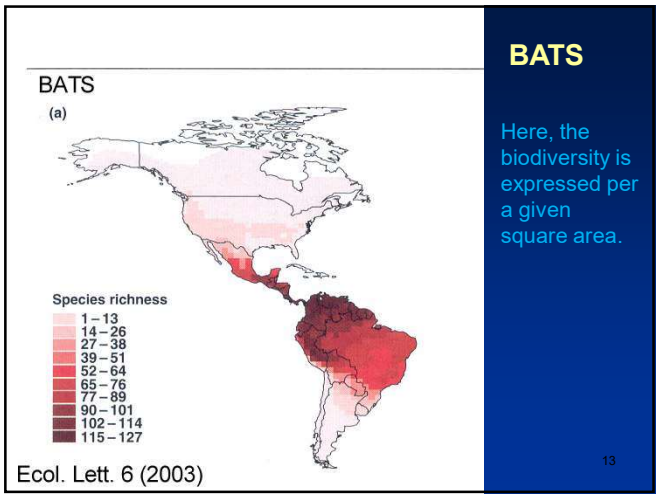

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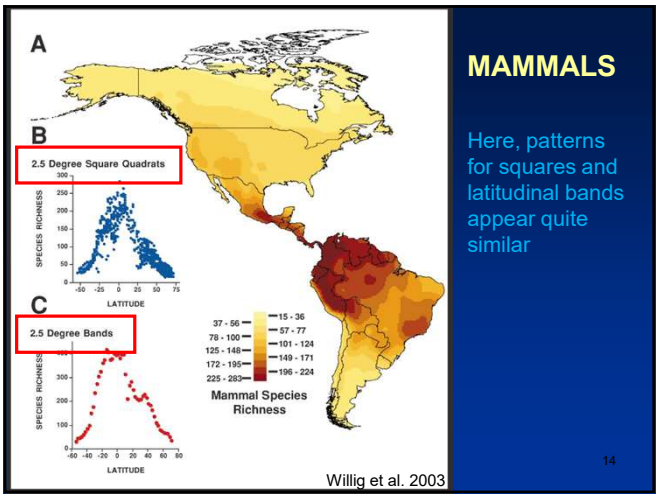

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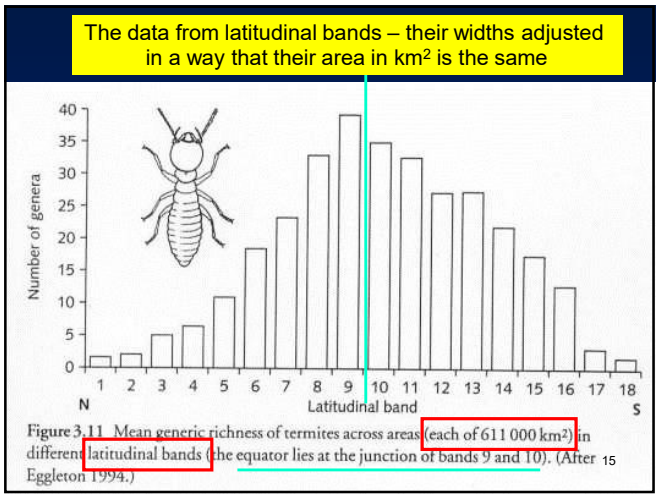

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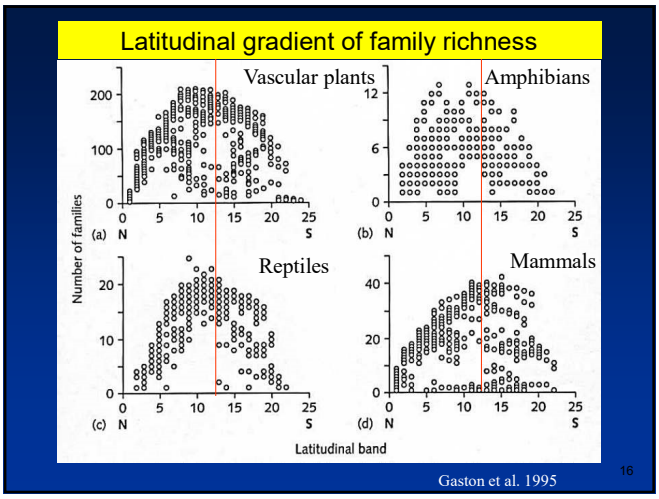

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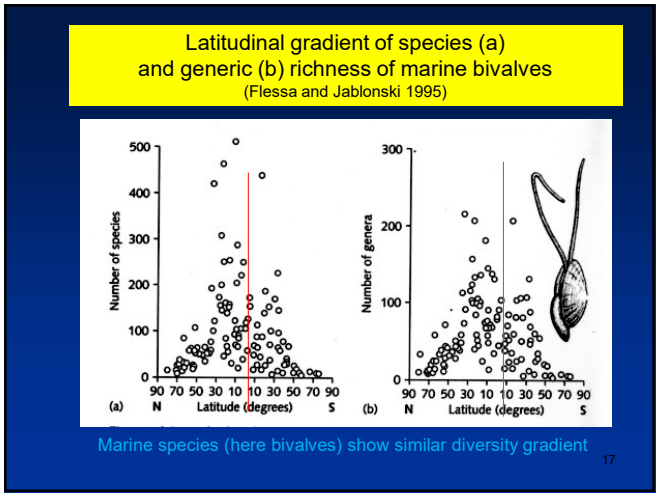

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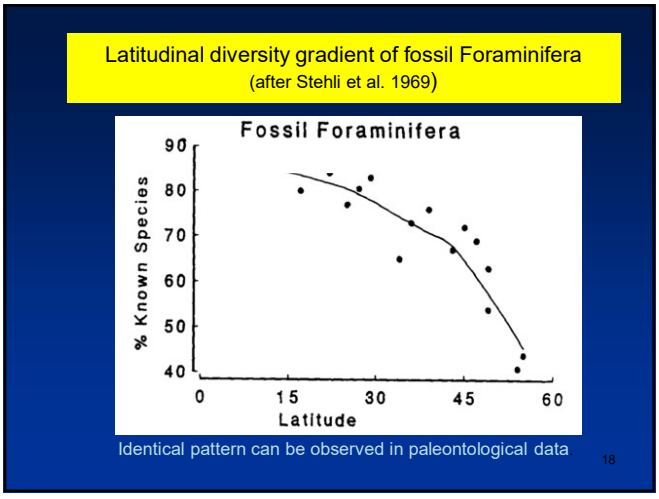

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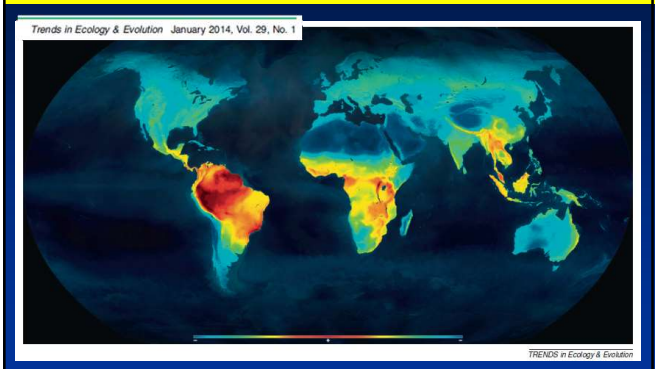
Modern day latitudinal biodiversity gradient of terrestrial vertebrates



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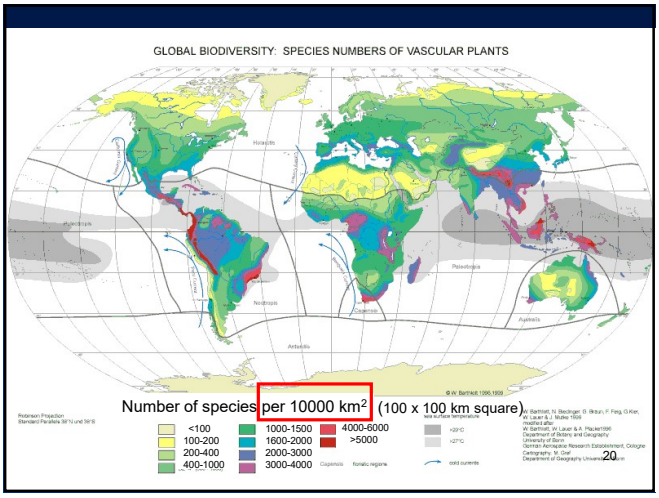

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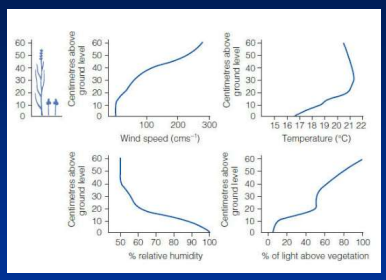
The animal diversity gradient can at least in part be a consequence of plant diversity

The effect of plants on microclimate



The structure of grassland vegetation and its effect upon the microclimate of the habitat …

Cox, C. Barry. Biogeography: An Ecological and Evolutionary Approach (p. 128). Wiley.

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Tropical rainforest

Santa Elena Reserve – Costa Rica

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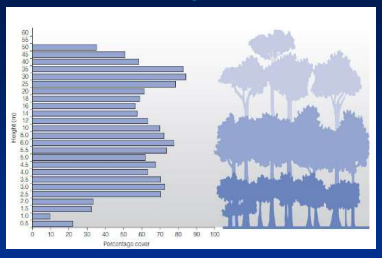
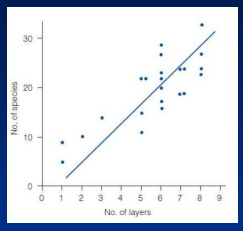
Profile of a tropical rainforest



The percentage leaf canopy cover at different heights above the ground. Note the stratification of the leaf cover into distinct layers.



The relationship between the number of bird species and the number of layers in the vegetation stratification.

Cox, C. Barry. Biogeography: An Ecological and Evolutionary Approach (p. 128). Wiley.

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There are some exceptions to the LDG

e.g., APHIDS – animals inversely correlated with plant diversity (4000 species, most of them live in the temperate zone)

Why aphids are not doing well in tropical forests?

Most aphid species feed on only one type of plant and are rather poor at locating them from a distance …

Picture: Kent Loeffler, Wikipedia
Public domain

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The great difficulty in studying LDG is the fact that most tropical species remain still unknown!

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EVERY YEAR NEW SPECIES OF BIRDS DISCOVERED

year	2010	2011	2012	2013
new sp.	5	3	7	24?

Formicivora grantsaui
BRASIL, 2007

Stiphrornis pyrrholaemus
GABON, 2008

Zosterops somadikartai,
TOGIAN ISLANDS, INDONESIA
2008

Orthotomus chaktomuk
CAMBODJA
2013

Jabouilleia naungmungensis
MYANMAR (BURMA), 2006

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„Lost World" – Foja Mts., Indonesia (New Guinea) 2005-2008
Dozens of new vertebrate species + many invertebrates

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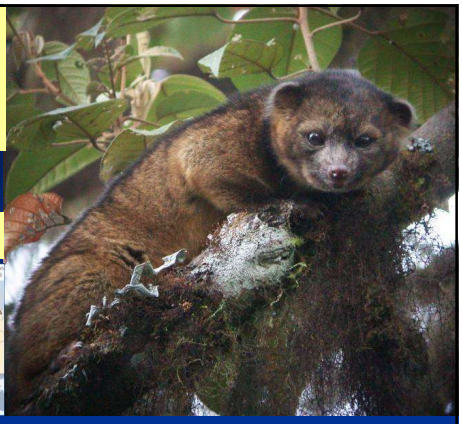
The Olinguito:
New mammal species discovered in 15 August 2013
first in a museum drawer and then found in the wild (Ecuador nad Colombia)

Bassaricyon neblina
(Procyonidae)



an arboreal carnivore mammal from the racoon family

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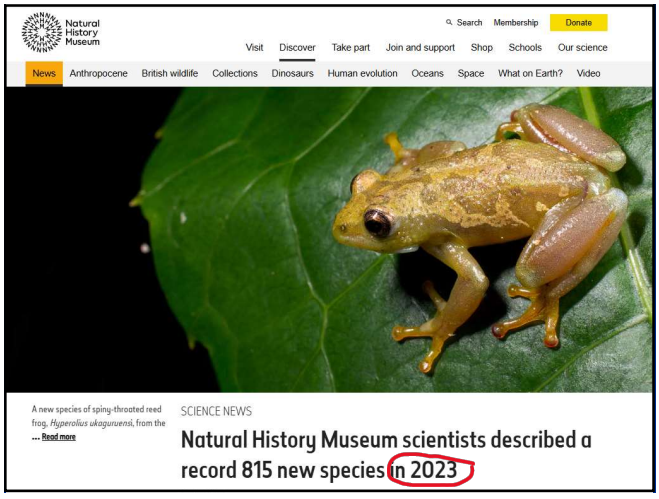

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EXAMPLES OF NEW SPECIES DISCOVERED IN 2023

Six new species of pygmy chameleons in Tanzania

A new species of spiny-throated frog in Tanzania

Five new species of snail-eating snakes in S. America

Three new Nautilus species in the Coral Sea

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A problem:

Latitudinal diversity gradient is a strongly confirmed phenomenon, although we do not know the total species diversity on the Earth …

In particular, the tropics are the least known areas …

We can only try to make estimations …

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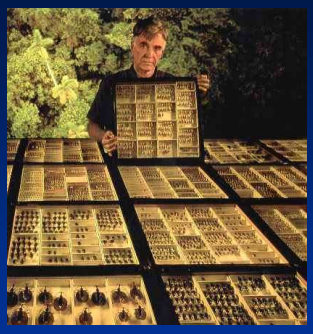

Terry L. Erwin

a curator at the
Dept. of Enthomology
National Museum
of Natural History
Smithsonian Institution
Washington DC

The first attempt to estimate the actual number of species (a scientific guess)

Tropical forests: Their richness in Coleoptera and other arthropod species, The Coleopterists Bulletin 36: 74–75 (1982)

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ERWIN'S ESTIMATE OF THE TOTAL SPECIES RICHNESS

19 trees *Luehea seemani* (Panama) fumigated
species of beetles collected **1 200**

Assumption 1: Average specifity of beetles = 13.5%
ergo: No. of specialised species per tree species **163**

Assumption 2: 50000 tree species are known from rainforests, each tree has specialized beetle species
ergo: total No. of specialised species **8 150 000**

Assumption 3: Beetles make up 40% species of Arthropods
ergo: No. of all arthropod species ..... **20 mln**

Assumption 4: 2 × more species in tree canopies than on forest floor
ergo: total No. of Arthropod species in rainforests ..... **30 mln**

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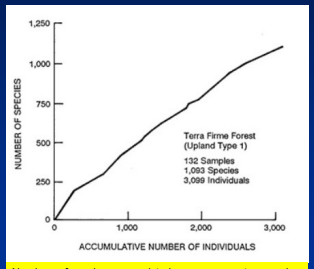
Biodiversity
Editors: E.O. Wilson and Frances M. Peter. 1988.
Washington (DC): National Academies Press (US);
ISBN-10: 0-309-03783-2ISBN-10: 0-309-03739-5

Chapter 13 The Tropical Forest Canopy. The Heart of Biotic Diversity (TERRY L. ERWIN)



Numbers of species accumulated per square meter sample in 12-meter-square plot (119 square meters sampled) in Upland Forest Type I at Tambopata Reserved Zone, Peru.

Most of the canopy beetles are 2-3-millimeter long.

Agra arrowi Liebke, a member of the top predatory carabid beetle group in tropical forest canopies.

https://www.ncbi.nlm.nih.gov/books/NBK219277/

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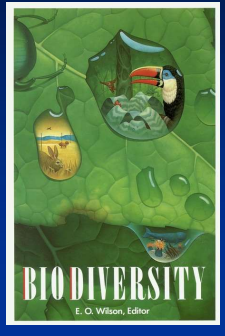

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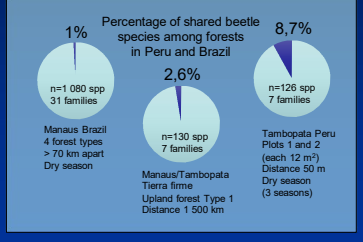

https://www.ncbi.nlm.nih.gov/books/NBK219277/

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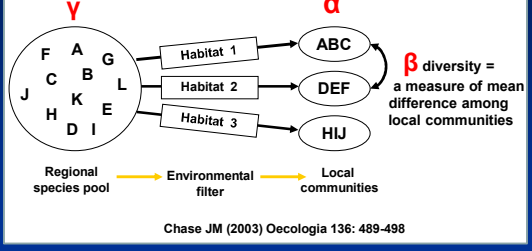
Species diversity (richness) measured
at various spatial scales (α, γ, β diversity)

γ diversity = number of species in a region consisting of numerous local communities

α diversity = number of species in a local community



Chase JM (2003) Oecologia 136: 489-498

Since in tropical rainforests both alfa and beta diversity are very high, consequently the regional species richness is very high

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HISTORY OF THE RESEARCH CONCERNING THE GEOGRAPHY OF SPECIES DIVERSITY

- Humboldt 1808
- Wallace 1878
- Dobzhanski 1950
- Hutchinson 1959
- MacArthur (et al.) 1965, 1969, 1972
- Pianka 1966

New papers are being constantly published: 322 papers in 2017-2023 with LDG or LBG keywords in *Web-of-Science*

MORE RECENT REVIEWS (WITH NEW HYPOTHESES)

- Rosenzweig 1992
- Brown 1988
- Currie 1991
- Rohde 1992
- Wright, Currie & Maurer 1993
- Turner, Lennon & Greenwood 1996
- Fraser & Currie 1996
- Rohde 1999
- Kaspari et al. 2000
- Willig et al. 2003
- Turner 2004
- Hillebrand 2004
- Mittelbach et al. 2007
- Quian 2010
- Brown 2014
- Usinowicz 2017

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Characteristic and discouraging statements (or conclusions) from important review papers

- **Pianka's (1966) review concludes by suggesting that all of the numerous mechanisms he lists operate at some spatial scales.**
- **Krebs's (1994) concludes that all of these hypotheses operate in some situations, but that history, climate and disturbance "seem most important".**
- **Begon, Harper and Townsend (1996) simply concluded that, "for most of these generalizations important exceptions can be found, and for most of them current explanations are not entirely adequate".**
- **Mittelbach et al. (2007) "A latitudinal gradient in biodiversity has existed since before the time of the dinosaurs, yet how and why this gradient arose remains unresolved".**
- **Belmaker and Jetz (2015) "Despite dedicated research, there is still no consensus on the determinants of broad-scale diversity gradients"**

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The multitude of potential factors can be reduced to four distinct explanations:

- **Solar radiation**
- **Climatic stability**
- **Duration (tropics are older)**
- **Surface area**

All ultimately associated with the spherical shape of the Earth!

Mark V. Lomolino (2020) Biogeography: a very short introduction. Oxford University Press

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Solar radiation: tropics benefit from more intense light and heat energy …

1. **Higher primary production, hence more animals (herbivores, carnivores …)**
2. **Higher temperature accelerates growth rate, hence shorter generation times …**
3. **More intense UV radiation – higher mutation rate …**
4. **Factors 2 and 3 combined potentially speed up evolution in the tropics …** (higher speciation rate … more species)

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Climatic stability: the lowest annual (and longer time) amplitudes are in the tropics

1. **Seasons are much less apparent across the surfaces most perpendicular to the sun — the tropics**
2. **Aseasonal climatic conditions may lead to a higher diversity by affecting interspecific interactions** (some examples later on)
3. **More stable conditions allow the evolution of more specialized niches (e.g., by disruptive selection)** (hence more species can be „packed" into the same area)

Why and when more specialized species have advantage over so called generalists?

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Tropics are older:

In contrast to the areas at higher latitudes, those in the Tropics today, have been in the Tropics for a much longer time …

1. **Natural selection had more time in the tropics for differentiation and speciation**
2. **More time allowed accumulating more species by evolution and/or by immigration …**
3. **Since tropics cover larger part of the globe, randomly drifting continents must have been spending more time under tropical conditions …**

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Surface area: Tropical land masses and oceans are larger

1. **Larger areas provide greater variety of resources, habitats, and potential niches …**
   hence can accommodate more species
2. **Can support larger populations, hence less likely to suffer extinctions …**
   Why extinction is more probable for small populations?
3. Have usually more barriers for dispersal (mountains, large rivers …) – which stimulates speciation

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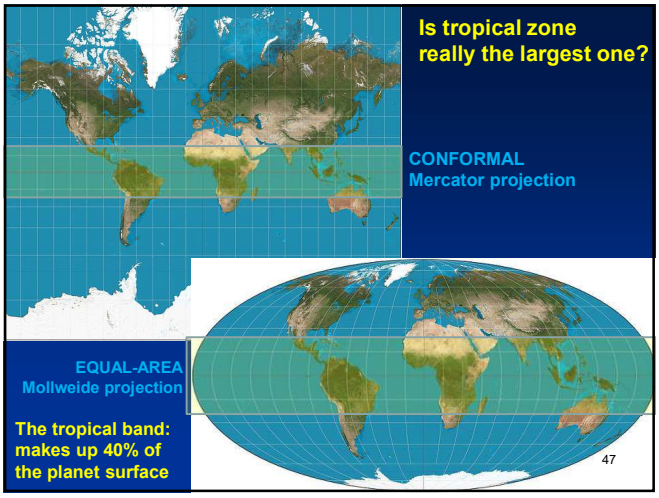

Is tropical zone really the largest one?

CONFORMAL Mercator projection

EQUAL-AREA Mollweide projection

The tropical band: makes up 40% of the planet surface

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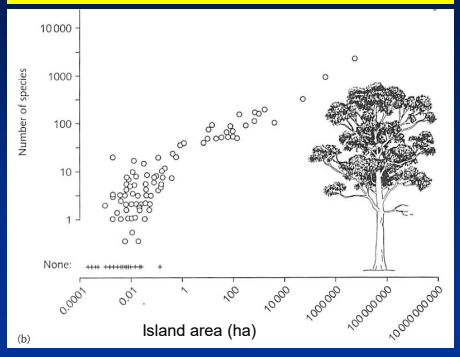
THE EFFECT OF THE AREA CAN BE BEST OBSERVED ON ISLANDS
e.g., number of tree species in relation to island area (Australia)



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LARGER AREAS OF RAINFORESTS HAVE MORE PRIMATE SPECIES

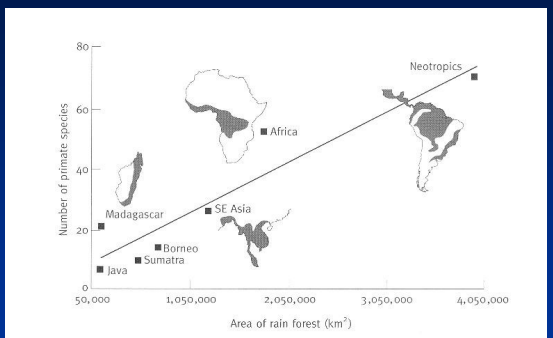

Fig. 3.3 Larger areas of rain forest have more primate species. (From Reed & Fleagle 1995.)

Primack i Corlett 2005) 49

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A digression:

Is the Earth spherical or flat?

The question is not absurd one for some people. The Flat-Earth Society has members all around the globe …

Flag of the United Nations

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Is the Earth spherical or flat?

Wikipedia, Creative Commons

World airline flight route map: one of the arguments used against the spherical Earth concept …

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Is water surface indeed always flat?

55

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The latitudinal diversity gradient, and its explanations, show the Earth must be a sphere

On a flat Earth:

- ❑ **There would be no Tropics at all …** (no insolation gradient on a flat surface)
- ❑ **There would be no seasonal differences …**
- ❑ **Randomly drifting continents would statistically spend the same time at each latitude**

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Examples of specific hypotheses or mechanisms proposed to explain latitudinal diversity gradient

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Historical hypotheses:

The LDG is a result of past geological, climatic and evolutionary events, most of which occurred millions of years ago …

Contemporary patterns of biodiversity cannot be understood by focusing only on contemporary ecological mechanisms

Some hypotheses assume the current state is not at equilibrium, i.e., there has not been sufficient time for animals and plants to disperse and adapt to the temperate habitats that became available after glaciation … (e.g., Center-of-origin and Time-for-speciation)

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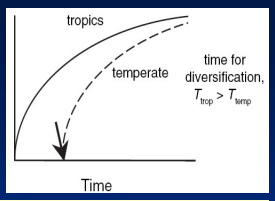
Two similar hypotheses propose historical mechanisms for gradients of species richness:

Centre of origin hypothesis
(Hennig 1979; Ricklefs & Schluter 1993)

Time for speciation
(Stephens & Wiens 2003)



Basic assumptions:

- ❑ Species originate in particular area and this affects their geographical distributions.
- ❑ The area occupied by the ancestor monophyletic group represents its centre of origin
- ❑ Diversification results from speciation and dispersion of new taxa away from the centre of origin.
- ❑ A diversity gradient develops: species richness is greatest at the centre of the range (where natural selection had more time) and decreases toward the periphery.
- ❑ Fossils provide evidence that indeed most lineages evolved in the tropics …

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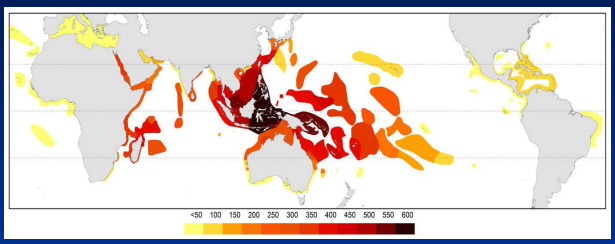
Pattern of global diversity of coral species

An example of „Center of origin – Center of diversity" concept?



Veron J.E.N., Stafford-Smith M.G., Turak E. and DeVantier L.M. (2016). **Corals of the World**. Accessed 24 Oct 2019.
http://www.coralsoftheworld.org/page/overview-of-coral-distributions/

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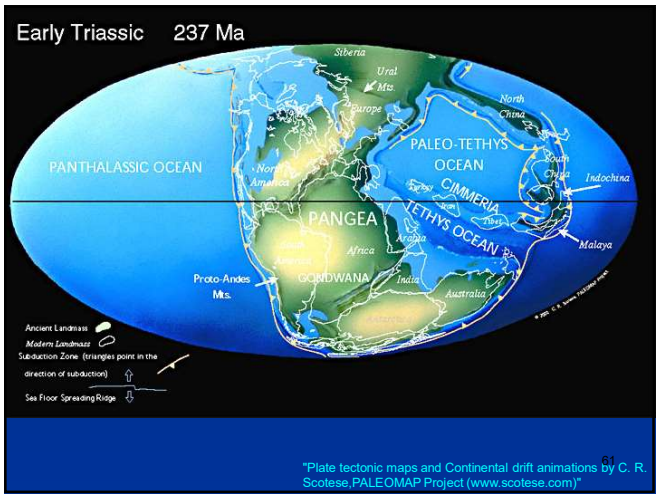

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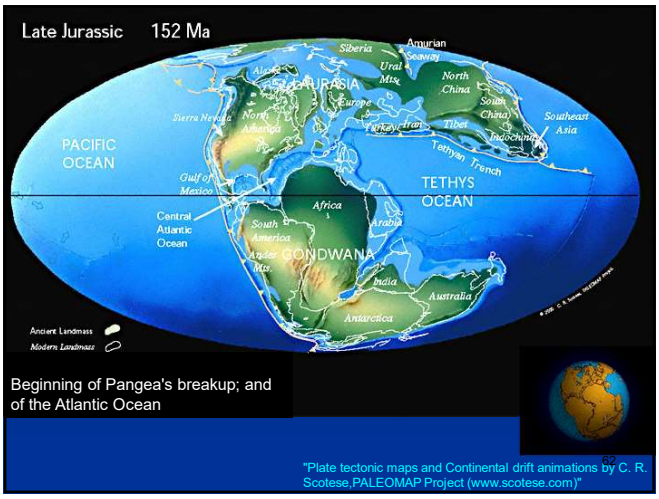

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Other Historical hypotheses:

Suggest that the LDG reflects a long-lasting, approximately steady-state relationship between abiotic conditions on Earth and evolutionary processes shaping biodiversity

e.g. „Out-of-the-Tropics" hypothesis

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Tropics as Cradle or Museum?

- **Cradle:** speciation rates in the tropics are higher than in other climatic zones.
- **Museum**: extinction rates in the tropics are lower than anywhere else.
- Or perhaps both at the same time? („**Out of the tropics**" hypothesis)

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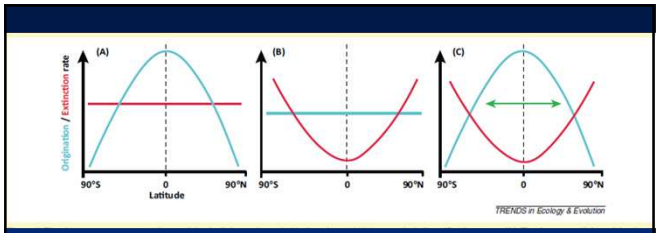

A. „Tropics as **THE CRADLE**": origination rates higher in the tropics

B. „Tropics as **THE MUSEUM**: extinction rates lower in the tropics

C. „**OUT of the tropics**": Origination faster, extinction lower, species disperse from the tropics to higher lattitudes …

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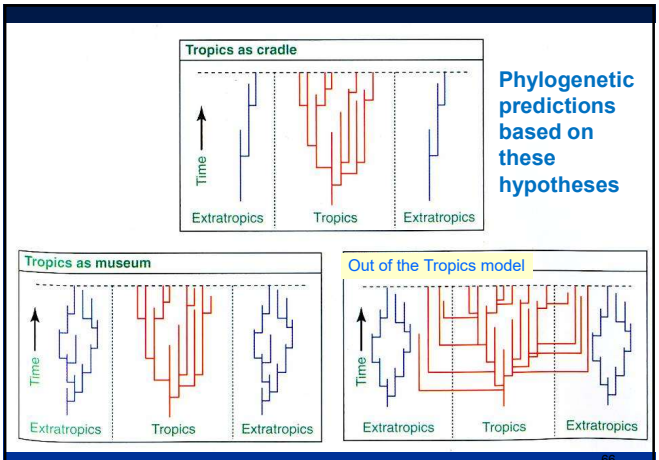

Phylogenetic predictions based on these hypotheses

Kricher 2011; 4.14

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Such models give different predictions but can they be verified?

Predictions derived from the Centre-of-origin hypothesis:

(1) Species richness declines toward the periphery of the range of a higher taxon;

(2) Taxa are more derived toward the periphery than the centre (average sequence distance from the ancestors is higher …)

(3) The average taxa age is lower toward the periphery than the centre;

(4) Ages and measures of derivedness are less variable toward the periphery of the range of a higher taxon …

Molecular methods allow now to verify such predictions

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An analysis of phylogenetic features of bat assemblages along latitudinal diversity gradient

Bat family Phyllostomidae represents a highly diverse group with approximately 53 genera and 141 spp.

(more than half of all bats found in the continental New World)

Stevens R.D. (2006)
Historical processes enhance patterns of diversity along latitudinal gradients. *Proc. R. Soc. B* 273: 2283–2289

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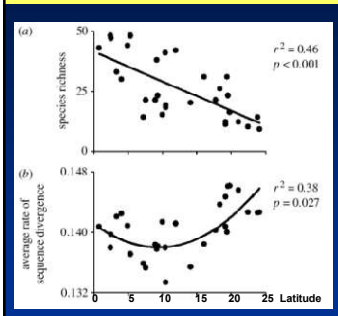
Results: This data support the idea that bats evolved in the tropical zone and later dispersed outside the tropics



Species richness clearly declines towards higher latitudes

The further away from the equator, the greater the sequence difference from the ancestor.

Dispersing species must adapt to new different conditions (faster diversification)

Stevens R.D. (2006)
Historical processes enhance patterns of diversity along latitudinal gradients. *Proc. R. Soc. B* 273: 2283–2289

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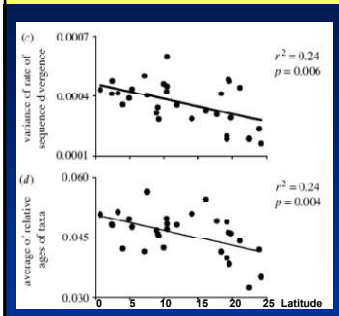
Results: This data support the idea that bats evolved in the tropical zone and later dispersed outside the tropics



The variance of the rate of sequence divergence declines toward the edge, (derived species dominate the range periphery, while both derived and primitive are at the centre) …

The youngest taxa are most far away from the equator (less time for speciation toward higher latitudes)

Stevens R.D. (2006)
Historical processes enhance patterns of diversity along latitudinal gradients. *Proc. R. Soc. B* 273: 2283–2289

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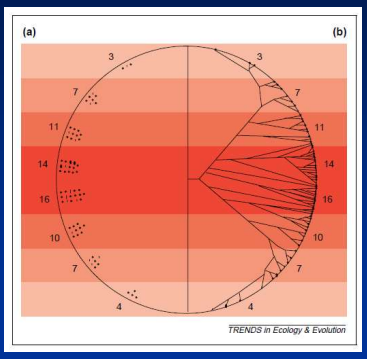
Comparison of reconstructed phylogenies of the lineages from latitude gradient allows verification of the predictions generated by hypotheses



Wiens & Donoghue 2004

An example:

- **Temperate lineages are usually late branches of tropical taxa**
- **Usually shallower differentiation between lineages in temperate climate areas …**

The example supports the „Out of the tropics" hypothesis

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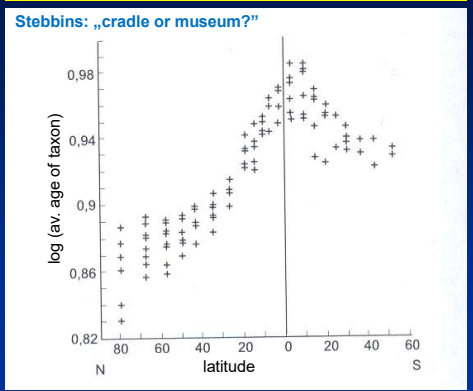
Average age of avian taxa in relation to latitude

Stebbins: „cradle or museum?"



Weiner 2003 — from Gaston & Blackburne 1996

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The rate of evolution hypothesis

- The rate of speciation is supposed to increase with temperature and solar radiation intensity:
  - higher rate of biochemical reactions
  - more free radicals
  - higher mutation rate
  - shorter generation time
  - stronger selection pressure

  (Rohde 1992)
- Recent study on a very large data base does not support this hypothesis

Orton et al. (2019) Is molecular evolution faster in the tropics? Heredity: 122: 513-524

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Is evolution „more creative" in the tropics?

Theodosius Dobzhansky

- The process of adaptation in the northern zone is primarily coping with the harsh physical environment and securing food
- Abiotic factors cause similar adaptations
- Evolution in the tropics is more about species interactions, coevolution, and mutualism than adaptations to the physical environment
- Biotic interactions cause more diversity, for example:
  - plant-herbivore interactions
  - predator-prey interactions
  - mutualistic interaction in competitive environment
- **Consequently, species living in more species-rich communities are exposed to more diverse selection pressures …** (diversity generates diversity?)

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Environmental energy

or „methabolic hypothesis" (Turner)

- Number of animal species (S) correlates with temperature and actual evapotranspiration
- Thermal conditions in tropical rainforests are stable and close to thermoneutrality …
- Individual energy budget of homeothermic animals is less loaded, enabling more expensive specializations (and/or more species in the same habitat) …

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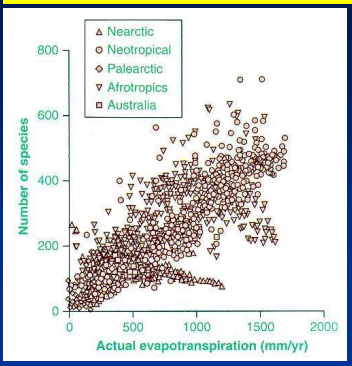
Productivity hypothesis



Kricher 2011, 4.21

Numerous examples show positive correlation of species richness with primary production PP or actual evapotranspiration (AET)

Here: avian biodiversity increases with actual evapotranspitration

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Productivity hypothesis

Tropical habitats due to higher PP can maintain more species

- **How to explain the possible mechanism?**
- **Why there are more species in a productive ecosystem and not just a larger abundance and biomass of the same species?**

Several possible explanations have been proposed:

- **More individuals hypothesis**
- **More specialization**
- **Dynamic equilibrium model**
- **One more trophic level**

Brown J.H. (2014) Why are there so many species in the tropics? J. Biogeogr. 41: 8–22

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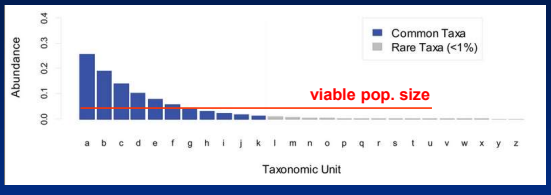
More-Individuals-Hypothesis



- **Typical species rank abundance distribution**
- **A viable population size concept …**
- **If higher productivity increases abundances of all species, more species would be above the viable population size …**

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More-Specialization

- Productivity is a sum of a variety of resources
- To support a specialist species a minimum amount of a given resource type is needed …
- At lower productivities some resources types are too rare to support a specialist species
- Higher productivity increases the amount of each resource type, hence more resource types support more specialist species

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Dynamic equilibrium models

- Higher productivity results in faster population growth rates
- Faster growth rates allow rapid recovery of population abundances after disturbances
- Populations with low abundances are more likely to go extinct
- Therefore, more productive communities have a higher equilibrium number of species …

(as long as the rate of disturbances prevents populations from becoming so abundant that competitive exclusion occurs)

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One More Trophic Level

- The number of trophic levels in a food web is limited by available energy
- Higher productivity results in longer food chains…
- Additional (higher) trophic level reduces population abundances below …
- Competitive exclusion is less likely with reduced population sizes
- Therefore, diversity increases with productivity (thanks to predators)

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Rapoport's rule

- Species geographical ranges are usually smaller closer to the equator
- Mechanism: in order to survive in seasonal climate species have to posses wider tolerance ranges due to the wide annual amplitude of physical factors
- This characteristic allows wider dispersion and facilitates overcoming geographical barriers (hence larger geographical ranges)
- Tropical species (living in mild and stable conditions) do not need adaptations to a wide range of physical condition
- Consequently, are more restricted in their latitudinal distribution (smaller geographical ranges)

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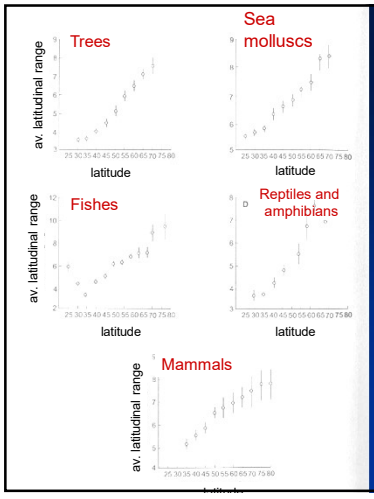

Rapoport's rule

Average latitudinal ranges of the taxa with the centres of distribution more distant from the equator are wider

from Stevens 1989; Weiner 2003

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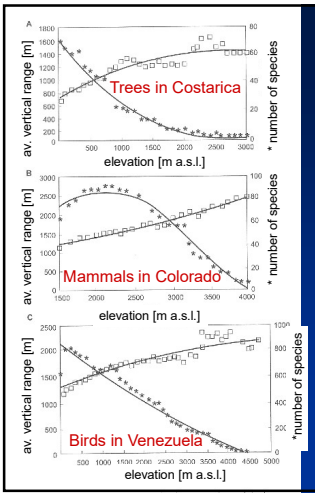

Rapoport's rule on elevation gradient

Vertical ranges of species are larger if their centre is located at higher elevation asl (squares)

With increasing elevation the numer of species decreases (stars)

Daniel Janzen (1967) "Mountain passes are higher in the tropics"

Stevens 1992; Weiner 2003

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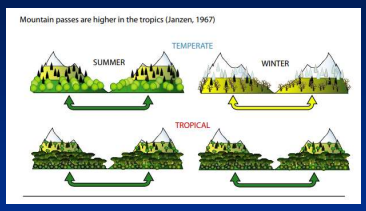
Are mountain passes higher in the tropics?



Rapoport's rule in short:

Compared to higher latitudes, tropical species are restricted to smaller geographic areas and narrower ranges of abiotic conditions.

This leads to a stronger genetic isolation and diversification (and higher species diversity).

Brown J.H. (2014) Why are there so many species in the tropics? J. Biogeogr. 41: 8–22

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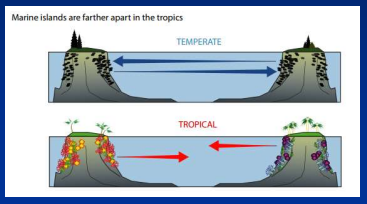
Why benthic (living on the bottom) marine invertebrates have more restricted geographic distributions compared to the species from colder areas?

Are marine Islands farther apart in the tropics?

- ❑ Most benthic marine invertebrates posses planktonic larvae that ensure dispersion making it possible to colonize new environments …
- ❑ Larvae drift in water column, carried by water currents, before settling down on the bottom and beginning the adult benthic phase …



Why planktonic larvae travel shorter distances in the tropics?

Brown J.H. (2014) Why Marine Islands Are Farther Apart in the Tropics. Am. Nat. 183: 842-846

Brown J.H. (2014) Why are there so many species in the tropics? J. Biogeogr. 41: 8–22

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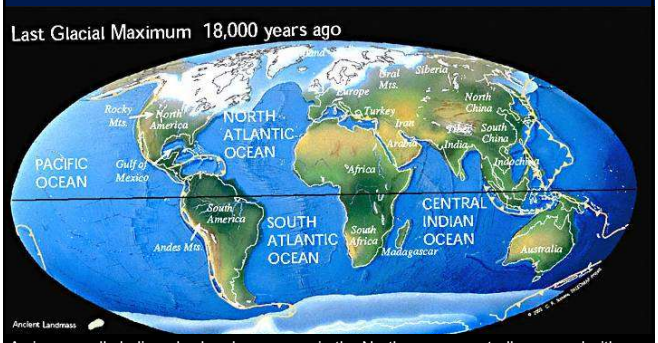
REFUGIA HYPOTHESIS



As is generally believed, when large areas in the North were repeatedly covered with thick layers of the ice during glaciations, the climate in the tropical zone did not change substantially. Hence the tropical biota had much longer uninterrupted time for development and speciation.

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REFUGIA HYPOTHESIS

Presumed changes of the Amazon rainforest extent during Pleistocene glaciations

RECENT PLEISTOCENE GLACIATIONS

Jürgen Haffer's hypothesis: During glacial periods, the Amazonian rainforest repeatedly shrunk into isolated fragments, which extended and joined again in interglacial periods. This stimulated divergence and speciation leading to today's species richness

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REFUGIA HYPOTHESIS

The centers of endemism (are presumed forest refugia during the dry phases of the Pleistocene)

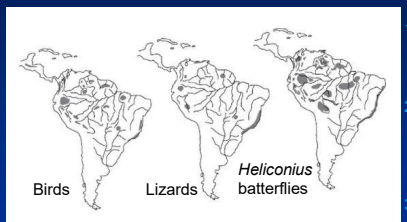

Figure 2-20 from: Kricher (2011) Tropical Ecology Princeton University Press. Kindle Edition

Criticism of the refugia model:

1) Centres of endemism of various taxa do not coincide…

2) Modern Pollen analyses from Amazonian lakes do not confirm such climatic changes …

3) Some centres of plant endemism turned out to be artefacts due to uneven plant sampling for herbaria …

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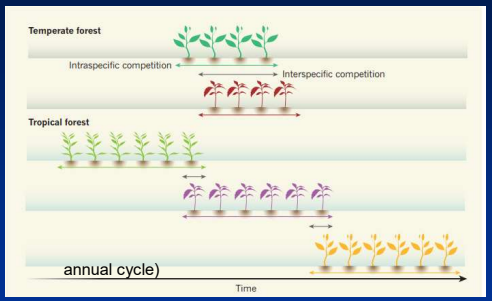
Can lack of seasonality promote species coexistence in tropical forests?



Short growing season: strong both itra- and interspecific competition

Long growing season: the intraspecific competition is stronger than interspecific competition

Gary G. Mittelbach 2017
A matter of time for tropical diversity
Nature

colours denote different species

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