Biodiversity in Tropical Rain Forests

Defining and measuring diversity across scales

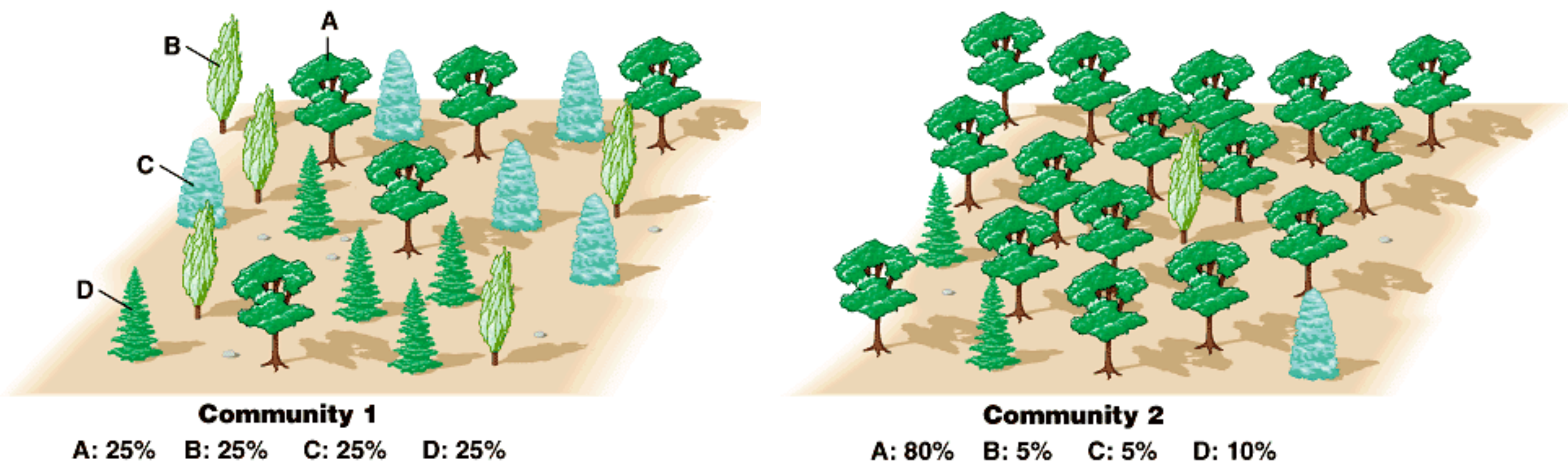
Species diversity gradients and hypotheses

Models for maintenance of diversity

Measuring Diversity

Species richness is the number of species in an ecosystem, or how many different species of a particular group inhabit a specific area

Species diversity measures incorporate the number of species and their relative abundances (evenness)

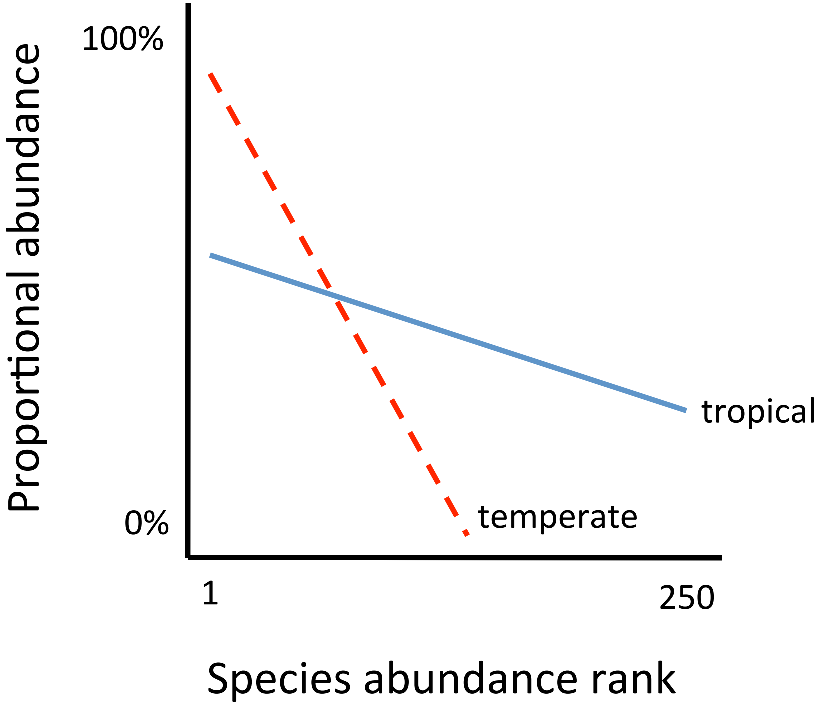


Consider these two communities that have the same richness but differ in evenness

Measuring Diversity

Species dominance patterns across regions:

Tropical areas tend to have more species, but those species tend to be numerically rare. In temperate regions, there are fewer overall species, many of which occur in high abundance.



Any individual tropical species accounts for a smaller proportion of the total abundance of individuals summed across all species.

Measuring Diversity

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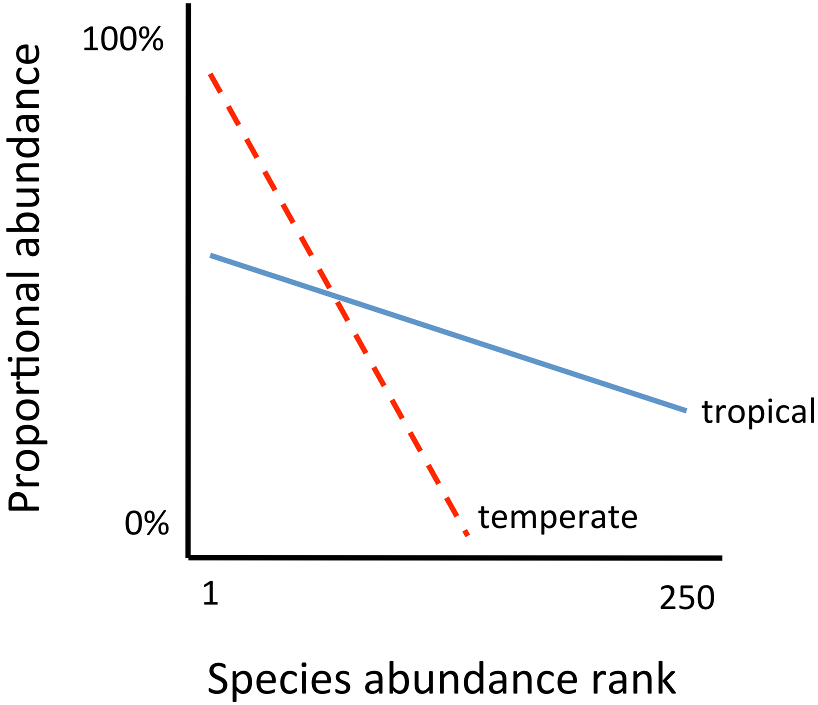
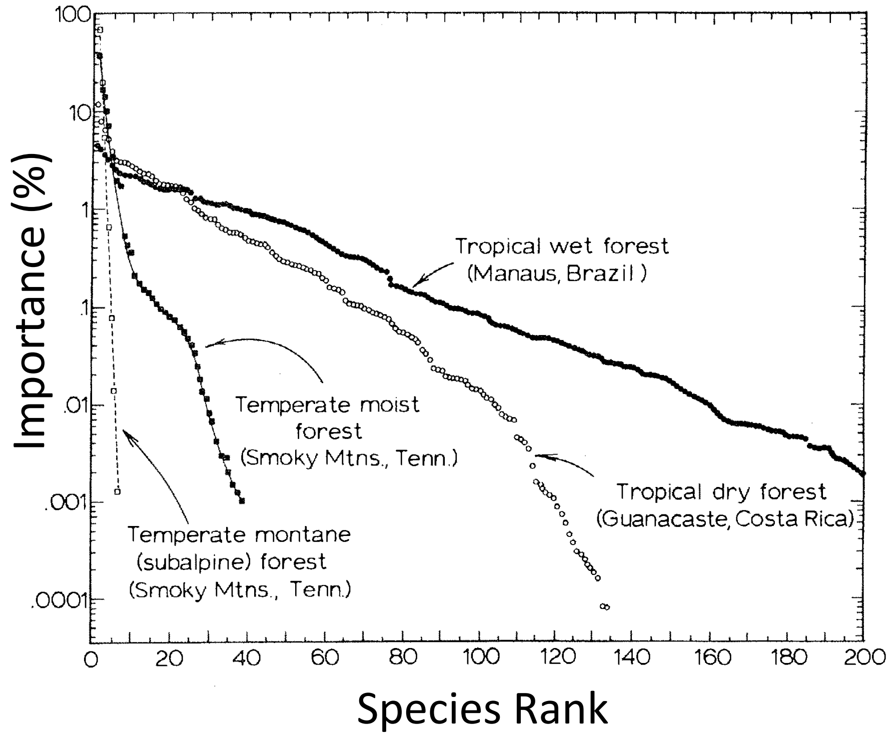




(Hubbell 1979)

Measuring Diversity

High species richness among different taxa is a hallmark of tropical regions (e.g., flowering plants of Sri Lanka)

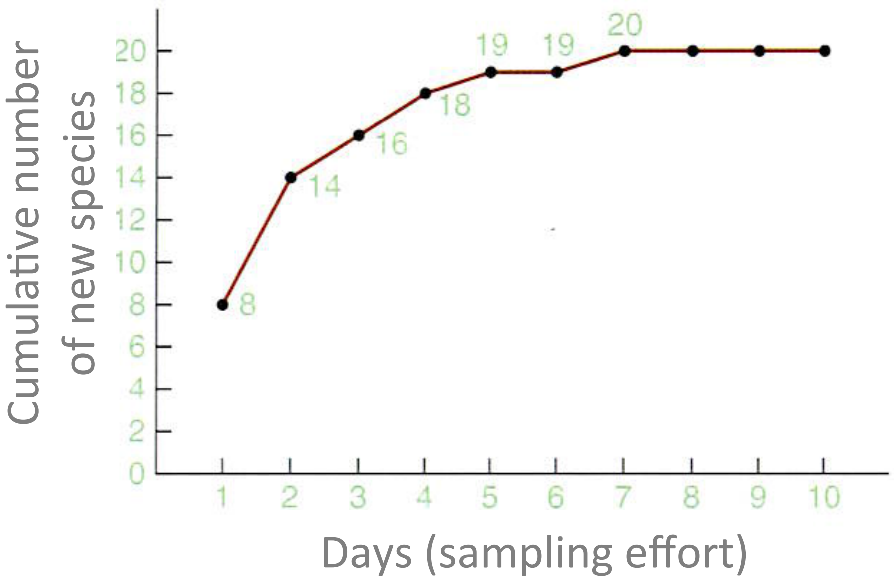
Measuring Diversity

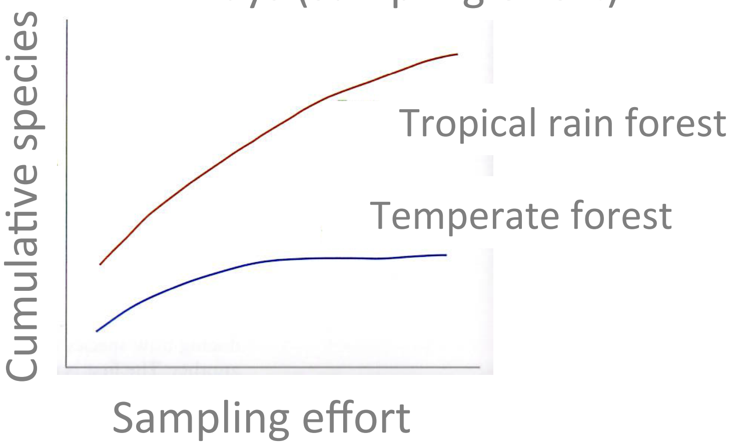
High species richness among different taxa is a hallmark of tropical regions (e.g., mammals of South America)

Measuring Diversity

Species richness is related to both sampling effort and sample area

	SPECIES	NEW SPECIES
Day 1	8	8
Day 2	9	6
Day 3	6	2
Day 4	9	2
Day 5	7	1
Day 6	8	0
Day 7	10	1
Day 8	7	0
Day 9	6	0
Day 10	11	0
$\bar{x}$ # Species per day	8.1	20 total species in the community





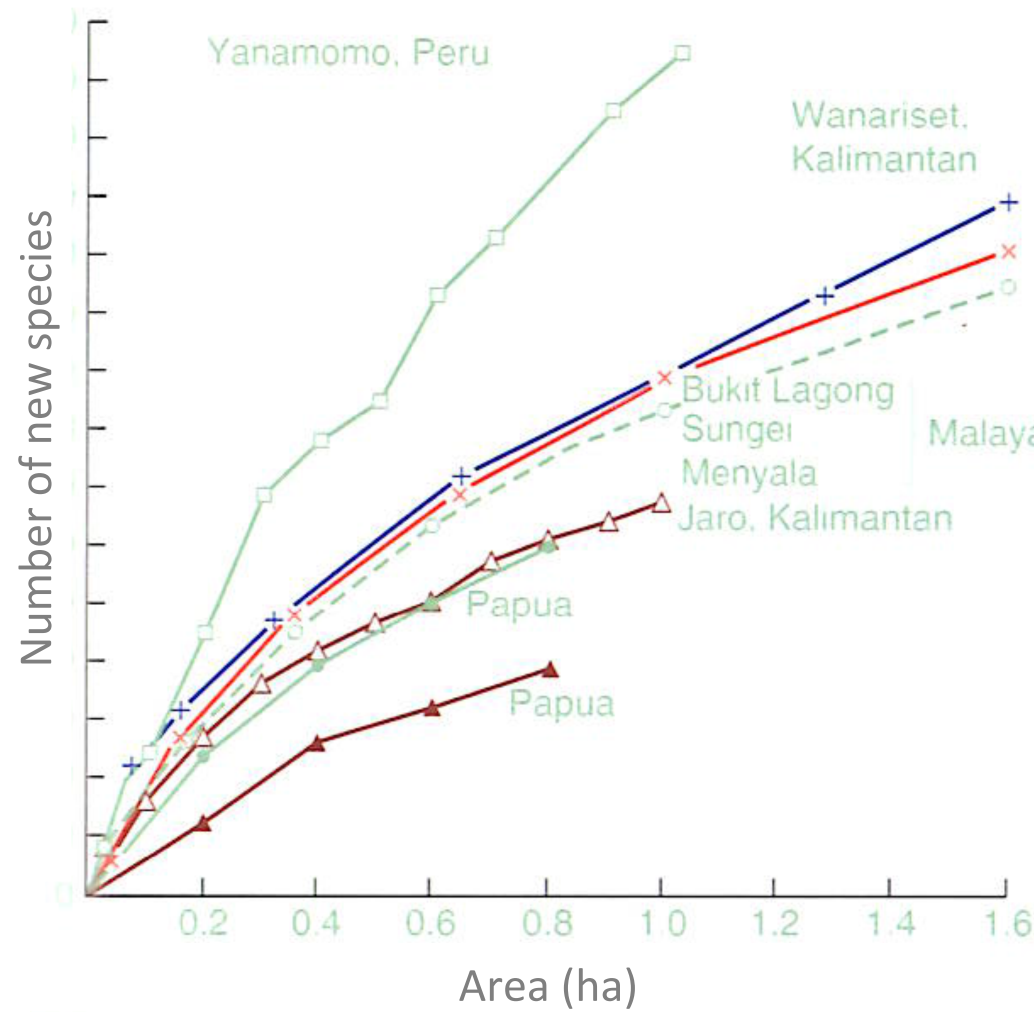
Measuring Diversity

Species richness is related to both sampling effort and sample area

Differences in species/area curves for evergreen tropical trees across forests

A very basic relationship relevant to conservation (loss of area directly translates into loss of species)

Area effects also probably important in considering global richness patterns



Measuring Diversity

Species diversity is often quantified using terms that reflect diversity across different spatial scales

Terminology can be confusing, since 'diversity' may refer to measures of richness, or richness & evenness (depends on what diversity index is used)

Alpha (α) diversity: number of species or diversity within a locality or habitat

Beta (β) diversity: change in the species composition between localities across space or an environmental gradient (proportion of shared species across sites)

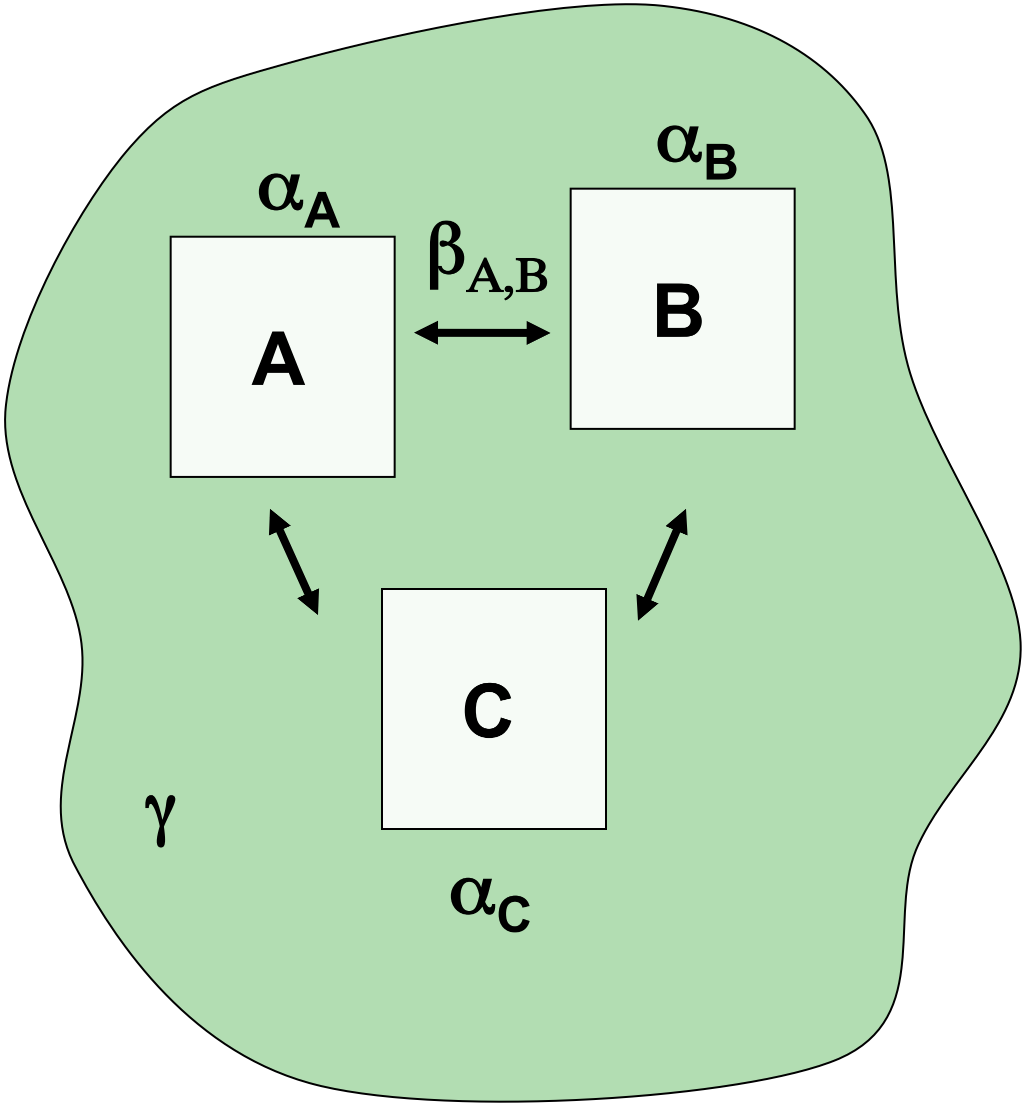
Gamma (γ) diversity: number of species or diversity within a larger region; a function of both alpha and beta diversity.

Spatial components of species diversity

Gamma (γ) diversity

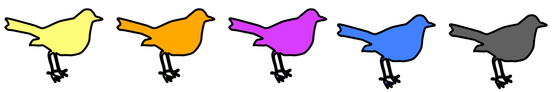
Alpha (α) diversity

Beta (β) diversity

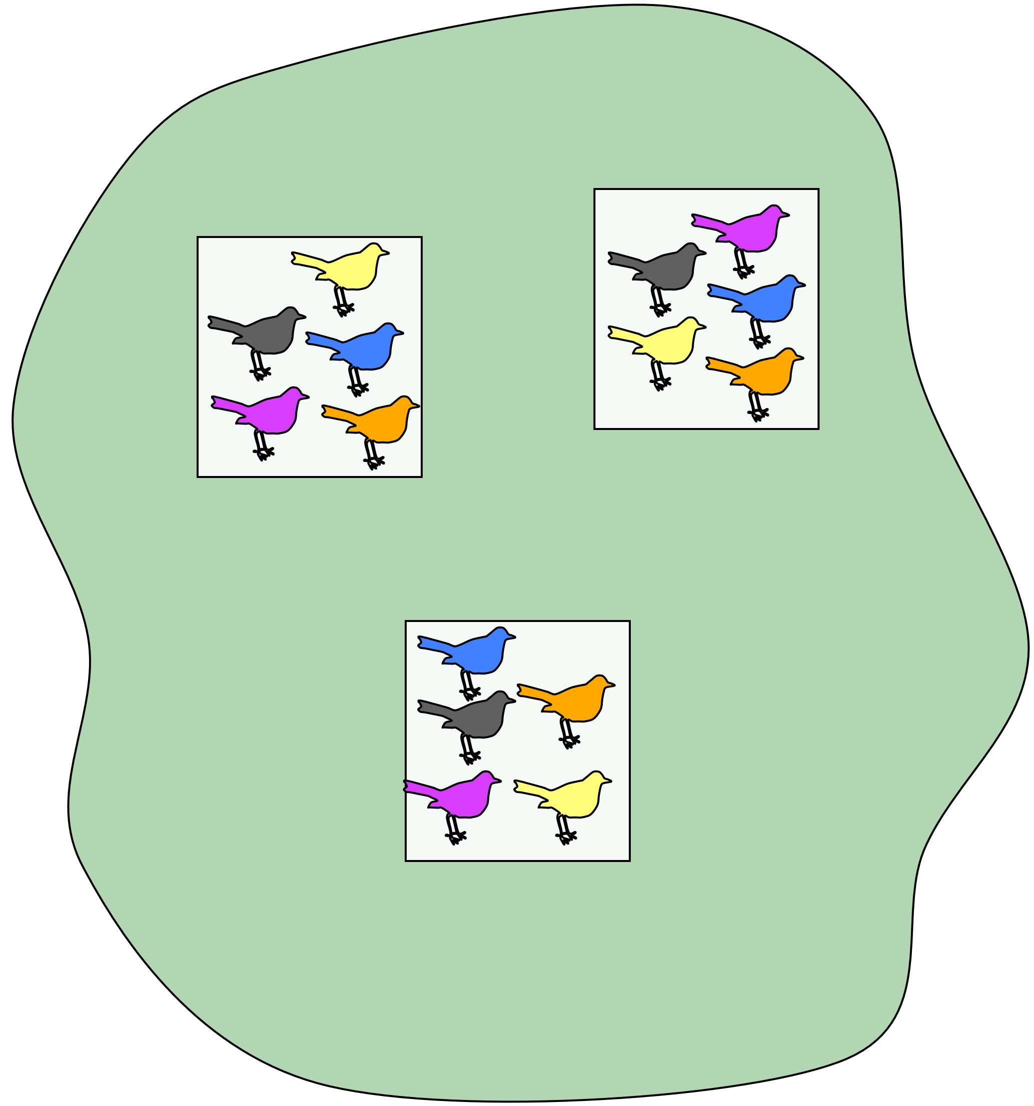


Patterns of Species Diversity

Regional pool (γ)



If α diversity ≅ γ diversity
→ low β diversity



Patterns of Species Diversity

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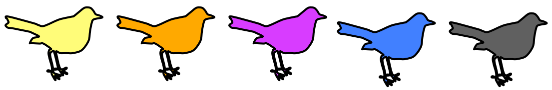
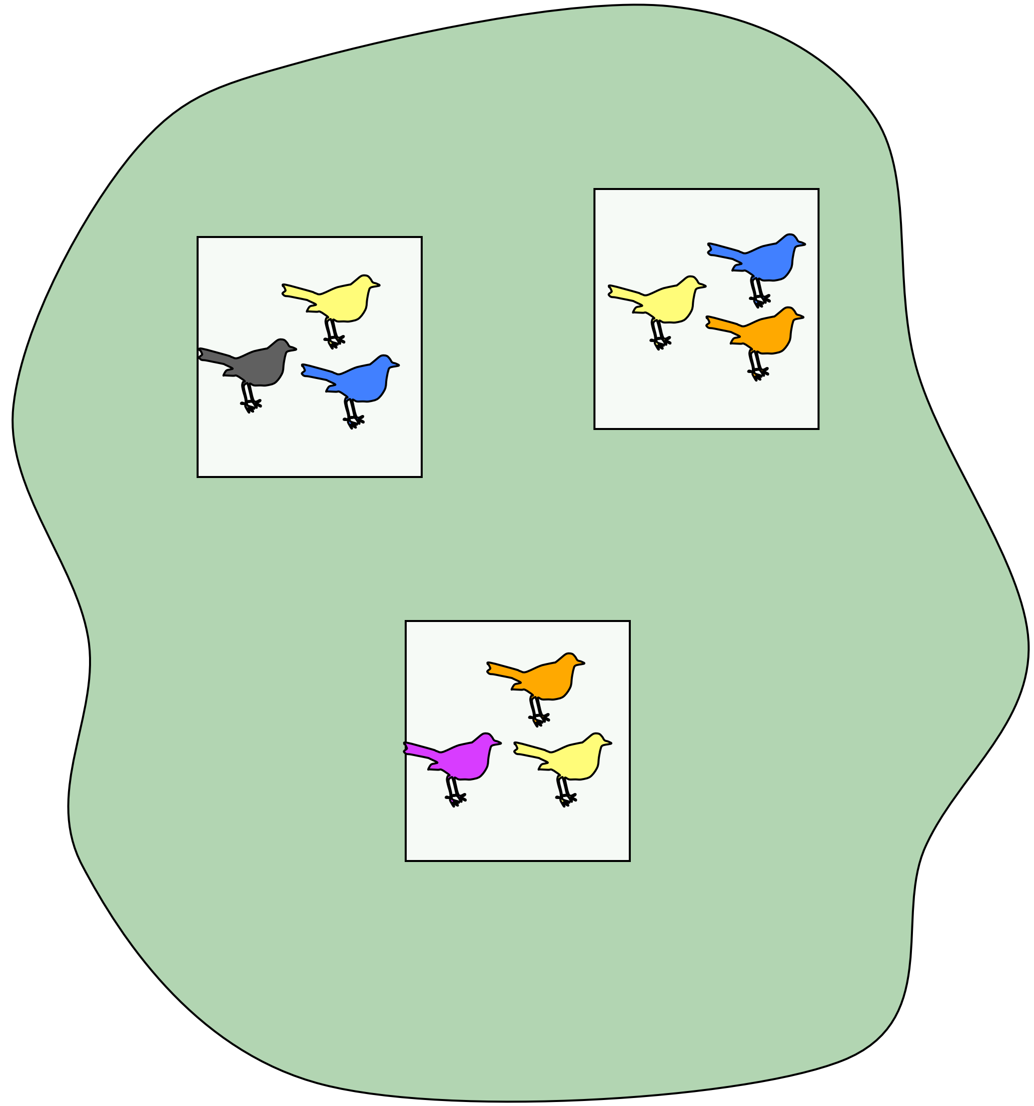


If α diversity $\cong$ γ diversity
→ low β diversity

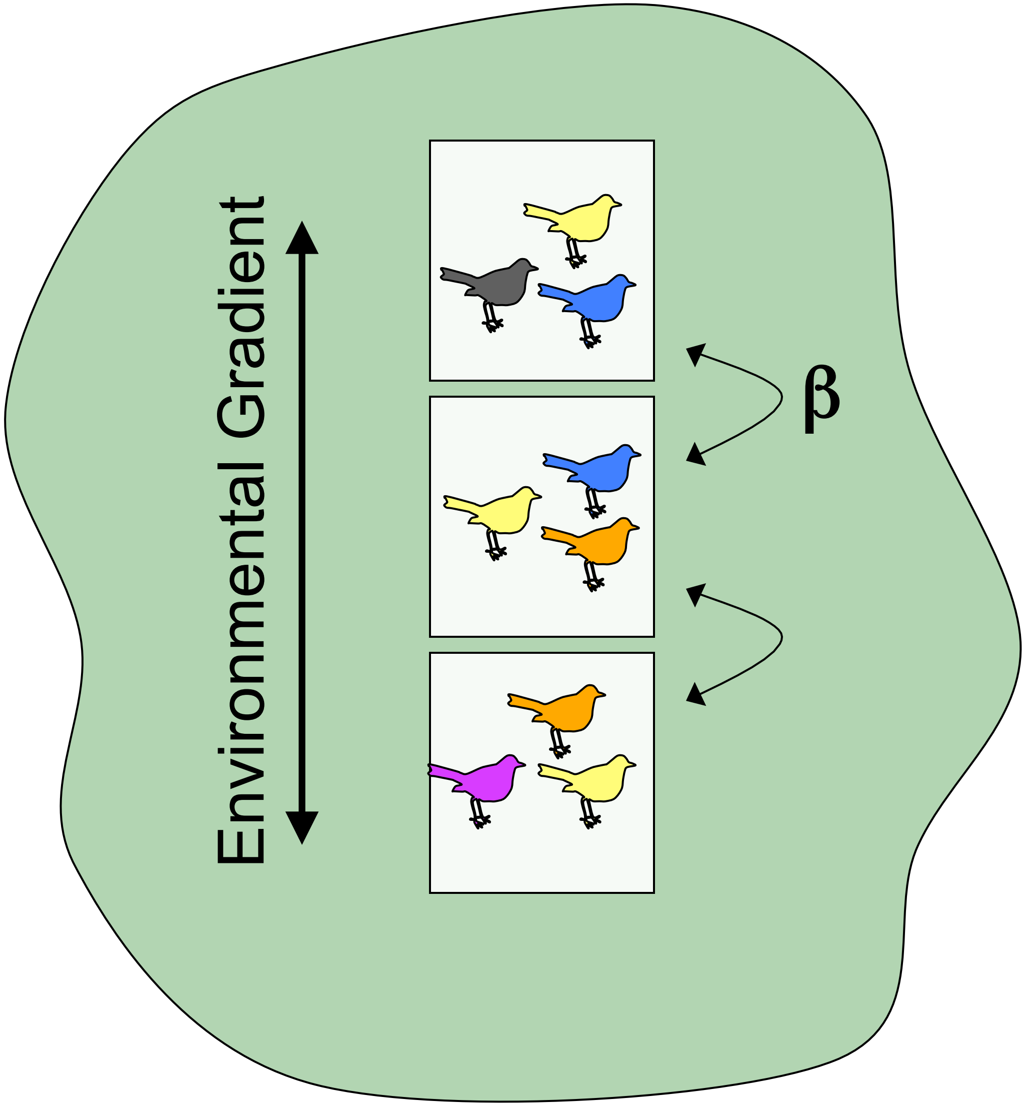
If α diversity $<$ γ diversity
→ high β diversity



Patterns of Species Diversity

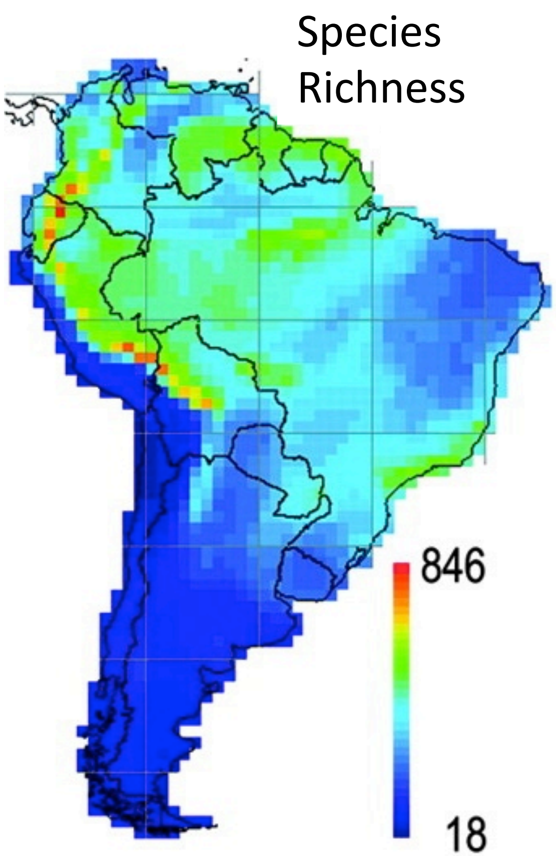
Species turnover:
beta diversity examined along axis of variation

How does the gradient affect composition?

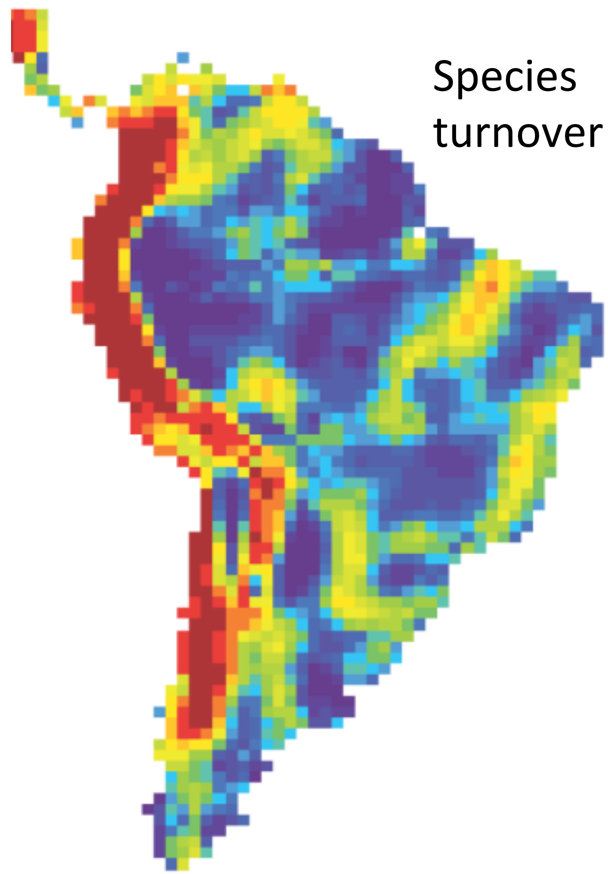


Species Diversity across South America

Comparisons in alpha and beta diversity for birds



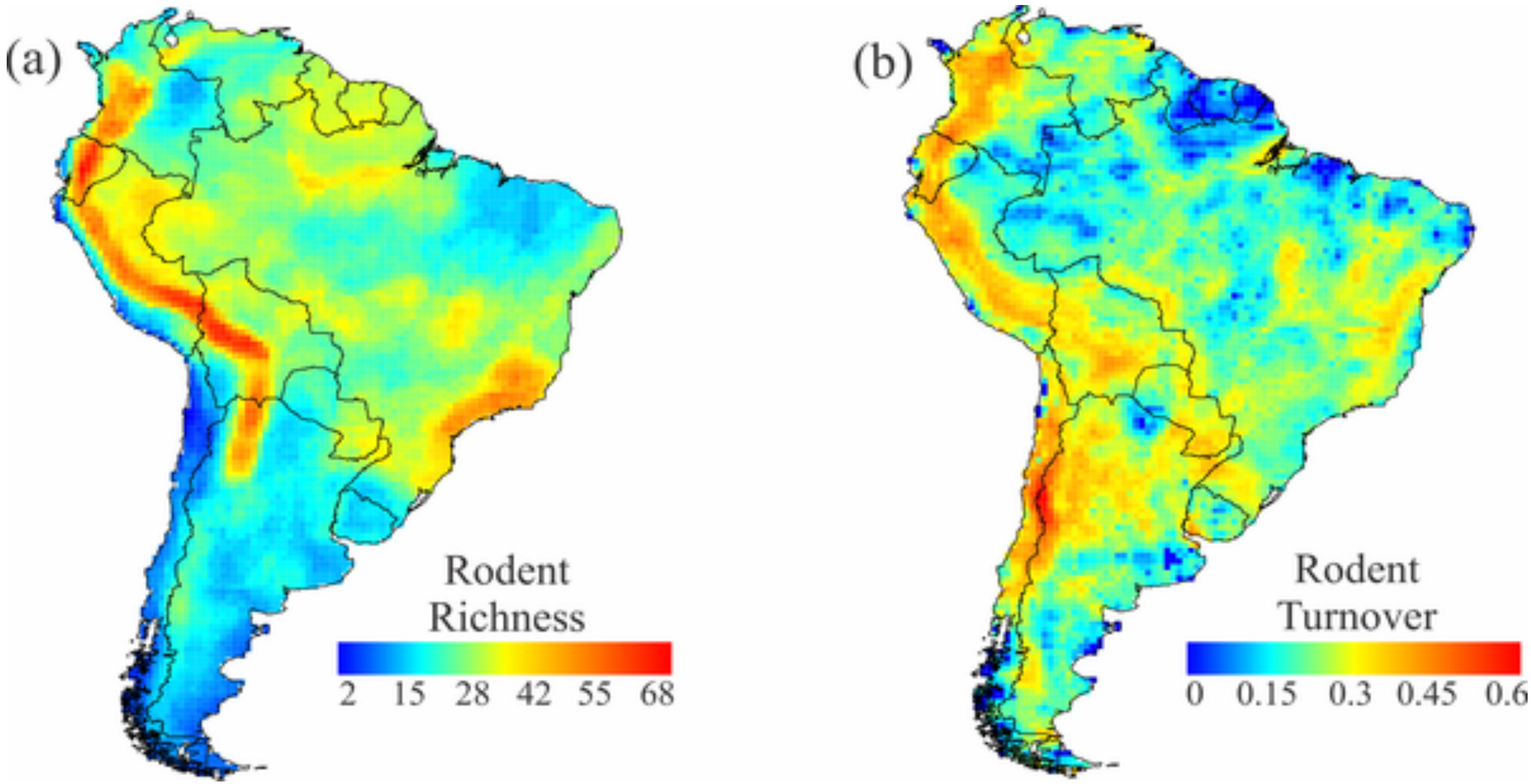
Graves & Rahbek 2005, *PNAS*



McKnight et al. 2007, *PLoS ONE*

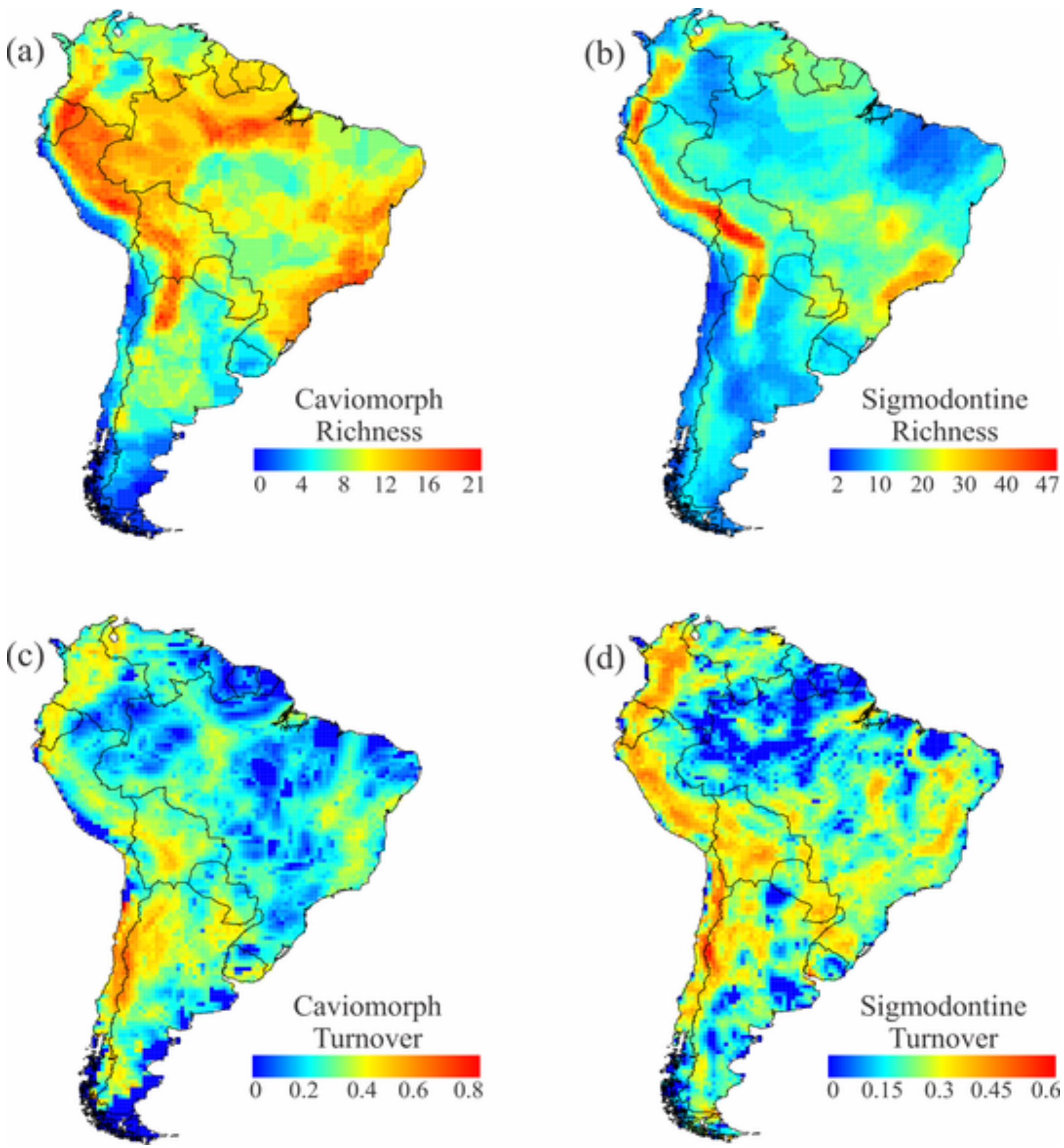
Species Diversity across South America

Comparisons in alpha and beta diversity for rodents



Maestri & Patterson 2016, PLoS ONE

Species Diversity across South America



Comparisons in alpha and beta diversity for rodents

Species Richness

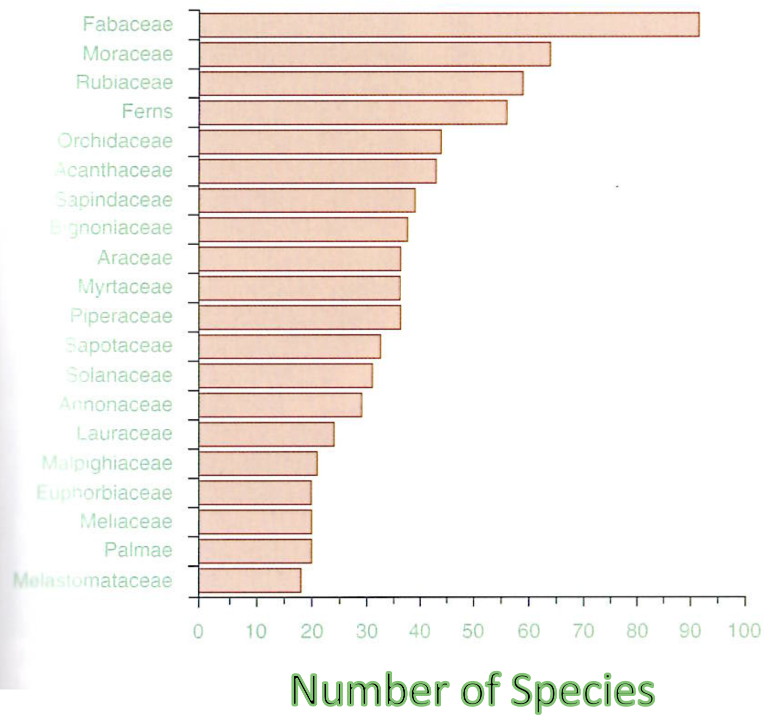
Species turnover

Maestri & Patterson 2016, PLoS ONE

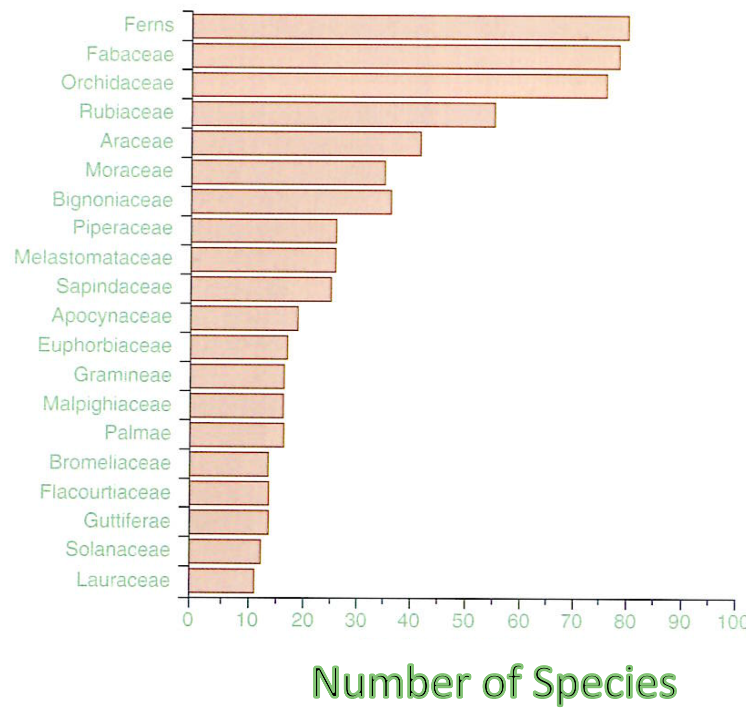
Broad scale comparisons in the Neotropics

Differences exist in species richness and composition of plant communities across the Neotropics (tree species richness greater in Amazonia, but epiphyte / shrub diversity greater in Central America)

Barro Colorado Island, Panama



Cocha Cashu, Peru



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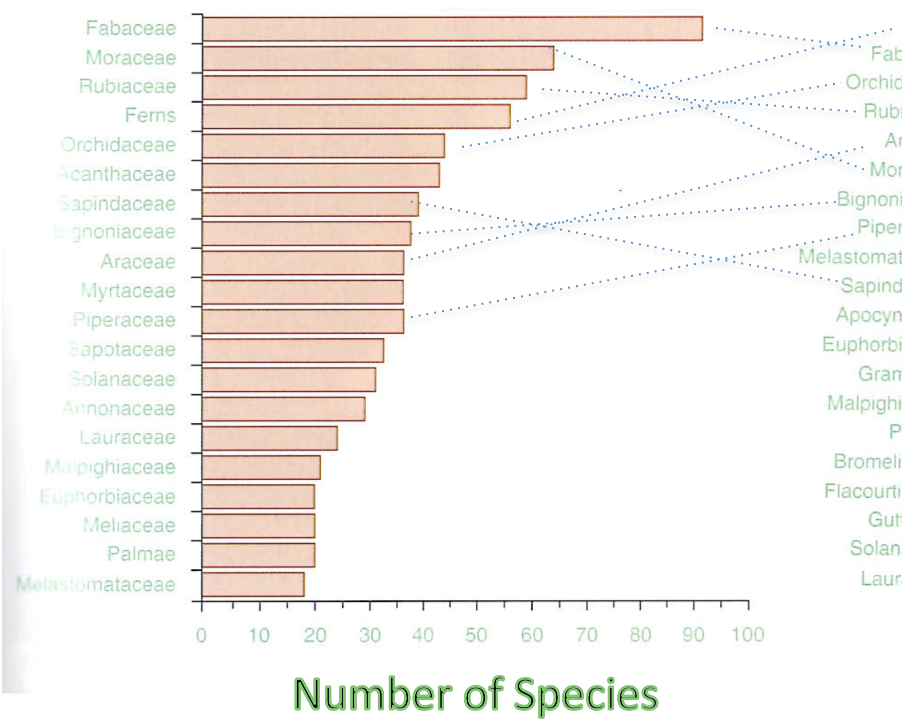

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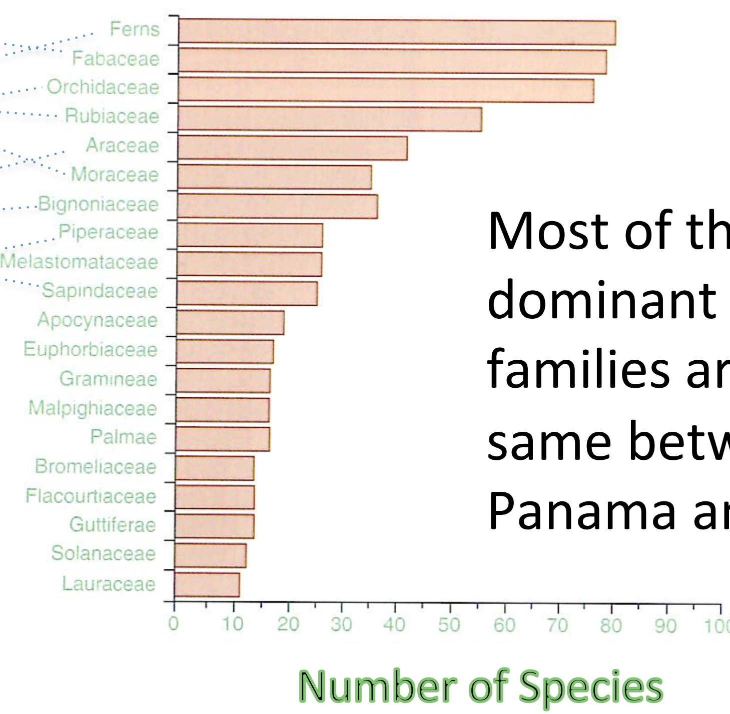


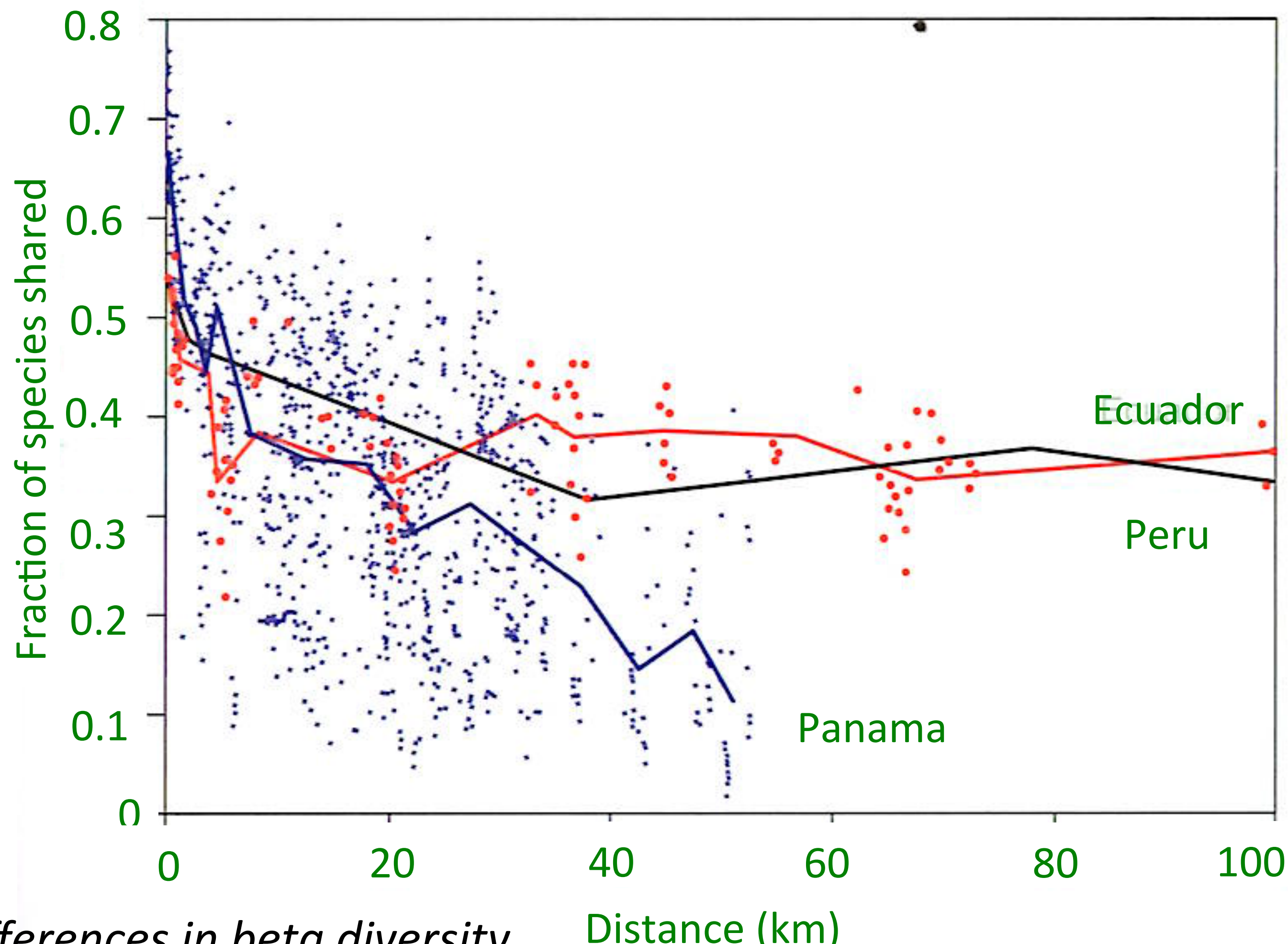
Most of the major dominant plant families are the same between Panama and Peru

Beta diversity across lowland forest

High beta diversity even among plots in close proximity

Similarity in species composition declines with increasing distance between plots

Surveyed tree plots in *terra firme* forest



What could explain differences in beta diversity between Panama and the sites in South America?

How many species?

Terry Erwin's forest canopy fogging experiment:

Extracted insects from the canopy of 19 individuals of *Luchea seemani,* a tropical tree species

Erwin identified ~1200 beetle species from the samples

Estimating ~70 tree species per hectare, and that ~13% are host specific, he estimated that 11,410 host-specific beetles could be found within a hectare of tropical forest.

Scaling up, to trees across the global tropics, Erwin estimated that there were ~ 8 million species of beetles!

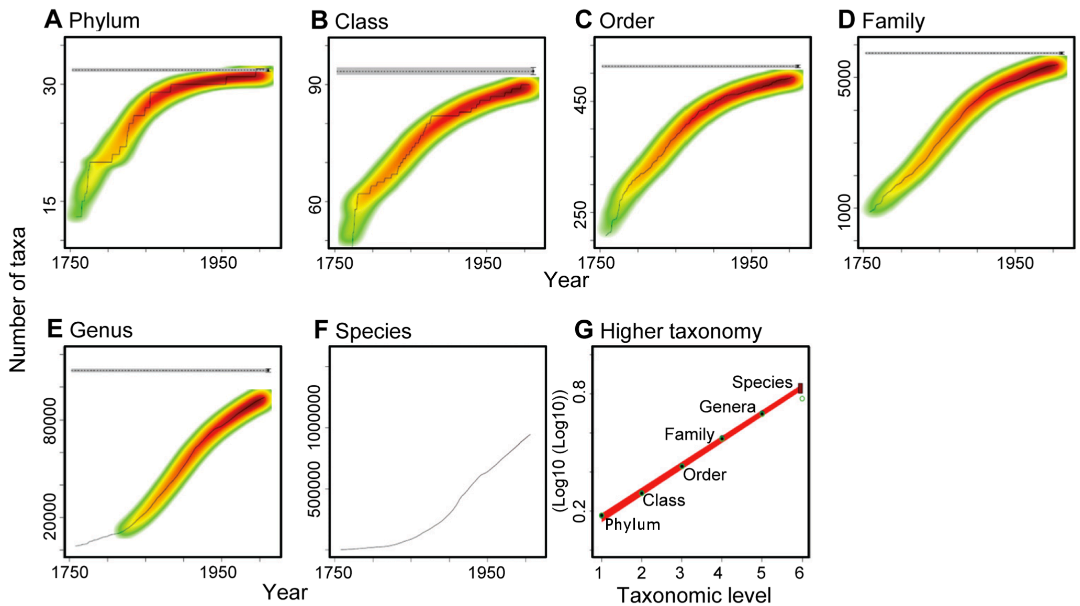
Total arthropod species may be as high as 30 million!

How many species?

A more recent study showed that the higher taxonomic classification of species (i.e., assignment of species to phylum, class, order, family and genus) follows a consistent and predictable pattern from which the total number of species in a taxonomic group can be estimated.

Validated against well-known taxa and applied to all domains of life, predicted:

~8.7 million ± 1.3 million SE eukaryotic species globally (~2.2 million are marine)



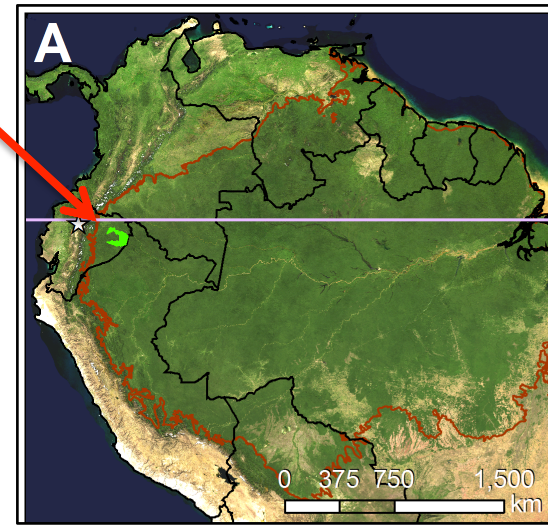
"In spite of 250 years of taxonomic classification and over 1.2 million species already catalogued in a central database, our results suggest that some 86% of existing species on Earth and 91% of species in the ocean still await description."

Mora et al. 2011, *PLoS Biology*

How many species?




130 species of amphibians recorded in Yasuni Biosphere Reserve, Ecuador



Leticia, Colombia – 98 species of anurans
Manu NP, Peru – 111 species of amphibians

Versus

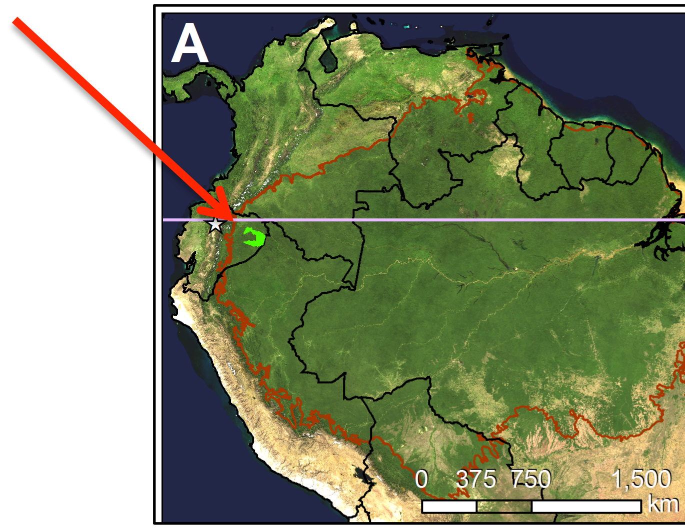
48 species of amphibians in Canada

Duellman 1992, *Scientific American*

How many species?




130 species of amphibians recorded in Yasuni Biosphere Reserve, Ecuador



"A total of 81 species actually live in Santa Cecilia, Ecuador (precisely the number of frog species in the entire U.S.). Although the diversity of frogs there is unusually high, 40 or more species are commonly found in tracts of rain forest no bigger than two square kilometers."

William Duellman 1992, *Scientific American*

Explaining the Latitudinal Diversity Gradient (LDG)

Dobzhansky (1950) suggested that, since all organisms are products of evolution, differences between tropical and temperate diversity must be due to differences in evolutionary patterns across latitudes

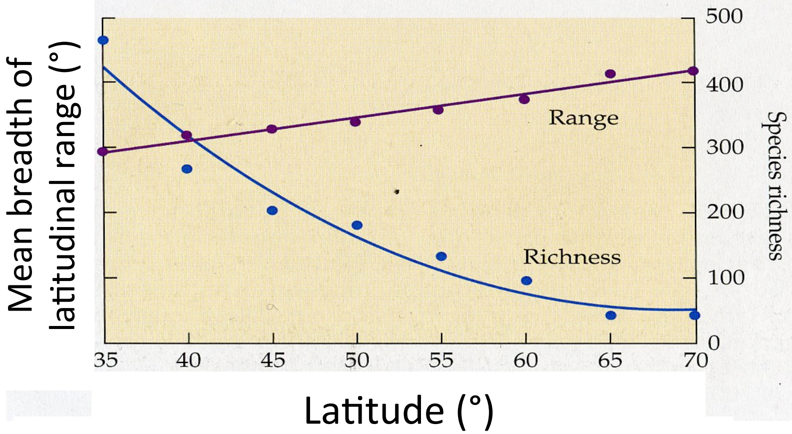
But the question of high species richness in the tropics also involves the maintenance of diversity – once species evolve, how are so many species accommodated within tropical systems?

(Some of the example hypotheses for the LDG focus on genesis, and others on maintenance, of diversity)

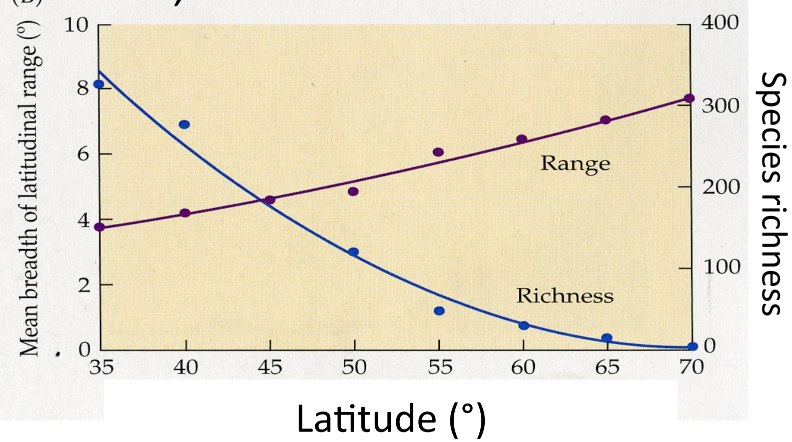
Explaining the Latitudinal Diversity Gradient

Rapoport's Rule: species tend to have larger range sizes at higher latitudes (or smaller range sizes at lower latitudes)

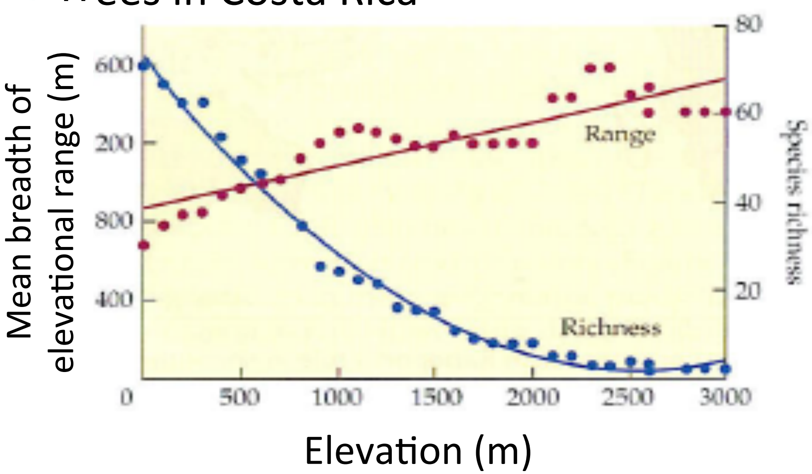
Marine mollusks, Pacific coast of N.A.



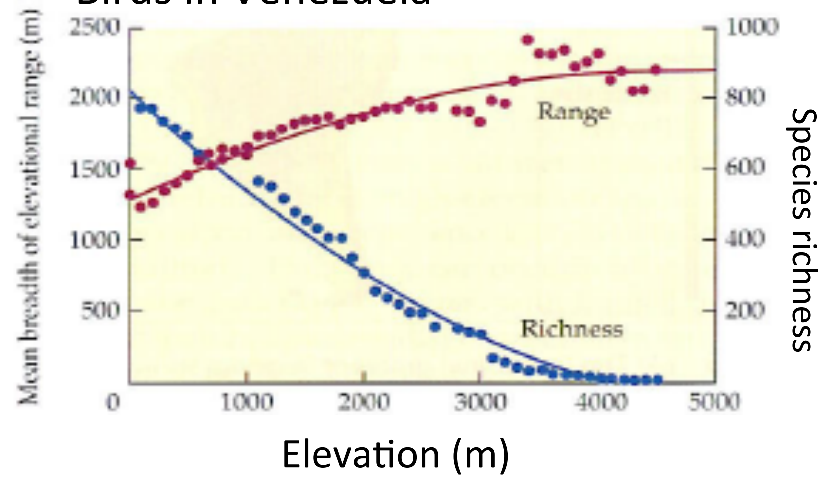
Trees, continental U.S. and Canada



Trees in Costa Rica



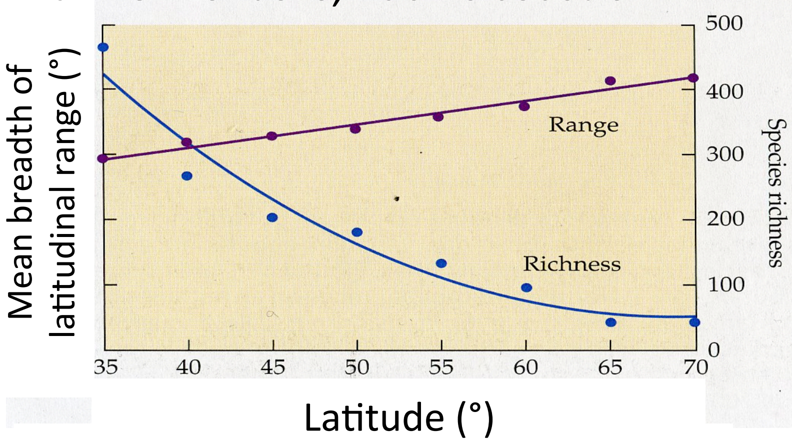
Birds in Venezuela



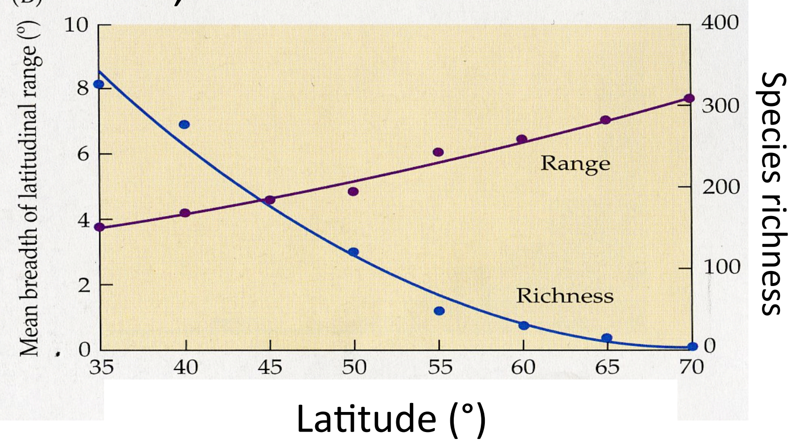
Explaining the Latitudinal Diversity Gradient

Rapoport's Rule: in the tropics, this pattern is shown across elevation

Marine mollusks, Pacific coast of N.A.



(B) Trees, continental U.S. and Canada



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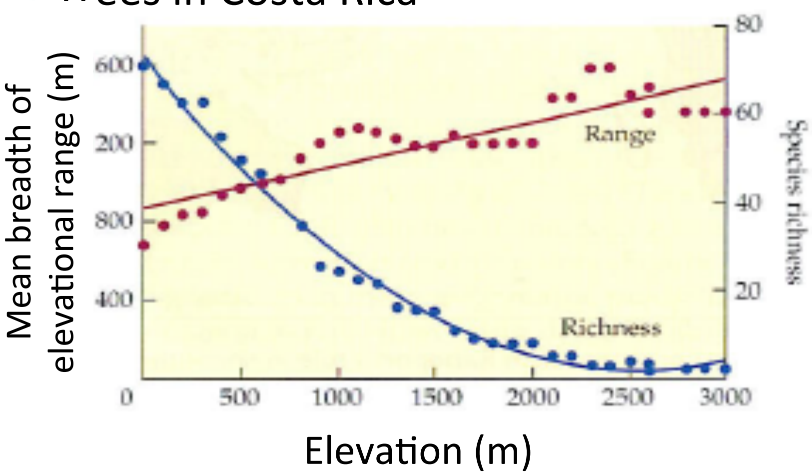
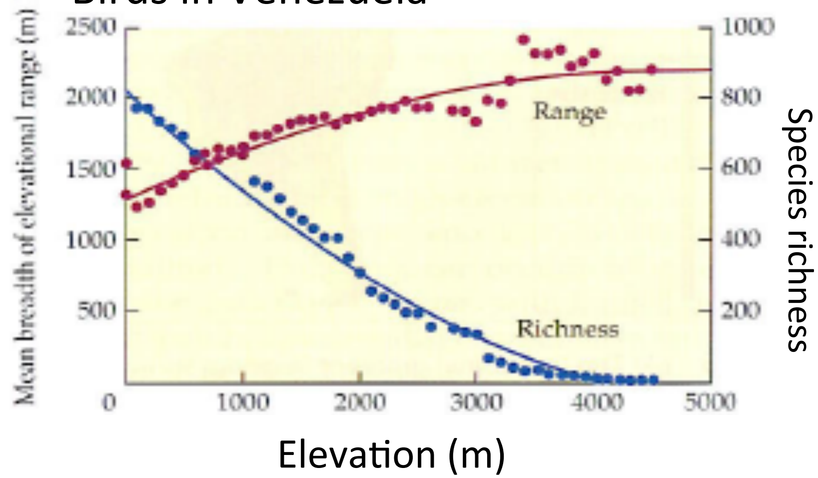
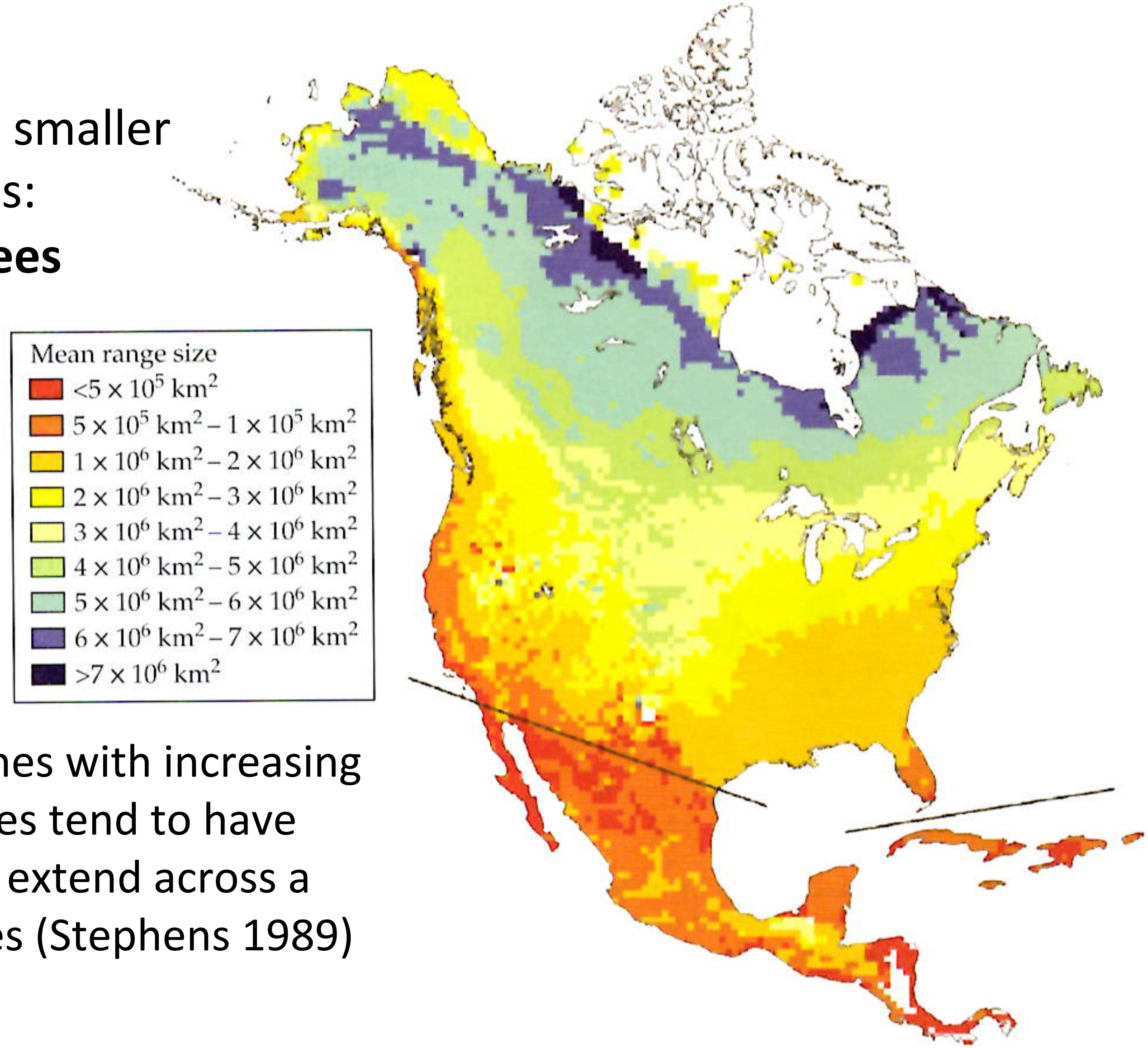


(B) Birds in Venezuela



Rapoport’s Rule: Range size increases with latitude

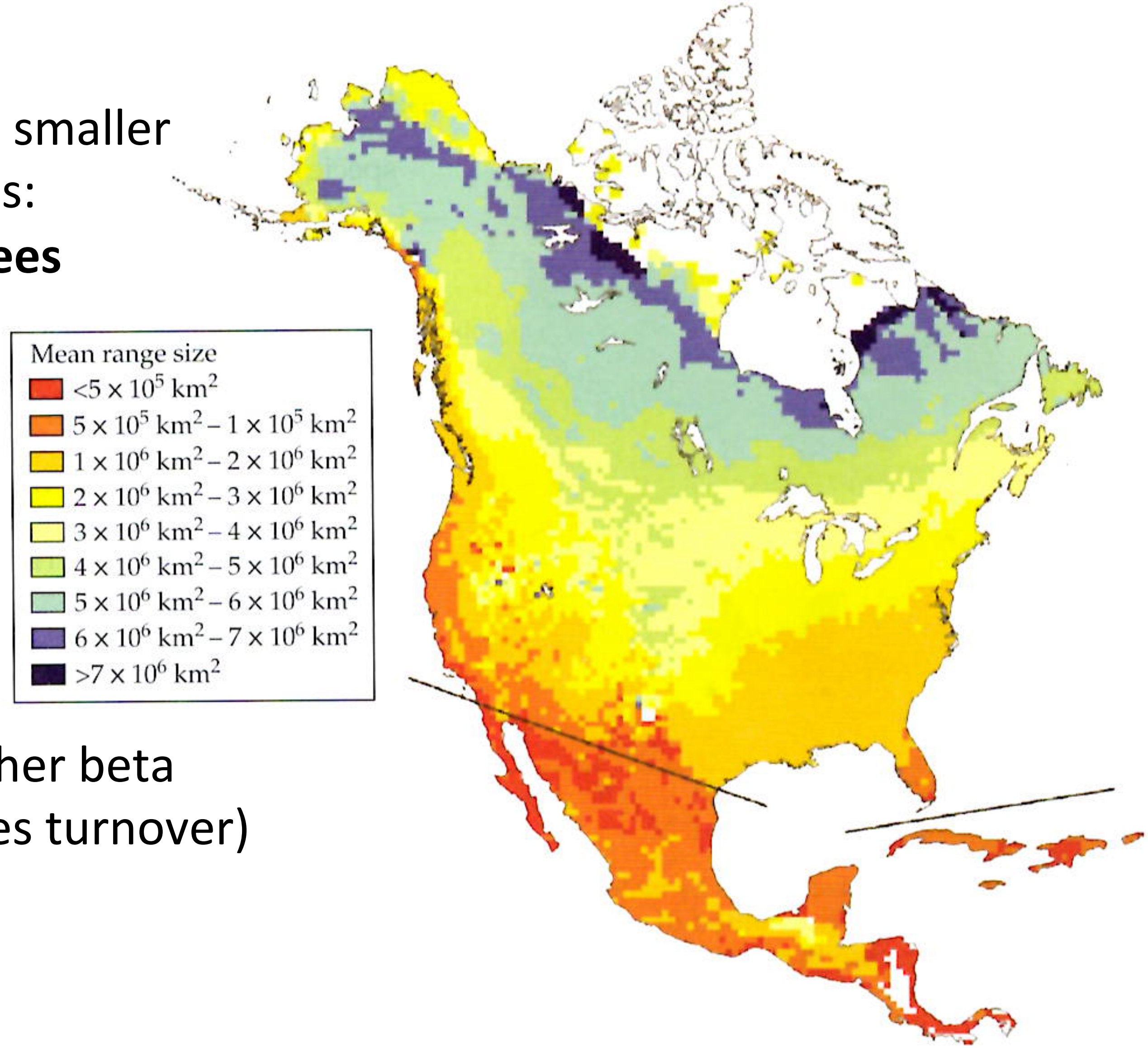
Species range size gets smaller towards lower latitudes:
for **North American trees**



As species richness declines with increasing latitude, remaining species tend to have geographical ranges that extend across a broader range of latitudes (Stephens 1989)

Rapoport's Rule: Range size increases with latitude

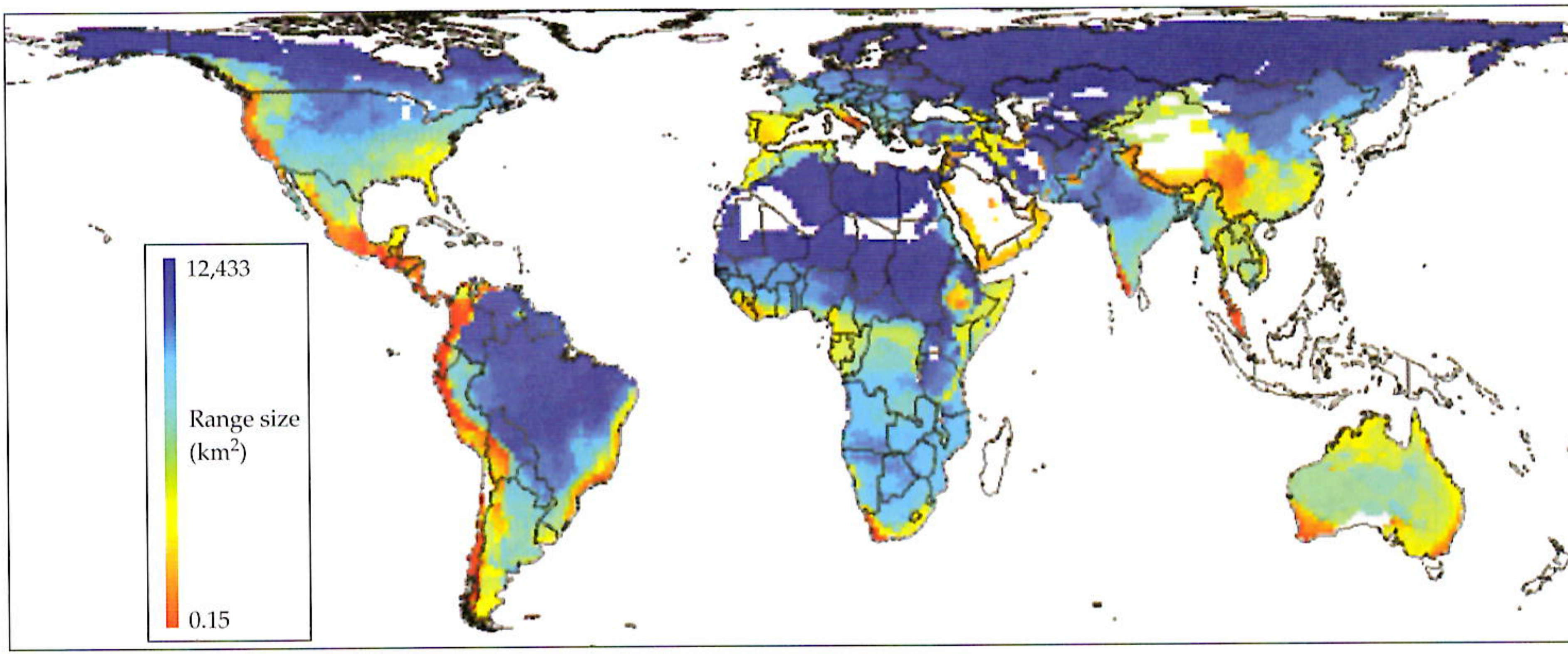
Species range size gets smaller towards lower latitudes:
for **North American trees**



This should lead to higher beta diversity (spatial species turnover) in the tropics

Rapoport's Rule: Range size increases with latitude (mostly)

Rapaport's rule is shown in geographic range size of **amphibians** (especially in North American and Asia), but reflects the influence of montane regions and coastal areas

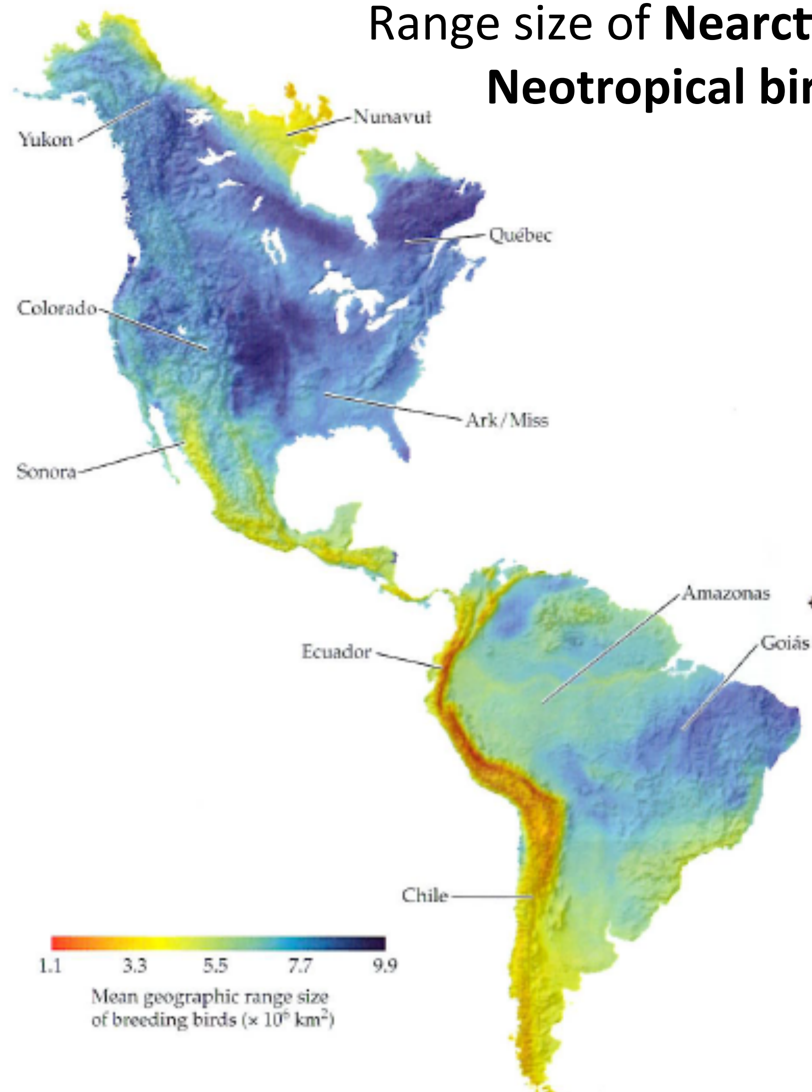


Rapoport's Rule: Range size increases with latitude (mostly)

Species in the tropics have smaller range sizes (generally)

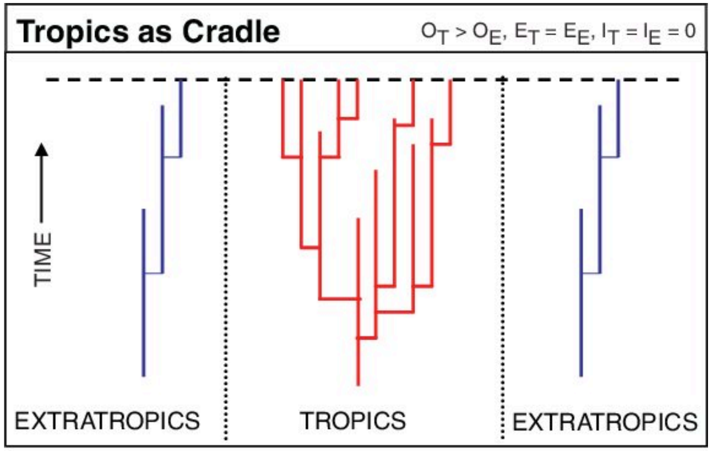
Geographic variables (topography, latitude, configuration of landmasses) also affect range size

Range size of **Nearctic/ Neotropical birds**

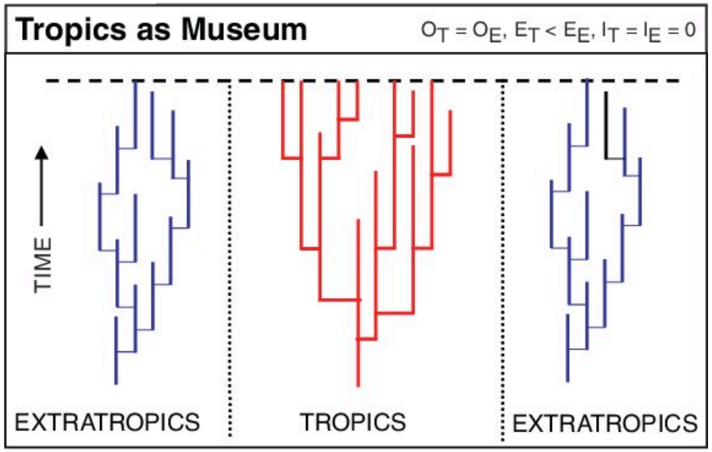


Are the tropics a cradle or a museum?

As a ‘cradle’ the tropics is suited to speciation: species generation is high, and species tend to accumulate



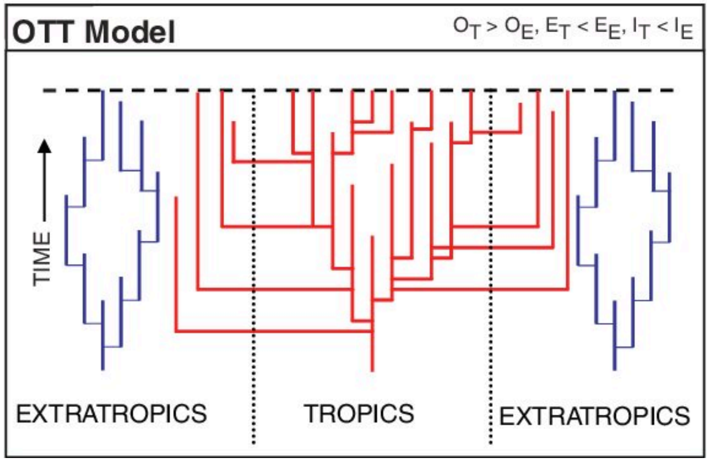
As a ‘museum’ the tropics experiences lower extinction – more ancient species tend to be kept, along with the new ones that evolve



Jablonsky et al. 2006, *Science*

Are the tropics a cradle or a museum?

Jablonsky and colleagues, in their assessment of bivalve mollusks, suggested that the 'cradle – museum' dichotomy is misleading.



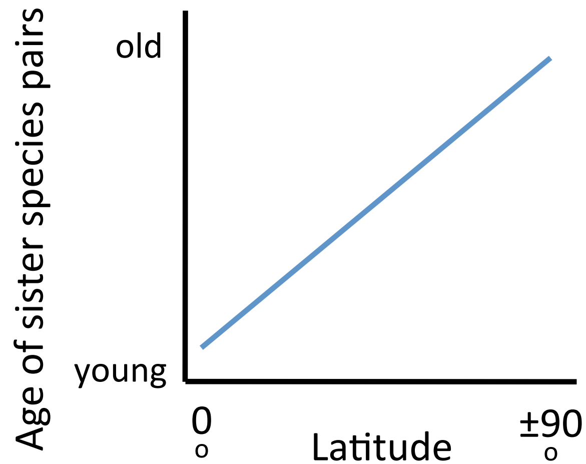
They proposed a new model – Out of The Tropics (OTT):
taxa originate in the tropics and expand pole ward over time without losing their tropical roots

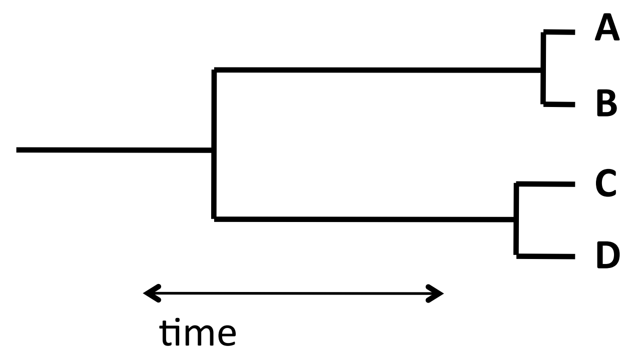
Jablonsky et al. 2006, *Science*

Are the tropics a cradle or a museum?

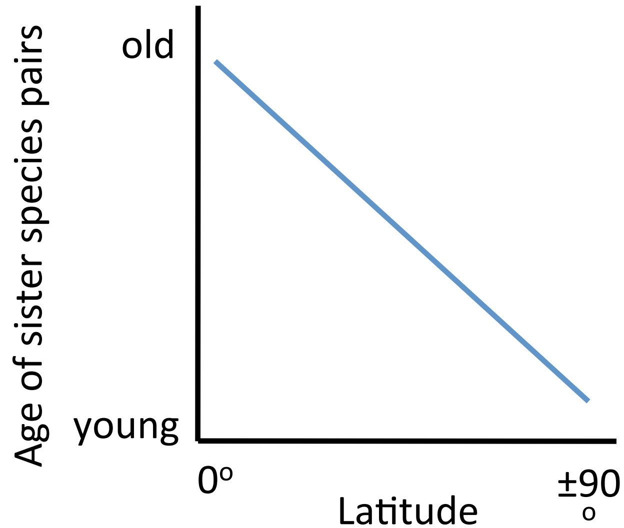
Other studies have addressed this question using age of sister taxa

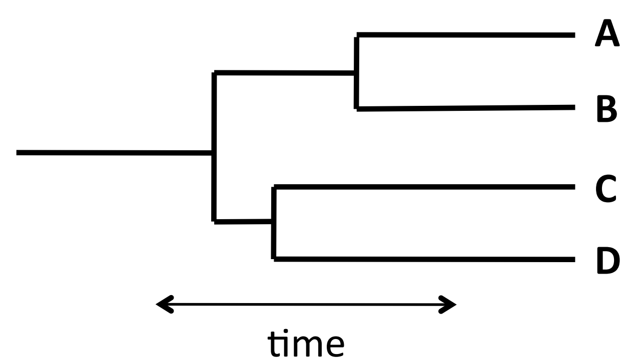
Tropical Cradle: divergences should be more recent between sister species





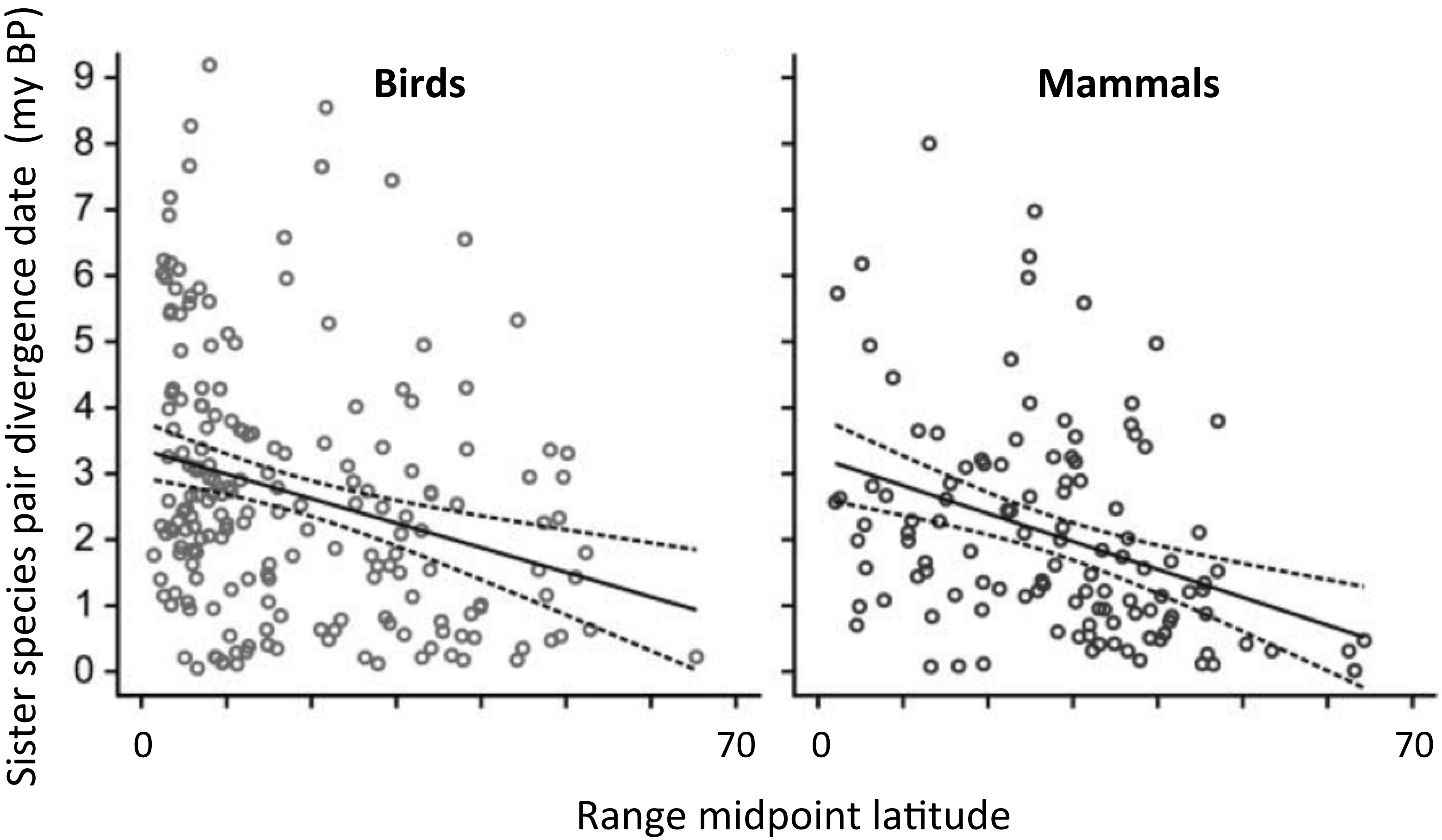
Tropical Museum: splits between sister taxa should be older





Weir & Schluter 2007

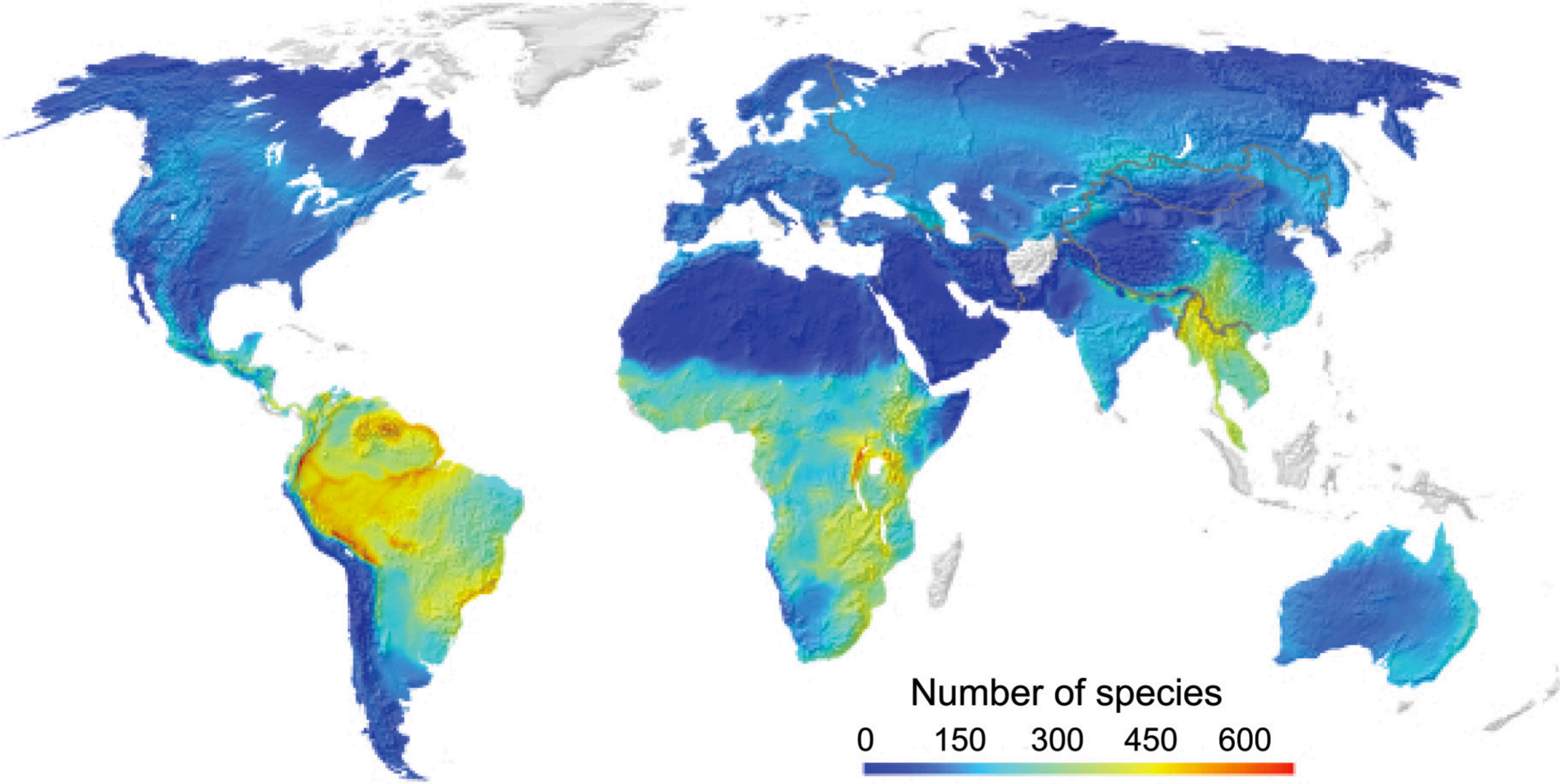
Are the tropics a cradle or a museum?



Weir and Schluter 2007

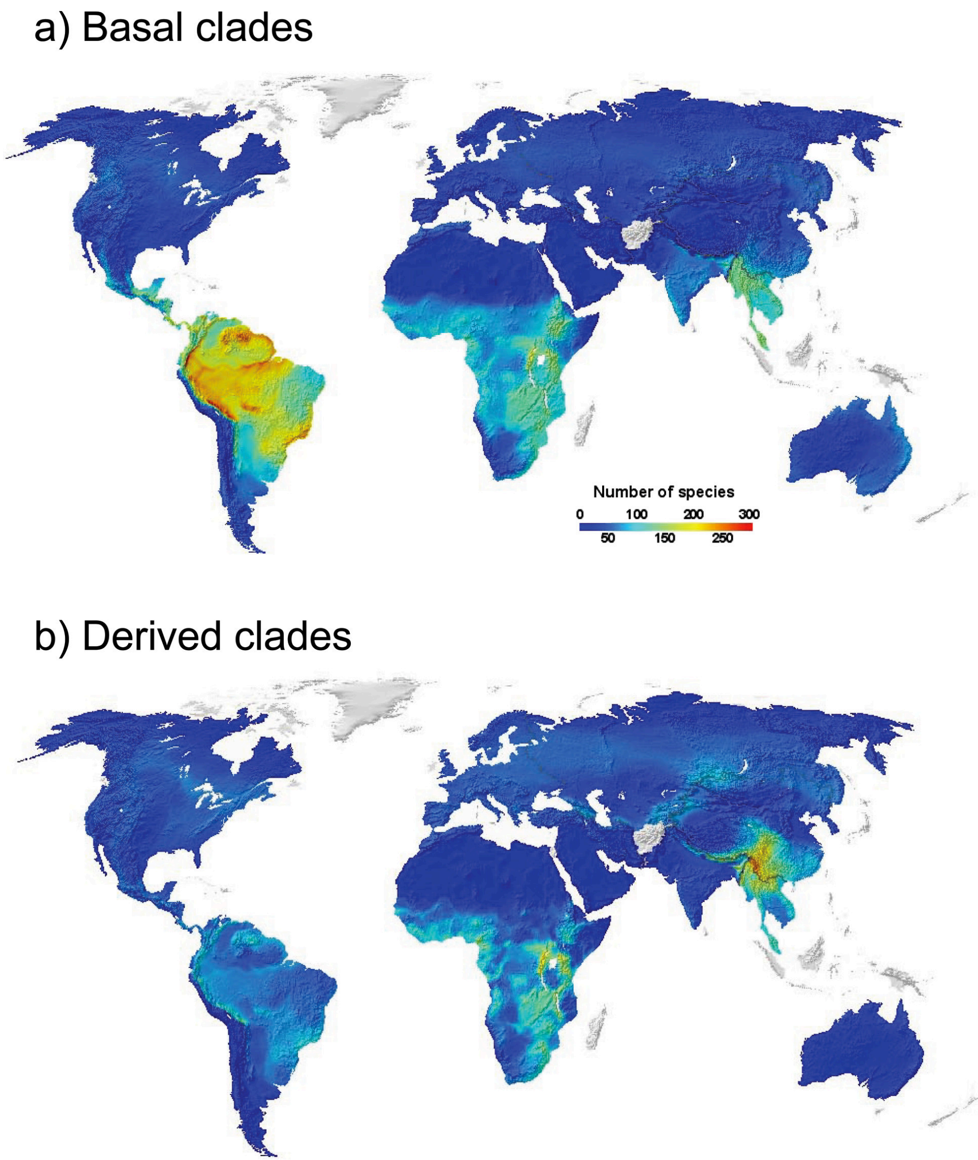
Are the tropics a cradle or a museum?

Geographical pattern of bird species richness



Hawkins et al. 2007, American Naturalist

Are the tropics a cradle or a museum?



Geographical pattern of richness for:

(a) 2,700 most basal species (in 54 families)

(b) 2,458 most derived species (in 16 families)

Hawkins et al. 2007, American Naturalist

Are the tropics a cradle or a museum?

Inga is a genus of tree (family Fabaceae) that have recently diversified (in the last 1.2 million years) – a cradle species cluster

Attributed to recent Andean mountain building episodes and Pleistocene climate changes

Inga acuminata – one of many species in this diverse genus of tropical forests

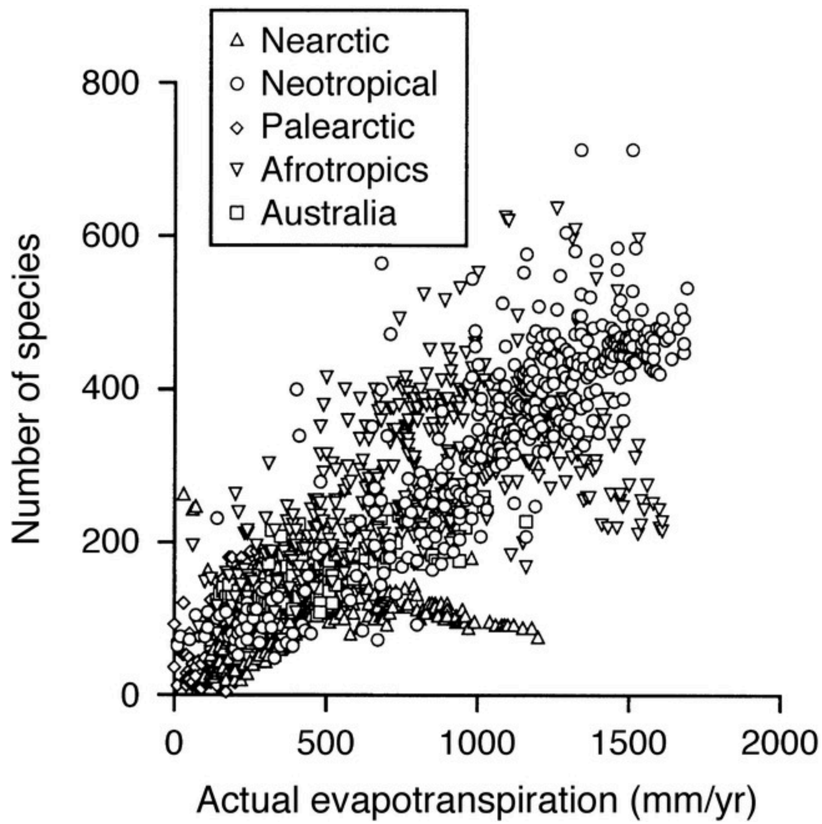
Tropical regions are rich not only in species, but in genera and families, which take longer to evolve. While *Inga* is a cradle species cluster, many families may be part of an old museum.

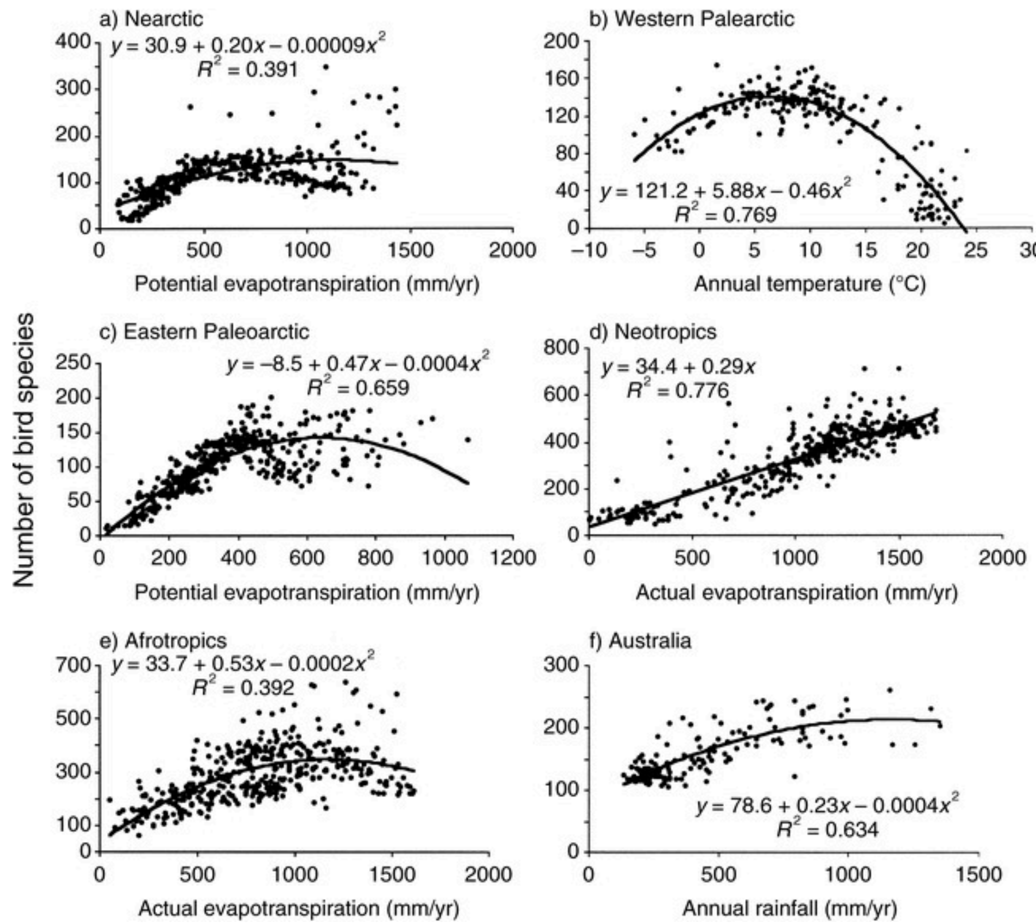
Different groups of species have been subject to different patterns of diversification.

Explaining the Latitudinal Diversity Gradient

Climate and energy availability: There are strong relationships between climate variables and species richness

For terrestrial birds:





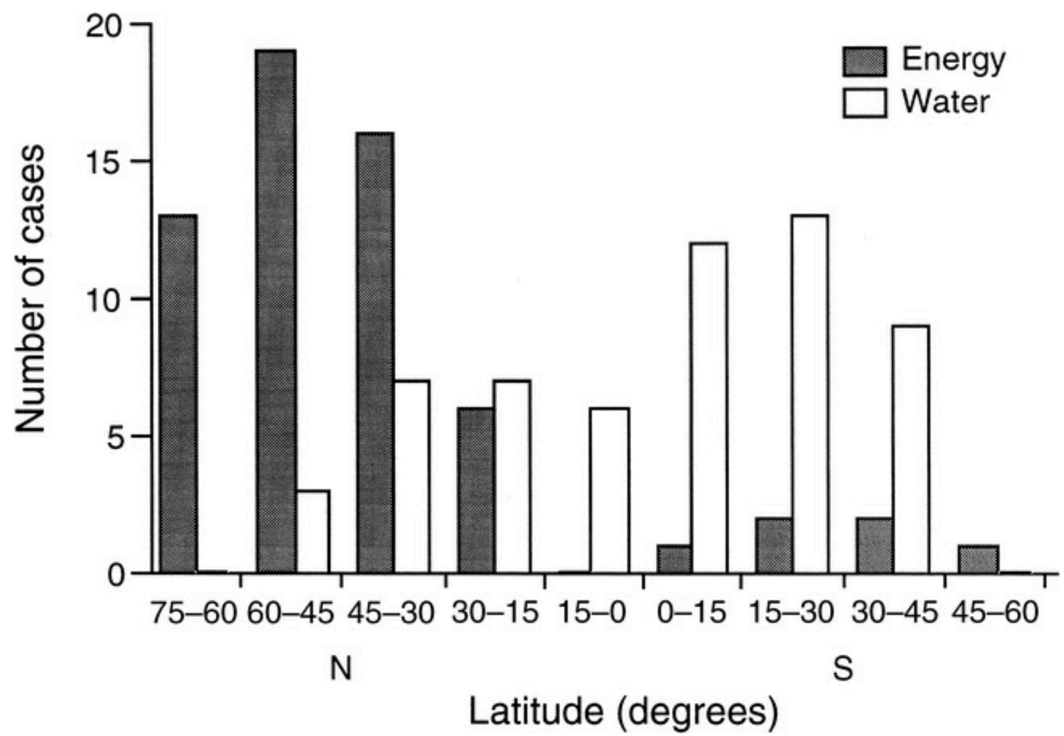
Hawkins et al. 2003a, *Ecology*

Explaining the Latitudinal Diversity Gradient

Climate and energy availability: There are strong relationships between climate variables and species richness

In a broader study with plants, invertebrates and vertebrates:

The same authors showed that species richness correlated with climate variables: precipitation, evapotranspiration, productivity, NPP



What varied among taxa was whether water, energy or their interaction best explained species richness

Hawkins et al. 2003b, *Ecology*

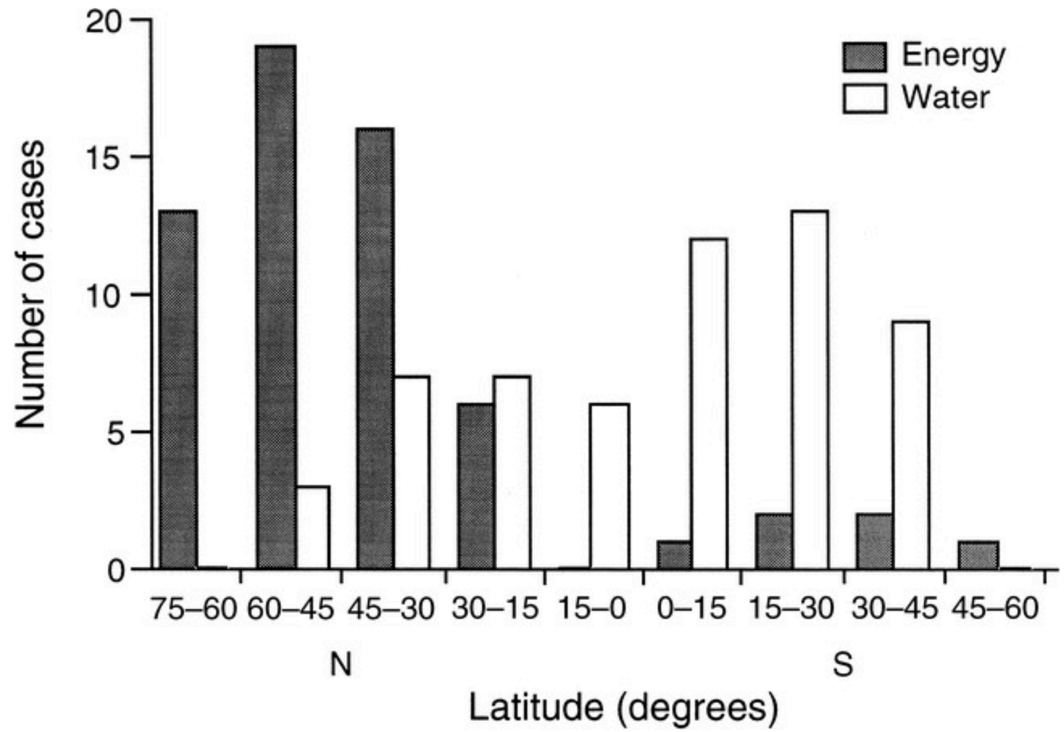
Explaining the Latitudinal Diversity Gradient

Climate and energy availability: There are strong relationships between climate variables and species richness

Climate variables that influence species richness shift with latitude:

In the far north, energy placed the strongest constraints on richness

In areas with high energy input, water was most responsible for constraining species richness



Hawkins et al. 2003b, *Ecology*

Explaining the Latitudinal Diversity Gradient

Does diversity in the tropics reflect “the perfect storm?”

– sensu John Kricher

- *Stability – time hypothesis*
- *Productivity – resource hypothesis*
- *Interspecific competition hypothesis*
- *Predation hypothesis*

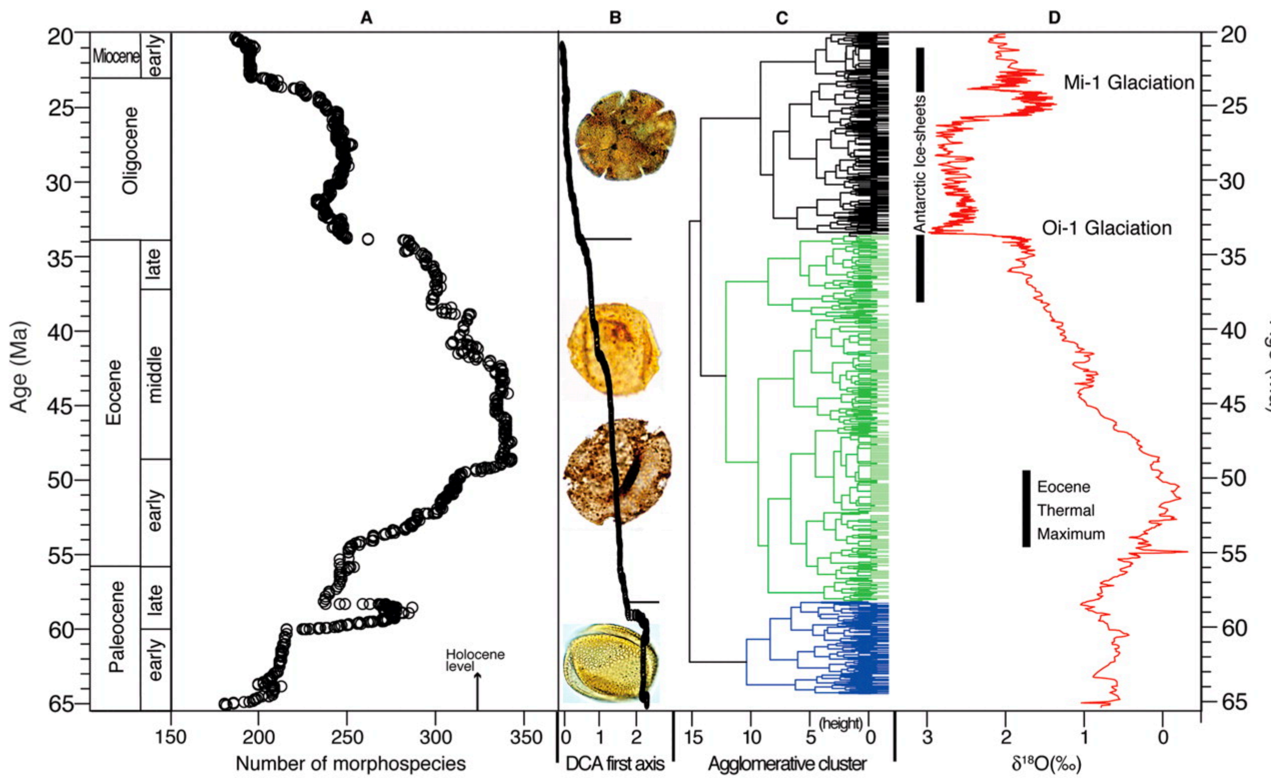
Together they may explain the generation and maintenance of high species richness

Explaining the Latitudinal Diversity Gradient

Stability - time hypothesis: suggests that the antiquity of the tropics, combined with the stable and equitable climate has allowed the generation and persistence of high species richness

A look at the pollen fossil record shows that the tropics has been very species rich over time

But little evidence shows that the tropics have been climatically stable (even though they were probably never climatically harsh)



Explaining the Latitudinal Diversity Gradient

Productivity-resources hypothesis: high plant productivity allows more species to be accommodated

Variables of climate that affect plant productivity strongly correlate with species richness

But how does high productivity translate into resources that support higher species richness?

Resources are distributed across a number of unique resources and substrates: vines and epiphytes

"I think there are so many species of insects because the world contains a very large amount of harvestable productivity that is arranged in a sufficiently heterogeneous manner that it can be partitioned among a large number of populations of small organisms." – Dan Janzen 1976

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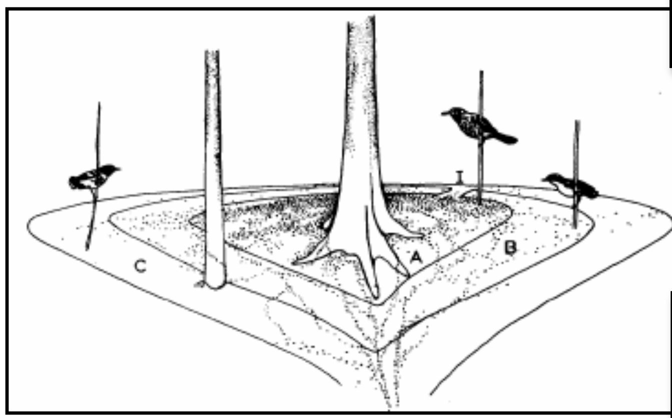
Resources are distributed across a number of unique resources and substrates: army ants allow the existence of "professional antbirds"



Willis & Oniki 1978

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Variables of climate that affect plant productivity strongly correlate with species richness

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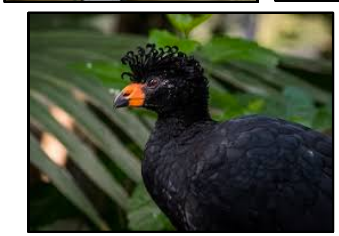
Resources are distributed across a number of unique resources and substrates: year-round availability of fruit



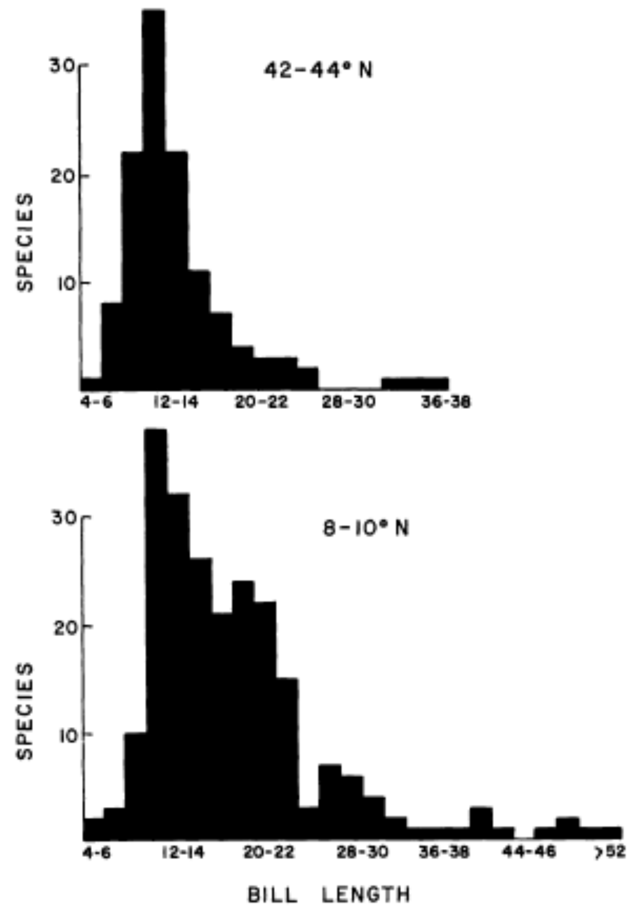


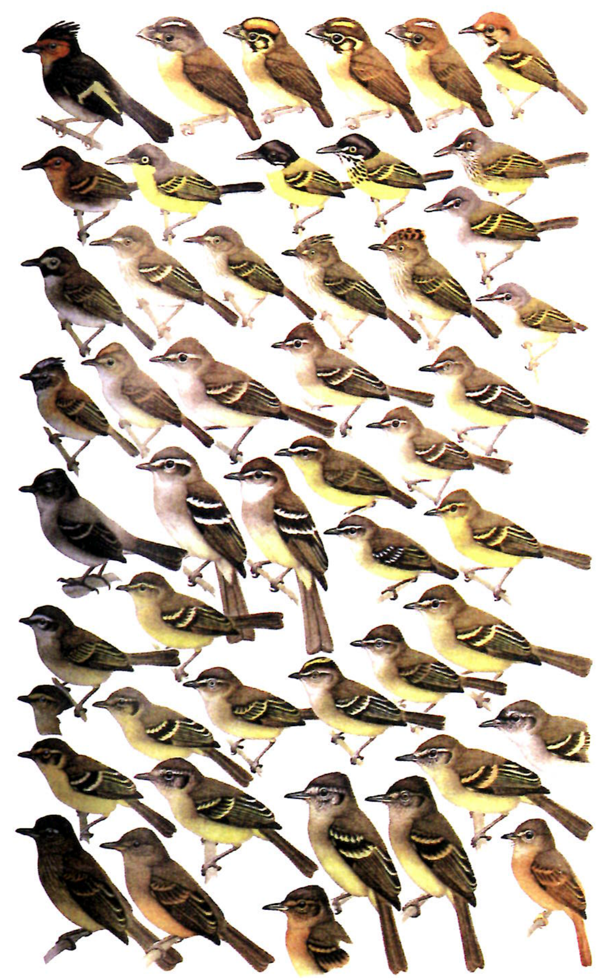
Explaining the Latitudinal Diversity Gradient

Productivity-resources hypothesis: high plant productivity allows more species to be accommodated

But how does high productivity translate into resources that support higher species richness?

Insectivorous birds in the tropics have a much wider range of bill lengths





Schoener 1971, *Condor*

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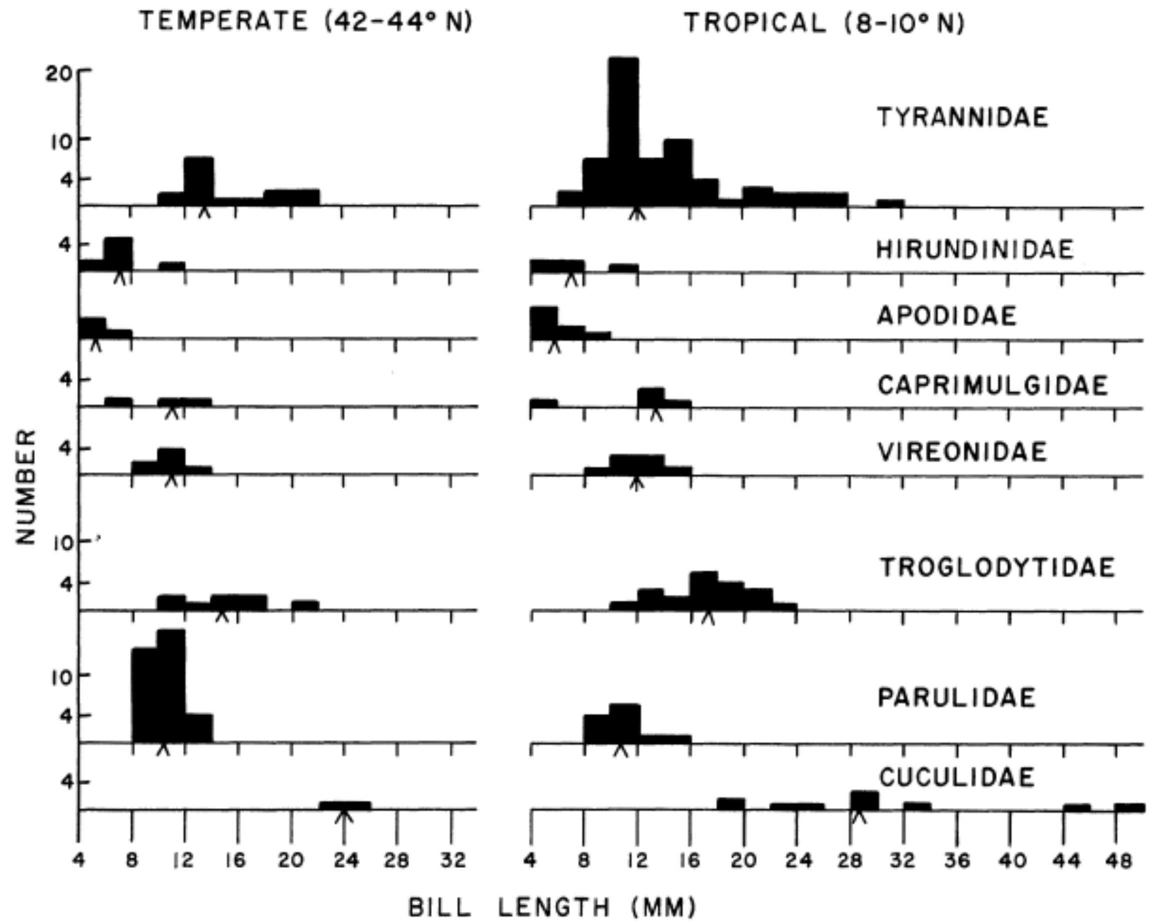

Schoener 1971, *Condor*

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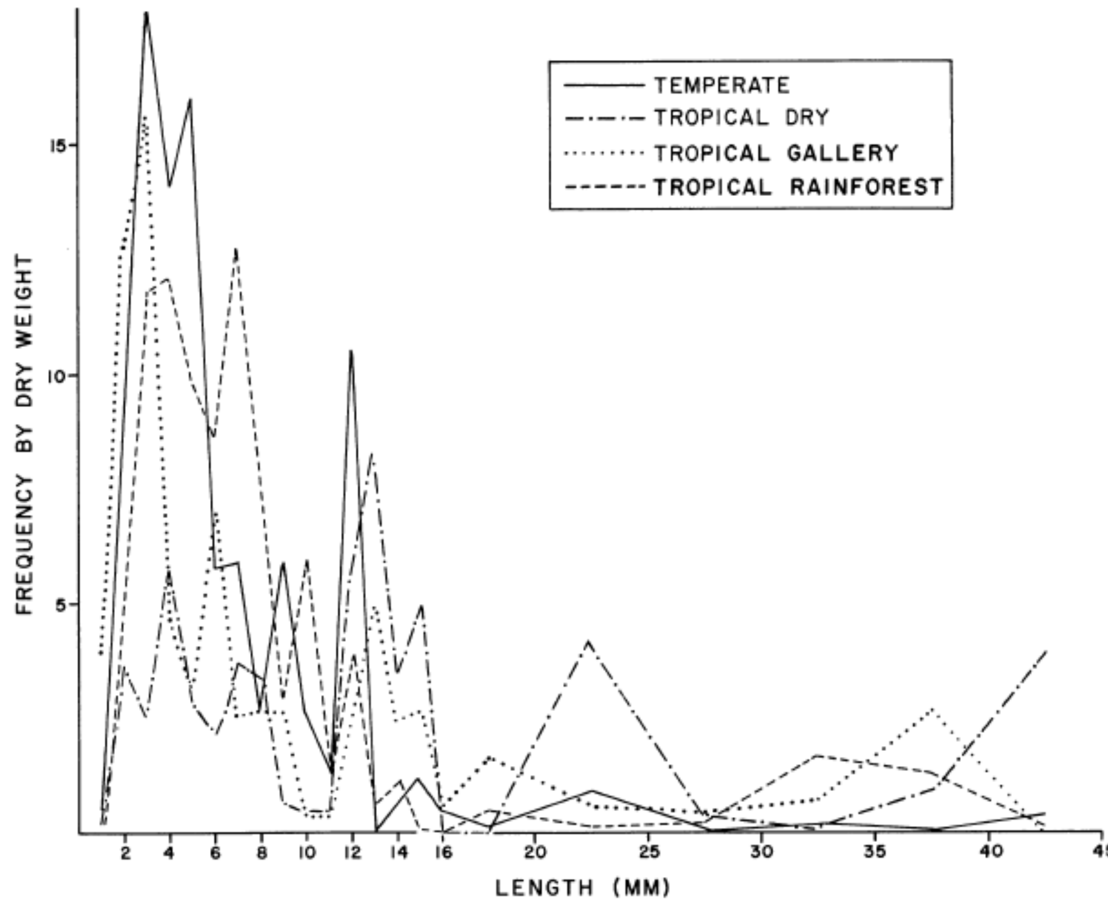
Frequency of arthropods by dry weight shows a much broader size range in tropics

The greater biomass of large arthropods extends the range of the food-size dimension that species can be placed



Schoener 1971, *Condor*

Explaining the Latitudinal Diversity Gradient

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But how does high productivity translate into resources that support higher species richness?

In some cases, additional resources lead to specialization

Black-and-white Owls and Bat Falcons are specialists on bats

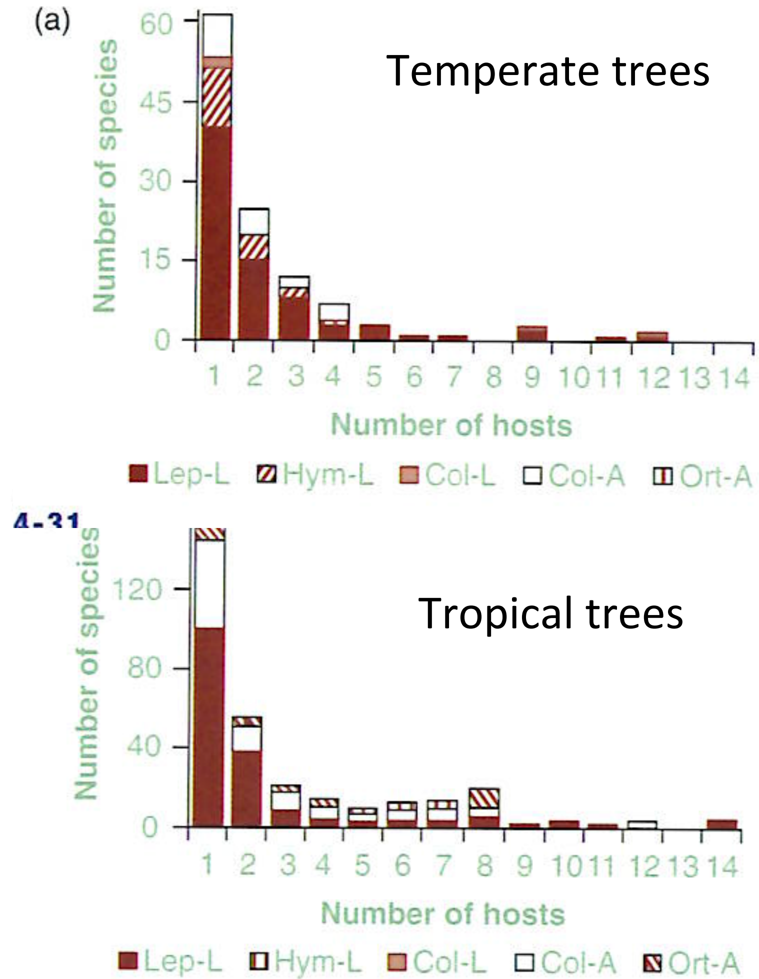
Explaining the Latitudinal Diversity Gradient

Productivity-resources hypothesis: high plant productivity allows more species to be accommodated

But how does high productivity translate into resources that support higher species richness?

In some cases, additional resources lead to specialization

But in other cases, such as host specificity of insects on tropical trees, specialization was no greater in the tropics than the temperate zone



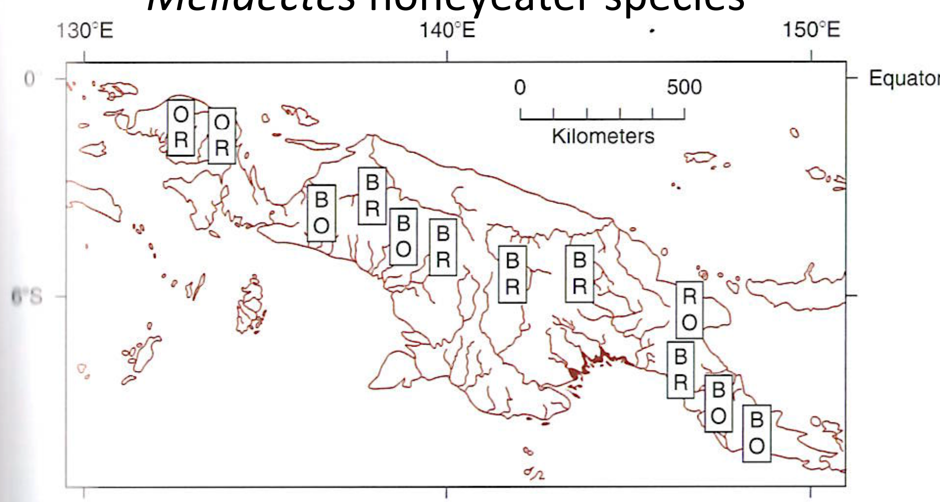
Novotny et al. 2006

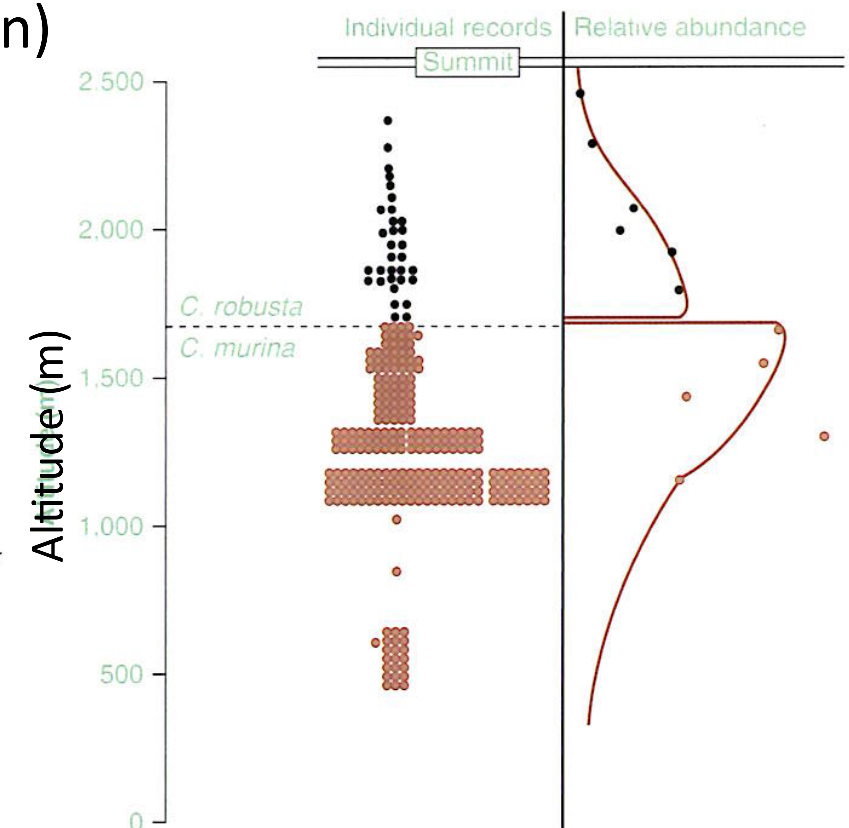
Explaining the Latitudinal Diversity Gradient

Interspecific competition hypothesis: high levels of competition have, over time, resulted in greater niche partitioning (a form of increased specialization)

Jared Diamond provided compelling evidence for competitive exclusion of honeyeaters and warblers in New Guinea

Checkerboard patterns in three *Melidectes* honeyeater species





Elevational replacements of two New Guinea warbler species

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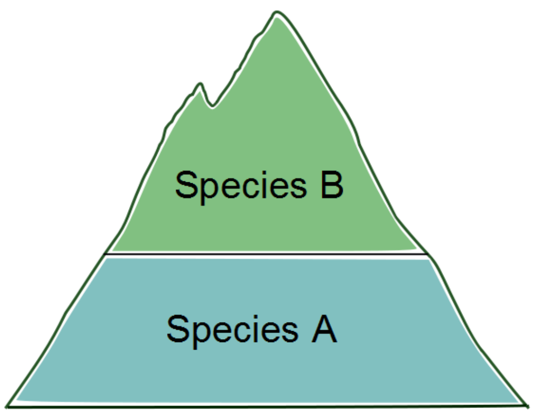

Cordillera Vilcabamba
Main Andes

A natural experiment examined niche breadth in birds

Species A and B are closely related ~ similar niche

In the main Andes:
- both species present
- ranges do not overlap

Terborgh & Weske 1975, Ecology

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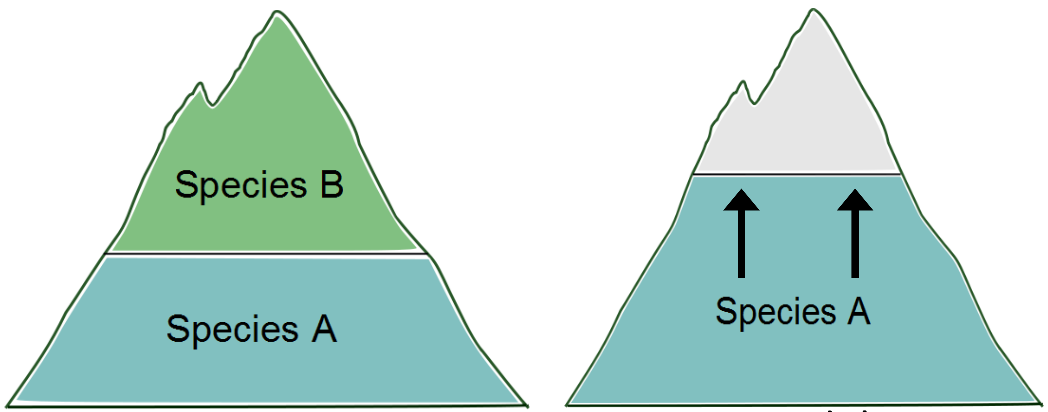

Cordillera Vilcabamba
Main Andes

Cerros del Sira
100 km from Andes

In a range isolated from the Andes:

- high elevation species absent
- low elevation species expands range upward

This comparison suggests that species show a compressed realized niche in the presence of competitors, and ecological release in their absence.

Terborgh & Weske 1975, Ecology

Explaining the Latitudinal Diversity Gradient

Predation hypothesis: by choosing the most abundant prey species, predators might allow other prey species to persist

The Neotropical eyelash viper is one of many predator species that may affect diversity patterns.

Predators can prevent prey species from competing to the point where extinction occurs

Predators switch their attention to the most abundant prey, so the rarer the species, the safer it is

This is a form of frequency- dependent selection (in this case, predation is the selective force)

Note: this effect does not predict extreme specialization – specialization might be less likely if predators keep competition levels low

Explaining the Latitudinal Diversity Gradient

Predation hypothesis: other top-down forces, like herbivory, may actually promote specialization.

White sand forest is a unique nutrient poor soil habitat that occurs in patches throughout the Amazon basin

White sand forest near Iquitos, Peru

Terra firme forest

Tree species are specific to each soil type

Species in white sand habitat are loaded with defense compounds in their leaves

Explaining the Latitudinal Diversity Gradient

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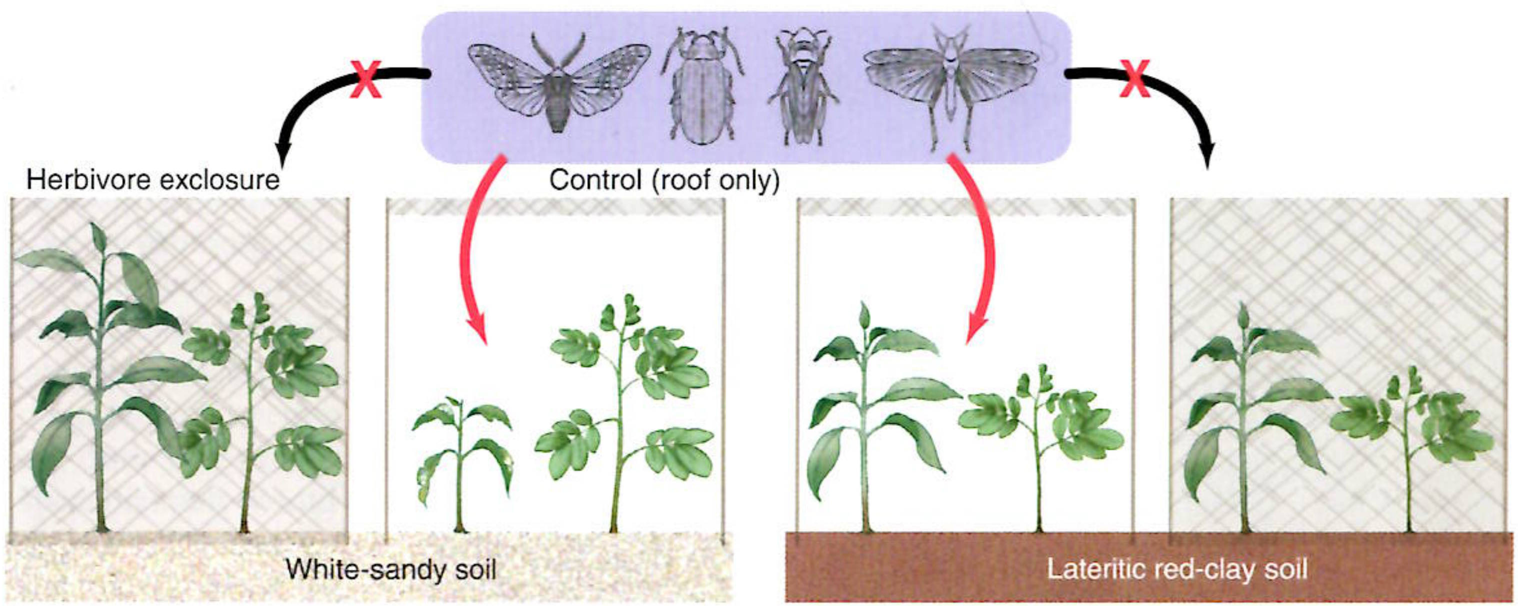
One study conducted transplant experiments of clay-soil and sandy-soil sapling species to the opposite soil type

Half of the transplants were protected from herbivores using exclosures



Fine et al. 2004, *Science*

Explaining the Latitudinal Diversity Gradient

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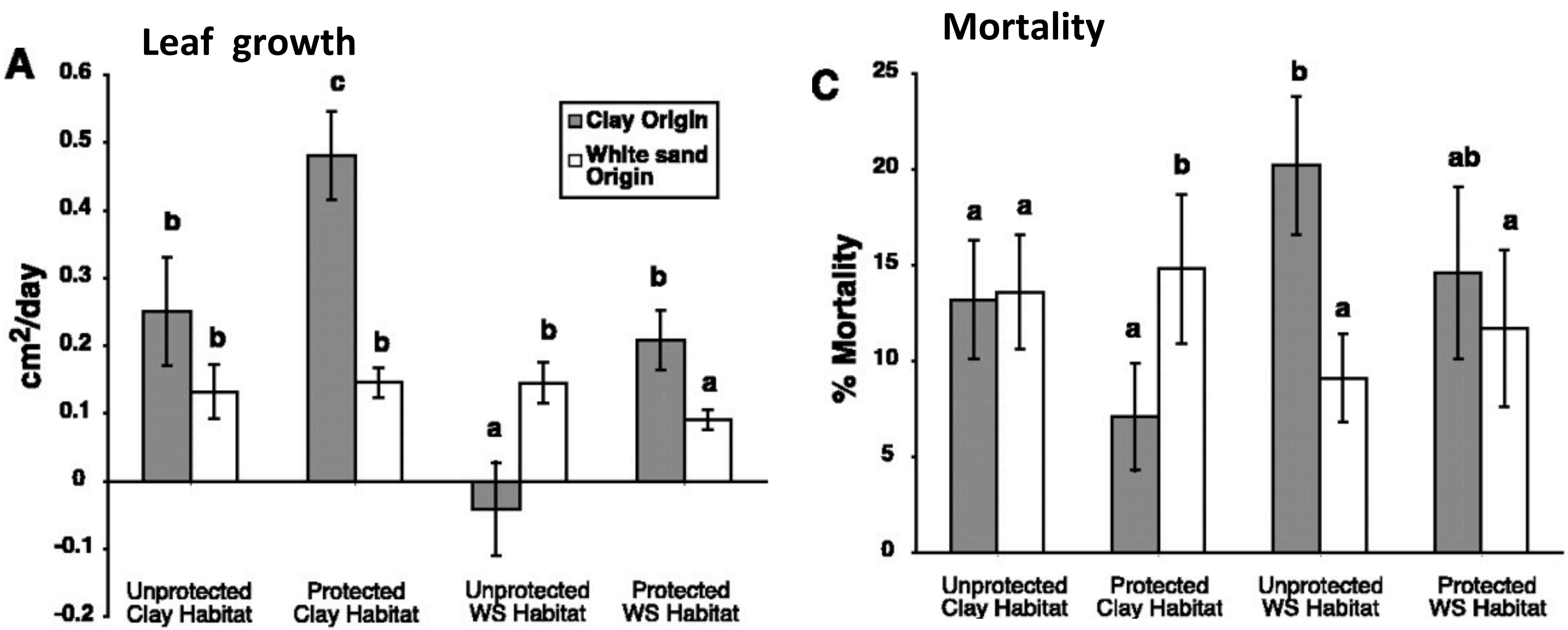
Clay-soil species grew *better* than WS species in white sand habitat when herbivores were excluded, but fared poorly when herbivores were not excluded



Fine et al. 2004, *Science*

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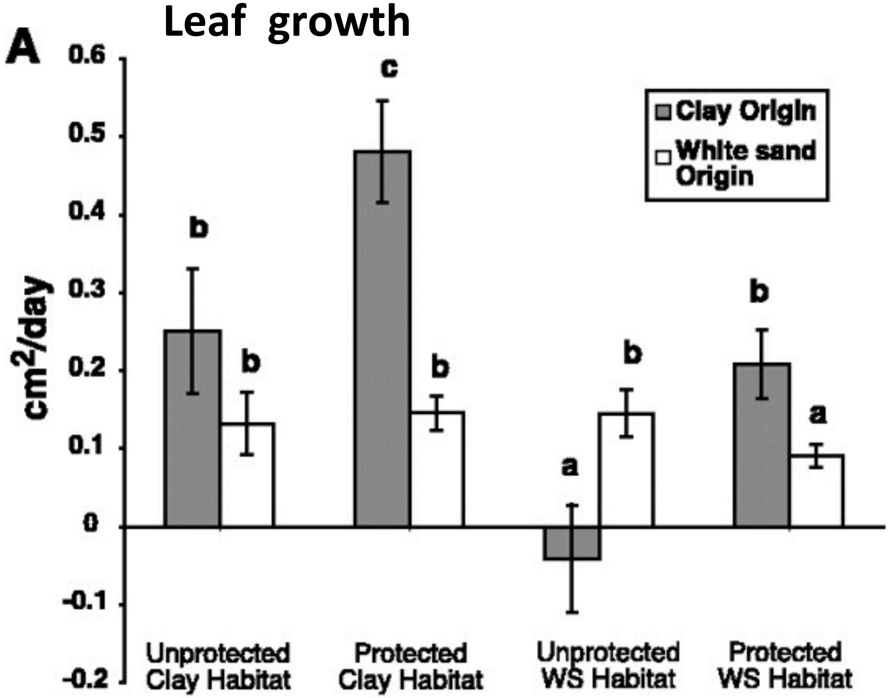
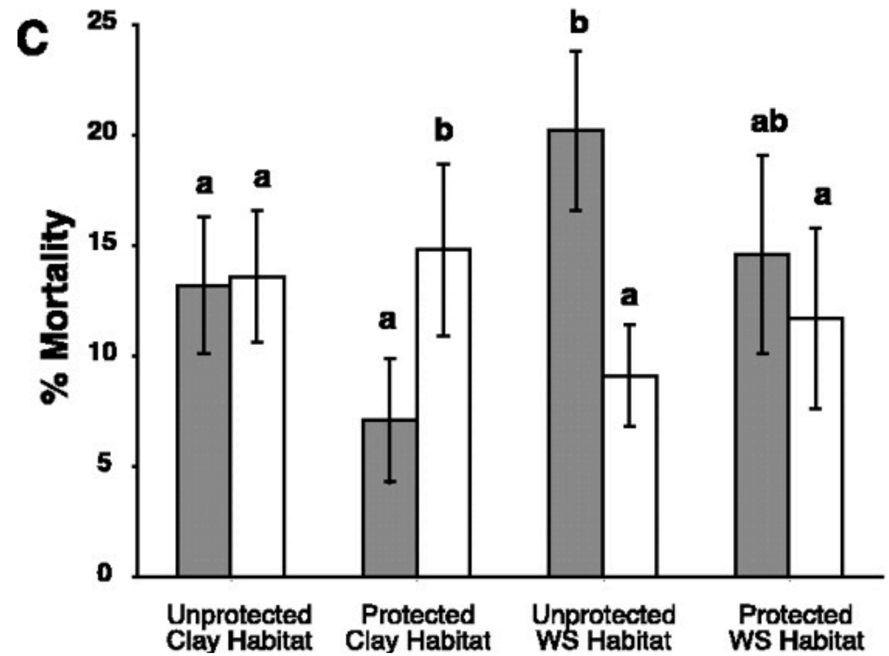
Speciation on white sands may have resulted from strong selection for defense compounds (sufficient to overcome gene flow from individuals on clay soil)

Leaf growth



Mortality



Fine et al. 2004, *Science*