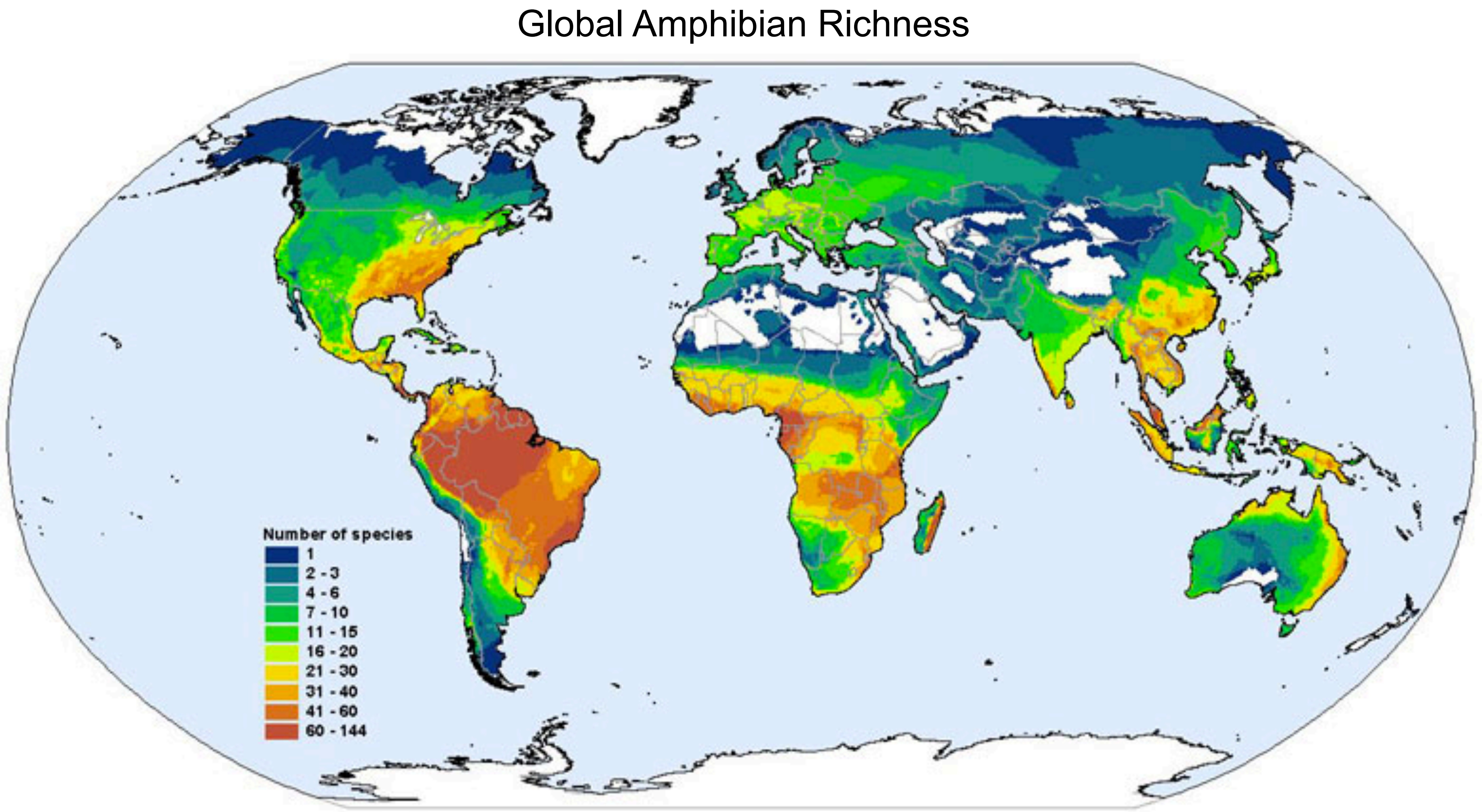
Patterns of Species Diversity



http://www.globalamphibians.org/

Goals and learning objectives

1) Define and understand different aspects of diversity – and how they are measured at different scales

2) Understand how the different components of diversity (alpha, beta, gamma diversity) contribute to the overall latitudinal diversity gradient

3) Describe the main hypotheses that have been proposed to explain the latitudinal gradient in diversity, along with *exceptions* to those models/ hypotheses

4) Be familiar with other kinds of diversity gradients and important latitudinal trends (Rapaport's Rule, Janzen's hypothesis)

Patterns of Species Diversity

Basic terms and quantifying species diversity:

Species *richness* is a basic property of communities and regions in biogeography.

Species richness: the number of species within a prescribed area, without regard to numerical abundance or ecological importance in a given community

Three levels of diversity indices:

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

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

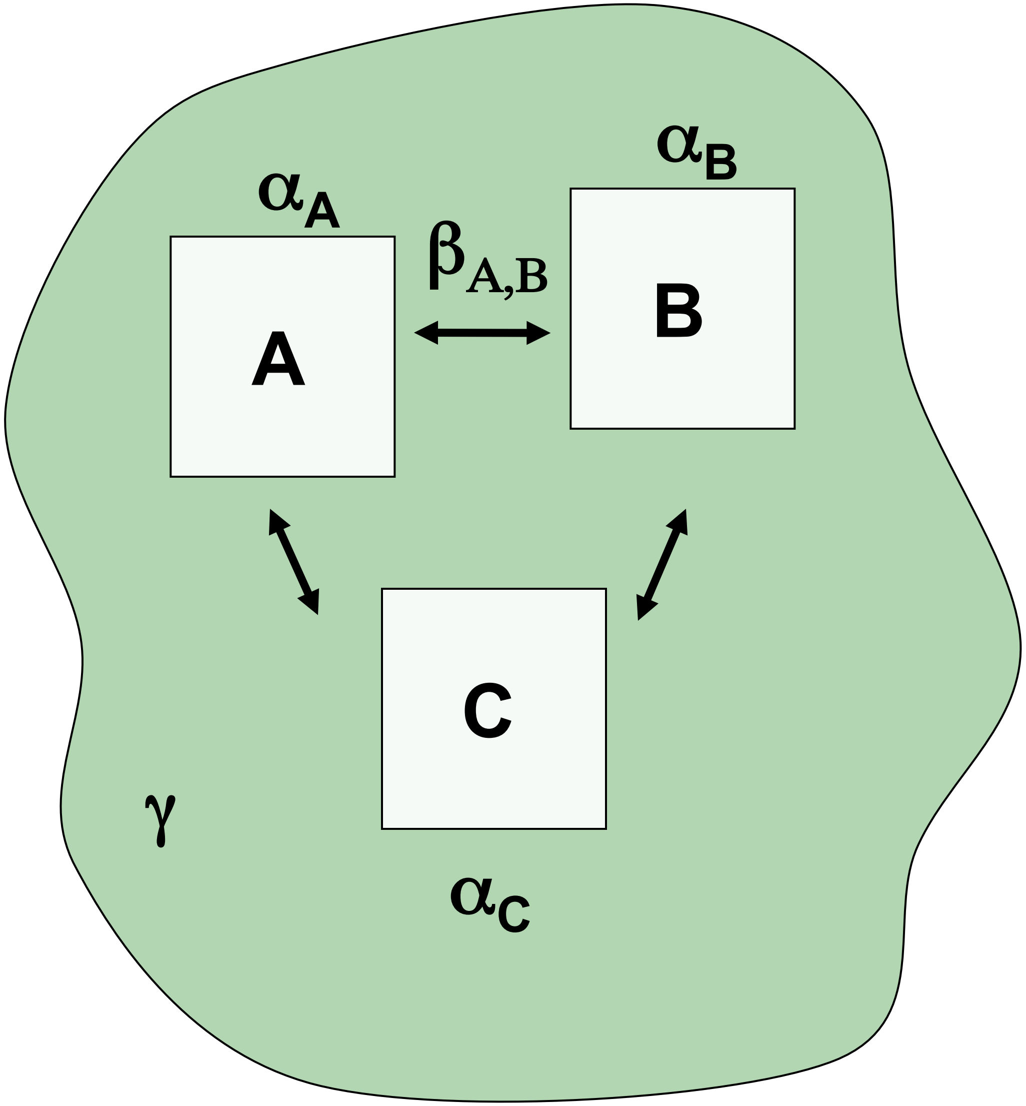
Gamma (γ) diversity: number of species within a larger region. Gamma diversity is a function of both alpha and beta diversity.

Recall: Spatial components of species diversity

Gamma (γ) diversity

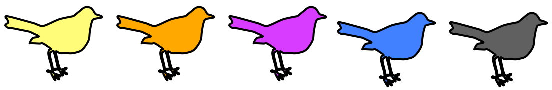
Alpha (α) diversity

Beta (β) diversity

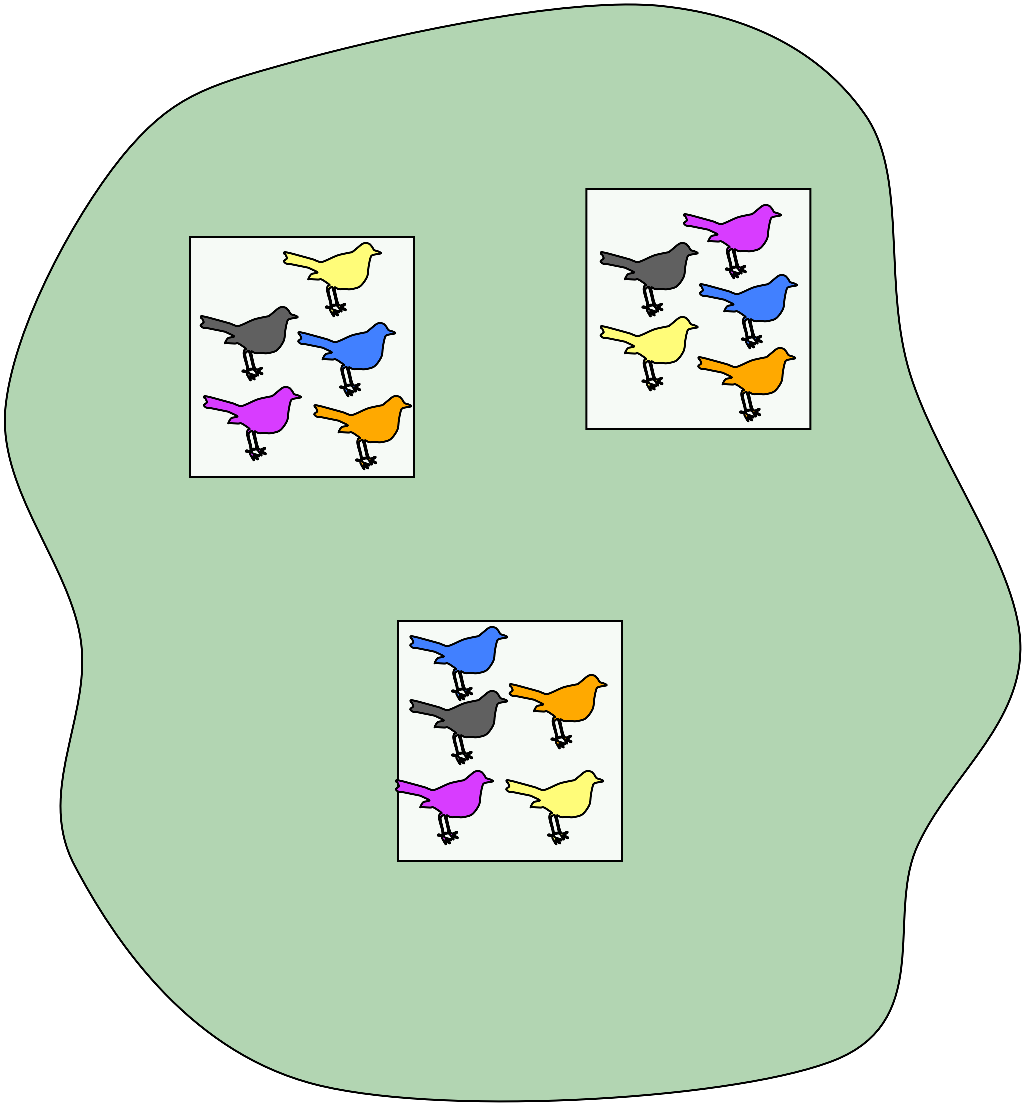


Patterns of Species Diversity

Regional pool (γ)

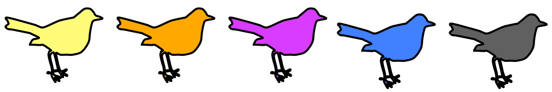


If α diversity ≅ γ diversity
→ low β diversity



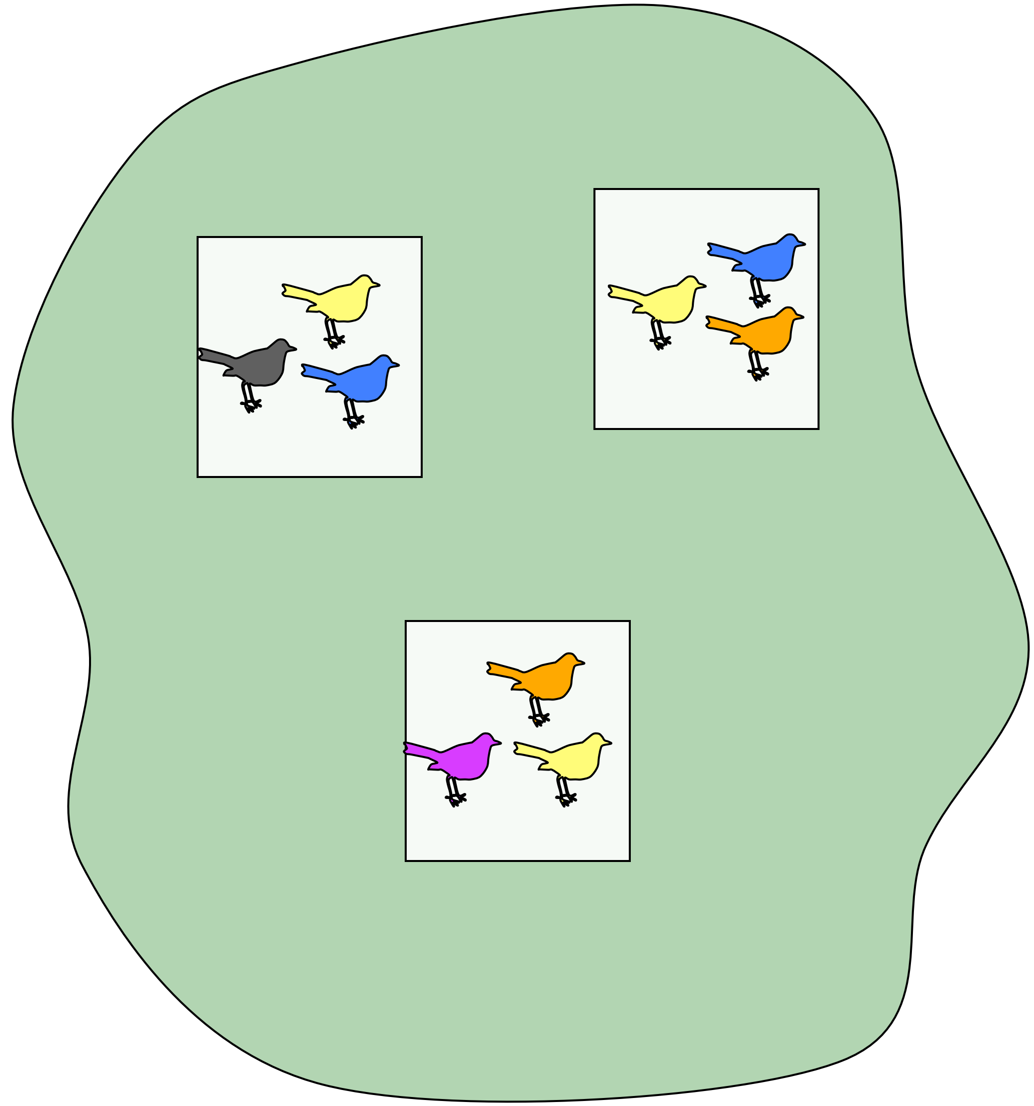
Patterns of Species Diversity

Regional pool (γ)



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

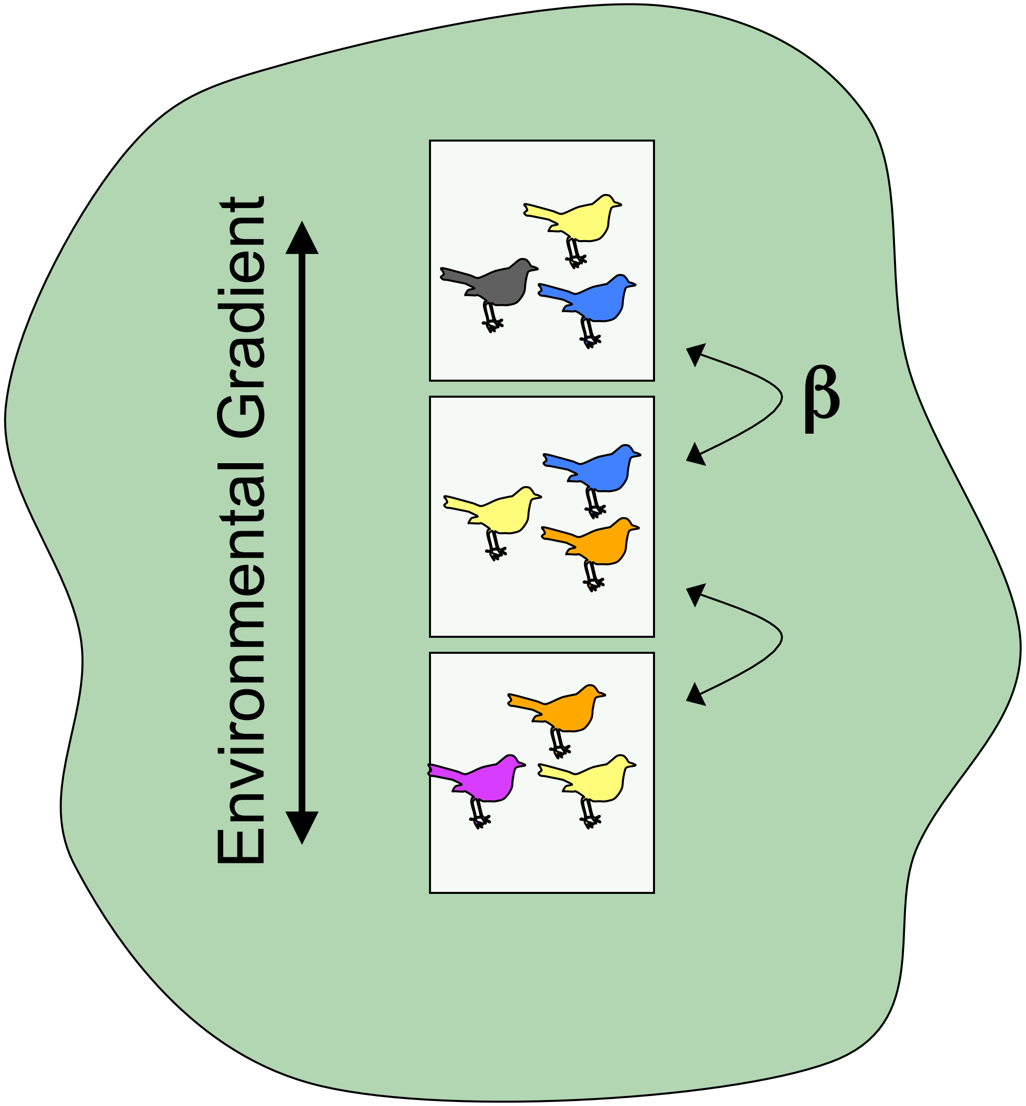
If α diversity < γ diversity
→ high β diversity



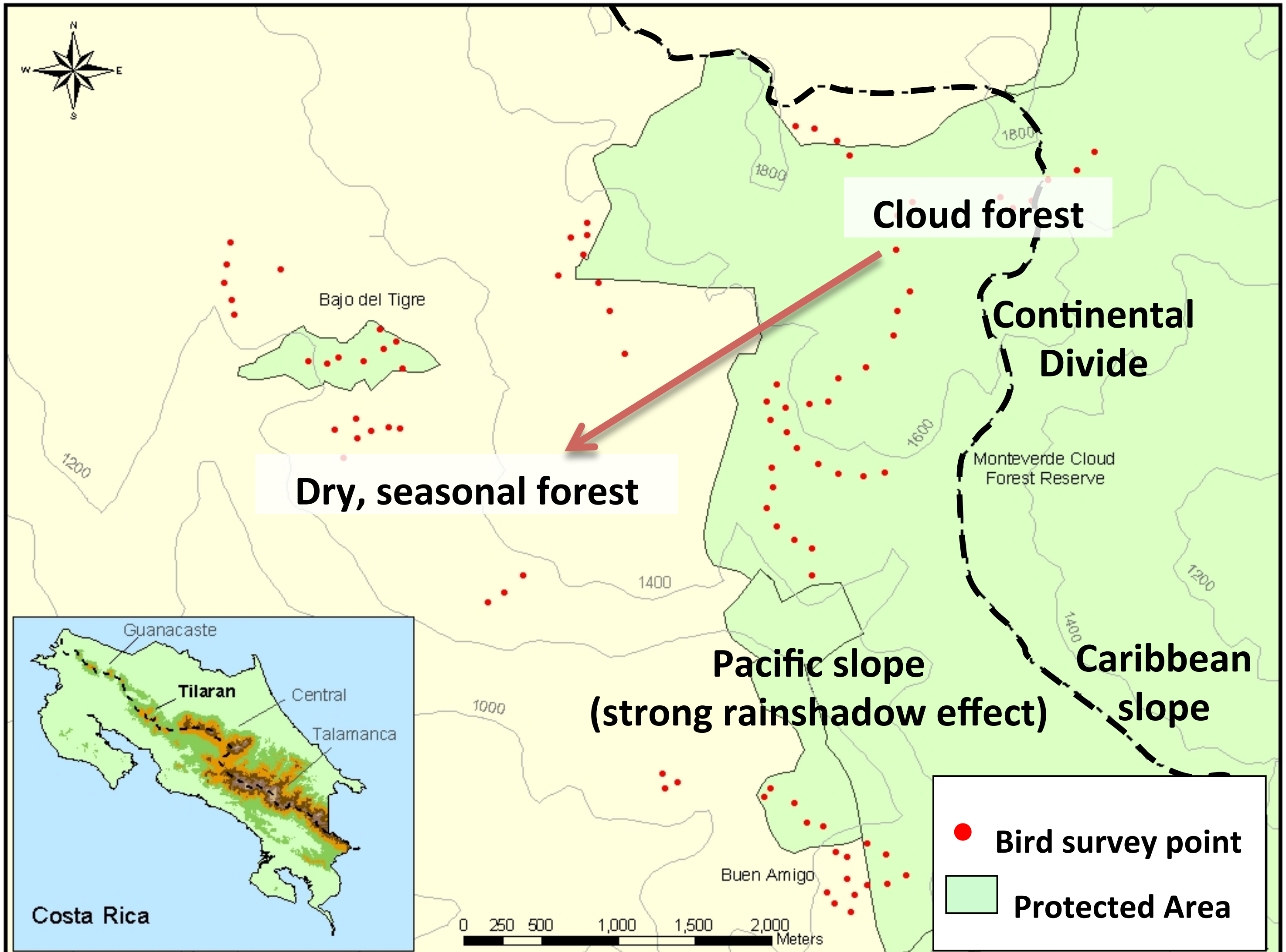
Patterns of Species Diversity

Species turnover:
beta diversity examined along axis of variation

How does the gradient affect composition?



Patterns of Species Diversity

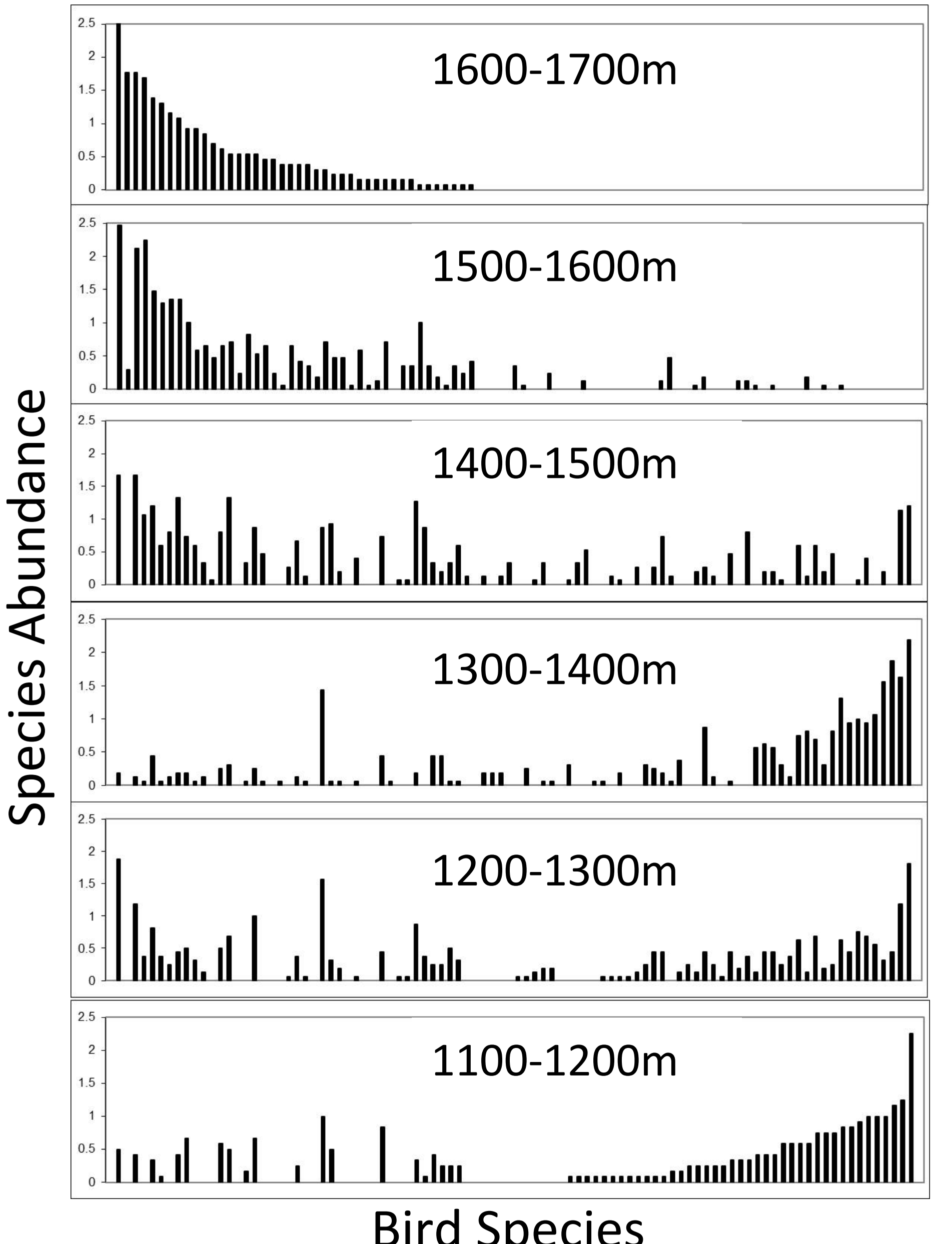


Tilarán Mountains, Costa Rica: 1100-1800m

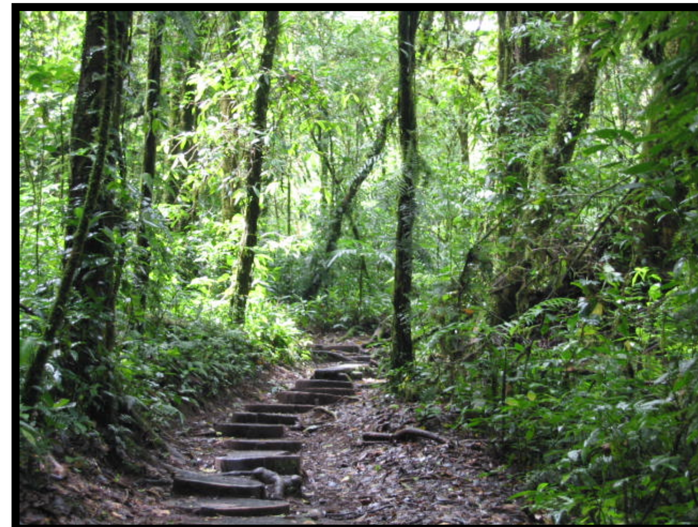
Change in bird community composition with elevation in Costa Rica.

Can look at beta diversity across elevation

Patterns of Species Diversity



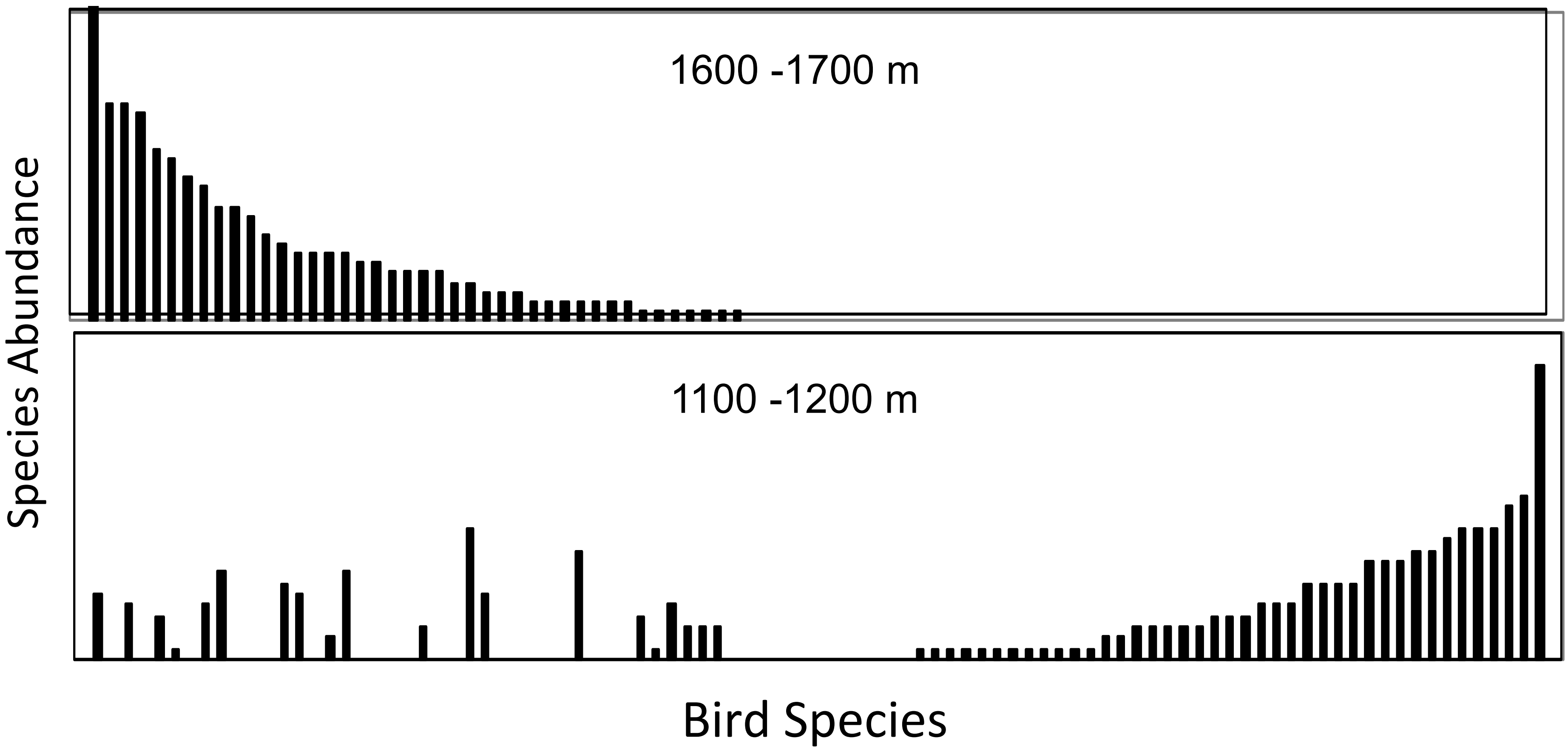
Visualizing beta diversity across elevational zones in Costa Rica



(Jankowski *et al.* 2009)

Patterns of Species Diversity

In 500m elevation, nearly 100% turnover in species...



Jankowski et al. 2009*, J. Anim. Ecol.*

Patterns of Species Diversity

Outline of topics in this section:

1) Demonstrating the latitudinal diversity gradient

2) Causes for the latitudinal diversity gradient

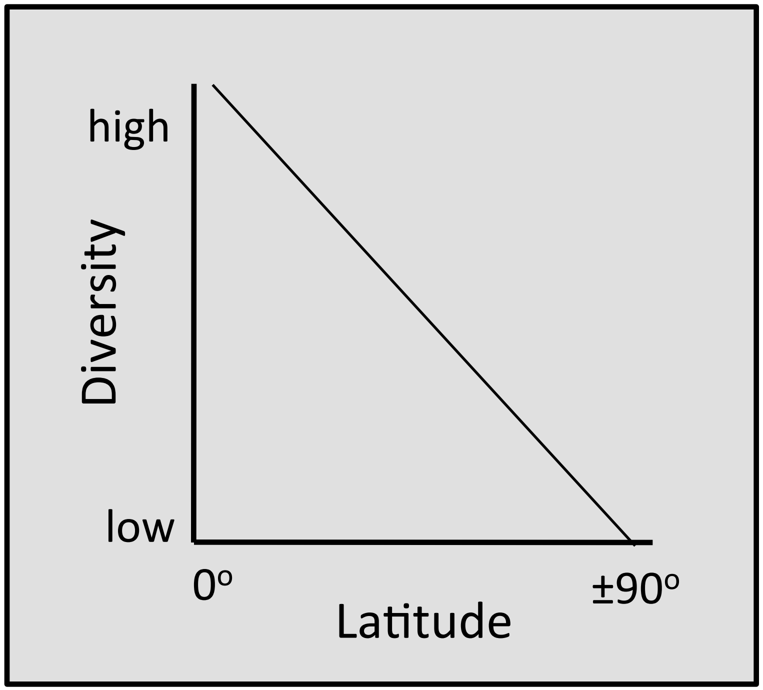
3) Synthesis

4) Other latitudinal trends

5) Other spatial diversity gradients

Latitudinal Diversity Gradient

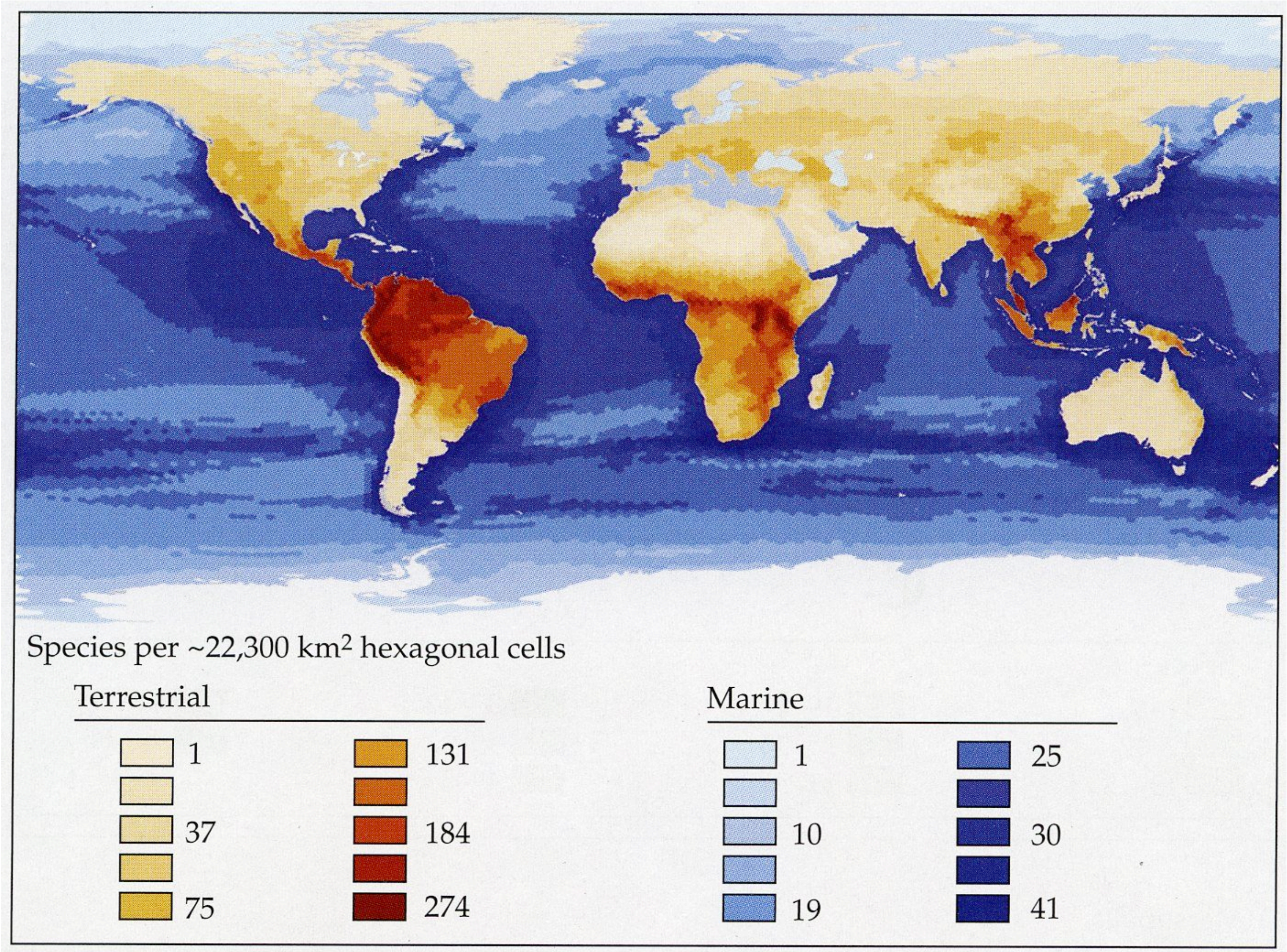
There is higher alpha, beta, and gamma diversity in the tropics.



Latitudinal Diversity Gradient

This gradient has been demonstrated across multiple and diverse taxa

Terrestrial and marine mammals:

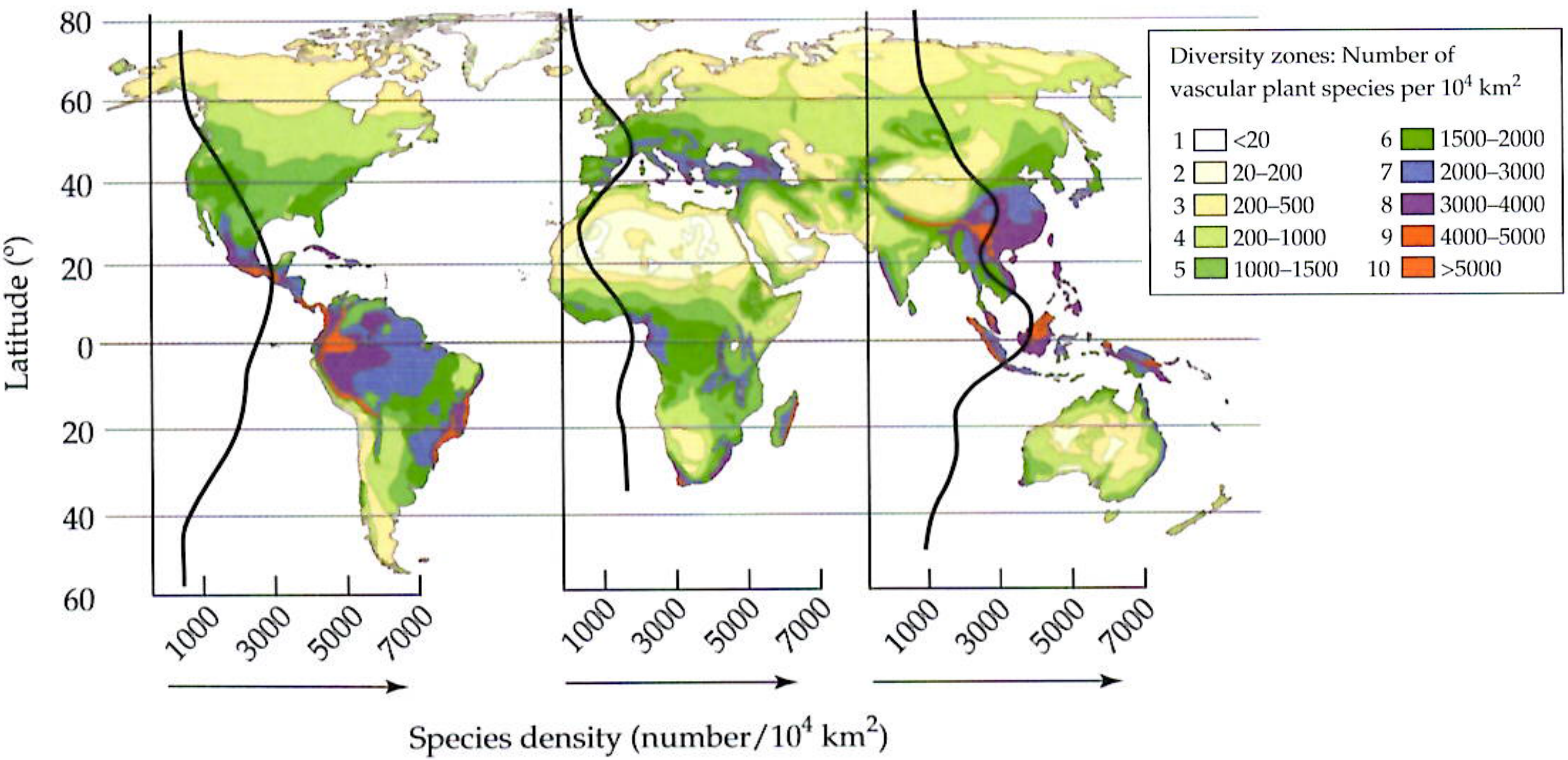


(all following global diversity maps from Lomolino *et al.* 2010)

Latitudinal Diversity Gradient

This gradient has been demonstrated across multiple and diverse taxa

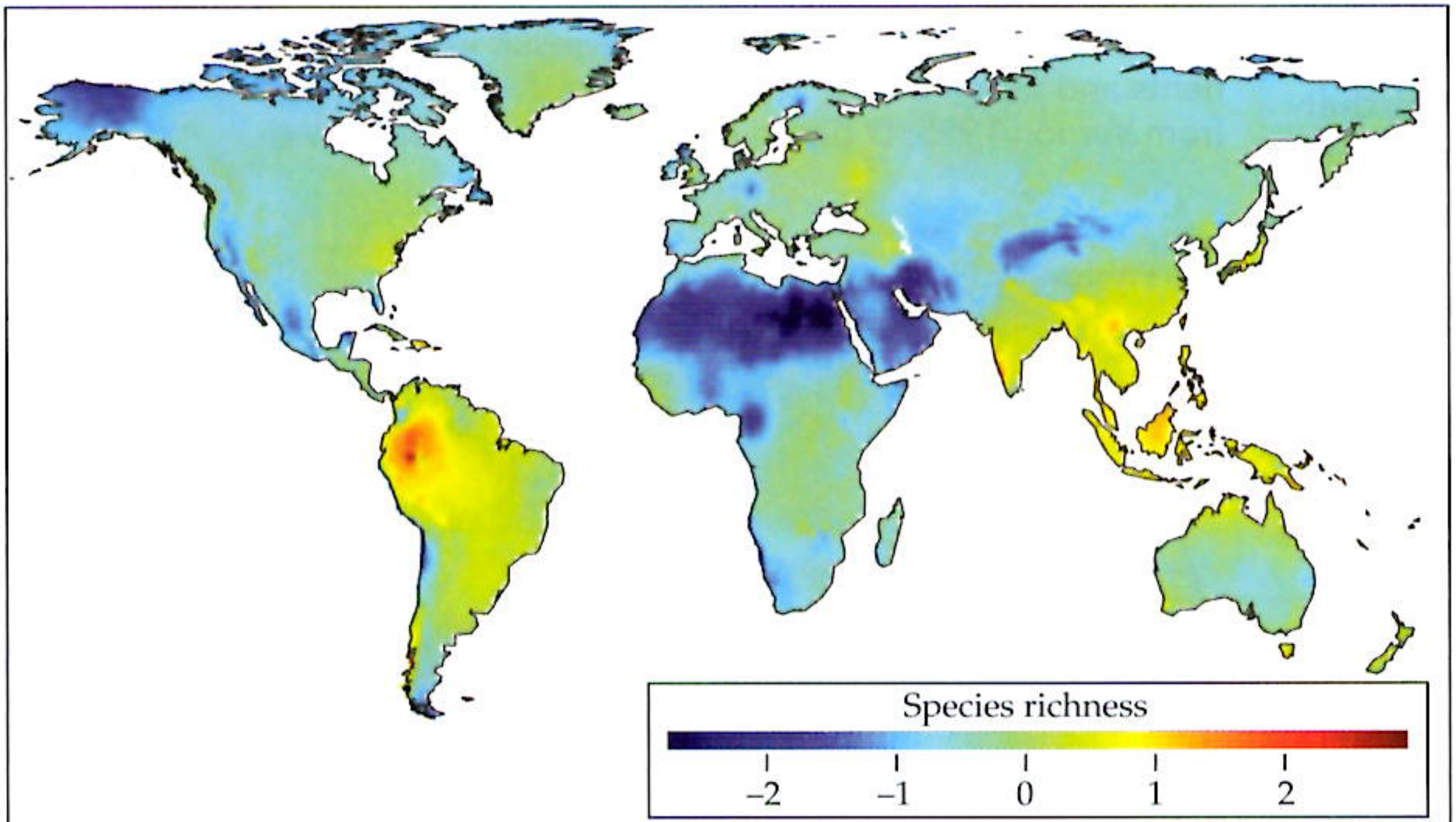
Vascular plants:



Latitudinal Diversity Gradient

This gradient has been demonstrated across multiple and diverse taxa

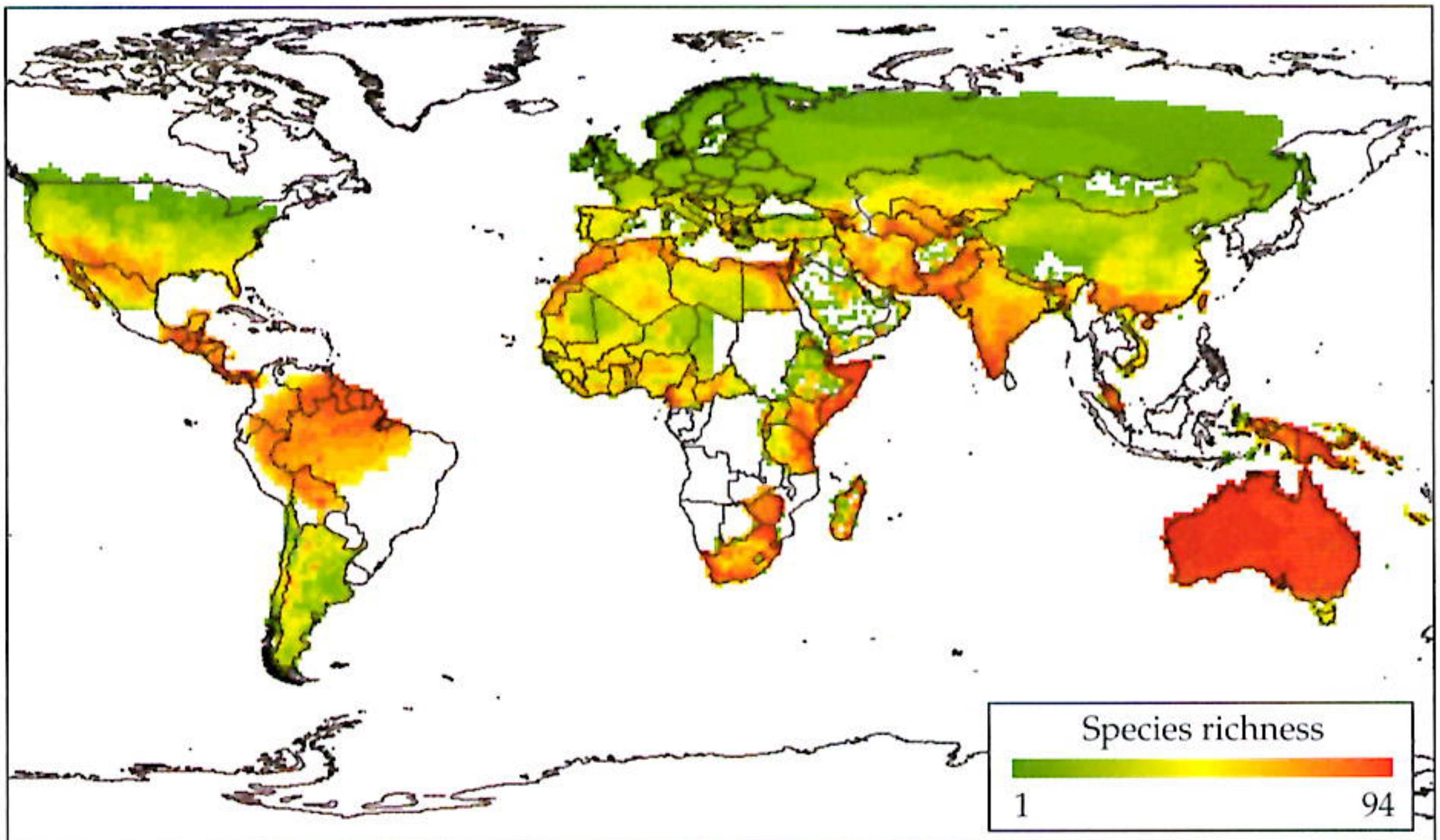
Soil fungi:



Latitudinal Diversity Gradient

This gradient has been demonstrated across multiple and diverse taxa

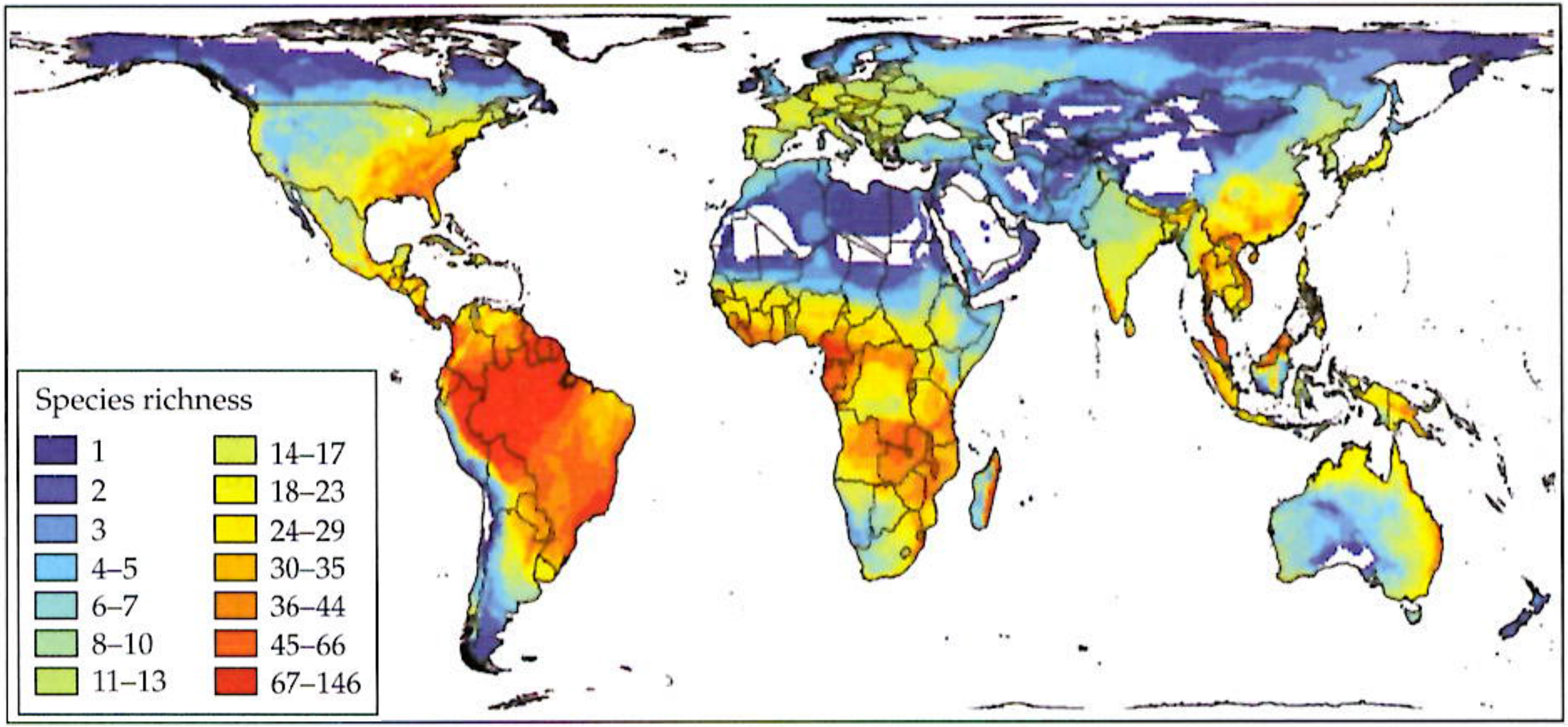
Lizards:



Latitudinal Diversity Gradient

This gradient has been demonstrated across multiple and diverse taxa

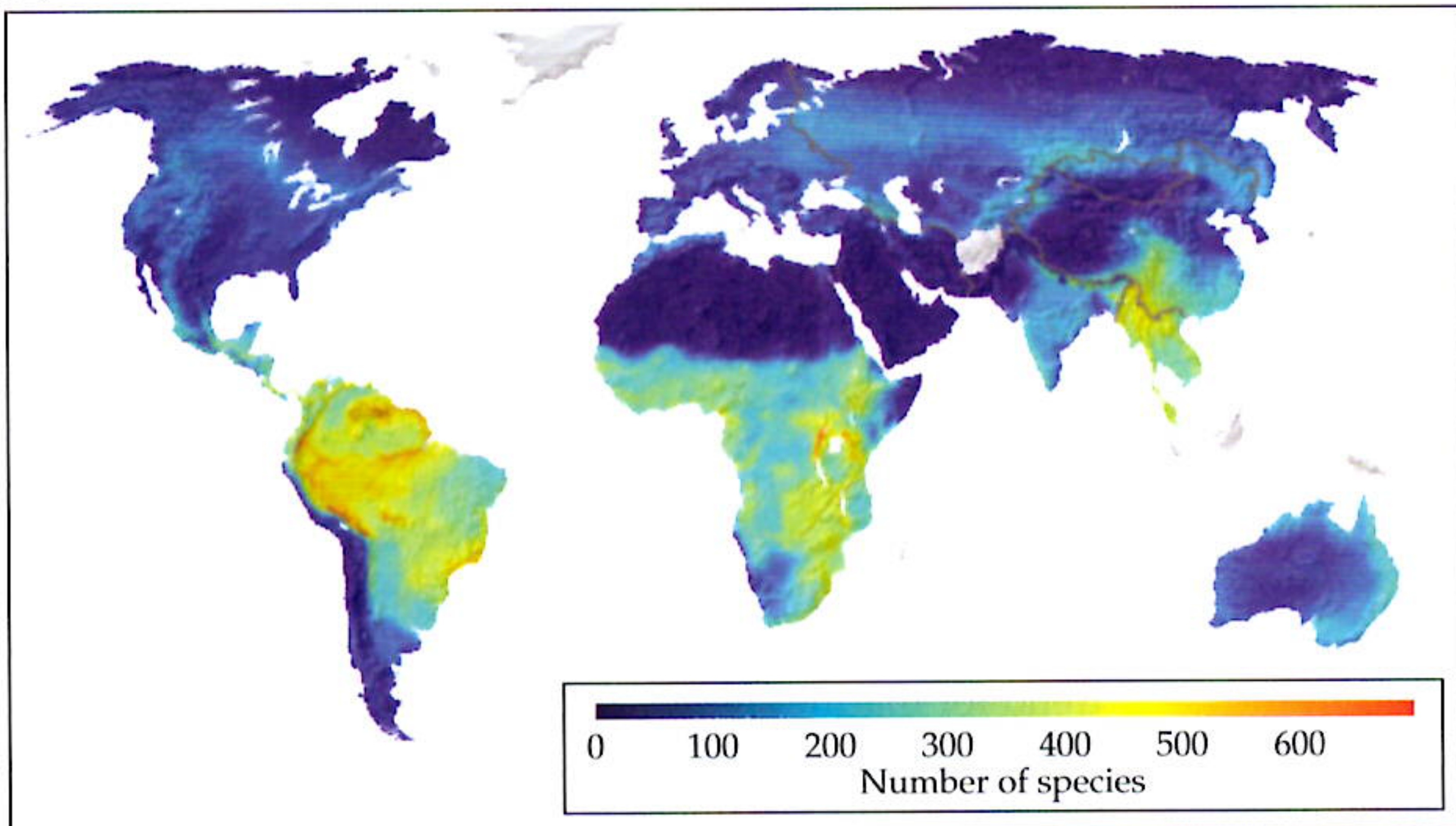
Amphibians:



Latitudinal Diversity Gradient

This gradient has been demonstrated across multiple and diverse taxa

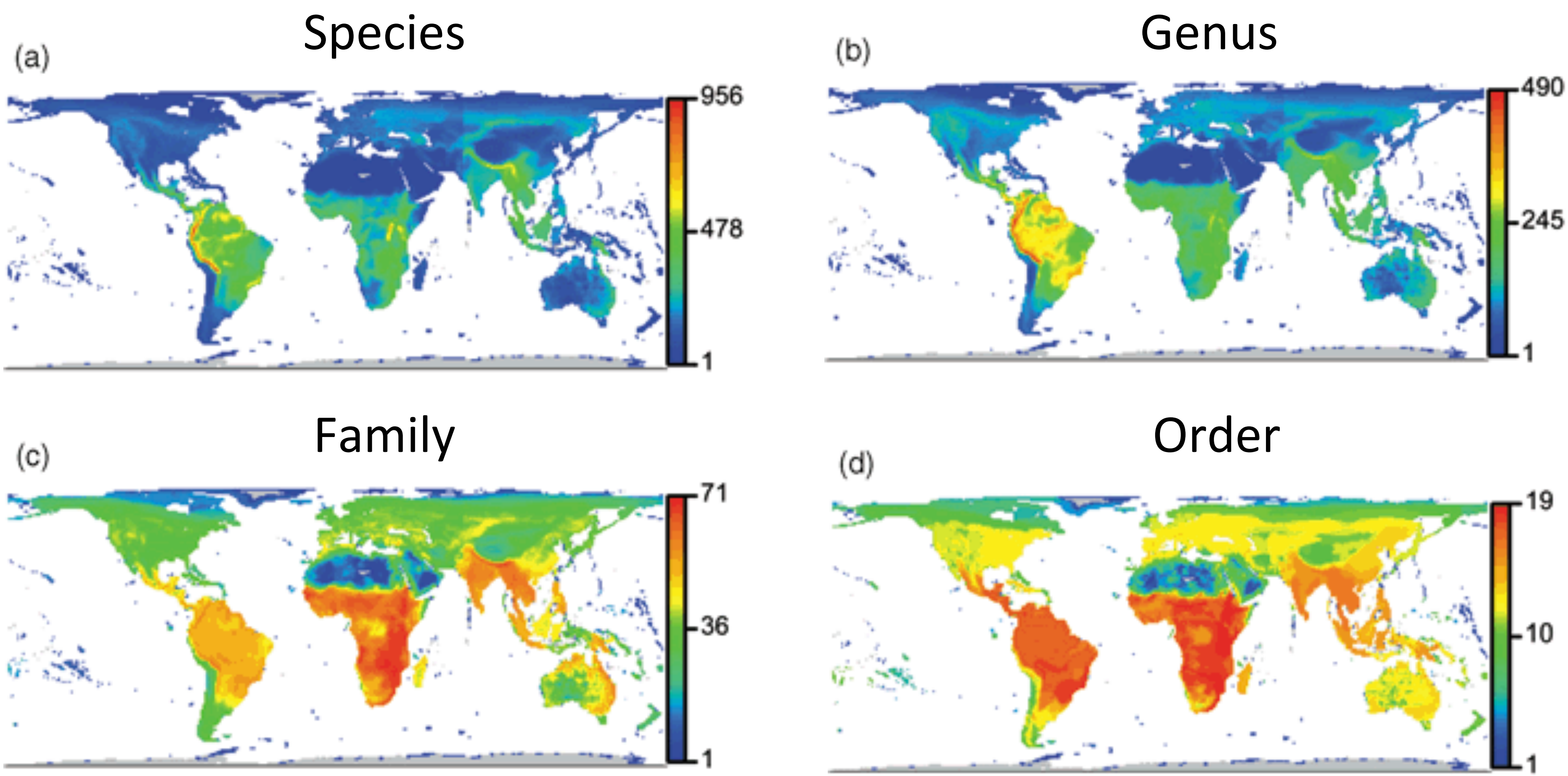
Birds:



(from Lomolino *et al.* 2010)

Latitudinal Diversity Gradient

The relationship holds across different levels of taxonomic organization (e.g., in birds)



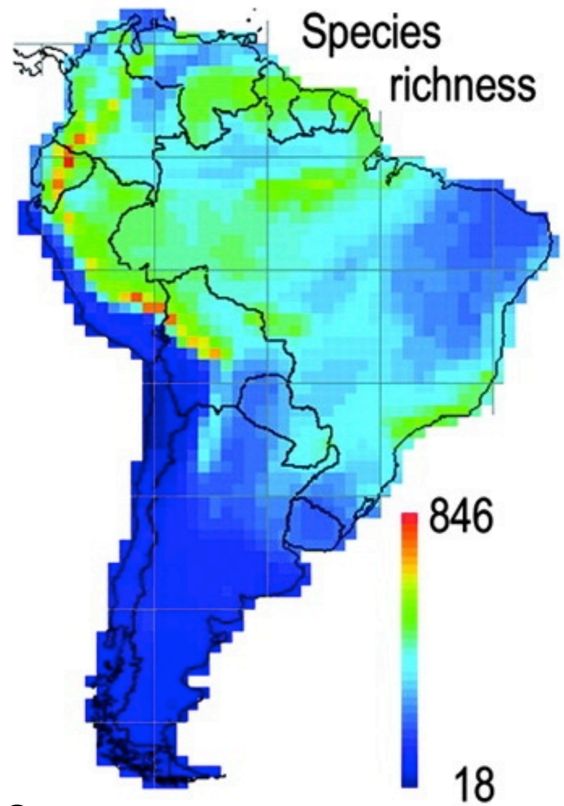
No. Species per 1° lat/long cell

Thomas *et al*. 2008, *Global Ecology and Biogeography*

Andean-Amazonian (Gamma) Diversity

3300 species in South America

2650 species in tropical Andes and Amazonian lowlands

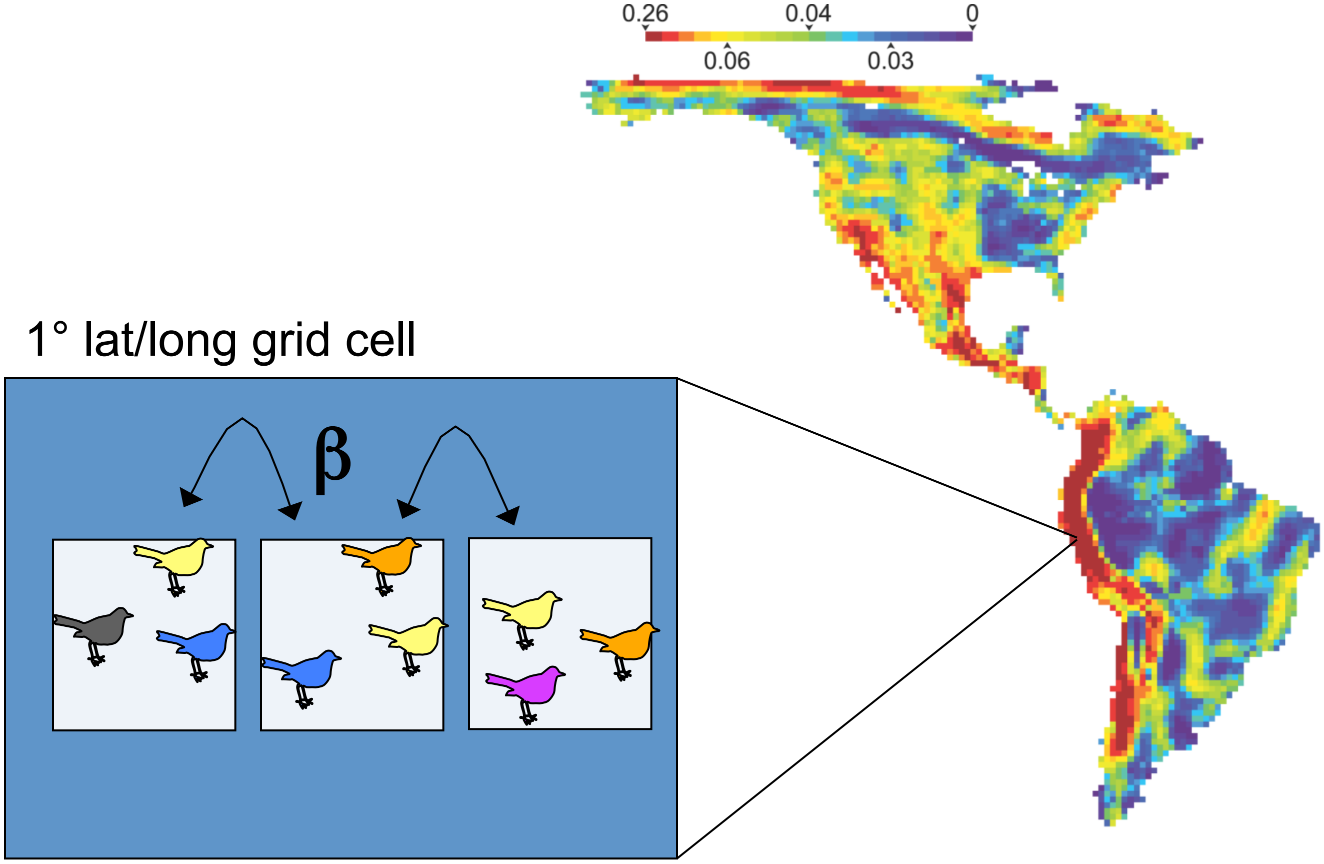


→ Number of species in each 1 degree grid cell

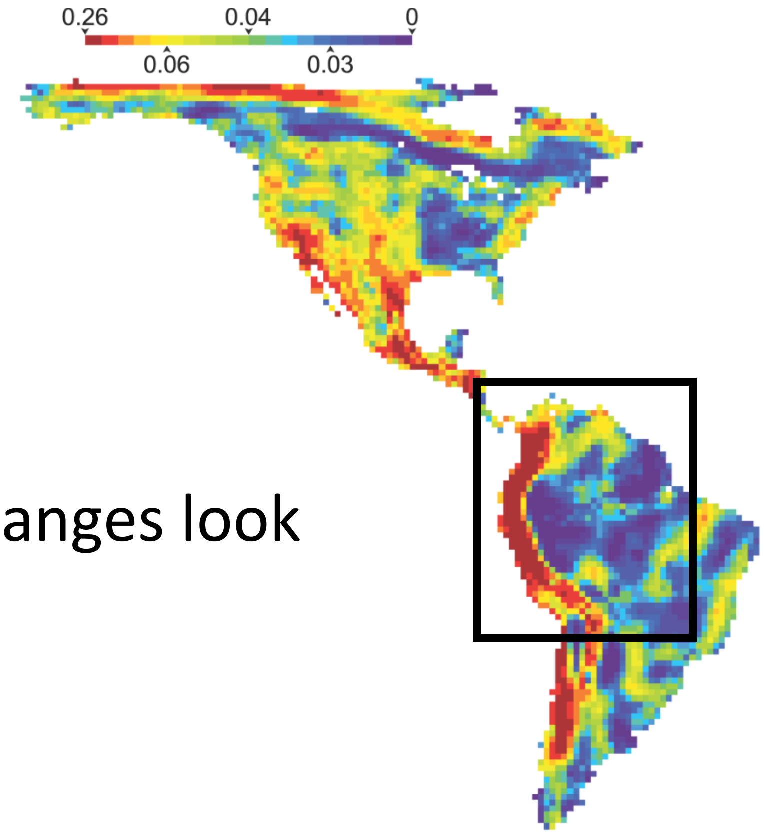
Note that within South America we see strong diversity trends from the Equator to southern latitudes

Graves & Rahbek 2005, *PNAS*

How does species composition change across space?
Beta-diversity (species turnover)



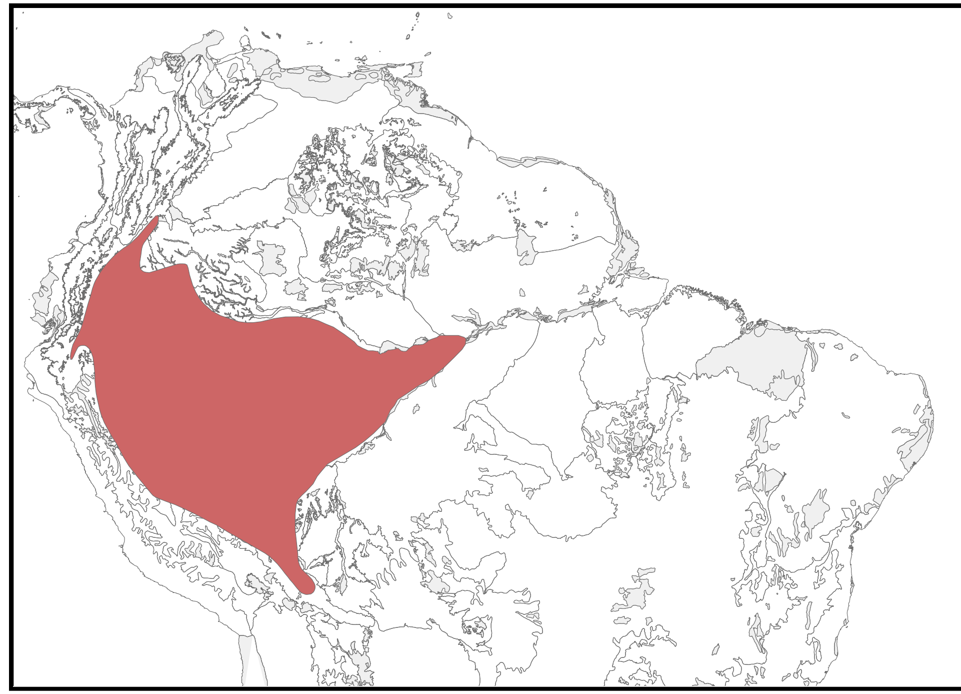
How does species composition change across space?
Beta-diversity (species turnover)



What do species' ranges look like in the tropics?

Expansive ranges of Amazonian birds

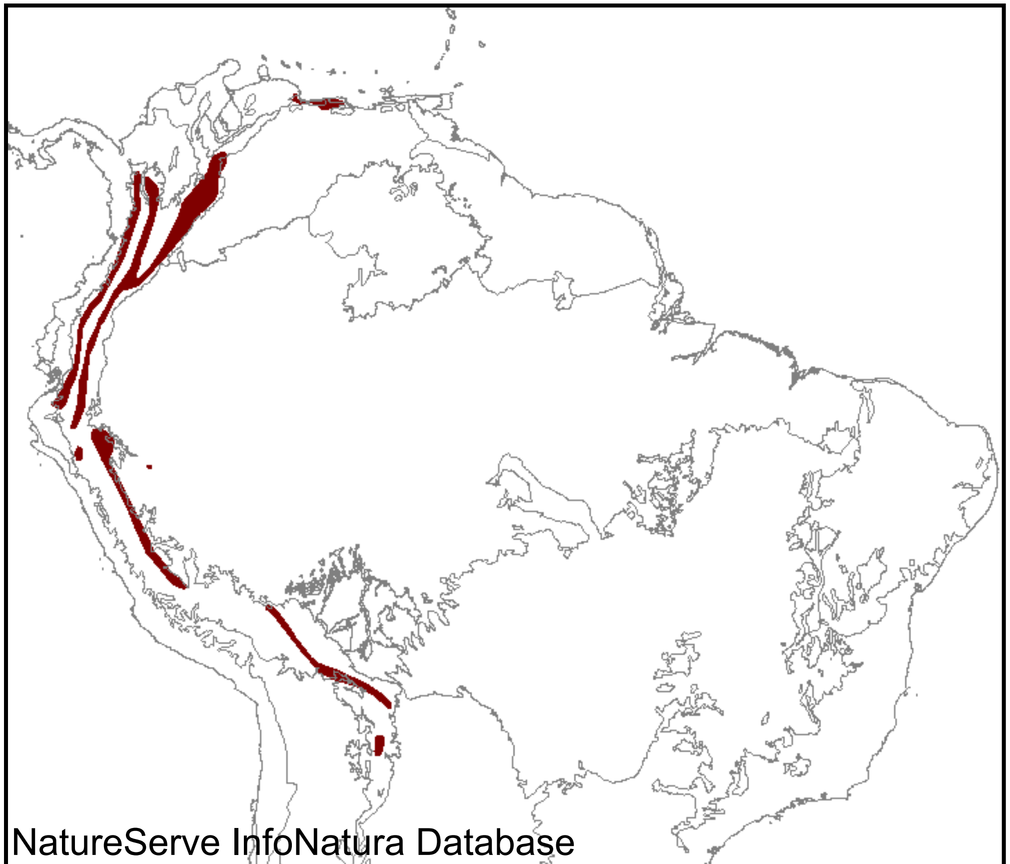
Hairy-crested Antbird
Rhegmatorhina melanosticta



Ridgely et al. 2005; Digital Distribution Maps of Birds of Western Hemisphere

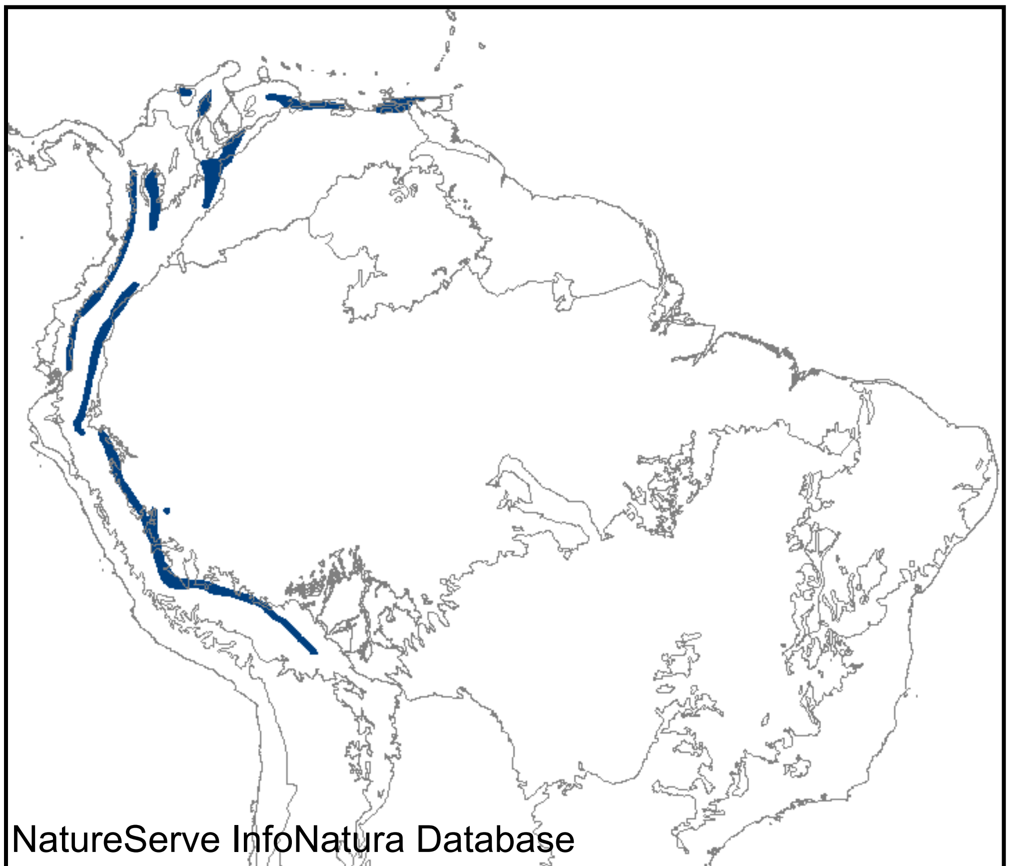
"Shoestring" distributions of montane birds

Blue-winged Mountain-Tanager
Anisognathus somptuosus



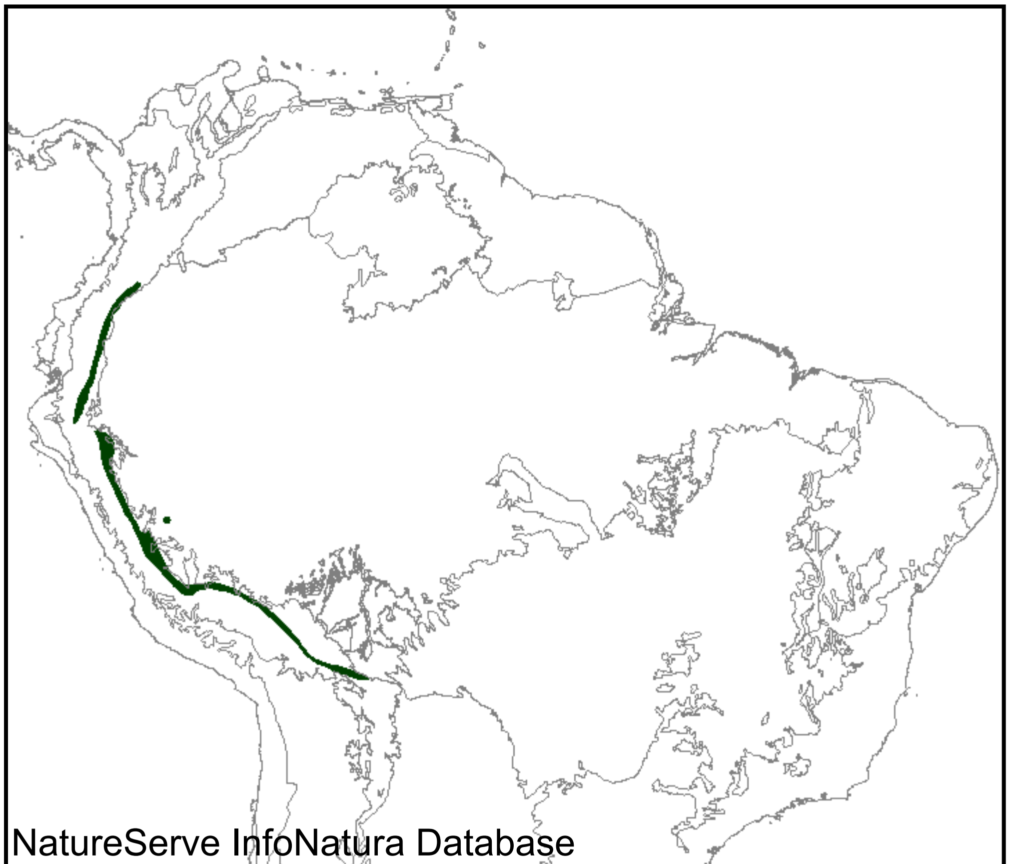
"Shoestring" distributions of montane birds

Long-tailed Antbird
Drymophila caudata

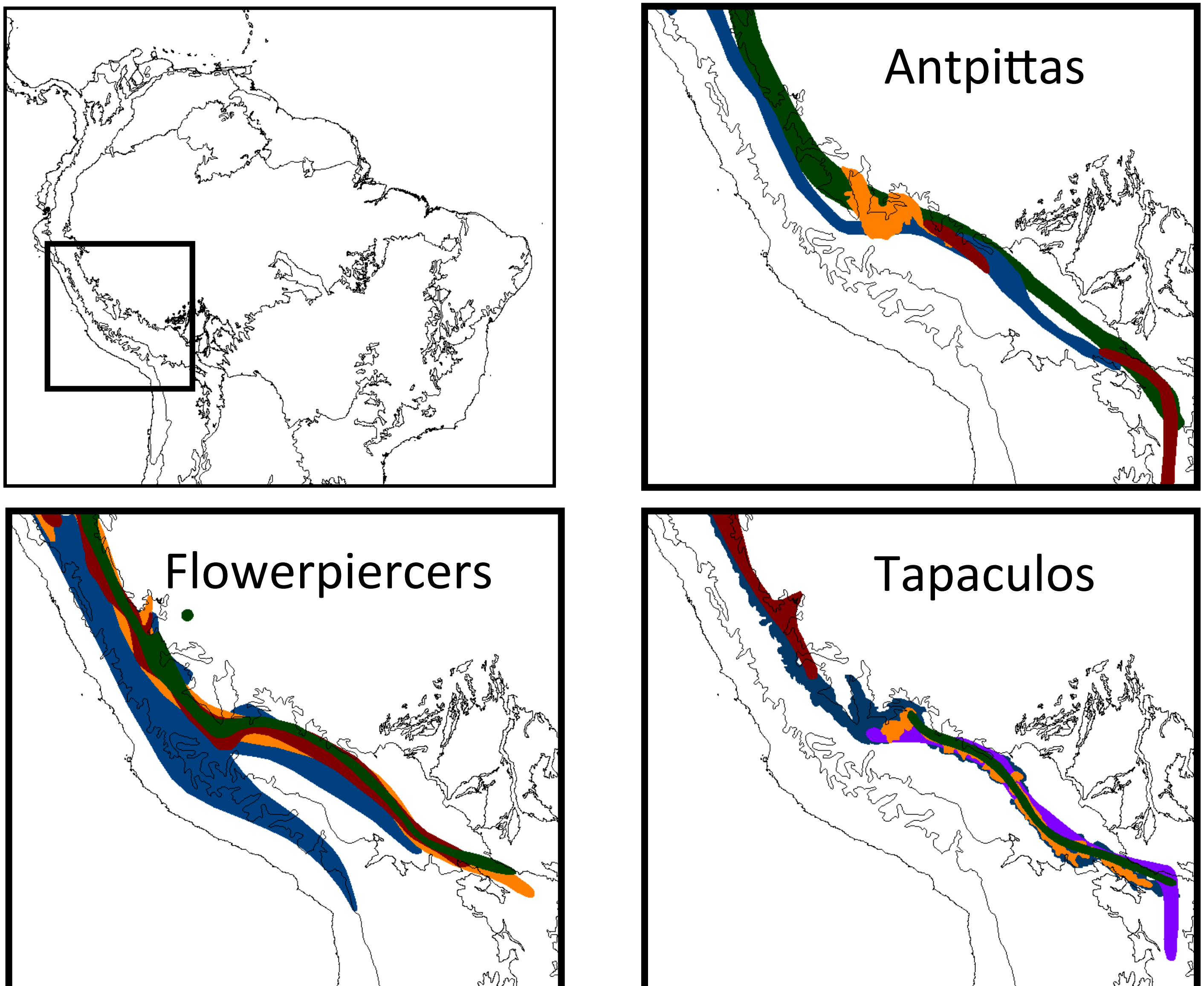


“Shoestring” distributions of montane birds

Deep-blue Flowerpiercer
Diglossa glauca



Communities in tropical mountains are defined by high species turnover or high beta diversity



NatureServe InfoNatura Database

…But is beta diversity really higher in the tropics?

Data for lizards, snakes and frogs show that ranges of montane species have higher overlap (i.e., show less species turnover) at high latitudes

(With higher overlap in elevational ranges, the average elevational range size of a species must be broader in the temperate zone)

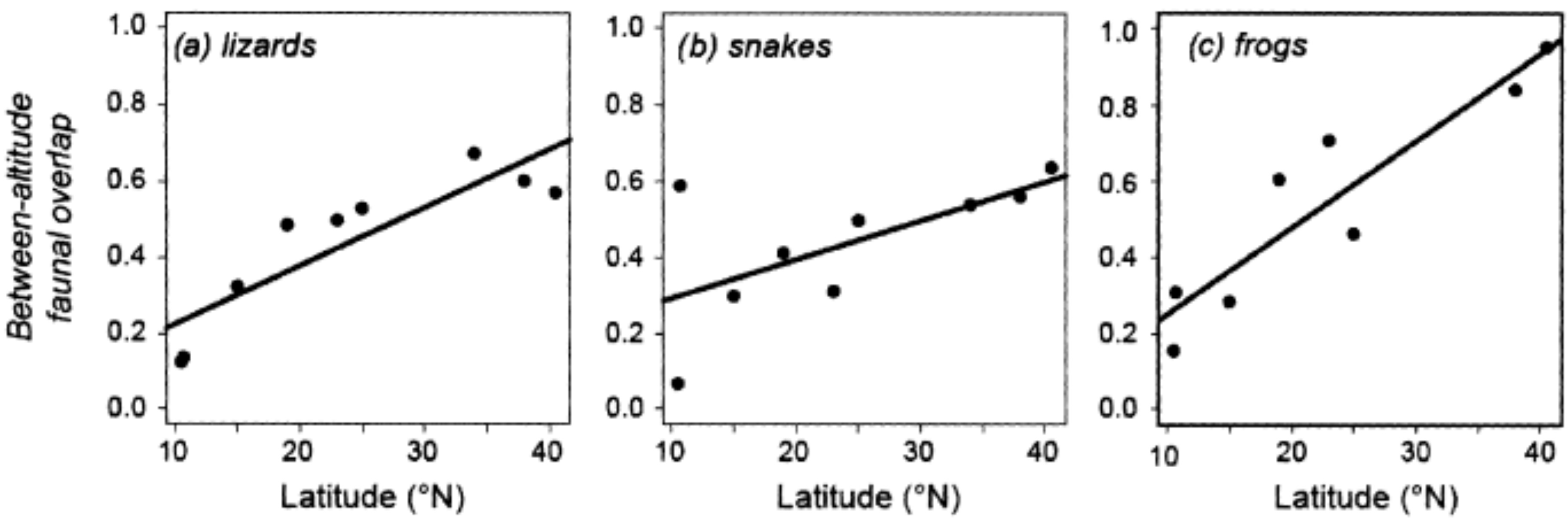


Fig. 5 Patterns of between-altitude faunal overlap for lizards, snakes, and frogs versus latitude. Faunas separated by altitude are much more similar in the temperate zone than in the tropics (based on data in Huey, 1978).

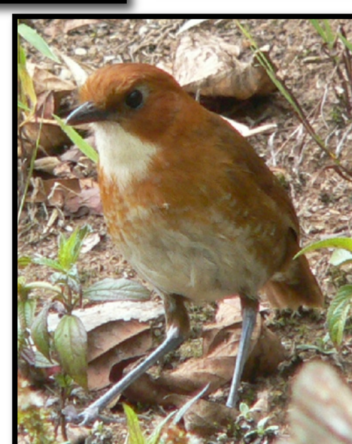
Figure from Ghalambor et al. 2006

Antbirds show high alpha, beta and gamma diversity

Family Thamnophilidae
Exclusively Neotropical
> 220 species





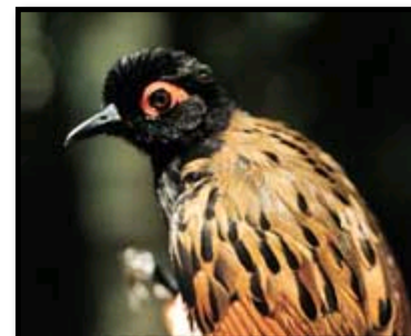
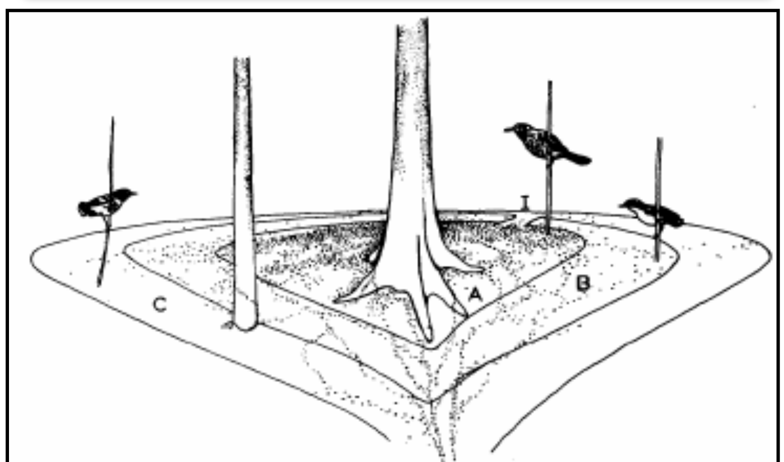




Antbirds show high alpha, beta and gamma diversity

Many antbirds follow army ant swarms and feed on flushed insects



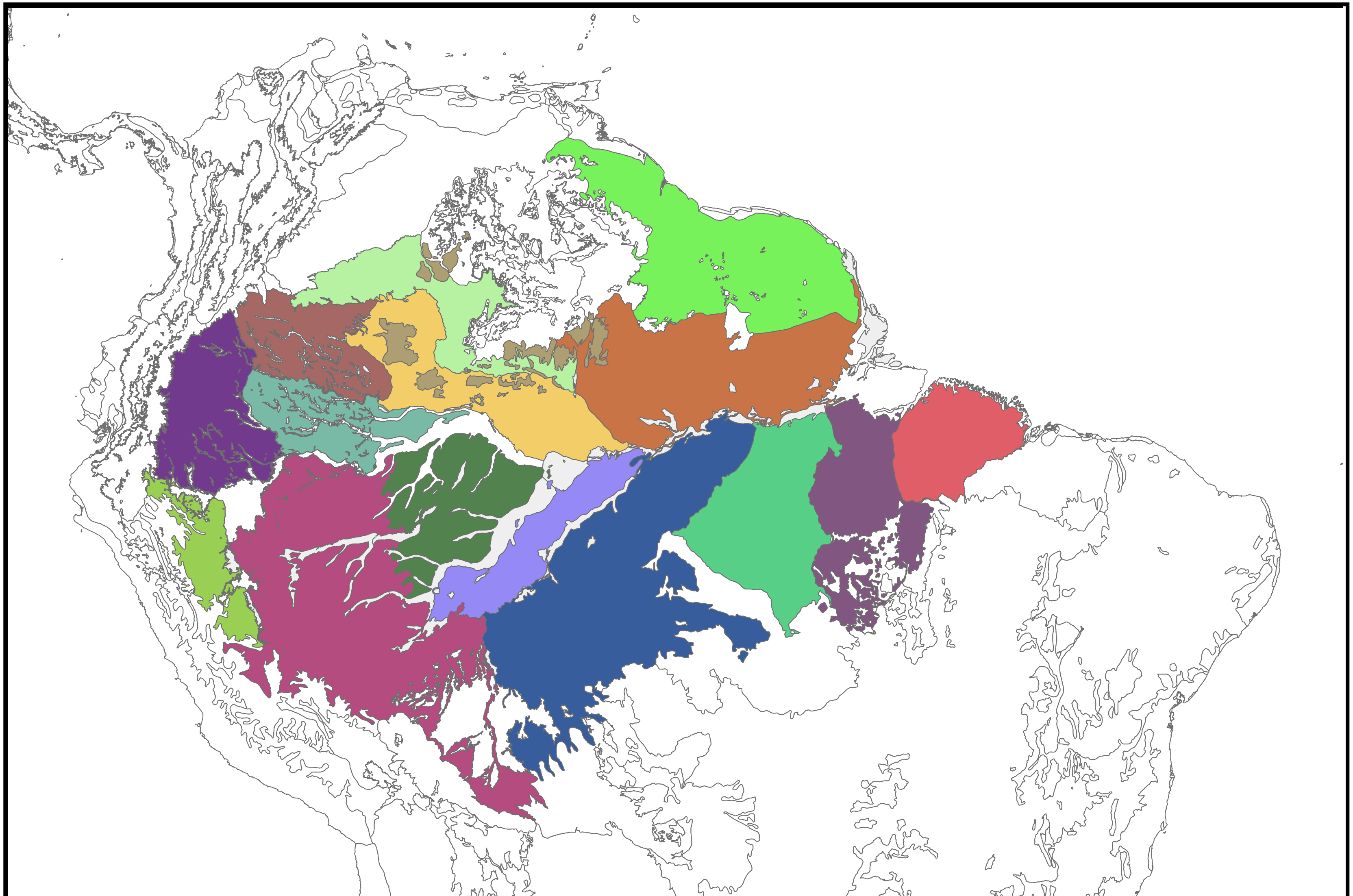


Willis & Oniki 1978

Antbirds show high alpha, beta and gamma diversity

Many species are restricted to several Amazonian ecoregions



Antbirds show high alpha, beta and gamma diversity

Other species are restricted to habitats created around river systems

Antbirds show high alpha, beta and gamma diversity

Habitats within Amazonian Ecoregions

Tropical Lowland Evergreen Forest

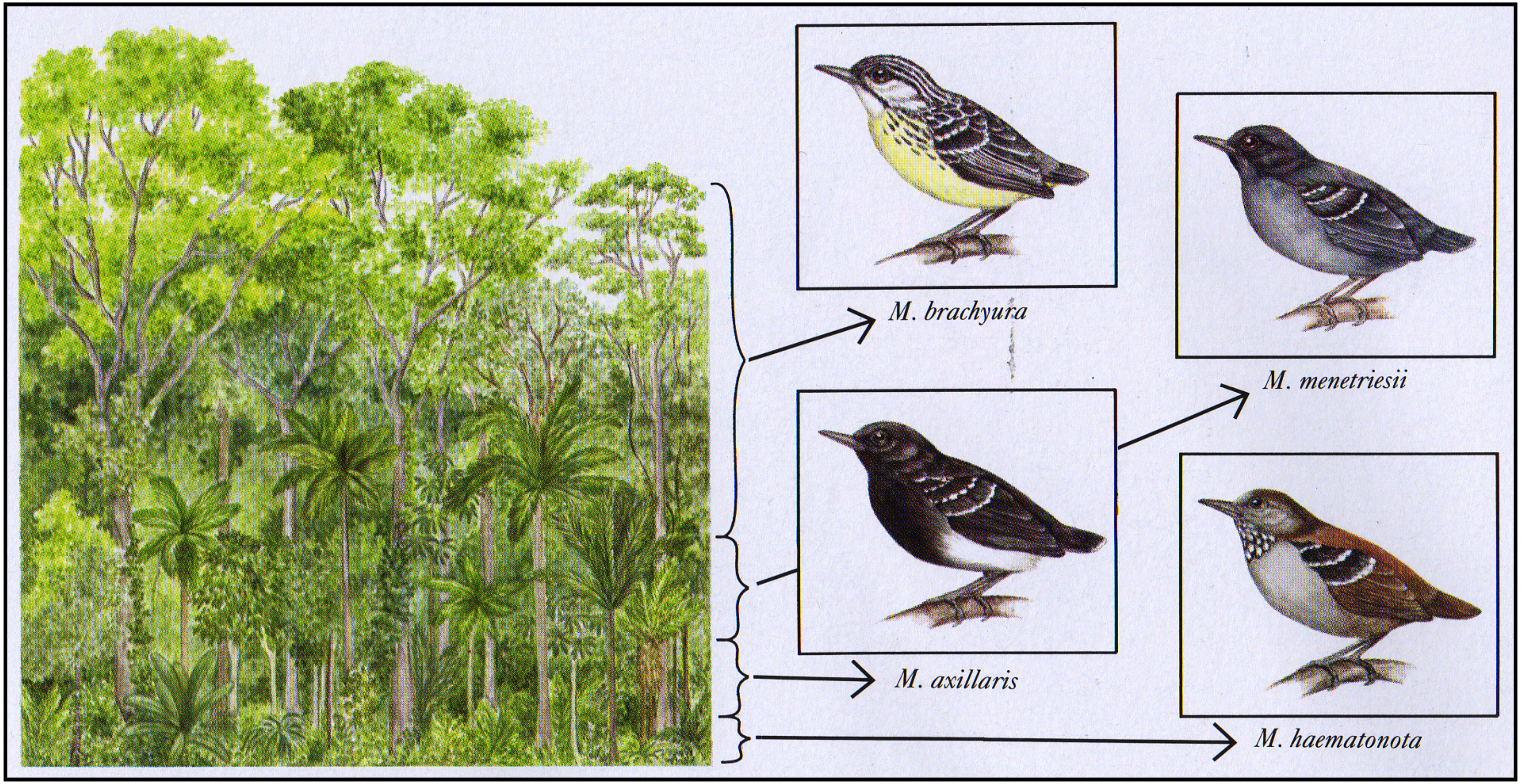
Flooded Tropical Evergreen Forest

River Edge & River Island Forest

White Sands Forest

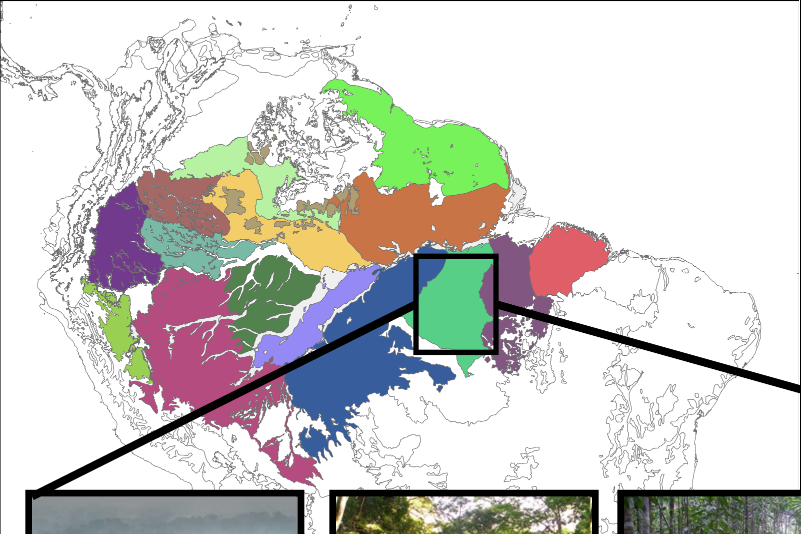
Antbirds show high alpha, beta and gamma diversity

Antbirds also show within habitat resource partitioning



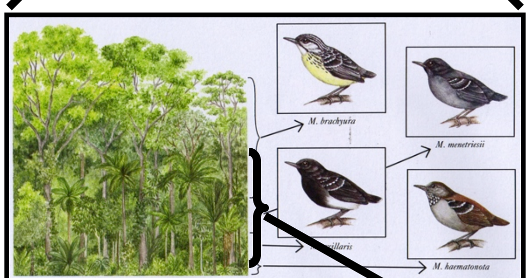
…evident in other tropical insectivore families, too.

Many factors contribute to antbird diversity and diversification

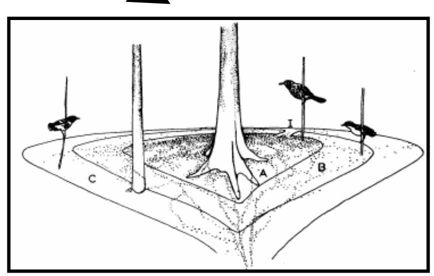


Geographic barriers to dispersal & historic events

Habitat partitioning



Microhabitat partitioning



Behavioural specialization

Latitudinal Diversity Gradient

There is higher alpha, beta, and gamma diversity in the tropics.

Combined taxa in North America:

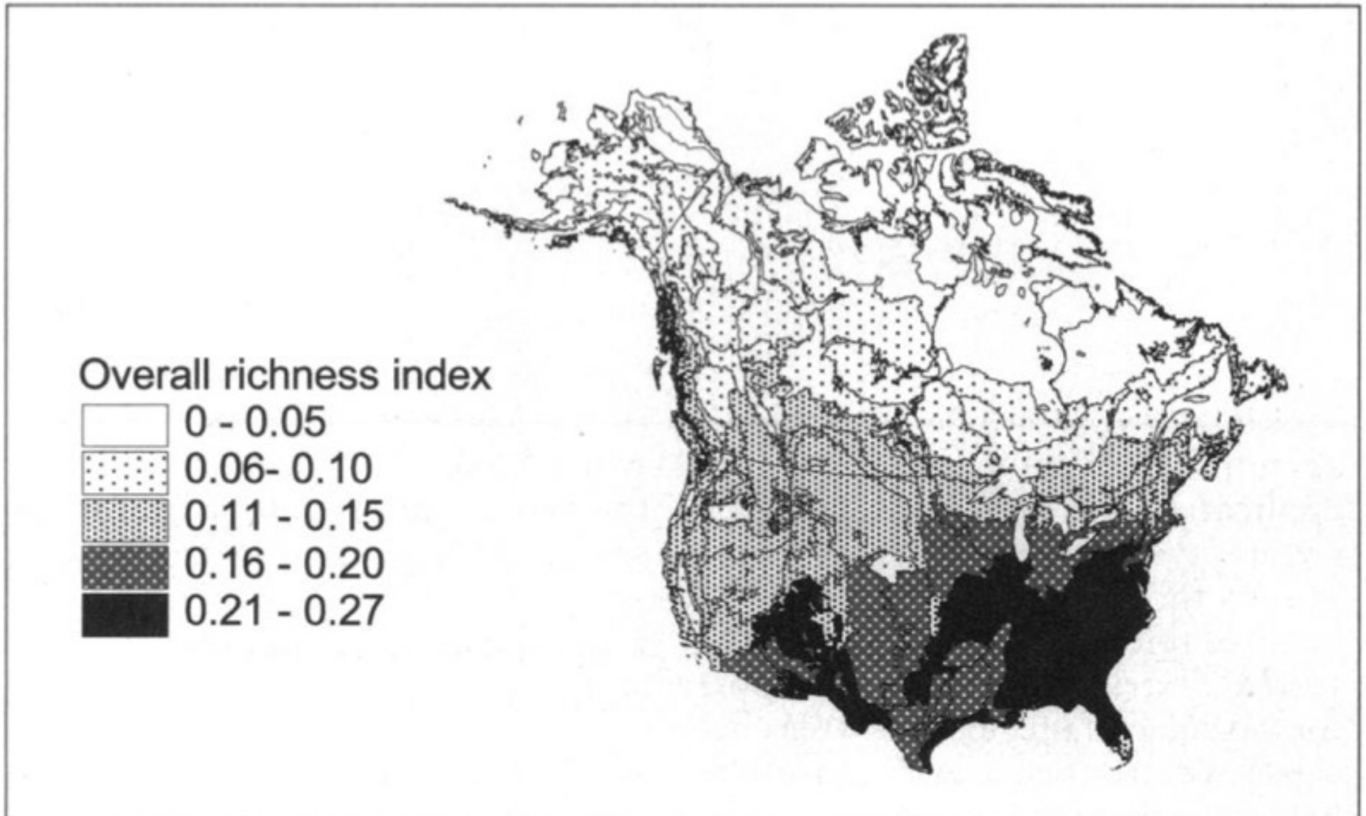
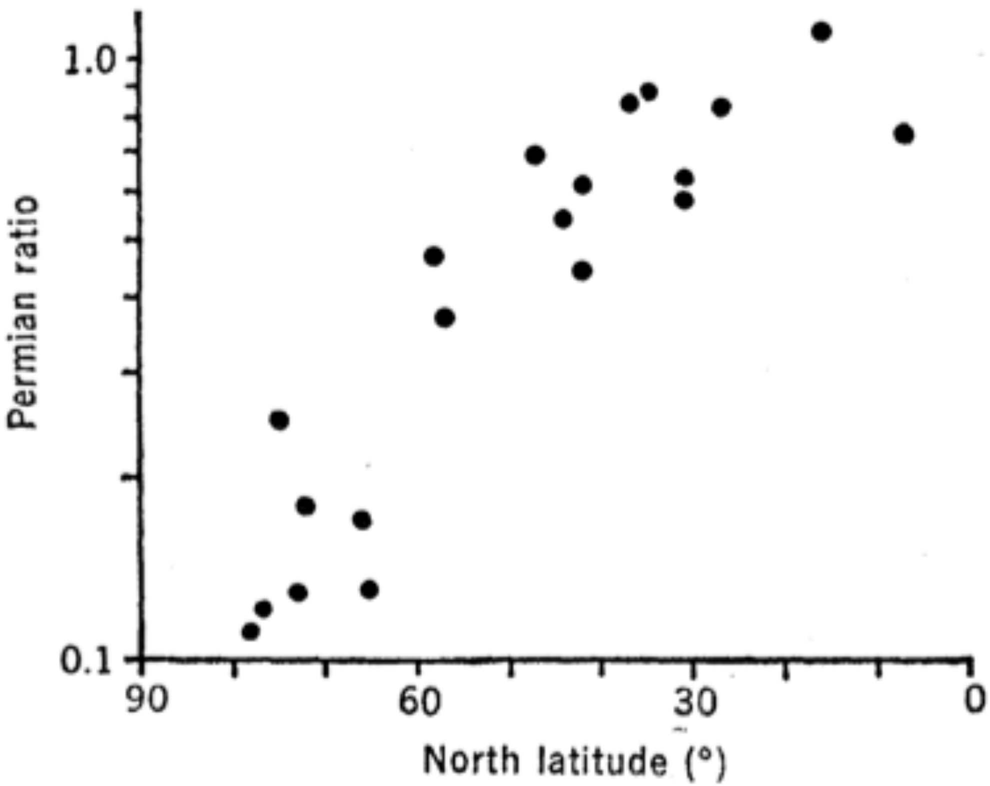


Figure 2. Map of overall richness index. This map incorporates richness values for all nine taxa: mammals, birds, reptiles, amphibians, butterflies, tiger beetles, land snails, trees, and nontree vascular plants.

(from Rickets *et al.* 1999)

Latitudinal Diversity Gradient

There is higher alpha, beta, and gamma diversity in the tropics.



The latitudinal gradient has also been observed in ancient faunas (e.g., in fossil remains of brachiopods deposited 270 mya), ranging from 7 to 80 degrees N latitude.

"Permian ratio" is a diversity metric that accounts for unequal sampling in geological record

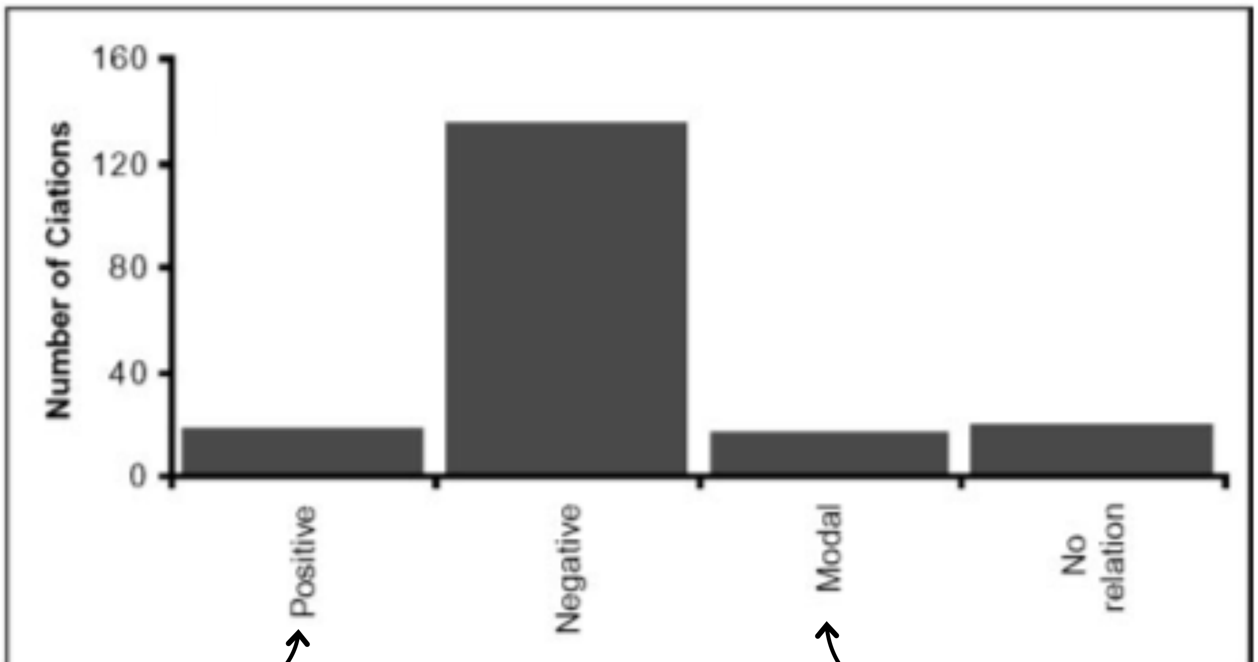
Gradient in diversity for Permian brachipods is similar to that typical of living organisms and Cretaceous planktonic foraminifera

(from Stehli *et al.* 1969)

Latitudinal Diversity Gradient

Exceptions:

Review of published accounts of diversity-latitude relationship:



(from Willig *et al.* 2003)

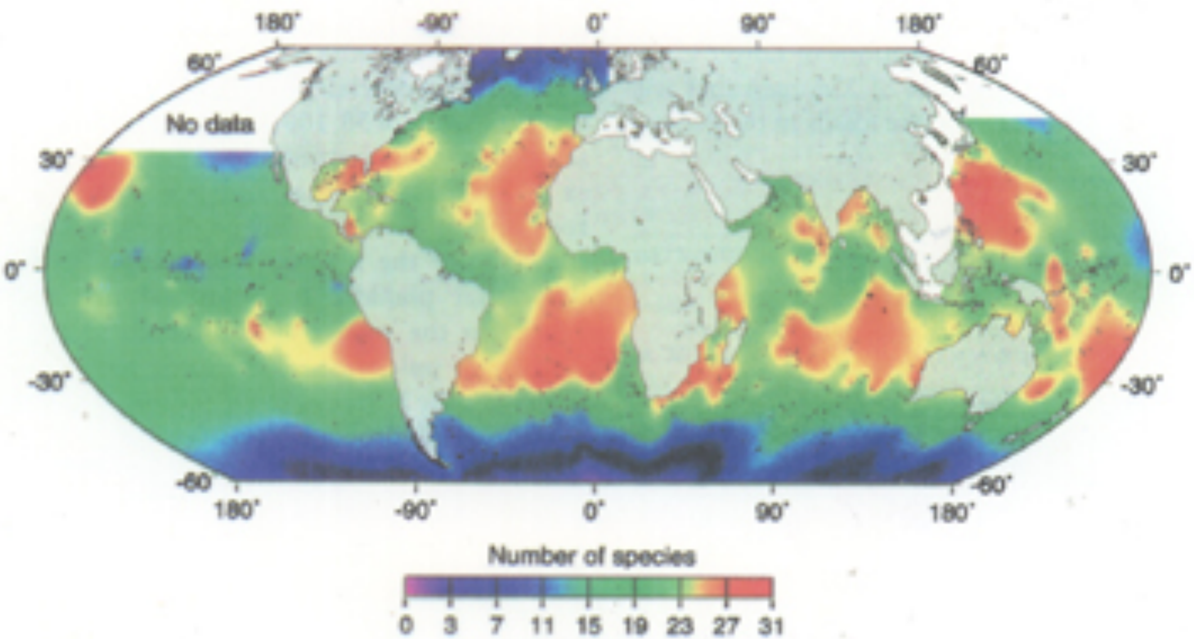
- Penguins
- Sandpipers
- Pelagic sea birds
- Pinnipeds (seals)

- Pine trees
- Aphids
- Zooplankton

Latitudinal Diversity Gradient

Exceptions:

Foraminiferan zooplankton diversity highest at intermediate latitudes:



What factors may drive this pattern?

What Causes the Latitudinal Diversity Gradient

Over 30 hypotheses have been suggested (we will cover ~7).
These categories can be useful for organizing these hypotheses:

1. null hypotheses

2. deterministic hypotheses

a. equilibrium models

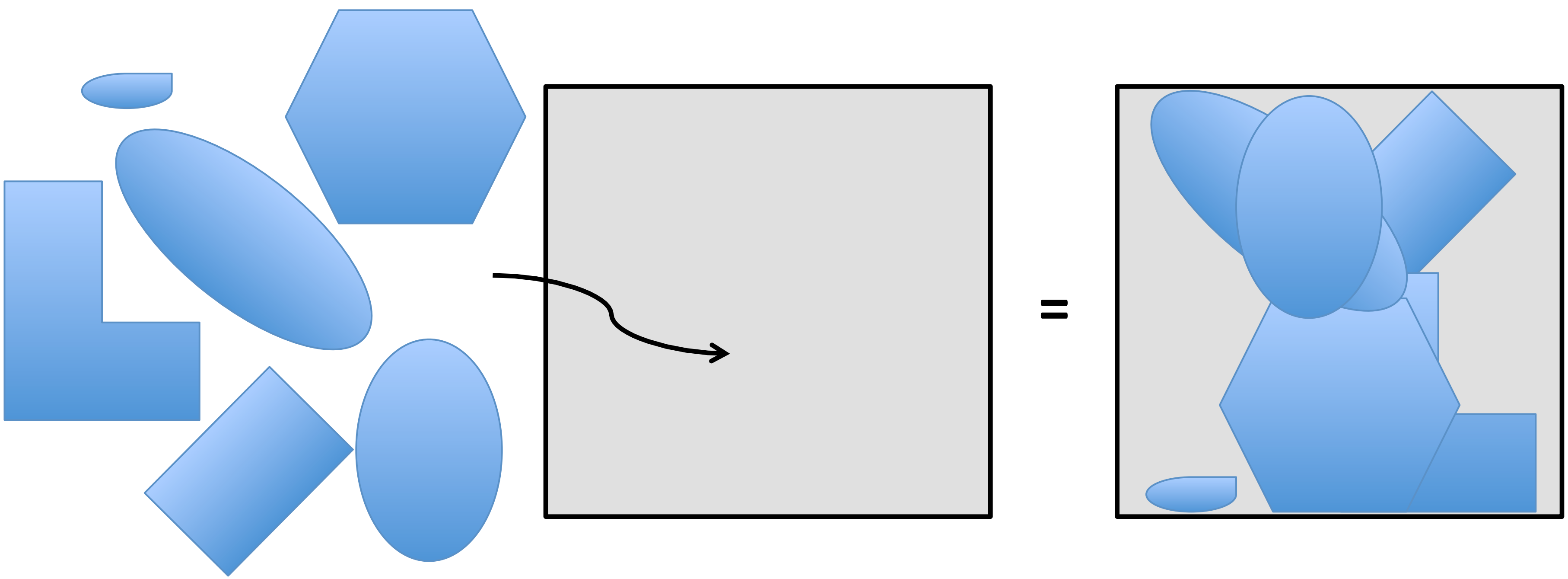
b. non-equilibrium models

What Causes the Latitudinal Diversity Gradient

Null hypotheses:

Patterns observed are artifacts of the way data are collected or presented.

Mid-domain effect*:* random distribution of geographic range boundaries between the "hard edges" of the poles results in the greatest range overlap mid-way between the poles - i.e., the equatorial regions (Colwell and Hurtt 1994).



Within any bounded gradient, randomly throwing ranges onto the landscape results in higher overlap of ranges in the center of the gradient ~ higher species richness

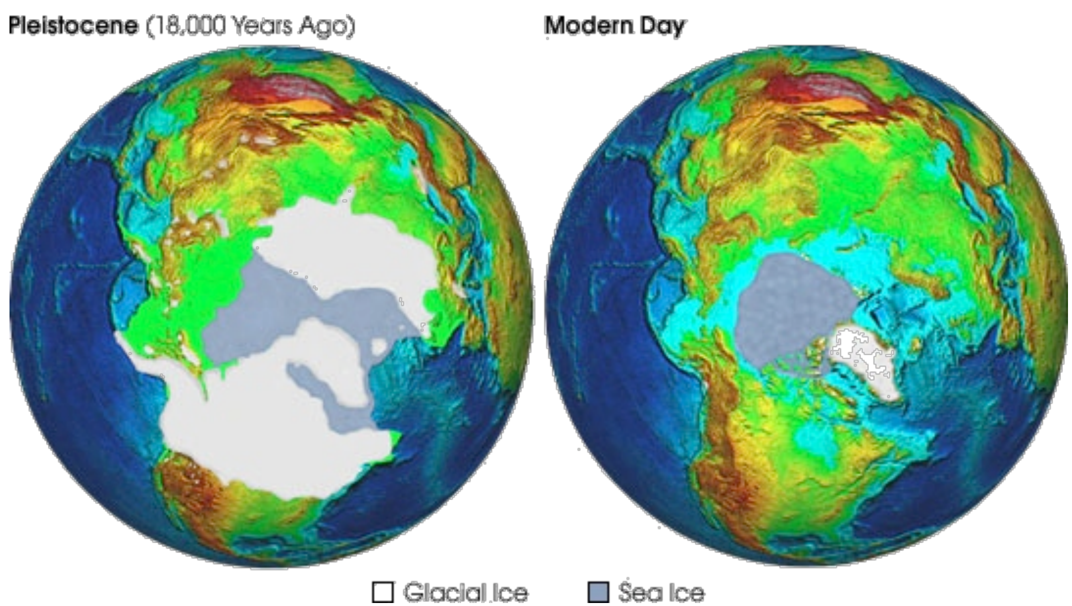
What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

A. Non-equilibrium models:

Communities have not yet reached a steady state.

e.g., *Historical perturbations*: species diversity is still in the process of increasing or decreasing after some historical disturbance.

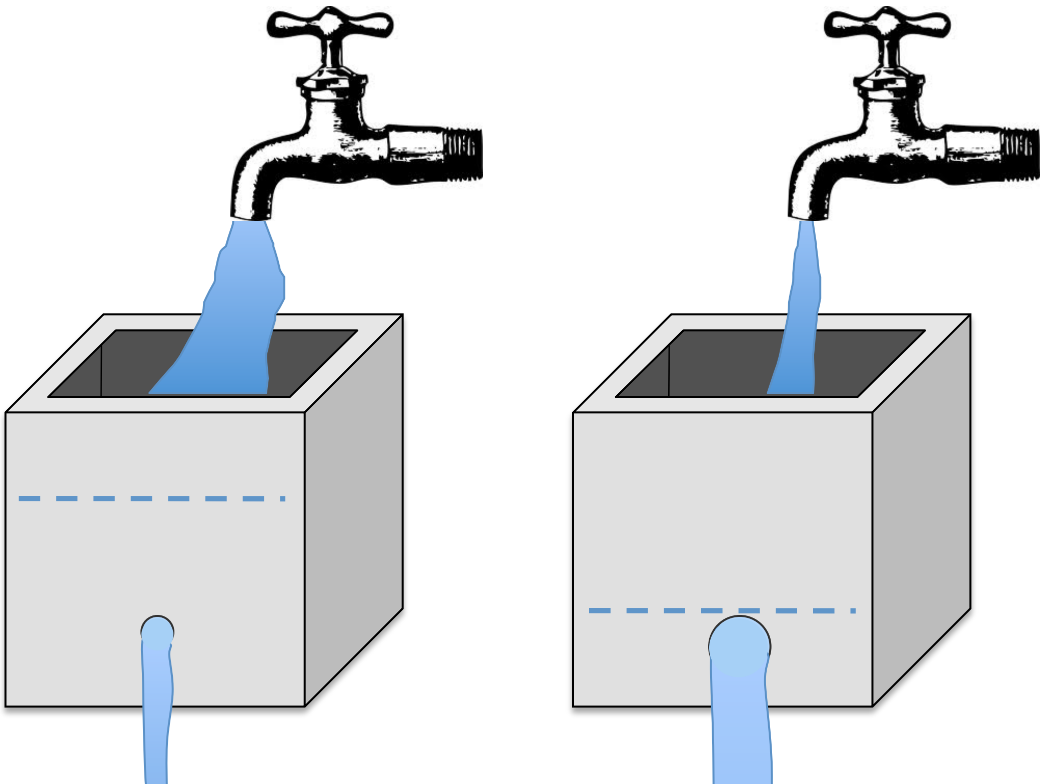


What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

B. Equilibrium models:

A steady state has been reached. The forces that increase diversity are balanced by those that reduce diversity such that species diversity remains fixed through time.

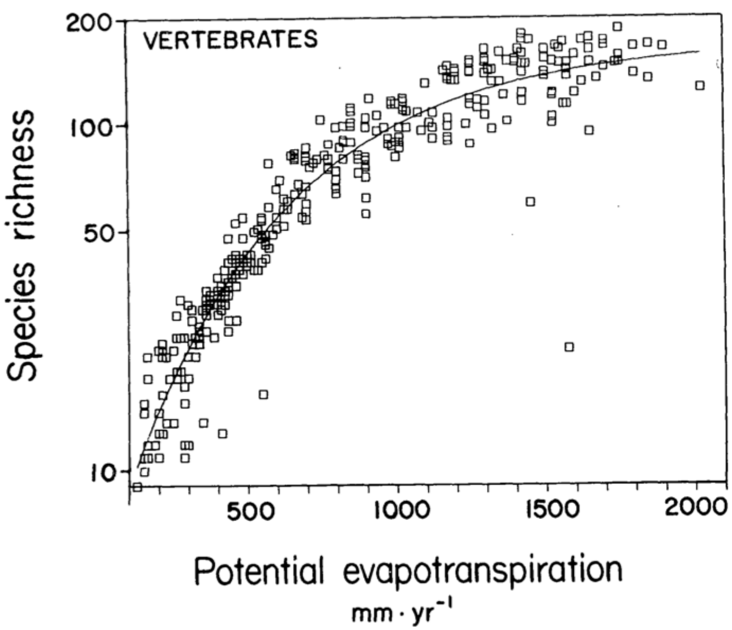


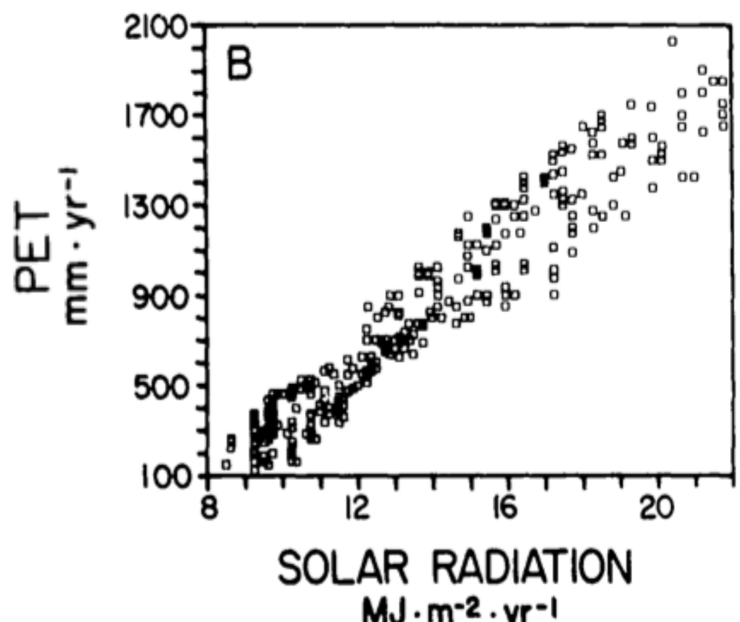
What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

B. Equilibrium models:

1. Productivity – the tropics receives more intense solar energy, supporting higher productivity of plant communities and promoting higher diversity of these producers and dependent consumers.





(From Currie 1991)

What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

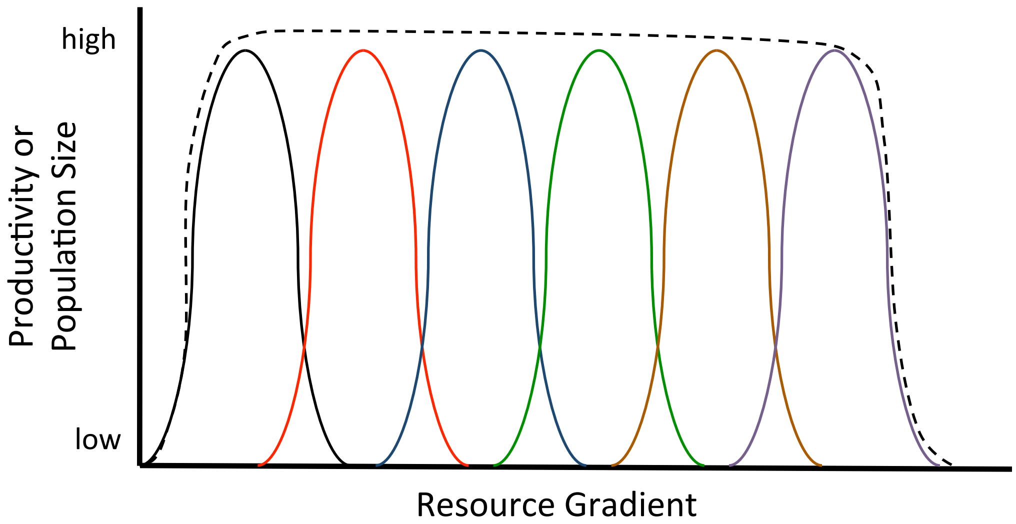
B. Equilibrium models:

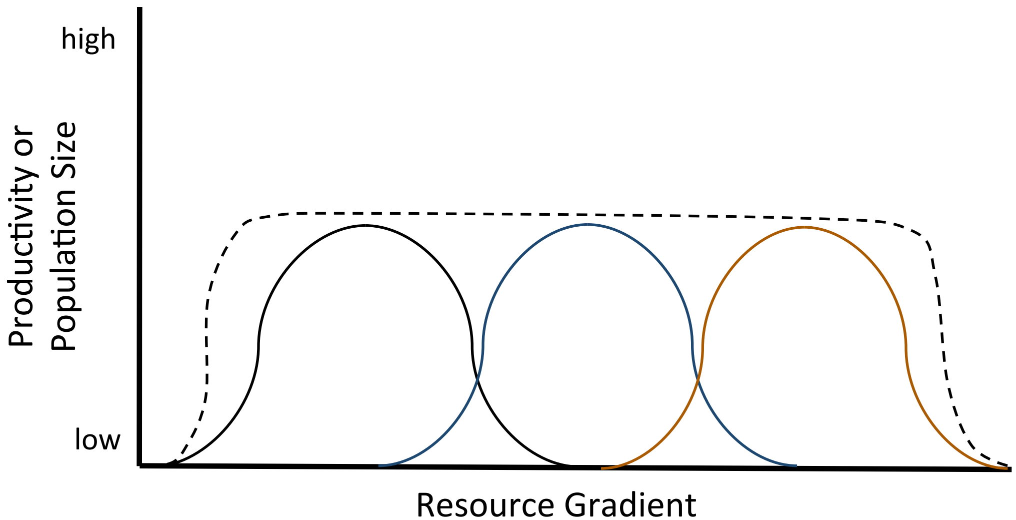
1. Productivity

Exceptions
(very productive, low diversity):

salt marshes

shallow eutrophic lakes





What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

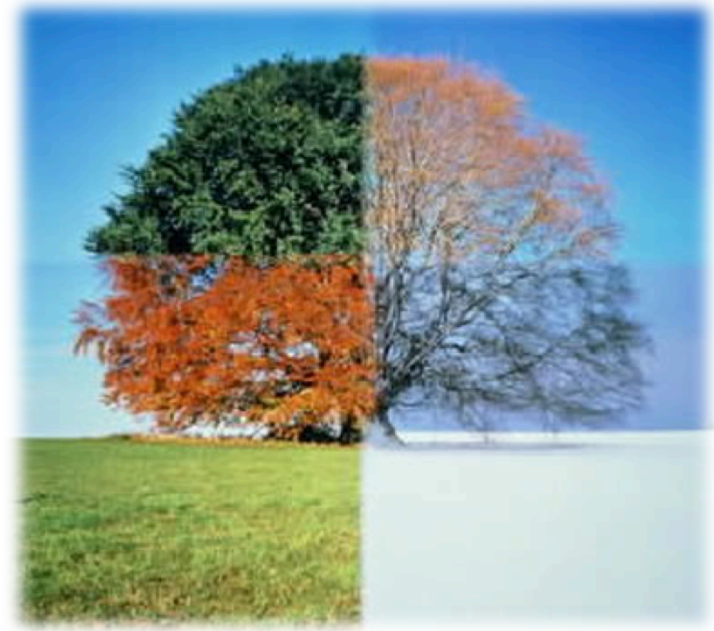
B. Equilibrium models:

2. Harshness - Harsh environments (e.g., icy and cold, hot and dry) have higher extinction rates, lower colonization potential, and less opportunity for resource specialization than more benign environments.

What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

B. Equilibrium models:



3. Temporal Stability - Variable climates prevent resource specialization, and hence tend to support fewer species.

Temporal variability tends to favour generalists at the expense of specialists.

Tropical species have more opportunity to adapt and specialize within more predictable environments

Exceptions (stable, low diversity):

deep ocean

What Causes the Latitudinal Diversity Gradient

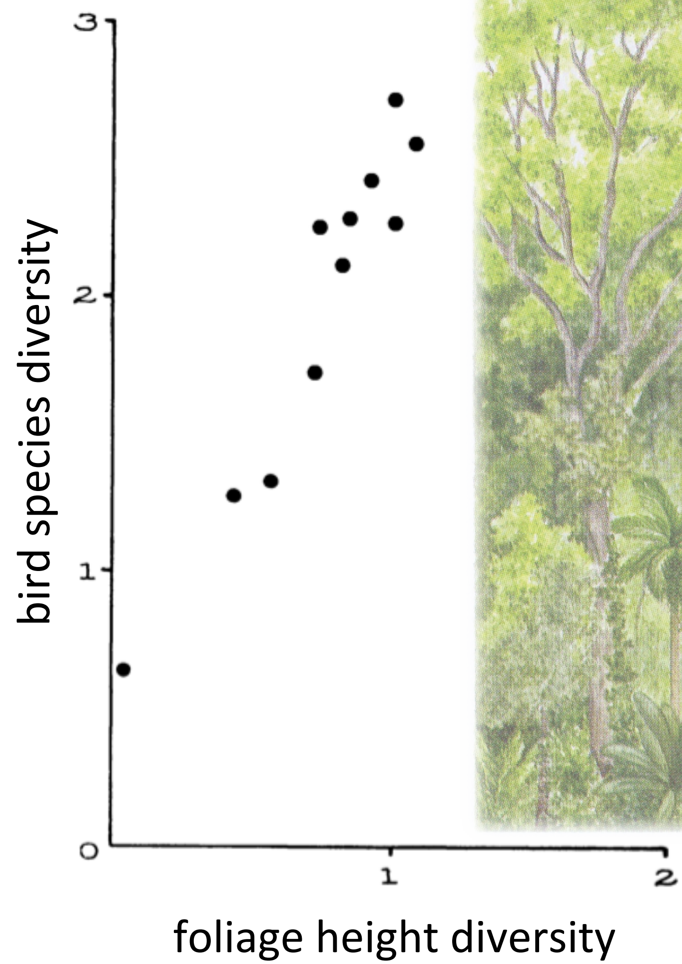
Deterministic hypotheses:

B. Equilibrium models:

4. Habitat heterogeneity –
Diversity is higher in more complex and heterogeneous habitats.
Diverse environments promote isolation resource specialization, speciation, and co-existence.

Tropical habitats tend to be more spatially/vertically heterogeneous with more complex habitats.

Exceptions (low heterogeneity, high diversity): marine plankton



Adapted from MacArthur & MacArthur 1961

What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

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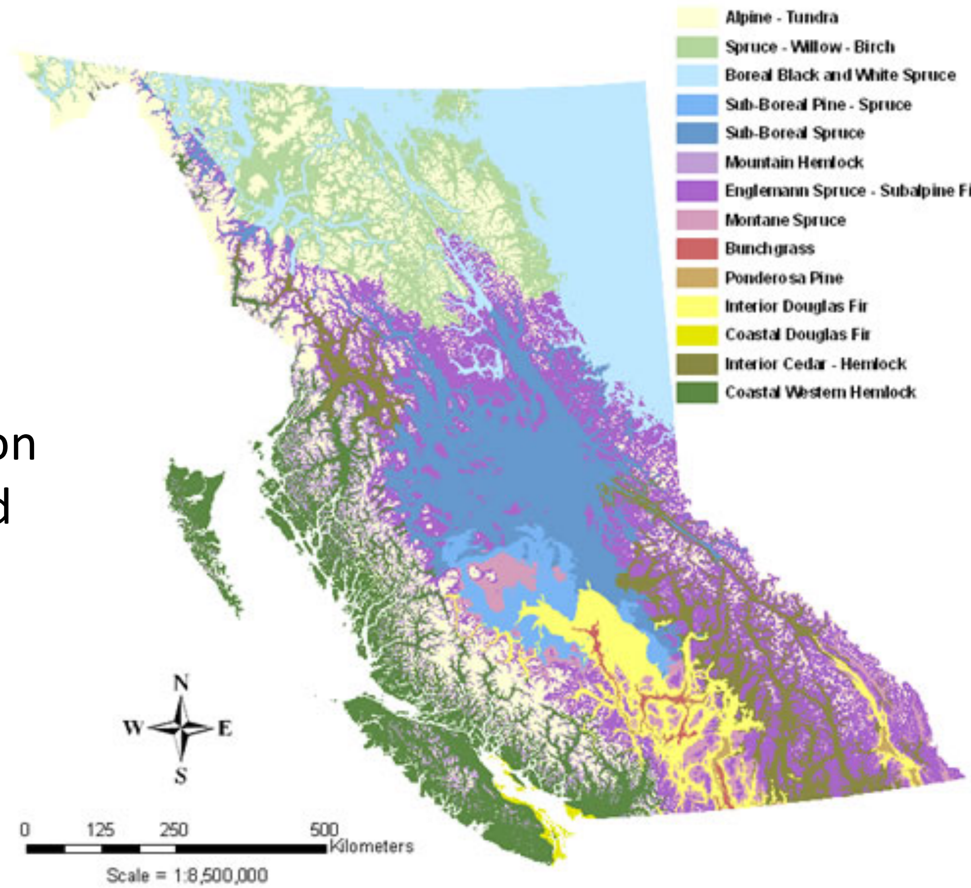


1140 native species of vertebrates in BC (most diverse topography, most biologically diverse province in Canada)

What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

B. Equilibrium models:

5. Interspecific Interactions - More species create a positive feedback of diversification through increased competition, predation, mutualism and parasitism – "diversity begets diversity"

E.g., predators tend to hold prey populations in check by preying on more abundant prey, preventing prey populations from increasing to levels at which they exclude each other (tropics have a high diversity of predators)

Epiphyte-laden tree in a tropical cloud forest

E.g., the tropics are inhabited by more host species, so diversity of parasites and other symbionts is also higher.

But is this a cause or a *consequence – still doesn't explain initial diversity*?

What Causes the Latitudinal Diversity Gradient

Deterministic hypotheses:

B. Equilibrium models:

6. Area - Tropics have greater area than either polar region due to curvature of the earth.

Species-area relationship is well established – recall predictions from the equilibrium theory of island biogeography

What Causes the Latitudinal Diversity Gradient

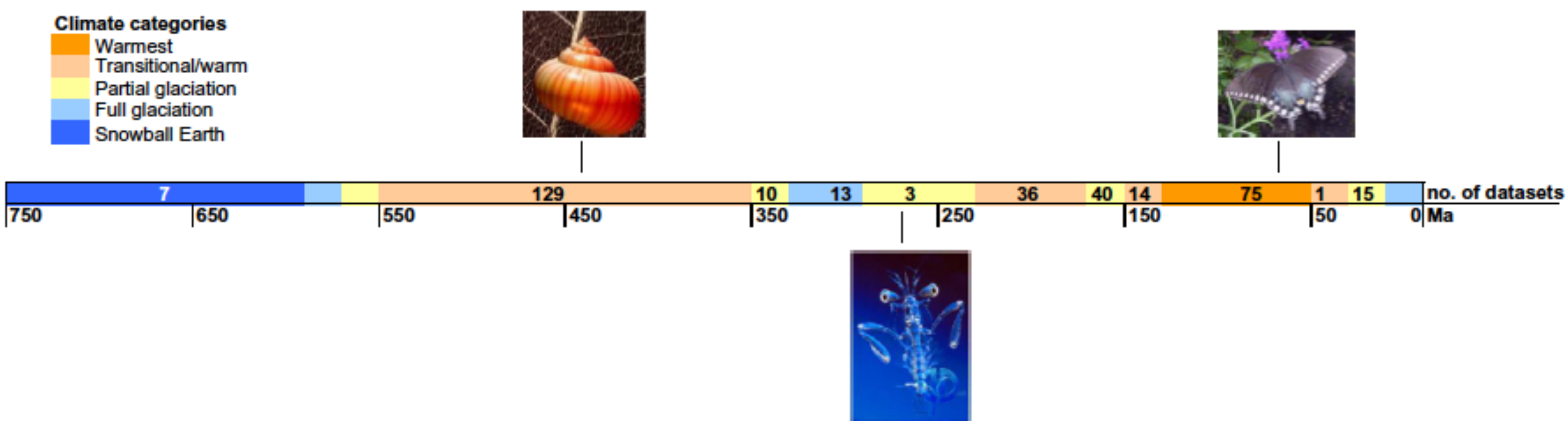
Deterministic hypotheses:

B. Non-equilibrium models:

7. Age - Romdal et al. analyzed the slope of the latitudinal gradient for 343 studies, representing plants and animals of marine and terrestrial realms.

Grouped time periods into palaeoclimatic categories

Compared the slope (steepness of the relationship) for different categories



What Causes the Latitudinal Diversity Gradient

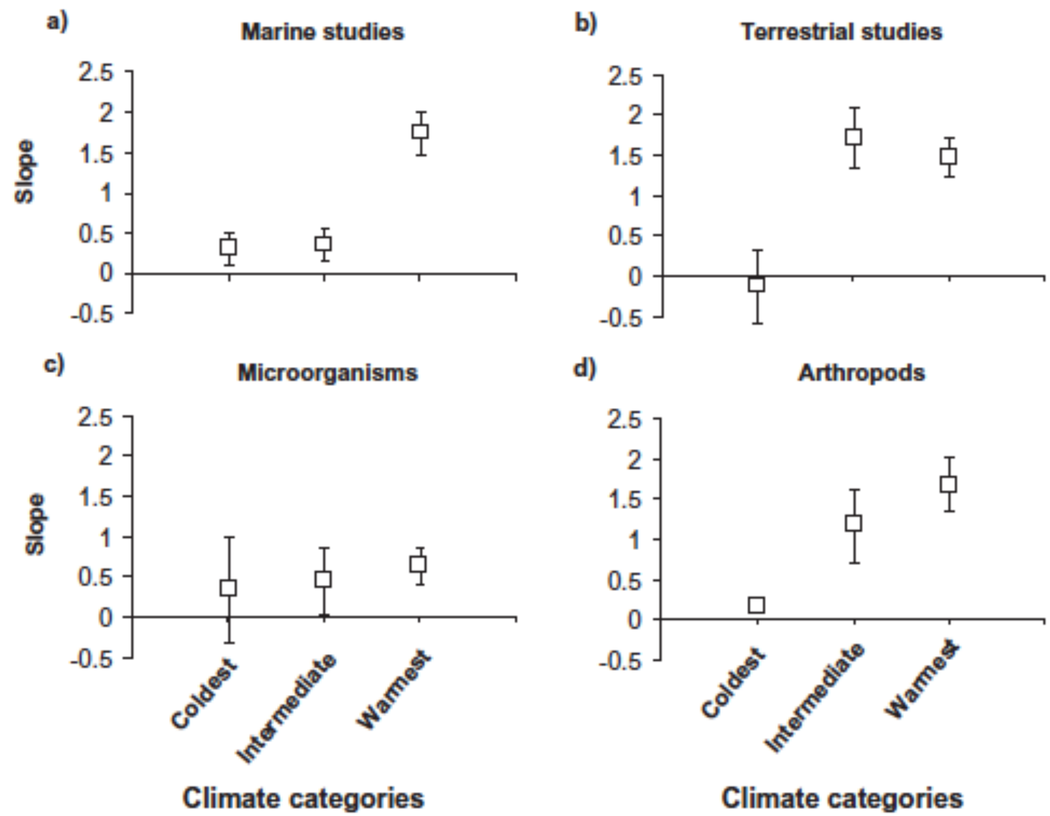
Deterministic hypotheses:

B. Non-equilibrium models:

7. **Age** - Latitudinal gradients for clades originating in warm climates are steeper, with a strong tropical affinity

For a variety of plants and animals of marine and terrestrial realms, most clades radiated in tropical climates.

Extant tropical diversity peak is created from lineages that adapted to a planet with tropical climate



Higher diversities have arisen among tropical clades because the earth has been predominantly tropical throughout most of its history.

Romdal et al. 2013

What Causes the Latitudinal Diversity Gradient

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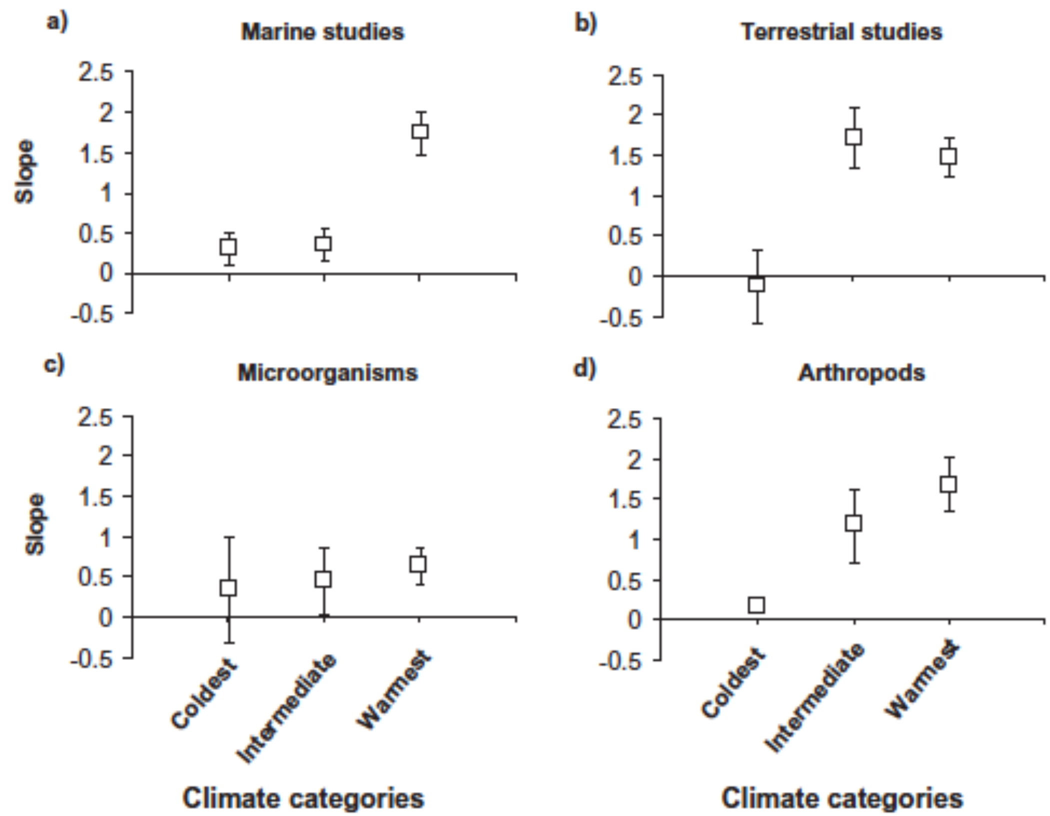


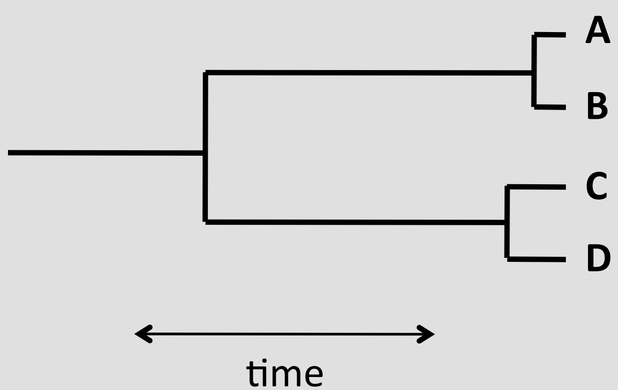
"Current diversity gradients carry the footprint of historical climates"
- Romdal et al. 2013

What Causes the Latitudinal Diversity Gradient

Are the tropics a diversity *cradle* or diversity *museum*?

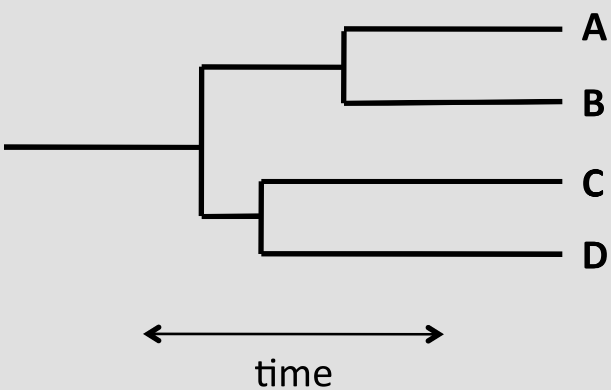
Tropical Cradle:

Young tropical sister species:



Tropical Museum:

Old tropical sister species:



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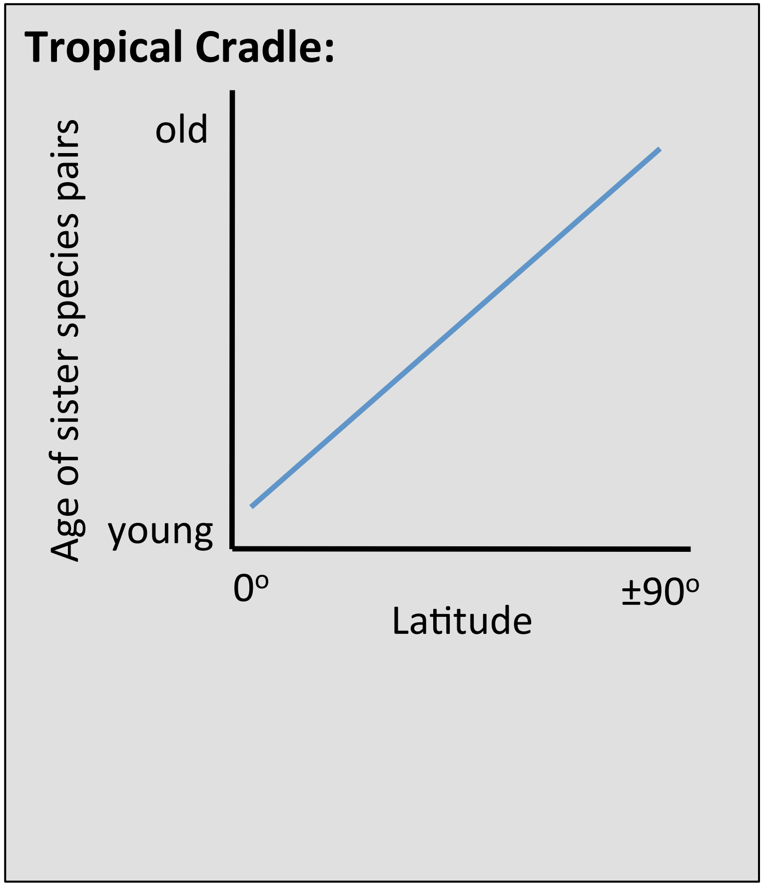

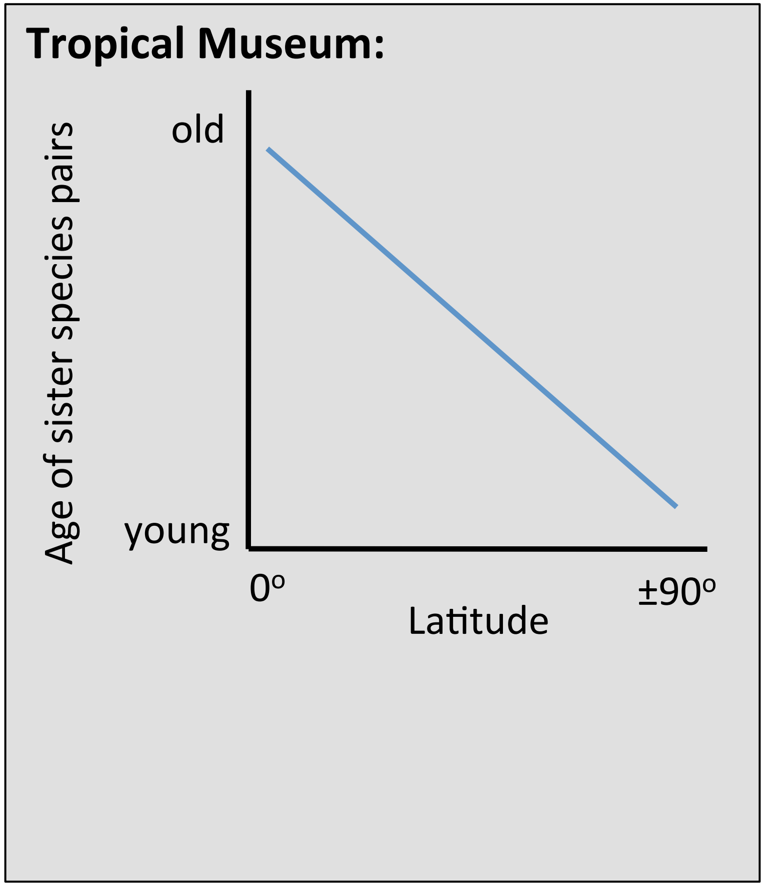

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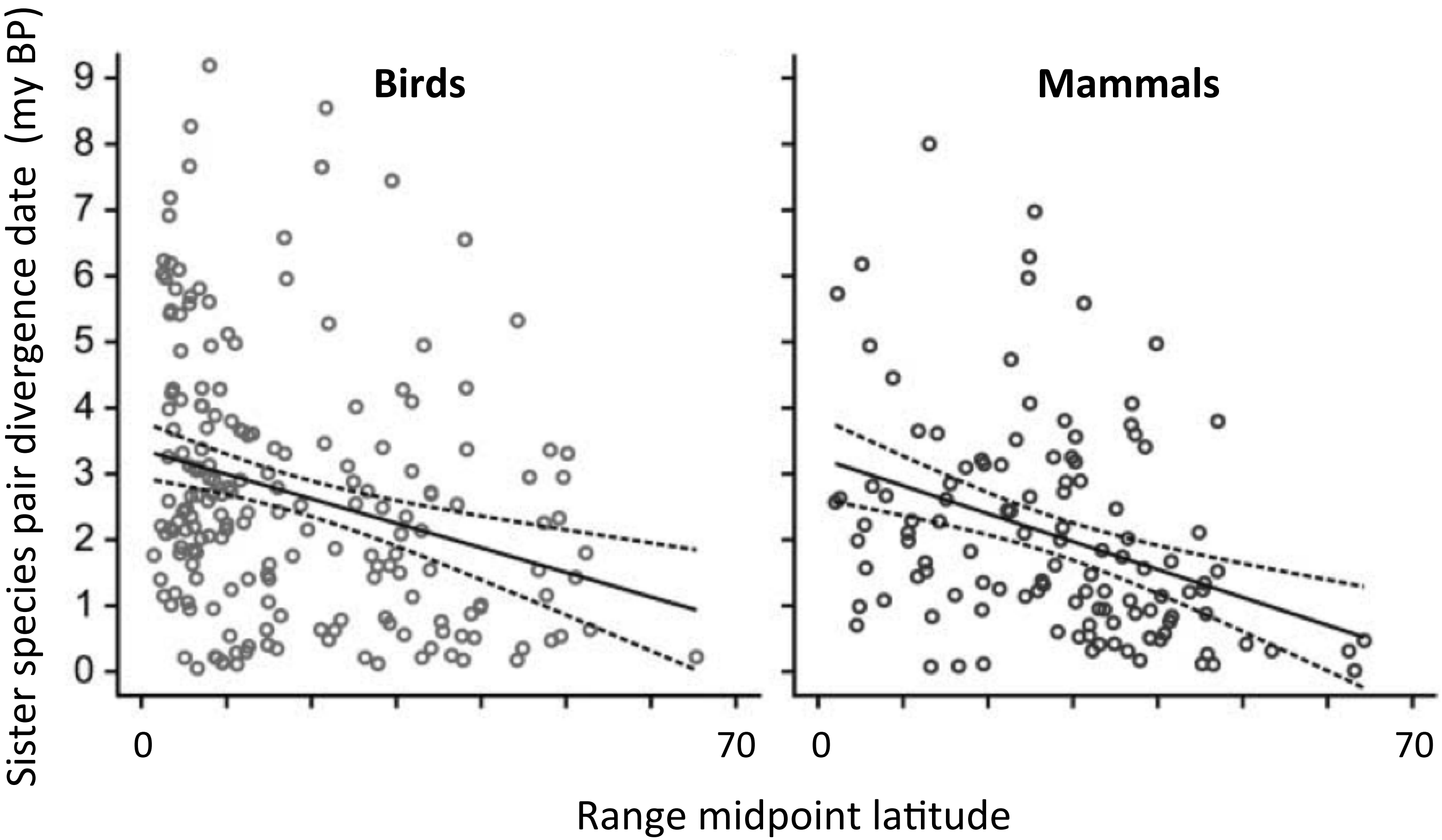


(from Weir and Schluter 2007)

Synthesis

Multiple factors together responsible for the diversity gradient:

	Area	Stability	Productivity	Harshness	Age
Tropics	+	+	+	-	+
Temperate	-	-	-	+	-

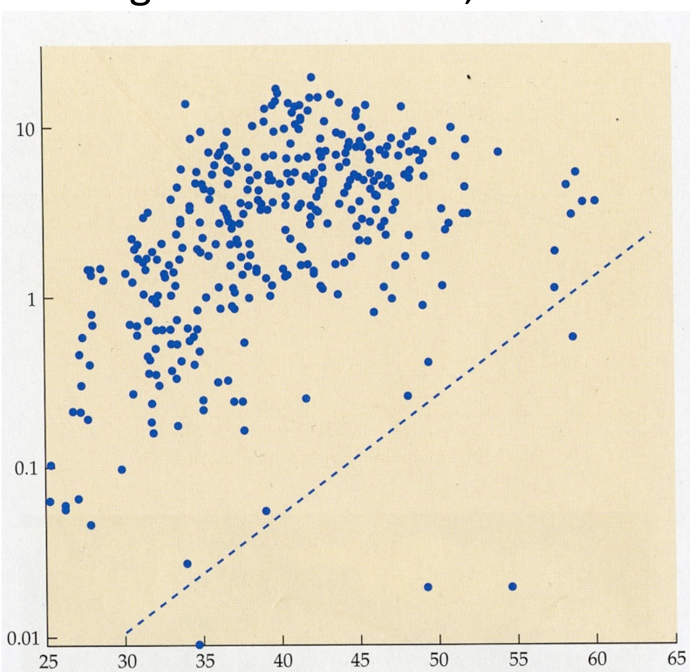
Other Latitudinal Trends

Rapoport's Rule

Rapoport's Rule: species tend to have larger range sizes at higher latitudes.

Breeding terrestrial birds, N.A.

Area of geographic range (10^6 km^2)



Geographic range centre (°Latitude)

Across bird species in North America, species with smaller geographical ranges (y-axis) tend to have range centres at lower latitudes (x-axis)

Note lack of species in right-hand lower portion of graph (i.e., few species with range centres at high latitude with small geographic ranges).

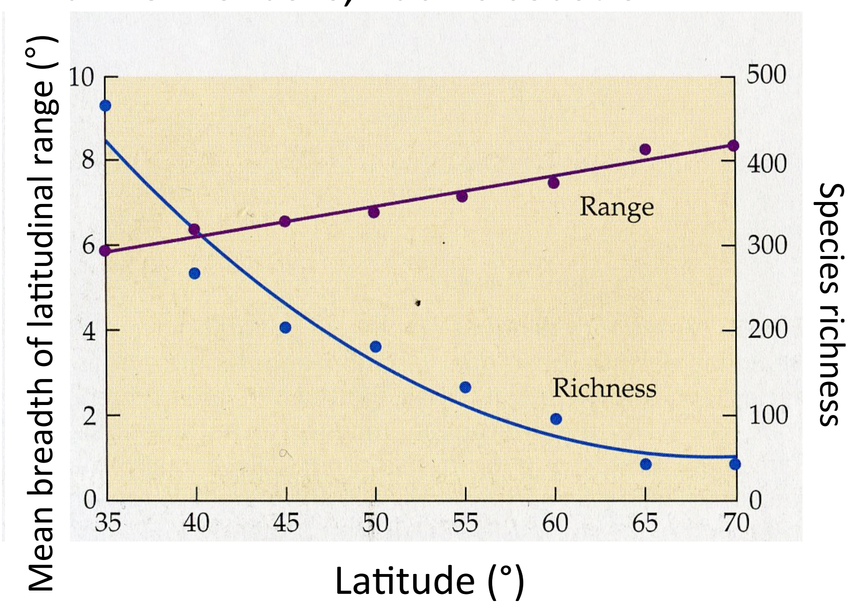
(from Lomolino *et al.* 2010)

Other Latitudinal Trends

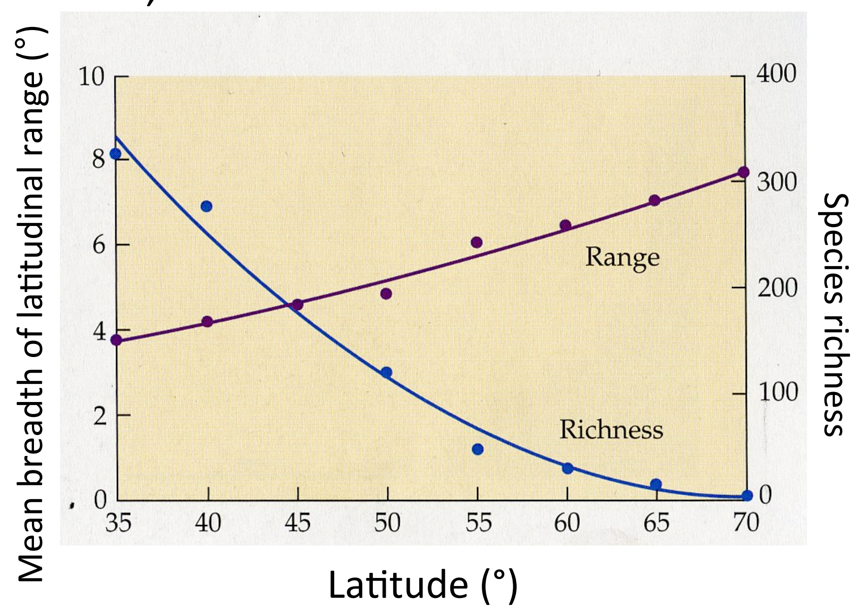
Rapoport's Rule

Rapoport's Rule: species tend to have larger range sizes at higher latitudes.

Marine mollusks, Pacific coast of N.A.



Trees, continental U.S. and Canada



Rapoport's rule as it relates to the latitudinal diversity gradient. As species richness declines with increasing latitude, remaining species tend to have geographical ranges that extend across a broader range of latitudes (Stephens 1989)

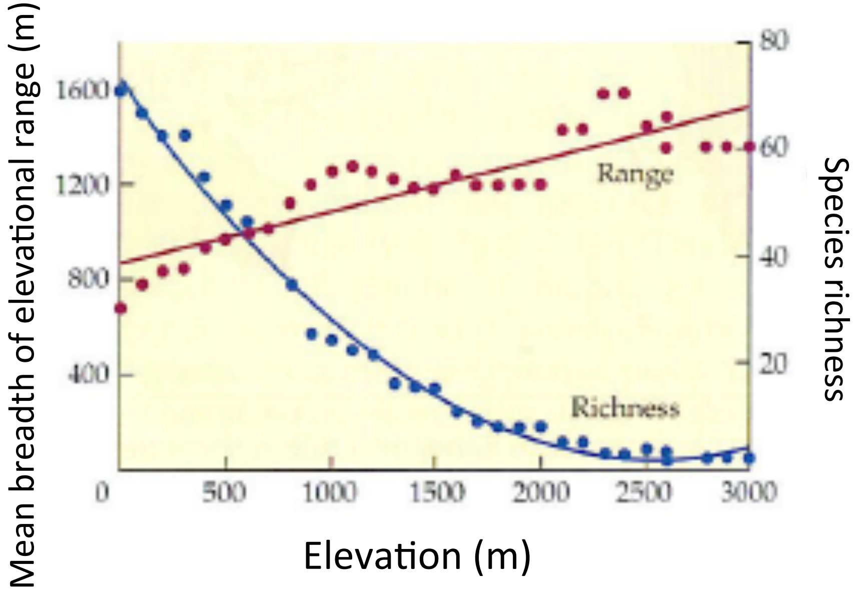
(from Lomolino *et al.* 2010)

Other Latitudinal Trends

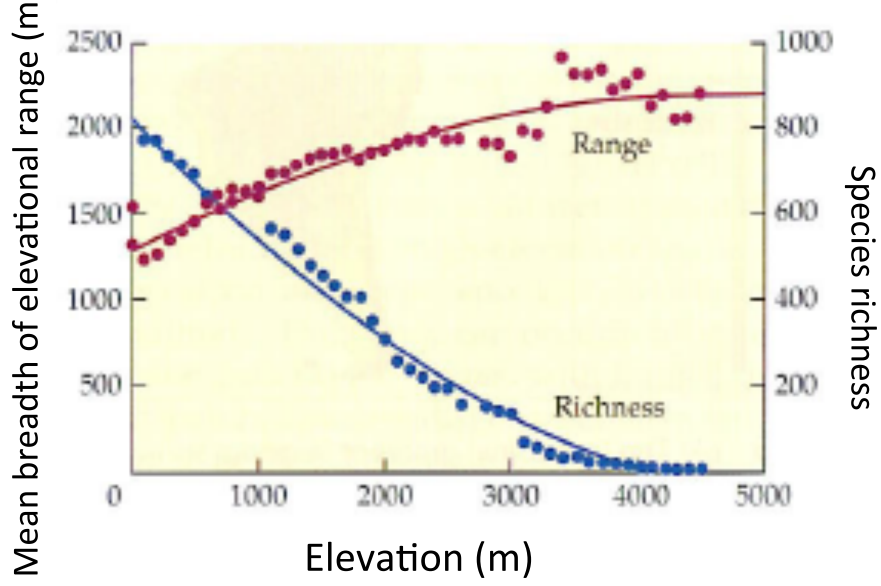
Rapoport's Rule

Rapoport's Rule: species tend to have larger range sizes at higher latitudes.

Trees in Costa Rica



Birds in Venezuela

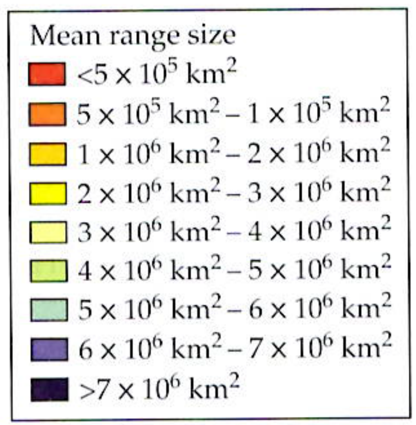


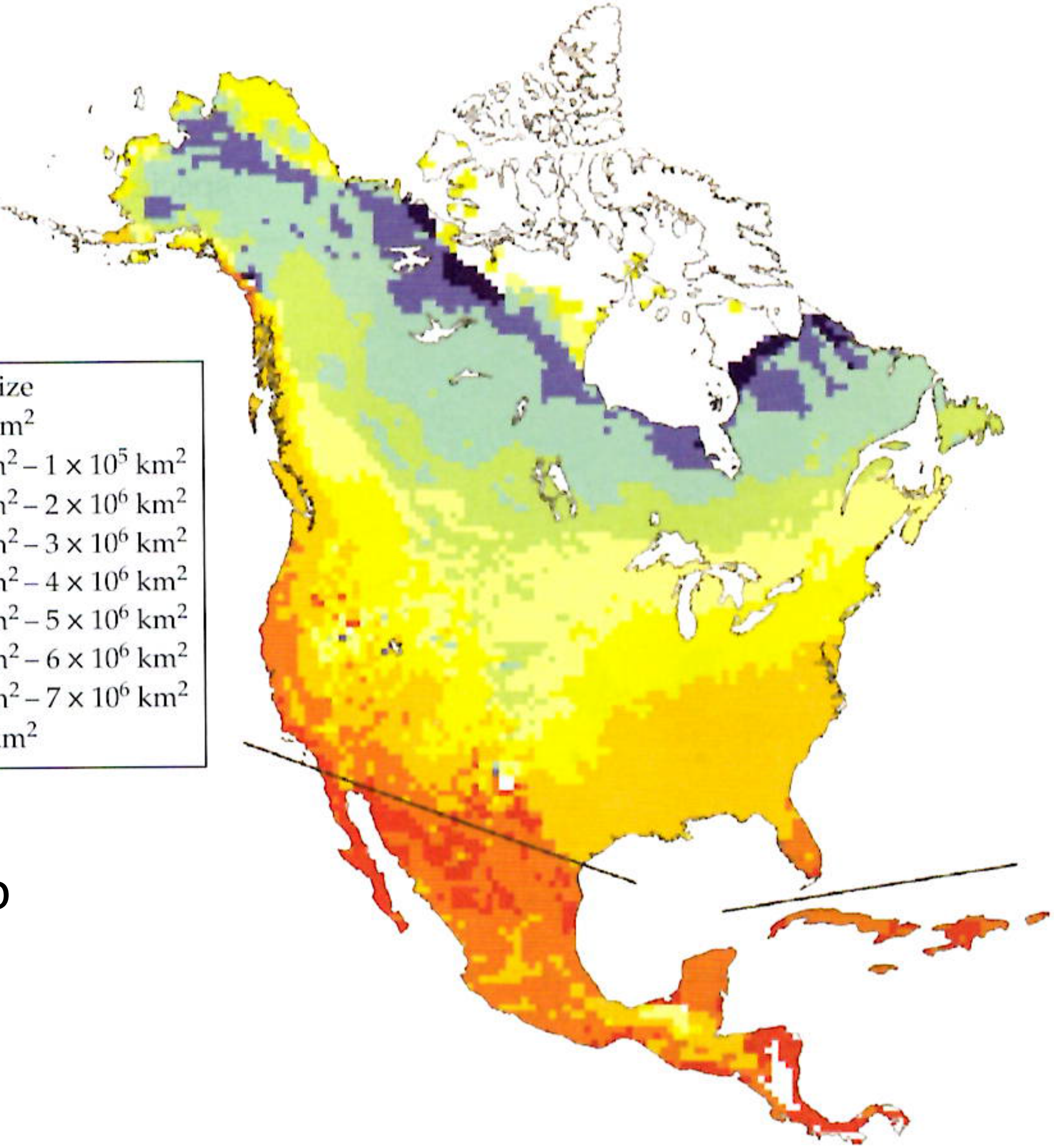
Rapoport's rule as it relates to the latitudinal diversity gradient. As species richness declines with increasing latitude, remaining species tend to have geographical ranges that extend across a broader range of latitudes (Stephens 1989)

Rapoport's Rule: Range size increases with latitude

Species range size gets smaller towards lower latitudes

This is shown for North American trees

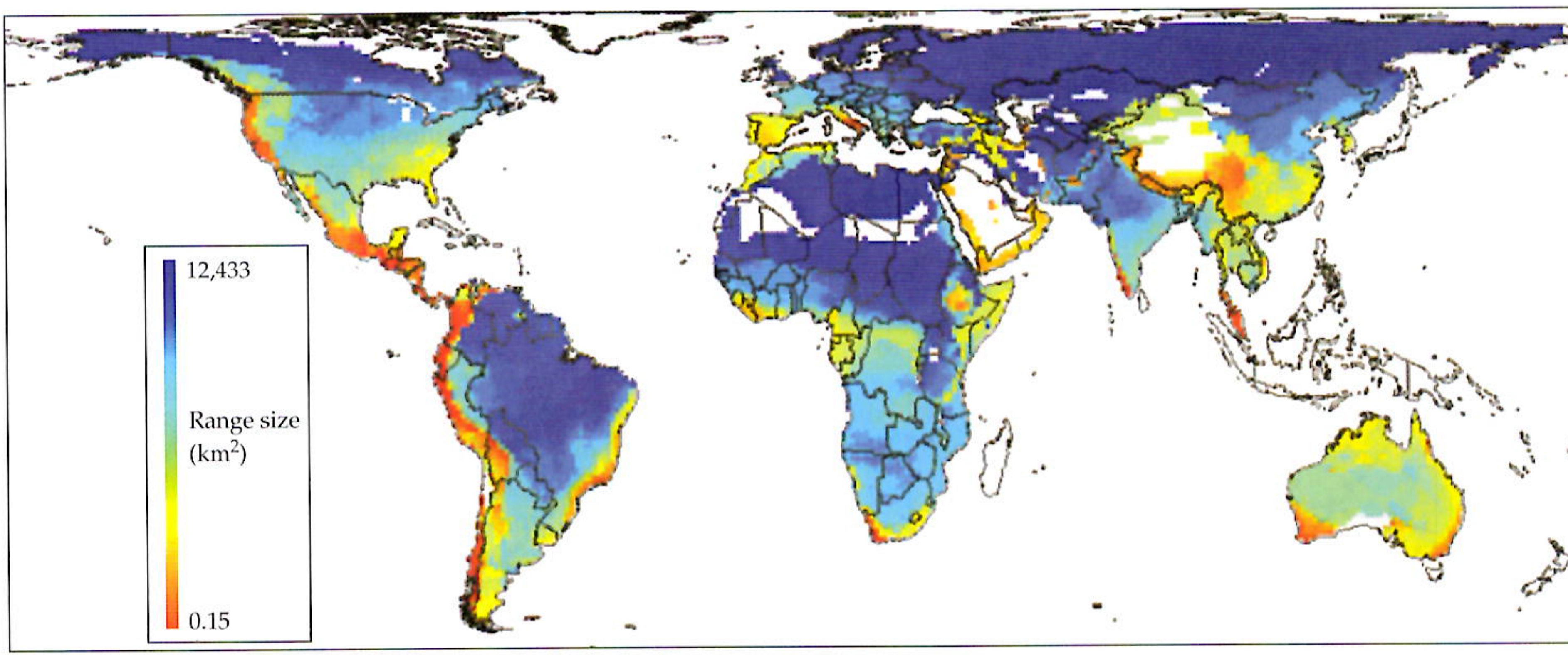




We would expect this to lead to higher beta diversity (species turnover) in the tropics

Rapoport's Rule: Range size increases with latitude

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



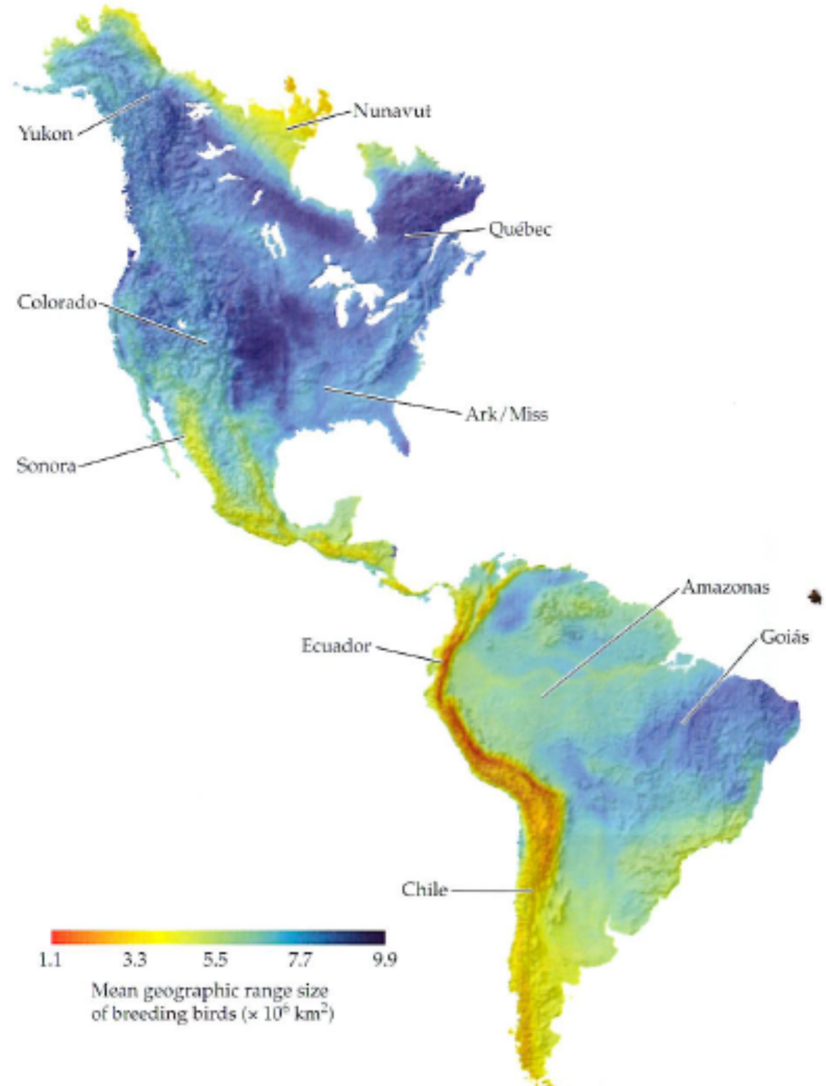
Rapoport's Rule: Range size increases with latitude

Species in the tropics have smaller range sizes (generally)

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

These variables influence climate conditions, productivity and seasonality of resources

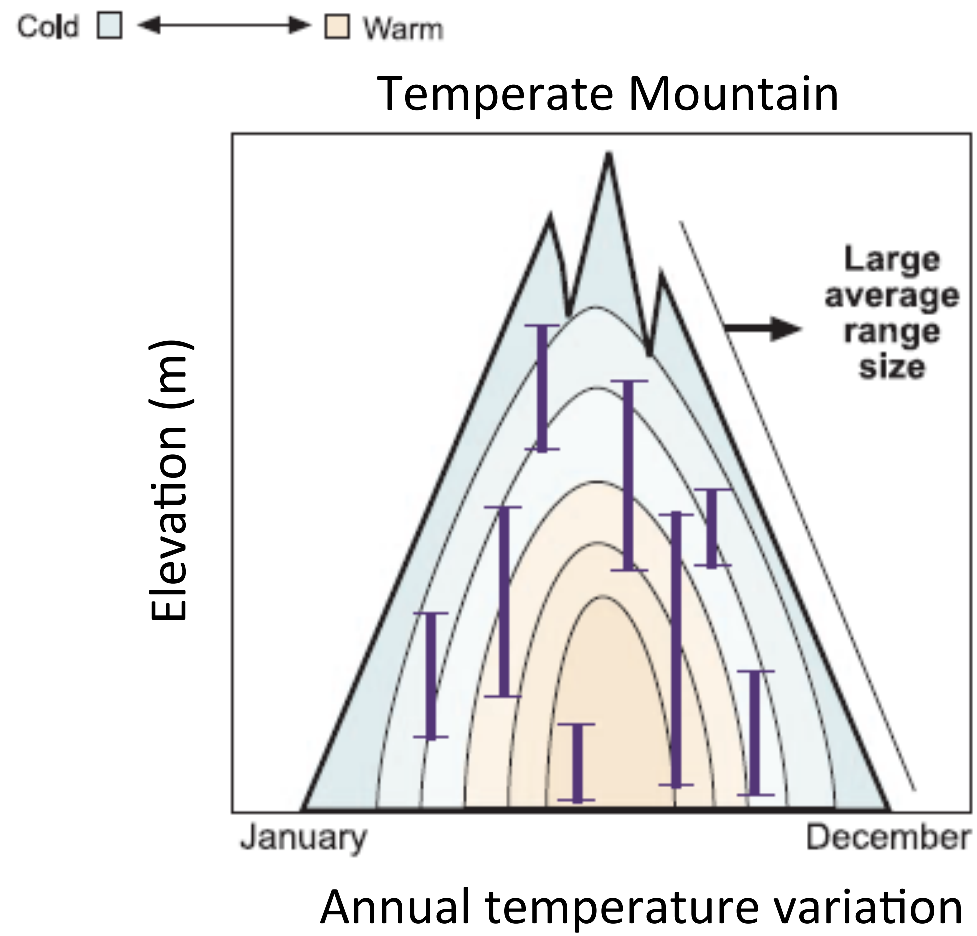
Range size of Nearctic/Neotropical birds



Other Latitudinal Trends

Recall Janzen's hypothesis – consistent with Rapoport's rule

Mountain passes are greater barriers to dispersal in the tropics than in temperate regions because there is less overlap in thermal regimes experienced at low and high altitudes in the tropics.



McCain 2009, *Ecol. Letters*; Janzen 1967, *American Naturalist*

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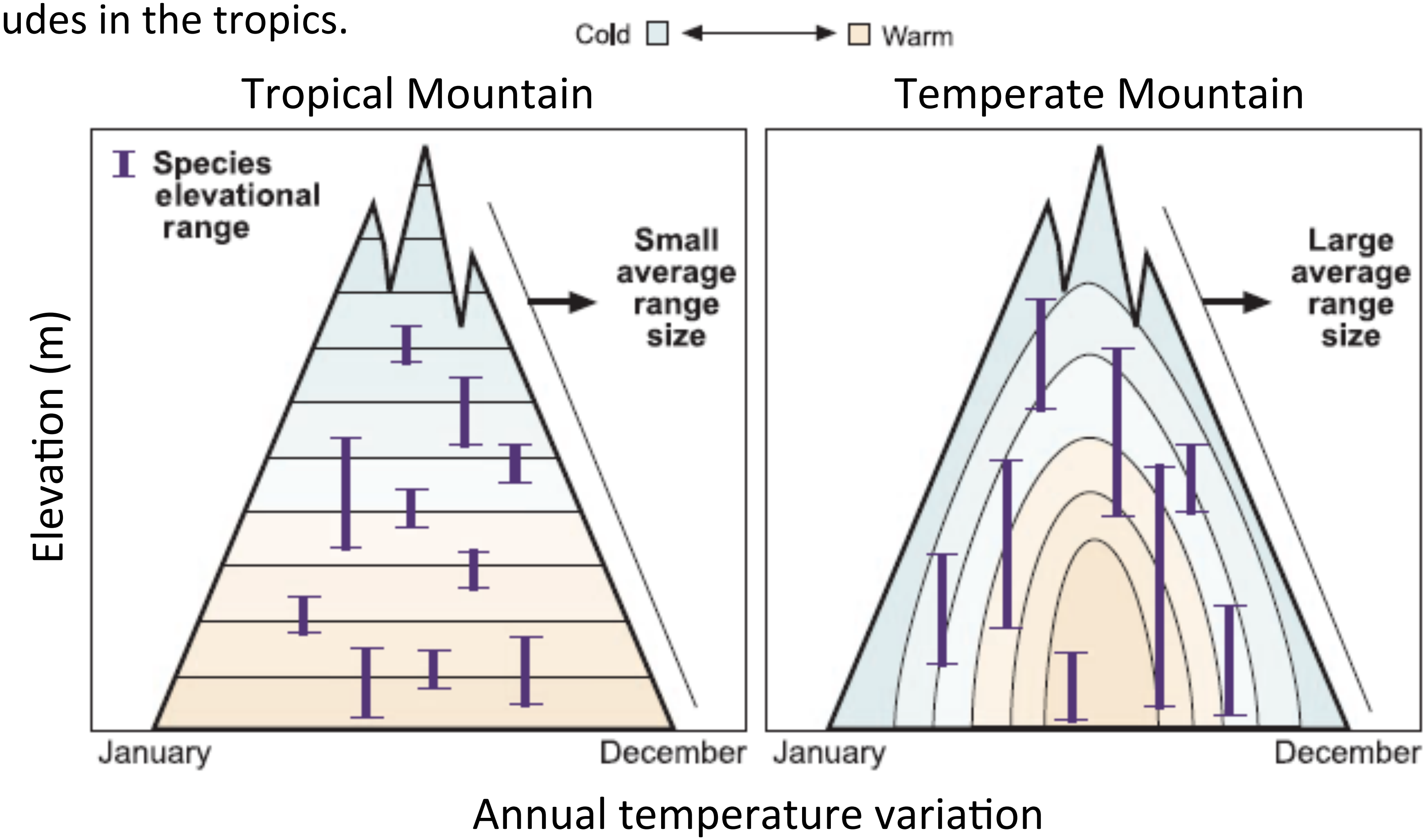

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Other Latitudinal Trends

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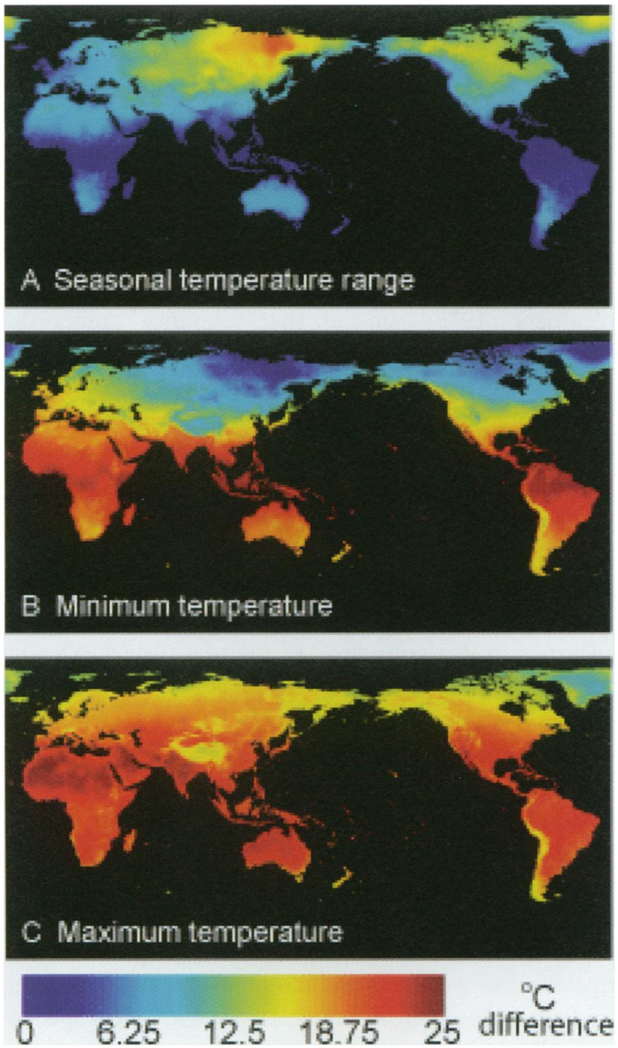
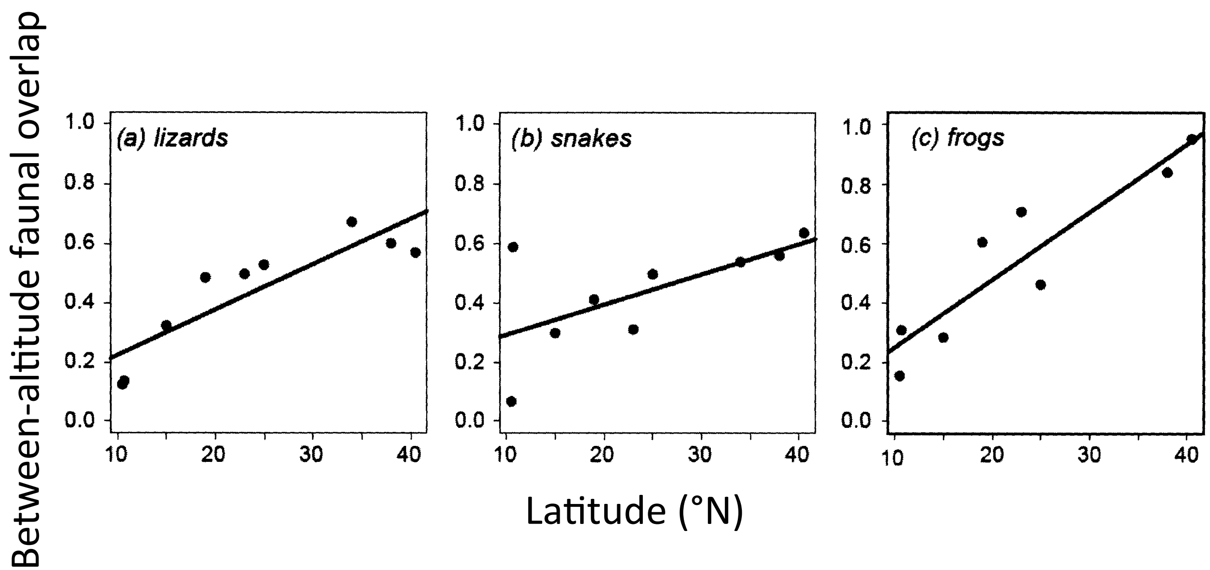


With stronger physiological dispersal barriers, we expect that species elevational ranges along mountainsides would be narrower in the tropics

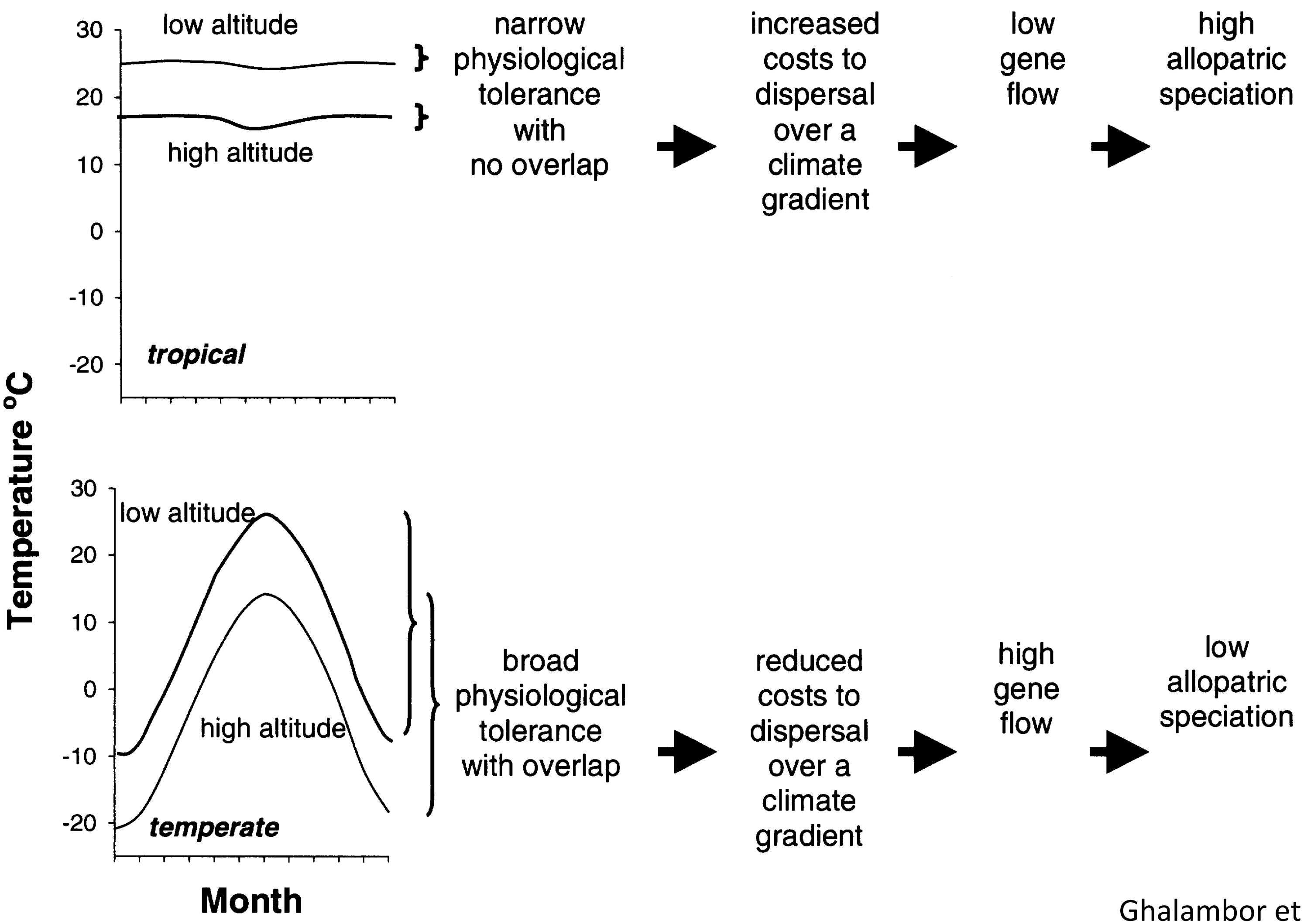
This leads to higher beta diversity in tropical mountains, or higher turnover moving across elevations, compared to temperate mountains



Ghalambor et al. 2006

Other Latitudinal Trends

With stronger physiological dispersal barriers, potential for isolation and allopatric speciation is higher in the tropics compared to the temperate zone

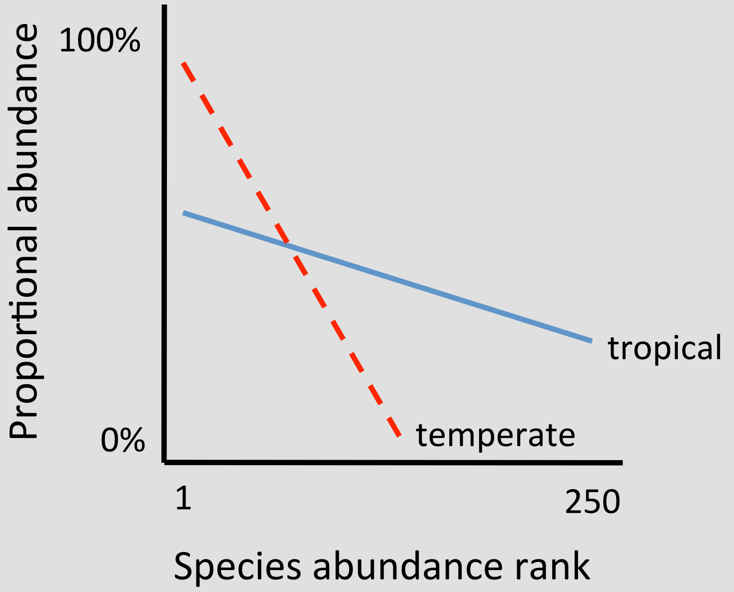


Ghalambor et al. 2006

Other Latitudinal Trends

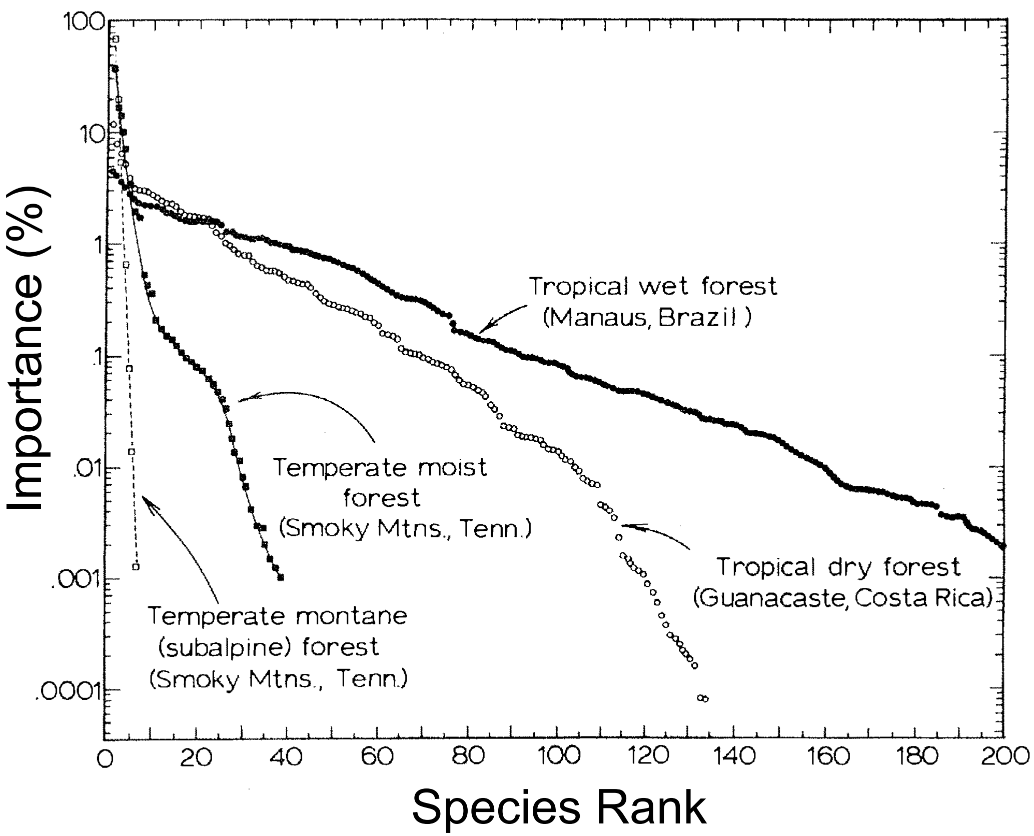
Species Dominance

Species Dominance: Tropical areas tend to have more species, but those species tend to be numerically rare. Any individual tropical species accounts for a smaller proportion of the total abundance of individuals summed across all species than the average species in temperate areas.



Other Latitudinal Trends

Species Dominance



Example in tropical tree communities

Tropical communities have higher species richness overall, but most species are rare – fewer species have high numerical abundance (x-axis)

Temperate communities have fewer species and are dominated by species with high numerical abundance (y-axis)

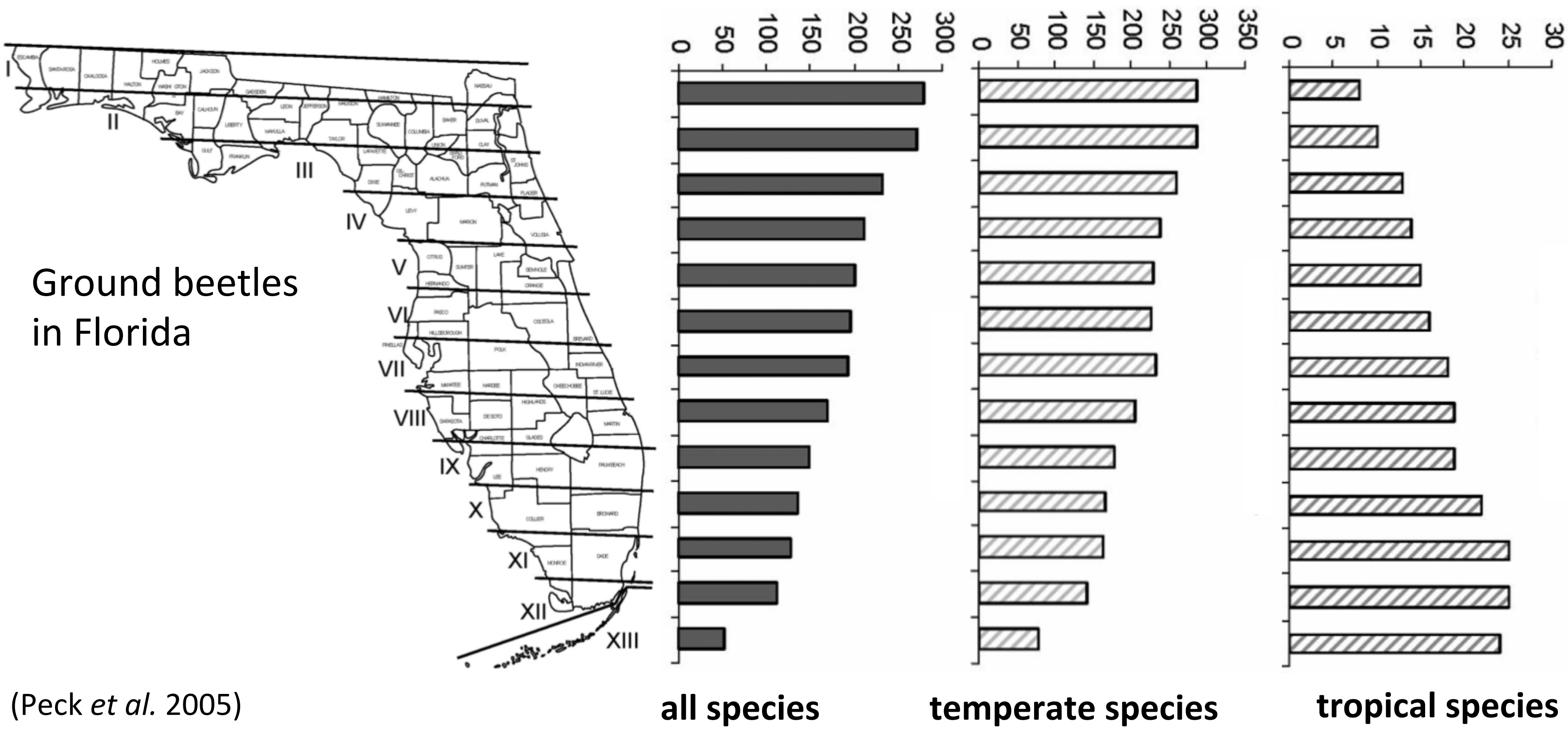
(Hubbell 1979)

Other Spatial Diversity Gradients

Peninsulas

Peninsula Effect: tendency for species richness to decrease towards the tip of a peninsula.

Ground beetles in Florida



(Peck *et al.* 2005)

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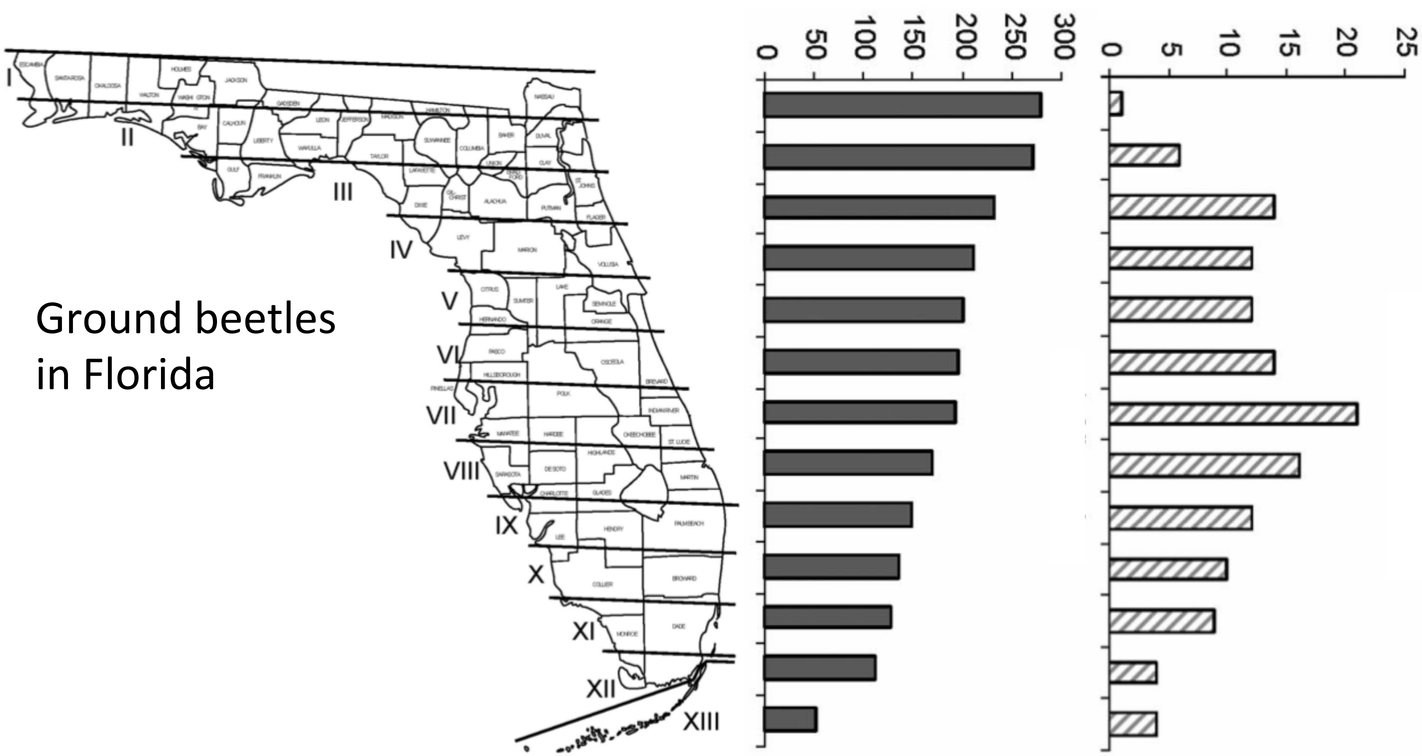

(Peck *et al.* 2005)

all species **endemic species**

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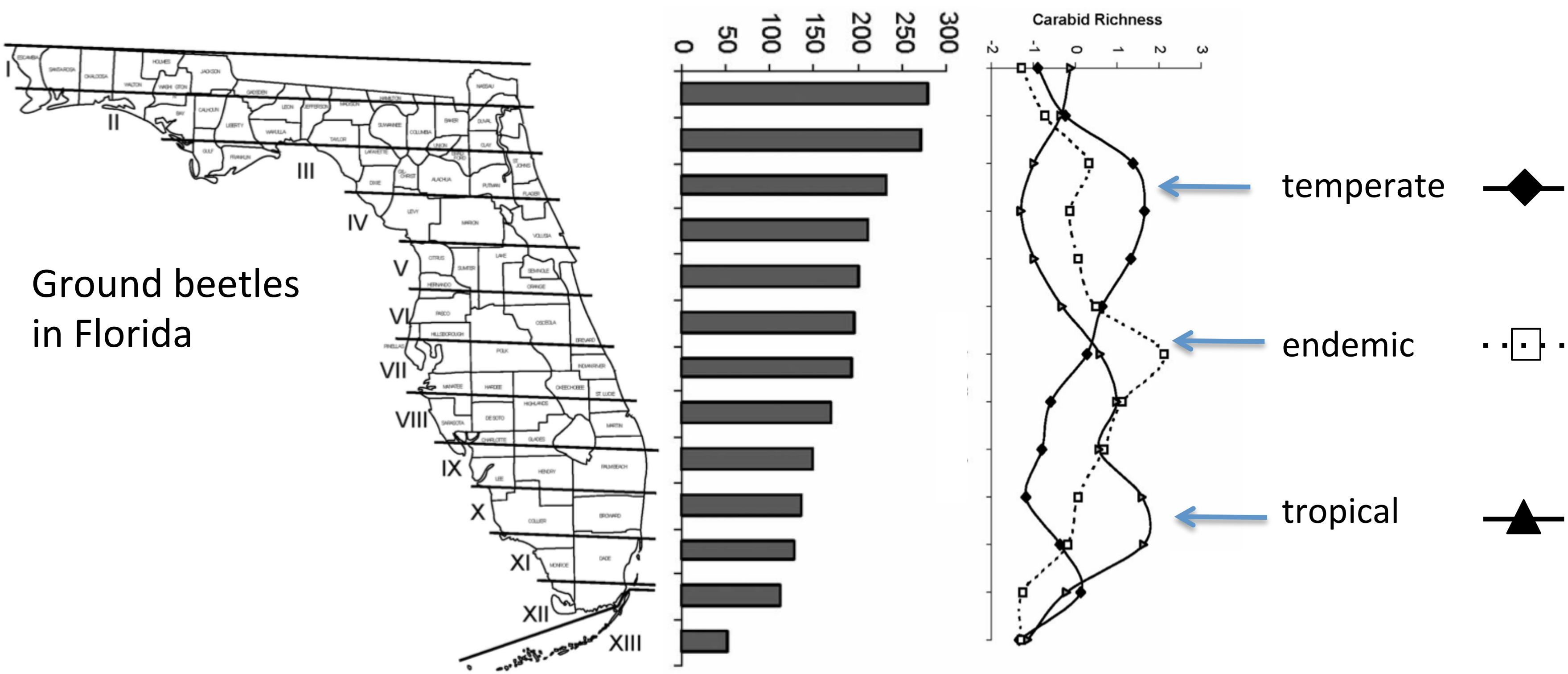


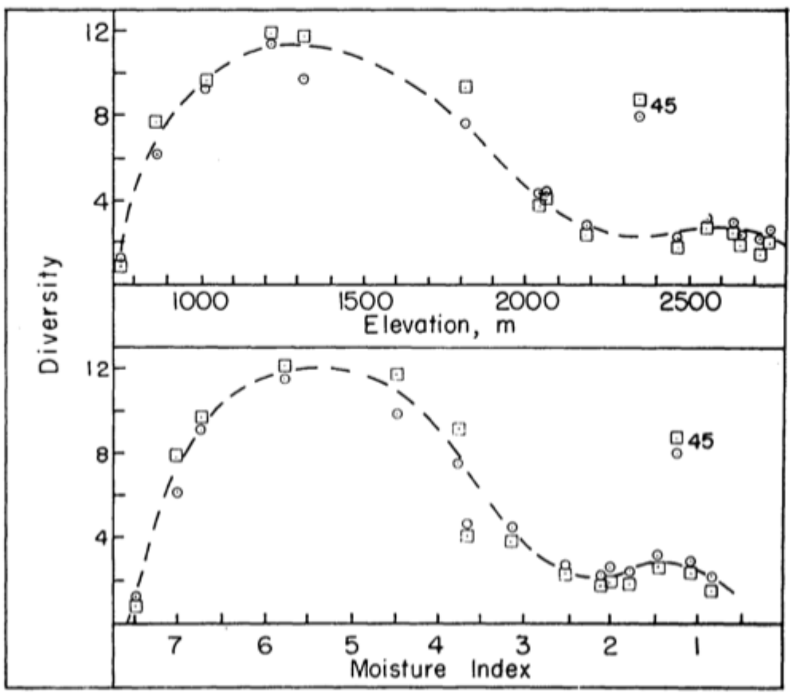
(Peck *et al.* 2005)

all species

Other Spatial Diversity Gradients

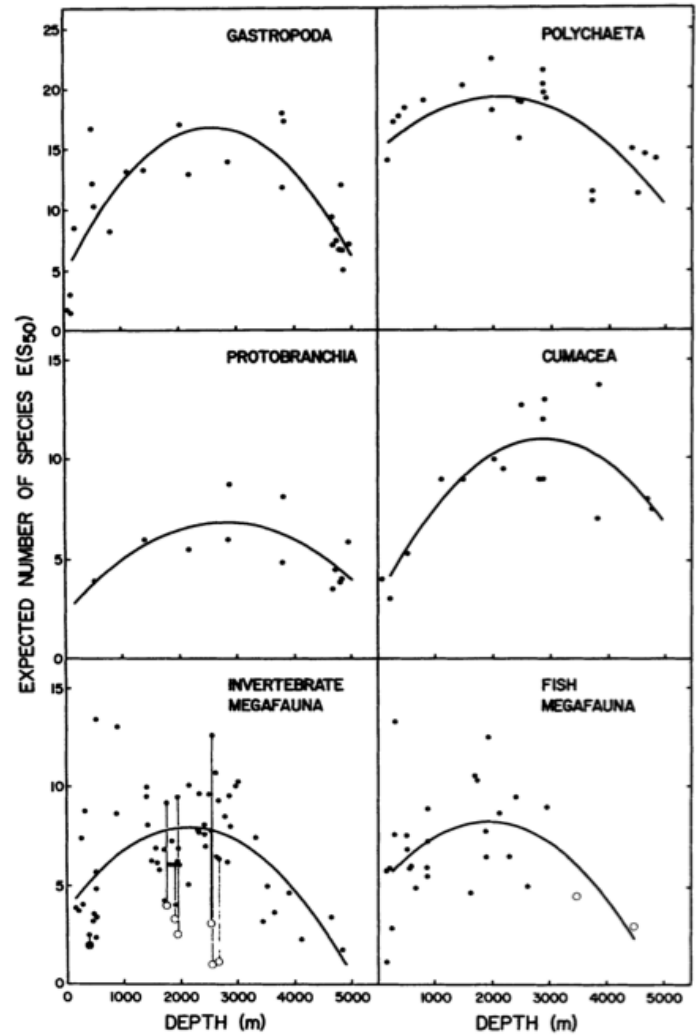
Altitude and Depth

Vegetation of Santa Catalina Mountains, AZ



(Whittaker and Niering 1975)

Marine fauna



(Rex 1981)

Patterns of Species Diversity

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Patterns of Species Diversity

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