

# Diversity Patterns III

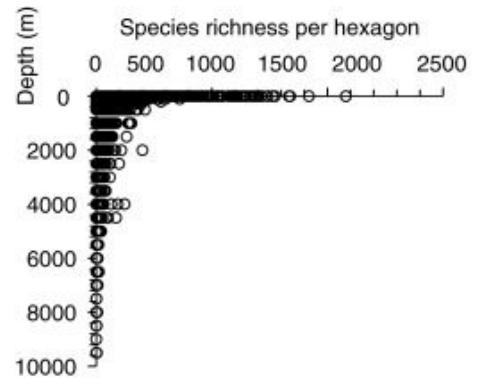
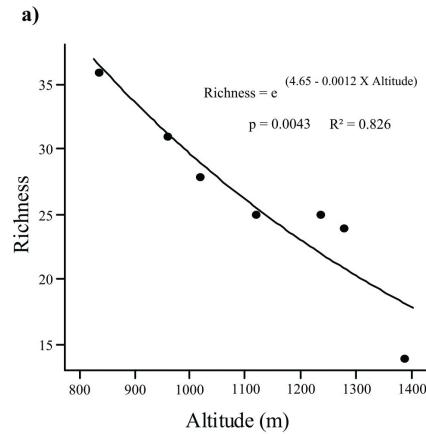
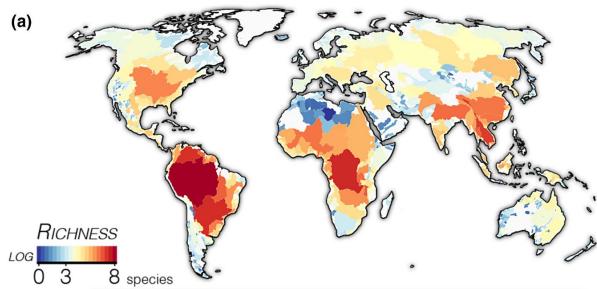
Today's Agenda:

- Quiz
- Drivers of Diversity

# Diversity patterns

We've spent the last few classes discussing patterns of diversity, but...

What drives differences in diversity? Any thoughts?



# Groups of hypothesized drivers

Your book splits hypothesized drivers in 4 groups:

- 1) Null model explanations
- 2) Ecological explanations
- 3) Historical explanations
- 4) Evolutionary explanations

# Groups of hypothesized drivers

Your book splits hypothesized drivers in 4 groups:

- 1) Null model explanations
- 2) Ecological explanations
- 3) Historical explanations
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Note that although these are discussed in terms of the latitudinal diversity gradient, they can be applied to other diversity patterns

# Null explanations of diversity

What do we mean by “null model”?

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“The null model is used as a term of comparison, to verify whether the object in question displays some non-trivial features (properties that wouldn't be expected on the basis of chance alone or as a consequence of the constraints), such as community structure” - Wikipedia

# Null explanations of diversity

What do we mean by “null model”?

“The null model is used as a term of comparison, to verify whether the object in question displays some non-trivial features (properties that wouldn't be expected on the basis of chance alone or as a consequence of the constraints), such as community structure” - Wikipedia

Note that null models can differ widely in how much biology is included!

# Null expectations: the mid-domain



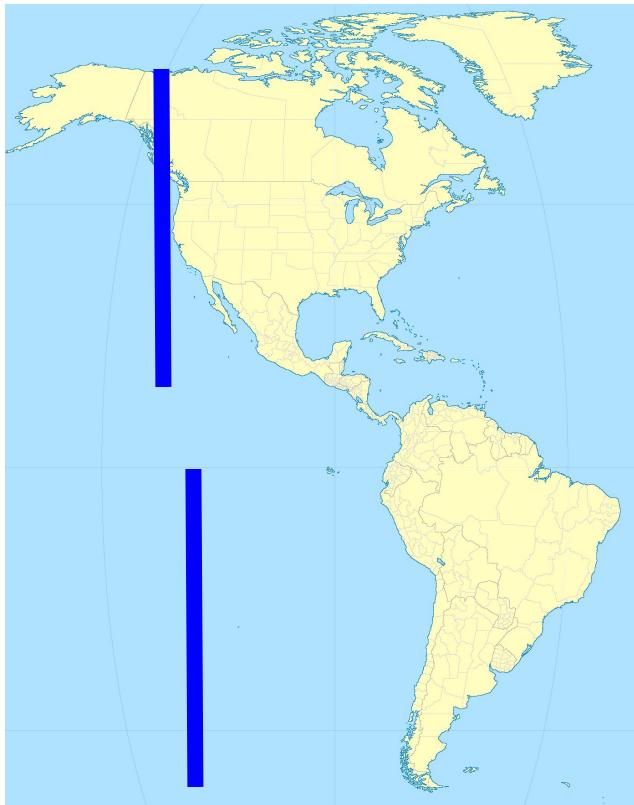
Species randomly added to a bounded region will tend to overlap more in the center

# Null expectations: the mid-domain



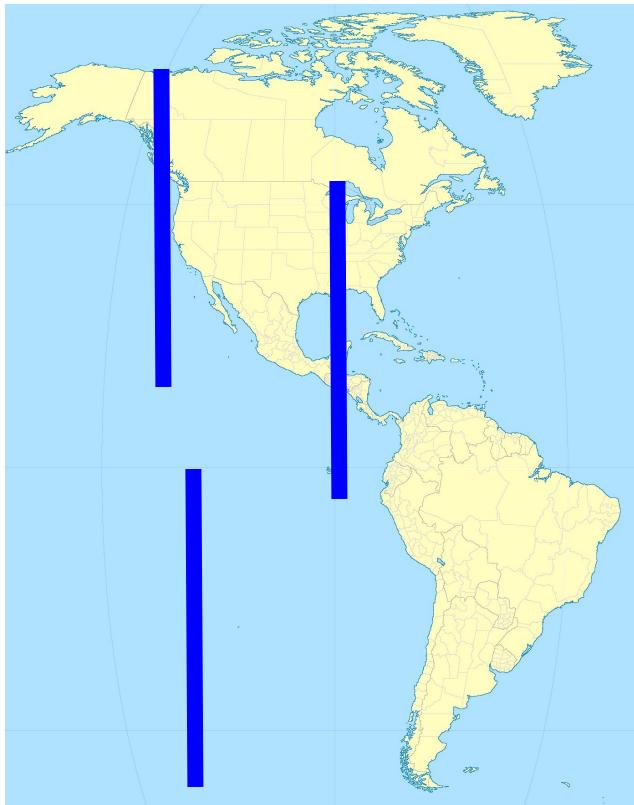
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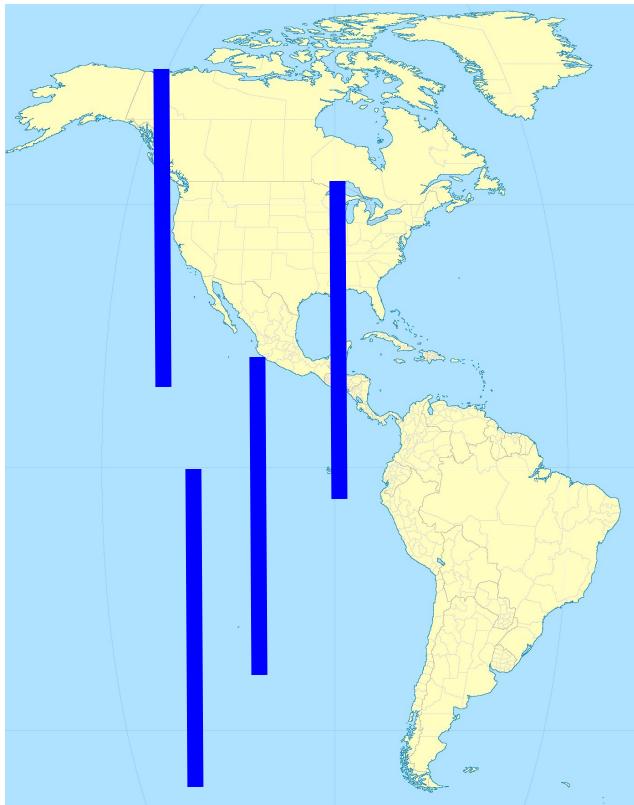
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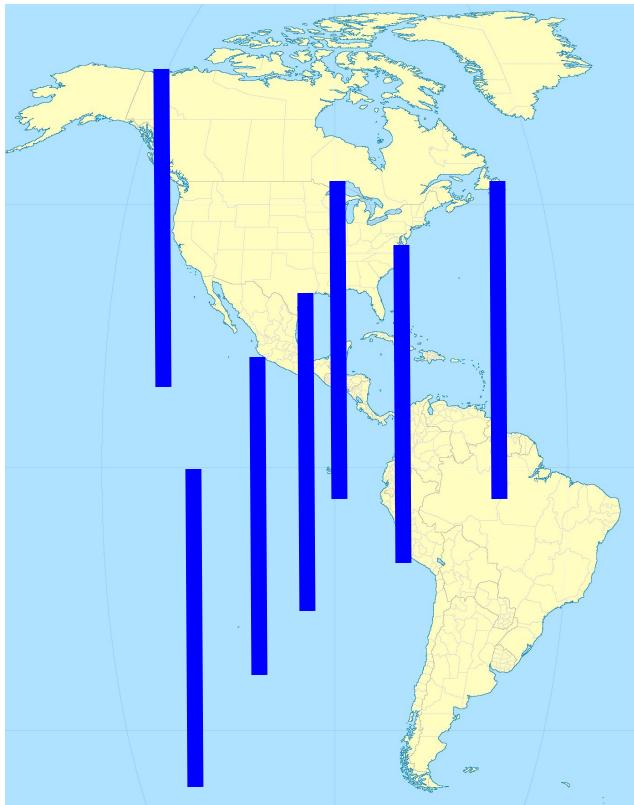
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# Null expectations: the mid-domain



Species randomly added to a bounded region will tend to overlap more in the center

# Null expectations: the mid-domain



Species randomly added to a bounded region will tend to overlap more in the center

Randomly placing species might give you a latitudinal diversity gradient

# Problems with the mid-domain hypothesis

- It should apply to ANY bounded regions (e.g., entries of continents, islands, etc.) in ANY direction (i.e., longitudinal as well as latitudinal)
- Is a globe really a bounded region?
- Inconsistent support when tested

# Testing the mid-domain hypothesis

Storch et al. tested this idea

- Randomly placed species using a spreading-dye algorithm
  - For each species, a random point was selected
  - then, adjacent areas were added until reaching the size of the species actual range
- Replicated 100 times

*Ecology Letters*, (2006) 9: 1308–1320

doi: 10.1111/j.1461-0248.2006.00984.x

LETTER

## Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity

David Storch,<sup>1,2\*</sup> Richard G. Davies,<sup>3</sup> Samuel Zajicek,<sup>1</sup> C. David L. Orme,<sup>4</sup> Valerie Olson,<sup>5</sup> Gavin H. Thomas,<sup>6</sup> Tzung-Su Ding,<sup>7</sup> Pamela C. Rasmussen,<sup>8</sup> Robert S. Ridgely,<sup>9</sup> Peter M. Bennett,<sup>5</sup> Tim M. Blackburn,<sup>6</sup> Ian P. F. Owens<sup>5,10</sup> and Kevin J. Gaston<sup>3</sup>

### Abstract

Spatial patterns of species richness follow climatic and environmental variation, but could reflect random dynamics of species ranges (the mid-domain effect, MDE). Using data on the global distribution of birds, we compared predictions based on energy availability (actual evapotranspiration, AET, the best single correlate of avian richness) with those of range dynamics models. MDE operating within the global terrestrial area provides a poor prediction of richness variation, but if it operates separately within traditional biogeographic realms, it explains more global variation in richness than AET. The best predictions, however, are given by a model of global range dynamics modulated by AET, such that the probability of a range spreading into an area is proportional to its

# Testing the mid-domain hypothesis

Storch et al. tested this idea

- Tested different models:
  - Species were randomly placed globally
  - Species were placed/expanded within ecoregions
  - Species were placed randomly, but preferentially expanded toward more productive regions

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LETTER

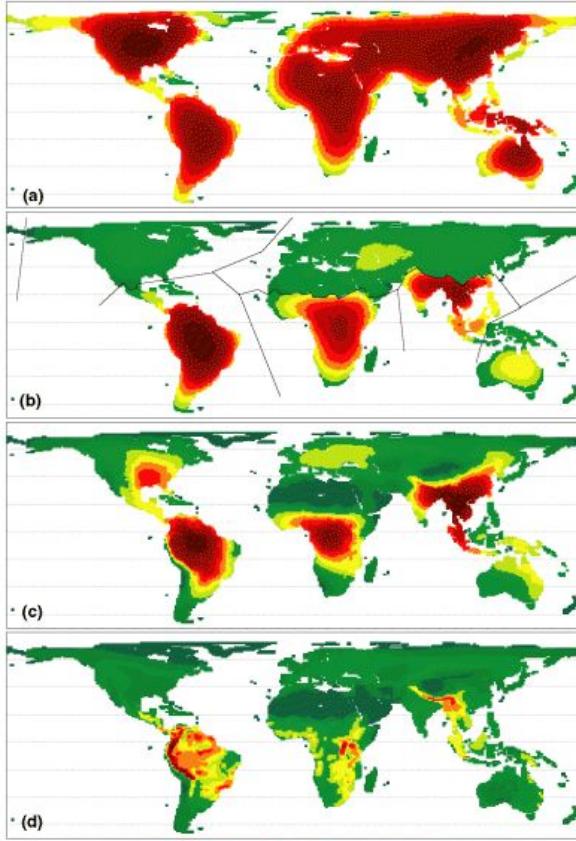
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# Testing the mid-domain hypothesis



Global Model

Ecoregion Model

Productivity-biased  
Model

Species richness

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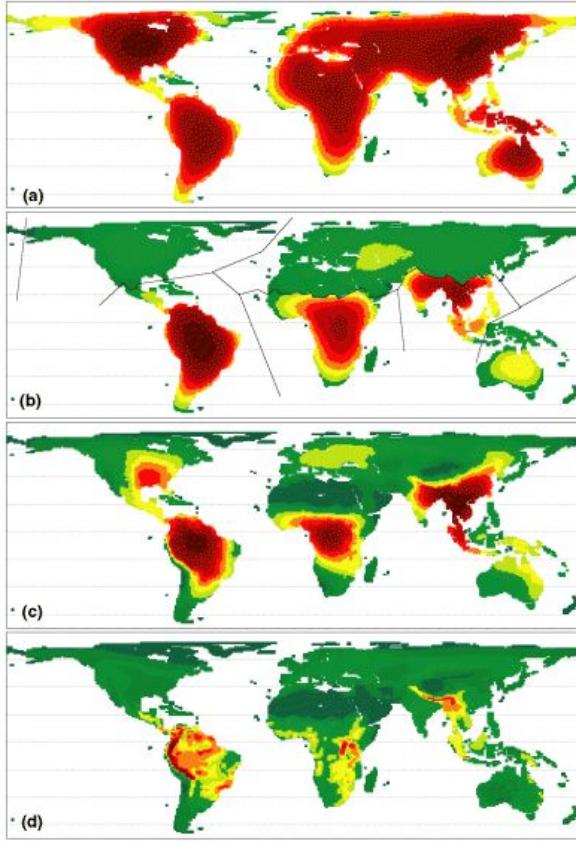
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Ecoregion Model

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Does not strongly support the MDE, but does suggest some neutral dynamics may be important

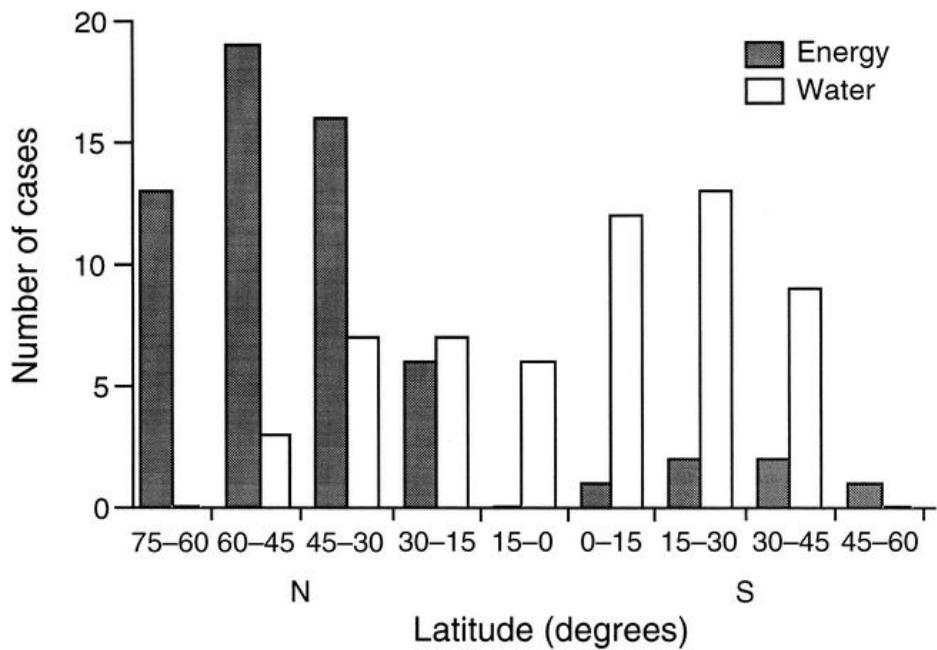
# Ecological hypotheses for diversity

- Climate-related hypotheses
- Productivity-related hypotheses
- Note that there is some overlap between these!

# Climatic Drivers of Diversity

Climate correlated with richness

- Animals: driver varies by latitude
- Plants: usually water, or water + energy



## CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecology, 84(12), 2003, pp. 3105-3117  
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### ENERGY, WATER, AND BROAD-SCALE GEOGRAPHIC PATTERNS OF SPECIES RICHNESS

BRADFORD A. HAWKINS,<sup>1,12</sup> RICHARD FIELD,<sup>2</sup> HOWARD V. CORNELL,<sup>3</sup> DAVID J. CURRIE,<sup>4</sup> JEAN-FRANÇOIS GUÉGAN,<sup>5</sup> DAWN M. KAUFMAN,<sup>6</sup> JEREMY T. KERR,<sup>7</sup> GARY G. MITTELBACH,<sup>8</sup> THIERRY OBERDORFF,<sup>9</sup> EILEEN M. O'BRIEN,<sup>10</sup> ERIC E. PORTER,<sup>10</sup> AND JOHN R. G. TURNER<sup>11</sup>

# Climate and Diversity

... but WHY?

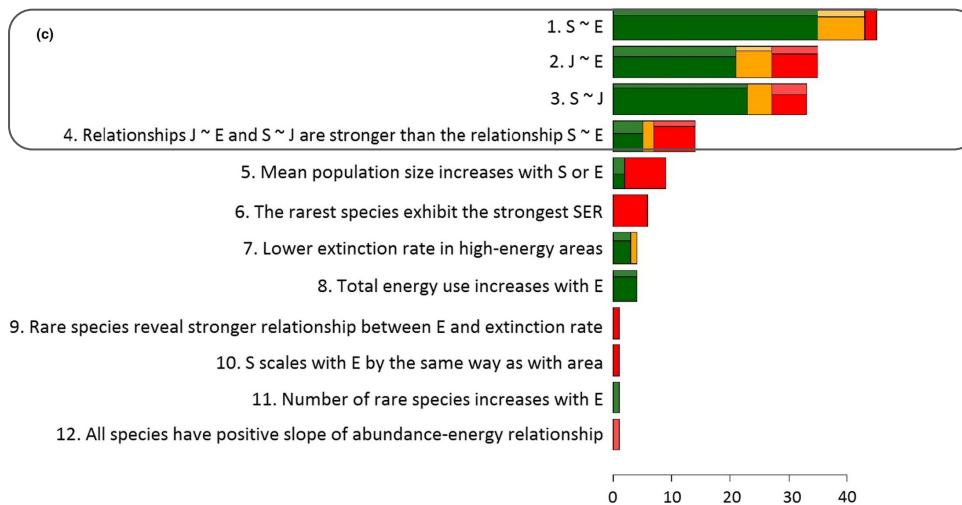
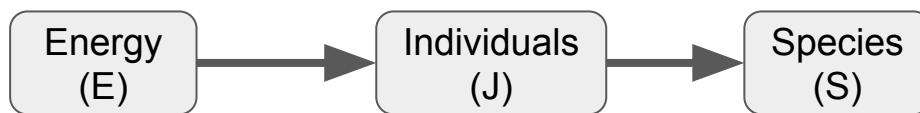
# Climate and Diversity

... but WHY?

## More Individuals Hypothesis:

- Assumes more individuals can be supported where there is higher productivity
- Assumes more individuals translates to more species
- Hence, high productivity should yield more species

# Testing the More Individuals Hypothesis



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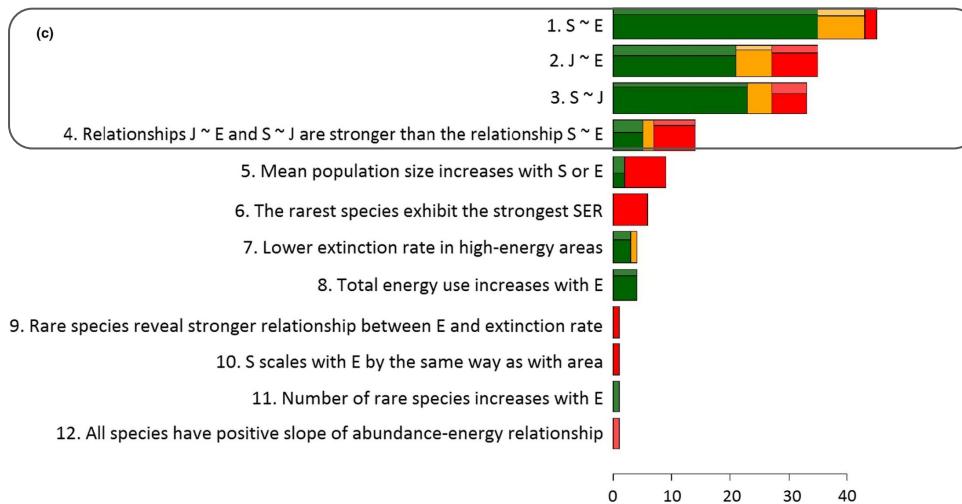
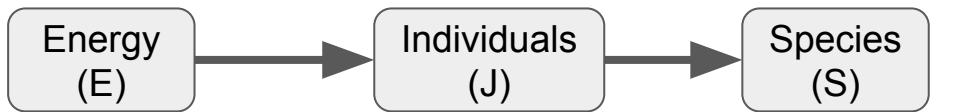
Review and Synthesis | [Full Access](#)

**The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship**

David Storch ✉ Eliška Bohdálková, Jordan Okie

First published: 16 April 2018 | <https://doi.org/10.1111/ele.12941> | Citations: 154

# Testing the More Individuals Hypothesis



- Relationships between E,J,S have mixed support
- Poor support when considering relative strengths

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# Issues with MIH

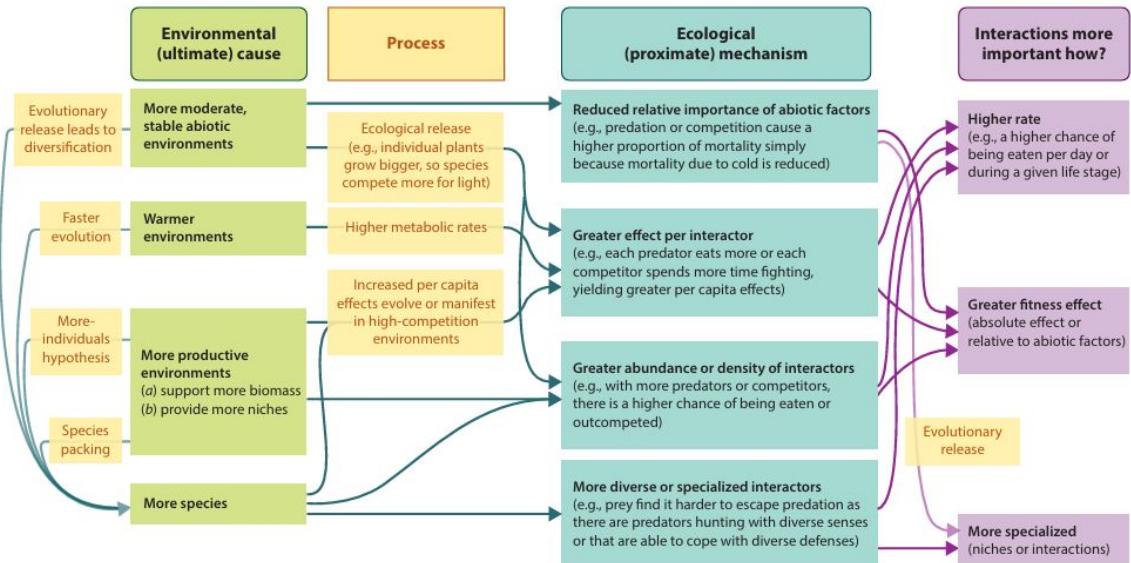
- Confounding relationships between species richness and productivity
- Plants often fail to show the pattern
- Quantitative analyses don't stand up well
- Recent work suggests that variation in abundances may also play a role

# Productivity and Diversity

We'll spend time on this when we cover Biodiversity and Ecosystem Functioning

# Other ecological hypotheses

- Species interactions
  - E.g., a greater role of natural enemies or mutualists in the tropics



Annual Review of Ecology, Evolution, and Systematics

Geographic Gradients in Species Interactions: From Latitudinal Patterns to Ecological Mechanisms

Anna L. Hargreaves

Department of Biology, McGill University, Montreal, Québec, Canada;  
email: anna.hargreaves@mcgill.ca

# Historical Explanations

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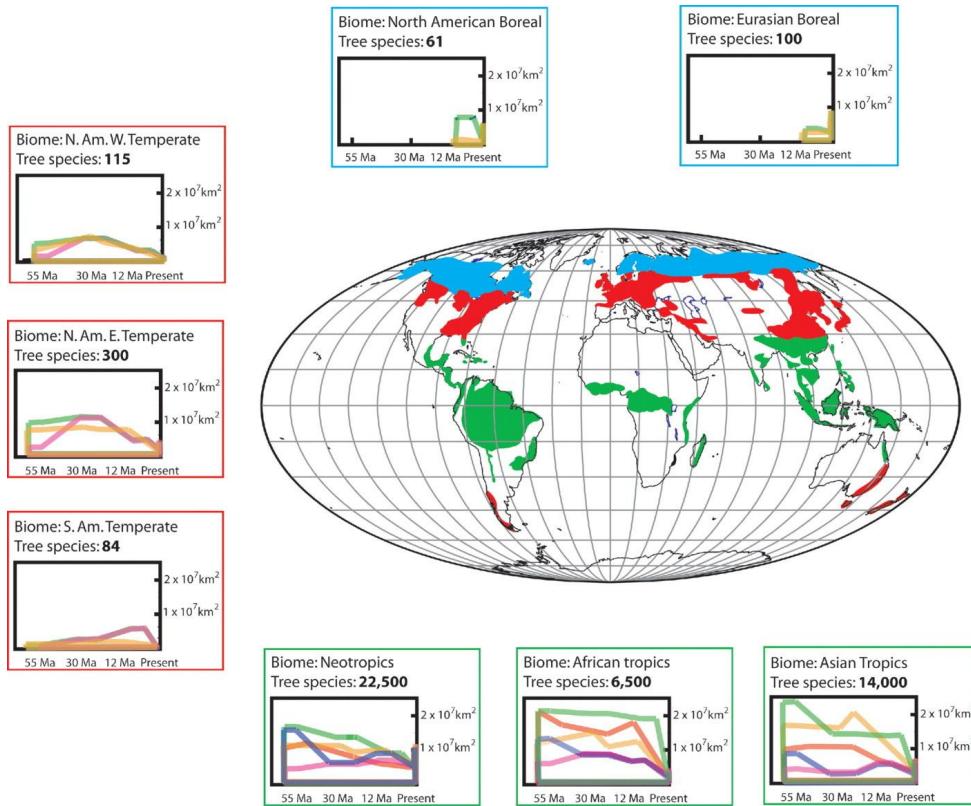
Time-integrated area hypothesis

# Historical Explanations

## Time-integrated area hypothesis

- Larger areas have more species
  - Higher speciation rates
  - Lower extinction rates
  - etc.
- Older areas have more species
  - More time to accumulate diversity

# Time-integrated area hypothesis



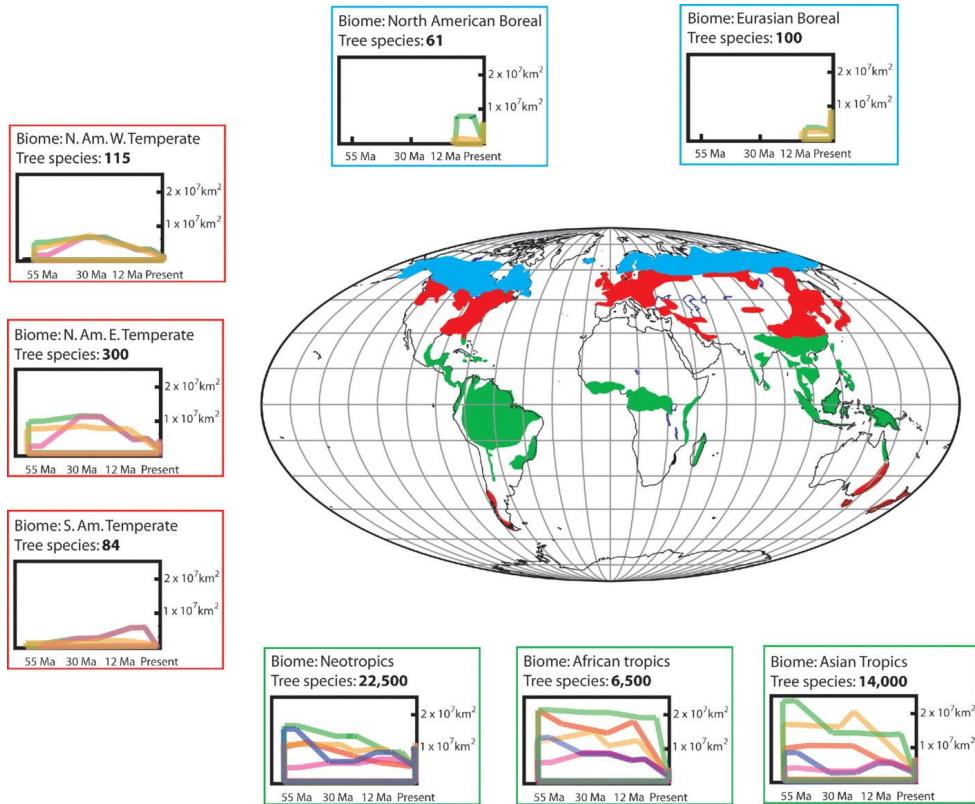
VOL. 168, NO. 6 THE AMERICAN NATURALIST DECEMBER 2006

## Notes and Comments

Evidence for a Time-Integrated Species-Area Effect on the Latitudinal Gradient in Tree Diversity

Paul V. A. Fine<sup>1,\*</sup> and Richard H. Ree<sup>2,†</sup>

# Time-integrated area hypothesis



**Table 2:** Results of the correlations between log (tree diversity) and log (time-integrated area) for the five interpretations shown in figure 1

Interpretation (source), cumulative time since	R <sup>2</sup>	P
Modern (Olson et al. 2001): Present	.13	.283
1 (Beerling and Woodward 2001): Eocene	.21	.151
Oligocene	.17	.211
Miocene	.01	.730
2 (Morley 2000): Eocene	.37	.046
Oligocene	.17	.211
Miocene	.01	.730
3 (Ziegler et al. 2003): Eocene	.47	.021
Oligocene	.39	.041
Miocene	.07	.426
4 (Scotese 2003): Eocene	.51	.014
Oligocene	.59	.006
Miocene	.61	.005
5 (Willis and McElwain 2002): Eocene	.57	.007
Oligocene	.53	.012
Miocene	.42	.030

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# Evolutionary Explanations

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- Variation in speciation rates
- Variation in extinction rate
- Tropical niche conservatism

# Cradles vs Museums

Diversification (speciation - extinction) rates may vary with latitude

- Could play a role in latitudinal diversity patterns
- However, this could be due to either
  - More speciation
  - Less extinction
  - A combination of the two

# Cradles vs Museums: Proposed mechanisms

## Speciation:

- Genetic Drift (higher in tropics, increases speciation)
- Climatic variation (higher in temp, decreases speciation)
- Speciation mechanisms (differ between temp and tropical)
- Geographic area (larger area = more speciation...or less)
- Evolutionary speed (higher in tropics, increases speciation)
- Biotic interaction (higher in tropics, increases speciation)

Ecology Letters, (2007) 10: 315–331  
doi: 10.1111/j.1461-0248.2007.01020.x

**REVIEW AND SYNTHESIS**

**Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography**

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**Abstract**  
A latitudinal gradient in biodiversity has existed since before the time of the dinosaurs, yet how and why this gradient arises remains unresolved. Here we review two major hypotheses for the origin of the latitudinal diversity gradient. The time and area hypothesis holds that tropical climates are older and historically larger, allowing more opportunity for diversification. This hypothesis is supported by observations that temperate taxa are often younger than, and nested within, tropical taxa, and that diversity is positively correlated with the age and area of geographical regions. The diversification rate hypothesis holds that tropical regions diversify faster due to higher rates of speciation (caused by increased opportunities for the evolution of reproductive isolation, or faster molecular evolution), or the increased importance of biotic interactions), or due to lower extinction rates. These paleontological evidence for higher rates of diversification in tropical clades, and palaeoecological data demonstrate higher rates of origination for tropical taxa, but mixed evidence for latitudinal differences in extinction rates. Studies of latitudinal variation in incipient speciation also suggest faster speciation

# Cradles vs Museums: Proposed mechanisms

## Extinction:

- Climatic variation (more stable climate in tropics, lower extinction rate)
- Geographic area (more area in tropics, lower extinction rate)

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**REVIEW AND SYNTHESIS**

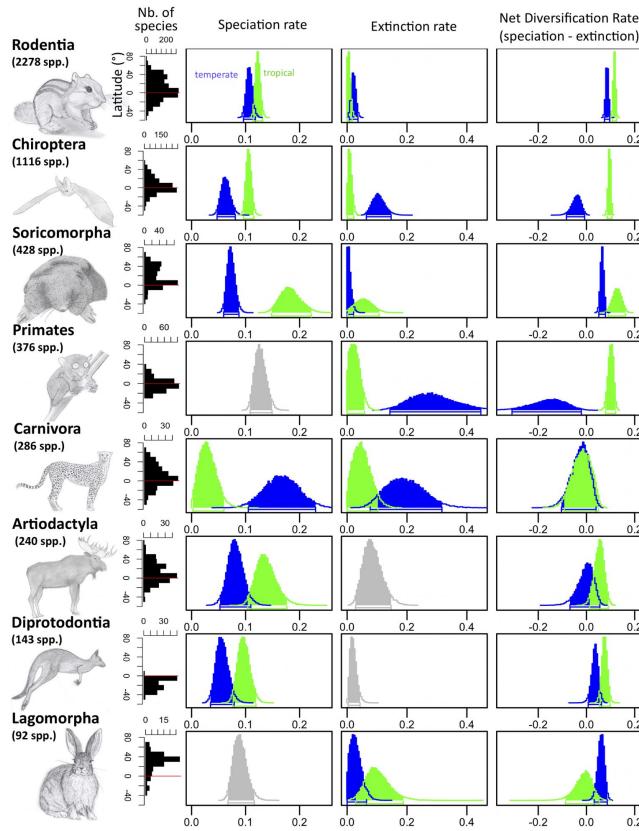
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# Cradles vs Museums: Testing with Phylogeny

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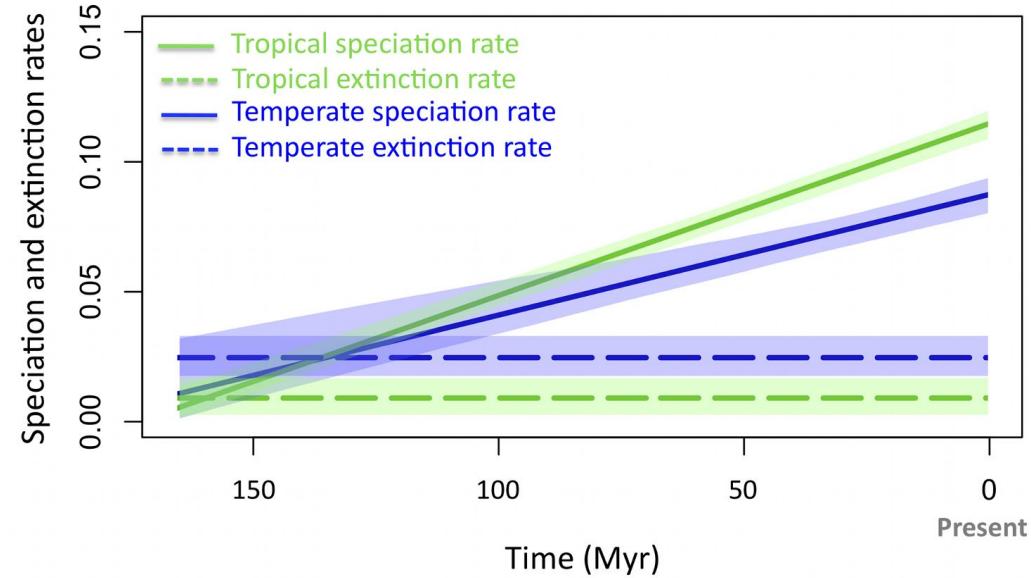
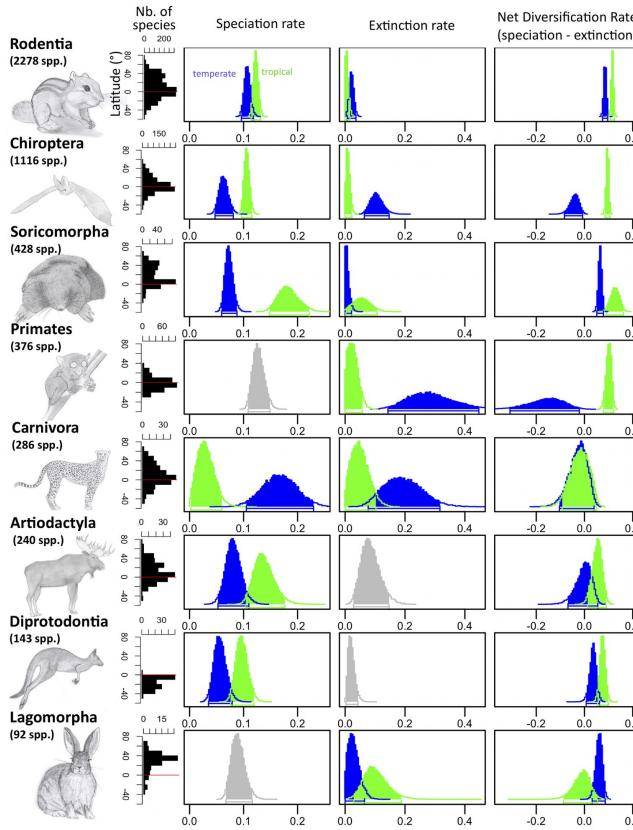
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PLOS BIOLOGY

Faster Speciation and Reduced Extinction in the Tropics Contribute to the Mammalian Latitudinal Diversity Gradient

Jonathan Rolland<sup>1,2\*</sup>, Fabien L. Condamine<sup>1</sup>, Frédéric Jiguet<sup>2</sup>, Hélène Morlon<sup>1</sup>

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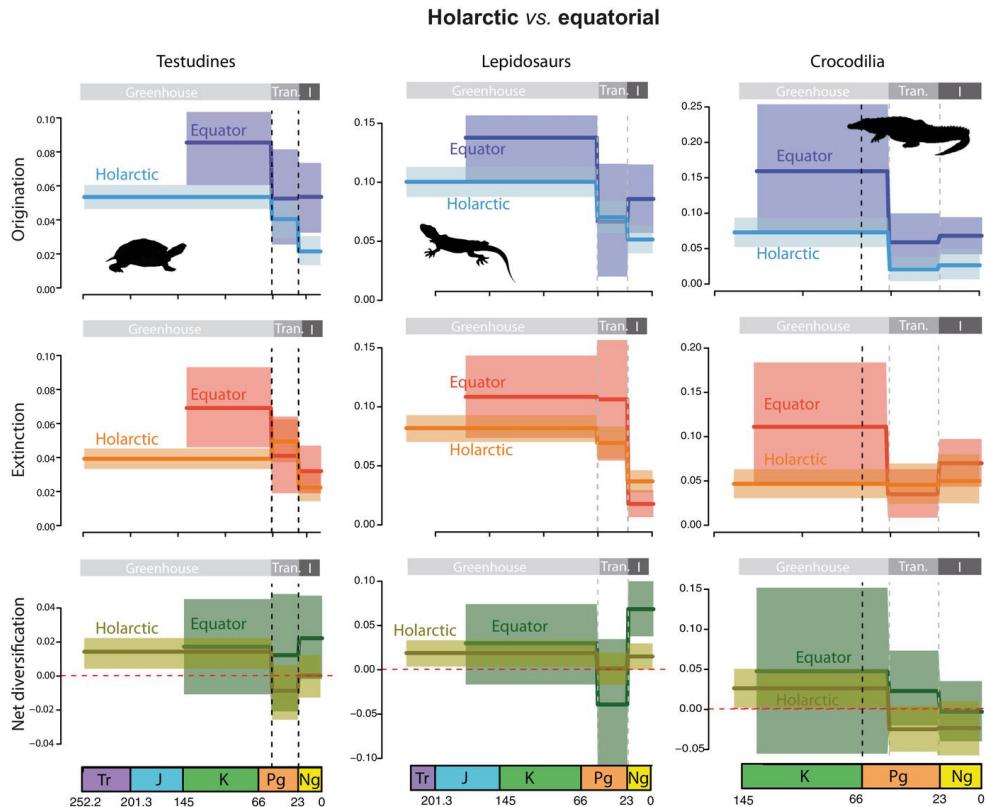
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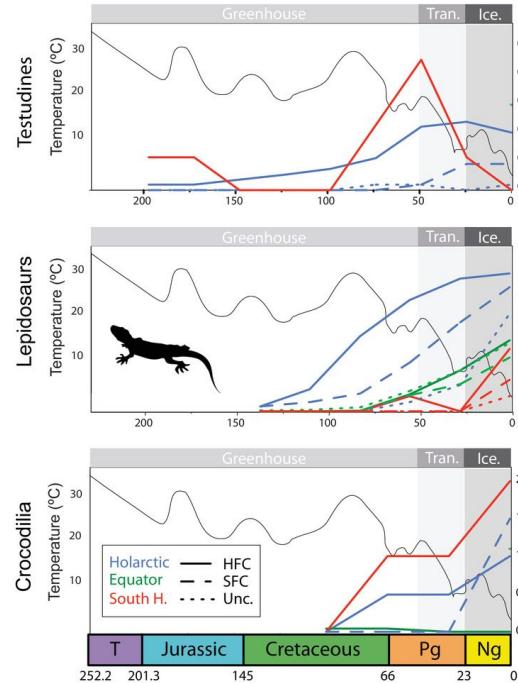
PLOS BIOLOGY

# Cradles vs Museums: Testing with Fossils

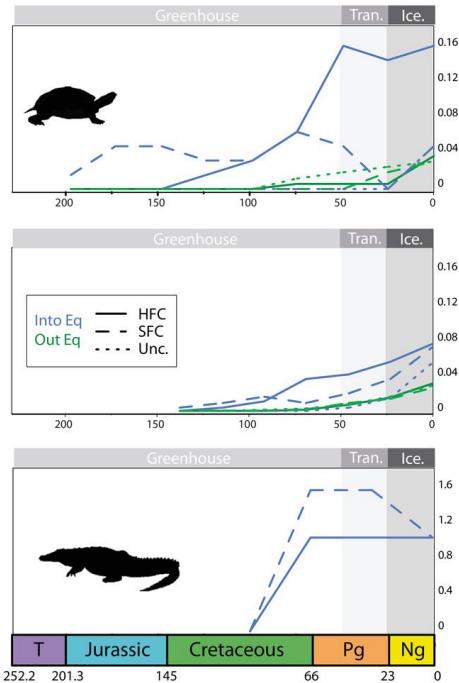


# Cradles vs Museums: Testing with Fossils

A Range extinction events



B Dispersal events

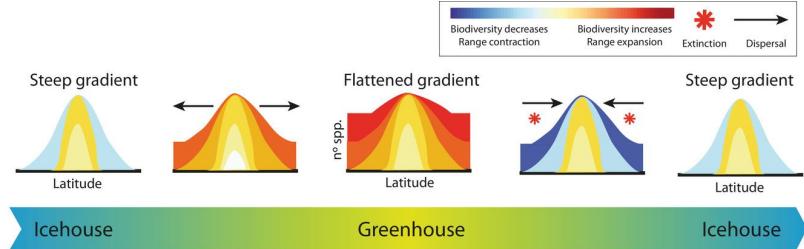
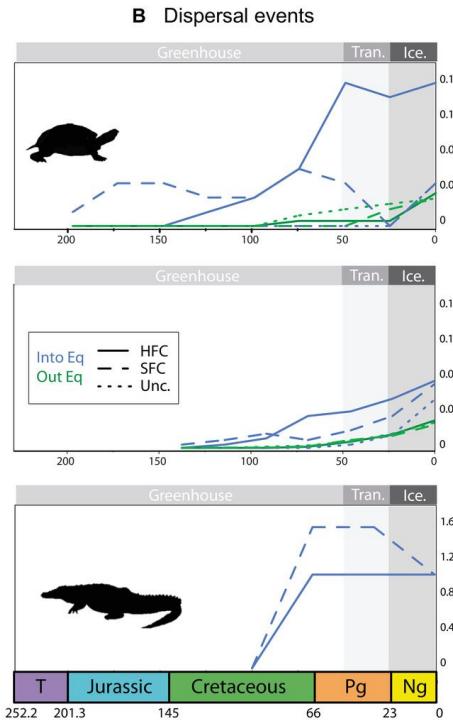
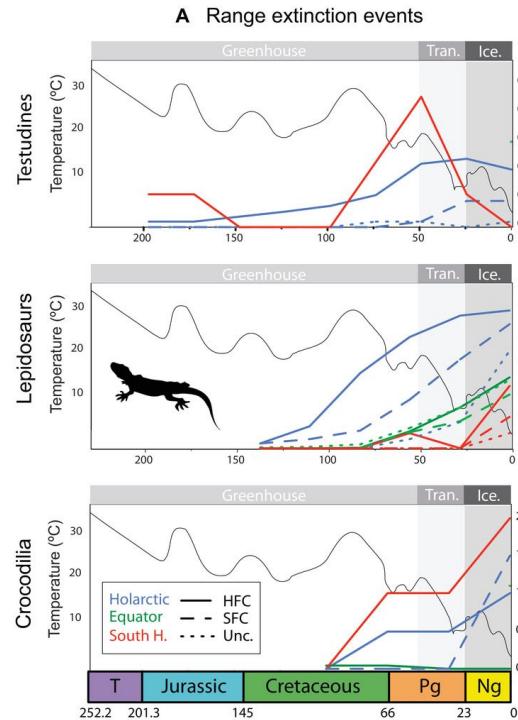


Ancient tropical extinctions at high latitudes contributed to the latitudinal diversity gradient\*

Andrea S. Meseguer<sup>1,2,3,4</sup> and Fabien L. Condamine<sup>2</sup>

doi:10.1111/evo.13967

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doi:10.1111/evo.13967

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SSCE ECOLOGY LETTERS

Andrea S. Meseguer<sup>1,2,3,4</sup> and Fabien L. Condamine<sup>2</sup>

# Evolutionary Explanations: Tropical Niche Conservatism

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**Niche conservatism:** tendency for niches to remain unchanged

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**Niche conservatism:** tendency for niches to remain unchanged

**Phylogenetic niche conservatism:** tendency for niches to remain unchanged along evolutionary lineages

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**Niche conservatism:** tendency for niches to remain unchanged

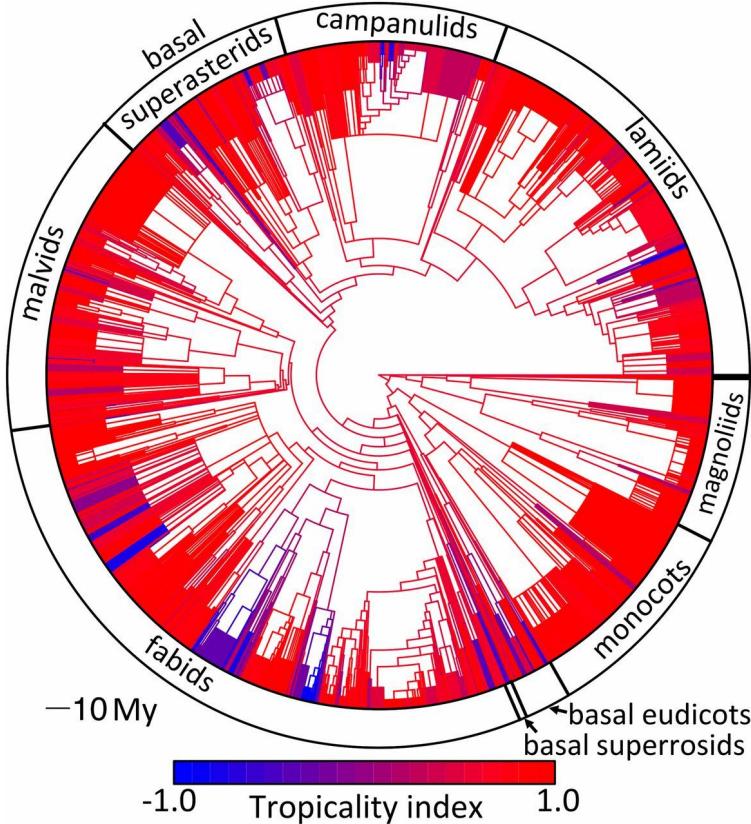
**Phylogenetic niche conservatism:** tendency for niches to remain unchanged along evolutionary lineages

**Tropical niche conservatism hypothesis:**

It's relatively difficult to evolve traits needed to persist in temperate areas

- Due to asymmetry of colonization and historical dominance of tropics, most species today are tropical with only fewer, younger lineages in temperate areas

# Evolutionary Explanations: Tropical Niche Conservatism

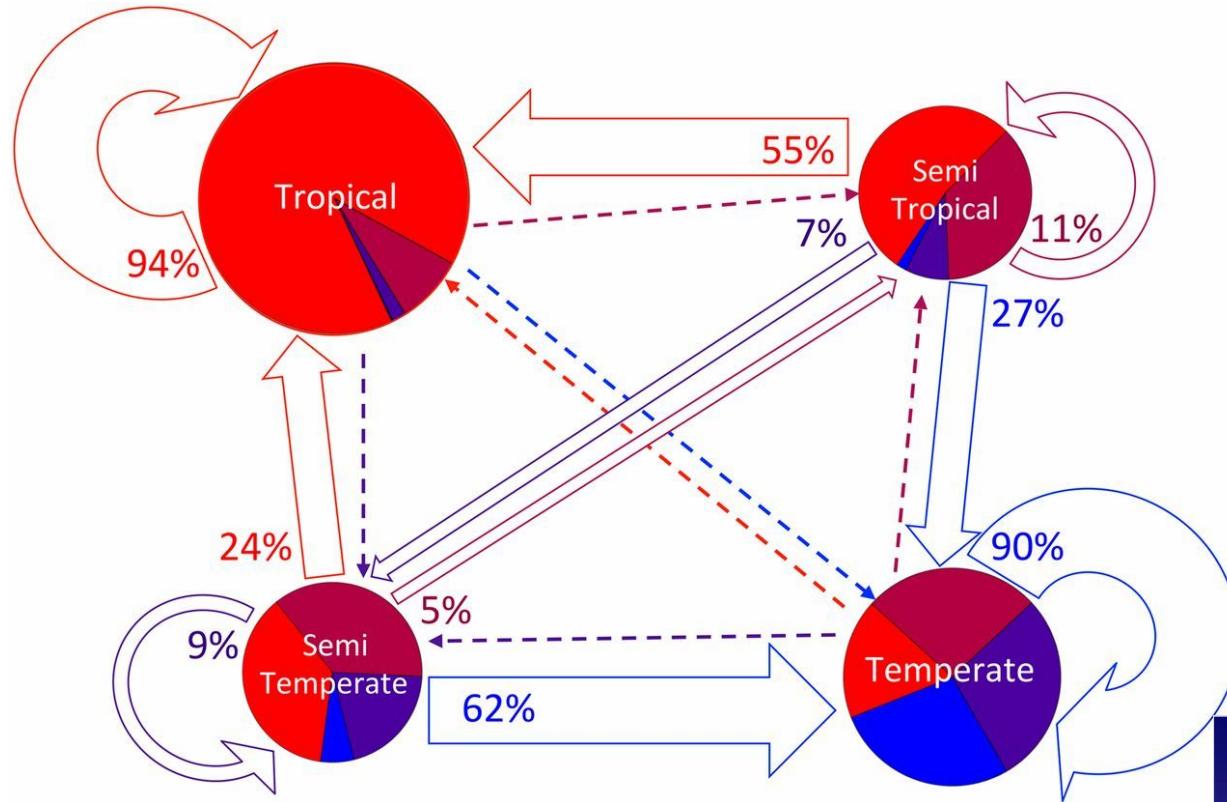


The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis

Andrew J. Kerkhoff<sup>a,1</sup>, Pamela E. Moriarty<sup>a,b</sup>, and Michael D. Weiser<sup>c</sup>



# Evolutionary Explanations: Tropical Niche Conservatism

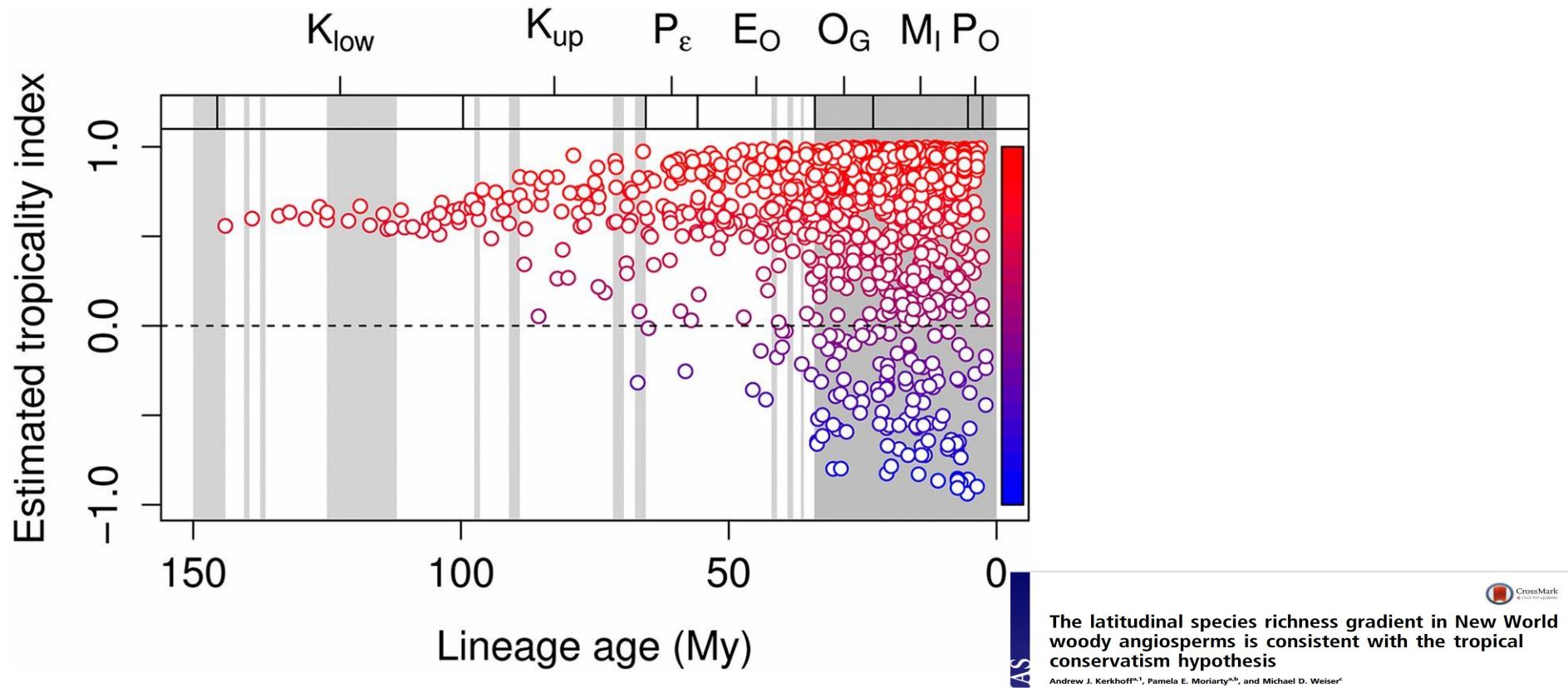


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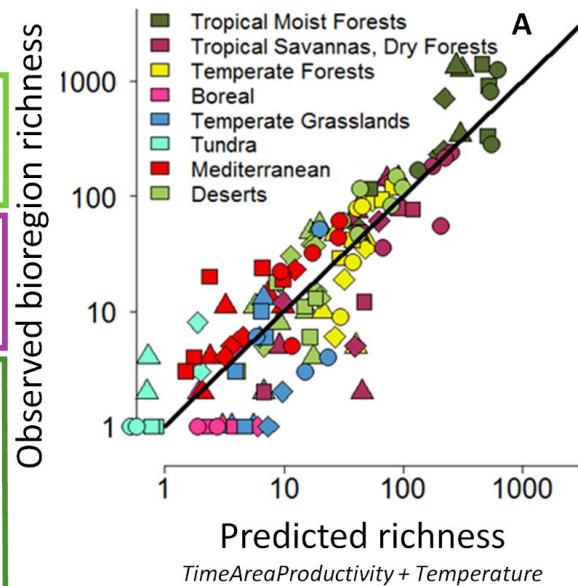
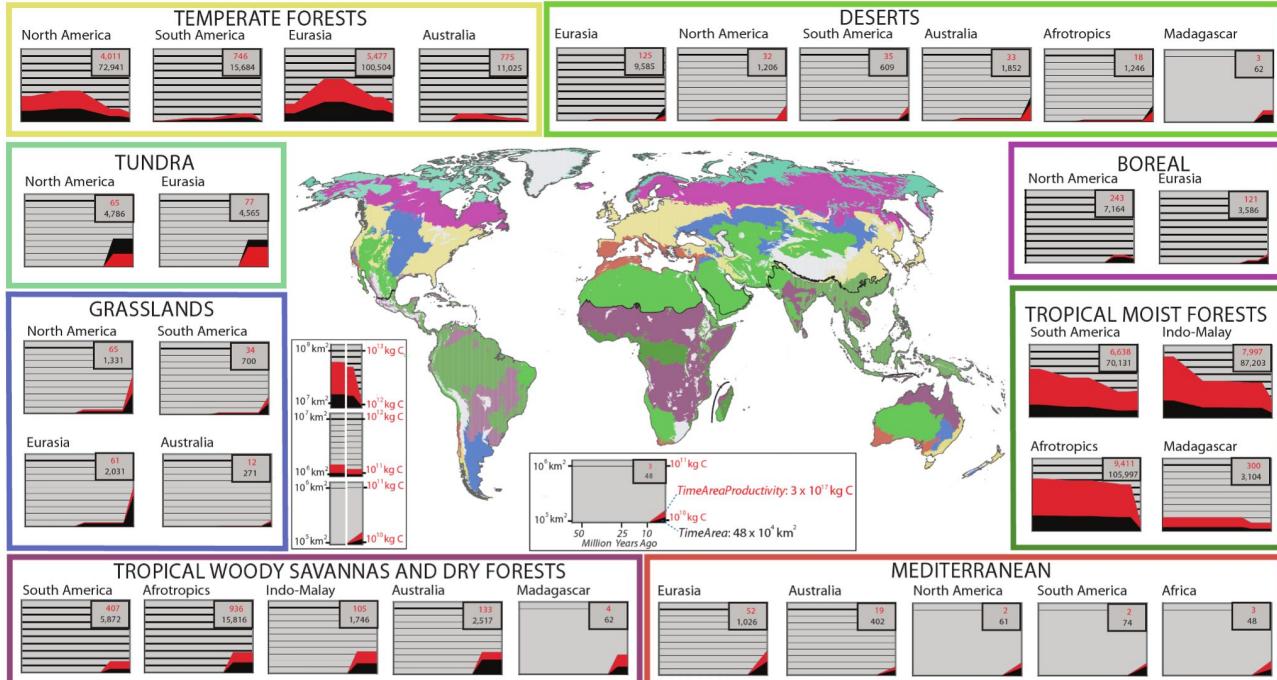


Which one is it?

# Which one is it?

- Probably a combination
- Studies that test multiple mechanisms are useful

## Combinations of factors



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PLOS BIOLOGY

# Global Gradients in Vertebrate Diversity Predicted by Historical Area-Productivity Dynamics and Contemporary Environment

# Testing Competing Mechanisms

RESEARCH PAPER

Global Ecology  
and Biogeography  
an journal

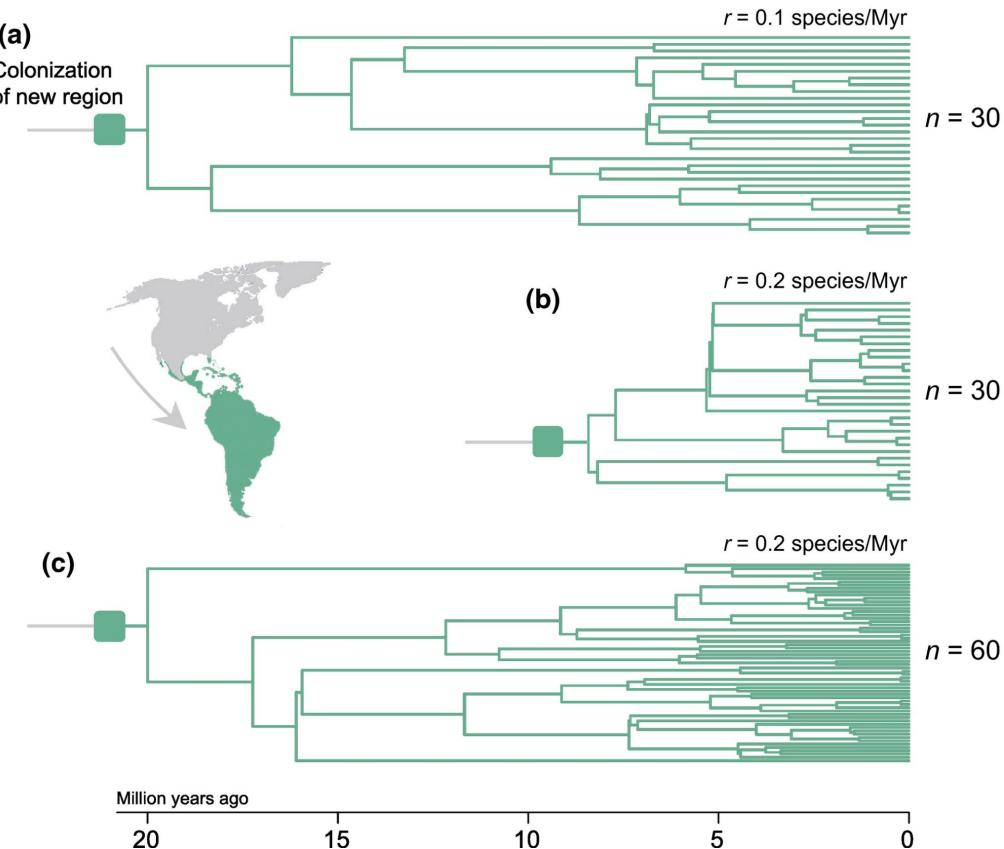
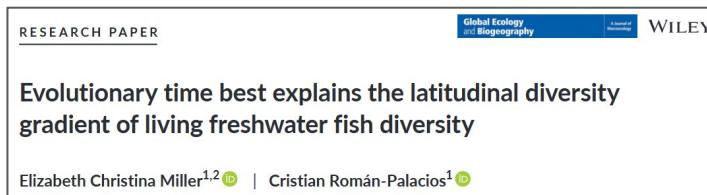
WILEY

Evolutionary time best explains the latitudinal diversity gradient of living freshwater fish diversity

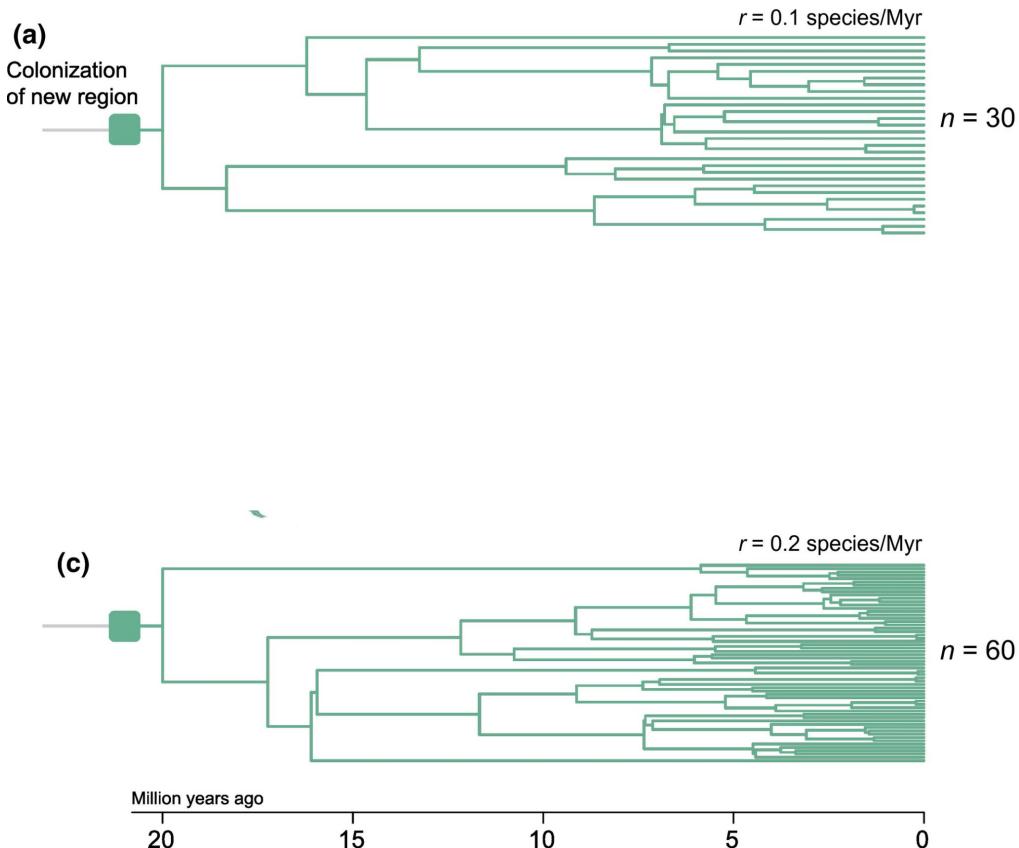
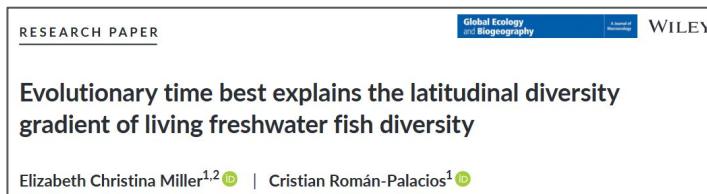
Elizabeth Christina Miller<sup>1,2</sup>  | Cristian Román-Palacios<sup>1</sup> 

Tested for relative importance of diversification rates vs. diversification time

# Testing Competing Mechanisms



# Testing Competing Mechanisms



# Testing Competing Mechanisms

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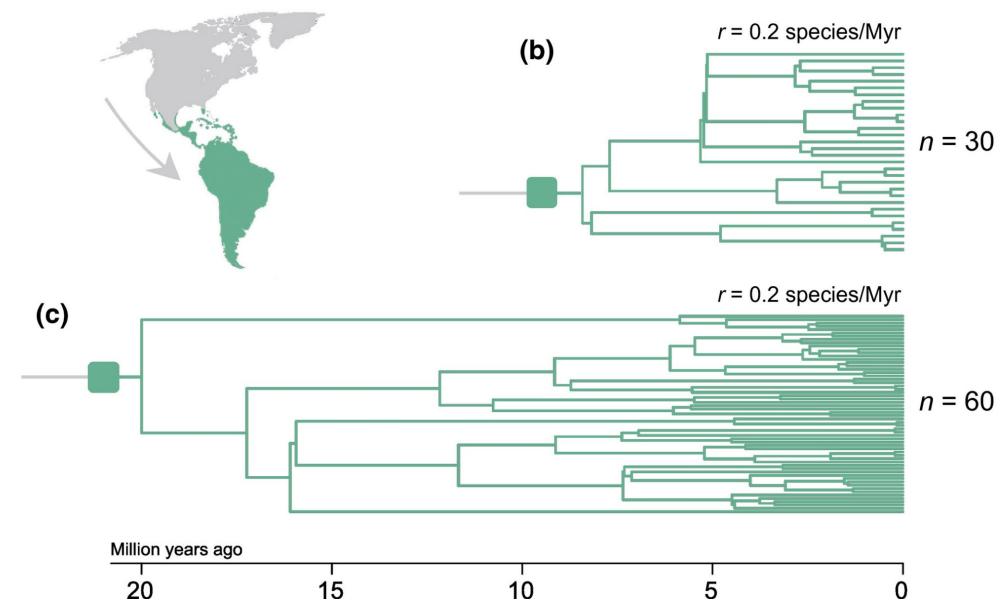
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30



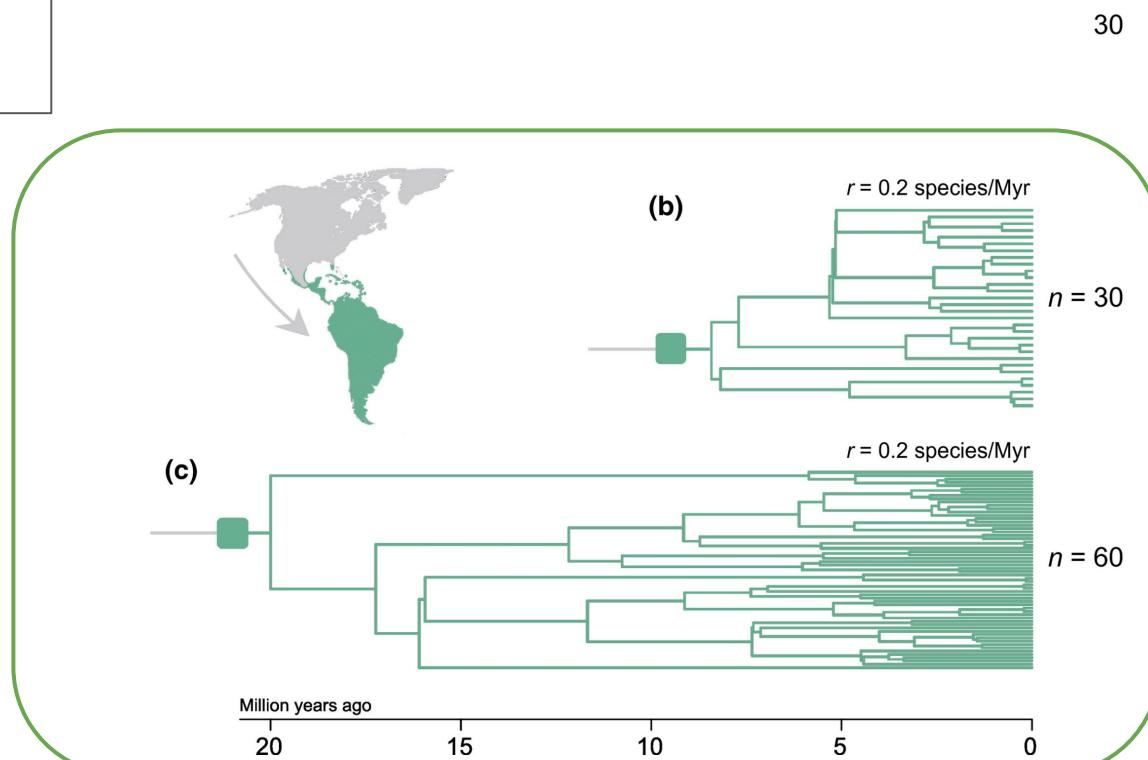
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# Further reading



ANNUAL  
REVIEWS **Further**

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## Ecological and Evolutionary Drivers of Geographic Variation in Species Diversity

Paul V.A. Fine

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email: paulfine@berkeley.edu

# These hypotheses apply beyond latitudinal patterns

Examples:

- Older vs. younger habitat types and resources
- Older vs. younger islands
- Productivity variation in aquatic environments
- Niche conservatism of other traits

Next class: Student presentations!