Why are there so many species in the tropics?

Why are tropical ecosystems so diverse?

WRONG QUESTION!

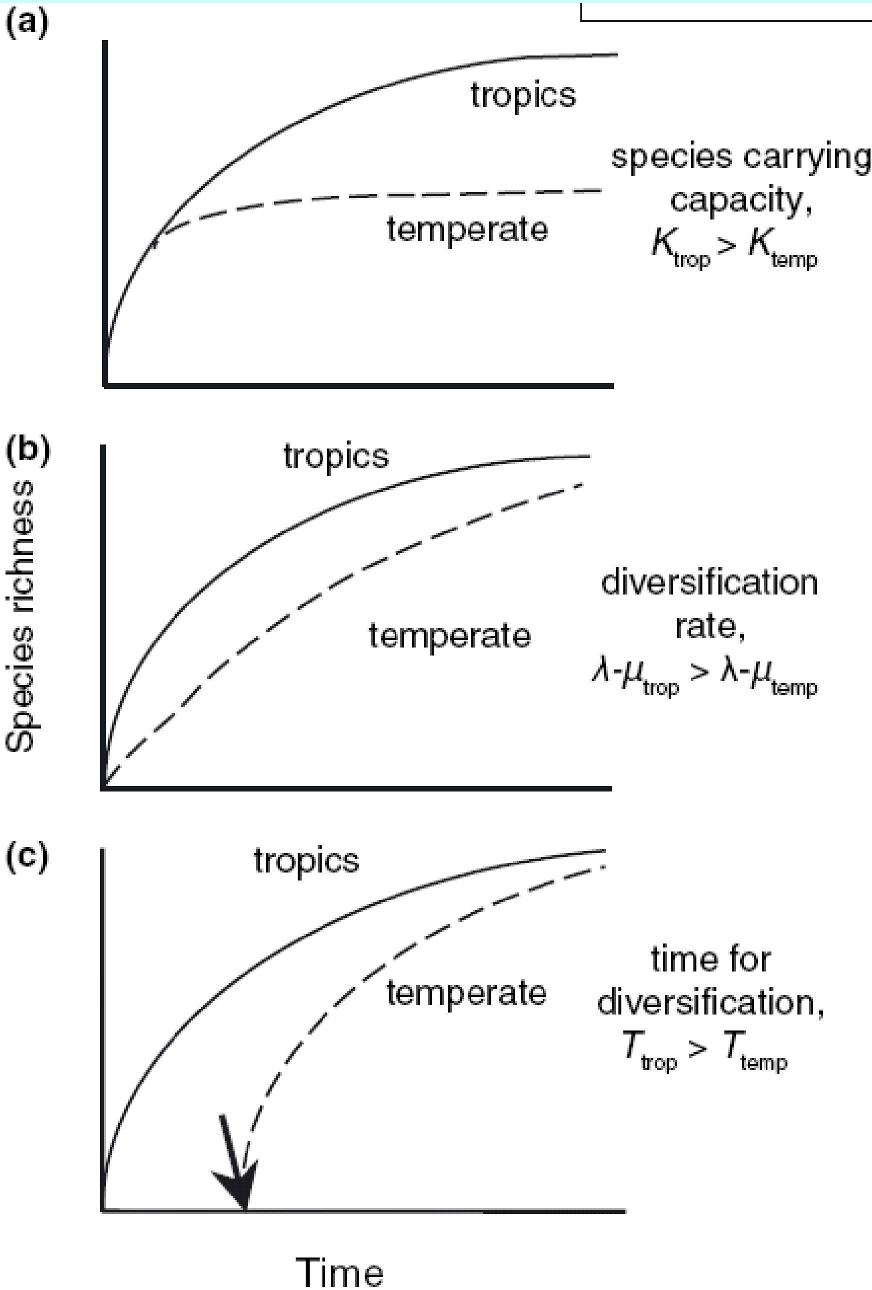
Why are the temperate ecosystems so species poor?

Simply because in recent times, they have been more or less permanently under or near some glacier

modern

last glacial maximum

Why are there so many species in the tropics?



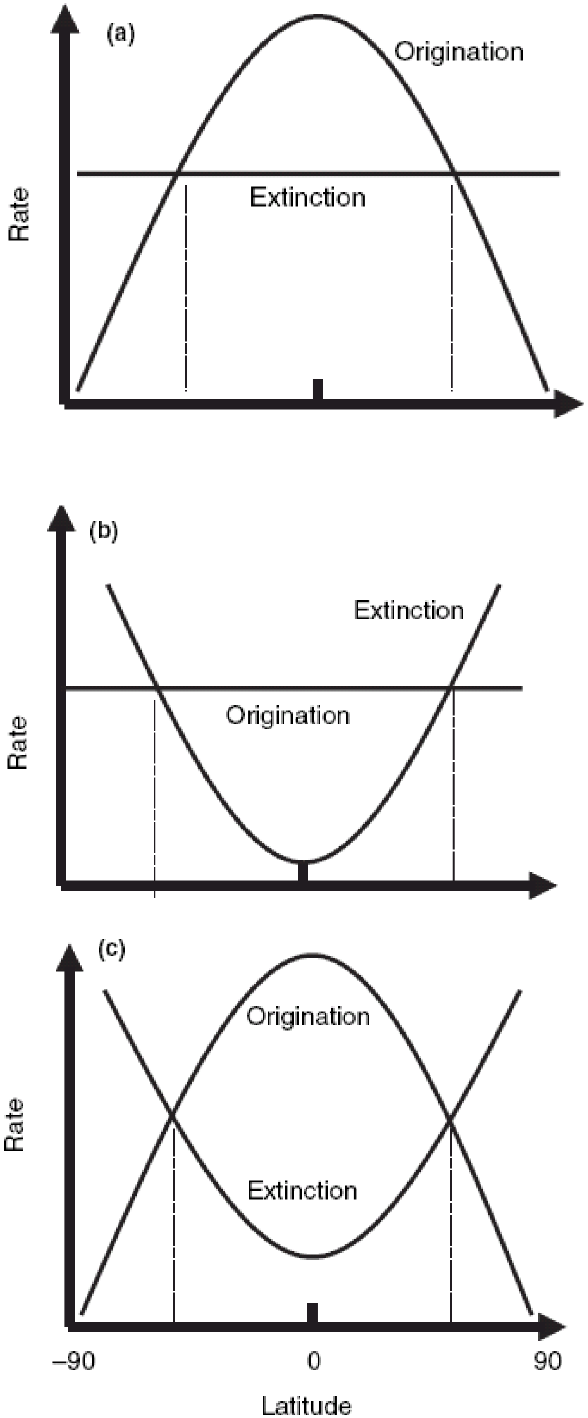
tropics may have

(a) higher carrying capacity than temperate areas

(b) higher diversification rate than temperate areas, which can be due to higher speciation and/or lower extinction rates

(c) longer time available for diversification than temperate areas

Mittelbach et al., Ecology Letters, (2007) 10: 315–331



Tropics: cradle or museum of biodiversity?

A: tropics as cradle
speciation in tropics higher than in temperate areas

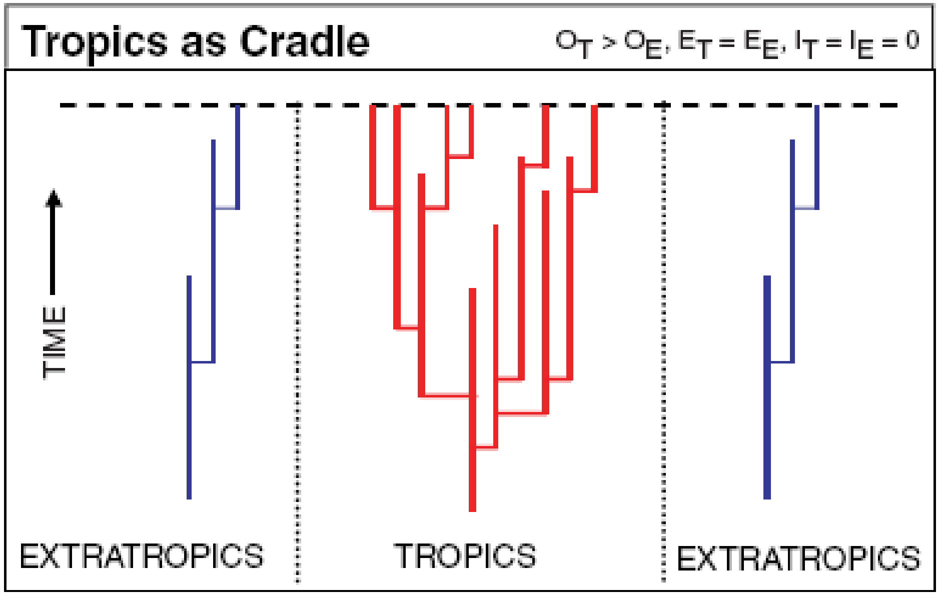
B: tropics as museum
extinction in tropics higher than in temperate areas

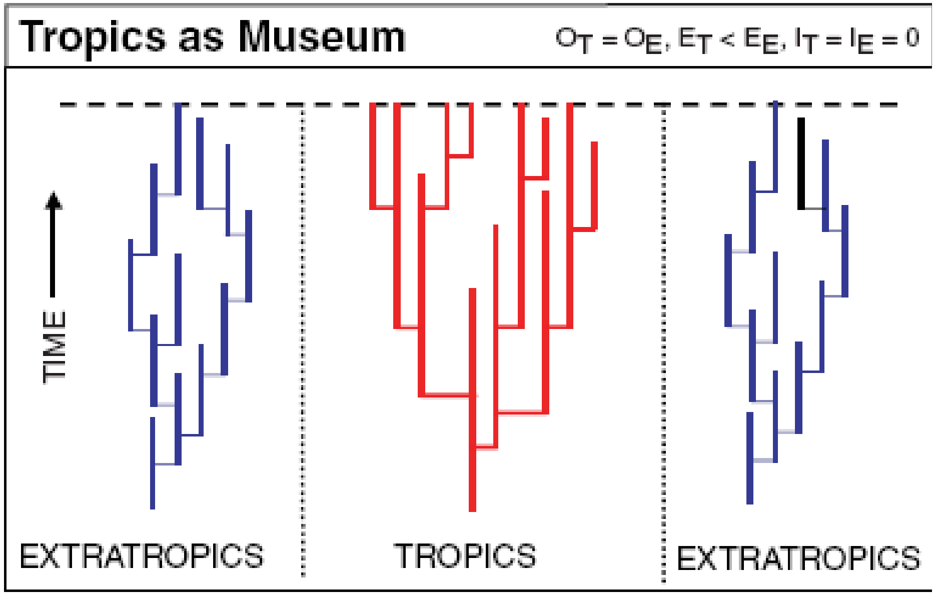
C: out of the tropics
tropics have higher speciation and lower extinction than in temperate areas, species disperse mostly from the tropics to temperate areas

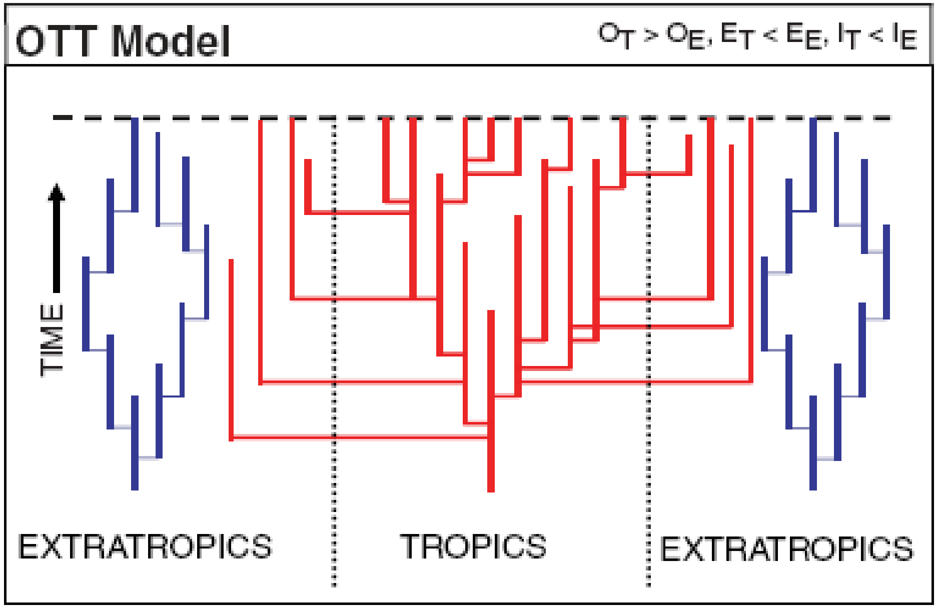
Arita and Vazquez-Dominigues, 2008, Ecology Letters 11:653

Tropics
as a cradle or a museum
of biodiversity?

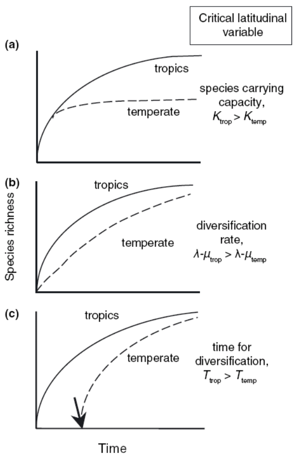
Probably both.







Why are there so many species in the tropics?



Higher carrying capacity in the tropics:

-- higher input of solar energy leading to higher biomass
-- higher plant diversity provides more niches to higher trophic levels

Diversification rates are higher in the tropics:

- higher speciation rates:

-- genetic drift in many small populations accelerates evolution
-- higher likelihood of parapatric and sympatric speciation in the tropics
-- larger area of the tropics provides more opportunities for isolation
-- narrower physiological tolerances in tropical species reduce dispersal
-- higher temperature increases evolutionary speed
-- stronger biotic interactions lead to greater specialization and faster speciation
-- more generations per year in some organisms (insects...) lead to faster evolution

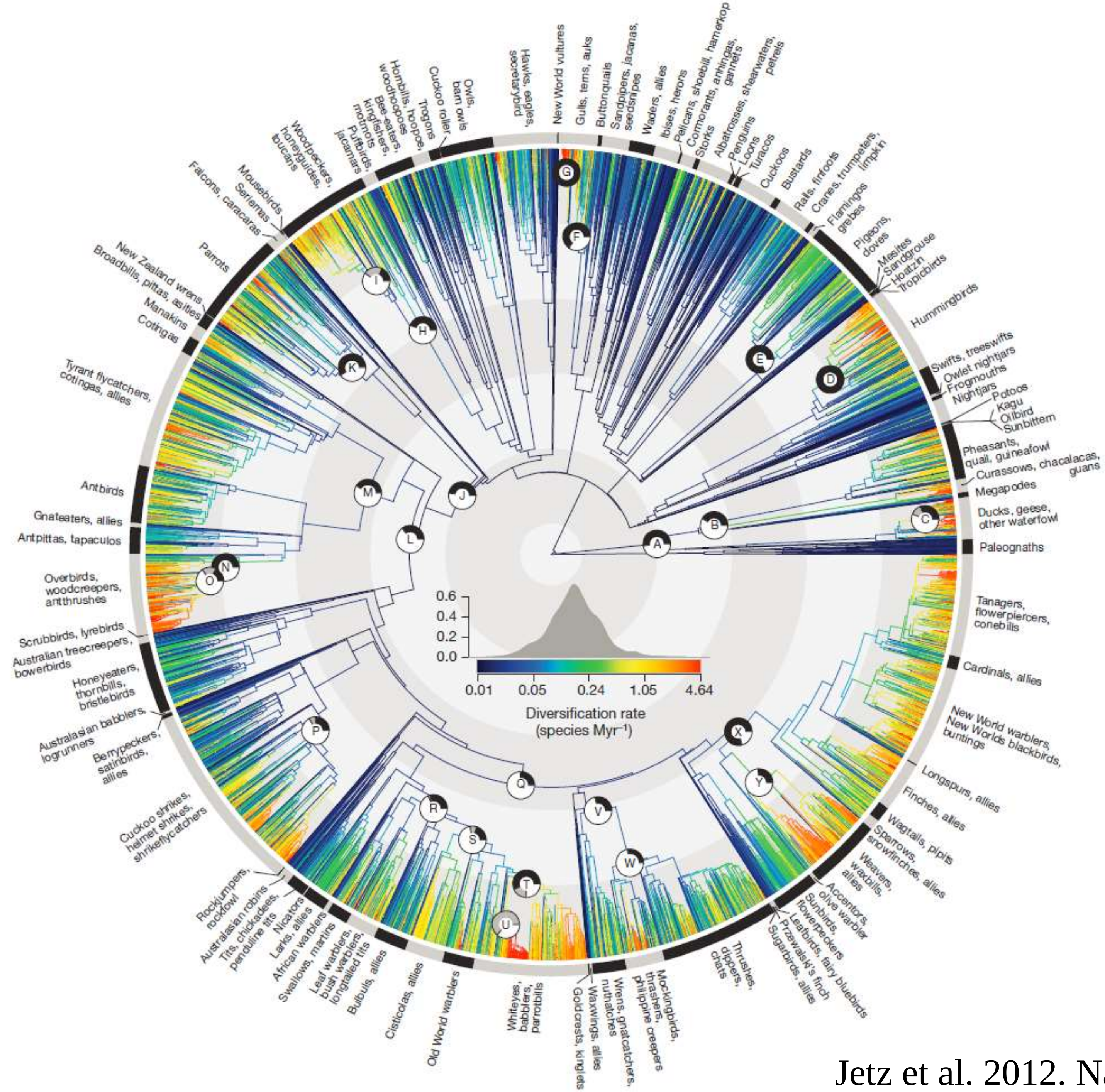
- lower extinction rates:

-- stability of tropical climate
-- larger tropical area leads to larger populations, geographic ranges and lower chance of extinction

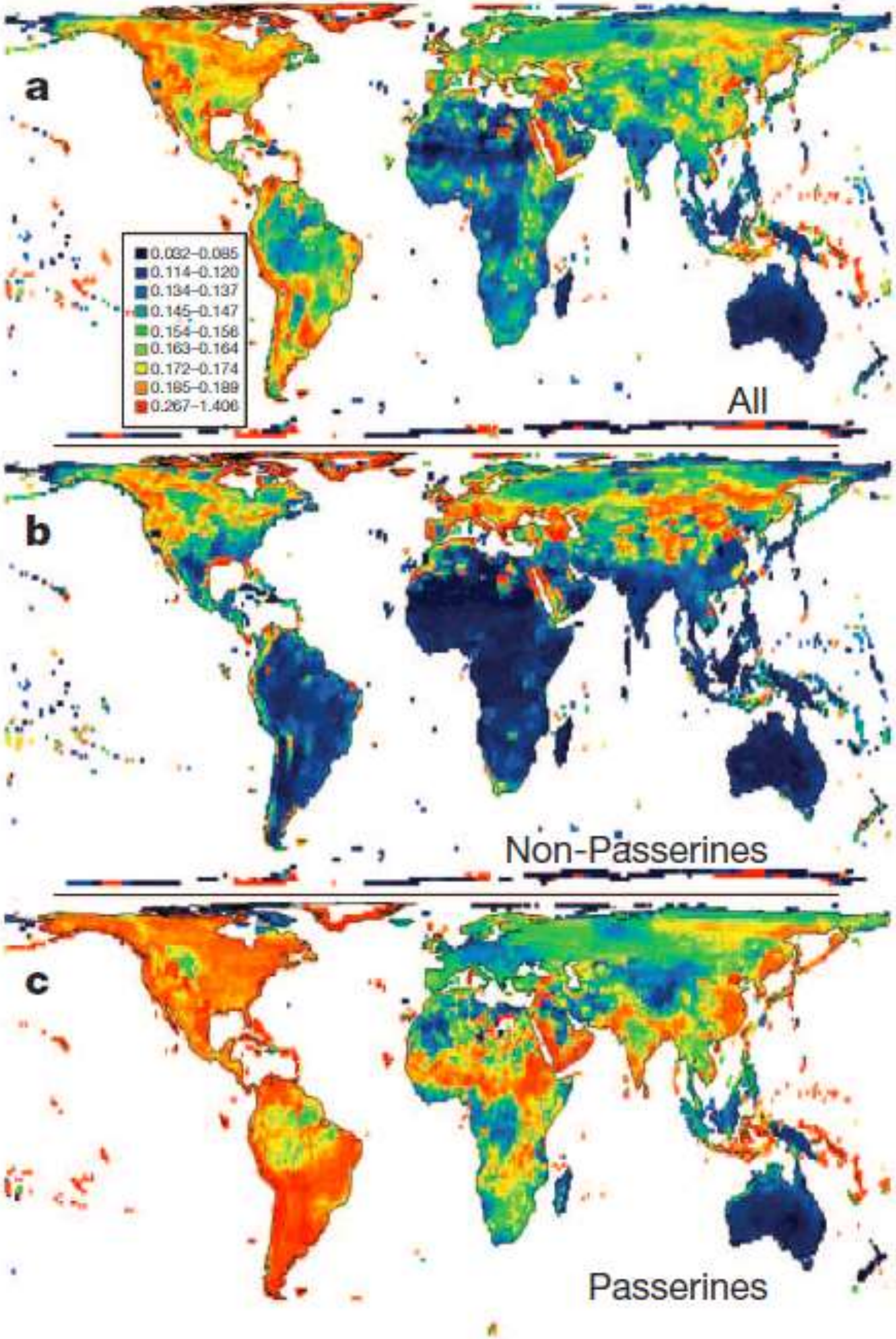
Time for diversification longer in the tropics:

-- tropical environments are older and many clades originated in the tropics
-- dispersal of clades out of tropics is limited and recent

Mittelbach et al., Ecology Letters, (2007) 10: 315–331

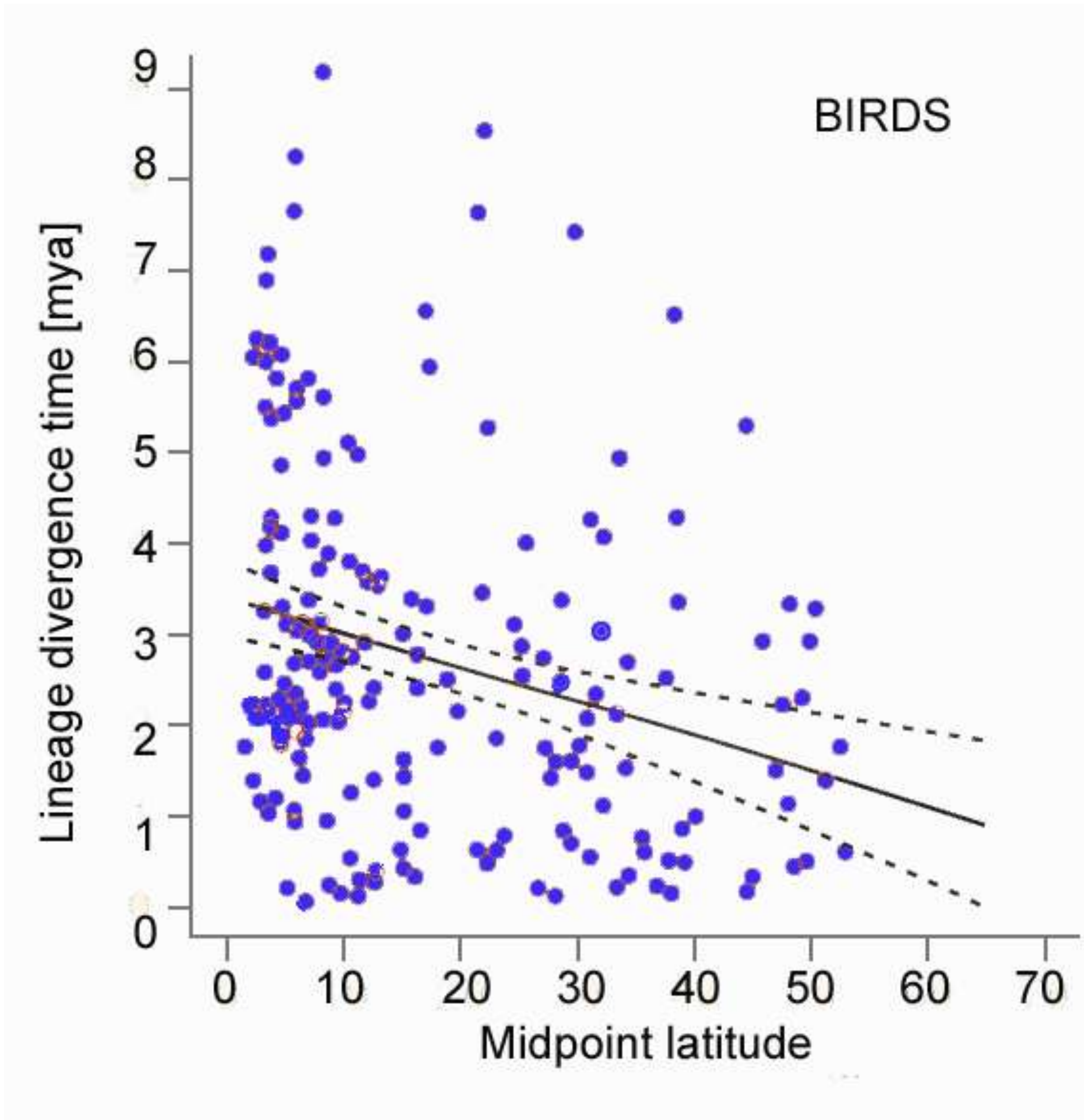


Jetz et al. 2012. Nature 4 9 1: 444

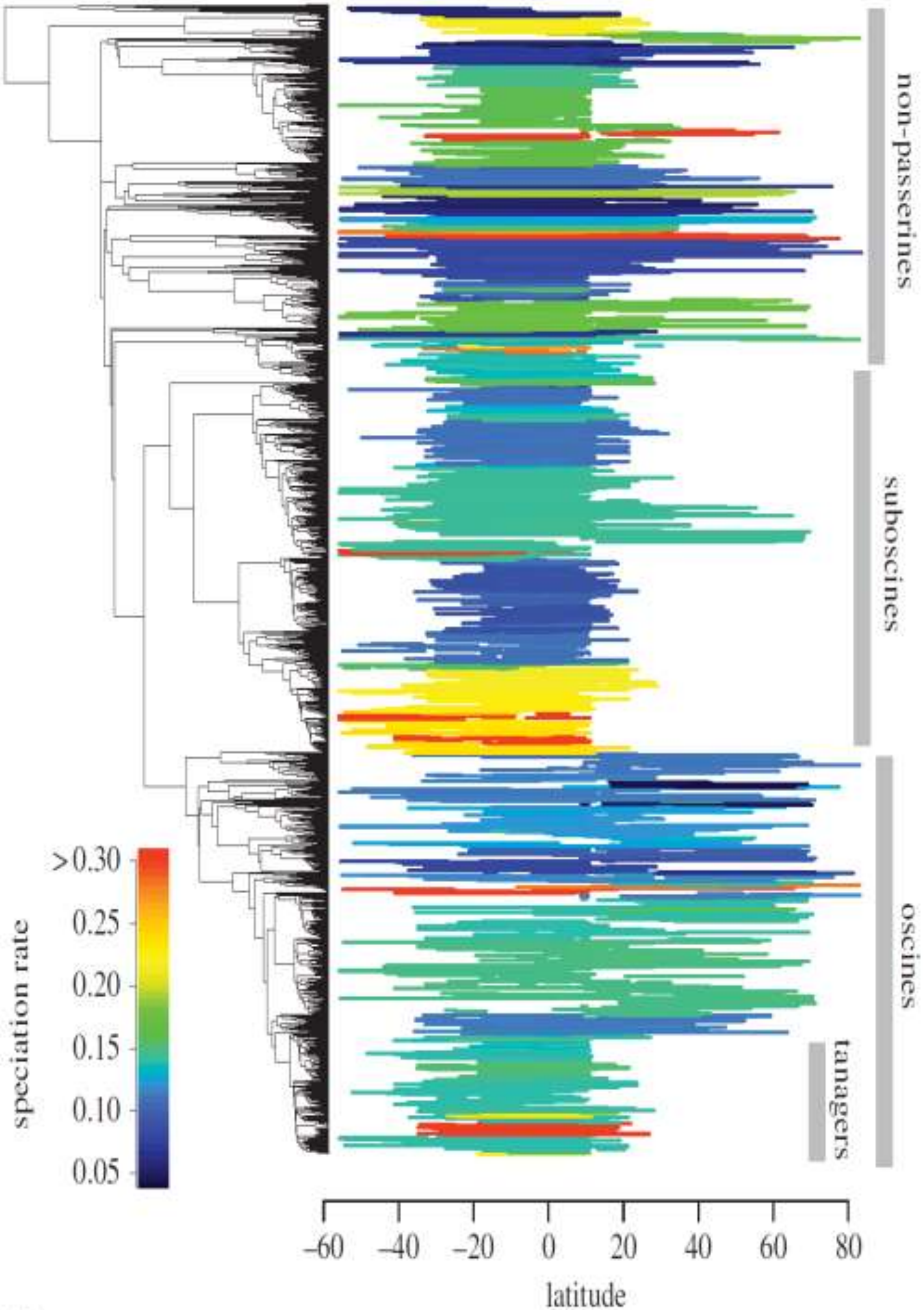


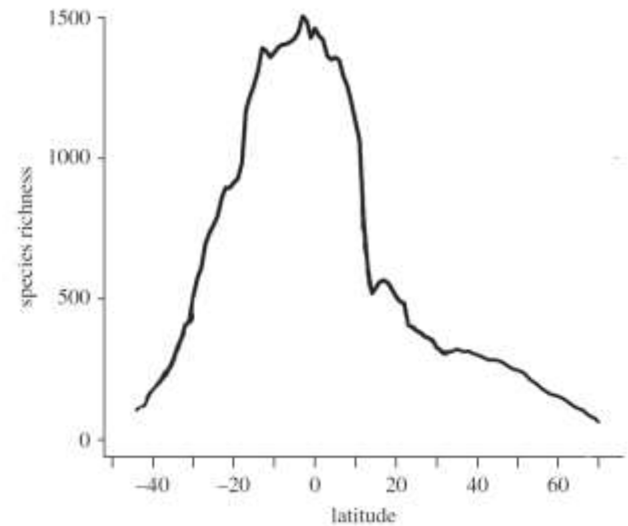
Geographic variation in species-level lineage diversification rate and the richness of high-diversification rate species. Mean assemblage diversification rate calculated as the geometric mean of all species in a grid cell assemblage, weighted by the inverse of their range size. a, All species; b, non-passerines; c, passerines.

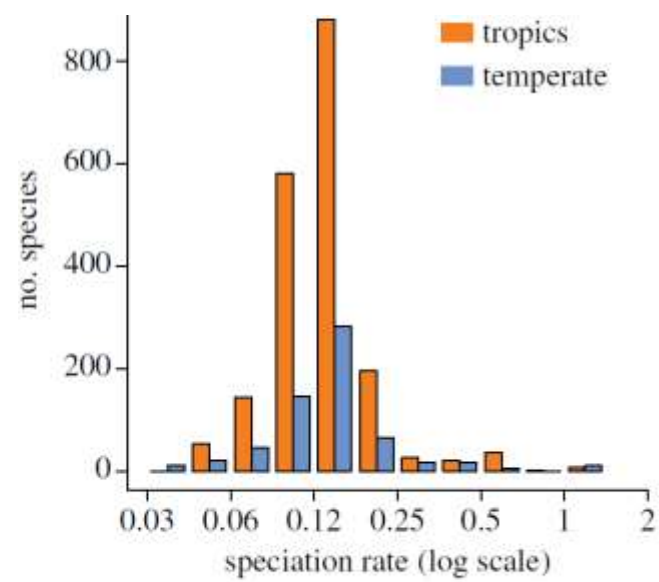
Sister lineages of birds: older splits tend to be tropical



Current speciation rates in New World birds: no cradle in the tropics

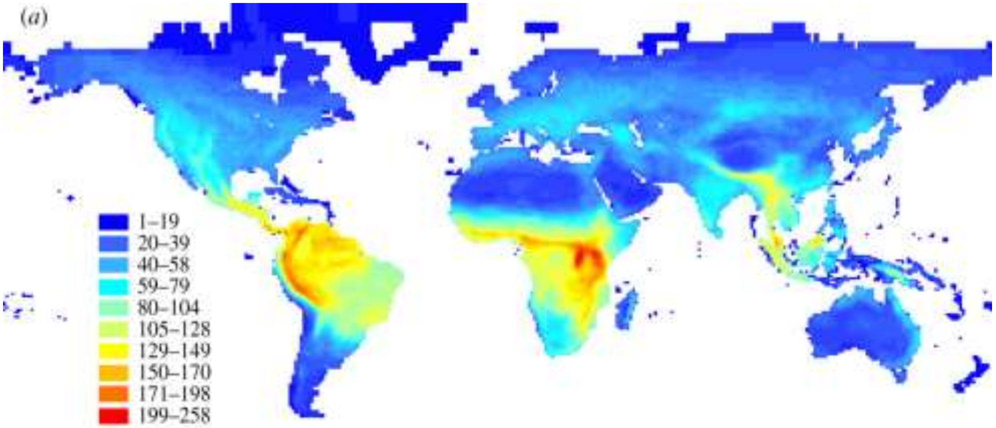




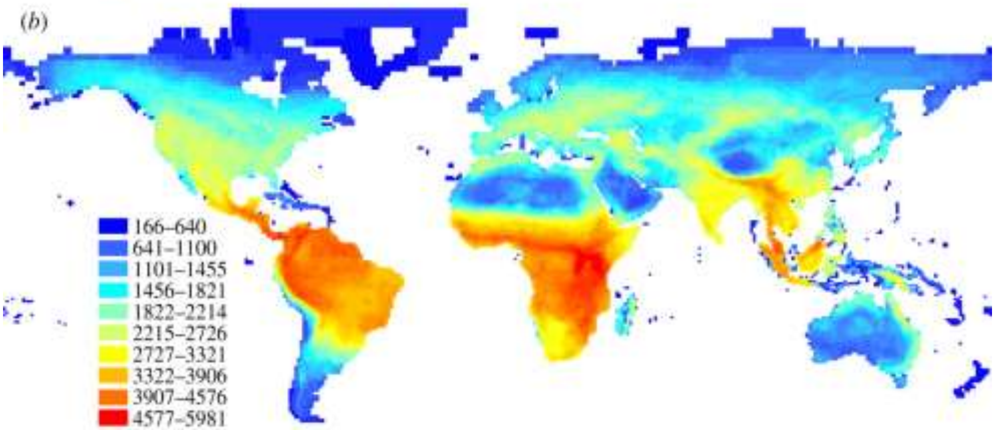


Rabosky et al. 2015 Proc. R. Soc. B 282: 20142889.

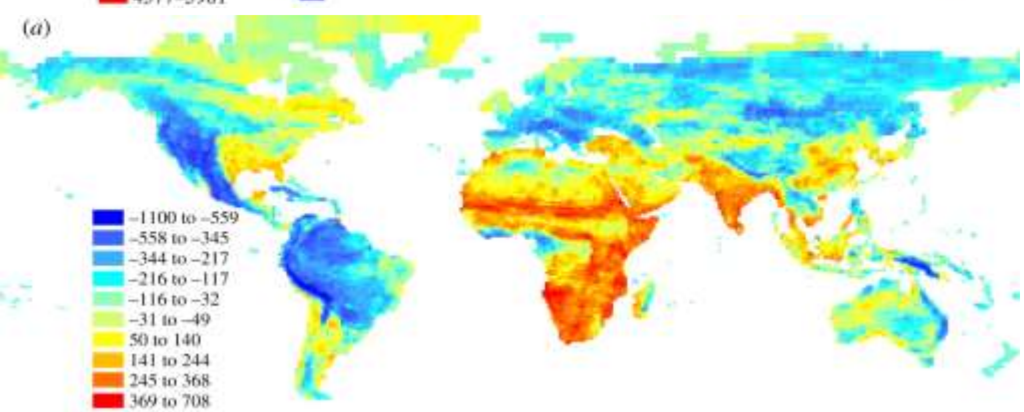
Global species richness and phylogenetic diversity of mammals



Species diversity per 100x100 km area

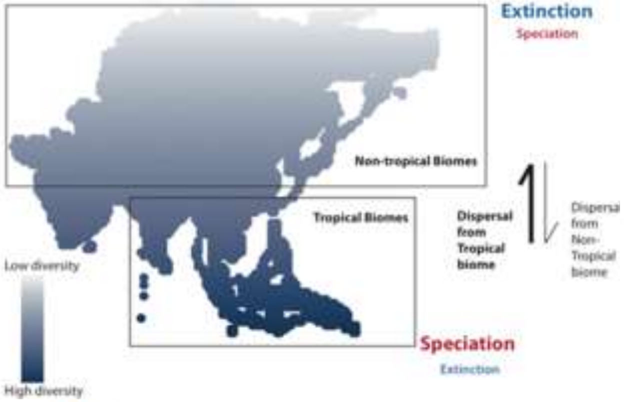


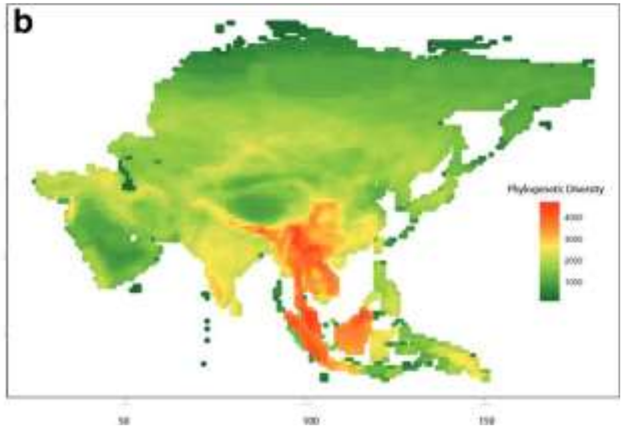
Phylogenetic diversity: summed branch lengths (in millions of years) of the evolutionary tree for the fauna within 100x100 km area



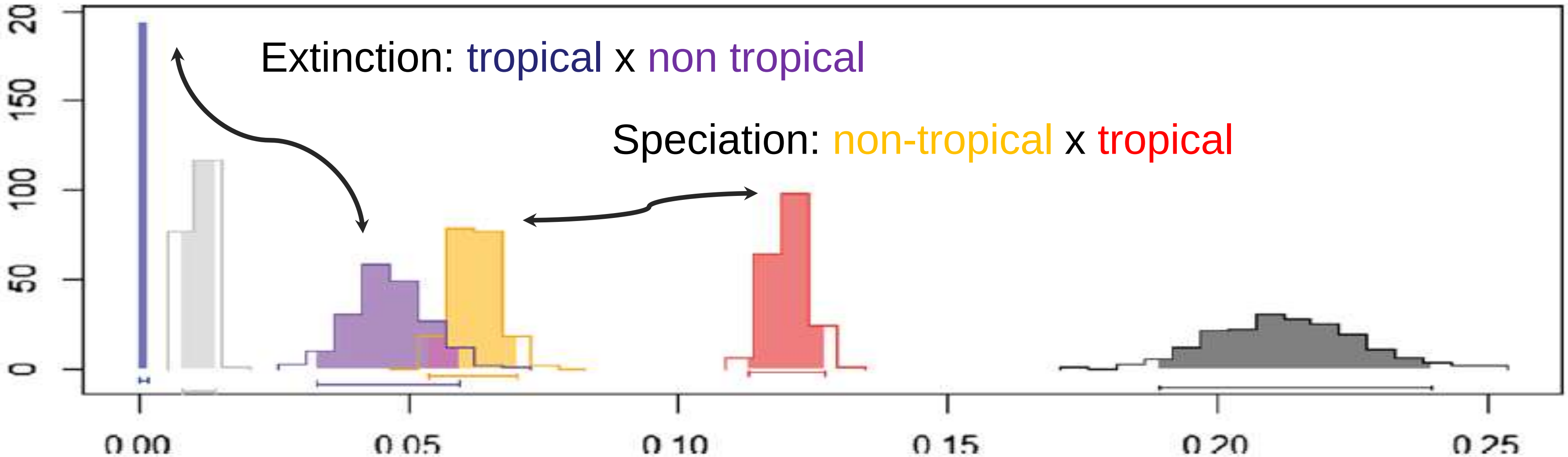
Residuals (millions of years) from a LOESS regression of phylogenetic diversity against the number of species within 100x100 km are

Davies & Buckley 2011. Phil. Trans. R. Soc. 366:2414-2425

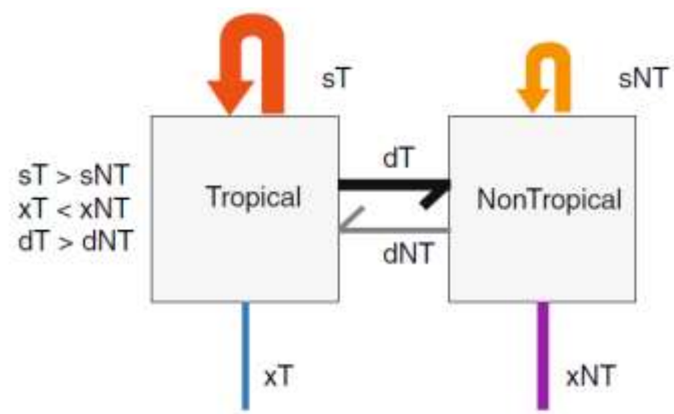




Tropical areas: cradle and museum for Asian mammals

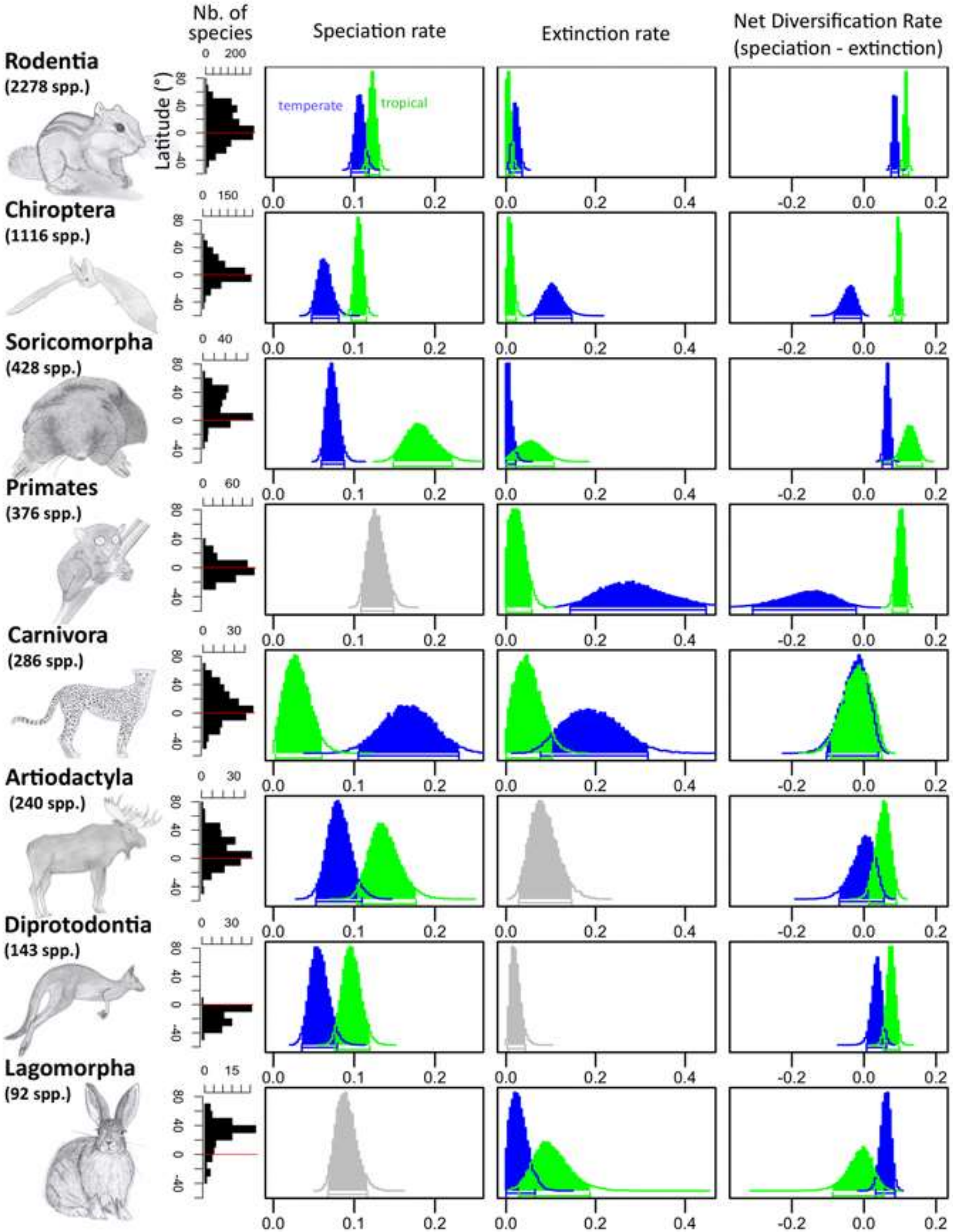


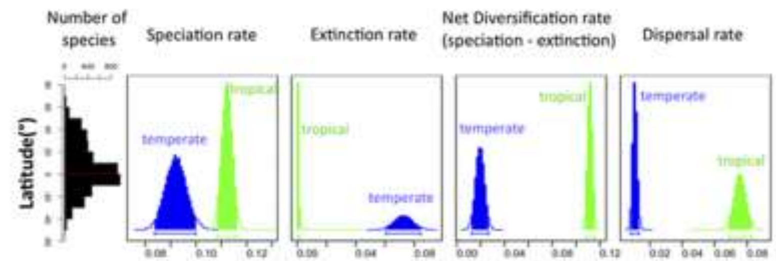
- Speciation in Tropical biome sT
- Speciation in NonTropical biome sNT
- Extinction in Tropical biome xT
- Extinction in NonTropical biome xNT
- Dispersal from Tropical biome dT
- Dispersal from NonTropical biome dNT

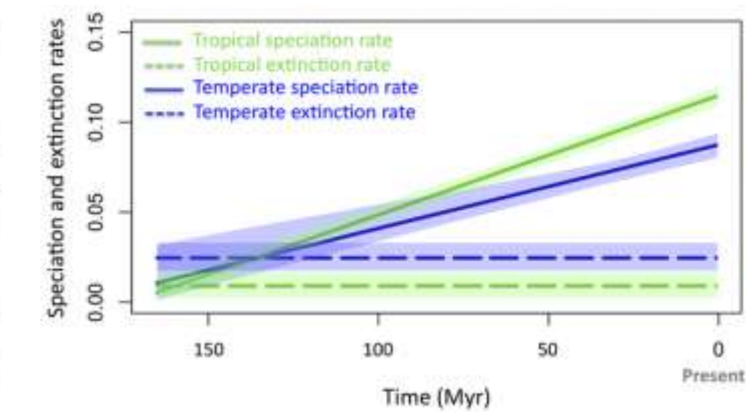


Tamma and Ramakrishnan BMC Evolutionary Biology (2015) 15:11

Diversification rates in mammals along a latitudinal gradient

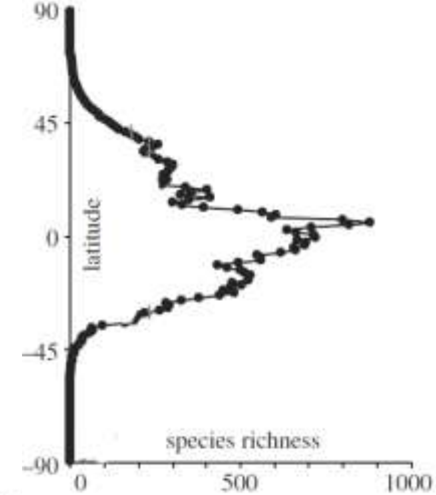


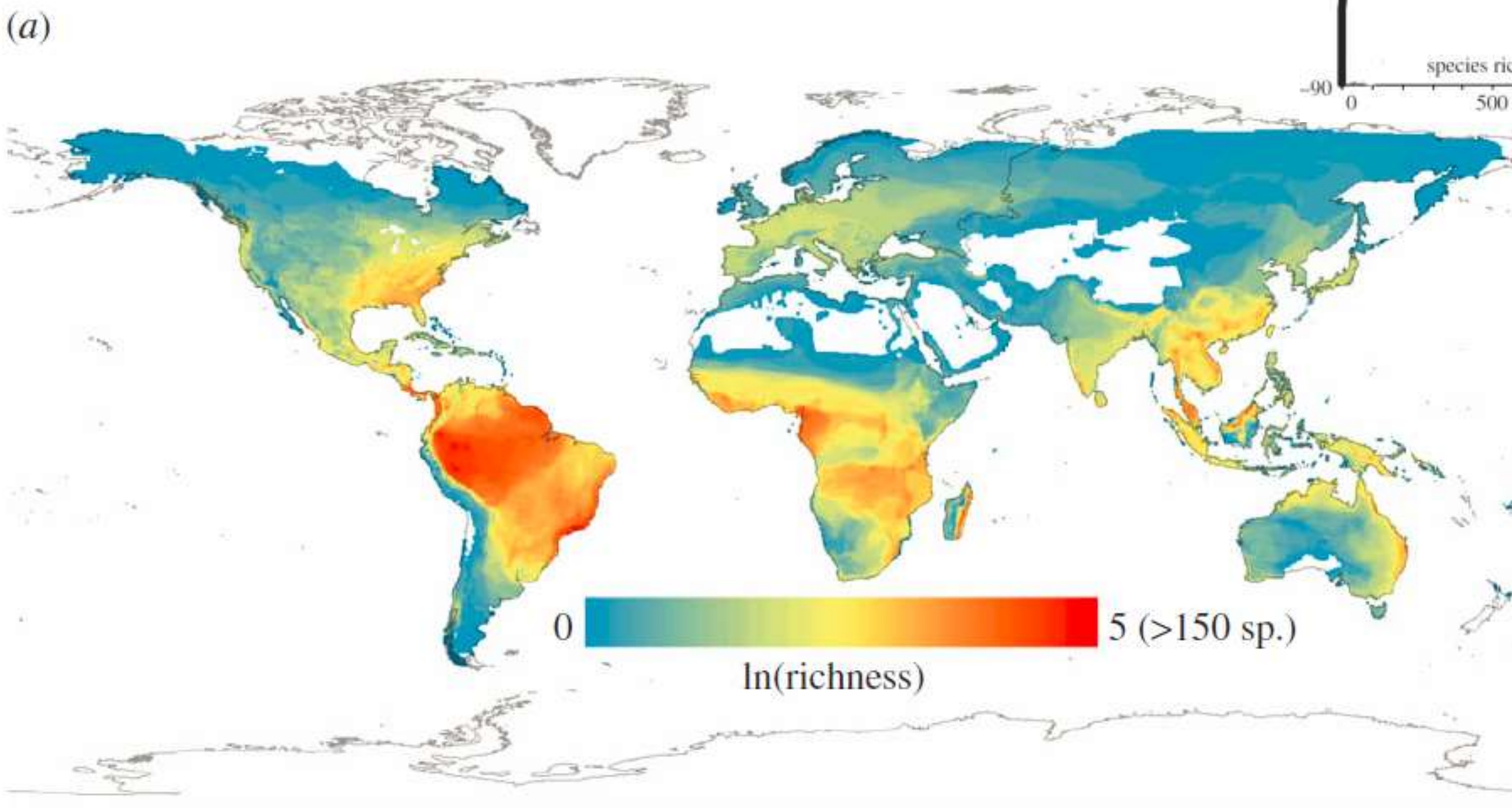




Rolland et al. (2014) PLoS Biol 12(1): e1001775

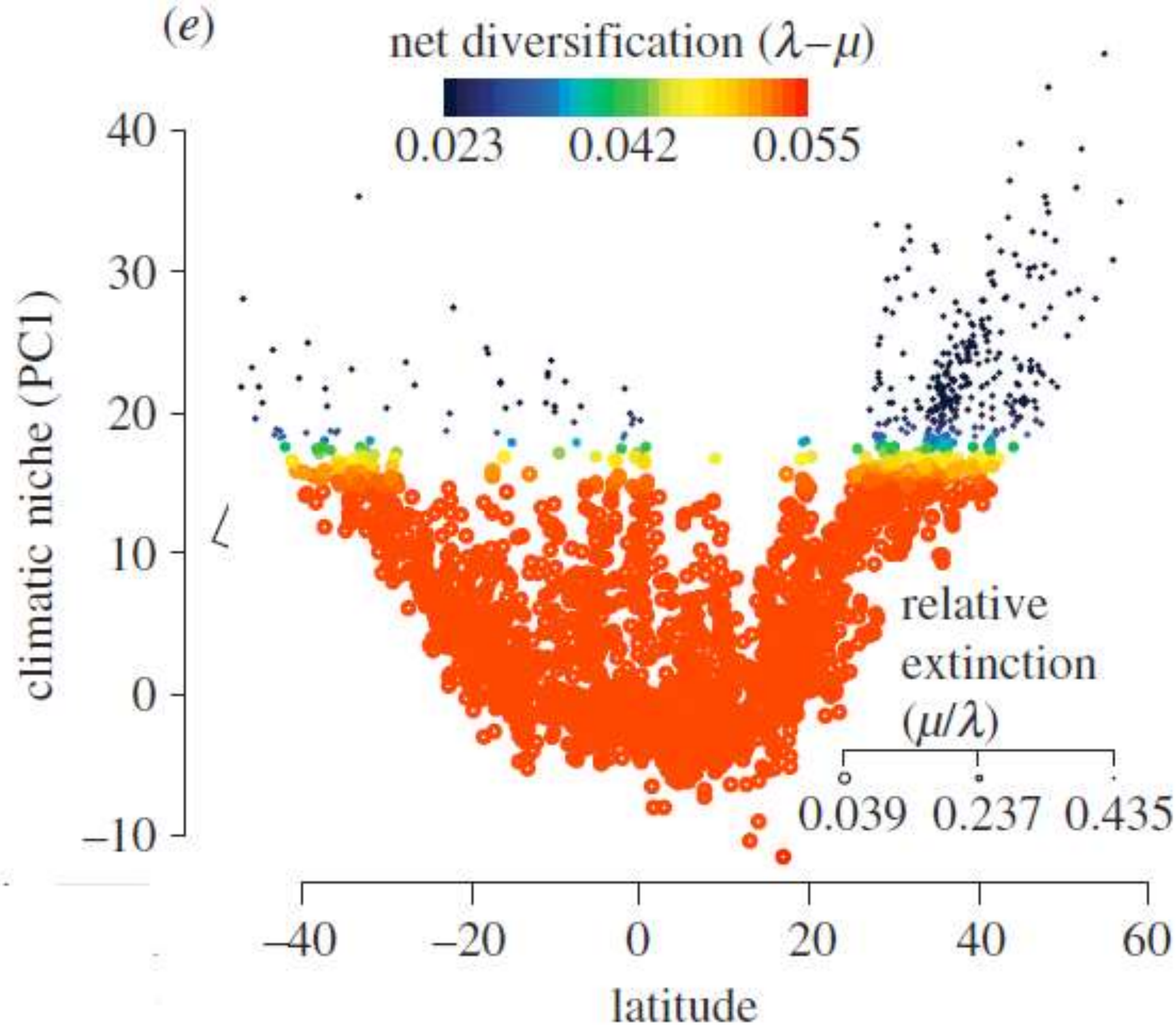
Global diversity of amphibians





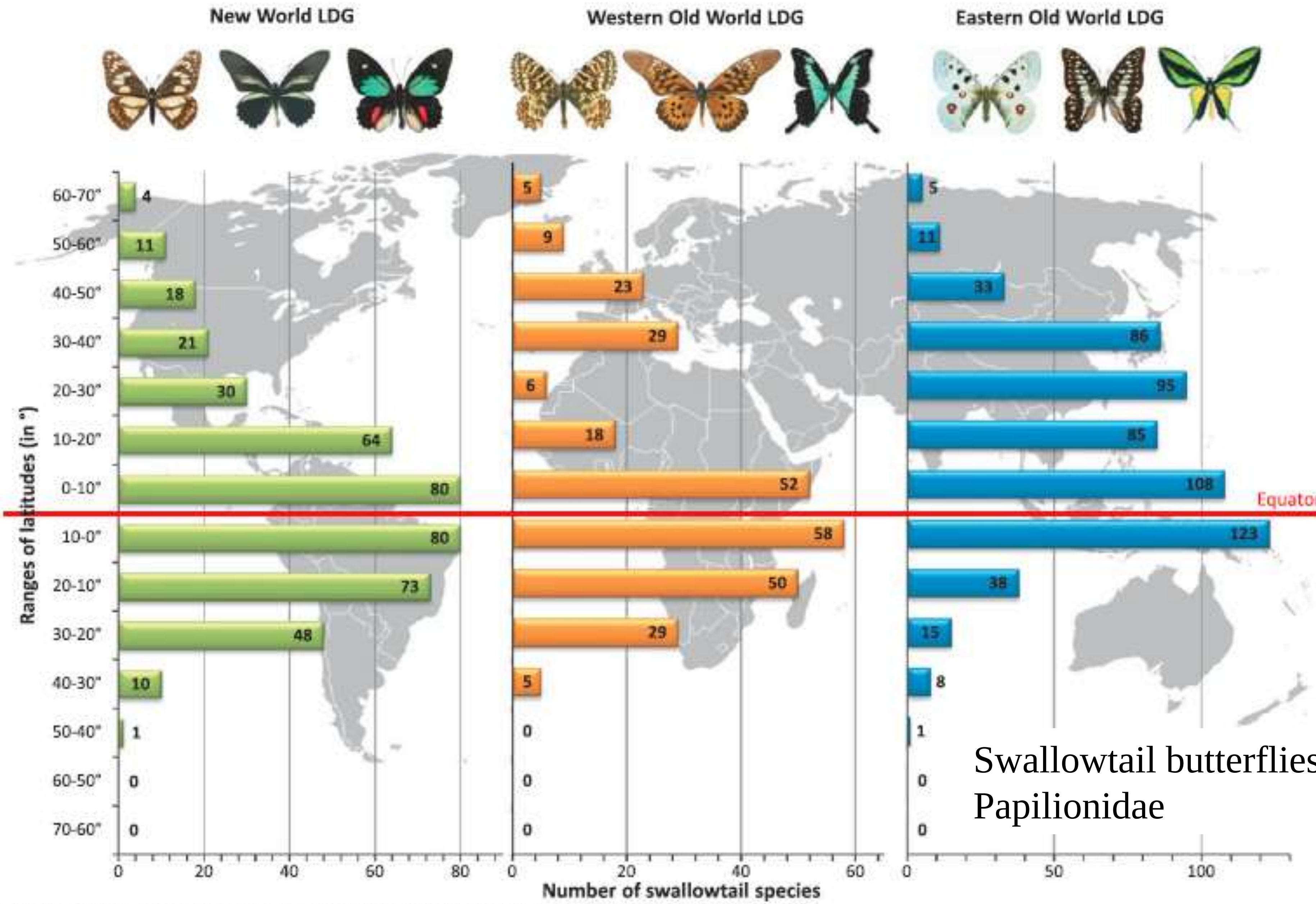
(a) Global richness of 6117 amphibians on a log scale in 58 grid cells;
(b) Latitudinal distribution of species

Pyron & Wiens 2013, *Proc. R. Soc. B* 2013 **280**



Plot of PC1 climate model versus latitude for amphibians, with species points coloured by estimated net diversification rate (r) and sized by relative extinction fraction (1; smaller circles indicate higher extinction), showing an increase in net diversification towards the equator.

Latitudinal patterns in butterfly species richness: parallel on all continents

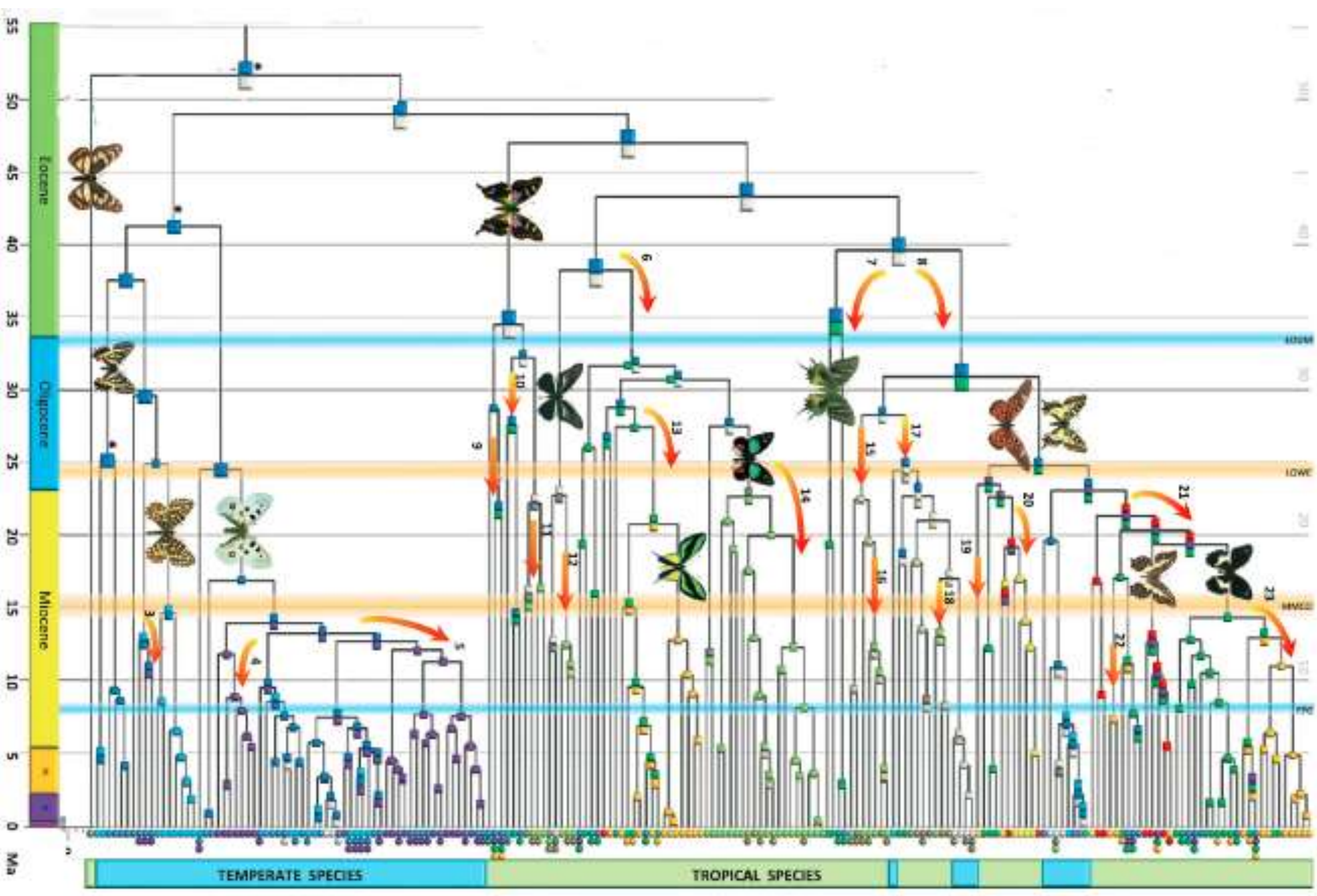


Swallowtail butterflies: Papilionidae

Figure 1 Latitudinal diversity gradients for swallowtail butterflies in three different parts of the world. Species richness increases from the poles toward the equator (red line) and applies to all tropical regions. One easily explained exception occurs in the western Old World, where a dip in species richness coincides with North African desert. Well-known species from each region are figured above. Data are compiled from various sources (e.g. Collins & Morris 1985).

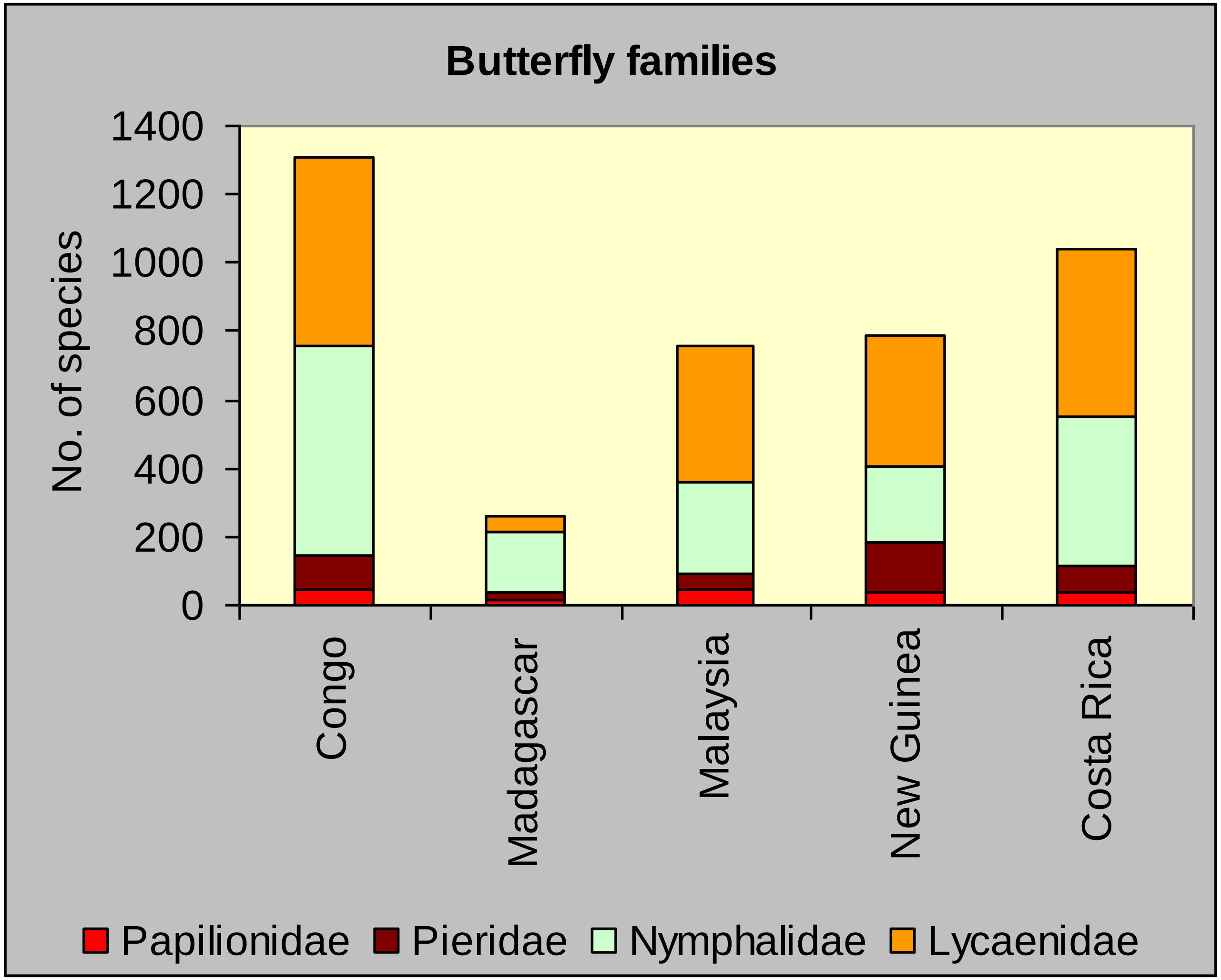
Condamine et al. Ecology Letters, (2012) 15: 267–277

Faster diversification (= speciation - extinction) in tropical than temperate papilionid butterflies



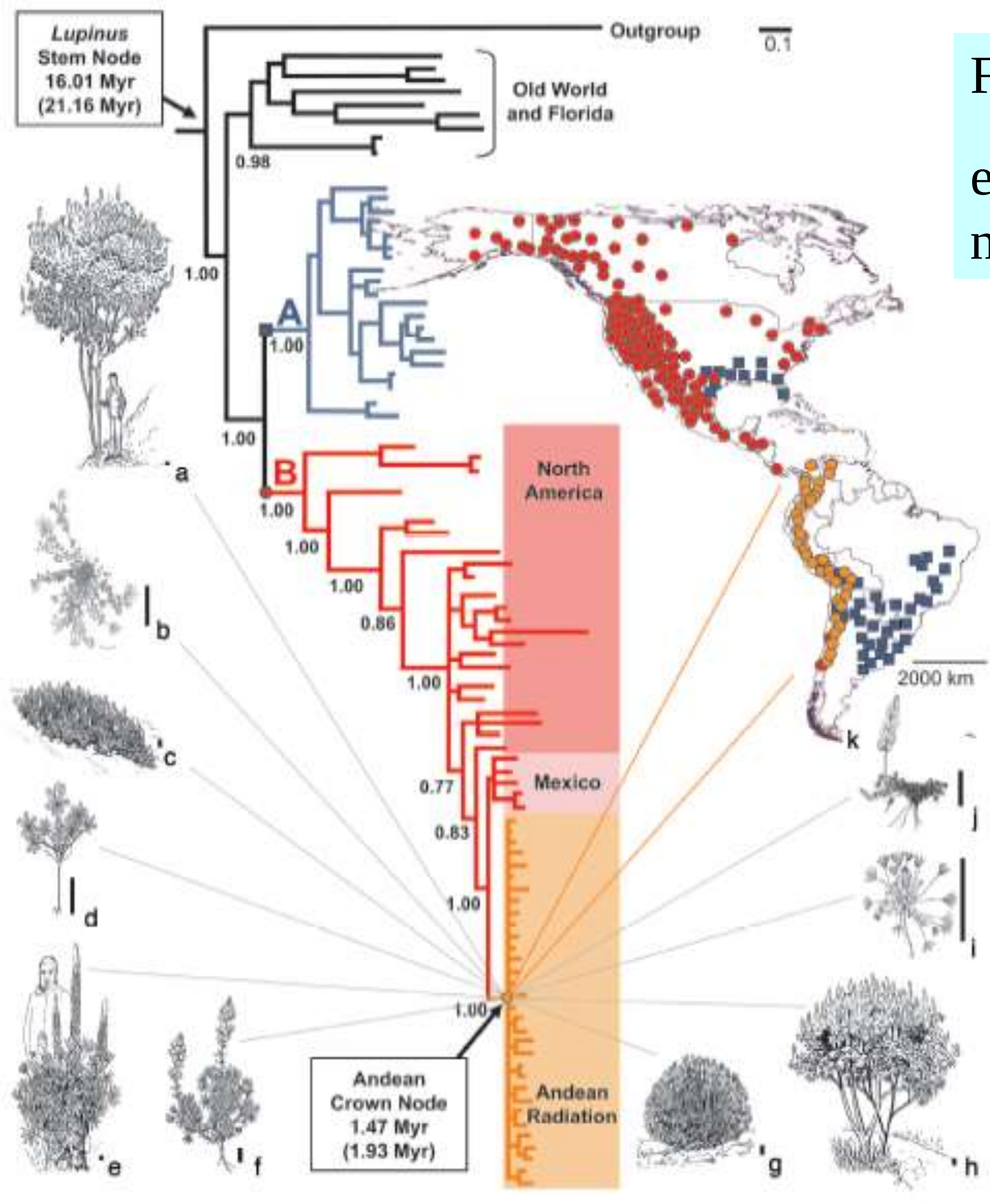
Condamine et al. Ecology Letters, (2012) 15: 267–277

Butterflies: parallel diversity patterns on all continents



Fabaceae diversification:

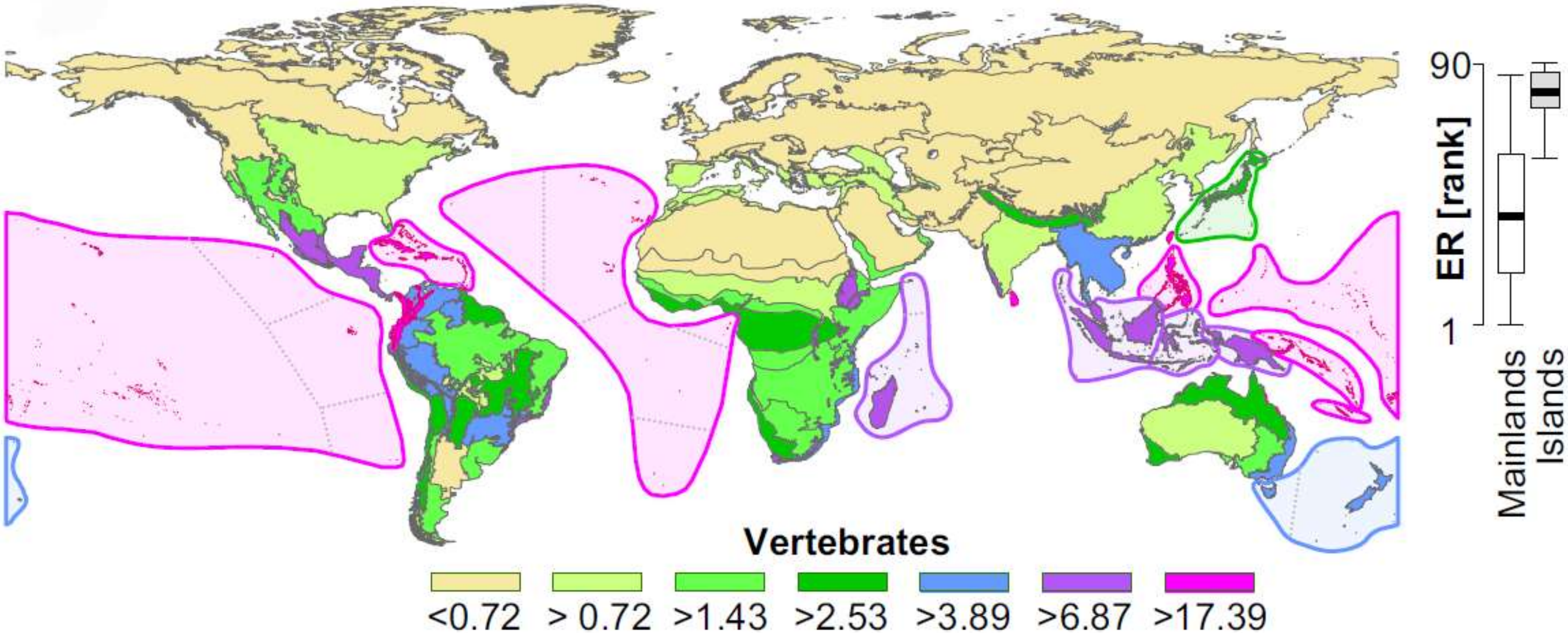
exceptionally fast in the newly uplifted Andes

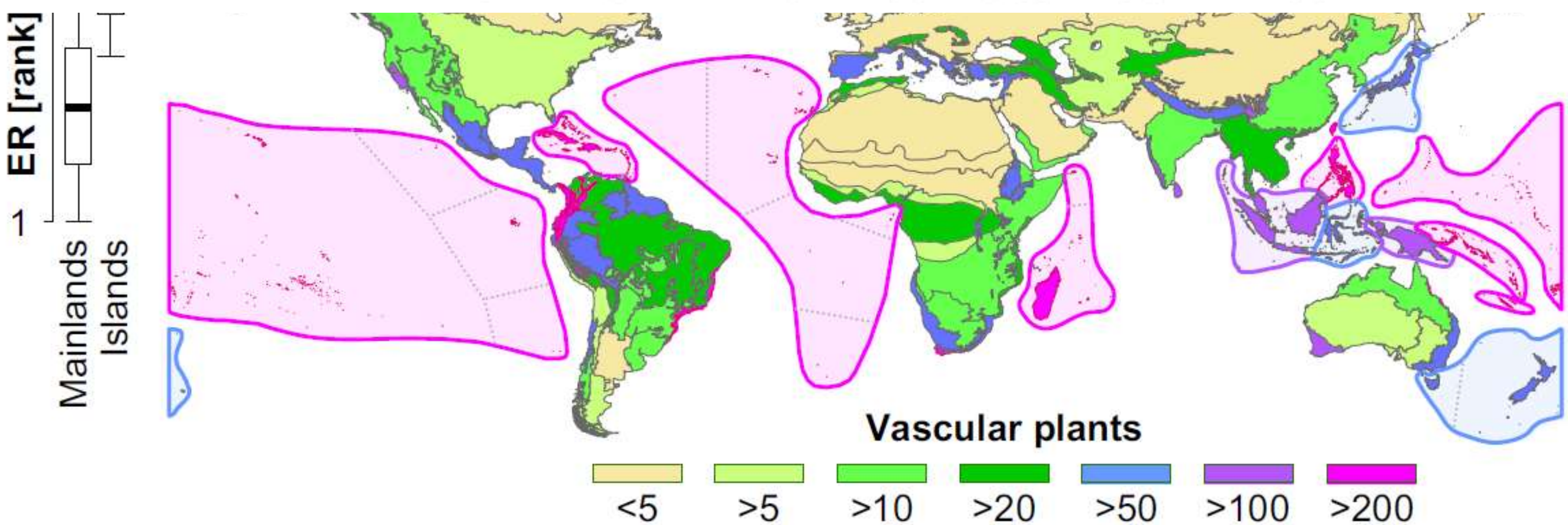


Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes

Colin Hughes* and Ruth Eastwood

Endemism richness (ER; range equivalents per 10,000 km2)





range equivalent: 1=entire range falls into given 10,000 km2 area, 0.5=50% of the species range etc.

Kier et al. 2009, PNAS 106, 9322–9327

Area of boreal, temperate and tropical habitats during past 55 million years

boreal (-40°C in winter)
temperate
tropical (above 0°C)

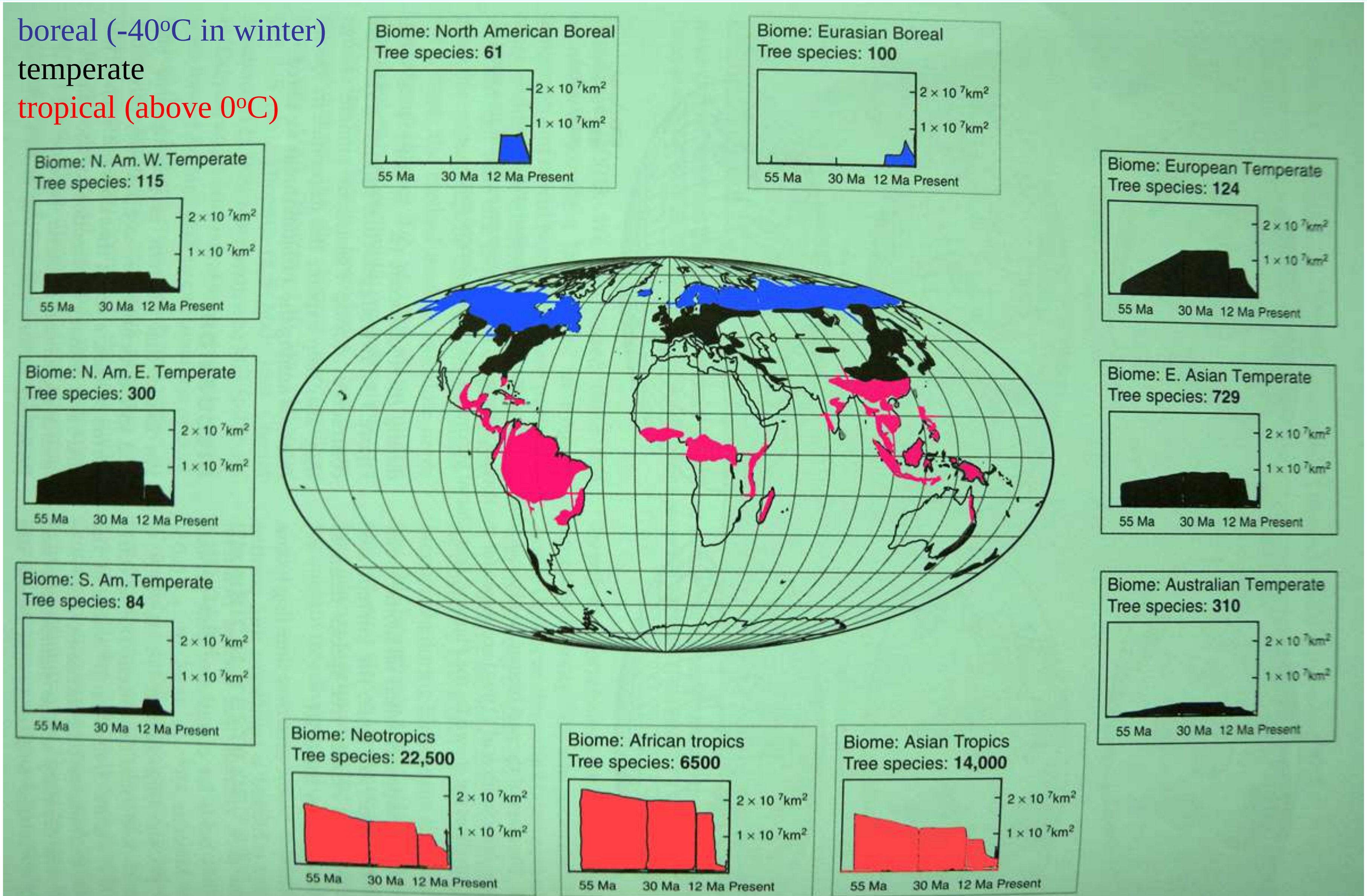
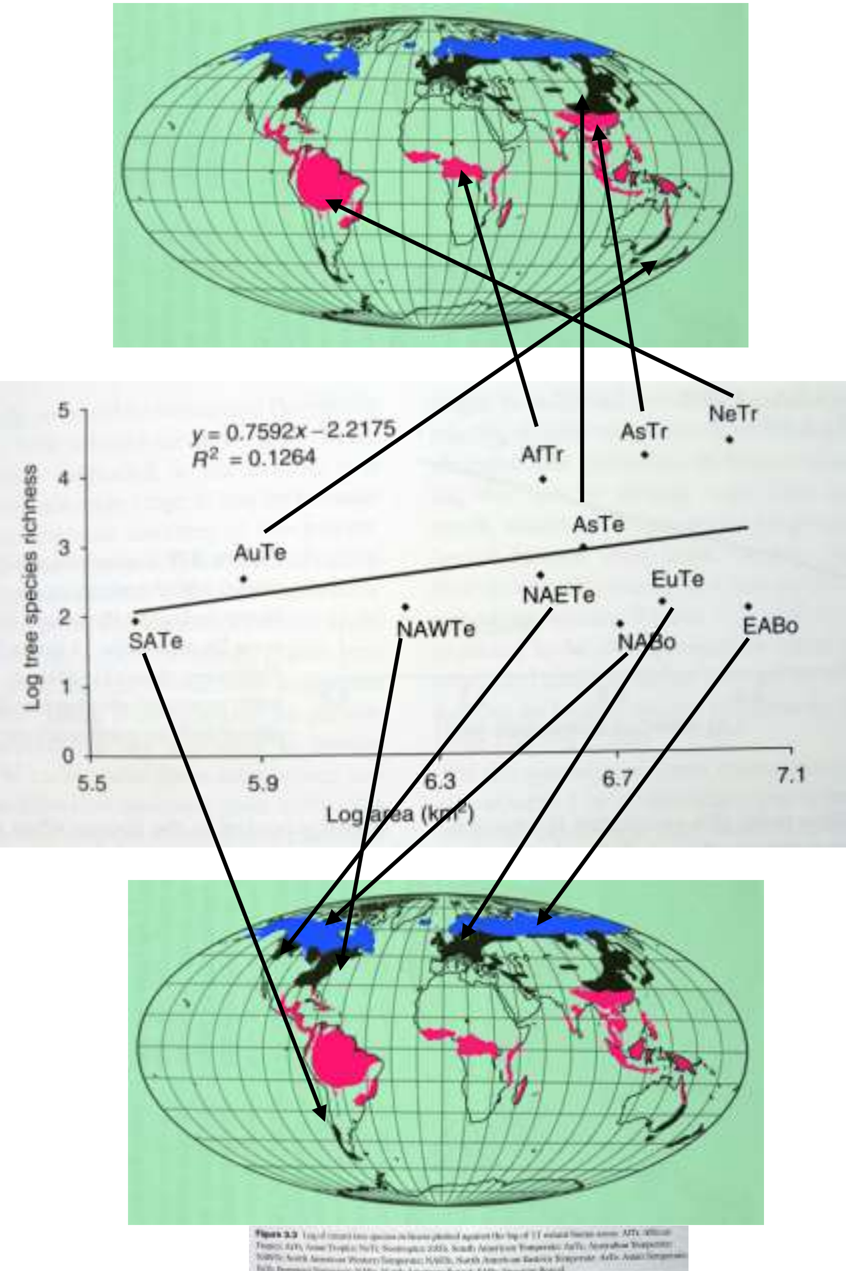
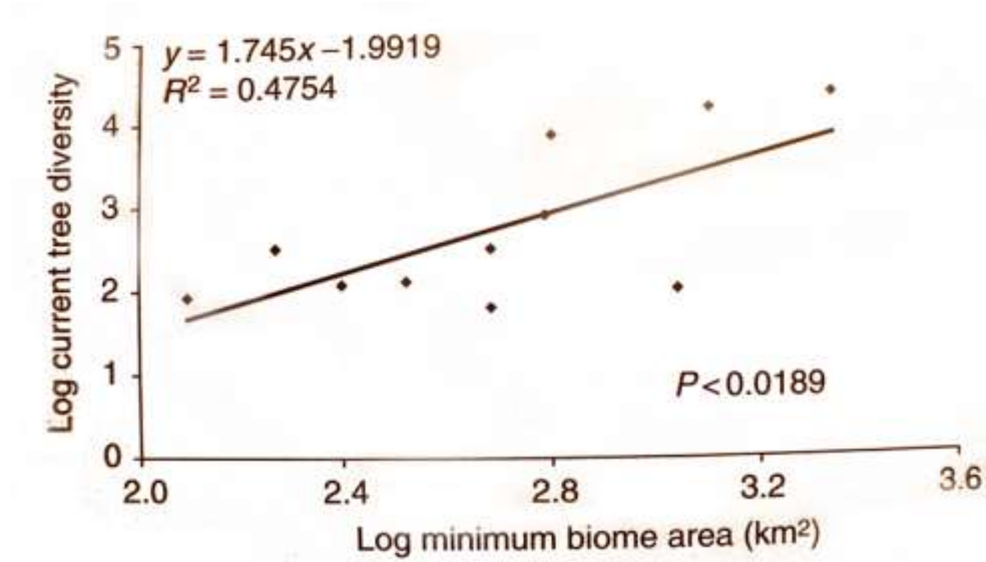


Figure 3.2 At center is a map showing the modern extent of the 11 biomes included in the analysis. *Surrounding the globe are the estimates for extant tree species richness and composite area–time measures for each biome. The area of each area–time plot was quantified, log-transformed and then correlated with log tree diversity to test for the time-integrated species–area effect.*

Fine at al. 2008 in Carson & Schnitzer: Tropical Forest Community Ecology

Species - area curve for boreal, temperate and tropical areas on different continents

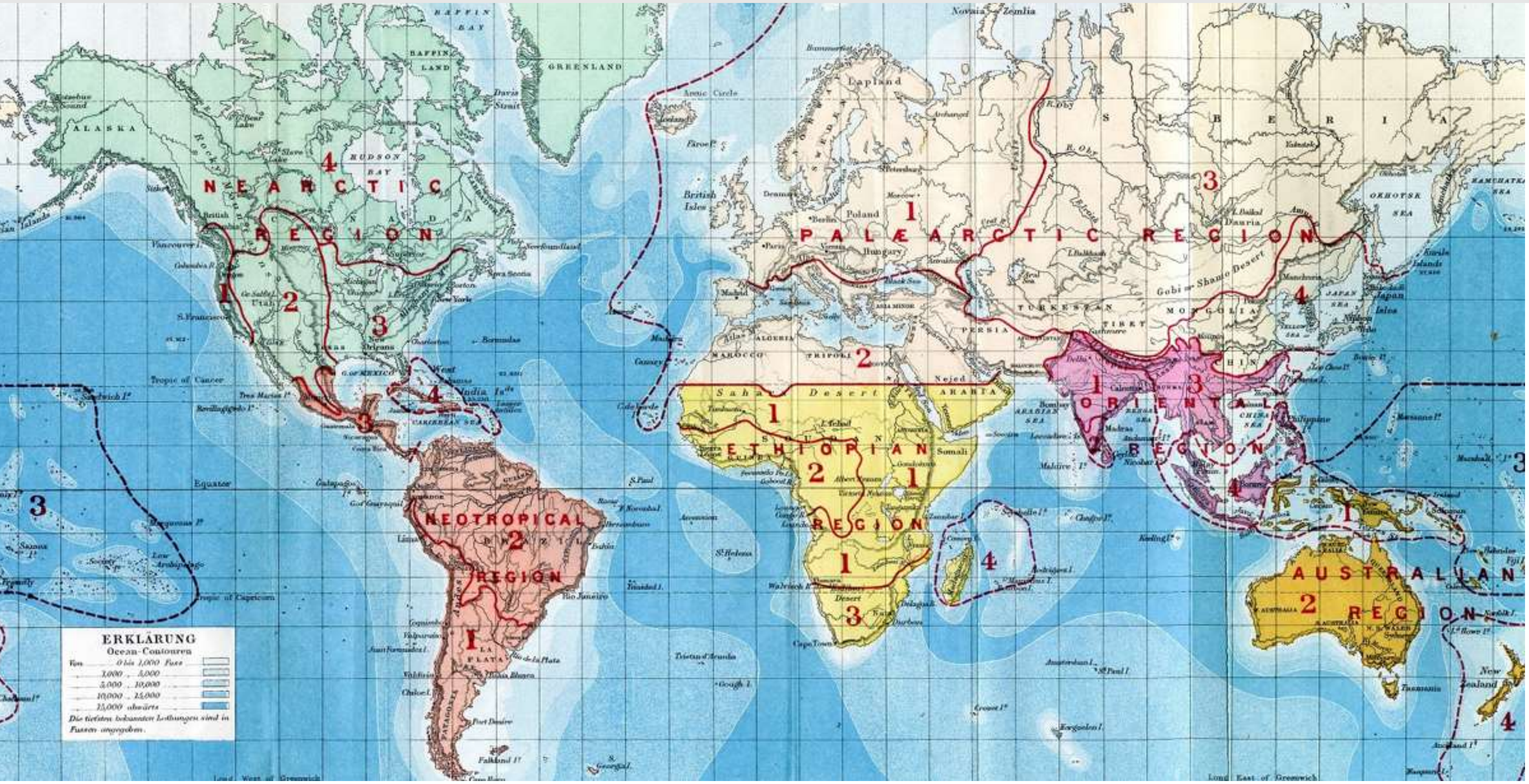




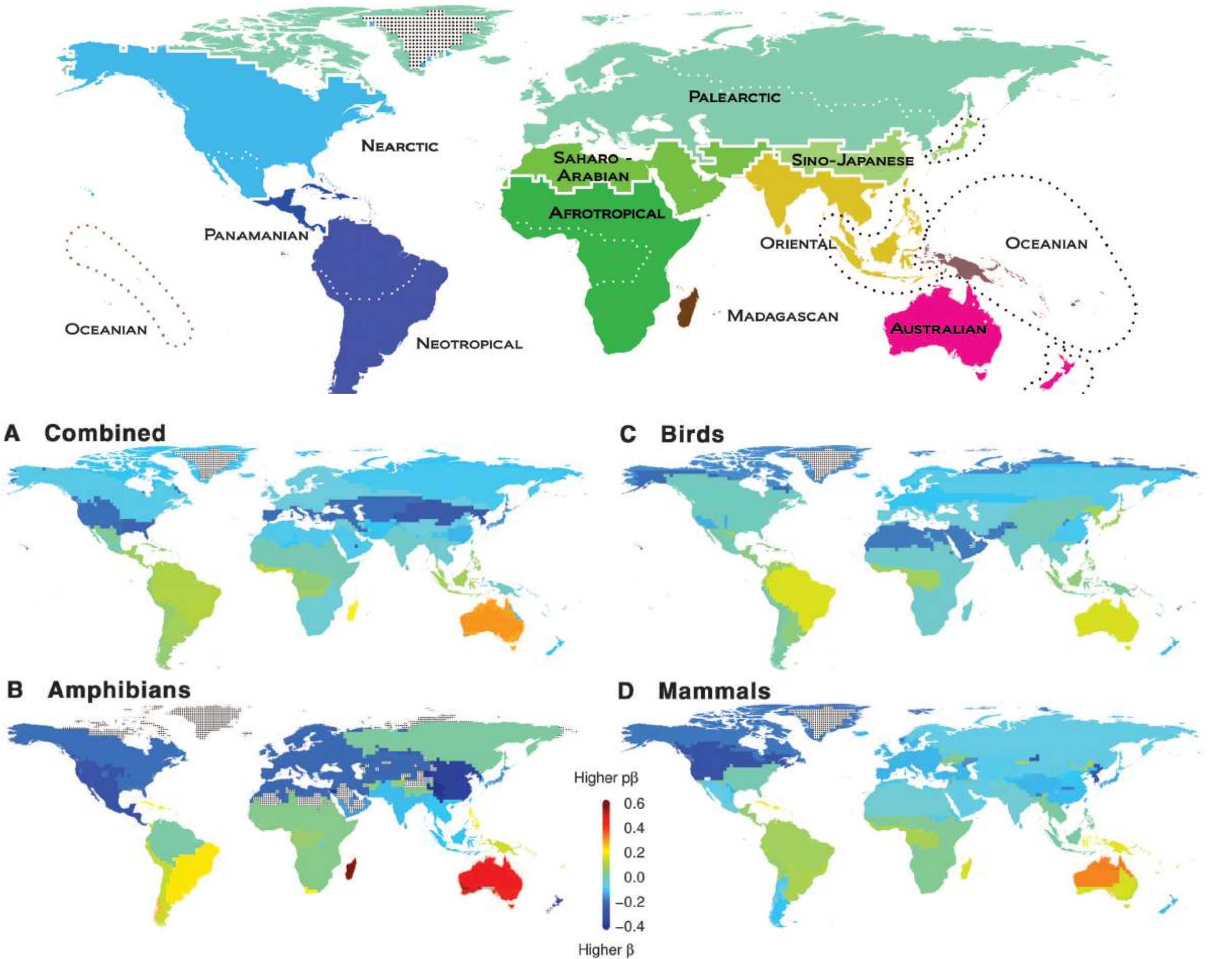
Weak correlation between tree species richness and geographic area [left] is significantly improved when the current area is replaced by minimum area during the Pleistocene and Holocene, i.e. past 2.6 million years [above].

Fine at al. 2008 in Carson & Schnitzer: Tropical Forest Community Ecology

An Update of Wallace's Zoogeographic Regions of the World (Holt et al. 2013, Science 339: 74)



An Update of Wallace's Zoogeographic Regions of the World (Holt et al. 2013, Science 339: 74)



Insects communities on tropical trees: extraordinary species richness

Table 8.17 Diversity of all insects, and of beetles, from individual tree crowns at selected sites

Location and tree	*N*	*S*	α
All insects			
Brunei, lowland forest (Stork 1991)			
Shorea johorensis # 1	2649	637	266
Shorea johorensis # 4	2166	566	249
Pentaspadon motleyi # 1	1020	288	134
Pentaspadon motleyi # 2	1431	524	298
Castanopsis sp.	3573	684	251
Beetles			
Central Panama, lowland moist forest (Erwin and Scott 1980)			
Luehea seemannii # 1	2085	335	113
Luehea seemannii # 2	1174	171	58
Luehea seemannii # 3	830	191	78
Luehea seemannii # 4	410	147	82
Luehea seemannii # 5	405	115	54
Northern Venezuela, lowland dry forest (Davies et al. 1997)			
Talisia sp.	975	292	141
Brownea grandiflora	393	168	111
Chrysophyllum lucentifolium	827	211	92
Brunei, lowland forest (Stork 1991)			
Shorea johorensis # 1	291	130	90
Shorea johorensis # 2	784	270	146
Shorea johorensis # 3	457	166	94
Shorea johorensis # 4	468	141	69
Castanopsis sp.	396	103	45
New Guinea, 500 m (Allison et al. 1993)			
Castanopsis acuminatissima 1	595	99	34
Castanopsis acuminatissima 2	496	125	54
New Guinea, 1200 m (Allison et al. 1993)			
Castanopsis acuminatissima 1	336	82	35
Castanopsis acuminatissima 2	299	86	40
New Guinea, 2100 m (Allison et al. 1993)			
Castanopsis acuminatissima 1	1829	234	71
Castanopsis acuminatissima 2	642	151	67

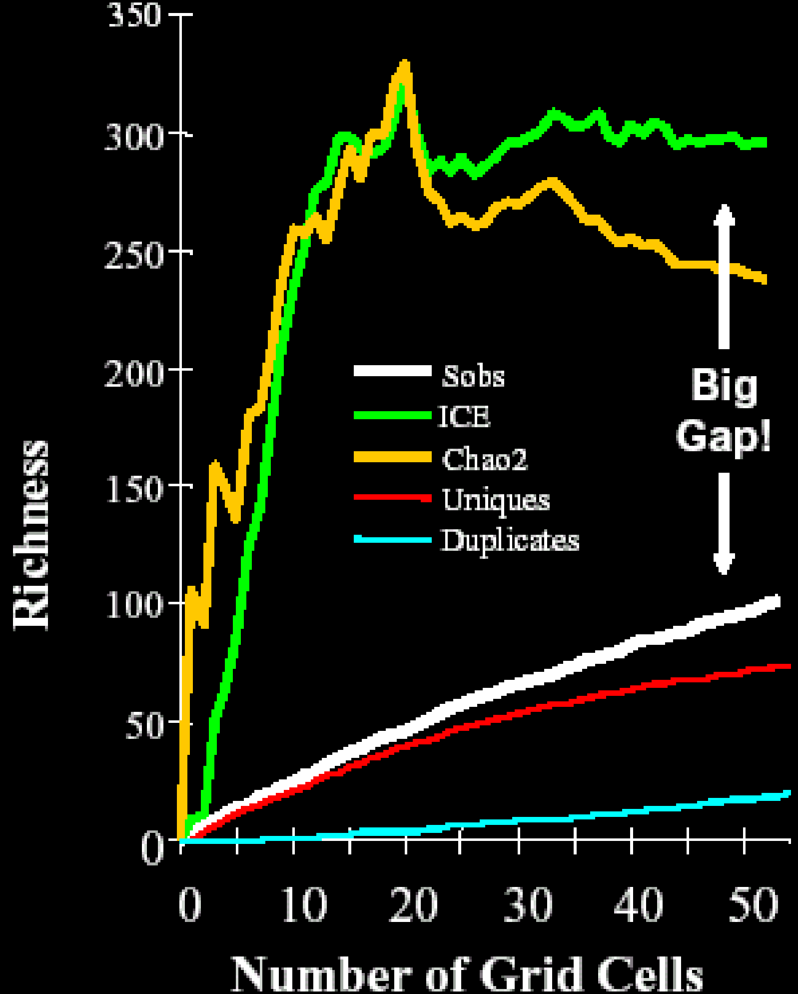
N, number of insects; *S*, number of species among them; and Fisher's α for insects collected by insectical fogging of the crowns of selected trees. Each row of numbers represents one tree's crown.

Individual tropical trees:

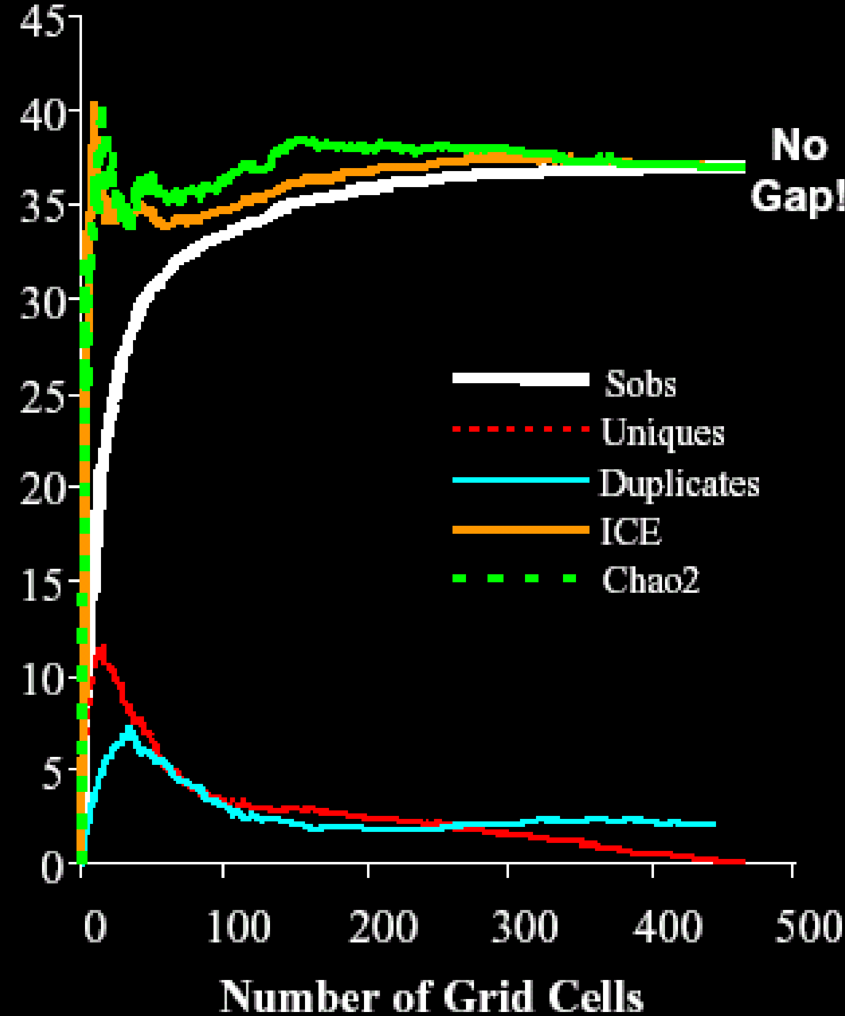
100-300 spp. of beetles
300-700 spp. of insects

Courtesy
Jonathan Coddington

Amazonian
Beetles v. Primates

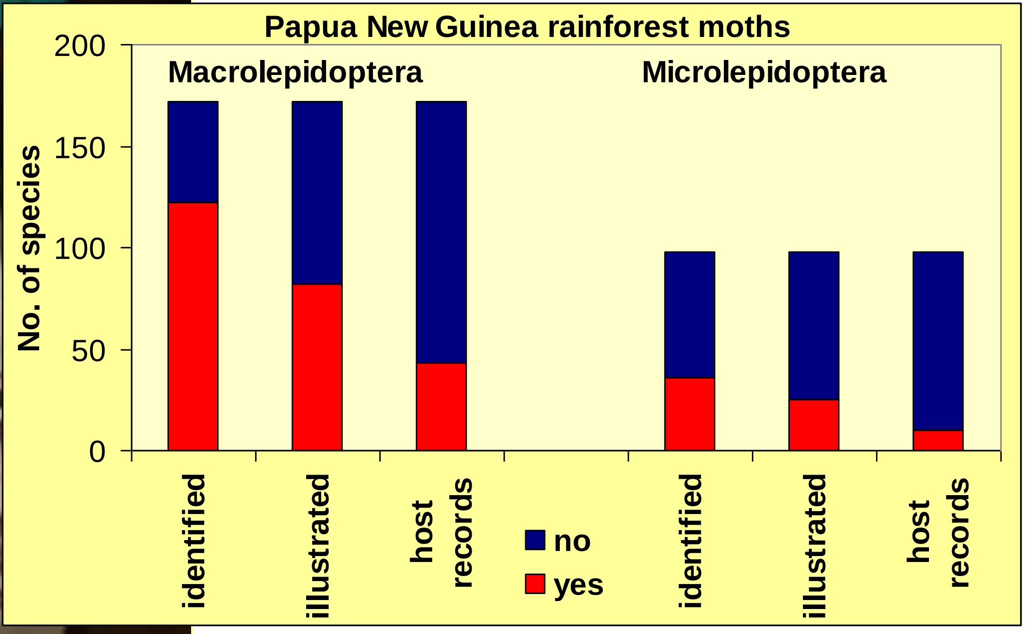


Not so Good!



Good!

Taxonomic impediment: the information on insect identity is locked in museum cabinets



Taxonomic knowledge of tropical insects: good enough only for butterflies, birds and a few other taxa - but not mammals

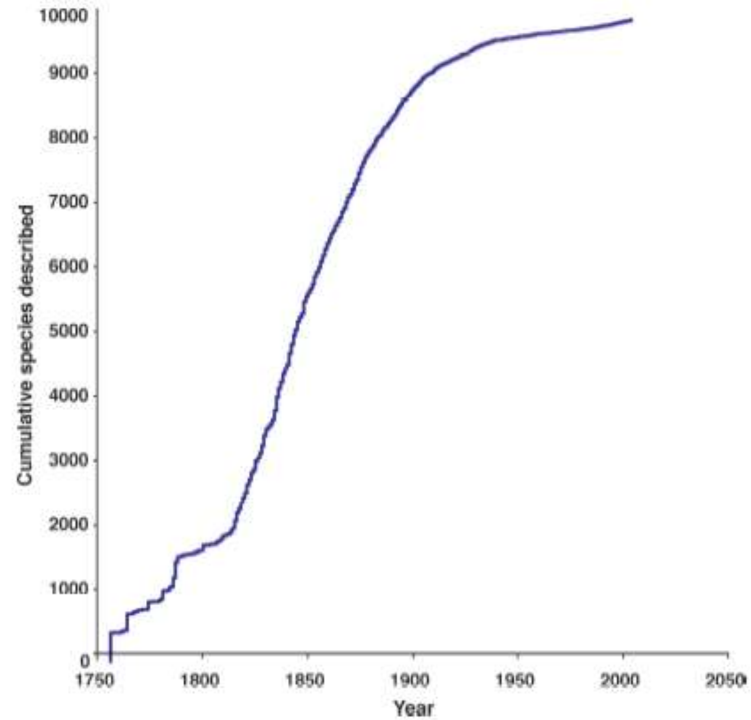
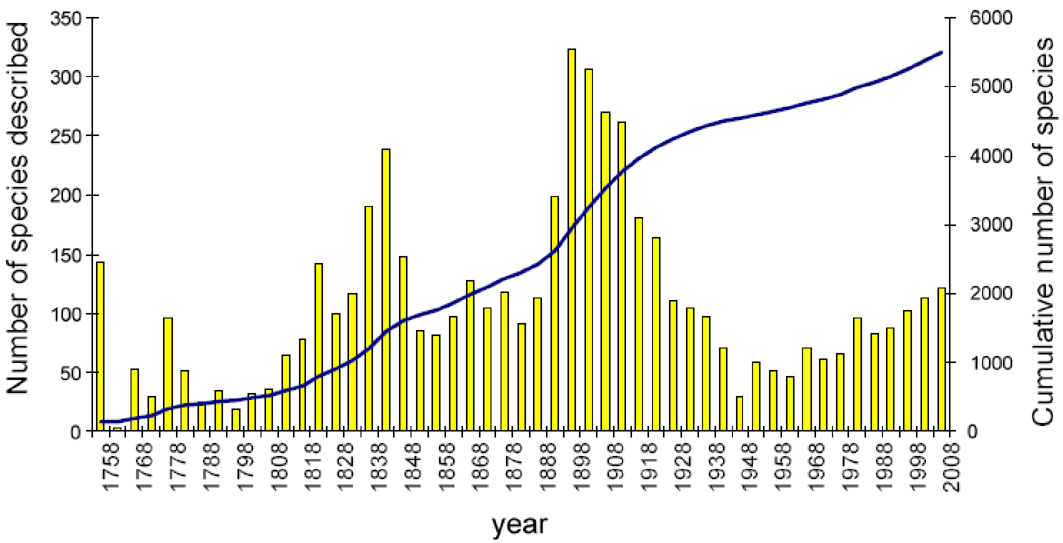


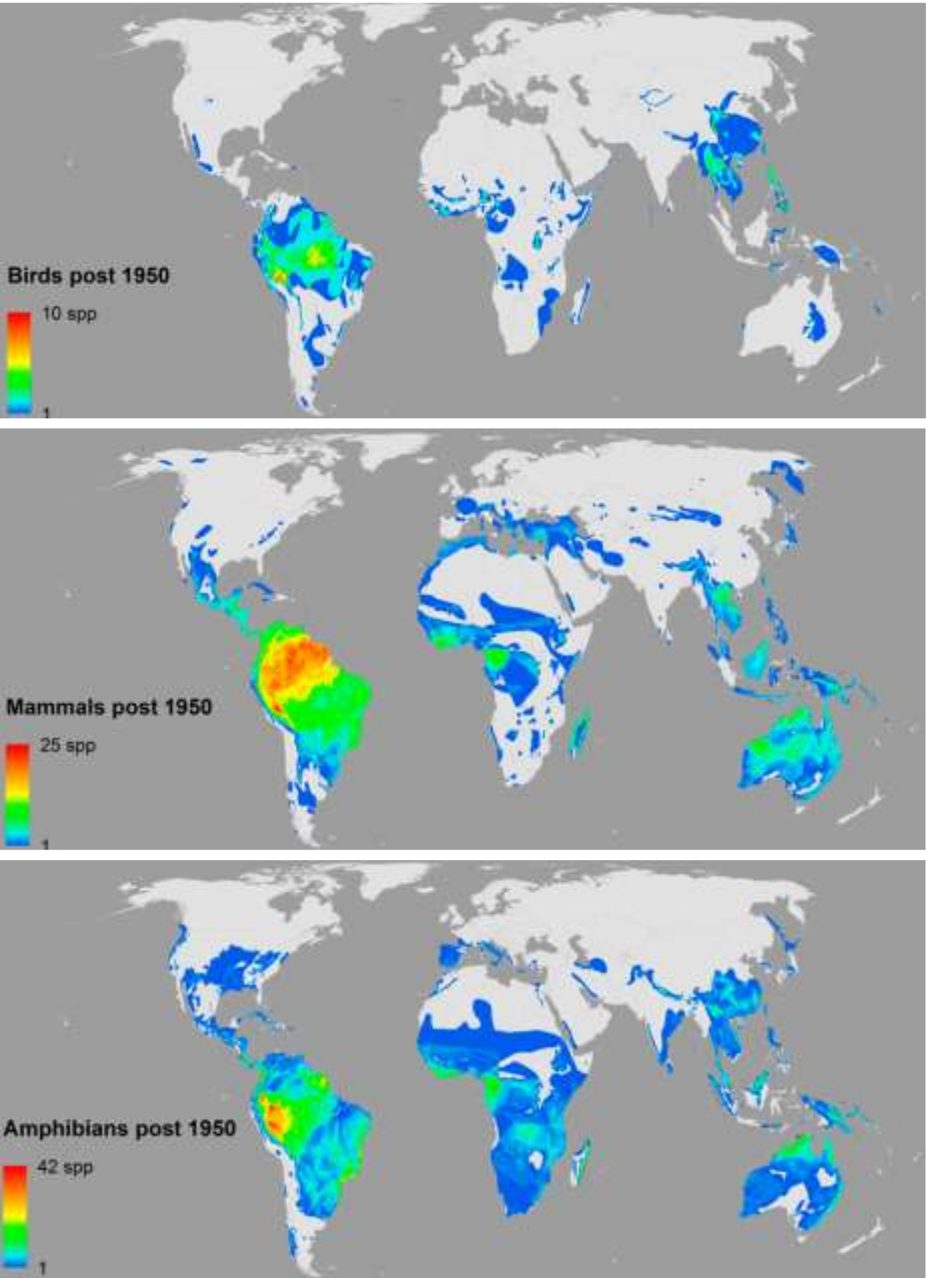
Fig. 1. Dates of description of the world's bird species. Data are available in supporting information, which is published on the PNAS web site.



Number of mammal species described each decade and cummulative number of mammal species

Schipper et al. 2008, Science 322:225

Species discoveries since 1950

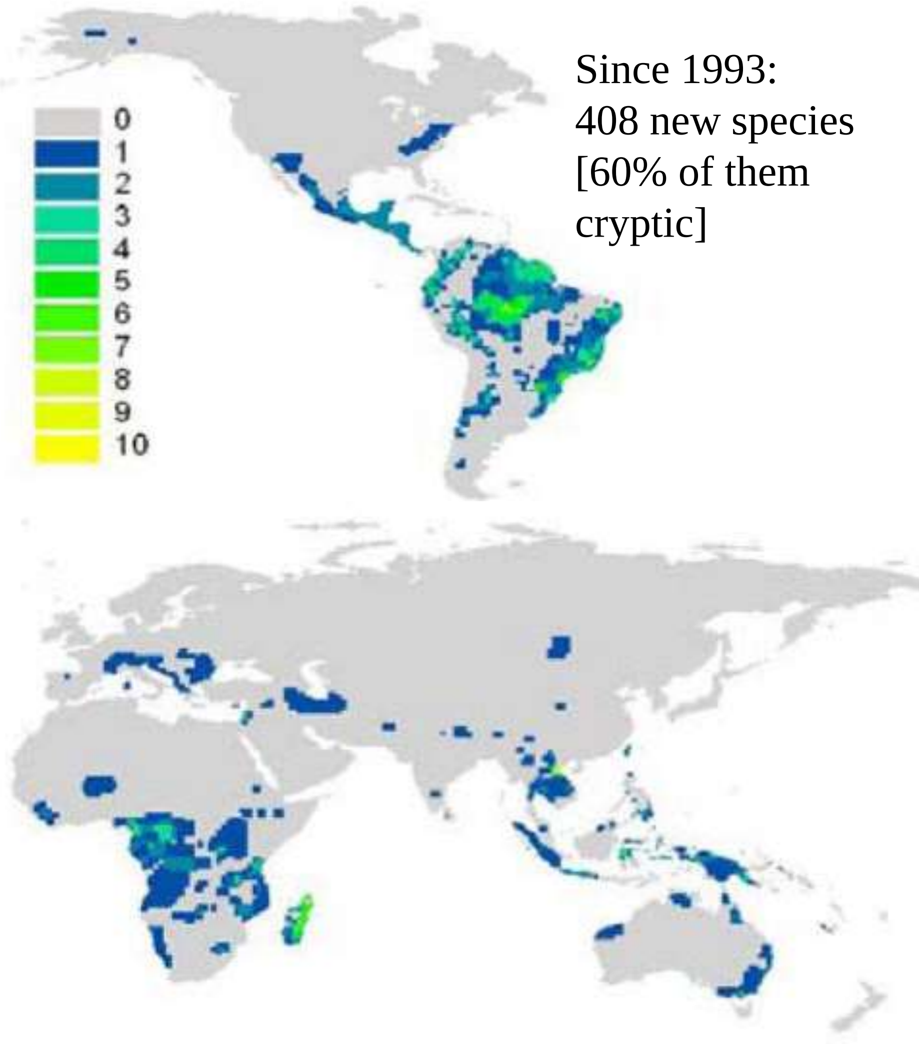


Jenkins et al. 2013, PNAS

Examples of mammals described in the last 15 years

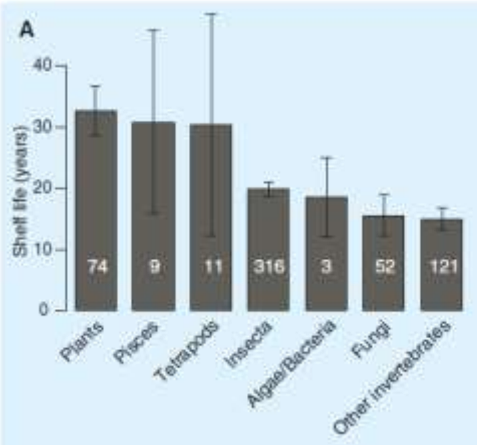
Fig. 1. Examples of new species of mammals discovered since 1993. From top left to bottom right, *Rungwecebus kipunji* (Copyright 2006, Tim Davenport/World Conservation Society). *Cuscomys ashanika* [Reproduced with permission from Emmons (*SI Appendix*) (Copyright 1999, American Museum of Natural History)]. *Bradypus pygmaeus* (Copyright 2007, Bill Haycher/National Geographic Society). *Mirza zaza* (Copyright 2006, David Haring/Duke Lemur Center). *Cebus queirozi* [Reproduced with permission from Pontes et al. (*SI Appendix*) (Copyright 2006, Magnolia Press)]. *Rhyncocyon udzunwensis* [Reproduced with permission from Rovero et al. (ref. 17) (Copyright 2007, The Zoological Society of London)]. *Macrotarsomys petteri* [Reproduced with permission from Goodman and Saorimalala (*SI Appendix*) (Copyright 2005, Biological Society of Washington)]. *Laonastes aenigmamus* (Copyright 2007, David Redfield/Florida State University). *Scotophilus marovaza* [Reproduced with permission from Goldman et al. (*SI Appendix*) (Copyright 2006, Polish Academy of Sciences)]. *Microgale jenkinsae* [Reproduced with permission from Goldman et al. (ref. 18) (Copyright 2006, The Zoological Society of London)].

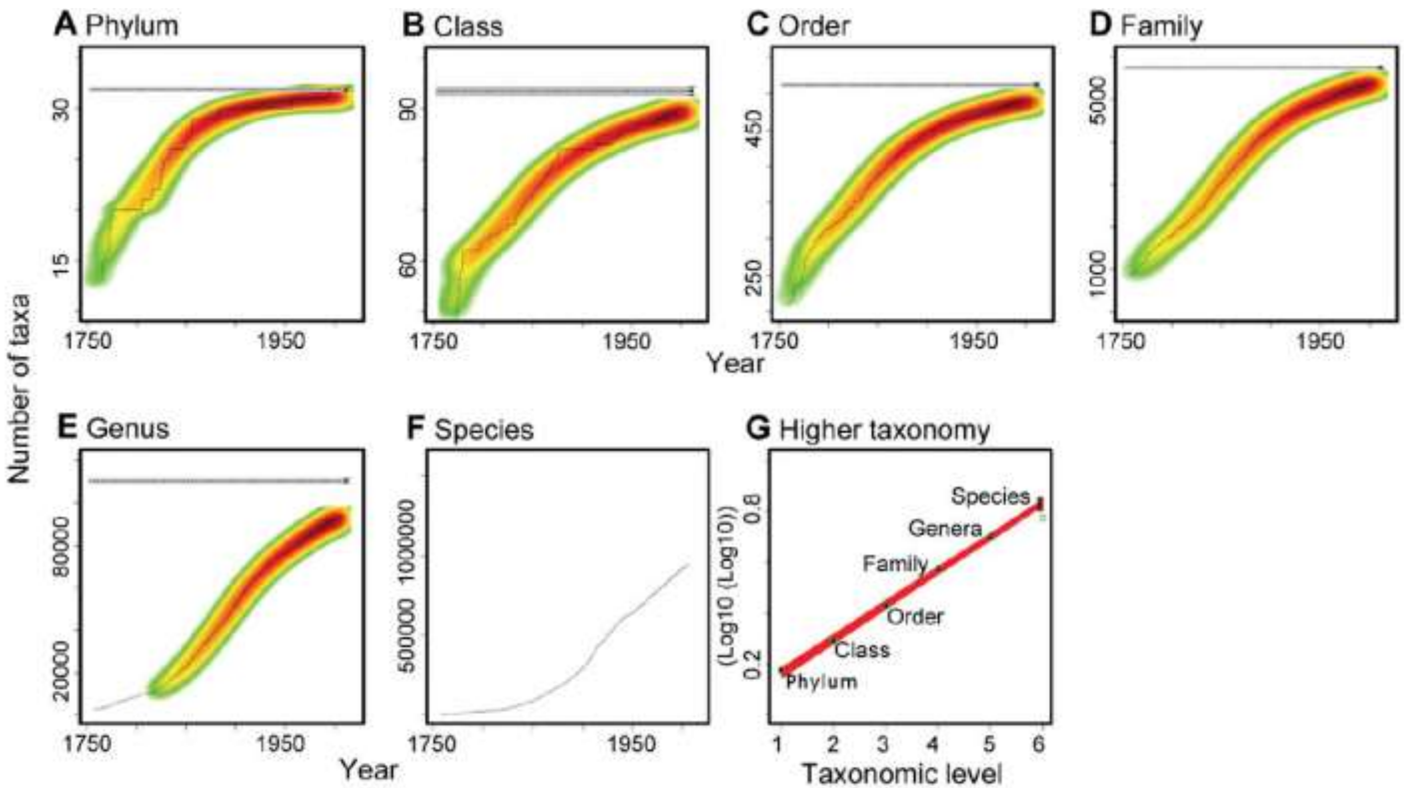
Since 1993:
408 new species
[60% of them cryptic]



Location of the species described since 1993

21 years of shelf life between discovery and description of new species





The accumulation of taxa. The horizontal dashed lines indicate the asymptotic number.

8.7 million (61.3 million SE) eukaryotic species globally,
incl. 2.2 million (60.18 million SE) marine.

Mora et al. PLOS Biology 2011, 9 e1001127

Fontaine et al. Current Biology 22: R944

A mayfly species unknown to science (Sepik river, New Guinea)

How many species are there on the Earth?

extrapolating from canopy fogging samples from 16 individual trees of *Luehea seemannii* in Panama, Erwin (1982) estimated global species richness of insects at 30 million species

CONSERVATION INTERNATIONAL

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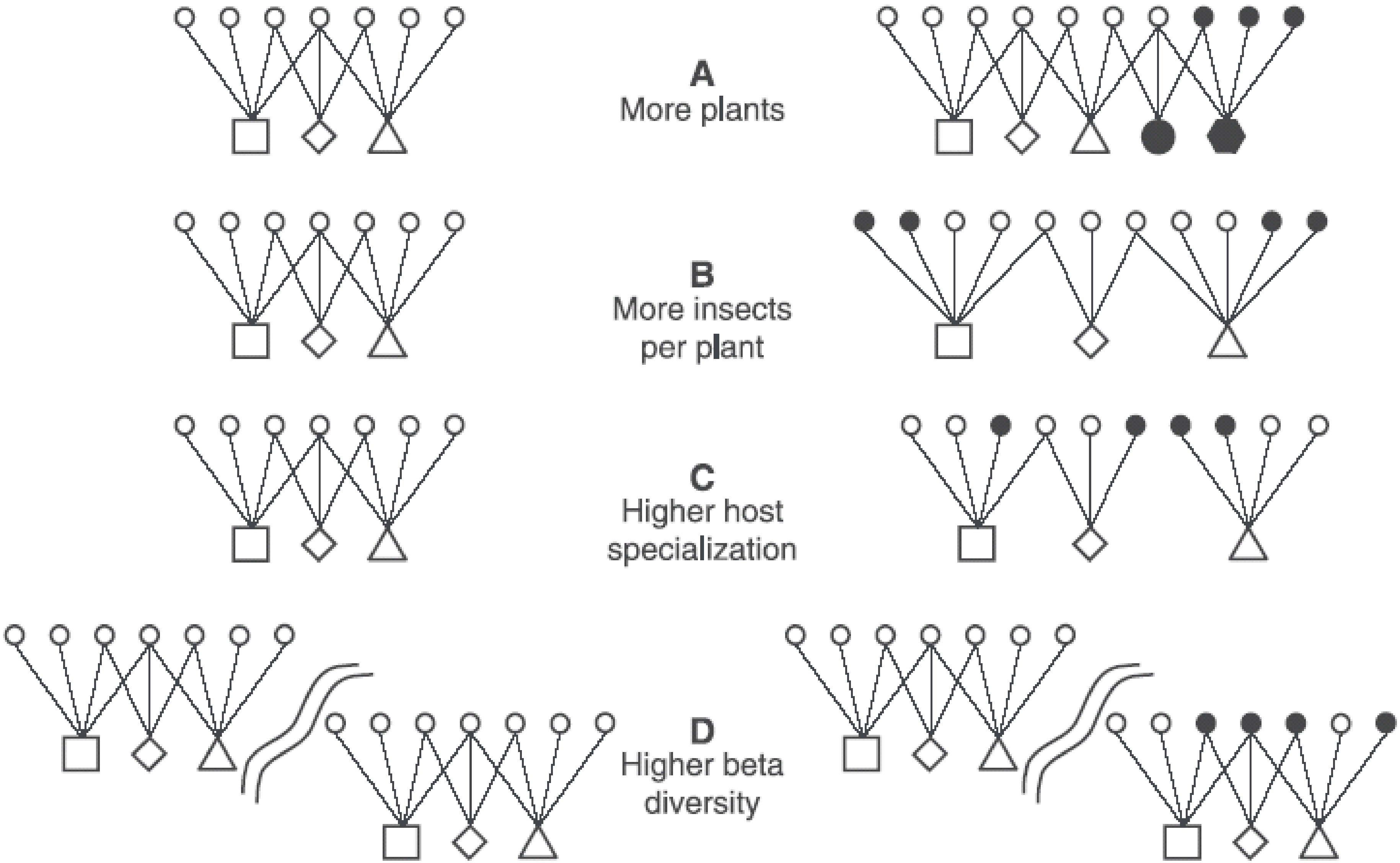
30 Million Insects Can't All Be Wrong

Table 2 Estimates of the global number of arthropod species

Variable	Coleoptera 1	Coleoptera 2	Coleoptera 3	Lepidoptera
A. No. of herbivore species per tree species	682*	32.9†	32.9†	30.8¶
B. Effective specialization	0.20*	0.24†	0.24†	0.51†
C. Correction for non-herbivorous species	1.20*	1.20*	1.20*	1.00†
D. Proportion of species from arthropods	0.40*	0.23‡	0.23‡	0.10#
E. Proportion of canopy fauna from total	0.66*	0.42‡	0.42‡	1.00†
F. No. of tropical tree species	50,000*	50,000*		
G. No. of plant genera in New Guinea			1,872§	1,872§
H. Proportion of New Guinea species from total			0.05‖	0.05‖
Global no. of arthropod species (A × B × C × F)/(D × E)	31,000,000	4,904,348		
Global no. of arthropod spp. (A × B × C × G)/(D × E × H)			3,672,376	5,881,075

Sources: *, from ref. 1; †, from this study; ‡, from ref. 4; §, from ref. 13; ‖, from ref. 19; ¶, our estimate of 26.1 externally feeding leaf-chewer species multiplied by 1.18 to account for herbivorous species from other guilds, based on ref. 30; #, from ref. 8. Coleoptera 1, estimate from ref. 1. Note that the Coleoptera 2 and Lepidoptera estimates are mutually independent because they are based on two entirely different sets of parameters.

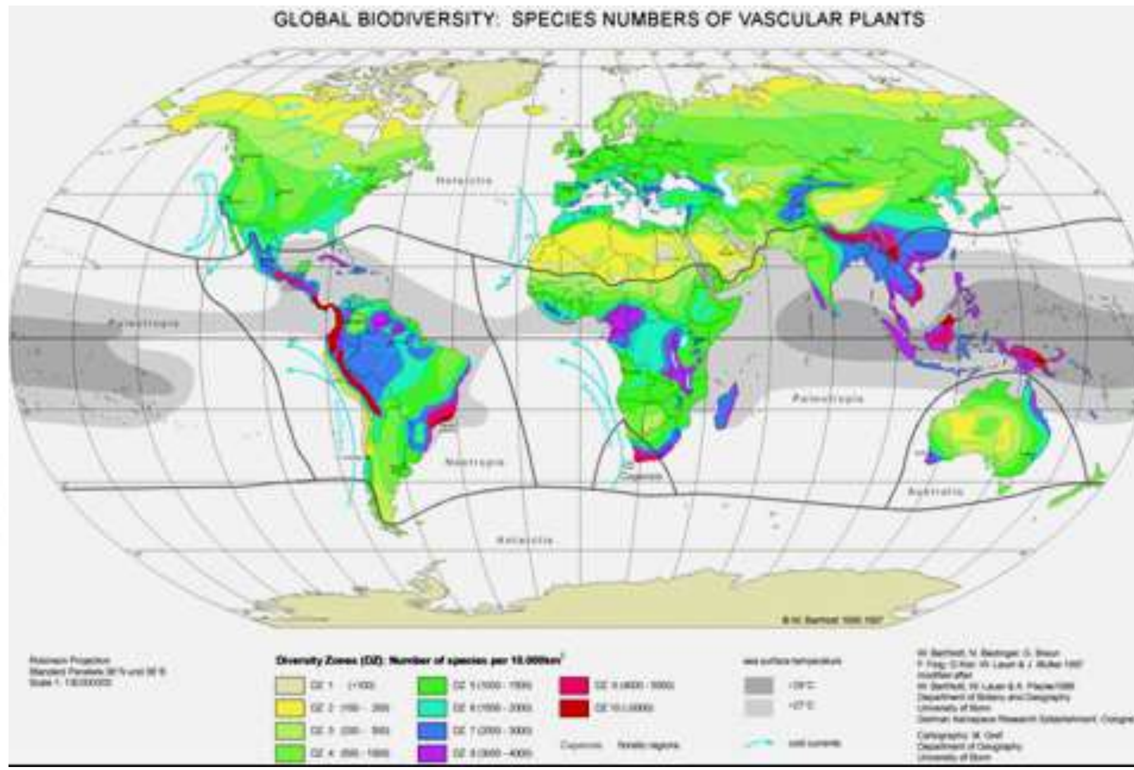
Why there are more herbivore species in the tropics than in the temperate zone?



Lewinsohn & Roslin, Ecology Letters, (2008) 11: 398–416

Latitudinal gradients in insect diversity:

explained by plants?



Barthlott et al. 2007 *Erdkunde* **61**, 305

Lewinsohn & Roslin (2008) Eco. Let. 11:398

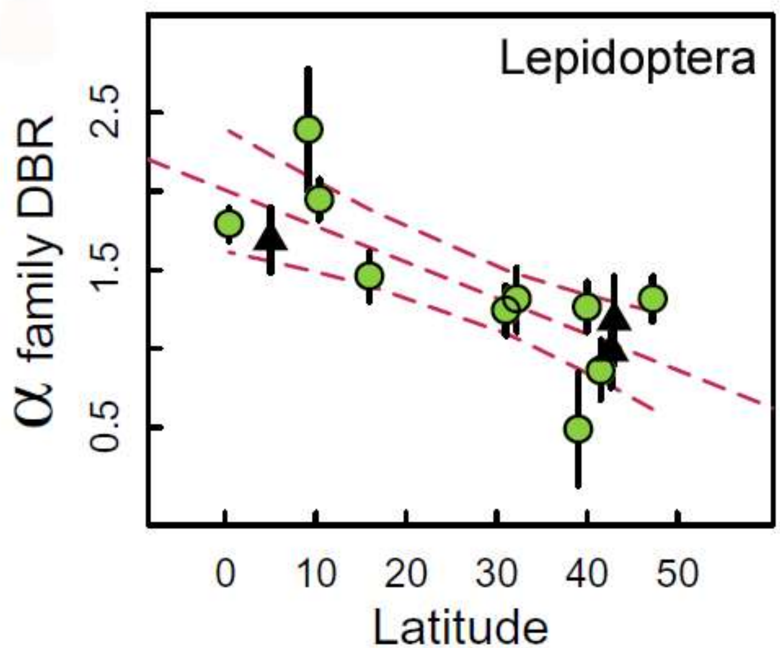
slide: Martin Volf

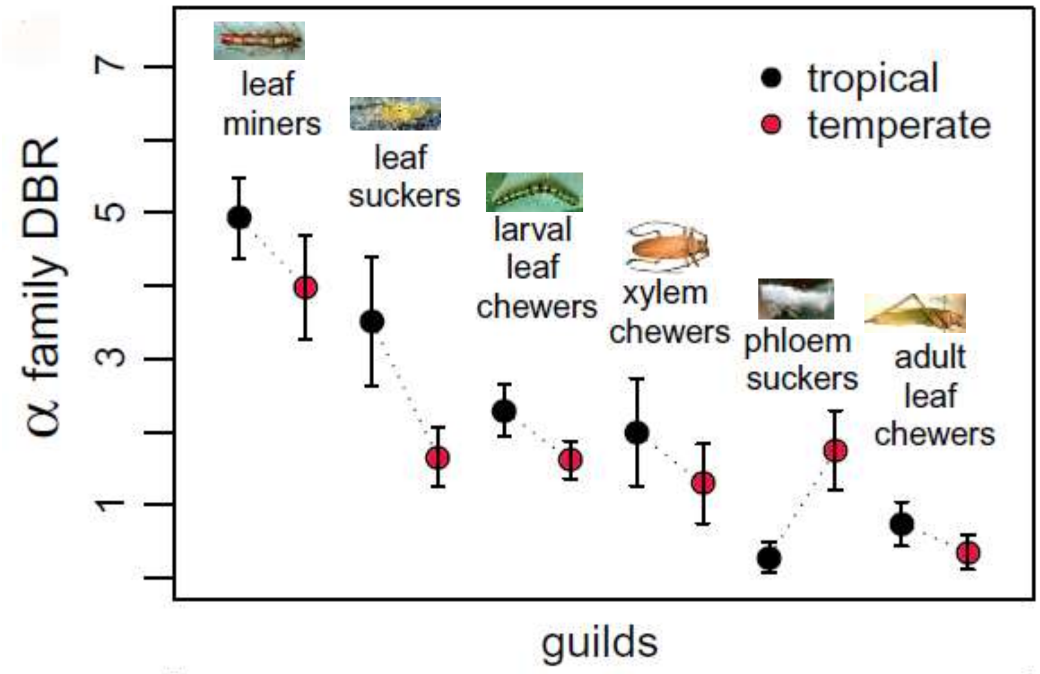
TEMPERATE

TROPICAL

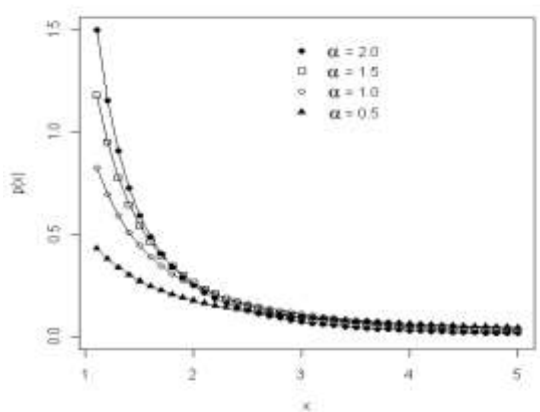
more plant species in the tropics

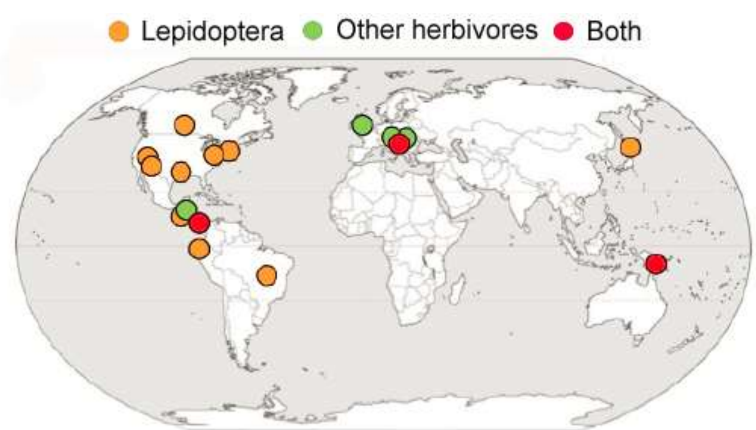
yes





Truncated discrete Pareto distribution



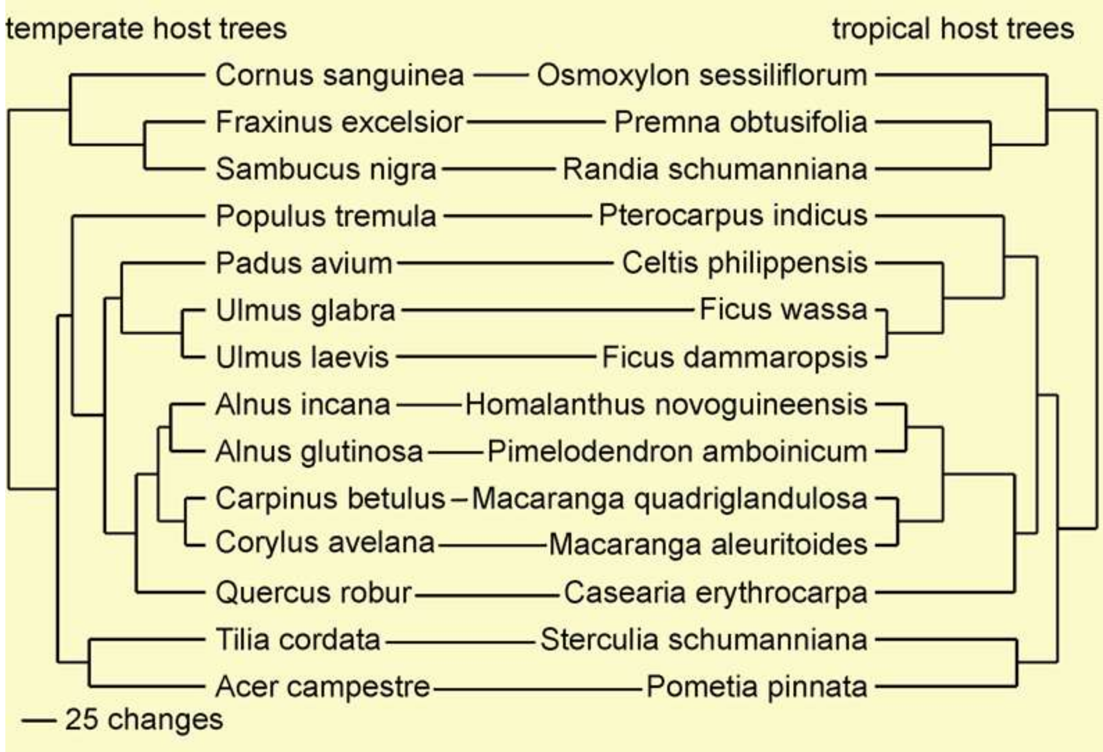


Comparing apples and oranges:

standardising phylogenetic diversity among disparate food webs along latitudinal gradients

Novotny et al. 2006, *Science* **313**:1115

temperate trees



tropical trees