Tropical systems: montane forest

Review key aspects of zonation and climate

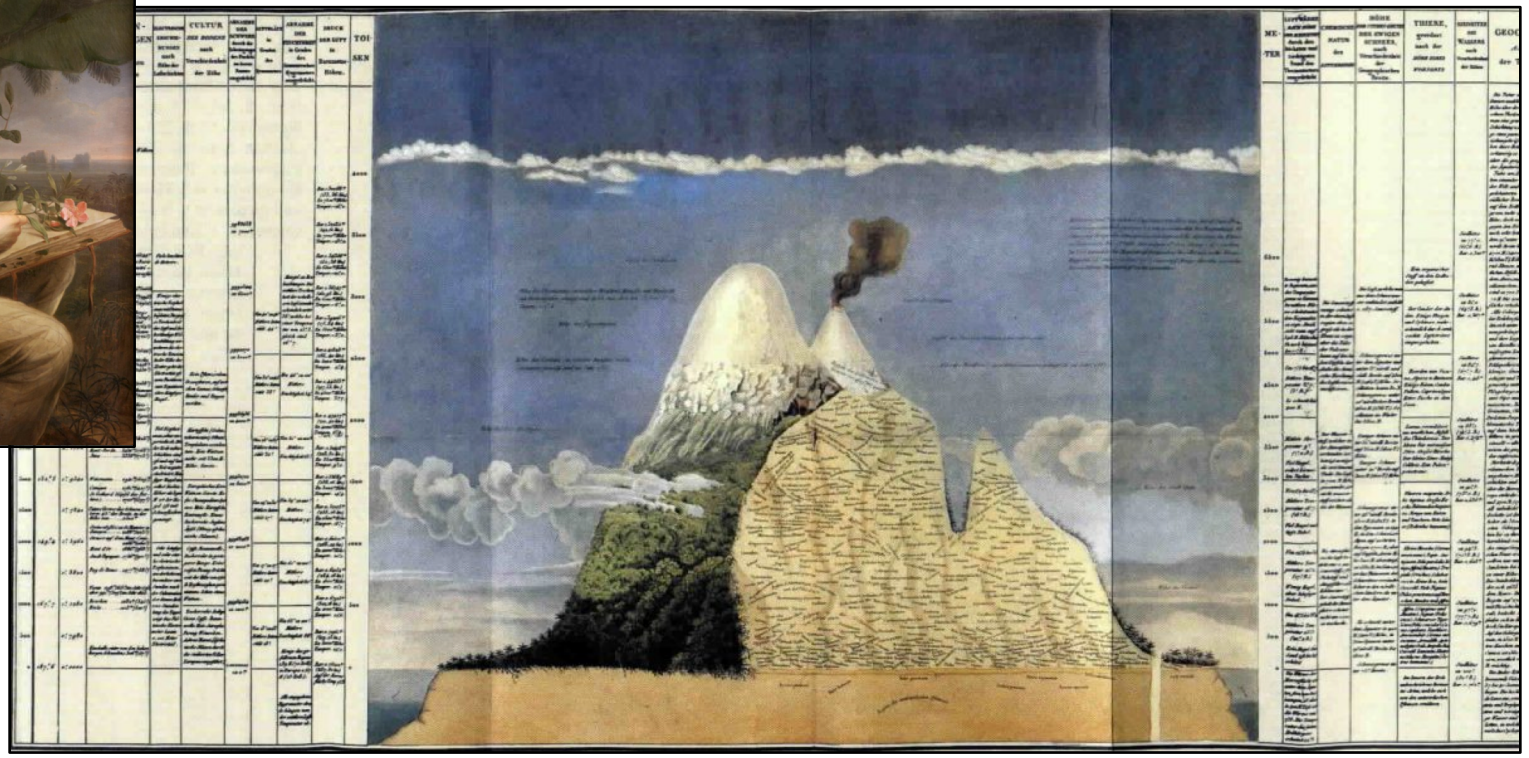
Vegetation features

Affects on diversity and distributions

Phylogenetic structure across elevational gradients

Recognition of changing diversity with elevation

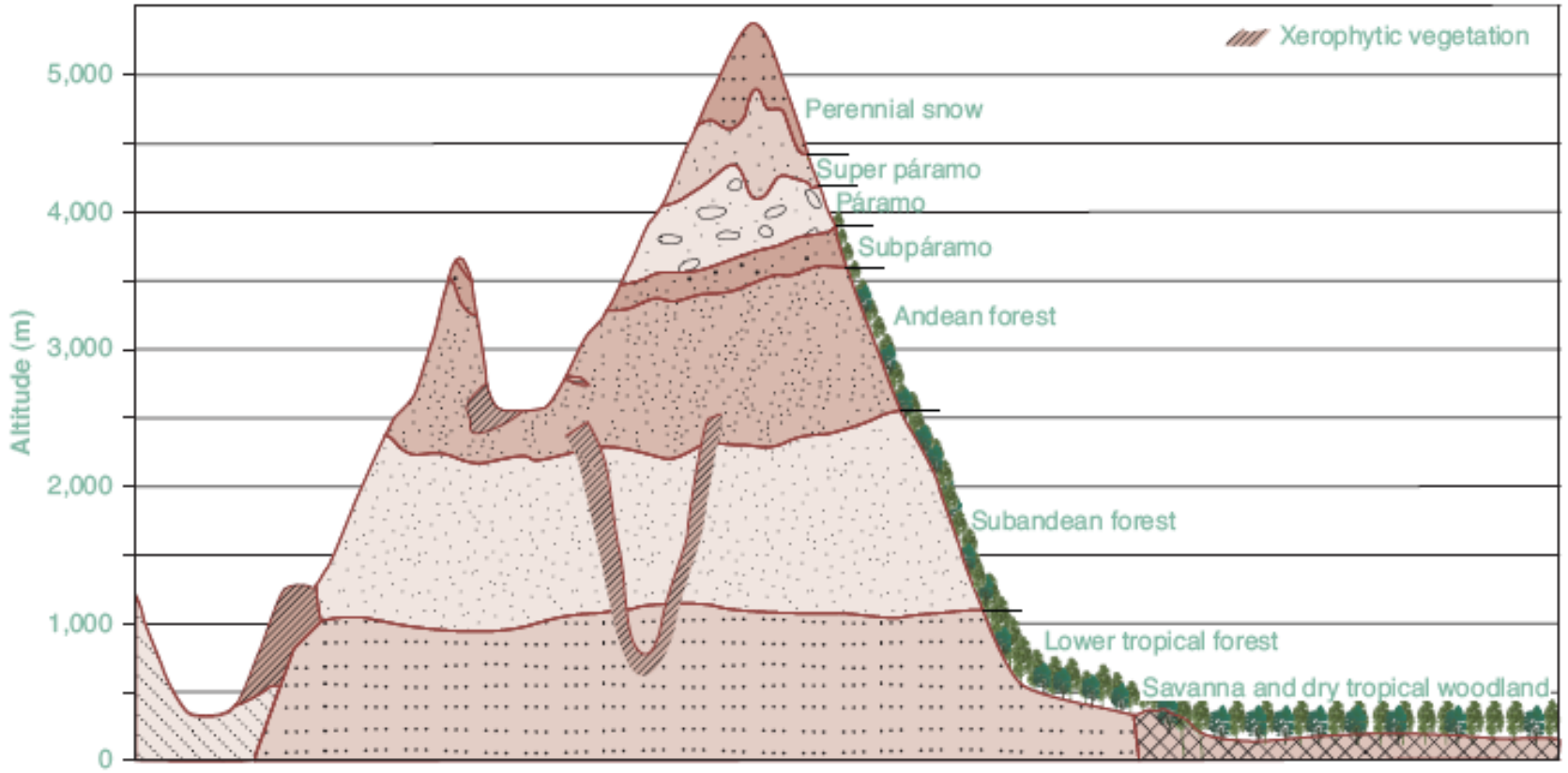
Alexander von Humboldt (1769-1859)



Humboldt explored the Neotropics in the early 1800's and first described changes occurring along tropical elevational gradients – this formed the backbone of concepts of plant associations and how community characteristics respond to the changing physical environment.

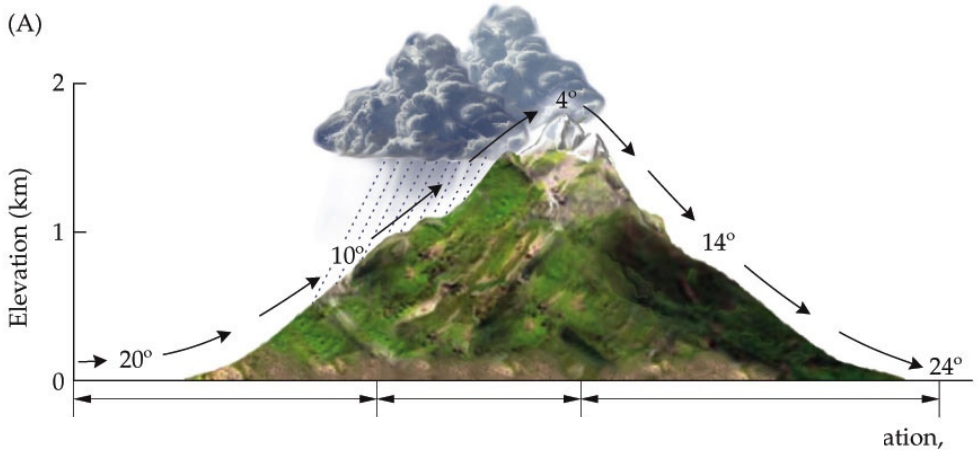
Zonation of vegetation belts across altitudes – Cordillera Oriental, Colombia

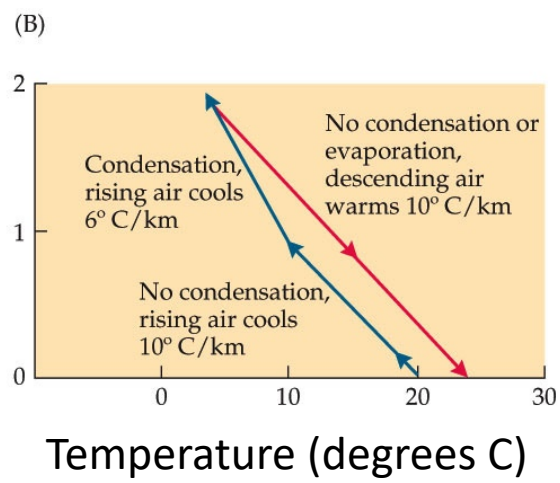
As temperature and precipitation change, there are correlated shifts in the structure and composition of vegetation from low to high elevations (vegetation zonation)



Recall how major temperature and precipitation gradients are generated

Air cools and loses moisture as it moves up slope (adiabatic cooling). When it descends on the other side, it warms (at a higher rate). This results in wet “windward” and dry “leeward” sides of a mountain



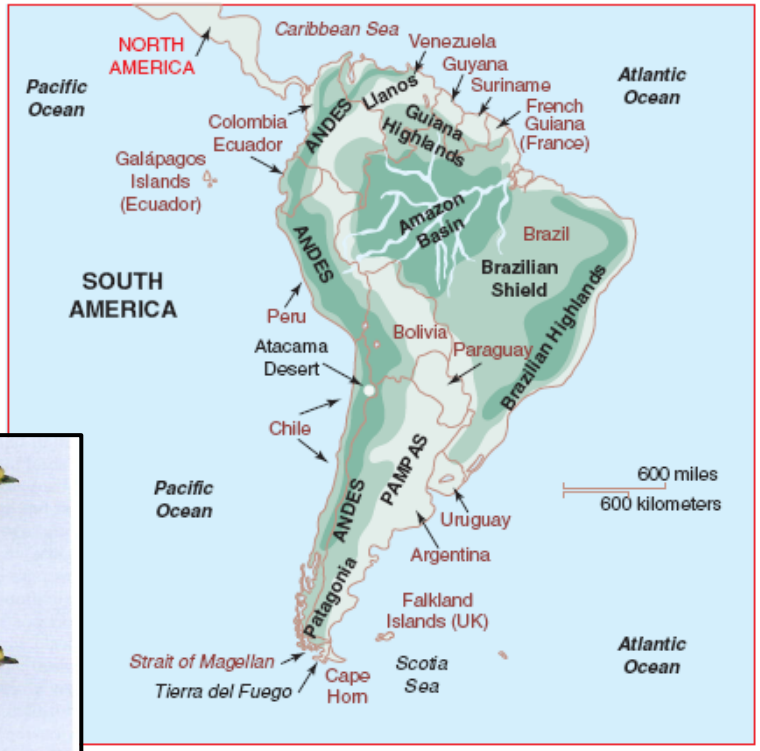


In Puerto Rico, drastic differences between windward and leeward slope habitats.

Extensive range of Andes in South America

These habitat zones or belts have linear, sinuous distributions along mountain chains

Reflected in the range shapes of montane species, which are limited to narrow elevational/habitat bands



Zonation of major habitats across tropical elevational gradient

Lower montane and cloud forest

Zonation of major habitats across tropical elevational gradient

Elfin and Polylepis Forest

(stunted forest below tree line)

Zonation of major habitats across tropical elevational gradient

Above treeline Paramo occurs in the Northern Andes and Central America, while *puna* grassland is dominant above treeline in the Central Andes and south


Frailejones of Colombian paramo


Puna of southern Peru

Zonation of major habitats across tropical elevational gradient

Much of the high Andean treeline is determined by anthropogenic factors

Peruvian farmers in highland communities set fires to maintain fresh grass sprouts for cattle

Fires can spread unimpeded across the landscape

Anthropogenic treeline at ~ 3400 m, sets upper limits of cloud forest species

Manu National Park, Peru (photos M. Chappell, Z. Peterson)

Unique features of montane cloud forest

Epiphytes – grow on other plants and contribute to forest canopy structure

Highest biomass of epiphytes is found in cloud forest, where they are important for hydrological and nutrient cycles

Unique features of montane cloud forest

~200 species of birds use epiphytes in foraging

Other species use it for nesting substrate

Nadkarni & Matelson 1989

Unique species of montane cloud forest

Many species of birds, amphibians and even mammals like the spectacled bear, are restricted to cloud forest

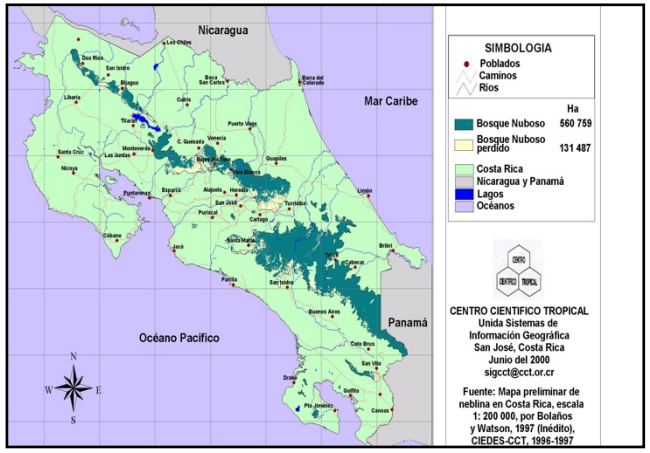
Cloud forests harbor many endemic species

Elfin Wood Warbler
endemic to cloud forest of Puerto Rico

Helmer et al. 2019, *PLOS ONE*

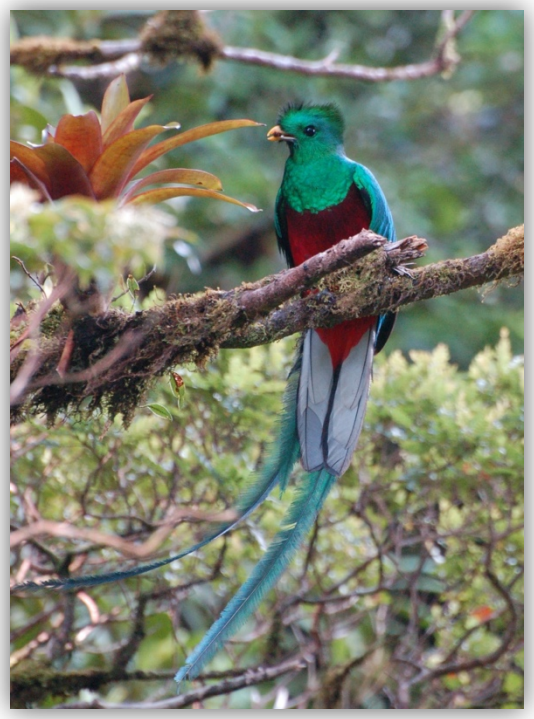
"In as few as 25 years, climate change could shrink and dry 60-80% of Western Hemisphere cloud forests, finds a study published today."

Cloud forests harbor many endemic species

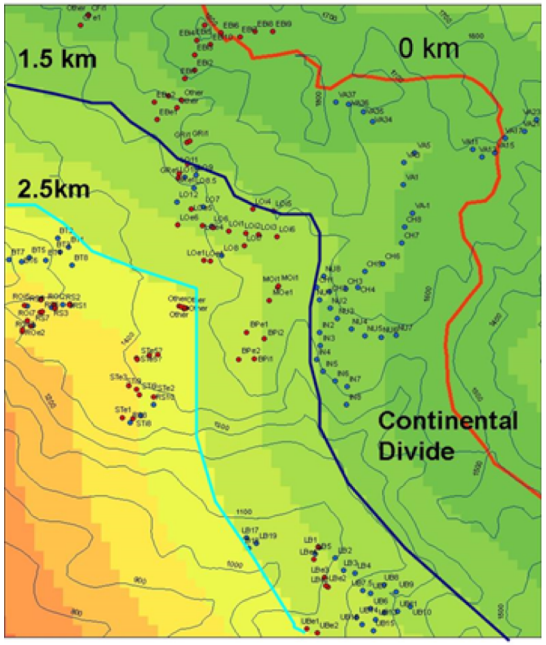


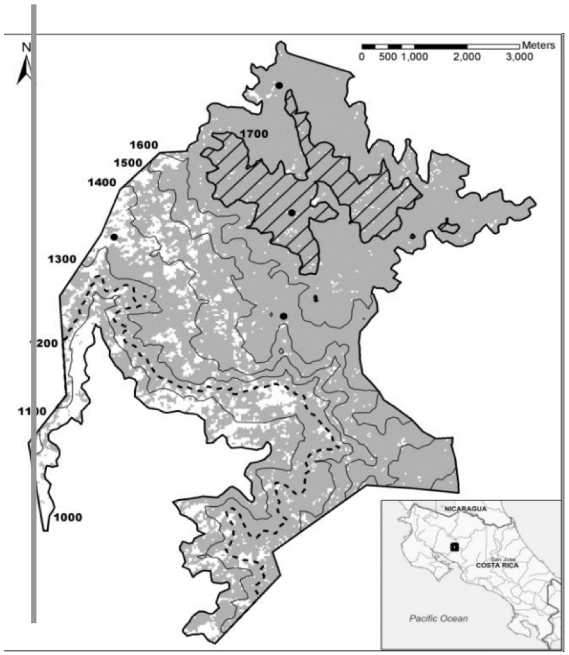
Endemic to cloud forest of Monteverde, Costa Rica:

- 24 amphibians
- 14 reptiles



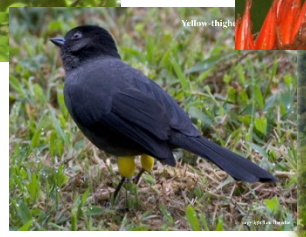
Cloud forests harbor many endemic species

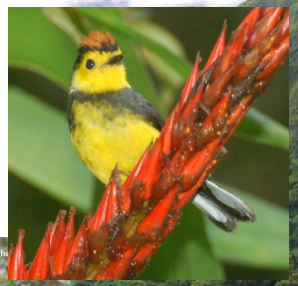




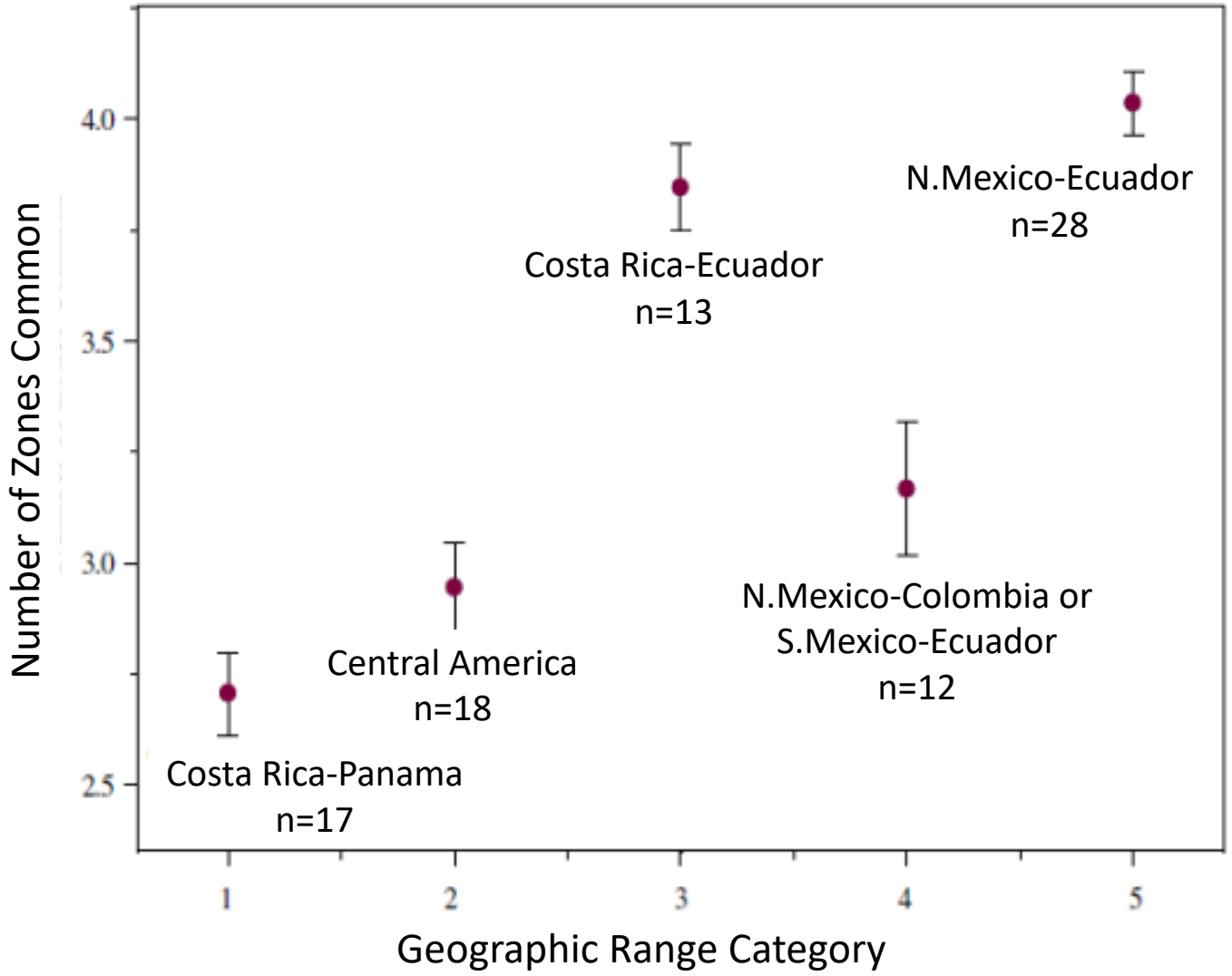
Monteverde has many species that are restricted to the mountaintop

40% of cloud forest species are endemic to Costa Rica – Panamanian highlands



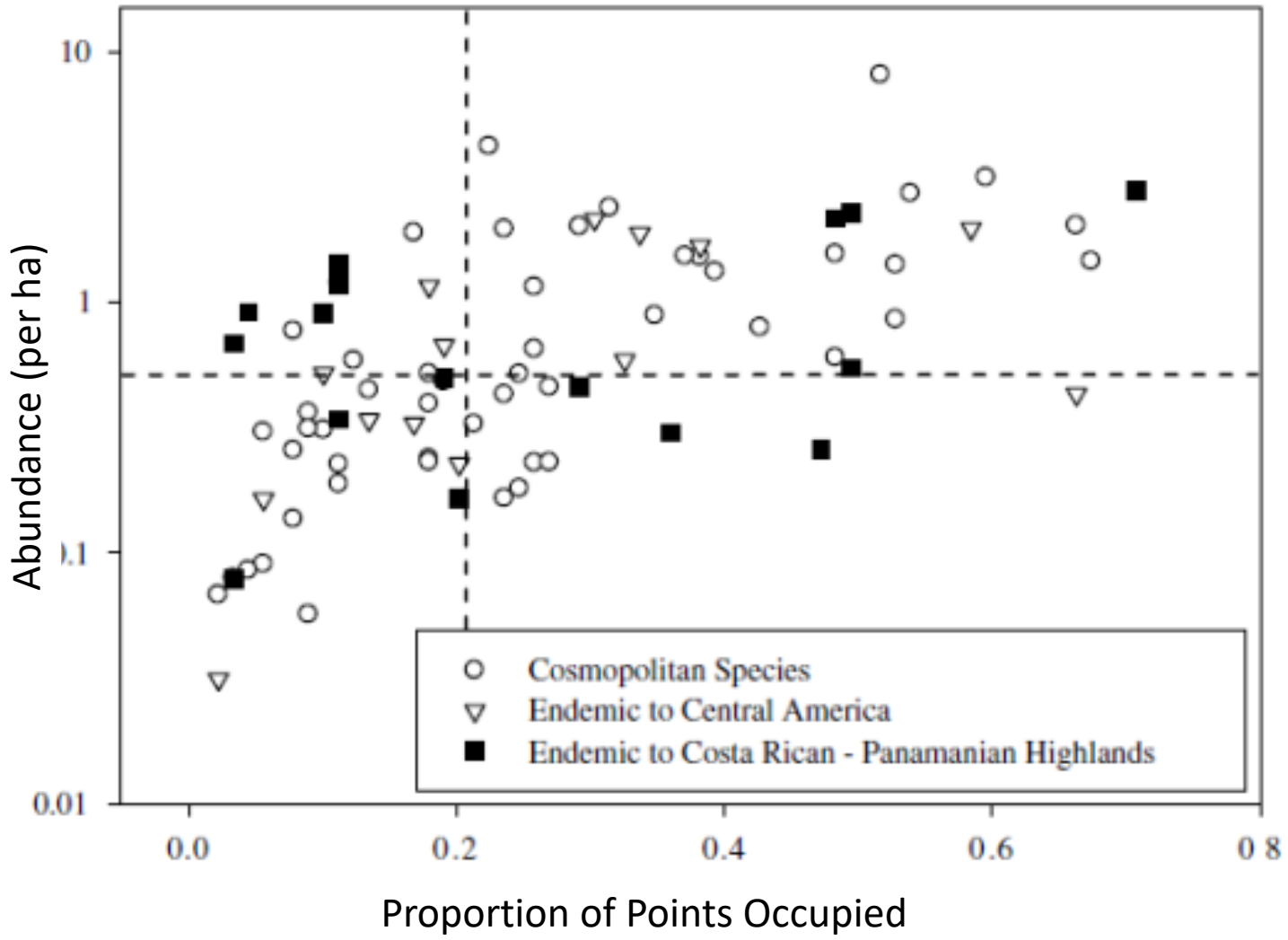


Species with restricted geographical ranges occur in fewer elevational zones



Jankowski & Rabenold 2007, *Biological Conservation*

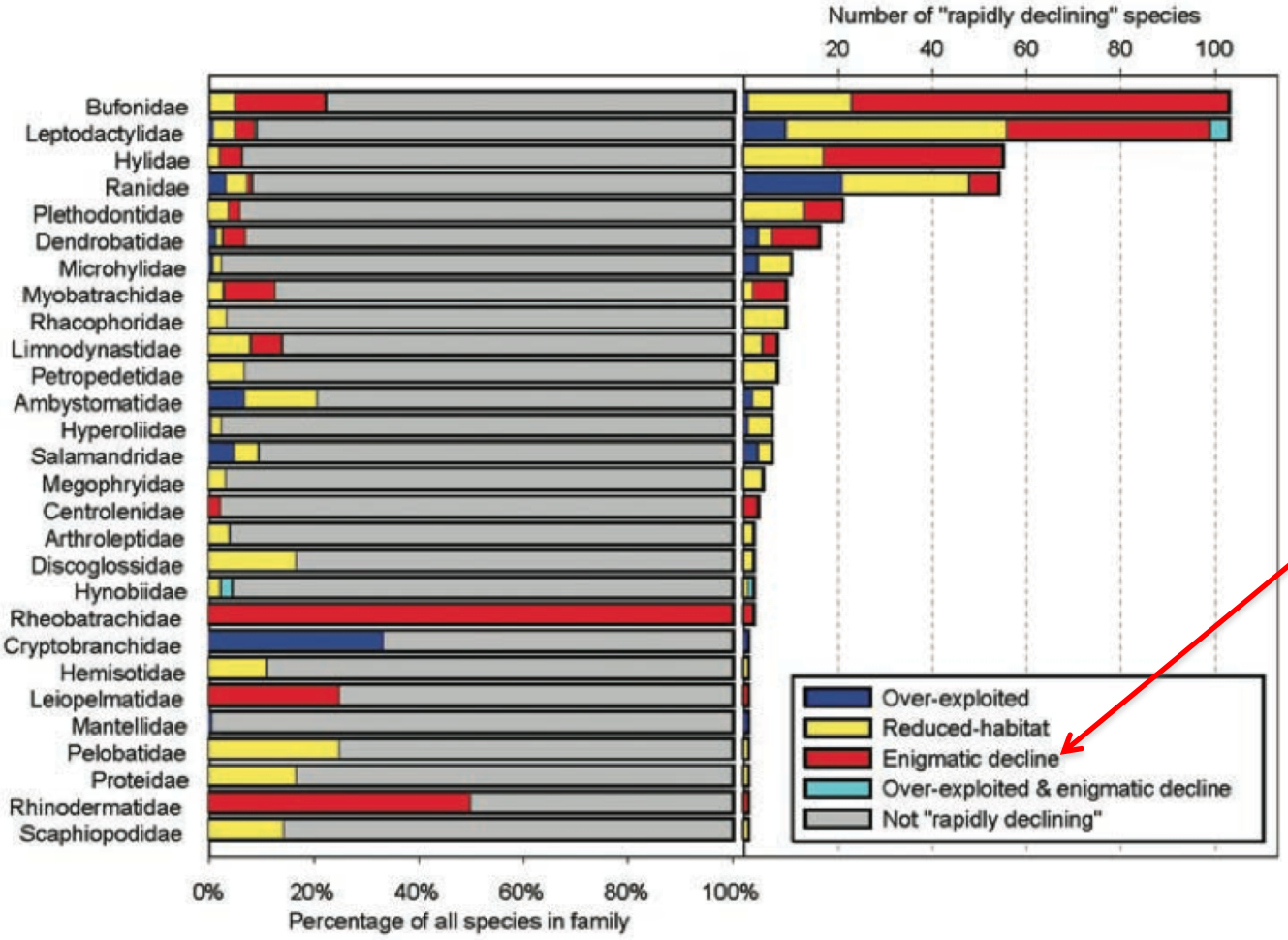
Species with narrower ecological distributions also tend to be numerically rare within their range



Jankowski & Rabenold 2007, *Biological Conservation*

The Golden toad and the global amphibian crisis

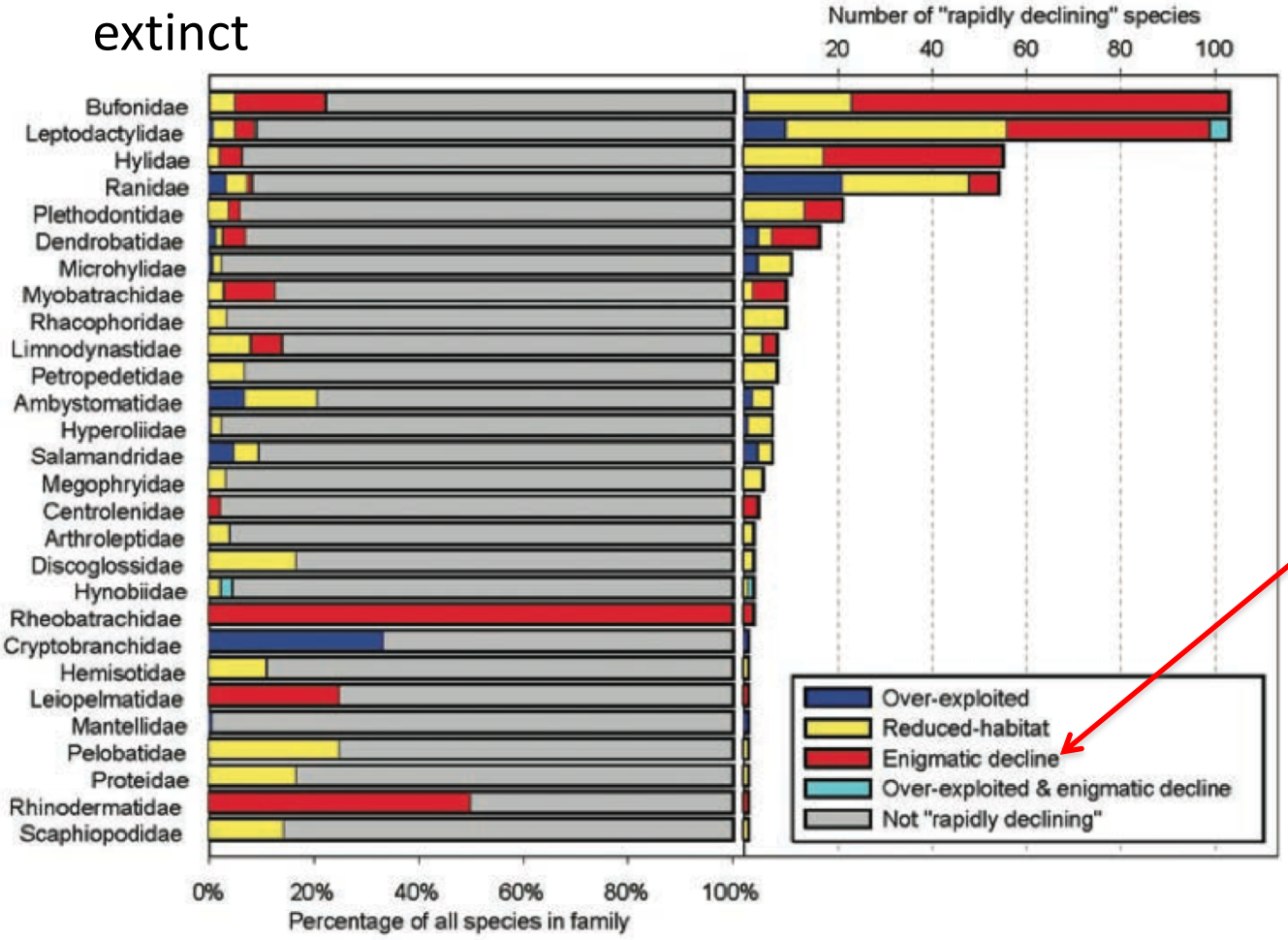
Extinction of the once super-abundant golden toad species, along with multiple other amphibian species in Monteverde, occurred over only ~3 years



Species showing dramatic declines even where suitable habitat remains, for reasons not fully explained.

The Golden toad and the global amphibian crisis

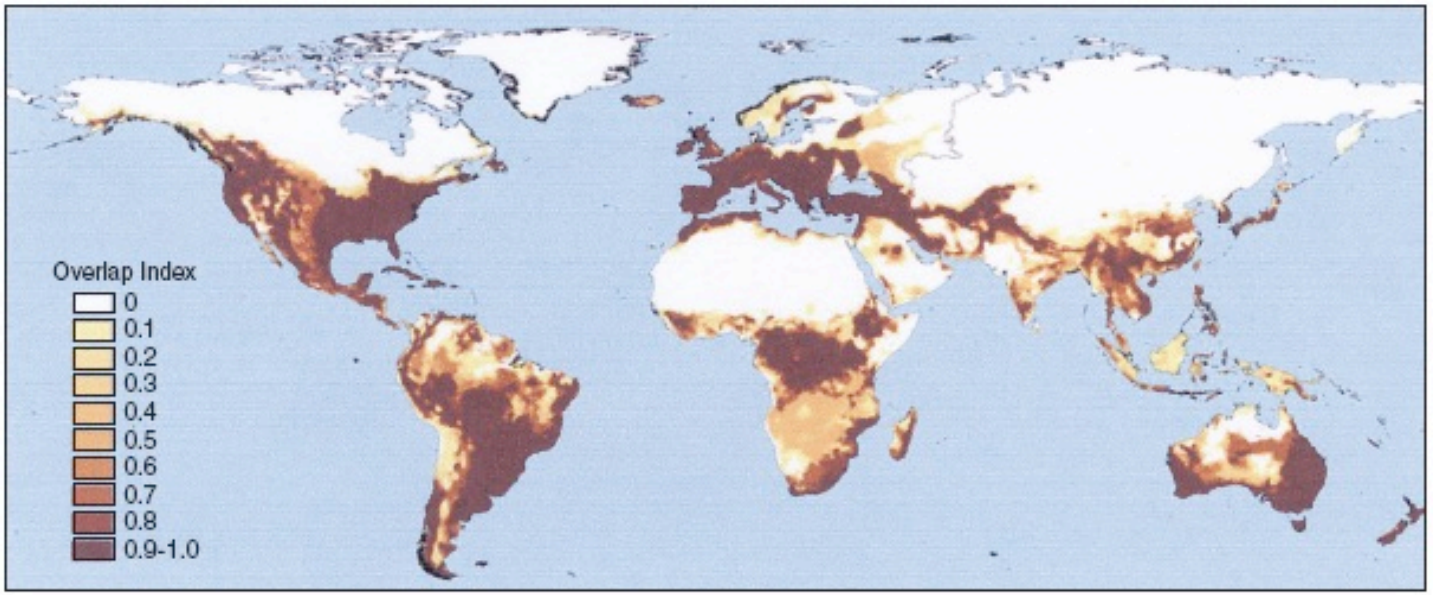
Within a few decades, there has been a 43% decline of amphibian species globally, 32.5% of which are threatened, 34 species extinct, 88 species possibly extinct



Species showing dramatic declines even where suitable habitat remains, for reasons not fully explained.

The Golden toad and the global amphibian crisis

The chytrid fungus (*Batachochytrium dendrobatidis*) is now the leading suspect in global amphibian declines – has low host specificity, and can persist outside the host.



Predicted distribution of the chytrid fungus fundamental niche, with darker colors showing more models predicting its presence in an area

Measuring diversity across elevations

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

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)

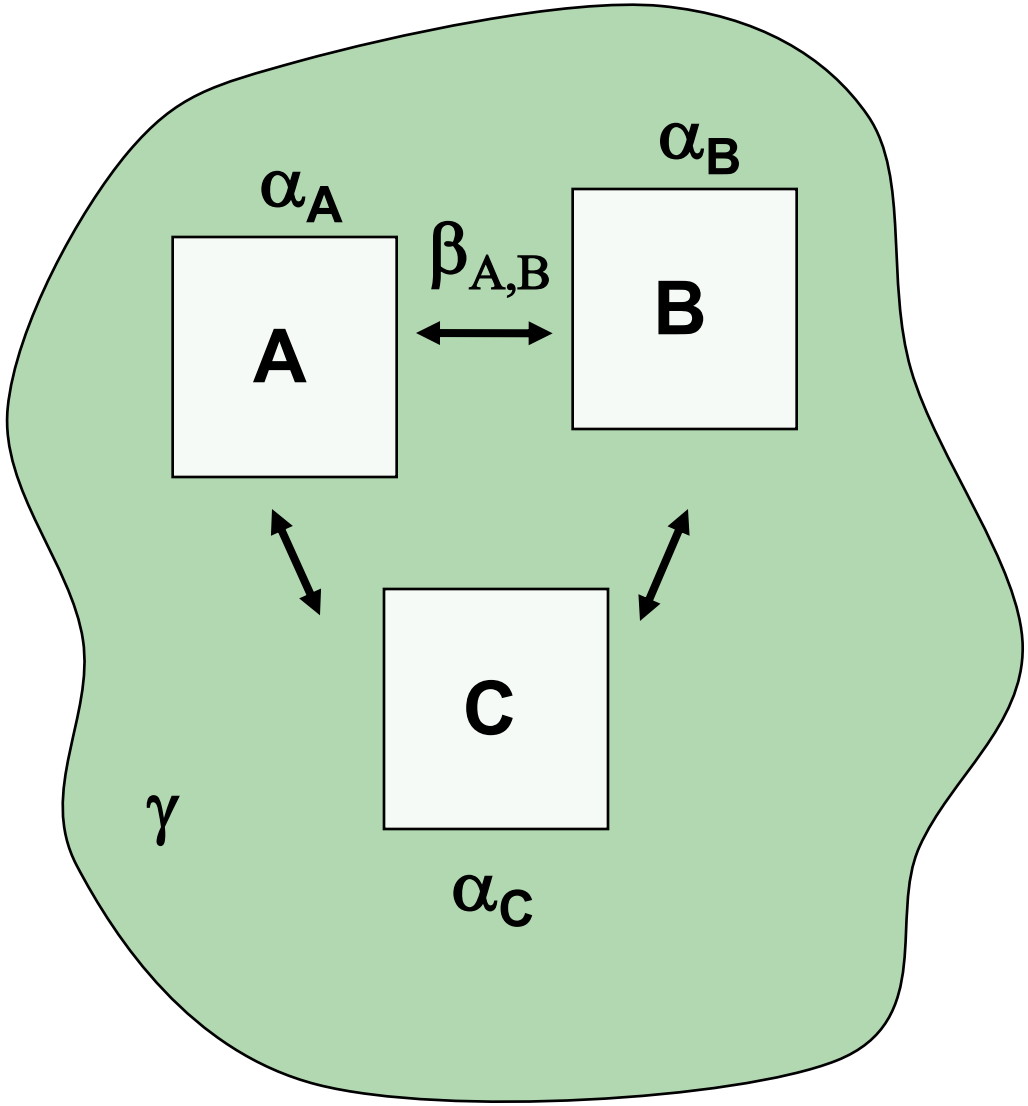
Gamma (γ) diversity: number of species or diversity within a larger region; a function of both alpha and beta diversity.

Measuring diversity across elevations

Gamma (γ) diversity

Alpha (α) diversity

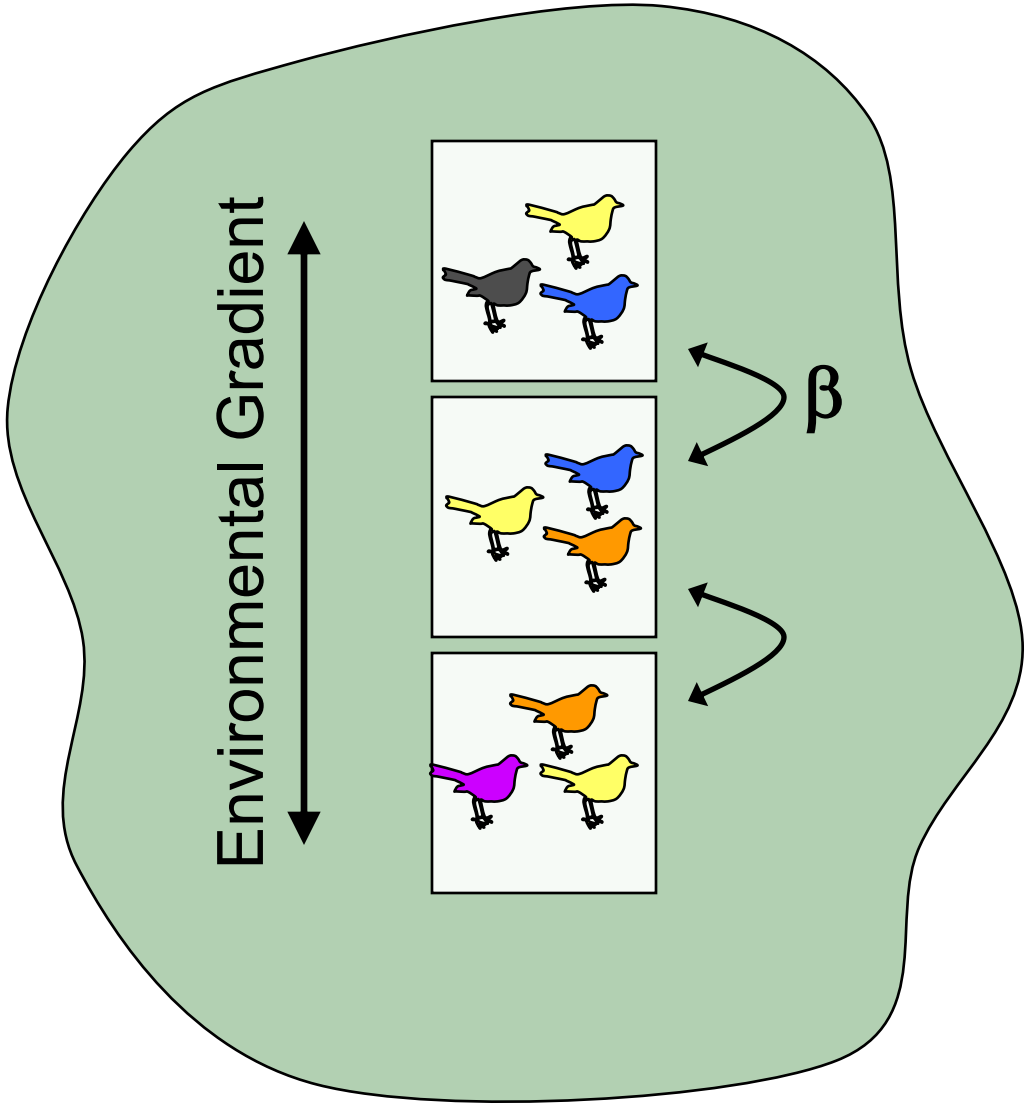
Beta (β) diversity



Measuring diversity across elevations

Species turnover:
beta diversity examined
along axis of variation

How does the gradient
affect composition?



Measuring diversity across elevations

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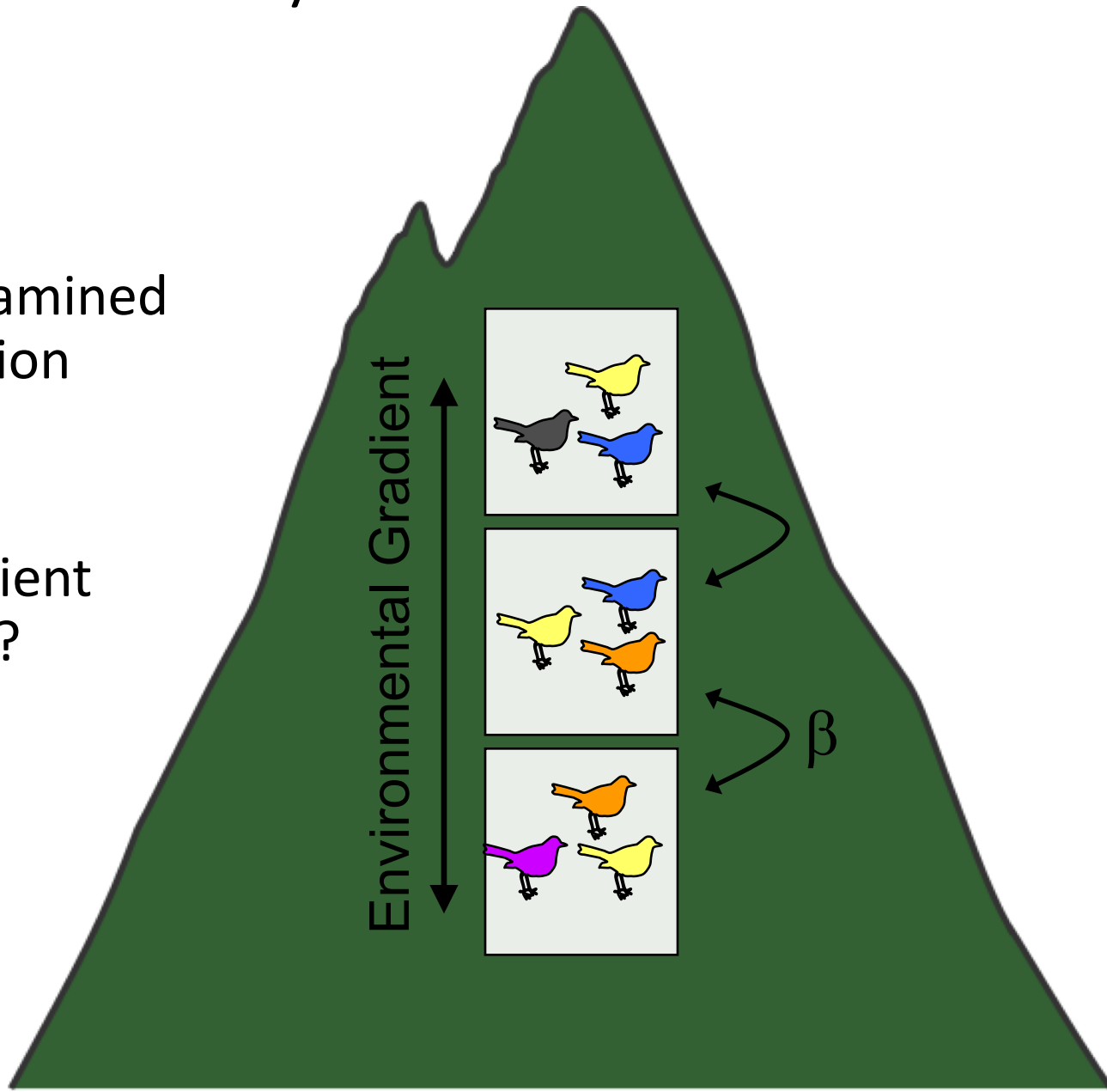
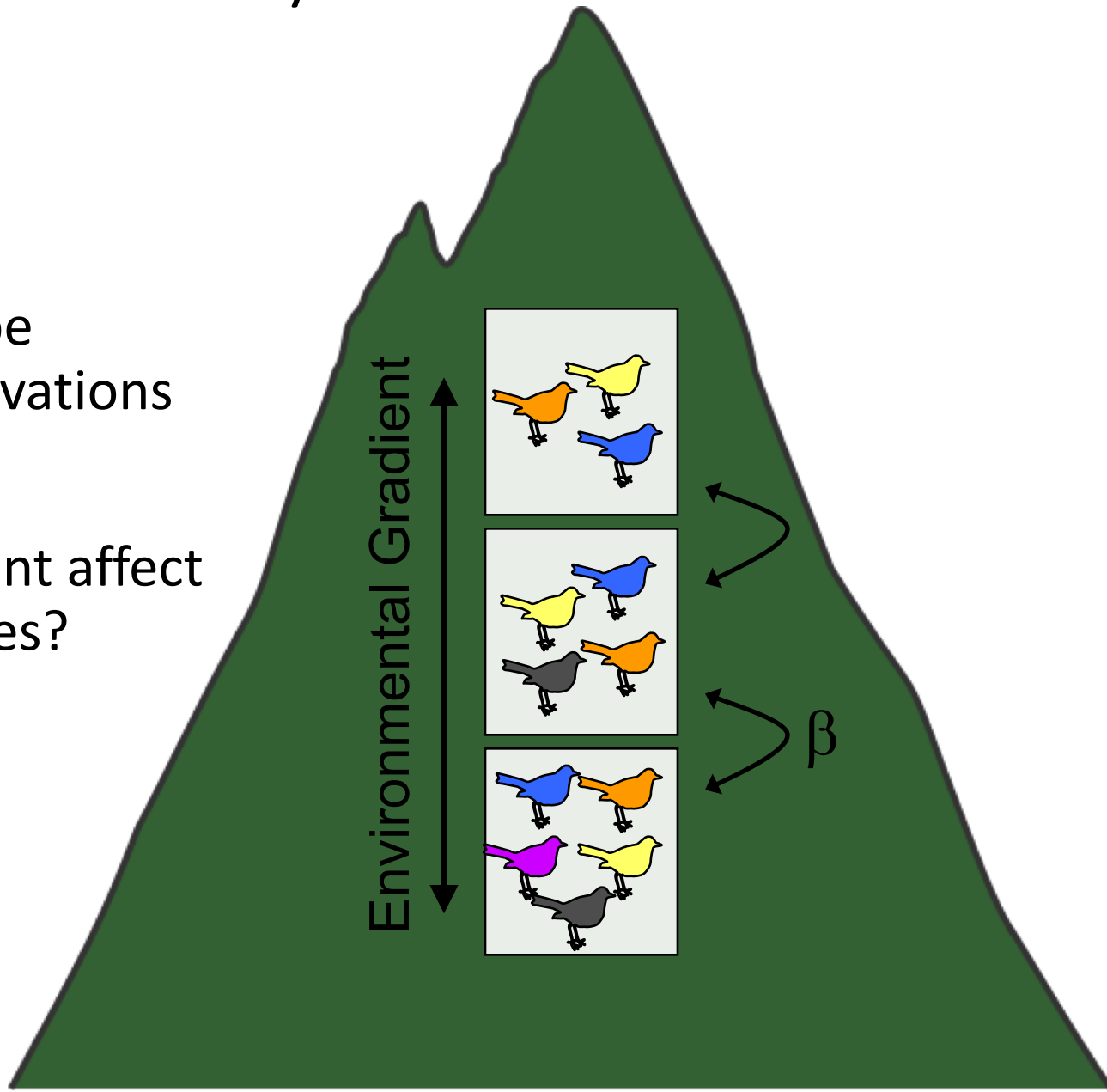


Measuring diversity across elevations

Species richness:

Alpha diversity can be compared across elevations

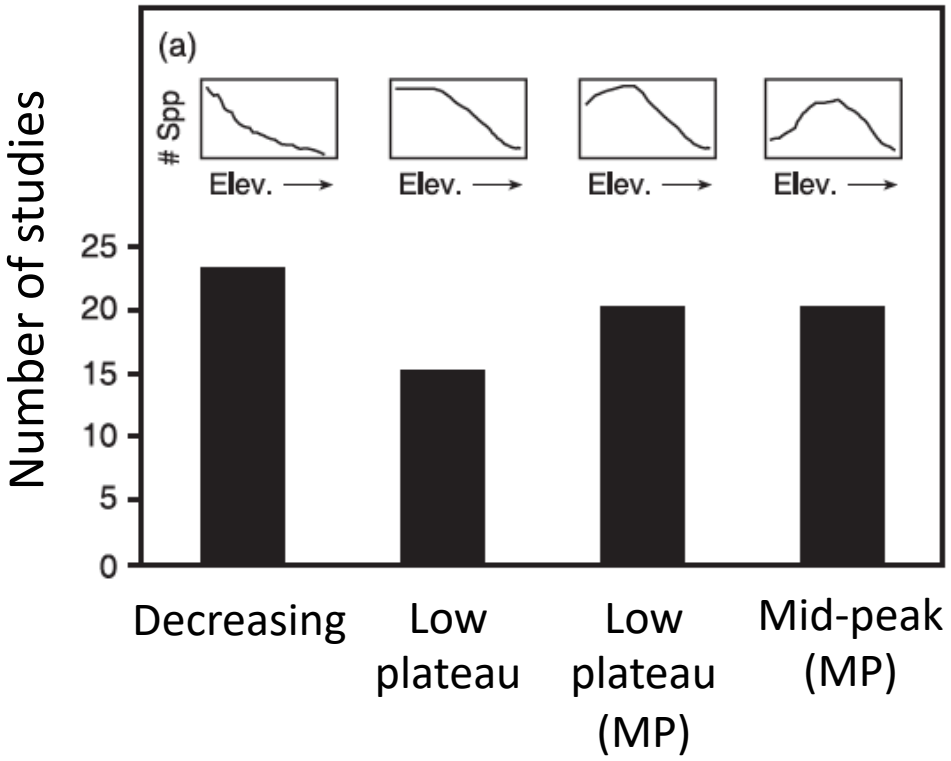
How does the gradient affect the number of species?

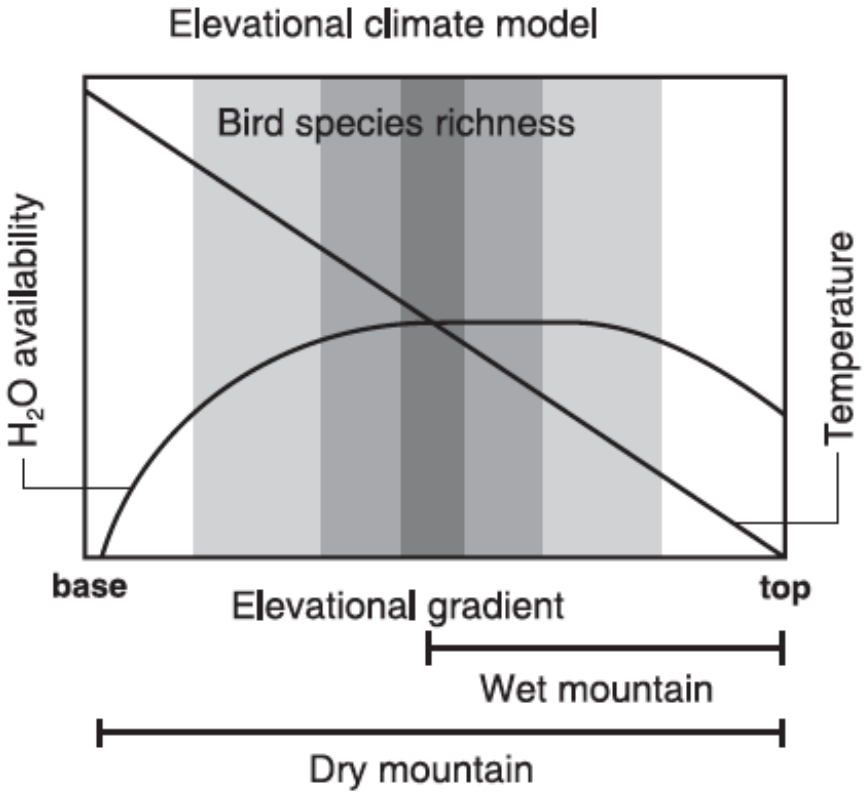


Measuring diversity across elevations

Species richness can show multiple relationships with elevation

McCain (2009) found that the shape of the relationship differs across wet and dry mountainsides





McCain 2009 Global Ecology & Biogeography

Measuring diversity across elevations

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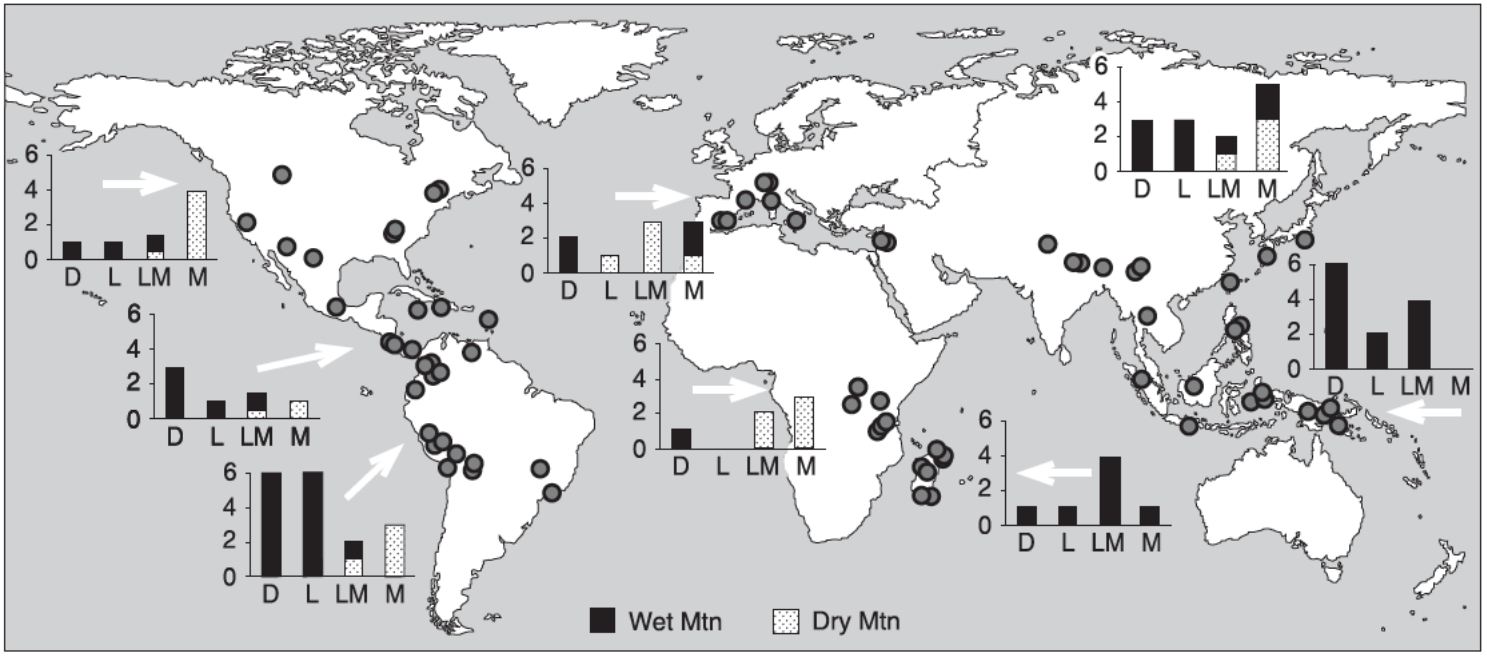
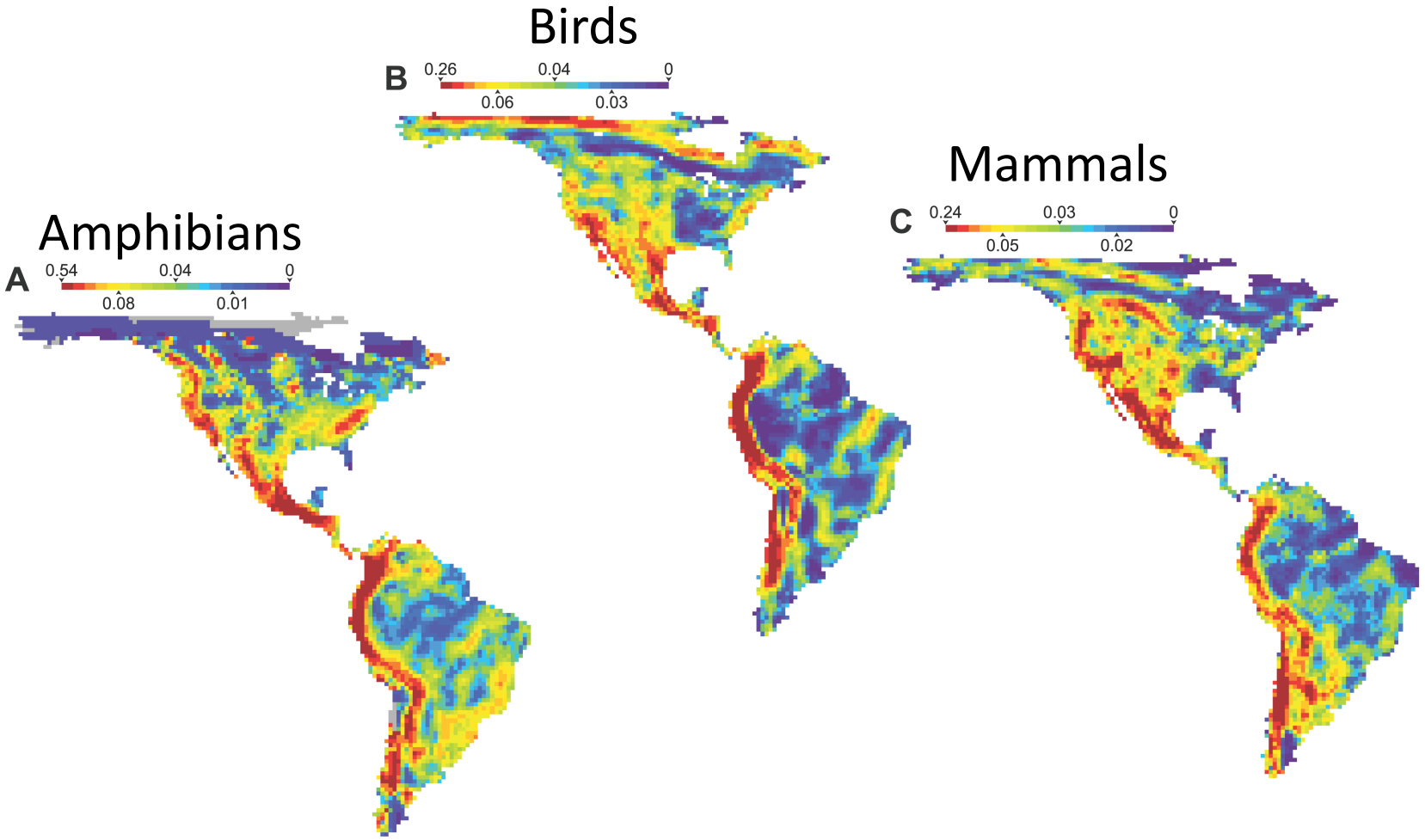


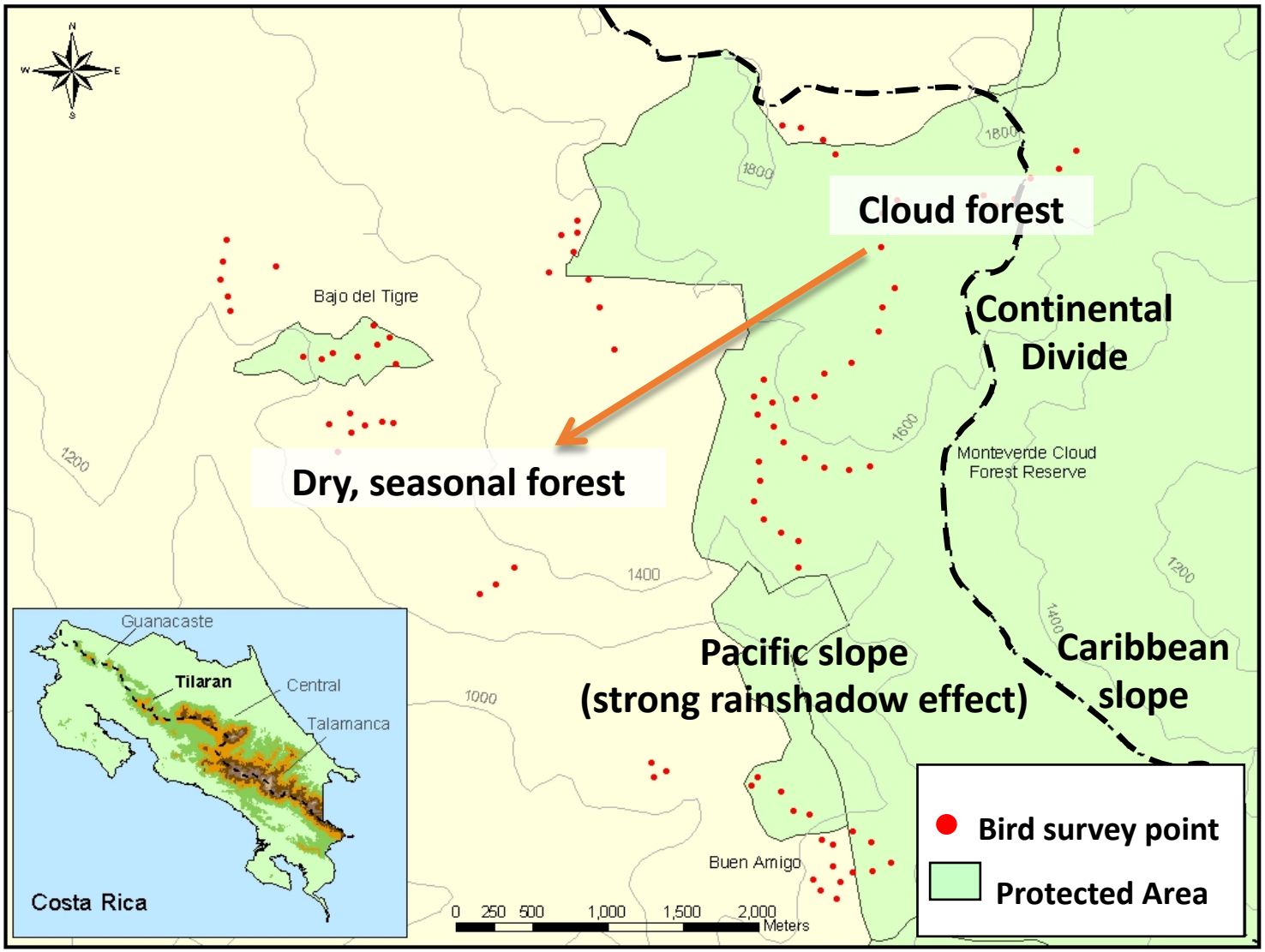
Meta-analysis shows frequency of four main elevational richness patterns across geographic regions and the number represented by wet- and dry-based mountains:
D = decreasing, L = low plateau, LM = low plateau with mid-peak, M = mid-peak

Beta-diversity maps for vertebrates (warm colors ~ high beta-diversity)



McKnight et al. 2007, *PLoS Biology*

Patterns of Species Diversity: Monteverde, Costa Rica



Used surveys to examine change in bird community composition with elevation Monteverde.

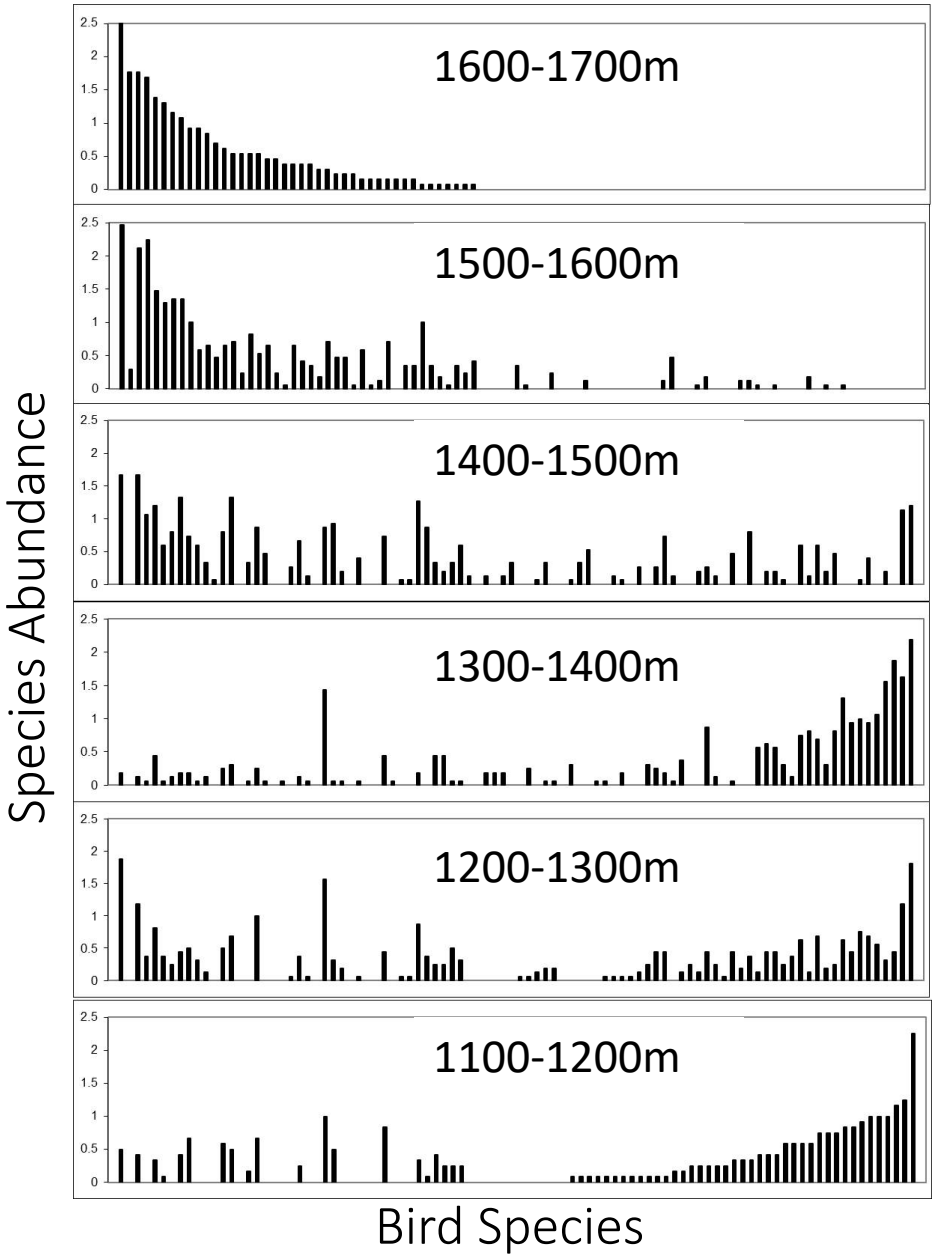
Can look at beta diversity across elevation

Tilarán Mountains, Costa Rica: 1100-1800m

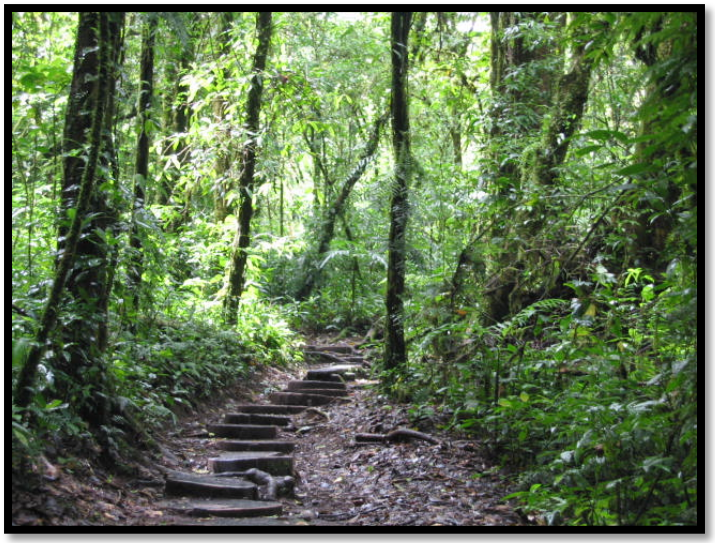
Predicting patterns in species turnover

In this mountain range, cloud moisture is determined by how far sites are from the continental divide

Patterns of Species Diversity: Monteverde, Costa Rica



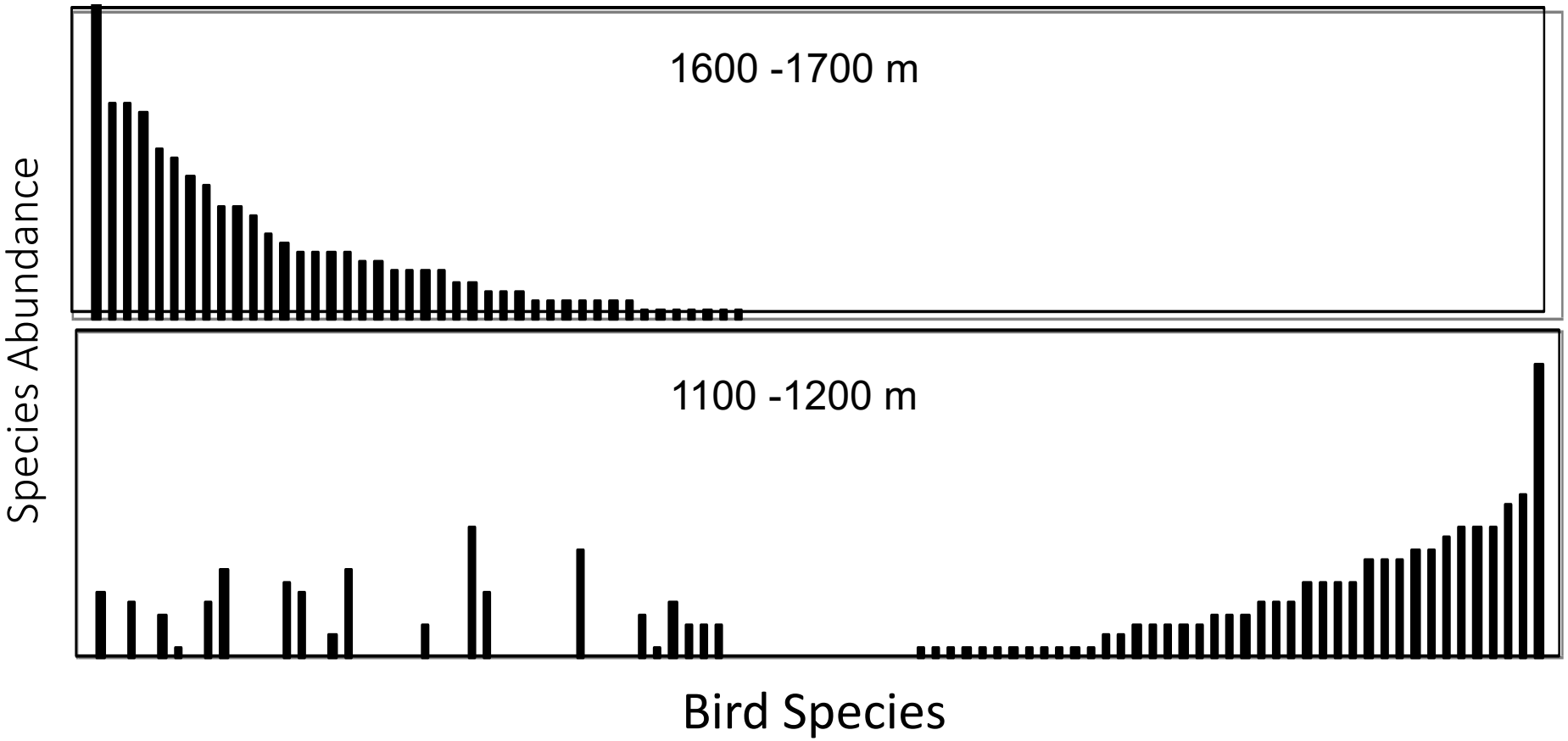
Visualizing beta diversity across elevational zones in Costa Rica



(Jankowski *et al.* 2009)

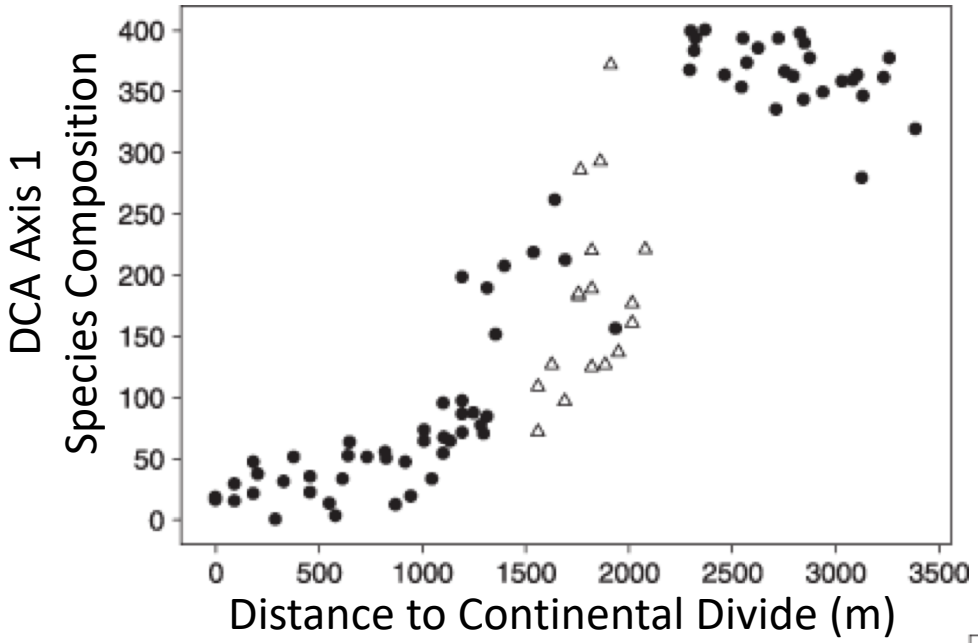
Patterns of Species Diversity: Monteverde, Costa Rica

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

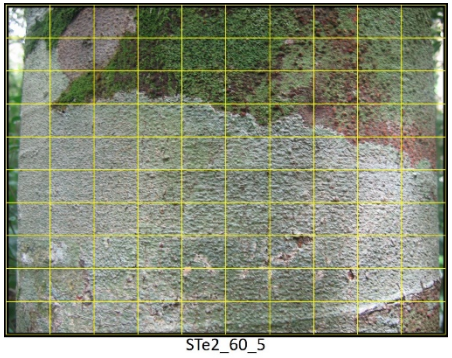


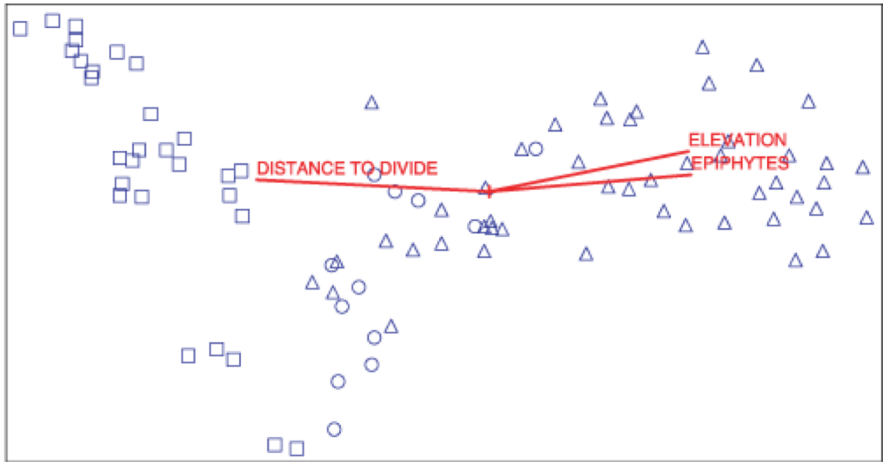
Jankowski et al. 2009*, J. Anim. Ecol.*

Changes in species composition are largely explained by the moisture gradient, and its impacts on vegetation



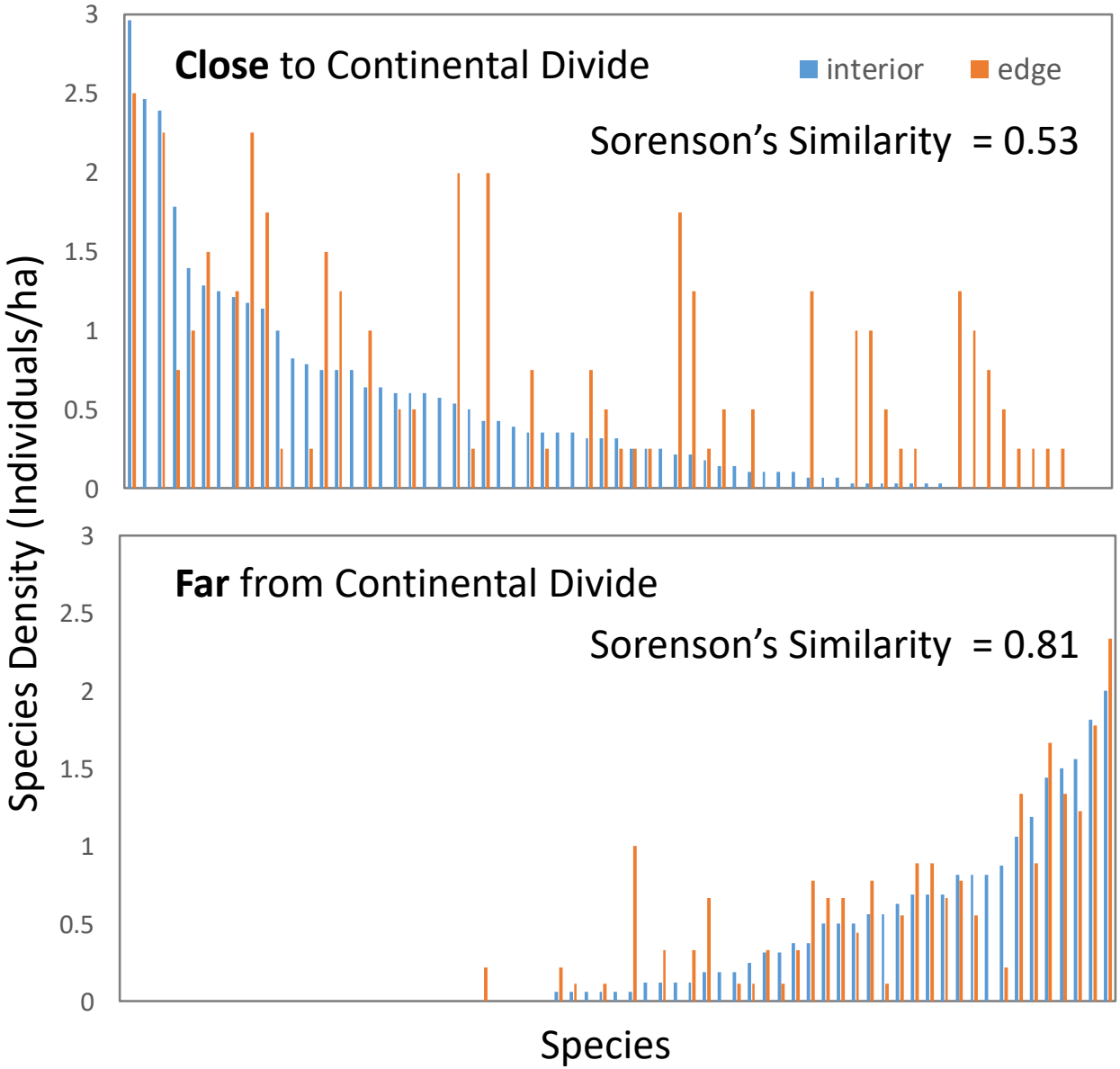
Epiphytes on tree trunks





Jankowski et al. 2009 *Journal of Animal Ecology*

Community differs between forest interior and edge



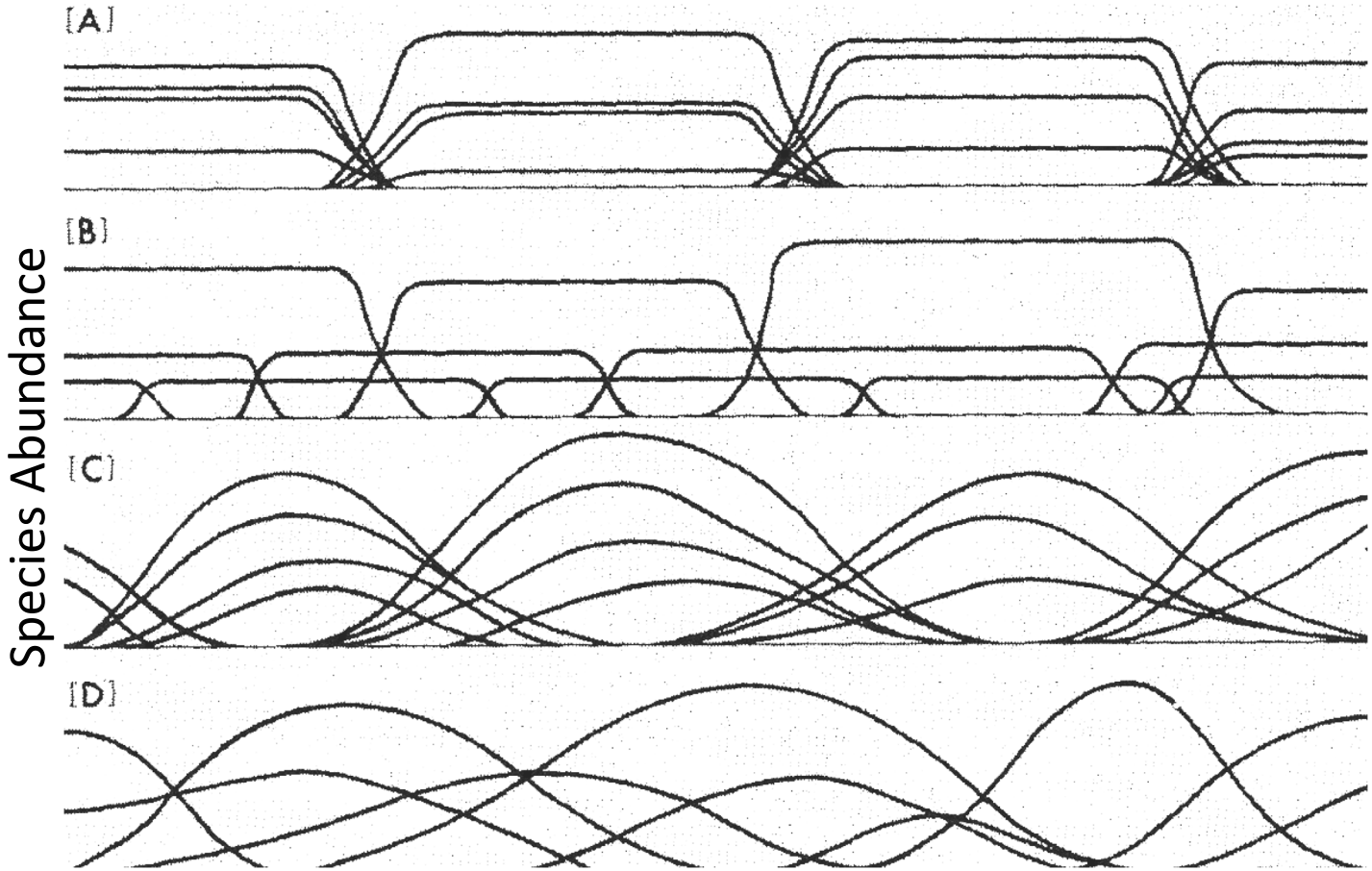
Cloud forest interior community differs greatly from dry edge habitat

In dry forest, communities differ little between interior and edge habitats

Kyle et al. *in Prep*

Patterns of species turnover: Are species distributions interdependent?

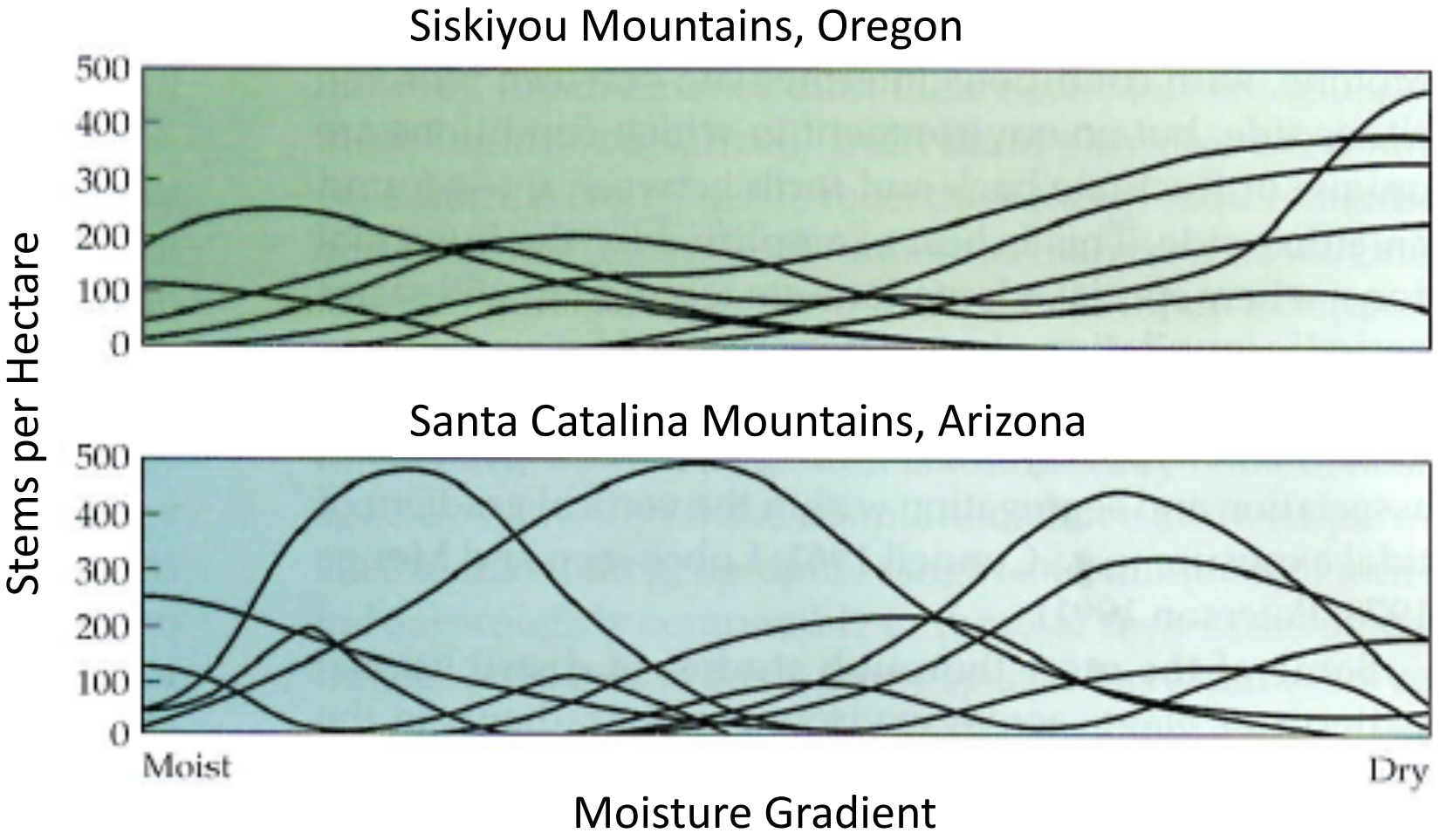
Whittaker (1975) combines individualistic and community-unit hypotheses including biotic processes to show alternative “idealized” community defintions



(From Whittaker 1975)

Patterns of species turnover: Are species distributions interdependent?

Whittaker tested hypothesized distribution patterns with trees species in two temperate mountain ranges (still hasn't been done in the tropics?)

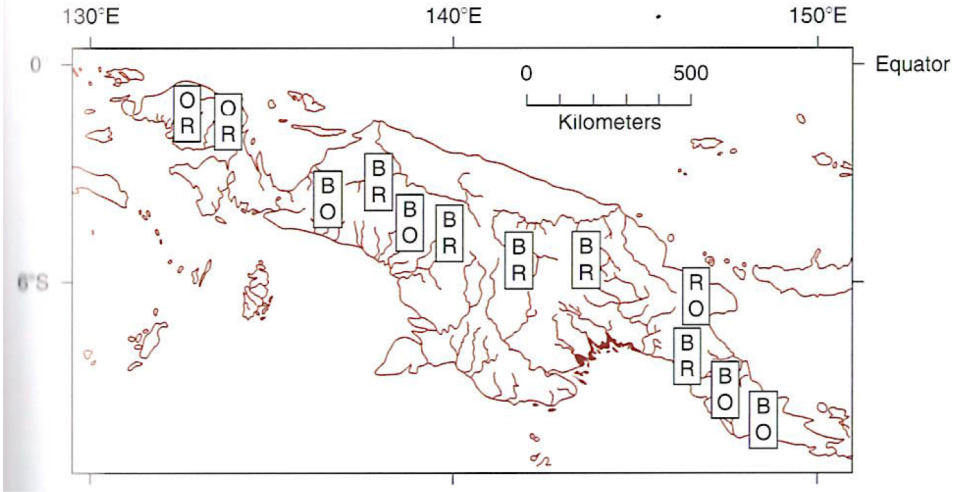


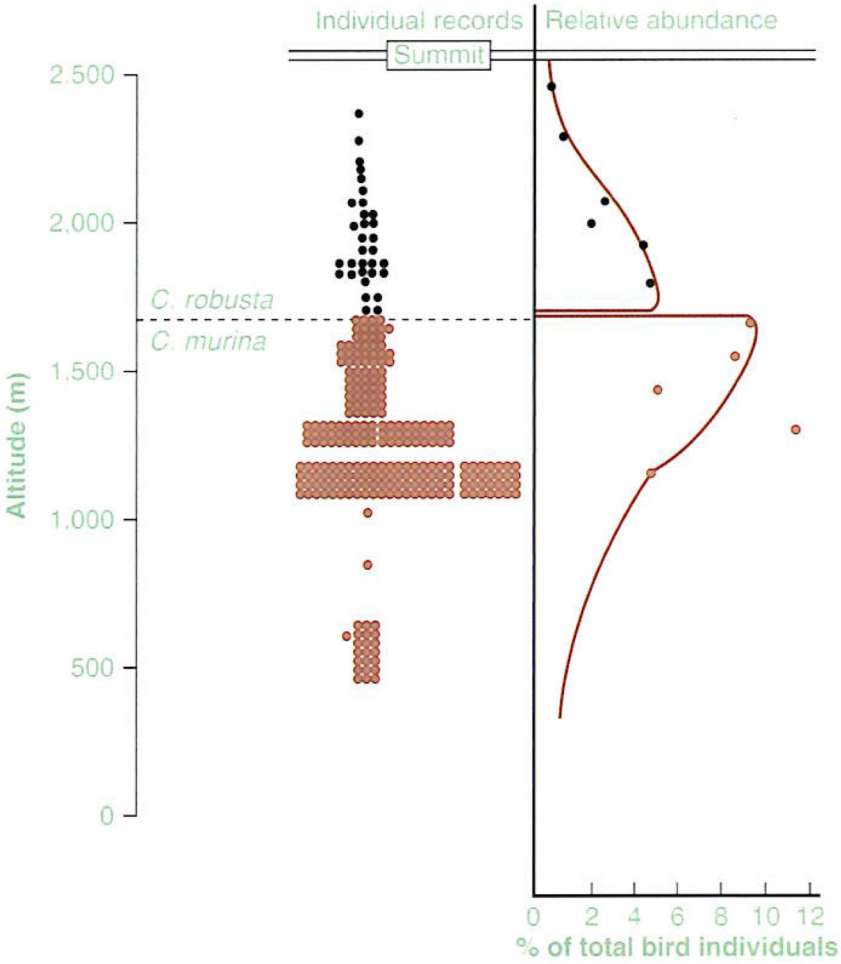
After Whittaker 1967, Lomolino et al. 2017

Patterns of species turnover: Are species distributions interdependent?

Other communities show distinct patterns where species distributions are certainly not independent: forbidden combinations of species and species replacements with elevation

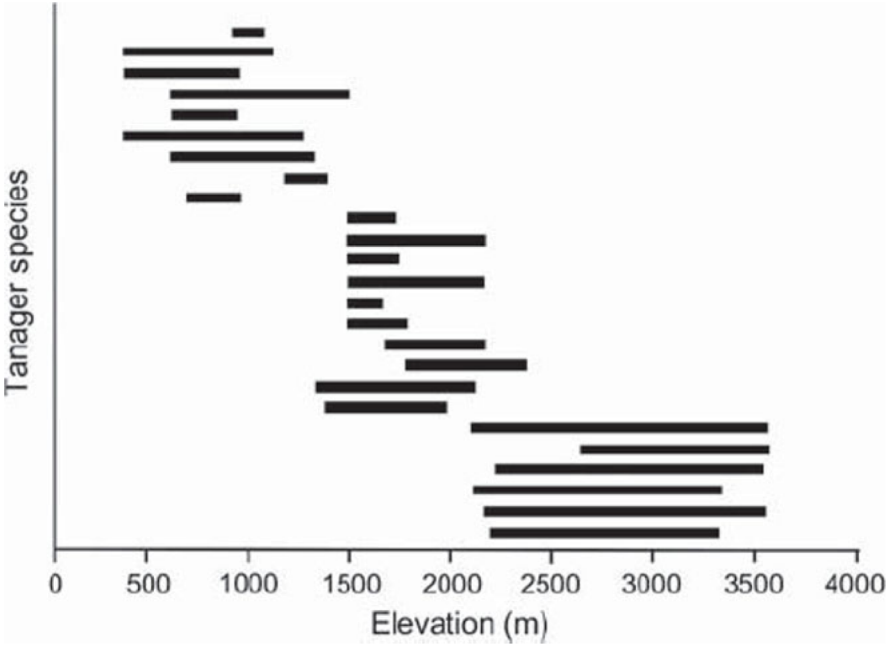
Jared Diamond (1975) demonstrated checkerboard patterns (forbidden combinations of species) in honeyeaters and warblers in New Guinea





Patterns of species turnover: Are species distributions interdependent?

Other communities show distinct patterns where species distributions are certainly not independent: species associated within mixed species flocks show high overlap in distributions and strong zonation across elevations



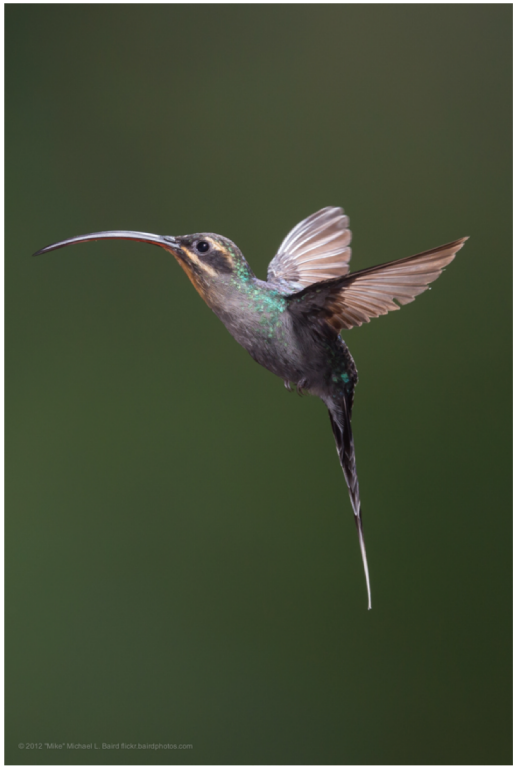
Note: high elevation tanagers also belong to a monophyletic clade

Data analyzed from Terborgh and Weske (1975) Ecology

What is the phylogenetic structure in diverse taxonomic groups along mountainsides?



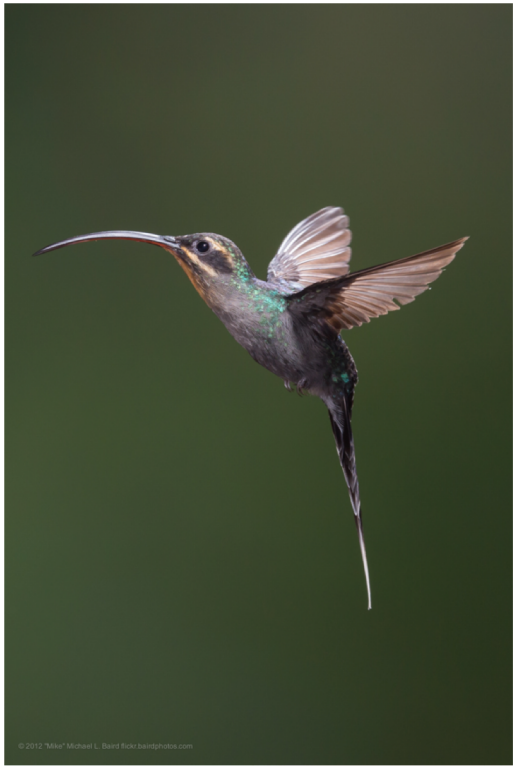



Most hummingbirds are found in tropical montane forest

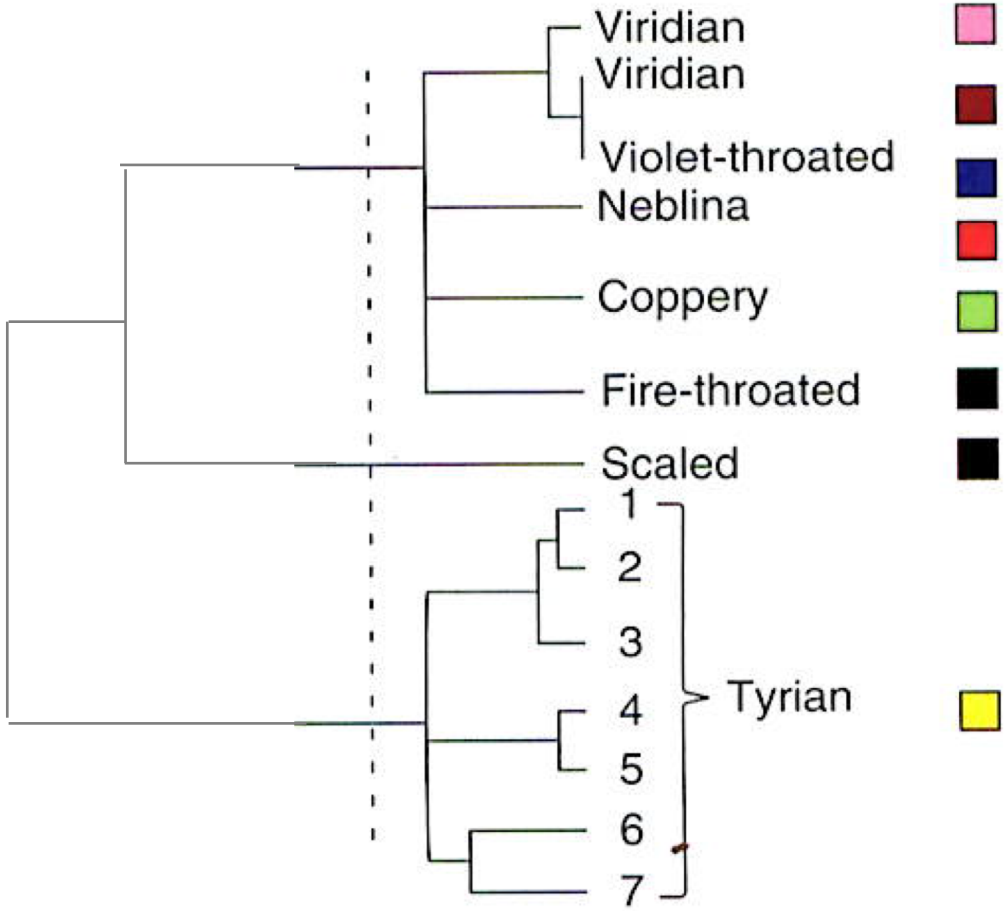


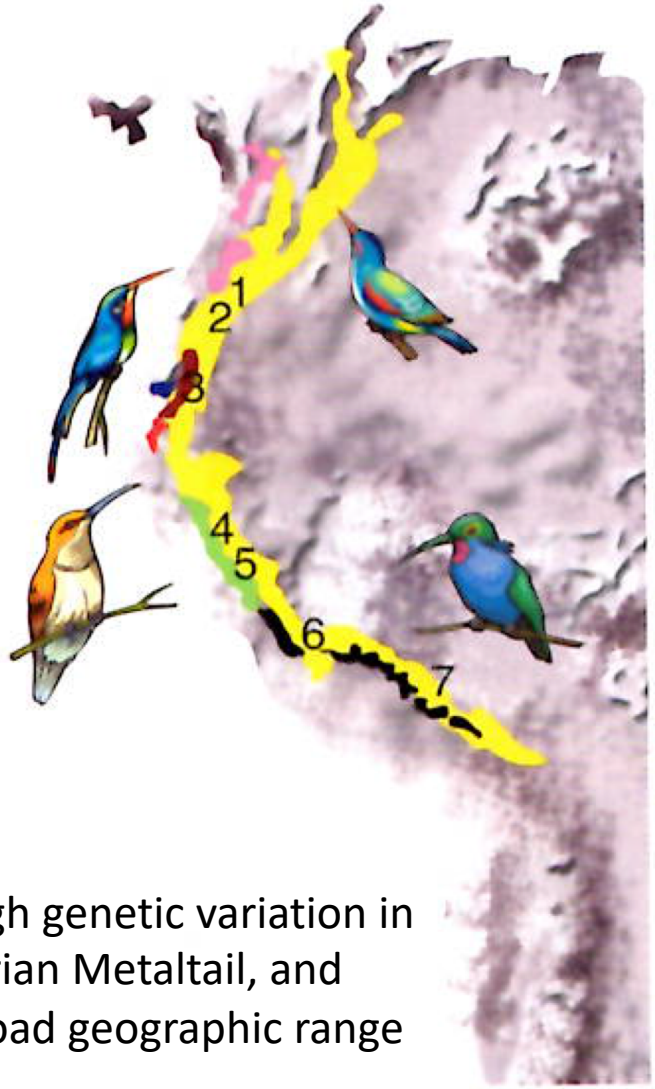



Hummingbirds show phylogenetic structure in communities across elevations

Phylogenetic relationships among Metaltail hummingbirds in the Andes

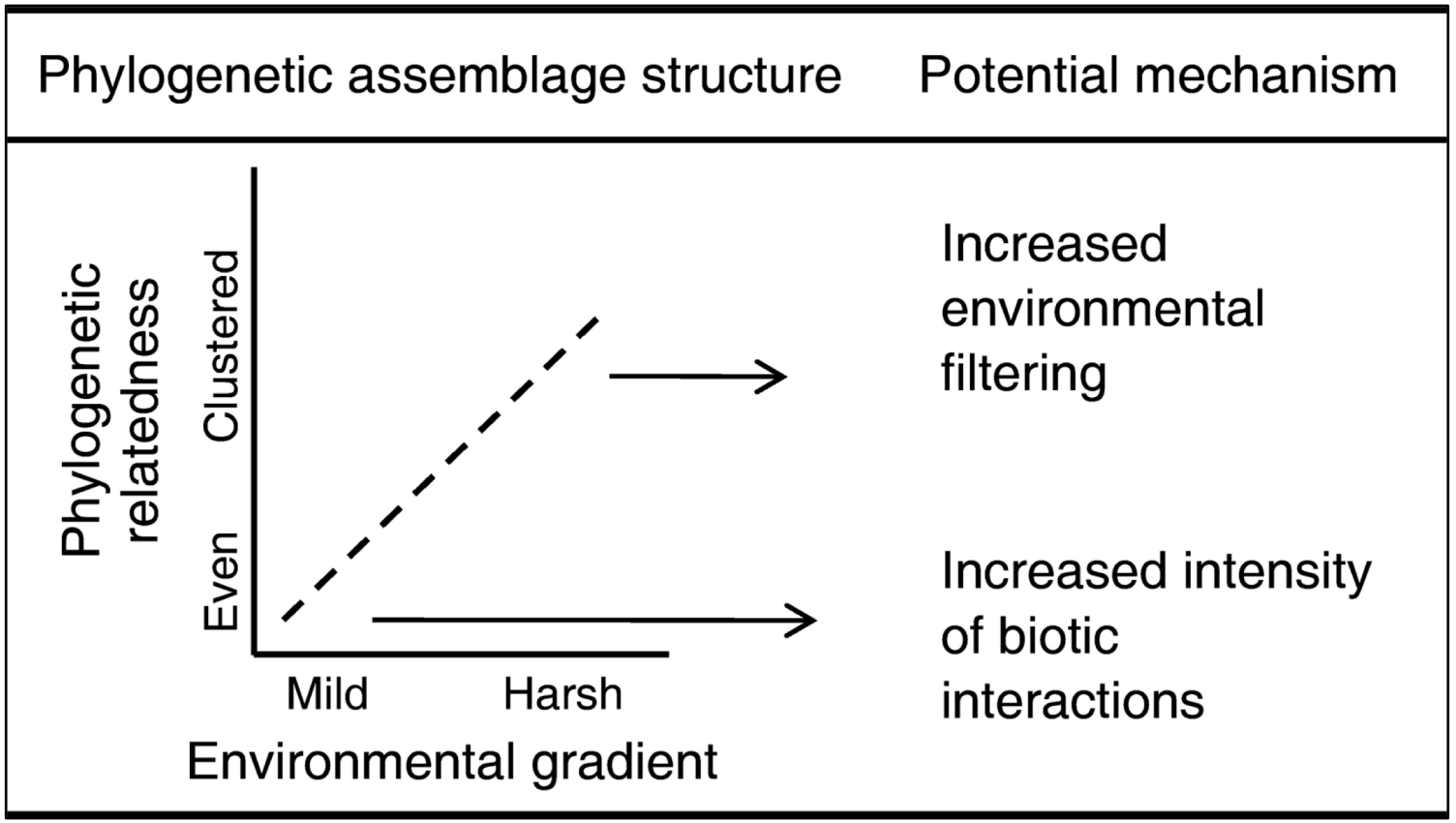




High genetic variation in Tyrian Metaltail, and broad geographic range

Hummingbirds show phylogenetic structure in communities across elevations

Proposed phylogenetic structure of communities:



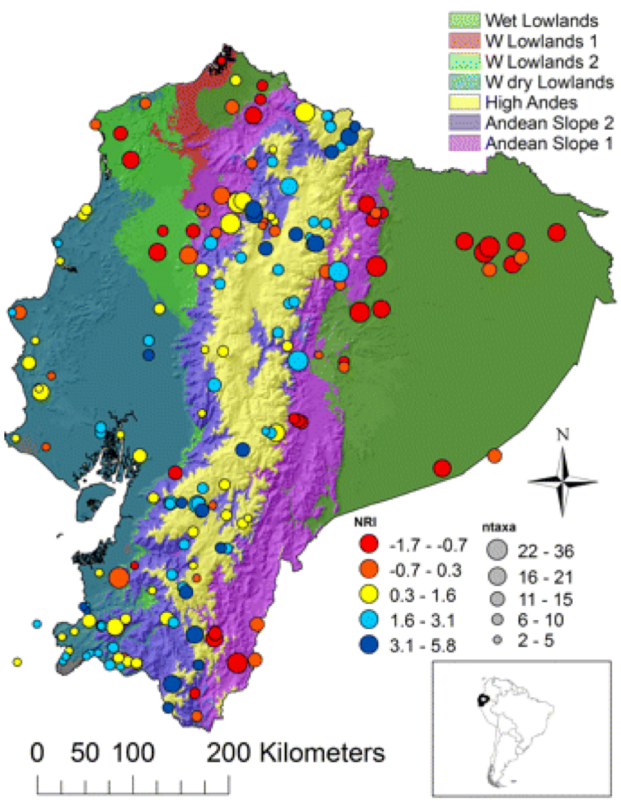
Hummingbirds show phylogenetic structure in communities across elevations

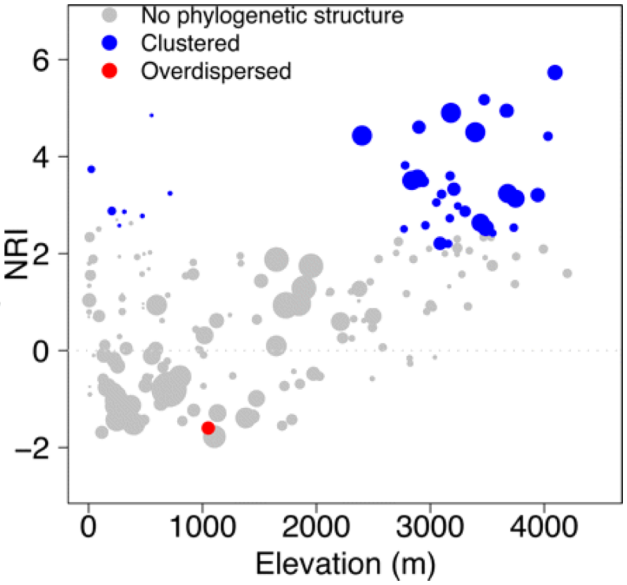
~330 species in the family of hummingbirds

70 species may occur along a single mountainside

High elevation communities were significantly and strongly clustered

Many lowland communities were phylogenetically overdispersed

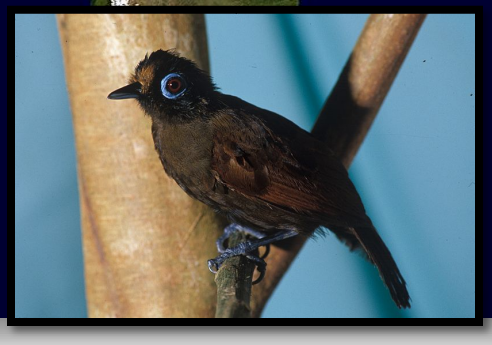




What about the phylogenetic structure of other groups? A case study with Neotropical birds

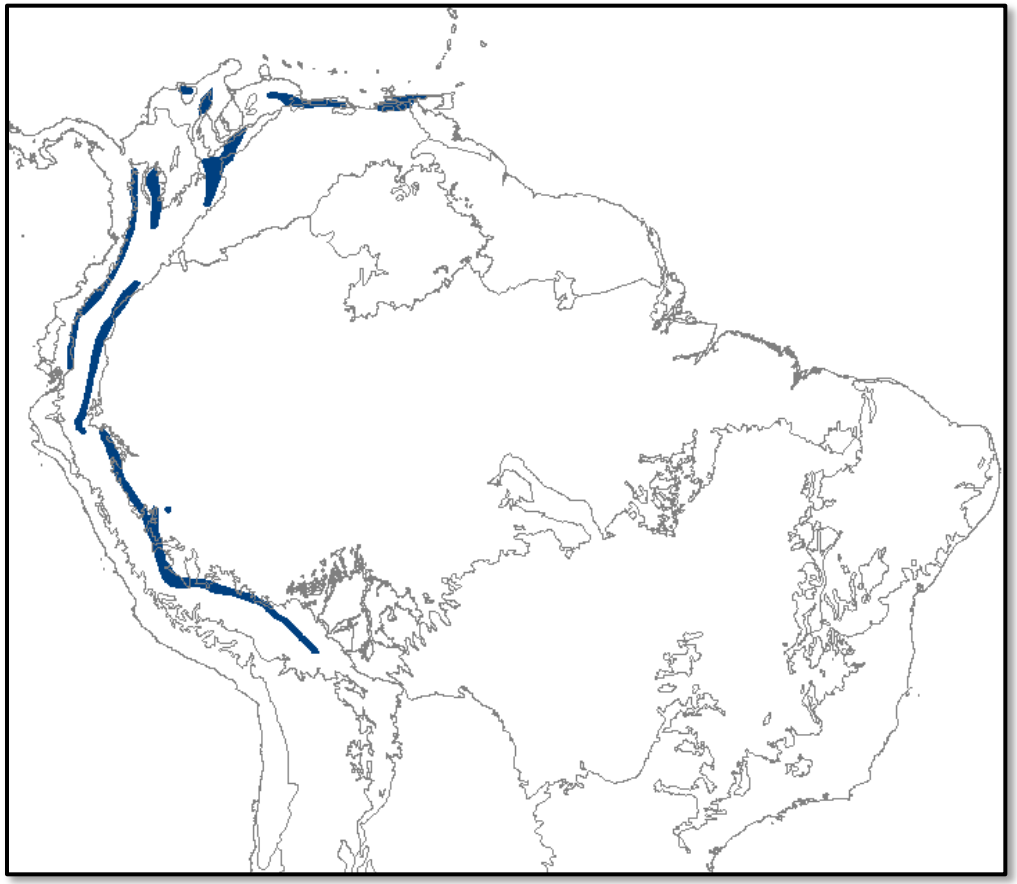
2650 species in tropical Andes and Amazonian lowlands

Represented by diverse families each with >200 species



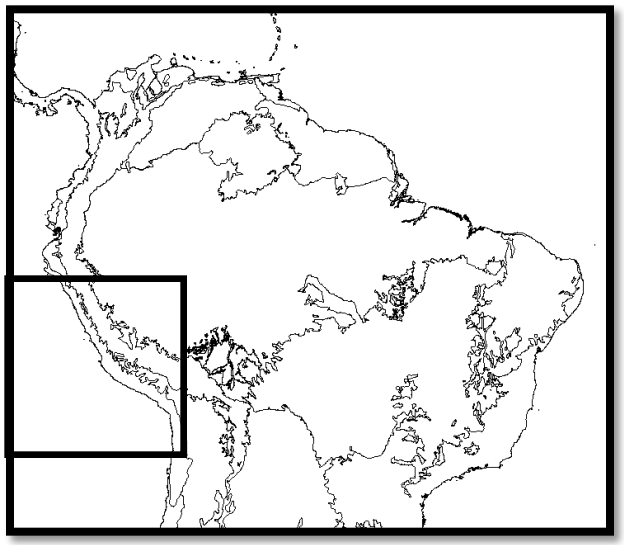
“Shoestring” distributions of montane birds

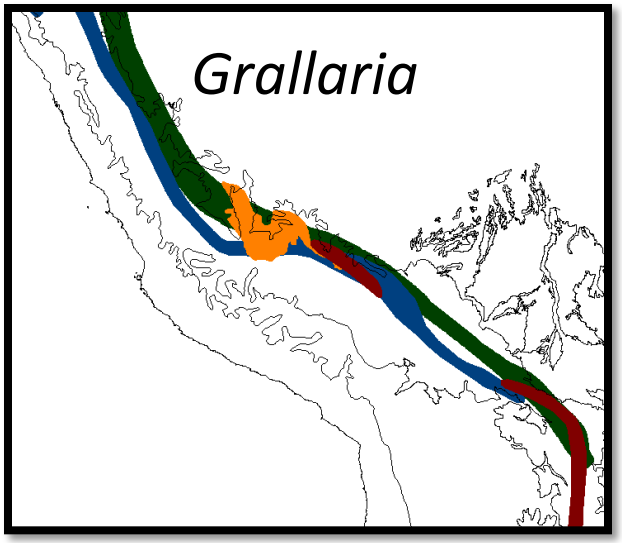
Long-tailed Antbird
Drymophila caudata

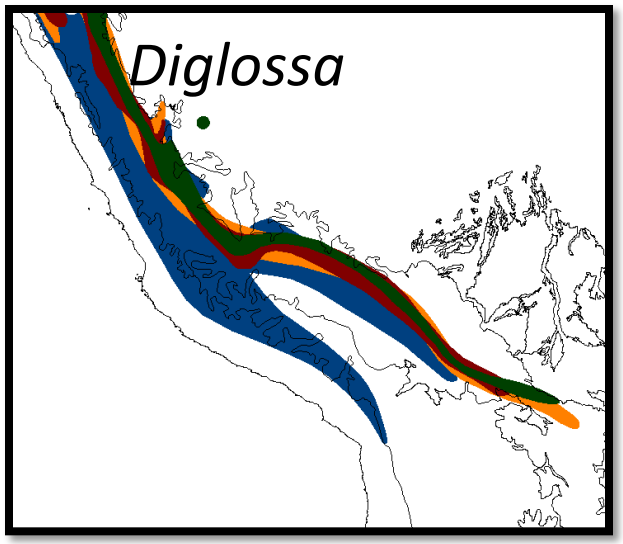


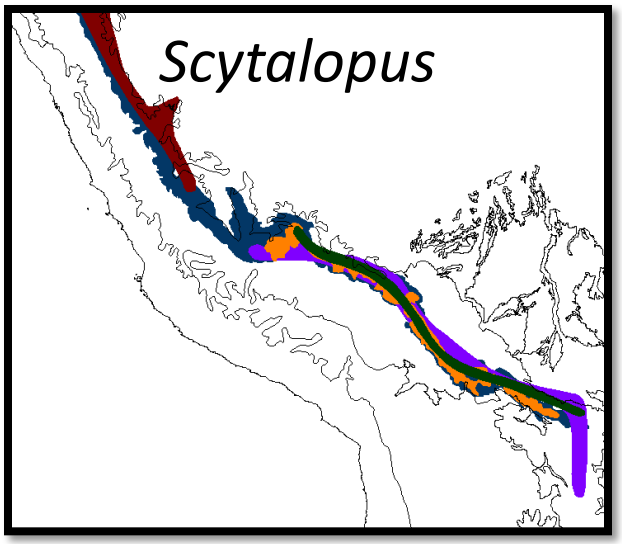
NatureServe InfoNatura Database

Narrow ranges of montane species generate high species turnover (high beta diversity)



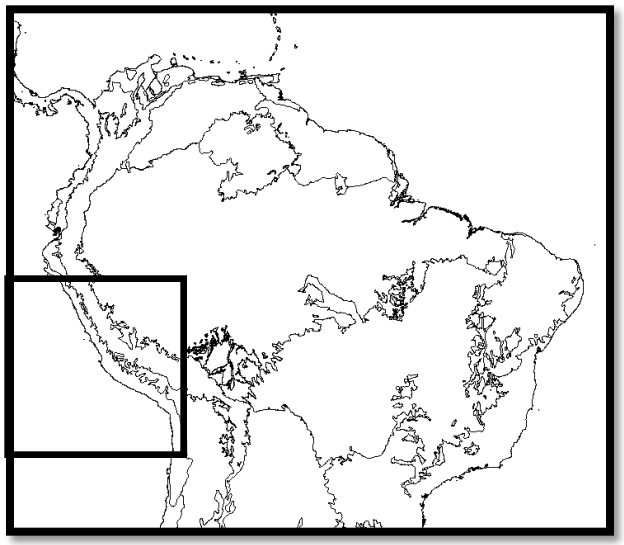


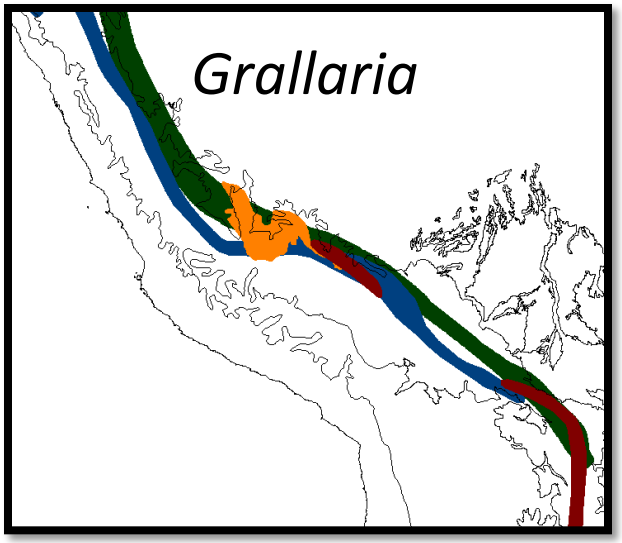


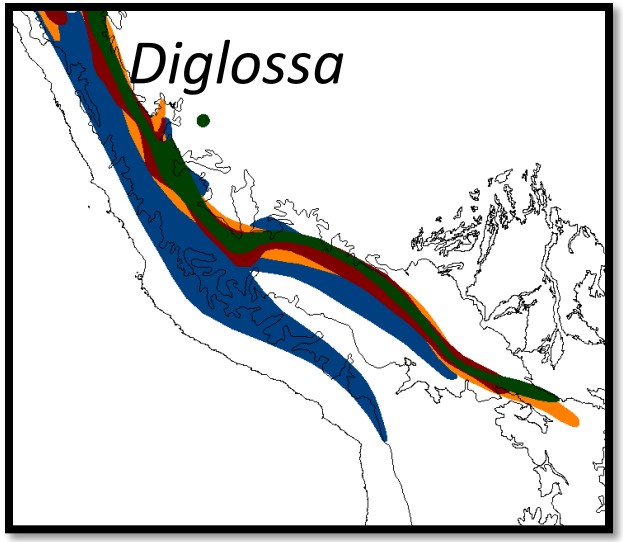


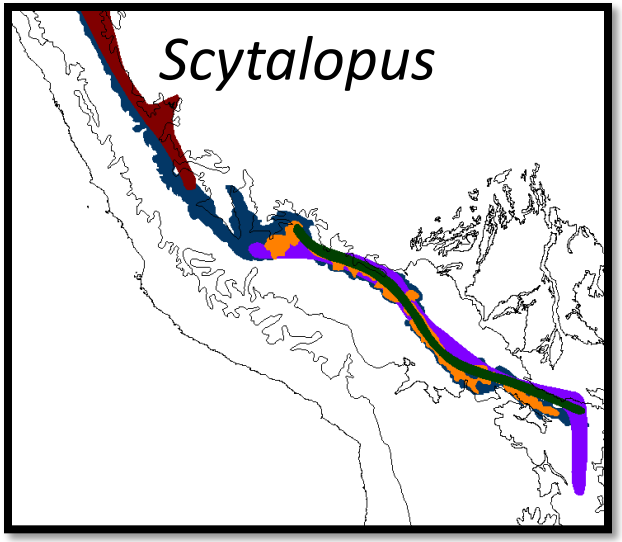
NatureServe InfoNatura Database

Distinct communities are found at different elevations
Do these communities show phylogenetic structure?





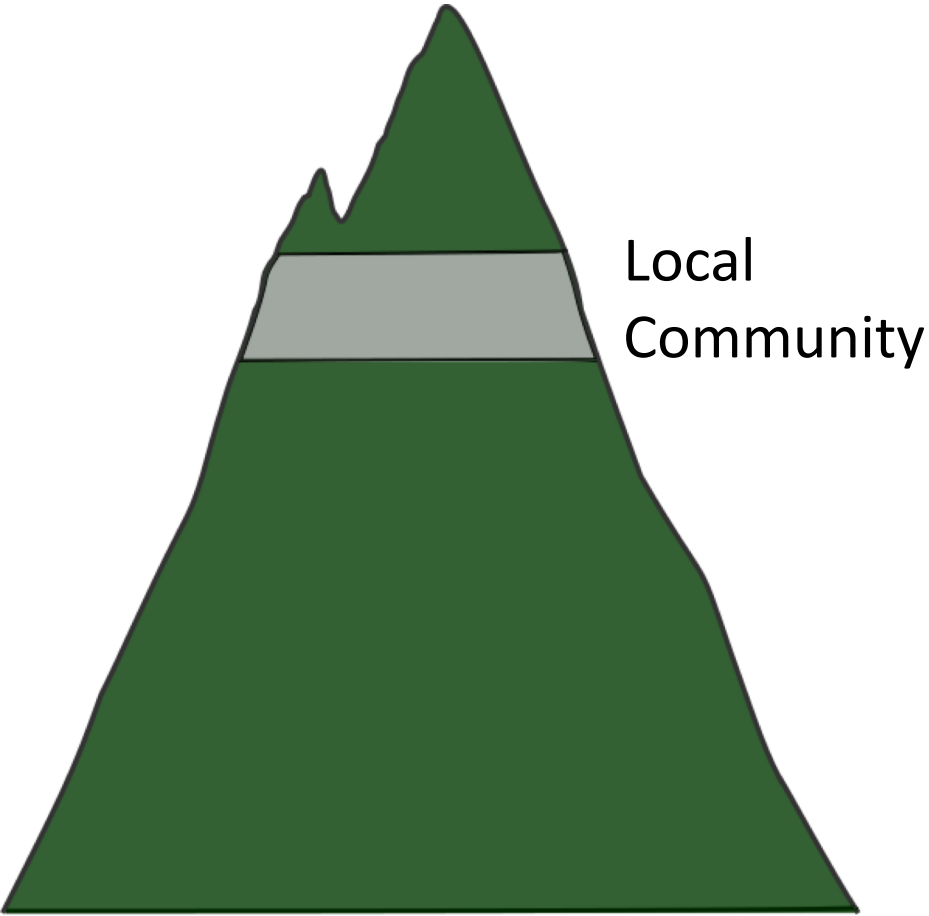




NatureServe InfoNatura Database

Distinct communities are found at different elevations
Do these communities show phylogenetic structure?

Ecological and evolutionary processes regulate community assembly



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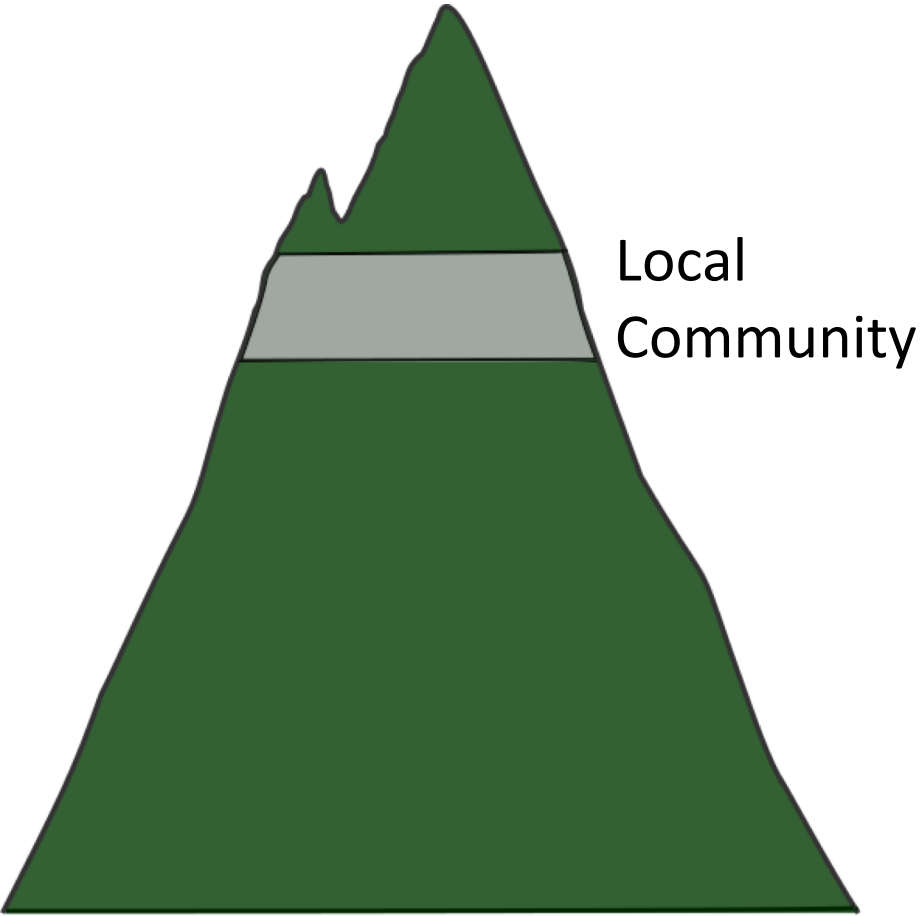


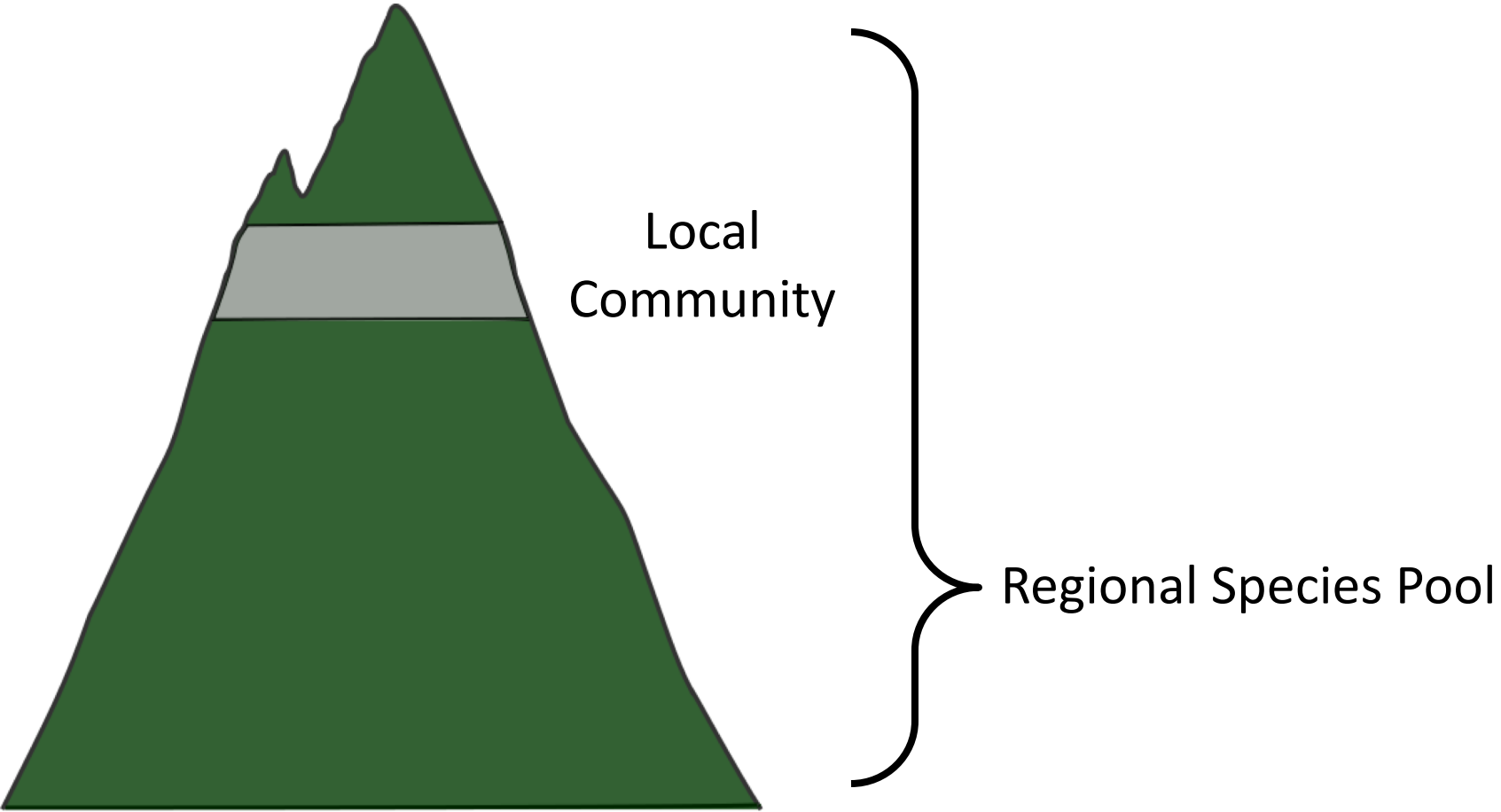
The local community is an area sampled within a larger region

Species in a local area should undergo some process of ecological sorting due to numerous types of interactions

Looking at relationships of co-occurring species can point us towards processes responsible for ecological sorting…

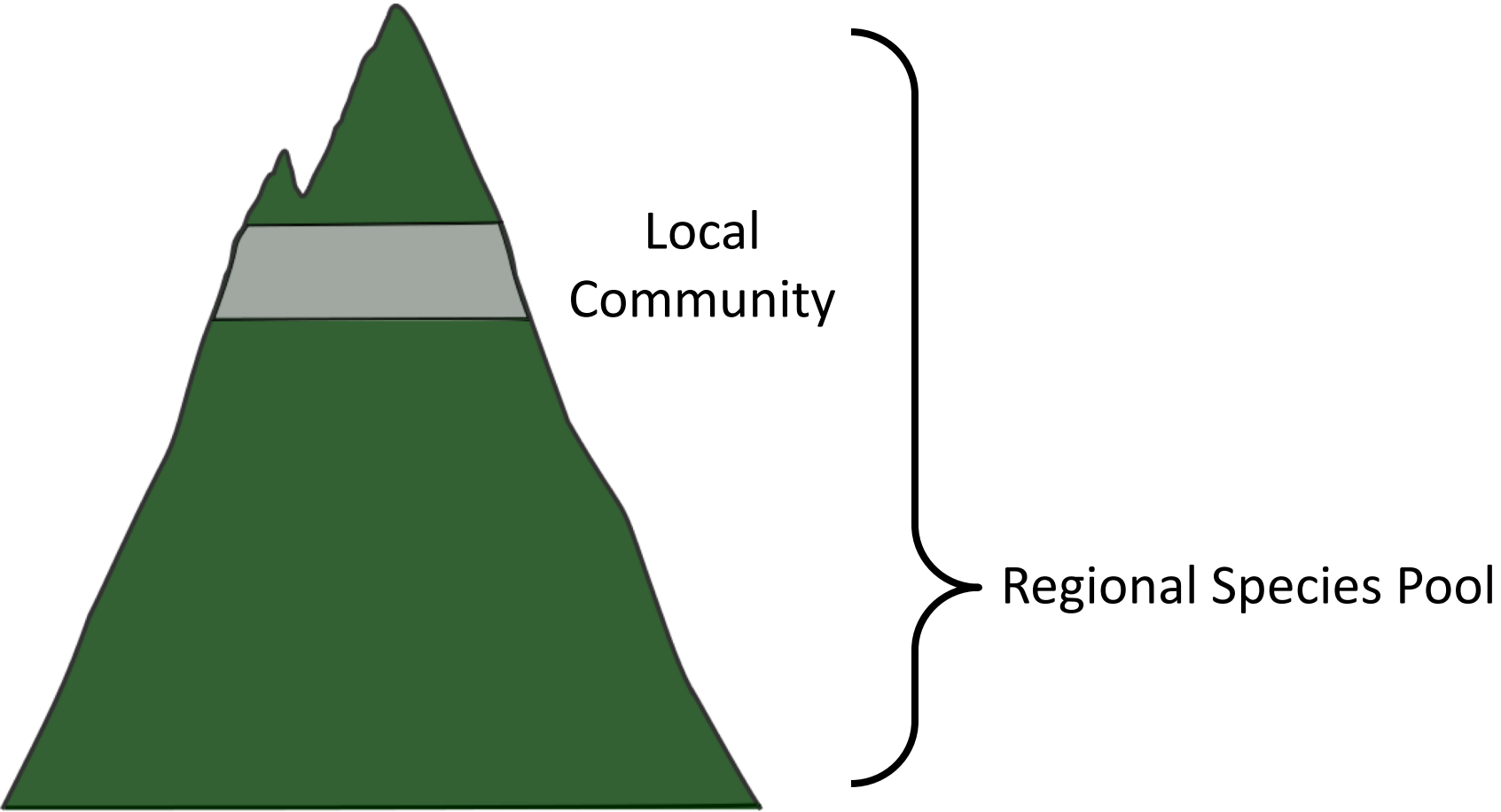
What can a phylogenetic perspective tell us?

Ecological sorting in communities due to habitat filters and species interactions



What can a phylogenetic perspective tell us?

Environmental gradients and biogeographic history of lineages influence dispersal, speciation and extinction



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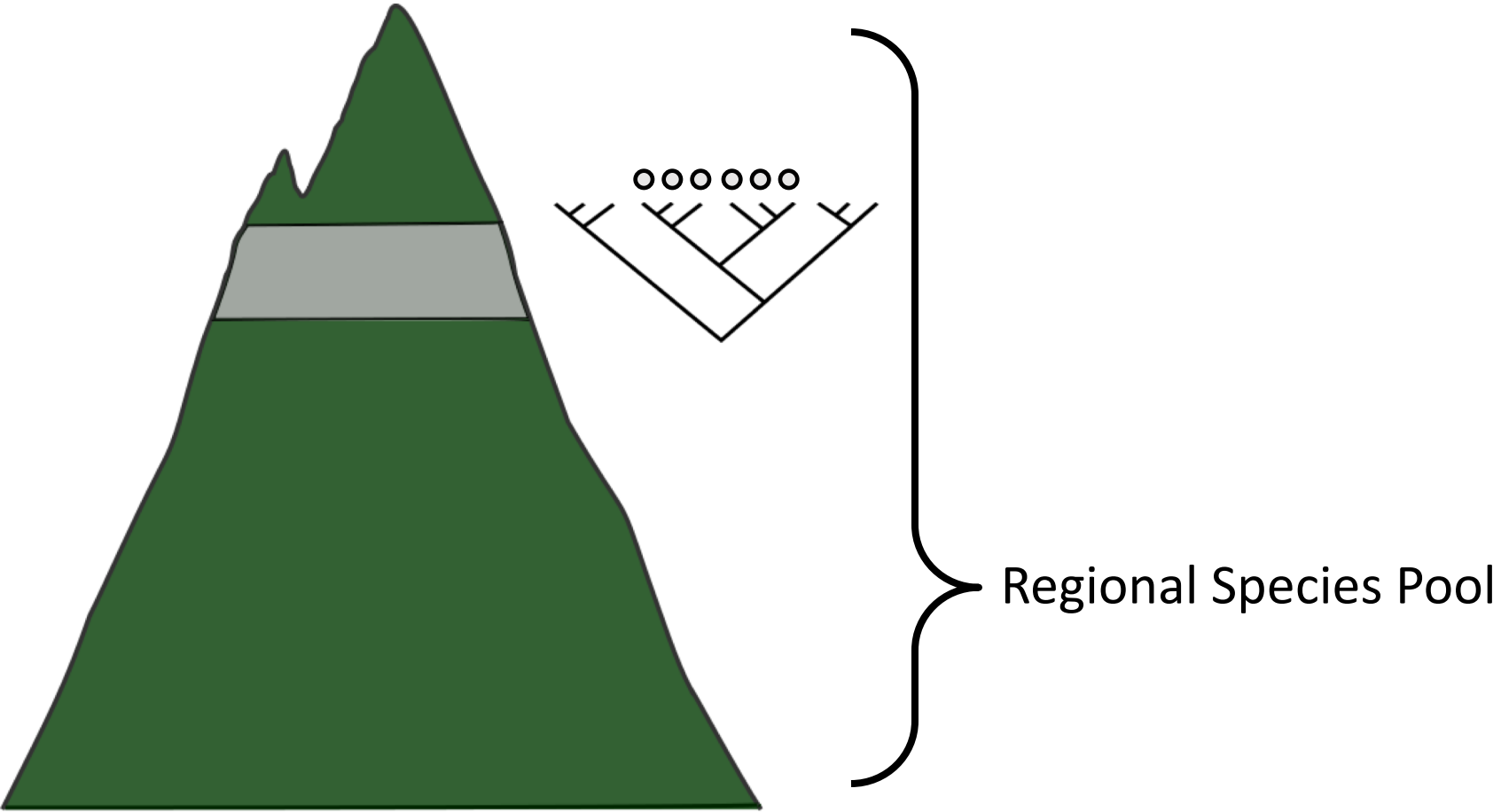
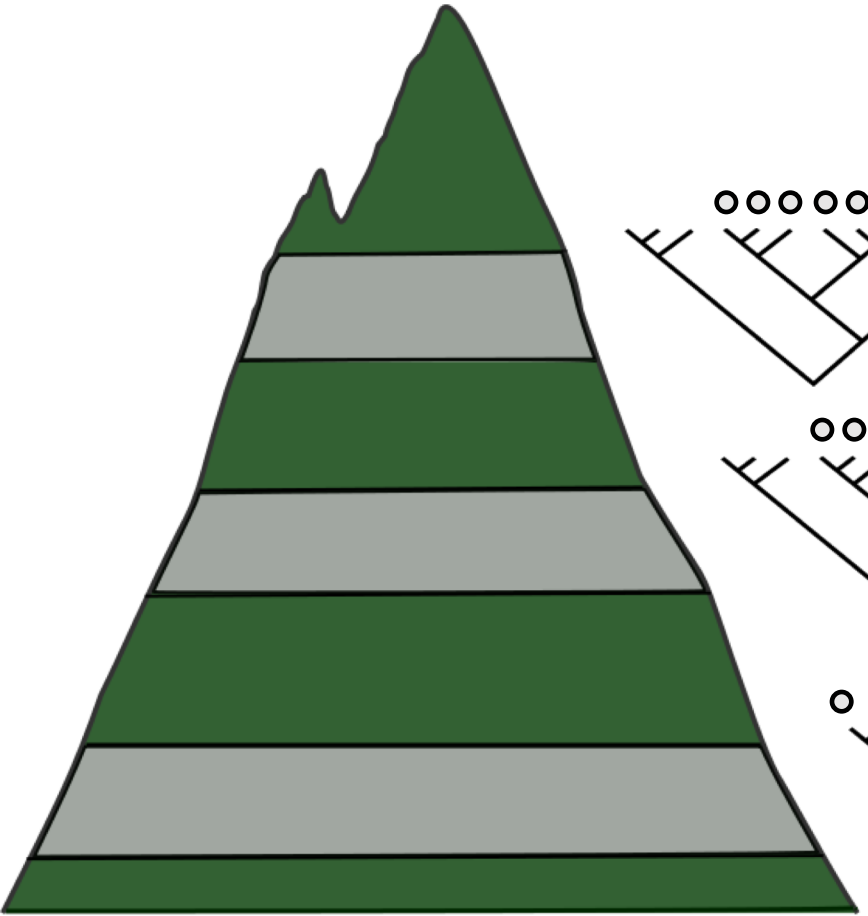
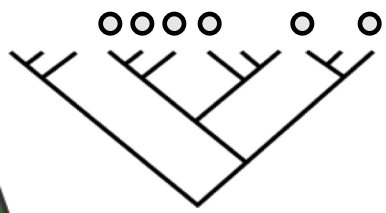


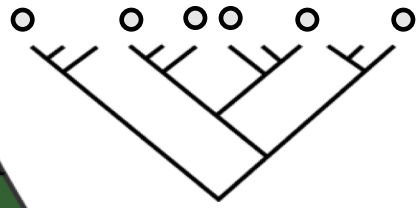
What can a phylogenetic perspective tell us?

How does the phylogenetic structure of communities change with elevation?



Phylogenetic Clustering
Co-occurring species are
more closely related



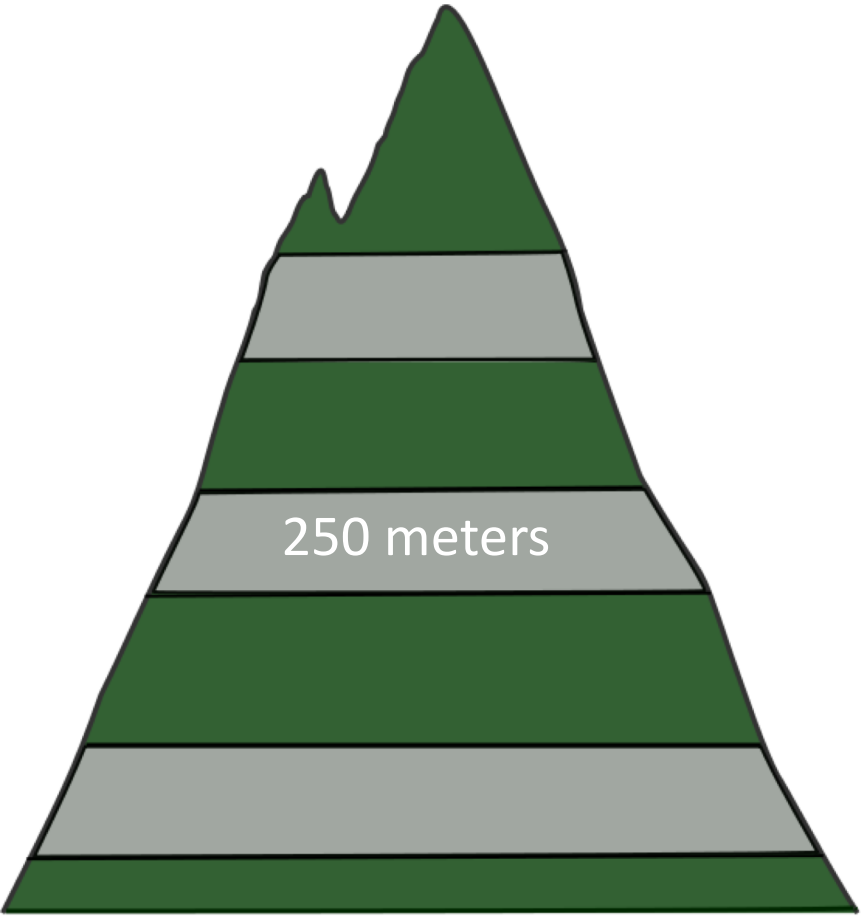


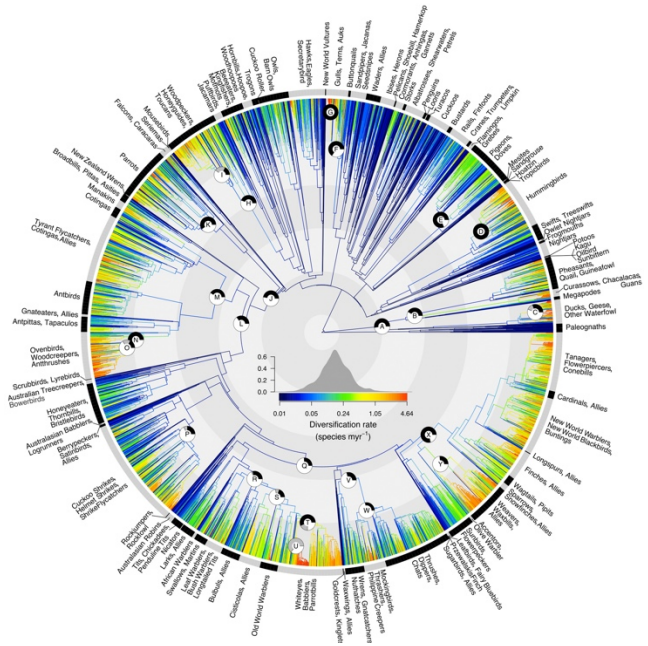
Phylogenetic Overdispersion
Co-occurring species are
more distantly related

A phylogenetic view of Andean bird communities

Used lists of species occurring in each 250-m elevational band

Combined with a distribution of 2,000 trees drawn at random (from Jetz et al., 2012)





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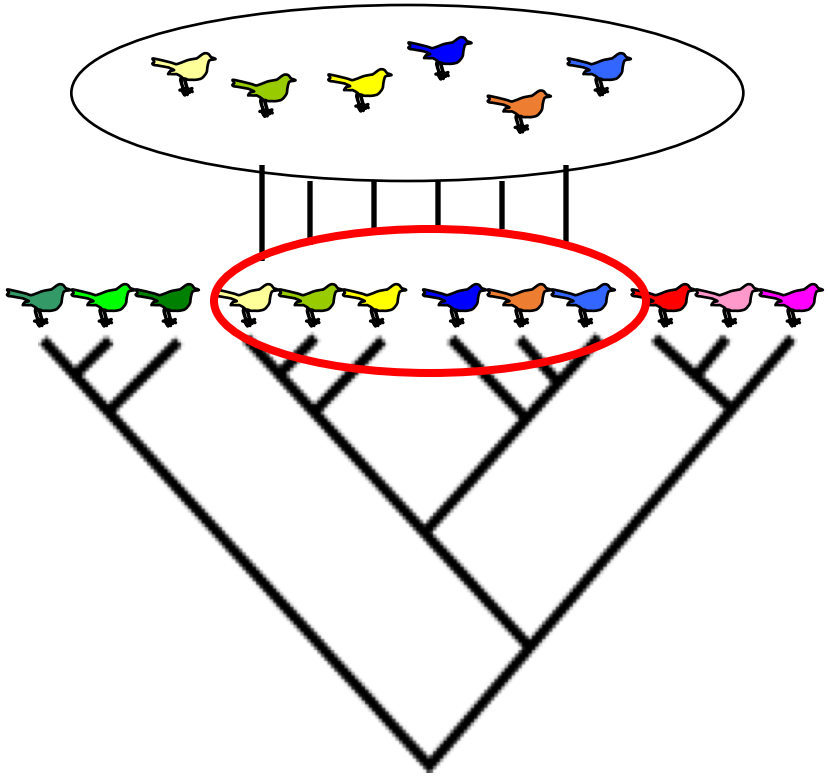

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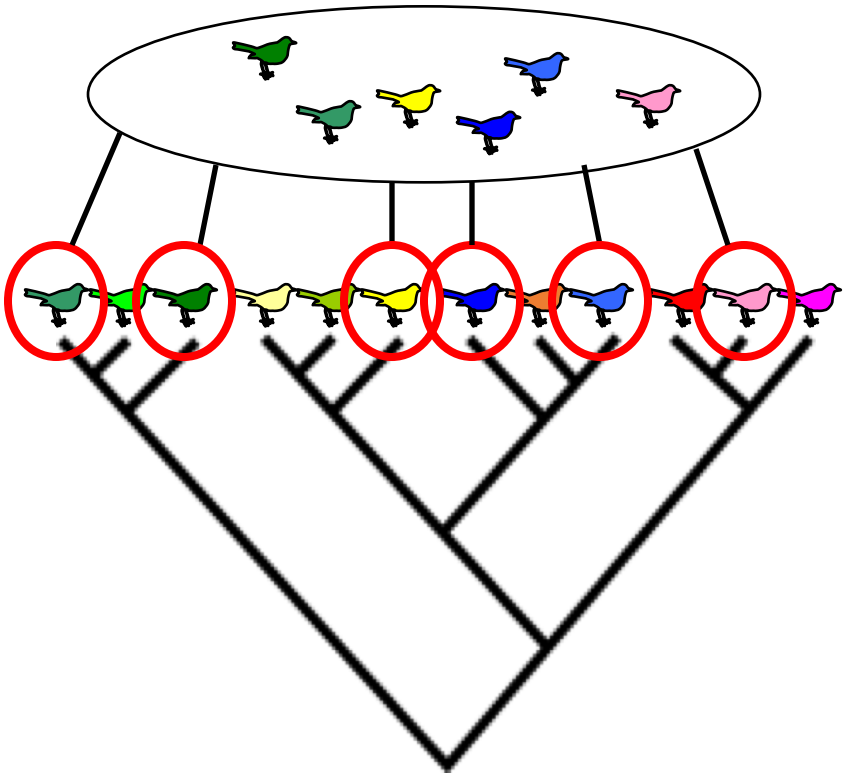
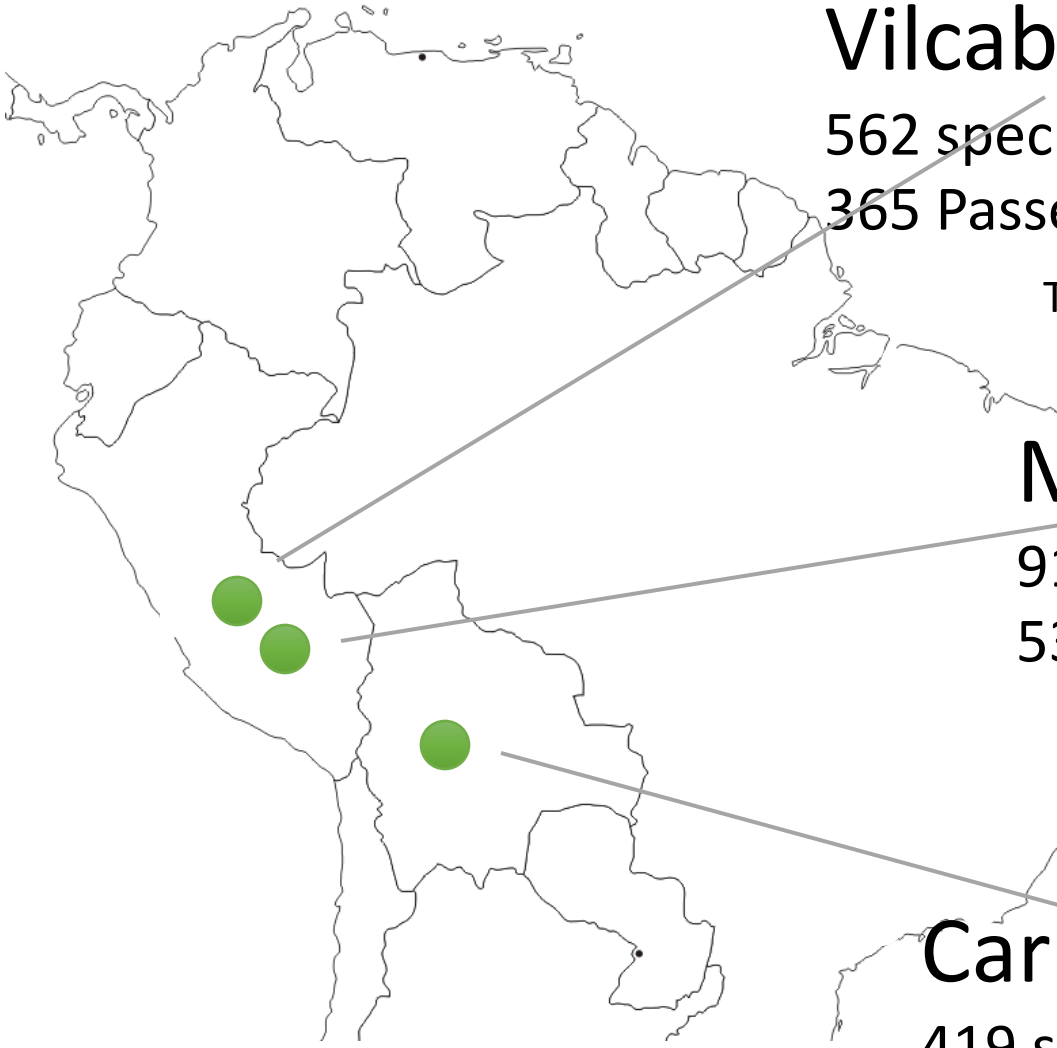


300-3600 meters



Vilcabamba

562 species
365 Passerines

Terborgh 1971, *Ecology*

Manu

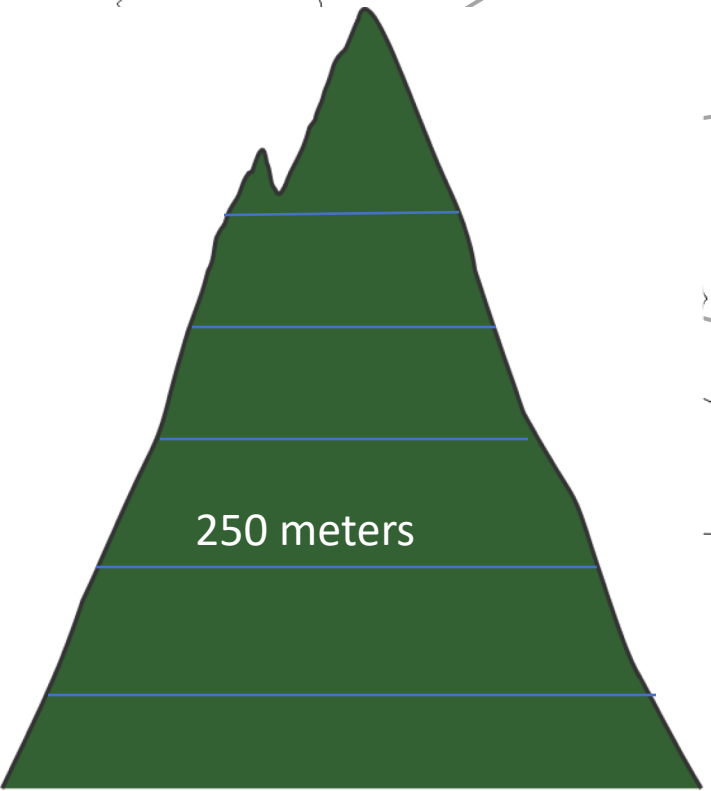
913 species
537 Passerines

Walker et al. 2006, *Fieldiana*

Carrasco

419 species
269 Passerines
unpublished

300-3600 meters



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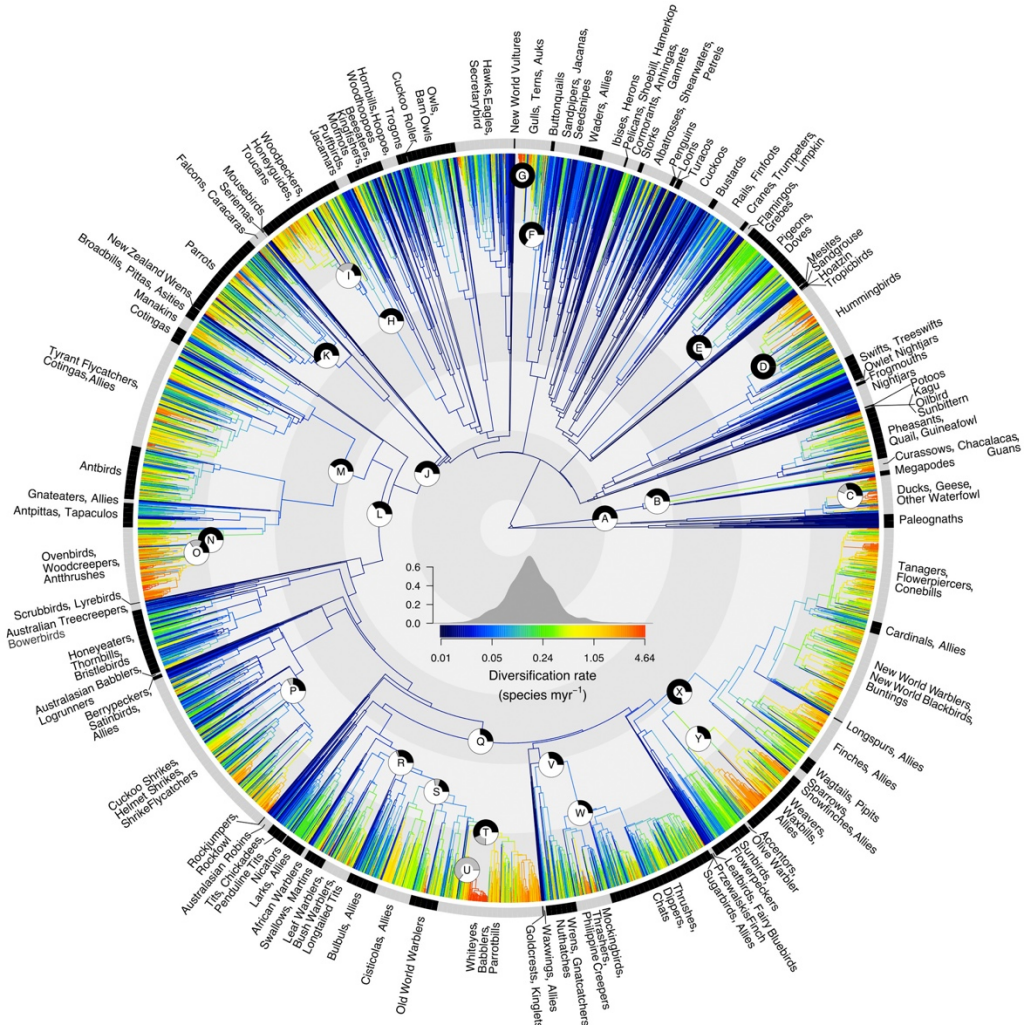


Distribution of 2,000 trees drawn at random from Jetz et al., 2012

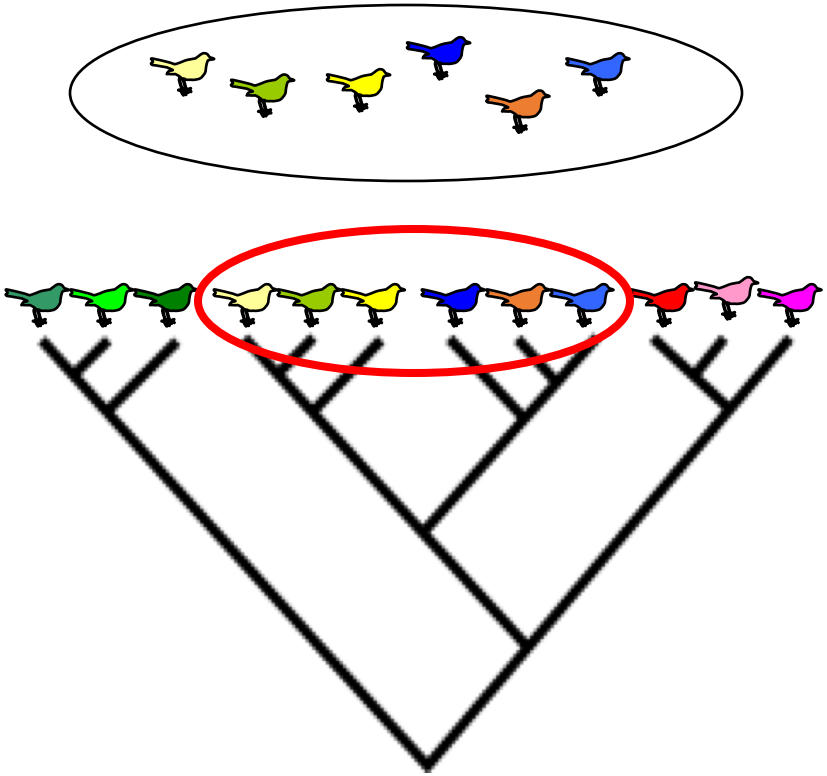
The global diversity of birds in space and time

W. Jetz, G. H. Thomas, J. B. Joy, K. Hartmann & A. O. Mooers

nature

Assess phylogenetic structure with null model

Mean phylogenetic distance (MPD)
for all pairwise species
combinations in local community



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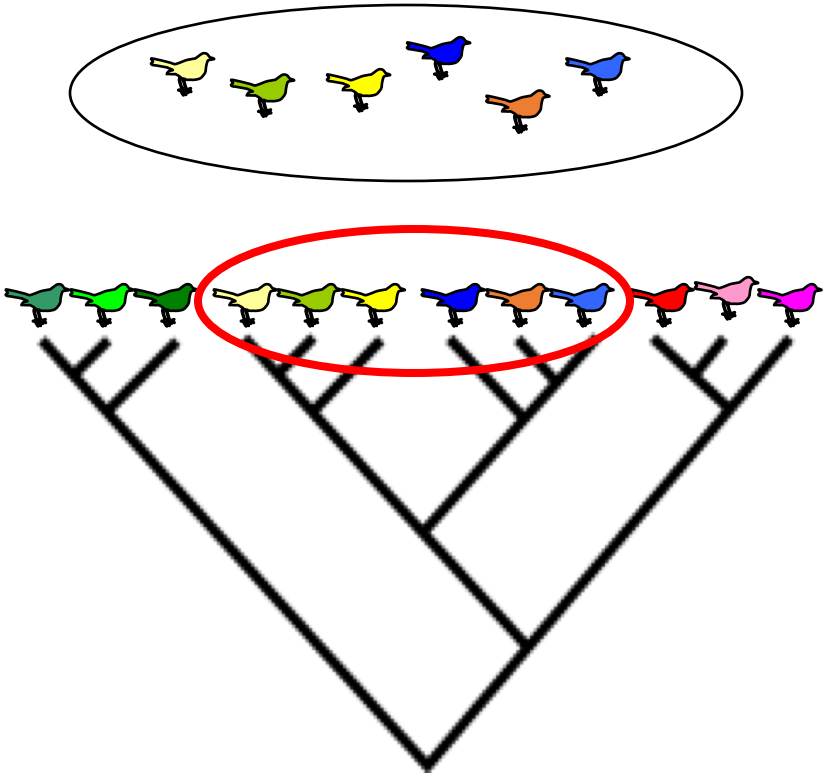
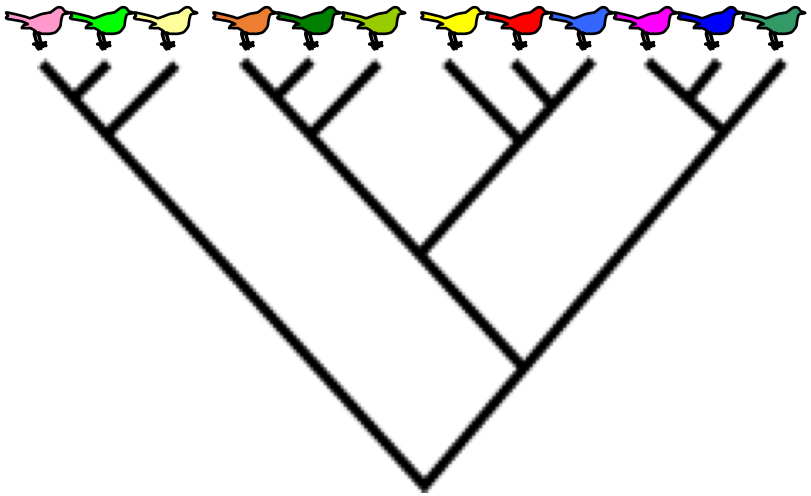


Randomize placement of species and recalculate (1000's of times)



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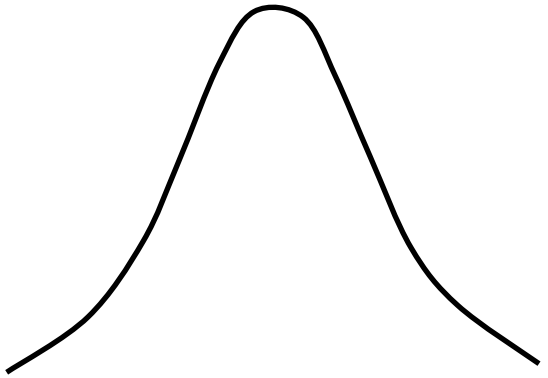

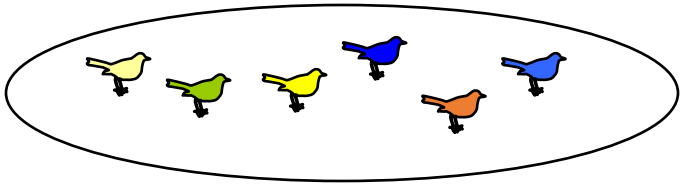

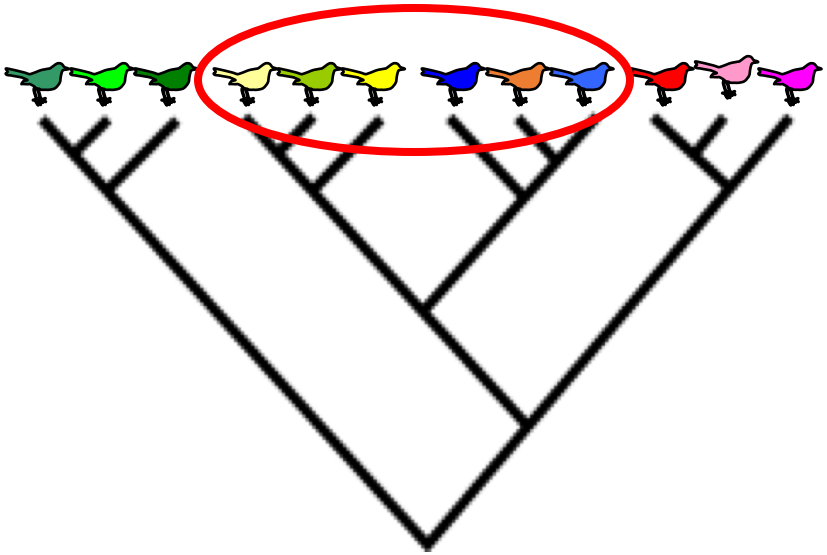

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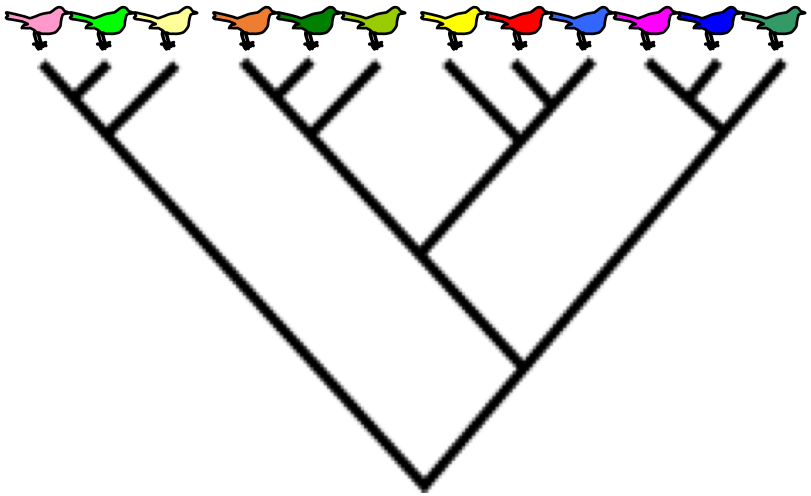

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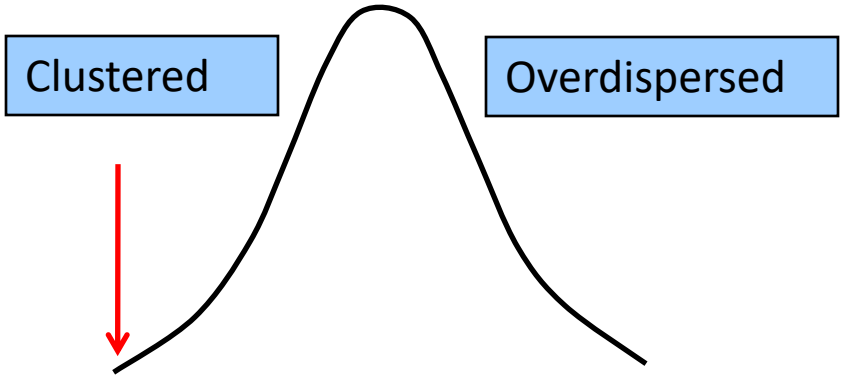

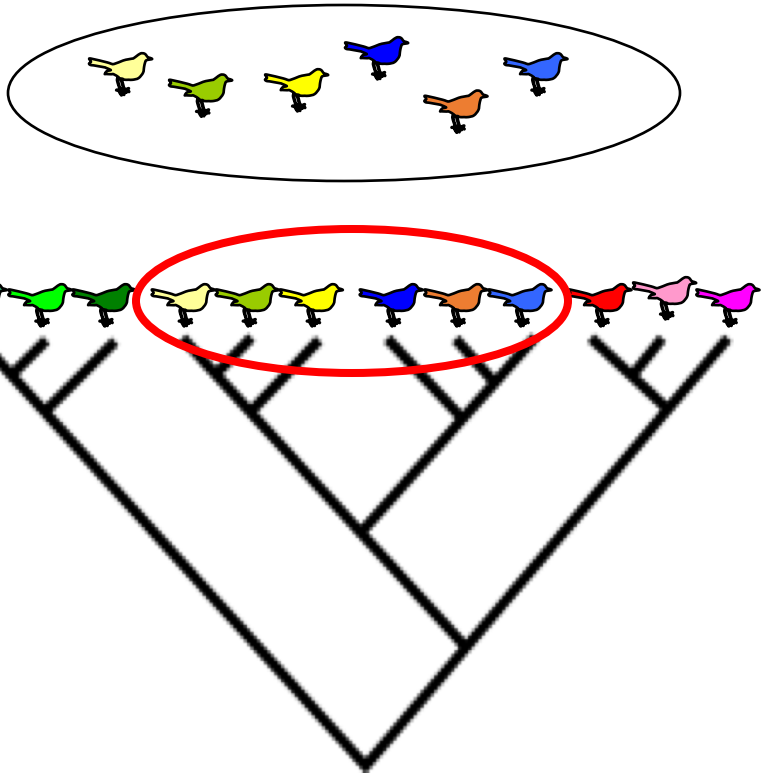

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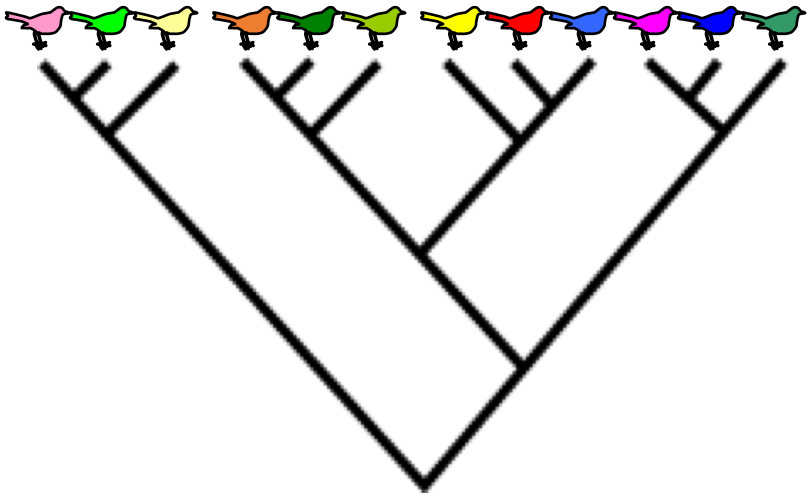
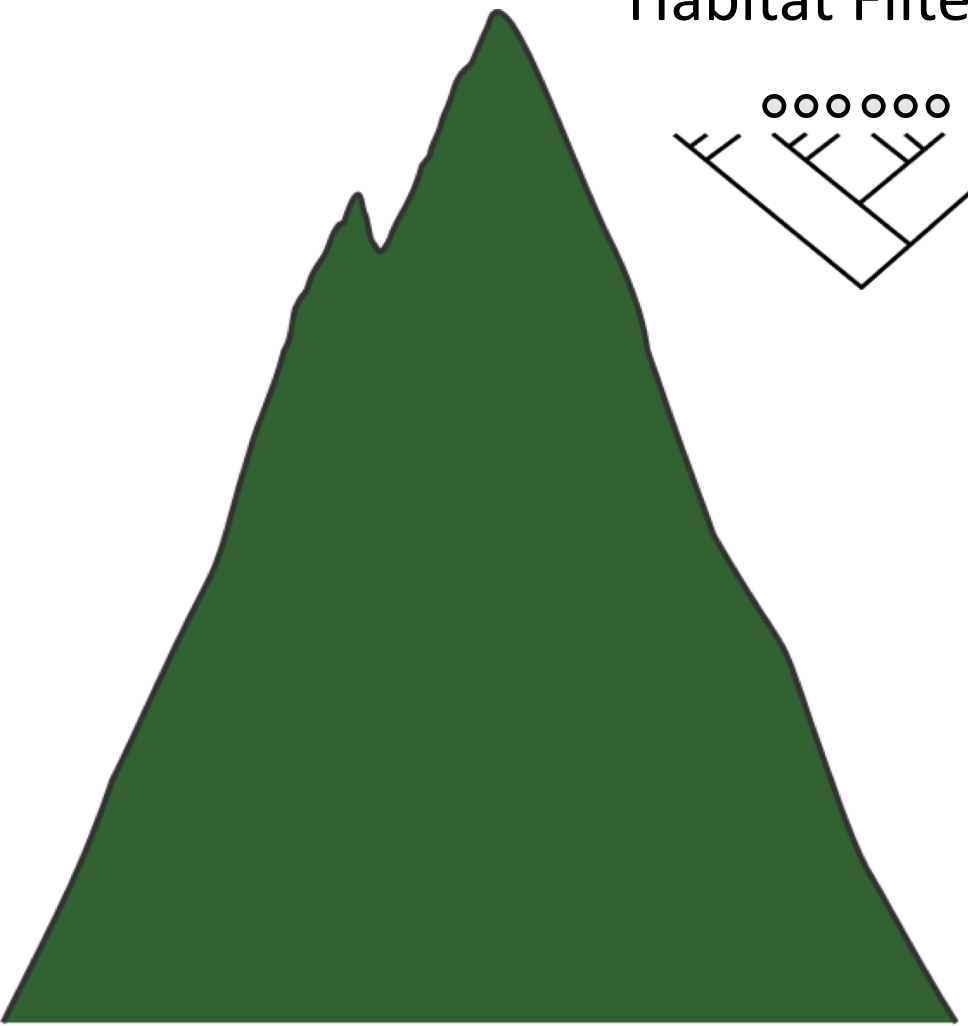


Prediction:
Overdispersion to phylogenetic clustering with elevation

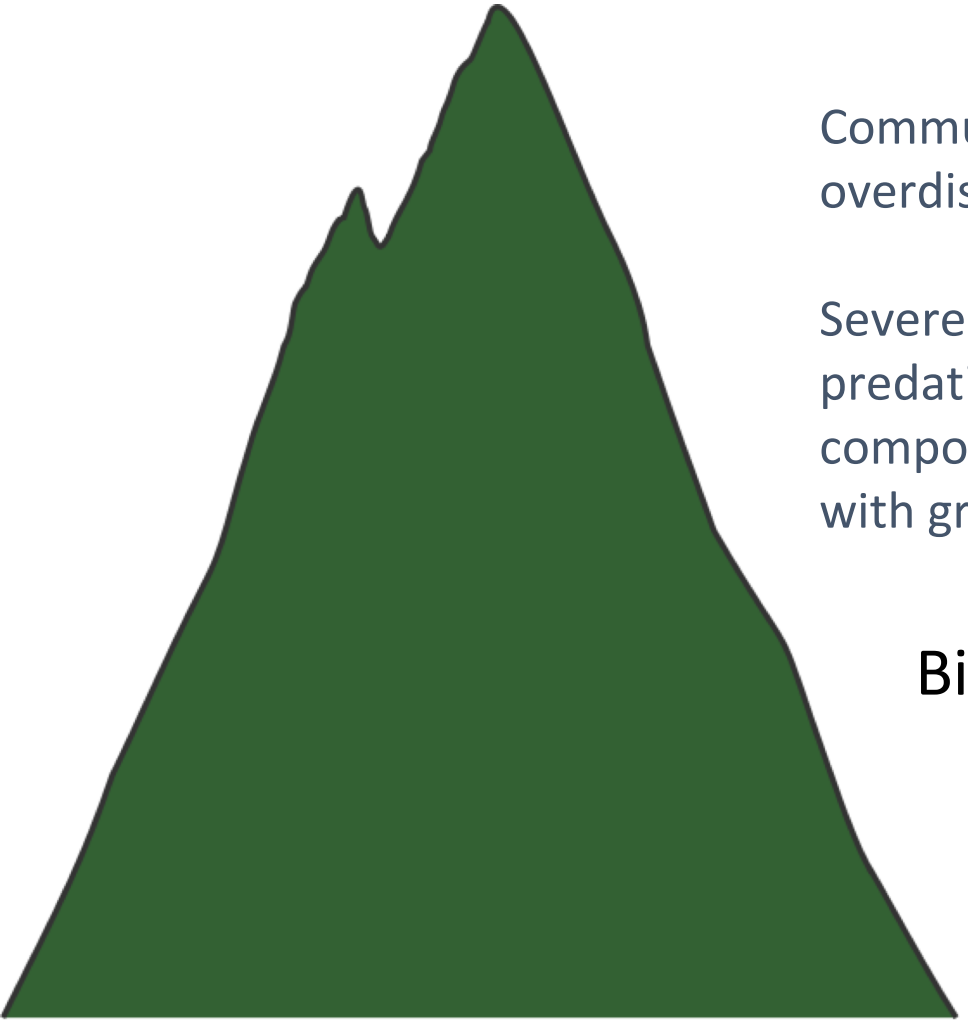


Habitat Filtering

Communities at high elevations should be clustered

Extreme abiotic conditions should pose a strong habitat filter, resulting in communities composed of similar species, with more similar traits

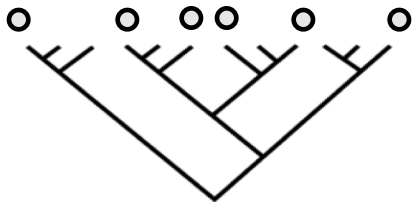
Prediction:
Overdispersion to phylogenetic clustering with elevation



Communities at low elevations should be overdispersed

Severe biotic pressures (like competition or predation) should result in communities composed of more distinct species, with greater differences in traits

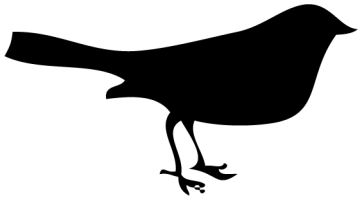
Biotic Interactions



Passeriformes

Thraupidae

Tyrannidae



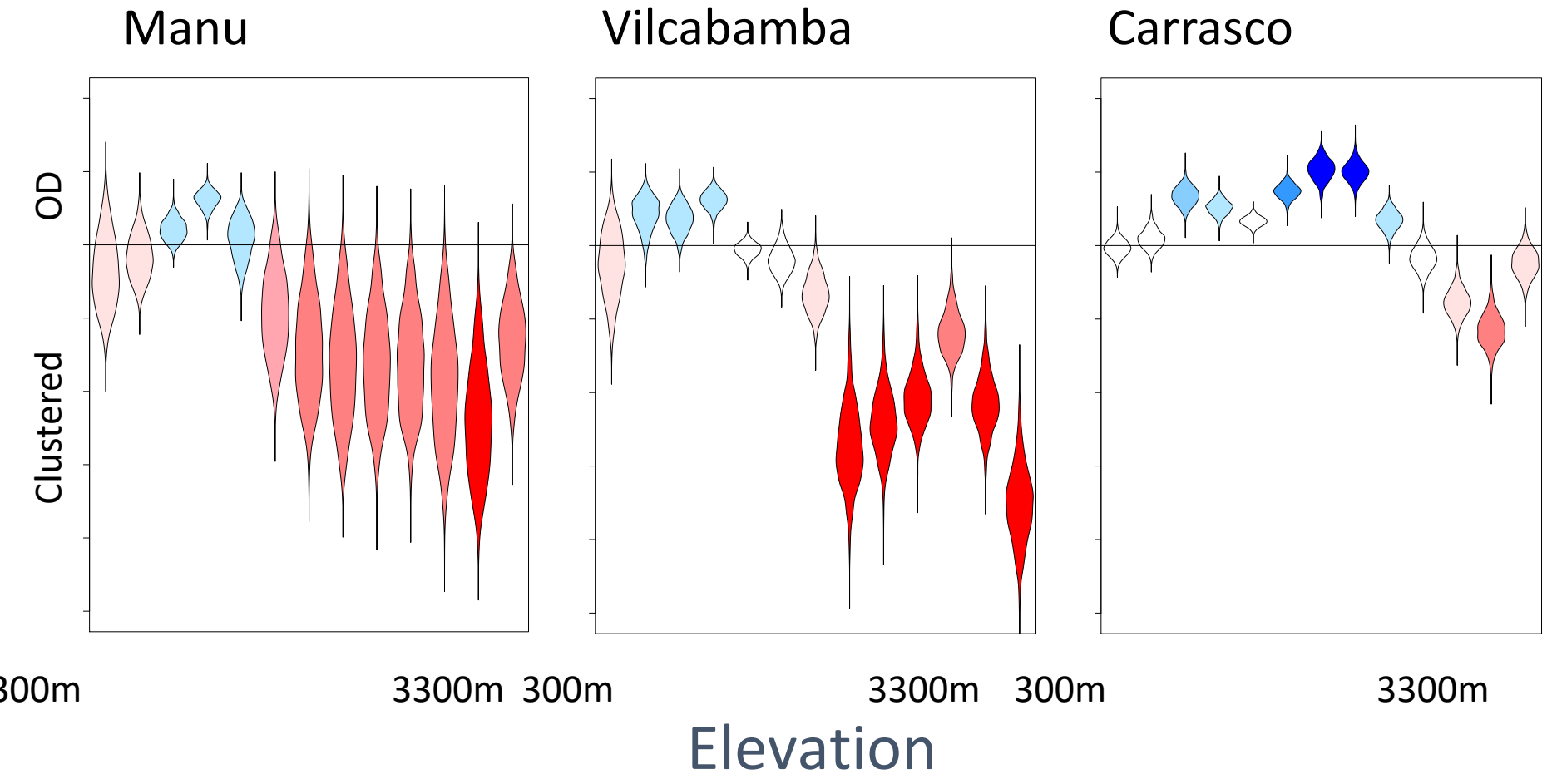
Thamnophilidae

Furnariidae

Trochilidae

Mean phylogenetic distance (MPD) plotted for diverse tropical bird families

Passerines



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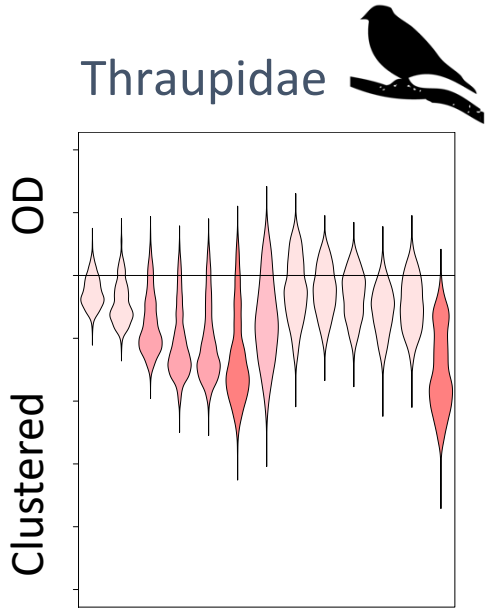
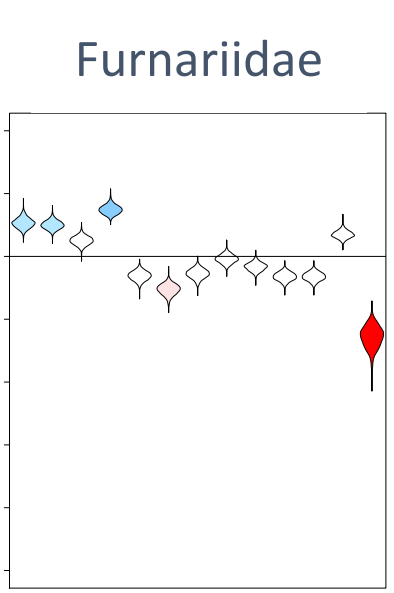
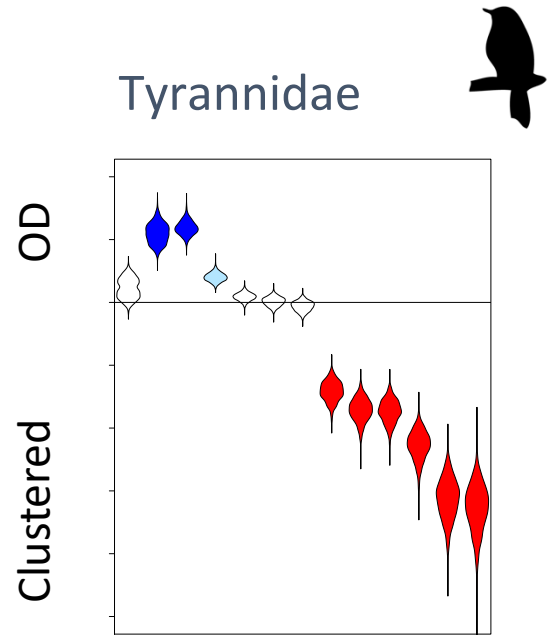
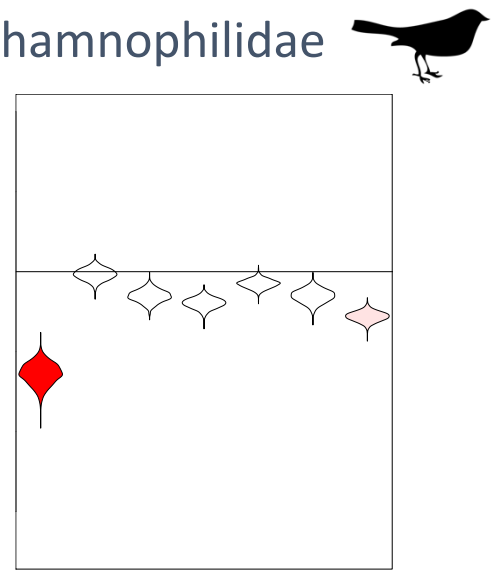
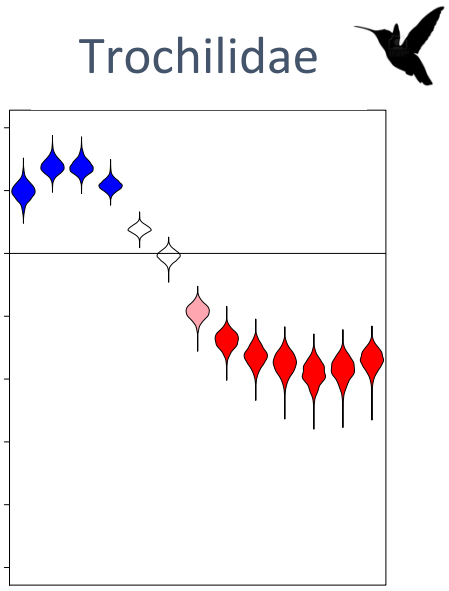


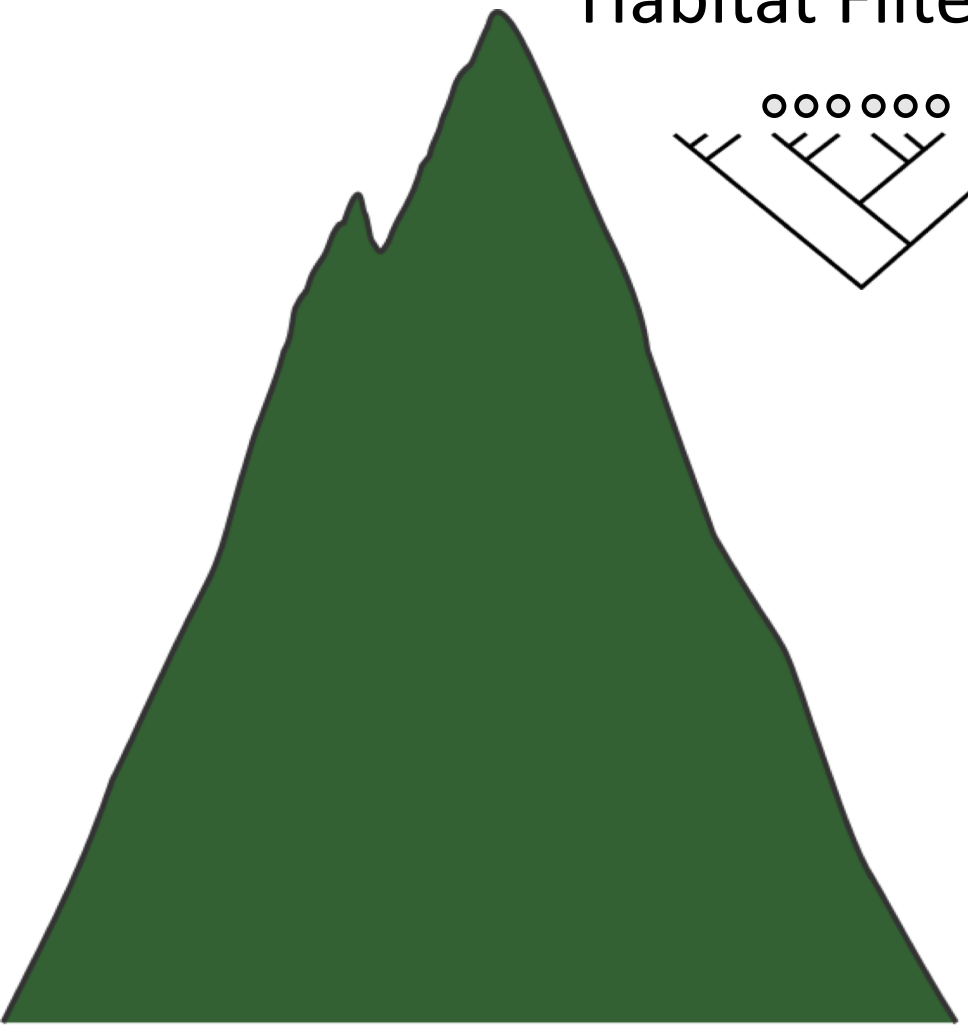








Overdispersion to phylogenetic clustering along the elevation gradient



Habitat Filtering

Biotic Interactions