



# Inside a tropical montane *forest*

Understanding patterns of plant diversity and  
ecosystem functioning across the Andes



Oxford Centre for Tropical Forests  
14 June 2019

---

Luis Cayuela

Tropical Ecology Lab ([www.grupoecologiatropical.com](http://www.grupoecologiatropical.com))  
Departamento de Biología y Geología, Física y Química Inorgánica  
Universidad Rey Juan Carlos



# what is a tropical montane forest





3500 m a.s.l.

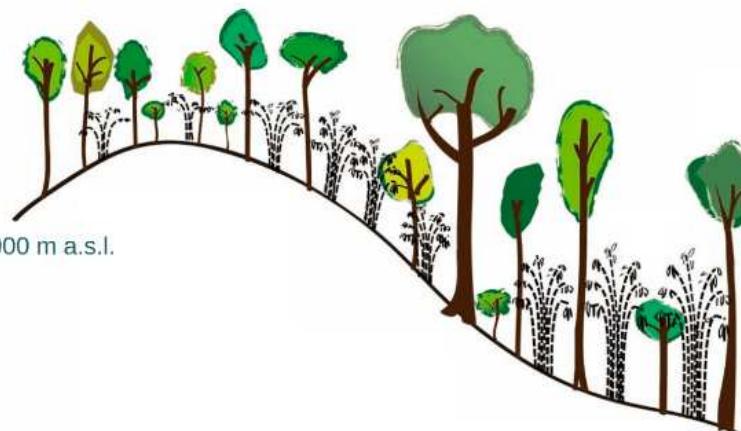
### Subalpine tropical montane forest

- Canopy: 1.5-9 m (1 layer)
- Emerging trees absent or up to 15 m
- Very small simple leaves
- Drip-tip leaves absent
- Buttressed roots absent
- Lianas absent
- Vascular epiphytes rare
- Abundant non-vascular epiphytes (70-80%)

Mean maximum temperature  
**<10°C**



2500 m a.s.l.



### Upper tropical montane forest (*elfin forest*)

- Canopy: 1.5-18 m (1 layer)
- Emerging trees absent or up to 25 m
- Small simple leaves
- Drip-tip leaves rare or absent
- Buttressed roots typically absent
- Lianas typically absent
- Frequent vascular epiphytes
- Abundant non-vascular epiphytes (70-80%)



1000 m a.s.l.

### Lower tropical montane forest

Mean minimum temperature  
**<18°C**

- Canopy: 15-33 m (2 layers)
- Emerging trees up to 30-40 m
- Occasional compound leaves / medium size
- Frequent drip-tip leaves
- Buttressed roots (occasional)
- Lianas (occasional)
- Abundant vascular epiphytes
- Frequent non-vascular epiphytes (25-50%)

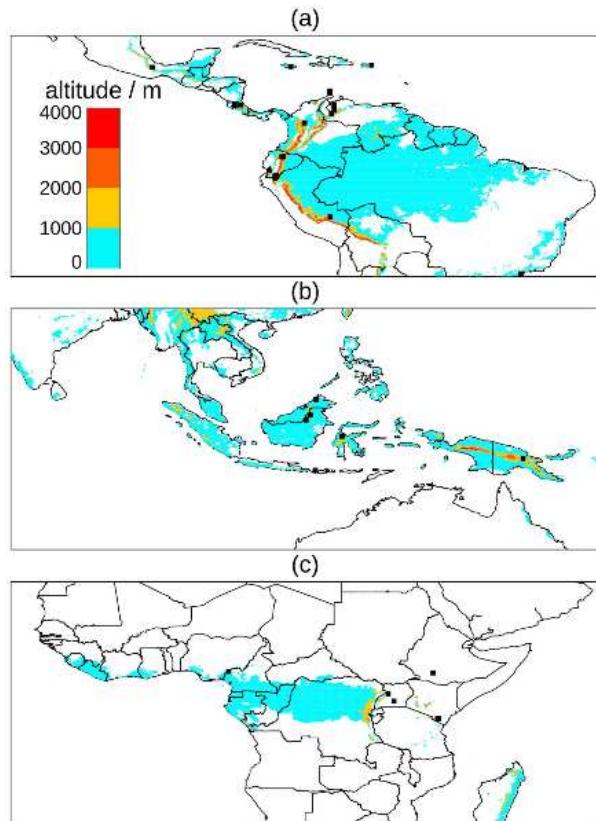


300 m a.s.l.

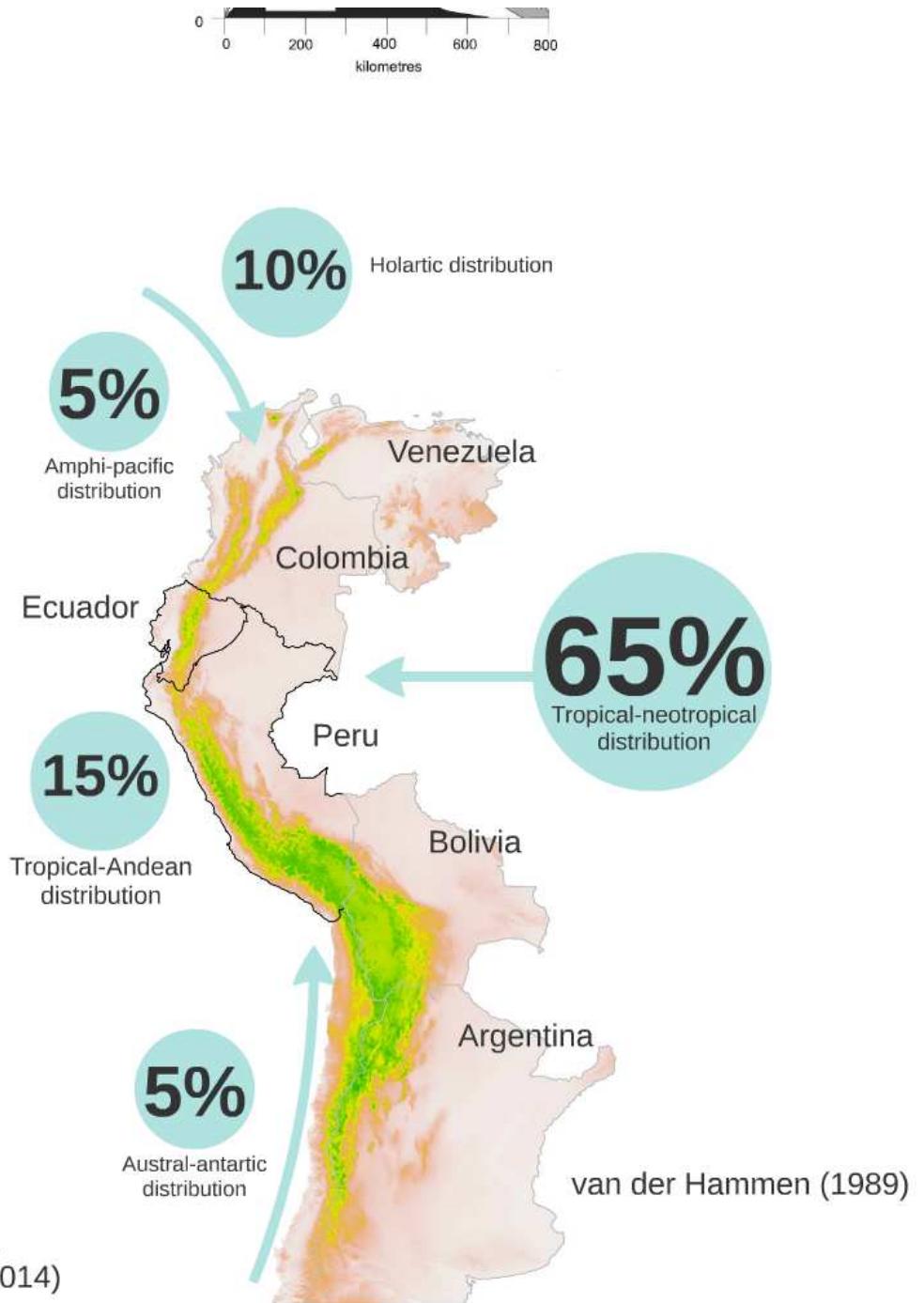
### Tropical rainforest

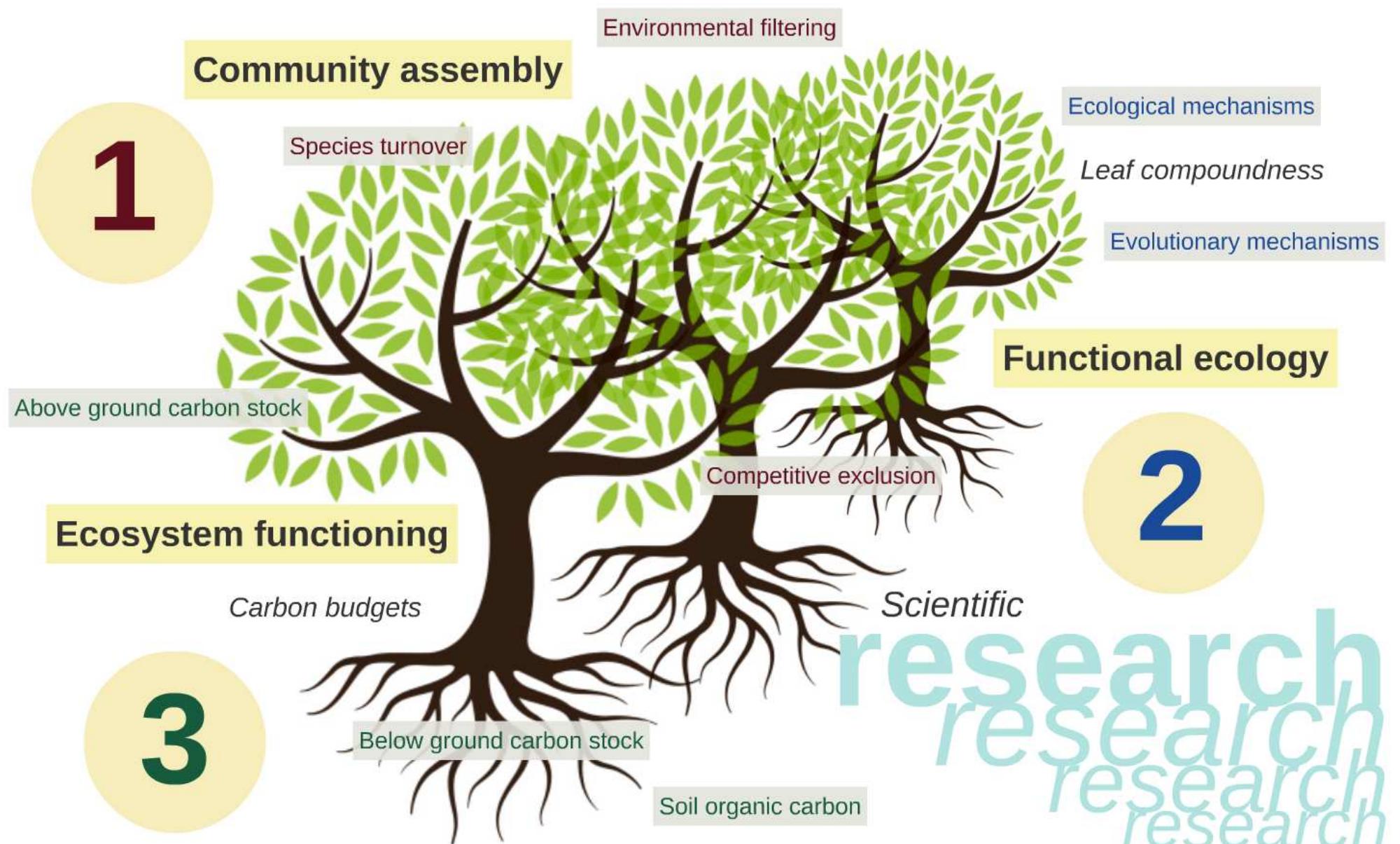
- Canopy: 25-45 m (3 or more layers)
- Emerging trees up to 60-70 m
- Large / compound leaves
- Abundant drip-tip leaves
- Buttressed roots
- Abundance of lianas
- Frequent vascular epiphytes
- Occasional non-vascular epiphytes

# Biogeography of the Andes



Spracklen &  
Righelato (2014)





Community assembly

# How can so many species co-exist?

## Plants



## Amphibians

81

Frog species

in just one site in the Amazonia of Ecuador!

Equivalent to all frog species of the USA

Duellman (1992)

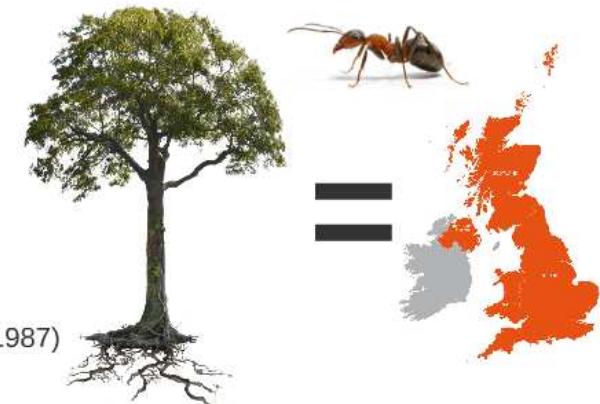
## Arthropods

Tambopata: 135 ant species

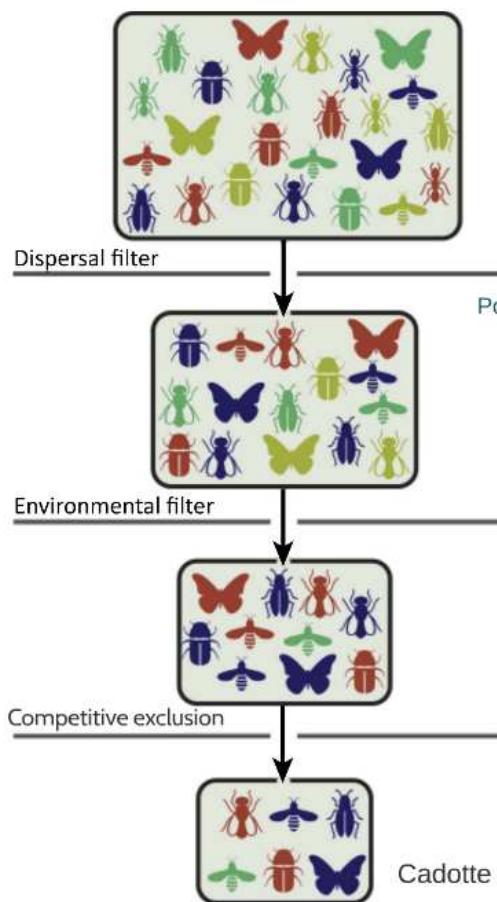
43

Ant species  
in just one tree!!!

Wilson (1987)

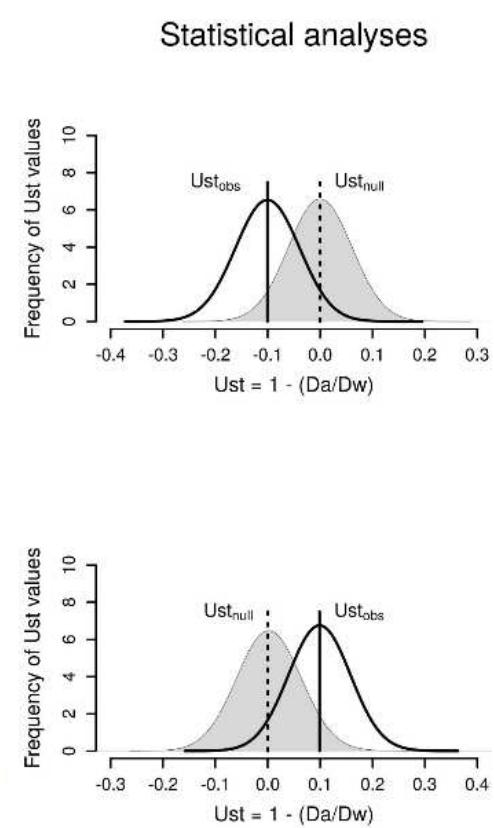
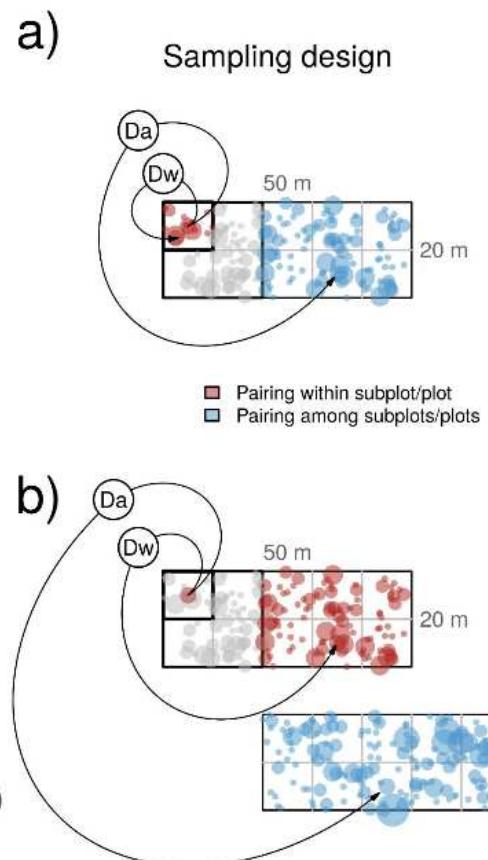


# Community assembly Looking into functional traits...



Bañares-de Dios et al. (in rev.)

Cadotte & Tucker (2017)



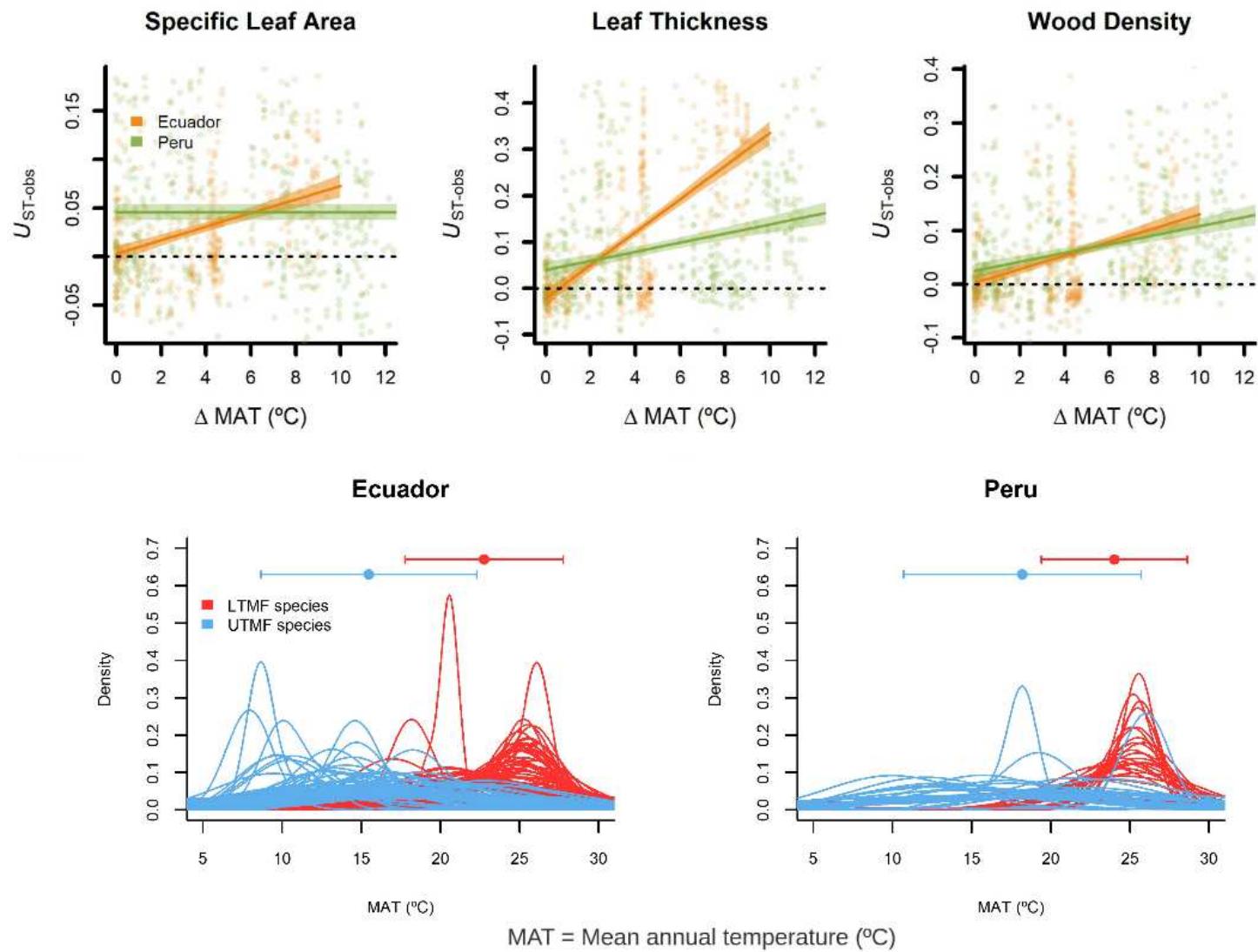
## Community assembly

# Results

### *In a nutshell:*

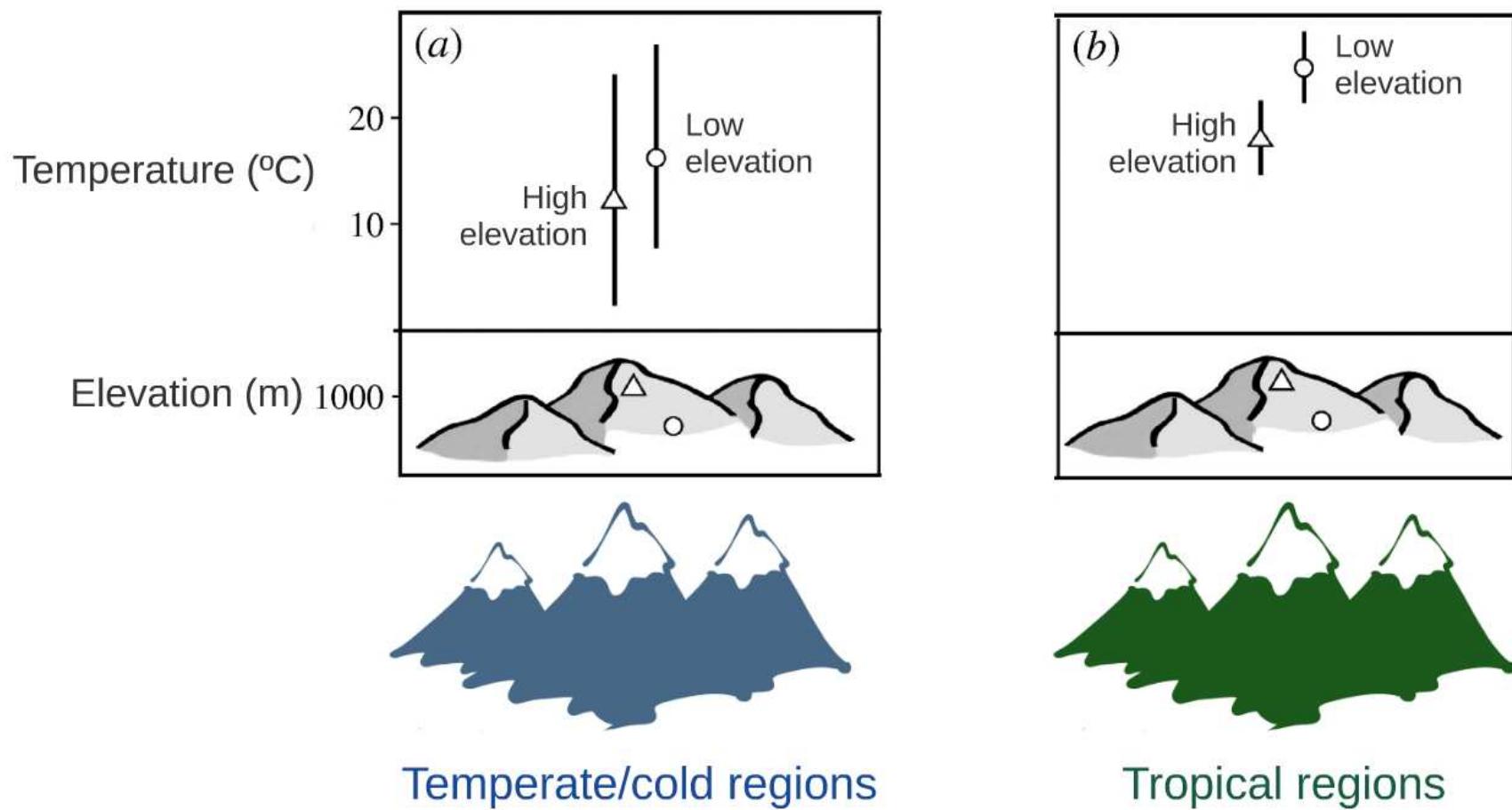
- Competitive exclusion at small spatial scales does not have an influence on community assembly
- Environmental filtering at larger spatial scales is the overriding process structuring TMF communities
  - Greater community functional differences were mostly the result of strong climatic affinities, maintained across the Neotropics

Bañares-de Dios *et al.* (in rev.)



Community assembly

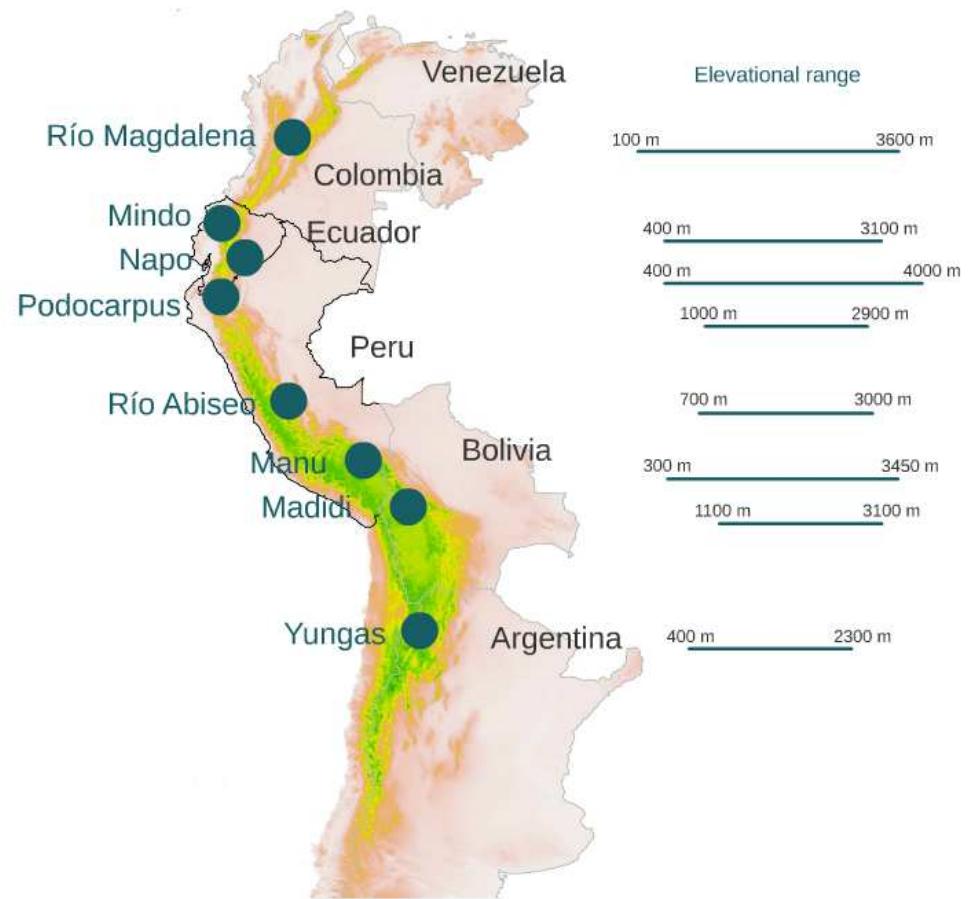
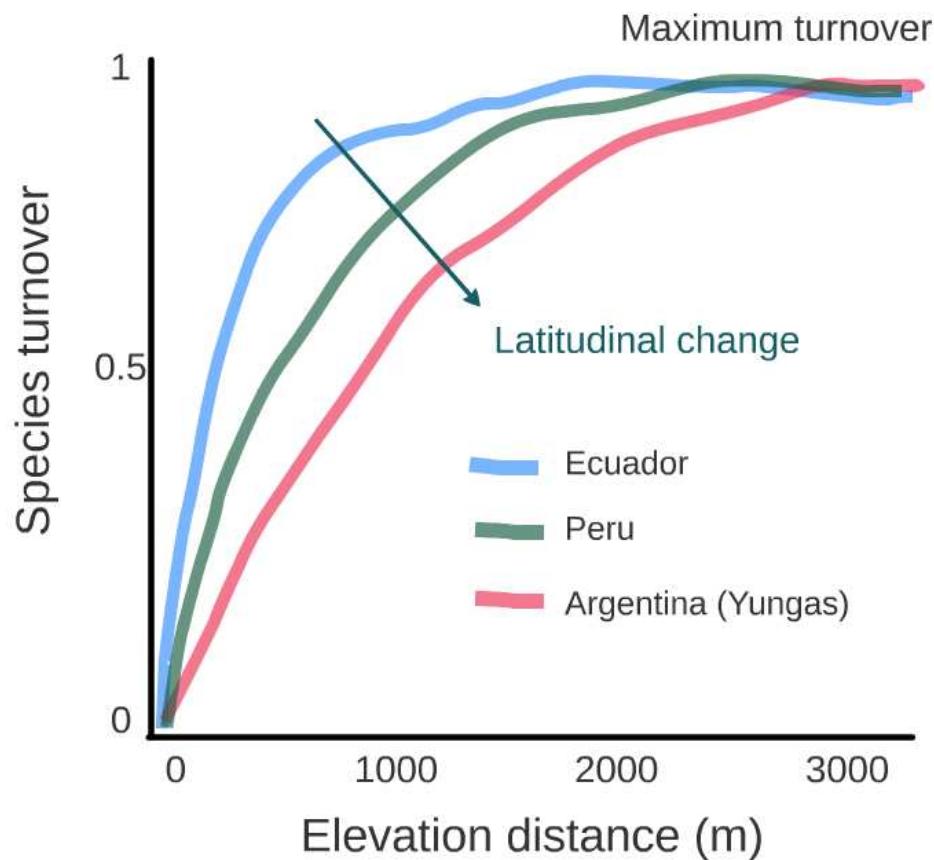
# Species turnover



Janzen (1976)

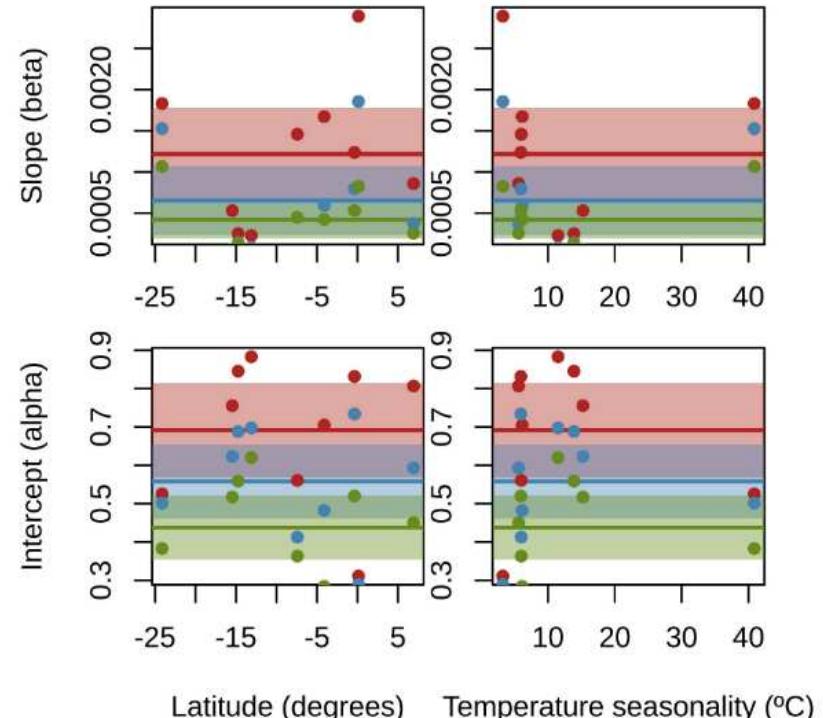
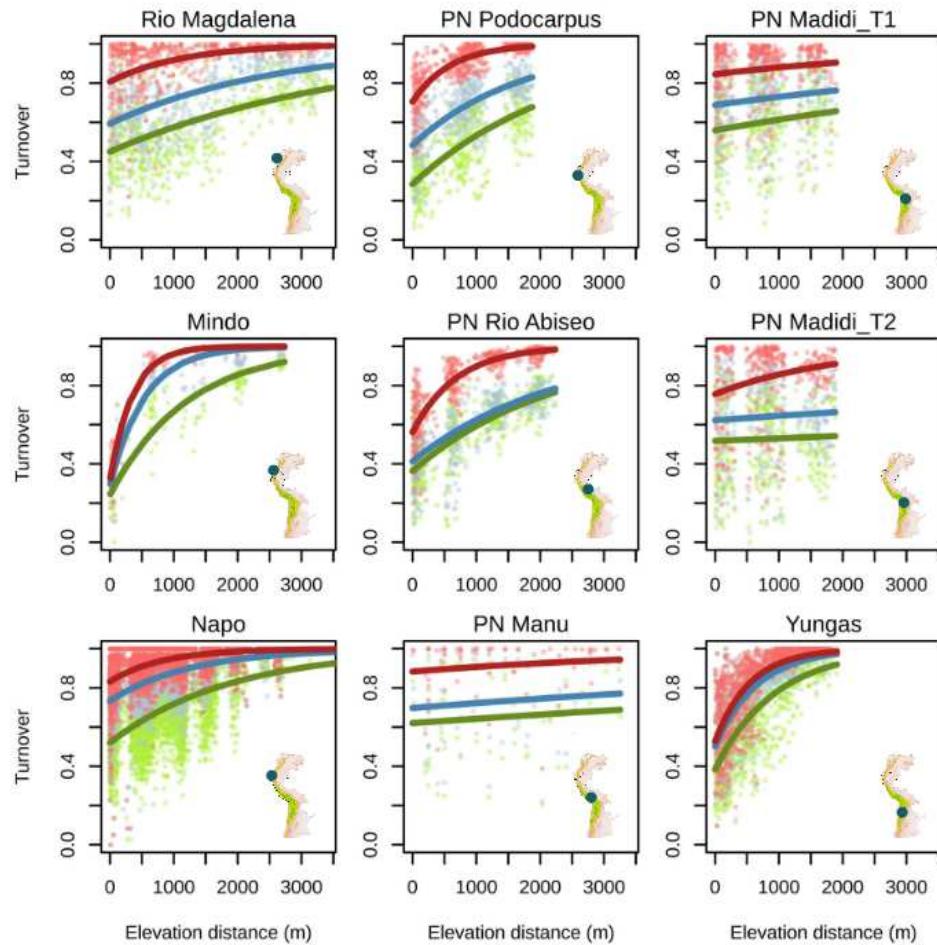
Community assembly

# Does turnover change with latitude?



## Community assembly

# Patterns... do they vary geographically?



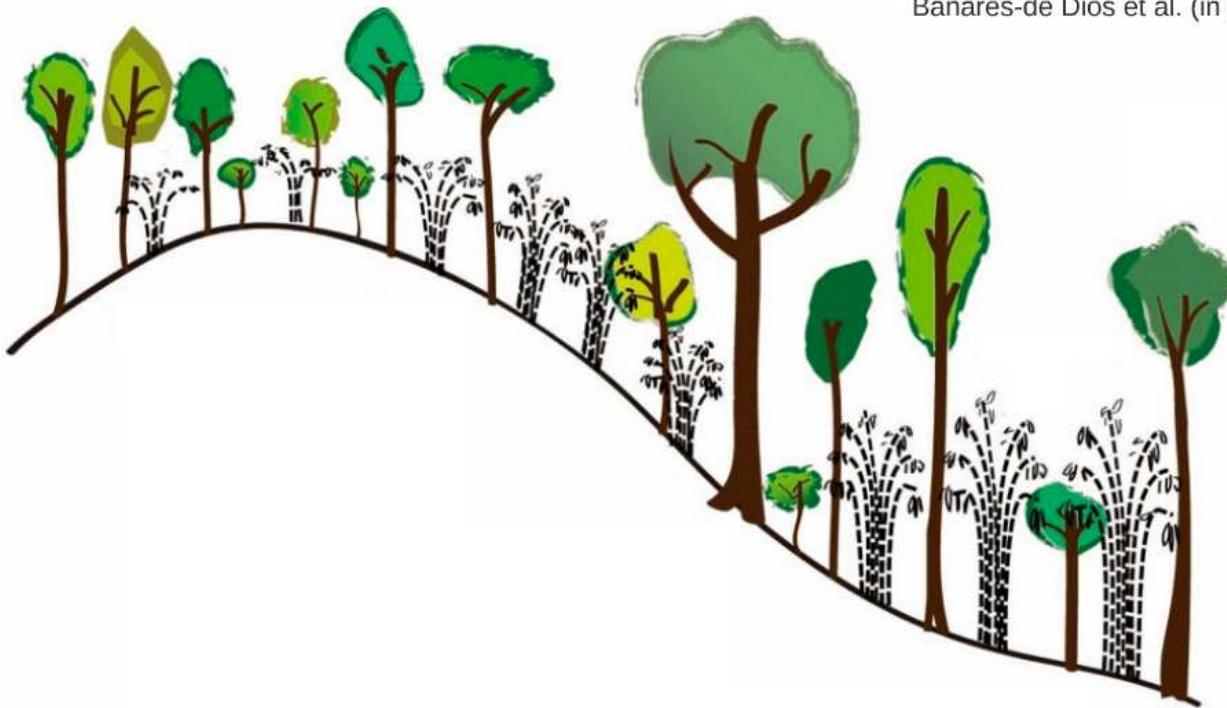
- Species turnover
- Genus turnover
- Family turnover

Cayuela et al. (in prep.)

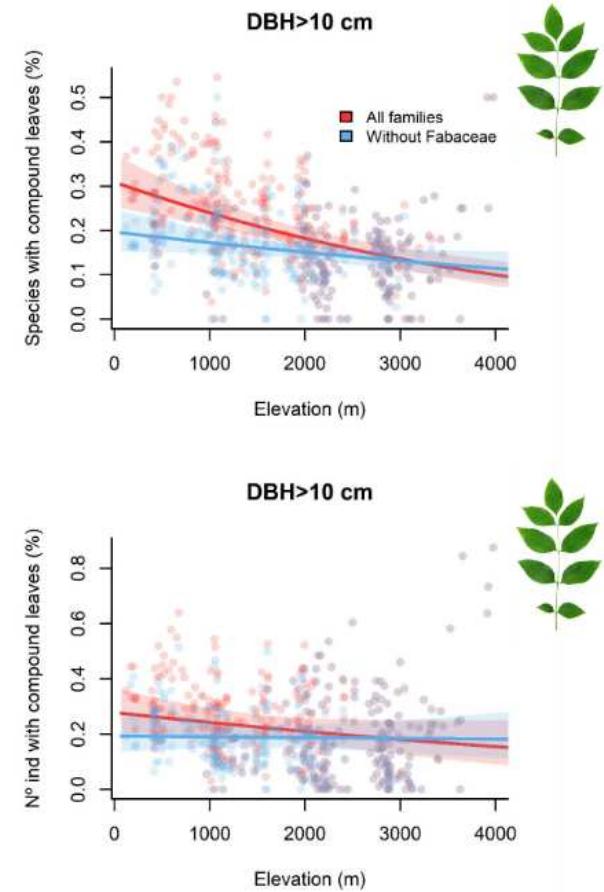
Do they change?

# What are compound leaves useful for?

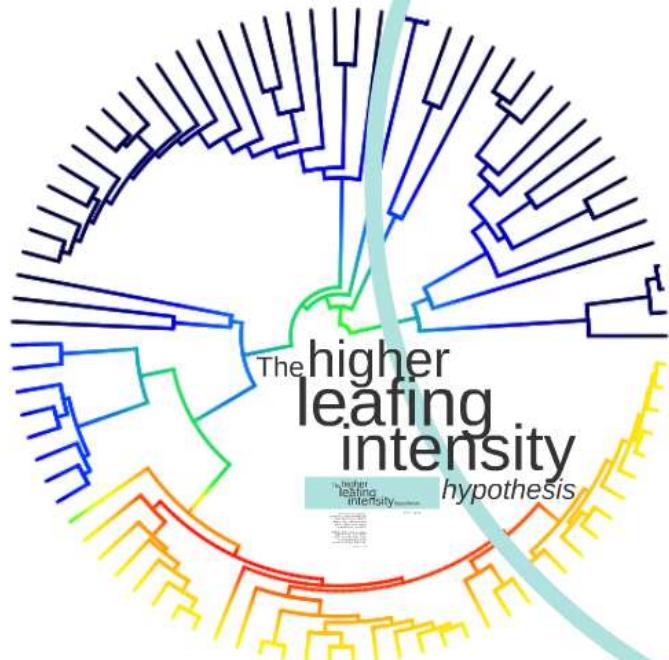
Do compound leaves decrease with elevation?



Bañares-de Dios et al. (in prep.)

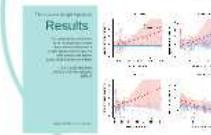


Mechanisms  
Mechanisms  
Mechanisms  
Mechanisms  
Mechanisms  
Mechanisms



# Evolutionary Ecological

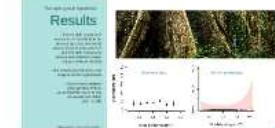
The seasonal drought hypothesis



The mechanical resistance hypothesis



The rapid growth hypothesis

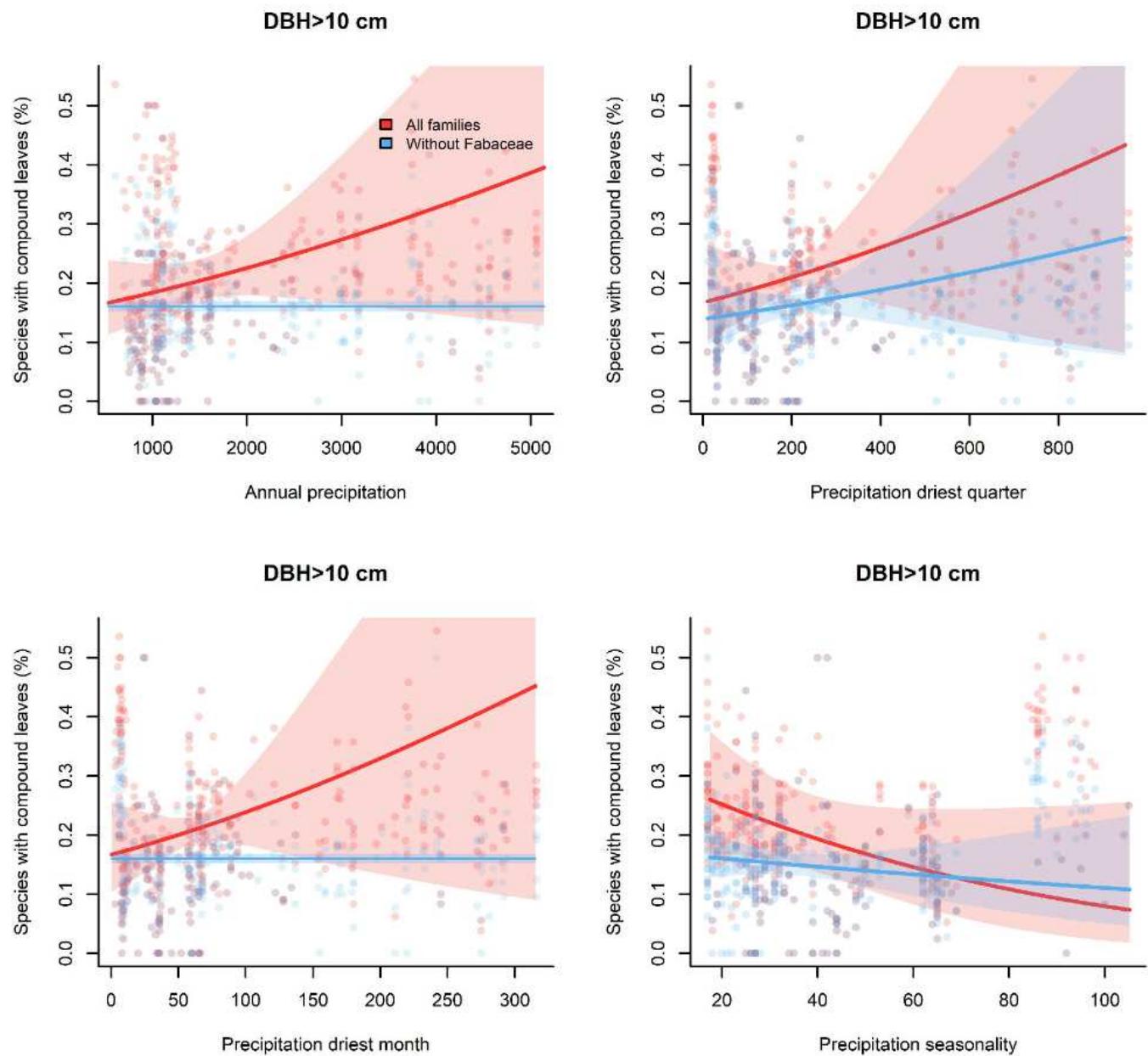


e seasonal drought hypothesis

# Results

- If compound leaves have lower transpiratory water loss, we would expect a higher proportion of species with compound leaves associated to drier conditions
  - Our results do show evidence for the opposite pattern

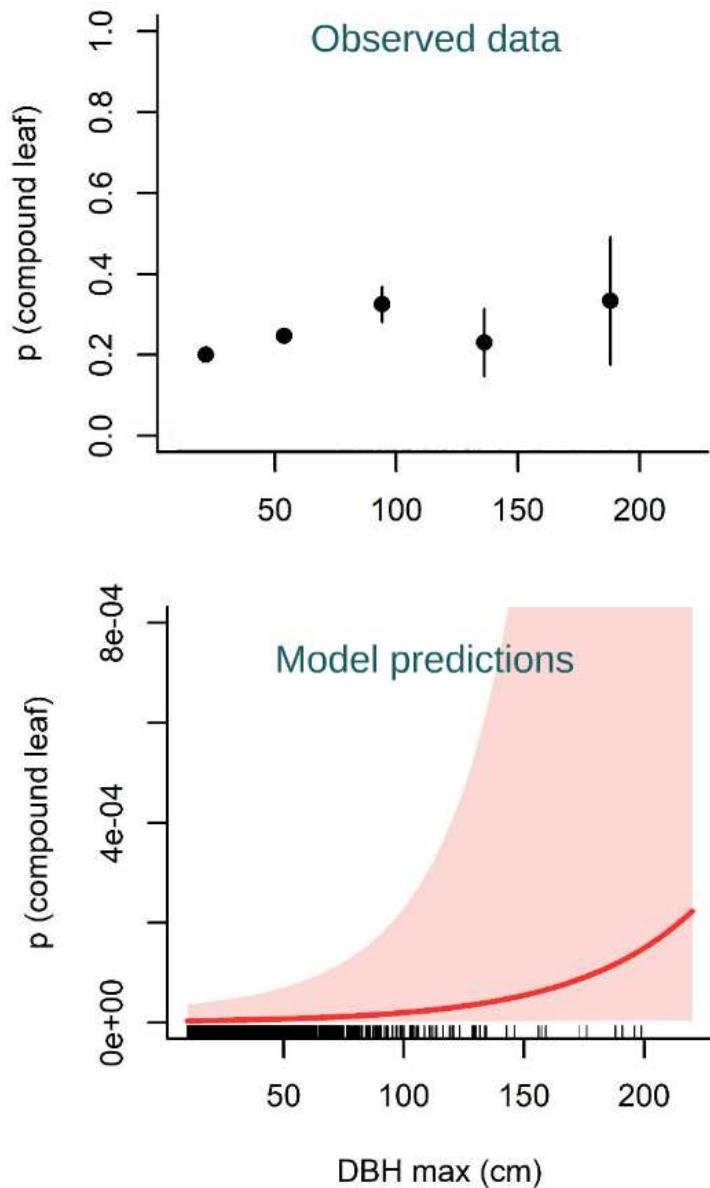
Bañares-de Dios et al. (in prep.)



mechanical resistance hypothesis

# Results

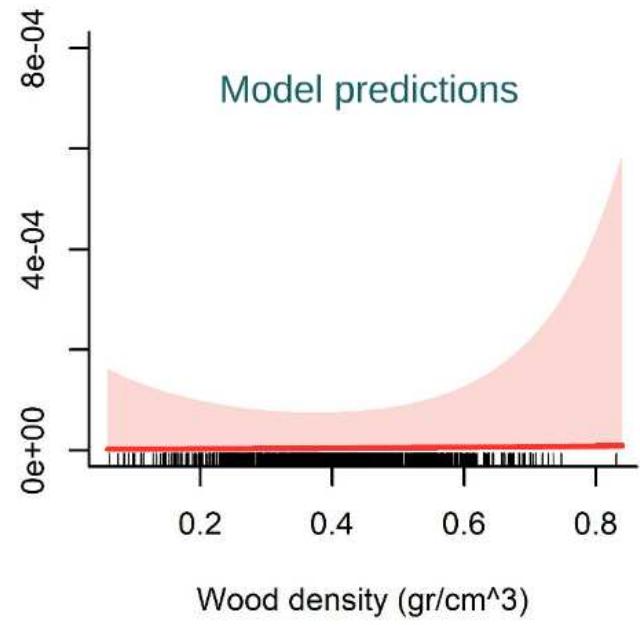
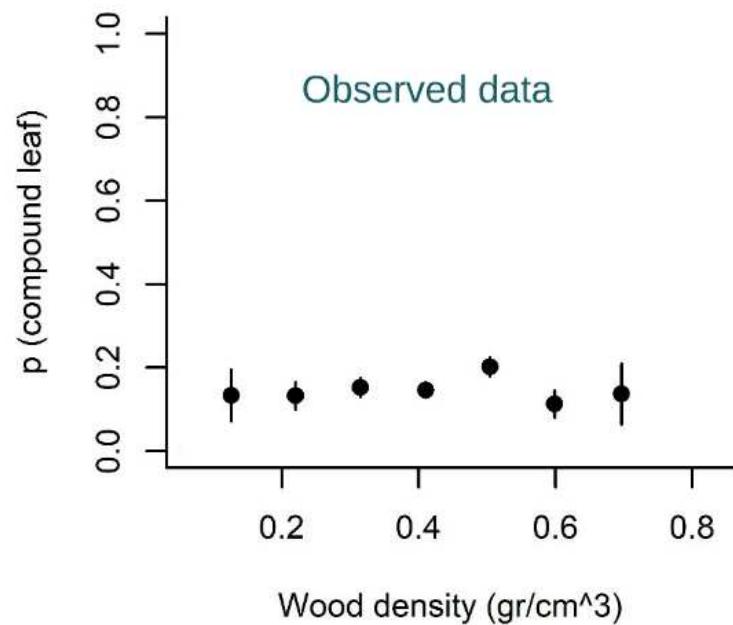
- Species with maximum higher DBH seems to have higher probabilities to have compound leaves
  - Random phylogenetic effects (genus and family membership) account for much of the observed variability ( $R^2 = 0.99$ )
    - When accounting for phylogenetic effects, the effect of maximum DBH on the probability of a species to have compound leaves was almost negligible ( $R^2 < 0.001$ )



The rapid growth hypothesis

# Results

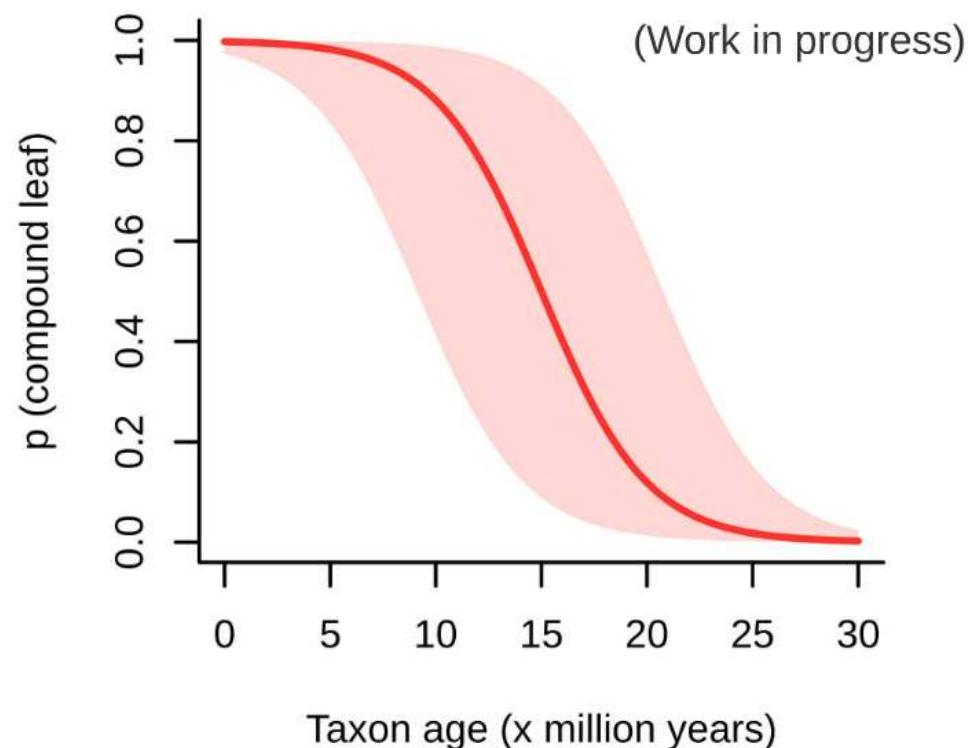
- If trees with compound leaves are more likely to be pioneer species, we would expect a higher proportion of species with compound leaves associated to lower values of wood density
- Our results do not show any support to this hypothesis
  - Once more, random phylogenetic effects accounted for much of the observed variability ( $R^2 = 0.99$ )



# The higher leafing intensity hypothesis

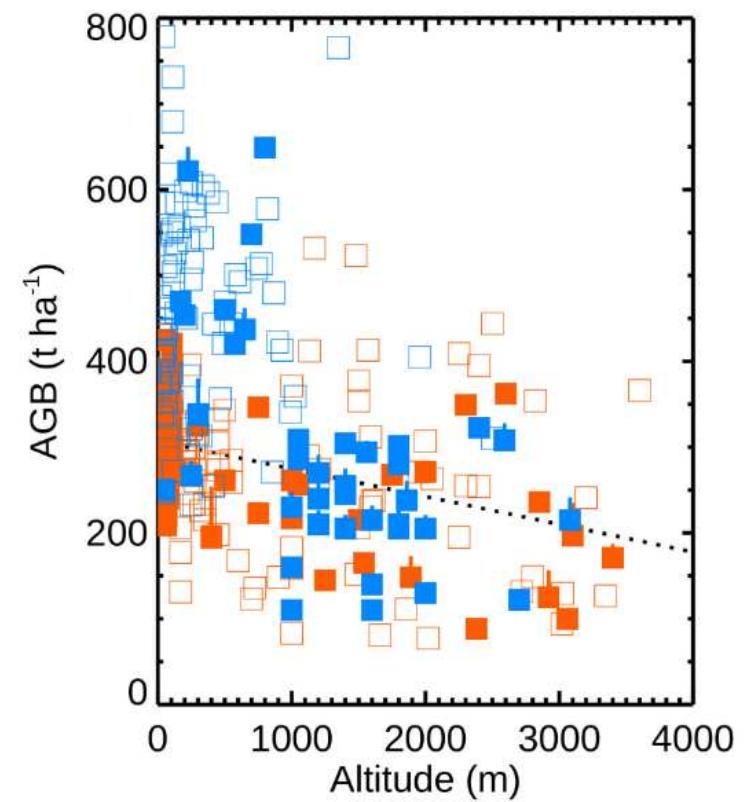
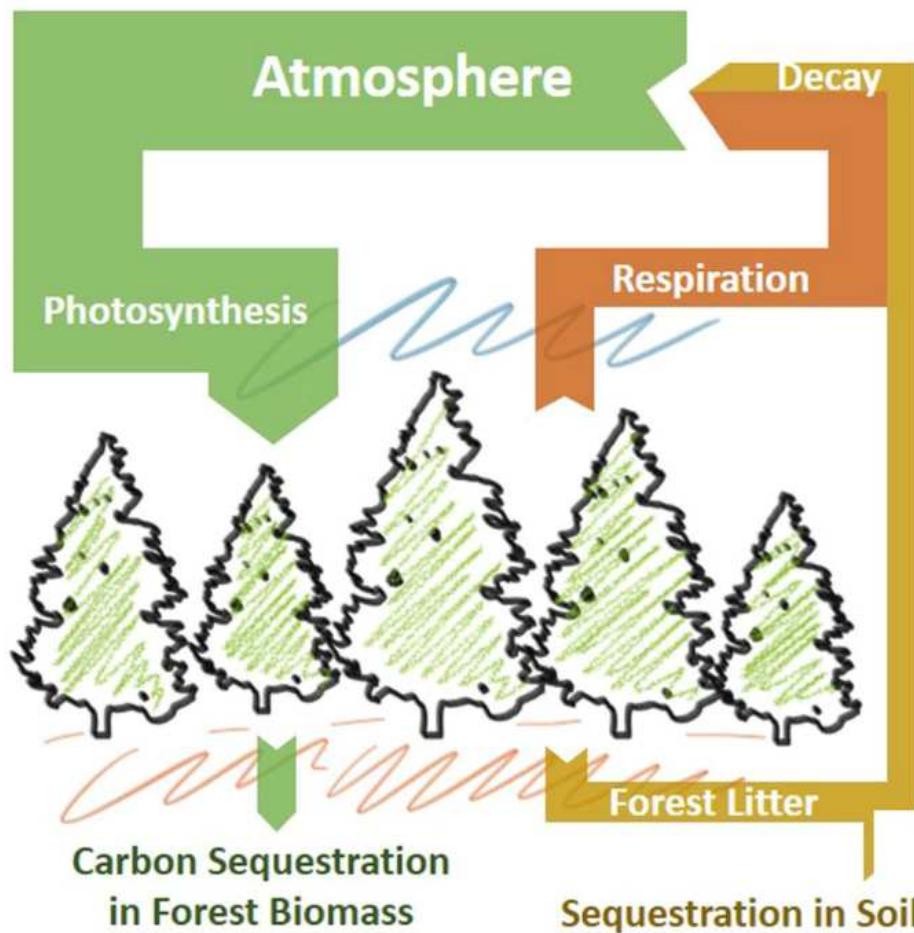
- Compound leaves could have evolved from ancestral simple leaves because the result was a leaf with smaller mass, which represents a trade-off of selection that favoured the production of more of them
- Producing more leaves generates a larger ‘bud bank’, and therefore more opportunities for generating novel adaptive mutations for transmission through the germ line

Aarsen (2012)



# Trade-offs in carbon budgets

Ecosystem functioning



Spracklen & Righelato (2014)

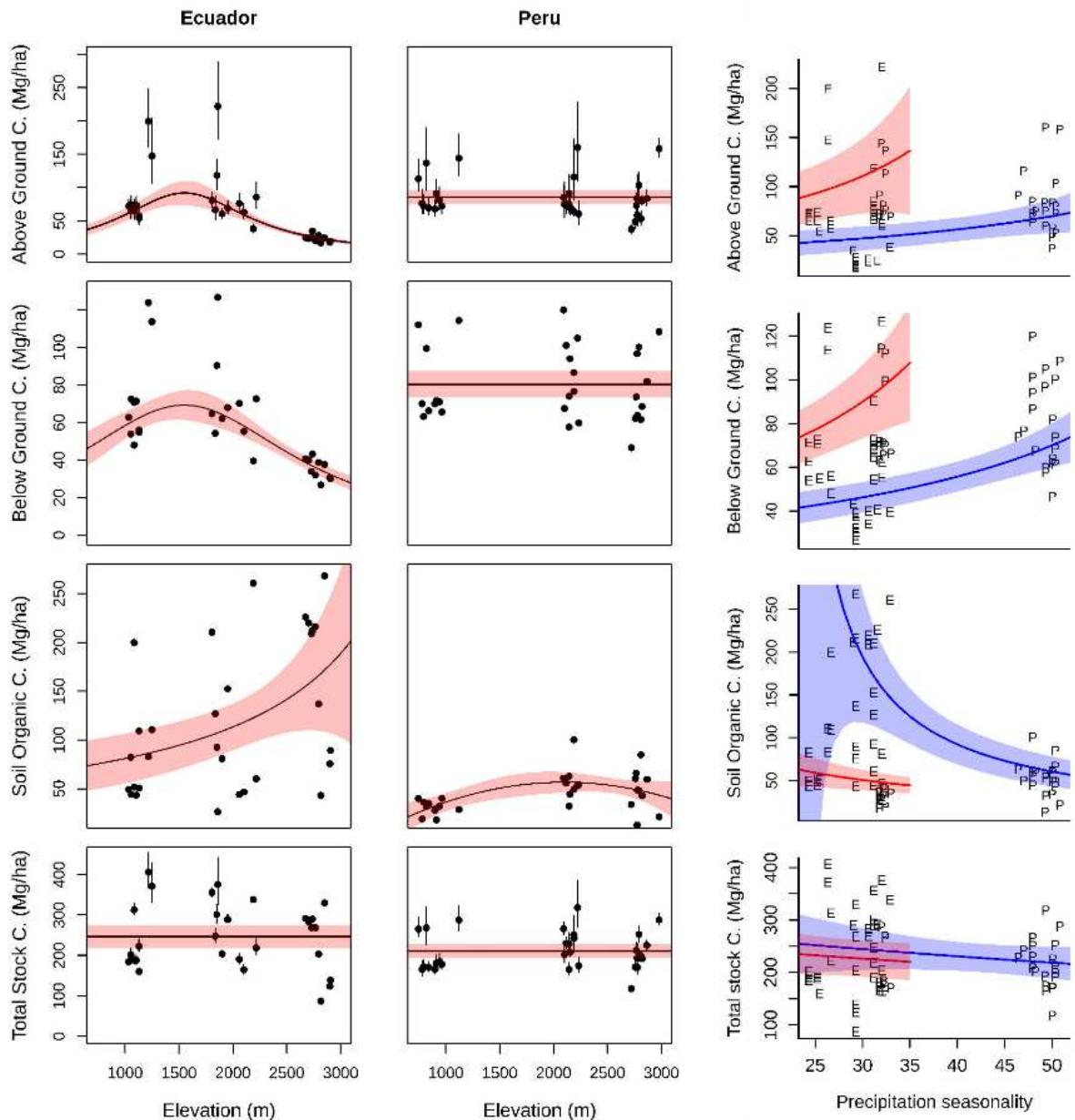
# Results

- Patterns of change with elevation for C stocks of the different forest compartments are not consistent

But... total C stock systematically did not change with elevation

- Temperature and precipitation seasonality might explain these patterns

de la Cruz *et al.* (in prep.)



A few  
take home  
messages





- Environmental filtering is the overriding process structuring TMF communities, whereas competitive exclusion has no effect
- Species turnover is exceptionally high in TMFs
  - No decline with latitude (no support to the "mountain passes hypothesis" (Janzen 1976) within the tropical belt)
- Compound leaves decline systematically with elevation in TMFs
  - No ecological explanation to such patterns
  - A strong phylogenetical signal
    - Might this be related to the 'higher leafing intensity' hypothesis?
- Carbon stocks in the different forest compartments do not vary consistently with elevation
  - There is no change in total carbon stocks along elevational gradients
  - Trade-offs might be explained by changes in precipitation seasonality, particularly at high elevations

# The *team* & funders

Funding agencies:



sDiv synthesis centre of iDiv



The *usual suspects*:



Guillermo Bañares de Dios



Gabriel M. de Carvalho



Manuel J. Macía



Iñigo Granzow de la Cerdá



Norma Salinas



Carlos Iván Espinosa



Jorge Armijos



Lydia de la Cruz