CForBio讲坛第58讲

Higher-order Interactions Enhance Latitudinal Tree Diversity Gradient

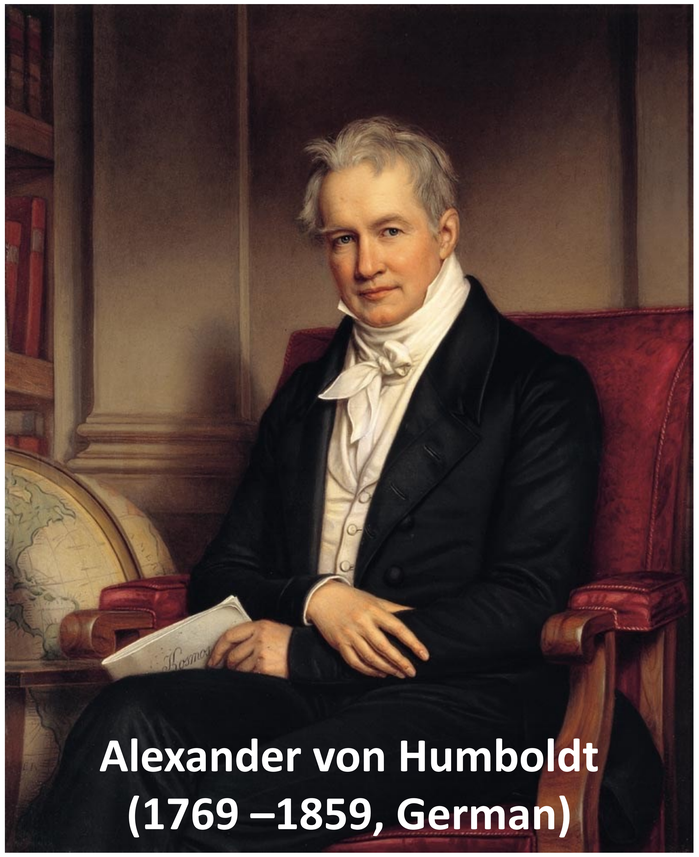
Yuanzhi Li| Junli Xiao| Yuan Jiang| Chengjin Chu

MAPPING (Microbe Animal Plant Plant Interaction Network Group)

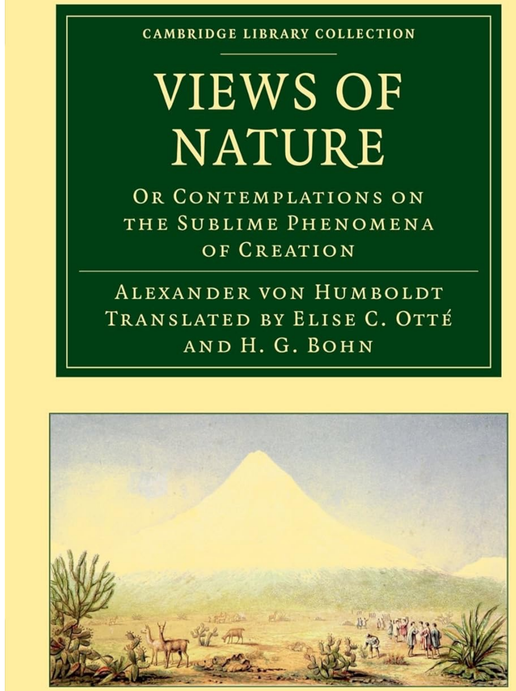
liyuanzhi@mail.sysu.edu.cn; chuchjin@mail.sysu.edu.cn

2026.05.18

Latitudinal Diversity Gradient (LDG)



Alexander von Humboldt
(1769 –1859, German)

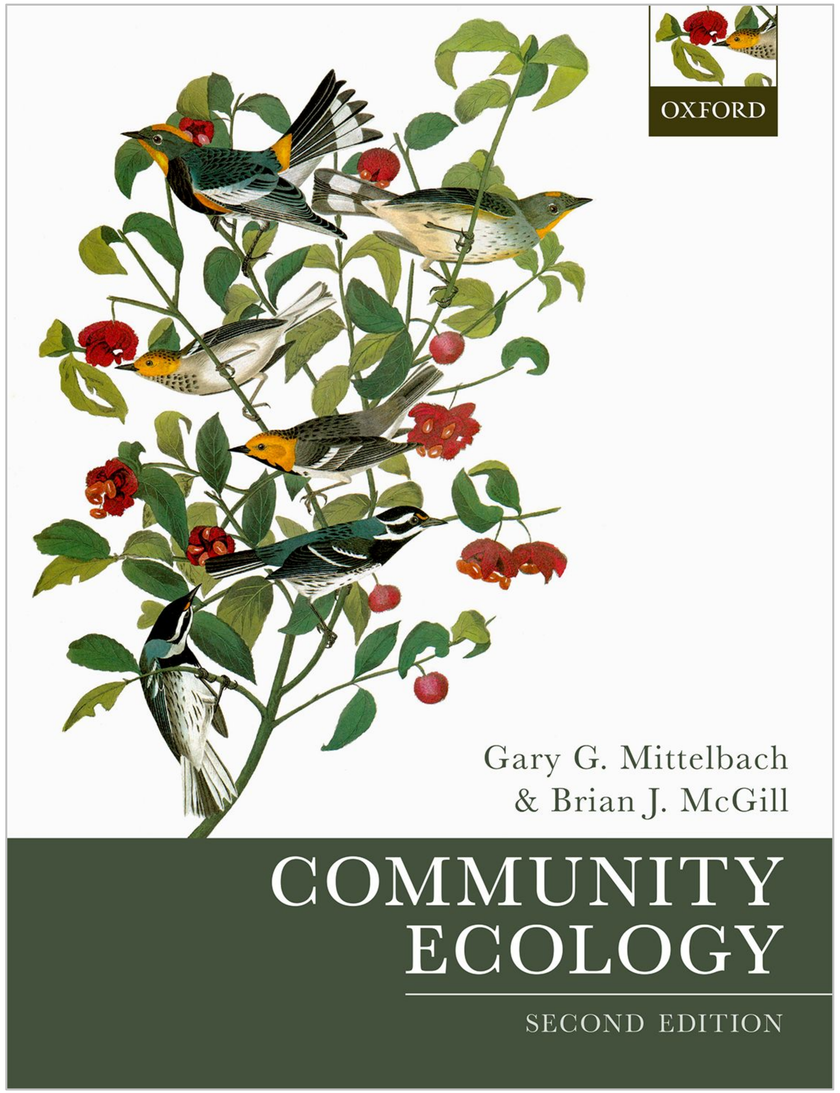


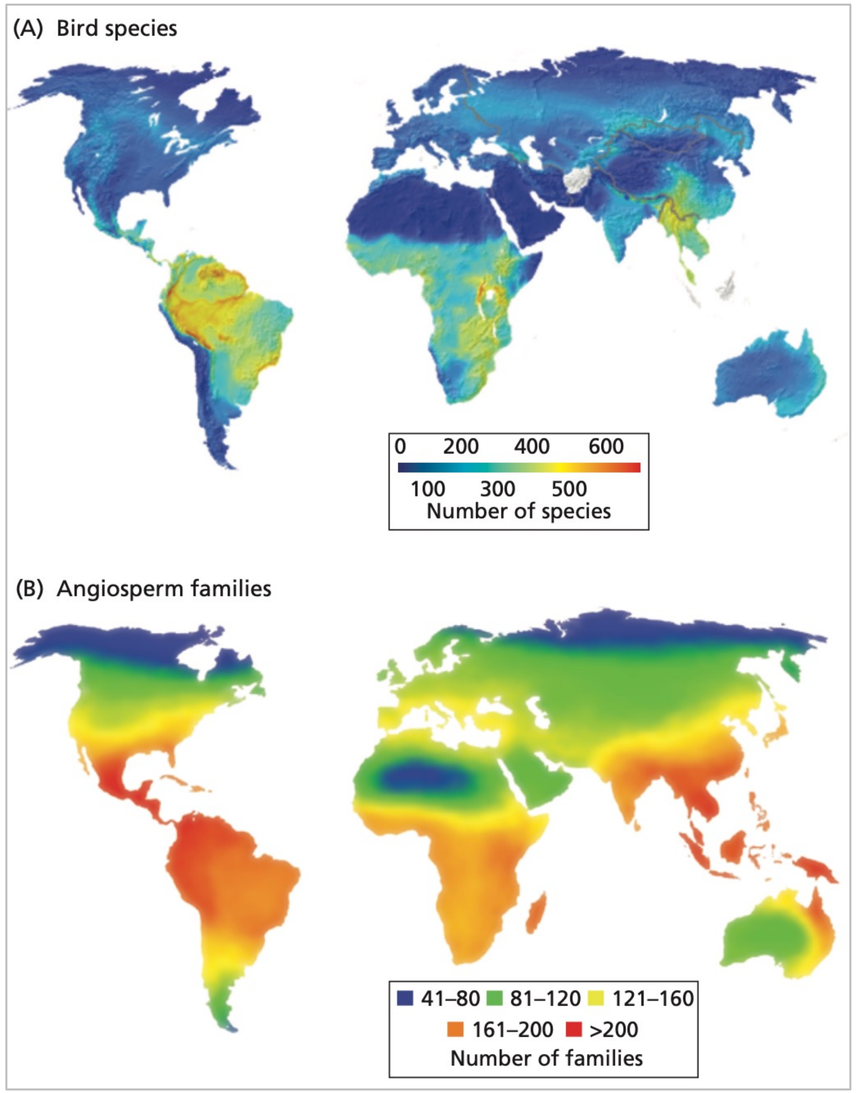
1850

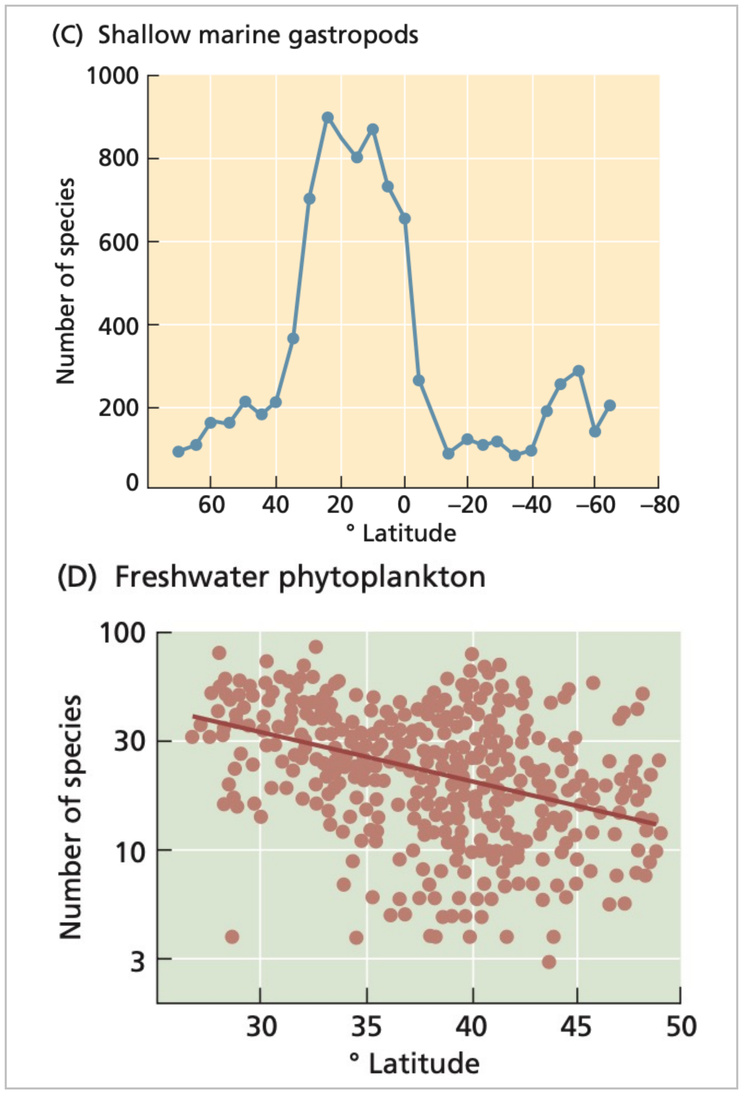
But although life is everywhere diffused, and although the organic forces are incessantly at work in combining into new forms those elements which have been liberated by death; yet this fulness of life and its renovation differ according to difference of climate. Nature undergoes a periodic stagnation in the frigid zones; for fluidity is essential to life. Animals and plants, excepting indeed mosses and other Cryptogamia, here remain many months buried in a winter sleep. Over a great portion of the earth, therefore, only those organic forms are capable of full development, which have the property of resisting any considerable abstraction of heat, or those which, destitute of leaf-organs, can sustain a protracted interruption of their vital functions. Thus, the nearer we approach the tropics, the greater the increase in variety of structure, grace of form, and mixture of colours, as also in perpetual youth and vigour of organic life.

Whether von Humboldt was right about why the latitudinal diversity gradient exists is beside the point. The funny thing is that his *ca.* 200-year-old idea represents one of the major hypotheses currently being tested by ecologists and biogeographers to account for geographical variation in species diversity (Hawkins, 2001, TREE).

Latitudinal Diversity Gradient (LDG)

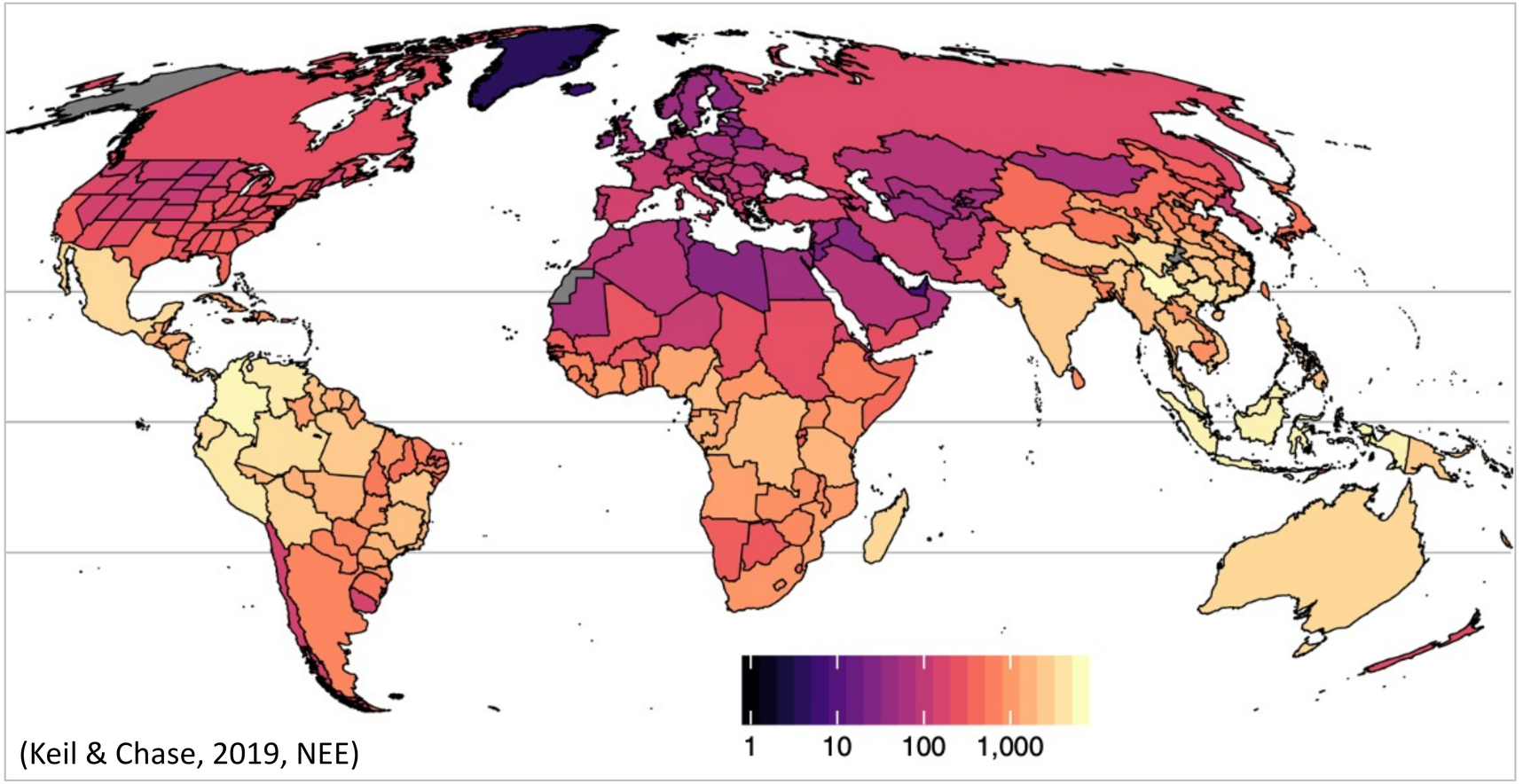




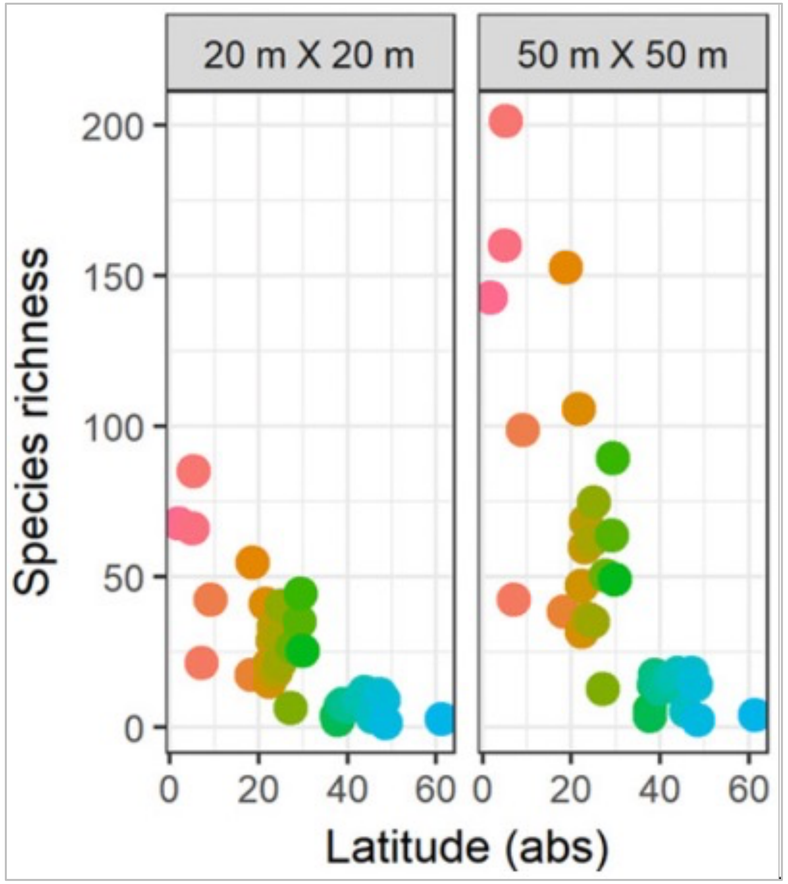


Latitudinal Diversity Gradient (LDG)

Latitudinal Tree Diversity Gradient



(Keil & Chase, 2019, NEE)



(Chu et al., 2019, Ecology Letters)

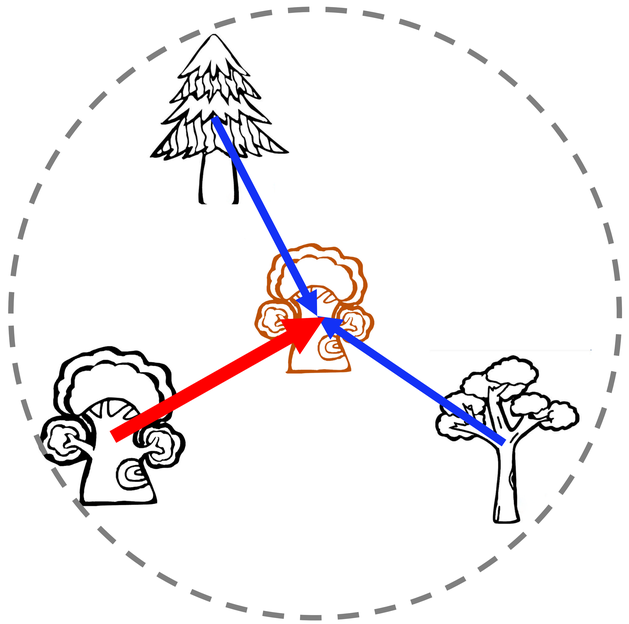
Latitudinal Diversity Gradient (LDG)

Table 1 Hypothesized drivers for large-scale gradients, their mechanistic bases, and their predictions about speciation, extinction, and specialization in tropical versus temperate bioregions

Hypothesis (citation)	Status in this review (citation if rejected)	Mechanism	Predict higher speciation rates in tropics?	Predict lower extinction rates in tropics?	Predict higher specialization rates in tropics?
Geographic area (W, R, M)	Included in area/energy/time hypothesis	Larger regions should have larger average population sizes, which should have higher speciation and/or lower extinction rates. Because speciation and extinction take time, area and time must be considered together.	Yes	Yes	No prediction
Tropical conservatism (M)	Included in area/energy/time hypothesis	See above	Yes	Yes	No prediction
Out of the tropics (M)	Included in area/energy/time hypothesis	See above	Yes	Yes	No prediction
Available energy/ productivity (W, R, P)	Included in area/energy/time hypothesis and ecological limits hypothesis	More energy should increase population sizes. This should increase speciation and reduce extinction rates (see above), as well as allow for a greater carrying capacity for species (see below)	Yes	Yes	Yes
Competition/niche width (R)	Included in ecological limits hypothesis	Regions with more available energy are able to support a higher equilibrium diversity, enforced by biotic interactions in a zero-sum relationship among community abundances within regions.	Yes	Yes	Yes
Climate stability/ambient energy (R, W)	Included in climate stability hypothesis	Regions with more climatic stability have lower extinction rates; climate stability promotes narrow physiological tolerances and specialization in general, increasing speciation rates, and isolates formed by allopatry are more likely to persist	Yes	Yes	Yes
Rapaport's rescue/narrow physiological tolerance (W, M)	Included in climate stability hypothesis	See above	Yes	Yes	Yes
Parapatric/sympatric speciation (M)	Included in climate stability hypothesis	See above	Yes	Yes	Yes
Spatial heterogeneity (P)	Included in climate stability hypothesis	See above	Yes	Yes	Yes
Evolutionary speed (W, R, M)	Included in evolutionary speed hypothesis	Regions with more temperature (kinetic energy) harbor organisms with faster metabolic rates and generation times, speeding up natural selection and speciation rates	Yes	No prediction	Yes
Competition/ predation (P)	Included in biotic interactions hypothesis	Regions with stronger biotic interactions could have increased speciation rates due to positive feedback on coevolutionary rates across a geographic mosaic and could have reduced extinction rates due to increased competition driving finer niche specialization or increased predation causing less competition and more coexistence.	Yes	Yes	Yes
Biotic interactions (M)	Included in biotic interactions hypothesis	See above	Yes	Yes	Yes
Genetic drift (R, M)	Rejected (R, M)	Genetic drift of small populations increase speciation probabilities in diverse systems	Yes	No prediction	No prediction
Geometric constraints/ mid-domain (W)	Rejected (C)	Large-scale gradients occur randomly	No prediction	No prediction	No prediction
Time (R, M)	Rejected (R, M)	More time to diversify	No prediction	No prediction	No prediction

Biotic interactions augment both diversification and coexistence in tropical bioregions (Fine, 2015, AREES).

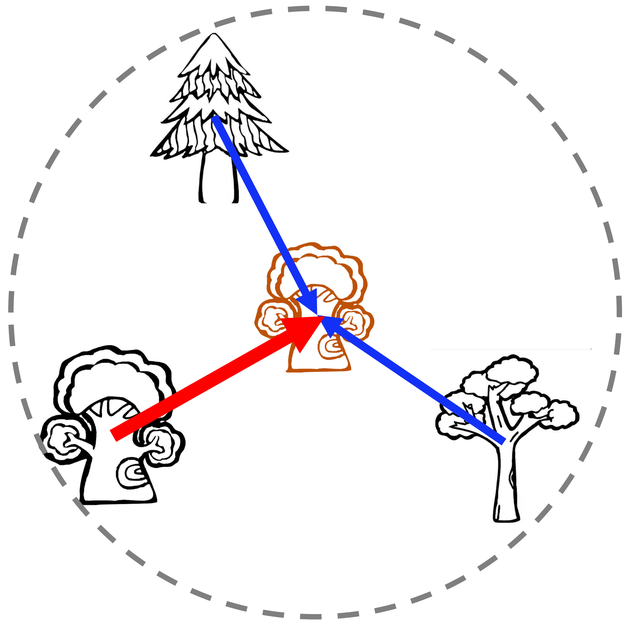
Conspecific Negative Density Dependence (CNDD)



CNDD is the process by which conspecific neighbors exert more negative effects on the performance of a focal tree than heterospecific neighbors as a results of natural enemies and/or competition for space and resources.

Stronger CNDD maintains higher diversity in lower latitudes?

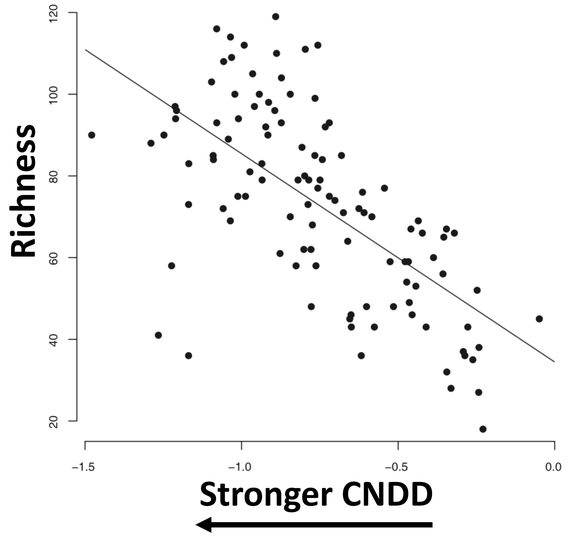
Conspecific Negative Density Dependence (CNDD)



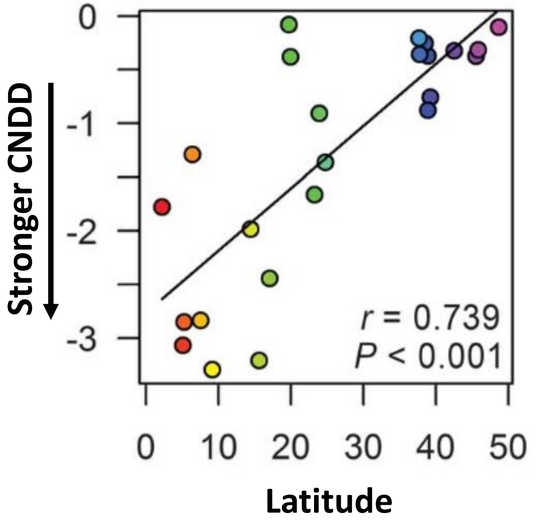
CNDD is the process by which conspecific neighbors exert more negative effects on the performance of a focal tree than heterospecific neighbors as a results of natural enemies and/or competition for space and resources.

Stronger CNDD maintains higher diversity in lower latitudes?

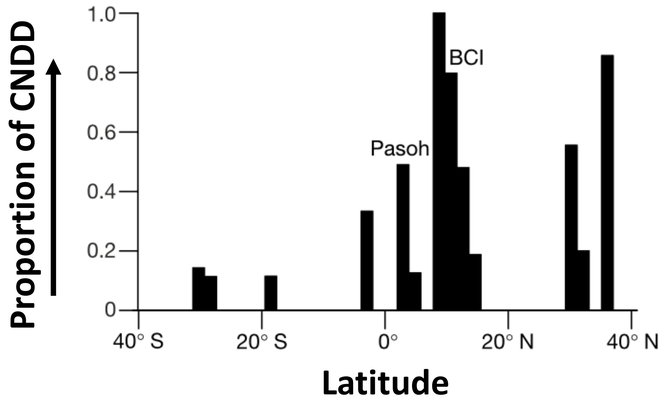
(√ Johnson et al., 2012, Science)



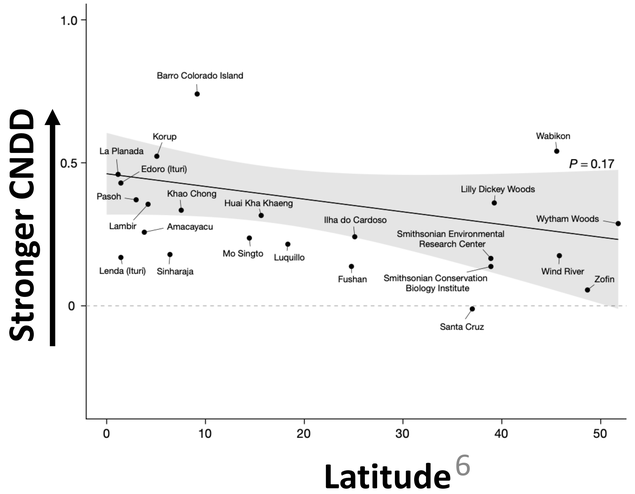
(√ LaManna et al., 2017, Science)



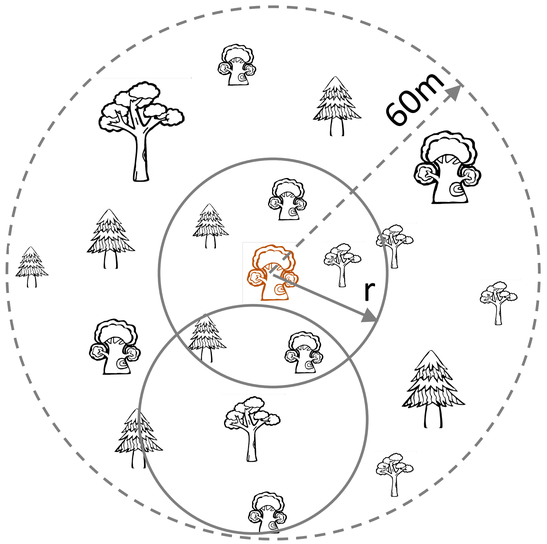
(× Lambers et al., 2002, Nature)



(× Hülsmann et al., 2024, Nature)



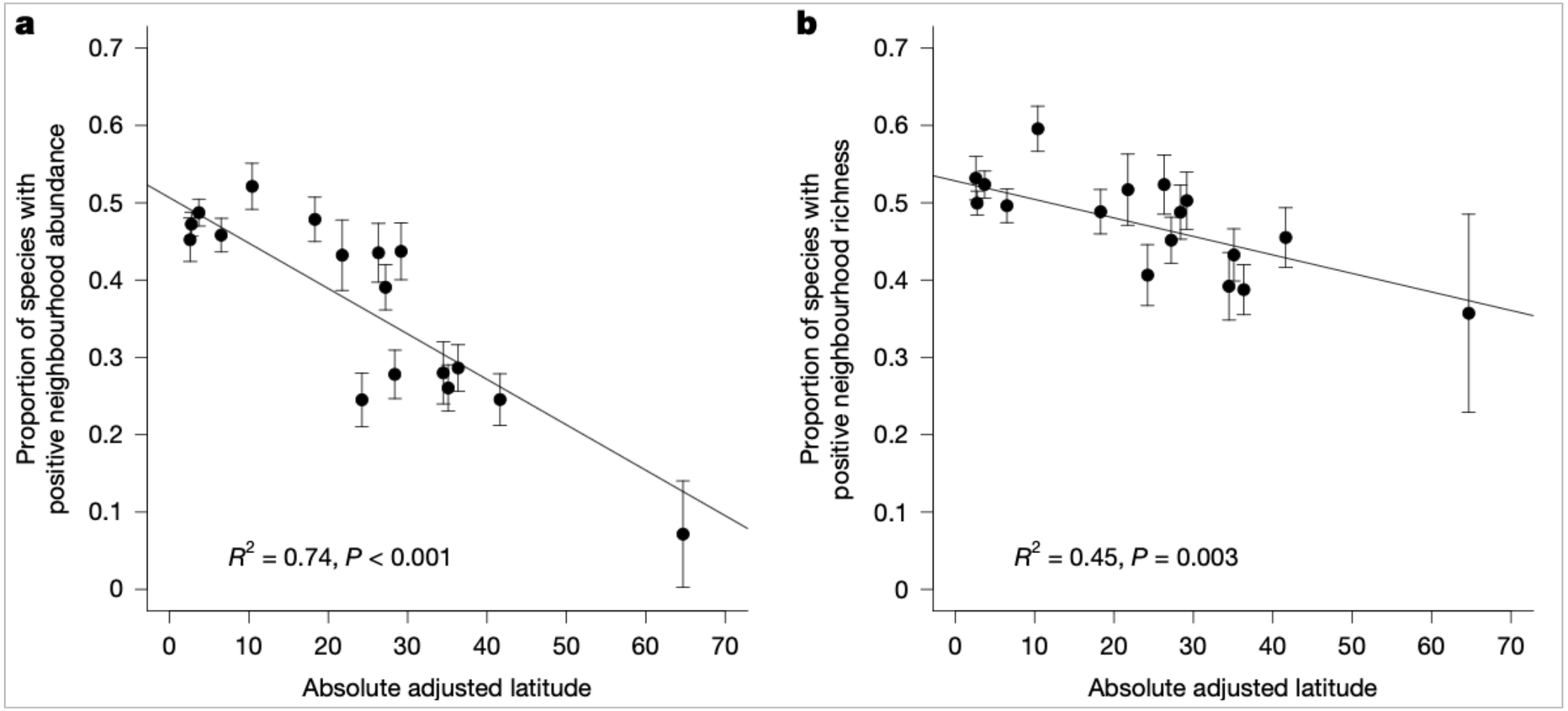
Facilitation (Positive Interaction)



$$IAAR_i(r) = \frac{1}{n_i}\sum_{j=1}^{n_i} N_{ij}(r)$$

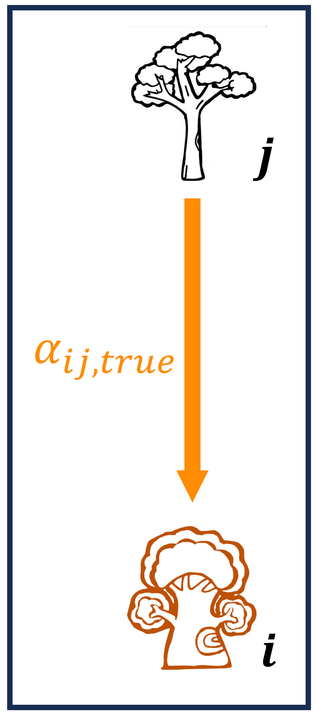
$$ISAR_i(r) = \frac{1}{n_i}\sum_{j=1}^{n_i} S_{ij}(r)$$

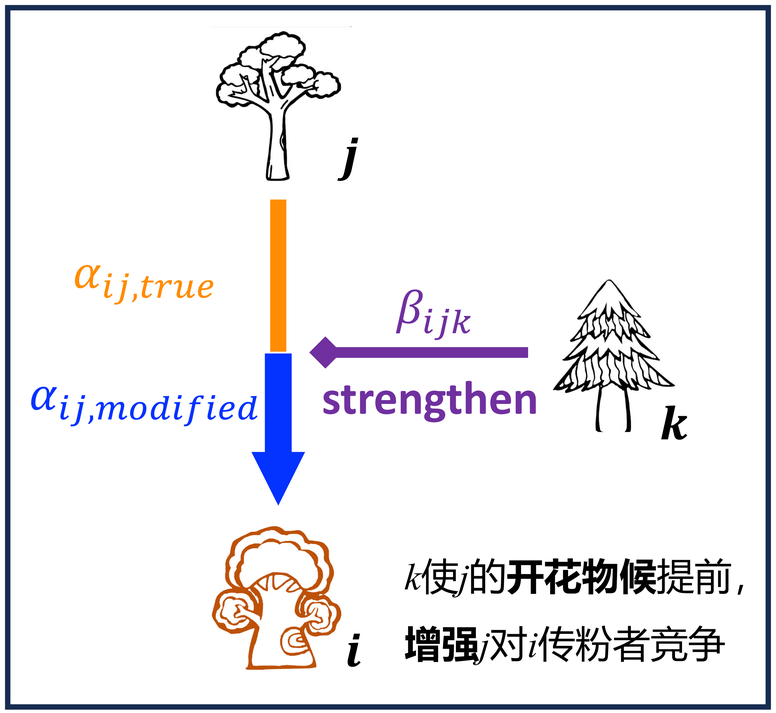
$$\frac{IAAR_i(r)}{IAAR_{0,i}(r)} > 1; \frac{ISAR_i(r)}{ISAR_{0,i}(r)} > 1$$

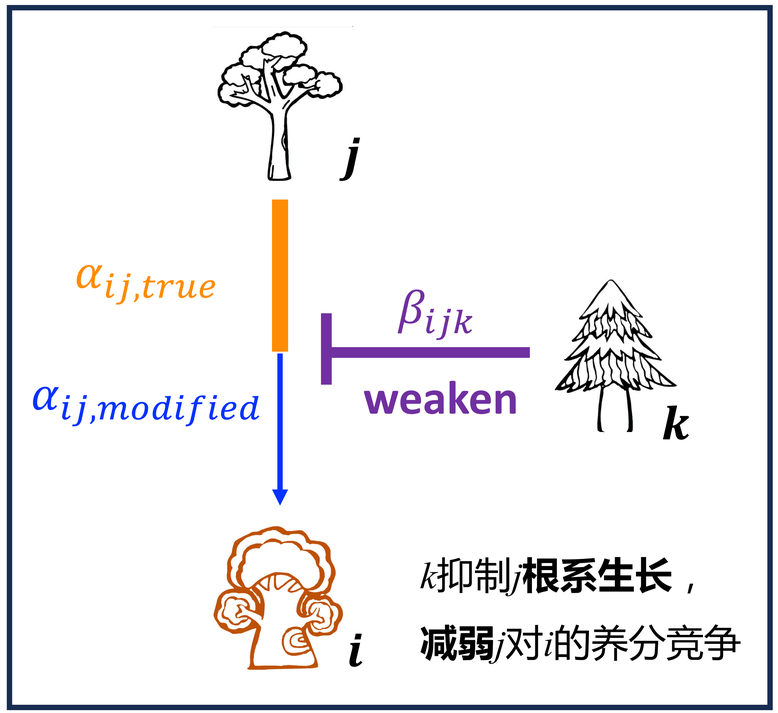


The decreasing facilitation at high latitudes (reduced abundance of legumes, non-arbuscular mycorrhizal associations, the weaker canopy nursing effect) weakens the strength of complementarity effect, thus reducing productivity and diversity (Xu et al., 2026, Nature).

Higher-order Interactions (HOIs)







HOIs emerge when pairwise interactions between two neighboring trees are modified by other neighbors

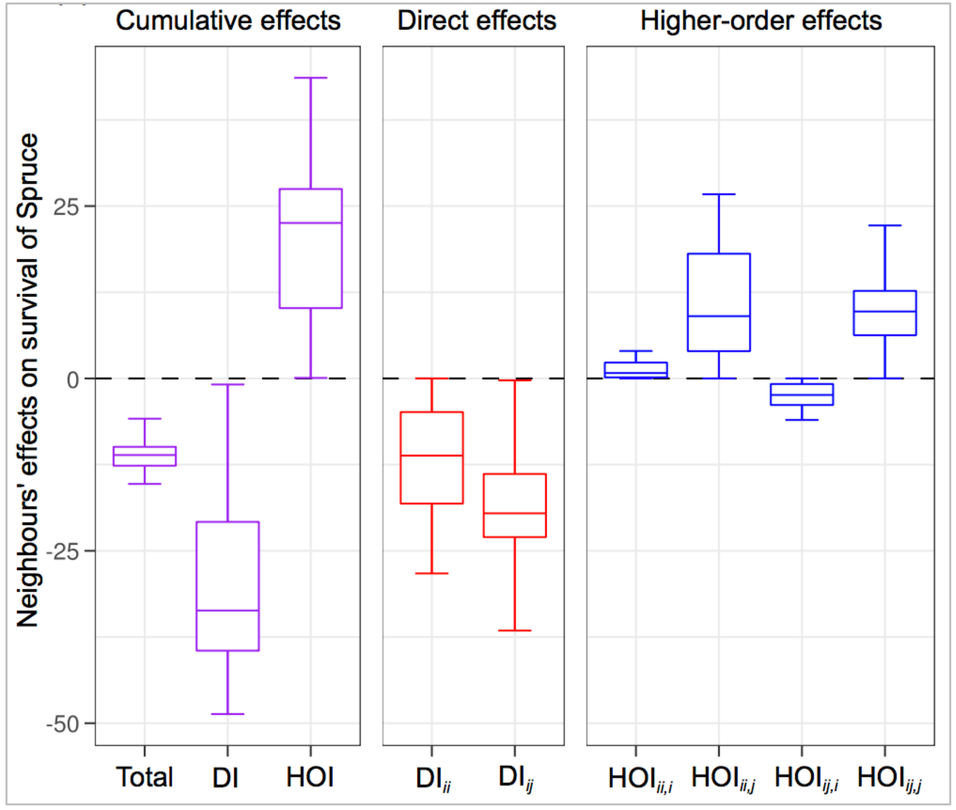
(also termed interaction modification or trait-mediate indirect interaction).

$$\alpha_{ij,modified} = \alpha_{ij}(N_k) = \alpha_{ij,true} + b_{ijk}N_k \Rightarrow \alpha_{ij,modified}N_j = \alpha_{ij,true}N_j + b_{ijk}\mathrm{N}jN_k$$

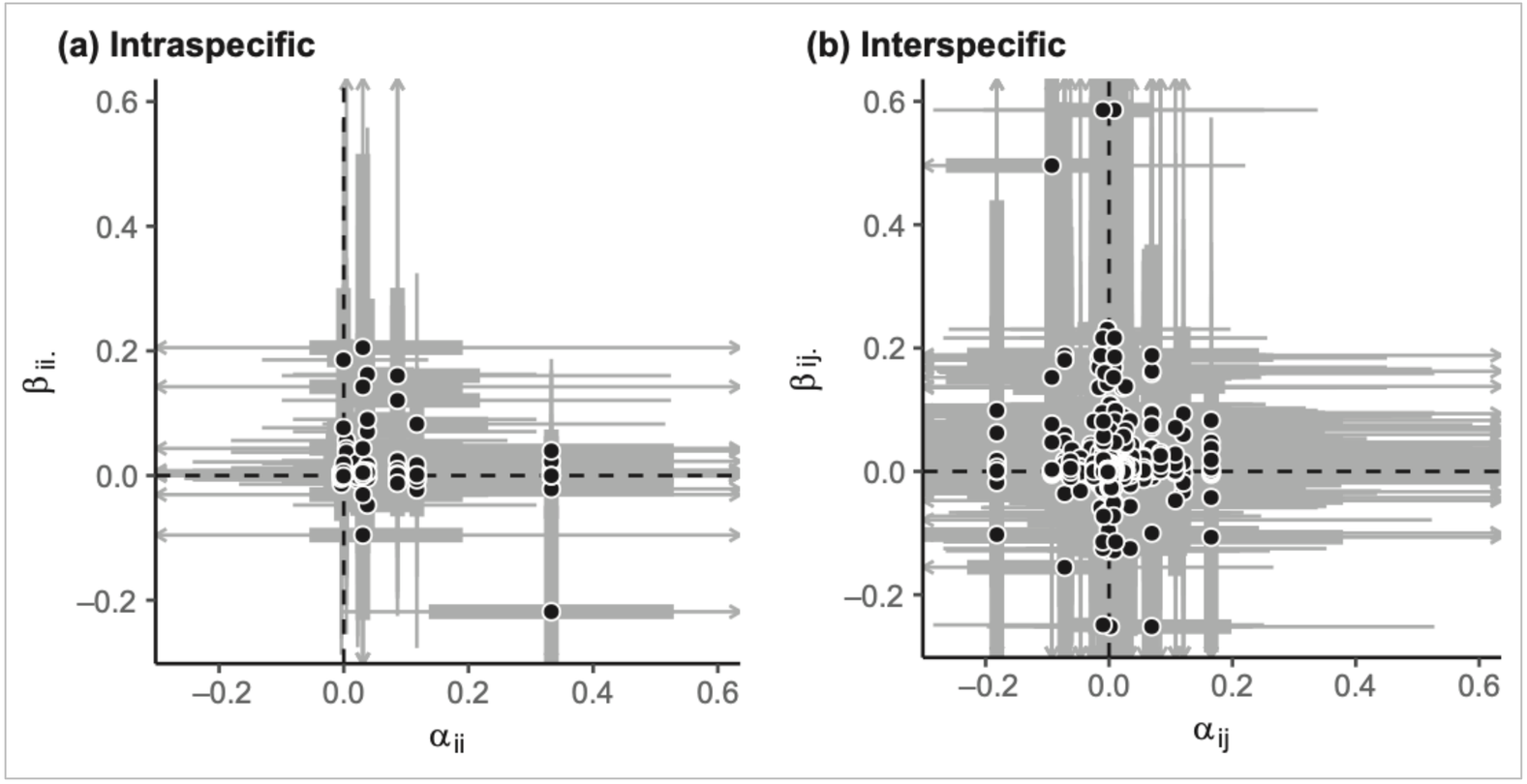
Few other questions in ecology have such great potential to radically shift how we think about the maintenance and fragility of biodiversity (Levine et al. 2017, Nature)

Higher-order Interactions (HOIs)

a temperate forest (Czech)



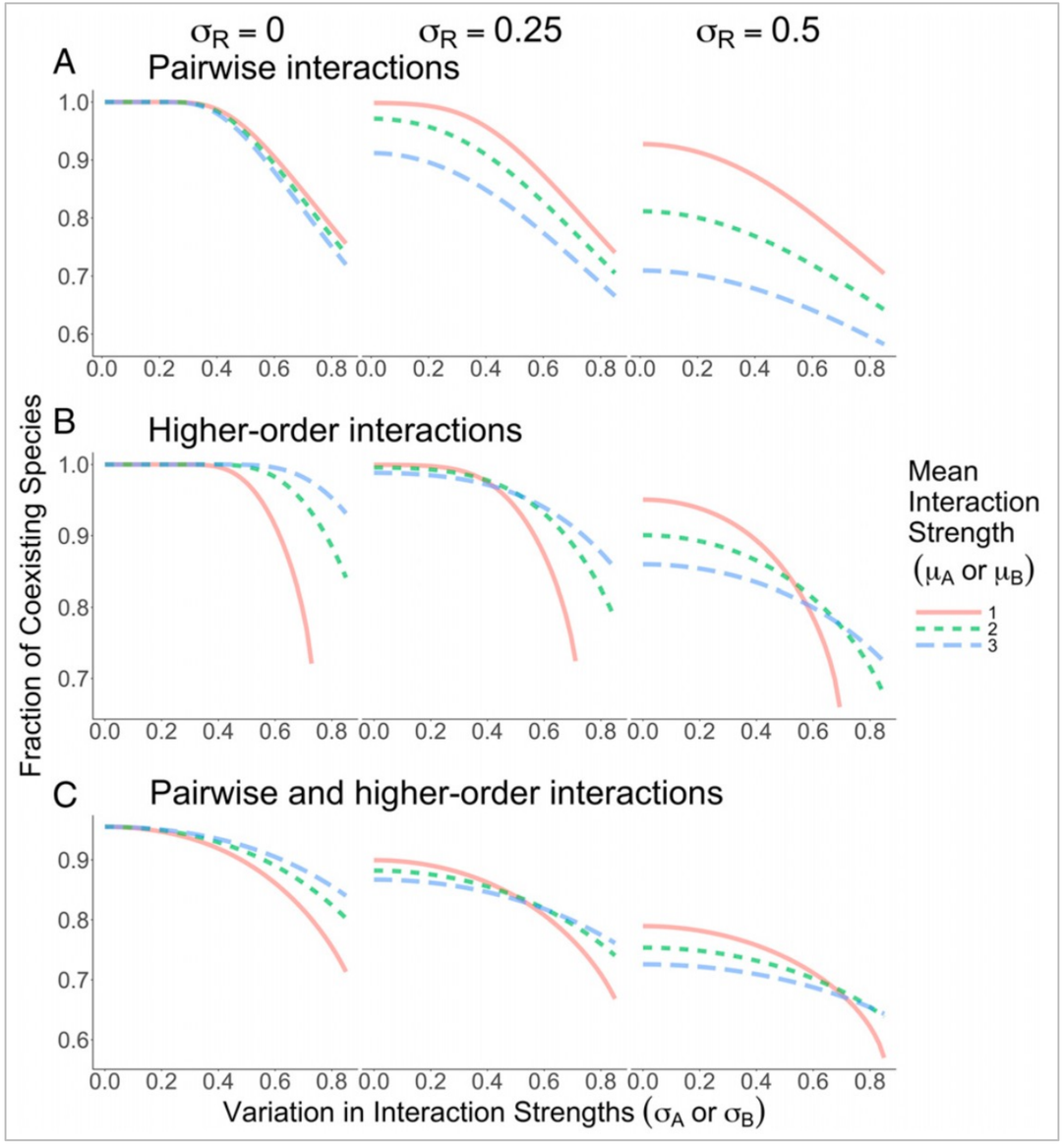
a tropical forest (Singapore)



HOIs weaken pairwise interactions (Li et al., 2021, NSR).

HOIs strengthen pairwise interactions (Lai et al., 2022, Ecology).

Higher-order Interactions (HOIs)



$$\frac{dN_i}{dt} = N_i\left(\begin{array}{c} r_i - \sum_j A_{ij}N_j \\ -\sum_{j,k} B_{ijk}N_jN_k \end{array}\right)$$

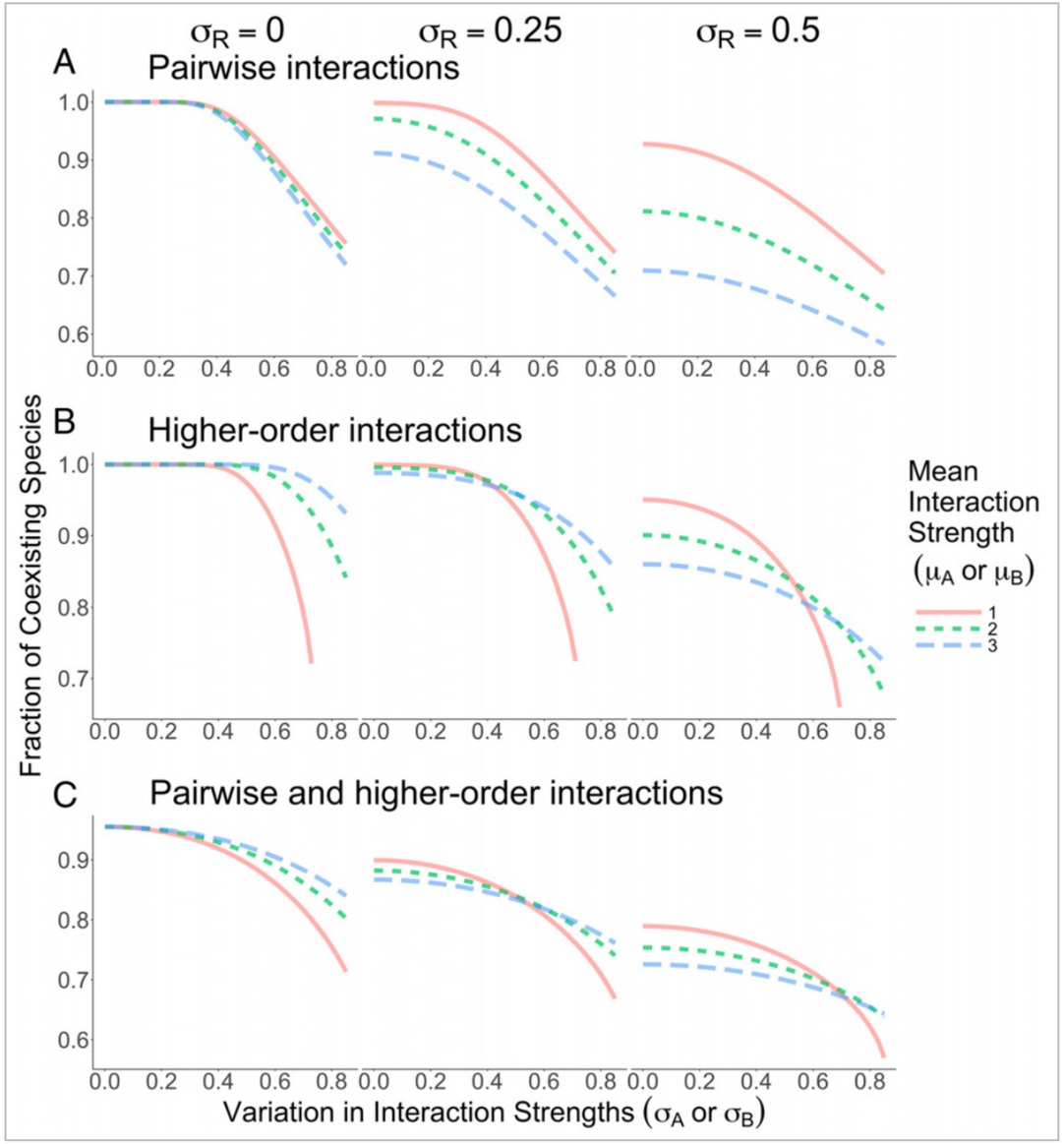
$r \sim N(\mu_R, \sigma_R^2)$,

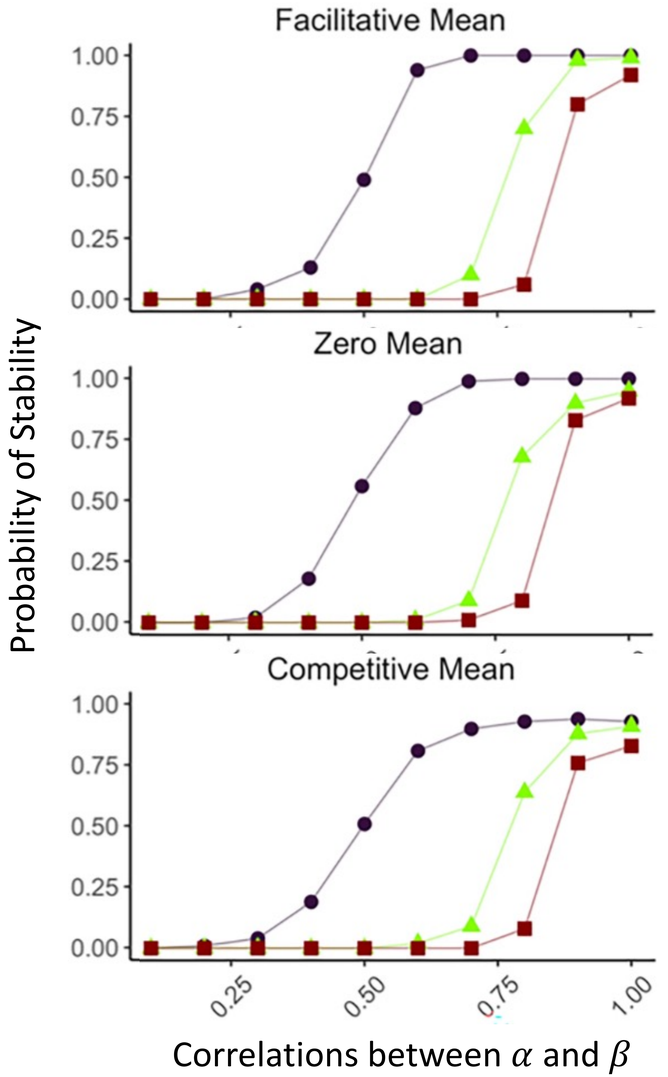
$A \sim N(\mu_A/S, \sigma_A^2/S)$

$B \sim N(\mu_B/S^2, \sigma_B^2/S^2)$

As strengths of HOIs became more variable across species, fewer species could coexist (Gibbs et al., 2022, PNAS)

Higher-order Interactions (HOIs)



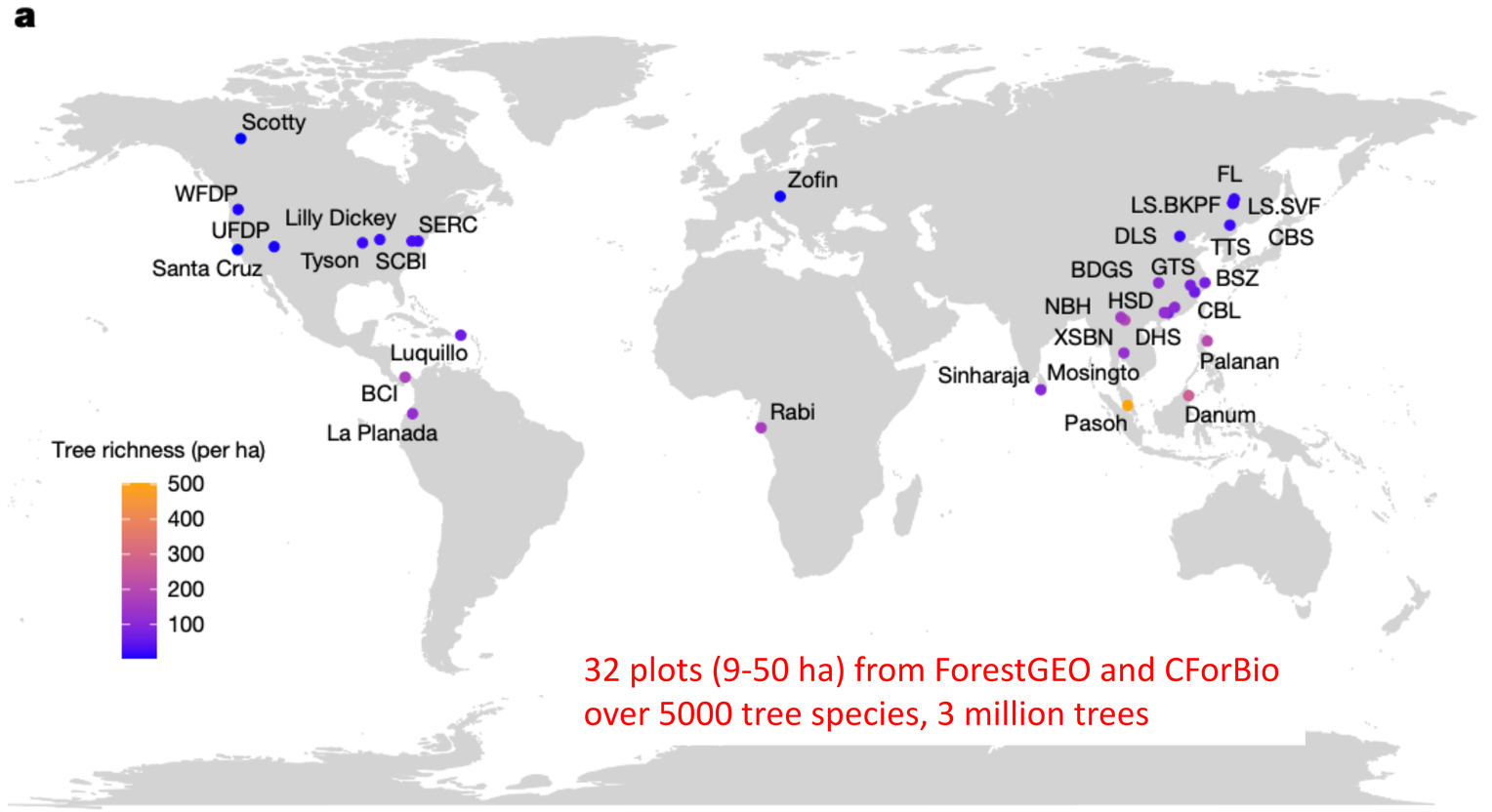


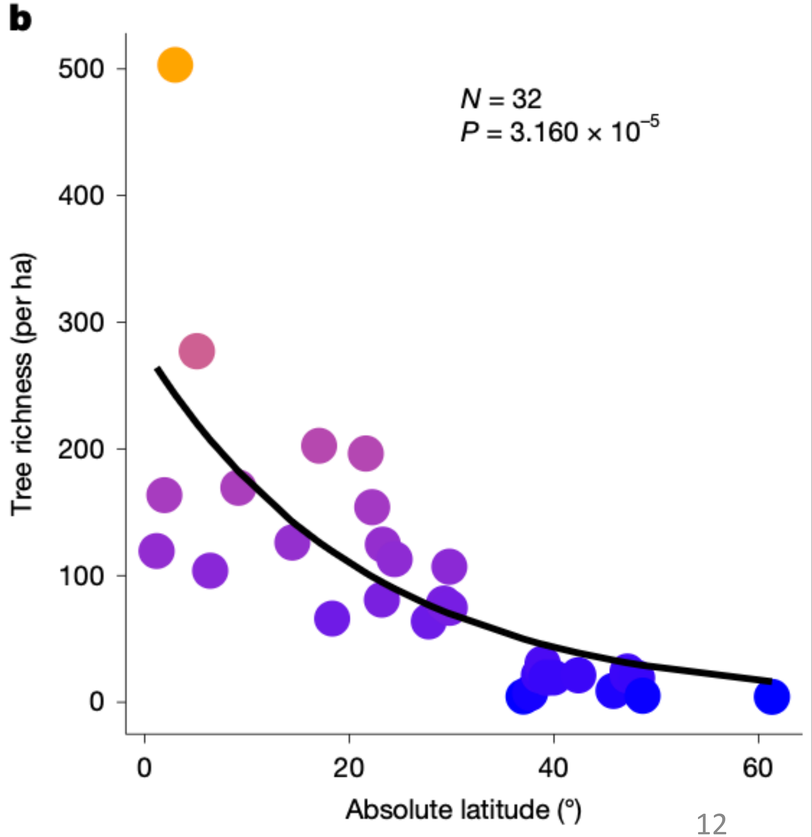
As strengths of HOIs became more variable across species, fewer species could coexist (Gibbs et al., 2022, PNAS)

Correlations between the pairwise and higher-order interactions do permit robust coexistence even in diverse systems (Gibbs et al., 2024, Ecology Letters)

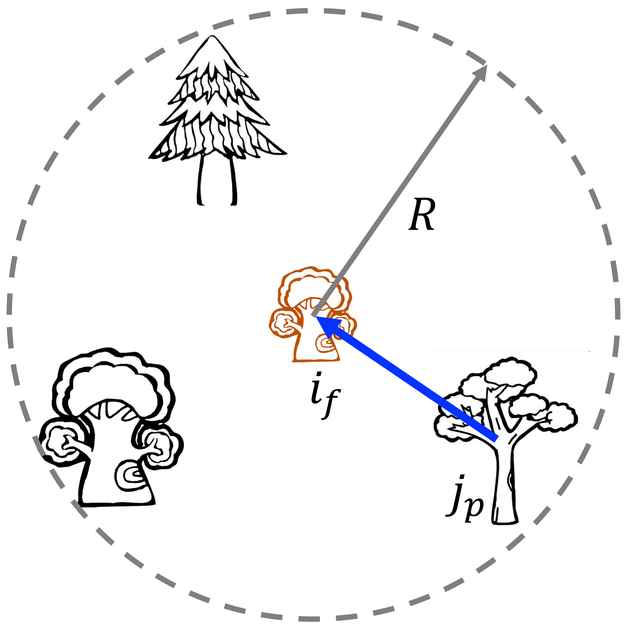
Three Key Questions

- ❑ Are HOIs prevalent among trees across forest plots? (Q1)
- ❑ How do pairwise interactions ($\alpha_{ij,true}$ and $\alpha_{ij,modified}$) and HOIs (β_{ijk}) vary with latitude? (Q2)
- ❑ How do latitudinal changes in HOIs contribute to the latitudinal tree diversity gradient? (Q3)





Growth Model with HOIs



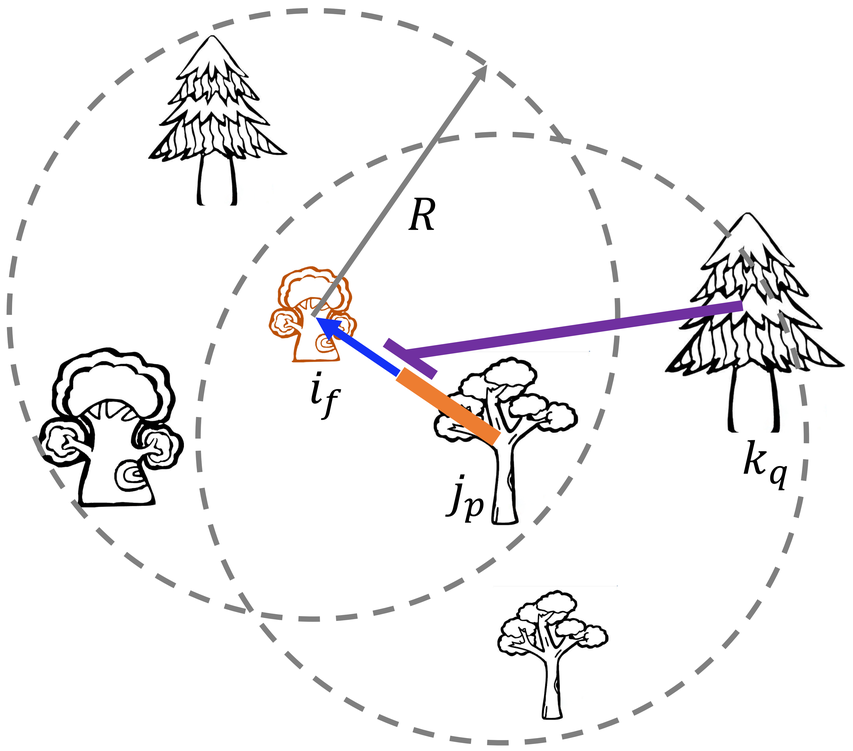
(I) Null models: $Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma}$

(II) Pair-only models: $Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma} \cdot e^{PAIR_{i_f}}$

$$PAIR_{i_f} = \sum_j \alpha_{ij} \cdot n_{j,i_f} \; ; n_{j,i_f} = \sum_{p=1}^{N_{j,i_f}} \frac{DBH_{j_p}^{u}}{d[i_f, j_p]^{v}}$$

(III) HOIs–inclusive models: $Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma} \cdot e^{PAIR_{i_f}} \cdot e^{HOI_{i_f}}$

Growth Model with HOIs



(Li et al., 2021, NSR; Li et al., 2026, Nature)

(I) Null models: $Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma}$

(II) Pair-only models: $Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma} \cdot e^{PAIR_{i_f}}$

$$PAIR_{i_f} = \sum\nolimits_j \alpha_{ij} \cdot n_{j,i_f}\,; n_{j,i_f} = \sum\nolimits_{p=1}^{N_{j,i_f}} \frac{DBH_{j_p}^{u}}{d\left[i_f, j_p\right]^{v}}$$

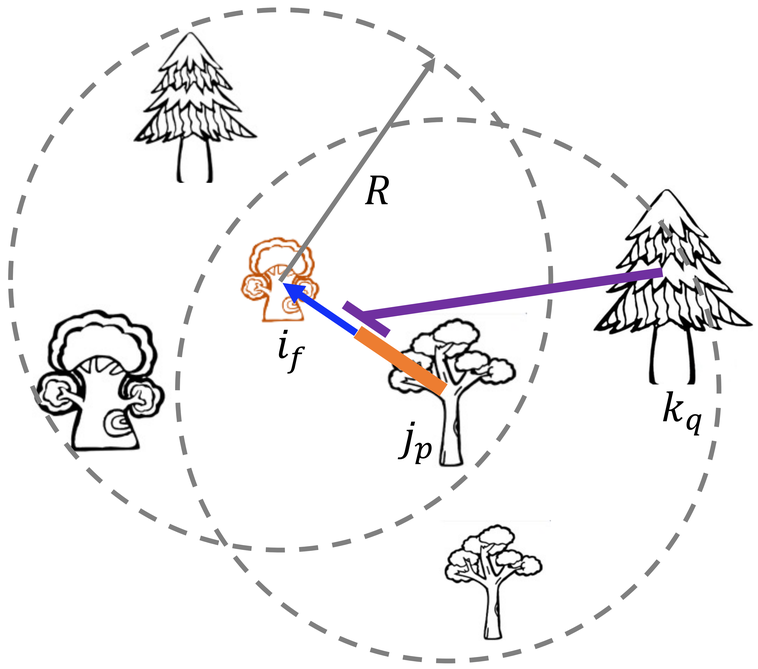
(III) HOIs–inclusive models: $Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma} \cdot e^{PAIR_{i_f}} \cdot e^{HOI_{i_f}}$

$$\sum\nolimits_j \alpha_{ij,modified} \cdot n_{j,i_f} = \sum\nolimits_j \left(\alpha_{ij,true} + \sum\nolimits_k \beta_{ijk} \cdot n_{k,j_p}\right) \cdot n_{j,i_f}$$

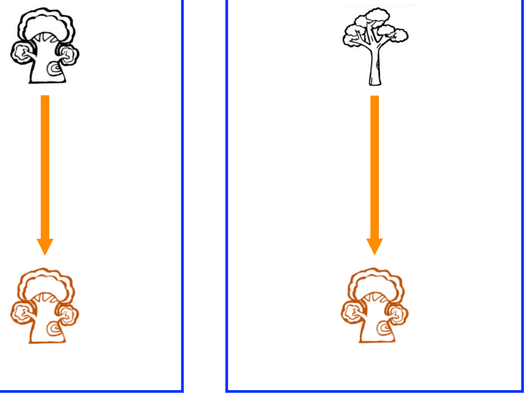
$$= \sum\nolimits_j \alpha_{ij,true} \cdot n_{j,i_f} + \sum\nolimits_j \sum\nolimits_k \beta_{ijk} \cdot n_{j,i_f} \cdot n_{k,j_p}$$

$$HOI_{i_f} = \sum\nolimits_j \sum\nolimits_k \beta_{ijk} \cdot n_{j,i_f} \cdot n_{k,j_p} \qquad A = \left[\alpha_{ij}\right]_{S\times S};\ B = \left[\beta_{ijk}\right]_{S\times S\times S}$$

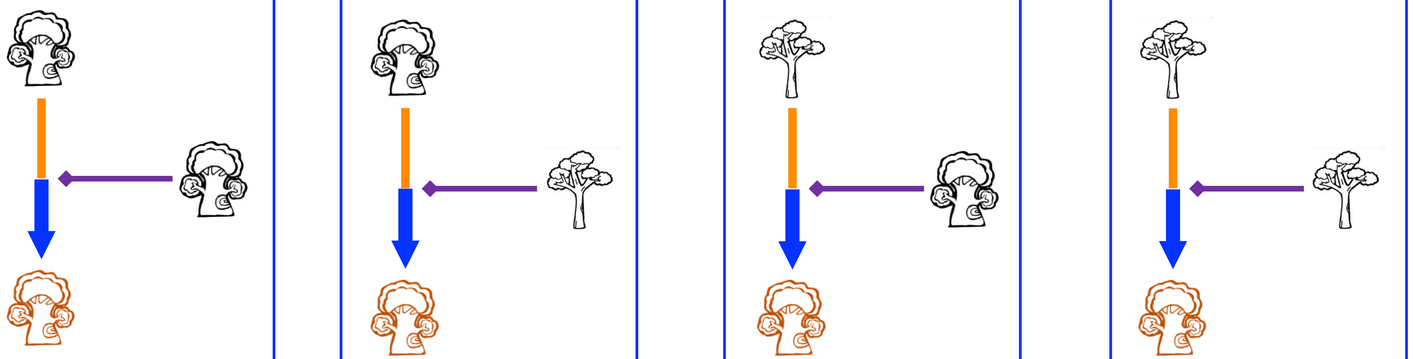
Growth Model with HOIs



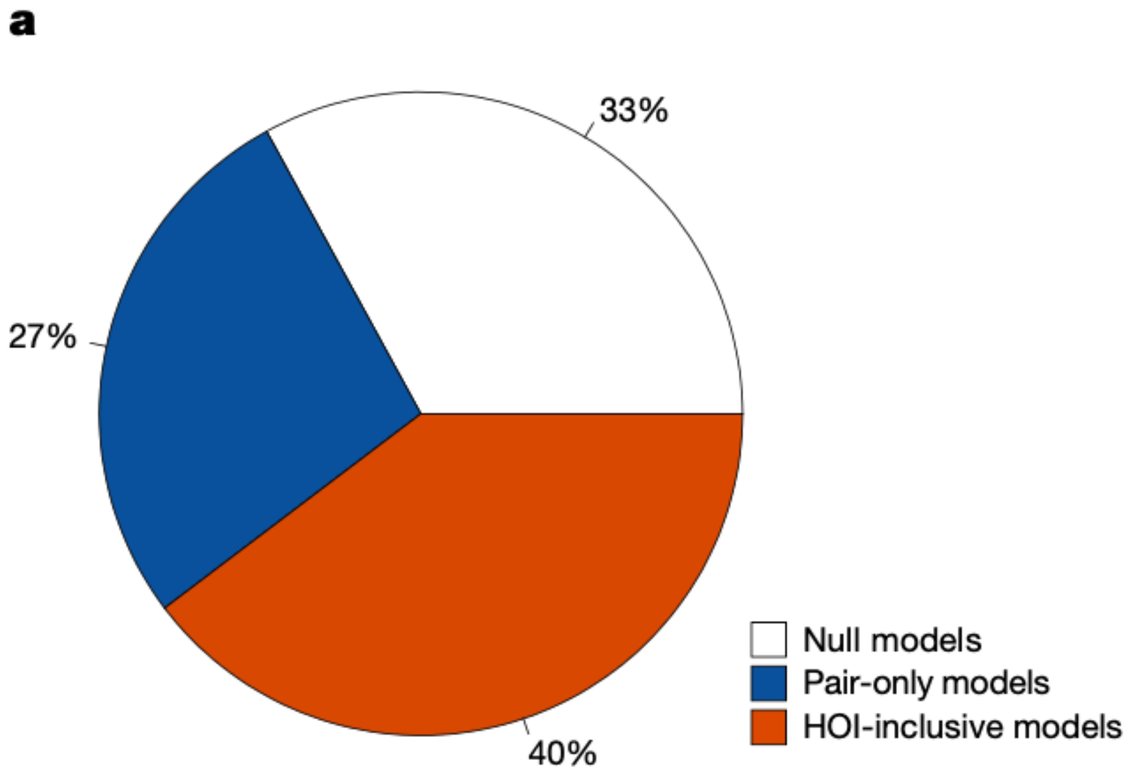
$$PAIR_{i_f} = \sum_j \alpha_{ij,true} \cdot n_{j,i_f} = \alpha_{ii,true} \cdot n_{i,i_f} + \alpha_{ih,true} \cdot n_{h,i_f}$$

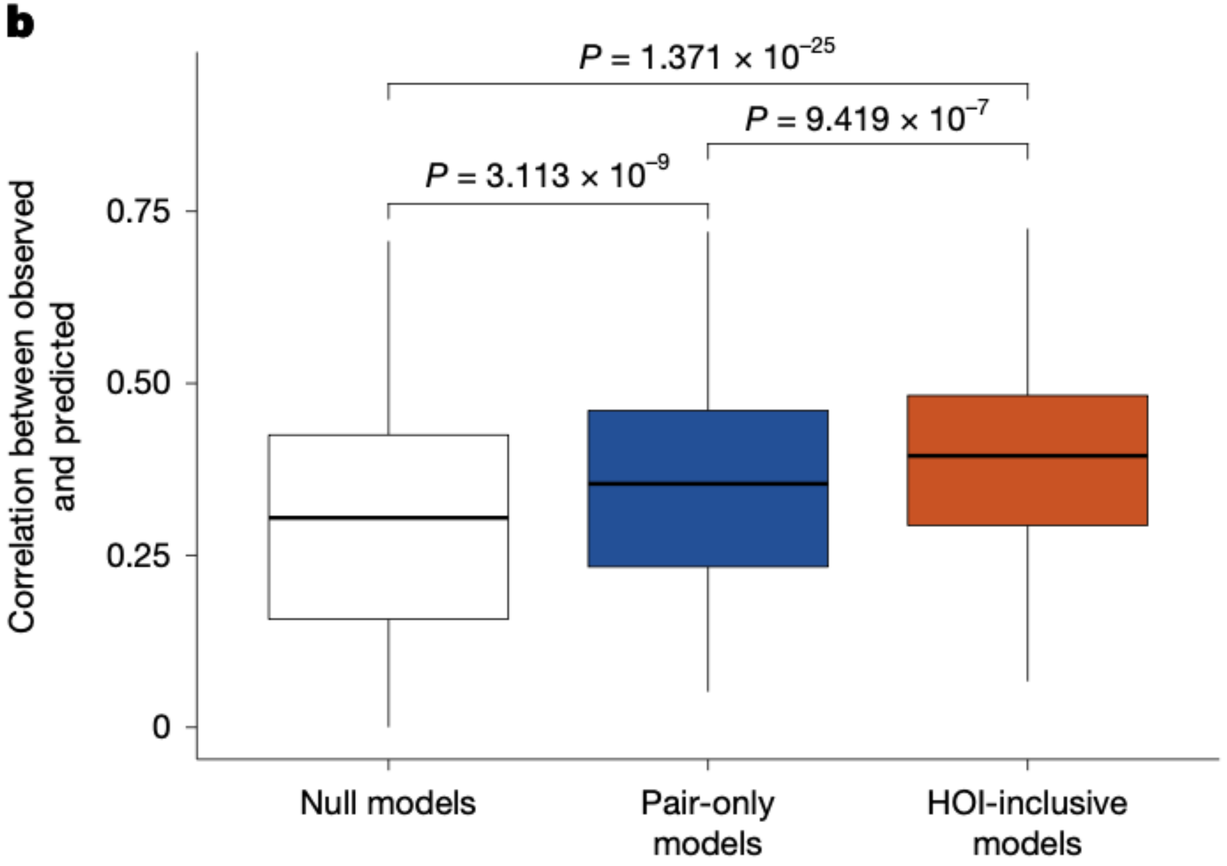


$$HOI_{i_f} = \sum_j \sum_k \beta_{ijk} \cdot n_{j,i_f} \cdot n_{k,j_p} = \beta_{iii} \cdot n_{ii,i_f} + \beta_{iih} \cdot n_{ih,i_f} + \beta_{ihi} \cdot n_{hi,i_f} + \beta_{ihh} \cdot n_{hh,i_f}$$



Prevalence of HOIs across forest plots (Q1)

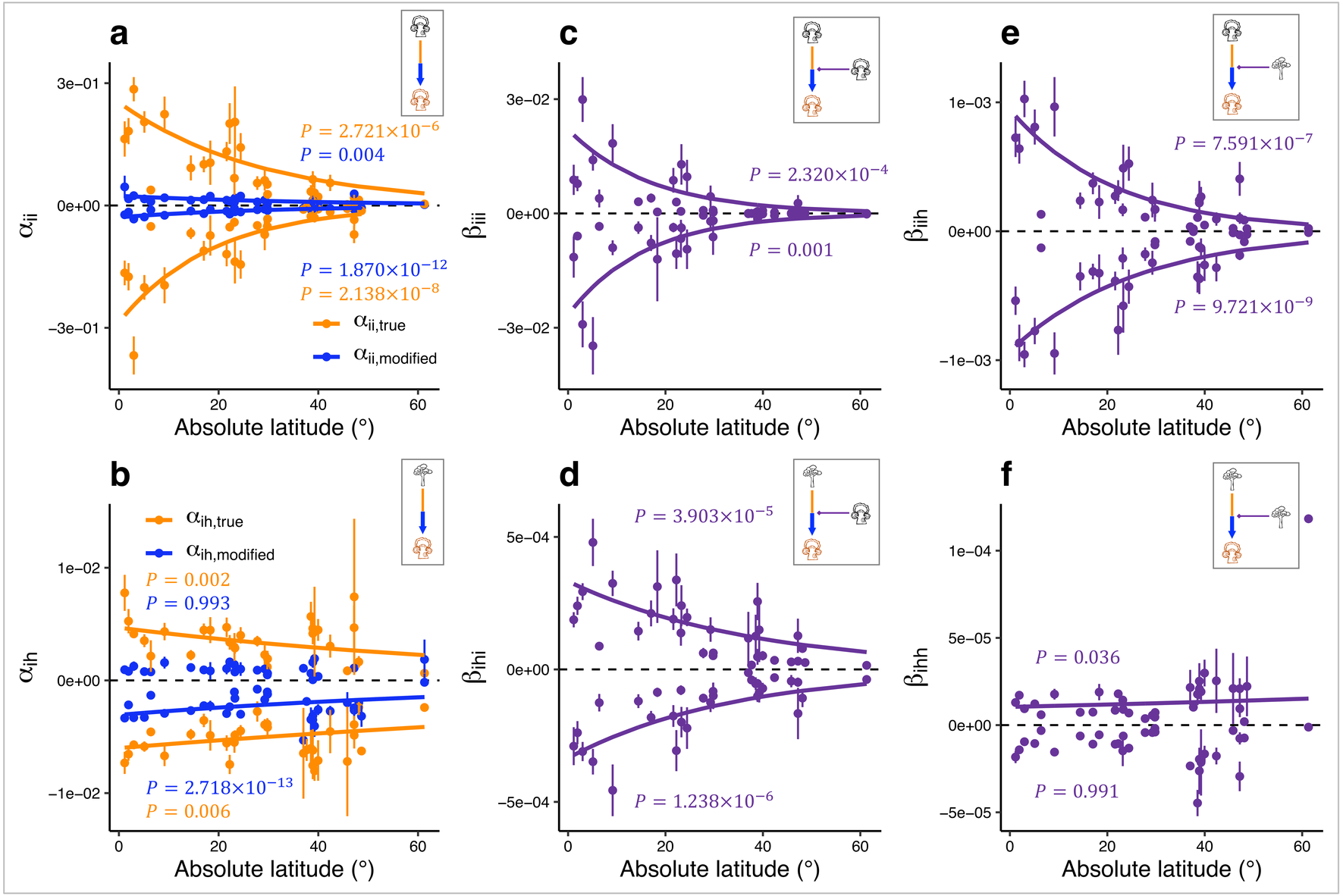




1,543 species-plot combinations (abundance>100)

Although HOIs have been reported at local scales in forests and other systems, our study shows that HOIs are ubiquitous in global forests, which highlight the importance and necessity of further exploration of their latitudinal patterns and ecological consequences.

Latitudinal decline in biotic interactions (Q2)



	α_{ii}	α_{ih}	β_{iii}	β_{iih}	β_{ihi}	β_{ihh}
α_{ii}	1.00	−0.17	−0.04	−0.96	0.11	0.19
α_{ih}	−0.17	1.00	0.05	0.19	−0.12	−0.89

Facilitations are frequent.

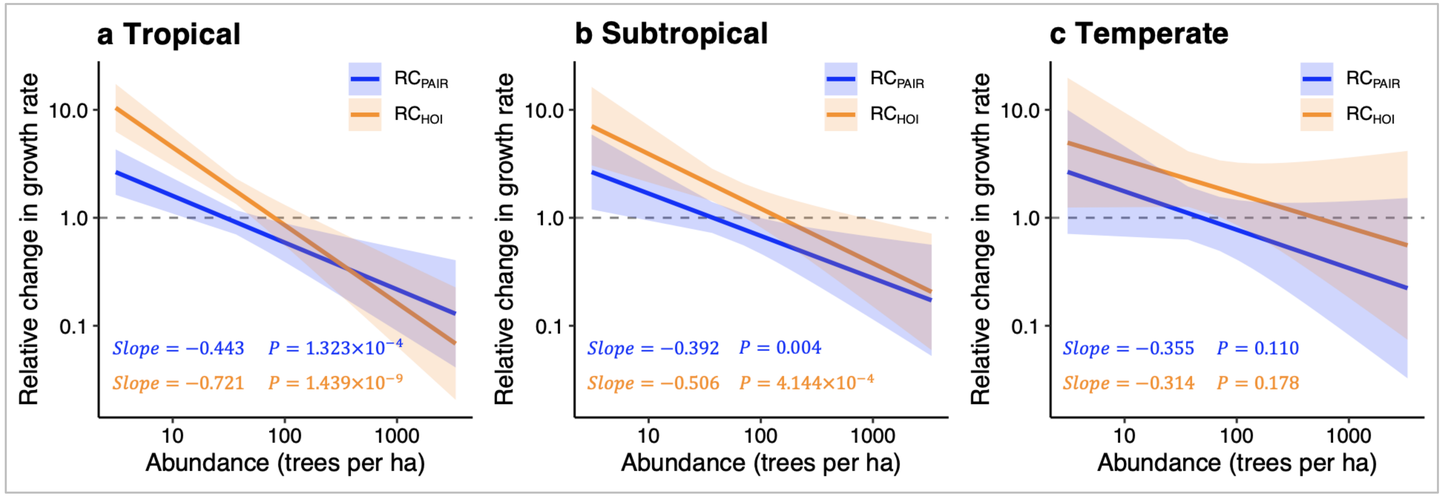
Biotic interactions decline.

HOIs weaken pairwise interactions.

Reconcile the divergent observations of latitudinal changes in CNDD.

HOIs enhance latitudinal tree diversity gradient (Q3)

Response	Effect	Estimate	s.e.	t	*P* value
RC_{Pair}	Intercept	1.494	0.507	2.945	0.003
	Abundance	−0.461	0.160	−2.888	0.004
	Latitude	−0.003	0.026	−0.095	0.924
	Abundance:latitude	0.002	0.007	0.336	0.736
RC_{HOI}	Intercept	3.586	0.531	6.752	2.07×10^{-11}
	Abundance	−0.864	0.167	−5.175	2.57×10^{-7}
	Latitude	−0.036	0.028	−1.309	0.19
	Abundance:latitude	0.012	0.007	1.680	0.093



$$Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma} \cdot e^{PAIR_{i_f}} \cdot e^{HOI_{i_f}}$$

$$RC_{Pair} = \sum_{f=1}^{N_i} e^{PAIR_{i_f}} / N_i$$

$$RC_{HOI} = \sum_{f=1}^{N_i} e^{HOI_{i_f}} / N_i$$

both the cumulative effects of pairwise interactions and HOIs promote the growth rates of rare species but suppress those of common species.

the stabilizing effect of HOIs becomes weaker towards higher latitudes, suggesting latitudinal changes in HOIs enhance the latitudinal tree diversity gradient.

Limitations and Future Directions

$$Growth_{i_f} = G_i \cdot DBH_{i_f}^{\gamma} \cdot e^{PAIR_{i_f}} \cdot e^{HOI_{i_f}}$$

$$PAIR_{i_f} = \alpha_{ii} \cdot n_{i,i_f} + \alpha_{ih} \cdot n_{h,i_f}$$

$$HOI_{i_f} = \beta_{iii} \cdot n_{ii,i_f} + \beta_{iih} \cdot n_{ih,i_f} + \beta_{ihi} \cdot n_{hi,i_f} + \beta_{ihh} \cdot n_{hh,i_f}$$

(I) Integrate different performances (IPM)

$$n_{t+1}(z') = \int_{\Omega} \big(s(z) \cdot G(z', z) + F(z', z)\big) n_t(z) dz$$

(Yang et al., 2025, GCB)

(II) Population-level Interactions

$$\alpha'_{ii} = ck_{ii}\alpha_{ii}$$

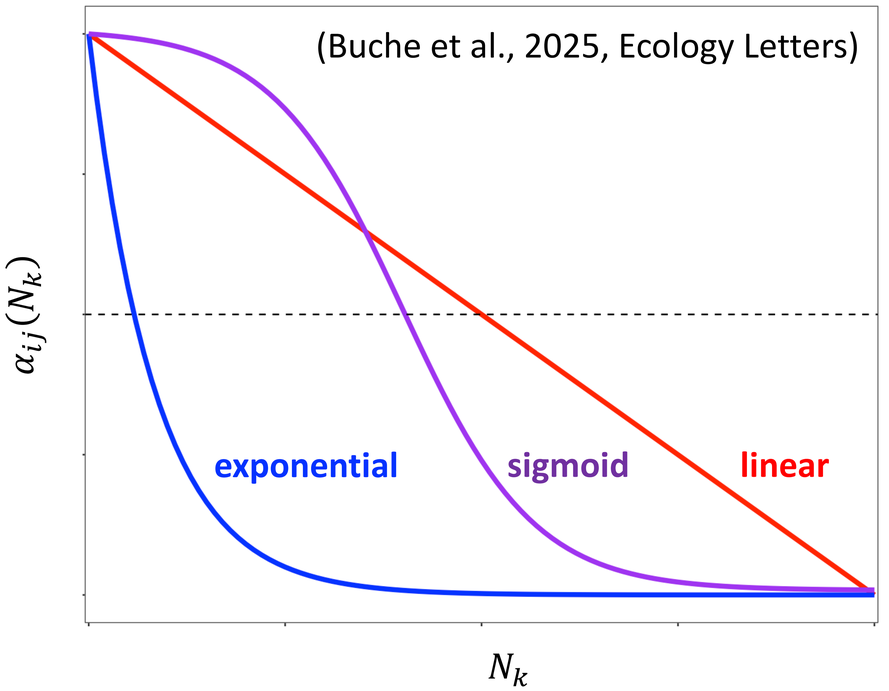
(Wiegand et al., 2021, NEE; Wiegand, 2025, Nature)

(III) Different Forms of Modification

linear: $\alpha_{ij}(N_k) = \alpha_{ij,true} + \beta_{ijk} N_k$

exponential: $\alpha_{ij}(N_k) = \alpha_{ij,true} + \beta_{ijk}[1 - \exp(hN_k)]$

sigmoid: $\alpha_{ij}(N_k) = \alpha_{ij,true} + \beta_{ijk} \dfrac{1 - \exp\big(h(N_k - N_0)\big)}{1 + \exp\big(h(N_k - N_0)\big)}$

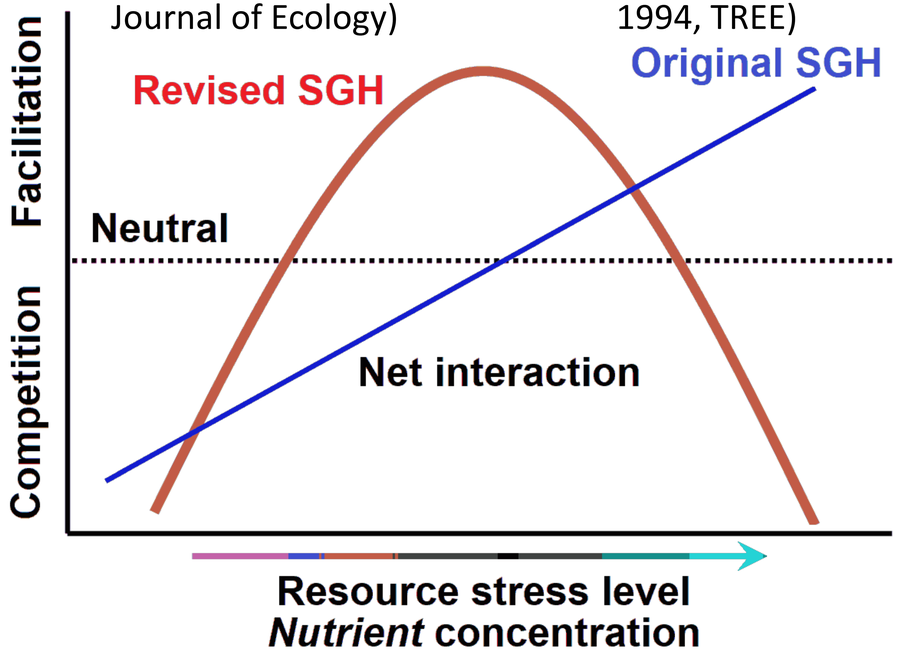


Limitations and Future Directions

Environmental Dependence of HOIs

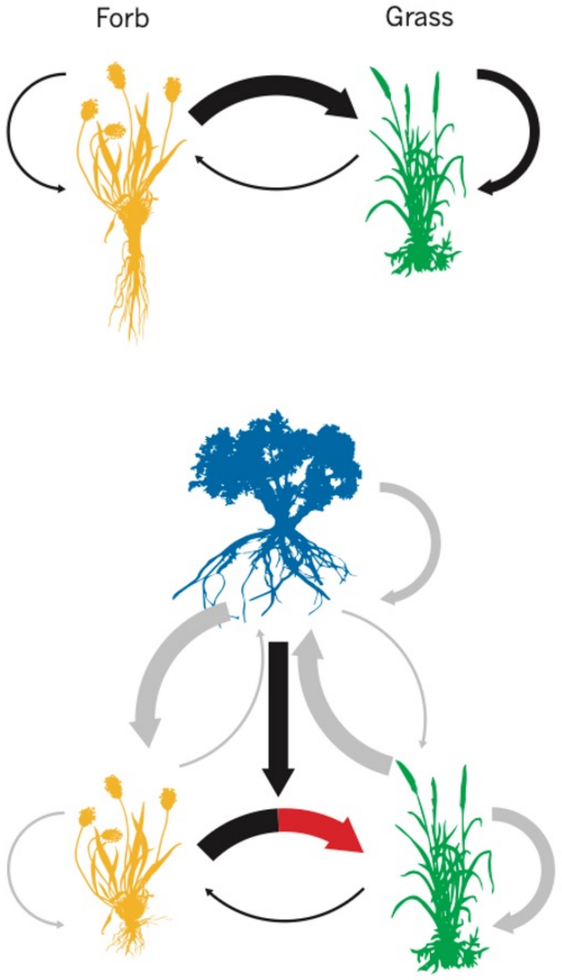
(Maestre et al., 2009, Journal of Ecology)

(Bertness & Callaway 1994, TREE)



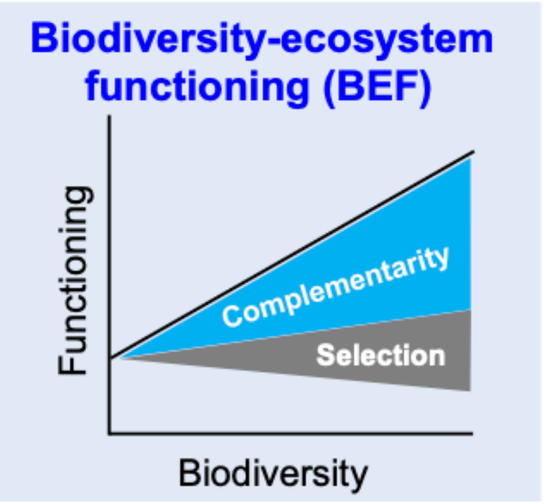
Strong (weak) HOI at low (high) enrichment in an experimental system of three ciliate species (Fox, 2023, Ecology).

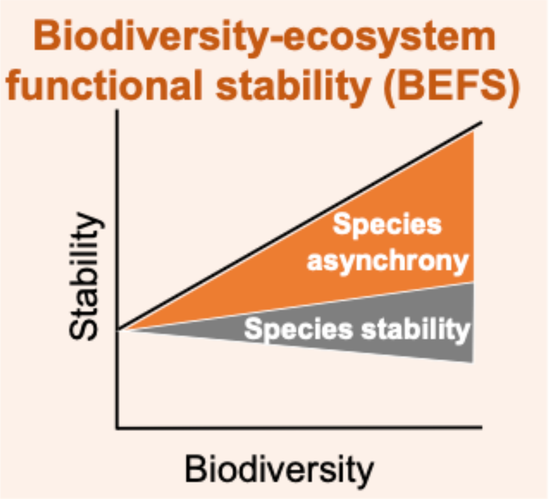
Trait-based Predictability of HOIs



(Levine et al., 2017, Nature)

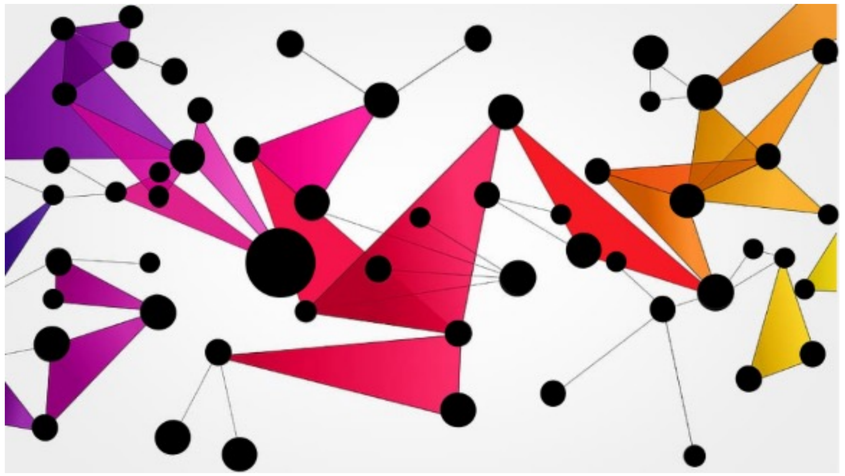
Contribution of HOIs to BEF





(Wang et al., 2024, TREE)

Limitations and Future Directions



communications physics

Explore content ⌄ About the journal ⌄ Publish with us ⌄

nature › communications physics › focus

Focus | **12 March 2021**

Higher-order interaction networks 2021

Guest Edited by Prof Ginestra Bianconi (Queen Mary University) in collaboration with our Editorial Board Member Prof Federico Battiston (Central European University).

communications physics

Explore content ⌄ About the journal ⌄ Publish with us ⌄

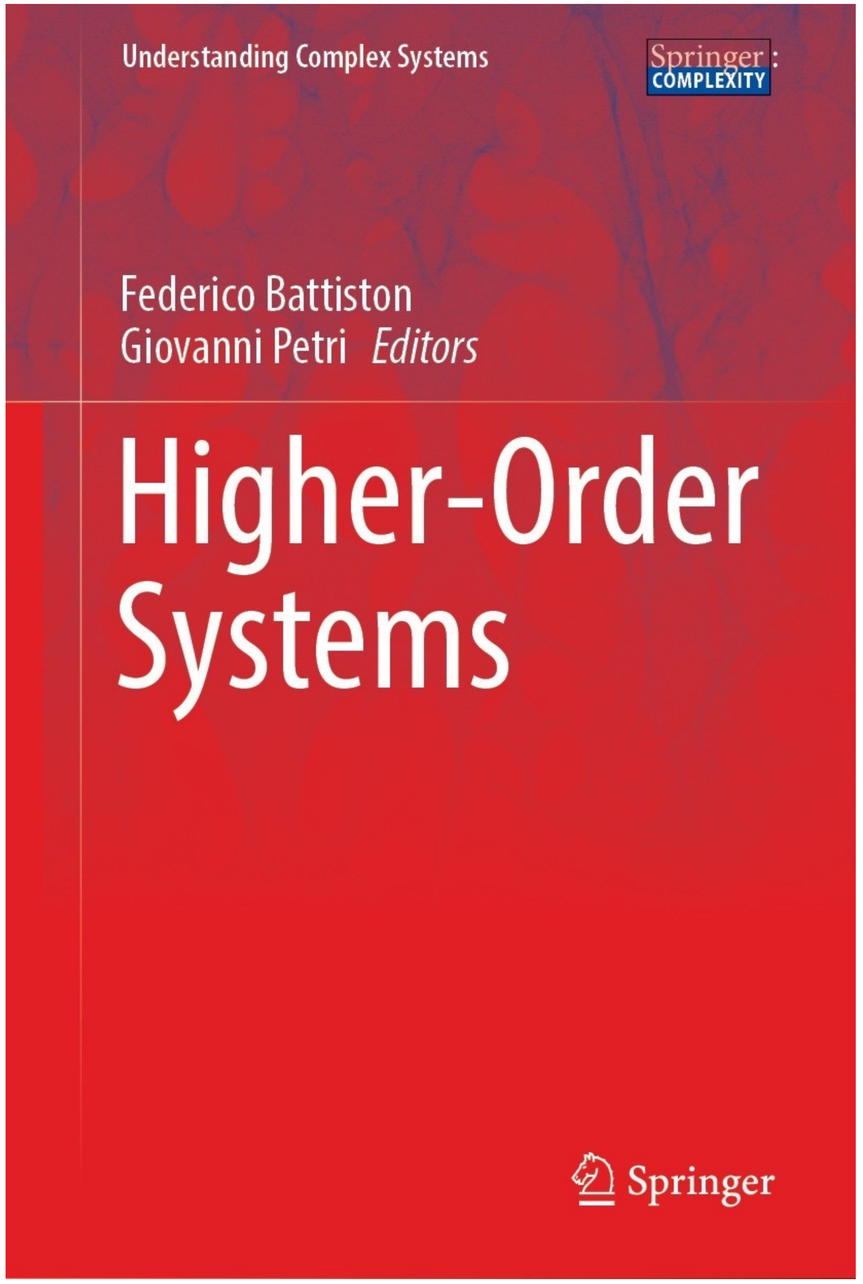
nature › communications physics › collection

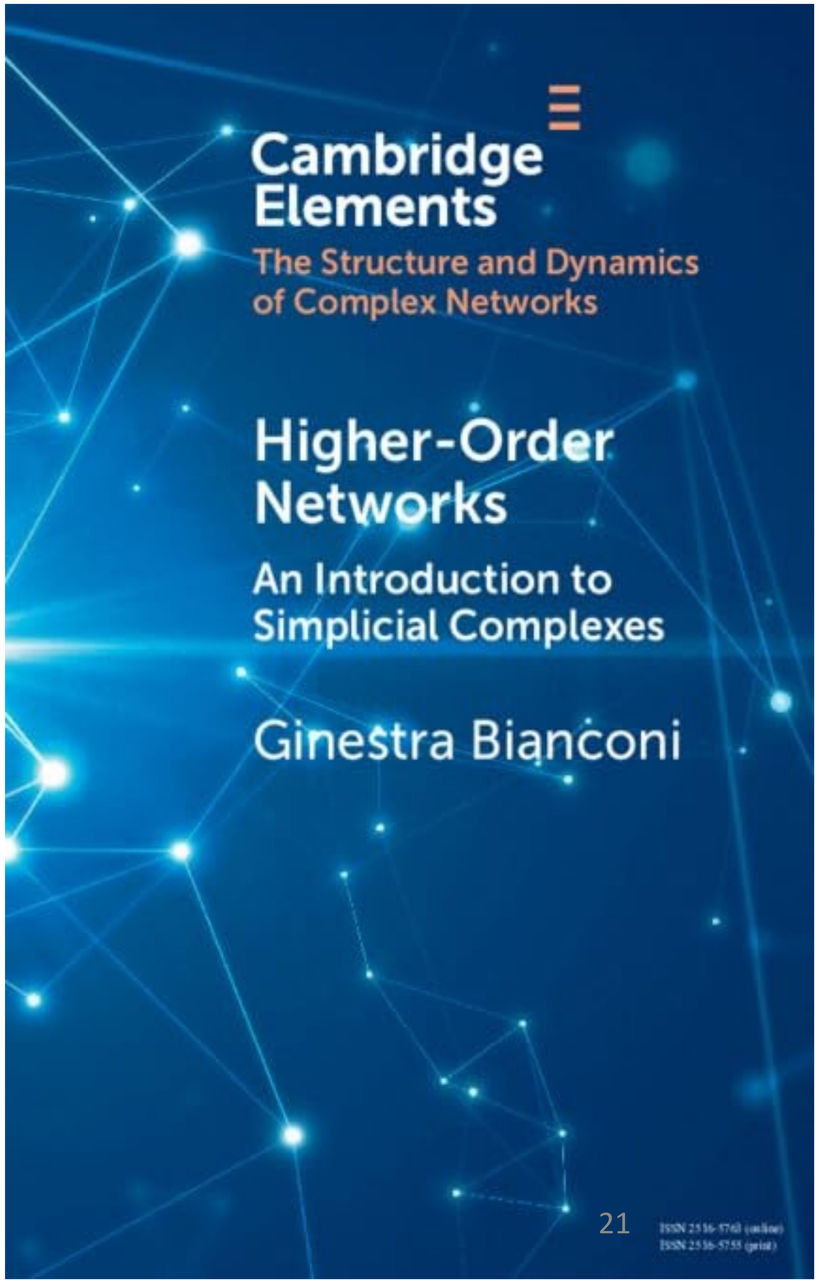
Collection | **12 November 2024**

Higher-order interaction networks 2024

Submission status
Closed

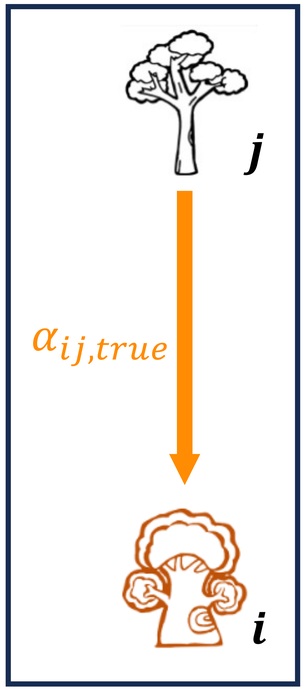
Submission deadline
28 February 2026

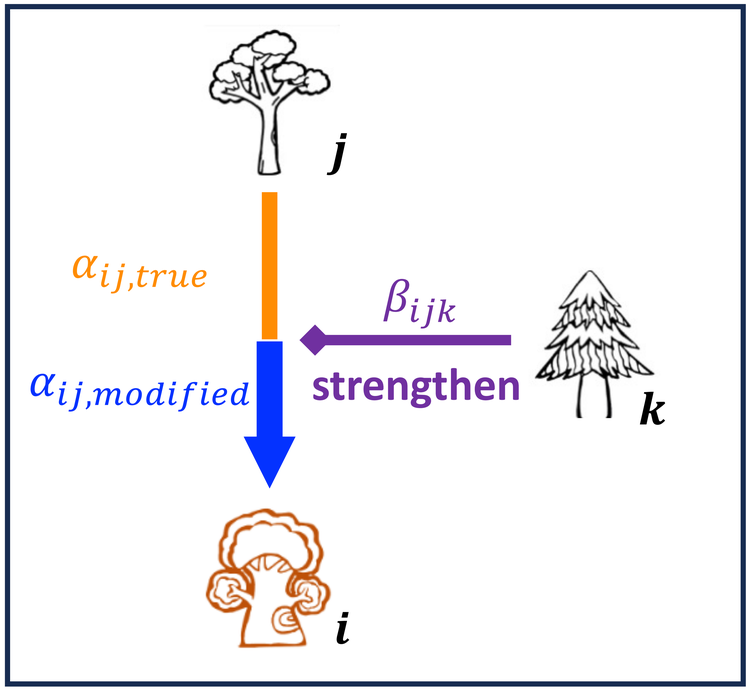


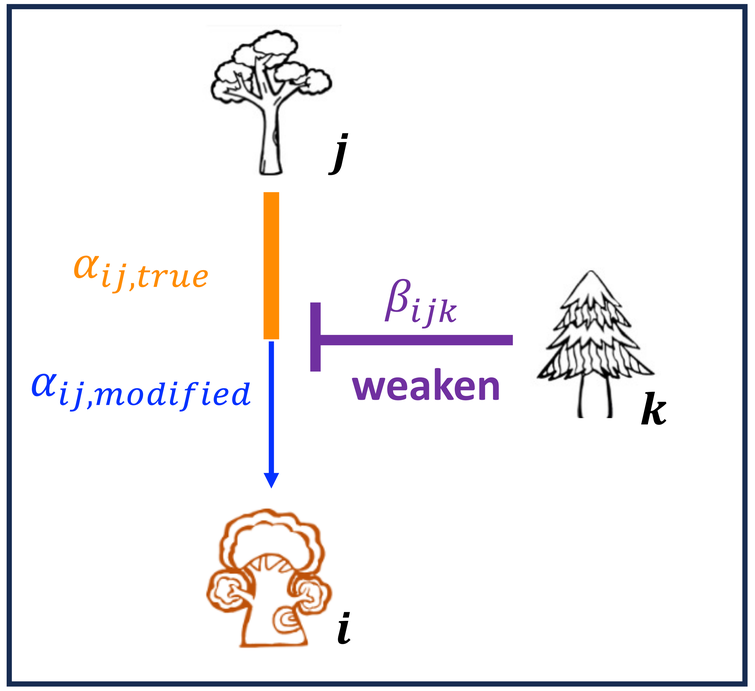


Take Home Message

- ❑ Are HOIs prevalent among trees across forest plots? Yes
- ❑ How do pairwise interactions ($\alpha_{ij,true}$ and $\alpha_{ij,modified}$) and HOIs (β_{ijk}) vary with latitude? Decline
- ❑ How do latitudinal changes in HOIs contribute to the latitudinal tree diversity gradient? Enhance









Thank You!

ForestGEO
GLOBAL EARTH OBSERVATORY NETWORK
Smithsonian

Forest Global Earth Observatory
Smithsonian Tropical Research Institute

16 May 2023

Subject: Invitation to 2023 ForestGEO Analytical Workshop

Yuanzhi Li

NANYANG TECHNOLOGICAL UNIVERSITY SINGAPORE

Asian School of the Environment
College of Science

Date: 29 May 2019

Subject: Invitation to 2019 ForestGEO Analytical Workshop

Invitee Name: Yuanzhi Li

国家自然科学基金委员会
NATIONAL NATURAL SCIENCE FOUNDATION OF CHINA
1986

ForestGEO
GLOBAL EARTH OBSERVATORY NETWORK

CForBio