# Metacommunities of Soil Microbiomes: Patterns, Processes, and Implications for Inference

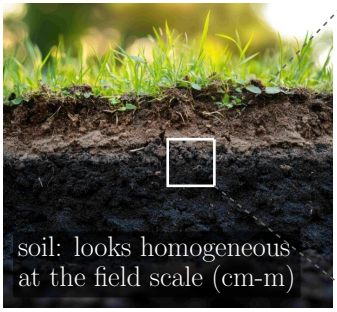
Ksenia Guseva

Symposium on Microbial (Meta-)Community Modeling

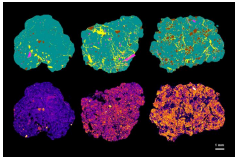
*21 October 2026*

# Soil across scales

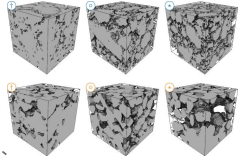
## Homogeneous to the eye, heterogeneous for microbes



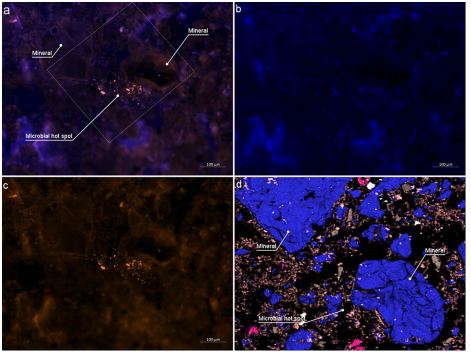

aggregates & pores (mm)



3D pore network



microbial hot spots (100 $\mu$m)




**Diversity:** $>$ 33 000 bacterial and archaeal taxa in a single soil sample

**Ecological importance:** nutrient cycling, plant growth, **carbon storage**

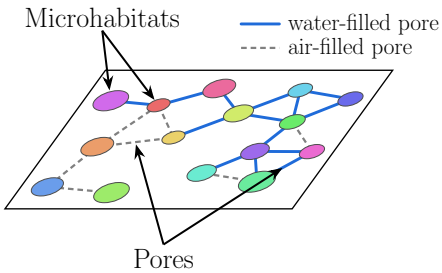
# Soil: a mosaic of microhabitats

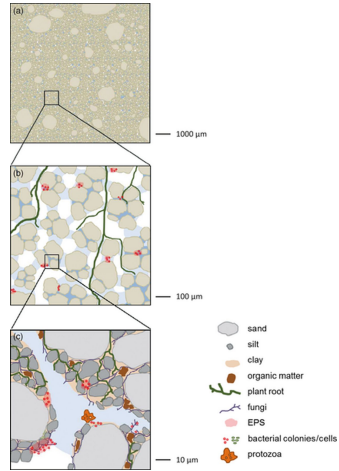
**Heterogeneity:** extreme at microbial scales

- pores and nested aggregates
- only $\sim 10^{-6}$ of surfaces colonized

$\Rightarrow$ more or less connected patches:
**metacommunities**

$\Downarrow$



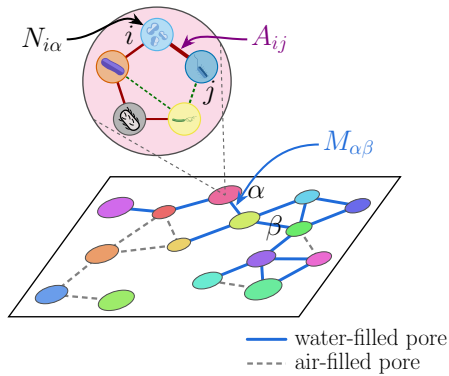

M. Vos, A. B. Wolf, S. J. Jennings, G. A. Kowalchuk, Micro-scale determinants of bacterial diversity in soil, *FEMS Microbiol. Rev.* **37**(6), 936-954 (2013)

# Patch Network (Microhabitats)

**Metacommunity generalized Lotka-Volterra model:**

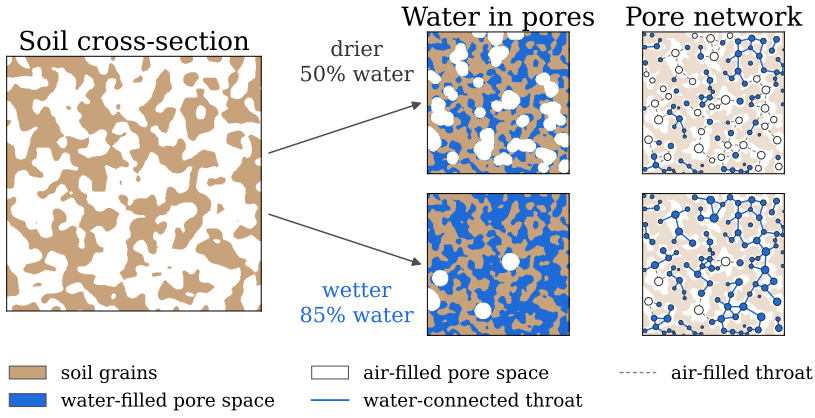
$$\frac{dN_{i\alpha}}{dt} = \underbrace{r_i\, N_{i\alpha}\Big(1 - \frac{1}{K_{i\alpha}} \sum_j A_{ij}\, N_{j\alpha}\Big)}_{\text{Local dynamics in patch } \alpha} + \underbrace{\sum_{\beta \neq \alpha} M_{\alpha\beta}\big(N_{i\beta} - N_{i\alpha}\big)}_{\text{Dispersal between patches}}$$

- $N_{i\alpha}$: abundance of species $i$ in patch (microhabitat) $\alpha$
- $r_i$: growth rate of species $i$
- $K_{i\alpha}$: carrying capacity of species $i$ in patch $\alpha$
- $A_{ij}$: interaction matrix, effect of species $j$ on species $i$ ($A_{ii} = 1$)
- $M_{\alpha\beta} = M_{\beta\alpha}$: symmetric connectivity matrix, dispersal rate between patches $\alpha$ and $\beta$; $M_{\alpha\beta} > 0$ only if they are connected by a pore



# Connectivity $M_{\alpha,\beta}$

## Pore networks




$\Rightarrow$ pores connected by water allow dispersal ($M_{\alpha\beta} > 0$); drying fragments the network

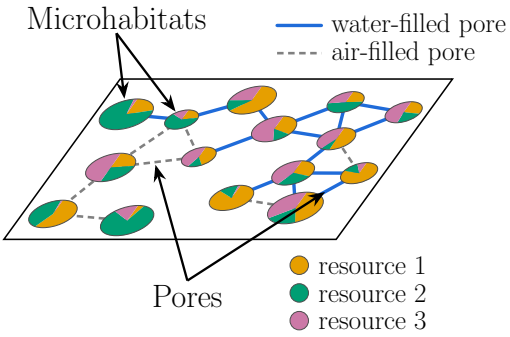
synthetic soil image and pore-network extraction (SNOW algorithm) with **PoreSpy**

J. T. Gostick *et al.*, PoreSpy: A Python toolkit for quantitative analysis of porous media images, *J. Open Source Softw.* **4**(37), 1296 (2019)

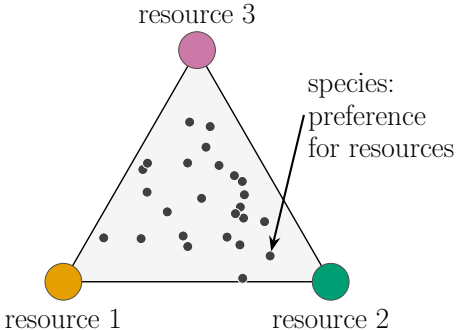
# Carrying capacity $K_{i\alpha}$

## Resources

**Microhabitats:** mix of 3 resources




**Species:** preference for resources

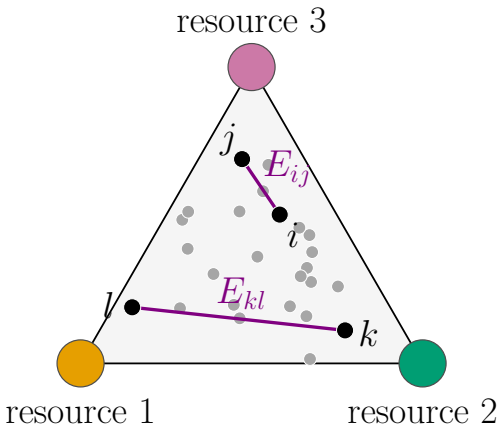



$\Rightarrow$ resources determine the carrying capacity of species $i$ in habitat $\alpha$: $K_{i\alpha} = \sum_k c_{ik}\, R_{k\alpha}$

$R_{k\alpha}$: amount of resource $k$ in patch $\alpha$ $\quad$ $c_{ik}$: preference of species $i$ for resource $k$

# Niche distance $E_{ij}$

## Resource preferences



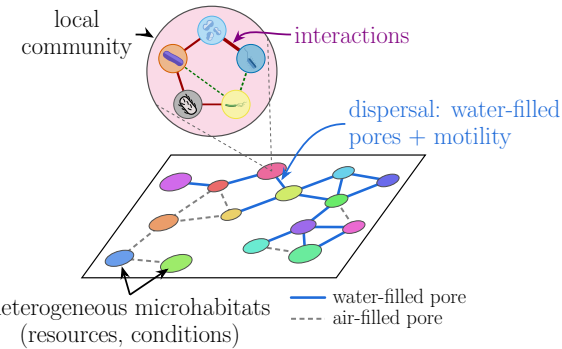

- species $i$: preferences $\mathbf{c}_i = (c_{i1}, c_{i2}, c_{i3})$, $\sum_k c_{ik} = 1$, a point in the triangle
- $E_{ij} = \|\mathbf{c}_i - \mathbf{c}_j\|$: distance between species $i$ and $j$ in the triangle
- **small** $E_{ij}$: similar preferences, species share the same **fundamental niche**
- **large** $E_{kl}$: preferences for **different resources**

# Soil metacommunities

## Overview

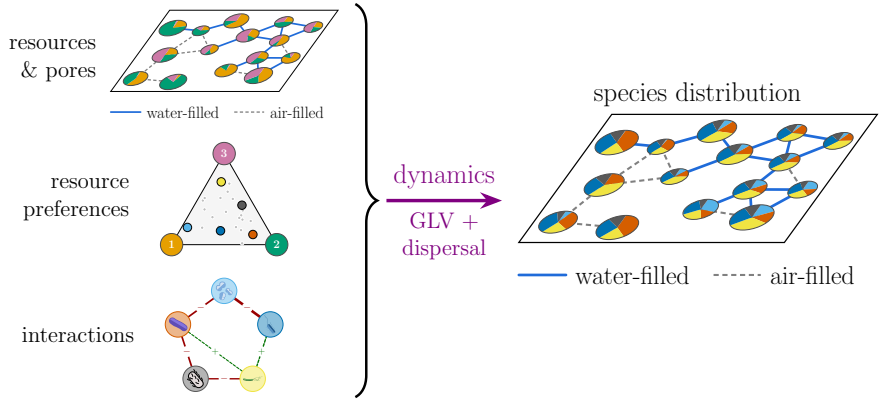
**The community in each microhabitat results from:**

- **spatial heterogeneity:** microhabitats differ in resources and conditions
- **resource-niche matching:** local resources vs. the species' fundamental niches ($K_{i\alpha}$, $E_{ij}$)
- **local population dynamics:** growth and interactions between species ($r_i$, $A_{ij}$)
- **dispersal:** through water-filled pores, set by soil water content and microbial motility ($M_{\alpha\beta}$)



# Forward problem

## From model ingredients to species distributions




**Research questions:**

- how do dispersal and connectivity (soil water content) shape local and regional diversity?
- when do species sorting, source-sink dynamics or homogenization dominate?

# Metacommunity dynamics

## Forward problem: from the model to community properties

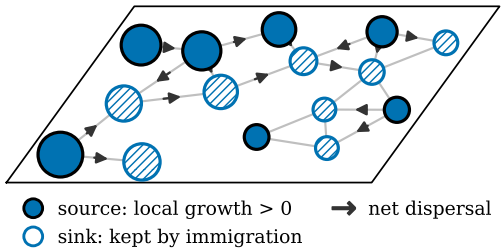
**Spatial structure:**

- segregation weakens competition [4]
- spatial variation stabilizes coexistence [2]

**Dispersal** (water content, motility)**:**

- **low:** species sorting by local resources [1]
- **intermediate:** source-sink rescue [1,3,5]
- **high:** homogenization, competitors lost [1,4]

source-sink dynamics of one species




[1] M. A. Leibold *et al.*, Ecol. Lett. **7**, 601 (2004); [2] P. Chesson, Aust. J. Ecol. **23**, 209 (1998); [3] G. Garcia Lorenzana, A. Altieri, G. Biroli, PRX Life **2**, 013014 (2024); [4] M. Mattei, A. Arenas, Phys. Rev. E **110**, 014404 (2024); [5] E. Mallmin, A. Traulsen, S. De Monte, arXiv:2505.01376 (2025)

# Metacommunity dynamics

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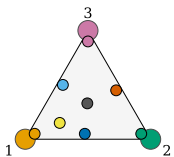
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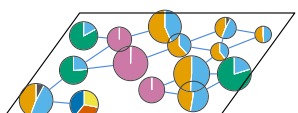
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species preferences



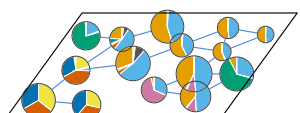

pie size ~ amount of resources

low dispersal



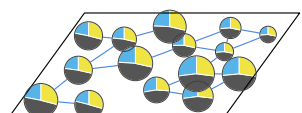
species per patch: 2.1
in the region: 8

intermediate dispersal



species per patch: 4.8
in the region: 8

high dispersal

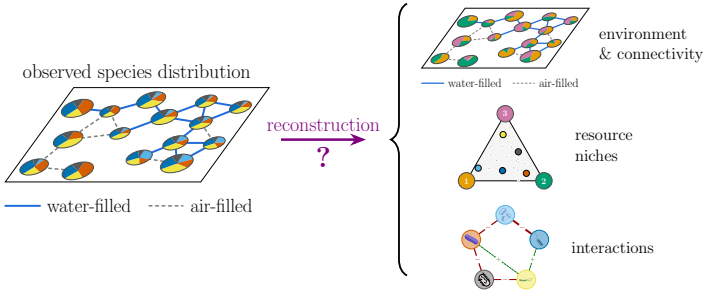


species per patch: 3.0
in the region: 3

[1] M. A. Leibold *et al.*, Ecol. Lett. **7**, 601 (2004); [2] P. Chesson, Aust. J. Ecol. **23**, 209 (1998); [3] G. Garcia Lorenzana, A. Altieri, G. Biroli, PRX Life **2**, 013014 (2024); [4] M. Mattei, A. Arenas, Phys. Rev. E **110**, 014404 (2024); [5] E. Mallmin, A. Traulsen, S. De Monte, arXiv:2505.01376 (2025)

# Inverse problem

## What do species patterns reflect?




**Patterns may reflect:**

- **environment:** niche matching
- **interactions:** competition, facilitation

**What hides the mechanisms:**

- **homogenization:**
  - *intrinsic:* dispersal, connectivity
  - *extrinsic:* sampling scale

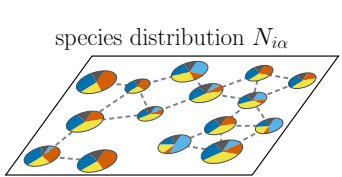


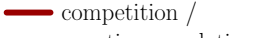
Sean Darcy

S. R. Darcy, C. Kaiser, K. Guseva, Environmental context shapes microbial co-occurrence, *bioRxiv* (2025), doi:10.1101/2025.08.05.668733

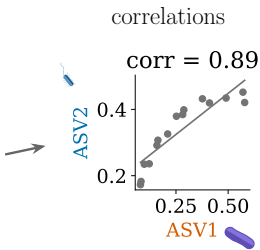
# Co-occurrence networks

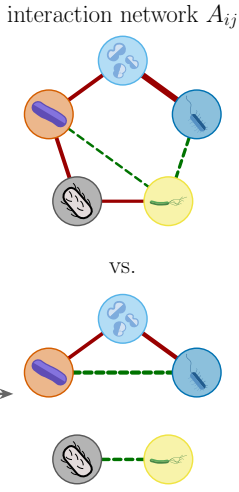
## From species distributions to networks




reconstructed edge:
$|\text{corr}| > 0.7$ across samples

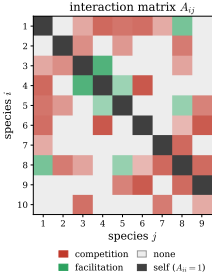


# Model set-up

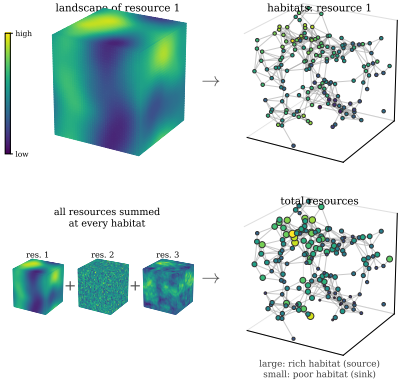
## Spatially explicit metacommunity GLV

### Interactions




- 10 species, 45 pairs: 40 % competition, 10 % facilitation, 50 % none
- random, symmetric, $|A_{ij}| \sim U(0.1, 0.5)$
- competition prevails among bacteria [1,2]

### Resources



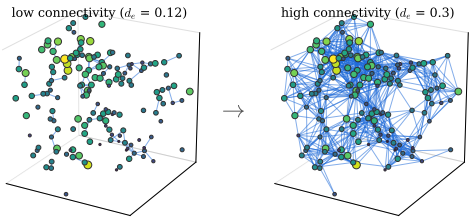

Resource-rich habitats are **sources**, poor ones **sinks**

[1] J. Kehe *et al.*, *Sci. Adv.* **7**, eabi7159 (2021); [2] J. D. Palmer, K. R. Foster, *Science* **376**, 581-582 (2022)

# Homogenization

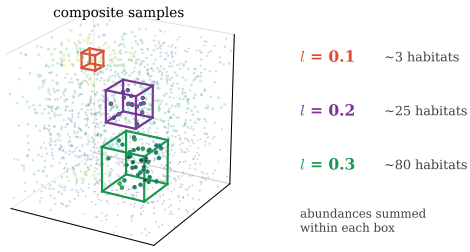
## Intrinsic and extrinsic

**Intrinsic:** dispersal, connectivity




Habitats exchange populations along their links: a larger connectivity radius $d_e$ links more habitats, communities become alike

**Extrinsic:** sampling scale

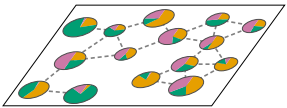



A sample pools all habitats in a volume of side $l$: larger samples average over more habitats

**Note:** intrinsic homogenization changes the communities themselves, while extrinsic homogenization only changes how they're observed.

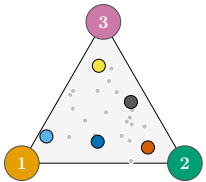
# Disconnected microhabitats

**Resources $R_{k\alpha}$**

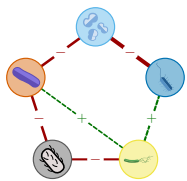


------ air-filled pores

**Preferences $\mathbf{c}_i$**



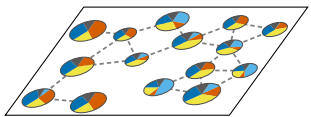

**Interactions $A_{ij}$**



competition

facilitation

**Species distribution $N_{i\alpha}$**



------ air-filled pores

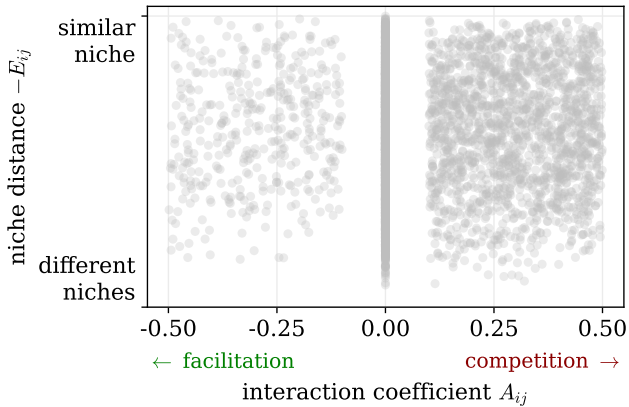
species distribution: steady state of the metacommunity GLV with $M_{\alpha\beta} = 0$

**Research question**

In disconnected microhabitats, are species distributions set by the local resources and species' preferences ($K_{i\alpha}$), or by the interaction network between species ($A_{ij}$)?

# Co-occurrence, interactions and niches

## Simulated species pairs

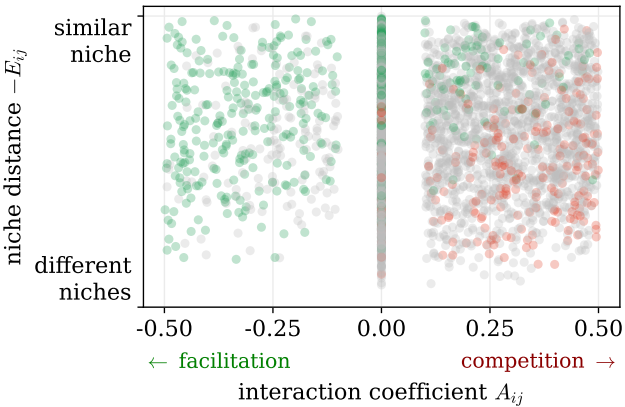



Species pairs:

- all species pairs

# Co-occurrence, interactions and niches

## Simulated species pairs

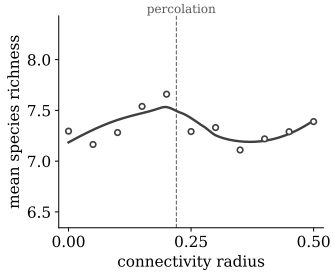


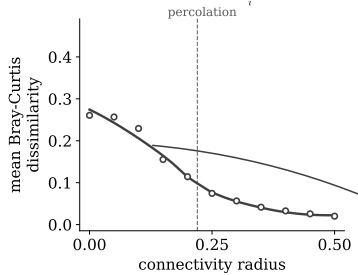

- Not all relationships detected
- Preference for the same resource may hinder the signal of competition

# The effect of intrinsic homogenization

## Connectivity

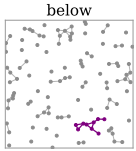
$$BC_{\alpha\beta} = 1 - \frac{2\sum_i \min(N_{i\alpha}, N_{i\beta})}{\sum_i (N_{i\alpha} + N_{i\beta})}$$

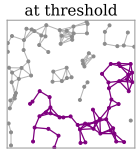


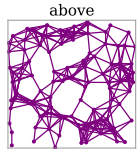









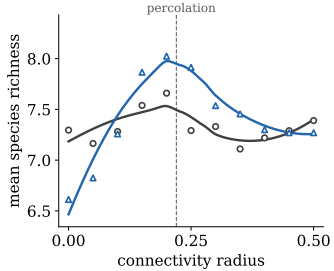



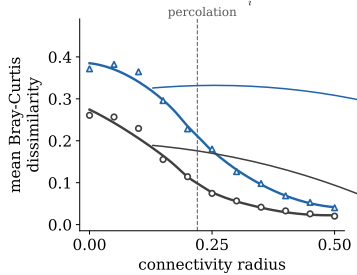

percolation: above a critical connectivity radius one connected network spans the whole system

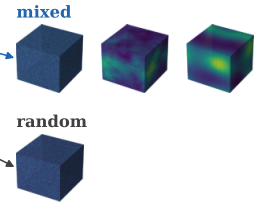
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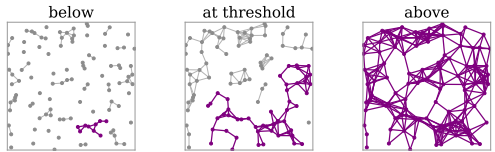
## Connectivity

$$BC_{\alpha\beta} = 1 - \frac{2\sum_i \min(N_{i\alpha}, N_{i\beta})}{\sum_i (N_{i\alpha} + N_{i\beta})}$$



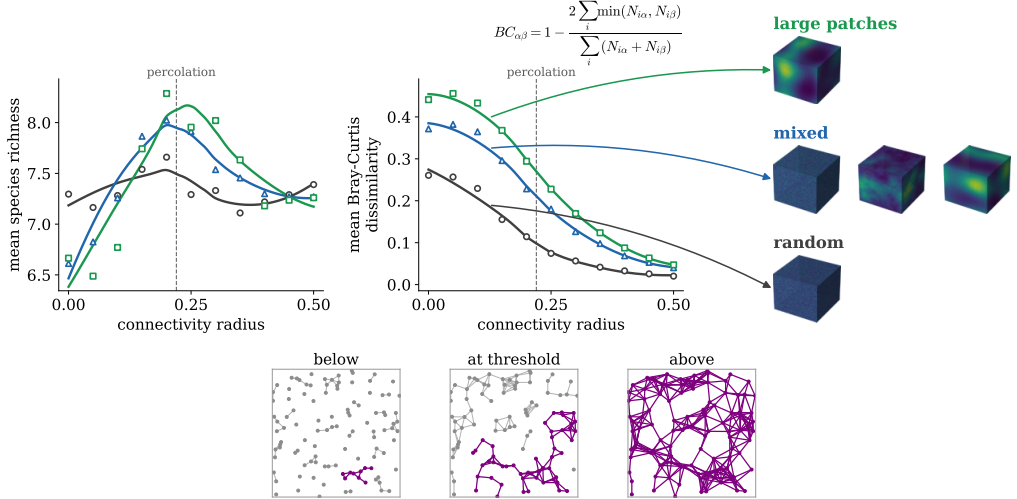




percolation: above a critical connectivity radius one connected network spans the whole system

# The effect of intrinsic homogenization

## Connectivity




percolation: above a critical connectivity radius one connected network spans the whole system

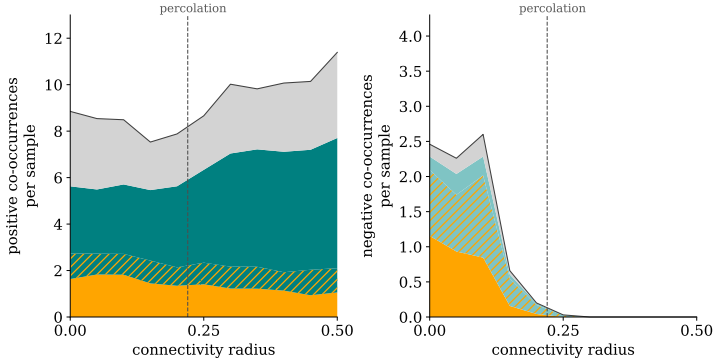
# The effect of intrinsic homogenization

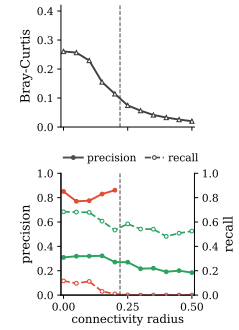
## Co-occurrences: random and mixed resource scenarios

**random resource scenario**



resources 1, 2, 3

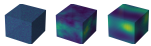


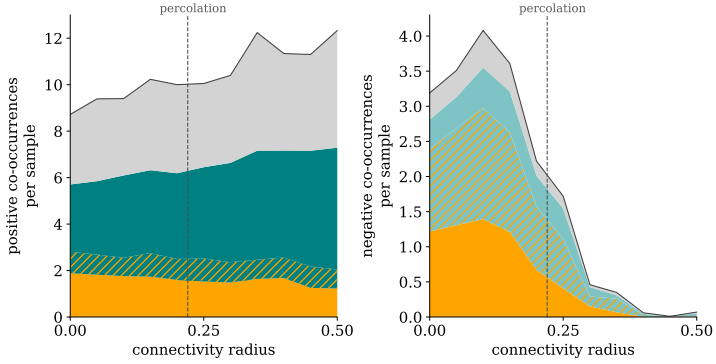
# The effect of intrinsic homogenization

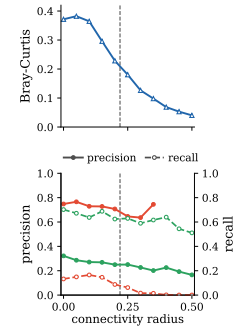
## Co-occurrences: random and mixed resource scenarios

mixed resource scenario



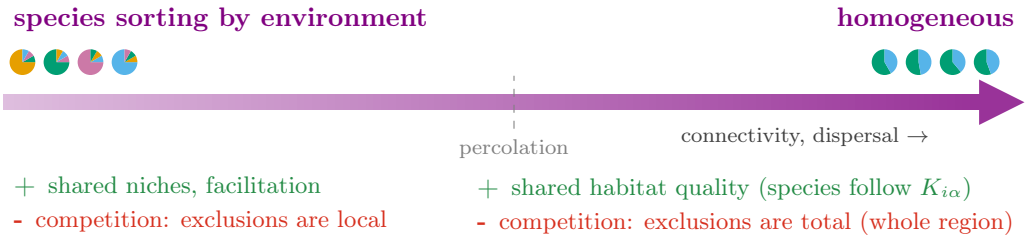
resources 1, 2, 3



# The effect of intrinsic homogenization

## What happens to co-occurrences

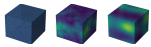



- **Positive co-occurrences increase**: species share rich habitats, not niches ⇒ mostly "undefined"
- **Negative co-occurrences vanish** above percolation:
  - *exclusion:* more than half of the competing pairs lose one partner in the whole region
  - *homogenization:* surviving competitors become uniform; what remains follows the environment

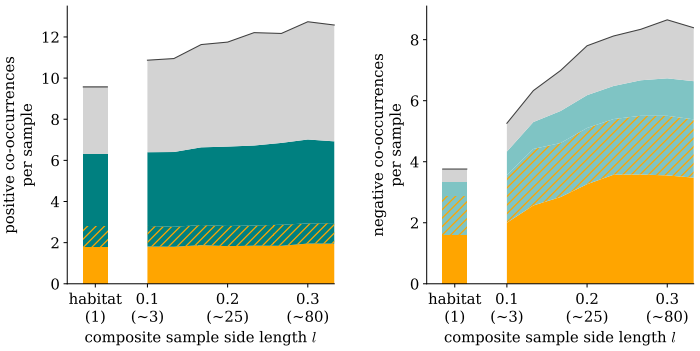
# The effect of extrinsic homogenization

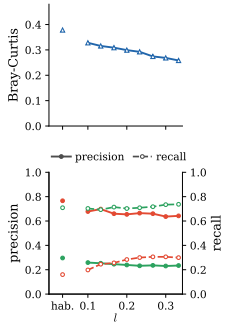
## Sampling scale in the mixed resource scenario

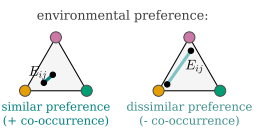
**mixed resource scenario**



resources 1, 2, 3



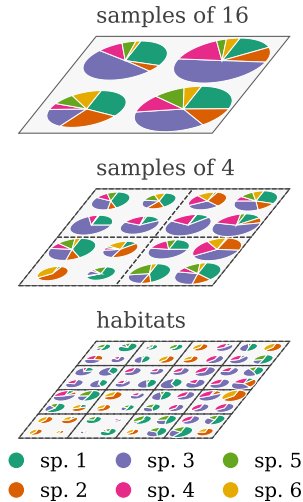



# The effect of extrinsic homogenization

## Why co-occurrences inflate with sample size

- **Inflation of co-occurrences** occurs when resources vary at different scales: pooling averages out the small-scale variation and keeps the large-scale structure
- **Positive:** pooling blurs niche differences ⇒ more co-occurrences, mostly "undefined" ⇒ lower precision
- **Negative:** pooled samples contain both competitors, in proportions that follow the patches ⇒ better detection of competition



# Conclusions

## Intrinsic and extrinsic homogenization

Both make samples more alike, but they act differently on co-occurrences:

| | **Intrinsic:** connectivity | **Extrinsic:** sampling scale |
|---|---|---|
| **Negative** | **lost:** competitors excluded or uniform | **better detected:** competitors dominate different patches |
| **Positive** | species follow habitat quality ⇒ lower precision | niche differences blurred ⇒ lower precision |

dispersal changes the communities, aggregation only how we observe them

S. R. Darcy, C. Kaiser, K. Guseva, Environmental context shapes microbial co-occurrence, *bioRxiv* (2025), doi:10.1101/2025.08.05.668733

Thank you!