

Fungi stabilize multi-kingdom community in a high elevation timberline ecosystem

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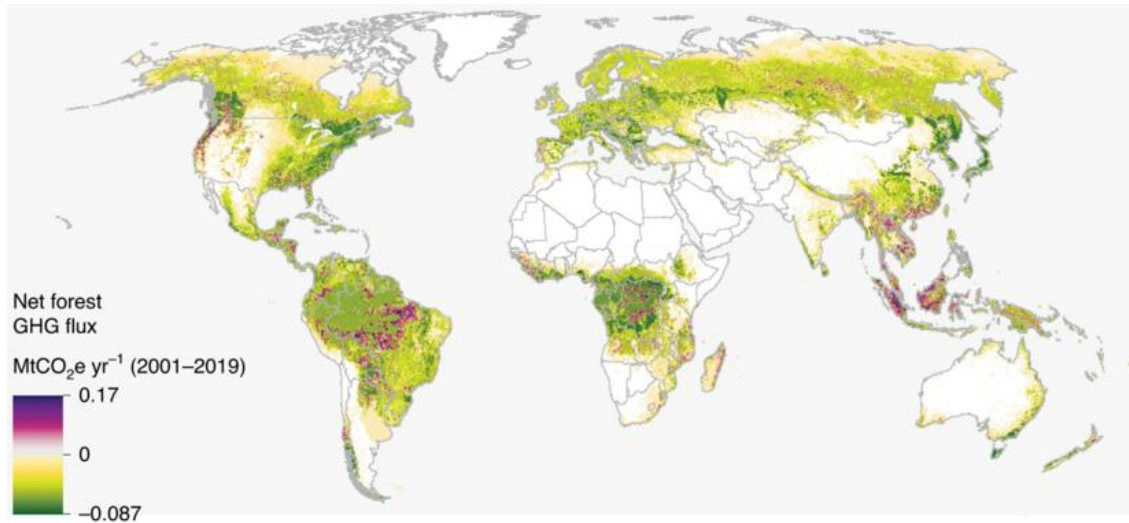
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Introduction

Global maps of twenty-first century forest carbon fluxes



Harris et al. 2021

Wildfire



Drought



Deforestation



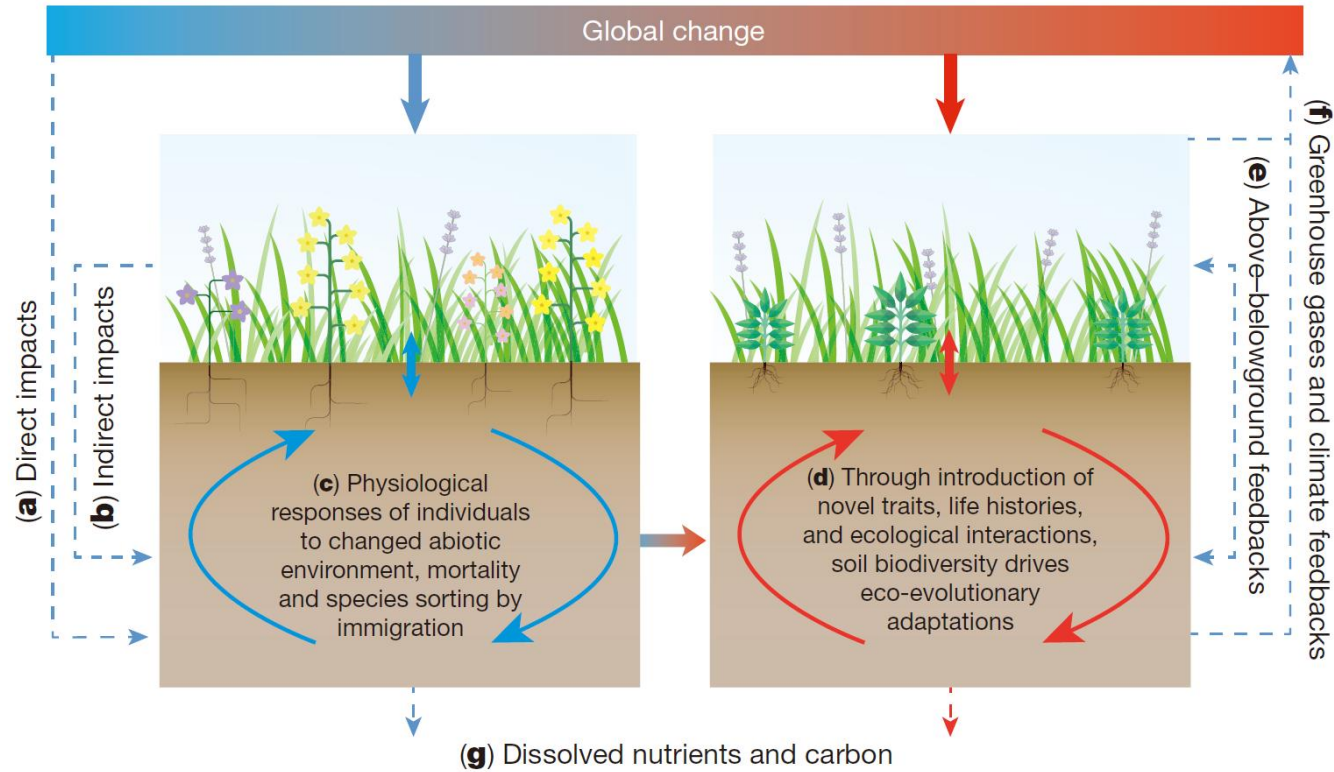
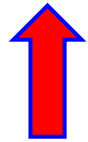
Insects and pathogens



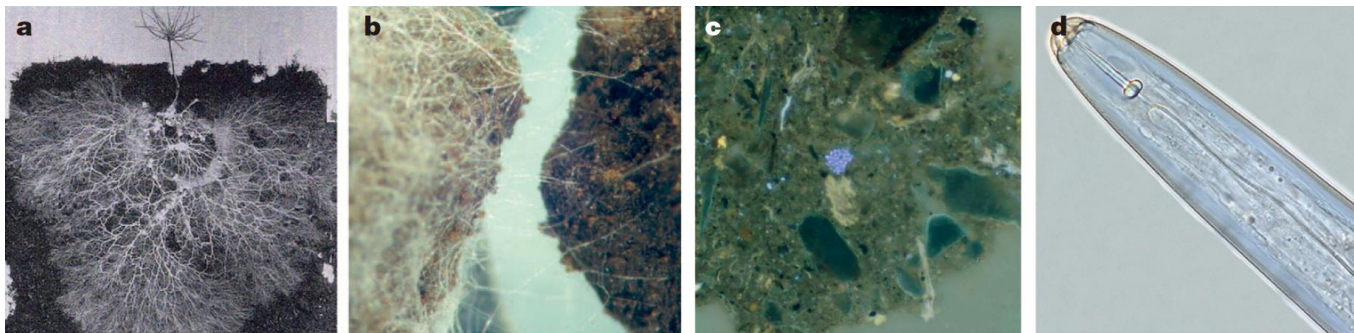
Millar et al. 2015

Introduction

- Shape aboveground biodiversity
- Drive biogeochemical processes
- Responses and feedbacks to global change



- Hyper-diverse belowground biota

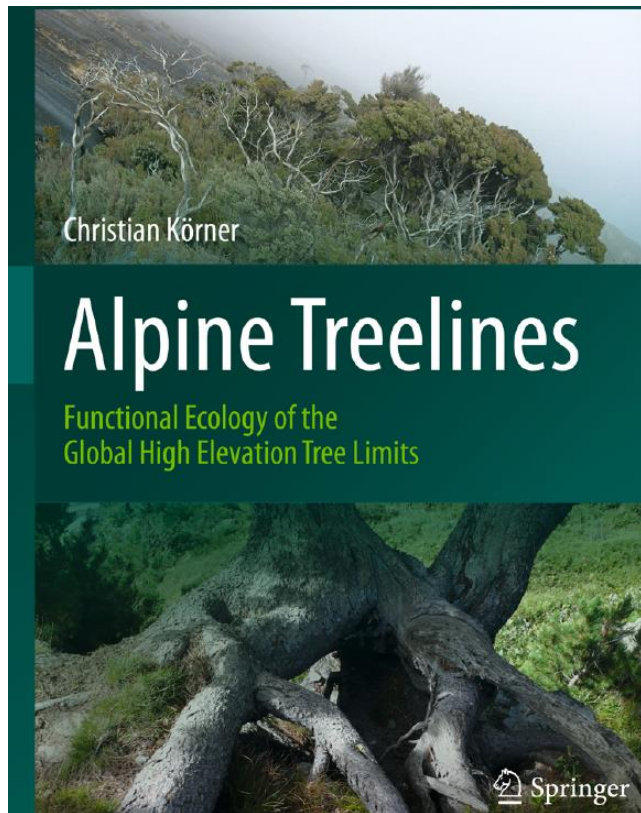


Bardgett & van der Putten 2014

Introduction

Timberline: a broad ecotone between closed forests and alpine grasslands or tundra

Timberline is highly sensitive to climate change and human activity

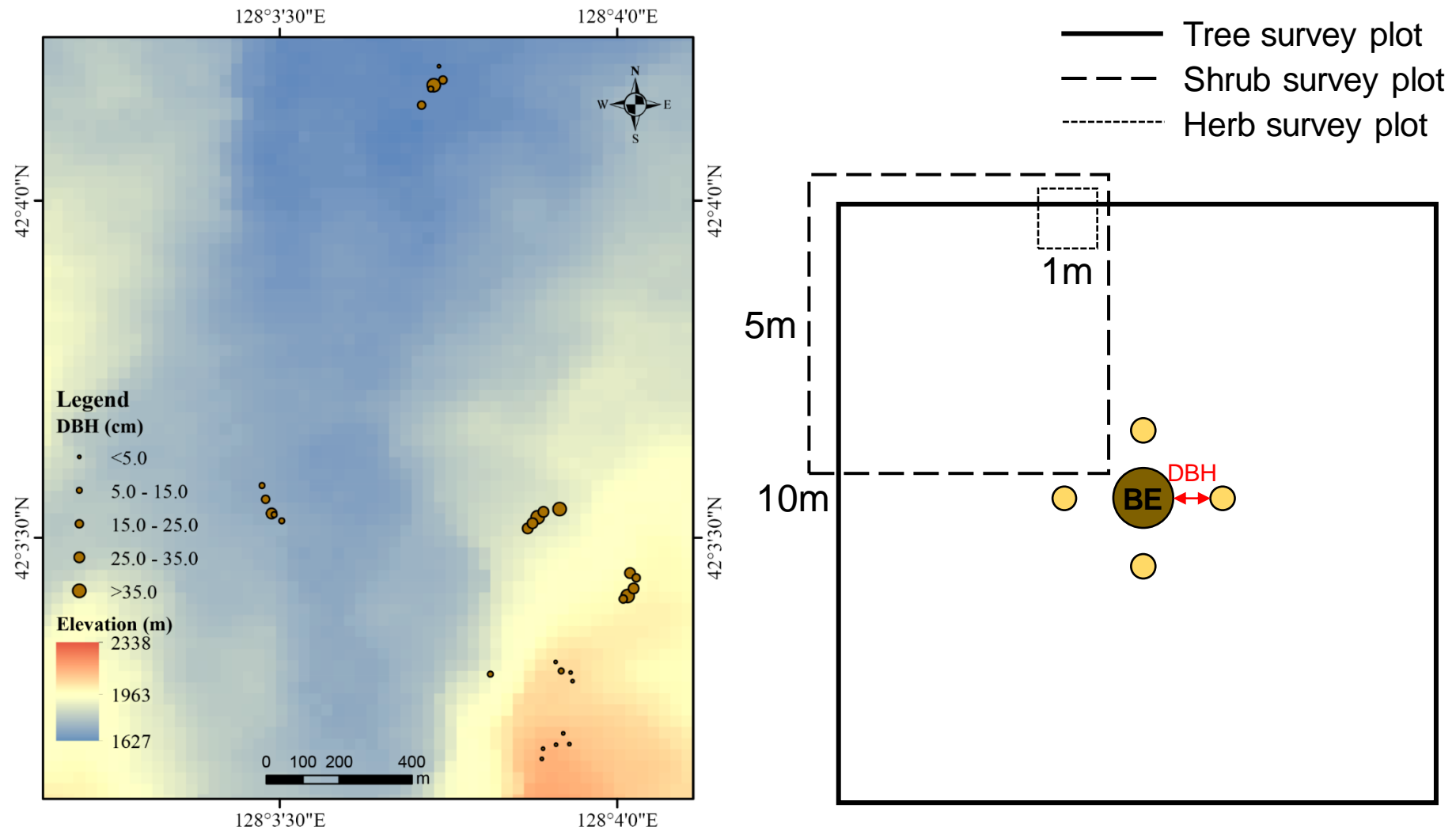


'The high elevation treeline will be understood, once the functional difference between trees and alpine shrubs is.'



Switzerland, 2012

Materials and Methods



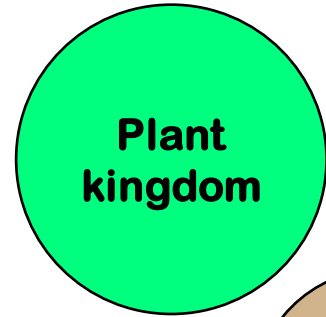
- The study area is located in the northern slope of Changbai Mountain, Northeast China.
- The soils neighboring 30 mature *B. ermanii* individuals were sampled along the elevation from 1688 to 2113 m.

Materials and Methods

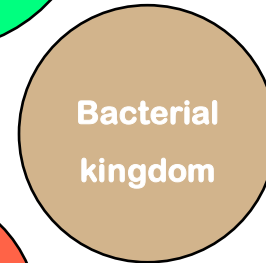
Plot Survey



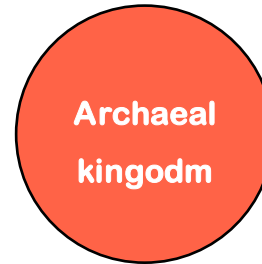
- Herbs
- Shrubs
- Trees



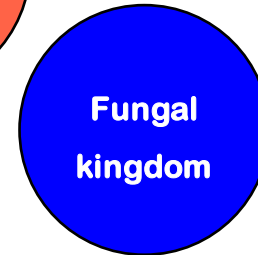
Plant kingdom



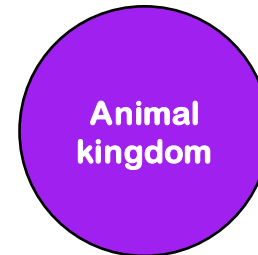
Bacterial kingdom



Archaeal kingdom



Fungal kingdom

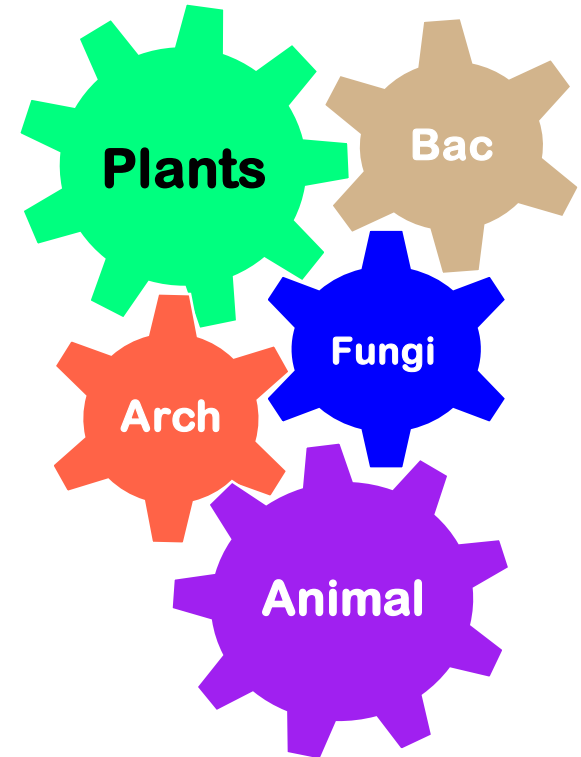


Animal kingdom

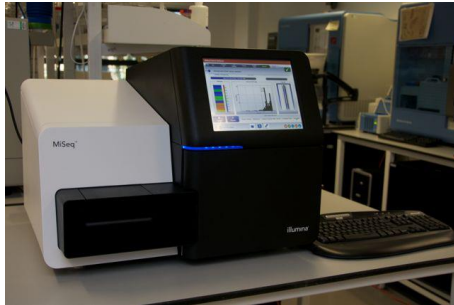
QIIME2

SPIEC-EASI

Multi-kingdom network

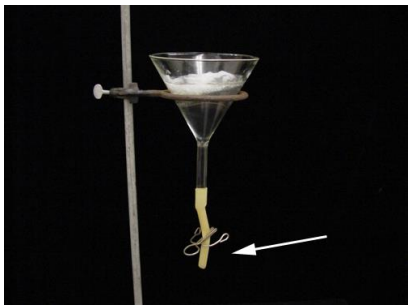


Soil DNA Sequencing

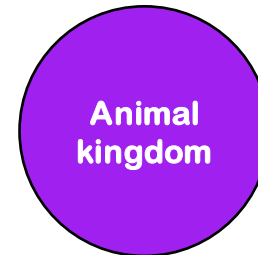


- Bacteria
- Archaea
- Fungi (ITS+18S-AMF)

Enrichment culture + Sequencing



→ Nematodes



Animal kingdom

Downstream analysis

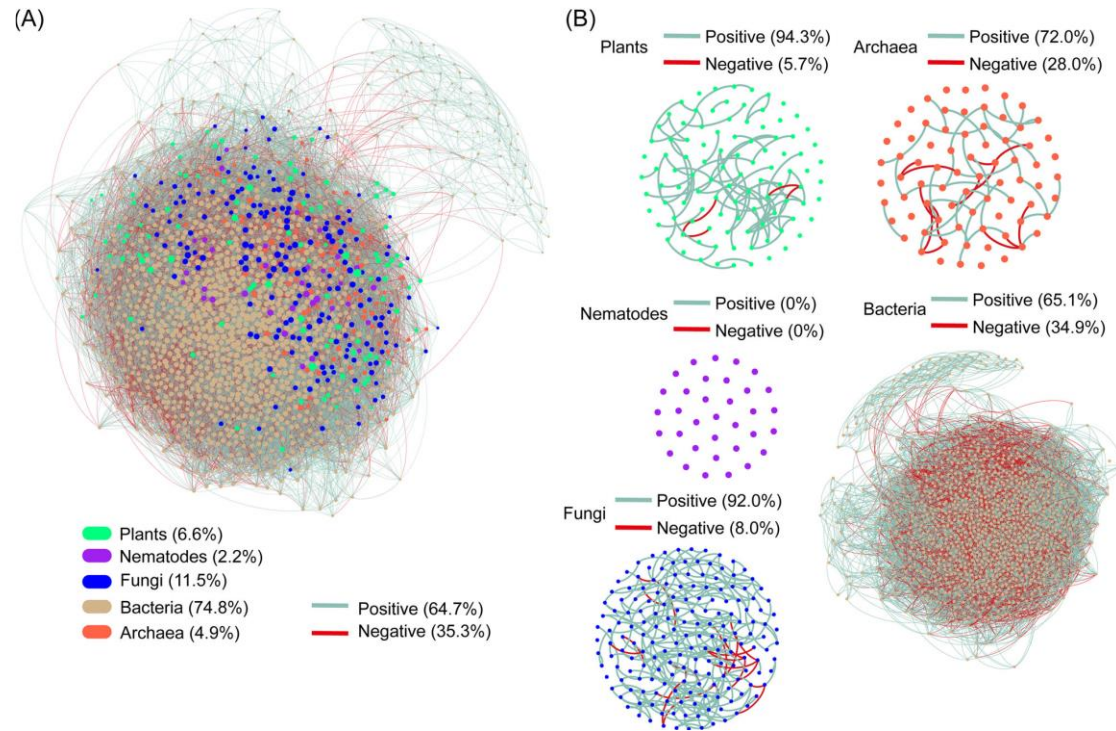


Scientific Hypotheses

- **Multi-kingdom network construction would largely increase the complexity and negative edge proportion when compared with that in single-kingdom networks.**
- **Species belonging to the fungal kingdom are crucial for the stability of multi-kingdom community association networks.**
- **Fungal community would be the “bridge” of the multi-kingdom community, linking aboveground and belowground communities.**

Results

Comparison of single-kingdom and multi-kingdom networks



(A) Single-kingdom network

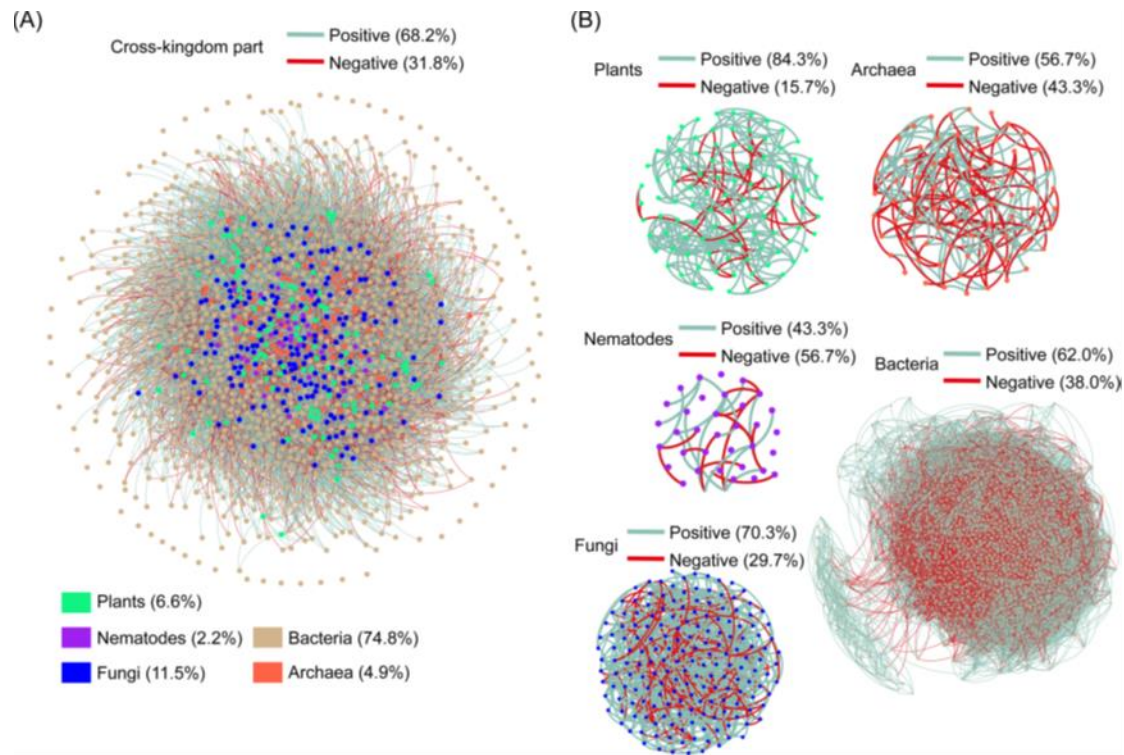
(B) Multi-kingdom network

Comparison of network topological parameters

	Node Number	Edge Number	Mean connectivity	Modularity	Average path length
Multi-kingdom	1550	28032	36.2	0.182	2.51
Plants	102	88	1.7	0.840	2.46
Nematodes	34	0	0	NA	NA
Fungi	178	286	3.2	0.695	5.81
Bacteria	1160	15824	27.3	0.208	2.67
Archaea	76	50	1.3	0.847	2.46

Results

Comparison of single-kingdom and multi-kingdom networks



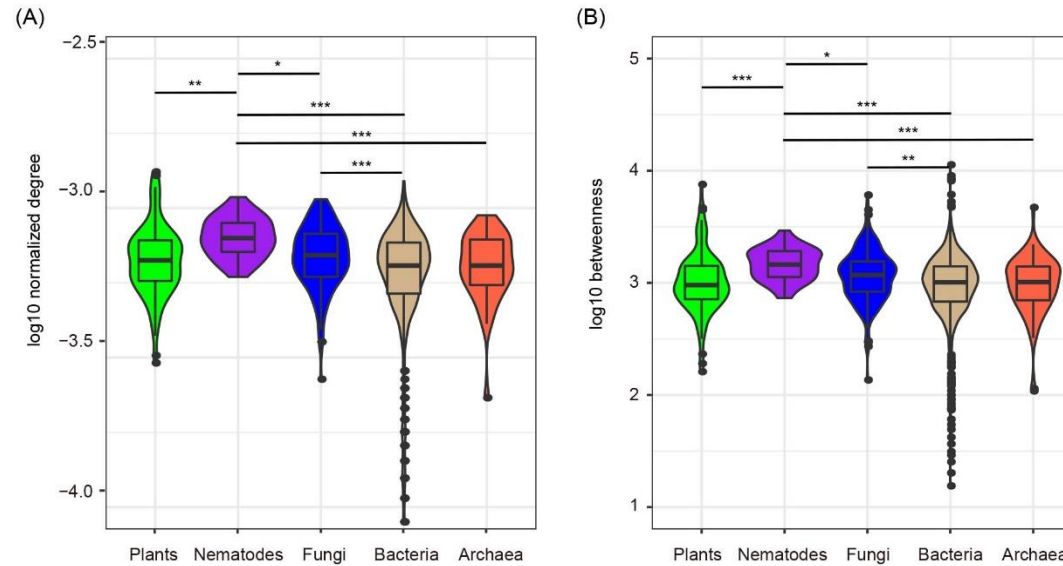
(A) The cross-kingdom subset
(B) The inner-kingdom subset

Comparison of network topological parameters

Network type	Node Number	Edge Number	Mean connectivity	Modularity	Average path length
Single-kingdom networks					
Plants	102	88	1.7	0.840	2.46
Nematodes	34	0	0	0	0
Fungi	178	286	3.2	0.695	5.81
Bacteria	1160	15824	27.3	0.208	2.67
Archaea	76	50	1.3	0.847	2.46
Within-kingdom subsets of multi-kingdom network					
Plants	102	262	5.1	0.615	3.62
Nematodes	34	30	1.8	0.595	3.57
Fungi	178	771	8.7	0.355	2.69
Bacteria	1160	16010	27.6	0.212	2.63
Archaea	76	187	4.9	0.436	2.98

Results

Node connectedness and centrality of plants, nematodes, fungi, bacteria, and archaea



The degree and betweenness of **fungi** were significantly larger than those of **bacteria**

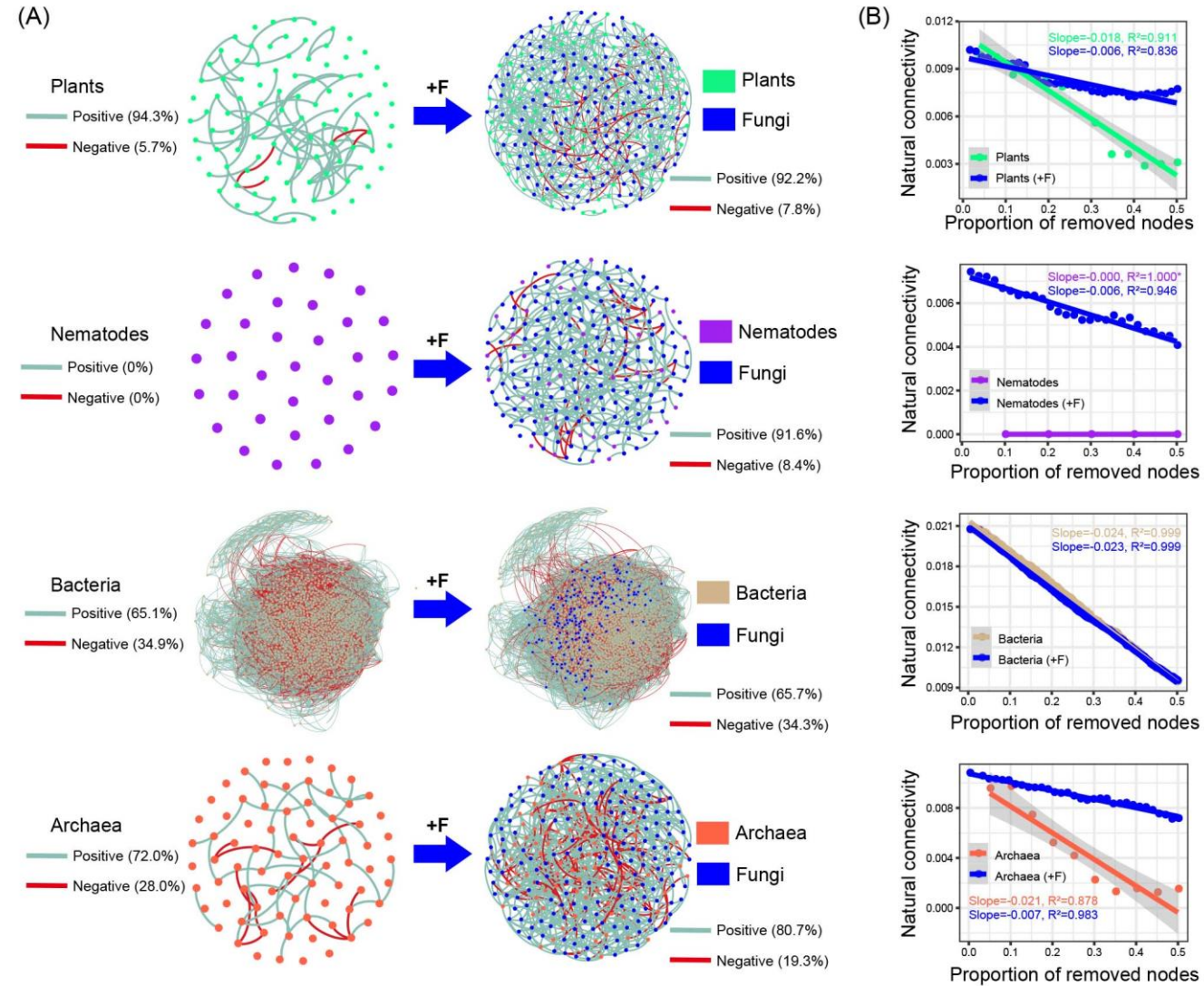
Degree: total number of links of one species

Betweenness: number of times that a species plays as “broker”

Results

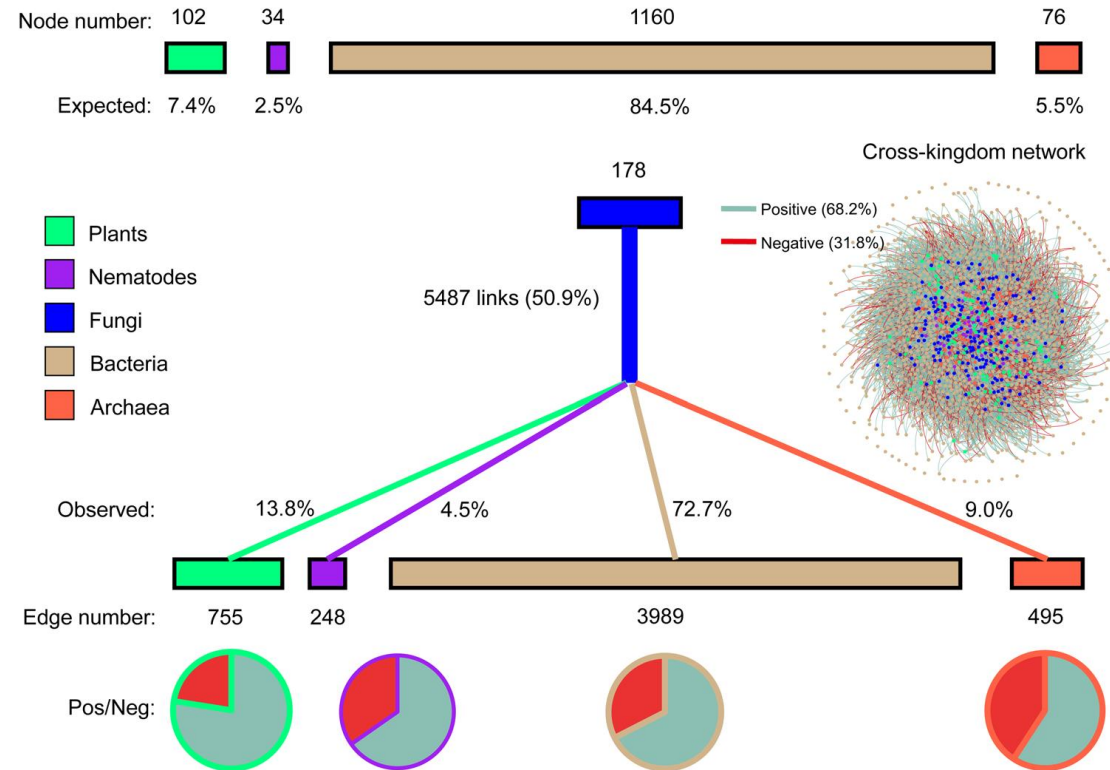
The additive impacts of fungal interactions on single-kingdom networks of plants, nematodes, bacteria, and archaea

The addition of **fungi** enhanced the network stability and connectedness of plants, nematodes, and archaea substantially



Results

Fungal links in the cross-kingdom part of multi-kingdom network



Compared to the randomized links of fungi, **fungi** were more prone to linking with **plants** and **archaea**

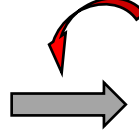
Results

Associations among fungi and other kingdoms at community level

Multiple Regression on Matrices

Nematodes R ² =0.201, P=0.001		
Variables	Coefficient	P
pH	0.047	0.001

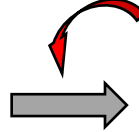
Add biotic interaction



Nematodes R ² =0.265, P=0.001		
Variables	Coefficient	P
pH	0.034	0.004
Fungal community	0.030	0.001

Fungi R ² =0.598, P=0.001		
Variables	Coefficient	P
Tree richness	0.011	0.005
ForestD	0.011	0.034
RMn	0.008	0.029
SM	0.014	0.001
pH	0.015	0.002
Conductivity	0.015	0.004
Plant community	0.023	0.001

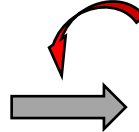
Add biotic interaction



Fungi R ² =0.605, P=0.001		
Variables	Coefficient	P
SM	0.013	0.003
pH	0.014	0.004
Conductivity	0.015	0.002
Plant community	0.027	0.001
Nematode community	0.008	0.017
Archaeal community	0.012	0.002

Archaea R ² =0.332, P=0.001		
Variables	Coefficient	P
Tree richness	0.038	0.001
DBH	0.018	0.014
Conductivity	0.027	0.004
Soil total Al	0.015	0.021
Soil total Fe	0.033	0.001

Add biotic interaction

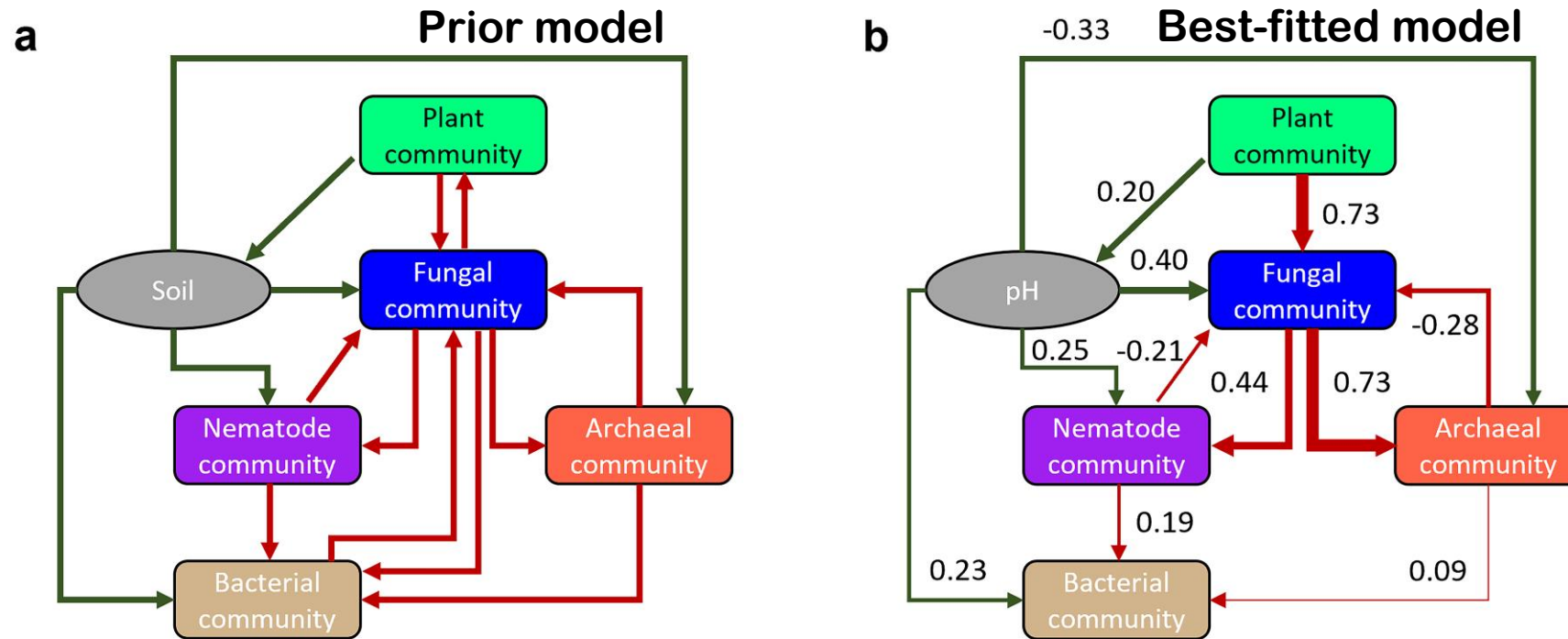


Archaea R ² =0.334, P=0.001		
Variables	Coefficient	P
Tree richness	0.029	0.001
DBH	0.019	0.001
Conductivity	0.016	0.009
Soil total Al	0.016	0.001
Soil total Fe	0.027	0.001
Fungal community	0.030	0.001

Results

Associations among fungi and other kingdoms at community level

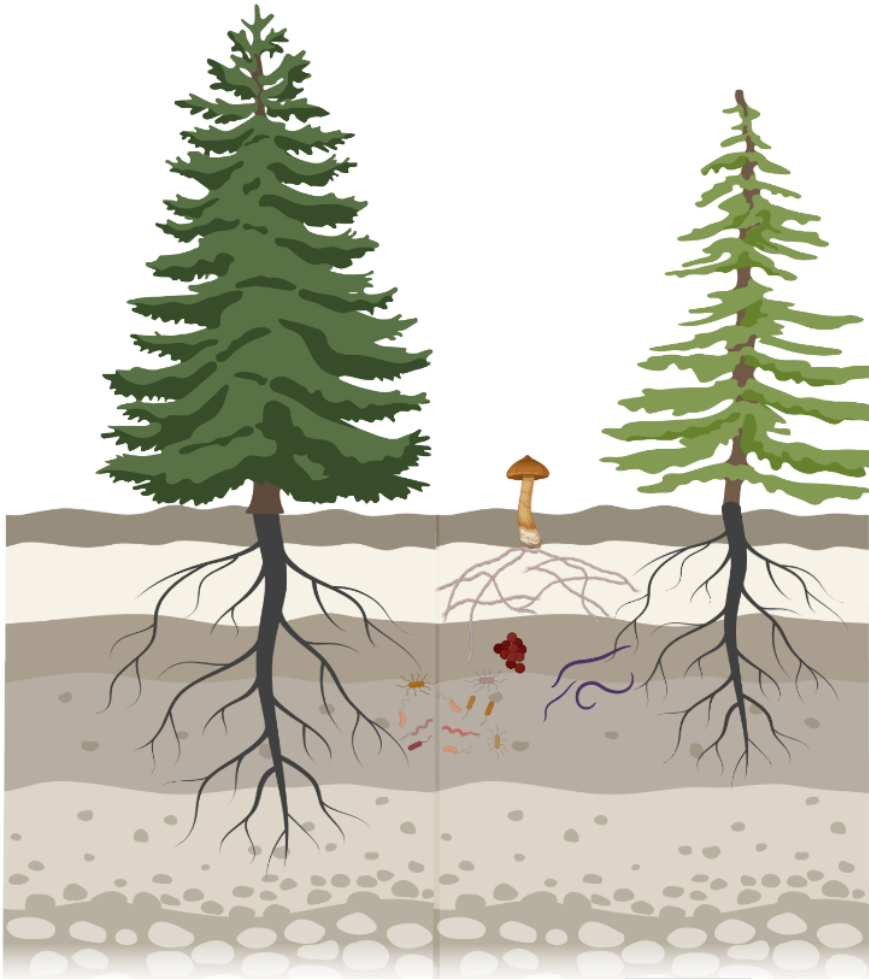
Structural equation modelling



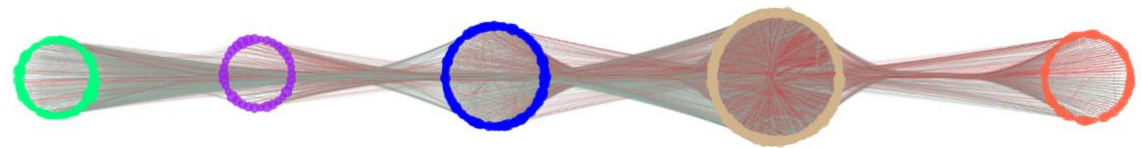
Expected 1: Plants → Soil → Soil biota
Expected 2: Plants ↔ Fungi ↔ Soil biota (excluding fungi)

Chi-square=0.519, Df=3, $P=0.915$
AGFI=0.997, RMSEA<0.001, AIC=36.519

Summary



- Multi-kingdom network construction increased network complexity and negative edge proportion.
- Fungi stabilized multi-kingdom network structure and linked above- and below-ground biota at community level.



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