

Synergistic effects of diazotrophs and arbuscular mycorrhizal fungi on soil biological nitrogen fixation after three decades of fertilization

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Introduction

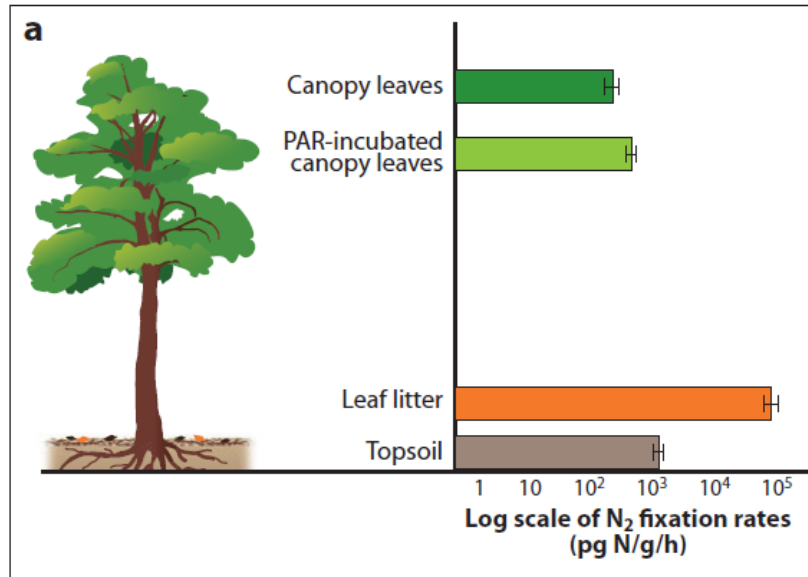
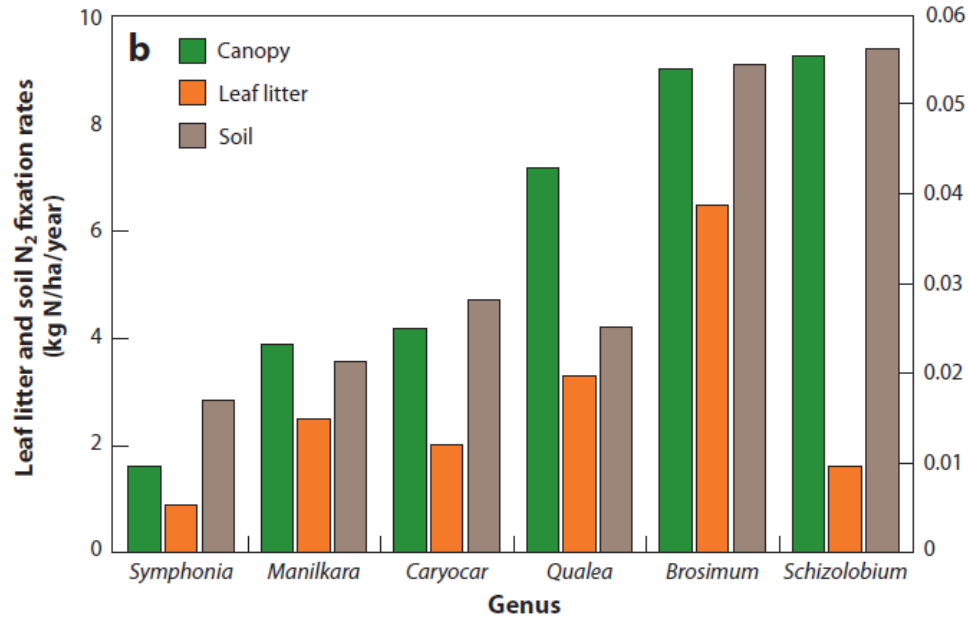
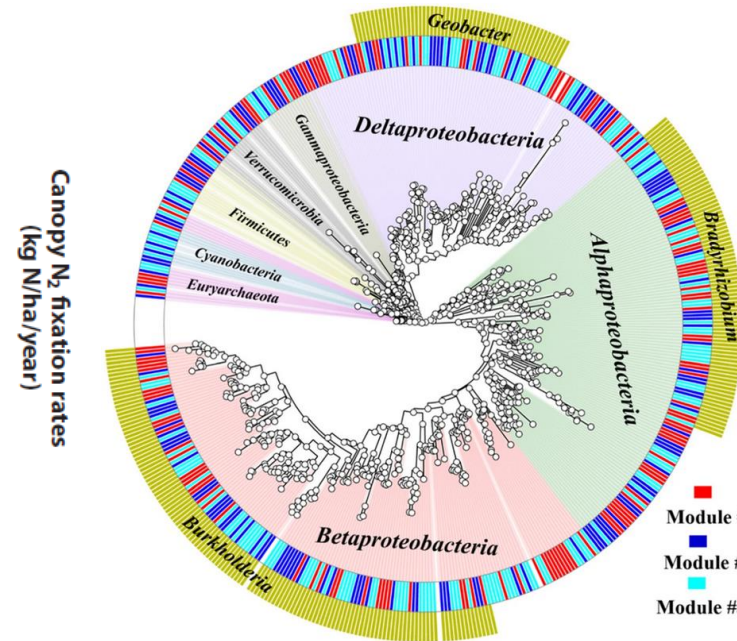


Table 1 Biome-scale estimates of terrestrial free-living and symbiotic N₂ fixation rates based on the literature^a

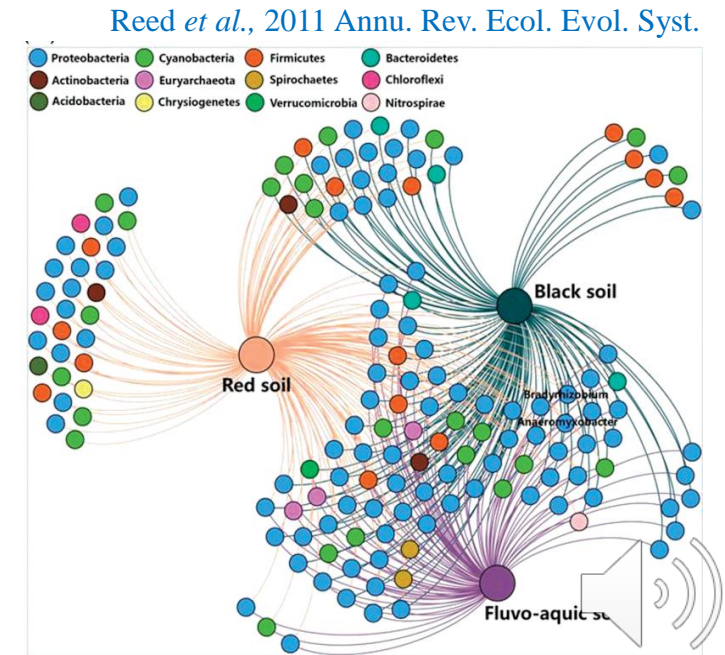
Biome	Free-living N ₂ fixation rates (kg N/ha/year)	Range in free-living N ₂ fixation rates (kg N/ha/year)	<i>n</i>	Range in symbiotic N ₂ fixation rates (kg N/ha/year)	<i>n</i>
Moist tundra and alpine tundra	1.5	0.4–3.0	7	1.0–4.9	3
Boreal forest and woodland	1.2	0.3–3.8	14	0.3–6.6	2
Temperate forests	1.7	0.01–12	38	1–160	17
Temperate grasslands	4.7	0.1–21	13	0.1–10	8
Tropical savanna	15.0	3–30	3	3–90	6
Tropical evergreen forest	7.8	0.1–60	19	5.5–16	4
Tropical floodplain	7.5	4.1–12	3	14–28.5	2
Tropical deciduous forest	3.3	3.3	1	7.5–30	3
Mediterranean shrubland	1.0	1.0	1	0.1–10	4
Desert	4.0	0.01–13	15	0.7–29.5	3



Reed *et al.*, 2011 Annu. Rev. Ecol. Evol. Syst.

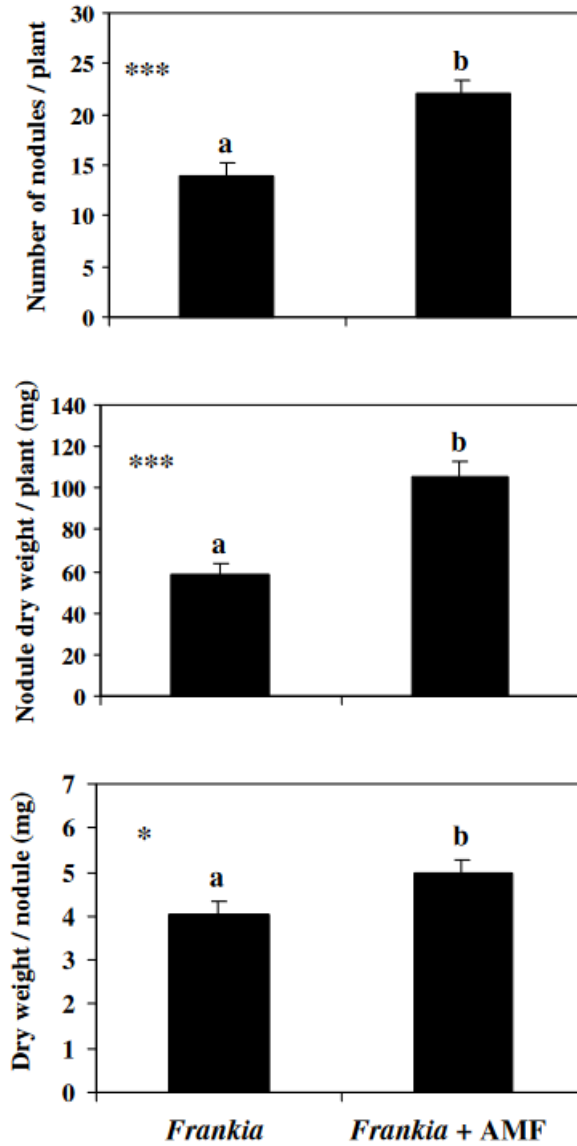


Fan *et al.*, 2019 Microbiome

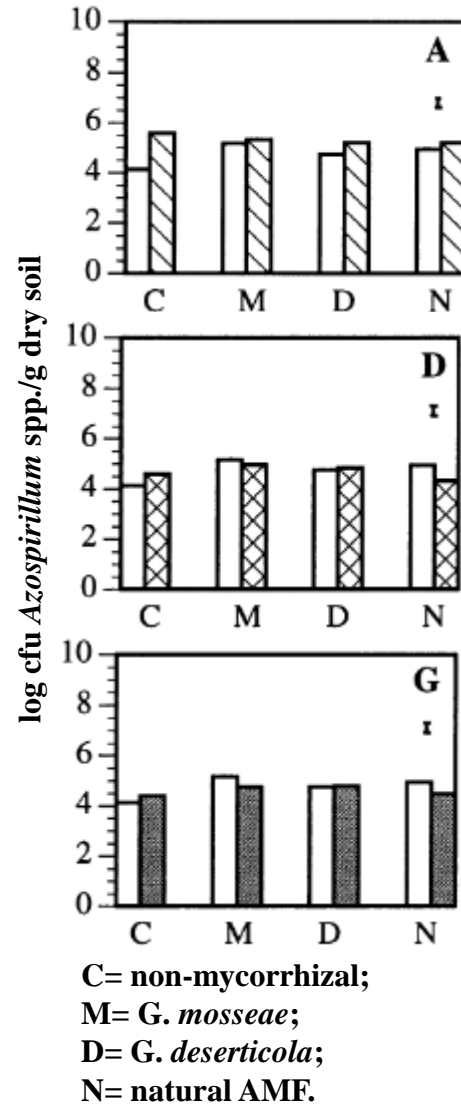


Han *et al.*, 2019 FEMS Microbiol. Ecol.

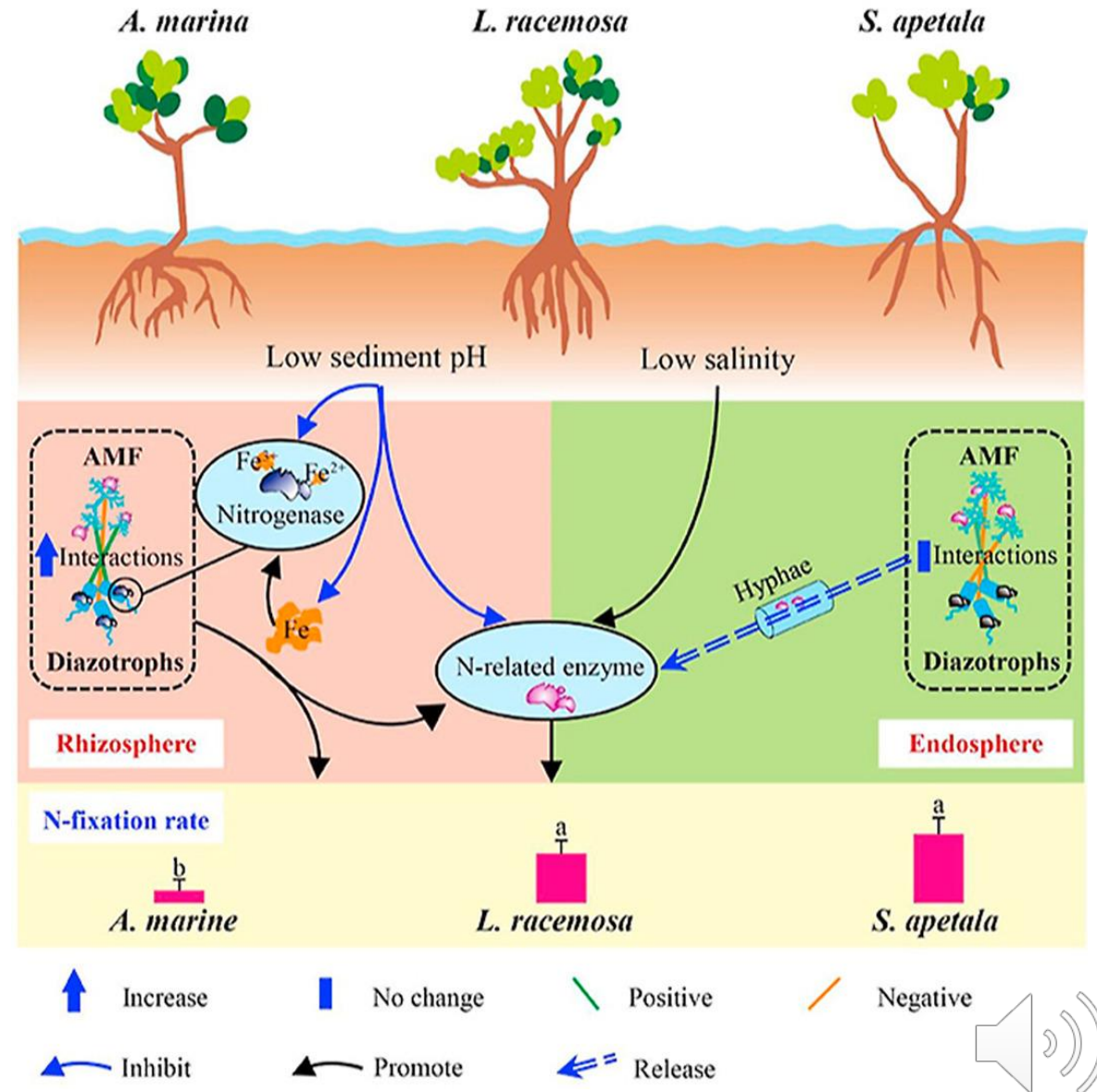
Introduction



Oliveira *et al.*, 2015 Chemosphere



Vázquez *et al.*, 2015 Appl. Soil Ecol.



Yu *et al.*, 2021 Soil Biol. Biochem.

Introduction

Four typical fertilization regimes



Chemical fertilizer



Cow manure



Wheat straw



Green manure

Wheat-maize intercropping system



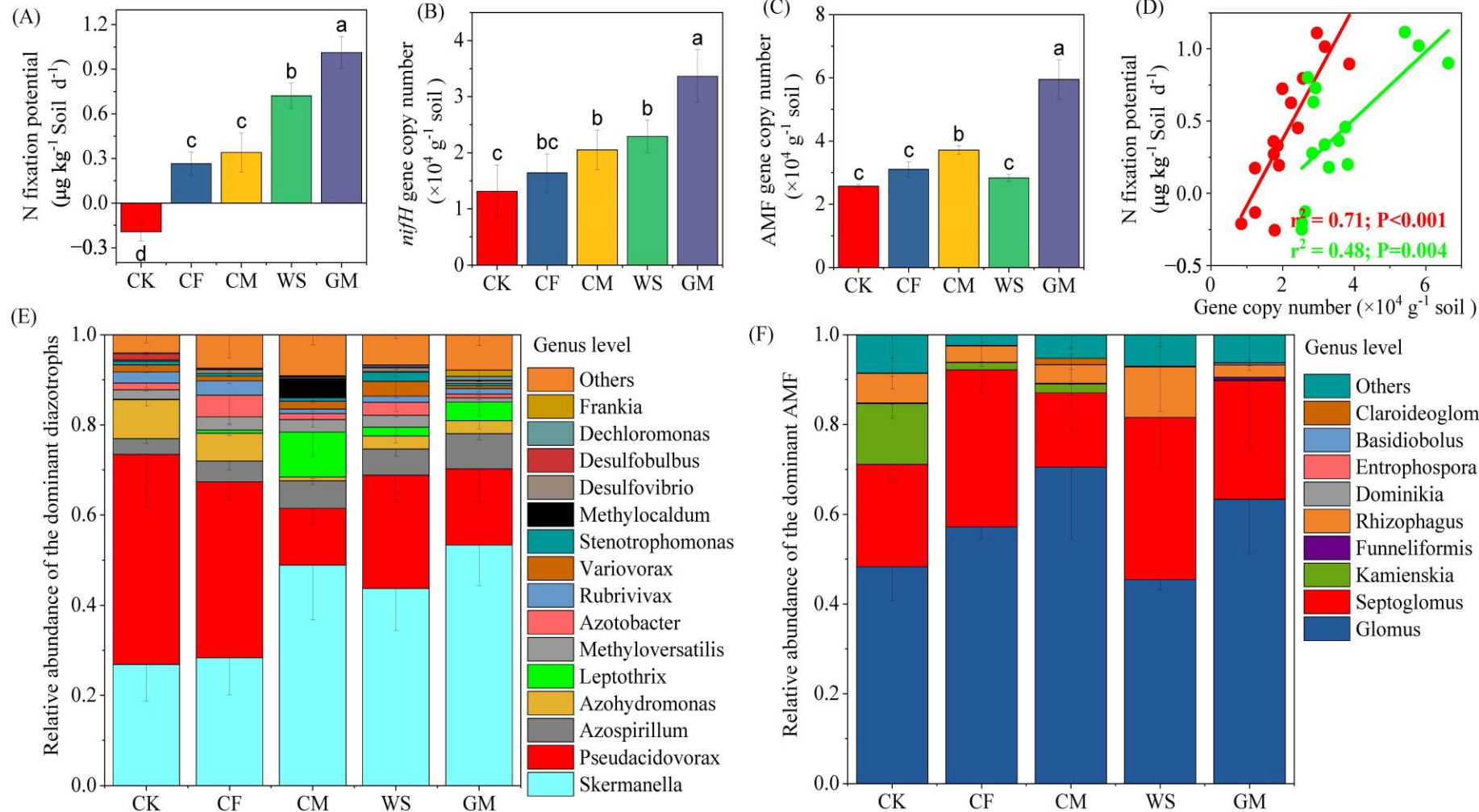
Hypothesis

- H1.** Long-term fertilization would inhibit the soil BNF and drastically alter the diazotrophic community structure that may no longer be required to fix atmospheric N;
- H2.** Compared to the entire microbial community, unique co-occurring ecological clusters of diazotrophs and AMF might predict BNF rates better;
- H3.** Long-term fertilization would lower the synergistic (positive) relationship between diazotrophs and AMF owing to the nutrient-rich environment in fertilization regime.



Results

Increased soil BNF rates, and improved N fixers and their helpers



- The BNF rates were promoted relative to the CK, showing an order of GM > WS > CM \approx CF > CK;

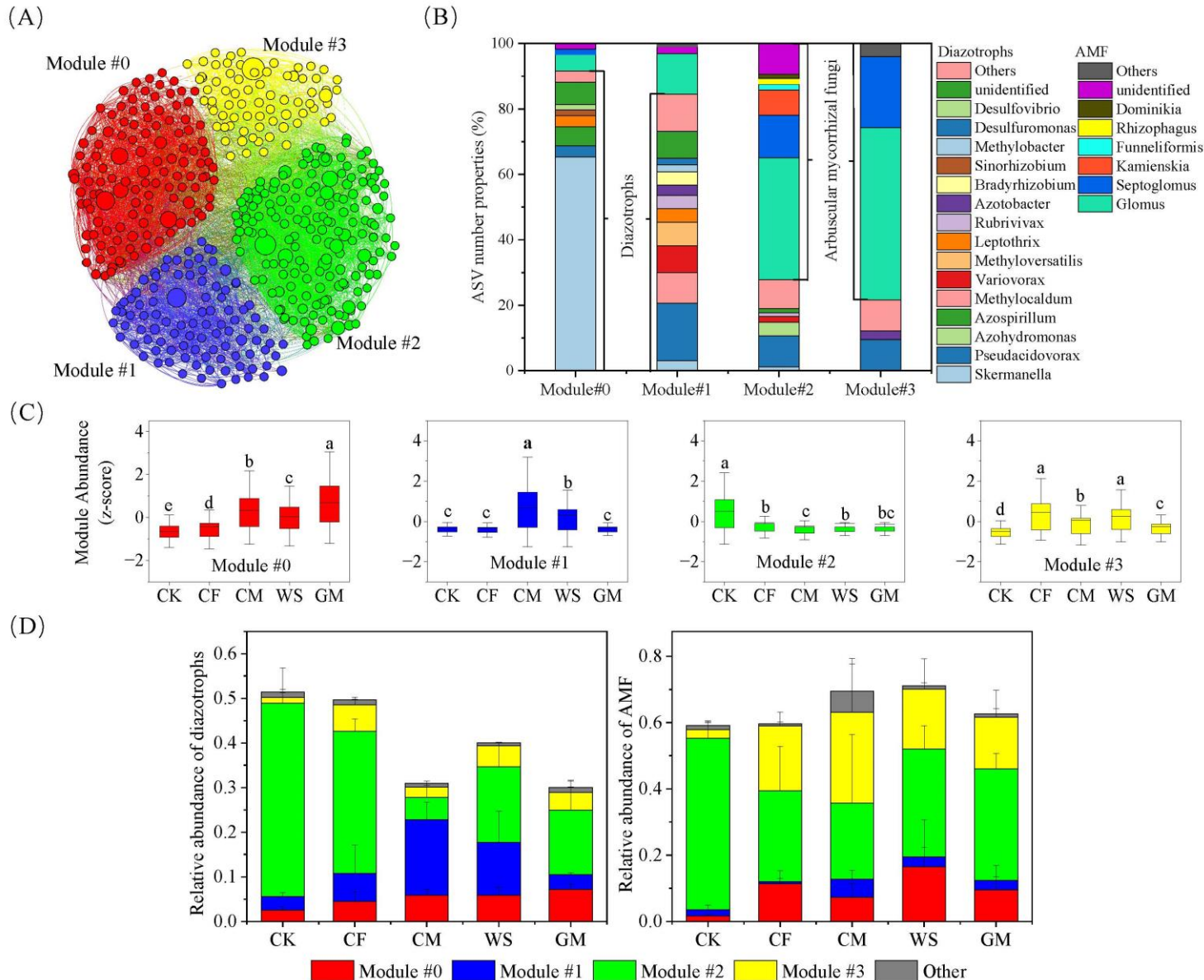
- Long-term organic fertilization increased the absolute abundance of diazotrophic and AMF communities;

- Green manuring increased the relative abundance of *Azospirillum* and *Skermanella*.



Results

Increased the relative abundance of Module #0 but reduced positive links between diazotrophs and AMF



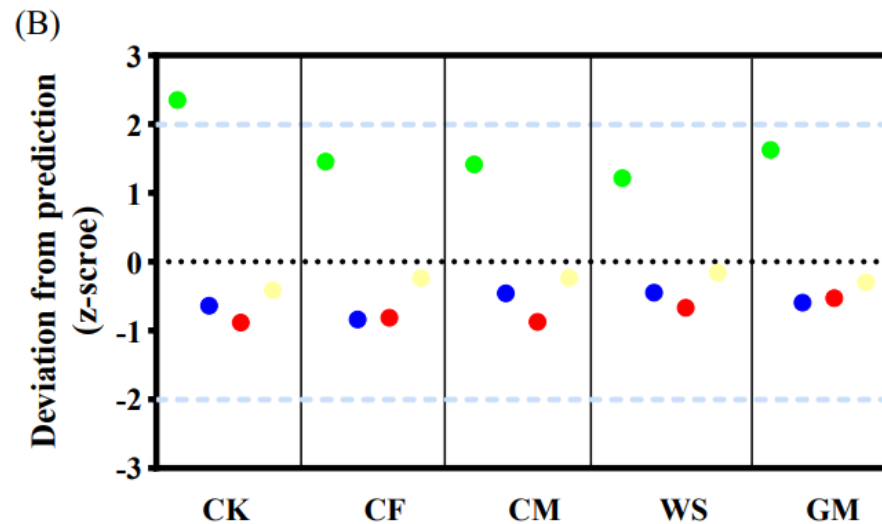
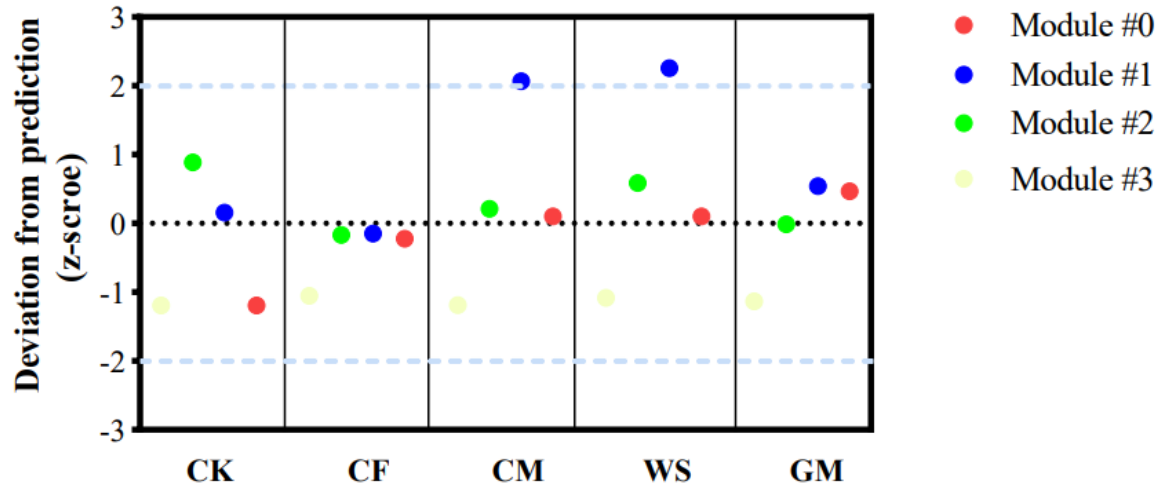
- **Module #0:** *Skermanella* and *Azospirillum*; **Module #1:** *Pseudacidovorax*, *Methylocaldum*, *Variovorax*, and *Methyloversatilis*; **Modules #2 and #3:** *Glomus* and *Septoglomus*
- Long-term fertilization increased the relative abundances of Modules #0 and #3, and GM treatment had the greatest enhancement in Module #0;
- Organic fertilization reduced synergistic relationships between diazotrophs and AMF.
- Green manuring increased the synergistic relationships within Module #0



Results

Selected against the microbes associated with Module #1 and Module #2

(A) Observed and Expected Phylogenetic Diversity

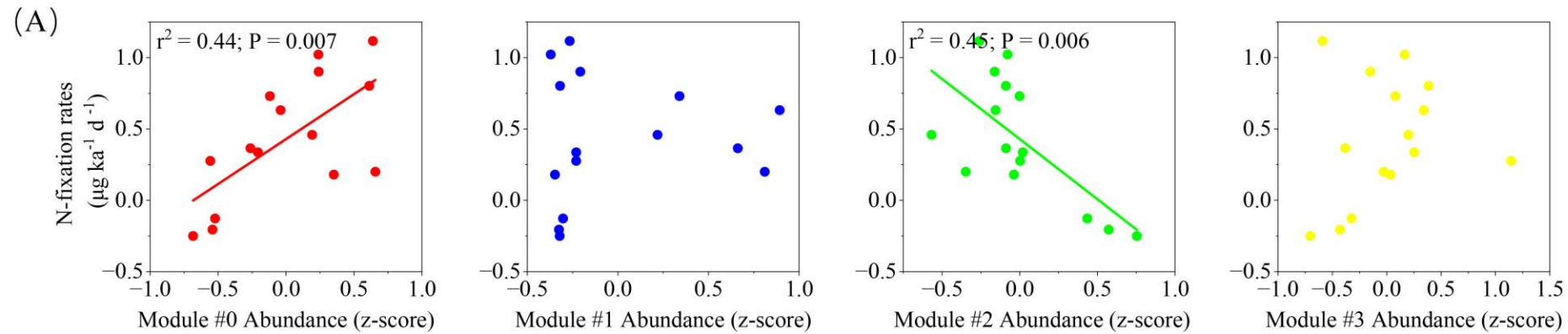


- Long-term CM and WS had been selected against the diazotrophs associated with Module #1, while long-term fertilization selected against the AMF associated with Module #2.
- The shift in observed PD of Module #1 was tightly linked with a large emergence of copiotrophic genera such as *Methylocaldum*, *Methyloversatilis*, and *Leptothrix* under CM and WS regimes;
- The changes in observed PD of Module #2 were closely linked with a large loss in *Kamienskia* sp., *Septoglomus* sp., and *Glomus* sp.

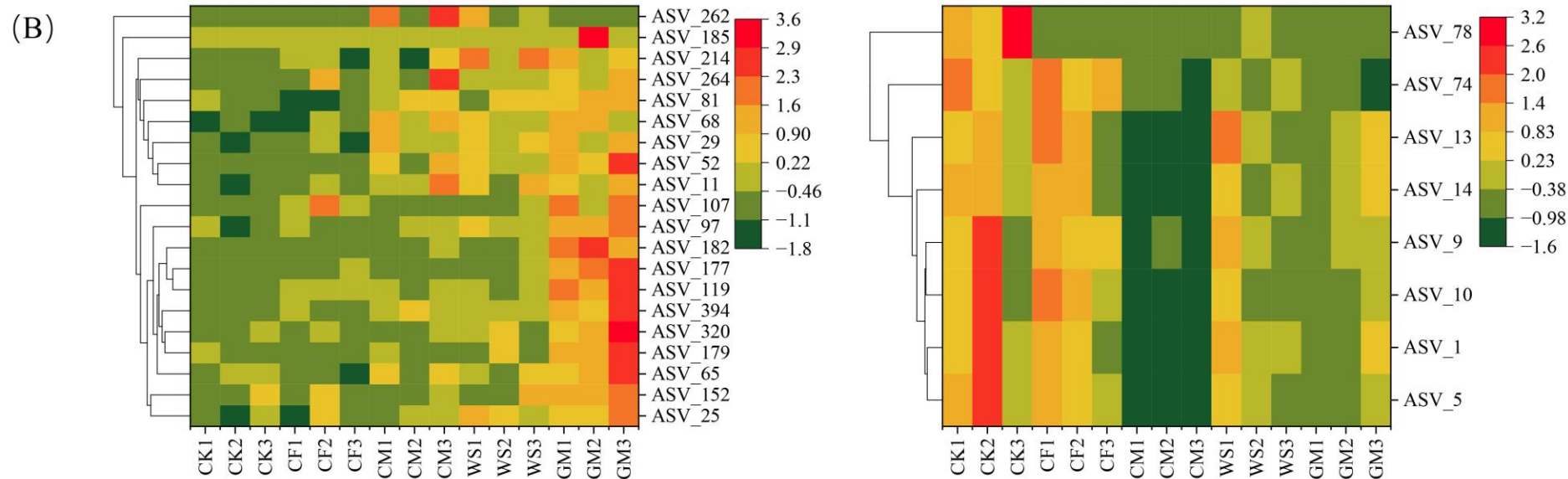


Results

Modules #0 and #2 were referred to as key ecological clusters



- Modules #0 and #2 were referred to as key ecological clusters, and enriched in GM and CK, respectively.

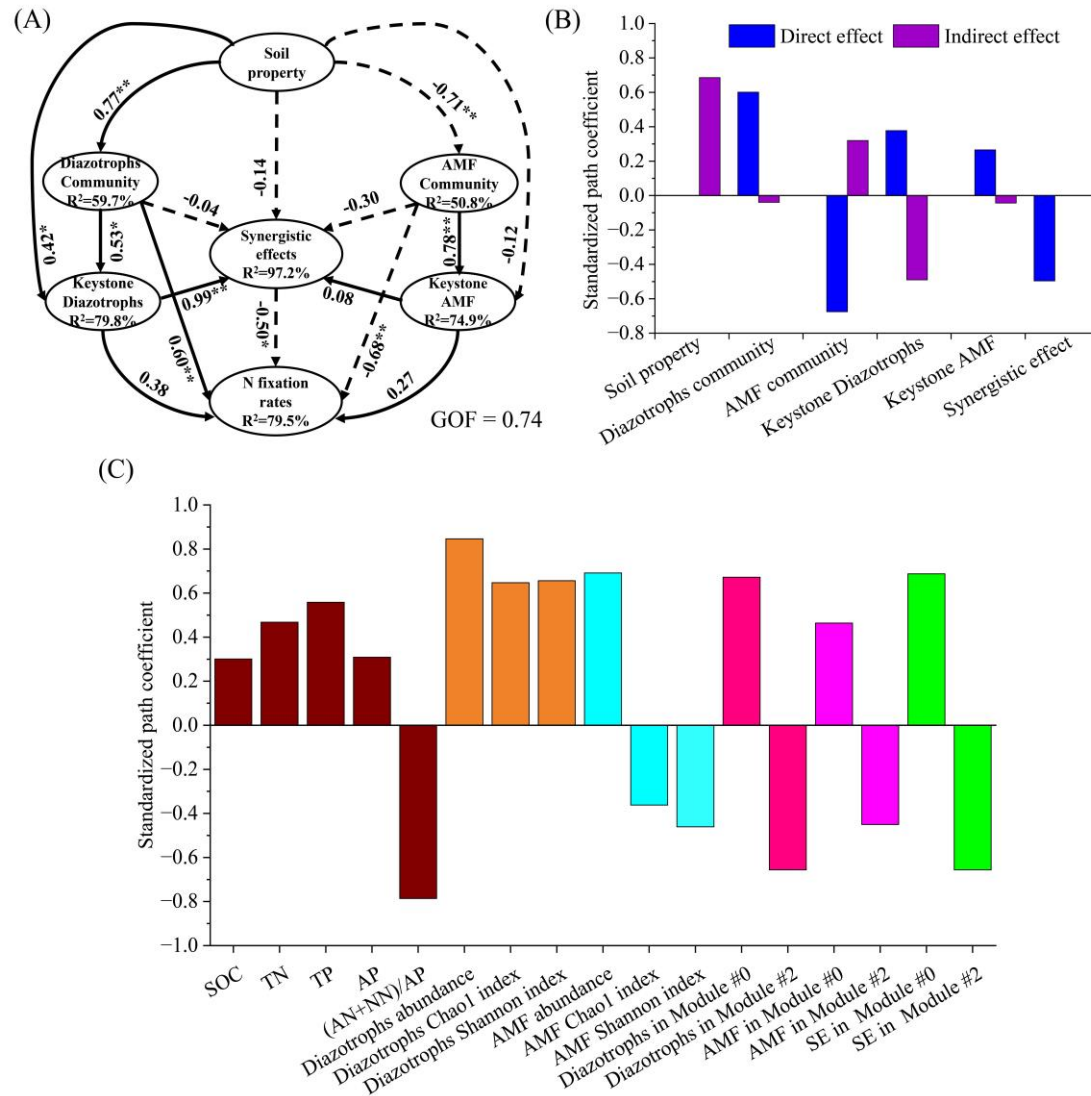


- In Modules #0 and #2, 15% (3/20) and 75% (6/8) of diazotrophic phylotypes showed a positive association with AMF.



Results

Diazotrophs in key ecological clusters had the second-strongest effect on BNF, after diazotrophic abundance



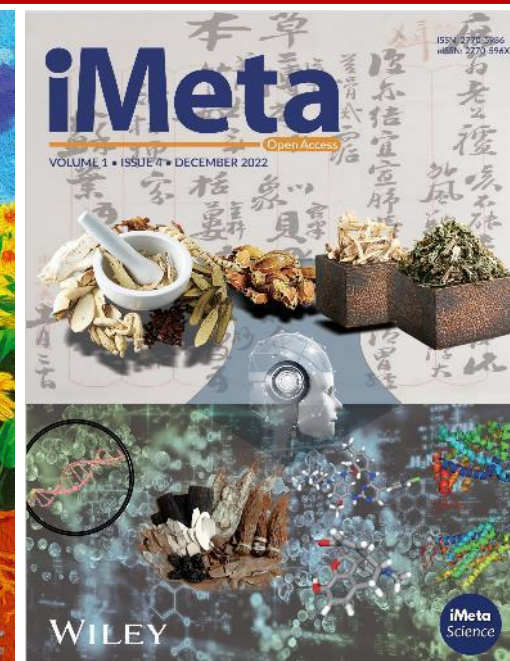
- Certain ecological clusters of diazotrophs and AMF rather than the entire microbial community promoted soil BNF;
- The relative abundance of diazotrophs in key ecological clusters had the second-strongest effect on BNF rates, the first being diazotrophic absolute abundance.



Summary

- Long-term fertilization increases soil BNF rates, and the green manure treatment rendered the highest enhancement;
- The increase in diazotrophic and AMF absolute abundance and the relative abundance of the key ecological cluster of Module #0 with dominant diazotrophs such as *Skermanella* and *Azospirillum*, strengthens soil BNF;
- Green manuring can reverse the decline (the synergistic functions of diazotrophs and AMF) within Module #0, and this had a positive correlation with the BNF rate;
- We highlights the novel findings about the soil BNF as affected by fertilization, i.e., diazotrophic and AMF absolute abundance and relative abundant of keystone phylotypes play important roles, the interspecies correlation between diazotrophs and AMF contributes significantly to the soil BNF, and green manuring is a more effective strategy for improving soil BNF rate.

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