RESEARCH ARTICLE SUMMARY

FUNGAL BIOGEOGRAPHY

# Global diversity and geography of soil fungi

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**INTRODUCTION:** The kingdom Fungi is one of the most diverse groups of organisms on Earth, and they are integral ecosystem agents that govern soil carbon cycling, plant nutrition, and pathology. Fungi are widely distributed in all terrestrial ecosystems, but the distribution of species, phyla, and functional groups has been poorly documented. On the basis of 365 global soil samples from natural ecosystems, we determined the main drivers and biogeographic patterns of fungal diversity and community composition.

**RATIONALE:** We identified soil-inhabiting fungi using 454 Life Sciences (Branford, CN) pyrosequencing and through comparison against taxonomically and functionally annotated sequence databases. Multiple regression models were used to disentangle the roles of climatic, spatial, edaphic, and floristic parameters on fungal diversity and community composition. Structural equation models were used to determine the direct and indirect effects of climate on fungal diversity, soil chemistry, and vegetation. We also examined whether fungal biogeographic patterns matched paradigms derived from plants and animals—namely, that species' latitudinal ranges increase toward the poles (Rapoport's rule) and diversity increases toward the equator. Last, we sought group-specific global biogeographic links among major biogeographic regions and biomes using a network approach and area-based clustering.

**RESULTS:** Metabarcoding analysis of global soils revealed fungal richness estimates approaching the number of species recorded to date. Distance from equator and mean annual precipitation had the strongest effects on richness of fungi, including most fungal taxonomic and functional groups. Diversity of most fungal groups peaked in tropical ecosystems, but ectomycorrhizal fungi and several fungal classes were most diverse in temperate or boreal ecosystems, and many fungal groups exhibited distinct preferences for specific edaphic conditions (such as pH, calcium, or phosphorus). Consistent with Rapoport's rule, the geographic range of fungal taxa increased toward the poles. Fungal endemicity was particularly strong in tropical regions, but multiple fungal taxa had cosmopolitan distribution.

**CONCLUSIONS:** Climatic factors, followed by edaphic and spatial patterning, are the best predictors of soil fungal richness and community composition at the global scale. Richness of all fungi and functional groups is causally unrelated to plant diversity, with the exception of ectomycorrhizal root symbionts, suggesting that plant-soil feedbacks do not influence the diversity of soil fungi at the global scale. The plant-to-fungi richness ratio declined exponentially toward the poles, indicating that current predictions—assuming globally constant ratios—overestimate fungal richness by 1.5- to 2.5-fold. Fungi follow similar biogeographic patterns as plants and animals, with the exception of several major taxonomic and functional groups that run counter to overall patterns. Strong biogeographic links among distant continents reflect relatively efficient long-distance dispersal compared with macro-organisms. ■

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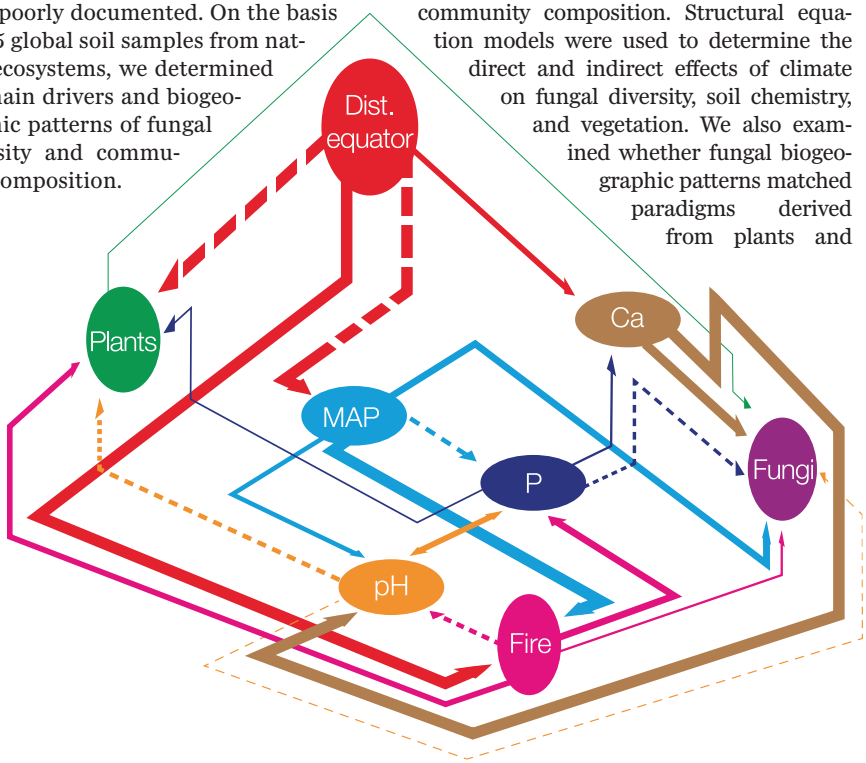


**Direct and indirect effects of climatic and edaphic variables on plant and fungal richness.** Line thickness corresponds to the relative strength of the relationships between the variables that affect species richness. Dashed lines indicate negative relationships. MAP, mean annual precipitation; Fire, time since last fire; Dist. Equator, distance from the equator; Ca, soil calcium concentration; P, soil phosphorus concentration; pH, soil pH.

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