New Phytologist

Commentary

Response of soil fungal ecological guilds to global changes

Fungi are eukaryotic microorganisms that play fundamental roles in regulating key ecosystem processes. They act as major decomposers of organic matter, contribute to carbon mineralization and sequestration, and act as crucial regulators of the soil carbon balance, which is a major priority for human survival in this century (Crowther *et al.*, 2019). Besides the free-living saprotrophs, many fungal species form symbiotic associations with plants or animals. As plant pathogens, fungi significantly influence plant primary production as well as plant species richness and community composition. In both animals and plants, an unprecedented number of fungal diseases have recently caused some of the most severe die-offs and are jeopardizing food security (Fisher *et al.*, 2012). By contrast, mycorrhizal fungi act as beneficial plant symbionts. Importantly, > 90% of all terrestrial plants, including the most important agricultural crops, largely depend on their mycorrhizal symbionts for uptake of water and mineral nutrients (Brundrett & Tedersoo, 2018). Mycorrhizal fungi can also provide protection against pathogens to their host plants. In return, terrestrial plants provide mycorrhizal fungi with carbon-rich compounds such as sugars and lipids (Brundrett & Tedersoo, 2018). Shifts among the above-listed fungal ecological guilds (i.e. a group of species that exploit/depend on the same resources) can, therefore, largely affect plant performance as well as various ecosystem processes. In this issue of *New Phytologist*, Rodriguez-Ramos *et al.* (2021; pp. 1105–1117) provide detailed evidence that the disturbance of temperate forests with bark beetle outbreaks, wildfires, and salvage and clear-cut logging, unequally affects different fungal ecological guilds. Aside from the importance for forestry and forest management practices, the results of Rodriguez-Ramos *et al.* also provide valuable insights into the response of forest soil fungi to consequences associated with the ongoing global changes.

While the impact of global change on the distribution of macroorganisms has been addressed in numerous studies, very little is still known about the effect of global change on the survival and distribution of soil fungi (Gange *et al.*, 2011). Among the various aspects of global change, changes in climate will likely result in severe ecosystem alterations. We are already facing increasing lengths of heat waves, and an unprecedented increase of temperature in high latitudes associated with long drought periods. Consequently, the frequency of large-scale forest wildfires and bark beetle outbreaks have largely increased over recent years (Pérez-Valera *et al.*, 2019). Rodriguez-Ramos *et al.* showed that these severe forest disturbances will result in a shift of fungal communities from those dominated by ectomycorrhizal fungi to those dominated by saprotrophs (i.e. tree-symbiotic fungi will be strongly negatively affected).

'. . . ongoing climate change will most likely severely disrupt ectomycorrhizal associations and increase the vulnerability of ectomycorrhizal plants to biotic and abiotic stresses, which can subsequently result in a further increase in large-scale forest disturbances.'

Several recent large-scale studies also documented contrasting responses of different soil fungal ecological guilds to climate change with potentially alarming consequences for ecosystems. While relative abundance of plant fungal pathogens will probably increase in most regions of the world in the near future because of the increasing global temperature (Delgado-Baquerizo *et al.*, 2020a), Steidinger *et al.* (2020), based on model predictions, forecast a substantial decline in ectomycorrhizal fungal diversity in North American coniferous forests. Even mitigation of greenhouse gas emissions during the 21st century would probably not stop the decline in ectomycorrhizal fungal diversity (Steidinger *et al.*, 2020). Similarly, a recent meta-study focused on soil mycobiome data across the world, identified that in general ectomycorrhizal fungi tend to have narrower climatic niches compared to free living saprotrophs or fungal plant pathogens (Větrovský *et al.*, 2019). Together these studies provide solid evidence that ongoing climate change will most likely severely disrupt ectomycorrhizal associations and increase the vulnerability of ectomycorrhizal plants to biotic and abiotic stresses, which can subsequently result in a further increase in large-scale forest disturbances.

How will these forest disturbances affect ecosystem functions? They can, in some cases, directly affect ecosystem functions with little or no effect on soil biodiversity (Zhou *et al.*, 2020), or they can affect soil abiotic properties (Pérez-Valera *et al.*, 2019). Ecosystem disturbances can cause substantial shifts in the dominant soil fungal guilds (from ectomycorrhizal to saprophytic fungi) and their biomasses (Rodriguez-Ramos *et al.*) or alter the complexity of microbial interaction networks (Wagg *et al.*, 2019), which in turn directly affect ecosystem functionality. To better understand the effect of global change and associated disturbances on ecosystem

This article is a Commentary on Rodriguez-Ramos *et al.* (2021), pp. 1105–1117.

functionality, all these causal relationships need to be disentangled. For example, biotic disturbances, such as insect outbreaks, that strongly affect initial litter quality, the key driver of early litter decomposition at global and regional scales (Djukic *et al.*, 2018), in the study of Rodriguez-Ramos *et al.* did not significantly affect soil abiotic properties or even microbial community composition. Although, it has been reported that higher intensities of insect outbreaks have strong effects on soil microbial communities (Štursová *et al.*, 2014; Pec *et al.*, 2017). By contrast, abiotic disturbances, such as wildfires, have been shown to strongly affect soil abiotic properties, which determined changes in the phylogenetic structure of soil microbial communities, which in turn affected indicators of ecosystem functioning (such as soil respiration, microbial biomass carbon, enzymatic activities, microbial and metabolic quotients) (Pérez-Valera *et al.*, 2019). The microbial quotient corresponds to the microbial biomass carbon per unit of organic carbon, whereas the metabolic quotient results from dividing respired carbon per unit of microbial biomass. Thus, future research needs to further explore these causal relationships by each disturbance type and soil fungal ecological guild.

Analyzing how different measures of biodiversity can explain or predict multiple ecosystem functions/services is one of the main tasks in ecosystem ecology. Global studies on the causal relationships between soil biodiversity and ecosystem functions have become increasingly common over the last few years. In this context, soil biodiversity has been measured as species richness (Delgado-Baquerizo *et al.*, 2020b), phylogenetic and functional diversity (Pérez-Valera *et al.*, 2019), and interaction network complexity (Wagg *et al.*, 2019). These biodiversity measurements have been linked to soil ecosystem multifunctionality, defined as a metric of aggregation of multiple ecosystem functions (Delgado-Baquerizo *et al.*, 2020b), which better explains the relationship with biodiversity than when analyzing each function individually. This research framework can be applied to understand the implications of forest disturbances on different soil fungal ecological guilds and ecosystem functions.

In a global soil survey, Delgado-Baquerizo *et al.* (2020b) found that plant richness and cover, soil properties (pH, carbon, percent of clay), and climate (aridity and mean annual temperature), in that order, affected soil biodiversity, which together with soil carbon, predicted ecosystem multifunctionality. The abundance of saprophytic fungi was more correlated to ecosystem functions such as nitrogen availability and soil respiration than mycorrhizal fungi, while only the former were correlated to phosphorus (P) availability (and the latter to P mineralization); both fungal guilds were equally correlated with the control of antibiotic resistance genes in soil (Delgado-Baquerizo *et al.*, 2020b). Thus, from these results, some ecosystem functioning implications caused by the shift from ectomycorrhizal to saprophytic fungi following abiotic disturbances (as found by Rodriguez-Ramos *et al.*) can be inferred. Interestingly, in a recent meta-analysis of 1235 climate change factor observations, Zhou *et al.* (2020) show that these changes do not always lead to a reduction in microbial diversity, although rare species are more affected. The impact of these changes in soil functions is explained by changes in microbial biomass and community structure rather than in alpha diversity (Zhou *et al.*, 2020). Applying a gradient of soil sieve-filtering (from 5 to 0.1 mm, or sterile soil) in a microcosm experiment, which can be taken as a disturbance intensity gradient, Wagg *et al.* (2019) found that multifunctionality, and bacterial and fungal richness and interaction network complexity decreased strongly along the gradient. Ecosystem functions, such as decomposition, leaching, and plant nutrient uptake, were also highly affected, with more fungal taxa involved in these functions than bacterial taxa (Wagg *et al.*, 2019).

Further studies on the effects of global changes on soil fungal guilds may need to incorporate some elements discussed here: causal relationships between disturbances and ecosystem functions and soil abiotic properties, and disturbance intensity gradients and timescales. Understanding the consequences of inevitable global changes on soil biota and ecosystem functioning has to be a primary interest of current biological research. We particularly need to assess the climate-driven changes in fungal species distribution and how this will affect plant physiology and ecosystems.

Acknowledgements

CM thanks the Universidad de O'Higgins postdoctoral fund and the Fondecyt project no. 1190642 (Chilean Government, ANID). PK thanks the Czech Science Foundation grant no. 18-26191S.

ORCID

Petr Kohout https://orcid.org/0000-0002-3985-2310
César Marín https://orcid.org/0000-0002-2529-8929

César Marín[1,2] and Petr Kohout[3,4]*

[1]Institute of Agri-food, Animal and Environmental Sciences (ICA3), Universidad de O'Higgins, San Fernando 3070000, Chile;
[2]Center of Applied Ecology and Sustainability, Pontificia Universidad Católica de Chile, Santiago 8320000, Chile;
[3]Institute of Microbiology, Czech Academy of Sciences, Vídeňská 1083, Prague, CZ-142 20, Czechia;
[4]Faculty of Science, Charles University, Viničná 7, Prague, CZ-128 44, Czechia
(*Author for correspondence: email petr.kohout@natur.cuni.cz)

References

Brundrett MC, Tedersoo L. 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist* **220**: 1108–1115.

Crowther TW, van den Hoogen J, Wan J, Mayes MA, Keiser AD, Mo L, Averill C, Maynard DS. 2019. The global soil community and its influence on biogeochemistry. *Science* **365**: eaav0550.

Delgado-Baquerizo M, Guerra CA, Cano-Díaz C, Egidi E, Wang JT, Eisenhauer N, Singh BK, Maestre FT. 2020a. The proportion of soil-borne pathogens increases with warming at the global scale. *Nature Climate Change* **10**: 550–554.

Delgado-Baquerizo M, Reich PB, Trivedi C, Eldridge DJ, Abades S, Alfaro FD, Bastida F, Berhe AA, Cutler NA, Gallardo A *et al.* 2020b. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution* **4**: 210–220.

Djukic I, Kepfer-Rojas S, Schmidt IK, Larsen KS, Beier C, Berg B, Verheyen K, Caliman A, Paquette A, Gutiérrez-Girón A *et al.* 2018. Early stage litter decomposition across biomes. *Science of the Total Environment* **628–629**: 1369–1394.

Fisher MC, Henk DA, Briggs CJ, Brownstein JS, Madoff LC, McCraw SL, Gurr SJ. 2012. Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**: 186–194.

Gange AC, Gange EG, Mohammad AB, Boddy L. 2011. Host shifts in fungi caused by climate change? *Fungal Ecology* **4**: 184–190.

Pec GJ, Karst J, Taylor DL, Cigan PW, Erbilgin N, Cooke JE, Simard SW, Cahill JF Jr. 2017. Change in soil fungal community structure driven by a decline in ectomycorrhizal fungi following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak. *New Phytologist* **213**: 864–873.

Pérez-Valera E, Goberna M, Verdú M. 2019. Fire modulates ecosystem functioning through the phylogenetic structure of soil bacterial communities. *Soil Biology and Biochemistry* **129**: 80–89.

Rodriguez-Ramos JC, Cale JA, Cahill JF Jr, Simard SW, Karst J, Erbilgin N. 2021. Changes in soil fungal community composition depend on functional group and forest disturbance type. *New Phytologist* **229**: 1105–1117.

Steidinger BS, Bhatnagar JM, Vilgalys R, Taylor JW, Qin C, Zhu K, Bruns TD, Peay KG. 2020. Ectomycorrhizal fungal diversity predicted to substantially decline due to climate changes in North American Pinaceae forests. *Journal of Biogeography* **47**: 772–782.

Štursová M, Šnajdr J, Cajthaml T, Bárta J, Šantrůčková H, Baldrian P. 2014. When the forest dies: the response of forest soil fungi to a bark beetle-induced tree dieback. *ISME Journal* **8**: 1920–1931.

Větrovský T, Kohout P, Kopecký M, Machac A, Man M, Bahnmann BD, Brabcová V, Choi J, Meszárošová L, Human ZR *et al.* 2019. A meta-analysis of global fungal distribution reveals climate-driven patterns. *Nature Communications* **10**: 5142.

Wagg C, Schlaeppi K, Banerjee S, Kuramae EE, van der Heijden MG. 2019. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. *Nature Communications* **10**: 4841.

Zhou Z, Wang C, Luo Y. 2020. Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nature Communications* **11**: 3072.

Key words: climate change, ectomycorrhizal fungi, insect outbreaks, logging, multifunctionality, pathogenic fungi, saprophytic fungi, wildfires.