



Editorial

Fungal community structure, development and function in decomposing wood



This special issue of Fungal Ecology focuses on recent exciting progress in understanding wood decay communities, and is based on the symposium on Fungal Community Structure, Dynamics and Function in Decaying Wood, which was held remotely during the 2020 Mycological Society of America (MSA) meeting (Mycology from the Cloud). About 400 audience members around the world tuned in to the symposium during the first fully remote MSA conference. Though we missed the in-person comradery, the accessibility of our fully remote symposium was notable. The symposium featured 6 speakers from several countries, and we have invited additional contributions to this special issue.

Over 70 Pg of carbon is stored in dead wood worldwide (Martin et al., 2021). A specialist group of basidiomycetes and xylariaceous ascomycetes are responsible for its breakdown, releasing carbon dioxide, water and mineral nutrients. Though some of these fungi are able to effect complete decomposition on their own, this rarely if ever happens in nature. Wood decomposition is usually brought about by a community of fungi which interact with each other, and with other organisms. The structure and activity of these communities change with time, and in response to the presence of other organisms and environmental conditions. Understanding fungal community structure, ecological interactions, and dynamics is essential for modelling and predicting ecosystem function in a globally changing environment. While solid progress has been made on describing wood decay communities using traditional methods, with modern technologies we are now able to achieve a deeper understanding.

High-throughput amplicon sequencing (HTS) methods are commonly used to characterize fungal community composition, and indeed, many of the papers in this special issue utilize these methods. Additionally, some papers highlight the utility of combining traditional methods, such as culturing and fruit body surveys, with HTS approaches not only to help validate results but also to help build culture collections for experimental work.

In addition to understanding important ecosystem processes, the study of wood decay communities can also advance understanding of community ecology in general. Abrego (2021) reviews the literature and explores opportunities for advancing ecological theory, using wood decay communities as a model system to examine important community assembly processes at multiple scales. The papers in this special issue also include experimental work and surveys, and use advanced methods to examine important ecological questions about wood-inhabiting fungal communities. These questions include: which fungi colonize living trees (Gilmartin et al., 2022); what are the patterns of dispersal, colonization and the role of animals in these processes (Fukasawa et al., 2021; Jusino et al., 2022, Menkis et al. 2020); how do wood-inhabiting fungal communities change through time (Lepinay et al., 2021;

Prylutskiy et al., 2021); and how do traits affect adaptation to changing environments (Jenssen et al., 2020), the composition of fungal communities (Birkmoe et al., 2021), and ecosystem processes (Maillard et al., 2022).

As we look closer into the fungal communities of living trees, the lines between endophytes and saprotrophs are blurring. Gilmartin et al. (2022) combined HTS of LSU and ITS, alongside culture-based methods, and demonstrated that the functional sapwood of living trees does indeed harbor decay fungi. Some of these fungi may be latent, but others may be facilitated via various sources of wounding and animal vectors.

An exciting emerging field in decay fungi is associations with wood-boring organisms, such as woodpeckers (Jusino et al., 2016; Elliott et al., 2019; Wainhouse and Boddy 2022). Multiple papers in this issue examine the role of vectors and damage in the colonization of fungi in living trees. For instance, acorn woodpeckers are associated with surprisingly diverse communities of saprotrophic fungi, including many wood decay species (Jusino et al., 2022). Moreover, these birds appear to help establish decay communities in living trees, much like red-cockaded woodpeckers (Jusino et al., 2016). Old trees and cavity excavators continue to be threatened by deforestation and habitat fragmentation. Menkis et al. (2020) examined a 6-y veteranization process as a conservation measure to provide microhabitat for fungi found in older living trees, such as those typically selected for cavity excavation by woodpeckers. We are gaining an understanding of the role of cavity excavators such as woodpeckers in fungal colonization and the maintenance of fungal diversity in living trees, and more experimental work is needed to determine the role of the excavators, the early successional fungi in holes, and the mechanistic processes that maintain these intricate symbioses.

Wood decay communities are dynamic, with conditions within the wood and the dominant fungal players changing as the substrate ages. Decay fungi can be present as latent endophytes in living trees, but may not fruit until specific stages in the decay process. Prylutskiy et al. (2021) found this to be the case for *Pleurotus calypttratus*, a species of conservation concern, and a fungus that seems to rely upon recently dead trees to fruit – but was also detected in living trees, using DNA-based molecular techniques. Although some species specialize on wood at various stages of decomposition, overall, there is stochasticity in fungal community composition as trees age (Lepinay et al., 2021).

Papers in this issue also address important phenotypic traits of wood-inhabiting fungi and their tree hosts. Even in one species of tree, there can be significant variation in nutrient content and secondary metabolites and that variation can help explain fungal community composition (Birkmoe et al., 2021). Significant individual level phenotypic variation exists among genets of *Phellolipilus nigrolimitatus*, which could have

implications for how some fungal species can adapt to climatic changes (Jenssen et al., 2020). Biotic and abiotic factors and tree species select for different functional groups of decay fungi, and climatic variables can ultimately affect fungal community composition and decay processes (Fukasawa et al., 2021; Maillard et al., 2022).

This collection of papers not only highlights how much has been learned about decay communities, but also helps illuminate the direction for future work. DNA-based work on fungal communities from environmental samples has come to rely upon relatively short-read sequencing, but long-read technologies may be more informative for future decay studies, especially for phylogenetic resolution. Fungal community characterization is a first step, but should be followed by mechanistic questions, which may require modern transcriptomics as well as other more traditional approaches, such as culture-based assays. As Peay (2014) emphasized, it is now relatively easy to accumulate large datasets from environmental samples, but we are often unable to interpret them due to insufficient basic information on fungal autecology and natural history. We concur with his suggestion that an important way forward is to combine environmental sequencing with molecular-based natural history, and other approaches.

References

- Abrego, N., 2021. Wood-inhabiting fungal communities: opportunities for integration of empirical and theoretical community ecology. *Fungal Ecol.*, 101112 <https://doi.org/10.1016/j.funeco.2021.101112>.
- Birkemoe, T., Nybakken, L., Andelic, M., Tangnæs, M.J., Sverdrup-Thygesen, A., Kauserud, H., Jacobsen, R.M., 2021. Secondary metabolites and nutrients explain fungal community composition in aspen wood. *Fungal Ecol.*, 101115 <https://doi.org/10.1016/j.funeco.2021.101115>.
- Elliott, T.F., Jusino, M.A., Trappe, J.M., Lepp, H., Ballard, G.A., Bruhl, J.J., Vernes, K., 2019. A global review of the ecological significance of symbiotic associations between birds and fungi. *Fungal Divers.* 98 (1), 161–194. <https://doi.org/10.1007/s13225-019-00436-3>.
- Fukasawa, Y., Matsukura, K., Stephan, J.G., Makoto, K., Suzuki, S.N., Kominami, Y., Takagi, M., Tanaka, N., Takemoto, S., Kinuura, H., Okano, K., 2021. Patterns of community composition and diversity in latent fungi of living *Quercus serrata* trunks across a range of oak wilt prevalence and climate variables in Japan. *Fungal Ecol.*, 101095 <https://doi.org/10.1016/j.funeco.2021.101095>.
- Gilmartin, E.C., Jusino, M.A., Pyne, E.J., Banik, M.T., Lindner, D.L., Boddy, L., 2022. Fungal endophytes and origins of decay in beech (*Fagus sylvatica*) sapwood. *Fungal Ecol.*, 101161 <https://doi.org/10.1016/j.funeco.2022.101161>.
- Jenssen, A.L., Kauserud, H., Maurice, S., 2020. High Phenotypic Variability in the Wood Decay Fungus *Phellolopius nigrolimitatus*. *Fungal Ecology*, 100982. <https://doi.org/10.1016/j.funeco.2020.100982>.
- Jusino, M.A., Lindner, D.L., Banik, M.T., Rose, K.R., Walters, J.R., 2016. Experimental evidence of a symbiosis between red-cockaded woodpeckers and fungi. *Proc. Biol. Sci.* 283, 20160106 <https://doi.org/10.1098/rspb.2016.0106>, 1827.
- Jusino, M.A., Hagemeyer, N.D., Banik, M.T., Palmer, J.M., Lindner, D.L., Smith, M.E., Koenig, W.D., Walters, E.L., 2022. Fungal communities associated with acorn woodpeckers and their excavations. *Fungal Ecol.*, 101154 <https://doi.org/10.1016/j.funeco.2022.101154>.
- Lepinay, C., Tláškal, V., Vrška, T., Brabcová, V., Baldrian, P., 2021. Successional development of wood-inhabiting fungi associated with dominant tree species in a natural temperate floodplain forest. *Fungal Ecol.*, 101116 <https://doi.org/10.1016/j.funeco.2021.101116>.
- Maillard, F., Jusino, M.A., Andrews, E., Moran, M., Vaziri, G.J., Banik, M.T., Fanin, N., Trettin, C.C., Lindner, D.L., Schilling, J.S., 2022. Wood-decay type and fungal guild dominance across a North American log transplant experiment. *Fungal Ecol.*, 101151 <https://doi.org/10.1016/j.funeco.2022.101151>.
- Martin, A.R., Domke, G.M., Doraisami, M., Thomas, S.C., 2021. Carbon fractions in the world's dead wood. *Nat. Commun.* 12, 889. <https://doi.org/10.1038/s41467-021-21149-9>.
- Menkis, A., Redr, D., Bengtsson, V., Hedin, J., Niklasson, M., Nordén, B., Dahlberg, A., 2020. Endophytes dominate fungal communities in six-year-old veteranisation wounds in living oak trunks. *Fungal Ecol.*, 101020 <https://doi.org/10.1016/j.funeco.2020.101020>.
- Peay, K.G., 2014. Back to the future: natural history and the way forward in modern fungal ecology. *Fungal Ecol.* 12, 4–9. <https://doi.org/10.1016/j.funeco.2014.06.001>.
- Prylutskyi, O., Yatsiuk, I., Savchenko, A., Kit, M., Solodianskin, O., Schigel, D., 2021. Strict Substrate Requirements Alongside Rapid Substrate Turnover May Indicate an Early Colonization: A Case Study of *Pleurotus calyptratus* (Agaricales, Basidiomycota). *Fungal Ecology*, 101098. <https://doi.org/10.1016/j.funeco.2021.101098>.
- Wainhouse, M., Boddy, L., 2022. Making hollow trees: inoculating living trees with wood-decay fungi for the conservation of threatened taxa-A guide for conservationists. *Global Ecol. Conserv.* 33, e01967 <https://doi.org/10.1016/j.gecco.2021.e01967>.

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