

## Meeting report

# Tracking signatures of selection in natural populations of ectomycorrhizal fungi – progress, challenges, and prospects

Environmental changes have a manifold effect on biodiversity. Although soil harbours most terrestrial biodiversity (Anthony *et al.*, 2023), including *c.* 90% of the fungal kingdom, little is known about the adaptation processes of natural populations of soil-dwelling organisms. Among these, ectomycorrhizal (ECM) fungi are involved in key mutualist interactions in forest ecosystems by providing water and nutrients to the host trees (Van Der Heijden *et al.*, 2015). Recent studies have shown large intraspecific genomic variation in ECM fungi (e.g. Tremble *et al.*, 2023a), raising questions about how natural selection affects ECM fungal populations. What are the signatures of adaptation in ECM fungal genomes? What are the strongest selective pressures occurring in local environments (Dauphin & Peter, 2023)? Given that environmental changes have become more pronounced in recent years (Dai, 2013), it is critical to improve our understanding of local adaptation in natural populations of these important organisms.

Against this backdrop, a 2-d symposium on the population and landscape genomics of ECM fungi was held at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL. The event was held on 5 and 6 September 2023, bringing together leading experts in the field of ecological genomics, to explore the latest advances and promising prospects. Drawing on the lively discussions at the event, this meeting report retraces the complementary approaches for tracking patterns of local adaptation, the methodological and analytical limitations currently encountered, and the emerging model organisms used to study the genomics of environmental adaptation in natural ECM fungal populations. The final section outlines some promising avenues for advancing the field and the overall biological knowledge of ECM fungi and their interacting host species.

## Latest advances in the study of local adaptation in forest ecosystems

Christian Rellstab (Swiss Federal Research Institute WSL, Switzerland) opened the symposium by presenting the main concepts used in the field of landscape genomics (Rellstab *et al.*, 2015), the best methodological practices for sampling and capturing environmental gradients (Dauphin *et al.*, 2023), potential insights gained from landscape genomics regarding gene variants under selection (Lotterhos, 2023), and recent statistical advances for testing genotype–environment associations (GEA). He showed that forests are the ecosystem most represented in landscape genomics studies (Dauphin *et al.*, 2023); however, very few studies have been conducted on fungi, let alone ECM fungi, and none have considered the interactions between forest organisms. He then illustrated how landscape genomics methods can be applied to ECM organisms (host and symbiont) by accounting for the neutral genetic structure of host and symbiont populations using either logistic regression or linear models to analyse haploid (e.g. from ascomycete mycelia) and diploid data (or population allele frequencies, for example from basidiomycete mycelia, sexual spore-bearing tissues in ascomycetes, basidiomycete fruitbodies, or host tree tissues), respectively. Finally, he highlighted the role of biotic and abiotic factors involved in local adaptation and formulated the issue of the nonindependence of predictors in relation to the response variable (Fig. 1).

## The rise of micro-environmental data and fungal genomic resources

Capturing selective pressures requires a high spatial and temporal resolution of environmental data and integrative geo-referenced databases (Dauphin *et al.*, 2023). Benjamin Dauphin (Swiss Federal Research Institute WSL, Switzerland) outlined state-of-the-art atmospheric microclimate data, that is the climatic conditions that occur under the forest canopy, and how they differ from the atmospheric macroclimate data usually used (Zellweger *et al.*, 2020). Next, he highlighted the substantial temperature differences, termed offset, between atmospheric and soil conditions at the same sampling locations, and the extent to which these new publicly available global maps (Lembrechts *et al.*, 2022) can be

Fungal symbiont genotype ~ Abiotic environmental factor(s) + Tree host genotype



**Fig. 1** Graph illustrating the nonindependence of predictors in relation to the response variable in host–symbiont interactions.

integrated with *in situ* soil measurements to identify the drivers of adaptive processes in soil-dwelling ECM fungi.

Francis Martin (INRAE, Nancy, France) synthesised 15 yr of large-scale genomic research since the publication of the first ECM fungal genome, *Laccaria bicolor*. He elaborated on how the over 2500 fungal genomes currently available in the US DOE Joint Genome Institute MycoCosm database enables in-depth research on: (1) tracking independent lifestyle transitions from saprotrophism to mutualism in ECM lineages (Miyauchi *et al.*, 2020); (2) linking genome characteristics to key ecological traits such as the decomposition of soil organic matter (Kohler *et al.*, 2015); and (3) identifying gene networks involved in the development and function of symbiosis (Lebreton *et al.*, 2021). He pointed out that only 0.5% of the 50 000 mycorrhizal fungal genomes have been sequenced to date, highlighting the need for additional high-quality fungal genomes.

Advances in genotyping-by-sequencing technologies have provided a wealth of new perspectives in population genomics research. Daniel Croll (University of Neuchâtel, Neuchâtel, Switzerland) introduced new genotyping approaches targeting short and long amplicons using Illumina and PacBio sequencing platforms, respectively, which have been applied to plant–fungal pathogen interactions (Bellah *et al.*, 2023; Stalder *et al.*, 2023). While the Illumina microfluidics-based pipeline is particularly powerful for monitoring new mutations arising in natural populations, the PacBio sequencing pipeline offers a wide range of applications for assessing phylogenetic relationships at the intraspecific level as well as colonisation processes in natural and human-affected environments. These are cost-effective, error-free, and scalable complementary genotyping approaches, applicable to small amounts of DNA, such as ECM root tips with exogenous materials.

## Traceable adaptive traits, experimental validation, and coevolution processes

Identifying phenotypic traits of adaptive relevance that can be measured in large numbers of fungal individuals in natural populations or under experimental conditions remains challenging. It is even more difficult to assess the impact of phenotypic variations, such as growth, melanin content, or mycelium exploration type, on fitness. Using experimental evolution to unravel the components of local adaptation, Anna Bazzicalupo (Royal Botanical Garden Kew, London, UK) showed how yeast lines respond to gradients of six heavy metals (cadmium, cobalt, copper, manganese, nickel, and zinc) and to what extent parallelism (i.e. cross-tolerance) and distinctness of resistance profiles to these heavy metals occur in fully controlled environments. She concluded that there are trade-offs in tolerance between heavy metals, likely established in an ancestral environment (Bazzicalupo, 2022), and that the polygenic nature of adaptation has led to numerous fitness profiles (A. Bazzicalupo *et al.*, unpublished data).

The symposium further stressed the need to validate findings derived from exploratory correlative approaches, such as GEA, and to further explore the genetic mechanisms underlying traits. For instance, Sara Branco (University of Colorado, Denver, USA)


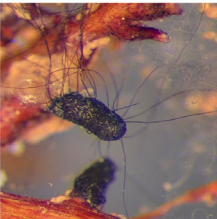




demonstrated the zinc tolerance of *Suillus luteus* strains isolated from contaminated and noncontaminated soils, highlighting the polygenic nature of adaptive traits. Interestingly, the genes involved in zinc tolerance encoding for metal binding, chelation, sequestration, and cell detoxification did not display high allelic differentiation, but seemed to confer metal tolerance through different expressions (Bazzicalupo *et al.*, 2020; Branco *et al.*, 2022). Zinc-tolerant *S. luteus* strains maintained constant growth under a zinc gradient, with lower metal accumulation in the mycelium than that reported for sensitive strains (Branco *et al.*, 2022). This was associated with a much greater variation in the expression of these genes in tolerant than susceptible strains.

Symbiotic or commensal organisms are likely to be affected by the evolutionary trajectory, demography, and local adaptation of their hosts. The coincidence of neutral and adaptive genetic processes between two interacting organisms can occur on both small and large spatial scales. For example, Sundry Maurice (University of Oslo, Oslo, Norway) illustrated how past and current land-use changes and habitat fragmentation have affected the population genetic diversity of the wood-decaying forest fungus *Phellolopilus nigrolimitatus*, a near-threatened species in Fennoscandia (IUCN). This study system enables the investigation of climate-driven local adaptation taking place in that area since the last glacial maximum and to infer the co-migration of host and wood-decomposing specialist populations (Sonstebo *et al.*, 2022), as *P. nigrolimitatus* is tightly dependent on its *Picea abies* host substrate. These climate-induced selection signatures in fungal populations are mirrored by *P. abies* populations that are known to have adapted locally to temperature and precipitation conditions (Milesi *et al.*, 2019).

Furthermore, Jason Hoeksema (University of Mississippi, Oxford, USA) addressed the role of reciprocal selection of coevolved species driving trait diversification and the dynamics of genotype–genotype interactions with consequences on the fitness of one or both partners. In this context, a common garden experiment established in a native *Pinus radiata* forest showed that ECM traits, such as exploration types, may be under selection, with some of these phenotypic traits significantly contributing to fungal biomass, relative growth rate, and survival (M. Rua & J. Hoeksema, unpublished data). In addition, much of the fungal diversity at the root tips was significantly associated with plant traits, raising questions about which plant and fungal genes are under selection and how selection differs among environments.

## Emerging model organisms for investigating adaptation of ECM fungi

In recent years, several collaborative initiatives have started in-depth studies on the eco-evolutionary processes of ECM fungal species and their inherent host species. The symposium highlighted three ascomycetes (*Cenococcum geophilum*, *Tuber melanosporum*, and *Tuber aestivum*) and three basidiomycetes (*Boletus edulis*, *Suillus brevipes*, and *Suillus luteus*) as model species, with varying degrees of population and adaptation studies performed at the genomic level (Fig. 2). Pioneering work has been carried out on *Suillus* species, combining laboratory and field experiments in pine

	Species	Host specificity	Mycelium sterile culturing	Population genetic information available <sup>2</sup>	Reference genome available <sup>3</sup>	Genome resequencing project	Pangenome project	Indication of (local) adaptation
	<i>Boletus edulis</i> (Bull.) Fr. (Basidiomycota)	Generalist on conifers and broadleaves	Yes	Yes (Hoffman <i>et al.</i> 2020)	JGI Myco-Cosm ( <a href="#">Boled5</a> )	Tremble <i>et al.</i> (2023a)	Tremble <i>et al.</i> (2023b)	Host preference Tremble <i>et al.</i> (2023b) genomic-based
	<i>Cenococcum geophilum</i> Fr. (Ascomycota)	Generalist on conifers and broadleaves	Yes	Yes	JGI Mycocosm ( <a href="#">Cenge3</a> )	Dauphin <i>et al.</i> (2021)	Ongoing	Soil water content, temperature Obase <i>et al.</i> (2017) ecological-based
	<i>Suillus brevipes</i> (Peck) Kuntze (Basidiomycota)	Specialist in two-needled pines	Yes	Yes	JGI Mycocosm ( <a href="#">Suibr2</a> )	Branco <i>et al.</i> (2015, 2017)	Ongoing	Soil salinity, climate Branco <i>et al.</i> (2022) <sup>4</sup> ecological-based genomic-based
	<i>Suillus luteus</i> ((L.) Fr.) Gray (Basidiomycota)	Specialist in two-needled pines	Yes	Yes	JGI Mycocosm ( <a href="#">Suilu4</a> )	Bazzicalupo <i>et al.</i> (2020)	Ongoing	Heavy metals, host specificity Branco <i>et al.</i> (2022) <sup>4</sup> ecological-based genomic-based
	<i>Tuber aestivum</i> Vittad. (Ascomycota)	Generalist, mainly broadleaves but also conifers	No <sup>1</sup>	Yes	JGI Mycocosm ( <a href="#">Tubae1</a> )	No	No	Temperature, precipitation Steidinger <i>et al.</i> (2022) ecological-based
	<i>Tuber melanosporum</i> Vittad. (Ascomycota)	Generalist, mainly broadleaves but also conifers	No <sup>1</sup>	Yes	JGI Mycocosm ( <a href="#">Tubme1v2</a> )	Payen <i>et al.</i> (2015)	No	Precipitation Buntgen <i>et al.</i> (2012) ecological-based

**Fig. 2** Emerging model organisms for studying the genomics of environmental adaptation in ectomycorrhizal fungi, presented at the symposium. <sup>1</sup>A few attempts have been successful, but it is not possible to subculture over the longer term; <sup>2</sup>reviewed in Vincenot & Selosse (2017); <sup>3</sup>the name of the reference genome given by the DOE Joint Genome Institute (JGI) is given in brackets; <sup>4</sup>and references therein. Photo credits: *Boletus edulis*, M. Danz [swissfungi.wsl.ch](https://www.swissfungi.wsl.ch); *Suillus brevipes*, M. Wood [mykoweb.com](https://www.mykoweb.com); *Suillus luteus*, M. Danz [swissfungi.wsl.ch](https://www.swissfungi.wsl.ch); *Tuber aestivum*, F. Staubli WSL.

forests to study plant–fungal mutualism and adaptation to salt environments and soils contaminated with heavy metals (Branco *et al.*, 2015; Bazzicalupo *et al.*, 2020). It is probably the most

promising model organism to date, with a high-quality pan-genome resource available, a well-known life cycle for inferring the demographic history of natural populations, and already advanced



knowledge of gene networks involved in adaptive traits. *Boletus edulis* is also at the heart of large-scale population genomic studies and appears to be an exciting model to better understand the dynamics of effective population size in the light of glacial oscillations (Etienne Brejon Lamartinière; University of Bielefeld, Bielefeld, Germany). The contrasting patterns of population genetic diversity between Alaskan and European lineages are of prime interest, as the Southern Peninsulas may serve as the main refugium and recolonisation source in North America, while a mosaic of microrefugia (nunataks) with complex recolonisation sources could occur in Europe. Echoing these sharp diversity patterns, a new resource of 22 reference genomes revealed that the species harbours one of the most diverse eukaryotic pan-genomes, with high structural variation but still preserves genomic synteny between lineages (Tremble *et al.*, 2023a,b).

*Cenococcum geophilum* is one of the most widespread ECM fungi found in temperate and boreal forest ecosystems. Highlighted by Martina Peter (Swiss Federal Research Institute WSL, Switzerland), this species has among the largest genome sizes in ECM fungi and unique genomic features, for example 80% of repeated elements that are strongly subject to repeat-induced point (RIP) mutations, a genome defence mechanism neutralising transposable elements (TE). Both TE and RIP activities represent driving forces for rapid adaptation (Lorrain *et al.*, 2021), and might partly explain the broad host and habitat range of this species. The ongoing *Cenococcum* pan-genome and resequencing projects aim to provide new insights into the genetic variants that enabled the ecological success of the species and the patterns of local adaptation to soil water conditions. *Tuber melanosporum* is one of the most economically and ecologically important ECM fungi world-wide. Marc-André Selosse (National Museum of Natural History, Paris, France) illuminated the symposium audience by showing how population genetics can inform the mating strategy and gene dispersal of black truffle populations (Selosse *et al.*, 2017). Based on experimental sites, he showed results supporting high inbreeding of black truffle populations, possibly due to isolation by distance, without evidence of male gamete dispersal. These findings highlight the complex life cycles of truffles and outline the main drivers that maintain the genetic diversity of their natural populations.

## Future directions

After 2 d of presentation and discussion, the symposium highlighted three key facets of ecological genomics in ECM fungi that require further research: (1) using genomic tools to improve our understanding of species life cycle processes and related traits; (2) characterising the relevant spatial and temporal scales over which natural selection is detectable in natural populations; and (3) applying local adaptation models based on environmental and genetic data to inform the conservation biology of soil-dwelling organisms, including ECM fungi. Progress in these research fields will rely on joining forces and interdisciplinary collaborations between population geneticists, ecologists, and molecular biologists. The study of belowground intraspecific biodiversity is still in its infancy, but it is timely to examine how natural selection affects it and what environmental factors push local populations of ECM

fungi to their physiological limits. This knowledge will certainly help to predict the fate of ECM fungi and, to some extent, the host tree species that interact with them in future forest ecosystems.

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