Ecology of Ascomycete genera – A searchable compilation of “Notes on genera: Ascomycota”

Guerreiro MA¹, Wijayawardene NN²,³, Hyde KD²,³,⁴ and Peršoh D¹

¹ AG Geobotany, Faculty of Biology and Biotechnology, Ruhr-Universität Bochum, Universitätstraße 150, 44801 Bochum, Germany
² Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand
³ Mushroom Research Foundation, 128 M.3 Ban Pa Deng T. Pa Pae, A. Mae Taeng, Chiang Mai 50150, Thailand
⁴ Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Science, Kunming 650201, Yunnan, People’s Republic of China


Abstract
DNA-metabarcoding of the fungal communities in environmental samples has greatly enhanced our knowledge of fungal diversity. However, linking taxonomic information to fungal traits is often challenging because of the immense species diversity encountered in most samples. This complicates inferring functional roles in ecosystem processes from biodiversity patterns. We have therefore made ecological traits of Ascomycete genera, compiled in a previous study, digitally accessible and searchable.

Key words – Fungal traits – High-throughput – Life modes

Introduction
Fungi are crucial for the functioning of most ecosystems on earth (e.g., Delgado-Baquerizo et al. 2017, Frąc et al. 2018). They usually form species-rich communities in their various habitats (Tedersoo et al. 2014, Hawksworth & Lücking 2017, Hyde et al. 2018). The application of cultivation-independent environmental PCR techniques has therefore greatly enhanced our knowledge of fungal diversity (e.g., Peršoh 2015, Baldrian 2017, López-Mondéjar et al. 2017, Jayawardena et al. 2018, Nilsson et al. 2018a). Such metabarcoding approaches use barcoding regions of the DNA (i.e. barcode sequences) to characterise composition of fungal communities (e.g., Creer et al 2016, Yahr et al. 2016, Raja et al. 2017). The obtained sequences are assigned to taxa by comparison with well-characterised reference sequences (e.g., Hibbett et al. 2016, Abarenkov et al 2018). This assignment is facilitated by the ever growing taxon coverage in the reference databases (Nilsson et al. 2018b), but in particular, remains challenging for samples of species-rich communities. Different reference databases and assignment workflows are however currently available to handle even the most complex high-throughput sequencing barcode data (Bálint et al 2016). While a comparative analysis of these database revealed major inconsistencies for species-level assignments, the assignments were largely consistent at the genus level (Abarenkov et al 2018).

Fungal traits are the key to link fungal activity to ecosystem processes and services (e.g., Koide et al. 2014, Peay 2014, Treseder & Lennon 2015). Such traits have been documented by...
mycologists since long before DNA sequencing was invented. Linking known traits to sequence data is therefore only achievable via taxonomic assignment. Extracting this knowledge from the literature is feasible for selected taxa, but challenging for hundreds to thousands of fungi usually detected in each sample by metabarcoding approaches. Two comprehensive trait databases are currently available for fungi: LIAS (Rambold et al. 2014) and FUNGuild (Nguyen et al. 2016). The former codes a vast variety of traits of lichenized fungi, while FUNGuild provides the trophic mode for >10,000 taxa and assigns them to an ecological guild.

The goal of this study was to advance ecological classification of fungi by providing a compilation of ecological data for Ascomycota. This was considered to complement the FUNGuild data, enabling comparative analyses and thus improving the assignment of fungal taxa to guilds. To achieve this goal, we compiled the data recently published by Wijayawardene et al. (2017) and made them searchable in a spreadsheet.

**Materials & Methods**

Information on the ecology of fungal genera was extracted from a recent compilation of genus level data (Wijayawardene et al 2017). We initially separated taxonomic from ecological information and references, according to the expression “type:” uniformly applied by Wijayawardene et al. (2017). Afterwards, we separated the ecological information from the references according to the expression “see”. The ecological information was then manually curated and unrelated information removed for each entry. In the following, we searched the ecological information for 142 terms (DOI 10.17605/OSF.IO/RNF5W). According to these terms, the presence of 47 traits was assessed, characterizing habitat, distribution, substrate and associated organism for the fungal genera, as well as the type of interaction with associated organisms (DOI 10.17605/OSF.IO/RNF5W). In addition, 12 terms indicating ambiguous or limited applicability of the characterizations are indicated. The searchable worksheet (DOI 10.17605/OSF.IO/RNF5W) was deposited in the repository of the Open Science Framework (https://osf.io) as Excel spreadsheet named ‘Ascomycota_EcoTraits_v181214.xlsx’ (https://osf.io/rnf5w/?view_only=2f9a372bbaa3f4716ae6f9d5550ecc2b8)

**Results**

Information was retrieved for 6617 of the 6794 genera of Ascomycota listed by Wijayawardene et al. (2017). Most genera of Ascomycota were classified as terrestrial (Table 1). More detailed assignment of the habitat was achieved for only 0.3 % of the terrestrial genera, while the habitat of 55 % of the aquatic genera was further specified as fresh- or seawater. The substrate or associated organism was specified for 2370 fungal genera. For 570 of the 753 plant-associated genera, the part of the plant which is colonized by the fungus was extracted from the original data. The type of interaction with their host or substrate was assessed for 5885 genera.

The Excel spreadsheet (supplementary information: DOI 10.17605/OSF.IO/RNF5W) lists information given in the original publication, as well as the extracted information for each genus. It also includes a worksheet with a column to paste a list of generic names. The original and extracted information is automatically assigned to each genus entered in the query column.

**Table 1** Character states assigned to the genera of Ascomycota. The number of genera classified accordingly is given in parentheses.

<table>
<thead>
<tr>
<th>Character</th>
<th>Character state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat I (5095)</td>
<td>Air (11), Terrestrial (4758), Water (481)</td>
</tr>
<tr>
<td>Habitat II (260)</td>
<td>Desert (1), Forest (7), Freshwater (59), Grassland (1), Indoor (6), Seawater (207)</td>
</tr>
<tr>
<td>Distribution (2214)</td>
<td>Arctic-montane (1), Neotropics (14), Subtropical (24), Temperate (228), Tropical (348), Widespread (1674)</td>
</tr>
<tr>
<td>Substrate (458)</td>
<td>Animal material (5), Excrement (107), Exudates (12), Food (28), Plant material (42), Soil (258), Stone (99)</td>
</tr>
</tbody>
</table>
Table 1 Continued.

<table>
<thead>
<tr>
<th>Character</th>
<th>Character state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Associated organism (2205)</td>
<td>Alga (978), Animal (364), Fungus (106), Lichen (228), Plant (753), Protist (3)</td>
</tr>
<tr>
<td>Associated organism subgroup (408)</td>
<td>Arthropod (188), Herbaceous plant (15), Moss (16), Vertebrate (75), Woody plant (172)</td>
</tr>
<tr>
<td>Colonized host plant part (570)</td>
<td>Endophytic (72), Epiphytic (133), Exudates (29), Generative parts (42), Leaf (186), Root (22), Stem (160)</td>
</tr>
<tr>
<td>Interaction type (5885)</td>
<td>Antagonistic (621), Associated (125), Biotrophic (163), Lichenized (966), Mutualistic (997), Mycorrhizal (9), Saprotrophic (4405)</td>
</tr>
<tr>
<td>Modifier (233)</td>
<td>Clinical (19), Dead (18), Decaying (26), Fossil (3), Living (52), Mangrove (22), Mostly (46), Often (4), One–some (26), Opportunistic (12), Rarely (14), Rotting (24)</td>
</tr>
</tbody>
</table>

Discussion

The purpose of the provided worksheet was to make the data compiled by Wijayawardene et al. (2017) digitally accessible. Therefore, the data were only structured and not modified. Accordingly, ecological information is provided for lichens, while the lichenized fungus is in the strict sense only (mutualistic) associated with algae. Data entries concerning the lichen ecology are easily removable from entries for lichenized (and lichenicolous) fungi. We included several modifiers (Table 1), which mostly indicate ambiguities in the classifications (see below). These also include the term “mangrove”, because for it is unclear for most fungi described from mangrove environments if they occur above ground (i.e. terrestrial) or at least temporarily below the water level (i.e. marine).

We provide a worksheet, which allows for rapid ecological classification of fungal genera according to Wijayawardene et al. (2017). Extended lists of genera ascertained by high-throughput approaches, such as metabarcoding, are easily processed. The compilation provides information on 6617 genera of Ascomycota, including 3395 genera not considered by the FUNGuild database (Nguyen et al. 2016). However, the presented compilation is supposed to complement FUNGuild and not to replace it. Wijayawardene et al. (2017) and FUNGuild both rely for the ecological classification of many genera on a limited number of references. Since these references mostly differ, comparative analyses of the results from querying of both datasets increases reliability of the classification.

FUNGuild and Wijayawardene et al. (2017) agree in the classification of many genera. For example, they list 887 and 966 genera of Ascomycota to include lichenized taxa, respectively. This is largely coherent, considering the different numbers of genera included. Furthermore, lichens are easily recognised as such and compiled in the most extensive databases available for fungi (Rambold et al. 2014). The number of genera of Ascomycota considered to form mycorrhizal associations, however, largely differs between FUNGuild (73 genera) and Wijayawardene et al. (2017; 9 genera). Agerer (2006) considered 48 genera of Ascomycota to include mycorrhizal taxa. These differences exemplify the uncertainty in classifying the type of (belowground) interaction between fungi and plants for many fungal species (Agerer 2006, Halbwachs et al. 2018). Discrepancies between the databases may accordingly reflect limitations in current knowledge and not necessarily erroneous data entries.

While congruency between the results from querying both databases certainly increases confidence, it does not guarantee absolute accuracy. An example is the genus Morchella, which is categorized as saprobe by FUNGuild and Wijayawardene et al. (2017). Even though the ecology of the genus is not fully understood, some species are known to be capable of forming mycorrhiza-like structures (Agerer 2006, Loizides 2017). Detailed literature research on the ecology, at least of the dominant species, is therefore currently still indispensable for ecological assessments inferred from taxonomic compositions of communities. This applies in particular for genera including species with different ecological traits. We consider a trait compilation on genus level nevertheless more
suitable for high-throughput metabarcoding approaches, because sequence-based taxonomic assignments are mostly less reliable on the species than on the genus level (Abarenkov et al 2018). An apparent accuracy of ecological assessments based on species traits may not be justified by limited reliability of species identification. In addition, it has to be considered that not only fungal genera may include ecologically distinct species, but that also species themselves may colonize distinct ecological niches (Selosse et al. 2018). We included a list of terms (“modifiers”) in the worksheet (DOI 10.17605/OSF.IO/RNF5W), to highlight genera, classifications of which require verification even if the data appear unambiguous in the compilation.

In conclusion, we consider making the extensive compilation of Ascomycota traits by Wijayawardene et al. (2017) digitally accessible one step on the way towards a comprehensive ecological classification of fungal taxa.

Acknowledgements

K.D. Hyde thanks the Thailand Research Fund for the grant award number: RDG6130001 entitled Impact of climate change on fungal diversity and biogeography in the Greater Mekong Subregion. The study was part of project PE 1673/4-1, funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation).

Accessibility of data

The searchable worksheet (DOI 10.17605/OSF.IO/RNF5W) was deposited in the repository of the Open Science Framework (https://osf.io) as Excel spreadsheet named ‘Ascomycota_EcoTraits_v181214.xlsx’ (https://osf.io/rnf5w/?view_only=2f9a372baa3f4716ae6f9d5550ec2b8). The worksheet includes the full descriptions and the classification of terms applied.

References


Loizides M. 2017 – Morels: The story so far. Field Mycology 18, 42–53.


