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Larger basidiomycetes growing on poroid lignicolous fungi show rot type-related colonization patterns

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Abstract

Poroid fungi that grow on the wood are frequently associated with other basidiomycetes that are often used as a substrate, also during fungal succession. This lifestyle has differing evolutionary origins, going back at least 100 million years. The use of fungal tissue as a substrate indicates that some fungicolous taxa could benefit from the higher nutrient contents compared to wood. These life modes relate to the dead and live fruiting bodies of the hosts. It may take forms such as commensalism, replacement, saprotrophy, displacement, and parasitism. These modes, often driven by competitive processes, imply different strategies that, in most cases, may be linked to the degrading capacities (rot types) of colonizers and hosts, i.e., to their enzymatic repertoire. This repertoire often includes glucanases, which are potentially able to cleave structural glucans of fungi. For investigating these assumptions, a compilation of published data of 95 taxa recorded in temperate and boreal biomes of the northern hemisphere was analyzed. A conspicuous, previously unpublished observation was that the members of most associations showed a higher ratio of white rotters than those among wood fungi in general. This phenomenon points to their highly developed enzymatic competence, which may also explain saprotrophy on dead fruit bodies. Future research should, above all, investigate molecular mechanisms involved in mycotrophic basidiomycetes.

Keywords – enzymatic competence – fungicolous – mycotrophy – parasitism – succession

Introduction

Fungi mainly grow on organic substrates that provide sufficient nutrients, such as humous soil, litter, wood, animal protein, and other fungi (Dix & Webster 1995). Many studies focused on fungus-fungus relationships, in most cases on microfungi (e.g., Baker 1987, Barnett 1963, Barnett & Binder 1973, Ehrlich & Ehrlich 1971, Eisfelder 1955, Eisfelder 1956, Gams et al. 2004, Jeffries 1995), often with taxa in culture (e.g., DeVay 1956, Griffith & Barnett 1967, Tsuneda & Thorn 1995). Fewer studies dealt with macromycetes (e.g., Helfer 1991). Henrici (2013) and Redhead et al. (1994) focused on the genus *Squamanita* of which all species parasitize on other agarics such as *Amanita*, *Galerina*, and *Hebeloma*. To some degree, Besl et al. (1989), Niemelä et al. (1995), and Runge (1980) studied larger basidiomycetes that grow on wood-colonizing poroid fungi (see Fig. 1) though a more comprehensive account was lacking.

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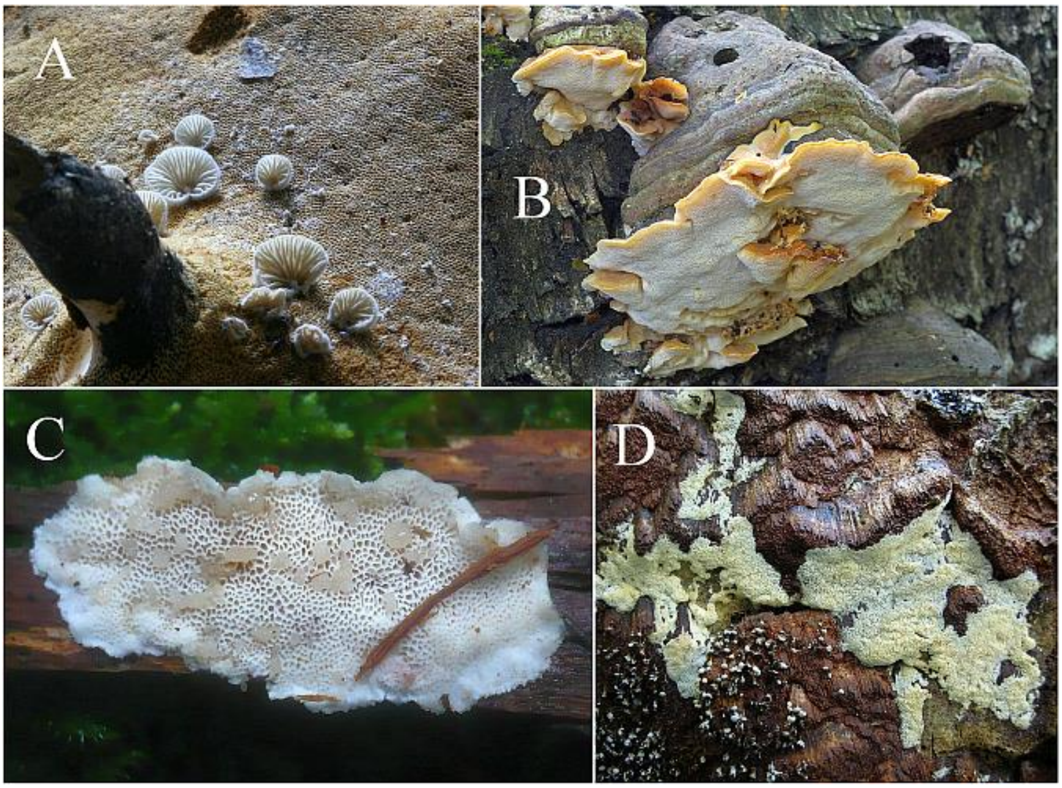

Fig. 1 – Examples of fungi growing on fruiting bodies of poroid fungi. A *Entoloma parasiticum* on a polypore, Penny Firth (CC BY-SA 3.0). B *Antrodiella pallescens* on *Fomes*, Urmas Ojango (CC BY-NC 2.0). C *Tremella polyporina* on *Cinereomyces lindbladii*, Gerhard Koller (CC BY-SA 3.0). D *Incrustoporia brevispora* on *Phellinidium ferrugineofuscum*, courtesy Tom Hofton

The difference between a lignicolous and a fungicolous lifestyle may predominantly be nutrient-related. Fungi contain significantly higher amounts of proteins, nitrogen, and sugars than woody substrates (See, e.g., Becker 1962, Khatua et al. 2017, Obodai et al. 2017, Schwalbe & Becker 1919). The evolutionary origins of basidiomycete mycotrophy reach at least back to the Cretaceous, as indicated by fossils in amber (Poinar Jr & Buckley 2007). Oberwinkler (2012) concluded that in the Agaricales/Russulaceae mycoparasitism is polyphyletic and may have developed from plant parasites. Studies on the origin of fungicolous saprotrophy among wood-associated fungi have, to our knowledge, not been undertaken. Besides nutritional considerations, the competition among wood fungi could be an additional or alternative explanation for the fungicolous lifestyle. Taxa that use the same or similar niche may have "sidestepped" by alternatively exploiting fruiting bodies, as it seems to be the case with, e.g., some ascomycete taxa (Chen 2017).

Associations of fungi on wood take many forms:

- Coexistence (commensalism) without mutual interference or non-combative replacement (colonization on the predigested substrate, synergistic relationship to predecessor) (Lange 1992, Niemelä et al. 1995); predecessor–successor relationships may be mediated by secondary metabolites (Heilmann-Clausen & Boddy 2005) (These types are not subject of this article)
- Saprotrophy on dead fruiting bodies (Besl et al. 1989)
- Exploitation of dead host mycelial channels to enter the substrate predigested by the predecessor (Jahn 1979, Niemelä et al. 1995)
- Combative displacement by hyphal dominance and/or exuding toxins (antibiosis) that inhibit mycelial growth (Dix & Webster 1995)

- Biotrophic parasitism by hyphal interference (haustorial, by fusion or penetration) and production of chitinases, glucanases, b-glucosidase, and cellulases (Jeffries 1995, Oberwinkler et al. 1984, Woodward & Boddy 2008)
- Necrotrophic parasitism by killing and exploiting foreign mycelia or trama (Jeffries 1995, Sun et al. 2019); only a few taxa of this type are obligate parasites (Sun et al. 2019)

A wide spectrum of fungicolous modes underscores the notion that the evolutionary origins are multifaceted. Direct interactions of poroid wood fungi with other basidiomycetes may include combative displacement, exploitation of dead host trama or their mycelial channels, and probably less often parasitism (Niemelä et al. 1995). With few exceptions, mycotrophic basidiomycetes that grow on poroid wood fungi also use wood as a substrate (Ryvarden et al. 2017). This trophic mode requires an enzymatic configuration that differs from basidiomycetes with other substrate preferences, such as soil (Baldrian 2008). There are, generally, two types of wood degraders among basidiomycetes: white and brown rotters, named after the colour of the wood they attack (Linnard et al. 2013). Most lignicolous taxa are white rotters, a type of rot that developed with the advent of angiosperms (Krah et al. 2018). They possess superior enzymatic capacities to digest celluloses and lignin by mainly employing glucanases and β-glucosidase and peroxidases for the latter, while brown rotters only degrade hemicelluloses and celluloses (Linnard et al. 2013, Schmidt 2006). Whether these capacities take a role in the mycotrophy of poroid lignicolous basidiomycetes has not been explored in the past. However, the enzymatic consortium of white rotters includes glucanases, which cleave structural glucans in fungi (Ruiz-Herrera 2012). Hence, we suspected that the mycotrophic lifestyle among poroid wood fungi might be linked to the enzymatic competence of the invaders/successors and their hosts, possibly for economizing energy expenses (Fukasawa et al. 2020) and, thus, avoiding competition.

Materials and methods

For investigating such patterns, we compiled and analyzed a database with information on direct interactions of poroid macrofungi and other basidiomycetes that colonize wood. Data were extracted from the literature that predominantly covered temperate and boreal biomes of the northern hemisphere (see Results section, Table 1). Relevant and representative data from the southern hemisphere are extremely scarce.

The database contained data on colonizers and their hosts, rot types, the vitality of the hosts, and lifestyle (facultative or obligate). This compilation is likely not complete mainly because many sources do not give sufficient details. For instance, Tomasi (1977) listed 24 taxa that grow on poroid fungi without specifying the host's status (live, dead). For exploring the relevance of enzymatic competence, we analyzed the rot type frequencies and compared these values with non-mycotrophic poroid wood fungi.

Results

Of the 97 invaders/successors found in published studies, 15 were loosely associated with dead fruiting bodies (fructification on dead fruiting bodies and adjacent wood), 68 were reported to grow on dead fruiting bodies without fructification on adjacent wood, and 20 on live fruiting bodies only (parasitic) (Table 1).

Table 1 Compilation of wood fungi associations (Key see below).

Invader/successor	Host/predecessor	a	d	l	rI	rH	Wood	Source
Antella niemelaei	*Hymenochaete*		x		w	w	no	1
Antella americana	*Hymenochaete*		x		w	w	yes	30
Antrodiella citrinella	*Fomitopsis pinicola*	x			w	w	yes	29

Table 1 Continued.

Invader/successor	Host/predecessor	a	d	l	rI	rH	Wood	Source
Antrodiella faginea	*Phellinus, Inonotus, Hymenochaete, Phellinopsis conchata, Daedaleopsis confragosa, Junghuhnia nitida, Fomitiporia punctata*	x			w	w	yes	1, 2
Antrodiella incrustans	*Daedaleopsis confragosa, Skeletocutis amorpha*		x		w	w	yes	2
Antrodiella pallasii	*Trichaptum*		x		w	w	no	1
Antrodiella pallescens	*Fomes fomentarius*	x			w	w	yes	1
Antrodiella parasitica	*Trichaptum abietinum*		x	x	w	w	yes	1
Antrodiella pirumspora	*Trametes trogii*		x		w	w	no	1
Antrodiella semisupina	*Fomes fomentarius, Phellinus*		x		w	w	yes	2
Antrodiella serpula	*Inonotus*	x			w	w	yes	1, 3
Aporpium macroporum	*Ganoderma applanatum*		x		w	w	yes	4
Basidiodendron caesiocinereum	*Gloeophyllum sepiarium, Fomes fomentarius**		x		w	w+b*	yes	5
Basidiodendron eyrei	*Tyromyces lacteus*			x	w	w	yes	6, 7
Boidinia furfuracea	*Gloeophyllum odoratum*		x		b	b	yes	5
Botryobasidium aureum	*Fomes fomentarius*		x		w	w	yes	5
Botryobasidium obtusisporum	*Fomes fomentarius*		x		w	w	yes	5
Botryohypochnus isabellinus	*Fomes fomentarius*		x		w	w	yes	5
Carcinomyces polyporinus	*Postia caesia, Postia tephroleuca*			x	b	b	no	3
Ceriporia aurantiocarnescens	*Trametes pubescens, Phellinus tremulae*		x		w	w	yes	8
Ceriporia purpurea	*Coriolopsis gallica*		x		w	w	yes	31
Ceriporia reticulata	*Bjerkandera, Coriolopsis, Inonotus, Phellinus Trametes*		x		w	w	yes	1, 31
Ceriporia sericea	*Fuscoporia ferruginosa*		x		w	w	yes	31
Ceriporia torpida	*Trametes*		x		w	w	yes	1
Ceriporia viridans	*Trametes, Ganoderma lipsiense*		x		w	w	yes	1,5
Ceriporiopsis mucida	*Gloeophyllum odoratum*		x		w	b	yes	5
Cinereomyces lindbladii	*Trichaptum*	x			w	w	yes	1
Coniophora olivacea	*Gloeophyllum odoratum*		x		b	b	yes	5
Diplomitoporus phellinicola	*Phellinus*		x		w	w	no?	9
Elmerina caryae	*Inonotus, Polyporus, Fomes, Ganoderma*		x		w	w	yes	1, 28
Entoloma parasiticum	*Cerioporus leptocephalus, Schizopora paradoxa, Coltricia perennis, Trametes versicolor*			x	w	w	yes	10, 11, 12, 24
Entoloma subdepluens	*Coltricia perennis*			x	w	w	no	13
Flaviporus citrinellus	*Fomitopsis*	x			w	b	yes	1
Galzinia incrustans	*Fomes fomentarius*		x		w	w	yes	5
Gloeoporus pannocinctus	*Fomes fomentarius*		x		w	w	yes	1
Hyphoderma setigerum	*Trametes hirsuta*		x		w	w	yes	5
Hyphodontia pallidula	*Gloeophyllum odoratum*		x		b	b	yes	5
Incrustoporia biguttulata	*Phellinidium ferrugineofuscum*		x		w	w	yes	14
Incrustoporia brevispora	*Phellinidium ferrugineofuscum*		x		w	w	yes	1
Incrustoporia chrysella	*Phellinus chrysoloma, Fomitopsis pinicola*, Trichaptum abietinum, Oxyporus corticola*		x		w	w+b*	yes	1, 14
Junghunia nitida	*Fomitiporia punctata*		x		w	w	yes	31
Junghuhnia pseudozilingiana	*Inonotus, Phellinus*		x		w	w	yes	1
Kurtia argillacea	*Gloeophyllum odoratum*		x		b	b	yes	5
Laxitextum bicolor	*Fomes fomentarius*		x		w	w	yes	5

Table 1 Continued.

Invader/successor	*Host/predecessor*	a	d	l	rI	rH	Wood	Source
Lenzites betulinus	*Trametes, Phanerochaete velutina, Stereum hirsutum, Vuilleminia comedens (at 20°C)*			x	w	w	yes	15, 16
Leptosporomyces galzinii	*Gloeophyllum sepiarium*		x		b	b	yes	5
Mucronella bresadolae	*Gloeophyllum odoratum*		x		b	b	yes	5
Mucronella calva	*Ischnoderma benzoinum*		x		w	w	yes	5
Naematelia aurantialba	*Stereum hirsutum*			x	w	w	yes	17
Odontia fallax	*Polyporus*		x		w	w	yes	18
Osteina rhodophila	*Rhodofomes roseus*		x		b	b	yes	19
Oxyporus corticola	*Phellinus tremulae*		x		w	w	yes	31
Paxillus involutus	*Phanerochaete velutina*			x	w	w	yes	20
Peniophorella praetermissa	*Fomes fomentarius, Odontia, Phanerochaete*		x		w	w	yes	5, 17
Peniophorella pubera	*Fomes fomentarius, Inonotus, Gloeophyllum odoratum**		x		w	w+b*	yes	5, 21
Phaeotremella fimbriata	*Stereum rugosum*			x	w	w	no?	22
Phaeotremella foliacea	*Stereum sanguinolentum*			x	w		yes	22
Phaeotremella frondosa	*Stereum rugosum*			x	w	w	no	22
Phaeotremella fuscosuccinea	*Stereum sanguinolentum*			x	w	w	no	22
Phanerochaete aculeata	*Fomes fomentarius*		x		w	w	yes	21
Phlebiopsis gigantea	*Heterobasidion annosum*			x	w	w	yes	15
Postia saxonica	*Daedalea quercina*		x		b	b	no	31
Piloderma byssinum	*Gloeophyllum sepiarium*		x		b	b	yes	5
Pseudotomentella mucidula	*Gloeophyllum odoratum*		x		b	b	yes	5
Pycnoporellus fulgens	*Fomitopsis pinicola*	x			w	w	yes	23
Resinicium bicolor	*Gloeophyllum odoratum*		x		w	b	yes	5
Rhizoctonia fusispora	*Pseudoinonotus dryadeus*		x		w		yes	5
Rigidoporus sanguinolentus	*Phylloporia ribis, Fomes fomentarius, Heterobasidion annosum*		x		w	w	yes	1, 5
Schizopora paradoxa	*Fomes fomentarius*		x		w	w	yes	31
Sidera vulgaris	*Heterobasidion annosum, Fomes fomentarius*		x		w	w	yes	1
Sistotrema brinkmannii	*Botryobasidium vagum, Fomes fomentarius, Ganoderma applanatum, Ganoderma carnosum, Daedaleopsis confragosa, Cerioporus varius, Ischnoderma benzoinum, Mensularia radiata, Trametes hirsuta, Ganoderma lucidum, Heterobasidion annosum, Bjerkandera adusta*		x		b	w+b	yes	5
Sistotrema sernanderi	*Daedaleopsis confragosa, Fomes fomentarius*		x		b	w	yes	5
Skeletocutis afrochrysella	*Phellinus*		x		w	w	no?	9
Skeletocutis carneogrisea	*Trichaptum*		x		w	w	yes	24
Skeletocutis kuehneri	*Trichaptum*	x			w	w	yes	1
Skeletocutis odora	*Phlebia centrifuga*		x		w	w	yes	14
Skeletocutis stellae	*Phellinus chrysoloma (predecessor?), Fomitopsis pinicola*	x			w	w	yes	14
Spongiporus rhodophilus	*Rhodofomes rosea*	x			b	b	yes	1
Steccherinum fimbriatellum	*Ganoderma*		x		w	w	yes	1
Syzygospora pallida	*Phanerochaete sordida*			x	w	w	no	25
Tomentella lateritia	*Gloeophyllum odoratum*		x		?	b	yes	5

Table 1 Continued.

Invader/successor	*Host/predecessor*	a	d	l	rI	rH	Wood	Source
Trametes gibbosa	*Bjerkandera*			x	w	w	yes	15
Trechispora candidissima	*Daedalea quercina*		?	?	b	b	yes	8
Trechispora cohaerens	*Fomes fomentarius*		x		w	w	yes	21
Trechispora farinacea	*Gloeophyllum odoratum*, Fomes fomentarius*, Daedalea quercina**		x		w	w+b*	yes	5
Trechispora mollusca	*Fomes fomentarius, Phellinus*		x		w	w	yes	1
Tremella encephala	*Stereum sanguinolentum*			x	w	w	yes	3
Tremella mesenterica	*Peniophora*			x	w	w	yes	3, 26
Tremella obscura	*Dacrymyces stillatus*			x	w	w	no	3
Tulasnella eichleriana	*Ischnoderma benzoinum*		x		w	w	yes	5
Tulasnella violea	*Daedaleopsis confragosa*		x		w	w	yes	5
Tylospora asterophora	*Coltricia perennis, Trichaptum abietinum*		x		w	w	yes	5
Tylospora fibrillosa	*Gloeophyllum odoratum*		x		b	b	yes	5
Vitreoporus dichrous	*Inonotus (obliquus), Fomes fomentarius, Fomitiporia punctata*		x		w	w	yes	1
Xenasmatella vaga	*Onnia, Phaeolus**		x		w	w+b*	yes	5
Xylodon asper	*Phellinus*		x		w	w	yes	5
Xylodon brevisetus	*Gloeophyllum odoratum*		x		b	b	yes	5

Key: a = associated (grows on a fruiting body and in its vicinity), d = on dead fruiting bodies, l = on live fruiting bodies, b = brown, w = white, rI = rot type of Invader, rH = rot type of Host, Wood = grows also on wood; asterisks denote rot types of hosts where appropriate; rot types according to Gilbertson and Bigelow (1998); taxonomy based on Index Fungorum (Index-Fungorum-Partnership 2020) and Mycobank (Mycobank 2004–2020). Sources: [1]Ryvarden et al. (2017); [2]Spirin & Zmitrovich (2003); [3]Jahn (1979); [4]Görke & Hahn (2016); [5]Besl et al. (1989); [6]Gilbertson & Bigelow (1998); [7]Setliff et al. (1983); [8]Bondartsev (1953/1971); [9]Leif Ryvarden[10]Noordeloos (1992); [11]https://mushroomobserver.org/; [12]http://www.texasmushrooms.org; [13]Buller (1924); [14]Spirin (2005); [15]Woodward & Boddy (2008); [16]Rayner et al. (1987); [17]Jeffries (1995); [18]Tomasi (1977); [19]Bernicchia et al. (2020); [20]Leake et al. (2003); [21]Volobuev et al. (2018); [22]Spirin et al. (2018); [23]Niemelä et al. (1995); [24]Helfer (1991); [25]Oberwinkler et al. (1984); [26]Zugmaier et al. (1994); [27]Jahn (1990); [28]https://nt.ars-grin.gov/fungaldatabases/fungushost/; [29]Wieners et al. (2016); Núñez & Ryvarden (2001); [31]Rivoire (2020)

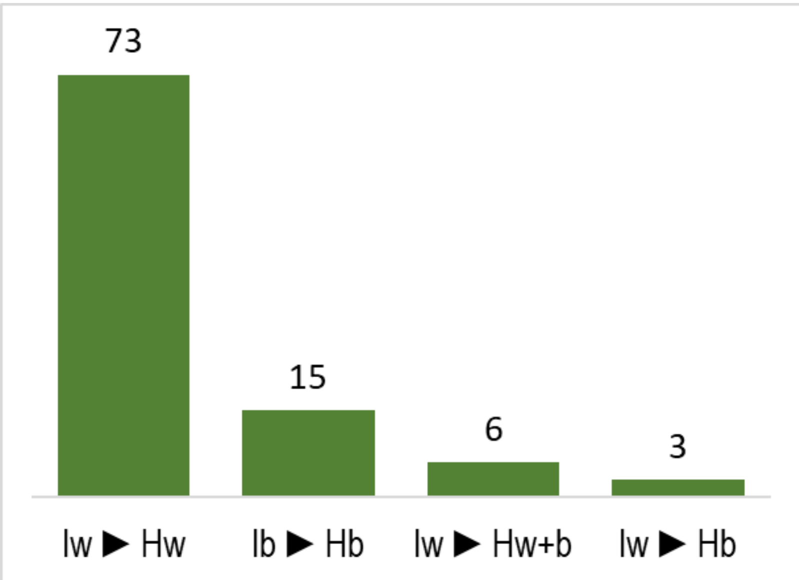

Fig. 2 – Variants of rot types between invaders/successors (I) and hosts/predecessors (H). w = white rot, b = brown rot. note that in two cases, the invader/successor rot type could not be identified.

The compilation revealed distinctive patterns with respect to the rot type of fruiting body colonizers. According to our analyses, 90% of invaders/successors were of the same rot type as their hosts/predecessors, 6% showed both rot types among the hosts/predecessors, and in three cases, a shift from white to brown rot was observed (Fig. 2). Moreover, the data suggest that eight invaders/successors depended on fruit bodies as hosts, including six parasitic taxa.

The ratio between white and brown rotters among the invaders (5.4:1, n = 91) differed from non-fungicolous poroid taxa (3.4:1, n = 643, Chi^2 p = 0.22 [not associated]; data not shown).

Discussion

Of the 95 associations recorded, a multifaceted picture emerged: (1) The fact that most invaders/successors use hosts/predecessors of the same rot type may indicate subsequent utilization of the “predigested” substrate. (2) This result and the high proportion of white rotters indicate a more pronounced ability of white rotters to use other poroid wood fungi as substrate. This capacity can be explained by their competence for degrading plant lignin by employing β-Glucosidase and peroxidases (Linnard et al. 2013), thus possibly lignin-analogous structural compounds of fungi (Davin et al. 2008). In addition, many basidiomycetes produce chitinases (Gooday et al. 1986) that could degrade fungal chitin. The same explanations may apply to invaders/successors that can colonize both white and brown rotters. To our knowledge, such phenomena have not been reported previously. (3) The exploitation of mycelial channels may be employed by an unknown number of taxa that succeed on dead fruiting bodies belonging to the same or different rot types, especially in the case of the rare brown rotting combinations (Ib ►Hb, see Fig. 2). Microscopical investigations and enzyme assays would be required to clarify this mode. (4) Of the six obligate taxa, five belong to the Tremellales, known to be parasitic (Kirk et al. 2011). The sixth species, *Entoloma subdepluens*, here noted as an obligate parasite, waits for the final confirmation of its obligate lifestyle, as is the case for some other *Entoloma* spp. (Czederpiltz et al. 2001). Some *Entoloma* spp. are assumed to be biotrophic (Tedersoo et al. 2010, Trudell et al. 2004). Like *Hygrocybe* s.l, some grassland *Entoloma* species avoid rich soils (belonging to the “CHEGD-fungi”), particularly regarding mineral nitrogen, which may indicate a biotrophic lifestyle (Griffith et al. 2013, Halbwachs et al. 2013). Therefore, it could well be that *Entoloma subdepluens* is a biotrophic parasite, while members of the Tremellales are necrotrophic parasites. To further clarify the underlying mechanisms, the stable isotope signature of *Entoloma subdepluens* should be determined.

To shed more light on the colonization modes of taxa that grow on dead poroid fruiting bodies, enzyme assays and physiological investigations should be employed. Moreover, molecular methods such as transcriptomics and genome sequencing could help uncover possible co-evolutionary processes that led to the observed colonization modes.

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