Commentary

Time to re-think fungal ecology? Fungal ecological niches are often prejudged

There is growing evidence that many fungi have more complex niches than previously imagined, and two articles in this issue of *New Phytologist*, based on different methodological approaches (Lofgren *et al.*, pp. 1203–1212; Martino *et al.*, pp. 1213–1229), support this. Both question whether the ability to colonize several ecological niches is a common phenomenon in fungi.

> '*. . . as readers, reviewers, researchers, or editors, we should be prepared to re-think fungal ecology, and describe niches beyond those our respective domains of research predict.*'

Fusarium graminearum is an American fungus that causes Fusarium Head Blight in cultivated grasses, which entails billions of dollars of losses during epidemics affecting wheat and barley. It causes the kernels to shrivel up due to the production of mycotoxins (trichothecenes), which also makes the seeds inedible. In this issue of *New Phytologist*, Lofgren *et al.* demonstrate a very different interaction with native North-American grasses. The fungus was isolated in 17 out of 25 asymptomatic native grass species, where it grew as a symptomless endophyte – by endophyte, we mean a fungus growing in living plant tissues which does not cause obvious symptoms or morphological modifications (e.g. no mycorrhiza) in terms of its impact on the host (Hardoim *et al.*, 2015). Interestingly, the accumulation of trichothecenes was often limited in these grass species, and Lofgren *et al.* verified the Koch's postulates by inoculating *F. graminearum* on native grasses, and established its potential for endophytism with reduced trichothecenes accumulation. There are additional barcoding reports that *Fusarium* spp. can be found as endophytes in various other plants (Bonito *et al.*, 2016; Glynou *et al.*, 2017). Thus, a major disease in introduced grasses in North America emerged from a common endophyte of native grasses, adding another example to the growing list of evidences that fungi which are reputedly 'phytopathogenic' can be recovered as endophytes from healthy plant tissue (Rodriguez *et al.*, 2009; Hardoim *et al.*, 2015; Almario *et al.*, 2017).

Some mycorrhizal fungi also have another ecological niche, as evidenced by recent research on fungal genomics. Martino *et al.*, in this issue of *New Phytologist*, assembled the draft genomes of three Leotiomycetes (Ascomycota), *Meliniomyces bicolor*, *M. variabilis* and *Rhizoscyphus ericae*, which form a particular type of mycorrhiza with some Ericaceae plants, the ericoid mycorrhiza. Analysis of these genomes confirms trends observed in another sequenced ericoid mycorrhizal Leotiomycete, *Oidiodendron maius* (Kohler *et al.*, 2015); namely, ericoid mycorrhizal fungi possess numerous enzyme-coding genes involved in the degradation of polysaccharides, proteins and lipids in a number similar (or even higher) to that found in related saprotrophic species. This can explain their saprotrophic survival and high-degrading abilities, long reported from *in vitro* cultivation. At the same time, they display several features of mycorrhizal fungi, such as an expansion of the gene family involved in nutrient uptake/exchange and an abundance of small secreted proteins (SSPs) that have important roles in biotrophic interactions. Additionally, Martino *et al.* studied gene expression and showed that 10–20% of these SSPs are induced during mycorrhizal interaction, a proportion similar to fungi from other mycorrhizal types (e.g. Kohler *et al.*, 2015). Most ericoid plants live in soils where the turnover in organic matter is slow (van der Heijden *et al.*, 2015), and where most phosphorus (P) and nitrogen (N) resources occur as organic compounds: the ability of ericoid mycorrhizal fungi to degrade organic matter is thus pivotal in host–plant adaptation.

Although they deal with different plant–fungal interactions, Lofgren *et al.* and Martino *et al.* both reveal fungi that do not exactly match the usually recognized ecological niches, but cover two of them in a larger, dual niche. Although this phenomenon has long been recognized, it is often considered to be an exception, rather than a general trend among fungi (e.g. 'multifunctional' fungi in Brundrett, 2006). Are dual niches kinds of exceptions, or do they tell us more? Here, we look at the literature to show and explain why occupation of more than one ecological niche may be common in fungi.

Do fungal ecological niches reflect more than mycologist's sociology?

Several other fungi display a dual niche, with two apparently unrelated aspects (Table 1). For example, some insect parasites are also plant endophytes, and they can transfer animal N to the plant (Behie *et al.*, 2012). Some years ago, several 'Ingoldian fungi', a set of ascomycetes which decay dead leaves in freshwater, were discovered in living leaves, and the tendency of their spores to concentrate in foam may allow aerial re-infection of living leaves (Sokolski *et al.*, 2006; Selosse *et al.*, 2008). Lichen-forming fungi from the genus *Stictis* were found to form a single complex of species with saprotrophic *Conotrema*, and these species have the

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This article is a Commentary on Lofgren *et al.*, **217**: 1203–1212 and Martino *et al.*, **217**: 1213–1229.

Table 1 Published examples of fungi with dual ecological niches, depending on hosts and conditions, with indication for the evolutionary trajectory of Fig. 1 whenever a scenario is proposed

Dual ecological niche	Fungal taxa	References	Evolutionary trajectory
Endophytic + phytoparasitic	*Fusarium graminearum*	Lofgren *et al.* (2018, this issue of *New Phytologist*, pp. 1203–1212)	(b)
Mycorrhizal + saprotrophic	Ericoid mycorrhizal Leotiomycetes	Martino *et al.* (2018, this issue of *New Phytologist*, pp. 1213–1229)	(a)
	Mycena[a]	Selosse *et al.* (2010); Grelet *et al.* (2017)	
	Basidiomycetes incl. *Coniophora*, *Hypholoma*, *Phellinus*[a]	Smith *et al.* (2017)	
Mycorrhizal + endophytic	Sebacinales incl. *Serendipita* (= *Piriformospora*) *indica*	Selosse *et al.* (2009); Weiß *et al.* (2016); Oliveira *et al.* (2014)	(a)
	Tuber melanosporum and *T. aestivum*	Gryndler *et al.* (2014); Schneider-Maunoury *et al.* (2018)	
	Tricholoma matsutake	Murata *et al.* (2013, 2014)	
Animal parasitic + endophytic	*Metarhizium* (=*Metacordyceps*)	Behie *et al.* (2012)	(in main text)
Lichenized + saprotrophic	*Stictis* – *Conotrema* complex	Wedin *et al.* (2004)	–
Endophytic + saprotrophic	*Chalara*	Koukol (2011)	(b)
	'Ingoldian fungi' (various Ascomycetes[b])	Sokolski *et al.* (2006); Selosse *et al.* (2008)	
	Xylariales	Davis *et al.* (2003)	

[a] The morphology of root colonization may differ from the 'standard' mycorrhizal morphology; however, considerable variations exist in mycorrhizal ultrastructure. For more detail, see discussions in the cited references.
[b] Ingoldian fungi include some Leotiomycetes, e.g. the genera *Tetracladium* or *Tricladium*.

ability to live as free-living saprotrophs and to form lichens ('optional lichenization'; Wedin *et al.*, 2004). Some important groups of saprotrophic fungi can form mycorrhizas, e.g. *Mycena* in orchids (Selosse *et al.*, 2010) or Ericaceae (Grelet *et al.*, 2017), or they can be common endophytes, such as Xylariales (Davis *et al.*, 2003) or *Chalara* spp. (Koukol, 2011). Recently, after inoculating 201 saprotrophic species on coniferous seedlings, Smith *et al.* (2017) evidenced biotrophic colonization in 17% of species, while three species induced formation of some characteristic features of ectomycorrhizas (see the Commentary by Baldrian & Kohout, 2017). Truffle species of the ectomycorrhizal genus *Tuber* (truffles) were shown to also colonize the roots of herbaceous plants where they likely live as endophytes (Gryndler *et al.*, 2014; Schneider-Maunoury *et al.*, 2018). Although the latter interaction is still poorly understood, it may account for a specific feature of truffles' habitat, the brûlé. This is a zone around trees colonized by truffles where vegetation grows poorly (Streiblová *et al.*, 2012), suggesting some interactions between truffles and herbaceous plants. The extent to which root endophytism of truffle contributes to the brûlé deserves closer investigation.

Interestingly, the presence of truffles on herbaceous plants was hidden to researchers for a long time because the primers used to specifically detect arbuscular mycorrhizal fungi (Glomeromycota, which associate with such plants) do not detect Ascomycota. There is even the possibility that additional ectomycorrhizal species colonize the roots of nonectomycorrhizal plants (Schneider-Maunoury *et al.*, 2018). When observing nature, we often see what we are specifically looking for: this may be one of the reasons why our understanding of fungal niches is long-standing, but not accurate. Mycorrhizologists study mycorrhizal fungi, lichenologists study lichens, pathologists study diseased plants, and specialists of decomposition research dead organic matter, etc. Our respective fields may prejudge our perceptions of what the fungal ecological niches really are, and beyond occasional discoveries, the organization of mycological sub-fields reinforce the prejudged niches.

Reinvestigation is now open, at a time where molecular tools are powerful enough to challenge current understanding of fungal ecological niches. DNA barcoding can investigate the spread of a given fungal species across ecosystem compartments and ecological niches (e.g. Wedin *et al.*, 2004; Selosse *et al.*, 2008). Now, high-throughput sequencing allows for the identification of many fungi in a single sample, and we can even find unexpected fungi in a surprising place. Of course, one has to be careful with fungal contaminations. But one also has to be careful with discarding (in good faith) relevant fungi from the data. This also means that additional controls, such as re-inoculation (Lofgren *et al.*) or direct visual observation (e.g. Smith *et al.*, 2017), are required before a new niche is confirmed. On the plant side, the potential for new niches expands the pool of possible fungal interactions.

Evolutionary trajectories, and species lost in translation

As Dobzhansky rightly said for biology, nothing in ecology makes sense, except in the light of evolution. The fungal niches as they are, even if they are larger than we have been thinking, result from an evolutionary process. Here, we propose a scenario that would give sense to (at least some) observed dual niches. It relies on an evolutionary tendency among fungi to shift ecological niches (what we call here evolutionary trajectories). Such trajectories often occur convergently in numerous independent taxa. Along a trajectory, some individuals or species may retain both the previous and the

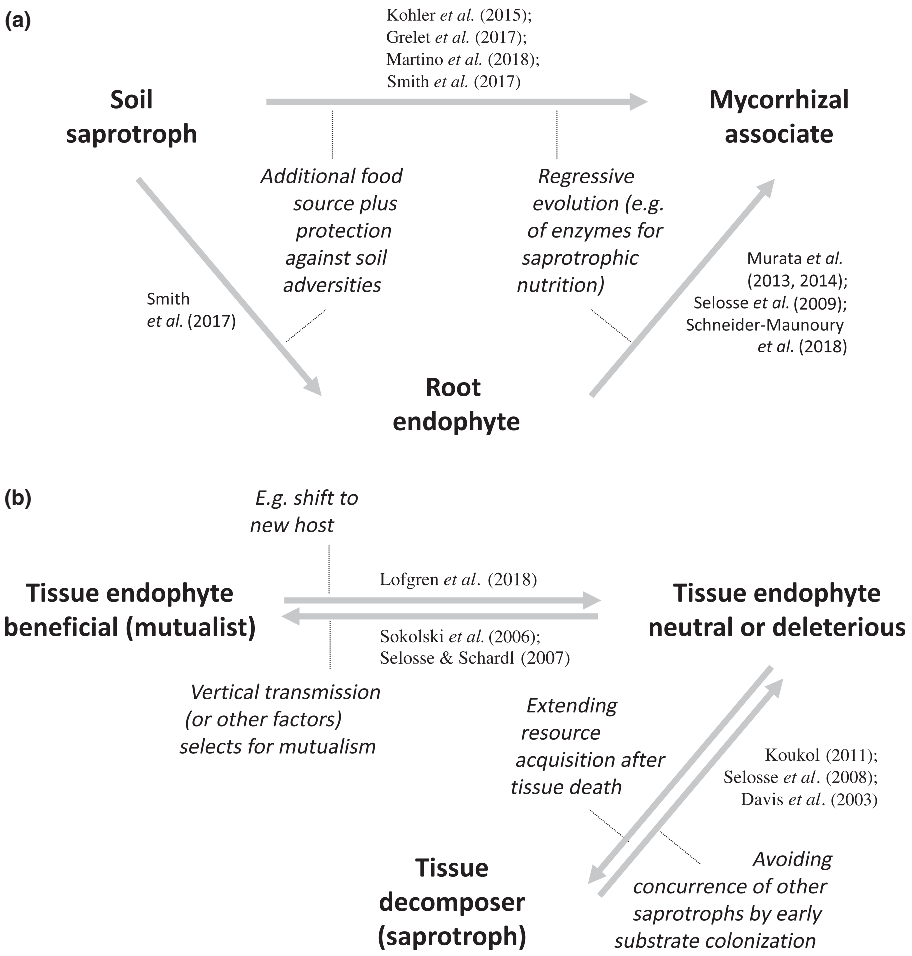

Fig. 1 Some evolutionary trajectories (grey arrows) between classical ecological niches (in bold), with some factors promoting the evolution in the direction of the arrow (italics). (a) Trajectories along the soil saprotrophy–mycorrhizal continuum, which mainly concern soil fungi; (b) trajectories along the saprotrophy–aerial endophytism continuum, which mainly concern fungi from aerial parts that may enter a vertical transmission through seeds. These trajectories and factors are not meant to be exhaustive but simply illustrate the way large, dual niches can arise in evolution. The cited work in the arrows refer to examples of fungi (also in Table 1) that occupy the two linked classical ecological niches, because they keep the previous and acquired niche in their evolution.

newly emerging niches, while others do not enter the niche enlargement, or fully shift to the new niche. For example, the finding that *Metarhizium* is both an insect parasite and a plant endophyte (Behie *et al.*, 2012) makes sense when considering the recurrent evolutionary shifts from animal to plant hosts in the Clavicipitaceae family (Spatafora *et al.*, 2007). While some clavicipitaceous species strictly associate with animals or plants, others are 'lost in translation' and colonize hosts from both kingdoms. Evolutionary trajectories are one of the drivers underlying dual niches, and we tentatively illustrate here a subset of possible trajectories (Fig. 1) involving fungi listed in this article (Table 1).

Many of the examples earlier, especially these reported by Martino *et al.* are relevant in the framework of the evolution to the mycorrhizal habit (Fig. 1a), a scenario that occurred many times in fungal evolution (Kohler *et al.*, 2015). We suggest two trajectories for this. First, a direct evolution from soil saprotrophic ancestors is possible, in a regressive evolution where many genes required for a saprotrophic free life are lost (van der Heijden *et al.*, 2015; Kohler *et al.*, 2015). Second, the mycorrhizal habit may have evolved from ancestors that were already able to colonize living plant tissues as endophytes (Brundrett, 2006). The latter pathway has been referred to as the 'waiting room' hypothesis (Selosse *et al.*, 2009; van der Heijden *et al.*, 2015). Following this hypothesis, root endophytism acts as a symbiotic 'waiting room', where biotrophic coexistence predisposes evolution towards a tighter mutualism with a more complex joint mycorrhizal morphogenesis. The latter pathway seems at least relevant for fungi mycorrhizal in ericoid hosts (Martino *et al.*) and orchids (Selosse & Martos, 2014). On the fungal side, it is phylogenetically supported in the Sebacinales, which evolved both ericoid and orchid mycorrhizal habits, as well as the ectomycorrhizal habit, from endophytic ancestors (Weiß *et al.*, 2016). The 'waiting room' hypothesis may explain why some ectomycorrhizal taxa, such as *Tuber* or *Tricholoma* (Table 1), also behave as root endophytes if they retain an ancestral niche. It may also explain why saprotrophic *Mycena* spp., which are also known to be endophytic (e.g. Glynou *et al.*, 2017; see references in Grelet *et al.*, 2017), also occur as mycorrhizal fungi in orchids or in Ericaceae (Table 1). However, one cannot fully exclude a reverse trajectory, where mycorrhizal abilities allow endophytic colonization in nonmycorrhizal hosts: in both cases, the observation of a dual niche would emerge from an evolutionary trajectory.

The transition from saprotrophy to endophytism, or vice-versa, is also described in fungi colonizing the aerial parts of plants (Fig. 1b), with a striking convergence in ascomycetous taxa that are both litter decayers and endophytes (Selosse *et al.*, 2008; Koukol, 2011). Recurrent transitions from saprotrophy to endophytism may explain the dominance of facultative endophytes in roots, which also behave as soil saprotrophs, e.g. in the Brassicaceae *Microthlaspi* (Glynou *et al.*, 2017) or in *Populus* (Bonito *et al.*, 2016). Noteworthy, among endophytes of aerial tissues, the trajectory from neutral or deleterious to mutualistic endophyte (Fig. 1b) is very relevant for plant physiology.

Considering the evolution of mutualism in endophytic interactions, plants offer a powerful selective pressure: vertical transmission. As opposed to animals, where newborns are axenic at birth, seeds can be colonized by maternal fungi during maturation on the mother plant, with colonization reaching seeds, fruit envelopes, or even the embryo itself (Tobias *et al.*, 2017). Vertical transmission generally selects for mutualism (Fig. 1b), because any partner harming its symbiont will produce offspring interacting with partners of lower quality, while any better altruist will improve the production of partners for its own offspring (Douglas, 2008). For example, in grasses, vertical transmission drove the emergence of protective endophytes with multiple favourable effects in the genus *Epichloë*, a group of parasitic fungi that destroy seeds to form spores for their own horizontal transmission. The mutualistic *Neotyphodium* evolved from such pathogenic ancestors through loss of sporulation and independent propagation entailing vertical transmission (Selosse & Schardl, 2007). The vertical transmission of *F. graminearum* in native North-American grasses observed by Lofgren *et al.* may account for the absence of mycotoxins (trichothecenes) and pathogenicity on these hosts. At the opposite end, the jump to new hosts (the introduced grasses), without previous coevolution and efficient vertical transmission, resulted in deleterious interactions. Thus, an evolutionary trajectory including the gain of vertical transmission can select for mutualism, and a given species may have a different outcome for the host depending on its transmission mode.

Final considerations

Beyond 'the' niche we attribute to one fungal species lie populations of individuals: dual niches, within a species, may not pertain to any individual. Some individuals may, for genetic and/or environmental reasons, be more prone to use one or another aspect of a niche, while other individuals may use the whole dual niche, as demonstrated in endophytic and ectomycorrhizal truffles (Schneider-Maunoury *et al.*, 2018). Understanding the intraspecific dimension of niche variation is promising for a micro-evolutionary approach, but remains a difficult, overlooked issue (Johnson *et al.*, 2012).

Phytoparasitism, lichenization, mycorrhiza, endophytism, saprotrophy may only be a part of many fungal ecological niches, which are more complex. We should remain open, and favour naive observations: as readers, reviewers, researchers, or editors, we should be prepared to re-think fungal ecology, and describe niches beyond those our respective domains of research predict. Let us especially pay attention to the works of teams such as Lofgren *et al.* and Martino *et al.*, which cross disciplinary borders. The latter's work nicely illustrates the set of tools, from morphological inspection and Koch's postulate to genomic and transcriptomic, that will allow us in the future to revisit fungal ecological niches. Tomorrow, we may investigate more details of how each of the various facets of the ecological niche shape fungal nutrition and reproduction.

On the plant science side, the comments earlier also underline the growing evidence that the endophytic fungome is of pivotal importance in plant functioning and evolution (Rodriguez *et al.*, 2009; Hardoim *et al.*, 2015), as exemplified by its role in the evolutionary trajectories proposed here (Fig. 1). A better understanding of the plant fungome, and its diversity and functions (Almario *et al.*, 2017; Glynou *et al.*, 2017), is now crucial.

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References

Almario J, Jeena G, Wunder J, Langen G, Zuccaro A, Coupland G, Bucher M. 2017. Root-associated fungal microbiota of nonmycorrhizal *Arabis alpina* and its contribution to plant phosphorus nutrition. *Proceedings of the National Academy of Sciences, USA* **114**: E9403–E9412.

Baldrian P, Kohout P. 2017. Interactions of saprotrophic fungi with tree roots: can we observe the emergence of novel ectomycorrhizal fungi? *New Phytologist* **215**: 511–513.

Behie SW, Zelisko PM, Bidochka MJ. 2012. Endophytic insect-parasitic fungi translocate nitrogen directly from insects to plants. *Science* **336**: 1576–1577.

Bonito G, Hameed K, Ventura R, Krishnan J, Schadt CW, Vilgalys R. 2016. Isolating a functionally relevant guild of fungi from the root microbiome of *Populus*. *Fungal Ecology* **22**: 35–42.

Brundrett MC. 2006. Understanding the roles of multifunctional mycorrhizal and endophytic fungi. In: Schulz B, Boyle C, Sieber TN, eds. *Microbial root endophytes. Soil biology (vol. 9)*. Berlin, Germany: Springer, 281–298.

Davis EC, Franklin JB, Shaw AJ, Vilgalys R. 2003. Endophytic *Xylaria* (Xylariaceae) among liverworts and angiosperms: phylogenetics, distribution, and symbiosis. *American Journal of Botany* **90**: 1661–1667.

Douglas AE. 2008. Conflict, cheats and the persistence of symbioses. *New Phytologist* **177**: 849–858.

Glynou K, Nam B, Thines M, Maciá-Vicente JG. 2017. Facultative root-colonizing fungi dominate endophytic assemblages in roots of nonmycorrhizal *Microthlaspi* species. *New Phytologist* **217**: 1190–1202.

Grelet G-A, Ba R, Goeke DF, Houliston GJ, Taylor AFS, Durall DM. 2017. A plant growth-promoting symbiosis between *Mycena galopus* and *Vaccinium corymbosum* seedlings. *Mycorrhiza* **27**: 831–839.

Gryndler M, Černá L, Bukovská P, Hršelová H, Jansa J. 2014. *Tuber aestivum* association with non-host roots. *Mycorrhiza* **24**: 603–610.

Hardoim PR, van Overbeek LS, Berg G, Pirttilä AM, Compant S, Campisano A, Döring M, Sessitsch A. 2015. The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiology and Molecular Biology Reviews* **79**: 293–320.

van der Heijden MGA, Martin FM, Selosse M-A, Sanders IR. 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist* **205**: 1406–1423.

Johnson D, Martin F, Cairney JWG, Anderson IC. 2012. The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. *New Phytologist* **194**: 614–628.

Kohler A, Kuo A, Nagy LG, Morin E, Barry KW, Buscot F, Canbäck B, Choi C, Cichocki N, Clum A *et al.* 2015. Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nature Genetics* **47**: 410–415.

Koukol O. 2011. New species of *Chalara* occupying coniferous needles. *Fungal Diversity* **49**: 75.

Lofgren LA, LeBlanc NR, Certano AK, Nachtigall J, LaBine KM, Riddle J, Broz K, Dong Y, Bethan B, Kafer CW *et al.* 2018. *Fusarium graminearum:* pathogen or endophyte of North American grasses? *New Phytologist* **217**: 1203–1212.

Martino E, Morin E, Grelet G-A, Kuo A, Kohler A, Daghino S, Barry KW, Cichocki N, Clum A, Dockter RB *et al.* 2018. Comparative genomics and transcriptomics depict ericoid mycorrhizal fungi as versatile saprotrophs and plant mutualists. *New Phytologist* **217**: 1213–1229.

Murata H, Yamada A, Maruyama T, Endo N, Yamamoto K, Ohira T, Shimokawa T. 2013. Root endophyte interaction between ectomycorrhizal basidiomycete *Tricholoma matsutake* and arbuscular mycorrhizal tree *Cedrela odorata*, allowing *in vitro* synthesis of rhizospheric "shiro". *Mycorrhiza* **23**: 235–242.

Murata H, Yamada A, Yokota S, Maruyama T, Endo N, Yamamoto K, Ohira T, Neda H. 2014. Root endophyte symbiosis *in vitro* between the ectomycorrhizal basidiomycete *Tricholoma matsutake* and the arbuscular mycorrhizal plant *Prunus speciosa. Mycorrhiza* **24**: 315–321.

Oliveira SF, Bocayuva MF, Veloso TGR, Bazzolli DMS, da Silva CC, Pereira OL, Kasuya MCM. 2014. Endophytic and mycorrhizal fungi associated with roots of endangered native orchids from the Atlantic Forest, Brazil. *Mycorrhiza* **24**: 55–64.

Rodriguez RJ, White JF Jr, Arnold AE, Redman RS. 2009. Fungal endophytes: diversity and functional roles. *New Phytologist* **182**: 314–330.

Schneider-Maunoury L, Leclercq S, Clément C, Covès H, Lambourdière J, Sauve M, Richard F, Selosse M-A, Taschen E. 2018. Is *Tuber melanosporum* colonizing the roots of herbaceous, non-ectomycorrhizal plants? *Fungal Ecology* **31**: 59–68.

Selosse M-A, Dubois M-P, Alvarez N. 2009. Do Sebacinales commonly associate with plant roots as endophytes? *Mycological Research* **113**: 1062–1069.

Selosse M-A, Martos F. 2014. Do chlorophyllous orchids heterotrophically use mycorrhizal fungal carbon? *Trends in Plant Science* **19**: 683–685.

Selosse M-A, Martos F, Perry B, Maj P, Roy M, Pailler T. 2010. Saprotrophic fungal symbionts in tropical achlorophyllous orchids. *Plant Signaling & Behavior* **5**: 349–353.

Selosse M-A, Schardl CL. 2007. Fungal endophytes of grasses: hybrids rescued by vertical transmission? An evolutionary perspective. *New Phytologist* **17**: 452–458.

Selosse M-A, Vohnik M, Chauvet E. 2008. Out of the rivers: are some aquatic hyphomycetes plant endophytes? *New Phytologist* **178**: 3–7.

Smith GR, Finlay RD, Stenlid J, Vasaitis R, Menkis A. 2017. Growing evidence for facultative biotrophy in saprotrophic fungi: data from microcosm tests with 201 species of wood-decay basidiomycetes. *New Phytologist* **215**: 747–755.

Sokolski S, Piché Y, Chauvet E, Bérubé JA. 2006. A fungal endophyte of black spruce (*Picea mariana*) needles is also an aquatic hyphomycete. *Molecular Ecology* **15**: 1955–1962.

Spatafora JW, Sung G-H, Sung J-M, Hywel-Jones NL, White JF. 2007. Phylogenetic evidence for an animal pathogen origin of ergot and the grass endophytes. *Molecular Ecology* **16**: 1701–1711.

Streiblová E, Gryndlerová H, Gryndler M. 2012. Truffle brûlé: an efficient fungal life strategy. *FEMS Microbiology Ecology* **80**: 1–8.

Tobias TB, Farrer EC, Rosales A, Sinsabaugh RL, Suding KN, Porras-Alfaro A. 2017. Seed-associated fungi in the alpine tundra: both mutualists and pathogens could impact plant recruitment. *Fungal Ecology* **30**: 10–18.

Wedin M, Döring H, Gilenstam G. 2004. Saprotrophy and lichenization as options for the same fungal species on different substrata: environmental plasticity and fungal lifestyles in the *Stictis–Conotrema* complex. *New Phytologist* **164**: 459–465.

Weiß M, Waller F, Zuccaro A, Selosse M-A. 2016. Sebacinales – one thousand and one interactions with land plants. *New Phytologist* **211**: 20–40.

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