

## Meetings

# Plants, fungi and oomycetes: a 400-million year affair that shapes the biosphere

## 10<sup>th</sup> New Phytologist Workshop on the 'Origin and evolution of plants and their interactions with fungi', London, UK, September 2014

In a rare gathering, genomics met palaeontology at the 10<sup>th</sup> New Phytologist Workshop on the 'Origin and evolution of plants and their interactions with fungi'. An eclectic group of 17 experts met at The Natural History Museum (London, UK) on 9–10 September 2014 to discuss the latest findings on plant interactions with fungi (Eumycota) and oomycetes (Oomycota = Peronosporomycota), with topics ranging from the fossil record and comparative genomics to symbiosis and phytopathology. The discussions were largely disseminated via social media (Box 1). Highly diverse plant–fungal interactions have formed the backbone of land ecosystems and biogeochemical cycles since the Palaeozoic (see Fig. 1 for geological timeframe). As summarized by Christine Strullu-Derrien and Paul Kenrick (The Natural History Museum, London, UK) the first land plants arose *c.* 470 million years (Myr) ago (Kenrick *et al.*, 2012; Edwards *et al.*, 2014), at which time fungi and oomycetes had already colonized terrestrial ecosystems. Following their terrestrialization, these microbes began to abound within plant fossils (Taylor *et al.*, 2014, and references therein). Ultimately, biological interactions sculpted the genomes of plants, fungi and oomycetes (e.g. Schmidt & Panstruga, 2011; Kohler *et al.*, 2015). Here we illustrate the picture that has emerged from the discussions at the 10<sup>th</sup> New Phytologist Workshop, and point to some pending questions.

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### Symbiotic origins

The emergence of land plants is often viewed as a symbiosis between a green alga with photosynthetic abilities that is unable to access water and minerals in the substrate, and a heterotrophic fungus predisposed to exploit soil resources (e.g. Selosse & Le Tacon, 1998; Selosse & Strullu-Derrien, 2015). Lichens have existed since

### Box 1 NPW10 and social media: from Twitter to Storify

As it has now become routine at New Phytologist Workshops and Symposia and other scientific conferences, many delegates live-tweeted scientific highlights and other tidbits. Questions from the community were relayed to the speakers through Twitter. This resulted in broader dissemination of the workshop topic and engagement with many more scientists than those who attended the 10<sup>th</sup> New Phytologist Workshop. A picture of a 407 Myr old slab of Rhynie Chert, the earliest known ecosystem of plants and fungi, was popular in the Twittersphere and was repeatedly retweeted. The #NPW10 tweets were archived in the Storify platform and received >10 000 page views a month after the workshop (<https://storify.com/KamounLab/npw10-10th-new-phytologist-workshop-origin-and-ev>).

the Devonian (Honegger *et al.*, 2013), but their apparent low frequency in the fossil record has argued against a major role during terrestrialization. As Marc-André Selosse (Muséum national d'Histoire Naturelle, Paris, France) and Dianne Edwards (University of Cardiff, UK) discussed, the affinities of the enigmatic Nematophytales – an extinct group that includes the gigantic *Prototaxites*, a widespread Devonian columnar organism, which could reach up to 9 m in height and 1 m in diameter – are still debated (Edwards *et al.*, 2013). A fungal affinity is suspected because of their distinctive filamentous organization, but since the contemporary plant biomass was likely insufficient to support large heterotrophs, it has been suggested that Nematophytales had photosynthetic abilities (Edwards *et al.*, 2013), or even a lichen-like nature (Selosse, 2002). Although remains of photobionts are still controversial, recent research bears out the lichenized nature of the much smaller thalloid forms (Edwards *et al.*, 2013; Honegger *et al.*, 2013). Together with evidence from other fossils (e.g. *Winfrenatia reticulata*; Taylor *et al.*, 1997), it now seems probable that lichens were a component of early terrestrial ecosystems, which bore a resemblance to modern cryptogam covers.

The terrestrialization of land plants (Embryophyta) is also a story of fungal symbiosis. Arbuscular mycorrhizas (AM) formed by Glomeromycetes are widespread in living plants, and Silvia Pressel and Jeffrey Duckett (The Natural History Museum, London, UK) summarized recent evidence from most basal lineages (e.g. liverworts, hornworts; Desirò *et al.*, 2013). Similarly, Maarja Õpik presented an overview of species diversity and modern distributions of AM fungi, based on a database hosted by her at the University of Tartu, Estonia (Õpik *et al.*, 2013). As noted by Martin Bidartando (Imperial College, London, UK) and others, the AM symbiosis can be considered ancestral in land plants (Bonfante & Selosse, 2010), and Christine Strullu-Derrien illustrated further support for this view, based on new fossils from the 407 Myr old Rhynie Chert

(Strullu-Derrien *et al.*, 2014). Here, the plant hosts were rootless, and arbuscules were formed in photosynthetic aerial axes, a mode of infection unknown in modern vascular plants but closely resembling that in living liverworts and hornworts. There is also a growing body of molecular developmental evidence: *Medicago* mutants deficient for the pathway required to perceive Glomeromycete signals that are critical for fungal colonization can be rescued by ortholog genes from liverworts or hornworts, supporting the ancestral origin of the plant–Glomeromycetes symbiosis (Wang *et al.*, 2010). Research on the origin of the genes acting in this pathway now focuses on algal lineages related to land plants, such as charophytes. Pierre-Marc Delaux (University of Wisconsin, Madison, WI, USA) suggested a stepwise evolution of the plant symbiotic ‘toolkit’ in algal ancestors, with several components predating the first land plants (Delaux *et al.*, 2013). Elements of this ‘toolkit’ may, therefore, first have facilitated the interactions between aquatic charophytes and diverse symbiotic microorganisms, later being recruited and further developed for AM evolution on land. A broader survey of the distribution and function of these genes within green algae is now desirable, and the investigation of living and fossil Charophyta–fungus interactions may offer further insights (Taylor *et al.*, 1992). Similarly, the strigolactones, another key component of the symbiotic plants–Glomeromycetes dialogue (Delaux *et al.*, 2012), might have been involved initially in non-symbiotic signalling pathways. Results are beginning to show how the origins of the finely interwoven relationship between Glomeromycetes and plants can be unpicked through a combination of palaeontological and molecular developmental approaches.

Recently, however, a new chapter in the story of land colonization through symbiosis was opened by two nearly concomitant discoveries: first, as Martin Bidartondo showed, extant basal land plants, such as liverworts, hornworts and lycophytes, associate with Mucoromycetes (Desirò *et al.*, 2013; Rimington *et al.*, 2015) in a symbiosis whose mutualistic nature is suspected in some cases at least (Field *et al.*, 2014); and second, Christine Strullu-Derrien showed a similar symbiosis in Devonian fossil land plants (Strullu-Derrien *et al.*, 2014). The reasons for such an ancient co-existence of two symbiotic lineages, the Glomeromycetes and the Mucoromycetes (two sister lineages; Tisserant *et al.*, 2012; Lin *et al.*, 2014), remain unclear: are their effects on the host plant redundant, which would make their co-existence more difficult to explain, or more likely, do they provide different benefits to the host? To answer these questions, more knowledge on extant Mucoromycetes associations would be desirable.

### From symbiosis to biogeochemical cycles

In addition to deriving mutual benefits through symbiosis, the rise of the cooperation between fungi and land plants is now thought to have had major impacts on biogeochemical cycles. Christopher Berry (University of Cardiff, UK) showed that complex plant communities with high biomass, such as forest-type ecosystems, arose as early as the Mid-Devonian (Stein *et al.*, 2012), probably in part due to efficient nutrient extraction by fungi supported by plant

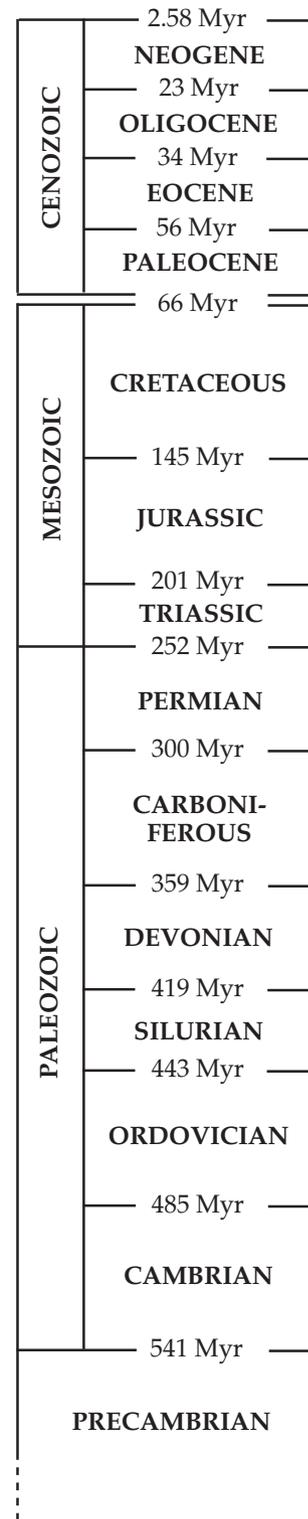


Fig. 1 A dated geological timeframe of the Phanerozoic, including the geological periods mentioned in the text (Cenozoic is not at same scale).

photosynthates. Two important consequences of the evolution of forests were increased weathering of calcium–magnesium silicates and the release of growth-limiting nutrients such as phosphorous from surface rocks, with diverse consequences that were emphasized by Timothy Lenton (University of Exeter, UK) and Jonathan

Leake (University of Sheffield, UK). First, the higher land-to-ocean calcium–magnesium flux increased ocean carbonate precipitation, drawing down atmospheric CO<sub>2</sub>. When incorporated into models of the geochemical carbon cycle, this effect equates to as much as an 80% drop in atmospheric CO<sub>2</sub> following the rise of land plants, contributing to a global cooling and possibly to the Late Ordovician glaciations (Bergman *et al.*, 2004; Lenton *et al.*, 2012). Second, Timothy Lenton stressed that biomass production, and the burial of a portion in sediments, caused a rise of atmospheric O<sub>2</sub>, with many biotic and abiotic consequences, such as the radiation of large predatory fish with high oxygen requirements (Dahl *et al.*, 2010) and the development of wildfire in terrestrial ecosystems, first seen in Late Silurian charcoals (Lenton, 2001; Scott *et al.*, 2014).

Following terrestrialization, changes in atmospheric CO<sub>2</sub> concentrations through the Phanerozoic are thought to have exerted critical controls on rates of plant-driven fungal weathering via photosynthate fluxes, regulating the land-to-ocean calcium, magnesium and phosphorous fluxes and stabilizing atmospheric chemistry. As noted by Jonathan Leake, the evolution of ectomycorrhizas (EM), where Ascomycetes or Basidiomycetes interact with vascular plants (gymnosperm and angiosperm tree taxa), appears to have selected for intensification of weathering, since EM display higher weathering abilities than AM roots (Quirk *et al.*, 2012, 2014; Thorley *et al.*, 2014). Direct fossil evidence of EM is sparse, with the oldest records dating to the Eocene (LePage *et al.*, 1997). However, fossils of EM hosting plant families appear in the fossil record or diversified much earlier during the Cretaceous (see Fig. 1 for geological time frame; Taylor *et al.*, 2011). Modelling approaches suggest that the rise of EM and the associated increase in weathering would have contributed to the CO<sub>2</sub> drawdown observed during the Cretaceous and over the past 120 Myr (Taylor *et al.*, 2011). This may be one of the causes for the lasting trend of reduction in atmospheric CO<sub>2</sub> and consequent climate cooling since the Paleocene–Eocene thermal maximum. In temperate soils, climatic conditions limit mineral weathering and microbial mineralization, so that EM plants, whose fungi have increased access to mineral resources as well as to organic nitrogen and phosphorus (see later), are particularly well adapted in these environments where they now dominate (Read, 1991; Selosse & Le Tacon, 1998). Understanding the relationships and feedbacks among palaeo-environmental conditions, biogeochemical cycles, and the evolution of the land flora is an exciting and developing area (Beerling & Berner, 2005). As Timothy Lenton pointed out, modelling is a powerful tool for testing how the successive stages in the evolution of plant–fungal interactions contributed quantitatively to changes in Earth climate and geochemistry (Bergman *et al.*, 2004; Taylor *et al.*, 2011).

### Fungi recycling plant remains

The evolution of land plants and their ancestors selected new enzymatic abilities in fungi feeding on plant tissues. For example, Mary Berbee (University of British Columbia, Vancouver, Canada) showed that pectinase genes are homologous in Ascomycetes,

Basidiomycetes, and early diverging fungi, including extant aquatic species living on algal remains: molecular clock dating indicates that 750 Myr, the estimated maximum age of origin of the pectin-containing ancestors of land plants, may represent the maximum age for the fungal ancestor that evolved such pectinases. Understanding this evolution again calls for more research on the interactions of extant aquatic fungi with algae closely related to land plants, and their use of algal pectin equivalents.

Later, land plants evolved new polymers such as lignin that in turn selected for new saprotrophic abilities in fungi. David Hibbett (Clark University, Worcester, MA, USA) reported that, based on comparative analyses of Agaricomycetes genomes (Basidiomycetes; Floudas *et al.*, 2012; Kolher *et al.*, 2015), peroxidases allowing lignin degradation by white-rot fungi might have originated during the Carboniferous period. The diversification of ligninolysis coincided with the decrease in the rate of organic carbon burial around the end of the Permian–Carboniferous, and the possibility of a causal role was much debated during the workshop. One caveat is our ignorance of when lignin degradation emerged in Ascomycetes, which can explain the report of white-rot as early as in the Upper Devonian (see Stubblefield *et al.*, 1985; although some doubt persists over the interpretation of the fossil fungi in this study). Moreover, the classical view of coal formation in wetlands under high rainfall and associated with tectonically induced subsidence (e.g. forearc basins or rift basins) holds for coals that accumulated later in geological history (e.g. Cretaceous coals; McCabe & Parrish, 1992). Even nowadays, ligninolysis requires high levels of oxygen and does not occur under the waterlogged conditions dominating the mire sediments where Carboniferous coals were formed. Thus, whereas the geological context of the formation of Euro-American Carboniferous coals remains unchallenged, the quality or the abundance of white-rot fungi could have placed further limits on organic matter recycling. Further research on fossil fungi in Late Palaeozoic ecosystems and on the evolution of white-rot in Ascomycetes will clarify the relative impacts of fungal evolution on carbon sequestration, especially during the Carboniferous.

### Recurrent evolutionary trends in interactions between fungi and plants

Not all fungi live on decaying land plants as saprotrophs: some evolved direct interactions with living tissues (biotrophy), and considerable genomics advances on biotrophic fungi were reported in London. Francis Martin (INRA, Nancy, France) explained how the evolution of EM, which occurred more than 80 times within Ascomycetes and Basidiomycetes (Tedersoo & Smith, 2013), entailed genome erosion with extensive loss of lignocellulose decay genes. Phylogenomic reconstructions suggest that extant EM clades derived with repeated gene loss from ancestral lineages of white-rot, brown-rot and litter decayers (Plett & Martin, 2011; Floudas *et al.*, 2012; van der Heijden *et al.*, 2015; Kohler *et al.*, 2015). This nicely explains why this transition occurred so frequently, whereas the reversion to saprotrophy, which would require the gain of many genes, is hitherto unknown. Nevertheless, some EM lineages have

retained some plant cell-wall degrading capabilities, which they do not utilize to assimilate carbon substrates but to access organic nitrogen and phosphorous (Rineau *et al.*, 2013). As Francis Martin pointed out, the ability to degrade plant cell wall materials found in some EM fungi means that they contribute to decomposition, but not that they are saprotrophs *sensu stricto*, since the mutualistic association remains their main or sole source of carbon. Polyphyletic evolution of the EM lifestyle is also marked by rapid genetic turnover in symbiosis-induced genes, some of which may reflect lineage-specific functional innovations, such as mycorrhiza-induced small secreted effector proteins (MiSSPs; Kohler *et al.*, 2015). Some of these effector proteins in EM fungi, such as MiSSP7, locally control plant immunity (Plett *et al.*, 2014); interestingly, this represents a convergence with effectors reported from Glomeromycetes, such as SP7 that has a role similar to MiSSP7 (Kloppholz *et al.*, 2011). Such effectors, in the similar context of a loss of the enzyme required for free life, are also abundantly found in the genomes of parasitic fungi (Schmidt & Panstruga, 2011), and represent a general adaptation to biotrophic life, as detailed in a recent Virtual Special Issue of *New Phytologist* (Kuhn & Panstruga, 2014).

Plant parasitism evolved independently in the oomycetes, a group of filamentous heterotrophic stramenopiles (Heterokonts) phylogenetically unrelated to Eumycota. Oomycetes, such as the Irish potato famine agent *Phytophthora infestans*, are common in modern ecosystems and often cause destructive epidemics in agriculture. The 10<sup>th</sup> New Phytologist Workshop highlighted their evolution to parasitism. Although distinctive features of oomycetes are somewhat difficult to detect in fossils, Christine Strullu-Derrien and Ben Slater (University of Birmingham, UK) reported recent discoveries of well-preserved materials that place the origin of oomycete–plant associations in the Devonian, if not earlier (Taylor *et al.*, 2006). Early plant-associated oomycetes colonized tissues of lycophytes, ferns, seed ferns and gymnosperms in Late-Palaeozoic–Early Mesozoic ecosystems and by that stage exhibited extensive diversification (Strullu-Derrien *et al.*, 2011; Slater *et al.*, 2013). The earliest evidence of parasitism dates back to the Carboniferous (*c.* 300 Myr; Strullu-Derrien *et al.*, 2011). However, how and when plant parasitism evolved in oomycetes remains unclear. On the one hand, it may have directly evolved from an ancestral algal parasitism, since many basal oomycete lineages are aquatic algal parasites (Beakes *et al.*, 2012). On the other hand, a secondary evolution from land saprotrophic oomycetes cannot be excluded, and would account for the absence of direct evidence for parasitism in the most ancient fossils. The evolution of plant parasitism in oomycetes may have been partly fuelled by gene transfer from pre-existing parasitic fungi (Richards *et al.*, 2011), and obligately parasitic oomycetes lost genes and pathways related to saprophytic life (Baxter *et al.*, 2010; Kemen *et al.*, 2011). Sophien Kamoun (Sainsbury Laboratory, Norwich, UK) reported that some species, such as *P. infestans*, evolved genomes with a distinctive ‘two-speed’ architecture, in which rapidly evolving repeat-rich genomic regions mediate adaptation and co-evolution with the host plants over time (Raffaele *et al.*, 2010; Raffaele & Kamoun, 2012). These regions are enriched in genes that are involved in host interactions and expressed *in planta*, such as effectors, resulting in dynamic co-

evolution with the host, specialization and occasionally host jumps to unrelated species (Raffaele & Kamoun, 2012; Dong *et al.*, 2014).

Interestingly, oomycetes reveal commonalities between pathogenesis and symbiosis. Sebastian Schornack (University of Cambridge, UK) reported that seven *Medicago truncatula* mutants deficient in AM colonization also display reduced root pathogenesis upon attack by the oomycete *Phytophthora palmivora* (Rey *et al.*, 2015), supporting the idea that pathogens have exploited the pathways by which plants accommodate mutualistic microbes. One of these mutants, RAM2, is impaired in the production of cutin monomers that promote colonization by both AM fungi and *P. palmivora* (Wang *et al.*, 2012). The current hypothesis is that cutin utilization has evolved to facilitate AM symbiosis, and was then secondarily co-opted by pathogenic oomycetes to penetrate host roots (Wang *et al.*, 2012). Thus, oomycetes have evolved in many respects to mimic fungi in their ability to interact with plants, especially given that plants have clearly evolved general mechanisms to accommodate microbes. In the future, further studies on parallel evolution between oomycetes and fungi will undoubtedly profit from both palaeontological and genomic investigations, but also from the use of common hosts as experimental systems for studying their biology (Rey *et al.*, 2015).

## Perspectives

The combination of palaeontological and genomic approaches in the workshop illustrated how the co-evolution of plants, fungi and oomycetes, over >400 Myr, has shaped their respective evolution and the geochemistry of earth, ocean and atmosphere. Several key areas would benefit from further cross-disciplinary developments. First, establishing the sequence in which events occurred, and their timing, is of crucial importance, hence the relevance of the fossil record for improved time-tree calibrations, in particular for oomycetes. Second, since all three groups have a marine ancestry, a better knowledge of their interactions in extant aquatic environments is crucial to understanding the origins of their terrestrial interactions – and phycologists should now be enrolled. Third, palaeobotanists and palaeomycologists are beginning to think in terms of cryptogam covers – including their fungal component – in early terrestrial ecosystems, yet the extent to which these resemble modern systems and the place of lichen-like associations remain open questions. Fourth, recognition of the importance of the rhizosphere to geochemical cycles through the Phanerozoic is growing, and we now need to develop further quantification of geochemical weathering under different vegetational and mycorrhizal regimes. Finally, we need a better understanding of the decomposition of lignocellulose during the mid- to late-Palaeozoic, which may have differed greatly to the modern carbon cycle. These areas are of key importance to improving current geochemical Earth System models. We hope that the emerging tools in palaeontology (such as X-ray synchrotron microtomography or confocal laser scanning microscopy) and the expansion of genomics (e.g. with the 1000 Fungal Genomes initiative; van der Heijden *et al.*, 2015) will enrich the cross-

disciplinary developments initiated in London, further enhancing and enlarging our view of the co-evolution between plants, fungi and oomycetes.

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## References

- Baxter L, Tripathy S, Ishaque N, Boot N, Cabral A, Kemen E, Thines M, Ah-Fong A, Anderson R, Badejoko W *et al.* 2010. Signatures of adaptation to obligate biotrophy in the *Hyaloperonospora arabidopsidis* genome. *Science* 330: 1549–1551.
- Beakes GW, Glockling SL, Sekimoto S. 2012. The evolutionary phylogeny of the oomycete "fungi". *Protoplasts* 249: 3–19.
- Beerling DJ, Berner RA. 2005. Feedbacks and the coevolution of plants and atmospheric CO<sub>2</sub>. *Proceedings of the National Academy of Sciences, USA* 102: 1302–1305.
- Bergman NM, Lenton TM, Watson AJ. 2004. COPSE: a new model of biogeochemical cycling over Phanerozoic time. *American Journal of Science* 304: 397–437.
- Bonfante P, Selosse M-A. 2010. A glimpse into the past of land plants and of their mycorrhizal affairs: from fossils to evo-devo. *New Phytologist* 186: 267–270.
- Dahl TW, Hammarlund EU, Anbar AD, Bond DPG, Gill BC, Gordon GW, Knoll AH, Nielsen AT, Schovsbo NJ, Canfield DE. 2010. A Devonian rise of atmospheric oxygen correlated to the radiations of terrestrial plants and predatory fish. *Proceedings of the National Academy of Sciences, USA* 107: 17911–17915.
- Delaux PM, Séjalon-Delmas N, Becard G, Ané JM. 2013. Evolution of the plant-microbe symbiotic 'toolkit'. *Trends in Plant Science* 18: 298–304.
- Delaux PM, Xie X, Timme RE, Puech-Pages V, Dunand C, Lecompte E, Delwiche CF, Yoneyama K, Bécard G, Séjalon-Delmas N. 2012. Origin of strigolactones in the green lineage. *New Phytologist* 195: 857–871.
- Desirò A, Duckett JG, Pressel S, Villarreal JC, Bidartondo MI. 2013. Fungal symbioses in hornworts: a chequered history. *Proceedings of the Royal Society B-Biological Sciences* 280: 1–8.
- Dong S, Stam R, Cano LM, Song J, Sklenar J, Yoshida K, Bozkurt TO, Oliva R, Liu Z, Tian M *et al.* 2014. Effector specialization in a lineage of the Irish Potato Famine pathogen. *Science* 343: 552–555.
- Edwards D, Axe L, Honegger R. 2013. Contributions to the diversity in cryptogamic covers in the mid-Palaeozoic: *Nematohallus* revisited. *Botanical Journal of the Linnean Society* 173: 505–534.
- Edwards D, Morris JL, Richardson JB, Kenrick P. 2014. Cryptospores and cryptophytes reveal hidden diversity in early land floras. *New Phytologist* 202: 50–78.
- Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Pressel S. 2014. First evidence of mutualism between ancient plant lineages (Haplomitriopsida liverworts) and Mucoromycotina fungi and its response to simulated Palaeozoic changes in atmospheric CO<sub>2</sub>. *New Phytologist* 205: 743–756.
- Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B, Martinez AT, Ollillar R, Spatafora JW, Yadav JS *et al.* 2012. The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* 336: 1715–1719.
- 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.
- Honegger R, Edwards D, Axe L. 2013. The earliest records of internally stratified cyanobacterial and algal lichens from the Lower Devonian of the Welsh Borderland. *New Phytologist* 197: 264–275.
- Kemen E, Gardiner A, Schultz-Larsen T, Kemen AC, Balmuth AL, Robert-Seilaniantz A, Bailey K, Holub E, Studholme DJ, Maclean D *et al.* 2011. Gene gain and loss during evolution of obligate parasitism in the white rust pathogen of *Arabidopsis thaliana*. *PLoS Biology* 9: e1001094.
- Kenrick P, Wellman CH, Schneider H, Edgecombe GD. 2012. A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 519–536.
- Kloppholz S, Kuhn H, Requena N. 2011. A secreted fungal effector of *Glomus intraradices* promotes symbiotic biotrophy. *Current Biology* 21: 1204–1209.
- 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*, in press. doi: 10.1038/ng.3223.
- Kuhn H, Panstruga R. 2014. Introduction to a *Virtual Special Issue* on phytopathogen effector proteins. *New Phytologist* 202: 727–730.
- Lenton TM. 2001. The role of land plants, phosphorus weathering and fire in the rise and regulation of atmospheric oxygen. *Global Change Biology* 7: 613–629.
- Lenton TM, Crouch M, Johnson M, Pires N, Dolan L. 2012. First plants cooled the Ordovician. *Nature Geoscience* 5: 86–89.
- LePage BA, Currah RS, Stockey RA, Rothwell GW. 1997. Fossil ectomycorrhizae from the Middle Eocene. *American Journal of Botany* 84: 410–412.
- Lin K, Limpens E, Zhang Z, Ivanov S, Saunders DGO, Mu D, Pang E, Cao H, Cha H, Lin T *et al.* 2014. Single nucleus genome sequencing reveals high similarity among nuclei of an endomycorrhizal fungus. *PLoS Genetics* 10: e1004078.
- McCabe PJ, Parrish JT. 1992. Tectonic and climatic controls on the distribution and quality of Cretaceous coals. *Geological Society of America Special Papers* 267: 1–16.
- Öpik M, Zobel M, Cantero JJ, Davison J, Facelli JM, Hiiesalu I, Jairus T, Kalwij JM, Koorem K, Leal ME *et al.* 2013. Global sampling of plant roots expands the described molecular diversity of arbuscular mycorrhizal fungi. *Mycorrhiza* 23: 411–430.
- Plett JM, Daguerre Y, Wittulsky S, Vayssières A, Deveau A, Melton SJ, Kohler A, Morrell-Falvey JL, Brun A, Veneault-Fourrey C *et al.* 2014. Effector MiSSP7 of the mutualistic fungus *Laccaria bicolor* stabilizes the *Populus* JAZ6 protein and represses jasmonic acid (JA) responsive genes. *Proceedings of the National Academy of Sciences, USA* 111: 8299–8830.
- Plett JM, Martin F. 2011. Blurred boundaries: lifestyle lessons from ectomycorrhizal fungal genomes. *Trends in Genetics* 27: 14–22.
- Quirk J, Andrews MY, Leake JR, Banwart SA, Beerling DK. 2014. Ectomycorrhizal fungi and past high CO<sub>2</sub> atmospheres enhance mineral weathering through increased below-ground carbon-energy fluxes. *Biological Letters* 10: 20140375.

- Quirk J, Beerling DJ, Banwart SA, Kakonyi G, Romero-Gonzalez ME, Leake JR. 2012. Evolution of trees and mycorrhizal fungi intensifies silicate mineral weathering. *Biological Letters* 8: 1006–1011.
- Raffaele S, Farrer RA, Cano LM, Studholme DJ, MacLean D, Thines M, Jiang RHY, Zody MC, Kunjeti SG, Donofrio MN *et al.* 2010. Genome evolution following host jumps in the Irish potato famine pathogen lineage. *Science* 330: 1540–1543.
- Raffaele S, Kamoun S. 2012. Genome evolution in filamentous plant pathogens: why bigger can be better. *Nature Reviews Microbiology* 10: 417–430.
- Read DJ. 1991. Mycorrhizas in ecosystems. *Experientia* 47: 376–391.
- Rey T, Chatterjee A, Buttay M, Toulotte J, Schornack S. 2015. *Medicago truncatula* symbiosis mutants affected in the interaction with a biotrophic root pathogen. *New Phytologist* 206: 497–500.
- Richards TA, Soanes DM, Jones MDM, Vasieva O, Leonard G, Paszkiewicz K, Foster PG, Hall N, Talbot NJ. 2011. Horizontal gene transfer facilitated the evolution of plant parasitic mechanisms in the oomycetes. *Proceedings of the National Academy of Sciences, USA* 108: 15258–15263.
- Rimington WR, Pressel S, Duckett JG, Bidartondo MI. 2015. Fungal symbioses of basal vascular plants: reopening a closed book. *New Phytologist* 205: 1394–1398.
- Rineau F, Shah F, Smits MM, Persson P, Johansson T, Carleer R, Troein C, Tunlid A. 2013. Carbon availability triggers the decomposition of plant litter and assimilation of nitrogen by an ectomycorrhizal fungus. *ISME Journal* 7: 2010–2022.
- Schmidt SM, Panstruga R. 2011. Pathogenomics of fungal plant parasites: what have we learnt about pathogenesis? *Current Opinion in Plant Biology* 14: 392–399.
- Scott AC, Bowman DMJS, Bond WJ, Pyne SJ, Alexander ME. 2014. *Fire on Earth: an introduction*. Chichester, UK: Wiley-Blackwell.
- Selosse M-A. 2002. Prototaxites: a 400 Myr old giant fossil, a saprophytic holobasidiomycete, or a lichen? *Mycological Research* 106: 642–644.
- Selosse M-A, Le Tacon F. 1998. The land flora: a phototroph–fungus partnership? *Trends in Ecology and Evolution* 13: 15–20.
- Selosse M-A, Strullu-Derrien C. 2015. Origins of the terrestrial flora: a symbiosis with fungi? In: Maurel M-C, Grandcolas P, eds. *Origins*. Les Ullis, France: EDP Sciences.
- Slater BJ, McLoughlin S, Hilton J. 2013. Peronosporomycetes (Oomycetes) from a Middle Permian permineralised peat within the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. *PLoS ONE* 8: e70707.
- Stein WE, Berry CM, VanAller Hernick L, Mannolini F. 2012. Surprisingly complex community discovered in the mid-Devonian fossil forest at Gilboa. *Nature* 483: 78–81.
- Strullu-Derrien C, Kenrick P, Pressel S, Duckett JG, Rioult J-P, Strullu D-G. 2014. Fungal associations in *Horneophyton ligneri* from the Rhynie Chert (c. 407 million year old) closely resemble those in extant lower land plants: novel insights into ancestral plant–fungus symbioses. *New Phytologist* 203: 964–979.
- Strullu-Derrien C, Kenrick P, Rioult JP, Strullu DG. 2011. Evidence of parasitic Oomycetes (Peronosporomycetes) infecting the stem cortex of the Carboniferous seed fern *Lyginopteris oldhamia*. *Proceedings of the Royal Society B: Biological Sciences* 278: 675–680.
- Stubblefield SP, Taylor TN, Beck CB. 1985. Studies of Paleozoic fungi V. Wood-decay in the Upper Devonian progymnosperm, *Callixylon newberryi*. *American Journal of Botany* 72: 1765–1773.
- Taylor L, Banwart S, Leake J, Beerling DJ. 2011. Modelling the evolutionary rise of the ectomycorrhiza on subsurface weathering environments and the geochemical carbon cycle. *American Journal of Science* 311: 369–403.
- Taylor TN, Hass H, Kerp H. 1997. A cyanolichen from the Lower Devonian Rhynie Chert. *American Journal of Botany* 84: 992–1004.
- Taylor TN, Krings M, Kerp H. 2006. *Hassiaella monospora* gen. et sp. nov., a microfungus from the 400 million year old Rhynie chert. *Mycological Research* 110: 628–632.
- Taylor TN, Krings M, Taylor EL. 2014. *Fossil fungi*. San Diego, CA, USA: Academic Press.
- Taylor TN, Remy W, Hass H. 1992. Devonian fungi: interactions with the green alga *Palaeonitella*. *Mycologia* 84: 901–910.
- Tedersoo L, Smith ME. 2013. Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. *Fungal Biology Reviews* 27: 83–99.
- Thorley RMS, Taylor LL, Banwart SA, Leake JR, Beerling DJ. 2014. The role of forest trees and their mycorrhizal fungi in carbonate rock weathering and its significance for global carbon cycling. *Plant, Cell & Environment*. doi: 10.1111/pce.12444.
- Tisserant E, Kohler A, Dozolme-Seddas P, Balestrini R, Benabdellah K, Colard A, Croll D, Da Silva C, Gomez SK, Koul R *et al.* 2012. The transcriptome of the arbuscular mycorrhizal fungus *Glomus intraradices* (DAOM 197198) reveals functional tradeoffs in an obligate symbiont. *New Phytologist* 193: 755–769.
- Wang B, Yeun LH, Xue J-Y, Liu Y, Ané J-M, Qiu Y-L. 2010. Presence of three mycorrhizal genes in the common ancestor of land plants suggests a key role of mycorrhizas in the colonization of land by plants. *New Phytologist* 186: 514–525.
- Wang E, Schornack S, Marsh J, Gobbato E, Schwessinger B, Eastmond P, Schultze M, Kamoun S, Oldroyd GED. 2012. A common signalling process that promotes mycorrhizal and oomycete colonisation of plants. *Current Biology* 22: 2242–2246.

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