When good relationships go bad

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Mycorrhizal associations of fungi and plants are usually viewed as mutually beneficial, but some non-photosynthetic plants cheat their fungal partners. Molecular tools can now be used to identify the fungi being exploited.

Mycorrhizae are ancient, widespread associations between fungi and the roots of many species of plants. In these symbioses, the plants supply carbohydrates (the products of photosynthesis) to their fungal partners, which reciprocate by facilitating the uptake of mineral nutrients from the soil. In a reversal of the usual relationship, some non-photosynthetic plants — termed epiparasites — obtain carbohydrates from mycorrhizal fungi that are also associated with photosynthetic plants in the immediate environment. In other words, epiparasites feed off green plants in their communities, and they do so via a fungal 'bridge'.

A barrier to understanding the ecology of mycorrhizal plants, including epiparasites, has been the difficulty of identifying the fungi with which they are associated. There are two main types of mycorrhizae, ectomycorrhizae (ECM) and arbuscular mycorrhizae (AM). The first type is produced by mushroom-forming fungi — including choice edibles such as truffles and chanterelles. The second is produced by soil fungi that belong to the taxonomic order Glomales. These fungi produce no above-ground structures in their life cycle, and reproduction is accomplished by large, multinucleate spores that are produced underground and on which the taxonomy of the group has traditionally been based (Fig. 1a).

Until now, all documented cases of epiparasitism have involved ECM fungi. This is surprising, because AM symbioses involve roughly 70% of all plant species — including many agricultural crops — and are ecologically much more widespread than ECM symbioses, which involve only about 30 plant families, mostly trees. On page 389 of this issue, Bidartondo *et al.*[1] provide the first molecular evidence that the fungal partners of two distantly related groups of epiparasites are AM fungi.

Bidartondo *et al.* used the polymerase chain reaction to amplify fungal ribosomal genes (rDNA) from the roots of epiparasites in the Corsiaceae (a group related to lilies) and the Gentianaceae (gentian family). Anatomical studies in these groups had suggested that AM fungi are present, but gave no clues to their precise identity. Bidartondo *et al.* generated sequences of the fungal rDNAs and compared them to a database of Glomales rDNA sequences. Evolutionary analyses of the rDNA sequences provided the necessary taxonomic resolution, and showed that both groups of epiparasites are highly specific for particular species of Glomales.

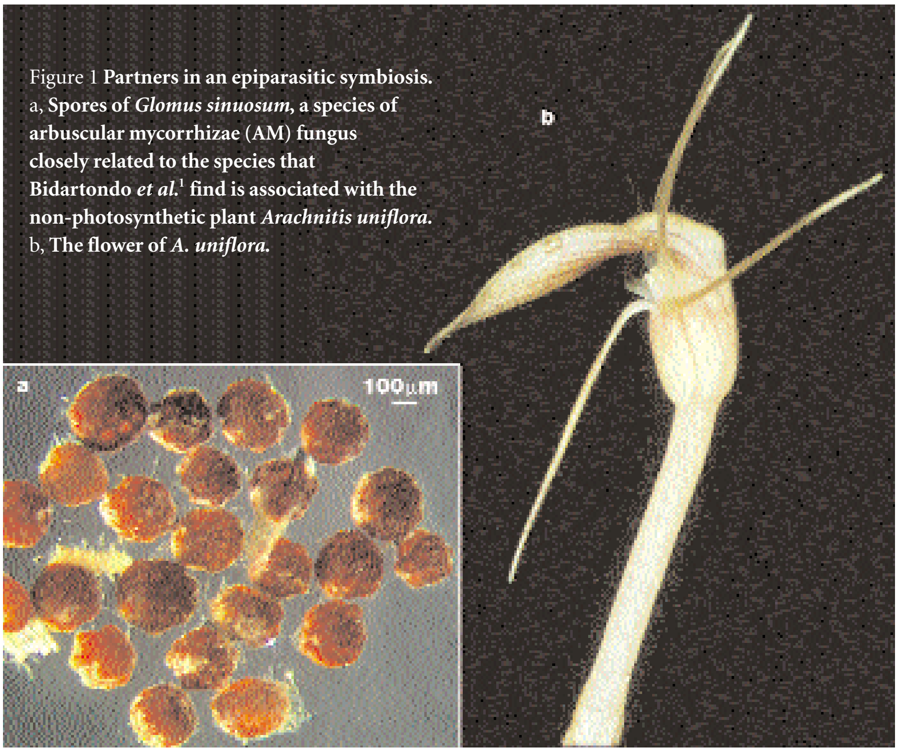

Figure 1 **Partners in an epiparasitic symbiosis. a, Spores of *Glomus sinuosum*, a species of arbuscular mycorrhizae (AM) fungus closely related to the species that Bidartondo *et al.*[1] find is associated with the non-photosynthetic plant *Arachnitis uniflora*. b, The flower of *A. uniflora*.**

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In the most intensively sampled species, *Arachnitis uniflora* (Corsiaceae; Fig. 1b), Bidartondo *et al.* found that eight plants in three populations were all associated with a single fungal species. Neighbouring green plants harboured the same fungus in their roots, suggesting that they could be the ultimate source of carbohydrates for *Arachnitis*, although they also contained other AM species not found in the roots of *Arachnitis*. These findings mirror those in ECM-associated epiparasites[2,3], which also have very narrow host ranges. The results are of interest to evolutionary biologists in general, because they support the view that host specialization is a common consequence of the evolution of parasitic lifestyles.

Species of Glomales have previously been regarded as ecologically equivalent: that is, they do not differ appreciably in the range of plant species with which they are linked[4]. One reason for this view is that although there are thought to be as many as 300,000 species of plants that form AM associations, there are only about 160 known species of Glomales. This is surely a gross underestimate of the actual diversity of Glomales, probably a consequence of their cryptic habit. Nevertheless, the striking disparity in apparent diversity of Glomales compared with that of AM-forming plants suggests that each species of Glomales must have many potential plant partners. The ecological-equivalence hypothesis is also supported by greenhouse studies involving pairings of individual species of fungi and plants, which have repeatedly shown that a single fungal species can form AM associations with many different plant species.

The results of Bidartondo *et al.* show that some kinds of AM associations are highly specific, and so contradict the idea that all species of Glomales are ecologically equivalent. The findings are less surprising in the context of studies indicating that, although species of Glomales are not absolutely host-specific, they exhibit ecological specialization under natural conditions. For example, the reproductive success of individual species of Glomales, measured in terms of spore production, varies according to the plant species with which they are associated[5,6]. Conversely, in greenhouse studies simulating natural plant communities, species of Glomales differ in their ability to promote growth of particular plant hosts[7]. The underlying mechanisms responsible for these differential growth effects are unknown. Bidartondo and colleagues' study[1] raises the tantalizing possibility that asymmetries in fungus-mediated transfer of carbohydrates between plants could be a factor.

The new work[1] is significant because it demonstrates that Glomales, which produce by far the most common form of mycorrhizae, can be drawn into epiparasitic associations. It also joins a growing body of research suggesting that mutualisms are not stable endpoints in evolution, but are inherently unstable and can be disrupted by conflicts of interest among the partners[8,9]. The breakdown of mutualisms can lead to parasitism[10] or even the complete dissolution of the symbiosis[11,12]. In the groups studied by Bidartondo *et al.*, the plants are parasitic on AM fungi and their associated green plants. At the other extreme, an AM fungal species, *Glomus macrocarpum*, has been implicated as the cause of stunt disease of tobacco plants[13].

Clearly, the characterization of AM symbioses as benign, stable associations does not reflect their dynamic nature. Functional and ecological studies are now needed to quantify the costs and benefits of mycorrhizal symbioses and to understand what causes them to shift along the continuum from mutualism to parasitism[14]. ■

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