From trophic cascade to mutualism: ecological genomics rectifies the concept of *Trichoderma* – plant interactions

Irina S. Druzhinina

Fungal Genomics laboratory (FungiG), the Key Laboratory of Plant Immunity, Nanjing Agricultural University, Nanjing, China
Fungal Diversity & Systematics, Department Accelerated Taxonomy, Royal Botanic Gardens Kew, Richmond, UK

ABSTRACT:
Ecophysiological profiling of *Trichoderma* (Hypocreales, Ascomycota) and the genus-wide metadata analysis documented the generally poor growth in soil, wood phytosaprotrophy, and multifaced direct interactions with taxonomically diverse fungi (*mycoparasitism, ammensalism,* and *competition*). *In vitro* studies of direct interactions with plants pointed to *commensalism* as *Trichoderma* frequently remains neutral. However, some *Trichoderma* species get isolated as facultative endophytes and thus form putative *mutualistic* interactions with plants. In line with this, the addition of *Trichoderma* inoculants (11 species) resulted in a significant increase of the *Solanum lycopersicum* (tomato) biomass and root growth. The evolutionary genomics study revealed that the origin of the genus coincided with the Cretaceous-Paleogene extinction event 66.5 MYA when it diverged from the ancestor shared *Hypomyces* and *Escovopsis* and showed that all these mycophagous genera were closely related to entomopathogenic Cordycipitaceae. Thus, this analysis explained mycoparasitism as the innate property of *Trichoderma*, while it did not uncover the nature of interactions with plants. The subsequent evolutionary analysis of plant cell wall degrading CAZymes (pcwdCAZymes) revealed that the formation of the genus was accompanied by the substantial enrichment of the initially limited pool of these enzymes through the massive lateral gene transfer from closely related Pezizomycotina fungi. However, numerous pcwdCAZymes families remained underrepresented in genomes making *Trichoderma per se* a still poor colonizer of plants but a phytosaprotroph. We then looked at the diversity of the effector-like proteins (cerato-platanins, hyphosphere proteins, and hydrophobins) that play a role in the plant pathogenicity of many fungi and found that despite some of them were slightly phytotoxic, their evolution in Hypocreales was explained by a function other than the interactions with plants.
Thus, being the top *mycoparasite* (~top predator) of mainly plant-pathogenic fungi, *Trichoderma* has a positive *indirect* impact on plants (*trophic cascade model*). These powerful indirect interactions occur when a predator (*Trichoderma*) limits the density of its prey (plant-pathogenic fungi) and thereby enhances the fitness of the next lower trophic level (plants). The results also suggest that the still rare *direct* interactions with plants can gain importance in the evolutionary future of some *Trichoderma* spp. However, whether they develop towards *mutualism* or *parasitism* is still challenging to predict.