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## **Cheating belowground interactions : diversity, ecology and distribution of mycoheterotrophy**

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## SUMMARY

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Mycoheterotrophy is a particular mode of life in which plants obtain carbohydrates from their associated fungal partners, instead of by using photosynthesis. It evolved multiple times independently within different land plant lineages, giving rise to over 500 species of achlorophyllous mycoheterotrophic plants. The majority of mycoheterotrophic plants exploit mycorrhizal fungi and thus, represent clear examples of cheating shifts from mutualistic interactions in the mycorrhizal symbiosis. Due to the complexity of mycorrhizal interactions and challenges in assessing the outcomes of this symbiosis – both for plants and fungi – mycorrhizal cheating has remained a poorly researched topic in plant ecology. This thesis aimed to shed light on the diversity, ecology and distribution of mycoheterotrophic interactions. In my approach, I considered that different drivers may be important at different scales and studied four levels of ecological complexity.

In chapter 2, the specificity of mycoheterotrophic interactions within the arbuscular mycorrhizal symbiosis was assessed at the organism level. Through the comparison of arbuscular mycorrhizal fungal communities of mycoheterotrophic *Thismia* species, surrounding plant species, and soil samples from different geographic locations, I was able to show that the mycoheterotrophic species consistently associate with a fungal community that is phylogenetically more restricted than autotrophic plants. These results support the view that mycoheterotrophic mycorrhizal interactions are highly specialized, and that this specificity is not caused by a limited local availability of arbuscular mycorrhizal fungi.

In chapter 3, biotic interactions between plants and fungi were studied in the framework of mycoheterotrophic plant coexistence scenarios at the population level. Since arbuscular mycorrhizal fungi are the main resources of tropical mycoheterotrophic plants, I tested the hypothesis that coexistence of arbuscular mycorrhizal mycoheterotrophic plants may be favored under symmetric patterns of fungal-host

overlap and diversity. Indeed, in communities of co-occurring mycoheterotrophic plant species in the field, and among the artificially-generated groups of mycoheterotrophic plants, we observe a trend towards increased phylogenetic diversity of fungal hosts among mycoheterotrophic plants with increasing overlap in their fungal hosts. These results indicate that fungus-mycoheterotrophic plant interactions can be better explained by understanding plant-plant interactions generated by sharing resources or fungal hosts.

In addition, edaphic abiotic factors potentially influencing the occurrence of mycoheterotrophic plants were assessed at the community level in chapter 4, through a comparison of soil chemistry and nutrients in plots where mycoheterotrophic plants were present with those lacking these plants. I found that soil pH, soil nitrate, and the interaction between soil potassium and nitrate concentrations were the best predictors for the occurrence of mycoheterotrophic plants in two lowland rainforests in South America. Mycoheterotrophic plant abundances decreased with an increase of nitrate, which suggests that these plants avoid high fertility patches. The trade balance model predicts that similar low-fertility conditions potentially favor a weak mutualism between plants and arbuscular mycorrhizal fungi. Therefore, I suggest that arbuscular mycorrhizal mycoheterotrophic plants potentially prefer conditions where local-scale mutualism is weak.

Finally, in chapter 5 I derived the global drivers for the distribution of mycoheterotrophy for both the arbuscular and the ectomycorrhizal symbiosis from species occurrence data of these plants. The results show that while mycoheterotrophy is globally distributed, mycoheterotrophic plants – regardless of their mycorrhizal status – avoid cold and highly seasonal climates, and show a strong preference for forests. However, arbuscular and ectomycorrhizal mycoheterotrophs show a strong global geographic segregation: arbuscular mycorrhizal mycoheterotrophs predominantly prefer broadleaved tropical evergreen forests, whereas ectomycorrhizal mycoheterotrophs are mainly found in broadleaved deciduous and evergreen needle-leaved forests in temperate regions. Temperature and precipitation variables – but not edaphic factors – are the best predictors explaining the distribution patterns of arbuscular and ectomycorrhizal mycoheterotrophs after accounting for the effects of forest type. Therefore I demonstrated that the global distribution of mycoheterotrophy is mainly determined by forest occurrence and type, while the occurrence of mycoheterotrophic plants is further limited by their evolutionary history and mycorrhizal type of their associations.

Together, the chapters of this thesis highlight the scale-dependent factors that explain the occurrence of mycoheterotrophy. Primarily, mycoheterotrophic plants require at least the presence of their associated fungal partners to persist, which should occur predominantly within humid forests. When these conditions are fulfilled, the balance between soil nutrients, instead of solely absolute concentrations of nutrients, influence the conditions that favour the occurrence of these plants, which also affects the stability of mycorrhizal networks. Lastly, resource competition may contribute to shape the specificity of fungal interactions of mycoheterotrophic plants, which can vary in degree of specialization respectively to each species. The broad approach taken in this thesis highlights many intriguing aspects about mycoheterotrophy that remain to be studied. Yet, it also shows how the study of mycoheterotrophy is important in the understanding of mycorrhizal symbiosis in general.