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Cheating belowground interactions : diversity, ecology and distribution of mycoheterotrophy

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CHAPTER 6

General discussion and synthesis

SOFIA I.F. GOMES

GENERAL DISCUSSION

Our knowledge on the mycorrhizal symbiosis has drastically increased in the past decades (van der Heijden *et al.* 2015). Yet, I believe that we are still only scratching the surface in discerning all the aspects of this intricate interaction. We struggle to disentangle a myriad of factors, biotic and abiotic, to broaden our understanding of the mycorrhizal symbiosis. In addition, there are still important technological challenges to overcome to allow us to grasp what is really going on at both sides of the interaction. Adding to this complexity is finding an objective evaluation of the outcomes of the interaction for each partner under several natural circumstances. However, despite these challenges, enormous progress has been made to comprehend the mechanisms underlying the dynamics of the mycorrhizal symbiosis, either using laboratory conditions (e.g. Bever *et al.* 2009; Kiers *et al.* 2011; Fellbaum *et al.* 2014), or under natural conditions (e.g. Simard *et al.* 1997).

The studies included in this thesis focused on field assessments of mycoheterotrophic plants. Because these plants are effectively cheating the mycorrhizal symbiosis, investigating the mechanisms that allow for this mode of life to exist and persist is particularly important for our understanding of the stability of this symbiosis. Mycoheterotrophy is locally rare, but has a worldwide distribution, and represents an extreme stage within the mutualism-parasitism continuum that spans mycorrhizal interactions (Bronstein 1994; Johnson *et al.* 1997; Egger & Hibbett 2004). Since mycoheterotrophic plants exploit mycorrhizal fungi, knowledge we derive from studying these plants, can be directly applicable to understand how the stability of the mutualistic interaction between plants and mycorrhizal fungi can be subverted.

My primary aim with this thesis was to expand our knowledge on the conditions under which mycoheterotrophy can occur (Figure 1). I investigated four aspects that proved promising to advance our comprehension on cheating within mycorrhizal interactions, specifically: fungal specificity, resource availability, local and global environmental drivers of mycoheterotrophy. To better understand this fascinating mode of life, I used the perspective of both the plant and fungal partners to investigate the biotic (chapters 2 and 3) and abiotic (chapters 4 and 5) factors that support mycoheterotrophy. In **chapter 2**, I showed that among five mycoheterotrophic *Thismia* species, and throughout their geographic range, the association with fungi is more specialized than those of their surrounding autotrophic plants. Also, my findings support the high fidelity towards fungal partners generally found in mycoheterotrophic plants, and highlight their ability

of partner choice by picking specific fungi from a broader pool of species. In **chapter 3**, I propose that species coexistence mechanisms among mycoheterotrophic plants can be explained in the light of the niche theory. By considering their fungal associates as resources, and based on the identity of co-occurring mycoheterotrophic species in communities in the field and simulated communities, I found that a possible strategy for mycoheterotrophic plants to maximize the chances of coexistence is the proportional increase of their fungal-host diversity with an increase in their fungal-host overlap. Because the occurrence of mycoheterotrophic plants is not restricted solely by their fungal-hosts, **chapter 4** investigates the importance of soil nutrient stoichiometry to the patchy occurrence of these plants. In that chapter, I found that the balance between nitrogen and potassium, and not phosphorus which is usually considered as the main driver of species diversity in tropical forests, plays an important role in understanding the local-scale conditions that allow the arbuscular mycorrhizal symbiosis to be cheated. These findings stress that the local stability of arbuscular mycorrhizal networks is probably influenced by the heterogeneity of soil characteristics at the local scale. Finally, in **chapter 5**, I investigated the global drivers for the occurrence of mycoheterotrophic plants. I found that these plants have a stronger preference to occur in forests than to follow the abundance of autotrophic plants associated with the same mycorrhizal type.

In the remainder of this final chapter, I will explore more widely the main findings of the previous chapters, considering their implications for the understanding of mycoheterotrophy, and more generally, of the mycorrhizal symbiosis, including the exploration of future steps to be taken towards a more complete view on this system.

Specificity of mycoheterotrophic interactions

As it is expected from a parasitic interaction, mycoheterotrophic plants show high specificity towards their fungal partners (but see exceptions in Hynson & Bruns, 2009; Roy *et al.* 2009). In **chapter 2**, I focused on the clade of *Thismia* species occurring in temperate climates to compare their fungal interactions with those of surrounding green plants, and the soil fungal pool, over their distribution range. This is the first study that evaluates mycorrhizal specificity of mycoheterotrophic plants considering ecological, evolutionary and geographic constraints. At least for this group of mycoheterotrophic species, their fungal interactions consistently presented a higher specificity level than the majority of the autotrophic plants in the surroundings, and both mycoheterotrophs and autotrophs associate with a subset of fungal partners from the larger available fungal

pool. However, availability of AM fungi targeted by these mycoheterotrophic plants alone were not sufficient to lead to occurrence of mycoheterotrophic plants (Merckx *et al.* 2017), suggesting that other unstudied ecological factors determine the limited occurrences of these specialized mycoheterotrophic plants, which was dealt with in more detail in **chapter 4**.

In **chapter 3**, the fungal diversity associated with mycoheterotrophic plants was also evaluated but spanning the sampling of plants to a wider taxonomical range, and targetting a different biome. As a general characteristic of the species included in

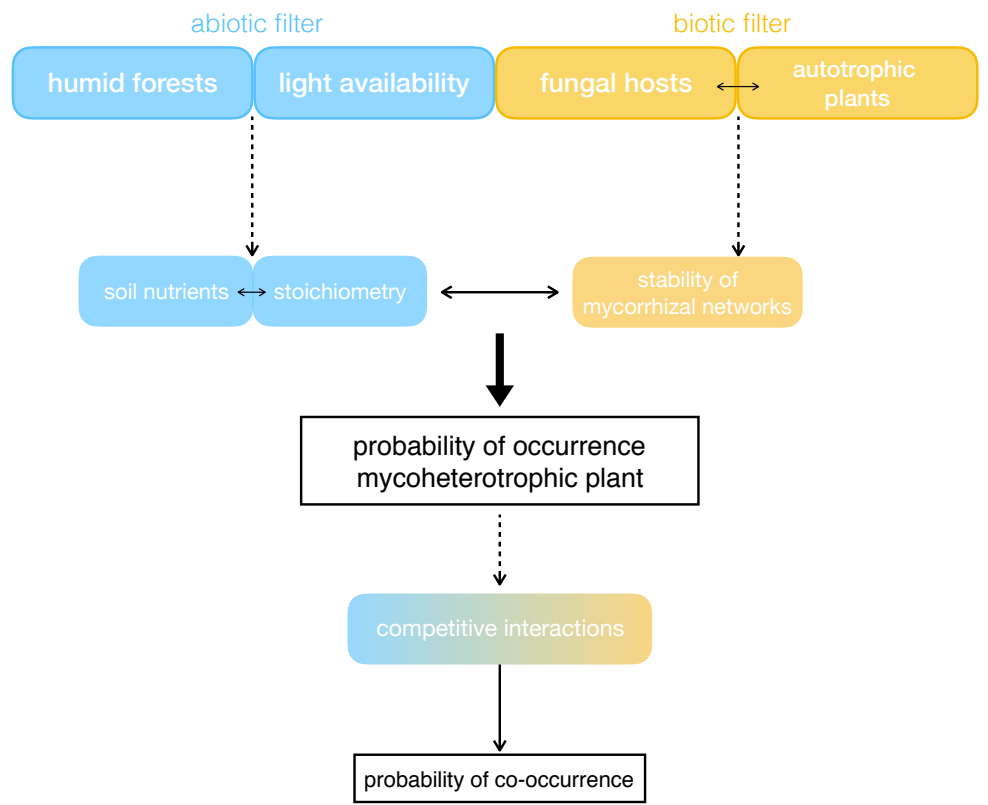


Figure 1 | Schematic representation of the factors that drive the occurrence of mycoheterotrophic plants (MH) as a summary of the chapters of this thesis. Mycoheterotrophic plants can be found inside forests (habitat; chapter 5), where their specific fungal partners are present (fungi; chapter 2) combined with edaphic factors favor conditions of weak mutualistic mycorrhizal symbiosis, at least in AM networks (edaphic factors; chapter 4), and which stable coexistence I determined by their competitive interactions (chapter 3).

that study, I showed that the 20 tropical mycoheterotrophic species collected tended to exploit more distantly related fungi than expected by chance. This finding may seem a priori contradictory with the high fungal specificity presented in **chapter 2**. However, from my point of view, this is a matter of the scale at which we look at these interactions, and the diversity of fungal pool considered in each chapter. A total of 60 individuals from five species were studied for **chapter 2**, while I used 140 individuals from 20 species for **chapter 3**. In addition, in **chapter 2** the fungal diversity of the mycoheterotrophic plants was compared in the context of total available local diversity, while in **chapter 3** the comparison was made among mycoheterotrophs, whose total diversity is more restricted. Thus, this means that among mycoheterotrophs, plants have the tendency to increase the diversity of their fungal interactions at the species level, but in comparison to the surrounding autotrophs and local fungal pool in the soil, these plants are more specialized. Furthermore, exclusively among mycoheterotrophic plants, there is a varying degree of specificity in their fungal interactions, as shown in **chapter 3**.

It is important to realize that the ITS2 region of arbuscular mycorrhizal fungi used in this study is hyper diverse, and the resolution for species delimitation is limited. This means that the high number of closely related sequences may reflect multiple genotypes within the same species or even different fungal individuals (Sanders *et al.* 1995). Thus, despite the general observation that most lineages of AM fungi can be part of a mycoheterotrophic interaction (Merckx *et al.* 2012), it may very well be that within the several distantly related lineages, only certain taxa, or genotypes within fungal species, are indeed being cheated. This remains to be confirmed.

Co-occurrence patterns of mycoheterotrophic plants

Since fully mycoheterotrophic plants entirely depend on their fungal partners for growth, these fungi are their primary nutritional resources. Therefore, the presence of specific fungal partners for a mycoheterotrophic plant is vital for its occurrence, and potentially mycoheterotrophic plants of different species may compete for the same fungal resources. According to the niche theory, species with high potential niche overlap are more prone to competitive exclusion (Macarthur & Levins 1967). Hence, even when conditions other than fungal availability are matched, competition with other mycoheterotrophs may limit the geographic expansion of certain species. In **chapter 3** I provided evidence that species co-occurrence of mycoheterotrophic plants can

contribute to shape the fungal diversity structure associated with each species, and can possibly act as drivers of the fungal community structure among mycoheterotrophs. Likewise, based on niche theory, it is possible that despite their restricted fungal associations, mycoheterotrophic plants benefit from associating with a higher diversity of fungal-hosts than expected by chance in order to increase their niche width, and therefore increase their chances to establish in new habitats. These results highlight the nutritional dependency of mycoheterotrophic plants on their fungal partners, and indicate that their mycorrhizal niche may be crucial for the understanding of their coexistence.

Ecological drivers of mycoheterotrophy

Even though the presence of specific fungal partners is essential for the occurrence of mycoheterotrophic plant species, the distribution of the host fungi alone is not likely to be sufficient to explain the occurrence of mycoheterotrophs (Yamato *et al.* 2016; Sheldrake *et al.* 2017; Merckx *et al.* 2017). Plants and fungi search for soil nutrients to satisfy their nutritional needs, thus edaphic factors can also contribute to the availability of the resources required determining specific niches to be occupied by mycoheterotrophic plants. In **chapter 4**, an interaction between potassium and nitrate availability, together with the effect of nitrate and pH were found to be the main drivers for the occurrence of mycoheterotrophy. This relationship between potassium and nitrate availability is well known to impact the effectiveness of the AM symbiosis (Ranade-Malvi, 2011). Furthermore, mycoheterotrophic plants avoided high fertility conditions, which coincide with a potential weak mutualistic mycorrhizal interaction, according to the trade balance model (Johnson 2010). Nonetheless, humidity is also an important predictor but not as much as soil nutrients. This suggests that the limiting factor for the occurrence of mycoheterotrophy is not their sensitivity to desiccation, as determined by water availability as extensively suggested (Maas *et al.* 1986; Leake 1994; Merckx 2013), but may be explained by soil nutrient stoichiometry and the stability of mycorrhizal networks. Mycoheterotrophs may indeed be sensitive to humidity levels, yet this can have a higher importance at a larger scale, since the forests where these plants have been collected are always characterized by high humidity levels (**chapter 5**). Moreover, the incidence of summers being drier than usual has been reported to reduce the reproduction levels of mycoheterotrophs (Leake 1994; Klooster & Culley 2009). This may indicate that the overall humidity conditions of certain forests, or even yearly drought events, already determine if any mycoheterotrophic plant can be found

in a certain forest. Then, for the patchy pattern at a fine scale, which is the main focus of this chapter, soil fertility plays a more crucial role, outweighing local differences in humidity.

I hypothesize that these edaphic factors do not solely represent preferences of the mycorrhizal fungi nor the mycoheterotrophic plants alone, but provide the necessary conditions under which cheating AM networks is possible. However, due to the intricate relationship between these plants and their fungi, it is hard to disentangle the abiotic factors that individually drive each partner within the interaction. Future studies should focus on measuring carbon and nutrient transfer between autotrophic plants and mycoheterotrophs, and compare the stability of the mycorrhizal networks considering the heterogeneity of soil properties. Furthermore, the edaphic drivers of EM mycoheterotrophic plants still remain to be studied, and are probably different from the ones described for the AM mycoheterotrophs, because they mostly occur in temperate forests (Phillips *et al.* 2013), which have different soil dynamics and nutrient economies compared to tropical forests (Vitousek & Sanford 1986).

Global preferences of mycoheterotrophic plants

Tailing the same rationale, mycoheterotrophic plants are expected to follow the distribution and / or abundance of autotrophic plants that associate with similar mycorrhizal types. Previous studies that found shared mycorrhizal fungi between mycoheterotrophs and surrounding autotrophs support such hypothesis (McKendrick *et al.* 2000; Waterman *et al.* 2013; **chapter 2**). However, other studies have shown that the distribution of species of *Thismia* (Merckx *et al.* 2017) and *Petrosavia* (Yamato *et al.* 2016) are limited by other factors than only the distribution or abundance of the associated AM fungi, since these fungi had more widespread distributions than the respective mycoheterotrophic plants. Considering the high specificity found in most of these plants, I hypothesized in **chapter 5** that the abundance of autotrophic plants associated with mycorrhizal fungi of the same type contributes to predict the distribution of mycoheterotrophic plants. I detected that it is definitely the case, yet it is not the main driving force at a global scale. Instead, the results showed that mycoheterotrophic plants preferably occur in forests worldwide, and in specific forests according to the mycorrhizal type they are associated with, suggesting that the environmental preferences of these plants are well represented in the abiotic conditions that characterize the respective forests. It is, thus, likely to find a considerable overlap in climatic conditions that drive the existence of

such forests, and the abundance of plants associated with each mycorrhizal type within these same forests. Nevertheless, these two mycorrhizal types are also abundant outside these forests. This may indicate why the distribution of mycoheterotrophic plants is better predicted by the occurrence of the specific forest type, and not necessarily by following the abundance patterns of the corresponding mycorrhizal types at a global scale. Furthermore, to a lesser extent, AM and EM mycoheterotrophs are also present in temperate and tropical regions, respectively, which do not follow the typical abundance of their mycorrhizal hosts. For both mycorrhizal types of mycoheterotrophic plants, hardly any other climatic or edaphic predictors were found to impact their distribution at a global scale, except the annual precipitation and the mean precipitation of the wettest month for the AM and EM mycoheterotrophs, respectively. This result further supports the explanation provided in **chapter 4** that different predictors may impact the occurrence of these plants at different scales. In this global scale analysis, the presence of certain types of forest was the main predictor, but climatic variables related to higher humidity levels were revealed to be also important for both mycorrhizal types, both in tropical and temperate regions (**chapter 5**). These achlorophyllous plants are well adapted to the low light conditions of forest floors, where they are able to avoid competition from autotrophic plants, which may also explain why they generally do not occur outside forests.

Implications

Understanding the mechanisms that underlie the maintenance of mutualistic interactions is still a major challenge for biologists. The mycorrhizal mutualism occurs in nearly all terrestrial ecosystems on Earth, and has been suggested to consist in an exchange of surplus resources (Brundrett 2002). Evolutionary theory considers mutualisms as reciprocal exploitations (Herre *et al.* 1999) in which each partner attempts to maximize the uptake of resources while minimizing their own costs, thus the mycorrhizal mutualism is expected to breakdown into cheating at the expense of cooperative partners (Kiers & Van Der Heijden 2006). Evaluating the symbiotic costs for the fungal partners is more difficult than for the plant hosts. Yet, mycoheterotrophic plants represent an ideal system to investigate the impacts of plants on their fungal partners, in which the fungal partners become the hosts for these cheater plants. It was not the goal of this thesis to measure such impacts of plants on their mycorrhizal partners, however. Instead I focused on what the interactions and the occurrence of mycoheterotrophic plants can teach us about the mycorrhizal symbiosis.

Based on the results presented in this thesis, I conclude that the occurrence of mycoheterotrophy, and thus cheating of the mycorrhizal mutualism, is influenced by an interplay of many factors, which have specific roles at different scales (Figure 1). Since mycoheterotrophic plants are completely dependent on particular fungal taxa, the presence of these fungi is the first and foremost limiting factor for their occurrence. These plants show generally high specificity towards their fungal interactions, and select their fungal partners from the local pool of taxa (**chapter 2**). Thus, either plants are highly picky and partner choice is key to determine the identity of their fungi, or ancestral lineages got stuck on specific fungi compatible with this mode of life, and fine-tuned their genetic machinery to exploit them, making host jumps a difficult step (Bidartondo & Bruns 2002).

Once mycoheterotrophic plants encounter the suitable environmental conditions, competitive interactions represent an important filter in determining their patterns of co-occurrence. The ability of mycoheterotrophic plants to associate with higher or lower diversity of AM fungi gives them different capabilities to compete with other mycoheterotrophic plants that rely on similar fungi. This differential ability provides the possibility to stably coexist and can be explained in light of the niche theory (**chapter 3**). This result also suggests that mycorrhizal fungi act as nutritional resources for mycoheterotrophic plants, which supports their status as exploitative cheaters, although direct physiological evidence is still lacking. Also, the general tendency, even if only at genotype level, to harbor a diverse fungal community in their roots, can lead to an increase in likelihood to find more efficient fungal partners to which, from the mycoheterotrophic plants point of view, they should remain engaged in a mycorrhizal association.

While the presence of their mycorrhizal partners acts as a primary biotic filter for the presence of mycoheterotrophic plants, ecological settings further narrow their occurrences. In **chapter 5**, I indicate that forests are the main habitats in which the subversion of the mycorrhizal mutualism is more likely to occur, but the reason for that preference still remains unknown. The photosynthetic capacity in forests increases with canopy height (Carswell *et al.* 2000), suggesting that forests may have large carbon availability enhancing mycorrhizal abundance (Treseder 2004), and potentially support larger fungal networks. Hence, forests represent habitats where there is a surplus of carbon supply, favoring a stable mutualistic interaction between plants and mycorrhizal fungi. Moreover, these achlorophyllous plants are well adapted to the very low light

conditions of forest floors, where they are able to avoid competition from autotrophic plants, which may also explain why they rarely occur outside forests (**chapter 5**). The assumption that mycoheterotrophy represents rare events within ecosystems should be treated with care, since I demonstrated that mycoheterotrophic plants have a worldwide distribution with clear preferences for particular forests according to their mycorrhizal type. This suggests that cheating mycorrhizal networks is a much more widespread phenomenon than previously thought (**chapter 5**). This phenomenon is

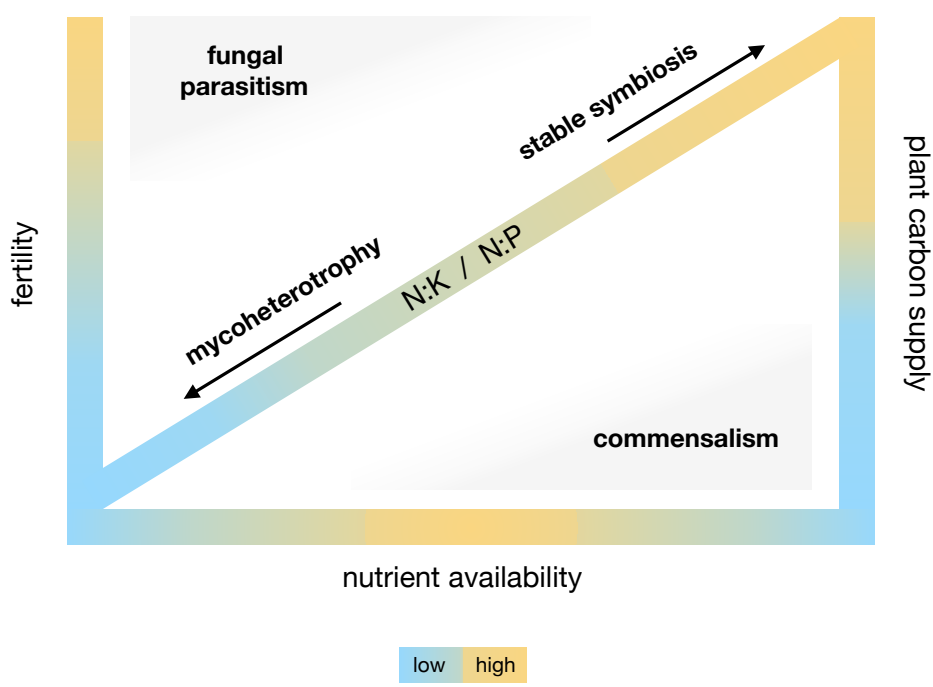


Figure 2 | Predicted outcome of mycorrhizal symbiosis according to soil fertility, nutrient availability, N:P and N:K ratios and, consequent, plant carbon supply to their arbuscular mycorrhizal partners. This model combines and updates previous predictions from Kiers & van der Heijden 2006 and Johnson 2010, based on the results obtained in chapter 4 of this thesis. At high N:P / N:K ratios and low nutrient availability, mycorrhizal symbiosis is expected to result in a strong mutualism with high C-for-P trade benefit. If nutrients become highly available, the C-for-P benefit decreases, and antagonistic fungal interactions are expected to occur. Plants are predicted to cheat the mycorrhizal symbiosis at lower N:P / N:K ratios and low fertility conditions. At low N:P / N:K ratios and low fertility, if N becomes limiting, C is the main limiting resource, favoring commensalistic interactions.

probably spread even wider, because this thesis did not include initial and partial states of mycoheterotrophy (Selosse *et al.* 2017).

Due to the soil nutrient heterogeneity, it seems that the performance of the mycorrhizal mutualism varies even at a local-scale, creating spatially constrained patches favorable for the occurrence of cheating, presenting the final filter. How mycoheterotrophic plants manage to either remain under the radar of the policy mechanisms that control cooperation in the mycorrhizal networks, or evolved ways to avoid the fungus to quit the exploitative interaction still remains to be comprehended. The stability of mycorrhizal networks is described to be influenced by resource availability of nutrients in the soil according to the trade balance model (Johnson 2010). My thesis highlights the importance of resource stoichiometry for the stability of these networks and places arbuscular mycorrhizal mycoheterotrophy in conditions of low nitrogen and potassium availability, which coincide with the predicted conditions for a weak mutualism between plants and mycorrhizal fungi (**chapter 4**). Based on this result, I propose a hypothetical model (Figure 2) where mycoheterotrophic plants could integrate the current models of mycorrhizal symbiosis outcome in the light of the plant assimilate availability as a function of nutrient availability (Kiers & van der Heijden 2006) and the trade balance model (Johnson 2010). This narrows down the hypothesis of whether mycoheterotrophic plants remain “unnoticed” or actively “trick” their mycorrhizal partners to remain engaged in this interaction to the latter. The former could suggest that mycoheterotrophic plants tap into mycorrhizal networks where there is a strong mutualistic interactions between partners, and therefore the exchange of carbon for nutrients at its maximum performance (Johnson 2010; Kiers & Van Der Heijden 2006), and they could be living on the carbon excess of these systems. The latter option suggests that mycoheterotrophic plants play an active role in keeping the mycorrhizal association, and future research should definitely address this topic further (see potential genetic mechanisms in Yuan *et al.* 2018). Understanding the circumstances under which mycoheterotrophic plants infiltrate mycorrhizal networks gives us valuable insights about the functioning of the mycorrhizal symbiosis. Despite representing an exception in respect to their relative abundance compared to autotrophic plants at the ecosystem level, mycoheterotrophic plants are prime examples of the most extreme outcome of mycorrhizal interactions within the mutualism-parasitism continuum (Bronstein 1994; Egger & Hibbett 2004), and their mere existence exposes the natural width of this symbiotic continuum. Because of the lack of a reciprocal rewarding

system, and their narrow diversity of associated fungal partners, mycoheterotrophic plants represent a system with decreased complexity compared to autotrophic plants ideal for the study of mycorrhizal symbiosis.

Taken together, the individual chapters of my thesis advance our understanding of why mycoheterotrophy does not occur in all forests worldwide, nor everywhere where the targeted fungal partners are available. At different scales, different drivers shape the probability of occurrence of mycoheterotrophic plants (Figure 1). A first filter that is imposed requires certain levels of humidity within forests to be able to harbor mycoheterotrophic plants, at the same time as their associated mycorrhizal partners are present within those forests. When this requirement is satisfied, conditions such as humidity levels or abundance of their mycorrhizal partners should not be a factor of importance. Instead, the patchy character of nutrient stoichiometry in the soil, which subsequently determines the performance of mycorrhizal networks at a local scale should determine the occurrence of mycoheterotrophic plants within the forests previously selected. This means that even if we find the local-scale conditions here described as suitable for the occurrence of mycoheterotrophic plants in any place in the world, it only makes sense to look for these plants if initially we selected forests that passed the first filter.

If we look inside particular forests where the specific fungal partners characteristic of the mycoheterotrophic plant species occur, we can potentially encounter a mycoheterotrophic plant in patches where soil conditions favor a weak AM mutualistic symbiosis. And on top of all these factors, and others that remain to be uncovered, we need to be in the right flowering season which varies among species and geography. So, finding a mycoheterotrophic plant is not about luck, but a complex interplay of biotic and abiotic factors.

Future perspectives

Mycoheterotrophic plants evolved from autotrophic mutualistic ancestors to exploit the same groups of mycorrhizal fungi that are mutualistic with green plants (Bidartondo *et al.* 2002). In this evolutionary journey, many phenotypic changes have culminated in the peculiar habits of these plants. Mycoheterotrophic plants are characterized by an obvious reduction of vegetative structures, absence of leaves and loss of photosynthesis, and of particular morphological features in the interface between plant and fungus in the roots (Imhof *et al.* 2013; Merckx 2013). Currently, considerable progress is being made

in uncovering the genetic background and consequences of the mycoheterotrophic mode of life. Sequencing full plastomes of several taxa have shown a considerable reduction of essential genes that participate in the photosynthetic apparatus, leading to the discovery of the smallest plastomes in land plants (Graham *et al.* 2017). Nonetheless, genome expansions have been also observed, suggesting a set of potential genes involved in sustaining this mode of life, and a recent study in a mycoheterotrophic orchid even revealed the largest mitochondrial genome within flowering plants (Yuan *et al.* 2018). Very soon whole genome assemblies of mycoheterotrophic plants will be available and further knowledge will be integrated at multiple levels to understand the evolution, persistence and functioning of mycoheterotrophy. A very hot topic in this area of research is to understand the dawn and persistence of cheating mycorrhizal interactions. Understanding cooperation within the mycorrhizal symbiosis is still quite challenging. Whole genome data will give important insights on the genetic machinery that was lost, gained, or modified, to allow for a cheating association with mycorrhizal fungi. These kind of studies will greatly contribute to explore the unique features that mycoheterotrophic plants display that distinguish them from autotrophic plants, in terms of how mycoheterotrophy impacts the relationship with their fungal partners, including exploring the genetic background responsible for the regulation of resource exchange. Also, knowing the genetic machinery that allows these plants to have a mycoheterotrophic nutrition will lead to more precise investigations on the actual extent of plant groups that can partially or fully rely on fungi for carbon supply, and maybe reveal that this phenomenon is taxonomically, and consequently geographically, more widespread than previously assumed.

Last, but not least, and perhaps even more defiant, is the perspective on mycoheterotrophy from the fungal point of view. The successful cultivation of these plants with their respective fungal partners, including the manipulation of environmental conditions, will be vital to understand the functionality of plants becoming mycoheterotrophic. Yet, it seems that the progress in this regard lacks behind in relation to our understanding of mycoheterotrophy from the plant's perspective. Due to the complexity of mycorrhizal networks in nature, mostly because of the intricate contribution of partners' identity and environmental conditions, it is necessary to disentangle the effect of the different players in the system. By comprehending when cheating is prone to occur, we will be able to grasp the constraints of at least one end of the mutualism-parasitism continuum that mycorrhizal symbiosis represents. This type of knowledge will greatly increase our understanding on the stability of one of the most

widespread mutualism on Earth. Besides, the occurrence of mycoheterotrophic plants at a global scale offers unique opportunities to have such perspective on mycorrhizal symbiosis in many different ecosystems, and involving an innumerable amount of plant and fungal species.

Hopefully, in the years to come, substantial progress will be made both in molecular methods and cultivation techniques, allowing to discover the secrets behind the mysterious relationship of plants cheating their mycorrhizal partners.

Final remarks

As with everything in life, every single-sided perspective will be incomplete. Times in science are gone that each discipline is restricted to specific subjects, disregarding the entirety of complex systems. To understand the nature of mycorrhizal symbiosis, or more specifically - as the aim of this thesis – of mycoheterotrophy, one needs to recognize the value of each of the individual parts and put the pieces together of the big puzzle that nature represents to mankind. Said so, there is not a single driver for the distribution of mycoheterotrophic plants. Besides, the combination of the drivers of each individual partner are not enough either to grasp the whole functioning of the system. In my opinion, to approach these kind of topics, besides from looking at its ecological and evolutionary aspects, one should consider as much as possible the interactions each organism entails in the complex web of life in space and in time.

THE EARTH HAS ITS MUSIC FOR THOSE WHO WILL LISTEN.

— George Santayana