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Global distribution patterns of mycoheterotrophy

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Abstract

Aim: Mycoheterotrophy is a mode of life where plants cheat the mycorrhizal symbiosis, receiving carbon via their fungal partners. Despite being widespread, mycoheterotrophic plants are locally rare, hampering the understanding of their global environmental drivers. Here, we explore global environmental preferences of mycoheterotrophy, and investigate environmental drivers of differential habitat preferences of mycoheterotrophic plants associated with arbuscular (AM) and ectomycorrhizal (EM) fungi.

Location: Global.

Time period: Current.

Major taxa studied: Mycoheterotrophic flowering plants.

Methods: We compiled the largest global dataset of epiparasitic mycoheterotrophic plant species occurrences and examined which environmental factors, including soil type, climate, vegetation type and distribution patterns of mycorrhizal autotrophic plants, relate to occurrence patterns of mycoheterotrophic plant species associated with AM and EM fungi.

Results: Mycoheterotrophic plant species avoid cold and highly seasonal climates and show a strong preference for forests. AM-associated mycoheterotrophs are predominantly found in broadleaved tropical evergreen forests whereas EM-associated mycoheterotrophs occur in temperate regions, mostly in broadleaved deciduous and evergreen needleleaved forests. The abundance of AM and EM autotrophic plants was a weaker predictor for mycoheterotrophs occurrences than forest type. Temperature and precipitation variables – but not edaphic factors – were the best predictors explaining the distribution patterns of mycoheterotrophs after accounting for the effects of forest type. For individual lineages, major differences in environmental preferences (often related to edaphic factors) occurred that were significantly associated with plant evolutionary relationships, indicating that these cheater plants have limited adaptive capabilities.

Main conclusions: The strong global geographical segregation of AM and EM mycoheterotrophs does not reflect the abundance of their potential autotrophic hosts, but seems to be driven by differential climate and habitat preferences. Our results highlight the non-trivial nature of mycorrhizal interactions, and indicate that identity of the partners is not enough to understand the underlying mechanisms promoting plant–fungal interactions in mycoheterotrophic plants.

KEYWORDS

arbuscular mycorrhiza, cheaters, ectomycorrhiza, forest type, global distribution, mycoheterotrophic plants

1 | INTRODUCTION

Mycoheterotrophy represents the breakdown of one of the most widespread and ecologically important mutualisms on Earth – the mycorrhizal symbiosis, where green plants exchange photosynthesized carbohydrates for mineral nutrients obtained by mycorrhizal fungi in the soil (Smith & Read, 2008). In this trophic strategy, cheater plants obtain carbon from their mycorrhizal partners. Mycoheterotrophic plants can use mycoheterotrophy in combination with autotrophy, or rely exclusively on their mycorrhizal fungi to obtain carbon, becoming fully mycoheterotrophic, and losing the ability to perform photosynthesis (Gebauer, Preiss, & Gebauer, 2016; Leake, 1994). Mycoheterotrophy has evolved multiple times independently in flowering plants (Merckx & Freudenstein, 2010), and occurs within the two most common mycorrhizal types: the arbuscular mycorrhizal (AM) and the ectomycorrhizal (EM) fungi (Leake, 1994; Smith & Read, 2008).

Fully mycoheterotrophic plants occur on every continent except Antarctica (Bidartondo & Bruns, 2002; Leake, 1994) and comprise around 500 species (Merckx, 2013). AM mycoheterotrophic plants occur mostly in tropical rain forests but occasionally grow in subtropical and even temperate regions, while EM mycoheterotrophs occur mostly in temperate zones but occasionally reach lower latitudes in mountain ranges (Merckx, 2013). Thus, this suggests a tropical versus temperate distribution of mycoheterotrophic plants according to their mycorrhizal type, which indicates that climate plays a major role in their distribution. Nonetheless, regardless of occurring in tropical or temperate areas, all mycoheterotrophic plants seem to share a preference for humid forests with dense overstorey in deep shade, with a thick layer of leaf litter on the forest floor where the occurrence of herbaceous plants is restricted (Cheek & Williams, 1999; Leake, 1994). Despite being widespread, mycoheterotrophic plants are often locally rare. However, when such a plant is found in the field, there is a high probability of finding other distantly related mycoheterotrophic species in the vicinity (Leake, 1994; Merckx, 2013). This suggests that mycoheterotrophic plants share environmental preferences both within and across tropical and temperate areas that still remain unexplored.

Because epiparasitic mycoheterotrophic plants obtain their carbon through a belowground fungal network, and ultimately from surrounding green plants (Bidartondo et al., 2002; Gomes, Aguirre-Gutiérrez, Bidartondo, & Merckx, 2017; Yamato, Takahashi, Shimono, Kusakabe, & Yukawa, 2016), the distribution of mycoheterotrophy might be limited by the abundance of the autotrophic potential host plants that act as a carbon source for their mycorrhizal fungi. Furthermore, besides the ecological drivers, the evolutionary history of mycoheterotrophic plants may also play an important role in their global distribution patterns as species tend to be restricted to biogeographical realms (Jonker, 1938).

Here, we explore global environmental preferences of mycoheterotrophy. Specifically, we test whether the differential distribution of mycoheterotrophic plants associated with AM and EM fungi can be better explained by soil and climate, by distinct types of vegetation, or by the distribution of autotrophic plants associated with the same mycorrhizal type, that is, AM versus EM dominant vegetation. Moreover, we explore potential drivers for the distribution of mycoheterotrophic plant lineages within each mycorrhizal type to investigate the habitat ranges that these lineages occupy. Understanding global preferences of full mycoheterotrophy will give us new insights into the environmental conditions where mycorrhizal cheating is likely to occur and therewith will enlarge our understanding of the ecology of mycorrhizas.

2 | METHODS

2.1 | Mycoheterotrophic plant species data

To study the global distribution of epiparasitic mycoheterotrophic plants, we compiled a dataset with world-wide observations of the large majority of fully mycoheterotrophic flowering plant species known to date (Merckx, 2013). We combined the records from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>) for the whole globe, the Botanical Information and Ecology Network (BIEN, <http://bien.nceas.ucsb.edu/bien/>) for America, the African Plant Database (<http://www.ville-ge.ch>) for Africa and personal datasets (Supporting Information Appendix S1). Our dataset included a total of 175 epiparasitic mycoheterotrophic plant species within 47 genera, with 21 species in Gentianaceae, 11 in Ericaceae, 5 in Polygalaceae, 15 in Liliales, 2 in Petrosaviaceae, 2 in Iridaceae, 79 in Dioscoreales and 40 in Orchidaceae. There are c. 500 known angiosperm mycoheterotrophs (Merckx, 2013). However, many tropical Orchidaceae mycoheterotrophs potentially associate with saprotrophic non-Rhizoctonia fungi (e.g., Lee, Yang, & Gebauer, 2015). Therefore, the number of angiosperm epiparasitic mycoheterotrophic species is likely to be considerably lower. Many species of mycoheterotrophic plants are rare and poorly represented in collections due to their inconspicuous habit and ephemeral appearance. Hence, despite the inevitable fragmentary nature of our database, our sampling covers all known mycoheterotrophic lineages and all regions where mycoheterotrophic plants are known to occur (Leake, 1994), except for India and Russia.

We assigned the mycorrhizal types AM or EM to the mycoheterotrophic plants in our dataset based on literature descriptions, and excluded those records of species associated with saprotrophic fungi or unverified mycorrhizal type (Supporting Information Appendix S1). A list of the data sources is found in the Appendix. Mycoheterotrophic plants associated with both

mycorrhizal types are not known. As mycorrhizal status is generally phylogenetically conserved (Feijen, Vos, Nuytinck, & Merckx, 2018), we extrapolated the mycorrhizal status to closely related species belonging to the same lineage (genus or family) for which reports are lacking. The mycorrhizal status of *Geosiris* remains to be studied, but we assigned this lineage to AM based on the AM status of other Iridaceae species (Wang & Qiu, 2006). Using these criteria, we extrapolated observed mycorrhizal status of 81 species to the total 175 species included in our dataset.

We created a 1-km² world-wide grid and recorded presences and absences of these plants in each grid cell considering their mycorrhizal types. To deal with different sampling efforts between grid cells, we did not consider abundance of plants and retained only presence/absence. In addition, to avoid including false absences in our analyses, we only considered grid cells where any mycoheterotrophic plant has been found. Thus, to understand the global drivers of a mycorrhizal type of mycoheterotrophs, we used those grid cells where mycoheterotrophic plants of that mycorrhizal type had been recorded as “present”, and the grid cells where mycoheterotrophs associated with the other mycorrhizal type had been recorded as “absent”.

After removing potentially incorrect occurrences, duplicate records and species records associated with the same mycorrhizal type in the same grid cell the compiled dataset contained 22,853 grid cells. In total, we considered 1,935 (8.5%) grid cells where individuals associated with AM fungi were present, and 20,918 (91.5%) grid cells where individuals associated with EM fungi were present. When AM and EM plants were both present in a single grid cell, which happened in 59 grid cells, they were assigned to both AM and EM individual datasets in the subsequent analyses.

2.2 | Global drivers of mycoheterotrophic plant distribution

We generated histograms of the distribution of mycoheterotrophic plants overlain with global patterns of climatic and edaphic conditions to highlight the environmental preferences of mycoheterotrophs (Supporting Information Figure S1). Mycoheterotrophic plants were shown to occur at a global scale with a clear dichotomy of tropics versus temperate regions in their distribution according to mycorrhizal type (see Results, Figure 1). Therefore, we focused our analysis on the drivers underpinning the differential distribution of AM- and EM-associated mycoheterotrophic plants. Given the obvious differences in temperature and precipitation regimes characteristic for tropics and temperate zones, we did not examine the global environmental drivers promoting the differential distribution of AM and EM mycoheterotrophs.

Instead, we examined if AM and EM mycoheterotrophs had distinct preferences for a specific type of vegetation. This would reflect the common description of mycoheterotrophic plants as understorey plants in closed canopy forests (Leake, 1994; Merckx, 2013). Alternatively, mycoheterotrophic occurrences may be associated with preference for habitats dominated by autotrophic plants of the same mycorrhizal type. This would reflect the reliance of these plants on the belowground mycorrhizal network for carbon uptake (Trudell, Rygielwicz, & Edmonds, 2003).

To investigate these alternative hypotheses, we considered the land-class categories from the Climate Change Initiative (CCI) Land Cover maps (ESA, 2015) to infer vegetation type. For the association with autotrophic plants featuring the same mycorrhizal type, we used the global maps of % biomass of autotrophic plants associated with

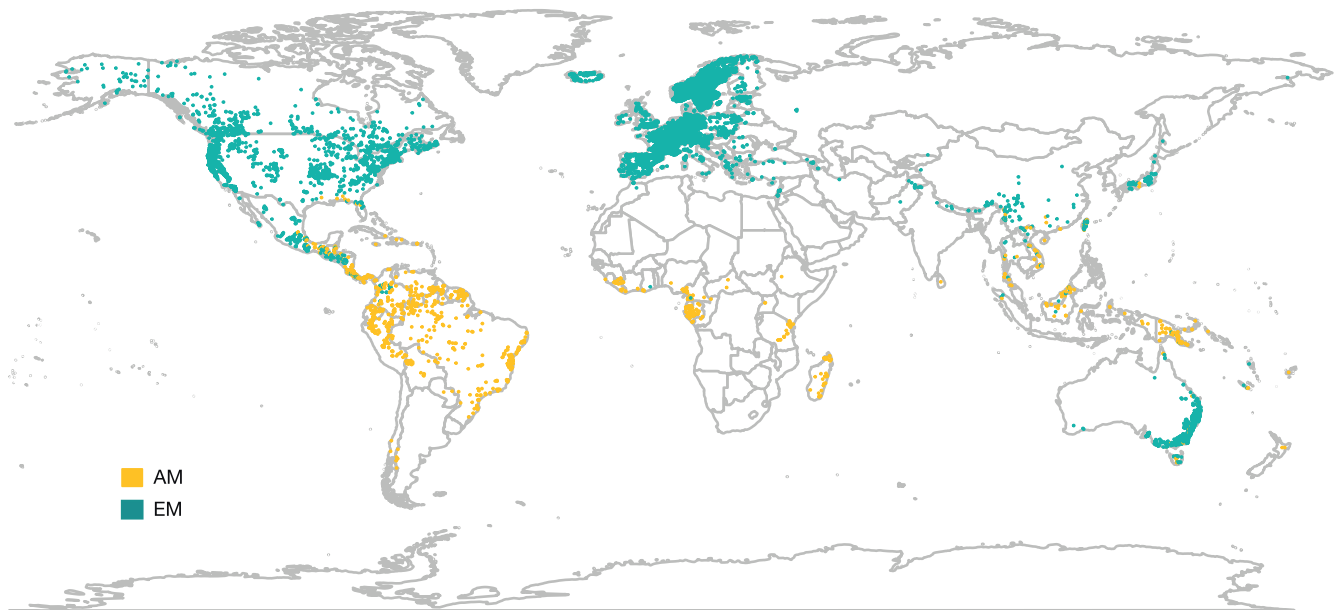


FIGURE 1 Global distribution of mycoheterotrophic plants associated with arbuscular (AM) and ectomycorrhizal (EM) fungi. Records were obtained from public databases (see Methods) [Colour figure can be viewed at wileyonlinelibrary.com]

AM and EM fungi (Soudzilovskaia et al., 2018), as proxy for the abundance of autotrophic plants. The Land Cover maps were obtained with a spatial resolution of 300 m, which we rescaled to the 1-km² grid used in this study. Maps on the abundance of plants associated with different mycorrhizal types were obtained at a resolution of 10 arc minutes, thus we obtained approximate estimates for autotrophic plants associated with each mycorrhizal per 1 km² grid. To reduce noise in our dataset caused by potential imprecision of coordinates, and by overlaying the vegetation and plant abundance maps, we excluded all records that were found in areas with no vegetation as epiparasitic mycoheterotrophs need to be associated with mycorrhizal fungi that are subsequently associated with surrounding green plants.

Climatic and edaphic factors are known to be important predictors of plant species and mycorrhizal fungi assemblages at large scales (Davison et al., 2015; Tedersoo et al., 2014). Hence, we tested the relative importance of these potential drivers for the distribution of mycoheterotrophic plants after accounting for the effects of vegetation type or abundance of their potential plant hosts. The climatic data, obtained from the WorldClim database at 1-km² resolution (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), describe temperature and precipitation annual trends, seasonality and extreme or limiting environmental factors world-wide. For the soil data, as these plants have generally shallow root systems (Leake, 1994; Merckx, 2013), we considered only edaphic variables in the top soil layer from the Harmonized World Soil Database (Batjes et al., 2009), which is a set of spatial databases of derived soil properties at a global scale. Furthermore, it is often assumed that these plants are sensitive to desiccation (Leake, 1994; Merckx, 2013), and therefore we also considered the actual evaporation, the evaporation stress factor, the root zone soil moisture and the surface soil moisture (Global Land Evaporation Amsterdam Model (GLEAM) maps; Martens et al., 2017) as potential drivers. To better understand the observed dichotomy in distribution of AM and EM mycoheterotrophic plant species, we explored environmental preferences separately for each mycorrhizal type.

2.3 | Environmental preferences of individual mycoheterotrophic lineages

Mycoheterotrophic plant species and genera are often restricted to particular biogeographical regions (Jonker, 1938; Mennes, Lam, et al., 2015; Merckx, 2013), suggesting that evolutionary relationships may shape the distribution patterns of these plants. Therefore, we tested whether the evolutionary history of mycoheterotrophic species limits their occurrence to particular ecozones. For this purpose, we considered the 15 independent shifts towards mycoheterotrophy represented by our data (Supporting Information Table S1). Based on recent phylogenetic insights, we considered four independent shifts in Gentianaceae represented by the genera *Voyria*, *Voyriella*, *Exacum* and *Exochaenium* (Merckx et al., 2013), two shifts in Ericaceae including *Monotropoideae* and *Pyrola* (Freudenstein, Broe, & Feldenkris, 2016), and a single shift in Polygalaceae: *Epirixanthes* (Mennes, Lam, et al., 2015), Liliales: Corsiaceae (Mennes, Moerland, Rath, Smets, & Merckx,

2015), Petrosaviaceae: *Petrosavia* (Cameron, Chase, & Rudall, 2003), Triuridaceae (Mennes, Smets, Moses, & Merckx, 2013) and Iridaceae: *Geosiris* (Goldblatt et al., 2008). In Dioscoreales, we recognized three shifts: *Afrothismia*, Thismiaceae s.s. and Burmanniaceae (Merckx et al., 2017). The latter group also contains chlorophyllous species, but recent evidence indicates that these are partially mycoheterotrophic (Bolin, Tennakoon, Majid, & Cameron, 2015), suggesting the presence of a strong predisposition for mycoheterotrophy in the most recent common ancestor of the family. Similarly, as all Orchidaceae are initially mycoheterotrophic and many are potentially partially mycoheterotrophic (Gebauer et al., 2016), we considered all species in this family to be part of a single lineage.

2.4 | Statistical analyses

To test whether mycoheterotrophic plants had a stronger preference for particular forest types or for co-occurring with autotrophic plants with the same mycorrhizal type, we examined four alternative binomial univariate generalized linear models testing the occurrence of AM and EM mycoheterotrophs separately versus (a) eight forest types, and (b) the abundance of autotrophic potential host plants. To build the univariate generalized linear models for the eight forest types for each mycorrhizal type, we attributed forest type to each record following the classification of the CCI Land Cover maps based on its coordinates. Then, we tested which forest type was better able to predict the presence/absence patterns of mycoheterotrophic plants. We selected the most parsimonious models based on the highest adjusted R^2 and the Bayesian information criterion (BIC) (Aho, Derryberry, & Peterson, 2014).

Once the variance explained by the selected predictor in the most parsimonious model was accounted for, we selected the residuals of this model. Through an ANOVA, we evaluated whether these residuals were related to environmental variables to understand if mycoheterotrophic plants had further preferences for particular environmental conditions. All predictors were standardized to avoid scaling variance issues due to different measurement scales. The selection of the predictors to be included in the models was performed in two steps. First, we excluded variables with $R^2 \leq .05$ in univariate linear regressions to avoid spurious correlations. Then, we assessed collinearity among variables by calculating the variance inflation factors (VIFs) in a stepwise manner, discarding the variable with the highest VIF at each step, until all the variables maintained in the final model had $VIF < 3$ (Zuur, Ieno, & Elphick, 2010) and Pearson correlation $< |.7|$ (Dormann et al., 2013). To evaluate the importance of each predictor, we calculated the omega squared (ω^2) as an unbiased effect size estimate on the amount of variance explained by each of the individual predictors in the linear models (Olejnik & Algina, 2000).

To investigate the biogeographical preferences of mycoheterotrophic plants regarding their evolutionary history, we ran a one-way permutational multivariate analysis of variance (perMANOVA with 99 permutations) for the AM and EM datasets separately.

We calculated a distance matrix based on the environmental variables as response variable, and we created a presence/absence matrix with the independent lineages as explanatory variable. Subsequently, multiple testing using BH corrections (Benjamini & Hochberg, 1995) suitable for large datasets was performed as a post hoc test. To visualize the environmental preferences of the mycoheterotrophic lineages, we applied principal component analysis (PCA) on the standardized environmental variables for each dataset separately. Moreover, we explored the environmental preferences of the various mycoheterotrophic lineages using a distance-based redundancy analysis (db-RDA), also separately for each dataset according to mycorrhizal type association. For the response variable, we created a presence/absence matrix of lineages with the total grid cells, and used all the environmental variables to build the best models, following the same procedures as described above. The significance of each variable in the final models was assessed using the function *permutest.cca*.

All analyses were carried out in R 3.4.1 (R Core Team, 2016) with the “vegan” (Oksanen et al., 2015) and “RVAideMemoire” (Maxime, 2017) packages.

3 | RESULTS

3.1 | Global distribution patterns of mycoheterotrophy

The global distribution of mycoheterotrophic plants showed a clear dichotomy with the AM plants occurring mainly in the tropics and EM plants in temperate areas (Figure 1). The Palaearctic is the most well-represented region in our study comprising 71.1% of the total number of records, followed by the Nearctic with 14.7%, Neotropics with 7.3%, Australasia with 4.3%, Afrotropics with 1.4% and finally Indomalaya with 1.2% of the total records.

When comparing the distribution of mycoheterotrophic plants with patterns in global climate and soil variables, we observed that

in general mycoheterotrophy has no strong preference for particular conditions except for occurring rarely in very cold and seasonal climates (Figure 2; see the other variables in Supporting Information Figure S1). The majority of mycoheterotrophs occurs in forests (Figure 3), with clear preferences for particular forest types: AM mycoheterotrophs occur mostly in broadleaved evergreen forest (Figure 4a), while EM mycoheterotrophs occur mostly in other forest types, preferring needleleaved evergreen forests, broadleaved deciduous forests, forests with mixed leaf habits and forests with shrub cover (Figure 4b). AM and EM mycoheterotrophic plants showed clear preferences for climatic conditions coinciding with their tropical and temperate distribution, respectively, but not for particular soil conditions (Supporting Information Figure S1). The selection of the most parsimonious models resulted in the evergreen forests (BIC: 6,936; Adj R^2 : .49 for AM; BIC: 6,784; Adj R^2 : .48 for EM) being the best predictor among all forest types (Supporting Information Table S2).

The global abundance of mycoheterotrophic plants seems to follow the global trend of AM autotrophic plant abundance (Figure 4c) better than that of the abundance of EM autotrophic plants (Figure 4d). However, models based on forest type were consistently significantly better than models including the autotrophic plants associated with AM type (BIC: 7,428.2; Adj R^2 : .45 for AM; BIC: 7,026.2; Adj R^2 : .46 for EM).

The analyses on the residuals of the best models – which had evergreen forest as the single predictor – showed that evergreen forests were the main predictors of the distribution of mycoheterotrophic plants, with climate and soil variables hardly showing any explanatory power, as only one climatic variable showed medium importance ($\omega^2 > .06$; Cohen, 1988) for either of the mycorrhizal types, namely annual precipitation (model coefficient: 0.12; $\omega^2 = .12$; Figure 5c) and the mean precipitation of the wettest month (model coefficient: -0.16 ; $\omega^2 = .11$; Figure 5d) for the AM and EM mycoheterotrophs, respectively. All the other predictors in the models had $\omega^2 < .06$ (Figure 5).

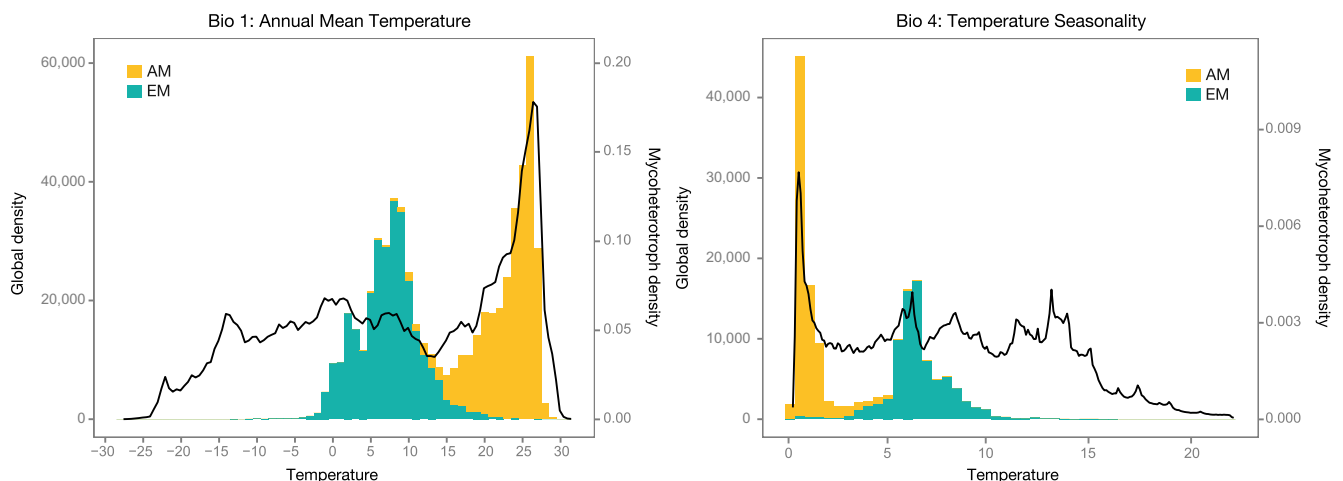


FIGURE 2 Climatic preferences of mycoheterotrophic plants (histograms) and global density of autotrophic plants (solid line) for the WorldClim dataset (Hijmans et al., 2005) variables of mean annual temperature (Bio 1) and temperature seasonality (Bio 4) [Colour figure can be viewed at wileyonlinelibrary.com]

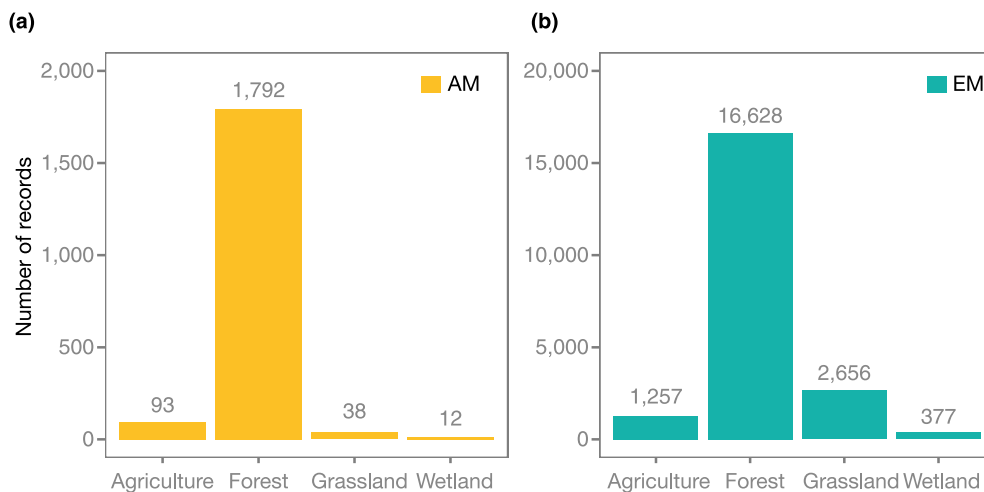


FIGURE 3 Land cover preference of mycoheterotrophic plants. The land cover categories were obtained using the Climate Change Initiative (CCI) Land Cover maps for arbuscular (AM; a) and ectomycorrhizal (EM; b) mycoheterotrophs. The numbers above the bars represent the number of records in each category [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Environmental preferences of lineages

The one-way perMANOVA indicated that mycoheterotrophic lineages showed preferences for specific biogeographical regions, both for AM ($df = 11$, Pseudo- $F = 9.0$, $R^2 = .05$, $p = .01$) and for EM fungi ($df = 2$, Pseudo- $F = 315.8$, $R^2 = .03$, $p = .01$), although explained variance by region was low. Pairwise permutation comparisons of lineage indicated differences between all AM lineages ($p = .013 - .044$), except for *Exochaenium* with *Afrothismia*, *Burmanniaceae*, *Exacum*, *Voyria*, *Voyriella* ($p = .054 - .760$), and *Petrosavia* with *Exacum* ($p = .213$). This exception may be an artefact due to the low number of records for *Exochaenium* in our dataset. For the EM dataset, pairwise permutation comparisons of lineage indicated significant differences among all the three EM lineages ($p = .010$).

The PCAs and the db-RDA indicated that mycoheterotrophic lineages associated with AM and EM fungi have different habitat preferences within tropical and temperate areas, respectively. For the AM mycoheterotrophs, we observed a significant clustering per lineage (see perMANOVA above), but this clustering did not lead to strong lineage separations (see Figure 6a) where the first two principal components explained 37.7% of the total variance. We found a weak correlation between the clustering of lineages with their climatic preferences in the db-RDA model ($df = 13$, Pseudo- $F = 10.67$, $p = .001$), where the first two constrained axes only explained 6% of the total variance (Figure 6c). For the EM mycoheterotrophs, we observed a significant clustering per lineage (see perMANOVA above), and stronger association per lineage within climate space than in the AM dataset (see the clearer clustering between lineages in the PCA, Figure 6b) where the first two principal components explained 33.8% of the total variance. The db-RDA model ($df = 15$, Pseudo- $F = 438.18$, $p < .001$) suggested that temperature variables, edaphic variables such as top soil clay, sodicity, gravel content, base saturation and the abundance of autotrophic plants associated with EM fungi together provide different habitats for the range of EM

mycoheterotrophic lineages analysed in this study (Figure 6d). The first two constrained axes explained 23% of the total variance.

4 | DISCUSSION

This is the first global study to assess the biogeography of mycoheterotrophs, taking into account both ecological and evolutionary aspects. According to our study, the trophic strategy of non-photosynthetic plants for obtaining carbon from mycorrhizal networks occurs in forests world-wide, following Leake's (1994) hypothesis, without specific environmental preferences except for avoiding very cold and seasonal climates. Apart from occurring often (AM mycoheterotrophs) or very rarely (EM mycoheterotrophs) in broadleaved evergreen forests, hardly any environmental predictor contributed to the segregated distribution of mycoheterotrophic plants according to their mycorrhizal type within tropical versus temperate forests. Climatic predictors such as mean annual precipitation and precipitation during the wettest month were the only variables that explained some variance in AM and EM mycoheterotrophic plant occurrence that had remained unexplained by forest type in the hierarchical models for AM- and EM-associated mycoheterotrophs, respectively. However, these variables had low explanatory power. Thus, humidity was revealed to be the only marginally important factor explaining the occurrence of mycoheterotrophy within evergreen (AM mycoheterotrophs) and other forests (EM mycoheterotrophs). The nearly exclusive occurrence in forests may be the result of a competitive advantage over other plants that grow in low-light conditions. Alternatively, forests in general may offer specific microhabitats, such as favourable humidity levels, supporting the patchy distribution of these plants (Leake, 1994), which are difficult to disentangle in a global-scale analysis. If indeed mycoheterotrophic plants are under the influence of specific microhabitats near the forest floor, this may explain why we found little evidence

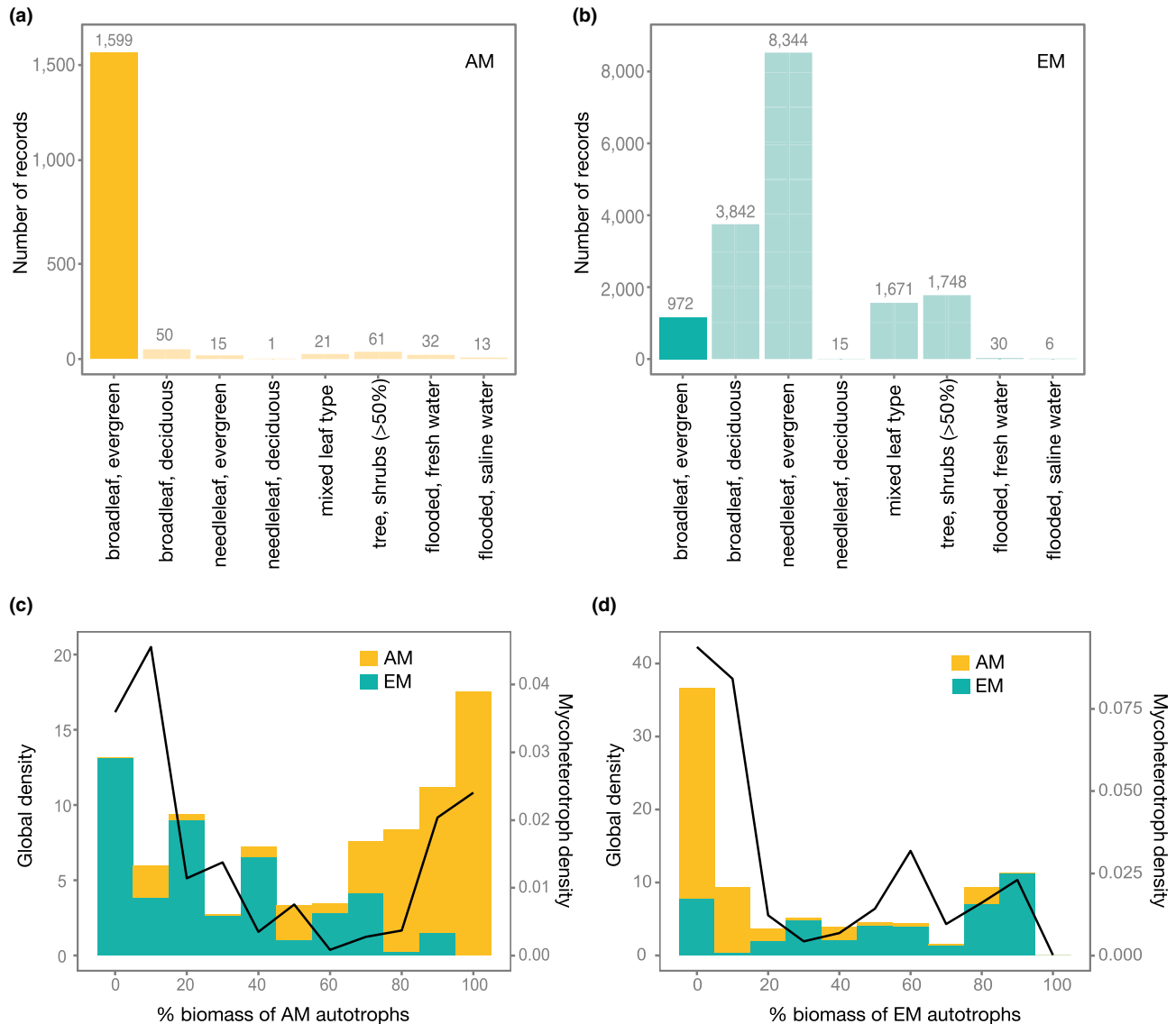


FIGURE 4 Mycoheterotrophic plant habitat preferences within forest types based on the categories of the Climate Change Initiative (CCI) Land Cover maps for arbuscular (AM; a) and ectomycorrhizal (EM; b) mycoheterotrophs. Filled bars highlight the forest type that best predicts the dichotomic distribution pattern among mycorrhizal types of these plants. The numbers above the bars represent the number of records in each category. Global density of autotrophic plants associated with AM (c) and EM fungi (d), and respective number of grid cells of mycoheterotrophic plant records per mycorrhizal type in our dataset (histograms). Solid lines represent the global trend followed by the autotrophic plants [Colour figure can be viewed at wileyonlinelibrary.com]

for the WorldClim climatic variables, as they represent atmospheric measurements which may not be representative of the microclimate in the understorey. This effect is potentially stronger in evergreen forests where canopies are more dense throughout the year, which can help understand why we found very little correlation between climatic variables measured above the canopy and the distribution of, particularly, the AM mycoheterotrophic lineages.

The evident dichotomic distribution of mycoheterotrophic plants according to mycorrhizal type between tropical and temperate forests (Figure 1) suggests a major importance of climate conditions in explaining this pattern, even though it coincides with a minimal importance of these same factors for explaining the distribution of AM and EM mycoheterotrophic plants within their

preferred forest types. Hence, climatic conditions do not restrict the wide range of niches that the mycoheterotrophic life strategy occupies. Also, these plants have been described to mainly occur in humus rich soils, which was not apparent from our analyses, perhaps due to the patchy character of soils at small scales that is not reflected in a global analysis.

The reliance of mycoheterotrophy on specific fungal partners for carbon uptake suggests that mycoheterotrophic plants could occur everywhere where the suitable fungal partner is present. AM fungi are abundant inside and outside the tropics and constitute important components of temperate forests (Phillips, Brzostek, & Midgley, 2013). At the same time, EM fungi are widespread in the tropics besides their predominant abundance in temperate areas

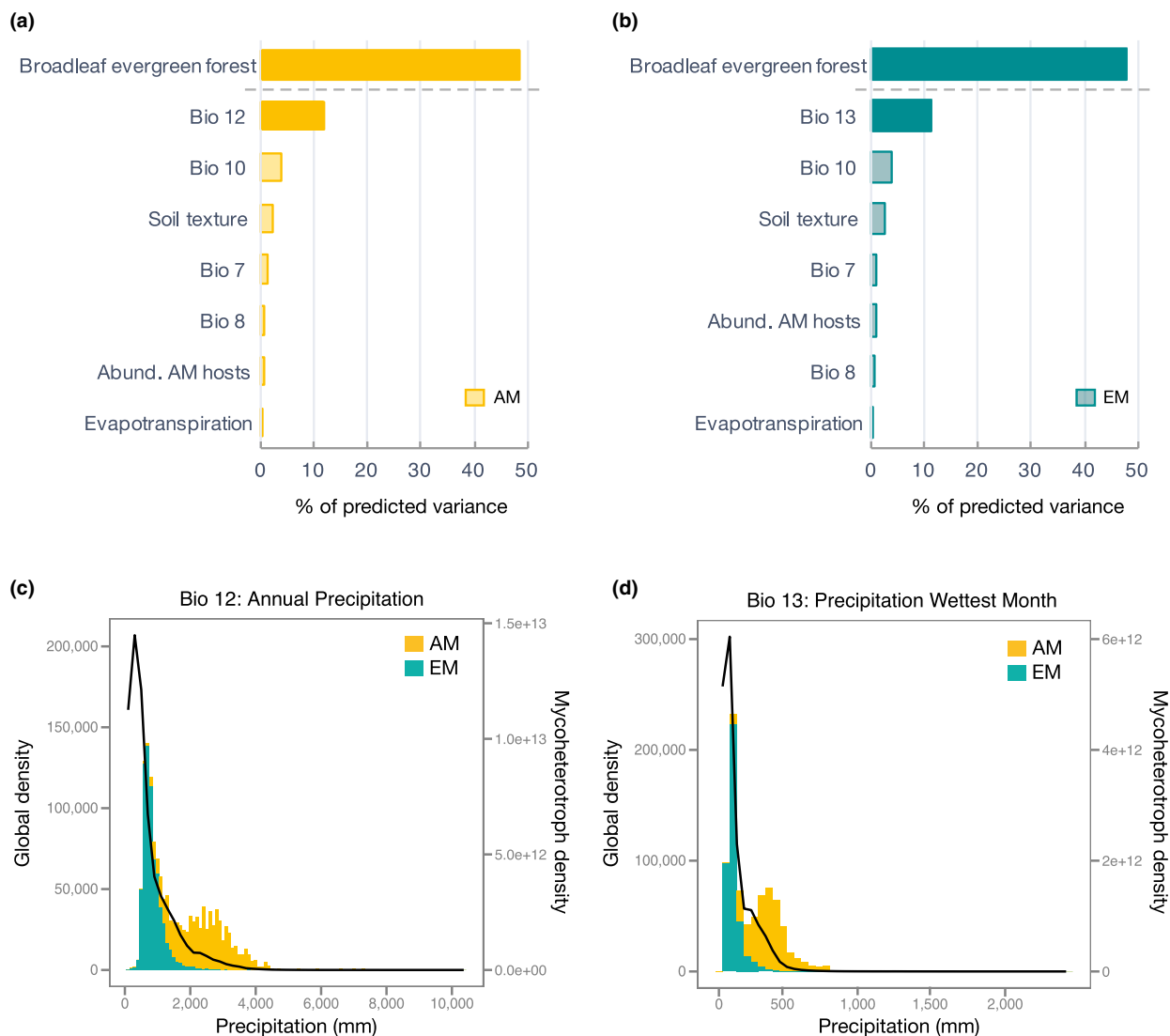


FIGURE 5 Ranking of selected predictors explaining the distribution of mycoheterotrophic plants associated with arbuscular (AM; a) and ectomycorrhizal (EM; b) fungi as a result of the generalized linear model (GLM; above dashed lines) and the ANOVA analyses on the residuals of the GLM (below dashed lines). Predictors are ranked according to the % of predicted variance reflecting their importance in the models. Important predictors are represented as filled bars. The climatic preferences of mycoheterotrophic plants (histograms) and global density of autotrophic plants (solid line) for predictors with medium importance, such as the annual precipitation (c) and the mean precipitation of the wettest month (d) are represented [Colour figure can be viewed at wileyonlinelibrary.com]

(Roy et al., 2016). However, in our study, AM mycoheterotrophs occur predominantly in AM-dominated forests in the tropics, while EM mycoheterotrophs avoid AM-dominated forests in temperate forests (see Figure 4). Therefore, the observed dichotomy in the distribution of AM and EM mycoheterotrophic plants does not reflect the global distribution pattern of AM and EM fungi, indicating that the distribution of particular mycorrhizal types does not constrain the global distribution of mycoheterotrophic plants. Evidently, our knowledge on the abundance of plants associated with each mycorrhizal type is limited, the only source available at the moment being the maps from Soudzilovskaia et al. (2018). These maps give a rough estimation of the abundance of plants associated with each mycorrhizal type and at a coarser resolution than our 1-km² grid cells with mycoheterotrophic plants records, highlighting the need

to develop more accurate proxies for mycorrhizal abundance at the global scale.

Previous studies, focusing on a finer taxonomic scale, suggested that the abundance of mycoheterotrophic plant species is related to the abundance of their specific fungal partners (Hazard, Lilleskov, & Horton, 2012; Yamato et al., 2016). This indicates that the mere presence of a suitable fungal partner is not sufficient to promote a mycoheterotrophic relationship of a plant with its mycorrhizal partners, even though the abundance of autotrophic plants supports the required mycorrhizal type. The habitat preferences associated with particular forest types likely restrict the distribution of mycoheterotrophic plants to a subset of environmental conditions of their fungal partners. Other factors that may constrain the occurrence of mycoheterotrophic plants is that they

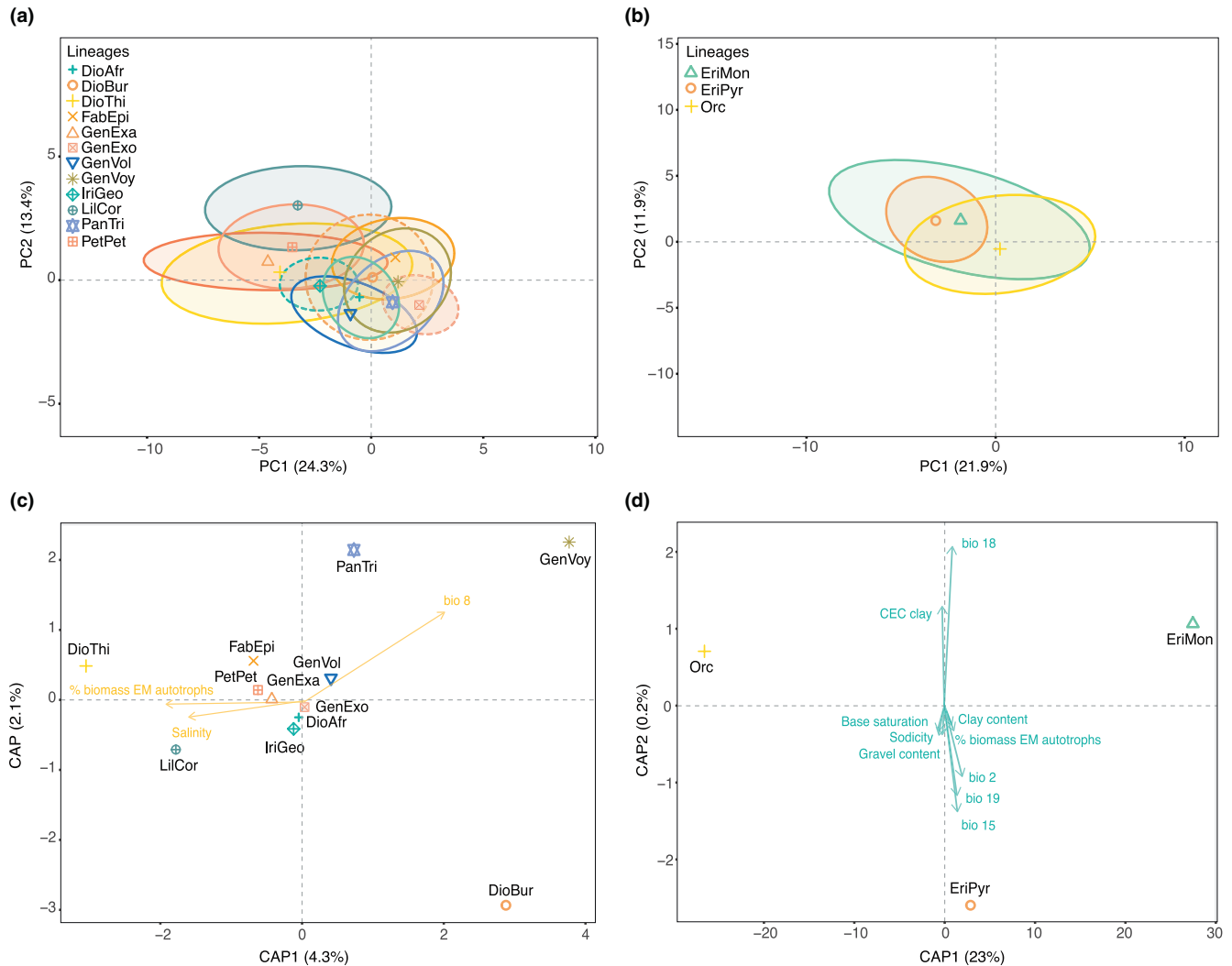


FIGURE 6 Principal components analysis of the environmental space occupied by mycoheterotrophic plants associated with arbuscular (AM; a) and ectomycorrhizal (EM; b) fungi. Due to the large amount of data points, the biplot was simplified by removing the clouds of points that represent the records in the dataset. Ellipses and respective centroids represent the environmental space occupied by each lineage. Variance explained by the first and second Principal Components (PC) is presented in between brackets. Distance-based redundancy analysis (db-RDA) model of the environmental preferences per lineage of mycoheterotrophic plants associated with AM (c) and EM (d) fungi. The arrows of the db-RDA represent the environmental variables that offer suitable habitat ranges for their occurrence. Variance explained by the first and second axis of Constrained Analysis of Principal Coordinates (CAP) is presented in between brackets. Bio 2 is the mean diurnal temperature range; bio 8 is the mean temperature of wettest quarter; bio 15 is the precipitation seasonality; bio 18 is the precipitation of warmest quarter; bio 19 is the precipitation of coldest quarter; CEC is cation exchange capacity. The lineages depicted in panels (a) and (c) correspond to *Afrothismia* (DioAfr), Burmanniaceae (DioBur), and Thismiaceae (DioThi) in Dioscoreales; *Epirixanthes* (FabEpi) in Polygalaceae; *Exacum* (GenExa), *Exochaenium* (GenExo), *Voyriella* (GenVol), and *Voyria* (GenVoy) in Gentianaceae; *Geosiris* (IriGeo) in Iridaceae; Corsiaceae (LilCor) in Liliales; Triuridaceae (PanTri) in Pandanales; and *Petrosavia* (PetPet) in Petrosaviaceae. The lineages in panels (b) and (d) are Monotropoideae (EriMon), *Pyrola* (EriPyr) in Ericaceae; and Orchidaceae (Orc) [Colour figure can be viewed at wileyonlinelibrary.com]

are likely to grow and reproduce only if their associated fungus is able to provide enough carbon from co-associated plants (Taylor & Bruns, 1997). This may be influenced by the dynamics within fungal networks, including their size, and the age, identity and fitness of their associated green plants (Fellbaum et al., 2014; Merckx, 2013). In addition, competition between fungal species may influence their ability to obtain photosynthesized carbohydrates as well (Bever, Richardson, Lawrence, Holmes, & Watson, 2009;

Kiers et al., 2011), and only permit the presence of cheaters under particular conditions.

Despite the ubiquitous occurrence of mycoheterotrophic plants in forests, individual lineages show clear preferences for particular environmental conditions, resulting in a significant clustering of mycoheterotrophic lineages in environmental space (see Figure 6). In the AM (arrows in Figure 6c) and EM lineages (Figure 6d), edaphic variables appear to create suitable habitat ranges for their distribution.

This suggests that edaphic factors are more relevant for the local distribution of individual mycoheterotrophic species than previously expected, and should be studied more in detail.

This clustering corresponds to a pattern of phylogenetic niche conservatism (Wiens et al., 2010), indicating spatial aggregation of related species. The strength of this spatial aggregation should depend on the dispersal ability of species (Cavender-Bares, Kozak, Fine, & Kembel, 2009), suggesting that mycoheterotrophic plants have limited dispersal capabilities. Despite their small seed size conferring a potential advantage promoting seed dispersal (Eriksson & Kainulainen, 2011), their habitat preference for dense close-canopy forests reduces their potential to disperse over large distances via wind (Wapstra, French, Davies, O'Reilly-Wapstra, & Peters, 2005). Many lineages, particularly those endemic to a single continent, are estimated to have evolved long after the breakup of Gondwana, further reducing their chances for effective intercontinental dispersal (Merckx, 2013). Thus, low dispersal capability together with the divergence history of these plants can be a viable explanation for the observed restricted distribution of certain clades to specific biogeographical regions (Jonker, 1938; Mennes, Lam, et al., 2015). This suggests an intricate connection between environmental factors and evolutionary history to explain the distribution patterns of mycoheterotrophic lineages.

The temperate versus tropical distribution pattern of AM and EM mycoheterotrophs also seems to have an evolutionary component. Interestingly, in the autotrophic common ancestor of the Monotropoideae and *Pyrola* lineages, there was a shift in mycorrhizal associations from AM fungi to ectomycorrhizas formed by Ascomycota and Basidiomycota, prior to the evolution of mycoheterotrophy. All other Ericaceae are derived from the same AM ancestry, which shifted to an interaction with ericoid mycorrhizal fungi (Lallemant et al., 2016). Within "core Ericaceae", mycoheterotrophy did not evolve. Similarly, for Orchidaceae, the specialized association with orchid mycorrhizal fungi involving members of Ascomycota and Basidiomycota was the result of a shift from the ancestral AM associations in the common ancestor of the family (Yukawa, Ogura-Tsujita, Shefferson, & Yokoyama, 2009). Moreover, the orchid's ability to recruit free-living saprotrophic fungi into novel mycorrhizae may also have led to niche expansions and radiations, including temperate habitats (Givnish et al., 2016). Yet remarkably, nearly all mycoheterotrophic lineages within Orchidaceae have shifted from orchid mycorrhiza towards an association with EM fungi, likely prior to the evolution of full mycoheterotrophy (Ogura-Tsujita, Yokoyama, Miyoshi, & Yukawa, 2012). The only exceptions are a few tropical fully mycoheterotrophic orchids in Southeast Asia (Waterman, Klooster, Hentrich, & Bidartondo, 2013), which grow on saprotrophic non-Rhizoctonia fungi. Thus, ericoid and the vast majority of orchid mycorrhizas (Rhizoctonia fungi) fail to support full mycoheterotrophy, despite their participation in partial mycoheterotrophic interactions (Gebauer et al., 2016). Furthermore, mycoheterotrophy in temperate regions evolved in lineages with pre-adaptations to form mycorrhizas with Ascomycota and Basidiomycota fungi, and nearly exclusively occurs through shifts towards EM fungi, but not

AM fungi. One explanation might be that because temperate forests are dominated by EM fungi, only these fungi are abundant enough to provide sufficient conditions of carbon availability to sustain mycoheterotrophic plants.

We may also use this evolutionary perspective to understand the wide distribution of mycoheterotrophy across many climatic zones as their association with EM fungi could have provided an advantage to plants to expand their niche from the tropics to colder and more seasonal areas (Wang, Tian, Xiang, & Liu, 2017). These colder and more seasonal climatic conditions are described to have been the main limitation for land plants to adapt and migrate out of the tropics during the Tertiary, potentially generating the latitudinal diversity gradient observed nowadays at a global scale (Wiens & Donoghue, 2004). This latitudinal diversity gradient also seems to be present for mycoheterotrophy. From the about 500 species described to date, most of the species occupy tropical areas (Merckx, 2013). This suggests that mycoheterotrophic plants may have been under similar climatic pressures as autotrophic plants in the colonization of temperate regions.

Yet, apart from their prevalence in the temperate Northern Hemisphere, mycoheterotrophic interactions through ectomycorrhizal fungi are present in tropical Asia, and tropical and temperate Australia, while they are absent on similar latitudes in Africa and South America. The pattern mostly reflects the distribution of ectomycorrhizal mycoheterotrophic Orchidaceae, and is likely to be caused by a combination of phylogenetic constraints of mycoheterotrophic plants themselves and historical biogeography of green ectomycorrhizal plants. Ectomycorrhizal trees are widely distributed across tropical Asia. This allows ectomycorrhizal mycoheterotrophic Orchidaceae to occur there (Roy et al., 2009), and diversify into temperate regions in Australia. In contrast, ectomycorrhizal trees are relatively rare in tropical Africa (Bâ, Duponnois, Moyersoen, & Diédhiou, 2012) and ectomycorrhizal mycoheterotrophic Orchidaceae are not known to occur there. Ectomycorrhizal trees are even rarer in tropical South America (Roy et al., 2017). Accordingly, ectomycorrhizal mycoheterotrophic Orchidaceae are also absent from the region. Interestingly, ectomycorrhizal mycoheterotrophs are also absent in the temperate South American forests found at high latitudes across the continent, where ectomycorrhizal trees are abundant (Fernández, Marchelli, & Fontenla, 2013). This could be explained by the absence of a link to other mycoheterotrophic ectomycorrhizal habitats in this region.

In conclusion, our study demonstrates that the global distribution of full 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. Thus, cheating belowground interaction networks is only possible under particular conditions, and the vulnerability of the mycorrhizal symbiosis to being cheated by plants differs among climatic regimes in the globe. AM interaction networks are more prone to be cheated in the tropics, while EM interaction networks are in temperate areas, despite the distribution of both mycorrhizal types across these regions. This suggests that the mutualistic

stability of mycorrhizal networks is context-dependent, and thus we should not expect to find a single underlying mechanism to understand the dynamics of plant-mycorrhizal interactions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ACCESSIBILITY

The data are available as Supporting Information.

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BIOSKETCH

Sofia Gomes is interested in the ecological and evolutionary aspects of the association between plants and mycorrhizal fungi, particularly in conditions that promote plants to cheat the arbuscular mycorrhizal mutualism.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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