3 Biogeography and Conservation

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3.1 Introduction

There is hardly a region in the world where mycoheterotrophy does not occur. As far as we know, all orchid species are dependent on fungi during germination and early development and are therefore classified as initial mycoheterotrophs (Chap. 1). Orchidaceae have a worldwide distribution and occur in almost every terrestrial ecosystem apart from deserts and permafrosts. The distribution of fully mycoheterotrophic species, however, is much more restricted and often shows intriguing patterns. Fully mycoheterotrophic flowering plants almost exclusively inhabit closed-canopy forests, and the majority of species occur in the tropical regions of the world. Many families and genera of mycoheterotrophic plants have remarkably widespread distributions that cross major dispersal barriers, and several botanists have suggested that these widespread lineages must be ancient (Engler 1888; Malme 1896; Jonker 1938; Rübsamen 1986; Leake 1994). In addition, the distribution ranges of mycoheterotrophic plants often show wide gaps ("disjunctions"). The mycoheterotrophic genus *Thismia* (Thismiaceae) even holds the status of what Robert Thorne considered one of the strangest distribution patterns in flowering plants (Thorne 1972), with two allegedly related species: one in northern USA and the sister species in Australia and New Zealand.

At local scale, the distribution of mycoheterotrophs is often highly patterned. Mycoheterotrophs can be extremely scarce, and some genera and species are known from only a few localities. It is not always clear whether this reflects true rarity or the plant's ability to remain unnoticed by collectors. Even in well-collected areas, the ephemeral nature of mycoheterotrophs makes their discovery challenging. In addition, some tropical species seem to have intriguingly fragmented distribution ranges, which, in some cases, appears to be linked with postulated glacial rainforest refugia (Cheek and Williams 1999; Franke 2004). Despite this rarity, certain localities and habitats seem to be more suited for mycoheterotroph survival: both in tropical and temperate zones, there is a tendency of unrelated species to grow together (e.g., Wallace 1975; Maas and Rübsamen 1986).

In general terms, the study of biogeography includes two distinct components. First, the distribution of species is determined by historical

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factors. Historical biogeography attempts to infer how evolutionary, geological, and climatic events have shaped the distribution of a particular lineage. Molecular phylogenetic hypotheses and divergence time estimates are particularly useful to test hypotheses in this context (de Queiroz 2005; Renner 2005). Unfortunately, the lack of a rigid phylogenetic framework still prevents inference of the historical biogeography of many mycoheterotrophic lineages. Nevertheless, the limited data that is available now allows us to evaluate the origin of the distribution patterns or disjunctions at least for a few mycoheterotrophic clades. In addition to historical events, the distribution of a species is also determined by ecological aspects. Mycoheterotrophic species seem to show very specific preferences toward certain (micro)habitats, a matter we discuss in detail below. In this context, the use of molecular techniques for the identification of root-inhabiting fungi has brought a new and interesting ecological association to the forefront of mycoheterotrophic biogeography. As many mycoheterotrophs show specialization toward narrow clades of fungi, it is often hypothesized that the distribution of their host fungi is a major determinant for the distribution of the plants. The study of the biogeography of fungi is still in its infancy, and to date, only a few studies have tested this hypothesis in detail. However, the development of next-generation sequencing techniques provides promising prospects to resolve such questions in the upcoming years.

Understanding distribution patterns is also essential for effective species conservation (Whittaker et al. 2005). The rapid and extensive destruction of habitats, particularly in the tropics, has become a serious threat to native biotas. Mycoheterotrophic plants are often restricted to areas that experience exceptional loss of habitat, and due to their localized distributions, many species are extremely vulnerable to extinction. Some species may already be on the brink of extinction, and only drastic conservation efforts can prevent their disappearance.

Here we provide a detailed overview of the global distribution of mycoheterotrophic plants. This overview is considerably biased toward angiosperm mycoheterotrophs, although we also discuss in short the distribution patterns observed in nonangiosperm lineages where mycoheterotrophy is mostly restricted to the gametophytes of lycophytes, ferns, and gymnosperms. The occurrence of mycoheterotrophy in nonangiosperm gametophytes remains poorly studied, thus preventing an in-depth discussion of their distribution and habitat preferences. The taxonomy and species numbers of the lineages discussed here are based on the information provided in Chap. 2. It is important to note that the majority of the species discussed here are only *putative* full mycoheterotrophs. The assumption that a species fully relies on mycoheterotrophy is, in most cases, based on the fact that leaves are absent and chlorophyll is lacking. However, the precise characterization of a species' trophic strategy requires careful investigation, which has been carried out for only very few species. Also, new species and localities are constantly discovered. Thus, our observations, particularly about number of species, are subject to change. Nevertheless, it is unlikely that undiscovered species and localities represent significant dissimilarities to the general patterns described here.

3.2 Distribution of Nonangiosperm Mycoheterotrophs

3.2.1 Liverworts

The only non-seed plant species with a completely mycoheterotrophic life cycle is the liverwort *Aneura mirabilis*. The species has been recorded from England, Germany, France, Portugal, Russia, Scandinavia, and Greenland. A liverwort species supposedly related to *Aneura mirabilis* is described from Costa Rica, but it remains unknown whether this species is a full mycoheterotroph (Crum and Bruce 1996; Wickett and Goffinet 2008).

3.2.2 Clubmosses

The genera *Huperzia* and *Lycopodiella*, with respectively fully mycoheterotrophic and putatively partially mycoheterotrophic gametophytes, have a true cosmopolitan distribution, although the diversity of *Lycopodiella* is highest in the New World and Australasia. Species of *Lycopodium* occur in temperate and tropical zones as well, but in the tropics, *Lycopodium* is restricted to montane regions.

3.2.3 Ferns

The gametophytes of *Botrychium* and *Ophioglossum* species (Ophioglossaceae) are achlorophyllous and thus putatively mycoheterotrophic. Both genera have a cosmopolitan distribution. The gametophytes of the only other Ophioglossaceae species, *Helminthostachys zeylanica* and *Mankyua chejuense*, have not been studied in detail. The former occurs in India and Sri Lanka, Southeast Asia, Japan, and Australasia, and the latter genus is endemic to Cheju Island (Korea).

Species of the two Psilotaceae genera *Psilotum* and *Tmesipteris* have subterranean mycoheterotrophic gametophytes. *Psilotum* has a pantropical distribution, with one species extending into temperate areas. *Tmesipteris* occurs in Southeast Asia, Australasia, Pacific, and New Zealand.

The gametophyte of *Stromatopteris moniliformis* (Gleicheniaceae), which is endemic to New Caledonia, is achlorophyllous as well and thus presumably mycoheterotrophic. Mycoheterotrophic gametophytes are also observed in species of the genus *Actinostachys* (Schizaeaceae), which are native to tropical America, Southeast Asia, and temperate regions in the southern hemisphere.

3.2.4 Gymnosperms

The remarkable *Parasitaxus usta* (Podocarpaceae) is the only achlorophyllous gymnosperm, but its mycoheterotrophic status remains doubtful. It is only found growing near or on the New Caledonian sickle pine (*Falcatifolium taxoides*), which occurs in dense evergreen rainforest on New Caledonia and the adjacent Île des Pins (Feild and Brodribb 2005; Eckenwalder 2009).

3.3 Distribution of Fully Mycoheterotrophic Angiosperms

3.3.1 Tropical Regions

The majority of fully mycoheterotrophic angiosperms—ca. 75% of all species—occur in the tropical zone ("tropics") between the Tropic of Cancer and the Tropic of Capricorn. This zone is dominated by tropical rainforest, the preferred habitat of mycoheterotrophs (Fig. 3.1). Tropical rainforest is the most diverse of all plant communities and occurs in areas with a warm wet climate without pronounced cold or dry seasons.

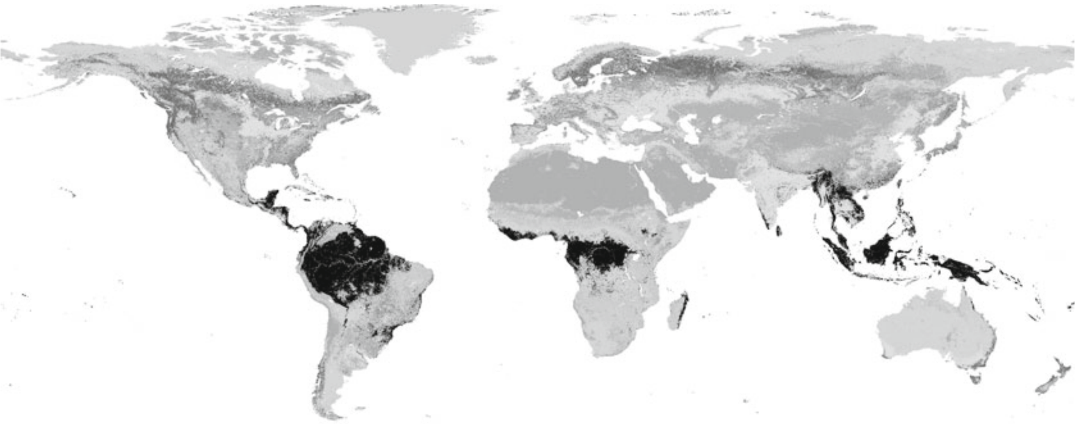

Fig. 3.1 Global distribution of tropical rainforest (*black*) in 2003. Map based on information obtained from NASA Earth Observations (2011)

Table 3.1 Approximate numbers of fully mycoheterotrophic angiosperm species, genera, and families for the main tropical regions discussed here

	Central and South America	Africa and Madagascar	Southwest India and Sri Lanka	Southeast Asia	Australasia	Pacific Islands
Families	7	6	4	9	7	3
Genera	24	19	10	29	17	9
Species	84	52	17	169	78	17

Numbers of species and genera are based on data from Chap. 2. Not all species included in this overview grow in tropical rainforest. Ericaceous mycoheterotrophs in tropical America and Asia, for example, are mainly restricted to coniferous and mixed forests at high elevations

Tropical rainforest is dominated by broad-leaved evergreen trees, and its multistoried canopy prevents light from penetrating to the forest floor.

The vast majority of tropical tree species form arbuscular mycorrhizas (AM), and AM interactions are the most common mycorrhizal associations in tropical rainforests (Smith and Read 2008). Most tropical mycoheterotrophic plants are associated with arbuscular mycorrhizal fungi, although mycoheterotrophic interactions involving ectomycorrhizal fungi (Orchidaceae and Ericaceae) and saprotrophic fungi (Orchidaceae) are also common. Ectomycorrhizal associations were long considered to be rare in the tropics, but we now know that at least three lineages of tropical trees form ectomycorrhizal associations (Alexander and Lee 2005). The most notable exception to the AM dominance in tropical forest is found in Southeast Asia. Rainforests in Southeast Asia are among the most diverse plant communities in the world and are characterized by high abundance of trees in the family Dipterocarpaceae, which are known to form associations with ectomycorrhizal fungi (Lee 1990).

While tropical rainforests on different continents are physiognomically very similar, their floras have little in common. This reflects their distinct geological and evolutionary histories (Morley 2000). In our overview, we adopt six major rainforest regions, loosely based on Primack and Corlett (2005): (1) Central and South America, (2) Africa and Madagascar, (3) India and Sri Lanka, (4) Southeast Asia, (5) Australasia, and (6) the Pacific Islands. Biologically, these regions can be subdivided into smaller areas, and we distinguish several smaller rainforest blocks in our discussion of each major region.

Mycoheterotrophs are represented in all these tropical rainforest regions, but their diversity is not equally distributed among the regions (Table 3.1). Southeast Asia contains by far the largest number of fully mycoheterotrophic species. On higher taxonomic level, the differences in diversity between the regions are less pronounced (Table 3.1), although there is little floristic overlap between the regions and many species and genera are endemic to a particular region.

3.3.2 Central and South America

Half of the world's current tropical rainforests are in South and Central America (Morley 2000; Primack and Corlett 2005), together referred to as the "Neotropics" or New World tropics (as opposed to the Paleotropics or Old World tropics). Centered on the Amazon River basin in northern and central Brazil and extending to the western foothills of the Andes and up into southern Mexico along the isthmus of Panama, the neotropical forests form the largest block of continuous rainforest on Earth (Fig. 3.2). The adjacent basin of the Orinoco River drains eastern Colombia and Venezuela and contains a large rainforest that extends into French Guiana, Surinam, and Guyana ("the Guianas"), sharing many characteristics with the Amazon River basin. A distinct patch of rainforest, the Brazilian Atlantic Forest (Mata Atlântica), runs along the coast of southeast Brazil from Recife in the north to Sao Paulo in the south. Due to excessive logging, less than 5% of the original Mata Atlântica remains; however, this forest still retains a high level of taxonomic diversity and endemism.

Fig. 3.2 Occurrence of rainforest in the Neotropics (*black*)

In Central America, rainforests extend from the Pacific coast of northwest South America to southernmost Mexico. Many larger islands of the West Indies were covered by rainforest as well, but very little of that forest now remains.

In comparison with Old World (paleotropical) tropical forests, neotropical rainforests are characterized by a high species diversity of trees belonging to the families Vochysiaceae, Bignoniaceae, Lecythidaceae, and Chrysobalanaceae. Another distinct feature of neotropical rainforests is the prominent presence of Bromeliaceae, which are the preeminent group of neotropical epiphytes (Primack and Corlett 2005). With an estimated 90,000 species of higher plants, the neotropical region is more species rich than the Paleotropics (Prance 1994). In terms of fully mycoheterotrophic plant species, however, the Neotropics contain only about a quarter of the number of species found in the Paleotropics (Table 3.1), with the flora of tropical America including ca. 80 species of fully mycoheterotrophs. The paucity of fully mycoheterotrophic species of orchids in the Neotropics is the main reason for this discrepancy. Despite the enormous diversity of tropical New World orchids, only seven species are achlorophyllous versus 17 species in tropical Africa and ca. 135 in tropical Asia.

With the exception of mycoheterotrophic Iridaceae (Madagascar), Petrosaviaceae (Southeast Asia), and Polygalaceae (Southeast Asia and Australasia), all angiosperm families with fully mycoheterotrophic species are present in the Neotropics. Of the 24 neotropical genera of mycoheterotrophic flowering plants, 17 are endemic: *Apteria*, *Dictyostega*, *Hexapterella*, *Marthella*, and *Miersiella* (Burmanniaceae); *Arachnitis* (Corsiaceae); *Lacandonia*, *Peltophyllum*, *Soridium*, *Triuris*, and *Triuridopsis* (Triuridaceae); *Degranvillea, Pogoniopsis*, *Uleiorchis*, and *Wullschlaegelia* (Orchidaceae); *Tiputinia* (Thismiaceae); and *Voyriella* (Gentianaceae). The Neotropics are also an important center of diversity for *Voyria* (Gentianaceae), *Gymnosiphon* (Burmanniaceae), and *Thismia* (Thismiaceae).

Although some neotropical mycoheterotrophic plant species are endemic to a restricted region, many species are widely distributed. *Apteria aphylla* (Burmanniaceae), for example, occurs from southern USA and the West Indies in the north to Paraguay and southern Brazil in the south (Maas et al. 1986). A similar distribution is observed in *Voyria aphylla* (Gentianaceae) (Maas and Ruyters 1986).

3.3.2.1 Central America

Many South American mycoheterotrophs reach their northern distribution limit in the rainforests of Central America. Central American forests also contain a few endemic mycoheterotrophic species, including *Lacandonia schismatica* (Triuridaceae), *Gymnosiphon panamensis* (Burmanniaceae), and *Voyria kupperi* (Gentianaceae). The only mycoheterotrophic orchids that grow in the rainforests of Central America are species of *Wullschlaegelia* (Orchidaceae). In terms of species richness, the floras of Panama and Costa Rica contain perhaps slightly more mycoheterotrophic species than other countries in Central America consistent with their increased species richness relative to surrounding regions.

Central America is also an important center of diversity for the orchid genera *Hexalectris* and *Corallorhiza*, which reach their southernmost distributions here. However, these mycoheterotrophs do not grow in rainforests but are found in a variety of habitats ranging from coniferous forest to mixed scrub forests and desert canyons (Salazar and Freudenstein 1998; Kennedy and Watson 2010). Central American coniferous forests at higher elevations are also home to *Hypopitys monotropa* and *Monotropa uniflora* (Ericaceae). The latter species reaches its southernmost distribution in the montane forests of Colombia (Wallace 1975). The distribution range of these species does not overlap with any rainforest species.

3.3.2.2 West Indies

The West Indies lack many groups of mycoheterotrophs that are found on continental South and Central America (e.g., Triuridaceae, Thismiaceae, *Voyriella*, and most Burmanniaceae genera). But species of *Apteria*, *Corallorhiza*, *Gymnosiphon*, *Voyria*, and *Wullschlaegelia* that are found in nearby continental forests have been recorded on many islands of the West Indies. Trinidad harbors a number of additional continental species (*Dictyostega orobanchoides*, *Hexapterella gentianoides*, and *Gymnosiphon divaricatus*) most likely as a result of its proximity to mainland South America. The rare monotypic genus *Marthella* (Burmanniaceae) is endemic to Trinidad.

3.3.2.3 Guianas and Amazonia

In South America, the Guianas are an important center of diversity for many mycoheterotrophic genera, in particular for *Voyria* and *Voyriella* (Gentianaceae), *Gymnosiphon* (Burmanniaceae), and *Sciaphila* (Triuridaceae). *Degranvillea dermaptera* (Orchidaceae) and *Thismia saülensis* (Thismiaceae) are endemic to this region. The adjacent Amazon rainforest is home to a high diversity of mycoheterotrophs, and several species are endemic to this region: *Sciaphila rubra*, *S. oligantha*, *S. corymbosa*, *Triuridopsis peruviana* (Triuridaceae), and the enigmatic species *Tiputinia foetida* and *Thismia melanomitra* (Thismiaceae) from Amazonian Ecuador. Many other mycoheterotrophs from the Amazon rainforest also occur in adjacent regions, particularly in the Guianas, Venezuela, and Colombia. There is little doubt that the forests of the Amazon Basin harbor many species that have yet to be discovered.

3.3.2.4 Southern Neotropics

Further to the south, many tropical mycoheterotrophic plants reach the edge of their distribution ranges in northern Paraguay and Bolivia. Contrarily, *Arachnitis uniflora* (Corsiaceae)

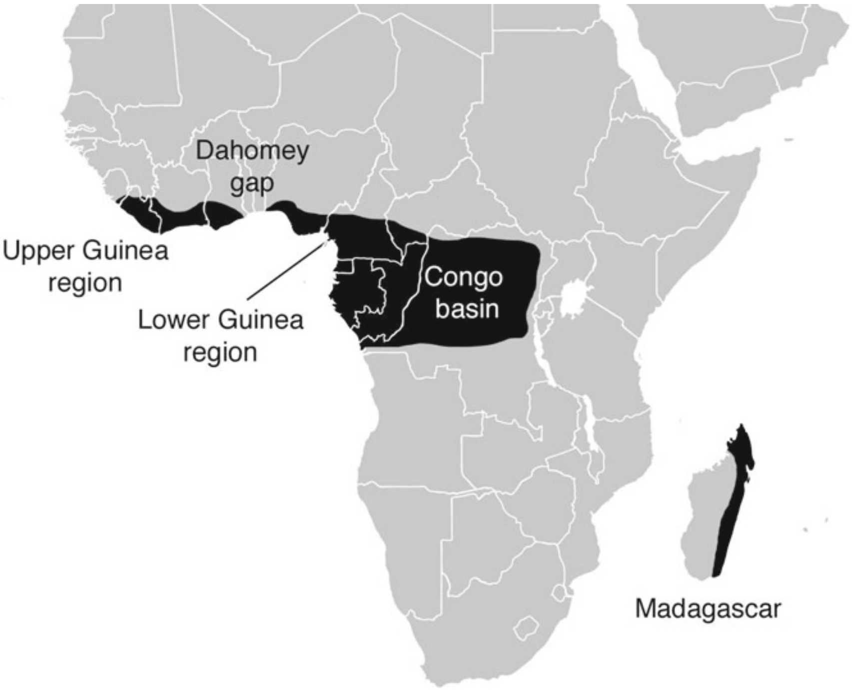

Fig. 3.3 Distribution of tropical rainforest (*black*) in Africa and Madagascar

reaches its most northern distribution in high-altitude rainforests of Bolivia that resemble the habitat of this species' southern Patagonian populations in Argentina and Chile (Ibisch et al. 1996).

3.3.2.5 Atlantic Forest

The Atlantic Forest (Mata Atlântica) on the Atlantic coast of Brazil is another important region for mycoheterotrophic plant diversity and has a high level of endemism: many species of *Thismia* (Thismiaceae) are endemic to this region (Maas et al. 1986), and the Mata Atlântica harbors the only known populations of *Lacandonia brasiliana*, *Peltophyllum caudatum*, *Triuris alata* (Triuridaceae), *Voyria obconica* (Gentianaceae), and *Pogoniopsis nidus-avis* (Orchidaceae). The Atlantic Forest is severely affected by habitat destruction, and many of these species are threatened with extinction.

3.3.3 Africa and Madagascar

Africa contains the second largest block of tropical rainforest, centered on the Congo River basin and continuing on the coast of the Gulf of Guinea to Sierra Leone but with a gap in the vicinity of Togo (the Dahomey Gap) (Fig. 3.3) (Morley 2000; White 2001). Tropical rainforest in East Africa is mostly restricted to small "islands," mainly centered on mountains. While these East African patches of rainforest cover only a small area, they contain a high percentage of endemic species due to their prolonged isolation from the forests of West and Central Africa. In Madagascar, tropical rainforest is mostly restricted to a 120 km-wide band along the eastern coast (Mittermeier et al. 1999), but due to intensive human activity, only very little of this forest remains today.

African rainforests are generally dryer, lower, and more open than rainforests found elsewhere (Morley 2000). They are relatively poor in plant species when compared with neotropical and Asian rainforests, a feature that has been attributed to the degrading effect of significant climatic changes during the Cenozoic and, more recently, to Pleistocene climatic fluctuations, although other factors such as human impact may have contributed as well (Plana 2004). African rainforests are particularly poor in palms and Lauraceae as well as in epiphytes and woody vines in general. The flora of tropical Africa is also notably poor in orchids, and it has been estimated that only 15% of the world's orchids occur in tropical Africa compared to 41% in tropical America and 34% in tropical Asia and New Guinea (Primack and Corlett 2005). Tropical Africa has always been considered relatively poor in number of mycoheterotrophic plant species (Leake 1994), but recent new discoveries started to alter this image (Cheek 2003a, b; Cheek et al. 2003, 2008; Franke 2004; Sainge et al. 2005; Cheek and Vanderburgt 2010; Cribb et al. 2010). Over 50 species of fully mycoheterotrophic plants are now known from Africa (including Madagascar) (Table 3.1). When compared to the total number of higher plants from tropical Africa (ca. 45,000; Beentje et al. 1994), the percentage of mycoheterotrophic species in the flora of Africa is not lower than that of the Neotropics, where ca. 80 species of mycoheterotrophs are recorded for an estimated 90,000 higher plants (Prance 1994). The continuous description of new taxa also illustrates the fact that certain areas in Africa remain undercollected and poorly characterized and that new discoveries, particularly from rainforests in Central Africa, are anticipated.

The mycoheterotrophic species from Africa and Madagascar belong to 19 genera, of which *Afrothismia* (Thismiaceae), *Auxopus*, *Brachycorythis* (Orchidaceae), *Kupea*, *Kihansia*, *Seychellaria* (Triuridaceae), and *Geosiris* (Iridaceae) are endemic. In general, the distribution of mycoheterotrophs in tropical Africa seems to be more patterned than in the Neotropics, as many species have very restricted distribution ranges. Exceptional widespread species include *Exochaenium oliganthum* (Gentianaceae), *Didymoplexis africana*, *Eulophia galeoloides*, and *Epipogium roseum* (Orchidaceae).

3.3.3.1 West and Central Africa

The main African rainforest block is centered in the Congo Basin and extends from the East African Albertine Rift mountains to the Atlantic Ocean in the West (Plana 2004). This rainforest region is known as the Lower Guinea Region. The Lower Guinea Region has a high diversity of mycoheterotrophic plants, and many mycoheterotrophs in Burmanniaceae, Orchidaceae, Thismiaceae, and Triuridaceae are endemic to this region (Cheek and Williams 1999; Franke 2007). These endemics include *Afrothismia* spp., *Oxygyne triandra* (Thismiaceae), *Auxopus letouzeyi*, *Gastrodia africana* (Orchidaceae), *Kupea martinetugei*, and *Sciaphila ledermannii* (Triuridaceae). The latter species is also found on the islands in the Gulf of Guinea along with *Epipogium roseum* (Orchidaceae) (Daniel 2010). A smaller western block of West African rainforest is found in the Upper Guinea Region, from Sierra Leone to Ghana (Plana 2004). This area is generally less diverse in mycoheterotrophs compared to the Lower Guinea Region. *Afrothismia* is remarkably absent from this region. Other mycoheterotrophs are generally shared with the Lower Guinea Region, including *Campylosiphon congestus*, *Gymnosiphon longistylus*, *G. bekensis* (Burmanniaceae), *Auxopus macranthus*, *A. kamerunensis*, *Epipogium roseum* (Orchidaceae), *Exochaenium oliganthum*, and *Voyria primuloides* (Gentianaceae). The species *Sciaphila africana* and *Gymnosiphon samoritoureanus* are endemic to the Upper Guinea Region.

3.3.3.2 East Africa

Rainforests in East Africa consist of small patches of forest on the East African mountains between about 1,200 and 2,500 m altitude. These "islands" of rainforests are generally surrounded by dry woodland (Primack and Corlett 2005). Although the total area of these rainforest patches is small, those on older mountains have potentially provided a stable habitat for a long period of time and have been isolated from the forests of West and Central Africa for millions of years. As a result, many of the plant and animal species are endemic to these mountains. Recent discoveries have stressed the importance of the coastal East African forests for mycoheterotrophic plant diversity (Cheek 2006). *Gymnosiphon usambaricus* (Burmanniaceae), *Afrothismia baerae*, *A. mhoroana* (Thismiaceae), *Seychellaria africana*, *Kihansia jonii*, and *Kupea lovettii* (Triuridaceae) are endemic to the region, and most of these species are known from very few restricted localities.

Kihansia jonii and *Kupea lovettii*, for example, have only been recorded at the Kihansi River Gorge in Tanzania (Cheek 2003b).

3.3.3.3 Madagascar

In Madagascar, mycoheterotrophs are restricted to the humid lowland forests along the eastern coastal strip and the subhumid forests above 600–800 m elevation. The flora of Madagascar largely evolved in isolation, and this explains the high level of endemism of mycoheterotrophic plants. Indeed, all fully mycoheterotrophic plant species that occur in Madagascar (and the adjacent Comores) are endemics. The Malagasy flora also includes one endemic mycoheterotrophic plant genus: *Geosiris* (Iridaceae), with one species known from Madagascar and the Comores and another species endemic to the island of Mayotte (Goldblatt and Manning 2010). Other mycoheterotrophic species are *Gymnosiphon danguyanus*, *G. marieae* (Burmanniaceae), *Seychellaria madagascariensis* (Triuridaceae), *Auxopus madagascariensis, Galeola humblotii*, and *Gastrodia madagascariensis* (Orchidaceae), although the generic identity of the latter has been disputed and this species may belong to *Didymoplexis* (Cribb et al. 2010). Another *Gastrodia* species (*G. similis*) is known from a single collection on La Réunion. With only eight species, Madagascar is rather poor in mycoheterotrophic plants, and most genera that occur on the east coast of Africa are absent from Madagascar (e.g., *Afrothismia*, *Kupea*, *Kihansia*). Another notable absence is that of the orchid *Epipogium roseum*, which has a widespread distribution in continental Africa, India and Sri Lanka, Southeast Asia, Australasia, and the Pacific Islands. In contrast, the genus *Seychellaria*, recorded from Madagascar, the Seychelles, and Tanzania, provides an interesting biogeographic link between Madagascar and continental Africa, perhaps indicating its potential for dispersal between Madagascar and the mainland. On the other hand, *Galeola*, for which one species is known from Madagascar and the Comores, is absent from continental Africa but is widespread in Southeast Asia. A biogeographic link between Madagascar and India/Southeast Asia is observed in several groups of organisms, including lizards (Macey et al. 2000), birds (Cooper et al. 2001), and amphibians (Bossuyt and Milinkovitch 2001), and is indicative of the geological past in which Madagascar separated from the India-Seychelles landmass several tens of millions of years after its separation from Africa (Storey et al. 1995).

3.3.4 India and Sri Lanka

India has a long but very narrow strip of rainforest running parallel to the west coast along the crest of the Western Ghats (Fig. 3.4). The southwest of the island of Sri Lanka supports rainforest as well. Southern India and Sri Lanka are separated by the relatively shallow Palk Strait, which allowed for intensive biotic interchange during the Pleistocene ice ages. As a result, Sri Lanka and the Western Ghats have very similar biota, although for some groups of fauna, differences are somewhat more pronounced than expected (e.g., Bossuyt et al. 2004). The rainforest of India and Sri Lanka has a vivid geological history and probably underwent more changes than any other rainforest region. The Indian Plate began to drift away from eastern Gondwana in the Early Cretaceous. While the Indian Plate drifted close to the African plate, it received diverse Late Cretaceous elements of the African tropical flora and lost temperate elements of the eastern Gondwanan gymnosperm flora (Morley 2000). The dramatic latitudinal and climatic changes that affected the Indian Plate during the Late Cretaceous and Tertiary, as it traveled from Gondwana and then collided with Asia, caused massive extinctions in its biota. Today, the Western Ghats–Sri Lanka rainforest covers only a very small area and is considered as a biodiversity hotspot under severe threat: 45.6% of the plant species that occur here are endemics (Myers et al. 2000).

This region contains ca. 17 fully mycoheterotrophic species within families Burmanniaceae, Orchidaceae, Thismiaceae, and Triuridaceae. Almost half of the mycoheterotrophic species from the Western Ghats–Sri Lanka hotspot are found nowhere else, while the

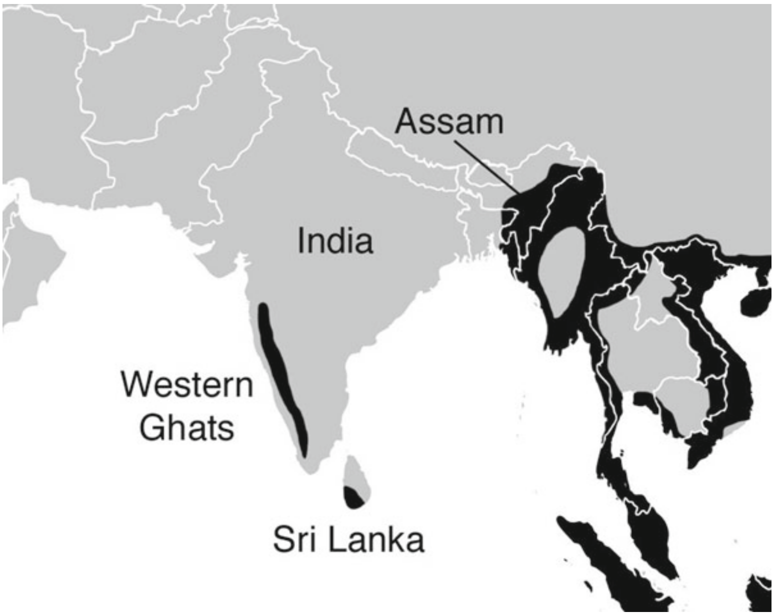

Fig. 3.4 Distribution of tropical rainforest (*black*) in India and Sri Lanka

widespread genera *Galeola* (Orchidaceae) and *Gymnosiphon* (Burmanniaceae) are remarkably absent from the southern India flora. In addition, apart from the single species in the endemic genus *Hyalisma* (Triuridaceae) and the widespread species *Aphyllorchis montana*, *Epipogium roseum* (Orchidaceae), and *Burmannia championii* (Burmanniaceae) (Mesta et al. 2011), the Western Ghats and Sri Lanka have no mycoheterotrophic species in common, indicating a high degree of local endemism in this region. For example, the enigmatic *Haplothismia exannulata* (Thismiaceae) is endemic to the Western Ghats and is only known from two restricted populations (Sasidharan and Sujanapal 2000). The rainforest of South India is also a habitat for three mycoheterotrophic *Burmannia* species: *B. candelabrum*, *B. indica*, and *B. stricta*. However, the latter two species are endemic to Southwest India. The Western Ghats also contains at least five mycoheterotrophic orchid species, of which two are endemic to the region (*Didymoplexis seidenfadenii* and *Gastrodia silentvalleyana*). In Sri Lanka, many Southeast Asian mycoheterotrophic species reach their westernmost distributions (e.g., *Sciaphila secundiflora*, *S. tenella*, *Cyrtosia javanica*, and *Eulophia zollingeri*). The island contains at least two endemic mycoheterotrophic species: *Thismia gardneriana* (Thismiaceae) and *Gastrodia zeylanica* (Orchidaceae).

The flora of India contains many other mycoheterotrophic species than those mentioned above, but all of these occur in the far northeastern state of Assam (e.g., *Burmannia nepalensis*, *Sciaphila khasiana*, *Chamaegastrodia shikokiana*, *Cymbidium macrorhizon*, *Eulophia zollingeri*, *Erythrorchis altissima*, *Galeola falconeri*, *Odontochilus asraoa*, *Aphyllorchis* spp., *Yoania* spp.). Biogeographically, these species have more in common with South China and Southeast Asia than with the Western Ghats–Sri Lanka rainforests.

3.3.5 Southeast Asia

Southeast Asia has one of the most complex geological histories in the world. The region has developed by the interaction of the Pacific, India–Australia, Eurasia, and several smaller tectonic plates, and as a result of this complicated past, several distinct centers of biological diversity can be identified within a small geographic range (Hall 1998; Sodhi et al. 2004). Until recently, rainforest covered most of the Malay Peninsula,

Fig. 3.5 Distribution of tropical rainforest (*black*) in tropical Asia and tropical Australasia. The barrier between Southeast Asia and Australasia is shown with a black line

Borneo, Sumatra, and Java (Fig. 3.5). This region is often referred to as "Sundaland," after the surrounding Sunda continental shelf. Lowland rainforest in this area has suffered considerably from human activity, particularly on Java. North of Sundaland rainforest extends into mainland Asia, including most of Cambodia, Laos, and Vietnam, and much of Thailand and Myanmar. However, due to the rain shadow of several long north–south mountain chains, most of the interior of Thailand and Myanmar is too dry to support rainforest. Farther north, rainforest covers South China and the southern tip of Taiwan, although most has now been cleared. The rainforests of Southeast Asia extend westward through Myanmar into Northeast India. Eastward rainforest covers Sulawesi and many of the smaller islands between Borneo and New Guinea ("Wallacea") (Fig. 3.5). As a whole, the tropical forests of Southeast Asia include four biodiversity hotspots (Indo-Burma, Sundaland, the Philippines, Wallacea) containing high concentrations of endemic species and undergoing immense and rapid habitat loss (Myers et al. 2000; Sodhi et al. 2004).

Southeast Asian rainforests can be characterized as "dipterocarp forests," with a canopy dominated by large trees of the family Dipterocarpaceae. Dipterocarps are particularly important forest elements of the Malay Peninsula, Borneo, Java, Sumatra, and the wetter parts of the Philippines. The dipterocarp forests of Southeast Asia are extremely rich in mycoheterotrophic plants. Except for Iridaceae mycoheterotrophs, all angiosperm families with fully mycoheterotrophic species are represented in Southeast Asia. Orchids are particularly species rich, with over 100 fully mycoheterotrophic species. The region is a center of diversity for mycoheterotrophic orchids of the genera *Aphyllorchis*, *Gastrodia*, *Didymoplexis*, *Didymoplexiella*, *Cyrtosia*, *Lecanorchis*, and *Galeola*. It is the only part of the world where fully mycoheterotrophic orchids of the genera

Cystorchis, *Platanthera*, *Silvorchis*, *Kalimantanorchis*, and *Tropidia* can be found. Other mycoheterotrophic orchids from Southeast Asia belong to *Erytrorchis*, *Pseudovanilla*, *Chamaegastrodia*, *Odontochilus*, *Cephalanthera*, *Epipogium*, *Eulophia*, and *Stereosandra*. The poorly known ericaceous genus *Cheilotheca*, which contains two mycoheterotrophic species, is also endemic to Southeast Asia: *Cheilotheca* species occur in pine and oak forest at high elevations, and therefore, their distribution does not overlap with other tropical mycoheterotrophs.

The region is also a major center of diversity for arbuscular mycorrhizal mycoheterotrophs in Burmanniaceae, *Petrosavia* (Petrosaviaceae), *Epirixanthes* (Polygalaceae), Thismiaceae, and Triuridaceae. The distribution of many genera of mycoheterotrophic plants from tropical Southeast Asia extends into the subtropics, mostly into subtropical China and Japan (e.g., *Thismia*, *Sciaphila*, *Gymnosiphon*, *Andruris*, *Exacum*, *Petrosavia*, *Cyrtosia*, *Erythrorchis*, *Lecanorchis*, *Aphyllorchis*, *Gastrodia*, *Odontochilus*, and *Didymoplexiella*). But many mycoheterotrophs from Southeast Asia are also found in Australasian rainforest, and a few species extend their distribution into Oceania. Particularly widespread species include *Aphyllorchis montana*, *Didymoplexis pallens*, *Stereosandra javanica*, *Epipogium roseum*, and *Eulophia zollingeri*.

3.3.5.1 Indochina

The rainforests of mainland Southeast Asia ("Indochina" or "Indo-Burma") are located in Cambodia, Laos, Vietnam, Myanmar, Singapore, Thailand, and South China (southeastern Tibet, southern Yunnan, Guangxi, southwestern Guangdong, Taiwan, and Hainan), although at higher latitudes, these rainforests are gradually replaced by monsoon and subtropical forests (Zhu 1997; Morley 2000). The area is rich in fully mycoheterotrophic plants, and the mycoheterotrophic flora consists of a mix of genera that are widespread in tropical Southeast Asia with genera that have a more temperate distribution. The majority of fully mycoheterotrophic species found here are orchids, and the region is an important center of diversity for the genera *Cyrtosia*, *Galeola*, *Lecanorchis*, *Chamaegastrodia*, and *Odontochilus*. Several species in these genera are endemic to the region. The Old World species of mycoheterotrophic *Cephalanthera* orchids are restricted to mainland Southeast Asia. Apart from Orchidaceae, mainland Southeast Asia contains full mycoheterotrophs that belong to *Burmannia*, *Gymnosiphon* (Burmanniaceae), *Petrosavia* (Petrosaviaceae), *Thismia* (Thismiaceae), *Sciaphila* (Triuridaceae), *Exacum* (Gentianaceae), and *Epirixanthes* (Polygalaceae). *Corsiopsis* (Corsiaceae) is endemic to the region; the only described species, *C. chinensis*, is known from a single collection from a subtropical forest in Guangdong, southern China (Zhang et al. 1999).

3.3.5.2 Sundaland

The major areas of rainforest of the Sundaland region are located in Borneo, Java, Sumatra, and Peninsular Malaysia. Sixty percent of the 25,000 plant species recorded from this region are endemic, but with natural habitat disappearing at an alarming rate, Sundaland is one of the most threatened rainforest areas of the world (Myers et al. 2000). This area is home to the most species-rich plant communities on Earth and is likewise one of the richest regions for fully mycoheterotrophic plants. The diversity of mycoheterotrophic orchids is particularly remarkable, with a high number of species of *Aphyllorchis* and *Gastrodia*. It is also a center of diversity for *Didymoplexiella* and *Didymoplexis*, and the mycoheterotrophic orchid genera *Kalimantanorchis*, *Tropidia*, and *Silvorchis* are endemic to Sundaland. Orchid genera *Cyrtosia*, *Erytrorchis*, *Galeola*, *Pseudovanilla*, *Cystorchis*, *Epipogium*, *Eulophia*, and *Stereosandra* are represented in this region by mycoheterotrophic species as well.

Sundaland rainforests are also rich in arbuscular mycorrhizal mycoheterotrophs. These belong to *Burmannia* and *Gymnosiphon* (Burmanniaceae), *Andruris*, *Sciaphila* (Triuridaceae), *Epirixanthes* (Polygalaceae), *Exacum* (Gentianaceae), *Petrosavia* (Petrosaviaceae), and *Thismia* (Thismiaceae). Several of these species are endemic to Sundaland, or even to a particular island within the Sundaland region. Of the three major islands, Borneo has by far the highest diversity of fully mycoheterotrophic species. The flora of Borneo contains at least 62 mycoheterotrophic species, which is more than the number of species known from all of tropical Africa. Endemism on Borneo is high and particularly pronounced in Orchidaceae and Thismiaceae: at least 16 species of mycoheterotrophic orchids are endemic to Borneo (*Aphyllorchis kemulensis*, *A. siantanensis*, *A. spiculaea*, *Cystorchis saprophytica*, *Didymoplexis latilabris*, *Didymoplexiella borneensis*, *D. cinnabarina*, *D. forcipata*, *D. kinabaluensis*, *Gastrodia grandilabris*, *G. sahabensis*, *G. spathulatha*, *Platanthera saprophytica*, *Kalimantanorchis nagamasui*, *Tropidia saprophytica*, and *T. connata*). All seven *Thismia* species recorded on the island are also endemic. The island of Java is also rich in mycoheterotrophs. The orchid genus *Silvorchis* is found nowhere else, and several *Didymoplexis* and *Gastrodia* species are endemic to Java as well.

3.3.5.3 Philippines

Until a few centuries ago, at least 95% of the Philippines was covered by tropical rainforest (Heaney and Regalado 1998). Today, only 3% of that rainforest remains, mainly in montane areas, and the Philippines has the questionable honor of being the second "hottest" diversity hotspot on Earth (Myers et al. 2000). The flora of the Philippines has fewer plant species than Sundaland and Indochina (which cover larger areas) but includes ca. 24 species of fully mycoheterotrophic angiosperms. Six species of *Sciaphila* (Triuridaceae) are native to the Philippines, but only a single mycoheterotrophic *Burmannia* species (*B. nepalensis*) and remarkably no *Gymnosiphon* species have been recorded for the Burmanniaceae. *Epirixanthes* (Polygalaceae), found throughout Australasia and Sundaland, is also absent. Mycoheterotrophic orchids from the Philippines are of the genera *Cyrtosia*, *Erythrorchis*, *Galeola*, *Lecanorchis*, *Pseudovanilla*, *Cystorchis*, *Aphyllorchis*, *Didymoplexis*, *Epipogium*, *Eulophia*, *Gastrodia*, and *Stereosandra*. Endemic mycoheterotrophs are *Aphyllorchis halconensis*, *Didymoplexis philippinensis*, *Pseudovanilla philippinensis* (Orchidaceae), *Exacum loheri* (Gentianaceae), and *Thismia gigantea* (Thismiaceae).

3.3.5.4 Wallacea

Wallacea includes the island of Sulawesi, the Maluku Islands, and the Lesser Sunda Islands. The area is one of the most geologically complex regions in the world. The islands originated from land fragments that rifted from Gondwana at different geological time periods, and they were never physically connected to Southeast Asia ("Wallace's Line") (Audley-Charles 1983). Due to their prolonged isolation, each island evolved highly endemic faunas, but the proximity of Sundaland caused a large influx of tropical Southeast Asian plants, which started during the mid-Miocene. The flora of Wallacea contains an estimated 10,000 species, of which ca. 1,500 are endemic (Myers et al. 2000). Ca. 21 species of mycoheterotrophic plants are known from Wallacea. Most of them have distribution ranges that include other parts of Southeast Asia, Australasia, or both: *Burmannia lutescens*, *B. championii*, *Gymnosiphon aphyllus*, *G. papuanus* (Burmanniaceae), *Sciaphila arfakiana*, *S. corniculata*, *S. densiflora*, *S. tenella* (Triuridaceae), *Petrosavia stellaris* (Petrosaviaceae), *Cyrtosia javanica*, *Cystorchis aphylla*, *Didymoplexis micradenia*, *Epipogium roseum*, and *Eulophia zollingeri* (Orchidaceae). *Gymnosiphon minahassae*, *Pseudovanilla ternatensis*, *Galeola nudifolia*, *Aphyllorchis acuminata*, *A. angustipetala*, *A. gracilis*, and *Gastrodia celebica* are endemic to the region. Remarkably, in Wallacea there are no records of *Thismia*, a genus that is otherwise widespread in Southeast Asia and Australasia.

3.3.6 Australasia

Most of the island of New Guinea is covered by what is now the third largest and most intact rainforest area of the world (Primack and Corlett 2005). Australia also supports a small area of rainforest in the northeast, along the coast between Cooktown and Townsville (Fig. 3.5). The geological history of New Guinea and Australia differs from that of Southeast Asia: New Guinea and

Australia are located on the Australian plate, while the rest of the Southeast Asian tropical forest is located on the Asian plate. The mid-Miocene collision of the Australian and Asian plate caused a large influx of Asian rainforest plants into New Guinea. The absence of a dry land connection prevented a similar influx of vertebrates. As a result, the composition of the flora of New Guinea is relatively similar to that of Southeast Asian rainforests, while their vertebrate faunas are very different. The rainforests of Australia were much less affected by the post-Miocene influx of Asian plants. The flora of Australian rainforests contains more Gondwanian and Australian components as well as more early diverging angiosperm families, such as Winteraceae, Eupomatiaceae, Monimiaceae, Lauraceae, and Cunoniaceae (Primack and Corlett 2005). Rainforests in New Guinea do contain Dipterocarpaceae trees, but they are much less dominant than in Southeast Asian rainforests.

Australasian rainforests harbor a high diversity of mycoheterotrophic plants, although the total number of mycoheterotrophic species is considerably lower than the number of species recorded from Southeast Asia (Table 3.1). Australasian mycoheterotrophs are part of seven different flowering plant families: Burmanniaceae, Thismiaceae, Triuridaceae, Corsiaceae, Polygalaceae, Orchidaceae, and Gentianaceae. Ca. 30 species belong to Orchidaceae—which is lower than the number of mycoheterotrophic orchids from Southeast Asia, but still high compared to the number of species occurring in Africa and the Neotropics. Reflecting their general floristic overlap, Australasian rainforests share many genera and species of mycoheterotrophs from rainforests in Southeast Asia and Oceania. A notable exception is the genus *Corsia* (Corsiaceae), of which all 25 species are endemic to Australasia. Conversely, Southeast Asian mycoheterotrophic species of *Petrosavia* (Petrosaviaceae), *Cyrtosia*, *Erythrorchis*, *Cystorchis*, *Odontochilus*, *Platanthera*, *Cephalanthera*, *Didymoplexiella*, *Tropidia*, and *Yoania* (Orchidaceae) do not occur in Australasia.

For mycoheterotrophic Orchidaceae, the region is an important center of diversity for *Pseudovanilla*, *Lecanorchis*, and *Aphyllorchis*. The orchid genera *Galeola*, *Didymoplexis*, *Epipogium*, *Eulophia*, *Gastrodia*, and *Stereosandra* are also represented by fully mycoheterotrophic species. Arbuscular mycorrhizal mycoheterotrophs in Australasia belong to the genera *Burmannia*, *Gymnosiphon* (Burmanniaceae), *Thismia* (Thismiaceae), *Sciaphila*, *Andruris* (Triuridaceae), *Epirixanthes* (Polygalaceae), *Exacum* (Gentianaceae), and *Corsia* (Corsiaceae).

3.3.6.1 New Guinea

By far the largest part of Australasian rainforest is found on New Guinea, and this is where most Australasian mycoheterotrophs occur. The world's second largest island is home to arbuscular mycorrhizal species of *Burmannia*, *Epirixanthes*, *Exacum*, *Gymnosiphon*, *Andruris*, *Sciaphila*, and *Thismia*. The island is also the center of diversity of the little-known genus *Corsia* (Corsiaceae), where 23 of the 25 described species occur as endemics. Mycoheterotrophic orchids belong to the genera *Galeola*, *Lecanorchis*, *Pseudovanilla*, *Aphyllorchis*, *Didymoplexis*, *Epipogium*, *Eulophia*, and *Gastrodia*. In addition to the 23 species of *Corsia*, island endemics include *Aphyllorchis elata*, *A. exilis*, *A. torricellensis*, *Didymoplexis torricellensis*, *Gastrodia crassisepala*, *G. papuana*, *Lecanorchis bicarinata*, *L. ciliolata*, *L. neglecta*, *Pseudovanilla gracilis*, *P. vanilloides* (Orchidaceae), *Burmannia micropetala*, *Thismia appendiculata*, *Andruris wariana*, *Sciaphila quadribullifera*, *S. papillosa*, *Gymnosiphon affinis*, *G. oliganthus*, and *G. pauciflorus*.

3.3.6.2 Australia

Tropical rainforest once covered Australia, but as a result of the continued northward drift of Australia, coupled with global climatic cooling, the climate of Australia became much drier in the Middle and Late Miocene and Late Pliocene, resulting in a withdrawal of tropical rainforests from all but the northeast coast region of Queensland. This tiny tip of tropical rainforest contains ca. 15 species of mycoheterotrophic angiosperms in the genera *Aphyllorchis*, *Andruris*, *Corsia*, *Didymoplexis*, *Epipogium*, *Eulophia*, *Gastrodia*, *Pseudovanilla*, and *Thismia*. Endemic mycoheterotrophs are *Thismia yorkensis*, *Corsia dispar*, *Andruris australasica*, *Aphyllorchis anomala*, *A. queenslandica*, *Didymoplexis pachystomoides*, *Gastrodia crebrifolia*, *G. queenslandica*, and *G. urceolata*.

3.3.6.3 New Caledonia and Vanuatu

The Southwest Pacific Island group of New Caledonia is also part of Australasia, and the region is recognized as a global biodiversity "hotspot" (Myers et al. 2000), with a very high degree of plant endemism (Jaffré et al. 1998). New Caledonia formed part of the eastern margin of Gondwana, until it became separated by the Tasman Sea about 90 million years ago (Ma) (Wilford and Brown 1994). Thus, the flora of New Caledonia results from a Gondwanan origin and mainly evolved in isolation (Jaffré 1992), although volcanic islands between Australia and the New Caledonian region could have facilitated plant migration during the Neogene (Wilford and Brown 1994), and island chains are also implicated along the Norfolk and Reinga Ridges toward New Zealand during this time (Herzer et al. 1997). In contrast to the continental origin of New Caledonia, the Vanuatu archipelago is oceanic in origin, and its development results from tectonic events ranging from 11.2 to 2.0 Ma (Kroenke and Rodda 1984). The flora of New Caledonia includes relatively few mycoheterotrophic plants, and none of them are endemic to the region except for the sole putative mycoheterotrophic gymnosperm *Parasitaxus usta*. New Caledonian mycoheterotrophic flowering plants include three Triuridaceae species (*Sciaphila densiflora*, *S. corallophyton*, and *S. corniculata*) and three orchids (*Didymoplexis micradenia*, *Dipodium squamatum*, and *Epipogium roseum*). Burmanniaceae are absent from the flora of New Caledonia, but the mycoheterotroph *Burmannia lutescens* occurs on the neighboring Vanuatu archipelago (Yohan Pillon, pers. comm.), which represents the easternmost distribution record for the family. Other Vanuatu mycoheterotrophs are *Sciaphila arfakiana*, *S. aneitensis* (Triuridaceae), *Didymoplexis micradenia*, *D. pallens*, *Dipodium squamatum*, *Epipogium roseum*, and *Gastrodia cunninghamii* (Orchidaceae) (van de Meerendonk 1984; Govaerts et al. 2011).

3.3.7 Pacific Islands

The islands in the Pacific Ocean are composed mostly of volcanic emergents and coral atolls that arose from the sea in geologically recent times, many of them in the Pleistocene. They were created either by hotspot volcanism or as island arcs pushed upward by the collision and subduction of tectonic plates. The islands range from tiny islets, sea stacks, and coral atolls to large mountainous regions containing complex ecosystems. Only these larger islands harbor tropical rainforests that are potential habitats for mycoheterotrophs. The flora of the islands is comprised entirely from long-distance dispersal events and is generally characterized by a low diversity but high endemism (Carlquist 1967). For mycoheterotrophic plants, only a few widespread species in Burmanniaceae, Triuridaceae, and Orchidaceae have been able to colonize some islands. Burmanniaceae are only present on the Caroline Islands, where *Burmannia ledermannii*, *Gymnosiphon aphyllus*, *G. papuanus*, and *G. okamotoi* occur. The latter is endemic to the islands. For Triuridaceae, *Sciaphila arfakiana* and *S. consimilis* have been recorded on Fiji (van de Meerendonk 1984). The latter species is widespread in Southeast Asia and is also found on the Caroline Islands, together with *S. corallophyton* and *S. multiflora*. Triuridaceae reach their easternmost distribution on Futuna, where the widespread *Sciaphila aneitensis* occurs. In Orchidaceae, the widespread species *Didymoplexis micradenia* occurs on the Marianas, Niue, Samoa, Tonga, Wallis–Futuna, and Caroline Islands, *D. pallens* is known from Niue, *Stereosandra javanica* from Samoa, and *Epipogium roseum* from Fiji. None of these species are endemic to the region. In contrast, *Pseudovanilla ponapensis* is only known from the Caroline Islands, and *Pseudovanilla anomala* is endemic to Fiji, but it is unclear whether these species are (partial) mycoheterotrophs. There are no records of mycoheterotrophic plants from French Polynesia and Hawaii. Whether this is the result of their isolated position or the absence of certain habitat characteristics necessary for the establishment of mycoheterotrophic plants remains unknown.

3.3.8 Temperate Regions

Similarly to the tropics, mycoheterotrophs in temperate regions are mainly restricted to forests. In temperate regions, forest coverage mainly consists of coniferous, deciduous, or mixed forests, and all these forest types provide habitats for mycoheterotrophic plants. Temperate forests predominantly occur in the northern hemisphere, although the southern hemisphere has small pockets of temperate forest as well. Temperate forests of the northern hemisphere are located in eastern North America, western North America, Europe (including southwestern Asia), and eastern Asia (Fig. 3.6). Many flora and fauna elements have a disjunct distribution across these forest regions, which is illustrated by the similarities of biotas between eastern North America and temperate Asia (Wen 1999; Donoghue et al. 2001). This current disjunct distribution has been attributed to the historical existence of a widespread evergreen vegetation type ("boreotropical" forest) earlier during the Tertiary, when warm and wet climatic conditions prevailed over northern latitudes (Milne and Abbott 2002). In response to climatic cooling from the start of the Oligocene, deciduous elements moved southward forming a northern hemisphere flora (the "mixed mesophytic forest") that contained a mix of deciduous and evergreen trees with increasing numbers of associated understory herbs (Tiffney 1985; Milne and Abbott 2002). During the Late Miocene to Pliocene, global temperatures dropped and the flora retreated, leading to increased extinction particularly in western North America. Further depauperation of the flora occurred during the Quaternary glaciations, which had a strong impact on the European flora (Milne and Abbott 2002; Donoghue and Smith 2004).

In the southern hemisphere, temperate forests are restricted to small patches in southern South America, South Africa, Australia, and New Zealand. These forests are thought to have originated from southern temperate Gondwanan floristic elements. The sequential breakup of Gondwana started 165 Ma ago and resulted in a successive division of the ancestral biota. However, there has been a documented exchange of plants between the major landmasses following their breakup; for example, trans-Tasman dispersal between Australia and New Zealand appears to be quite common (Hill 2004; Sanmartin and Ronquist 2004).

The diversity of mycoheterotrophic plants in temperate regions is lower than in the tropics, with temperate mycoheterotrophs mainly belonging to Ericaceae and Orchidaceae. In contrast to the dominance of arbuscular mycorrhizal mycoheterotrophs in the tropics, mycoheterotrophic interactions in temperate regions generally rely on ectomycorrhizal fungi. Nevertheless, many predominantly tropical arbuscular mycorrhizal mycoheterotrophic families extend their distribution into subtropical and even temperate regions, particularly in Asia (e.g., *Thismia*, *Petrosavia*, *Sciaphila*).

3.3.9 North America

North America contains a large variety of different forest types, providing habitat for a very distinct group of mycoheterotrophs. Of a total of 30 fully mycoheterotrophic species in North America, only the two widespread species *Hypopitys monotropa* and *Monotropa uniflora* (Ericaceae) occur outside North America, indicating a high level of continental endemism. The distribution of the partial mycoheterotroph *Corallorhiza trifida* (Orchidaceae) extends only into temperate Eurasia. North American forests are particularly rich in ericaceous mycoheterotrophs: with the exception of *Cheilotheca* and *Monotropastrum*, all genera of ericaceous mycoheterotrophs occur here. Many Ericaceae genera are endemic to North America (*Monotropsis*, *Pterospora*), most occurring only in western North America (*Pityopus*, *Allotropa*, *Hemitomes*,

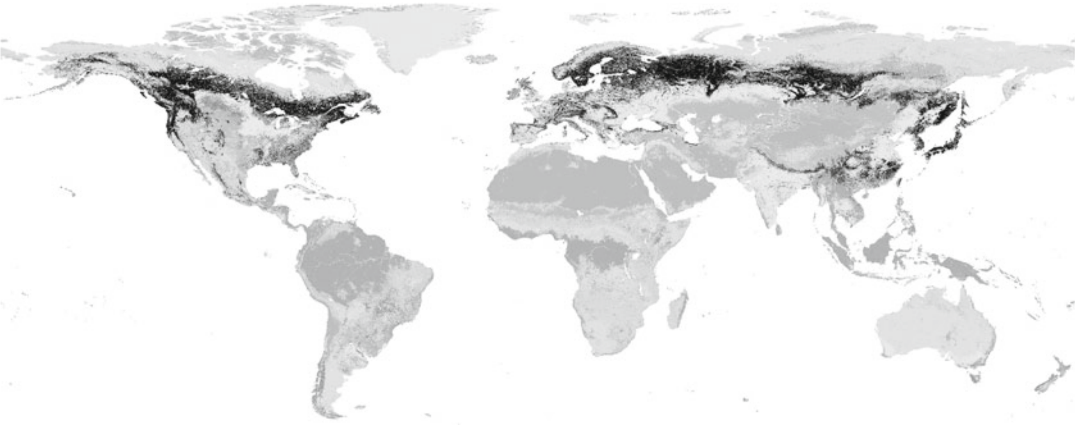

Fig. 3.6 Distribution of coniferous and mixed forest (*black*) in the temperate parts of the northern hemisphere. Map based on information obtained from NASA Earth Observations (2011)

Pleuricospora, *Sarcodes*). The only fully mycoheterotrophic species in *Pyrola* (Ericaceae), *P. aphylla*, is also endemic to North America.

North American mycoheterotrophic orchids include *Cephalanthera austiniae*, all *Corallorhiza* species, all *Hexalectris* species, and the partial mycoheterotroph *Liparis liliifolia.* As far as is known, these mycoheterotrophs are associated with ectomycorrhizal fungi. In contrast, the North American partially mycoheterotrophic Gentianaceae species of *Bartonia* and *Obolaria* are associated with arbuscular mycorrhizal fungi (Cameron and Bolin 2010). The full mycoheterotroph *Thismia americana* (Thismiaceae), which has been recorded from a prairie near Chicago, was probably also associated with arbuscular mycorrhizal fungi (see further). This species is probably extinct.

3.3.10 Europe

The temperate forests of Europe are less diverse in plant species than those of North America. This difference has been explained by greater survival of plant species in North America during the Quaternary glaciation, although some evidence indicates that floristic differentiation between Europe and North America started in the late Tertiary (Davis 1983). The diversity of mycoheterotrophic plants in Europe is likewise significantly lower than that of North America and temperate Asia. The coniferous, mixed, and deciduous forests of Europe harbor only seven mycoheterotrophic species, the ericaceous *Hypopitys monotropa* and six orchid species: *Neottia nidus-avis*, *Limodorum abortivum*, *L. rubriflorum*, *L. trabutianum*, *Corallorhiza trifida*, and *Epipogium aphyllum.* The distribution range of some of these species extends into North Africa and temperate Asia.

3.3.11 Temperate Asia

In temperate Asia, mycoheterotrophic flowering plants occur in coniferous, mixed, and deciduous forests. Toward the south, there is a transition from temperate through subtropical forests into the tropical rainforest of Indochina, allowing for influx of tropical mycoheterotrophic groups. Typical temperate elements are the genera *Hypopitys* and *Monotropa* (Ericaceae), of which both monotypic species are present in temperate Asia. Other ericaceous mycoheterotrophs *Monotropastrum humile* and *M. sciaphilum* occur in the subtropical zones of Asia. There is a relatively large diversity of fully mycoheterotrophic orchids in temperate and subtropical Asia. With about 13 species, *Neottia* is particularly species rich. Five species of *Aphyllorchis*, a genus with a center of diversity in tropical Asia, are found in South and Central China and Tibet. All tree species of *Epipogium* are found in temperate and subtropical Asia as well. *Yoania japonica* and *Y. prainii* are also present in the subtropical zone of Asia, as well as *Risleya atropurpurea.* In addition, the distribution of a few *Burmannia* (Burmanniaceae) species extends into Central China, Assam, and Nepal (e.g., *B. nepalensis*, *B. wallichii*, *B. itoana*, *B. cryptopetala*, *B. chinensis*).

3.3.12 Japan

The flora of Japan includes a large number of mycoheterotrophic plants. The wet subtropical evergreen forest in southern Japan is a habitat for many species of arbuscular mycoheterotrophs that belong to genera with a mainly tropical distribution: *Burmannia*, *Thismia*, *Petrosavia*, *Andruris*, and *Sciaphila.* Three species of *Oxygyne* (Thismiaceae) have been discovered in these forests as well, which is remarkable since the only other species of the genus is recorded from Cameroon. With ca. 25 species, the Japanese flora is also rich in fully mycoheterotrophic Orchidaceae. Genera with a mainly tropical distribution, as well as genera from temperate Asia, are represented in Japan. Japanese mycoheterotrophic orchids include *Cyrtosia septentrionalis*, *Erythrorchis altissima*, *Lecanorchis* spp., *Chamaegastrodia shikokiana*, *Odontochilus poilanei*, *Aphyllorchis montana*, *Cymbidium macrorhizon*, *Didymoplexiella siamensis*, *Epipogium japonicum*, *E. roseum*, *Eulophia zollingeri*, *Gastrodia* spp., *Neottia* spp., *Stereosandra javanica*, and *Yoania* spp. Lastly, three ericaceous mycoheterotrophs *Hypopitys monotropa*, *Monotropa uniflora*, and *Monotropastrum humile* occur in Japan as well.

3.3.13 South Chile and Argentina

Temperate forests in southern South America are located on the Pacific coast of southern Chile, on the west-facing slopes of the southern Chilean coast range, and the Andes Mountains in both Chile and Argentina down to the southern tip of South America (Patagonia). These wet *Nothofagus* forests are home to *Arachnitis uniflora* (Corsiaceae), an arbuscular mycorrhizal mycoheterotroph that also occurs in tropical Bolivia and on the Falkland Islands (Ibisch et al. 1996).

3.3.14 South Africa

In South Africa, forests have a patchy distribution and occur in frost-free areas with more than 725 mm rainfall during the wet season. Indigenous forest is the smallest biome in South Africa (Eeley et al. 1999). Only two mycoheterotrophic orchid species have been recorded from the South African flora. *Didymoplexis verrucosa* is endemic to KwaZulu-Natal. *Gastrodia sesamoides*, which occurs natively in South and East Australia, was introduced to South Africa and is naturalized in the Cape Province near Kirstenbosch (Linder and Kurzweil 1999; Linder et al. 2005; Cribb et al. 2010).

3.3.15 Temperate Australia, Tasmania, and New Zealand

The forests of temperate Australia and Tasmania comprise ca. eight species of mycoheterotrophic orchids, and all of them are endemic to this region. *Cryptostylis hunteriana*, *Burnettia cuneata*, and *Dipodium roseum* are endemic to southeast Australia, and the latter two also occur in Tasmania. *Erythrorchis cassythoides* and *Dipodium variegatum* are endemic to East Australia, and *Gastrodia lacista* is endemic to western Australia. Temperate Australia is also the only place in the world where the enigmatic underground orchid, *Rhizanthella*, is found. Three species of *Rhizanthella* are known: *R. gardneri* from southwest Australia and *R. slateri* and *R. omissa* from southeast Australia. In southwest Australia, *Rhizanthella* is found growing in much drier habitats than the eastern Australian species. The temperate rainforests and wet sclerophyll forests in New South Wales, Victoria, and

Tasmania are also home to the arbuscular mycorrhizal mycoheterotroph *Thismia rodwayi* (Thismiaceae). Another *Thismia* species, *T. clavarioides*, is only known from Morton National Park in New South Wales.

In New Zealand, mycoheterotrophs only occur on the North Island, mostly in coniferous podocarp forests and broadleaf evergreen forests. Apart from *Thismia rodwayi* (Thismiaceae) and *Danhatchia australis* (Orchidaceae), which also occurs in Australia, all New Zealand mycoheterotrophs are endemic and belong to Orchidaceae: *Corybas cryptanthus*, *Gastrodia cunninghamii*, and *G. minor* (Moore and Edgar 1970).

3.4 Biogeographic Patterns

3.4.1 General Patterns of Diversity

Most fully mycoheterotrophic angiosperms occur in the tropics, and—in terms of the number of species—Southeast Asia is the most important region. Southeast Asia contains more than twice the number of mycoheterotrophic species found in the Neotropics (Table 3.1). This difference is remarkable but is almost solely the result of the high number of mycoheterotrophic orchid species in Southeast Asia (Fig. 3.7). Indeed, the flora of the Neotropics includes only seven species of mycoheterotrophic orchids. With 17 species, the diversity of orchid species in Africa and Madagascar is only slightly higher. In tropical Asia, the mycoheterotrophic orchid diversity peaks, with 27 species in Australasia and ca. 100 species in Southeast Asia. Most of these species belong to species-poor genera, although a few genera, such as *Lecanorchis*, *Aphyllorchis*, and *Gastrodia*, are particularly species rich. Mycoheterotrophic orchids associate with saprotrophic or ectomycorrhizal fungi, while tropical tree species are generally associated with arbuscular mycorrhizal fungi (Smith and Read 2008). However, in Southeast Asia—and to a lesser extent also in Australasia—tropical forests are dominated by Dipterocarpaceae trees which are known to form associations with ectomycorrhizal fungi (Lee 1990). These mycorrhizal networks

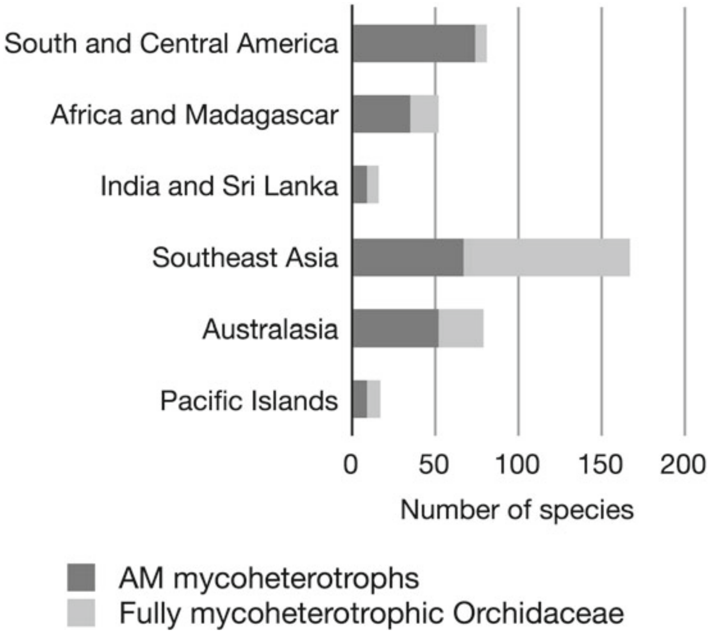

Fig. 3.7 Comparison of the species richness between major rainforest regions for arbuscular mycorrhizal (AM) mycoheterotrophs and mycoheterotrophic Orchidaceae, which associate with ectomycorrhizal and saprotrophic fungi

are potential “hosts” for ectomycorrhizal mycoheterotrophic orchids: indeed, mycoheterotrophic orchids from a dipterocarp forest in Thailand have been found to obtain carbon from dipterocarps through shared ectomycorrhizal fungi (Roy et al. 2009). Thus, it is possible that the dominance of ectomycorrhizal trees in Asian rainforests explains the high number of mycoheterotrophic orchids in these forests.

Differences between major rainforest regions in the number of arbuscular mycorrhizal mycoheterotrophs are less pronounced. The Neotropics have the most species, but in comparison with floras of Southeast Asia and Australasia, which have in general less plant species but also cover a smaller area, species diversity of AM mycoheterotrophs is more pronounced in tropical Asia (Fig. 3.7). However, the Neotropics are home to 19 genera of AM mycoheterotrophs, Africa and Madagascar have 12 genera of AM mycoheterotrophs, and Southeast Asia and Australasia only have nine and eight genera, respectively, or ten when considered as one area. Generic diversity in the Neotropics is particularly high in Burmanniaceae and Triuridaceae (Table 3.2). It has been hypothesized that Burmanniaceae originated in South America (or western Gondwana) and only reached the Old World during the Eocene (Merckx et al. 2008). The early diversification of Burmanniaceae in the Neotropics may explain the comparatively high number of genera in this region.

In the temperate zone, East Asia and Japan are the most species-rich regions for mycoheterotrophic plants. Their floras contain a mix of temperate and subtropical elements and are particularly rich in fully mycoheterotrophic orchids. Influx from the tropics probably also explains the high number of arbuscular mycorrhizal mycoheterotrophs in these regions (e.g., species of *Burmannia*, *Thismia*, *Sciaphila*, *Petrosavia*). The number of mycoheterotrophic species in North America is only slightly lower than in Asia and Japan. The diversity of Ericaceae in North America is remarkable, and the region is also relatively rich in mycoheterotrophic orchids (e.g., *Corallorhiza*, *Hexalectris*). The diversity of mycoheterotrophs in Europe is relatively low. Besides a few mycoheterotrophic orchids, European forests only contain the most widespread ericaceous mycoheterotroph *Hypopitys monotropa* and no arbuscular mycorrhizal species. Perhaps this is due to the lack of an historical connection with tropical floras, restricting all present-day mycoheterotrophic plants to be relictual elements of taxa with an ancient boreotropical distribution.

In the southern hemisphere, the much higher proportion of sea to land creates conditions favoring temperate rainforest on west-facing coasts (Beard 1990). The identity of mycoheterotrophic plants in these forests is very different from that of their northern hemisphere counterparts, and the species diversity is lower. Most mycoheterotrophs in the forests of the southern hemisphere belong to groups with mainly tropical distributions, indicating independent tropical origins of the southern hemisphere mycoheterotrophs. Southern hemisphere mycoheterotrophs include both species that are living on arbuscular mycorrhizal fungi (*Thismia*, *Arachnitis*) and orchids linked with ectomycorrhizal or saprotrophic fungi, but mycoheterotrophic Ericaceae are absent from the southern hemisphere.

3.4.2 Widespread Distributions

A few tropical mycoheterotrophic families are particularly widespread. Burmanniaceae and Triuridaceae can be found in all rainforest regions of the world (Table 3.2). Thismiaceae have a similar distribution but are absent from Madagascar and the Pacific Island region. Mycoheterotrophic Gentianaceae and Orchidaceae are also found in nearly all tropical regions, but their mycoheterotrophic species have evolved independently in different lineages. These lineages show little overlap in their distribution ranges, and it is likely that mycoheterotrophy has evolved on different continents independently. At the genus level, *Sciaphila* (Triuridaceae) has the most widespread distribution, and it is only absent from East Africa, Madagascar, and Southwest India. However, in these regions, Triuridaceae are represented by *Seychellaria* and *Hyalisma*, which may be

Table 3.2 List of families with fully mycoheterotrophic species present in each rainforest region

Central and South America	Africa and Madagascar	India and Sri Lanka	Southeast Asia	Australasia	Pacific Islands
Burmanniaceae (8/24)	Burmanniaceae (3/10)	Burmanniaceae (1/4)	Burmanniaceae (2/15)	Burmanniaceae (2/8)	Burmanniaceae (2/4)
Corsiaceae (1/1)	Gentianaceae (2/2)	Orchidaceae (4/7)	Corsiaceae (1/1)	Corsiaceae (1/26)	Orchidaceae (5/8)
Ericaceae (1/2)	Iridaceae (1/2)	Thismiaceae (2/2)	Ericaceae (1/2)	Gentianaceae (1/1)	Triuridaceae (2/5)
Gentianaceae (2/19)	Orchidaceae (7/17)	Triuridaceae (2/3)	Gentianaceae (1/4)	Orchidaceae (9/28)	
Orchidaceae (4/7)	Thismiaceae (2/13)		Orchidaceae (21/99)	Polygalaceae (1/2)	
Thismiaceae (2/14)	Triuridaceae (4/8)		Petrosaviaceae (1/3)	Thismiaceae (1/3)	
Triuridaceae (6/17)			Polygalaceae (1/5)	Triuridaceae (2/12)	
			Thismiaceae (1/24)		
			Triuridaceae (2/15)		

For each family the number of present genera/species is indicated between brackets congeneric with *Sciaphila. Gymnosiphon* (Burmanniaceae) is extremely widespread in the tropics as well, yet has not been recorded in India, Sri Lanka, and Australia. The distribution of *Burmannia* (Burmanniaceae) is also pantropical, although the genus is represented in East Africa and Madagascar by chlorophyllous species only. There is only one fully mycoheterotrophic *Burmannia* species in the Neotropics, which limits the South American distribution range of *Burmannia* mycoheterotrophs. In Orchidaceae, there are no tropical mycoheterotrophic genera that occur both in the Old and the New World, although a few Old World genera are extremely widespread (e.g., *Epipogium*, *Didymoplexis*, *Eulophia*).

In the temperate zones, Monotropoideae (Ericaceae) are extremely widespread, spanning the entire northern temperate region and extending into the tropics both in South America and Southeast Asia. *Hypopitys* is the most widespread genus of this group, and its distribution is almost identical to the entire Monotropoideae. *Corallorhiza* (Orchidaceae) is also widespread and occurs both in the temperate zone of the Old and the New World. In the Old World, however, the genus is represented only by *C. trifida*, which retains chlorophyll but obtains most of its carbon from fungi. Mycoheterotrophic *Neottia* species (Orchidaceae) also have a widespread distribution, ranging from Europe and North Africa into Asia and Japan.

3.4.3 Widespread Species

While many species of mycoheterotrophic plants have restricted distributions (see "Rarity"), some species have remarkable widespread distribution ranges. In the Neotropics, *Apteria aphylla* (Burmanniaceae) and *Voyria aphylla* (Gentianaceae) are particularly widespread, and their distribution almost completely overlaps with that of the entire neotropical rainforest biome. However, the Old World tropics are home to species with an even wider distribution especially given the challenges to dispersal across Old World tropical forests. The orchid species *Epipogium roseum* has the most widespread distribution of all tropical mycoheterotrophic plants. The species occurs throughout tropical Africa, India and Sri Lanka, South China, Japan, Southeast Asia, Australasia, and the Pacific Islands. Remarkably, *Epipogium roseum* has not been reported from Madagascar. Another widespread mycoheterotrophic orchid is *Didymoplexis pallens*, which occurs from Afghanistan to India, Southeast Asia, Australasia, and the Pacific Islands. The distribution of *Eulophia zollingeri* is only slightly more restricted and covers Sri Lanka, South China, Southeast Asia, Japan, and Australasia.

Hypopitys monotropa (Ericaceae) and the partial mycoheterotroph *Corallorhiza trifida* have boreotropical distributions that cover almost the entire northern temperate region. The distribution of *Monotropa uniflora* is slightly more restricted as this species is absent from Europe and most of temperate Asia. The orchid *Epipogium aphyllum* is extremely widespread in the temperate regions of Europe, Asia, and Japan but is not known from North America.

While widespread species in the Neotropics are members of lineages that are associated with arbuscular mycorrhizal fungi (e.g., *Apteria aphylla*, *Voyria aphylla*), widespread species in the Paleotropics are generally orchids that are associated with saprotrophic fungi (e.g., *Epipogium roseum*, *Eulophia zollingeri*). Widespread northern temperate species are all associated with ectomycorrhizal fungi (e.g., *Hypopitys monotropa, Monotropa uniflora*, *Corallorhiza trifida*, *Epipogium aphyllum*).

3.4.4 Disjunct Distribution Patterns

The distributions of a few groups of mycoheterotrophic plants show remarkable disjunctions (i.e., distributions that are geographically separated). On familial level, the distribution of Corsiaceae is intriguing: *Arachnitis* grows in Argentina, Chile, Bolivia, and the Falkland Islands, *Corsia* has its center of diversity in New Guinea and the Solomon Islands, and *Corsiopsis* was collected once in southern China (Fig. 3.8a). A Southern American–Australasian–Chinese disjunction is unusual in flowering plants, although similar patterns are observed at both familial

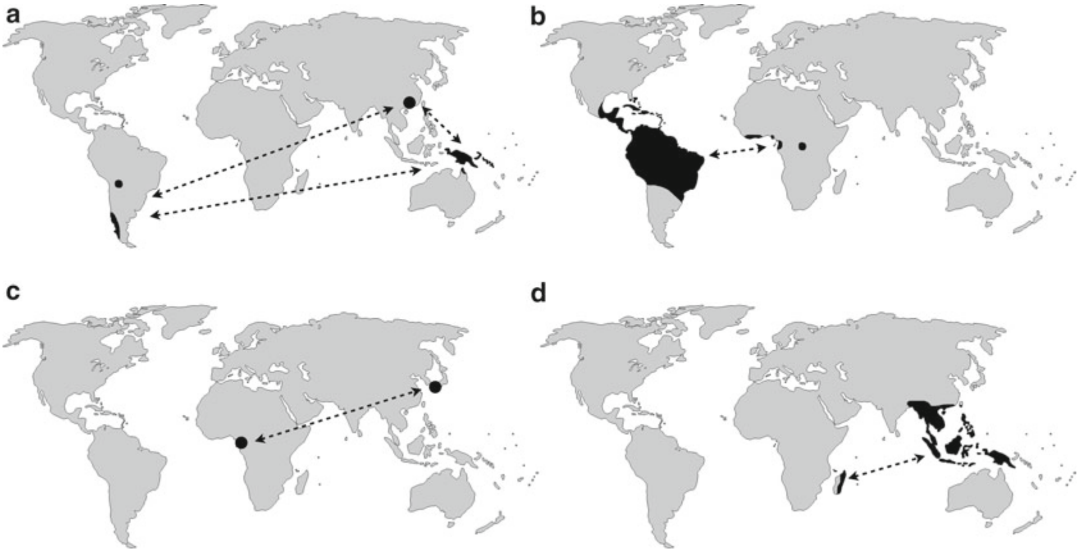

Fig. 3.8 Examples of disjunct distribution patterns in mycoheterotrophic plants. (**a**) The distribution of Corsiaceae. The *large dot* represents the single locality of *Corsiopsis*. Note the disjunct distribution of *Arachnitis* in South America. (**b**) The trans-Atlantic distribution of *Voyria* (Gentianaceae). (**c**) Species of *Oxygyne* (Burmanniaceae) have only been found in Cameroon and Japan. (**d**) *Galeola* (Orchidaceae) is widespread in Southeast Asia and Australasia, but one species is endemic to Madagascar and the Comores. See text for further discussion

(Stylidiaceae; Good 1974) and generic (*Coriaria*; Coriariaceae) level (van Balgooy 1966; Zhang et al. 1999). The South American–Australasian disjunction (*Arachnitis*–*Corsia*) in the family has been hypothesized to result from a Gondwanan tectonic link through Antarctica (Zhang et al. 1999). However, there is doubt that all genera of Corsiaceae are closely related (Neyland and Hennigan 2003; Petersen et al. 2006), and molecular phylogenetic studies are needed to resolve this issue.

At the generic level, disjunct distributions are quite common in full mycoheterotrophs. An interesting disjunct pattern is observed in *Voyria* (Gentianaceae), which comprises 18 species from tropical South and Central America and one species from tropical West Africa (Fig. 3.8b). It has been hypothesized that this pattern is either the result of a long-distance dispersal event or the relictual distribution of a previously continuous, boreotropical distribution across the North Atlantic (Albert and Struwe 1997). Due to the estimated origin of the Gentianaceae (ca. 50 Ma; Yuan et al. 2003), it is unlikely that this distribution is caused by ancient continental drift (vicariance). The small dustlike seeds of *Voyria* make a dispersal event plausible, although Albert and Struwe (1997) note that the seeds of the African *Voyria* species and its presumed neotropical sister species are not among the most highly modified for wind dispersal compared to other species in the genus. Also, a scenario of migration through Laurasia during the Eocene (e.g., Davis et al. 2002) cannot be excluded. Disjunct relationships between Africa and the Neotropics are not uncommon. Very similar South American–West African disjunctions are present in the plant families Rapateaceae and Bromeliaceae, which have been explained as the result of long-distance dispersal events rather than continental drift (Givnish et al. 2004; Renner 2004).

In Thismiaceae, some notable disjunct distribution patterns are found in *Thismia* and *Oxygyne*. *Thismia* is widespread in tropical South America, Southeast Asia, and Australasia but is absent from Africa. The occurrence of *Thismia* in the Chicago area, many thousands of kilometers from other *Thismia* populations, still remains unexplained (see below). The distribution of *Oxygyne*, with records only from Cameroon and Japan, also represents an extreme case of a geographic disjunction unique in flowering plants (Fig. 3.8c).

However, this distribution pattern has to be interpreted with caution as the relationships between the African and Japanese specimens of *Oxygyne* are in need of close investigation.

In Triuridaceae, *Seychellaria* occurs in Madagascar, the Seychelles, the Comores, and Eastern Africa (Tanzania). Vollesen (1982) suggested that this distribution pattern results from the breakup of Gondwana during the Cretaceous. But Madagascar and Africa have been separated since ca. 120 Ma (Rabinowitz et al. 1983; Ali and Aitchison 2008), and most African–Malagasy plant disjunctions have been explained by dispersal (Yoder and Nowak 2006). Thus, dispersal by wind or water (Renner 2004; Ali and Huber 2010), perhaps aided by the occurrence of land bridges (McCall 1997), may offer a more plausible explanation for the current distribution of *Seychellaria.* Other Triuridaceae genera have disjunct distribution ranges as well, although the pattern may be influenced by collecting bias: *Kupea* occurs both in Cameroon and Tanzania, but the genus was only recently discovered, and it is possible that populations exist connecting these two regions. The South American genus *Triuris* has a patchy distribution with large gaps between collection sites, but this also may reflect a sampling artifact rather than its actual distribution.

Geographic disjunctions are also observed in several mycoheterotrophic lineages within Orchidaceae. Species of *Galeola*, which are all putative full mycoheterotrophs, occur in tropical forests in Southeast Asia and New Guinea. However, one species, *G. humboltii*, is endemic to Madagascar and the Comoros (Fig. 3.8d). The achlorophyllous species of *Cephalanthera* occur as disjunct between North America and Southeast Asia, but the distribution of achlorophyllous *Cephalanthera* species overlaps with that of the achlorophyllous species and also covers intervening areas. It is not yet clear whether full mycoheterotrophy arose more than once in the genus. In this case, the apparent disjunct distribution may in fact be indicative of multiple origins of mycoheterotrophy in a particular lineage.

In Australia, *Rhizanthella gardneri* from western Australia is separated from its relatives *R. omissa* and *R. slateri* in southeastern Australia by 3,500 km of desert. Dixon (2003) suggests that *Rhizanthella* may have been present in the paratropical forests that once covered the Australian continent. These forests disappeared when the climate of Australia became much drier in the Middle and Late Miocene and Later Pliocene, possibly separating *Rhizanthella* populations to their current distribution.

Lastly, in liverworts, the mycoheterotrophic species *Aneura mirabilis* (Aneuraceae) occurs in northwestern Europe and Greenland. A species thought to be closely related to *Aneura mirabilis* has been reported from Costa Rica providing an interesting disjunction (Crum and Bruce 1996). However, it remains to be confirmed if the species from Costa Rica is the closest relative of *Aneura mirabilis* or if this disjunct distribution is also the result of convergent evolution of mycoheterotrophy in *Aneura.*

At the species level, it is mainly tropical mycoheterotrophic species that have disjunct distributions. In many cases (e.g., tropical species in Thismiaceae and Triuridaceae), these may represent sampling artifacts because the species are known from only very few collections. A few "real" disjunctions are notable. *Thismia rodwayi* (Thismiaceae) occurs on Tasmania, mainland Australia (Victoria, New South Wales, and Queensland), and the North Island of New Zealand. This distribution may be the result of long-distance seed dispersal but can also be interpreted as a relict of a widespread ancestor (e.g., Heads 2009). It is doubtful whether there still is genetic exchange between the populations on different landmasses. Another disjunction can be found in the distribution of *Arachnitis uniflora* (Corsiaceae), where Bolivian populations are separated from populations in southern Argentina, southern Chile, and the Falkland Islands by a 2,000–km-broad-belt of vegetation types that are clearly unsuitable habitat for *Arachnitis*: the Atacama desert, high mountain deserts and grasslands of the Andes, dry forests, the shrubby "monte" vegetation, and the Patagonian grasslands (Ibisch et al. 1996). While recent long-distance dispersal remains a possible explanation for this pattern, Ibisch et al. (1996) hypothesized that the current gap was bridged along the Andes by islands of montane forests during glacial times (18,000–19,000 years ago (ya)) allowing *Arachnitis* to migrate into Bolivian tropical montane forests when the postglacial era started (10,000–11,000 ya) (Ibisch et al. 1996).

Hypopitys monotropa and *Monotropa uniflora* (Ericaceae) have remarkable transoceanic distribution ranges as well: the two species are found in temperate zones on both sides of the Pacific Ocean. *Monotropa uniflora* grows in large parts of North America extending into montane regions of Central and South America. It also occurs in Asia, where it is found in Japan, southern China, India to Nepal, and Bhutan (Wallace 1975). *Hypopitys monotropa* has an even wider distribution that mainly overlaps with that of *M. uniflora* but also includes temperate Europe. Thorne (1972) categorized this distribution as "circumboreal." Although there are no divergence time estimates for these species, migration through Beringia, a land bridge that connected North America and temperate Asia at various times during the Pleistocene ice ages, seems the most likely explanation for this distribution pattern (Donoghue and Smith 2004).

The partial mycoheterotroph *Corallorhiza trifida* (Orchidaceae) also has a circumboreal distribution, while all other *Corallorhiza* species are restricted to the New World. *Corallorhiza trifida* is not the earliest diverging species in the genus (Freudenstein and Senyo 2008; Barrett and Freudenstein 2008) and possibly dispersed through Beringia, similar to the dispersal hypothesized for both *Monotropa* and *Hypopitys* (see above).

3.5 Biogeographic History

3.5.1 Distributions of Families and Genera: Vicariance Versus Long-Distance Dispersal

In his treatment of the Burmanniaceae, Adolf Engler noted the transoceanic distribution of several genera and assumed that these genera must be extremely old: "Aus dem Vorkommen der Gattungen *Burmannia, Gymnosiphon, Dictyostega* und *Thismia* in der alten und neuen Welt ergiebt sich, dass die Familie der Burmanniaceae sehr hohen Alters sein muss und dass höchstwahrscheinlich in der Tertiärperiode ihre Verbreitung sich bis nach den Polen hin erstreckt hat" (Engler 1888, p. 46). Written at a time when the Earth's geography was assumed to have been stable, ancient dispersal across the poles seemed the only possible explanation for the widespread distribution of these genera. In 1915, the German meteorologist Alfred Wegener published his theory of continental drift (Wegener 1915), although, due to the lack of convincing mechanisms that might have caused the movement and splitting of huge landmasses, his theory only became widely accepted in the 1960s after the discovery of plate tectonics. From that time, the fragmentation of Gondwana became an appealing explanation for the widespread and disjunct distribution patterns observed in many groups of plants (Raven and Axelrod 1974) and has been used to explain the disjunct distribution of Corsiaceae (Zhang et al. 1999) and *Seychellaria* (Vollesen 1982). However, the application of molecular dating of lineage divergences has suggested that most cases of transoceanic distributions are unlikely to be the result of tectonic vicariance simply because the lineages are too young to have been dispersed through ancient land connections (Renner 2004; de Queiroz 2005).

The lack of fossil data and hypotheses of phylogenetic relationships have prevented detailed studies on the biogeographic histories of most mycoheterotrophic groups to date. There is only one series of fossils that may be assigned to an extant mycoheterotrophic lineage. These fossils are from the Late Cretaceous (about 90 Ma) and were found in New Jersey (Gandolfo et al. 1998). A phylogenetic analysis based on morphological characters placed the two fossil genera *Mabelia* and *Nuhliantha* within extant Triuridaceae (Gandolfo et al. 2002). However, it remains questionable whether these plants were in fact mycoheterotrophic because the fossilized material only consists of flowers (Gandolfo et al. 2002). Moreover, the fossilized pollen lacks distinctive features of pollen of extant members of the Triuridaceae (Furness et al. 2002). If the fossils represent genuine remnants of Triuridaceae, they

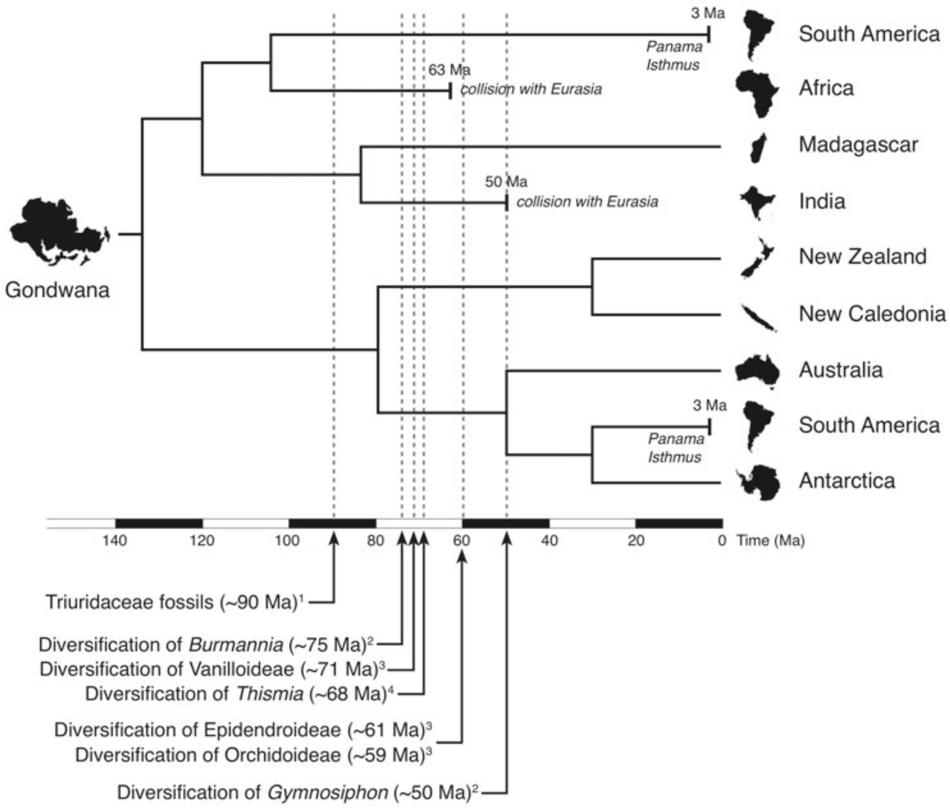

Fig. 3.9 Geological area cladogram showing the progressive breakup of Gondwana. *Vertical lines* indicate collisions between landmasses. South America is shown twice to illustrate its separation from both Africa and Antarctica. Representations of landmasses are not drawn to scale. Cladogram modified from Sanmartin and Ronquist (2004) and Cox and Moore (2010). [1] Age estimate from Gandolfo et al. (2002). Fossils were found in North America (Laurasia). [2] Mean molecular clock estimate taken from Merckx et al. (2008). [3] Molecular clock estimates of crown node ages of Orchidaceae subfamilies taken from Ramirez et al. (2007). [4] Mean molecular clock estimate from Merckx et al. (2010a). In this study, *Thismia* is paraphyletic and includes *Haplothismia* and *Tiputinia*

show that the family occurred at higher latitudes than today, at least during the Late Cretaceous when the climate was warmer than present. Also, if major Triuridaceae lineages had diverged by the Late Cretaceous, the breakup of Gondwana may have played a significant role in the distribution of the family (Fig. 3.9). Nevertheless, the occurrence of *Sciaphila* species on isolated oceanic islands (e.g., Bonin, see Fosberg and Sachet 1980; Fiji, see van de Meerendonk 1984) indicates that long-distance dispersal is certainly an important factor in the widespread distribution of this genus and probably for Triuridaceae in general.

In the absence of fossil data, divergence time estimates for biogeographic reconstructions can be obtained through broadscale molecular clock analyses which allow for inclusion of fossil data from distant groups or by using secondary calibration points. These strategies have been used to investigate the biogeographic history of Burmanniaceae (Merckx et al. 2008). The obtained age estimates suggest that Burmanniaceae genera are relatively ancient and diverged from each other during the Cretaceous probably in South America. However, the obtained hypothesis suggests that the widespread genera *Burmannia* and *Gymnosiphon* reached their transoceanic distribution range during the Eocene, when the breakup of Gondwana was well under way (Fig. 3.9). This demonstrates that both genera obtained their current pantropical distribution by dispersal, probably aided by various land bridges. In particular, dispersal of *Burmannia* and *Gymnosiphon* out of South America may have been possible by "boreotropical" migration routes: during the Eocene, global temperatures peaked, and tropical vegetation occurred at high latitudes. This allowed for migration of tropical flora between the Neotropics and the Paleotropics over the "North Atlantic Land Bridge" (Tiffney 1985; Davis et al. 2002). The disjunct distribution of *Voyria* (Gentianaceae) between the Neotropics and Africa has also been explained as a relict of an ancient boreotropical distribution (Albert and Struwe 1997; see above). Similarly, molecular clock analyses suggest a Cretaceous origin for Thismiaceae, but diversification occurred well after the breakup of Gondwana, rendering a "Gondwanian aborigine" explanation for its widespread distribution unlikely (Merckx and Bidartondo 2008; Merckx et al. 2010a; Fig. 3.9).

In Orchidaceae, mycoheterotrophy evolved multiple times independently in subfamilies Vanilloideae, Orchidoideae, and Epidendroideae, all of which diversified after the start of the breakup of Gondwana (Ramirez et al. 2007; Fig. 3.9; Chap. 5). Thus, any mycoheterotrophic genus in Orchidaceae with a distribution that covers multiple Gondwanan fragments must have acquired their distribution through dispersal rather than vicariance. The widespread genus *Gastrodia*, for instance, with a distribution that covers tropical Africa, Madagascar, Southeast Asia, Australasia, and the Pacific Islands, belongs to the Epidendroideae. *Gastrodia* therefore diverged and diversified after the breakup of Africa, Madagascar, and India (Fig. 3.9) and must have migrated by long-distance dispersal. Similar observations can be made for widespread genera *Didymoplexis*, *Galeola*, *Epipogium*, *Eulophia*, and *Gastrodia*. In addition, distributions that include oceanic islands must have been the result of long-distance dispersal (e.g., *Stereosandra*).

In conclusion, widespread lineages of mycoheterotrophic plants are generally too young to have acquired their distribution by tectonic vicariance. In some cases, temporary land bridges may have aided migration between fragments of Gondwana. However, we hypothesize that transoceanic dispersal has been the most important factor in the widespread distributions of mycoheterotrophic plants. Most mycoheterotrophic plants produce large amounts of small dustlike seeds which promotes dispersal and increases the likelihood of reaching suitable microsites for recruitment (Eriksson and Kainulainen 2011).

3.5.2 Species Distributions

Only few phylogeographic studies on fully mycoheterotrophic plants have been carried out. Recent phylogeographic studies on *Hypopitys monotropa* in North America (Beatty and Provan 2011a) and Europe (Beatty and Provan 2011b) provide the first detailed hypotheses about the glacial history of a mycoheterotrophic plant species (see also Chap. 6). Population genetic data and ecological niche modeling suggest that the current east–west disjunct distribution of *H. monotropa* in North America results from the existence of separate eastern and western refugia during the last glaciation. In Europe, *H. monotropa* probably recolonized northern Europe from refugia in the Balkans and southern Europe, a scenario that is suggested for many European taxa (Provan and Bennett 2008). The high species diversity of mycoheterotrophic plants in tropical postulated glacial refugia (see further) suggests that glacial and interglacial cycles that characterized the Quaternary period (ca. 2.6 Ma to present) have had a significant effect on the distributions of tropical mycoheterotrophic species as well.

3.6 Habitat Characteristics

3.6.1 Light

Most mycoheterotrophic plants grow in forests with a dense overstory that produces deep shade. Probably due to the lack of light, these microhabitats often have little or no herbaceous ground flora (Leake 1994; Cheek and Williams 1999). Since mycoheterotrophs do not require light to grow, the occurrence of most of these plants to deeply shaded sites lacking herbaceous autotrophs suggests their mode of life evolved to provide escape from competitive exclusion in the shaded conditions of forest understory habitats (Bidartondo et al. 2004). Indeed, in partially mycoheterotrophic orchids, it has been shown that low light levels result in strong mycoheterotrophy, while higher irradiances successively drive the orchids toward autotrophy (Preiss et al. 2010).

3.6.2 Water

Besides their preference for low-light habitats, the availability of water seems an important feature for mycoheterotrophic plant habitats. Bakshi (1959) noted that *Pterospora* is particularly associated with moist soils. Summerhayes (1951) assumed that a moist but well-drained soil is thought to favor the fungal symbiont of *Epipogium aphyllum.* Mycoheterotrophic plants from tropical rainforests seem to prefer local habitats with very moist soils as well (Maas et al. 1986; Cheek and Williams 1999). Moreover, some species are often found near perennial or seasonable streams (Maas et al. 1986; Cheek and Williams 1999; Taylor and Roberts 2011). In Africa, areas with a high diversity of mycoheterotrophic plants seem to overlap with postulated rainforest refugia (Cheek and Ndam 1996). The occurrence of these refugia is strongly correlated with rainfall as well (Linder 2001), indicating minimal seasonality and a stable, moist environment year-round. In general, mycoheterotrophs seem to prefer habitats with high rainfall and short dry seasons. For example, on Mount Kupe, one of the richest sites for mycoheterotrophic plants in Africa, annual rainfall exceeds 4,000 mm with only 3 months with less than 100 mm precipitation (Hofer et al. 2000). Similarly, Reserva Ducke in Brazil receives over 2,000 mm of rainfall and has a dry season of 3 months (Iriondo and Latrubesse 1994; ter Steege et al. 2003). There is some evidence that mycoheterotrophic plants are sensitive to desiccation. In dry summers, the flowering stems of *Monotropa uniflora*, *Hypopitys monotropa*, and *Neottia nidus-avis* suffer severely from drought and often fail to expand before drying out (Snetselaar and Whitney 1990; Leake 1994). Klooster and Culley (2009) observed that a drought in the summer and fall of 2007 likely contributed to the overall decline in reproductive effort and output of *Monotropa* with some populations experiencing 100% floral abortion.

3.6.3 Soil Types

Both in temperate and tropical zones, mycoheterotrophic plants occur on a variety of soil types, including organic soils, clay, loam, and white sand (Wallace 1975; Maas et al. 1986; Maas and Ruyters 1986). They generally prefer acidic soils. Reported soil pH values for mycoheterotrophic habitats in temperate regions range from 5.2 to 6.2 (Wallace 1975; Gebauer and Meyer 2003; Bougoure et al. 2008), but Merckx et al. (2010b) reported a soil pH of 3.8 at a tropical rainforest site in French Guiana where *Dictyostega* and *Voyria* species were found. Mycoheterotrophs are often found in places with a thick layer of decaying leaf litter (Graham 1953; Paul 1964; Van Royen 1972; Richards 1976; Maas and Ruyters 1986). In some cases, their flowers fail to emerge through this layer, for example, *Monotropsis* (Copeland 1939), *Thismia rodwayi* (Campbell 1968), *Epipogium* and *Neottia* spp. (Davies et al. 1988). *Rhizanthella* species remain entirely underground when flowering and fruiting (George 1980).

The roots of some species, for example, *Voyria rosea* and *Campylosiphon purpurascens*, can penetrate the soil to a depth of 20 cm and more (Maas et al. 1986; VSFTM pers. oberv.). Contrarily, the roots of a few species (e.g., *Voyria aphylla*, *V. flavescens*, *V. primuloides*, *Afrothismia foertheriana*) are entirely located in the uppermost soil strata, which consists of lose decaying leaf litter (Franke 2002; Franke et al. 2004; VSFTM and CDS pers. observ.).

3.6.4 Elevation

Mycoheterotrophic plants occur from sea level to montane forests generally up to 2,000 m. In North America, Monotropoideae can occur up to

4,000 m (Wallace 1975). In the Neotropics, *Apteria*, *Dictyostega*, and *Gymnosiphon* species are sometimes found above 2,000 m (Maas et al. 1986). In East Africa, mycoheterotrophs often occur at high elevations; *Epipogium roseum* is recorded from Mount Kilimanjaro at 2,500 m (Cheek and Williams 1999). In New Guinea, species of *Corsia* generally inhabit forests between 900 and 1,500 m, extending into the upper part of lowland forest and into montane forest (Van Royen 1972).

3.6.5 Plant Communities

Mycoheterotrophic plants occur in a variety of forest communities. In temperate zones, Monotropoideae occur in forests dominated by conifers (pines and cypress), beech, and oak (Wallace 1975; Ogura-Tsujita et al. 2009). Similarly, fully mycoheterotrophic orchids are generally found in forests dominated by pines, beech, and oak trees (Gebauer and Meyer 2003; Bidartondo et al. 2004; Zimmer et al. 2008; Taylor and Roberts 2011). These forests tend to have higher pH soils than other temperate forest habitats.

Information on plant communities is purely anecdotal for species that occur in the tropics. In the Neotropics, species of *Gymnosiphon* (Burmanniaceae) are often found in *Mora* forest (Maas et al. 1986). In West Africa, *Afrothismia* (Thismiaceae) occurs in proximity of a wide variety of rainforest trees, including species of *Cola*, *Diospyros*, and *Tabernaemontana* (Franke 2004; Sainge et al. 2005; Dauby et al. 2007). Tropical mycoheterotrophic orchid species of *Aphyllorchis* and *Cephalanthera* have been found in Fagaceae and Dipterocarpaceae forest in Thailand (Roy et al. 2009). In Southeast Asia, mycoheterotrophic plants are sometimes found in bamboo thickets, for example, *Epirixanthes* (Chen et al. 2008), *Thismia* (Chantanaorrapint 2008), and *Gastrodia confusa* (Ogura-Tsujita et al. 2009).

Arbuscular mycorrhizal mycoheterotrophs are sometimes reported from forest communities dominated by ectomycorrhizal trees. In New Guinea, species of *Corsia* (Corsiaceae), for example, are mostly found in beech and oak forests (Van Royen 1972). In Southeast Asia, species of *Thismia* are often collected from forest dominated by Dipterocarpaceae or Fagaceae trees (Jarvie 1996; Yang et al. 2002; Tsukaya and Okada 2005). In Japan, *Oxygyne shinzatoi* (Thismiaceae) has been found in *Castanopsis* forest (Yokoyama et al. 2008). However, in Argentina, *Arachnitis uniflora* (Corsiaceae) was found to link with the same arbuscular mycorrhizal fungi as *Osmorhiza chilensis* (Apiaceae), *Austrocedrus chilensis* (Cupressaceae), and *Nothofagus dombeyi* (Nothofagaceae) (Bidartondo et al. 2002). The latter species had been previously reported as ectomycorrhizal (Fontenla et al. 1998).

A very strong preference toward a particular plant community is observed for the underground orchid *Rhizanthella gardneri* (Orchidaceae), which only occurs in *Melaleuca uncinata* thickets in West Australia (Bougoure et al. 2008). In Tasmania, *Thismia rodwayi* (Thismiaceae) is always found in wet forest dominated by *Eucalyptus* trees (Wapstra et al. 2005).

3.6.6 Exceptional Habitats

There are plenty of exceptions to the general habitat preferences listed above. In the Neotropics, *Apteria aphylla* (Burmanniaceae) and several *Voyria* species (Gentianaceae) are known to occur in wet grasslands and savannas (Maas et al. 1986). *Arachnitis* (Corsiaceae) has been recorded on the treeless East Falkland Island, “growing in sand amongst rocks on an eroded sandstone ridge” (Cribb et al. 1995). In Africa, mycoheterotrophic *Brachycorythis* orchids occur in woodland and wooded grassland (Cheek and Williams 1999). Monotropoideae are often found in open vegetations, such as dune slacks (Wallace 1975; Leake 1994). The enigmatic species *Thismia americana* (Thismiaceae) was discovered in the margin of a grass field (Pfeiffer 1914), and the western underground orchid *Rhizanthella gardneri* grows in shrublands, in habitats of low-nutrient availability and high light levels (Bougoure et al. 2008). *Hexalectris spicata* (Orchidaceae) occurs in diverse habitats: from swamps to oak canyons rising out of the desert (Luer 1975). And while mycoheterotrophic species are usually terrestrial, *Voyria spruceana* and *V. aphylla* (Gentianaceae) have been found growing as epiphytes up to 30 m high in trees in Colombia (Groenendijk et al. 1997). *Burmannia kalbreyeri* (Burmanniaceae) is also known to grow epiphytically, but this species retains chlorophyll and has well-developed leaves (Maas et al. 1986). Lastly, several species of *Sciaphila* (Triuridaceae) are often found growing on termite nests (van de Meerendonk 1984; Maas and Ruyters 1986), and Franke (2002) reported a specimen of *Voyria flavescens* (Gentianaceae) growing top of a termite mound of *Embiratermes neothenicus* (Isoptera, Nasutitermitinae).

3.6.7 Population Size

Even within suitable habitats, populations of mycoheterotrophic plants are mostly thinly scattered. Population sizes are usually small, with less than 15 individuals per population, but plants can only be detected when aboveground parts are present (flowering and fruiting stages), so the actual population size is difficult to determine. In some cases, populations of over hundreds of flowering specimens have been reported (e.g., *Gymnosiphon* Cheek and Williams 1999; *Burmannia* Fensham 1993).

3.6.8 Co-occurrence

Many authors have noted that different species of mycoheterotrophs (often from different families), both in temperate and tropical zones, have the tendency to grow together (e.g., van der Pijl 1934; Jonker 1938; Van Royen 1972; van de Meerendonk 1984; Maas and Rübsamen 1986; Cheek and Williams 1999). Indeed, after a mycoheterotrophic plant is spotted in a forest, closer inspection of the area will often reveal other species growing close by (Maas et al. 1986; Cheek and Williams 1999). There is no explanation for this phenomenon. A few authors have suggested that co-occurring mycoheterotrophs are possibly sharing the same mycorrhizal fungus (Cheek and Williams 1999; Cheek 2003b) but no evidence has been found to support this. In contrast, Merckx et al. (2010b) sampled specimens of *Voyria aphylla* (Gentianaceae) and *Dictyostega orobanchoides* (Burmanniaceae) co-occurring at a rainforest plot in French Guiana and found that they were associated with nonoverlapping AMF lineages. A specimen of *Campylosiphon purpurascens* (Burmanniaceae) that occurred at this spot was found to utilize distinct fungal lineages as well (VM, unpublished data). Similarly, Courty et al. (2011) identified distinct lineages of arbuscular mycorrhizal fungi in roots of *Voyria aphylla* (Gentianaceae), *Apteria aphylla*, and *Gymnosiphon* sp. (Burmanniaceae) growing at a site in Guadeloupe. Interestingly, many patches of rainforest in French Guiana that are rich in mycoheterotrophic Burmanniaceae and Gentianaceae are also inhabited by the mycoheterotrophic orchid *Wullschlaegelia calcarata* (Orchidaceae) (VSFTM pers. oberv.), yet *Wullschlaegelia* is associated with saprotrophic fungi (Martos et al. 2009), while Burmanniaceae and Gentianaceae exploit arbuscular mycorrhizal mycorrhiza. In the temperate forests of Northwest America, different species of ericaceous mycoheterotrophs are often found growing together (Wallace 1975) but are each specialized on different mycorrhizal fungi (Bidartondo and Bruns 2001, 2002). Similarly, Taylor and Bruns (1999) investigated the mycorrhizal associations of the mycoheterotrophic orchids *Corallorhiza maculata* and *C. mertensiana* over a wide geographic range and found that they never shared fungal species, even when growing intermixed. In these cases, co-occurrence of mycoheterotrophs cannot be explained by specialization on the same "host" fungus. The pattern may reflect access to different resources by different fungal taxa and thus would result from competition rather than convergence. Plant sister species that occur in sympatry but grow with different fungal lineages may result from a speciation process driven by mycorrhizal specialization (Chap. 5). Other factors that may cause co-occurrence of mycoheterotrophs include similar preferences of mycoheterotrophs and/or their associated mycorrhizal fungi toward certain microhabitats or similar dispersal biases.

3.7 Biodiversity Hotspots

A few localities are notorious for their high number of mycoheterotrophic species. For example, Mount Kupe in Southwest Cameroon is often cited as the richest site for mycoheterotrophic plants in Africa (Cheek and Cable 1997; Franke 2004). Two decades of intensive surveys on the slopes of this mountain have revealed twelve different mycoheterotrophic species, including two *Afrothismia* species yet to be described (Franke 2007; Moses N. Sainge, pers. comm.). Therefore, Mount Kupe is home to about one-fourth of all mycoheterotrophic species known from continental tropical Africa. The adjacent Mount Cameroon has a comparable diversity of mycoheterotrophic plants, although some species may be extinct due to extensive habitat destruction (Schlechter 1906; Cheek and Williams 1999; Franke et al. 2004). Mount Kupe and Mount Cameroon are part of the Lower Guinea rainforest region, which is a center of diversity and endemism for mycoheterotrophic plants (see above) and for flowering plants in general (Linder 2001; Plana 2004). The stunning diversity of plants in this region can be explained by modern patterns in rainfall seasonality, while the high level of endemism is probably related to paleoclimatic fluctuations, and the area has likely served as a rainforest refugium during glacial maxima (Linder 2001; Plana 2004). In Africa, centers of diversity of mycoheterotrophic plants all occur in areas that have been thought to be glacial refugia. Since many mycoheterotrophic plants are vulnerable to disturbance, have very narrow habitat preferences, and seem to have very slow dispersal rates, it has been proposed that mycoheterotrophic plants may be suitable indicators of Pleistocene rainforest refugia (Cheek and Ndam 1996; Cheek and Williams 1999).

Another mycoheterotrophic plant “hotspot” is the Reserva Ducke near Manaus (Brazil). In an area of only 100 km^2, no less than 22 mycoheterotrophic species have been found, or over 25% of the total species diversity of mycoheterotrophic plants in the Neotropics. Two species of Triuridaceae (*Sciaphila oligantha* and *S. rubra*) are endemic to the reserve (Ribeiro et al. 1999; Maas and Rübsamen 1986; Maas and Maas 2005). The Reserva Ducke is characterized by an extremely high diversity of flowering plants (Ribeiro et al. 1999). Patterns of tree diversity in the Amazon rainforest have been linked to soil gradients and the current climate, and particularly rainfall seasonality (ter Steege et al. 2003, 2006), although recent research has indicated that paleoclimate probably had a much greater effect on current patterns of tree diversity than current climate (Hoorn et al. 2010; ter Steege et al. 2010). Indeed, the high diversity of plant species found in Reserva Ducke has been attributed to its position at the contact point among several Tertiary and Quaternary refugia, indicating that its diversity may have been enhanced by the coalescence of the distributions of former allopatric species in this area (Oliveira and Daly 1999; Oliveira and Mori 1999).

The most species-rich locality of mycoheterotrophic plants in Southeast Asia is Mount Kinabalu in Malaysian Borneo. Since botanical explorations on the slopes of the 4,095 m high mountain started in the second half of the nineteenth century, 29 species of fully mycoheterotrophic plants have been recorded. These include 16 species of orchids, of which *Didymoplexiella kinabaluensis* and *Gastrodia spathulata* (formerly *Neoclemensia spathulata*) have not been found elsewhere (Wood et al. 2011). Burmanniaceae and Thismiaceae are both represented with two fully mycoheterotrophic species, Triuridaceae with five species, Polygalaceae with three fully mycoheterotrophic species, and Petrosaviaceae with a single species (Beaman and Beaman 1998; Beaman and Anderson 2004). Mount Kinabalu is ca. 1.5 million years old and therefore comparatively young in geological terms. The flora is exceptionally diverse with a high percentage of endemicity (Wong and Phillipps 1996; Wood et al. 2011). The high diversity of plant species on Mount Kinabalu has been attributed by the occurrence of a wide range of soil types and climatic conditions. The endemic species of Mount Kinabalu may be relicts of ancient, more widespread distribution ranges, or recent species that result from rapid adaptive radiation, catastrophic selection and drift, and dispersal of propagules from distant and neighboring mountain systems (Wong and Phillipps 1996).

Other areas with high numbers of mycoheterotrophic species include Saül (French Guiana) (Clarke and Funk 2005) and Mabura (Guyana) (Ek and ter Steege 1997). In temperate Northwest America, mainly in the coastal areas of northern California, Oregon, and Washington, there are many small "hotspots" where distribution ranges of several Monotropoideae species overlap (Wallace 1975).

Molecular clock evidence indicates that Burmanniaceae and Thismiaceae have Cretaceous origins and major diversification began shortly after the mass extinctions at the K/T boundary, suggesting that glacial periods may have had a significant influence on their current distributions (Merckx and Bidartondo 2008; Merckx et al. 2008). In addition, these analyses indicate that speciation events within mycoheterotrophic Dioscoreales lineages predate the Pleistocene glaciations. Based on this evidence, it seems that during glacial maxima rainforest refugia have acted as "museums" of ancient lineages of mycoheterotrophic Dioscoreales rather than as speciation "engines" (see Plana 2004). However, mycoheterotrophic species of other families that are endemic to a particular hotspot may result from recent speciation events. For example, several species of orchids endemic to Mount Kinabalu have evolved from vertical altitudinal radiation of lowland congeners or dispersal from neighboring mountain systems most likely after the uplift of the mountain (1.5 million years ago) and can be considered as "neoendemics" (Barkman and Simpson 2001; Wood et al. 2011). The endemic mycoheterotrophic orchids of Mount Kinabalu may therefore be recent species as well. Thus, hotspots of mycoheterotrophic plant diversity may be both "museums" and "cradles" of diversity.

3.8 Endemism and Rarity

Mycoheterotrophic plants are seldom found in high abundances. That does not mean that all species are rare. Some species have wide distribution ranges and occur in a variety of habitat types (e.g., *Hypopitys monotropa*, *Epipogium roseum*). But even widespread mycoheterotrophs may still be extremely rare on a local scale. *Epipogium aphyllum*, for example, has a widespread distribution in temperate Eurasia, but on a local scale, it is often considered to be extremely rare. In Britain, it has been frequently described as the rarest orchid and even as Britain's rarest plant (Taylor and Roberts 2011). In addition, many mycoheterotrophs seem to have very limited distribution ranges and/or have extremely low abundances (e.g., known from very few populations). For example, most neotropical *Thismia* species are only known from one or two collections (Maas et al. 1986). A large number of African mycoheterotrophs are also known from only one or two localities (e.g., species in the genera *Afrothismia*, *Kupea*, *Kihansia*, *Oxygyne*, *Auxopus*, and *Gastrodia*). Similarly, the enigmatic underground orchid (*Rhizanthella gardneri*) is known from only a handful of sites in Southwest Australia (Bougoure et al. 2008). Numerous other mycoheterotrophic species from all continents share this apparent rarity.

It is important to note that our knowledge about the occurrence of fully mycoheterotrophic plants may be considerably biased by the plants' ability to remain unnoticed by collectors. Many species, particularly those from tropical rainforests, are only known from remote areas where botanical inventories have yet to be carried out. Moreover, mycoheterotrophs can only be spotted when they are flowering or fruiting, mostly for a short period of time only and often in the wet season, when few botanists are eager or able to enter the forest. The rest of the year, they remain underground hiding from discovery, and they may not even flower each year. We lack detailed information on the phenology of most mycoheterotrophs, but, for example, in the ghost orchid (*Epipogium aphyllum*), it has been observed that populations can disappear for up to 30 years between successive flowering episodes at the same site (Leake 1994). This suggests that some mycoheterotrophs may have very cryptic flowering cycles. Finally, mycoheterotrophs are generally very difficult to spot due to their small size and hyaline coloration. They often fail to protrude above the dense leaf litter and remain covered by fallen leaves,

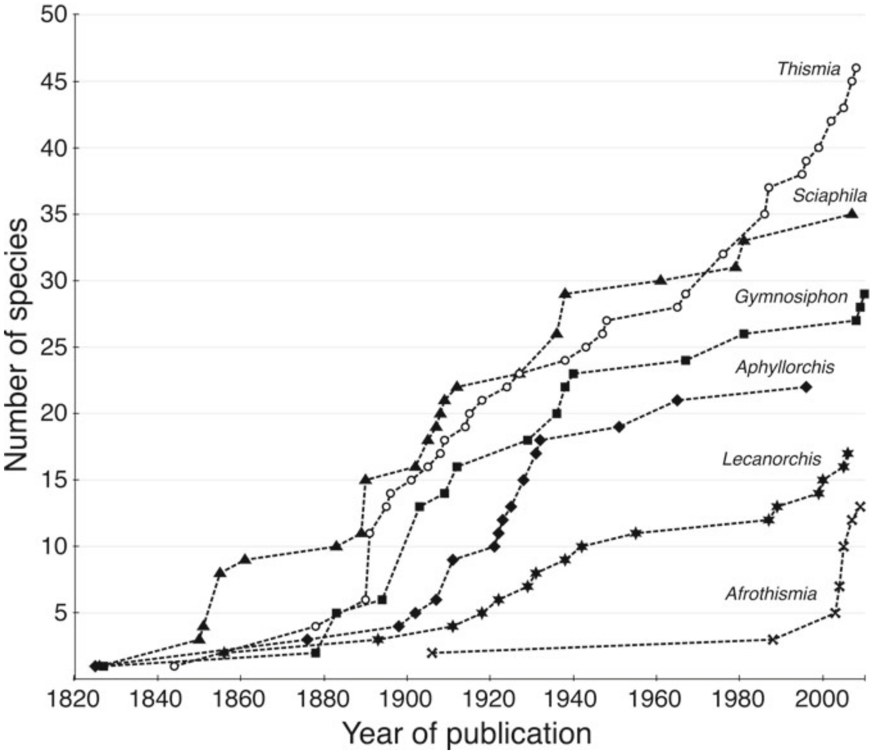

Fig. 3.10 Number of species in a selection of mycoheterotrophic genera that occur in the tropics (*Thismia*, *Sciaphila*, *Gymnosiphon*, *Aphyllorchis*, *Lecanorchis*, and *Afrothismia*) and their year of publication. Data based on the World Checklist of Selected Plant Families (2010)

even when flowering. It is little wonder that mycoheterotrophs are often spotted by mushroom hunters or by a botanist during a sanitary break; some species may be more abundant than we presume because we just fail to find them even when actively looking for them. The fact that new species are constantly being described and thus escaped discovery for a long time illustrates the secret nature of mycoheterotrophs (Fig. 3.10).

Some new species were spotted only after extensive long-term monitoring. Notorious is the discovery of two new *Afrothismia* (Thismiaceae) species in Korup Forest Dynamic Plot in Cameroon (Sainge and Franke 2005; Sainge et al. 2005). This 50-ha plot was established in 1994 and is constantly monitored, yet two *Afrothismia* species escaped discovery for almost a decade, despite the fact that a path through the plot was also going through one of the *Afrothismia* populations (Franke 2007). The spectacular species *Tiputinia foetida* (Thismiaceae), with a flower of 5 cm in diameter, was discovered in 2005 in a biological station in Ecuador growing within a meter of the path linking the station's dining hall to the laboratory (Woodward et al. 2007).

The influence of collection effort has been addressed for the rare species *Thismia rodwayi* (Roberts et al. 2003; Wapstra et al. 2005). From its discovery in 1890 until 2002, there were only five records of *T. rodwayi* in Tasmania (Roberts et al. 2003). Since the discovery of two specimens at a new site in Tasmania, subsequent searches on this and other sites with similar habitat characteristics revealed a total of 110 *T. rodwayi* flowers (Roberts et al. 2003), and *T. rodwayi* is now known from 26 sites from 7 disparate locations in Tasmania (Wapstra et al. 2005) (Fig. 3.11). Although these numbers certainly do not upgrade *T. rodwayi* to a common species, it can be concluded that it is at least more abundant

Fig. 3.11 Distribution of *Thismia rodwayi* (Thismiaceae) in Tasmania. (**a**) A flower of *T. rodwayi*. (**b**) Known distribution of *Thismia rodwayi* based on records before 2002. (**c**) Distribution of *T. rodwayi* based on all records up to 2005. Maps adapted from Roberts et al. (2003) and Wapstra et al. (2005)

than presumed by previous collections. As standard biological inventories failed to encounter *T. rodwayi* (Roberts et al. 2003), another conclusion that can be drawn from this study is that this species, and other inconspicuous mycoheterotrophs, can only be reliably recorded by targeted surveys. Because very few botanists search tropical rainforests specifically for mycoheterotrophic plants, the majority of collections result from chance encounters, hence explaining the lack of collections for so many known mycoheterotrophic species. The few intensive searches for mycoheterotrophic plants that have been carried out lead, in many cases, to the discovery of unexpected mycoheterotrophic plant diversity or even to the discovery of undescribed taxa (e.g., Franke 2007).

Despite the probable impact of collection effort, there is no doubt that the paucity of records for many mycoheterotrophic species is the result of “real” rarity and high local endemism (Kruckeberg and Rabinowitz 1985). This is obvious for species that are part of well-known floras (e.g., *Epipogium aphyllum* in Britain, *Thismia americana* in North America). In lesser-known tropical regions, differences in rarity among species are becoming more obvious with targeted collecting. Comparing herbarium records between species with similar habit, it becomes clear that some species are encountered more frequently than others (Fig. 3.12). In the Neotropics, for example, there is a very pronounced difference in collection frequency between mycoheterotrophic Burmanniaceae and Gentianaceae on the one hand and Thismiaceae and Triuridaceae on the other. This can only be explained by differences in distribution and abundance. According to Harper (1981), rare plant species can be classified based on space, group, or time relatedness. Space-limited species may be locally abundant but only occur in a limited number of sites. Their distributions may be restricted due to high niche specificity or dispersal barriers. These species are often local endemics. Group-dependent species occupy a specialized niche with a limited distribution, associated with certain ecotypes often at ecological frontiers for species. Rarity in time-dependent species results from fluctuations in population numbers following adverse sporadic or cyclical events, such as drought or fire (Swarts and Dixon 2009). Most rare mycoheterotrophic species seem to belong to the first and second categories, although time-dependent rarity may occur as well.

The influence of abiotic factors on the distribution of mycoheterotrophic plants remains to be determined. The fact that (rare) mycoheterotrophs of different species are often found growing at the same site, but in association with different fungi, possibly indicates that distribution of mycoheterotrophic species, or their associated fungi, is restricted by adaptations to similar

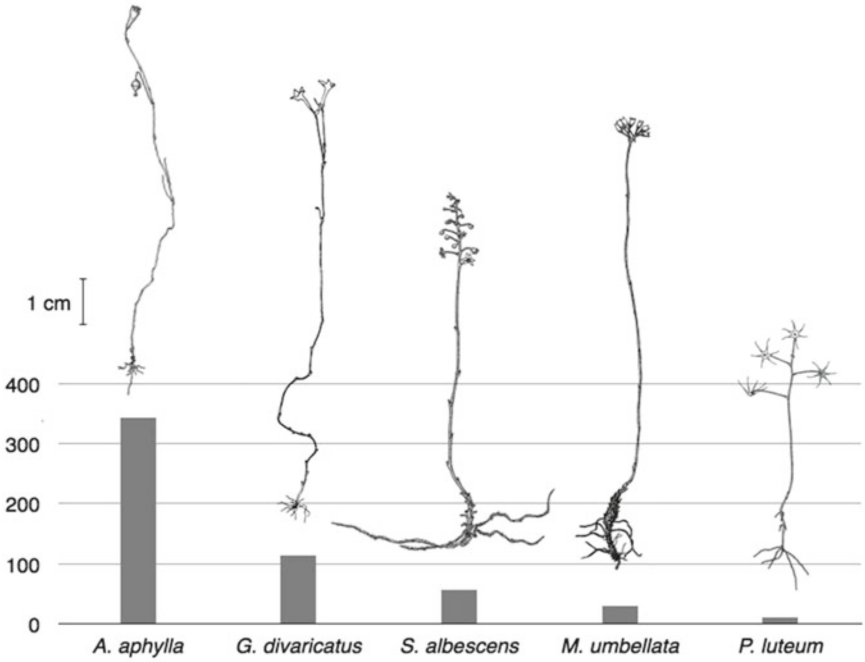

Fig. 3.12 The number of herbarium records cited in the Flora Neotropica for a selection of neotropical Burmanniaceae (*Apteria aphylla*, *Gymnosiphon divaricatus*, *Miersiella umbellata*) and Triuridaceae (*Sciaphila albescens*, *Peltophyllum luteum*). Data obtained from Maas et al. (1986) and Maas and Rübsamen (1986). For comparison, the habit of each species drawn at the same scale is shown above

microhabitats. These microhabitats can be characterized by certain abiotic factors such as soil type, humidity, and water availability. Alternatively, this pattern of co-occurrence may be explained by similar dispersal and colonization patterns.

Next to abiotic factors, biotic dependency may play an important role in the distribution range and abundance of mycoheterotrophic plants (Fig. 3.13). As fully mycoheterotrophic plants are completely dependent on their (often very specific) associated fungi, the availability of these fungi will be essential for the plant's establishment. Mycoheterotrophs that are specialized on rare fungi may thus be a priori severely limited in their distribution range. The range of the fungi may be restricted to certain abiotic habitat requirements and dispersal barriers (see further). In addition, some mycorrhizal fungi may also show specificity toward particular autotrophic plants. This can create a very complex tripartite biotic dependency for a mycoheterotrophic plant. For example, *Rhizanthella gardneri* is associated with a specific fungus, which is possibly only able to form ectomycorrhizas with *Melaleuca uncinata* (Bougoure et al. 2009). Furthermore, it is possible that the host fungus is not always able to serve as a suitable host for a mycoheterotrophic plant. Theoretically, a mycoheterotrophic plant will only successfully grow and reproduce if its associated fungus is able to provide enough carbon from coassociated trees or, in case of saprotrophic fungi, from dead material. For obligate mycorrhizal fungi, this may be influenced by the size of their network and the number, age, and identity of its associated autotrophic plants. Competition between different fungus species may influence their ability to allocate nutrients as well (Bever et al. 2009).

Specificity to aboveground biotic interactions may also induce rarity (Swarts and Dixon 2009). Specialized pollination systems, in a manner similar to the level of specialization in mycorrhizal associations, may play a role in causing rarity in

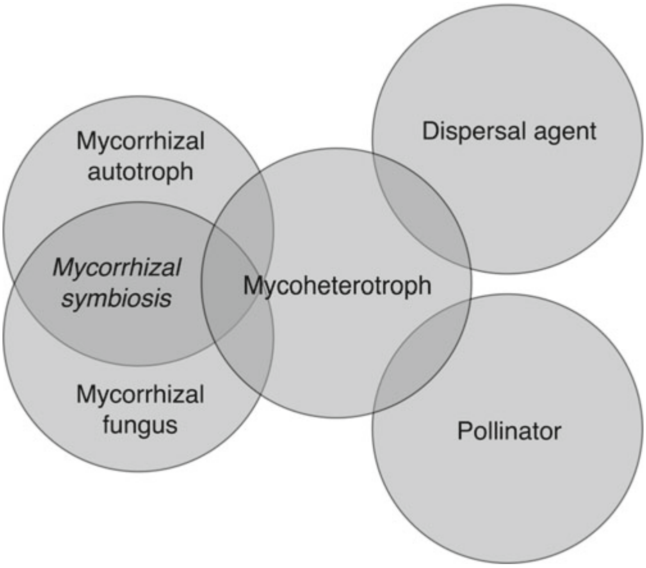

Fig. 3.13 Primary biotic agents that may limit the abundance and distribution of mycoheterotrophic plants. Overlap indicates potential biological dependency of the mycoheterotroph on that factor. See text for further discussion. Figure based on Swarts and Dixon (2009)

mycoheterotrophs. It has been hypothesized that mycoheterotrophic plants that show high specificity in their mycorrhizal interactions probably have generalist pollination syndromes and/or exhibit autogamous self-pollination due to the evolutionary instability inherent to specializing on two lineages (Bidartondo 2005). We know little about the pollination strategy of mycoheterotrophic plants, but support for Bidartondo's hypothesis concerning absence of specialized pollination syndromes has been found for mycoheterotrophic orchids (Dressler 1981; Benzing and Atwood 1984; Arditti 1992; Molvray et al. 2000) and mycoheterotrophic plants in general (Leake 1994). However, detailed studies on the reproductive biology of *Hypopitys*, *Monotropa*, and *Monotropsis* (Klooster and Culley 2009) and *Voyria* (Hentrich et al. 2010) revealed the presence of outcrossing and specialization in pollination interactions (see Chap. 7). Therefore, it is possible that, in some cases, both pollinator and fungal specificity affects the distribution mycoheterotrophic plants (Waterman and Bidartondo 2008). Comparative population approaches (Thompson 2005), where both mycorrhizas and reproductive traits for multiple populations of a single mycoheterotrophic species are examined, are needed to explore the effect of both mutualisms on the distribution of mycoheterotrophs. A recent study has addressed this interaction for achlorophyllous orchids of the tribe Coryciinae, which show specificity both in pollinators and associated fungi (Waterman et al. 2011). Interestingly, when orchids were subjected to transplant experiments, it was found that effective pollination does not occur outside native regions, whereas effective fungi can be recruited. This strongly suggests that pollination specificity has more influence on the local distribution of the species than does mycorrhizal specificity. However, it can be argued that mycorrhizal selection pressure is less influential for initially mycoheterotrophic plants than for full mycoheterotrophs that completely rely on the allocation of adequate nutrients from the fungi for their entire life cycle.

Finally, specialization toward seed dispersal agents may limit plant distributions as well. This factor seems to have little impact on mycoheterotrophs, which produce large amounts of dust seeds that are presumably dispersed by wind (Leake 1994; Eriksson and Kainulainen 2011). However, the dust seeds of orchids generally disperse only over short distances, and long-distance dispersal seems to be rare (Diez 2007; Jacquemyn et al. 2007). In *Voyria*, there is evidence of endozoochory (Hentrich et al. 2010), and seed dispersal of the rare underground orchid *Rhizanthella gardneri* is thought the carried out by a native mammal that is now extirpated from all known localities of the orchid (Dixon 1991). Therefore, limitations to seed dispersal cannot be ruled out as a determining factor in the distribution of mycoheterotrophic plants.

3.9 Extinct Species

According to the IUCN Red List, a taxon is extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historical range have failed to record an individual (IUCN 2010). Since many mycoheterotrophic species, particularly those occurring in tropical rainforests, grow in inaccessible areas and are extremely difficult to spot (see above), it is impossible to declare any mycoheterotrophic species as extinct with confidence. Even when the type locality is destroyed and a species has not been seen for many decades, it is still possible that other populations escaped discovery. Sometimes species have been rediscovered after a notably long hiatus. *Haplothismia exannulata* (Thismiaceae) was rediscovered at its type locality in India in 2000, 49 years after its discovery and only a few years after being declared "extinct" (Sasidharan and Sujanapal 2000). The second collection of *Thismia clavigera* (Thismiaceae) was made 115 years after the first and over 1,000 km from the type locality (Stone 1980).

Despite these rediscoveries, many other rare species have not been collected for a remarkably long period of time. For some, it remains plausible they have escaped extinction. For example, *Marthella trinitatis* (Burmanniaceae) is only known from Mount Tucuche on Trinidad and was last collected in 1898 (Maas et al. 1986). But large patches of undisturbed forests are still present on Mt. Tucuche, retaining the possibility of a rediscovery of this species (Paul Maas, pers. comm.). In other cases, however, chances for survival of the species seem grim because the type locality and surrounding habitat has been destroyed. One of the most famous, now destroyed, localities is the "Alto Macahé" near Nova Friburgo (Rio de Janeiro), which is part of the coastal rainforest of southeast Brazil. In the nineteenth century, John Miers and Auguste Glaziou collected many remarkable mycoheterotrophic plants at this location. As a result, Alto Macahé is the type locality of *Peltophyllum caudatum* (Triuridaceae), *Thismia fungiformis*, *T. caudata*, *T. macahensis*, *T. janeirensis*, and *T. glaziovii* (Thismiaceae). Of these species, only *Thismia janeirensis* and *T. glaziovii* were later collected at another location. All other species have not been recorded since the type collection, and because 95% of the original Mata Atlântica rainforest has been replaced by farmland (Prance et al. 2000; Murray-Smith et al. 2009), little hope remains that these species escaped extinction (Maas et al. 1986). A similar fate was suffered by the endemics of Mount Cameroon, where most of the forest has been replaced by farmland, thereby destroying the type localities of *Oxygyne triandra*, *Afrothismia pachyantha*, *A. winkleri* (Thismiaceae), and *Burmannia densiflora* (Burmanniaceae) (Schlechter 1906, 1921). The latter two species were later found at other nearby locations, but *Oxygyne triandra* and *Afrothismia pachyantha* have not been collected for more than 100 years and may be extinct.

Arguably, the most mysterious of all mycoheterotrophic plant discoveries is that of *Thismia americana* (Thismiaceae). This tiny plant was discovered in August 1912 by Norma E. Pfeiffer in a low prairie near Chicago, Illinois (USA) (Pfeiffer 1914). *Thismia americana* was observed at this locality for several subsequent summers and was probably last seen in 1916. The type locality of *Thismia americana* has been replaced by an industrial complex, and numerous attempts to relocate this enigmatic species have been unsuccessful. Therefore, the species is currently listed as "possibly extinct" (Lewis 2002). *Thismia* species are generally found in the leaf litter of moist tropical rainforests in South and Central America, Southeast Asia, and Australasia, although some species occur in subtropical and temperate rainforests in Japan, Australia, and northern New Zealand. While this widespread distribution indicates that there is considerable variety in ecological preferences among *Thismia* species, the occurrence of a *Thismia* species in a prairie in temperate North America, more than 3,500 km from the nearest *Thismia* site (southern Costa Rica), is truly remarkable. The average temperature in the Chicago area lowers to −5°C during winter, by far the lowest temperature for any Thismiaceae site. This led Pfeiffer (1914) to the suggestion that the plant was perennial and that the underground parts of the plant were able to hibernate. Based on morphological similarities, it has been suggested that the closest known relative of *T. americana* is *T. rodwayi* from Australia and New Zealand (Jonker 1938; Maas et al. 1986; but see Thiele and Jordan 2002), forming one of the "most anomalous disjunctions known in flowering plants" (Thorne 1972, p. 407). Was this *Thismia* population the result of a human introduction, a recent long-distance dispersal, or the last remnant of an ancient boreotropical *Thismia* distribution? Unless the plant is rediscovered, this mystery will remain unsolved. Many people assume that the species is still present in the area. The only certainty is that if *T. americana* still exists, it is extremely difficult to find. In a letter to Prof. Warren H. Wagner in 1956, Pfeiffer recalled that it took her 3 h to relocate the plants when she returned to the exact same spot shortly after her first discovery.

3.10 Distribution of Host Fungi

The distribution of mycoheterotrophic plants is strongly geographically patterned both on global and local scales. This may be the result of constraints imposed by the physical environment or the biogeographic history of the plant lineages (see above). However, as many mycoheterotrophic plants show specificity toward narrow lineages of fungi (see Chaps. 5 and 7), an obvious question emerges: is the distribution of mycoheterotrophic plants also limited by the distribution of their associated fungi?

On a broad geographic scale, a correlation between the distributions of mycoheterotrophs and their host fungi seems apparent. Arbuscular mycorrhizal mycoheterotrophs are almost exclusively found in tropical forests, where the native trees form arbuscular mycorrhizal associations. In contrast, ectomycorrhizal mycoheterotrophic orchids and Ericaceae species are mainly restricted to temperate forests where ectomycorrhizal associations are predominantly formed by the native tree species. Forests of Southeast Asia, with their pronounced diversity of mycoheterotrophic orchids, are dominated by large trees of the family Dipterocarpaceae which are known to form associations with ectomycorrhizal fungi (Lee 1990; Moyersoen 2006). Indeed, species of *Aphyllorchis* and *Cephalanthera* mycoheterotrophs have been shown to use ectomycorrhizal fungi to obtain carbon from dipterocarps (Roy et al. 2009), and it is likely that many other mycoheterotrophic orchids from tropical Asia rely on similar associations.

A few ericaceous mycoheterotrophs do occur at tropical latitudes: *Cheilotheca* is restricted to Southeast Asia, and the distribution of the mostly temperate *Monotropa uniflora* reaches as far south as Colombia (Wallace 1975). However, tropical ericaceous mycoheterotrophs grow in pine, beech, and oak forests at high elevations where the presence of ectomycorrhizal fungi allows the establishment of these species. Interestingly, there are several reports of arbuscular mycorrhizal mycoheterotrophs growing in forests dominated by ectomycorrhizal trees (see above). In these cases, the arbuscular mycorrhizal "host" is likely associated with arbuscular mycorrhizal understory plants.

On a finer spatial scale, the relation between mycoheterotroph and fungus distributions is a much more complicated issue. Why are some mycoheterotrophs rare, even when their habitat is relatively common (e.g., *Rhizanthella*)? Are these mycoheterotrophs associated with "rare" fungi, and is their distribution limited by that of the fungus? In contrast to the obvious distribution limitations of specialized holoparasitic plants imposed by their host plant range, the relationship between the distribution range of mycoheterotrophic plants and their associated fungi is far less obvious. A major obstacle to assess this question is our lack of detailed knowledge of the distribution ranges of fungi. Historically, the assumption that fungi and other eukaryotic microorganisms have "global" geographic ranges was widely accepted. This would imply that the distributions of fungi are independent of biogeography and if conditions are right, the appropriate fungi will appear (de Candolle 1820). Similar environments, tropical rainforests, for example, would thus harbor similar fungi, and the potential distribution of mycoheterotrophic plants would be constrained by the physical environment rather than the distribution of their associated fungi. Recently, the assumption that "every fungus is everywhere" has been challenged by molecular studies of historical biogeography, ecology, and population genetics of fungi (Taylor et al. 2006; Lumbsch et al. 2008; Öpik et al. 2010; Peay et al. 2010a). These studies show that although some fungi are capable of long-distance dispersal (Moncalvo and Buchanan 2008), the actual distributions of most species reflect the same major dispersal barriers (e.g., oceans and mountains) that drive vicariance events in other organisms (James et al. 1999; Matheny et al. 2009). Geographic patterning is also evident at a more local scale (Collier and Bidartondo 2009; Peay et al. 2010b). This implies that the actual distribution of fungi is not necessarily equal to the potential distribution and that mycoheterotrophs that are specialized on particular fungi may fail to invade new areas solely because their obligate host fungi are not present. However, evidence that availability of fungi poses a real limitation to the distribution ranges of some mycoheterotrophic plants is not eminent. One speculative example for this phenomenon may be presented by the Hawaiian Islands. Despite the presence of seemingly suitable habitats, mycoheterotrophic plants are absent from the flora of Hawaii. In addition, only three species of orchids are native to the Hawaiian Islands, a surprisingly small number for a tropical region (Ziegler 2002). This is remarkable, because the small dust seeds of orchids seem ideal for long-distance dispersal by air, and both mycoheterotrophic and green orchids are found on remote Pacific Islands like Vanuatu, Fiji, and Samoa. Carlquist (1980) hypothesized that orchid seeds may not be resistant to freezing temperatures of the upper air layers or that the pollination requirements of potential colonizing species are not met. Another possible explanation for the scarcity of orchids—and the absence of mycoheterotrophic plants in general—in Hawaii may be the absence of suitable fungi necessary for their establishment. Similarly, a limited number of suitable ectomycorrhizal plants may explain the absence neottioid orchids in the Macaronesian region (Liebel et al. 2010).

On a smaller geographic scale, there is evidence that the rarity of the full mycoheterotroph *Pterospora andromedea* (Ericaceae) in eastern North America is influenced by the distribution and rarity of its fungal symbiont. A recent study by Hazard et al. (2011) showed that *P. andromedea* from the east coast of North America consists of a single haplotype that grows only with a single narrow lineage of *Rhizopogon* fungi. This fungal lineage appears to be rare in eastern white pine forests, and this may be a contributing factor to the rarity of eastern *P. andromedea* plants. In contrast, in western North America, five haplotypes of *P. andromedea* have been identified, and these haplotypes show preference for either *Rhizopogon salebrosus* or *R. arctostaphyli*, even when they co-occur (Bidartondo and Bruns 2002). Kjøller and Bruns (2003) found that these fungus species are common in the soil spore bank of the Sierra National Forest in western North America, where *P. andromedea* is common as well. Similarly, the initial mycoheterotroph *Caladenia huegelii*, a rare terrestrial orchid from Australia, partners with a specific Sebacinales fungus, which is ecologically efficacious only under a highly limited range of habitat and environmental conditions. Thus, rarity of this orchid species is potentially caused by a high degree of mycorrhizal specialization (Swarts et al. 2010). A similar study on species of *Drakaea* orchids from western Australia showed that all species show high mycorrhizal specificity and germinate only in a particular microhabitat. However, within this microhabitat, rare and common species exhibit no difference in germination rates, and both germinate in suitable habitat not currently occupied. The extreme rarity of some *Drakaea* species is therefore attributed to their highly specific pollination systems rather than their mycorrhizal specificity (Phillips et al. 2011).

A putative case of plant rarity induced by the rarity of a specific fungal symbiont is the distribution of the western underground orchid (*Rhizanthella gardneri*), which is only known from five sites in Southwest Australia (Bougoure et al. 2008). *Rhizanthella gardneri* is found in *Melaleuca uncinata* shrublands, in habitats of low-nutrient availability and high light levels. However, comparison between *Rhizanthella* sites revealed that *R. gardneri* can tolerate a range of habitat conditions and may be more widespread than previously thought, given that there are extensive areas of *Melaleuca* thickets with similar habitat characteristics across Southwest Australia (Bougoure et al. 2008). Underground orchids are extremely difficult to find, and thus, additional populations may remain to be discovered. However, *Rhizanthella* orchids seem to be linked with *Melaleuca uncinata* plants by a specific *Ceratobasidium* fungus (Bougoure et al. 2009). A possible explanation for the scarcity of *Rhizanthella* populations compared to the wide range of sites that appear to be suitable habitat may be found in the availability of the required fungus. Similarly, the rarity of *Petrosavia sakuraii* in the understory of Japanese cypress plantations—a common vegetation type in Japan—may be the result of a preference of the mycoheterotroph toward specific and range-restricted fungi (Yamato et al. 2011).

These observations suggest that mycorrhizal specificity may play an important role in both the global and local distribution of mycoheterotrophic plants, in addition to other biogeographic and ecological factors. However, it must be noted that for mycoheterotrophic plants, host specificity does not necessarily lead to restricted geographic ranges. The mycoheterotrophic orchid *Eulophia zollingeri* has an extremely wide distribution in tropical and subtropical Asia, yet individuals from seven populations in Japan, Myanmar, and Taiwan were found to associate with the same narrow lineage of fungi related to *Psathyrella candolleana* (Coprinaceae). Based on this observation, the authors conclude that a mycoheterotrophic plant can achieve a wide distribution even with a high mycorrhizal specificity, so long as the fungal partner is widely distributed (Ogura-Tsujita and Yukawa 2008).

3.11 Threats

3.11.1 Value of Diversity

Mycoheterotrophic plants do not have a direct economical value. They are not useful for consumption or for pharmaceutical purposes with the only exception being *Gastrodia elata* (Orchidaceae), used in Chinese traditional medicine (Xu and Guo 2000). Mycoheterotrophs are not essential ecological components of forest habitats; however, their presence in forest ecosystems may offer an indirect economical value through recreational services for humans. While few people will actually visit forests only to see mycoheterotrophic plants, most will be intrigued when they encounter one due to their exceptional and often mysterious habit. Rare plants hardly ever reach the status as a “flagship” species, such as the Galápagos tortoise or the giant panda, but they certainly add an unusual biological aspect to an ecosystem that can be appreciated by visitors. Apart from this value, mycoheterotrophic plants present a unique model system to study mycorrhizal mutualisms and ecological symbioses in general. Their inability to fix carbon through photosynthesis clearly shows the potential of mycorrhizal fungi to transport carbon, and perhaps other nutrients, between plants. This has led to the discovery of partial mycoheterotrophic plants. In addition, mycoheterotrophic plants offer excellent research opportunities to study the evolution of multipartite symbioses.

Like all organisms, mycoheterotrophic plants carry a certain “existence value” (Primack 2008). Existence value can be defined as the amount that people are willing to pay to prevent species from going extinct, habitats from being destroyed, and genetic variation from being lost (Martín-Lopez et al. 2007). As a unique part of their ecosystems (deciduous forests, rainforests, savannas, etc.), their presence contributes to the existence value that is attached to these ecosystems. In addition, their rarity is sometimes used in favor of protection of specific areas. An example is *Kupea martinetugei* (Triuridaceae), which is often used to support conservation efforts for the threatened rainforest on Mount Kupe in Cameroon (Cheek et al. 2004; Baird 2006). The genus *Kihansia* (Triuridaceae) is one of the endemics of the Kihansi River Gorge in Tanzania, and its presence draws attention to the necessity of conservation efforts for protection of this severely threatened habitat (Davis and Mvungi 2004). Also, the charismatic underground orchids of Australia are often featured to highlight conservation necessity (Swarts and Dixon 2009). And *Thismia americana* still helps to protect native prairie in the Calumet area near Chicago, USA, even though it was last seen almost 100 years ago (Chew 2004).

Lastly, fully mycoheterotrophic plants offer serious potential for horticulture. “Exceptional” plants, such as rare orchids and carnivorous plants, have always generated interest from plant enthusiasts. Indeed, commercial growing of rare or bizarre plants is a profitable business. If the difficulties of culturing fully mycoheterotrophic plants can be overcome, these “ghost plants” will find their way into the greenhouses of orchid collectors but may also attract the attention of the average consumer looking for an extraordinary plant.

3.11.2 Habitat Destruction

The major threat for the existence of mycoheterotrophic plants is habitat destruction. This is the inevitably result of the expansion of human populations and human activities. Habitat destruction is the primary cause of the loss of biodiversity in terrestrial ecosystems (Pimm and Raven 2000). It is likely that most of the original habitat of some tropical mycoheterotrophic species has already been destroyed. The distribution of many mycoheterotrophic plants overlaps with the biodiversity “hotspots” assigned by Myers et al. (2000). These areas comprise exceptional concentrations of endemic species and are undergoing exceptional loss of habitat. Particularly strongly affected are the Philippines and Indo-Burma, where less than 5% of the primary vegetation is retained (Myers et al. 2000). For mycoheterotrophic plants, endemism is particularly pronounced in the biodiversity hotspots of Sundaland, the Western Ghats and Sri Lanka, Madagascar, the Eastern Arc and Coastal Forests of Tanzania/Kenya, West Africa, and the Atlantic Forest in Brazil. These areas rank among the “hottest” hotspots with the highest number of endemics and the most severe habitat loss (Myers et al. 2000). The effect of habitat loss on mycoheterotrophic plant diversity is probably best illustrated by Brazil’s Atlantic Forest, where only 5% of the original vegetation remains (Murray-Smith et al. 2009; Fig. 3.14). Several Thismiaceae and Triuridaceae species are only known from this biodiversity hotspot. Because most of the historical localities of these species are now destroyed, little hope remains for their survival (Maas et al. 1986; Maas and Rübsamen 1986).

Apart from habitat destruction, habitat fragmentation is an important factor that contributes to the loss of biodiversity in ecosystems. Habitat fragments are not only isolated from one another by a highly modified or degraded landscape, but edges of each fragment experience an altered set of environmental conditions, referred to as “edge effects” (Primack 2008). It remains unclear how this affects diversity of mycoheterotrophic plants, but effects may be profound. It can be assumed that various edge effects, such as a lower canopy density, lower relative humidity, and lower soil-moisture content (Laurance et al. 2002), will have significant influence on the occurrence of mycoheterotrophic plants. Their occurrence may be even more influenced by the availability of their host fungi. Little is known about the effect of fragmentation, isolation, and concurrent edge effects on the belowground diversity. A few studies have shown that ectomycorrhizal fungal species richness is significantly reduced on smaller and more isolated habitat fragments in temperate (Peay et al. 2007, 2010b) and tropical forests (Tedersoo et al. 2007). Similar observations have been made for

Fig. 3.14 The original distribution of the Atlantic Forest in Brazil in 1500 AD and its distribution in the 1990s. Adapted from Morellato and Haddad (2000)

saprotrophic fungi (Penttilä et al. 2006). For ectomycorrhizal fungi, species composition may be very different at edges (Dickie and Reich 2005). All these factors may influence host availability and thus successful establishment for mycoheterotrophic plants. Mycoheterotrophic plants that are specialized on particular "rare" fungi may thus be in jeopardy if habitat size proves to be a strong determinant of fungal richness.

Even without destruction or fragmentation, ecosystems can suffer from human activities causing pollution. Pollution that impacts plant and fungal diversity is commonly caused by pesticides, sewage, fertilizers from agricultural fields, industrial chemicals and wastes, emissions from factories and automobiles, and sediment deposits from eroded hillsides (Relyea 2005). Pollution can significantly alter plant species richness, and there is no doubt that its negative impact will affect mycoheterotrophic plants as well (Brandle et al. 2001; Stevens et al. 2004).

3.11.3 Global Climate Change

The emission of greenhouse gasses has been steadily increasing over the past 100 years. There is convincing scientific evidence that the increased levels of greenhouse gasses produced by human activity have affected the world's climate and ecosystems already and that these effects will increase in the future (Primack 2008). Global surface temperatures have increased by 0.6°C during the last century and are likely to increase by 2–4°C by 2100 (Solomon et al. 2007). This global warming will affect a complete set of climate characteristics, leading to a global climate change. The effect of global climate change on rainforests remains poorly known. Different rainforest regions may experience different effects. It is expected that there is severe risk of forest retreat, especially in eastern Amazonia, Central America, and parts of Africa, but there are also indications for potential of expansion in other regions, for example, around the Congo Basin (Malhi et al. 2009; Zelazowski et al. 2011).

Global climate change may be especially harmful for montane forests and their associated mycoheterotrophs. The vegetation zonation on tropical mountains is strongly controlled by temperature. A 3°C warming would result in temperature zones moving 500 m vertically up the mountain, permitting lowland plants to migrate upward and eliminating the species in the highest zones (Pounds et al. 1999; Foster 2001). In the northern temperate zone, it is expected that global warming-induced changes in the ratio of extinctions and colonizations at the northern and southern boundaries of species ranges will result in northward range shifts for many species. However, given the current landscape fragmentation of forest habitats and the short time period involved, colonization will be very difficult for most forest plant species, and their survival will depend on their environmental tolerance. Plants with low environmental tolerance may be replaced by mobile generalist species invading from the south (McKinney and Lockwood 1999; Honnay et al. 2002). The fragmented distribution patterns of many mycoheterotrophic plant species suggests slow dispersal rates and/or high ecological specificity. Therefore, we hypothesize that temperate mycoheterotrophic plants are particularly vulnerable to global climate change. At least for one mycoheterotrophic species, *Hypopitys monotropa* in Europe, the impact of global climate change has been estimated using species distribution modeling based on projected future climate (Beatty and Provan 2011b). The results indicate that climate change will have substantial impact on the distribution range of the species, with a loss of southern and central European populations, and a potential northward expansion. Finally, there is no doubt that global climate change will affect diversity on all levels, including diversity of mycorrhizal fungi (Bellgard and Williams 2011). Changes in community structures of mycorrhizal fungi may have an indirect effect on the occurrence of mycoheterotrophic plants as well.

3.11.4 Disturbance

It is unclear whether (limited) human disturbance, such as selective logging, is a threat for mycoheterotrophs. It is often noted that mycoheterotrophic species prefer areas that have been devoid of disturbance in recent history (Cheek and Williams 1999; Taylor and Roberts 2011). This seems to suggest that mycoheterotrophic plants are sensible to disturbance or that recolonization of areas that have been prone to disturbance is slow. However, little research has been done on this issue. Bergman et al. (2006) studied the distribution of the mycoheterotrophic orchid *Wullschlaegelia calcarata* in a rainforest in Puerto Rico and concluded that its occurrence is correlated with land use history as the orchid was most abundant in areas which had been minimally impacted by human activity. Fensham (1993) reported that a fully mycoheterotrophic *Burmannia* species on Bathurst Island, Australia, prefers monsoon forest sites that are cleared of leaf litter by seasonal flooding, but their occurrence is negatively influenced by disturbance by pigs. However, in Tasmania, *Thismia rodwayi* often occurs at sites that have been subject to intensive and relatively recent forest activities, including clear-cutting and regeneration burns (Roberts et al. 2003). Similarly, there are many records of mycoheterotrophs that have been collected from secondary forests (Maas and Rübsamen 1986; Maas and Ruyters 1986; Lok et al. 2009; Cheek and Vanderburgt 2010; Klooster and Culley 2010; Pendry 2010). In Japan, the rare mycoheterotroph *Petrosavia sakuraii* occurs in *Chamaecyparis obtusa* plantations (Yamato et al. 2011). *Eulophia zollingeri* is frequently found in the introduced *Calliandra calothyrsus* forest in Java (Comber 1990). Therefore, at least some species are able to withstand moderate disturbance or have the ability to migrate into areas that have been affected by human activities. A key factor in the recolonization of secondary forests may be the presence of preferred host fungi, although other factors such as the presence of specific pollinators, seed dispersal barriers, or abiotic requirements may be of importance as well.

Herbivory may also have a negative impact on reproductive success of mycoheterotrophs (Klooster and Culley 2009; Taylor and Roberts 2011). Thus, introduction of herbivores into mycoheterotrophic plant habitats could pose potential threat for the local distribution of mycoheterotrophs. Finally, rare mycoheterotrophic plants may suffer from overzealous botanists, who collect specimens and trample populations during searches (Taylor and Roberts 2011).

3.11.5 Vulnerable Taxa

Only a dozen of mycoheterotrophic plant species are featured in the IUCN Red List (2010). Those that are listed are all categorized as "threatened" and range from "vulnerable" to "critically endangered." Unfortunately, this low number illustrates the incomplete state of the list rather than the absence of vulnerability of mycoheterotrophic species. Due to the continuing loss of rainforest area, it can be assumed that many rainforest mycoheterotrophs are at risk of extinction. In particular, species that are known from only a few localities, close to human settlements or outside protected areas, and species with a very limited distribution ranges and small population sizes are threatened. More intensive studies on the occurrence and distribution of mycoheterotrophic plants, particularly in the tropics, are urgently needed to assess the conservation status of these species. At the current rate of habitat destruction in the tropics, it is likely that some mycoheterotrophic plant species become extinct before they are even discovered.

3.12 Conservation

3.12.1 Habitat Conservation

Protecting populations is the key to preserving species. The best and most straightforward strategy to protect mycoheterotrophic plants is to protect the habitats in which they occur. Large parks are probably the only way to preserve complete rainforest ecosystems, but smaller rainforest reserves can also play a valuable role in the protection of rainforest species. Besides legal protection, investments in management are essential to preserve the biodiversity within protected areas.

3.12.2 Inventory and Monitoring

Our knowledge about the abundance and ecology of most species of mycoheterotrophs remains very poor. Only through careful inventories and observations in the field can the true status of a species and its habitat be determined. In addition, because flowering times of mycoheterotrophic plants can be cryptic, the conservation status of a species can only be established by studying populations over time. Detailed inventory studies and long-term ecological monitoring often lead to the discovery of new populations and new species, stressing the importance of these types of studies as well as our limited knowledge about mycoheterotrophic plant distributions (e.g., Roberts et al. 2003; Franke 2007; Cheek and Vanderburgt 2010).

3.12.3 Establishing New Populations

Conservation of rare and endangered species can be supported by establishing new populations. It is unclear whether this strategy is applicable to rare mycoheterotrophic plants. Seed germination of fully mycoheterotrophic orchids and Ericaceae has been achieved by burying seed packages near ectomycorrhizal trees (McKendrick et al. 2000b; Bidartondo and Bruns 2001; Bidartondo 2005), showing the possibility of introducing (or reintroducing) mycoheterotrophs into existing suitable habitats. However, given the paucity of knowledge on ecological requirements of mycoheterotrophs (mycorrhiza, pollinators, etc.), only crude assessments can be made to ensure a site is suitable for introduction of a species. Given the high ecological specificity of many mycoheterotrophic species, establishing new populations may be extremely difficult. Translocation of mycoheterotrophic plants from natural populations into new sites either as propagated seeds or as adult plants is likely to lead to failure due to the breakage of vital mycorrhizal connections, but if attempted, one should take care to fully characterize the existing mycoheterotrophic flora of the transplant area in order to avoid any negative impacts on existing mycoheterotroph populations.

3.12.4 Ex Situ Conservation

The best strategy for the conservation of biodiversity is the preservation of existing ecosystems. However, if the last remaining populations of a rare and endangered species are too small to maintain the species, if they are declining despite conservation efforts, or if the remaining individuals are found outside protected areas, then in situ—or on-site—preservation may not be effective. It is likely that the only way species in such circumstances can be prevented from going extinct is to maintain individuals in artificial conditions under human supervision (Primack 2008). The worlds' botanic gardens are a safe house for many plant species: about 80,000 species of plants are currently being cultivated (Guerrant et al. 2004), and several of these species are extinct in the wild. Botanic gardens thus play a key role in plant conservation, and this aspect should become even more important in the future. However, due to the complexity of their mode of life, cultivation of mycoheterotrophic plants remains problematic and, in most cases, currently impossible. There are several reports of successful germination and subsequent development of mycoheterotrophic orchids. Umata (1995, 1999) reported successful in vitro germination and formation of lateral roots of *Erythrorchis altissima. Gastrodia elata* and *Epipogium roseum* have been in vitro germinated and grown up to the formation of flowers (Xu and Mu 1990; Xu and Guo 2000; Yagame et al. 2007). In these experiments, the orchids germinated and grew in media that were inoculated with saprotrophic fungi, presumably closely related or identical to those with which the plants grow in nature. Asymbiotic germination to and cultivation to flowering stage have been reported for *Cymbidium macrorhizon* (as *Cymbidium nipponicum*) and *Didymoplexis pallens* (Mizuno et al. 1991; Irawati 2002). Successful long-term cultivation of mycoheterotrophs that are associated with fungi that are mycorrhizal with surrounding trees has not been achieved to date. Bruns and Read (2000) were able to germinate seeds of *Sarcodes* and *Pterospora* (Ericaceae) in vitro with ectomycorrhizal *Rhizopogon* fungi, which were isolated from mature plants in nature, but further development of seedlings could not be accomplished. Adult plants of *Thismia rodwayi*, *Afrothismia winkleri*, and *A. foertheriana* (Thismiaceae) have been grown for considerable amounts of time after transplantation from the field to the laboratory, but it remains unclear whether an effective tripartite symbiosis (mycoheterotroph–fungus–autotroph) was achieved under these conditions (Wood 2010; Franke, pers. comm.; VM pers. obs.). Establishment of such tripartite symbioses have been successfully accomplished in microcosm studies linking naturally germinated seedlings of the partial mycoheterotroph *Corallorhiza trifida* and seedlings of *Betula* and *Salix* trees by a shared mycorrhizal fungus (McKendrick et al. 2000a). Similar microcosm experiments successfully linked *Aneura mirabilis* and *Betula* seedlings by a shared mycorrhizal fungus (Read et al. 2000). Nevertheless, more research is urgently needed to investigate ex situ cultivation possibilities for mycoheterotrophs.

Ex situ seedling culture and subsequent reintroduction into appropriate habitats have been successfully achieved for orchids (e.g., McKendrick 1995; Yam et al. 2010) and may similarly be used for conservation purposes of mycoheterotrophic plants. However, there is a potential danger to this approach. It is observed that some orchids are able to germinate and develop ex situ with a wider range of mycorrhizal fungi than those found in natural populations (Masuhara and Katsuya 1994; Perkins and McGee 1995). Similar observations have been made for the germination of mycoheterotrophic Ericaceae (Bruns and Read 2000; Bidartondo 2005). Introducing these plants into natural habitats will also lead to the introduction of an "alien" fungus with potential ecological harm (Zettler et al. 2005).

3.13 Conclusions

Mycoheterotrophic plants are found in all forest biomes of the world and show a pronounced preference for damp habitats with primary forest and a closed canopy cover. The diversity of mycoheterotrophic flowering plants peaks in the tropics and is particularly high in Southeast Asia. Many families, genera, and species of mycoheterotrophic plants have a widespread distribution that covers multiple continents. Evidence from molecular clock analyses suggests that most widespread lineages are too young to have acquired their distribution before the breakup of Gondwana. While some transoceanic distribution may be explained by migration over temporary land bridges, oceanic dispersal probably played the most important role in the acquisition of widespread distributions. Due to their minute habit and ephemeral occurrence, mycoheterotrophic plants are not often found and collected. For many species, the paucity of records is also the result of extreme rarity and high local endemism. The rarity of mycoheterotrophic plants is probably related to particular habitat preferences. High specificity toward particular lineages of fungi may significantly limit the dispersal potential of mycoheterotrophs, although specificity toward other biotic (pollinators, dispersal agents, plant communities) and abiotic factors (humidity, soil composition) may be influential as well. The continuous destruction of their habitats and the increase of global temperatures threaten many species with extinction, and a few species may already have disappeared. The protection of their habitats is the best and currently the only way for the effective conservation of mycoheterotrophic plants.

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