

Chapter 5

Altitudinal Gradients in Mycorrhizal Symbioses

The Current State of Knowledge on How Richness and Community Structure Change with Elevation

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5.1 Introduction

Montane habitats generally are recognized as biodiversity hotspots as well as areas of high endemism (Lomolino 2001). Despite representing about one-eighth of the world's land area outside Antarctica, mountains harbor about one-third of all terrestrial species (Spehn et al. 2012; Antonelli 2015). Ever since the first scientific studies of Darwin, Wallace and von Humboldt on mountain biota, documenting changes in species richness and community composition has been at the center of ecological and biogeographic studies (Lomolino 2001; McCain and Grytnes 2010). Mountains provide unique opportunities to test various ecological theories and, to some extent, to study possible effects of climate change as they are characterized by gradients of abiotic factors, such as temperature, available moisture, etc. (Guo et al. 2013). However, in most organismal groups we still lack answers to fundamental questions regarding patterns of taxonomic richness and community composition (Lomolino 2001; Guo et al. 2013).

5.2 Environmental Factors

Numerous abiotic factors that shape biological communities change more or less predictably with increasing elevation. Among these, temperature is the most predictable with an average decrease of ca. 0.6 °C per 100 m elevation increase (Barry 2008). Changes in precipitation, another environmental factor crucially important

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for living organisms, along altitudinal gradients is much less predictable in general terms due to its complex relationship with regional climate and topography (Barry 2008). In mid- and high latitudes, precipitation tends to increase with elevation, while tropical mountains often show little variation in rainfall along an altitudinal gradient or exhibit a moderate mid-elevation peak (McCain and Grytnes 2010). There are several other environmental factors that interplay with temperature and precipitation to determine biological productivity. Among these, solar radiation, cloud cover, soil type, and nutrient content also vary substantially with elevation, as does surface area due to geometric constraints. For example, cloud forests, perhaps the most characteristic vegetation type of tropical montane habitats, are created by largely persistent cloud cover at certain elevations. Living organisms occupy different habitats along altitudinal gradients according to their physiological requirements for abiotic factors (temperature, water availability, etc.) and based on their interaction dynamics with other species. The resulting, largely predictable, changes in habitat and community structure with increasing elevation have been a focal point for ecological and evolutionary research and have contributed to the understanding of spatial patterns of biodiversity and their underlying mechanisms.

5.3 General Altitudinal Patterns in Terrestrial Ecosystems

Most studies focusing on biological communities along altitudinal gradients have focused on changes in richness (i.e., the number of taxa) of various taxonomic groups of vascular plants, insects, and vertebrates. Most studied organismal groups have been reported to display either a monotonal decline in richness with increasing elevation, a mid-elevation peak, or some combinations of the two, e.g., low-elevation richness plateau followed by a mid-elevation peak or by a monotonal decline (Colwell et al. 2004; Cardelús et al. 2006; McCain 2009).

Patterns of monotonal decline have generally been attributed to the decrease in environmental energy (e.g., temperature) and the decrease in suitable habitat area (Stevens 1992; Rosenzweig 1995). Possible explanations for mid-elevation peak in richness include increased rainfall and relative humidity and the mostly geometric effect of overlapping distributions of species with broad elevation range as observed in various organismal groups (Colwell and Lees 2000; Grytnes and Vetaas 2002; Sanders 2002; Colwell et al. 2004; McCain 2004; Cardelús et al. 2006; Grytnes et al. 2008). In some instances, in groups specialized in habitats with sparse vegetation (e.g., lichens), species richness can increase with elevation (Grytnes et al. 2006; Geml et al. 2014).

It has been noted repeatedly that certain altitudinal patterns of richness correlate with functional groups and, because ecological function often is evolutionarily conserved, with taxonomic groups. In other words, various ecological groups of plants and animals have been shown to exhibit diversity peaks at different elevations (Cardelús et al. 2006; McCain 2009; McCain and Grytnes 2010; Guo et al. 2013). Considering their particular importance to mycorrhizal fungi, it is noteworthy that,

among plants on a global level, trees generally have higher richness in lower elevations, while shrubs and herbs tend to be most diverse in mid-elevations (Guo et al. 2013).

5.4 The Distribution of Fungi Along Altitudinal Gradients

5.4.1 *General Aspects*

The vast majority of studies on the effect of elevation on richness have focused on vascular plants and animals, while information on changes in richness and community composition of fungi along elevation gradients remains scarce. The limited number of relevant fungal studies used various techniques and often targeted specific groups, such as morphological identification of macrofungi (Kernaghan and Harper 2001; Gómez-Hernández et al. 2012), freshwater ascomycetes (Shearer et al. 2015), culturable soil ascomycetes (Devi et al. 2012), and root-colonizing arbuscular mycorrhizal fungi (Gai et al. 2012); DNA sequencing of leaf and root endophytic fungi (Coince et al. 2014), bryophyte-associated fungi (Davey et al. 2013), wood-inhabiting fungi (Meier et al. 2010), and ectomycorrhizal root tips (Bahram et al. 2012; Nouhra et al. 2012; Coince et al. 2014; Miyamoto et al. 2014; Jarvis et al. 2015; Rincón et al. 2015); and deep DNA sequencing of soil samples (Geml et al. 2014; Merckx et al. 2015; Rincón et al. 2015). For non-mycorrhizal fungi, the first results show either nonsignificant effect of elevation on richness (Meier et al. 2010; Davey et al. 2013; Geml et al. 2014; Rincón et al. 2015) or a more or less monotonic decrease in species richness with increasing elevation (Devi et al. 2012; Gómez-Hernández et al. 2012; Geml et al. 2014; Shearer et al. 2015), often depending on the taxonomic or functional groups in question. Moreover, the vast majority of these studies from different biomes detected strong compositional shifts with increasing elevation, regardless of richness (e.g., Meier et al. 2010; Gómez-Hernández et al. 2012; Davey et al. 2013; Geml et al. 2014; Merckx et al. 2015; Rincón et al. 2015).

5.4.2 *Arbuscular Mycorrhizal Fungi*

Arbuscular mycorrhizal fungi (phylum Glomeromycota) are obligately symbiotic and form mycorrhizal associations with ca. 80% of land plants, including ca. 200,000 species of herbs, grasses, trees, hornworts, and liverworts (Davison et al. 2015). Despite their Paleozoic origin that coincided with the colonization of land by plants, extant taxa of Glomeromycota mostly appeared and achieved global distribution after the major continental shifts of the Mesozoic (Davison et al. 2015). The number of taxa is estimated to be between 340 and 1600 based on molecular

studies, and the vast majority of them occur in more than one continent and in multiple climatic zones (Davison et al. 2015; Van der Heijden et al. 2015).

The accumulating data suggest that, despite their large spores being more suited for short-distance dispersal, arbuscular mycorrhizal fungi are surprisingly effective dispersers even across considerable geographic distances over long timespans and that the regional species pool at any given locality represents a relatively large portion of the total global diversity (Davison et al. 2015; Van der Heijden et al. 2015). At the global level, the primary factors that are expected to determine the composition and richness of arbuscular mycorrhizal fungal communities are geographic distance, climate, and edaphic factors, in particular precipitation and soil pH (Davison et al. 2015; Öpik and Davison 2016). For example, arbuscular mycorrhizal fungal richness has been shown to correlate negatively with latitude (Davison et al. 2015) and positively with soil pH (Porter et al. 1987; Coughlan et al. 2000). Overall, the relative importance of dispersal to environmental filtering seems to depend on geographic scale and shows substantial variation (Vályi et al. 2016).

Given their obligately symbiotic lifestyle, vegetation is expected to have a strong influence on the distribution of arbuscular mycorrhizal fungi. Even though plant species richness does not correlate with the taxonomic richness of Glomeromycota on a global scale (Tedersoo et al. 2014), vegetation type does influence both richness and community composition of arbuscular mycorrhizal fungi at smaller spatial scales (Davison et al. 2015; Vályi et al. 2016). In addition to marked microclimatic and edaphic differences among distinct habitats on a landscape scale, the identity and distribution of host plants can influence the spatial distribution of arbuscular mycorrhizal fungi even within relatively homogenous habitats. For example, despite the apparent lack of species-level specificity in arbuscular mycorrhizal symbioses, different plant species often associate with different sets of glomeromycete species from the species pool of a given site (Sýkorová et al. 2007; Gosling et al. 2013; Vályi et al. 2016). Functional differences among arbuscular mycorrhizal fungi likely explain at least partly such preferential associations among certain host–symbiont pairs (Davison et al. 2011). For example, it has been shown that host plants and arbuscular mycorrhizal fungi with similar life strategies, e.g., competitiveness and tolerance for stress or disturbance, preferentially associate with each other (Chagnon et al. 2013).

There have been only a handful of studies documenting changes in root colonization, community composition, and/or richness of arbuscular mycorrhizal fungi along altitudinal gradients. Ruotsalainen et al. (2004) did not find statistically significant shift in root colonization of several herb species along an elevation gradient ranging from sea level to 1400 m a.s.l. in subarctic Norway based on morphological assessments. Similarly, Fisher and Fulé (2004) found no correlation of root colonization of corn seedlings by arbuscular mycorrhizal fungi across soil samples taken from various forest types between 2595 and 3308 m a.s.l. in Arizona, USA. Lugo et al. (2008) morphologically identified arbuscular mycorrhizal fungi in rhizospheric soil samples taken from underneath various grass species in Puna vegetation in the Andes between 3320 and 3870 m a.s.l. Despite the relatively short gradient (550 m) that featured a single vegetation type, the authors observed

that species richness of arbuscular mycorrhizal fungi decreased significantly with increasing elevation (Fig. 5.1). A follow-up study from Lugo et al. (2012) based on an extended set of field sites ranging from 3220 to 4314 m a.s.l. in the same region documented significant decrease in root colonization in the sampled grass species. This trend was evident both in total colonization rates in all samples and within host plant species. Gai et al. (2012) compared species richness and root colonization rate of arbuscular mycorrhizal fungi along a Tibetan elevation gradient between 1990 and 4648 m a.s.l. The vegetation types ranged from subtropical broad-leaved forest, through various temperate conifer forests to alpine scrubland and meadow. Both species richness and root colonization rate decreased significantly with increasing elevation regardless of host plant identity, particularly above 3000 m a.s.l. (Gai et al. 2012) (Fig. 5.1). Geml et al. (2014) used DNA metabarcoding of soil samples to characterize soil fungal communities in the subtropical Yungas forests of the Andes. Their sampling sites ranged from 405 to 2160 m a.s.l., representing the three major forest types: piedmont, montane, and montane cloud forest. The results showed strong compositional turnover with increasing elevation and revealed that although total fungal richness did not change with increasing elevation, richness estimates changed markedly in several fungal groups. In particular, richness of operational taxonomic units (OTUs) of arbuscular mycorrhizal fungi was negatively correlated with elevation (Geml et al. 2014) (Fig. 5.1). As part of a multi-taxon study on the evolution of endemism on Mt. Kinabalu in Malaysia, Merckx et al. (2015) analyzed DNA metabarcoding data generated from soil samples taken along an altitudinal gradient from 425 to 4000 m a.s.l. and showed that the majority of phylogenetic lineages in the genus *Glomus* were restricted to low elevations. Finally, Bonfim et al. (2016) found strong altitudinal turnover of arbuscular mycorrhizal fungi in a Brazilian Atlantic Forest gradient from 80 to 1000 m a.s.l., but, in contrast to other studies, the authors found greatest richness at the highest sampling site. Given the low number of sites along their single gradient, site-specific confounding factors may at least in part explain these results (Bonfim et al. 2016).

The emerging picture from the above studies is that both richness and abundance of arbuscular mycorrhizal fungi show a more or less monotonous decrease with increasing elevation, although regional deviation from this general pattern may exist. As noted above, there are various environmental factors that correlate with elevation at differing spatial scales. While the decrease in temperature with increasing elevation is predictable globally, biotic and edaphic factors can change along an altitudinal gradient on a more local scale and could strongly influence the distribution of arbuscular mycorrhizal fungi. For example, soil pH often is negatively correlated with elevation, particularly in areas with an increase in precipitation and resulting changes in vegetation and soil organic matter (Gai et al. 2012; Geml et al. 2014), and several of these factors likely contribute to the decrease in richness. On the other hand, the dataset of Lugo et al. (2008) suggests that even temperature per se may influence richness, when vegetation and edaphic factors remain comparable along the gradient. The positive correlation between arbuscular fungal richness and temperature is also supported by their higher richness in low latitudes on a global scale, as noted above.

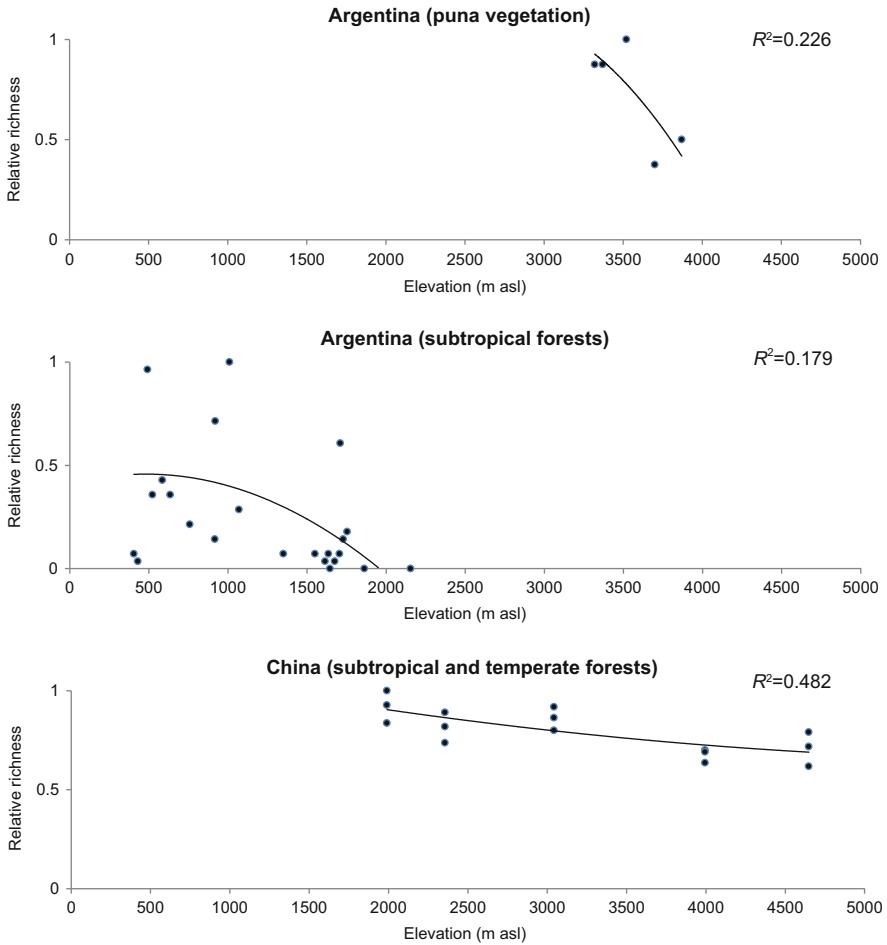


Fig. 5.1 Relative richness of arbuscular mycorrhizal fungi as a function of elevation based on data from previous studies: Puna vegetation in Argentina (Lugo et al. 2008), subtropical forests in Argentina (Geml et al. 2014), and subtropical and temperate forests in China (Gai et al. 2012). Relative richness was calculated in relation to the highest per-site richness value in each study. Correlation coefficients were inferred using quadratic regression

5.4.3 *Ectomycorrhizal Fungi*

Ectomycorrhizal symbioses worldwide involve ca. 6000 plant species and more than 20,000 fungal species (Rinaldi et al. 2008; Brundrett 2009). Although only about 2% of the estimated number of plant species form ectomycorrhizal associations (Brundrett 2009), the vast majority of them are woody plants and include the ecologically and economically most important trees in most of the forested areas of the world, with possible exception of Neotropical lowland forests (Chap. 20). Plant

families involved in ectomycorrhizal symbioses include Betulaceae, Dipterocarpaceae, Fagaceae, Nothofagaceae, Pinaceae, and certain lineages in Cistaceae, Fabaceae, Juglandaceae, Myrtaceae, Nyctaginaceae, Polygonaceae, Rosaceae, Salicaceae, Tiliaceae, etc. (Chap. 19). According to the latest syntheses (Tedersoo and Smith 2013; Chap. 6), the ectomycorrhizal habit has evolved independently in ca. 80 fungal lineages that comprise more than 250 genera, mostly in the phyla Basidiomycota and Ascomycota. Most ectomycorrhiza-forming taxa likely radiated in the Cretaceous and Paleogene, as orders of Agaricomycetes and Pezizales probably originated around 200 and 150 million years ago, respectively, based on molecular clock estimates (Berbee and Taylor 2001; Chap. 1). These estimates, however, postdate the evolution of Pinaceae, the oldest extant plant family that form ectomycorrhizal symbiosis, whose oldest fossils are dated to 156 million years ago (LePage 2003; Tedersoo and Smith 2013).

On a global scale, ectomycorrhizal fungal richness is primarily influenced by the relative proportion and species richness of host plants, soil pH, mean annual temperature, and mean annual precipitation (Tedersoo et al. 2012, 2014). Specifically, richness of ectomycorrhizal fungi has repeatedly been shown to peak at intermediate annual temperatures (between 5 and 20 °C) and at mid-latitudes, particularly in northern temperate forests. In terms of soil pH, ectomycorrhizal fungi are known to prefer slightly acidic to neutral pH. The majority of ectomycorrhizal fungi have broad host range and associate with hosts representing a wide range of taxonomic groups, while several others are more specific to plant families or even genera (Molina et al. 1992). Richness and density of host plants correlate positively with ectomycorrhizal fungal richness both on global and more regional scales (Tedersoo et al. 2014). In fact, Pinaceae is most dominant in northern mid-latitudes where the richness peak of ectomycorrhizal fungi is observed (Tedersoo et al. 2014; Chap. 18).

Many ectomycorrhizal fungi in low- to mid-latitudes show dispersal limitation and pronounced phylogeographic patterns (Geml et al. 2008; Peay et al. 2012; Branco et al. 2015), while arctic-alpine species generally exhibit high level of intercontinental gene flow (Geml 2011; Geml et al. 2012). The global study of Bahram et al. (2013) on ectomycorrhizal fungal communities showed a strong impact of latitude, but not longitude, on phylogenetic community turnover, confirming the abovementioned differences in the dispersal capabilities among fungi inhabiting different latitudes. These studies suggest that ectomycorrhizal fungal species tend to have much more restricted geographic distribution than arbuscular mycorrhizal fungi and that differences in the size and composition of the regional species pools of ectomycorrhizal fungi likely influence strongly their altitudinal patterns in a given region.

Similarly to arbuscular mycorrhizal fungi, the number of studies on changes in richness and community composition of ectomycorrhizal fungi along altitudinal gradients is low. The few relevant studies largely investigated different geographic regions with distinct vegetation and climatic conditions and reported several types of observed patterns, which makes comparisons difficult (Fig. 5.2). Kernaghan and Harper (2001) collected sporocarps of ectomycorrhizal fungi along multiple

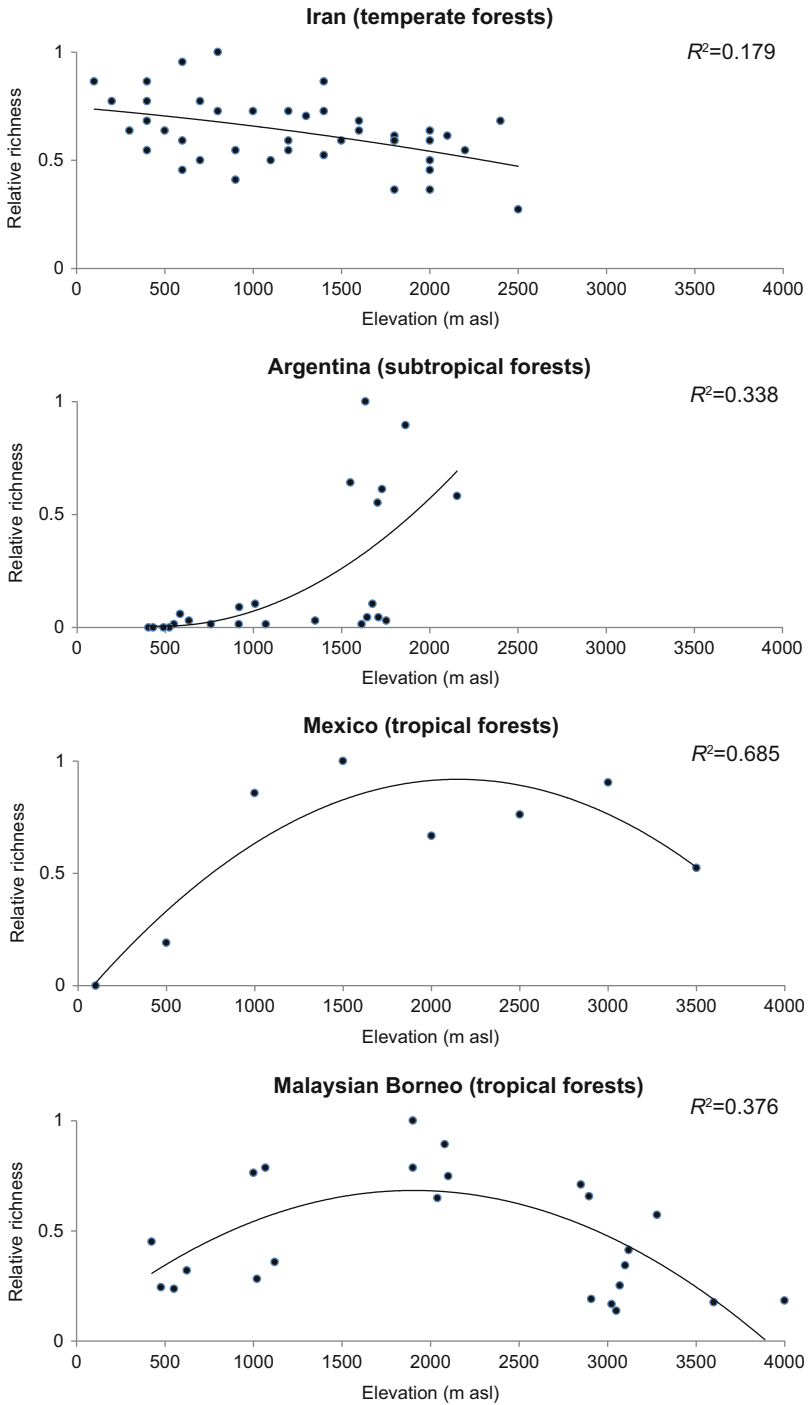


Fig. 5.2 Relative richness of ectomycorrhizal fungi as a function of elevation based on data from previous studies: temperate forests in Iran (Bahram et al. 2012), subtropical forests in Argentina

transects spanning the subalpine/alpine treeline ecotone (between 2000 and 2500 m a.s.l.) at two sites in Alberta, Canada. They found that richness and diversity of ectomycorrhizal fungi decreased with elevation despite the fact that host plant diversity was highest at the ecotone. Bahram et al. (2012) analyzed DNA sequence data generated from root tips of 367 ectomycorrhizal fungal species in mixed deciduous forests of Iran, ranging from sea level to ca. 2700 m a.s.l. The authors found that richness of ectomycorrhizal fungi declined with increasing elevation, partly explained by the decrease of rare species at high elevations due to their reduced competitive abilities under increased environmental stress (Bahram et al. 2012). In temperate forests in Argentina, Nouhra et al. (2012) compared sporocarp production of hypogeous fungi associated with *Nothofagus* species and reported higher richness in lower (800–900 m a.s.l.) than in higher elevations (1700–1800 m a.s.l.). Unlike the previous papers, Miyamoto et al. (2014) found highest richness of ectomycorrhizal fungi at mid-elevations on Mt. Fuji in Japan based on DNA sequences generated from root tips representing 73 ectomycorrhizal fungal species sampled between 1100 and 2250 m a.s.l. The authors contributed the observed patterns to the geometrical effect of overlapping elevation ranges (Miyamoto et al. 2014). The above studies spanned multiple vegetation types including different hosts that covaried with elevation, although ectomycorrhizal hosts were dominant throughout the sampled altitudinal gradients. In order to identify the role of abiotic drivers while keeping the host identity constant, Counce et al. (2014) analyzed pyrosequencing data of ectomycorrhizal root samples of *Fagus sylvatica* along multiple altitudinal gradients in France and Spain and found no statistically significant change in ectomycorrhizal fungal richness. Using the same methodology, similar results were obtained by Jarvis et al. (2015) and Rincón et al. (2015) regarding ectomycorrhizal fungi associated with *Pinus sylvestris* in various western European mountains. It is important to note, however, that all of the above studies showed compositional differences in ectomycorrhizal fungal communities along the altitudinal gradients as well as among the different regions regardless of the observed patterns of richness. In addition to the influence of host plant identity and abundance, temperature, precipitation, and edaphic factors, particularly soil moisture, pH, and C/N ratio, appear to be most influential in shaping ectomycorrhizal fungal communities in temperate mountains (Counce et al. 2014; Jarvis et al. 2015; Miyamoto et al. 2015; Rincón et al. 2015).

Even though substantially fewer studies have been published on the distribution of ectomycorrhizal fungi in subtropical and tropical mountains, studies from Mexico, Costa Rica, and northwestern Argentina concordantly suggest that richness of ectomycorrhizal fungi is by far the highest in montane cloud forests that generally occur between 1500 and 3000 m a.s.l. (Mueller et al. 2006; Gómez-Hernández et al.



Fig. 5.2 (continued) (Geml et al. 2014), tropical forests in Mexico (Gómez-Hernández et al. 2012), and tropical forests in Malaysian Borneo (Geml et al. 2017). Relative richness was calculated in relation to the highest per-site richness value in each study. Correlation coefficients were inferred using quadratic regression

2012; Geml et al. 2014; Wicaksono et al. 2016). Furthermore, a high percentage of ectomycorrhizal fungi appear to be restricted to montane cloud forests (Mueller et al. 2006; Wicaksono et al. 2016). The distribution of ectomycorrhizal hosts has been thought to shape the observed patterns strongly, because in these Neotropical regions the diversity and abundance of ectomycorrhizal host plants are by far the greatest in montane habitats, while low-elevation forests tend to harbor very few hosts (Mueller et al. 2006; Geml et al. 2014). The single published study on the distribution of ectomycorrhizal fungi in Palaeotropical mountains is that of Geml et al. (2017) on Mt. Kinabalu in Malaysian Borneo. Similar to the Neotropical studies, the data from Kinabalu indicated highest richness in most ectomycorrhizal fungal lineages in the mid-elevation montane forests, with the exception of tomentelloid fungi that showed a monotonal decrease in richness with increasing elevation. The high richness and restricted distribution of many ectomycorrhizal fungi in the montane forests suggest that mid-elevation peak richness is primarily driven by environmental characteristics of this habitat and not by the mid-domain effect (Geml et al. 2017). On Mt. Kinabalu, despite the decrease in host richness, the total relative basal area of ectomycorrhizal hosts is relatively constant (37–47%) along the sampled elevation gradient (Aiba and Kitayama 1999). This suggests that, in addition to host availability, ectomycorrhizal richness in subtropical and tropical mountains appears to peak at intermediate temperatures and high levels of available moisture, similar to the abovementioned latitudinal trends on a global scale. Tropical mountain environments are characterized by mid-elevation condensation zones where available moisture is usually the highest (Whitmore 1984; Rahbek 2005). As a result, many organismal groups that rely on high humidity show highest richness and abundance in montane cloud forests, e.g., orchids (Wood et al. 1993), ferns (Parris et al. 1992; Grytnes and Beaman 2006), epiphytic plants (Cardelús et al. 2006; Grytnes and Beaman 2006), bryophytes (Ah-Peng et al. 2012), and snails (Liew et al. 2010). Considering the distribution of ectomycorrhizal fungi, it is important to point out that tropical montane cloud forests are among the most vulnerable terrestrial ecosystems to climate change (Foster 2001; Pacheco et al. 2010; Wicaksono et al. 2016), as rising temperatures are resulting in a shifting cloud base that threatens their long-term survival (Still et al. 1999).

5.4.4 *Orchid Mycorrhizal Fungi*

While the knowledge on the altitudinal distribution of arbuscular mycorrhizal and ectomycorrhizal fungi is still rudimentary, much less attention has been paid to elevation patterns in other mycorrhizal fungi, such as those that form orchid and ericoid mycorrhizae. Most fungi that form mycorrhizas with orchids are facultative symbionts of orchids. Generally, fungi associated with green-leaved (i.e., only partially myco-heterotrophic) orchids mostly are saprotrophic, while nonphotosynthetic (fully myco-heterotrophic) orchids tend to associate with ectomycorrhizal fungi (Dearnaley et al. 2013). Furthermore, different species of orchids, as well as various life stages of the same orchid species, often represent different intermediate positions between the fully

autotrophic and fully heterotrophic spectrum of trophic mode (Dearnaley et al. 2013). Sebaciales, Ceratobasidiaceae, and Tulasnellaceae include most fungi that form mycorrhizas with orchids, but representatives of a wide range of other fungal taxonomic groups, particularly those that form ectomycorrhizas with trees, such as Pezizales, Russulales, Thelephorales, etc., can be associated with orchids as well, mostly in forests (Selosse et al. 2002; McCormick et al. 2004; Taylor et al. 2004; Waterman and Bidartondo 2008; Illyés et al. 2010; Dearnaley et al. 2013).

Despite the fact that substantial work has been done on the ecology of orchid mycorrhizal associations, there are very few published studies on their distribution at different elevations (Chap. 8). Taylor and Bruns (1999) investigated mycorrhizal specialization in nonphotosynthetic orchids *Corallorhiza maculata* and *C. mertensiana* in California. All symbiotic fungi found in the samples belonged to the ectomycorrhizal Russulaceae, and the authors found no shared fungal symbionts between the two orchid species. Moreover, there was a strong correlation with habitat and orchid mycorrhizal community composition, as populations of *C. maculata* above 2000 m a.s.l., corresponding to *Abies* forest, had no fungi in common with populations below 2000 m a.s.l. in forests dominated by *Pinus* and *Pseudotsuga* (Taylor and Bruns 1999).

Autotrophic orchids tend to be less specific with respect to mycorrhizal symbionts, ranging from “weedy” orchid species that associate with a broad range of fungi to locally endemic orchid species with more specialized symbionts (Suárez et al. 2006, 2008; Bonnardeaux et al. 2007; Rasmussen and Rasmussen 2009). The family Orchidaceae is most diverse in the tropics, and within tropical regions, their richness and abundance peak in mid-elevation montane forests (Küper et al. 2004; Cardelús et al. 2006; Acharya et al. 2011). Therefore, it is reasonable to hypothesize that orchid mycorrhizal fungal diversity and abundance may be highest in these montane forests. In addition, Kartzinel et al. (2013) found high spatial turnover of mycorrhizal symbionts of *Epidendrum firmum* in montane forests of Costa Rica, although neither biogeographic nor large-scale environmental factors were significantly correlated with community composition of orchid mycorrhizal fungi. Alternatively, differences in land use and fine-scale environmental factors may better explain the high spatial heterogeneity.

5.4.5 *Ericoid Mycorrhizal Fungi*

Most known ericoid mycorrhizal fungi can also grow as soil saprotrophs, while some can simultaneously colonize roots of other plants as well to form endophytic or ectomycorrhizal associations (Villarreal-Ruiz et al. 2004; Horn et al. 2013; Van der Heijden et al. 2015). Most fungi that are known to form ericoid mycorrhizas belong to the ascomycete order Helotiales and the basidiomycete order Sebaciales (Selosse et al. 2007; Walker et al. 2011; Geml et al. 2015; Van der Heijden et al. 2015). Even though members of Ericaceae, mostly evergreen or deciduous shrubs, can be found in all continents except Antarctica, they generally prefer cool and

relatively moist climates and acidic, nutrient-poor soils (Walker et al. 1994; Ojeda et al. 1998). The only published study specifically devoted to comparing community structure of ericoid mycorrhizas along an elevation gradient focused on fungal symbionts of *Vaccinium membranaceum* in Canada (Gorzalak et al. 2012). The study featured *V. membranaceum* root samples taken from various vegetation types, such as low- and mid-elevation spruce and hemlock forests, subalpine spruce and fir community, and alpine tundra at ca. 875, 1225, 1800, and 1925 m a.s.l., respectively. Gorzalak et al. (2012) isolated a total of ten fungal species from the root samples. Although all of them were found in multiple elevation sites and per-site richness values differed a little, there was substantial turnover in community composition: high-elevation fungal communities, characterized by *Rhizoscyphus ericae* and *Meliniomyces* sp., differed from lower elevation communities, where *Phialocephala fortinii*, *Cryptosporiopsis* sp., and *Neonectria radicola* were dominant.

In the tropics, ericaceous plants tend to be restricted to montane habitats, particularly between 1000 and 3000 m a.s.l. (Luteyn 1989, 2002; Beaman and Beaman 1990; Kreft et al. 2004; Giriraj et al. 2008). Geml et al. (2014) found that richness in Helotiales and Sebaciniales in the subtropical Andean forests was highest in the montane cloud forest zone (1500–3000 m a.s.l.). This pattern was particularly strong in Helotiales that included several indicator taxa with significant specificity and fidelity to the montane cloud forest. In addition to comprising numerous fungal species capable of forming ericoid mycorrhizas, both orders include many taxa with saprotrophic, root endophytic, or ectomycorrhizal trophic modes (Tedersoo et al. 2010). Therefore, studies specifically targeting ericaceous plants and their symbionts are needed to test whether or not the above trend holds (Chap. 9).

5.5 Conclusions

Despite significant advances in our knowledge on the diversity, distribution, and ecology of mycorrhizal fungi in the last decades, there is still very little known on how abiotic and biotic factors that correlate with elevation influence mycorrhizal communities. The first studies reviewed above suggest that altitudinal patterns of richness of mycorrhizal fungi are somewhat similar to those observed with respect to latitudinal gradients. For example, when considering the full range of biomes from tropical lowland forests to cold-dominated ecosystems, richness of arbuscular mycorrhizal fungi decreases with increasing altitude (and latitude), while ectomycorrhizal fungal richness tends to peak in mid-elevation (and mid-latitude) forests with temperate climates. Therefore, climate appears to be important in shaping the distribution of mycorrhizal fungi along altitudinal gradients in a variety of ways, e.g., by affecting microbial processes (e.g., decomposition) and edaphic factors, by altering species interaction dynamics among fungi and other members of the soil biota, and by influencing the abundance and diversity of hosts, etc. Distribution of hosts, which is also influenced by their biogeographic history, has

substantial influence on the above patterns, particularly in ectomycorrhizal fungi that associate with only ca. 2% of plant species and tend to have higher host specificity than arbuscular mycorrhizal fungi. Orchid and ericoid mycorrhizal symbioses, by definition, are also spatially limited by the distribution of Orchidaceae and Ericaceae, respectively. However, unlike most ectomycorrhizal fungi, both orchid and ericoid mycorrhizal fungi can grow as saprotrophs and/or root symbionts of a wide range of plants, and, therefore, the distribution of these fungal taxa is not restricted to areas where orchids and ericaceous plants occur. Carefully planned and executed studies, ideally featuring altitudinal gradients across multiple geographic regions, are needed to statistically evaluate the contributions of globally relevant (e.g., temperature) and regionally (e.g., precipitation, host biogeography) or locally (e.g., edaphic factors) idiosyncratic variables to explain altitudinal patterns in mycorrhizal fungal richness as well as community composition.

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