# Chapter 7
# Diversity in Soil Fungi, Protists, and Microarthropods

**Matthias C. Rillig, Tessa Camenzind, Julia Gawlik, Ingeborg Haug, Valentyna Krashevska, Mark Maraun, Dorothee Sandmann, and Stefan Scheu**

## 7.1 Introduction and Background

This chapter is one of the three that are concerned with current preserving services of a biodiversity hotspot of the South-Ecuadorian Andes. While the other two chapters (Chaps. 6 and 8) deal with plants and aboveground animals, here we cover selected soil biota groups. These are the arbuscular mycorrhizal (AM) fungi, forming a key mutualism with plant roots in tropical forests, soil microarthropods and testate amoebae, which are crucial components of the soil food web. While separated into chapters, it is clear that these components are interdependent and interact in various ways (e.g., Wardle et al. 2002). For example, plant diversity can have a strong influence on AM fungal diversity and vice versa (e.g., van der Heijden et al. 1998), at least as known from temperate ecosystems (mostly grasslands). Other microorganisms including bacteria and saprobic fungi, as well as decomposer invertebrates and their interactions, affect plant performance and thereby ecosystem processes (Scheu et al. 1999, 2005; Wardle 2002; Scheu 2003). Thus, it is important to consider these components together.

*Preserving Services and Soil Biota.* Preserving services refer to the maintenance of genetic or species diversity irrespective of any function. Soil biota generally play a key role in preserving services, since the reservoir of organismal diversity in soil is

M.C. Rillig (✉) • T. Camenzind
Institut für Biologie, Freie Universität Berlin, Berlin, Germany
e-mail: matthias.rillig@fu-berlin.de

J. Gawlik
Georgraphic Institute, University of Erlangen, Erlangen, Germany

I. Haug
Eberhard Karls-Universität Tübingen, Tübingen, Germany

V. Krashevska • M. Maraun • D. Sandmann • S. Scheu
J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Göttingen, Germany

typically vast, greatly exceeding the aboveground diversity of biota in terrestrial ecosystems (Wardle 2002). The strategy taken in research summarized in this chapter was not to tackle belowground diversity exhaustively, but to instead focus on a number of key groups. These are, for soil microbes, the group of AM fungi, for soil protists, testate amoebae, and for soil microarthropods, oribatid mites.

## 7.2 Methods

Terrestrial vascular plants of the natural forest were compared with strongly modified vegetation types (pastures, pine plantations, and bracken fern areas). The methods are described in greater detail in Chap. 8.

In order to assess molecular diversity of root-colonizing AM fungi we conducted a survey of the small subunit (SSU), comparing pristine forest with reforestation sites. The mycobionts were examined by molecular tools as given in Haug et al. (2010), additionally the primers AML1 and AML2 (Lee et al. 2008) were used. Operational Taxonomic Units (OTUs) were defined as surrogates for species on the basis of sequence similarity by use of OPTSIL (Göker et al. 2009) at <1 % divergence. In addition, we also carried out a morphological survey of root colonization at ×200 magnification.

Testate amoebae are unicellular protists and represent major consumers of bacteria in many terrestrial ecosystems in particular acidic forests such as the studied montane tropical rainforests (Krashevska et al. 2010, 2012a, b). They were extracted by washing soil and litter samples over filters, inspected under the microscope, and live specimens and empty shells were determined to species (see Chap. 18). Oribatid mites represent major soil mesofauna taxa reaching maximum density in acidic forests (Maraun and Scheu 2000) including the studied system (Maraun et al. 2008). They predominantly feed on fungi but are trophically diverse with some species functioning as not only primary decomposers but also predators (Schneider et al. 2004; Heidemann et al. 2011). They were extracted from soil cores of a diameter of 5 cm by heat (Kempson et al. 1963).

## 7.3 Results

### 7.3.1 Changes in Plant Diversity as a Driver of Other Diversities

The highly diverse natural forests in the San Francisco valley are exposed to a strong land use pressure. As a consequence large areas have been deforested and converted into pastures (see Chap. 2). This land use change causes a strong impact on plant diversity which is clearly shown by a differing vegetation composition and

Fig. 7.1 Distribution of plant species in the natural forest, on anthropogenic sites, and in both systems (data from Peters et al. 2010)
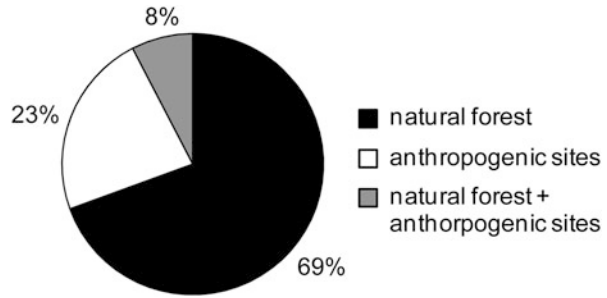


the loss of the vast majority of natural forest species (Peters et al. 2010; Chap. 8). With the conversion of the multi-storied natural forest ecosystem into a single or double layered anthropogenic replacement system about 90 % of the forest species (without epiphytes) are lost. Furthermore, species number average per 100 m$^2$ decline from 114 forest species to 39 on the pasture sites. Exchange ratio between both sites is very low and just 8 % of 880 plant species can be found on both sites (Fig. 7.1). The vast majority of species growing on human influenced sites, except the introduced fodder grass species, is native and has their distribution center in the Andes.

The data reported here are for aboveground diversity surveys; however, they will translate to the belowground as well, in terms of carbon input from living roots (rhizodeposition), from dead roots (root litter), and aboveground litter input.

## 7.3.2  Soil Fungi: Arbuscular Mycorrhizal Fungi

AM fungi are considered keystone mutualists in many terrestrial ecosystems; they are clearly the dominant mycorrhizal association type in tropical mountain forests in Southern Ecuador, with 112 out of 115 examined forest tree species forming this association (Kottke and Haug 2004).

Given the vast difference between the natural forest and the anthropogenic replacement system, the pasture, in terms of the respective plant community type and species composition, a strong effect on this group of plant root symbionts is expected. Additional factors contributing to any community divergence are higher frequency of disturbance through fire, altered microclimate, as well as soil properties (see Chaps. 1 and 2; Beck et al. 2008a, b).

In tropical ecosystems, disturbance by natural phenomena (e.g., treefall gaps and landslides) as well as by slash and burn or other agricultural practices may affect AM fungal diversity and abundance (Allen et al. 1998; Cuenca et al. 1998; Bastias et al. 2006). Already Janos (1980) proposed that a transformation of primary forests towards managed systems will impact the root-associated mycorrhizal fungi, even though he rather focused on the state of mycotrophy of the newly arising plant community.

Previous studies on the AM status of forests and pastures do not clearly support this view. The abundance/inoculum potential of AM fungi in soil and roots tended to not be reduced (Fischer et al. 1994; Maldonado et al. 2000; Guadarrama et al. 2008; Stürmer and Siqueira 2011), although methodologies applied may alter the outcome of a study (Muthukumar et al. 2003). Changes concerning the AM fungal community composition are complex. Picone (2000) compared tropical lowland forests in Costa Rica with converted pastures, finding a similar species composition and no decline in species diversity, though gamma-diversity was significantly reduced. Johnson and Wedin (1997) reported the same pattern in Costa Rican dry forests. Conversely, Gavito et al. (2008) found higher species richness in primary forests and a change in species composition in a tropical dry ecosystem in Mexico, whereas Stürmer and Siqueira (2011) report the lowest species richness in pristine forests in the Brazilian Amazon. These data were collected by analyzing spore communities, which generally raises problems because sporulation patterns can be affected by biotic and abiotic factors (Bever et al. 1996; Clapp et al. 1995). PCR-based methods provide a novel tool to directly assess fungal diversity in the roots itself. Few studies in the tropics applied molecular tools on this topic (e.g., Aldrich-Wolfe 2007). Basing on the analysis of only one tree species growing in tropical premontane forests in Costa Rica, seedlings planted into adjacent pastures formed a distinct mycorrhizal community. In the data described in the present chapter, the AM fungal community is likewise surveyed using a molecular approach.

A morphological comparison of AM fungal root colonization revealed no obvious divergence between forests and pastures, regarding both the abundance of AM fungal structures and the morphological traits. The percentage of AM fungal root colonization in the pristine forest has been assessed for various root samples collected at the NUMEX plots (2,020 and 2,120 m a.s.l., 3°59′S, 79°05′W; see Fig. 1.2; Chap. 23). Percentage of root colonization is on average 40–50 % (T. Camenzind, unpublished data). Roots sampled on the near reforestation plots and pastures were studied as well and the AM fungal colonization was examined visually after staining. These samples were well colonized throughout with no apparent morphological differences to the forest.

A small subunit (SSU)-based molecular survey of root-colonizing AM fungi comparing pristine forest with reforestation sites was conducted. In the pristine forest mycorrhizal roots were sampled from trees, planted (Kuptz et al. 2010) and naturally regenerated (seedlings). On reforestation sites of different successional stages, mycorrhizal roots were taken from tree seedlings of four planted native species (Günter et al. 2009) and surrounding trees, shrubs, and grasses. Members of Archaeosporales, Diversisporales, and Glomerales were found on all sites, with the Glomerales dominating. Omitting the singleton-OTUs, a total of 56 OTUs were found: 35 OTUs on the reforestation plots, 42 OTUs in the pristine forest, of these 21 OTUs occurring in both systems (Fig. 7.2a). No plant specific OTUs were recognizable. Few OTUs were found in high numbers, many in low numbers (Fig. 7.2b). Most of the frequent OTUs occurred in both systems. The results not only indicate a slight decrease in AM fungal richness and changes in species
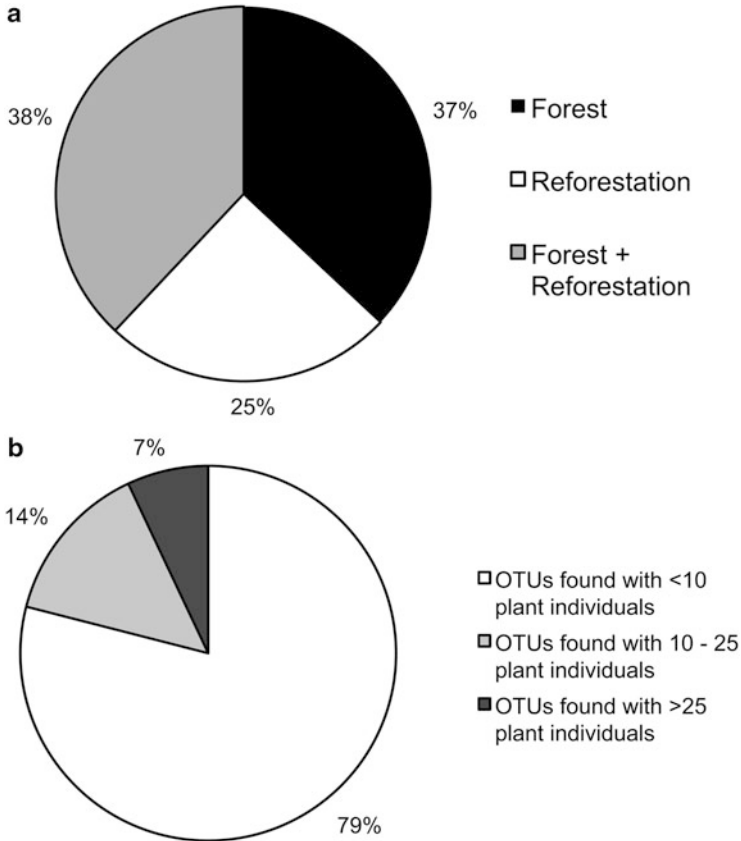
**Fig. 7.2** (**a**) Distribution of the occurrence of AM fungal Operational Taxonomic Units (OTUs) in the ecosystems of pristine forest, reforestation sites, and both systems. (**b**) Percentage of AM fungal OTUs found on different numbers of plant individuals

composition on the reforestation sites but also show a high fraction of AM fungi that are robust to the system change.

### 7.3.3 Soil Protists and Microarthropods: Testate Amoebae and Oribatid Mites

Micro- and mesofauna form main components of the soil food web and essentially affect decomposition of organic matter and thereby carbon and nitrogen cycling (Bradford et al. 2002; Hackl et al. 2005; Wilkinson and Mitchell 2010), but this remains poorly investigated in particular in tropical ecosystems (Coleman et al. 2004; Scheu et al. 2005).

Soil bacteria and fungi are imbedded in a complex food web in soil. Major consumers of bacteria include unicellular organisms such as testate amoebae, and major consumers of fungi include microarthropods such as oribatid mites. Both are considered to play an important role in regulating prey abundance and thereby decomposition processes in virtually all ecosystems on earth. This is also likely to be true in tropical montane rain forests of southern Ecuador, in particular since macrofauna decomposers are relatively rare in these ecosystems (Maraun et al. 2008; Scheu et al. 2008). Over the last 6 years we investigated the response of microorganisms, testate amoebae, and microarthropods to altitudinal changes (Krashevska et al. 2007; Scheu et al. 2008). Further, we explored the limitation of microorganisms and testate amoebae by carbon and nutrients (Krashevska et al. 2010), their dependency on litter quality (Illig et al. 2008; Krashevska et al. 2012a) and response to the exclusion of precipitation (Krashevska et al. 2012b). Here we summarize these findings and show how sensitively these components of tropical montane rainforests respond to environmental changes and to changes of altitude. As opposed to AM fungi, no comparable data are available for the comparison of forest and replacement system, so this aspect cannot be discussed.

### 7.3.3.1    Testate Amoebae

The density of testate amoebae live specimens was at maximum at 2,000 m, lower at 3,000 m and lowest at 1,000 m a.s.l. (Fig. 7.3a). Parallel to the density of live specimens, total density of testate amoebae peaked at 2,000 m, was similar at 3,000 m and lower at 1,000 m (Krashevska et al. 2007). Species number of live specimens did not change with altitude (Fig. 7.3b). In contrast, total species number decreased significantly in the order $2,000 \leq 3,000 < 1,000$ m. Krashevska et al. (2007) identified a total of 135 taxa and only few more species are to be expected, as suggested by rarefaction analysis (Fig. 7.4a). Indeed, in the last few years we found only few more species. Generally, more than 160 taxa of testate amoebae were identified in more than 200 samples. In comparison with plant diversity (about 1,200 species; Homeier and Werner 2007) protist diversity in the studied tropical montane rainforests is low, however, compared to testate amoebae diversity in a rain forest of Puerto Rico (104 species), in a temperate forest in Germany (62 species) and in acidic soils in Chile (94 species) the number of species of testate amoebae in the studied tropical montane rain forests of Ecuador is high. High species diversity is particularly remarkable as with a maximum of about 3,000 live specimens and about 13,000 total ind./g dry weight the density of testate amoebae is low compared to the above mentioned ecosystems with densities of 23,000–370,000 ind./g dry weight (Bonnet 1966; Wanner 1989; Bamforth 2007). The results suggest that the diversity but not the density of testate amoebae in tropical mountain forests is high exceeding that in other tropical forests and temperate forests. Additionally, the majority of the taxa found are geographically widespread, less than 10 % are endemic and we judge that less than 5 % are new to science. However, more detailed studies including molecular investigations are
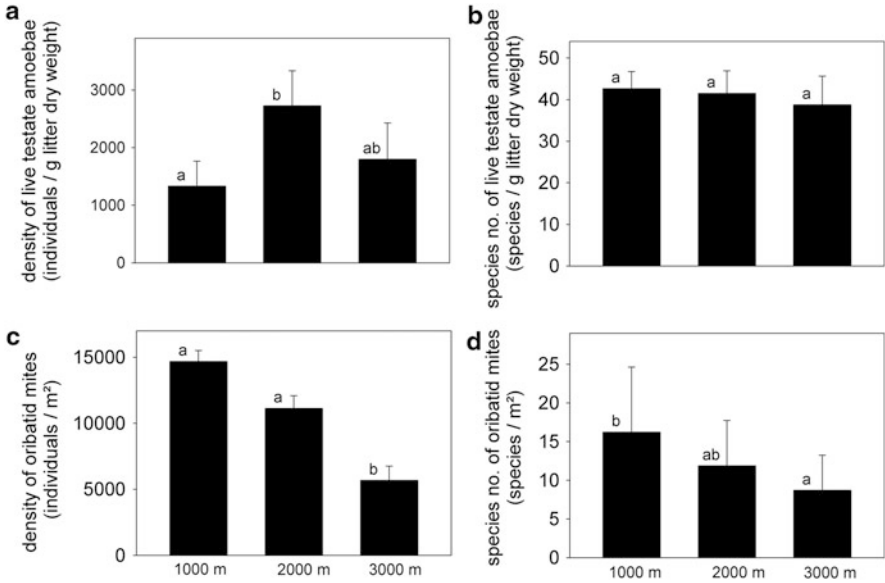
**Fig. 7.3** Density and species richness of live testate amoebae (**a** and **b**, respectively) and oribatid mites (**c** and **d**, respectively) in the litter/fermentation layer at three altitudes (1,000, 2,000, and 3,000 m a.s.l.) of the studied tropical montane rainforests. Means with SE; bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$)
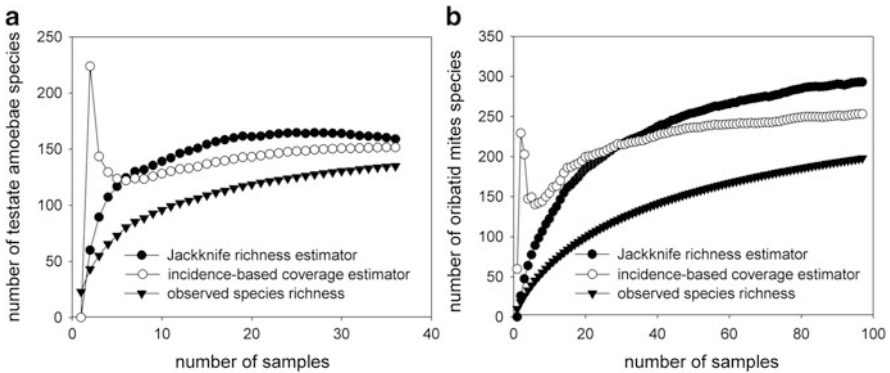


**Fig. 7.4** Sample-based rarefaction curves and corresponding estimators for testate amoebae (**a**) and oribatid mites (**b**)

needed to confirm these findings. As abiotic conditions at the study site are rather beneficial for soil invertebrates such as protists, low density of testate amoebae suggests low availability of resources with nitrogen presumably being most important (Iost et al. 2008; Krashevska et al. 2010).

### 7.3.3.2   Oribatid Mites

Total density of oribatid mites significantly decreased with increasing altitude in order $1,000 \leq 2,000 < 3,000$ m with $13,452 \pm 740$, $10,942 \pm 946$ and $5,597 \pm 1,090$ ind. m$^{-2}$, respectively (Fig. 7.3c). These densities resemble those of other tropical forests (rainforest in French Guiana ca. 25,000 ind. m$^{-2}$, Kounda-Kiki et al. 2004; rainforest in Australia ca. 43,000 ind. m$^{-2}$, Plowman 1981) but are much lower compared to acidic deciduous forests of the temperate zone and boreal forests where oribatid mites reach densities of $>200,000$ ind. m$^{-2}$ (Maraun and Scheu 2000). Surprisingly and in contrast to adult oribatid mites, the density of juveniles significantly increased with increasing altitude (data not shown). The higher proportion of juveniles at higher altitudes at least in part is likely due to longer developmental time of juveniles resulting from lower temperature. Corresponding to the density the average number of species found in one sample strongly decreased with increasing altitude (Fig. 7.3d). The total number of identified species also decreased with altitude, in particular at the highest altitude, with 169, 178, and 73 taxa at 1,000, 2,000, and 3,000 m, respectively. The number of species which exclusively occurred on one altitude decreased with increasing altitude with 60 %, 52 %, and 27 % at 1,000, 2,000, and 3,000 m, respectively, suggesting that at higher altitude the number of ubiquitous species increases.

In more than 350 samples investigated, a total of 335 taxa of oribatid mites were identified along the three study sides at 1,000, 2,000, and 3,000 m. The number of species corresponded with those estimated by rarefaction analysis (Fig. 7.4b). Although very preliminary, we estimate the number of new species to be high; about 40 % of the identified species could not be named with certainty using keys of Balogh (1972, 1988), Balogh and Balogh (1988, 2002), Balogh et al. (2008), Weigmann (2006) and others. Some new species have already been described (Niedbala and Illig 2007), but a wealth of work remains to be done. However, compared to the number of herbivore species above the ground, the number of oribatid mite species in soil is low as indicated by, e.g., the $>1,000$ species of geometrid moths found at the studied tropical montane rainforests (Brehm et al. 2003; Fiedler et al. 2008; see Chap. 6). This supports suggestions that compared to above the ground the latitudinal gradient in belowground animals is less pronounced (de Deyn and van der Putten 2005; M. Maraun, unpubl. data).

## 7.4   Conclusions

In this chapter we showed that in a comparison of forest and the anthropogenic replacement system, AM fungal richness was not greatly changed, even though there were strong changes in the associated plant community. It would be interesting to compare such patterns also for other soil biota groups such as other symbionts or decomposer microorganisms.

In a comparison of altitudinal patterns at three elevations, it became evident that the diversity of belowground animals, such as protists and microarthropods, does not approach that of aboveground animals, such as herbivores. Some groups showed strong altitudinal patterns (oribatids), whereas others (testate amoebae) did not.

Overall, the results highlight that considerably more effort is necessary to understand the relationship between above- and belowground diversities in these tropical forests: what is a hotspot for some organism groups does not necessarily have to be equally "hot" for others, but why this is so is not yet clear. Perhaps it is due to cryptic diversity below the level currently examined, but maybe there are also system-inherent reasons that explain why symbiont or decomposer subsystem diversity does not track the diversity of the aboveground component.

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