Chapter 10
Arbuscular Mycorrhizal Fungal Communities Pushed Over the Edge – Lessons from Extreme Ecosystems

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Abstract The diversity and structure of soil microbial communities are crucial elements in understanding the ecological impacts of rapidly changing environments. One important group of soil microbes is the ubiquitous plant symbiotic arbuscular mycorrhizal (AM) fungi. Their diverse communities are shaped by complex interactions of their abiotic and biotic environments. Locally extreme ecosystems have proven to be useful for natural long-term experiments in the ecology and evolution of AM fungi, giving an insight into much-needed processes of adaptation and acclimation of natural communities to abiotic stress. For example, data from natural CO_2 springs (mofettes) show that when exposed to extreme long-term stress (soil hypoxia and elevated soil CO_2 concentrations) specific and temporary stable AM fungal communities form with a high abundance of specialised, stress-tolerant taxa. Moreover, in both natural– and human-impacted ecosystems there are several such cases. This chapter covers a wide range of extremes (abiotic stresses) in the pedosphere, from high to low temperatures, drought and floods, hypoxia, salinity, and soil pollution. An overview of several specific stressed environments where AM fungal community ecology has been studied is presented. In some of these cases, locally extreme environments have already been used and could further serve as a powerful tool to study slow ecological and evolutionary processes that normally require long-term observations and experiments to study them.

Keywords Abiotic stress • Arbuscular mycorrhizal fungi • Soil biodiversity • Community ecology • Extreme ecosystems • Global change • Glomeromycota • Microbial ecology • Mofettes

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10.1 Introduction

Understanding mechanisms regulating the diversity and structure of soil microbial communities is urgently required for predicting the ecological impacts of rapidly changing environments. Arbuscular mycorrhizal (AM) fungal communities are diverse and near ubiquitous, symbiotically interacting with most terrestrial (Fitter and Moyersoen 1996; Smith and Read 2008), and some aquatic (e.g. Baar et al. 2011; Kohout et al. 2012; Sudová et al. 2015; Moora et al. 2016), plants. What structures their communities in natural ecosystems remains a matter of debate; however, it is clear that a complex combination of abiotic and biotic factors are determinants of AM fungal community composition. The direct effect of abiotic stress on AM fungal communities is less well understood than the impact it may have on their host plants. Recently, two hypotheses have been proposed predicting how AM fungi may respond to abiotic stress (Millar and Bennett 2016). The first, the stress exclusion hypothesis, predicts that AM fungal abundance and diversity will decrease with persistent abiotic stress, mostly by means of competitive exclusion of less tolerant taxa to a particular or combination of stress factors. The second, the mycorrhizal stress adaptation hypothesis, predicts that AM fungi will evolve in response to abiotic stress to maintain their fitness. While it is still not clear which are the main mechanisms behind AM fungal stress response, the authors of the study conclude that abiotic stress can have effects on AM fungi independent of the effects on the host plant (Millar and Bennett 2016). Moreover, there have been some studies in which the direct effects of abiotic factors on AM fungal communities have been well documented. Data from natural CO_2 springs (mofettes), for example, show AM fungal community response to long-term soil hypoxia. Mofettes are a valuable ecosystem in which studies in ecology and evolution are possible with the system serving as a long-term natural experiment (Maček et al. 2011, 2016a; Šibanc et al. 2014). The latter can be used to gain much-needed insight into the adaptation of natural communities and their ecological networks to the changing environment, including climate change.

However, apart from soil hypoxia (for a review see Maček 2017), there are many other stress factors that may even be more common in natural– and agro-ecosystems and still need more attention in the context of studies of soil microbial ecology. Here, AM fungi present just one but nevertheless functionally important and diverse group of organisms. The abiotic stress can be defined as a shift in any non-living factor within the environment away from the optimal condition or away from the condition to which most organisms in that environment have become adapted (Millar and Bennett 2016). Since natural ecosystems are often noisy and therefore challenging for research, one way of eliminating at least some of the variability is a study of locally extreme environments (for a review see Maček et al. 2016a). In extreme environments, selective pressures are sometimes long-term and relatively constant, providing ideal conditions for examining the genetic adaptation of biological communities to specific conditions (Maček et al. 2011, 2016a). Abiotic stresses, however, include a range of different factors, such as, for example, high and low temperatures, drought and floods, hypoxia, salinity, and different types of soil pollution. In this chapter, an overview of some specific environments where AM fungal diversity and community ecology has been studied will be presented. As a well-documented example, mofettes or natural CO_2 springs, serving as a model natural ecosystem for soil hypoxia research, are presented as a case study (Maček et al. 2016a; see Sect. 10.3.2).

10.2 Arbuscular Mycorrhiza

About 80% of all vascular plant species form arbuscular mycorrhiza, which is an underground symbiotic association between plants and AM fungi (Smith and Read 2008) (Figs. 10.1 and 10.2). This is a functionally important group of soil fungi involved in many terrestrial ecosystem processes (Fitter 2005; Rosendahl 2008). The symbiosis is ancient, over 450 million years old, and was significant in enabling the colonisation of land by plants (Redecker et al. 2002). AM fungi were accompanying plants in their transition from water to land from the very beginning and have been evolving in a range of diverse terrestrial and aquatic ecosystems. They are important players in key soil functions such as biogeochemical cycling of essential macronutrients and minerals, and maintenance of soil structure. For plants, there are several benefits of being mycorrhizal; AM fungi facilitate plant mineral nutrient uptake from the soil, affect plant water relations, and pathogen and pollutant resistance and tolerance (Smith and Read 2008). Indeed, as the most exposed function, mycorrhizal fungi provide significant amounts of N and P to their host plants in

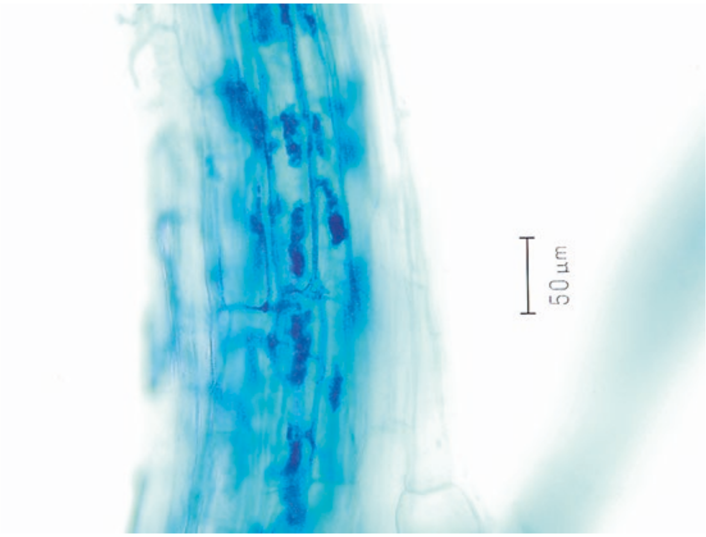

Fig. 10.1 AM fungi – root colonisation with abundant arbuscules in the root cortex of a C4 grass *Setaria pumila*

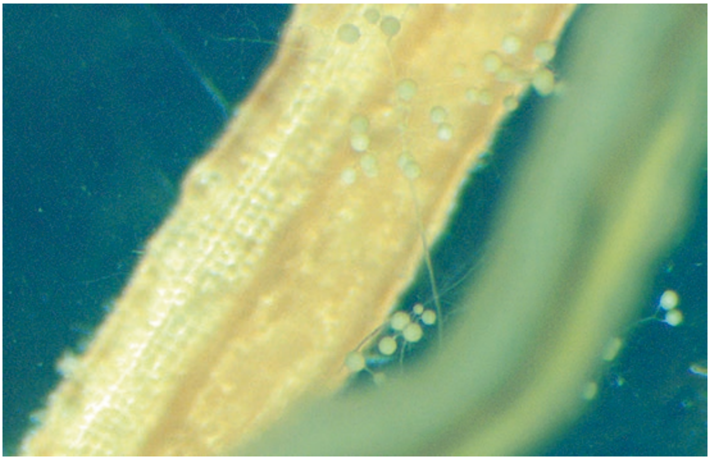

Fig. 10.2 Spores and extra-radical hyphae of AM fungus *Rhizophagus irregularis* around transformed *Medicago truncatula* roots in *in vitro* culture

natural ecosystems, especially those with reduced soil nutrient availability (see Fitter 2005; van der Heijden et al. 2015).

Therefore, AM fungi are common in many stressed environments and have been shown to increase plant survival and vitality in such ecosystems. They acquire all their carbon from the host plants and have central roles (e.g. nutrient cycling) in many habitats. Several indicators exist that the benefits provided to plants by AM fungi will become even more important due to increased abiotic stresses caused by climate change (e.g. Hanson Welzin 2000).

Understanding AM fungal ecology and identification of the main predictors of their community-level processes applies to a wide range of habitats. By delivering to the plant a range of benefits, they have a profound effect on plant community dynamics and diversity (Fitter 2005; van der Heijden et al. 2015). Recent molecular studies have shown, that communities of AM fungi in nature are more diverse than originally thought on the basis of spore morphology. AM fungal spores still serve as the main taxonomic characteristic since AM fungi cannot be identified morphologically in roots (Merryweather and Fitter 1998) (Figs. 10.1 and 10.2). It is known, however, that soil spore counts do not reflect the AM fungal diversity in plant roots and are not necessarily correlated with physiologically active AM fungal taxa forming mycorrhiza (e.g. Clapp et al. 1995; Renker et al. 2005). Since the morphological features of the structures of AM fungi in plant roots only allow low levels of identification, molecular approaches are needed for a more detailed description of their communities. The majority of the ecological studies on AM fungi are constructed on DNA-based techniques that have been developed to quantify AM fungi in field-collected soil and plant roots since the 1990s (e.g. Helgason et al. 1998).

Although over 250 morpho-species of the ph. Glomeromycota have been described (Walker and Trappe 1993; Schüßler 2008), molecular data show that significantly more AM fungal taxa exist, however those are currently known solely by their environmental sequences (e.g. Helgason et al. 2002; Öpik et al. 2013, 2014). With improved DNA-based identification methods, such as next generation sequencing (NGS), our ability to study soil microbial diversity has started to increase (e.g. Roesch et al. 2007; Öpik et al. 2009; Schloss 2009; Lemos et al. 2011; Dumbrell et al. 2011), allowing the characterisation of important mechanisms structuring natural AM fungal communities and tracking their seasonal dynamics (e.g. Dumbrell et al. 2011). The heterogeneous and dynamic nature of soil ecosystems, however, still makes it challenging to study the effect of the soil environment on natural microbial communities *in situ*.

10.3 AM Fungal Diversity in Extreme Ecosystems

Extreme environments have been defined as having one or more environmental parameters showing values permanently close to the lower or upper limits known for life (ESF – European Science Foundation report 2007). Therefore, for non-adapted organisms, an extreme environment is simultaneously a highly stressful one. The diversity of extreme environments is vast and can include several abiotic factors, ranging from physical (e.g. extremely high and extremely low temperatures), resource availability (e.g. limited water and O_2), to different types of pollution.

AM fungal diversity has been studied in several extreme ecosystems (Fig. 10.3); however, the use of molecular methods in the characterisation of their communities,

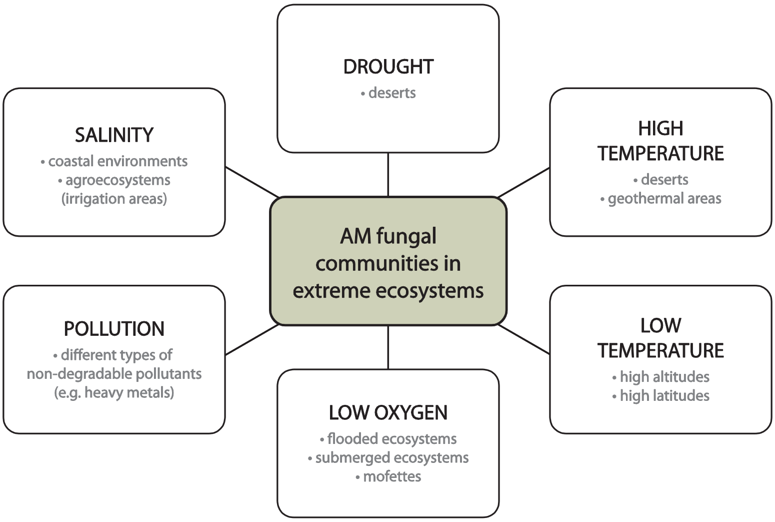

Fig. 10.3 AM fungal diversity (communities) and abiotic stress in selected extreme ecosystems that show potential for serving as long-term experimental sites in ecology and evolution

along with detailed description of relevant abiotic and biotic factors impacting their community structure, or even their temporal stability, is still limited. In most cases, AM fungal communities have not been sampled to saturation, and more intensive sampling might result in detecting additional taxa and would allow for a more realistic description of the patterns in the community ecology of this group of organisms. For example, the next generation sequencing (NGS) approaches (e.g. Dumbrell et al. 2011, 2016) may reveal other new taxa to be present, in particular, the rare ones, which are usually found only with the use of a higher-throughput methodology. The latter allows more intense sampling and is increasing the number of the analysed sequences (Dumbrell et al. 2016). Specifically, there is a need to target some less studied habitats, including aquatic and extreme environments (Fig. 10.3), where a combination of different approaches and expertise is needed. In particular, uniting species– (taxonomy) and community–oriented (ecology) approaches would be a major advantage in studying AM fungal community ecology and global diversity patterns (Öpik and Davison 2016).

10.3.1 Temperature and Drought

Both extremes, very high and very low temperatures can be problematic for life, since temperature stress disrupts metabolic processes in living organisms (e.g. protein stability, enzymatic reactions, changes in membrane fluidity and electron flow). Along with challenging temperatures, limited water availability is accompanying both extremes. Cell dehydration is not only common in dry and hot places, like deserts, but also occurs during freezing stress caused by extracellular ice crystal formation.

The community composition of AM fungi in northern latitudes remains poorly investigated (Francini et al. 2014; Öpik and Davison 2016), while there have been some reports of AM fungi in Swiss alpine sites (e.g. Oehl et al. 2012; Oehl and Körner 2014). One of the reasons may also be a limited number of projects involving AM fungal researchers that have access to those sites. In addition, arctic and alpine tundra are dominated by ericaceus plant species which host diverse networks of root-associated fungi forming other types of symbiosis in which AM fungi are not common (Toju et al. 2016). Indeed, in a recent study using high-throughput sequencing, fungal communities in alpine tundra were shown to be dominated by the taxa from the ascomycete order Helotiales and basidiomycete order Sebacinales, which are known to embrace ectomycorrhizal fungal lineages allied to ericoid mycorrhizal ones (Tedersoo et al. 2009, 2014). Despite the deep sequencing of root-associated fungal community compositions in the study of Toju et al. (2016), only a very small number of AM fungal sequences were found, which shows that arbuscular mycorrhiza is rare in those habitats and that diversity of AM fungi is low, as also seen in other studies (Francini et al. 2014; Varga et al. 2015). This is in accordance with the general knowledge that AM symbiosis usually dominates in milder and warmer abiotic environments (Read 1991). Nevertheless, other vegetation types and plant hosts that are known to form a symbiosis with AM fungi should also be more thoroughly examined for AM fungal diversity, both in alpine and arctic areas.

Indeed, the few reports on AM fungal diversity in arctic and alpine areas show that there also is a high number of taxa that are adapted to extreme conditions in the indigenous AM fungal communities (e.g. Francini et al. 2014). A similar observation was also found in an alpine site in Switzerland (Dom summit, at 4,505 m asl) known as the coldest place where angiosperm plant life is found, where five different species of AM fungi were found colonising *Saxifraga oppositifolia* (Oehl and Körner 2014). In those conditions the capability of the fungi to form long-surviving spores and retaining their viability after long-term cold conditions with freezing temperatures is vital (Varga et al. 2015). In addition, root colonisation from other AM fungal structures (e.g. vesicles) is also possible, and in such conditions some adaptive traits of fungi may be present, either colonising new roots from the existent structures in the roots or the ability for germination under cold conditions just above freezing temperatures, as observed for *Archaeospora trappei* from Dom summit, a species that is not known to form vesicles (Oehl and Körner 2014).

On the other end of temperature extremes, there have been several reports on the diversity of AM fungi in deserts, for example from the Arabian Peninsula (Al-Yahya'ei et al. 2010; Symanczik et al. 2014a), and Eritrea in East Africa (Harikumar et al. 2015), with several descriptions of new species based on spore morphology and in some cases also molecular identification (e.g. Symanczik et al. 2014b). Furthermore, geothermal vents are another specific high-temperature environment where AM fungal communities were studied. This was done in the geothermal and non-thermal grasslands in the Yellowstone National Park (USA), where plants experience rooting zone temperatures of 45 degrees C or more (Appoloni et al. 2008; Lekberg et al. 2011), and in geothermal areas of Iceland (Appoloni et al. 2008). Five of the seven operational taxonomic units (OTUs) detected in Iceland were also found in Yellowstone National Park. A subset of three OTUs was determined to be associated with geothermal conditions in the field sites analysed, while the AM fungal communities in geothermal soils include both unique OTUs and generalist fungi that occur across a broad range of environmental conditions (Appoloni et al. 2008). With the exception of an apparent generalist fungal type closely related to *Glomus intraradices*[1], AM fungal community composition in the Yellowstone National Park was highly correlated with soil pH and pH-driven changes in soil chemistry, and the large differences in soil temperature and differences in plant community composition were only secondary factor affecting the AM fungal community (Lekberg et al. 2011). Soil pH has also been confirmed in other studies as the main abiotic driver of AM fungal community composition (e.g. Dumbrell et al. 2010).

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[1] The names from the original papers have been used in this Chapter, as some authors are following the nomenclature preceding the major modifications published by Schüßler and Walker (2010), and Oehl et al. (2011). See also Öpik et al. (2013) for comparison between names.

10.3.2 Anaerobic Stress

Hypoxia (low O_2 concentration) or even anoxia (lack of O_2) in plant rhizosphere are common phenomena that can be consequence of flooding, submergence, soil compaction, or are a specific characteristic of some extreme ecosystems (e.g. due to geological CO_2 release in natural CO_2 springs (mofettes), after displacing soil O_2 with CO_2 or sometimes water) (Maček et al. 2016a; Maček 2017). Plants and soil fungi are known to be obligate aerobes and are sensitive to O_2 deficiencies in their environment since they need a sufficient amount of this gas to support their aerobic metabolism. Large areas of land are flooded each year and climate change models projections show the extreme events resulting in increased areas of flooding to become even more frequent and severe in the future (Hirabayashi et al. 2013). Therefore, anaerobic soil conditions will be an even more common phenomenon both in natural and agroecosystems.

Most of the studies of AM fungal diversity in submerged ecosystems (in the context of permanent plant root and aerial system flooding) come from aquatic macrophyte vegetation from the oligotrophic and ultraoligotrophic lakes of northern Europe (e.g. Baar et al. 2011; Sudová et al. 2015; Moora et al. 2016, for review see also Maček 2017). Only very recently, and empowered by the newly developed molecular tools, researchers have looked further into AM fungal community composition in these specific ecosystems. Diverse AM fungal communities have been found in the roots of an aquatic macrophyte *Littorella uniflora*, with several AM fungal taxa present, including the taxa from the genera *Glomus, Acaulospora*, and *Archaeospora* (Baar et al. 2011; Kohout et al. 2012), and a significant share of previously non-recorded sequences. The latter has been reported also from a recent study on AM fungal communities inhabiting the roots of submerged aquatic plant *Lobelia dortmanna* (Moora et al. 2016). A new AM fungal species, *Rhizoglomus melanum*, was also recently described and isolated from the rhizosphere of aquatic macrophytes from the freshwater lake Avsjøen in Norway (Sudová et al. 2015). Those aquatic plants have characteristic aeration systems allowing rapid O_2 diffusion from the shoots to the roots and are known for high radial O_2 losses from their roots into the sediment (Smolders et al. 2002). The AM fungi appear to be dependent on the high O_2 concentrations in the roots and surrounding root zones of the aquatic plants (Wigand et al. 1998), and this appears to be a consistent and important component of AM fungal habitats in hypoxic soils.

Natural CO_2 springs, or mofettes, are another ecosystem with long-term soil hypoxia and relatively well-described communities of AM fungi (Maček et al. 2011, 2016a, see Fig. 10.4). These are tectonically or volcanically active sites with CO_2 gas vents, through which ambient temperature geological CO_2 reaches the surface (Vodnik et al. 2006, 2009; Maček et al. 2012, 2016a; Maček 2013). Here, O_2 in the soil atmosphere is largely displaced by CO_2. Thus far, only the research by Maček et al. (2011, 2016a), studying the impact of elevated CO_2 and soil hypoxia on the diversity of AM fungal communities, has focused on the diversity of AM fungi from these habitats. In this study, significant levels of AM fungal community turnover (beta diversity) between soil types and the numerical dominance of specific AM

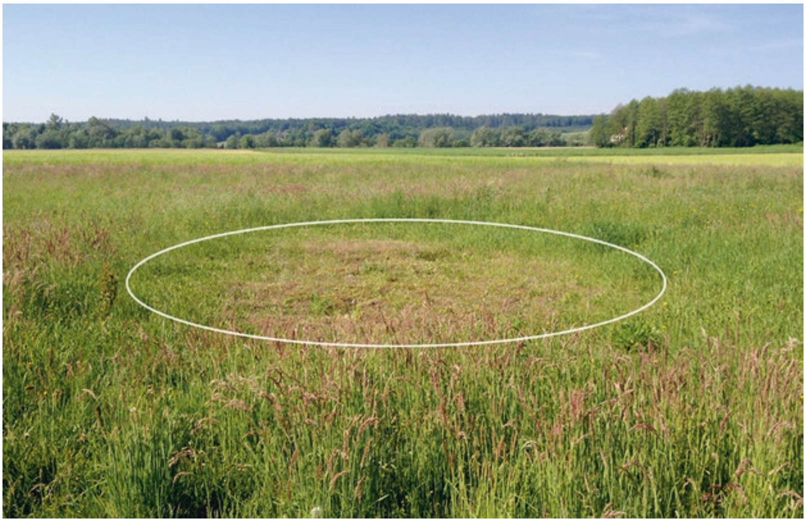

Fig. 10.4 Mofette area (natural CO_2 springs) with geological CO_2 exhalations causing long-term soil hypoxia (Stavešinci mofette, Slovenia). Inhibition in vegetation growth due to elevated geological CO_2 and soil hypoxia can be seen centrally around the mofette (*white line*)

fungal taxa when exposed to soil hypoxia were found. This work strongly suggests that direct environmental selection acting on AM fungi is a major factor regulating AM fungal communities (Maček et al. 2011). Moreover, mofette research has allowed a further step of using locally extreme environments as natural experiments where important questions in ecology and evolution can be investigated (Maček et al. 2016a). Extreme, persistent, and directed abiotic pressures have been shown to result in a more stable system with highly specific and partially predictable composition of microbial communities, dominated by the adapted taxa consistently present in high abundance in those soils (e.g. Maček et al. 2016a). This has already been confirmed for several groups of mofette microbes: archaea and bacteria (Šibanc et al. 2014), AM fungi (Maček et al. 2011, 2016a), as well as some higher organisms, including soil fauna (Hohberg et al. 2015; Schulz and Potapov 2010), and plants (Maček et al. 2016a). For more details, mofettes have been throughly presented as a case study and as a natural long-term experimental site in ecology in a chapter of a recent thematic issue of *Advances in Ecological Research*, titled '*Large Scale Ecology: Model Systems to Global Perspectives*' (Maček et al. 2016a).

10.3.3 Salinity

Some plants can survive (salt-tolerant plants) or even thrive (halophytes) in high salt concentrations. Salinity stress has both osmotic (causing water deficits) and cytotoxic effects (accumulation of toxic ions in the cells) that affect both groups of organisms in mycorrhizal symbiosis, plants, and fungi. Along with the coastal areas where salinity is naturally present, it is estimated that 20% of all irrigated land is currently affected by salinity stress. The occurrence and community composition of AM fungi was investigated in several coastal areas where biota has been naturally exposed to long-term salt stress. Some example ecosystems across the globe would be: (i) a NaCl salt marsh site of the island Terschelling, Atlantic coast, the Netherlands, (ii) a K_2CO_3 marsh at Schreyahn, Northern Germany (Wilde et al. 2009), (iii) coastal vegetation on Okinawa island in Japan (Yamato et al. 2008, 2012), (iv) Saemangeum reclaimed land in South Korea (Krishnamoorthy et al. 2014), and marsh and sand dunes vegetation in Cabo de Gata Natural Park in Spain (Estrada et al. 2013). The overall biodiversity of AM fungi, based on molecular and morphological analyses, was reported to be relatively low at most of those sites, though a relatively high diversity of 30 AM fungal morphospecies from 13 genera, including some newly described species has also been reported for some areas (e.g. Estrada et al. 2013). As for other extreme environments, there is a need for more diversity and community ecology studies, including those using higher-throughput techniques to thoroughly characterise these ecosystems regarding their soil biological communities composition.

10.3.4 Pollution – Toxins (e.g. Heavy Metal Polluted Soil)

Soil contamination, caused by large amounts of pollutants, is becoming a major problem on a global scale (EEA 2007, The EU Environment, State and Outlook). In particular, heavy (toxic) metals are a major concern as they are non-degradable and persist in soil, thus causing permanent long-term stress to all biota present (e.g. Maček et al. 2016b). Heavy metals are known to cause severe toxicity and include zinc, copper, cobalt, nickel, mercury, lead, cadmium, silver and chromium.

By using molecular methods, AM fungal communities have also been described in sites polluted with heavy metals (e.g. Zarei et al. 2008, 2010; Hassan et al. 2011; Maček et al. 2016b). Among other abiotic factors toxic metal concentration in soils have been shown to have an important impact on the composition of AM fungal communities (Zarei et al. 2008, 2010; Hassan et al. 2011). Many reports indicate a reduction of AM fungal diversity in heavy metal polluted areas, based both on spore morphology (e.g. Griffioen 1994; Pawlowska et al. 1996; Leyval et al. 1997; del Val et al. 1999) and molecular data (e.g. Zarei et al. 2008, 2010; Hassan et al. 2011). A predominance of the taxa within the genus *Glomus*[1] has been reported in most of the studied areas with severe heavy metal disturbance (e.g. Whitfield et al. 2004; Vallino et al. 2006; Zarei et al. 2008; Sonjak et al. 2009; Hassan et al. 2011), as well as other human-impacted environments, such as agricultural sites, phosphate-contaminated sites (Daniell et al. 2001; Renker et al. 2005), and sites with fungicide treatments (Helgason et al. 2007). Zarei et al. (2008) analysed the diversity of AM fungal associated to *Veronica rechingeri* growing in the heavy metal-polluted soil of the Anguran Zn and Pb mining region in Iran. Three species could be separated morphologically, while phylogenetic analyses revealed seven different AM fungal MOTUs in plant roots, all within the genus *Glomus*[1]. Some MOTUs were only found at sites with the highest and lowest soil heavy metal contents and some in both, which is a pattern also observed in other studies (e.g. Zarei et al. 2010; Hassan et al. 2011). Thus, the patterns of new taxa identifications are also showing in extreme environments that entirely originate from the human-impacted pollution.

10.4 Conclusions

Extreme environments have for a long time been explored as ecosystems of particular interest. The ecology of extremophiles has long been a rich source of knowledge about the evolution and functions relevant to stress adaptation, of microbes from different phylogenetic groups (e.g. Gostinčar et al. 2010). Many initial studies have aimed to describe those systems from different aspects, including the diversity of abiotic factors and biological communities. AM fungi are diverse in many extreme environments, but those ecosystems have not yet been largely used to study general principles in AM fungal biology, ecology and evolution (Maček et al. 2016a).

Experimental manipulation of soils is challenging, and gives conflicting results, possibly because few studies have the long-term manipulation necessary to observe adaptive change (e.g. Jansa et al. 2003). This is also one of the reasons that in locally extreme environments some important fundamental, but still unanswered, questions in microbial ecology may be addressed, including those that involve the response of soil microbes to long-term disturbance or environmental change, and questions about the predictability of microbial community composition patterns (Maček et al. 2016a). Therefore, as a potential natural source for studying general principles in microbial ecology, extreme ecosystems have a wider importance to the scientific community that extends beyond stress ecology *sensu stricto* and descriptions of extreme ecosystems *per se*.

Importantly, questions on long-term (press) related changes in soil microbial communities are relevant to many human drivers of long-term nature, including climate change, pollution, nutrient input, land-use change and others. However, in particular questions about the stability against press perturbations have received relatively little attention so far. The introduction of NGS methods into ecology can largely change this (see Dumbrell et al. 2016). These tools are allowing us to obtain an exceptional amount of data in a relatively short time. This is a key condition to be fulfilled in order to understand the complex temporal and spatial patterns in soil microbial communities along with their environmental drivers and consequently increase our capacity to predict their response to human impacts and global change.

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