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Summary of the Doctoral thesis

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Biochemické markery funkce půdního mikrobiálního společenstva a vliv antropogenního stresu

Biochemical markers of soil microbial community and functioning and antropogenic stress

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Abstract

The soil microbial community has a major impact on ecosystem processes on a global scale. Anthropogenic stress has a significant effect on the composition, biomass and activity of the microbial community. In addition, this effect depends not only on the anthropogenic activity, but also on the environmental conditions. Modern analytical and molecular methods, including the use of biochemical markers, can be well used to monitor changes in the microbial community. These methods do not monitor the community directly, but detect the substances that are secreted and transformed by microbes and, last but not least, those that are part of them. The amount of these biochemical markers reflects the biomass, condition and taxonomic composition of a particular microbial community. In the presented work, these markers were used to monitor the response of microorganisms in various ecosystems which are affected directly or indirectly by human activity. The results of the dissertation are presented in four articles. Three of them have been published in international journals with IF and one is prepared in the form of a manuscript for publication.

The first publication presents the results of research exploring the impact of traditional agriculture in Papua New Guinea on the soil microbial communities, soil organic matter and soil nutrients. With the exception of the available P, no significant differences were found between the areas variously affected by agriculture. This indicates the sustainability of traditional and proven cultivation practices. The second publication, which is attached as a manuscript, shows the significant effect of the non-native invasive plant Piper aduncum on the soil microbial community and on the nutrients in the soil, also in Papua New Guinea. The third publication deals with the occurrence of arbuscular mycorrhizal (AM) and ectomycorrhizal fungi (EcM) on spoil heaps after brown coal mining in the Sokolov region; the subject of the study was a gradient of early successional herbaceous and woody vegetation. Here it was found that the coexistence of Calamagrostis epigejos and Salix caprea favor EcM at the expense of AM. In the fourth article, the significant influence of tourism on the composition of the microbial community of cave soils is confirmed by means of markers.

This work provides a broader view of the application of biochemical markers in soils affected by direct or indirect human activity. It provides new information that can be used in practice as a basis for decision-making and planning.

1. Introduction

The most abundant living components of the soil, are microorganisms. For example, 1 g of soil contain aprox. 10^6-10^9 bacterial cells , and especially in the rhizosphere of some plants there are up to several tens of thousands of species (de Vrieze 2015). Microorganisms also play an important role in functioning of ekosystem and ekosystem services such as decomposition and mineralization, nitrogen fixation, carbon sequestration, etc. (Bardgett a van der Putten 2014; Fierer 2017). The microorganisms are affected by environmental factors, as well anthropogenic influences and management. The microbial community of soil may be characterized by its size, composition and activity (Harris a Steer 2003). To characterize these, a number of methods is used based on the analysis of biochemical markers and components. The determination of the biomass of soil microorganisms, diversity and activity provides information on soil health and processes.

Soil microorganisms play an important role in the global carbon cycle. Soil organic carbon represents the largest terrestrial carbon pool containing about three times more carbon than the atmosphere (Intergovernmental Panel on Climate Change 2000). Even small changes in the soil organic carbon pool may significantly affect atmospheric carbon concentration and have a strong feedback effect on climate change (Lal 2004; Minasny et al. 2017). Soil organic carbon stock is very sensitive to changes in management and land use with tropical soils being particularly vulnerable (Feller a Beare 1997; Ogle et al. 2005). The vulnerability of tropical soils may be further increased by agriculture practices (Bayer et al. 2002; McGrath et al. 2001; Ogle et al. 2005). However, some forms of traditional agriculture have slight or non-significant effect on soil organic matter and microbial communities (**Publication 1**).

Tropical rain forest ecosystems face many threats (Sala 2000) including impact of alien invasive species which can influence not only biodiversity but also provisioning of ecosystem services (Cardinale et al. 2012; Costanza et al. 1997). Invasive plants may affect the composition of soil microorganisms (Callaway a Ridenour 2004; Jordan et al. 2008, **Publication 2**), sometimes in the ways that promote plant invasion (Callaway a Ridenour 2004). These effects can be caused by the accumulation of root exudates, allelochemicals and modification of nutrient availability by alien plants (Ehrenfeld 2003; Vilà et al. 2011).

The relationship between plants and soil microorganisms are also important for ecosystem development and restoration. Mycorrhizal fungi serve is the major link between plants and soil and contributing to plant uptake of essential nutrients such as nitrogen and phosphorus (Smith a Read 2009) while increasing plant resistance to water deficiency to some microbial pathogensand and to water deficiency (Augé 2001; Dugassa et al. 1996). Arbuscular mycorrhizal (AM) fungi and ectomycorrhizal (EcM) fungi form the two most important types of mycorrhizal symbioses in temperate zones (Smith a Read 2009). Differences in functional traits of AM and EcM fungi enable these two distinctive mycorrhizal types to provide their associated host plants advantages in different environments. Coexistence of AM and EcM plants may affect fungal communities in roots of both species, including their mycorrhizal symbionts (Publication 3). Natural sites undergoing spontaneous plant succession (e.g. after coal mining) are particularly suitable for research on AM–EcM fungal interactions.

Microorganisms can respond sensitively to different changes in soil. Caves are unique ecosystems with specific environment. In particular, cave sediments affected by exogenous material associated with human access can serve as a good indicator of the human impact on caves (Adetutu et al. 2012, **Publication 4**). Analysis of microbial biomass and diversity can be useful for evaluation of environmental stress due to the tourist traffic. These information can be helpful for cave management.

2. Aims of the study

Publication 1: To evaluate the impact of the traditional slash-and-burn agriculture on microbial community, soil organic matter and nutrients, in the environment of the tropical rainforest in Papua New Guinea.

Publication 2: To explore the impact of the invasive shrub *Piper aduncum* on the soil microbial community and selected nutrients on the same old successional plots in the tropical rainforest in Papua New Guinea.

Publication 3: To describe the occurrence of ectomycorrhizal and arbuscular mycorrhizal fungi depending on the successional vegetation of *Salix caprea* and *Calamagrostis epigejos* in soils formed on post mining sites.

Publication 4: To investigate the effect of unregulated cave tourism on the microbial community in cave sediment.

3. Material and methods

Publication 1: The study was conducted in and around the Wanang village in the Madang province, Papua New Guinea. The village is surrounded by a mosaic of primary rain forest and secondary vegetation regenerating after shifting agriculture. The plots for the study represented active gardens, old gardens (5–10 years since disturbance), secondary forest (20–40 years since disturbance), and primary forest (more than 60 years since disturbance). The soil samples were collected from two depths (0–5 and 5–10 cm). Air-dried homogenized soil was used for soil analyses (total C, N, P, and C fractions of soil and available P, Ca, Mg, K, NO_3, pH). Freeze-dried homogenized soil was used for analysis of PLFAs.

Publication 2: The study area was situated in the lowland tropical rain forest in the Papua New Guinea (Madang province). The study sites were located around the Wanang and Ohu villages. In Wanang, eight approximately 10-year-old abandoned gardens were selected, four of which were invaded by *P. aduncum* while the remaining four, treated as control plots, remained without *P. aduncum*. In the Ohu village, where most of the secondary vegetation was invaded by *P. aduncum*, the effect of experimental removal of *P. aduncum* was studied. At each site, three soil cores (5 cm deep and 5 cm in diameter) were mixed into one composite sample for each of two depths (0–5 and 5–10 cm). Furthermore, the second most terminal leaf from three sweet potato plants and a 5 x 5 cm leaf section from the second most terminal leaves of three banana plants were sampled at each site. Samples for PLFA and DNA analyses were freeze-dried. Soil and leaf samples were air-dried and analyzed for soil properties and nutrient content.

Publication 3: Samples were collected at three different sites (20-year-old) on the post mining area (NW Bohemia, Czech Republic; 500–600 m a.s.l.). At each of the three sites, five samples containing roots of the target plant species and surrounding soil were taken from three different microenvironments: 1. spots predominantly occupied by the early succession-dominant, AM-hosting grass *Calamagrostis epigejos*; 2. spots beneath the canopy of *Salix caprea* trees (dual host with EcM fungi prevailing) covering ca 5 m^2 of bare land under the tree canopy and where herbaceous plants occur only sporadically; and 3. contact zone outside of the tree canopy area where the roots of these two species interacted. The sand bags were placed at the sites. Sand bags consisted of 7 × 7 cm nylon mesh bags (mesh size 40 μm) filled with 10 g of pure, sterilized silica sand. The sand samples were used for ergosterol and neutral lipid fatty acids (NLFA) analysis. Dried homogenized soil was used for assessing the mycorrhizal inoculation potential (MIP) and soil chemistry. DNA was extracted from roots.

Publication 4: The study area were sandstone caves situated in the NNR Kaňon Labe (Labe Canyon), PLA Labské pískovce (Elbe Sandstone Mountains). In each of the caves, sediment samples were taken along the gradient of the walkway from the cave entrance. Two types of samples were collected: samples affected by trampling in the part of cave where the majority

of visitors step, and non-affected in the part where stepping is unlikely. The samples were analysed for soil properties, phospholipid fatty acids (PLFAs) and enzyme activities and nutrients. Rate of cave tourism was determined from log-books which are located in all caves in the area.

4. Results and discussion

Publication 1: Kukla, J., Whitfeld, T., Cajthaml, T., Baldrian, P., Veselá-Šimáčková, H., Novotný, V., Frouz, J., 2019. The effect of traditional slash-and-burn agriculture on soil organic matter, nutrient content, and microbiota in tropical ecosystems of Papua New Guinea. Land Degrad. Dev. 30, 166–177. https://doi.org/10.1002/ldr.3203

The traditional slash-and-burn agriculture which are followed by the tillage and modern western agriculture style can leads to loss of soil organic matter and their degradation. Slash-and-burn agriculture typically affects spacious areas in the tropical zone. Due to evaluation the effect of the traditional slash-and-burn agriculture the soil properties were studied by a chronosequence represented at the active gardens. The abandoned gardens (5–10 years old), secondary forest in the deserted garden sites (20–40 years old) and primary forest where have not been the evidence of the cultivation over the last 60 years. Ther were no significant differences observed between the individual successional stages. No diffences were observed in the total C, N, and P and in the C fractions, pH, conductivity or microbial biomass. In addition, stocks of C, N, and P in the soil did not differ between the successional stages. On the other side, the concentration of available P, Ca, Mg, K, and NO_3 was higher in the active gardens. The litter was absent in the active gardens, and the highest amount of the litter on the soil surface was found in the primary forest. The study shows that the traditional slash-and-burn agriculture had a significant effect on the nutrient availability but no effect on the total CNP stocks and the soil C fractions.

Publication 2: Kukla, J., Heděnec, P., Baldrian, P., Cajthaml, T., Novotný, V., Moradi J., Whitfeld, T.J.S., Frouz, J. The plant invasion of *Piper aduncum* altered soil microbiota and nutrient content in shifting areas of Neotropical lowland forests in Papua-New Guinea (manuscript)

Piper aduncum is a Neotropical invading species which successfully occupies the secondary vegetation fallows in the patches after slash-and-burn agriculture in Papua New Guinea. The soil samples were collected from same old plots. The research was focused on the comparison of the soil chemistry and the soil biota of the sites invaded and uninvaded by *P. aduncum*. The soil invaded by *P. aduncum* had significantly lower P content in the shallower layer at 0−5 cm under the surface and lower NO_3^-, N and C content in the deeper layer at 5−10 cm under the surface than soil under the secondary vegetation which was not invaded by *P. aduncum*. The *P. aduncum* plots also manifested lower biomass of soil microorganisms which was proven by phospholipid fatty acid (PLFA) analysis. PLFA and the next generation sequencing methods revealed that the composition of microbial communities also differed between the soils with and without *P. aduncum* however there was no difference in the abundance of the soil macrofauna. In addition, the soil chemistry and the foliar nitrogen in the gardens specified as the slash and burn secondary vegetation with a history of five years of experimental exclusion of *P. aduncum* was studied. These selected gardens did not differ in the soil chemistry from the control gardens, although *P. aduncum* removal was associated with a higher content of N in the

sweet potatoes leaves (*Ipomoea batatas*), but not in the bananas (*Musa* spp.). Our results suggest that *P. aduncum* may decrease the fertility of food gardens established after slashing and burning of secondary vegetation.

Publication 3: Knoblochová, T., Kohout, P., Püschel, D., Doubková, P., Frouz, J., Cajthaml, T., Kukla, J., Vosátka, M., Rydlová, J., 2017. Asymmetric response of root-associated fungal communities of an arbuscular mycorrhizal grass and an ectomycorrhizal tree to their coexistence in primary succession. Mycorrhiza 27, 775–789. DOI: 10.1007/s00572-017-0792

This study focused on the arbuscular mycorrhizal (AM) grass *Calamagrostis epigejos* and predominantly ectomycorrhizal (EcM) tree *Salix caprea* co-occur. These plants were observed at the post-mining sites spontaneously colonized by these species and other vegetation. AM herbaceous vegetation was replaced by predominantly EcM woody species during the succession. For better understanding the interaction of AM and EcM plants during vegetation transition, the study of the reciprocal effects of these species' was set on the base of the coexistence of their root-associated fungi (RAF). The root and the soil samples were collected from three different microenvironments: stand of *C. epigejos*, under *S. caprea* canopy, and contact zone where roots of these species interacted together. In the roots RAF communities and mycorrhizal colonization were determined and the soil was tested for EcM and AM inoculation potentials. Despite the composition of the RAF communities in both plant species were significantly affected, the effect was higher in the case of *C. epigejos* RAF communities than in that of *S. caprea* RAF communities. The observation showed significantly decreasing AM fungal abundance in the soil as well as AM colonization and richness of AM fungi in *C. epigejos* root in the presence of *S. caprea*. Changes observed in the abundance and community composition of AM fungi might constitute an important factor in transition from AM-dominated to EcM-dominated vegetation during succession.

Publication 4: Kukla, J., Holec, M., Trögl, J., Holcová, D., Hofmanová, D., Kuráň, P., Popelka, J., Pacina, J., Kříženecká, S., Usťak, S., Honzík, R., 2018. Tourist Traffic Significantly Affects Microbial Communities of Sandstone Cave Sediments in the Protected Landscape Area "Labské Pískovce" (Czech Republic): Implications for Regulatory Measures. Sustainability 10, 396. DOI: 10.3390/su10020396

The step-compression of the cave sediment significantly increased the ratios of fungi/bacteria and gram-positive to gram-negative (G+/G−) phospholipid fatty acids (PLFA) as well as PLFA of actinobacteria, but the activities of phosphatases, glucosidases and oxidases were decreased significantly in the sediments modified by anthropogenic stres. The absolute numbers of visitors were known and there were set the positive correlation with the G+/G− ratio and the sediment nutrients while there were observed the negative correlation with the activity of peroxidases. These results indicate the significant effect of anthropogenic stres on microbial sediment communities which is most likely caused by the introduction of the nutrients into the caves. Acording to this results the cave attendance policy is recommended.

5. Conclusions

The microbial community has a crucial role in a number of important processes in soil. However due to its character, it has been difficult to study it effectively in earlier times. The

composition, biomass and activity of microbial communities can be studied using biochemical markers. More recently, due to the advances in analytical methods, analysis of these markers has become more accessible and microbiology has become a dynamically developing discipline. As the number of studies increases, so does the level of knowledge about the behavior of microorganisms and the environmental and anthropogenic effects on the microbial community. It is important to understand the response of microorganisms to these effects in a wide variety of habitats.

A significant form of anthropogenic stress is soil disturbance by agriculture, which can be problematic especially in tropical ecosystems. In Papua New Guinea, it has been found that the traditional slash-and-burn agricultural system does not have a significant effect on the soil microbial community, nor on the soil organic matter. This suggests that the traditional way of farming is relatively soil-friendly and sustainable and that the microbial community is able to cope relatively well with some types of stressors.

Biological invasions are a serious global problem, but their impact on soil has not been well understood. Many disturbed plots in Papua New Guinea are invaded by *P. aduncum* shrubs. It has a significant negative effect on soil nutrients and microbial biomass and also changes the microbial community composition when compared to control areas with native vegetation. This may be caused by the allelopathic substances in the roots and leaves *of P. aduncum* and indicates a strong link between the invasive plant and the soil microorganisms.

Relationships between plants and microorganisms play an essential role during succession. Post-mining sites are very specific habitats where ecosystem development processes can be observed in real time. *S. caprea* has been found to suppress ectomycorrhizal fungi in the rhizosphere of *C. epigejos* grass. The results suggest that the sensitivity of soil microorganisms to the presence of some plants can be one of the mechanisms causing shifts from grassland to young forest.

Microbial communities colonize almost all natural habitats, even those relatively poor in nutrients and low in productivity. In an isolated cave environment, the influence of tourist traffic, in this case represented by trampling, on the microbial community in the sediment compared with unaffected sediment can be well monitored using biomarkers. Changes in the community composition (fungi/bacteria ratio or G +/G- ratio) were found. The positive correlation of the microbial biomass with the attendance rate also points to the influence of tourism on the microbial community and Suggests that microbial biomass could be used as indicator of cave attendance. Such approach could be helpful in developing strategies for cave conservation.

The use of biochemical markers in all these studies helped to explain the under-explored effects of direct and indirect anthropogenic stress and biological processes on the soil microbial community. This knowledge can serve as a basis for decision-making or can refine prediction of changes in global nutrient cycles and ecosystem processes.

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Curriculum Vitae

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Kukla, J., Heděnec, P., Baldrián, P., Cajthaml, T., Novotný, V., Moradi J., Whitfeld, T.J.S., Frouz, J. The plant invasion of *Piper aduncum* altered soil microbiota and nutrient content in shifting areas of Neotropical lowland forests in Papua-New Guinea (manuscript)

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