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FUNCTIONAL REDUNDANCY OF SOIL MICROBIOTA – DOES MORE ALWAYS MEAN BETTER?

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Abstract. The proper and healthy functioning of the soil depends largely on the microorganisms abundance, including the total number of bacteria and fungi, but also their diversity. The increase in the biodiversity also increases the functional capabilities of the ecosystem but from a certain point, a further increase in the biodiversity does not bring any new features, so the general biochemical and metabolic profile of the ecosystem remains constant. It is also suggested that the loss of one or more species does not dramatically affect the functioning of the ecosystem, because the same functions can be represented by many different species. This phenomenon is called a functional redundancy and makes the soil a very stable environment with a high buffering capabilities, more often called the "soil memory". On the other hand, some unique biochemical processes are characteristic for a small group of species, for example, nitrogen fixation or toxic compounds degradation. The loss of the specialized species may lead to the decrease of a rare genes occurrence in the soil, resulting in the loss of nutrients or the accumulation of toxins.This article presents the current findings on functional redundancy in terms of soil microorganisms and its implications to the soil functioning.

Keywords: functional redundancy, soil microbiota, soil memory, biodiversity

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INTRODUCTION

The soil processes, such as organic matter decomposition, mineralization, neutralisation of toxins, or maintenance of nutrients at the stable level depend primarily on the soil microorganisms. Many studies show the correlation between microbial community composition and the soil metabolic profile (Navarro-Noya *et al.* 2013). Despite the very rapid development of modern research methods, the number of known species of microorganisms varies between 0.1 and 10%, depending on the ecosystem studied. This knowledge is very limited especially for cultivated soils in agroecosystems because the very dynamic changes in the microbial composition and the soil functioning depend on the season, the stage of plant growth, type of soil, and, finally, the agrotechnical management (Torsvik and Ovreas 2002). Regardless of the limited knowledge, the position of science is consistent in that the diversity of microorganisms has a direct impact on the stability of different ecosystems, from water and soil, to the human body. Over the last decades, attention has been paid to the preservation of biodiversity, including microorganisms, for example, by more sustainable soil cultivation (Panizzon *et al.* 2015). On the other hand, there is a strong position that the soil is such a huge reservoir of diverse individuals and, consequently, an inexhaustible source of functions that the environmental changes do not cause a damage to the whole ecosystem. This is explained by performing the same functions by many different representatives, and even with the loss of one or more species, there are plenty of others ready to take over the same role. This phenomenon is called a functional redundancy, making the soil a very stable environment (Jurburg and Salles 2015). Nevertheless, many studies prove that the soil ecosystem has its limits in response to changing environment, and that microorganisms are often endemic. This causes that some ecosystems are functioning properly only in the original environment which is caused by coevolution of microorganisms and their adaptation to environmental conditions (Keiser *et al.* 2011). Moreover, one of the studies has shown that different microbial communities have not become similar under the same conditions, suggesting that the original composition of microorganisms could be a predictor of the responses of a particular ecosystem and its development (Pagaling *et al.* 2014). For that reason, it is increasingly common to classify microorganisms communities not on the basis of their taxonomic affiliation but on their functions. The presence of a particular species in the soil does not indicate its interactions with the environment, as more than 80% of the microbial cells in the soil are temporarily not active. They represent a specific reservoir or bank of potential functions that are activated only under the specific conditions (Lennon and Jones 2011).

THE SPECIES RICHNESS IS BENEFICIAL FOR LESS COMMON FUNCTIONS

It is well known that most of the basic metabolic processes in the soil such as respiration, carbon turnover, organic matter decomposition are performed by all of the microorganisms, or at least by most of them. Changes in the environment will not cause significant fluctuations in the level of these processes. On the contrary, what will happen with the rare functions carried out only by a specific group of the soil microbiome?

In one of the experiments (Girvan *et al.* 2005) two soils differing originally in the species richness were compared. The subject of the study was a comparison of the ability of mineralization of different carbon sources by soil communities after application of toxic substances (copper sulfate and benzene) which caused a non-selective decline in biomass and overall diversity. There was no significant difference in the mineralization of the easily accessible carbon source (wheat shoots) that is a broad scale function. Interestingly, the mineralization of 2,4-dichlorophenol, which is known as a narrow niche function, was initially impaired in both soils. Shortly before the end of the experiment, the soil of greater diversity recovered the ability to benzene mineralization. After 9 weeks, both soils recovered their original microbial composition and functionality. Similar conclusions can be drawn from another experiment (Griffiths *et al.* 2000) in which authors gradually reduced the number of different species by repeating the fumigation followed by the regeneration phases. The large reduction in the diversity did not reduce the basic respiration or decomposition levels but resulted in the reduction of nitrification, denitrification and methane oxidation, indicating that the specific processes are more sensitive to environmental changes.

Each of the metabolic functions depends directly on the genes encoding specific enzymes. It turns out that the species redundancy which often also leads to the functional redundancy favors another phenomenon. More species may increase the presence of different genes variants in the population which products perform the same function, that is the isofunctional diversity of enzymes. In addition to enhancing the functional capabilities of the entire population, such isoenzymes have a great advantage, they can mutually complement each other depending on the conditions. It was also proved (Horemans *et al*. 2016) that to perform one function, in this case linuron degradation, the cooperation of several species is beneficial. Some of the species only initiate the degradation (hydrolysis) and do not have the downstream genes (downstream catabolism). One of these synergistic interactions was found in a consortium consisting of *Variovorax sp.* (converts linuron to 3,4-dichloroaniline) and *Comamonas testosteroni* (removes 3,4-dichloroaniline) (Dejonghe *et al.* 2003). If one of these species is missing, the pesticide or its intermediate form still remains in the soil and results in toxicity.

THE AGROTECHNICAL MANAGEMENT ALTERS THE MICROORGANISMS COMPOSITION

Cultivation is one of the most influential human activities as far as the properties and functioning of the soil are concerned (Navarro-Noya *et al.* 2013). A strong relationship between agrotechnical management, the microbiome composition and its functionality was proved by Sun *et al.* (2016). The team showed that the combination of no tillage and crop rotation improves the soil biological parameters and its quality. The greater abundance of microorganisms was observed in a 0–5 cm depth and it was correlated to the higher organic carbon and total nitrogen in the soil. Other studies seem to confirm the effect of the type of the tillage, but not a crop rotation, on the amount of total organic carbon in the soil, by increasing the biomass of microorganisms. However, this only affects some crops, but often the effect is either reversed or negligible. Moreover, it is suggested that only fast growing microorganisms are sensitive to temporary changes in nutrient availability or level of hydration and that the change in their occurrence does not necessarily entail changes in the metabolic level of the soil and its functioning (Navarro-Noya *et al.* 2013).

Monitoring changes in species diversity is not always correlated with a change in the functioning of the ecosystem. An example is the result of research on metabolism levels after adding nutrients and organic matter during the decomposition (Banerjee *et al.* 2016). Although the modification of the substrates caused a shift in the number of some species up to 300-folds, the total richness and evenness was reduced but the biomass was increased. A smaller number of species did not affect the decline in organic matter decomposition. However, there was an increase in the number of key species (including *Acidobacteria* in bacteria and *Fusarium* in fungi), which probably contributed to maintaining a steady level of metabolism. This suggests that functional redundancy in the examined environment ensured a metabolic equilibrium despite the shift of species taxa. This is another proof that increasing the number of species does not affect the improvement of metabolic parameters of the whole community, at least in terms of general processes such as respiration or organic matter decomposition.

Very important conclusions have been made in an experiment (Attard *et al.* 2010) that has shown the influence of the tillage on the shift of bacterial communities in terms of nitrite-oxidizing bacteria. It turned out that tillage can have long-term effects, causing the decrease of soil potential nitrite oxidation (PNO). What is more, in the soil that has been cultivated for 14 years with no-tillage, the PNO level was twice as high as in continuously tilled. After the conversion from no-tillage to tillage soil management, the PNO level decreased and the number of nitrite-oxidizing bacteria shifted from *Nitrobacter*- to *Nitrospira* related bacteria, which are negatively correlated to potential nitrate oxidation levels. Even after the cessation of tillage, this parameter did not increase and the

Nitrobacter-to-*Nitrospira* ratio did not return to the optimal level for even up to 17 months. This experiment is an example of irreversible, at least long-term, phenomena of the change in microbial composition of the soil caused by the human activity. Despite the huge buffering capacity of the soil, it has failed to maintain its homogeneity, not only on the taxonomic but also on the functional level, probably reaching a new state of equilibrium. Functional redundancy in this case has led to the shift of nitrogen turnover by other representatives (from *Nitrobacter* to the less efficient *Nitrospira*), but this has resulted in a reduction in the rate of nitrogen conversion. This directly affects the availability of nitrogen for plants, and consequently, deterioration of crop quality. The failure to return to the previous state may also result from the establishment of favorable conditions for the more adaptively, *Nitrospira* group. This state is very difficult to change especially if alternative species require more time to grow and have a lower metabolic rate. The last conclusion that can be drawn from this analysis is the need for consideration in applying treatments intended to improve the soil parameters. These changes may be more permanent than it was supposed, and the environment may never return to its original state.

CONCLUSIONS

The functional redundancy is a phenomenon not fully understood and requires deeper research, however, it is known that more diverse communities enrich different ecosystems in more potentially useful capabilities of metabolism, organic matter decomposition, toxins neutralization and environmental stress resistance. Almost 160 years ago, in *On the Origin of Species*, Charles Darwin stated that more productive systems are based on species diversity compared to individual species. Although his words referred to plants, it turns out that his statement has numerous affirmations in various ecosystems, including the soil microbiome. The most observable results of the species diversity decrease are in the case of microorganisms carrying rare, but important genes, responsible for such processes as nitrogen fixation or pesticides degradation. The exclusion of such species from the population can result in a significant decrease in system efficiency, reduction in nutrient content and the accumulation of toxic substances. At the same time, it was repeatedly reported that the soil is a very stable and resistant environment, having strong buffering properties. The changes in species composition in most of the cases are not altering the general respiration, organic matter decomposition and many others “broad scale” functions. That strong stability is ensured by the diversity of microorganisms, which are performing the same or similar functions. Despite the soil’s ability to return to equilibrium, it is important to mention that greater than environmental changes, can be human influences on microbial composition and its functioning. Different agrotechnical managements may alter the microbiome structure, sometimes in irreversible manner. The initial state retrieval often lasts for several decades and is highly dependent on the original composition of bacteria, fungi and protozoa that inhabit the soil.

Answering the question whether "more always means better?", there is no clear answer in the context of soil microorganisms. It is believed that the composition of the microbe instead of species redundancy is most significant in the healthy and proper maintenance of the soil. On the other hand, the functional diversity depends directly on the number of different representatives, so greater biodiversity offers a wider range of possible functions.

REFERENCES

[1] Attard, E., Poly, F., Commeaux, C., et al., 2010. *Shifts Between Nitrospira- and Nitrobacter-Like Nitrite Oxidizers Underlie the Response of Soil Potential Nitrite Oxidation to Changes In Tillage Practices*. Environmental Microbiology, 12, 2: 315–326, **http://doi.org/10.1111/j.1462-2920.2009.02070.x**

[2] Banerjee, S., Kirkby, C.A., Schmutter, D., et al., 2016. *Network Analysis Reveals Functional Redundancy and Keystone Taxa Amongst Bacterial and Fungal Communities During Organic Matter Decomposition in an Arable Soil*. Soil Biology and Biochemistry, 97: 188–198, **http://doi.org/10.1016/j.soilbio.2016.03.017**

[3] Dejonghe, W., Berteloot, E., Goris, J., et al., 2003. *Synergistic Degradation of Linuron by a Bacterial Consortium and Isolation of a Single Linuron-Degrading Variovorax Strain*. Applied and Environmental Microbiology, 69, 3: 1532–1541, **http://doi.org/10.1128/AEM.69.3.1532-1541.2003**

[4] Girvan, M. S., Campbell, C. D., Killham, K., et al., 2005. *Bacterial Diversity Promotes Community Stability and Functional Resilience after Perturbation*. Environmental Microbiology, 7, 3: 301–313, **http://doi.org/10.1111/j.1462-2920.2005.00695.x**

[5] Griffiths, B.S., Ritz, K., Bardgett, R.D., et al., 2000. *Ecosystem Response of Pasture Soil Communities to Fumigation-Induced Microbial Diversity Reductions: An Examination of the Biodiversity-Ecosystem Function Relationship*. Oikos, 90, 2: 279–294, **http://doi.org/10.1034/j.1600-0706.2000.900208.x**

[6] Horemans, B., Bers, K., Romero, E.R., et al., 2016. *Functional Redundancy of Linuron Degradation in Microbial Communities in Agricultural Soil and Biopurification Systems*. Applied and Environmental Microbiology, 82, 9: 2843–2853, **http://doi.org/10.1128/AEM.04018-15**

[7] Jurburg, S.D., Salles, J.F., 2015. *Functional Redundancy and Ecosystem Function – The Soil Microbiota as a Case Study*. Biodiversity in Ecosystems – Linking Structure and Function. InTech, **http://doi.org/10.5772/58981**

[8] Keiser, A.D., Strickland, M.S., Fierer, N., Bradford, M.A., 2011. *The Effect of Resource History on the Functioning of Soil Microbial Communities is Maintained Across Time*. Biogeosciences, 8, 6: 1477–1486, **http://doi.org/10.5194/bg-8-1477-2011**

[9] Lennon, J.T., Jones, S.E., 2011. *Microbial Seed Banks: The Ecological and Evolutionary Implications of Dormancy*. Nature Reviews. Microbiology, 9, 2: 119–130. **http://doi.org/10.1038/nrmicro2504**

[10] Navarro-Noya, Y.E., Gómez-Acata, S., Montoya-Ciriaco, N., et al., 2013. *Relative Impacts of Tillage, Residue Management and Crop-Rotation on Soil Bacterial Communities in a Semi-Arid Agroecosystem*. Soil Biology and Biochemistry, 65, 86–95, **http://doi.org/10.1016/j.soilbio.2013.05.009**

[11] Pagaling, E., Strathdee, F., Spears, B.M., 2014. *Community History Affects the Predictability of Microbial Ecosystem Development*. The ISME Journal, 8, 1: 19–30, **http://doi.org/10.1038/ismej.2013.150**

[12] Panizzon, J.P., PilzJúnior, H.L., Knaak, et al., 2015. *Microbial Diversity: Relevance and Relationship Between Environmental Conservation and Human Health*. Brazilian Archives of Biology and Technology, 58,1: 137–145, **http://doi.org/10.1590/S1516-8913201502821**

[13] Sun, B., Jia, S., Zhang, S., et al., 2016. *No Tillage Combined with Crop Rotation Improves Soil Microbial Community Composition and Metabolic Activity.* Environmental Science and Pollution Research, 23, 7: 6472–6482, **http://doi.org/10.1007/s11356-015-5812-9**

[14] Torsvik, V., Ovreas L., 2002. *Microbial Diversity and Function in Soil: From Genes to Ecosystems*. Current Opinion in Microbiology, 5, 3: 240–245, **http://doi.org/10.1016/S1369-5274(02)00324-7**