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Grant Proposal

Microbial diversity-ecosystem function relationships across environmental gradients

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Abstract

In light of increasing anthropogenic pressures on ecosystems around the globe, the question how biodiversity change of organisms in the critical zone between Earth's canopies and bedrock relates to ecosystem functions is an urgent issue, as human life relies on these functions. Particularly, soils play vital roles in nutrient cycling, promotion of plant growth, water purification, litter decomposition, and carbon storage, thereby securing food and water resources and stabilizing the climate. Soil functions are carried to a large part by complex communities of microorganisms, such as bacteria, archaea, fungi and protists. The assessment of microbial diversity and the microbiome's functional potential continues to pose significant challenges. Next generation sequencing offers some of the most promising tools to help shedding light on microbial diversity-function relationships. Studies relating microbial diversity and ecosystem functions are rare, particularly those on how this relationship is influenced by environmental gradients. The proposed project focuses on decomposition as one of the most important microbial soil ecosystem functions.

The researchers from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig combine an unparalleled range of expertise from next generation sequencing-based analysis of microbial communities ("meta-omics") to soil ecology and biodiversity-ecosystem function research. This consortium will make use of soil samples from large international networks to assess microbial diversity both at the taxonomic and functional level and across the domains of life. By linking microbial diversity to functional measurements of decomposition and environmental gradients, the proposed project aims to achieve a comprehensive scale-independent understanding of environmental drivers and anthropogenic effects on the structural and functional diversity of microbial communities and subsequent consequences for ecosystem functioning.

Keywords

Biodiversity research, ecosystem functions, microbial ecology, decomposition, nutrient cycling

List of participants

Funded applicants: François Buscot, Nico Eisenhauer, Anna Heintz-Buschart, Kirsten Küsel, Carl-Eric Wegner

Co-applicants with project responsibility: Simone Cesarz, Antonic Chatzinotas, Carlos Guerra, Johannes Sikorski

International cooperation partner: Ika Djukic

Further project group: Guillaume Pantoine, Tesfaye Wubet

Third parties involved in the project

The project is performed in cooperation with international partners. Ika Djukic (Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf; - Switzerland; ika.djukic@umweltbundesamt.at) coordinates the global efforts of TeaComposition, the soil samples of which will be analysed in this project. Ika Djukic is not financially involved beyond the provision of the teabags to the cooperating scientists. There is no financial involvement in the proposed analyses for either partner.

Next generation sequencing will be performed at a DFG Sequencing Centre, the NGS Competence Center Tübingen (NCCT), Germany.

State of the art and preliminary work

Human activities are altering the biodiversity of ecosystems around the globe, which has provoked concern regarding potential consequences for ecosystem functions. The notion

that biodiversity could be an important determinant of ecosystem functions stems from observations of natural communities (Elton 1958) as well as from theoretical models (Tilman et al. 1997; Yachi and Loreau 1999) and has been around for decades. Hundreds of biodiversity-ecosystem function (BEF) experiments have revealed that biodiversity is essential for the provisioning of various ecosystem functions and services (Cardinale et al. 2012; Naeem et al. 2012). Given the limitations of these experiments in realistically representing the non-random biodiversity loss (Haddad et al. 2008) determined by the simultaneous interplay of abiotic and biotic filters in time and space (Götzenberger et al. 2011; Wardle 2016), future BEF research has to answer the question: How does non-random biodiversity loss affect ecosystem functioning in real ecosystems? Answering this question is particularly important in order to apply BEF results to, e.g., agriculture and biodiversity conservation. However, this is also a very challenging question as biodiversity change and species turnover may be hard to predict due to multiple co-occurring and interacting global change drivers and their context-dependent effects on different organisms and interactions (Schmid and Hector 2004). Environmental change and heterogeneity determine both the biodiversity and the functioning of ecosystems (Fig. 1A). In addition, changes in biodiversity can have significant effects on ecosystem functioning, which can be masked by strong environmental gradients (Fig. 1B; Isbell et al. 2013).
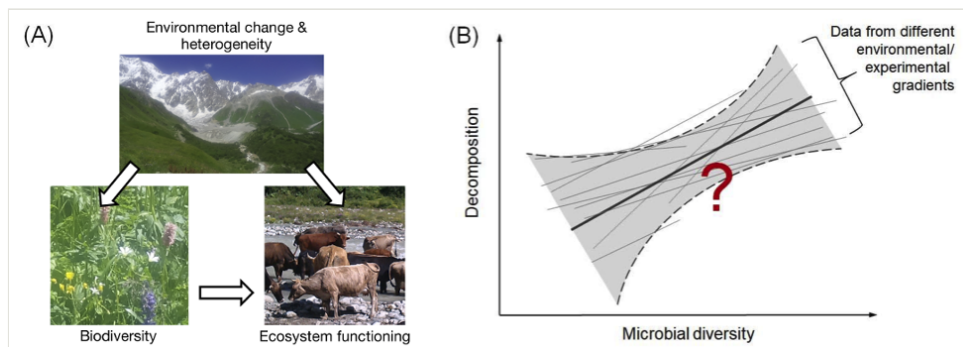

Figure 1. doi

A Environmental change and heterogeneity determine the biodiversity and the functioning of ecosystems (modified after Eisenhauer et al. 2016). In addition, changes in biodiversity can have significant effects on ecosystem functioning, which can be masked by strong environmental gradients. Only by accounting for environmental heterogeneity can the role of biodiversity for ecosystem functioning be wholly realized (Grace et al. 2016). **B** Hypothesized positive relationship between microbial diversity and decomposition (overall positive relationship with confidence intervals; no real data was used to create this figure). The diversity gradient in soil microbes is supposed to be caused by different environmental conditions. The different grey lines indicate BEF relationships across different experimental and environmental gradients.

Future approaches to study BEF relationships should thus move from studying the relationships between random species loss and ecosystem functioning to the complex interplay between anthropogenic drivers, non-random biodiversity changes (including gains, losses, and changes in evenness/dominance and composition/traits), ecosystem

functioning, and ecosystem services at multiple spatial and temporal scales. Given these complications, evidence for significant BEF relationships across environmental gradients is scarce (e.g., Grace et al. 2016). However, recently developed international networks of collaborating researchers now allow for the study of BEF relationships across environmental gradients (e.g., Djukic et al. 2018).

Currently, most BEF studies focus on aboveground diversity, although the ecosystem functions are driven by belowground biological processes. In particular, soils play pivotal roles in important terrestrial ecosystem functions including nutrient cycling, sustaining plant growth, water purification, litter decomposition, and carbon storage (Bardgett and van der Putten 2014, Wall et al. 2015). Microbial communities in the soil drive these critical functions (Quince et al. 2008), which is why they are often referred to as the 'functional backbones' of terrestrial ecosystems (van der Heijden et al. 2008). Soil microbial communities are among the most diverse in the world, with key taxa comprising bacteria, archaea, fungi and protists. The high levels of soil microbial diversity have led to the assumption that many taxa are functionally redundant. However, at least for bacteria, it appears that rare and common taxa play fundamentally different roles in ecosystem functioning (Rivett and Bell 2018, Delgado-Baquerizo et al. 2016). Soil microbial communities drive plant diversity and productivity (van der Heijden et al. 2008). However, globally, belowground alpha diversity is not always correlated with above-ground diversity (Cameron et al. 2019). Soil microbial diversity is also only poorly correlated with plant diversity, especially for bacteria and fungi, and therefore focusing on plant diversity is not helpful to predict responses of soil microbiomes, e.g., to global change factors (Prober et al. 2014) or biodiversity loss (Fanin et al. 2019). As a consequence, while plant diversity influences soil microbial biomass (Chen et al. 2019) and plant community composition may improve predictions of microbial communities, the variation in microbial communities explained by plant community composition at the global scale is low (Leff et al. 2018). Recent research has revealed strong spatial variability in the distribution of soil microbial diversity (Ramirez et al. 2017, Delgado-Baquerizo et al. 2018) and functional capacity (Bahram et al. 2018), and has revealed major drivers of bacterial alpha-diversity across biomes (Delgado-Baquerizo and Eldridge 2019). However, data on soil biodiversity still is very limited (Cameron et al. 2018) and has rarely been linked to ecosystem functions. Therefore, a more comprehensive understanding of BEF relationships for soil microbiomes is urgently needed.

Although microcosm experiments suggest positive microbial BEF relationships (e.g., Tiunov and Scheu 2005, Jousset et al. 2011), just a few studies address the potential links between microbial diversity and ecosystem functions in natural ecosystems and across broad environmental contexts (Soliveres et al. 2016). A key challenge is to quantify the functional roles of microbial taxa to understand how ecosystem properties change at spatial and temporal scales. A number of different methods for the assessment of soil microbial communities and their diversity currently co-exist, including the most commonly employed meta-barcoding (amplicon sequencing) estimates of relative abundances of highly resolved taxonomic groups and microbial diversity. Increasingly, studies assess microbial traits and gene content by metagenomics and, more rarely, expressed functions

by metatranscriptomics and metaproteomics. Due to their different aims and different resolutions, these techniques can lead to diverging conclusions, but integration of both taxonomic and trait data is expected to improve predictions of ecosystem functions (Fry et al. 2018). Traditionally, overall respiration rates and specific *in vitro* enzyme activities have often been measured. While most studies employ a combination of some of the mentioned techniques and relate the results to drivers or response variables, systematic comparisons are rare (Fierer et al. 2012). While data collected in independent studies can be combined to improve predictions (Johnston and Sibly 2018), sequencing-based profiles are hardly ever collected in the same studies as ecosystem function data. Hence, data on soil biodiversity are not as coherent and exhaustive as the ones on aboveground biodiversity (Cameron et al. 2018). It is therefore necessary to employ comprehensive methods that deliver the most predictive read-outs for ecosystem function and response to changes.

Among the important functions fulfilled by soil microbial communities that are strongly influenced by soil conditions, climate, and human activities (e.g., Tedersoo et al. 2014, Leff et al. 2015) is the breakdown of organic matter. Litter decomposition and the cycling of the respective nutrients influences plant productivity, and therefore aboveground biodiversity and carbon storage within the soil (Hättenschwiler et al. 2005). The microbial actors and their enzymes are well described under controlled conditions (Schneider et al. 2012). Noteworthy, organisms from all domains of life interact in this process. Copiotrophic, fast growing bacteria degrade easily accessible substrates. Oligotrophic, slow growing bacteria feed on more recalcitrant substrates. In particular the more recalcitrant fractions of litter are more efficiently decomposed by saprotrophic fungi (van der Wal et al. 2013). Mycorrhizal fungi also play a significant role in litter decomposition, as they on the one hand have stimulatory effects, and on the other hand contribute to stabilization of litter-derived carbon (Verbruggen et al. 2015). Microbial grazers and predators also shape the microbial community and the turnover rates (Geisen et al. 2015, Xiong et al. 2017).

We lack a systemic understanding of how this cycling potential is influenced by local (e.g. along soil profile) and interregional variations (climate, soil type, stoichiometry) via their impacts on soil biodiversity. For the longest time, global litter decomposition has been considered to be mainly controlled by climate (temperature and moisture) and litter quality (i.e. the chemical composition; Tenney and Waksman 1929). While climatic drivers are often observed (Sherman and Steinberger 2012), further important controllers may exist (Keiser et al. 2014, Bradford et al. 2015). Soil microbial communities are prime candidates for these controllers (Couˆteaux et al. 1995, Hättenschwiler et al. 2005, Manzoni et al. 2008, Allison et al. 2013). For example, N-fertilization is consistently observed to lower litter decomposition (Knorr et al. 2005). A possible reason for lower decomposition rates may be lower microbial biomass, as observed in N-fertilized grasslands (Treseder 2008, Riggs and Hobbie 2016, Zhang et al. 2018). Despite high functional redundancy, certain functions can be reduced or lost when microbial diversity declines (Singh et al. 2014). For carbohydrate active enzymes in particular, shifts in genetic diversity have been observed, e.g. in response to precipitation (Diamond et al. 2019). Precipitation is a major driver of both litter decomposition (Djukic et al. 2018) and bacterial functional diversity (Bahram et al. 2018), suggesting a significant relationship between functional diversity and decomposition as an

ecosystem function, but it is unknown whether this will be true across biomes. While factors like climate, soil conditions, and fertilization directly influence the soil microbiomes (e.g., Tedersoo et al. 2014, Ramirez et al. 2017, Leff et al. 2015), indirect effects through changes in litter quality are also observed (Meier and Bowman 2008). It is therefore important to assess decomposition of standardized materials (Keuskamp et al. 2013) to explore general relationships between microbial diversity and decomposition.

With the proposed project, we aim to perform an integrative, global assessment of the relationship between microbial diversity and litter decomposition in the soil, using a set of existing monitoring platforms operating along environmental gradients (Fig. 1B). This project builds on the successful establishment of a "network of networks" on litter decomposition (Djukic et al. 2018). In an unprecedented initiative, experimental and observational ecological networks have been united using a common methodology to assess litter decomposition (Keuskamp et al. 2013). In preparation of this proposal, this network conducted a concerted and highly standardized soil sampling campaign for the analysis of soil microbial communities. The analysis of microbial taxa and functional diversity using a standardized set of next generation sequencing (NGS)-based tools in relation to functional measurements of decomposition processes should enable us to determine how to combine the available technologies most effectively in BEF research as well as in mechanistic microbiological studies. These analyses necessitate substantial investment in the form of NGS, being applied for within this proposal.

Given the strong societal relevance of global soil biodiversity and function (Bardgett and van der Putten 2014), high levels of integration between scientific disciplines as well as spatial and temporal scales are required. The applicant iDiv members cover a uniquely broad expertise ranging from the analysis of microbial communities by NGS to soil biodiversity and function research that has little parallel worldwide. Researchers at iDiv have started compiling a comprehensive dataset on the global distribution of soil biodiversity (www.idiv.de/sworm), which will be hosted in EDAPHOBASE (https://portal.edaphobase.org) as a first trial for a global soil biodiversity database hosted by iDiv (such as outlined in Ramirez et al. 2015). These data demonstrate for the first time at a global level that hotspots and coldspots of aboveground (mammals, birds, and amphibians, and vascular plants) and soil biodiversity (soil macrofauna, and fungi) do not always coincide (Cameron et al. 2019).

Moreover, some of the PIs have been active participants in the TeaComposition network (Djukic et al. 2018), and all PIs are now leading an initiative to study microbial diversity-function relationships across the sites worldwide. In this study, decomposition measurements have been taken by our international partners together with a collection of soil. From the 395 projected field sites (Fig. 2, 790 samples), 258 (516 samples) were already pre-processed for soil functional analysis in our labs (soil aggregate stability, soil respiration, and microbial biomass). 402 samples have been processed to extract DNA in our labs and the remaining samples are expected to arrive until the end of June 2019.
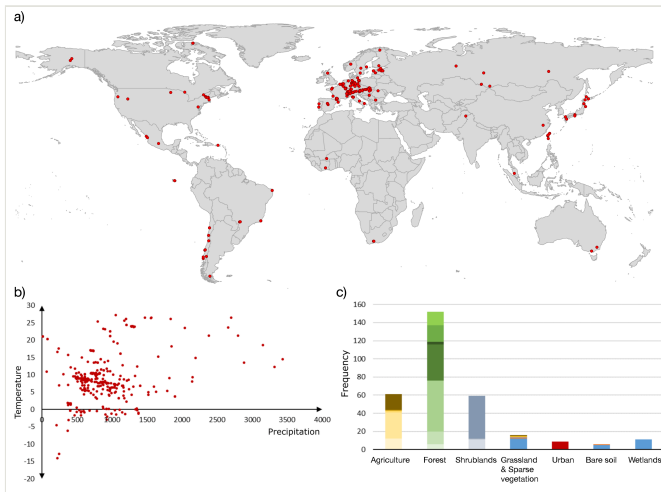
Figure 2. doi

Overview of the sample collection. Decomposition, as a central soil function, and the biodiversity of involved microbial communities will be studied in a large, international monitoring network (sampling locations indicated in a) to assess the generality of microbial biodiversity-function relationships across climates (mean annual air temperature and annual precipitation in b) and land use and cover types (c).

In summary, this project will foster integration between the above-mentioned approaches to reach a **comprehensive scale-independent understanding of environmental drivers and anthropogenic effects on the structural and functional diversity of microbial communities and the subsequent consequences for ecosystem functioning**. Therefore, we will produce extensive datasets on the main soil microbial taxa (bacteria, archaea, fungi, and protists) across a global network of sites in relation **to climate and land use**. Functional relationships will be deduced by multivariate analyses (e.g., structural equation modelling; Grace et al. 2016) of **data on microorganisms, physicochemical parameters, and ecosystem functions (decomposition, including litter mass loss and soil microbial respiration)**. Building on the TeaComposition network will enable us to create unique synergies between an existing, vibrant global network of collaborators working on litter decomposition and cutting-edge next generation sequencing of the soil biodiversity that drives decomposition processes. By doing this, our ultimate goal is to optimize an approach that can be used as standard for future global soil biodiversity and function analyses in relation to different environmental (change) drivers.

Project-related publications

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4. European Commission, Joint Research Centre. 2016. Global Soil Biodiversity Atlas - Earth Sciences Research - EU Bookshop. bookshop.europa.eu/en/global-soil-biodiversity-atlas-pbLBNA27236/. Contributors: **Küsel K**, Totsche KU, Trumbore SE, **Buscot F**; Chapter III - Geographical and temporal distribution, p. 73.

5. Ivanova AA, **Wegner CE**, Kim Y, Liesack W, Dedysh SN. (2016). Identification of microbial populations driving biopolymer degradation in acidic peatlands by metatranscriptomic analysis. Molecular Ecology 25: 4818-4835.

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8. Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, Alt F, Arndt H, Baumgartner V, Binkenstein J, Birkhofer K, Blaser S, Blüthgen N, Boch S, Böhm S, Börschig C, **Buscot F**, Diekötter T, Heinze J, Hölzel N, Jung K, Klaus VH, Kleinbecker T, Klemmer S, Krauss J, Lange M, Morris EK, Müller J, Oelmann Y, Overmann J, Pašalić E, Rillig MC, Schaefer M, Schloter M, Schmitt B, Schöning I, Schrumpf M, Sikorski J, Socher SA, Solly EF, Sonnemann L, Sorkau E, Steckel J, Steffan-Dewenter I, Stempfhuber B, Tschapka M, Türke M, Venter PC, Weiner CN, Weisser WW, Werner M, Westphal C, Wilcke W, Wolters V, Wubet T, Wurst S, Fischer M, Allan E (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536: 456-459.

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10. Guerrero-Ramirez NR, Craven D, Reich PB, Ewel JJ, Isbell F, Koricheva J, Parrotta JA, Auge H, Erickson HE, Forrester DI, Hector H, Joshi J, Montagnini F, Palmborg C, Piotto D, Potvin C, Roscher C, van Ruijven J, Tilman D, Wilsey B and **Eisenhauer N** (2017) Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. Nature Ecology & Evolution 1: 1639-1642.

Objectives and work programm

Anticipated total duration of the project

iDiv is a Research Centre of the DFG, established in 2012, currently in the second funding phase (October 2016 - September 2020). The integrative project "Microbial diversity-ecosystem function relationships across environmental gradients" described here runs since November 2017, with monthly meetings, and supported by an iDiv postdoc (Dr. Carlos Guerra) since June 2018. The DFG-funded NGS applied for in this proposal should take place **in the first half of 2020** (see Table 1). Data analysis and integration will proceed in 2020 and 2021.

Table 1.

Project duration: NGS should be performed in the first half of 2020.

	2017-2019	2020 II	2020 III	2020 IV	2021 I	2021 II
Sample collection	x					
Interaction with NGS centre	x	ship samples &receive data				
Data processing amplicons			x			
Data processing metagenomics			x	x		
Integration					x	x
Publication						x

Objectives

This project **aims to explore the relationship between microbial diversity and decomposition**, as a major ecosystem function carried out by microbes of the soil, **across environmental contexts** (Fig. 2). The principle of this project is to make use of established infrastructures, networks and expertise. This project builds on the engagement of iDiv within the TeaComposition network (teacomposition.org; Djukic et al. 2018), where measurements of decomposition and organic matter turnover have been performed. **This project would not only greatly benefit from NGS-based assessment of the microbial taxonomic and functional diversity, but combining NGS-based microbial diversity data with available data on decomposition will allow an unprecedented survey of the generality of microbial BEF relationships, and the synthesis of the different projects to derive a scale-independent understanding of environmental drivers and anthropogenic effects of microbial diversity and function** (Fig. 1B).

Despite the global origin of the samples contributed by the TeaComposition network, there are several unifying characteristics, which will enable integration of the results. To investigate the direct effects of different environmental drivers on soil biodiversity and related functions, the network analyses a standardized decomposing material. Sampling

procedures have been synchronized, and the same sequencing approaches will be used for all samples. Decomposition rates at all sites after 3 months, 1 year, and 2 years have been determined in the framework of TeaComposition (Djukic et al. 2018). In preparation of this proposal, soil has been collected in a standardized way for next generation sequencing and respiration measurements (Eisenhauer et al. 2010) at the same time (synchronized with the 2-year litter decomposition assessment). Respiration measurements have already been performed. As a result, the project has at its disposal a unique collection of functionally characterised globally distributed soil samples. Moreover, the collection enables the study of environmental gradients that are likely to induce considerable changes in the soil microbial community composition and diversity, which is the prerequisite for studying microbial BEF relationships in different contexts.

This study makes use of a network of decomposition experiments across the globe, with more than 350 participating sites (Fig. 2a). These sites cover different land use types, land use intensities, soil types, and climates (Fig. 2b&c). Climate data, decomposition rates, physicochemical parameters, microbial activity and biomass (Eisenhauer et al. 2010), stability (Pérès et al. 2013) of the experimental plots will be related to the results of the sequencing-based surveys. One of the main advantages and novelties of this project and its experimental approach is that we will collect information on the structure and capacity of the microbial community, and its ecological functions, at the same spatial grain and across very different environmental gradients at large spatial scale (global climatic gradients and different soil types).

Although human activities have accelerated global biodiversity change and have threatened the supply of ecosystem services, global biodiversity assessments, syntheses, and predictions are based primarily on a few well-studied aboveground taxa including plants and vertebrates (e.g., Millennium Ecosystem Assessment; IUCN red lists; Eisenhauer et al. 2019). In contrast, soil biodiversity has been neglected from several global biodiversity assessments and conservation actions, although it represents a major terrestrial biodiversity pool, supports key ecosystem services, and is increasingly under pressure due to human activities (Wall et al. 2015, Cameron et al. 2018, Cameron et al. 2019). Even the current IPBES regional assessments report this as an important gap that hampers the ability of scientists and decision-makers to provide governance strategies that include the conservation and protection of soil biodiversity at local to global scales (Cameron et al. 2019). Accordingly, in a meeting of the Intergovernmental Technical Panel on Soils held in June 2018, understanding global soil biodiversity dynamics was defined as a critical priority for the coming 2 years to support effective action. However, to efficiently communicate the implications of human actions for soils and soil biodiversity, we need to better understand

1.   the drivers of soil microbial diversity, and
2.   the consequences for important functions.

In this context, the NGS data will directly contribute to inform about the global and local relations between soil biodiversity and decomposition. By doing this at multiple scales, it will also support the development of complex causal models that will integrate the global

model intercomparison project for soils [Soil-MIP, https://soil-modeling.org/science-panels/Soil-MIP] and will be linked to global soil biodiversity assessments. The NGS data will be used in at least one integrative publication in a high-ranking journal and a data descriptor. In addition, the data will greatly advance the global soil biodiversity database [EDAPHOBASE, https://portal.edaphobase.org], and support the global biodiversity network of the Group in Earth Observations (www.geobon.org).

Work programme incl. proposed research methods

The presented project is a collaborative effort with contributions of each of the PIs. In an integrative effort, all key soil microbial taxa (bacteria, fungi, archaea, and protists) will be comprehensively profiled in a worldwide collection of functionally characterised soil samples by the collaborating groups using amplicon sequencing. To establish a link between the soil microbial molecular functional capacity and ecosystem functions, the samples will be further analysed using shotgun metagenomics, yielding information on functional diversity and distribution patterns of molecular functions related to decomposition. The resulting unprecedented dataset will allow us to study relationships between microbial diversity and ecosystem functions as well as ecosystem multifunctionality.

We will synthesize data on microbial diversity-ecosystem function relationships across the target taxa and functions to develop a scale-independent understanding of environmental drivers and anthropogenic effects on the structural and functional diversity of microbial communities and the subsequent consequences for ecosystem functioning (Fig. 1B). Such integrative and comprehensive information is critical to better understand the drivers of soil microbial communities, biodiversity risks and potential functional consequences to parametrize global to local models of biodiversity and function distribution and to predict future potential future changes.

In particular, the tasks shared by the project partners are:

- communication with NGS centre and DFG, coordination of sample shipping (DNA from 2 x 395 soil samples collected worldwide within the TeaComposition network (Djukic et al. 2018), presently stored at iDiv) (*A. Heintz-Buschart*)
- devising and implementing the data management plan, data transfer from NGS centres and sharing among consortium (*A. Heintz-Buschart*)
- coordination of NGS data processing, bioinformatics support (*A. Heintz-Buschart*)
- analysis of prokaryotic community structure and diversity of 800 soil samples (*K. Küsel*, in collaboration with T. Wubet and J. Sikorski)
- analysis of eukaryotic community structure and diversity of 800 soil samples (*F. Buscot*, in collaboration with A. Chatzinotas)
- analysis of functional diversity in 395 soil samples (*A. Heintz-Buschart*, in collaboration with *K. Küsel* and *C.-E. Wegner)*
- analysis of occurrence of decomposition-related genes in 395 soil samples (*C.-E. Wegner*, in collaboration with *K. Küsel* and *A. Heintz-Buschart)*

- relating decomposition data to data on soil microbial biomass, microbial respiration, soil aggregate stability (all generated in the Eisenhauer lab), and microbial community composition (*N. Eisenhauer* in collaboration with S. Cesarz and I. Djukic)
- to study microbial diversity-function relationships across large environmental gradients (*N. Eisenhauer* in collaboration with C. Guerra and S. Cesarz)
- to perform microbial diversity-function analyses related to litter decomposition across large environmental gradients (*N. Eisenhauer* in collaboration with C. Guerra, I. Djukic, J. Sikorski and *A. Heintz-Buschart*)
- preparation and documentation of meetings of project consortium (*A. Heintz-Buschart* in collaboration with C. Guerra)
- dissemination of results (*all project partners*)

Project background

This project will be carried out within the TeaComposition network, taking advantage of a globally distributed research infrastructure on decomposition of organic matter and aims at providing a more comprehensive understanding of biosphere-atmosphere carbon feedback. It is a global low cost and "easy-to-join" initiative that is open for international collaboration. In addition to the global sampling approach, the research conducted in this network will provide an improved understanding of decomposition for leading experiments and observation networks, such as ILTER, CLIMMANI, TreeDivNet, and GLORIA. Decomposition trials have already been analysed (12 and 24 months litter mass loss) and published (three months litter mass loss; Djukic et al. 2018).

Sampling design and soil data

This study uses experiments and observation networks at more than 350 sites worldwide (Fig. 3a). Each site consists of 2 blocks, with 2 tea bag types that represent different litter qualities (Djukic et al. 2018). Soil samples in each block were taken with 24 months litter mass loss measurements in July and August of 2018 and December 2018 to February 2019 on the on the Northern and Southern hemisphere, respectively (395 sites with 2 blocks = 790 samples). All participants follow a standard sampling protocol and report environmental variables, such as annual average air temperature, annual precipitation and annual average temperature amplitude, as well as soil properties such as pH, organic carbon and total nitrogen content. The participants have received sampling kits to cleanly handle soil samples. Sampling kits contain vials with RNAlater for DNA analyses and plastic vials for fresh soil samples, allowing for subsequent functional analyses: soil microbial biomass, respiration (Eisenhauer et al. 2010), and aggregate stability analyses (Kemper and Rosenau 1986), indicating soil stability a potentially important determinant of soil erosion control and soil sustainability (Lehmann et al. 2017). Functional soil analyses of the fresh soil aliquots taken at the same time as the sequencing sample comprise soil microbial biomass and respiration and the percentage of water-stable soil aggregates. These results will be used to calculate an aggregated index of ecosystem multifunctionality (Lefcheck et al. 2015, Eisenhauer et al. 2018).

Sequencing requirements

Both blocks of all 395 sites will be analysed by amplicon sequencing (790 samples in total). Deep microbial community profiles will be generated based on four regions within the rRNA operons, that are specifically informative for the major microbial taxa in soil, namely 16S V4 for bacteria and many archaea, ITS for fungi and two 18S regions for fungi and protists. A total of 400,000 read pairs per sample are required. In addition, shotgun metagenomics of one of the blocks in each site will be performed to derive measures of functional diversity and to survey the occurrence of genes involved in decomposition, such as carbohydrate-active enzymes. We estimate a depth of 50 million read pairs per sample to be informative for this aim.

Sequencing data analysis

Amplicon sequencing data will be processed separately for each target using established pipelines based on frameworks such as Mothur (Schloss et al. 2009) and high-resolution approaches (DADA2; Callahan et al. 2016), consisting of quality control and filtering, high-resolution clustering and taxonomic annotation, with taxon specific settings and databases (Öpik et al. 2010, Guillou et al. 2012, Quast et al. 2013, Kõljalg et al. 2013). From the resulting, whenever possible taxonomically annotated, operational taxonomic units or sequence variants, common diversity metrics will be derived.

Whole shotgun metagenomic data will be processed using a pipeline already set up on the high performance computing infrastructure at the iDiv, starting from quality filtering and *de novo* assembly (Narayanasamy et al. 2016). After separation of eukaryotic and prokaryotic assembled contiguous sequences (West et al. 2018), open reading frames and genes will be called and functionally using suitable tools and reference databases (Stanke et al. 2006, Ter-Hovhannisyan et al. 2008, Keilwagen et al. 2016, Seemann 2014). In addition to broad-scope databases (Huerta-Cepas et al. 2016, El-Gebali et al. 2018), we will perform focused annotations of carbohydrate-active enzymes (Huang et al. 2018) and modules of decomposition genes (Konietzny et al. 2014). Unassembled reads will be mapped to a published soil microbial gene catalogue (Bahram et al. 2018). An extended, uniformly annotated gene catalogue based on our gene-centric analysis and the existing collection will serve to estimate functional diversity and redundancy, as well as determine occurrence patterns of genes involved in decomposition processes. Taxonomic annotation of the contiguous sequences will be performed (Wood and Salzberg 2014) against reference genomes (Parks et al. 2018, Mendler et al. 2019). The same database can be used as secondary reference for the amplicon sequencing based 16S rRNA gene sequence variants to allow for integration of both data sets. Genome-centric analyses, based on *k*-mer frequencies, coverage and presence of single-copy essential genes can be added to link gene functions of interest to highly abundant taxa (Heintz-Buschart et al. 2016) to assess functional adaptations to the studied environmental gradients.

Together, the amplicon and shotgun data will yield deeply sampled measures of bacterial, archaean, fungal and protist taxonomic and phylogenetic diversity, complemented by

measures of global and decomposition-specific genetic functional diversity of the more abundant taxa.

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Data integration

We will test if significant BEF relationships across environmental gradients exist, in particular with respect to microbial diversity measures and decomposition. We expect an overall positive relationship with heterogeneous slopes in diversity gradients caused by different environmental drivers (Fig. 1B).

Like done in previous synthesis projects (e.g. Thakur et al. 2015, Craven et al. 2016a, Craven et al. 2016b, Isbell et al. 2015, Guerrero-Ramírez et al. 2017), a meta-database will be created. Multivariate statistical analyses like SEM will allow separating effects of environmental drivers on soil microbial diversity and decomposition from effects of soil microbial diversity on decomposition (Fig. 1; Grace et al. 2016, Giling et al. 2018). Structural equation models will consider the covariance structure of the multivariate dataset, and will thus allow investigating particular mechanistic paths of interest (here: microbial diversity effects on decomposition) by accounting for different environmental drivers (Lange et al. 2015, Grace et al. 2016). Notably, such an analysis requires the separation of environmentally driven variations in biodiversity and function from biodiversity-ecosystem function relationships (Eisenhauer et al. 2016, De Laender et al. 2016, Giling et al. 2018). This can only be achieved with large data sets that cover different environmental gradients, such as done in Grace et al. 2016 for a global network of grassland experiments. These analyses will allow us to test the overall hypothesis and conceptual model illustrated in Fig. 1, stating that microbial diversity drives decomposition processes across environmental contexts, once these environmental gradients are considered in the analyses (Giling et al. 2018). Analyses and results will be discussed in mini-workshops at iDiv (1-2 days), and the respective paper is expected to be published in an international high-profile journal.

Data handling

This project will integrate existing data, as detailed above, with data sets to be derived from NGS. In the long-term, the NGS data pertaining to specific geographic locations will remain of value to the research community. The publication of the datasets are not restricted by privacy concerns. Samples and data are subject to the CBD (see section 2.5).

The data management plan for this project will be devised and implemented by Anna Heintz-Buschart in consolation with all project partners, and if necessary supported by the Biodiversity Informatics Unit of iDiv. The following measures are foreseen in order to make the generated data available for future re-use: The NGS data will be made publicly

available at the time of the publication of results, or at the very latest at the end of the project, in international public databases in openly documented standard data formats. In these databases, the data will be findable, publically accessible, linked to the databases hosting other types of data from the project, together with data descriptors in standard formats, and therefore the data will be interoperable and reusable (according to the FAIR - findable, accessible, interoperable, reusable - principles). The publication of a data descriptor in an open access journal such as Scientific Data or Giga Science is foreseen. Raw NGS reads will be submitted to the NCBI's short read archive or the European Nucleotide Archive ENA, which links them to geo-referenced 'biosample' data handles that will contain also soil and plant residue physicochemical parameters and sample metadata. Environmental and ecosystem function data will also be submitted and cross-linked within the PANGAEA database and have a DOI of the iDiv data portal (https://idata.idiv.de). Derived data types such as reconstructed genomes will likewise be submitted to dedicated, open databases fulfilling Minimal Information standards. All computational workflows used to process the NGS data will be linked to the published datasets and will be open source, in order to ensure reproducible bioinformatics. They will be kept in sustainable repositories, such as CERN's Zenodo, where they are accessible via a DOI. The data management plan foresees that all long-term data will have been submitted to public databases by the end of the project and no long-term costs will be incurred for the consortium.

Other information

The NGS analyses are subject to the Convention on Biological Diversity (CBD). The applicants are familiar with the CBD and the DFG's guidelines on the CBD. The applicants will ensure that all analyses will conform to the rules of the CBD. As no use beyond basic research and no commercialization are envisaged, a simple ABS contracts will be sufficient.

Material transfer agreement with the collaborating scientist abroad (and in Germany) have been signed. The applicants have localised the national contact points and inquired for the processes in the participating countries. We are optimistic that PICs and MATs can be achieved for the remaining countries. To comply with all legal regulations, the applicants receive support by "Dezernat für Forschungs- und Transferservice" of Leipzig University.

Budget: Requested modules/funds

This project proposal is to request funding of NGS analyses, as detailed in section 2 of this proposal. Sufficient funding for all other costs are available to the applicants within the framework of iDiv. Therefore, no funding is requested for any of the following points:

Funding for Staff; Direct Project Costs; Equipment up to 10 000 €, Software and Consumables; Travel Expenses; Visiting Researchers; Expenses for Laboratory Animals; Project-related publication expenses; Instrumentation; Equipment exceeding 10 000 €; Major Instrumentation exceeding 50 000 €.

Other costs: NGS costs

This proposal is for NGS costs of an on-going project within the DFG Research Centre iDiv, which is not covered by the current iDiv business plan or any of the experimental platforms and networks. All costs beside the NGS costs will be carried by the applicants and iDiv funding. The proposed project will incur sequencing costs of **202 172 €**, as detailed in the quotations and Counselling Reports from the DFG NGS centre in Tübingen. Table 2 details the allocation of the project funds to the experimental work packages and the applicants.

Table 2.

Budget.

Method	Samples	Targets	Costs	cost details
Amplicon sequencing	800	4	75 241 €	• Amplicon generation and sample preparation: 12.78 € × 3200 = 40 911 € • Sequencing on MiSeq (optional on NovaSeq: 34 330 €
Metagenomics	395	1	121 561 €	• Library preparation (Illumina Nextera Flex): 66.08 € × 395 = 26 101 € • Sequencing on NovaSeq (6 Flow Cells S2): 15 805 € × 6 = 100 830 €
		total	**202 172 €**	
		per PI	**40 434 €**	

Justification: Amplicon sequencing is requested as the only reliable method to deeply profile all target soil taxa, including rare taxa, and assess inter-kingdom interactions. The proposal foresees the use of the NGS centre's automation and high-throughput sequencers, potentially including a highly multiplexed approach to enable the high number of samples. To perform functional profiling of the prominent taxa, metagenomics measurements are requested. Both targeted and shotgun technologies are combined to compare and facilitate changes from amplicon-based to whole genome techniques if sequencing volumes and depth per € increase further in the future.

Project requirements

Applicants' employment status information

Applicants are detailed in Table 3.

Table 3.

Applicants.

Last name	First name	Title	Employment and funding body
Heintz-Buschart	Anna	Dr.	Bioinformatics Unit of German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, employed by Helmholtz Centre for Environmental Research GmbH – UFZ, fixed term contract, funded by the German Research Foundation - DFG (FZT 118 – iDiv)
Küsel	Kirsten	Prof. Dr.	Friedrich Schiller University - Institute of Biodiversity, permanent
Wegner	Carl-Eric	Dr.	Friedrich Schiller University - Institute of Biodiversity, fixed term contract, funded by Friedrich Schiller University
Eisenhauer	Nico	Prof. Dr.	Professor at German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig and Leipzig University, permanent
Buscot	François	Prof. Dr.	Helmholtz Centre for Environmental Research GmbH – UFZ, Soil Ecology Department, permanent

Composition of the project group

This project will involve several researchers of iDiv and the PIs' working groups at Friedrich-Schiller-University Jena and the UFZ contributing their experience to the experimental work packages and/or the integration, see Table 4.

Table 4.

Project group.

Last name	First name	Title	Employment, duration and funding body
Guerra	Carlos	Dr.	Experimental Interaction Ecology group at iDiv and Leipzig University, fixed term contract, funded by the German Research Foundation - DFG (FZT 118 – iDiv)
Cesarz	Simone	Dr.	Experimental Interaction Ecology group at iDiv and Leipzig University, permanent
Sikorski	Johannes	Dr.	Leibniz Institute DSMZ - German Collection of Microorganisms and Cell Culture, permanent
Chatzinotas	Antonis	Dr.	Helmholtz Centre for Environmental Research GmbH – UFZ, permanent
Wubet	Tesfaye	Dr.	Helmholtz Centre for Environmental Research GmbH – UFZ, permanent

Scientific equipment

The proposed projects make use of existing experimental platforms and computing infrastructure. For the analysis of the NGS data in all WPs, the high-performance computing cluster of UFZ and iDiv will be used.

Funding program

Research Grants

Grant title

Microbial diversity-ecosystem function relationships across environmental gradients

Hosting institution

Helmholtz-Centre for Environmental Research GmbH - UFZ, Halle, Germany

University Leipzig, Germany

Friedrich-Schiller-University Jena, Germany

Conflicts of interest

The authors have declared that no competing interests exist.

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