Higher spatial than seasonal variation in floodplain soil eukaryotic microbial communities

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Abstract

Beta diversity is a key component of biodiversity with implications ranging from species dynamics to ecosystem functioning. However, β-diversity and its drivers have received little attention, especially for micro-eukaryotes which play key roles in soil functioning. We studied the diversity of soil micro-eukaryotes in a Swiss lowland floodplain using high-throughput Illumina sequencing of soil DNA. We determined the temporal *vs*. spatial patterns of soil micro-eukaryotic α- and β-diversity in six contrasted habitats sampled over one year. We identified the drivers of these patterns among soil conditions and functions and identified indicator taxa of habitats in each season. We found higher spatial than temporal variability and a strong space-time interaction in soil micro-eukaryotic diversity patterns as well as in their edaphic drivers, which contrasts with previous observation of bacterial diversity patterns. Our results show that, although soil micro-eukaryotic diversity indeed varies seasonally, it is correlated most strongly with edaphic variables and vegetation but the strength of correlations with individual drivers varied seasonally. Microbial diversity patterns and their drivers can thus differ quite substantially among seasons and taxa. Despite the dominance of spatial patterns, the temporal component of microbial diversity should not be ignored to accurately estimate the diversity and the complexity of soil microbial community assembly processes. Given the importance of soil microbial diversity for ecosystem functioning such knowledge is relevant for land management.

Keywords: soil protist; beta diversity; spatiotemporal dynamics; soil physico-chemical conditions; soil ecosystem functions; riparian ecosystem.

1. Introduction

Soil microbial eukaryotes (here including protists and fungi, but excluding micro-metazoans) are highly diverse and play central roles in soil food webs (Geisen 2016). They are thus key actors of biogeochemical cycling: they influence nutrient cycling and energy fluxes in soils via the microbial loop (Bonkowski 2004), thus contributing to soil fertility (Barrios 2007; de Vries *et al.* 2013). However, there are still significant gaps in basic knowledge of the diversity and ecology of soil microbial eukaryotic communities. Notably, analyses of seasonal dynamics of soil microbial eukaryotic communities are rare and limited to a relatively small range of ecosystem types.

With the development of high-throughput multi-taxa identification using environmental DNA, hereafter eDNA metabarcoding (Taberlet *et al.* 2012), more efficient and complete characterization of microbial eukaryotic diversity is possible. Indeed, macroecological patterns such as the latitudinal biodiversity gradient, which are well documented in macro-organisms, were also observed in several major groups of soil fungi, but not in ectomycorrhizal fungi (Tedersoo *et al.* 2014). Similarly, morphological and molecular studies showed an increase of diversity toward the equator for euglyphid testate amoebae (Lara *et al.* 2016) or towards mid-latitudes where the water-energy balance is maximal for all testate amoebae (Fernández *et al.* 2016). There is compelling evidence that at least some micro-eukaryote taxa are not globally distributed, and that the composition of communities diverges considerably across large geographic distances (Foissner 2006; Heger *et al.* 2013). Furthermore, environmental distance-decay similarity in diatom communities were shown to be comparable to that observed in macro-organisms (Astorga *et al.* 2012). Morphological- and DNA-based fine-scale analyses of the spatial variations of soil microbial eukaryotic communities are scarce (Mitchell *et al.* 2000; Acosta-Mercado & Lynn 2002). But, Fiore-Donno *et al.* (2019) have shown, using a metabarcoding approach, that the spatiotemporal heterogeneity of edaphic factors can drive the changes in microbial eukaryotic community compositions highlighting the importance of deterministic niche-based processes. Despite the methodological progress, studies investigating the patterns of diversity distribution and biogeography of microbial eukaryotes are less numerous than for bacteria and often do not consider temporal changes. The few studies that have investigated the temporal changes of soil microbial eukaryotic communities have revealed a marked seasonality (Lamentowicz *et al.* 2013; Fiore-Donno *et al.* 2019; Levy-Booth *et al.* 2019; Zhao *et al.* 2019). A better characterization of the relative importance of seasonal as compared to spatial variability in soil microbial eukaryotic communities can improve our understanding of community assembly processes, and is necessary to clarify the patterns and drivers of diversity and biogeography of soil microbial communities.

Beta diversity measures the differences in community composition among sites within a region of interest (Whittaker 1960). Many different definitions and metrics of beta diversity exist (Tuomisto 2010). In its additive form (i.e. $\beta = \gamma - \alpha$), beta diversity can be defined as the amount by which the species richness of the entire (regional) dataset exceeds that of a single sampling unit of mean species richness (Tuomisto 2010). This approach allows quantifying the relative importance of alpha and beta diversity for total gamma diversity. While it is widely used for the study of macro-organisms (Wagner *et al.* 2000; Gering *et al.* 2003; Tylianakis *et al.* 2005; Schmidt *et al.* 2017), such an approach has, to our knowledge, never been used to assess the variability of soil microbial eukaryotic communities.

We focus on the spatiotemporal variability of soil microbial eukaryotes in riparian soils. Floodplains, at the interface between the riverbed and the surrounding upland terrestrial ecosystems (Sedell et al., 1989), are among the most diverse environments on earth. They are characterized by sharp environmental gradients and are strongly influenced by the seasonal dynamic of the river. Riparian soils contain a high diversity of eukaryotic microorganisms (Foissner, Chao & Katz 2007; Baldwin *et al.* 2013), that is very heterogeneously distributed among the various floodplain habitats (Binkley *et al.* 1997). Previous studies about the seasonal variations of soil microbial eukaryotic communities were conducted in habitats with relatively low spatial variability in environmental conditions such as temperate rainforests (Levy-Booth *et al.* 2019), agricultural soils (Zhao *et al.* 2019), and grasslands (Fiore-Donno *et al.* 2019) which might lead to a biased view of the relative importance of spatial and seasonal beta diversity. In the few cases where protist communities of temporarily flooded systems were investigated, and where the temporal dimension was included, marked seasonal patterns were observed (Simon *et al.* 2015; Sisson *et al.* 2018). A better knowledge on the patterns and drivers of soil micro-eukaryotic diversity in a broader range of ecosystems types is needed to improve our understanding of the structure and functions of soil ecosystems in general. Dynamic systems such as floodplains characterized by irregular perturbations have to this date not been studied for soil micro-eukaryotes. And, virtually nothing is known about the seasonal variability of floodplain soil microbial eukaryotic communities despite strong and well-known seasonal changes in climate and flood dynamic. Riparian soils are thus ideal model ecosystems to investigate the spatiotemporal variability of soil microbial eukaryotic communities.

We present the results of a field survey of soil microbial eukaryotic communities in a Swiss lowland floodplain. The survey was conducted in six contrasted characteristic floodplain habitats with four seasonally replicated sampling campaigns. The purpose of this study was to examine the richness and turnover (beta diversity) of microbial eukaryote taxa in relation to the spatial, temporal, and edaphic characteristics of the selected habitats. As our focus is on taxa richness and turnover to quantify the spatiotemporal changes of soil micro-eukaryotic assemblages, we decomposed the total diversity into spatial and temporal components. Finally, we related these indices to measured variables reflecting soil conditions and functions. We expected a stronger contribution of habitats to total beta diversity because of the marked differences in soil conditions and functions (Samaritani *et al.* 2011), vegetation type (Fournier *et al.* 2013), and soil organism groups (Fournier et al. 2012a, Fournier et al. 2012b, Fournier et al. 2015) at the study site. However, we expected the important seasonal changes in soil and climate to induce significant temporal changes of soil microbial eukaryotic communities. Our results confirmed these expectations by showing that beta diversity (spatial and temporal) contributes to a greater extent to total gamma diversity than local alpha diversity. And, although important, seasonal changes in soil microbial eukaryotic communities were less marked than spatial ones. These results highlight the importance of considering both the spatial and temporal changes for understanding soil microbial eukaryotic diversity and functions.

2. Experimental procedure

2.1. *Study site*

The study was conducted in a restored section of the River Thur in north-western Switzerland. River Thur flows through the Swiss Plateau from Mount Säntis to the Rhine. Its regime is similar to that of alpine rivers, with peak flow generally occurring in spring after snowmelt and in summer and fall after large storms. The study site is a 1.5 km long recently restored section of the river located in a peri-urban / agricultural region of Switzerland (long-term maximum, mean, and minimum flow rates are 1130, 50, and 2 $m^3 s^{-1}$, respectively; 1904–2005: http://www.hydrodaten. admin.ch/en/index.html). More information about the study site can be found in Schirmer *et al.* (2014) and Woolsey *et al.* (2007).

2.2. *Sampling design*

Six habitats were distinguished based on flood dynamics (assessed using topographic conditions: distance to the river and elevation) as well as soil and vegetation characteristics (*Gravel, Grass, Willow bush, Mixed forest, Willow forest,* and *Pasture*; Fig. S1). *Gravel* is characterized by frequent floods (average = 24 floods y^{-1}), patches of poorly developed soils (Calcaric Regosols), and pioneer vegetation. *Grass* is characterized by frequent floods (average = 17 floods y^{-1}), more developed soils (Calcaric Regosols) with a high spatial and temporal heterogeneity (Samaritani et al., 2011), and dense vegetation dominated by tall herbs (*Phalaris arundinacea*). *Willow Bush* experiences on average three floods per year and has soils of average depth (Calcaric Fluvisols) where willow bushes (mostly *Salix viminalis*) were planted. *Mixed Forest* is subjected to limited influence of flooding (0.2 flood y^{-1}), has deep soils (Calcaric Fluvisols), and is dominated by mixed deciduous tree species (*Acer pseudoplatanus, Fraxinus excelsior*). *Willow Forest* occurs at a similar distance to the river than *Mixed Forest*, but at a slightly lower elevation. It experiences on average 0.5 flood per year, has deep soils with more hydromorphic features than *Mixed forest* (Calcaric Gleyic Fluvisols), and the vegetation is dominated by old willows (*Salix alba*). Finally, *Pasture* lies outside the restored section of the river and is still protected from floods by levees (number of floods per year < 0.2), has the most developed soils (Calcaric Fluvisols), and harbors the typical vegetation of a grassland. The number of floods per year per habitat was calculated in Fournier et al. (2015). The soil taxonomy was assessed by Fournier et al. (2013) according to the World reference base for soil resources (IUSS Working Group 2006). Four plots were sampled in each habitat and each plot was sampled four times (spring = 09.04.2008; summer = 08.07.2008; autumn = 08.10.2008; and winter = 09.01.2009; N = 24 * 4 = 96 samples). This design aimed at capturing a maximum of the fine-scale spatial and temporal heterogeneity within the study site without *a priori* knowledge of environmental conditions.

2.3. Soil physico-chemical conditions

Soil physico-chemical variables were presented by Samaritani *et al.* (2011). *Soil texture* (sand; silt; clay) was measured on dried samples using the pipette method (Gee & Bauder 1986). The percentage of *total organic carbon (TOC)* of dried, homogenized soils was measured using a TOC analyzer (Shimadzu, Tokyo, Japan) after HCl (10%) acid digestion to remove carbohydrates. *Total carbon and nitrogen contents* were measured using an automatic element analyzer (Shimadzu, Tokyo, Japan). The Olsen P method was used as a proxy of *available P* (Kuo 1996). *Soil temperature* (T) at 5 cm depth was continuously measured during this study in each plot at 30 min resolution with

TidBit v2 temperature loggers (Bourne, MA, USA). *Soil Moisture (SM)* was estimated at each sampling time by measuring the weight loss upon drying 20 g of fresh soil at 105 °C for 24 h. See Samaritani et al. (2011) for further details about the measurements of soil conditions.

2.4. Ecosystem functioning proxies

Four variables indicative of soil functioning were selected and measured in each plot and season: basal respiration, microbial biomass (carbon and nitrogen), and enzymatic activity. These variables are ecosystem functioning proxies that can be linked to ecosystem services such as decomposition, nutrient cycling and carbon storage. *Basal respiration* (BR) was measured in a closed soil-chamber system connected to a Li-8100 infrared gas analyzer (LI-COR Inc., Lincoln, NE, USA) (Samaritani *et al.* 2017). The gas flow and the CO_2 concentration were recorded and the BR was calculated according to Rieder *et al.* (2013). Fluxes are reported as mmol CO_2 h^{-1} g^{-1} soil dry weight. *Microbial biomass Carbon* (MC) and *Nitrogen* (MN) were determined by chloroform fumigation-extraction (Vance *et al.* 1987; Frey *et al.* 2006; Samaritani *et al.* 2011). MC and MN data were expressed in mg kg^{-1} soil dry weight. *Enzymatic activity* (EA) was estimated by fluorescein diacetate analysis (see Samaritani *et al.* 2017 for more information). Fluorescein diacetate (FDA) is hydrolysed by proteases, lipases and esterases and can therefore be used to determine the microbial activity (Söderström, 1977; Schnürer and Rosswall, 1982; Adam and Duncan, 2001). The formation of a yellow color was assessed at 490 nm by spectrophotometer. The intensity of the resulting yellow color is indicative of the amount of enzymatic cleavage of the FDA molecule (colorless) and the overall enzymatic activity in the sample. The results were expressed in mg of degraded FDA h^{-1} g^{-1} soil dry weight.

2.5. DNA extraction

We used aliquot of soil DNA from the study of Samaritani et al. (2017). Briefly, a 0.5 g subsample of fresh soil and 0.75 g glass beads (0.1 mm diameter) were suspended in 1 ml extraction buffer (0.2 M Na_3PO_4 [pH 8], 0.1 M NaCl, 50 mM EDTA, 0.2% CTAB). The DNA was purified by chloroform extraction with 2 ml chloroform. The DNA was precipitated by the addition of 3 ml of precipitation solution (20% PEG 6000, 2.5 M NaCl). The supernatant was removed and the samples were air dried for 20 min, and re-suspended in AE buffer (10 mM TrisCl, 0.5 mM EDTA, pH9; Qiagen, Hilden, Germany) at 1 ml AE per g of extracted soil (dry weight equivalent). The extracted DNA was examined by electrophoresis on agarose gels (1% w/v in Tris-Borate-EDTA buffer), quantified using PicoGreen and stored at -20 °C.

2.6. 18S rRNA amplification and Illumina sequencing

The microbial eukaryotic communities were investigated using high-throughput Illumina sequencing. The V9 SSU rRNA hypervariable region was amplified with the general eukaryotic primer pair 1380f/1510r (Amaral-Zettler *et al.* 2009). The forward primers were tagged with 96 different 9 nucleotides long keys. In a total volume of 30µl we added 1ng of DNA, 6µl of 10xPCR buffer, 0.6µl of each primer, 0.6µl of each dNTP 400µM (Promega), and 0.2µl of 0.05U µl-1 Hotstar Taq-polymerase (Qiagen). PCR amplification was performed with a PTC-100 thermocycler (MJ Research, Waltham, MA, USA). Each PCR reaction was repeated in triplicates and a negative control was run for each differently tagged primer combination was run. Amplification conditions followed Amaral-Zettler et al. (2009) protocol: 3 minute denaturation at 94°C, followed by 30 cycles of 30s at 94°C, 60s at 57°C, and 90s at 72°C and final extension at 72°C for 10 minutes.

The three PCR products from each sample were combined and purified through Zymo columns. Then, approximately 4 ng of amplicons for each sample were pooled together. Amplicons were quantified by fluorometry with the QuBit HS dsDNA kit (Life Technologies, Carlsbad, CA). A DNA library was prepared for Illumina sequencing following New England Biolabs's kit NEBNext DNA Sample Prep Master Mix Set 1. The 100bp paired-end sequencing run was performed with the Illumina HiSeq2000 platform at the Genomics Core Facility of Brown University (Providence, USA). The sequencing provided a total of 221,625,392 barcoded reads. The amplicon data are available on EMBL European Nucleotide Archive under project number: PRJEB35438 (ERP118478).

2.7. *Sequence data processing and taxonomic assignment*

The absence of sequencing primers in the dataset was verified using cutadapt (Martin 2011). The analysis of the reads was then done with the DADA2 package (version 1.12) in *R version* 3.5.0 (R Development Core Team 2018). The DADA2 pipeline includes the following steps: filtering, dereplication, sample inference, chimera identification, and merging of paired-end reads. DADA2 infers exact amplicon sequence variants (ASVs) from sequencing data (Callahan *et al.* 2016). The ASVs were then taxonomically assigned with QIIME2 (Bolyen *et al.* 2018) using a pre-trained Naive Bayes classifiers (Silva Ref NR 99, release 132) (Quast *et al.* 2012). All ASVs which were not assigned to Nucletmycea or a protist group were removed from the dataset. After this all ASVs representing less than 1% of the average sampling depth were removed (from 14900 ASVs to 13909 ASVs). This was done to remove potential technical artifacts.

2.8. Spatial and temporal changes of ASV richness

The analyses were first focused on the changes in ASV richness among habitats and seasons. The importance of seasons, habitat types, and their interaction as potential drivers of changes in soil micro-eukaryotic ASV richness was assessed. A linear model using ASV richness as a response and habitats and seasons as the two explanatory variables (i.e. without interaction, adjusted $R^2 = 0.31$, P <

0.001) was computed. A second linear model using the same variables was then computed, but, this time, considering an interaction between seasons and habitats (adjusted $R^2 = 0.54$, $P < 0.001$). An ANOVA showed that including the interaction improved the model ($P < 0.001$). Because the interaction between seasons and habitats was significant, these variables (and their interaction) were considered together instead of individually.

The extent to which spatiotemporal, soil condition, and soil function variables explained the variation in ASV richness was then assessed using a variation partitioning analysis (Peres-Neto *et al.* 2006; Legendre & Legendre 2012). More specifically, the variation of ASV richness was partitioned into a spatiotemporal fraction (i.e. interaction between seasons and habitats), a soil function fraction, and a soil condition fraction. Generalized Linear Models (GLM) with ASV richness as response and six variables reflecting soil conditions alongside four variables reflecting soil functions as descriptors were used to assess the importance of soil condition and soil function variables within each season. Soil silt and clay content were removed before analyses because of collinearity.

2.9. Beta diversity: ASV turnover among habitats and seasons

In order to estimate the relative importance of the spatial and temporal turnover of ASV per habitat as well as at the floodplain scale (i.e. within and among habitats), an additive partitioning of total ASV diversity (gamma) into alpha, beta spatial, and beta temporal components was conducted. Through additive decomposition, β-diversity is explicitly an average amount of diversity just as is α-diversity (Veech et al. 2002). This approach thus allows direct comparison of alpha and beta diversities which is particularly relevant for testing theoretical concepts and developing conservation and/or management applications. The additive partitioning of diversity was done following the method of Tylianakis et al. (2005) (see also: Veech *et al.* 2002; Crist *et al.* 2003). Alpha diversity (α) was defined as the mean number of ASV per plot per season. The temporal turnover in ASV between seasons was calculated for each plot (β_{TPlot}) within a given habitat type as: the total number of ASV found within that plot (over the entire year) minus the mean number of ASV per season for that plot (α). Overall β_T was calculated as the mean β_{TPlot} for a given habitat type. Spatial turnover (β_S) was calculated as the total number of ASV found within a habitat type over the entire year minus the mean number of ASV per plot of that habitat type (over the entire year). Therefore, the overall diversity of a habitat type can be described as $\gamma = \alpha + \beta_T + \beta_S$.

The drivers of community compositional changes were then investigated using PERMANOVA applied on a Bray-Curtis dissimilarity matrix (function ADONIS, R package "vegan"; Oksanen *et al.* 2015). Seasons (time), habitat (space), and their interaction (space-time) were used as explanatory variables. As for ASV richness, there was a significant space-time interaction (whole model: adjusted $R^2 = 0.34$, $P < 0.001$; interaction term: adjusted $R^2 = 0.2$, $P = 0.001$). The variation in ASV dissimilarity was then partitioned into a spatiotemporal fraction (i.e. interaction between seasons and habitats), a soil function fraction, and a soil condition fraction (Peres-Neto *et al.* 2006; Legendre & Legendre 2012). Finally, the importance of soil condition and soil function variables within each season was explored using PERMANOVA with ASV dissimilarity as response and six soil condition and four function variables as descriptors. As for ASV richness, soil silt and clay content were removed before analyses because of collinearity.

2.10. Indicator ASV

Indicator ASVs were searched for each habitat in each season. The indicative value (IndVal) of each ASV for each habitat per season was assessed using the function "multipatt" of the R package "indicspecies" (De Cáceres, Legendre & Moretti 2010). This approach calculates an Indicator Value (IndVal) index to measure the association between a species (here ASV) and a group of sites (here habitats; Dufrêne & Legendre 1997). The statistical significance of this relationship was assessed using a permutation test.

All statistical analyses were performed in *R version* 3.6.1 (R Development Core Team 2016).

3. Results

3.1. Metabarcoding of riparian soil microbial eukaryote environmental DNA.

A total of 11,280,627 microbial eukaryote reads belonging to 14,900 distinct amplicon sequence variants (ASVs) were identified in the studied riparian soils. Overall, the dominant taxonomic groups in proportion of sequences were Fungi (36%), Cercozoa (15%), Ciliophora (8%), Bacillariophyta (diatoms) (6%), Chrysophycaea (3%), and Peronosporomycetes (="Oomycetes") (3%), while 30% of all ASVs belonged to less abundant taxonomic groups.

3.2. Spatiotemporal changes in ASV richness

ASV richness varied considerably over space and time (Fig. 1A). The most striking differences among habitats were observed in summer and winter. ASV richness was least variable among habitats in autumn where a large intra-habitat variation was observed. In agreement, the interactions of seasons and habitats explained an important part of the variation in ASV richness (adjusted R^2 = 0.36; Fig. 1B). Part of this variation can be explained by changes in soil conditions (adjusted R^2 = 0.1) and soil functions (adjusted R^2 = 0.08). We also found strong difference in the importance and effect of soil conditions and functions within each season (Table 1).

[Here Fig. 1 and Table 1]

3.3. Spatiotemporal variability in soil microbial eukaryotic assemblages

The turnover of species was higher among habitats (β_S) than seasons (β_T), (Fig. 2A) indicating that the community composition of soil microbial eukaryotes varied more spatially than seasonally. The temporal turnover of species was higher than alpha diversity in all habitats. However, the temporal turnover was about half of the spatial turnover within each habitat. Furthermore, the relative importance of the spatial turnover of species increased at the floodplain scale highlighting the heterogeneity among habitats. We found a similar pattern for the six most abundant taxonomic groups with little variability among groups (Fig. S2). We further found that the interaction between habitat and seasons explained 14 % of the variation in community composition whereas soil conditions and functions each explained about 2 % of this variation (Fig. 2B). We also found strong changes in the importance of soil conditions and functions within each season (Table 2).

[Here Fig. 2 and Table 2]

3.4. Indicator ASVs

We found several indicator ASVs for each habitat in each season, but with important differences in the number and type of indicators (Fig. 3). In spring and autumn, the number of indicator ASVs was clearly higher in *Pasture*. In winter, however, the highest number of indicators was observed in *Gravel*. We also observed differences among taxonomic groups. For example, diatoms were associated to *Gravel* in winter and Cercozoa were more frequently associated to the three habitats further away from to the river (*Mixed forest, Willow forest,* and *Pasture*).

[Here Fig. 3]

4. Discussion

Soil microbial eukaryotes are highly diverse and play key roles in soil functioning (Geisen et al. 2018). Currently, however, the spatial and, especially, temporal patterns of soil microbial eukaryotic beta diversity remains poorly known and our main goal was to characterize these patterns and understand their drivers in a highly dynamic natural and complex ecosystem. Characterizing soil microbial eukaryotic spatiotemporal beta diversity will improve our understanding of community dynamics as well as our capacity to anticipate future changes in soil ecosystem structure and functions.

The present study is, to our knowledge, the first that presents a detailed assessment of soil microbial eukaryote ASV richness and spatiotemporal beta diversity in riparian soils. Soil microbial eukaryotic richness and beta diversity were surveyed using a DNA-based approach over an entire year along a gradient of very heterogeneous habitats encompassing strong changes in flood dynamics, vegetation, and soil conditions and functions. Our results highlight a strikingly important contribution of beta diversity to total microbial eukaryotic diversity within the floodplain. Specifically, the spatial and, to a lesser extent, temporal turnover of ASVs are the main sources of microbial eukaryotic diversity within the floodplain. This contrasts with previous studies based on microscopic observations highlighting a high local diversity of microbial eukaryotes and a relatively high local/global species ratio of soil microbial eukaryotes (e.g. Finlay 2002; Fenchel & Finlay 2004). Such studies, however, characterized a limited fraction of the total diversity by lumping large numbers of genetically very different organisms into single morphospecies (Bass *et al.* 2007; Heger *et al.* 2013) which likely greatly underestimates the importance of beta diversity (Singer *et al.* 2018). The advent of high throughput metabarcoding studies now allows a more complete and objective assessment of biodiversity patterns and a reassessment of existing knowledge. In a study of Neotropical rainforest soils, Lentendu et al. (2018) found a high alpha and low beta diversity for several groups of microbial eukaryotes. However, this study was done in rainforest habitats only (i.e. it does not include a gradient of habitats ranging from bare soils to relatively dense forests contrary to our study) and was based on a single sampling campaign, thus not considering the temporal aspect of beta diversity, which might explain the low beta diversity observed. In contrast, Benke et al. (2010), studying the spatiotemporal changes of protist communities in marine environments, found that the temporal variation was as pronounced as the spatial differences between depths. And Chénard et al. (2019) observed a higher seasonal variation in coastal waters exposed to the influence of the monsoon. In our case, the temporal variation is less pronounced than the spatial one. We attribute this difference as reflecting the higher spatial heterogeneity of soils as compared to marine ecosystems.

We observed a high spatiotemporal complexity in the edaphic drivers of soil microbial eukaryotic alpha and beta diversities. Indeed, a strong interaction between seasons and habitats determines ASV richness and beta diversity. And, seasonal analyses of the drivers of ASV richness and beta diversity show important shifts in variable importance (R^2) as well as shifts in the direction of the relationship (Table 1 and 2). While other studies, in agreement with our results, have highlighted the importance of soil water availability (Bates *et al.* 2013; Geisen *et al.* 2014; Fiore-Donno *et al.* 2019), C and N cycling (Krashevska *et al.* 2010), and soil temperature (Tsyganov *et al.* 2011) as drivers of microbial eukaryote taxa, to our knowledge no study has assessed the importance of proxies for soil ecosystem functioning alongside soil conditions and the seasonal shifts in these drivers. These shifts are likely to have important consequences for biogeochemical processes in soil ecosystems (Levy-Booth *et al.* 2019). For example, soil moisture has negative effect on richness in spring and summer and a positive effect on richness in winter. In agreement with these results, Geisen et al. (2014) showed a non-linear effect of soil water availability on soil protists suggesting maximum abundance of soil protists at intermediate levels of soil water availability. Most of the other studied soil variables showed complex seasonal shifts in importance and/or effects that likely reflects flooding dynamics, and biogeochemical cycles in the soil ecosystems. Interestingly, we observed a floodplain-scale homogenization of soil microbial eukaryotic communities in autumn (i.e. no significant differences in composition among habitats). This homogenization likely resulted from floods occurring shortly before the sampling campaign. Floods can bring propagules from outside the floodplain and move soil material among habitats resulting in increased dispersal at the floodplain scale. Dispersal in metacommunities has indeed the potential to increase immigration in local communities resulting in homogenization at the metacommunity scale (Fodelianakis *et al.* 2019).

The present study also highlights the role of deterministic processes for soil microbial eukaryotic diversity. The high beta diversity and the identification of several ASVs as specific to a particular season and habitat (Fig. 3) suggests a direct response to environmental heterogeneity, as reported for testate amoebae (Fournier *et al.* 2012) and macro-invertebrates at the same site (Fournier *et al.* 2015). Previous studies have already highlighted that different habitat types (e.g., seawater versus soils) harbour different suites of microbial eukaryotes (Bates *et al.* 2013). And the role of a variety of environmental factors in determining soil microbial eukaryotic community structure and richness is well established (Krashevska *et al.* 2010; Bates *et al.* 2013; Geisen *et al.* 2014; Fiore-Donno *et al.* 2019). As such, it is likely that species sorting is a major driver of soil microbial eukaryotic diversity patterns (Leibold *et al.* 2004; Pandit *et al.* 2009; Singer *et al.* 2018). However, at a finer scale, soil microbial eukaryotes were also shown to have a stochastic distribution in boreal forest soils (Bahram *et al.* 2016), a result most likely due to the short environmental gradient sampled. Thus, the degree of environmental heterogeneity covered in a study likely determines the inferred strength of stochastic versus deterministic processes for the assembly of soil microbial eukaryotic communities with the importance of deterministic niche-based processes increasing together with heterogeneity (e.g. along environmental gradients) (Jassey *et al.* 2011).

Our results contrast with a previous study at the same study site showing a much higher temporal than spatial variation of bacterial communities (Samaritani *et al.* 2017). Studies showing a higher spatial than temporal beta diversity of soil bacteria also exists (e.g. Lauber *et al.* 2013).

However, these studies were conducted over larger spatial extent and the importance of dispersal limitation is thus likely to be higher than in our study. Two interrelated hypotheses can explain the observed differences in spatiotemporal beta diversity between soil microbial eukaryotes and bacteria. Microbial eukaryotes typically have longer life span and generation time than bacteria. Despite large variation in life strategies within micro-eukaryotes and within bacteria, microbial eukaryotes can, in general, be considered as K-strategists while bacteria would then be r-strategists, and thus the diversity patterns of microbial eukaryotes should be driven (and explained) by local adaptation (r-K selection; MacArthur & Wilson 1967; Pianka 1970). In addition, microbial eukaryotes might have a lower passive dispersal capacity (e.g. by wind and flood) than bacteria due to their larger (by microbial standard) size (Wilkinson *et al.* 2012). It can thus be expected that local niche-based processes and dispersal limitations play a larger role for protists than for bacteria. In agreement with this, a recent study in marine ecosystems highlighted lower sorting/dispersal effect ratios for bacterial communities as compared to protist communities (Wu *et al.* 2018).

Our study, however, did not consider some potentially important factors for soil microbial eukaryotic diversity. For example, seasonal shifts from bacteria-based to fungal-based decomposition pathways should modify the availability of food resources potentially causing shifts in the composition of the phagotrophic component of the soil microbial eukaryotic communities. Indeed, previous studies have identified highly specialized fungal feeder microbial eukaryote taxa (Petz *et al.* 1985; Foissner 1999) that would be negatively impacted by a decrease in the abundance of fungi in the soil. However, some protists are generalist feeders that are also capable of facultative mycophagy (Geisen *et al.* 2016). Furthermore, some protists are autotrophs, mixotrophs or osmotrophs and are thus not or only marginally affected by the relative abundance of fungi vs bacteria. In any case, the lower temporal than spatial variation suggest that eukaryotes can cope with potential seasonal shifts in prey availability either by being flexible in their feeding source or by encysting. More specific investigations are needed to understand the implications of our results for the whole microbial foodweb. In addition, studies at larger spatial scale or experimental approaches might complement our results about the role of dispersal for beta diversity and its changes across spatial scales. Similarly, our study does not consider the inter-annual or intra-seasonal variability in soil microbial communities which are expected to be smaller than the inter-seasonal variability but might still represent a significant fraction of the total diversity. And, because our approach is based on eDNA, our data might include ASVs derived from extracellular DNA, encysted, or inactive organisms. Finally, our study raises the question of the role of floods for microbial taxa dispersal within the floodplain. Indeed, floods can bring propagules from outside the floodplain and move soil material among habitats thus increasing dispersal and stochasticity potentially leading to homogenization of community composition at the floodplain scale. As such, one can expect low spatial structuring of communities. However, our results do not support this view and rather point toward the importance of local environmental filtering for community structure.

5. Conclusions

We demonstrated the existence of both spatial and temporal turnover in floodplain soil microbial eukaryotic diversity mirroring the spatiotemporal patterns of biogeochemical processes in these ecosystems. Our results also illustrate the value of spatial monitoring of soil biodiversity across habitats within a complex ecosystem. The observed temporal dynamics illustrate the value of seasonal sampling for biodiversity assessment to accurately estimate the diversity and the complexity of assembly processes of soil microbial communities. Sound measurements of the patterns and drivers of soil microbial diversity is needed to understand the relationships between biodiversity and ecosystem functions. This, in turn, allows to assess the impact of environmental changes and management options including restoration efforts on a range of ecosystems.

Conflict of interests

The authors declare no conflict of interest regarding the publication of this article.

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Table and figure legends

Table 1. Predictors in generalized linear models for floodplain soil micro-eukaryotic amplicon sequence variants (ASV) richness per season, their coefficient (Z), and significance (P). GLMs were fitted assuming a Poisson error distribution and using the logarithm as the link function. Bolded characters highlight significance (α < 0.05).

		Spring		Summer		Autumn		Winter	
		(R^2 = 0.56)		(R^2 = 0.61)		(R^2 = 0.51)		(R^2 = 0.8)	
		Z	P	Z	P	Z	P	Z	P
Soil conditions	Soil moisture	**-2.446**	**0.014**	**-12.461**	**>0.001**	1.837	0.066	**5.745**	**>0.001**
	Soil temperature	**2.082**	**0.037**	**21.63**	**>0.001**	-1.459	0.145	**2.149**	**0.032**
	Sand	1.802	0.071	**-10.511**	**>0.001**	**-10.102**	**>0.001**	0.177	0.859
	Organic carbon	**-4.215**	**>0.001**	**-13.692**	**>0.001**	**-12.639**	**>0.001**	**-3.73**	**>0.001**
	Available phosphorus	**3.118**	**0.002**	1.183	0.237	**13.147**	**>0.001**	**12.863**	**>0.001**
	Total nitrogen	**3.327**	**0.001**	**13.936**	**>0.001**	**4.845**	**>0.001**	-1.447	0.148
Soil functions	Basal respiration	**-2.292**	**0.022**	**12.225**	**>0.001**	**9.432**	**>0.001**	**-4.565**	**>0.001**
	Enzymatic activity	**2.684**	**0.007**	**3.735**	**>0.001**	0.657	0.511	**-8.354**	**>0.001**
	Microbial carbon	**5.432**	**>0.001**	**9.289**	**>0.001**	**-16.266**	**>0.001**	**4.241**	**>0.001**
	Microbial nitrogen	**-2.167**	**0.030**	-0.531	0.596	**12.318**	**>0.001**	0.613	0.540

Table 2. Predictors in PERMANOVA for floodplain soil micro-eukaryotic community dissimilarity (Bray-Curtis) per season, their partial R-squared (R^2), and significance (P). Bolded characters highlight significance (α < 0.05).

		Spring		Summer		Autumn		Winter	
		(R^2 = 0.49)		(R^2 = 0.47)		(R^2 = 0.5)		(R^2 = 0.49)	
		R^2	P	R^2	P	R^2	P	R^2	P
Soil conditions	Soil moisture	**0.055**	**0.044**	0.047	0.205	**0.064**	**0.014**	0.037	0.583
	Soil temperature	**0.075**	**0.002**	0.058	0.073	**0.074**	**0.007**	0.038	0.49
	Sand	**0.060**	**0.018**	0.056	0.099	0.044	0.192	**0.099**	**0.001**
	Organic carbon	0.043	0.249	0.039	0.463	0.041	0.302	0.040	0.384
	Available phosphorus	0.038	0.536	0.044	0.294	0.048	0.13	0.040	0.366
	Total nitrogen	0.042	0.273	0.045	0.265	0.046	0.153	0.037	0.61
Soil functions	Basal respiration	0.034	0.84	0.049	0.197	0.053	0.064	**0.051**	**0.052**
	Enzymatic activity	**0.053**	**0.042**	0.036	0.663	0.038	0.444	**0.055**	**0.033**
	Microbial carbon	0.039	0.452	0.060	0.071	0.046	0.169	0.046	0.147
	Microbial nitrogen	0.049	0.078	0.037	0.543	0.042	0.292	0.049	0.086

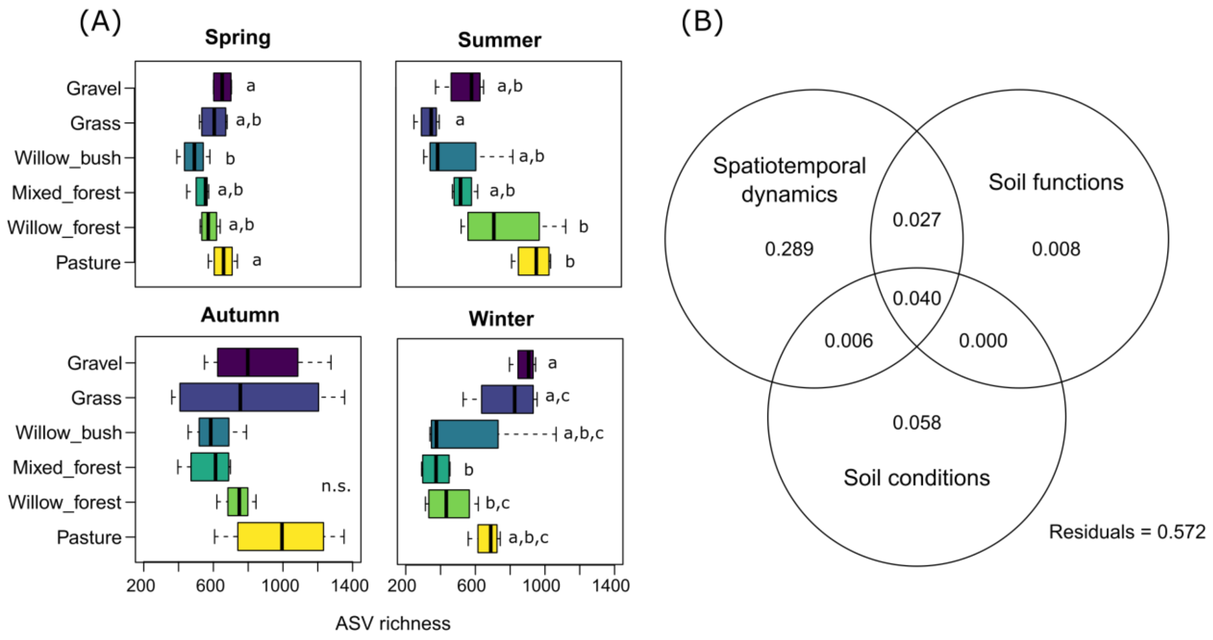

Fig. 1. (A) Changes in floodplain soil micro-eukaryotic amplicon sequence variants (ASV) richness among habitats per season. Letters indicate pairwise differences in mean (Tukey honest differences). Colors highlight the six different habitats. (B) Partitioning of the variation in ASV richness among spatiotemporal (36.2%), soil condition (10.4%), and soil function (7.5%) components.

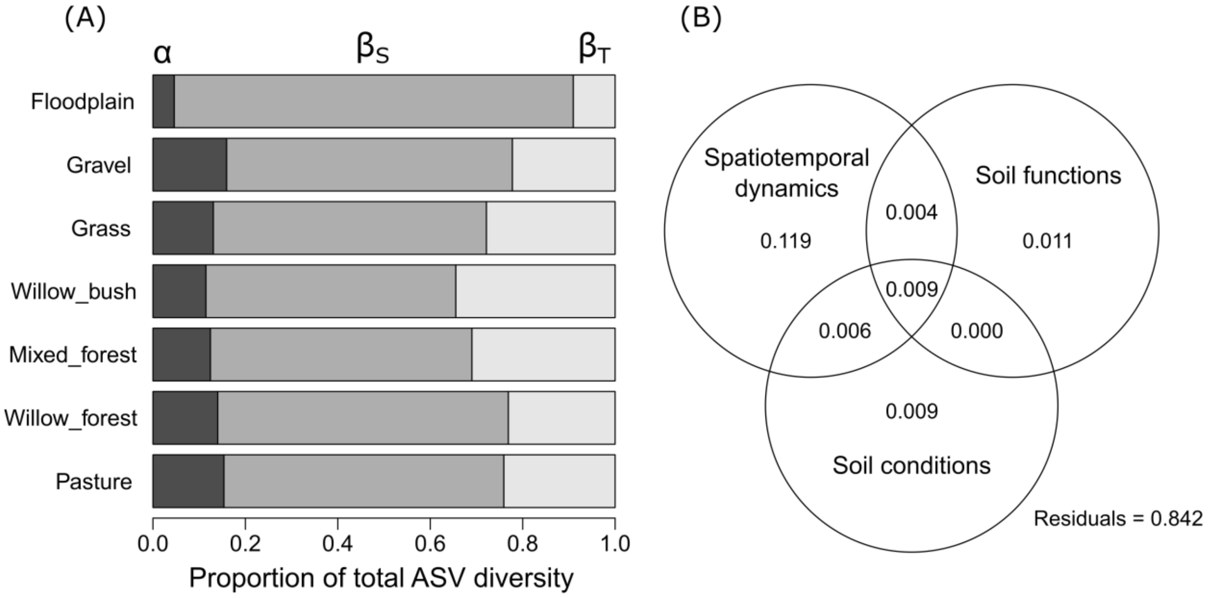

Fig. 2. Spatiotemporal turnover of floodplain soil micro-eukaryotic taxa (amplicon sequence variants - ASV). (A) Partitioning of total diversity (γ) into local diversity (α), temporal species turnover (β_T), and spatial species turnover (β_S) per habitat ($\gamma = \alpha + \beta_T + \beta_S$). This analysis shows a higher spatial than temporal turnover of soil microbial eukaryotic taxa both at the floodplain scale and within habitats. (B) Partitioning of the variation in ASV community composition among spatiotemporal (13.8%), soil condition (2.4%), and soil function (2.4%) components.

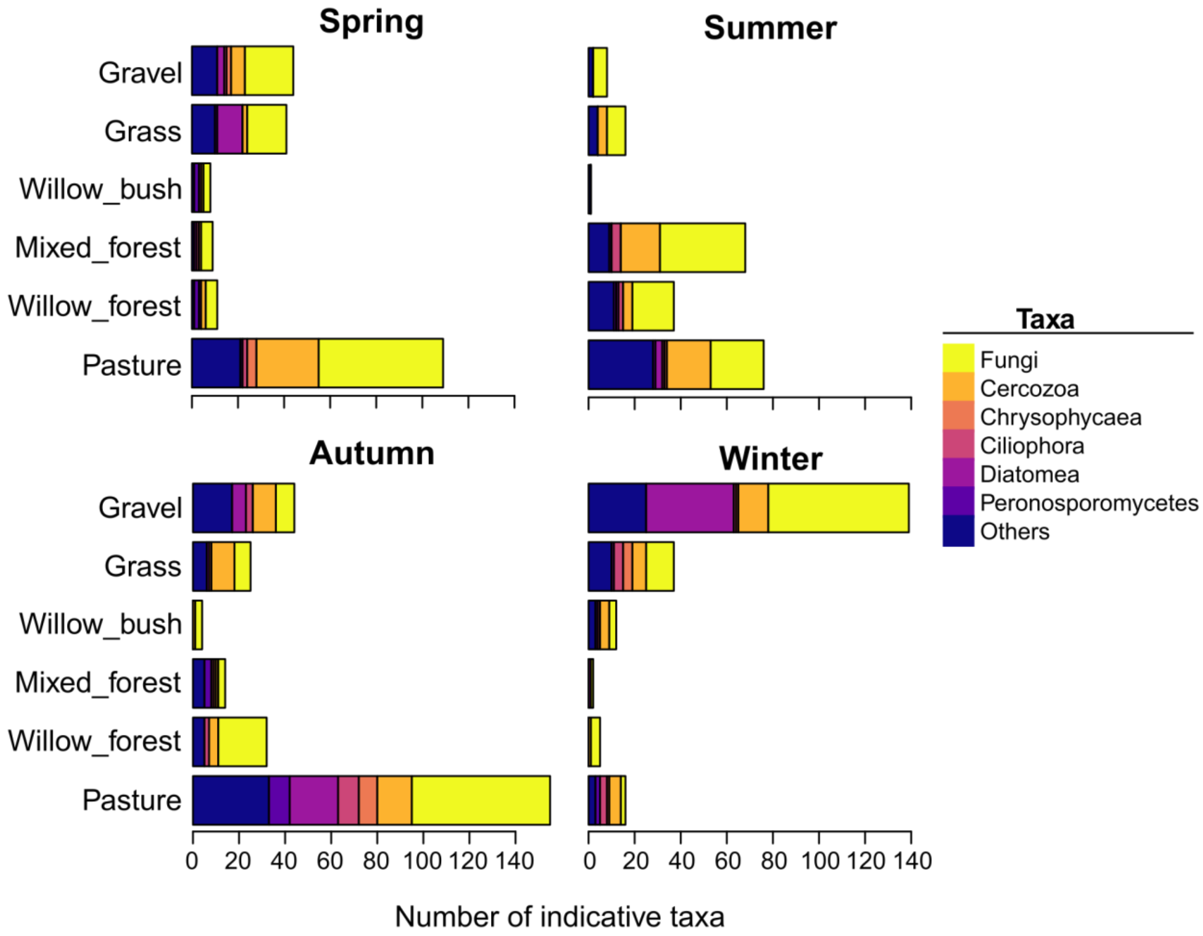

Fig. 3. Indicator ASVs (amplicon sequence variants) of floodplain soil micro-eukaryotes for each habitat at each season. Only ASVs with significant IndVal values (indicator values; De Cáceres, Legendre & Moretti 2010) are shown. Colors show the different taxonomic groups. Other are ASVs belonging to less abundant taxonomic groups.

Appendix A. Supplementary information

Higher spatial than seasonal variation in floodplain soil eukaryotic microbial diversity

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Table S1. List of indicator ASVs for each season and habitat.

ASV_ID	season	habitat	taxa	indval	pval
472	Spring	Gravel	Cercozoa	0.810	0.005
823	Spring	Gravel	Cercozoa	0.707	0.005
826	Spring	Gravel	Cercozoa	0.695	0.040
445	Spring	Gravel	Cercozoa	0.620	0.030
429	Spring	Gravel	Cercozoa	0.590	0.035
301	Spring	Gravel	Cercozoa	0.456	0.010
78	Spring	Gravel	Chrysophycaea	0.770	0.020
717	Spring	Gravel	Ciliophora	0.654	0.035
124	Spring	Gravel	Diatomea	0.764	0.005
97	Spring	Gravel	Diatomea	0.705	0.025
143	Spring	Gravel	Diatomea	0.689	0.035
129	Spring	Gravel	Diatomea	0.594	0.045
350	Spring	Gravel	Fungi	0.866	0.015
396	Spring	Gravel	Fungi	0.866	0.005
418	Spring	Gravel	Fungi	0.866	0.020
655	Spring	Gravel	Fungi	0.866	0.020
512	Spring	Gravel	Fungi	0.762	0.005
317	Spring	Gravel	Fungi	0.758	0.020
373	Spring	Gravel	Fungi	0.757	0.010
628	Spring	Gravel	Fungi	0.752	0.020
647	Spring	Gravel	Fungi	0.748	0.045
8	Spring	Gravel	Fungi	0.748	0.010

862	Spring	Gravel	Fungi	0.742	0.005
412	Spring	Gravel	Fungi	0.738	0.030
521	Spring	Gravel	Fungi	0.735	0.025
571	Spring	Gravel	Fungi	0.696	0.025
858	Spring	Gravel	Fungi	0.672	0.015
864	Spring	Gravel	Fungi	0.669	0.035
376	Spring	Gravel	Fungi	0.663	0.035
890	Spring	Gravel	Fungi	0.644	0.040
526	Spring	Gravel	Fungi	0.629	0.005
878	Spring	Gravel	Fungi	0.605	0.015
343	Spring	Gravel	Fungi	0.522	0.040
199	Spring	Gravel	Others	0.901	0.005
208	Spring	Gravel	Others	0.748	0.030
62	Spring	Gravel	Others	0.739	0.020
840	Spring	Gravel	Others	0.725	0.035
233	Spring	Gravel	Others	0.717	0.040
270	Spring	Gravel	Others	0.689	0.020
919	Spring	Gravel	Others	0.684	0.030
261	Spring	Gravel	Others	0.659	0.015
904	Spring	Gravel	Others	0.641	0.040
231	Spring	Gravel	Others	0.640	0.040
850	Spring	Gravel	Others	0.615	0.020
289	Spring	Grass	Cercozoa	0.866	0.030
164	Spring	Grass	Diatomea	0.785	0.005
150	Spring	Grass	Diatomea	0.775	0.030
101	Spring	Grass	Diatomea	0.624	0.020
111	Spring	Grass	Diatomea	0.614	0.030

165	Spring	Grass	Diatomea	0.587	0.005
131	Spring	Grass	Diatomea	0.468	0.030
66	Spring	Grass	Diatomea	0.465	0.005
525	Spring	Grass	Fungi	0.866	0.030
513	Spring	Grass	Fungi	0.812	0.005
28	Spring	Grass	Fungi	0.793	0.010
22	Spring	Grass	Fungi	0.751	0.040
401	Spring	Grass	Fungi	0.701	0.005
657	Spring	Grass	Fungi	0.697	0.040
5	Spring	Grass	Fungi	0.659	0.005
500	Spring	Grass	Fungi	0.656	0.015
32	Spring	Grass	Fungi	0.639	0.040
532	Spring	Grass	Fungi	0.636	0.005
416	Spring	Grass	Fungi	0.624	0.025
33	Spring	Grass	Fungi	0.616	0.030
893	Spring	Grass	Fungi	0.559	0.030
912	Spring	Grass	Others	0.750	0.040
207	Spring	Grass	Others	0.633	0.030
264	Spring	Grass	Others	0.633	0.035
267	Spring	Grass	Others	0.509	0.015
448	Spring	Willow_bush	Cercozoa	0.431	0.015
763	Spring	Willow_bush	Ciliophora	0.625	0.040
557	Spring	Willow_bush	Fungi	0.866	0.010
576	Spring	Willow_bush	Fungi	0.781	0.025
538	Spring	Willow_bush	Fungi	0.766	0.010
517	Spring	Willow_bush	Fungi	0.563	0.035
843	Spring	Willow_bush	Others	0.719	0.010

430	Spring	Willow_bush	Others	0.493	0.020
42	Spring	Willow_bush	Peronosporomycetes	0.820	0.015
43	Spring	Willow_bush	Peronosporomycetes	0.692	0.040
433	Spring	Mixed_forest	Cercozoa	0.648	0.035
432	Spring	Mixed_forest	Cercozoa	0.613	0.045
752	Spring	Mixed_forest	Ciliophora	0.619	0.010
249	Spring	Mixed_forest	Diatomea	0.573	0.015
274	Spring	Mixed_forest	Fungi	0.753	0.030
313	Spring	Mixed_forest	Fungi	0.692	0.015
803	Spring	Mixed_forest	Fungi	0.664	0.045
357	Spring	Mixed_forest	Fungi	0.639	0.020
546	Spring	Mixed_forest	Fungi	0.608	0.020
928	Spring	Mixed_forest	Others	0.622	0.040
477	Spring	Willow_forest	Cercozoa	0.746	0.025
245	Spring	Willow_forest	Diatomea	0.677	0.030
564	Spring	Willow_forest	Fungi	0.728	0.030
582	Spring	Willow_forest	Fungi	0.728	0.030
556	Spring	Willow_forest	Fungi	0.694	0.020
304	Spring	Willow_forest	Fungi	0.685	0.020
534	Spring	Willow_forest	Fungi	0.637	0.020
175	Spring	Willow_forest	Others	0.748	0.025
55	Spring	Willow_forest	Peronosporomycetes	0.866	0.015
47	Spring	Willow_forest	Peronosporomycetes	0.579	0.035
463	Spring	Pasture	Cercozoa	0.896	0.010
297	Spring	Pasture	Cercozoa	0.866	0.020
298	Spring	Pasture	Cercozoa	0.866	0.015
578	Spring	Pasture	Cercozoa	0.866	0.020

778	Spring	Pasture	Cercozoa	0.866	0.020
789	Spring	Pasture	Cercozoa	0.866	0.020
793	Spring	Pasture	Cercozoa	0.866	0.015
798	Spring	Pasture	Cercozoa	0.866	0.020
807	Spring	Pasture	Cercozoa	0.866	0.020
810	Spring	Pasture	Cercozoa	0.866	0.015
852	Spring	Pasture	Cercozoa	0.866	0.015
618	Spring	Pasture	Cercozoa	0.787	0.015
821	Spring	Pasture	Cercozoa	0.765	0.020
295	Spring	Pasture	Cercozoa	0.760	0.020
468	Spring	Pasture	Cercozoa	0.741	0.040
479	Spring	Pasture	Cercozoa	0.740	0.020
641	Spring	Pasture	Cercozoa	0.722	0.005
832	Spring	Pasture	Cercozoa	0.713	0.025
775	Spring	Pasture	Cercozoa	0.706	0.005
457	Spring	Pasture	Cercozoa	0.691	0.015
773	Spring	Pasture	Cercozoa	0.686	0.005
834	Spring	Pasture	Cercozoa	0.678	0.030
822	Spring	Pasture	Cercozoa	0.603	0.010
706	Spring	Pasture	Cercozoa	0.593	0.035
794	Spring	Pasture	Cercozoa	0.576	0.010
459	Spring	Pasture	Cercozoa	0.566	0.035
619	Spring	Pasture	Cercozoa	0.528	0.035
172	Spring	Pasture	Chrysophycaea	1.000	0.005
82	Spring	Pasture	Chrysophycaea	0.866	0.015
84	Spring	Pasture	Chrysophycaea	0.866	0.015
68	Spring	Pasture	Chrysophycaea	0.647	0.030

768	Spring	Pasture	Ciliophora	0.763	0.015
670	Spring	Pasture	Ciliophora	0.714	0.045
757	Spring	Pasture	Ciliophora	0.661	0.040
356	Spring	Pasture	Fungi	1.000	0.005
610	Spring	Pasture	Fungi	1.000	0.005
488	Spring	Pasture	Fungi	0.934	0.005
403	Spring	Pasture	Fungi	0.912	0.005
629	Spring	Pasture	Fungi	0.903	0.005
425	Spring	Pasture	Fungi	0.902	0.005
642	Spring	Pasture	Fungi	0.891	0.005
587	Spring	Pasture	Fungi	0.879	0.010
361	Spring	Pasture	Fungi	0.866	0.015
363	Spring	Pasture	Fungi	0.866	0.020
367	Spring	Pasture	Fungi	0.866	0.015
379	Spring	Pasture	Fungi	0.866	0.020
486	Spring	Pasture	Fungi	0.866	0.015
492	Spring	Pasture	Fungi	0.866	0.020
597	Spring	Pasture	Fungi	0.866	0.015
603	Spring	Pasture	Fungi	0.866	0.020
605	Spring	Pasture	Fungi	0.866	0.020
612	Spring	Pasture	Fungi	0.866	0.020
886	Spring	Pasture	Fungi	0.866	0.015
397	Spring	Pasture	Fungi	0.858	0.005
353	Spring	Pasture	Fungi	0.826	0.005
483	Spring	Pasture	Fungi	0.824	0.010
277	Spring	Pasture	Fungi	0.805	0.005
365	Spring	Pasture	Fungi	0.795	0.010

276	Spring	Pasture	Fungi	0.794	0.015
593	Spring	Pasture	Fungi	0.787	0.015
14	Spring	Pasture	Fungi	0.775	0.020
390	Spring	Pasture	Fungi	0.772	0.025
541	Spring	Pasture	Fungi	0.772	0.020
548	Spring	Pasture	Fungi	0.761	0.020
307	Spring	Pasture	Fungi	0.755	0.020
305	Spring	Pasture	Fungi	0.751	0.005
508	Spring	Pasture	Fungi	0.743	0.025
645	Spring	Pasture	Fungi	0.732	0.005
654	Spring	Pasture	Fungi	0.722	0.005
423	Spring	Pasture	Fungi	0.722	0.020
321	Spring	Pasture	Fungi	0.719	0.045
568	Spring	Pasture	Fungi	0.713	0.015
493	Spring	Pasture	Fungi	0.705	0.020
371	Spring	Pasture	Fungi	0.700	0.045
607	Spring	Pasture	Fungi	0.691	0.045
369	Spring	Pasture	Fungi	0.668	0.005
569	Spring	Pasture	Fungi	0.665	0.010
516	Spring	Pasture	Fungi	0.659	0.035
340	Spring	Pasture	Fungi	0.637	0.025
604	Spring	Pasture	Fungi	0.603	0.035
520	Spring	Pasture	Fungi	0.593	0.035
575	Spring	Pasture	Fungi	0.588	0.035
888	Spring	Pasture	Fungi	0.580	0.005
335	Spring	Pasture	Fungi	0.555	0.020
325	Spring	Pasture	Fungi	0.480	0.005

868	Spring	Pasture	Fungi	0.469	0.045
35	Spring	Pasture	Others	1.000	0.005
730	Spring	Pasture	Others	1.000	0.005
920	Spring	Pasture	Others	1.000	0.005
720	Spring	Pasture	Others	0.909	0.005
906	Spring	Pasture	Others	0.890	0.005
37	Spring	Pasture	Others	0.866	0.020
186	Spring	Pasture	Others	0.866	0.015
193	Spring	Pasture	Others	0.866	0.015
222	Spring	Pasture	Others	0.866	0.020
229	Spring	Pasture	Others	0.866	0.015
238	Spring	Pasture	Others	0.866	0.015
669	Spring	Pasture	Others	0.866	0.015
782	Spring	Pasture	Others	0.866	0.020
784	Spring	Pasture	Others	0.796	0.005
785	Spring	Pasture	Others	0.721	0.010
93	Spring	Pasture	Others	0.613	0.045
916	Spring	Pasture	Others	0.605	0.010
844	Spring	Pasture	Others	0.575	0.005
908	Spring	Pasture	Others	0.569	0.015
227	Spring	Pasture	Others	0.563	0.005
738	Spring	Pasture	Others	0.558	0.025
689	Spring	Pasture	Others	0.539	0.025
39	Spring	Pasture	Peronosporomycetes	0.751	0.030
329	Summer	Gravel	Fungi	0.866	0.025
551	Summer	Gravel	Fungi	0.818	0.025
554	Summer	Gravel	Fungi	0.700	0.035

590	Summer	Gravel	Fungi	0.676	0.010
553	Summer	Gravel	Fungi	0.662	0.035
869	Summer	Gravel	Fungi	0.657	0.040
901	Summer	Gravel	Others	0.866	0.025
715	Summer	Gravel	Others	0.652	0.035
701	Summer	Grass	Cercozoa	0.749	0.010
635	Summer	Grass	Cercozoa	0.693	0.005
470	Summer	Grass	Cercozoa	0.612	0.040
293	Summer	Grass	Cercozoa	0.501	0.010
585	Summer	Grass	Fungi	0.866	0.020
558	Summer	Grass	Fungi	0.861	0.005
881	Summer	Grass	Fungi	0.759	0.020
505	Summer	Grass	Fungi	0.597	0.015
563	Summer	Grass	Fungi	0.587	0.010
419	Summer	Grass	Fungi	0.585	0.015
560	Summer	Grass	Fungi	0.516	0.005
577	Summer	Grass	Fungi	0.465	0.005
725	Summer	Grass	Others	0.673	0.005
252	Summer	Grass	Others	0.595	0.005
726	Summer	Grass	Others	0.575	0.015
631	Summer	Willow_bush	Others	0.757	0.035
776	Summer	Mixed_forest	Cercozoa	0.898	0.005
467	Summer	Mixed_forest	Cercozoa	0.892	0.005
456	Summer	Mixed_forest	Cercozoa	0.866	0.020
779	Summer	Mixed_forest	Cercozoa	0.866	0.025
800	Summer	Mixed_forest	Cercozoa	0.866	0.010
799	Summer	Mixed_forest	Cercozoa	0.740	0.040

464	Summer	Mixed_forest	Cercozoa	0.738	0.020
711	Summer	Mixed_forest	Cercozoa	0.711	0.005
708	Summer	Mixed_forest	Cercozoa	0.709	0.005
707	Summer	Mixed_forest	Cercozoa	0.690	0.040
812	Summer	Mixed_forest	Cercozoa	0.676	0.005
705	Summer	Mixed_forest	Cercozoa	0.665	0.010
774	Summer	Mixed_forest	Cercozoa	0.640	0.010
709	Summer	Mixed_forest	Cercozoa	0.600	0.015
469	Summer	Mixed_forest	Cercozoa	0.544	0.045
620	Summer	Mixed_forest	Cercozoa	0.511	0.015
671	Summer	Mixed_forest	Ciliophora	0.866	0.020
273	Summer	Mixed_forest	Ciliophora	0.749	0.030
751	Summer	Mixed_forest	Ciliophora	0.710	0.005
764	Summer	Mixed_forest	Ciliophora	0.643	0.020
272	Summer	Mixed_forest	Ciliophora	0.575	0.005
422	Summer	Mixed_forest	Fungi	1.000	0.005
404	Summer	Mixed_forest	Fungi	0.907	0.005
630	Summer	Mixed_forest	Fungi	0.906	0.005
586	Summer	Mixed_forest	Fungi	0.901	0.005
481	Summer	Mixed_forest	Fungi	0.898	0.005
427	Summer	Mixed_forest	Fungi	0.896	0.005
494	Summer	Mixed_forest	Fungi	0.879	0.005
608	Summer	Mixed_forest	Fungi	0.878	0.005
484	Summer	Mixed_forest	Fungi	0.866	0.010
504	Summer	Mixed_forest	Fungi	0.866	0.025
594	Summer	Mixed_forest	Fungi	0.866	0.025
650	Summer	Mixed_forest	Fungi	0.866	0.025

660	Summer	Mixed_forest	Fungi	0.866	0.025
583	Summer	Mixed_forest	Fungi	0.861	0.005
409	Summer	Mixed_forest	Fungi	0.832	0.005
489	Summer	Mixed_forest	Fungi	0.818	0.005
364	Summer	Mixed_forest	Fungi	0.807	0.005
644	Summer	Mixed_forest	Fungi	0.800	0.020
398	Summer	Mixed_forest	Fungi	0.790	0.005
552	Summer	Mixed_forest	Fungi	0.771	0.010
362	Summer	Mixed_forest	Fungi	0.769	0.010
595	Summer	Mixed_forest	Fungi	0.762	0.025
561	Summer	Mixed_forest	Fungi	0.755	0.025
596	Summer	Mixed_forest	Fungi	0.746	0.035
592	Summer	Mixed_forest	Fungi	0.746	0.035
574	Summer	Mixed_forest	Fungi	0.690	0.010
570	Summer	Mixed_forest	Fungi	0.686	0.015
333	Summer	Mixed_forest	Fungi	0.677	0.035
891	Summer	Mixed_forest	Fungi	0.668	0.040
623	Summer	Mixed_forest	Fungi	0.645	0.045
872	Summer	Mixed_forest	Fungi	0.627	0.015
519	Summer	Mixed_forest	Fungi	0.609	0.025
887	Summer	Mixed_forest	Fungi	0.587	0.005
867	Summer	Mixed_forest	Fungi	0.527	0.005
324	Summer	Mixed_forest	Fungi	0.507	0.035
189	Summer	Mixed_forest	Others	0.866	0.010
221	Summer	Mixed_forest	Others	0.866	0.025
230	Summer	Mixed_forest	Others	0.798	0.005
194	Summer	Mixed_forest	Others	0.766	0.010

714	Summer	Mixed_forest	Others	0.748	0.015
676	Summer	Mixed_forest	Others	0.739	0.040
924	Summer	Mixed_forest	Others	0.723	0.035
907	Summer	Mixed_forest	Others	0.631	0.020
228	Summer	Mixed_forest	Others	0.618	0.005
845	Summer	Mixed_forest	Others	0.561	0.005
625	Summer	Mixed_forest	Others	0.548	0.045
61	Summer	Mixed_forest	Peronosporomycetes	0.838	0.005
299	Summer	Willow_forest	Cercozoa	0.743	0.030
446	Summer	Willow_forest	Cercozoa	0.678	0.045
704	Summer	Willow_forest	Cercozoa	0.654	0.035
460	Summer	Willow_forest	Cercozoa	0.515	0.020
761	Summer	Willow_forest	Ciliophora	0.726	0.040
745	Summer	Willow_forest	Ciliophora	0.723	0.005
341	Summer	Willow_forest	Fungi	0.776	0.025
26	Summer	Willow_forest	Fungi	0.758	0.040
572	Summer	Willow_forest	Fungi	0.758	0.005
282	Summer	Willow_forest	Fungi	0.720	0.040
877	Summer	Willow_forest	Fungi	0.705	0.035
286	Summer	Willow_forest	Fungi	0.703	0.010
352	Summer	Willow_forest	Fungi	0.699	0.015
338	Summer	Willow_forest	Fungi	0.691	0.025
883	Summer	Willow_forest	Fungi	0.687	0.015
870	Summer	Willow_forest	Fungi	0.685	0.030
382	Summer	Willow_forest	Fungi	0.645	0.045
543	Summer	Willow_forest	Fungi	0.644	0.025
897	Summer	Willow_forest	Fungi	0.640	0.040

649	Summer	Willow_forest	Fungi	0.622	0.045
11	Summer	Willow_forest	Fungi	0.589	0.025
209	Summer	Willow_forest	Others	0.866	0.010
929	Summer	Willow_forest	Others	0.866	0.025
787	Summer	Willow_forest	Others	0.758	0.015
741	Summer	Willow_forest	Others	0.751	0.045
216	Summer	Willow_forest	Others	0.733	0.005
687	Summer	Willow_forest	Others	0.699	0.025
239	Summer	Willow_forest	Others	0.698	0.005
181	Summer	Willow_forest	Others	0.675	0.040
191	Summer	Willow_forest	Others	0.660	0.025
921	Summer	Willow_forest	Others	0.647	0.045
57	Summer	Willow_forest	Peronosporomycetes	0.866	0.025
802	Summer	Pasture	Cercozoa	0.910	0.005
825	Summer	Pasture	Cercozoa	0.807	0.005
601	Summer	Pasture	Cercozoa	0.799	0.015
839	Summer	Pasture	Cercozoa	0.777	0.005
791	Summer	Pasture	Cercozoa	0.761	0.010
830	Summer	Pasture	Cercozoa	0.752	0.015
811	Summer	Pasture	Cercozoa	0.731	0.020
290	Summer	Pasture	Cercozoa	0.714	0.040
471	Summer	Pasture	Cercozoa	0.713	0.045
851	Summer	Pasture	Cercozoa	0.709	0.020
699	Summer	Pasture	Cercozoa	0.705	0.005
434	Summer	Pasture	Cercozoa	0.693	0.025
614	Summer	Pasture	Cercozoa	0.678	0.040
292	Summer	Pasture	Cercozoa	0.675	0.035

827	Summer	Pasture	Cercozoa	0.643	0.015
637	Summer	Pasture	Cercozoa	0.633	0.040
437	Summer	Pasture	Cercozoa	0.610	0.030
797	Summer	Pasture	Cercozoa	0.609	0.015
302	Summer	Pasture	Cercozoa	0.509	0.025
743	Summer	Pasture	Ciliophora	0.736	0.040
758	Summer	Pasture	Ciliophora	0.720	0.040
754	Summer	Pasture	Ciliophora	0.646	0.045
240	Summer	Pasture	Diatomea	0.744	0.035
163	Summer	Pasture	Diatomea	0.742	0.020
154	Summer	Pasture	Diatomea	0.672	0.035
113	Summer	Pasture	Diatomea	0.588	0.025
643	Summer	Pasture	Fungi	0.907	0.005
7	Summer	Pasture	Fungi	0.866	0.015
539	Summer	Pasture	Fungi	0.866	0.010
540	Summer	Pasture	Fungi	0.866	0.020
328	Summer	Pasture	Fungi	0.827	0.010
866	Summer	Pasture	Fungi	0.808	0.010
349	Summer	Pasture	Fungi	0.782	0.015
662	Summer	Pasture	Fungi	0.763	0.025
6	Summer	Pasture	Fungi	0.753	0.025
544	Summer	Pasture	Fungi	0.751	0.045
875	Summer	Pasture	Fungi	0.744	0.010
31	Summer	Pasture	Fungi	0.743	0.040
417	Summer	Pasture	Fungi	0.718	0.030
12	Summer	Pasture	Fungi	0.714	0.040
315	Summer	Pasture	Fungi	0.712	0.025

374	Summer	Pasture	Fungi	0.708	0.025
310	Summer	Pasture	Fungi	0.707	0.040
381	Summer	Pasture	Fungi	0.705	0.010
514	Summer	Pasture	Fungi	0.692	0.035
30	Summer	Pasture	Fungi	0.674	0.025
3	Summer	Pasture	Fungi	0.608	0.010
176	Summer	Pasture	Others	0.866	0.020
251	Summer	Pasture	Others	0.866	0.010
719	Summer	Pasture	Others	0.866	0.020
913	Summer	Pasture	Others	0.866	0.010
917	Summer	Pasture	Others	0.750	0.025
260	Summer	Pasture	Others	0.750	0.040
204	Summer	Pasture	Others	0.749	0.030
911	Summer	Pasture	Others	0.747	0.010
910	Summer	Pasture	Others	0.744	0.020
786	Summer	Pasture	Others	0.743	0.030
88	Summer	Pasture	Others	0.725	0.045
205	Summer	Pasture	Others	0.699	0.020
90	Summer	Pasture	Others	0.697	0.040
203	Summer	Pasture	Others	0.696	0.045
926	Summer	Pasture	Others	0.688	0.035
925	Summer	Pasture	Others	0.687	0.020
783	Summer	Pasture	Others	0.684	0.015
728	Summer	Pasture	Others	0.679	0.030
685	Summer	Pasture	Others	0.677	0.025
210	Summer	Pasture	Others	0.666	0.040
271	Summer	Pasture	Others	0.662	0.040

268	Summer	Pasture	Others	0.634	0.025
190	Summer	Pasture	Others	0.628	0.030
258	Summer	Pasture	Others	0.582	0.020
905	Summer	Pasture	Others	0.574	0.030
686	Summer	Pasture	Others	0.507	0.020
58	Summer	Pasture	Peronosporomycetes	0.734	0.040
613	Fall	Gravel	Cercozoa	0.866	0.005
795	Fall	Gravel	Cercozoa	0.866	0.005
835	Fall	Gravel	Cercozoa	0.646	0.005
454	Fall	Gravel	Cercozoa	0.627	0.015
828	Fall	Gravel	Cercozoa	0.613	0.005
809	Fall	Gravel	Cercozoa	0.532	0.020
639	Fall	Gravel	Cercozoa	0.530	0.045
796	Fall	Gravel	Cercozoa	0.529	0.010
440	Fall	Gravel	Cercozoa	0.514	0.005
838	Fall	Gravel	Cercozoa	0.480	0.040
443	Fall	Gravel	Cercozoa	0.446	0.030
770	Fall	Gravel	Ciliophora	0.784	0.005
672	Fall	Gravel	Ciliophora	0.744	0.020
674	Fall	Gravel	Ciliophora	0.694	0.040
250	Fall	Gravel	Diatomea	0.866	0.015
141	Fall	Gravel	Diatomea	0.730	0.035
121	Fall	Gravel	Diatomea	0.701	0.025
139	Fall	Gravel	Diatomea	0.664	0.040
162	Fall	Gravel	Diatomea	0.620	0.005
170	Fall	Gravel	Diatomea	0.505	0.010
167	Fall	Gravel	Diatomea	0.488	0.020

130	Fall	Gravel	Diatomea	0.464	0.005
65	Fall	Gravel	Diatomea	0.447	0.030
873	Fall	Gravel	Fungi	0.756	0.005
312	Fall	Gravel	Fungi	0.752	0.035
581	Fall	Gravel	Fungi	0.713	0.030
523	Fall	Gravel	Fungi	0.701	0.005
535	Fall	Gravel	Fungi	0.671	0.005
599	Fall	Gravel	Fungi	0.667	0.040
392	Fall	Gravel	Fungi	0.665	0.045
496	Fall	Gravel	Fungi	0.602	0.005
413	Fall	Gravel	Fungi	0.583	0.035
4	Fall	Gravel	Fungi	0.525	0.025
266	Fall	Gravel	Others	0.866	0.005
632	Fall	Gravel	Others	0.866	0.015
899	Fall	Gravel	Others	0.866	0.025
922	Fall	Gravel	Others	0.768	0.005
91	Fall	Gravel	Others	0.762	0.025
724	Fall	Gravel	Others	0.732	0.030
256	Fall	Gravel	Others	0.719	0.010
853	Fall	Gravel	Others	0.680	0.020
698	Fall	Gravel	Others	0.679	0.005
716	Fall	Gravel	Others	0.678	0.040
855	Fall	Gravel	Others	0.663	0.030
624	Fall	Gravel	Others	0.661	0.005
177	Fall	Gravel	Others	0.655	0.045
234	Fall	Gravel	Others	0.630	0.035
206	Fall	Gravel	Others	0.617	0.005

694	Fall	Gravel	Others	0.616	0.040
262	Fall	Gravel	Others	0.576	0.030
232	Fall	Gravel	Others	0.571	0.015
259	Fall	Gravel	Others	0.550	0.005
442	Fall	Grass	Cercozoa	0.866	0.010
438	Fall	Grass	Cercozoa	0.776	0.010
431	Fall	Grass	Cercozoa	0.716	0.030
633	Fall	Grass	Cercozoa	0.707	0.010
831	Fall	Grass	Cercozoa	0.675	0.035
617	Fall	Grass	Cercozoa	0.641	0.030
278	Fall	Grass	Cercozoa	0.638	0.040
476	Fall	Grass	Cercozoa	0.589	0.045
702	Fall	Grass	Cercozoa	0.581	0.045
640	Fall	Grass	Cercozoa	0.572	0.015
621	Fall	Grass	Cercozoa	0.537	0.015
837	Fall	Grass	Cercozoa	0.516	0.015
710	Fall	Grass	Cercozoa	0.516	0.020
441	Fall	Grass	Cercozoa	0.490	0.015
478	Fall	Grass	Cercozoa	0.455	0.030
76	Fall	Grass	Chrysophycaea	0.632	0.045
753	Fall	Grass	Ciliophora	0.648	0.035
140	Fall	Grass	Diatomea	0.757	0.020
622	Fall	Grass	Fungi	0.866	0.010
280	Fall	Grass	Fungi	0.863	0.005
533	Fall	Grass	Fungi	0.740	0.005
370	Fall	Grass	Fungi	0.654	0.030
359	Fall	Grass	Fungi	0.636	0.025

542	Fall	Grass	Fungi	0.591	0.030
661	Fall	Grass	Fungi	0.587	0.020
323	Fall	Grass	Fungi	0.461	0.040
680	Fall	Grass	Others	0.865	0.005
847	Fall	Grass	Others	0.775	0.020
842	Fall	Grass	Others	0.653	0.005
909	Fall	Grass	Others	0.626	0.015
237	Fall	Grass	Others	0.598	0.035
737	Fall	Grass	Others	0.556	0.010
818	Fall	Grass	Others	0.477	0.015
475	Fall	Willow_bush	Cercozoa	0.866	0.010
509	Fall	Willow_bush	Fungi	0.866	0.010
515	Fall	Willow_bush	Fungi	0.866	0.010
690	Fall	Willow_bush	Others	0.650	0.030
777	Fall	Mixed_forest	Cercozoa	0.584	0.035
74	Fall	Mixed_forest	Chrysophycaea	0.866	0.015
567	Fall	Mixed_forest	Fungi	0.762	0.010
591	Fall	Mixed_forest	Fungi	0.685	0.045
692	Fall	Mixed_forest	Others	0.866	0.015
902	Fall	Mixed_forest	Others	0.715	0.010
235	Fall	Mixed_forest	Others	0.644	0.035
677	Fall	Mixed_forest	Others	0.480	0.010
48	Fall	Mixed_forest	Peronosporomycetes	0.618	0.020
44	Fall	Mixed_forest	Peronosporomycetes	0.608	0.025
46	Fall	Mixed_forest	Peronosporomycetes	0.552	0.005
300	Fall	Willow_forest	Cercozoa	0.866	0.005
465	Fall	Willow_forest	Cercozoa	0.780	0.005

636	Fall	Willow_forest	Cercozoa	0.682	0.015
462	Fall	Willow_forest	Cercozoa	0.662	0.025
638	Fall	Willow_forest	Cercozoa	0.640	0.045
765	Fall	Willow_forest	Ciliophora	0.900	0.005
769	Fall	Willow_forest	Ciliophora	0.763	0.005
766	Fall	Willow_forest	Ciliophora	0.683	0.030
598	Fall	Willow_forest	Fungi	0.900	0.005
320	Fall	Willow_forest	Fungi	0.866	0.005
402	Fall	Willow_forest	Fungi	0.866	0.005
588	Fall	Willow_forest	Fungi	0.866	0.010
611	Fall	Willow_forest	Fungi	0.866	0.005
389	Fall	Willow_forest	Fungi	0.784	0.005
584	Fall	Willow_forest	Fungi	0.776	0.005
405	Fall	Willow_forest	Fungi	0.759	0.005
485	Fall	Willow_forest	Fungi	0.758	0.005
482	Fall	Willow_forest	Fungi	0.757	0.005
562	Fall	Willow_forest	Fungi	0.755	0.010
609	Fall	Willow_forest	Fungi	0.750	0.010
366	Fall	Willow_forest	Fungi	0.743	0.020
491	Fall	Willow_forest	Fungi	0.737	0.035
420	Fall	Willow_forest	Fungi	0.707	0.020
487	Fall	Willow_forest	Fungi	0.688	0.025
355	Fall	Willow_forest	Fungi	0.687	0.005
426	Fall	Willow_forest	Fungi	0.680	0.030
346	Fall	Willow_forest	Fungi	0.680	0.010
332	Fall	Willow_forest	Fungi	0.678	0.015
334	Fall	Willow_forest	Fungi	0.675	0.045

387	Fall	Willow_forest	Fungi	0.632	0.030
179	Fall	Willow_forest	Others	0.774	0.005
223	Fall	Willow_forest	Others	0.683	0.025
848	Fall	Willow_forest	Others	0.682	0.020
92	Fall	Willow_forest	Others	0.645	0.015
89	Fall	Willow_forest	Others	0.645	0.005
461	Fall	Pasture	Cercozoa	0.857	0.005
815	Fall	Pasture	Cercozoa	0.810	0.010
296	Fall	Pasture	Cercozoa	0.784	0.005
780	Fall	Pasture	Cercozoa	0.766	0.005
788	Fall	Pasture	Cercozoa	0.761	0.015
458	Fall	Pasture	Cercozoa	0.758	0.020
291	Fall	Pasture	Cercozoa	0.753	0.010
817	Fall	Pasture	Cercozoa	0.750	0.015
781	Fall	Pasture	Cercozoa	0.739	0.025
790	Fall	Pasture	Cercozoa	0.738	0.025
616	Fall	Pasture	Cercozoa	0.691	0.045
447	Fall	Pasture	Cercozoa	0.676	0.010
451	Fall	Pasture	Cercozoa	0.667	0.035
450	Fall	Pasture	Cercozoa	0.646	0.020
627	Fall	Pasture	Cercozoa	0.621	0.045
428	Fall	Pasture	Cercozoa	0.619	0.040
473	Fall	Pasture	Cercozoa	0.608	0.035
615	Fall	Pasture	Cercozoa	0.555	0.045
303	Fall	Pasture	Cercozoa	0.462	0.010
453	Fall	Pasture	Cercozoa	0.442	0.005
75	Fall	Pasture	Chrysophycaea	0.831	0.005

69	Fall	Pasture	Chrysophycaea	0.795	0.005
174	Fall	Pasture	Chrysophycaea	0.782	0.015
70	Fall	Pasture	Chrysophycaea	0.776	0.015
79	Fall	Pasture	Chrysophycaea	0.713	0.015
72	Fall	Pasture	Chrysophycaea	0.594	0.025
80	Fall	Pasture	Chrysophycaea	0.537	0.005
87	Fall	Pasture	Chrysophycaea	0.520	0.035
748	Fall	Pasture	Ciliophora	0.866	0.005
755	Fall	Pasture	Ciliophora	0.818	0.005
771	Fall	Pasture	Ciliophora	0.771	0.015
713	Fall	Pasture	Ciliophora	0.755	0.015
756	Fall	Pasture	Ciliophora	0.753	0.015
718	Fall	Pasture	Ciliophora	0.722	0.005
749	Fall	Pasture	Ciliophora	0.710	0.030
854	Fall	Pasture	Ciliophora	0.707	0.035
760	Fall	Pasture	Ciliophora	0.681	0.015
762	Fall	Pasture	Ciliophora	0.644	0.005
122	Fall	Pasture	Diatomea	0.866	0.005
158	Fall	Pasture	Diatomea	0.866	0.005
116	Fall	Pasture	Diatomea	0.785	0.005
99	Fall	Pasture	Diatomea	0.781	0.005
155	Fall	Pasture	Diatomea	0.761	0.005
103	Fall	Pasture	Diatomea	0.756	0.005
63	Fall	Pasture	Diatomea	0.754	0.025
142	Fall	Pasture	Diatomea	0.754	0.015
149	Fall	Pasture	Diatomea	0.745	0.020
118	Fall	Pasture	Diatomea	0.744	0.005

104	Fall	Pasture	Diatomea	0.739	0.015
135	Fall	Pasture	Diatomea	0.679	0.020
120	Fall	Pasture	Diatomea	0.676	0.005
107	Fall	Pasture	Diatomea	0.675	0.010
128	Fall	Pasture	Diatomea	0.671	0.010
152	Fall	Pasture	Diatomea	0.660	0.015
242	Fall	Pasture	Diatomea	0.647	0.030
123	Fall	Pasture	Diatomea	0.612	0.005
112	Fall	Pasture	Diatomea	0.565	0.010
136	Fall	Pasture	Diatomea	0.559	0.045
108	Fall	Pasture	Diatomea	0.548	0.030
102	Fall	Pasture	Diatomea	0.542	0.015
160	Fall	Pasture	Diatomea	0.508	0.010
144	Fall	Pasture	Diatomea	0.492	0.040
19	Fall	Pasture	Fungi	1.000	0.005
874	Fall	Pasture	Fungi	0.908	0.005
283	Fall	Pasture	Fungi	0.906	0.005
385	Fall	Pasture	Fungi	0.892	0.005
400	Fall	Pasture	Fungi	0.882	0.005
308	Fall	Pasture	Fungi	0.866	0.005
424	Fall	Pasture	Fungi	0.866	0.005
580	Fall	Pasture	Fungi	0.866	0.015
653	Fall	Pasture	Fungi	0.866	0.005
885	Fall	Pasture	Fungi	0.866	0.005
668	Fall	Pasture	Fungi	0.836	0.010
511	Fall	Pasture	Fungi	0.825	0.005
318	Fall	Pasture	Fungi	0.807	0.015

311	Fall	Pasture	Fungi	0.807	0.005
871	Fall	Pasture	Fungi	0.789	0.005
351	Fall	Pasture	Fungi	0.781	0.010
316	Fall	Pasture	Fungi	0.779	0.005
547	Fall	Pasture	Fungi	0.775	0.005
386	Fall	Pasture	Fungi	0.775	0.005
25	Fall	Pasture	Fungi	0.771	0.005
378	Fall	Pasture	Fungi	0.771	0.005
663	Fall	Pasture	Fungi	0.770	0.005
652	Fall	Pasture	Fungi	0.768	0.005
550	Fall	Pasture	Fungi	0.765	0.005
658	Fall	Pasture	Fungi	0.760	0.005
501	Fall	Pasture	Fungi	0.757	0.015
506	Fall	Pasture	Fungi	0.757	0.005
646	Fall	Pasture	Fungi	0.752	0.025
857	Fall	Pasture	Fungi	0.748	0.015
347	Fall	Pasture	Fungi	0.747	0.010
20	Fall	Pasture	Fungi	0.746	0.030
319	Fall	Pasture	Fungi	0.741	0.005
336	Fall	Pasture	Fungi	0.738	0.020
892	Fall	Pasture	Fungi	0.736	0.040
393	Fall	Pasture	Fungi	0.736	0.025
860	Fall	Pasture	Fungi	0.726	0.005
573	Fall	Pasture	Fungi	0.721	0.035
388	Fall	Pasture	Fungi	0.720	0.030
528	Fall	Pasture	Fungi	0.717	0.005
865	Fall	Pasture	Fungi	0.709	0.005

518	Fall	Pasture	Fungi	0.705	0.005
384	Fall	Pasture	Fungi	0.704	0.005
415	Fall	Pasture	Fungi	0.696	0.005
348	Fall	Pasture	Fungi	0.694	0.025
930	Fall	Pasture	Fungi	0.673	0.035
18	Fall	Pasture	Fungi	0.669	0.005
287	Fall	Pasture	Fungi	0.650	0.030
24	Fall	Pasture	Fungi	0.649	0.010
665	Fall	Pasture	Fungi	0.648	0.015
354	Fall	Pasture	Fungi	0.629	0.030
306	Fall	Pasture	Fungi	0.605	0.030
499	Fall	Pasture	Fungi	0.604	0.010
531	Fall	Pasture	Fungi	0.590	0.005
399	Fall	Pasture	Fungi	0.585	0.030
894	Fall	Pasture	Fungi	0.573	0.005
527	Fall	Pasture	Fungi	0.553	0.035
326	Fall	Pasture	Fungi	0.547	0.035
9	Fall	Pasture	Fungi	0.541	0.040
859	Fall	Pasture	Fungi	0.534	0.010
395	Fall	Pasture	Fungi	0.532	0.015
342	Fall	Pasture	Fungi	0.531	0.010
407	Fall	Pasture	Fungi	0.518	0.005
879	Fall	Pasture	Fungi	0.517	0.035
218	Fall	Pasture	Others	0.903	0.005
742	Fall	Pasture	Others	0.899	0.005
733	Fall	Pasture	Others	0.892	0.005
196	Fall	Pasture	Others	0.866	0.005

217	Fall	Pasture	Others	0.866	0.005
736	Fall	Pasture	Others	0.866	0.015
36	Fall	Pasture	Others	0.849	0.005
684	Fall	Pasture	Others	0.845	0.005
255	Fall	Pasture	Others	0.821	0.005
265	Fall	Pasture	Others	0.780	0.005
841	Fall	Pasture	Others	0.775	0.015
729	Fall	Pasture	Others	0.765	0.005
696	Fall	Pasture	Others	0.763	0.015
195	Fall	Pasture	Others	0.762	0.015
225	Fall	Pasture	Others	0.760	0.015
213	Fall	Pasture	Others	0.752	0.015
918	Fall	Pasture	Others	0.747	0.015
236	Fall	Pasture	Others	0.743	0.005
846	Fall	Pasture	Others	0.734	0.015
183	Fall	Pasture	Others	0.733	0.035
849	Fall	Pasture	Others	0.732	0.020
732	Fall	Pasture	Others	0.723	0.005
688	Fall	Pasture	Others	0.721	0.015
681	Fall	Pasture	Others	0.711	0.035
679	Fall	Pasture	Others	0.711	0.020
914	Fall	Pasture	Others	0.706	0.030
220	Fall	Pasture	Others	0.694	0.020
683	Fall	Pasture	Others	0.685	0.035
735	Fall	Pasture	Others	0.685	0.010
198	Fall	Pasture	Others	0.685	0.015
184	Fall	Pasture	Others	0.681	0.015

723	Fall	Pasture	Others	0.671	0.040
226	Fall	Pasture	Others	0.666	0.005
739	Fall	Pasture	Others	0.664	0.035
219	Fall	Pasture	Others	0.655	0.010
94	Fall	Pasture	Others	0.636	0.020
201	Fall	Pasture	Others	0.622	0.035
721	Fall	Pasture	Others	0.590	0.040
56	Fall	Pasture	Peronosporomycetes	1.000	0.005
50	Fall	Pasture	Peronosporomycetes	0.866	0.005
51	Fall	Pasture	Peronosporomycetes	0.866	0.005
41	Fall	Pasture	Peronosporomycetes	0.749	0.025
38	Fall	Pasture	Peronosporomycetes	0.734	0.005
52	Fall	Pasture	Peronosporomycetes	0.732	0.020
60	Fall	Pasture	Peronosporomycetes	0.713	0.005
59	Fall	Pasture	Peronosporomycetes	0.691	0.005
54	Fall	Pasture	Peronosporomycetes	0.686	0.005
53	Fall	Pasture	Peronosporomycetes	0.566	0.035
444	Winter	Gravel	Cercozoa	1.000	0.005
697	Winter	Gravel	Cercozoa	0.866	0.020
700	Winter	Gravel	Cercozoa	0.866	0.010
806	Winter	Gravel	Cercozoa	0.866	0.010
452	Winter	Gravel	Cercozoa	0.767	0.010
449	Winter	Gravel	Cercozoa	0.740	0.020
829	Winter	Gravel	Cercozoa	0.734	0.005
600	Winter	Gravel	Cercozoa	0.709	0.015
436	Winter	Gravel	Cercozoa	0.692	0.020
816	Winter	Gravel	Cercozoa	0.683	0.040

712	Winter	Gravel	Cercozoa	0.676	0.045
703	Winter	Gravel	Cercozoa	0.644	0.025
792	Winter	Gravel	Cercozoa	0.621	0.020
808	Winter	Gravel	Cercozoa	0.569	0.045
71	Winter	Gravel	Chrysophycaea	0.773	0.015
81	Winter	Gravel	Chrysophycaea	0.733	0.040
747	Winter	Gravel	Ciliophora	0.866	0.020
34	Winter	Gravel	Diatomea	0.866	0.020
110	Winter	Gravel	Diatomea	0.866	0.020
115	Winter	Gravel	Diatomea	0.866	0.020
126	Winter	Gravel	Diatomea	0.866	0.020
133	Winter	Gravel	Diatomea	0.866	0.015
148	Winter	Gravel	Diatomea	0.866	0.015
151	Winter	Gravel	Diatomea	0.866	0.010
241	Winter	Gravel	Diatomea	0.828	0.005
147	Winter	Gravel	Diatomea	0.821	0.005
146	Winter	Gravel	Diatomea	0.812	0.025
134	Winter	Gravel	Diatomea	0.752	0.010
156	Winter	Gravel	Diatomea	0.728	0.025
137	Winter	Gravel	Diatomea	0.724	0.020
153	Winter	Gravel	Diatomea	0.697	0.020
127	Winter	Gravel	Diatomea	0.693	0.015
138	Winter	Gravel	Diatomea	0.689	0.040
246	Winter	Gravel	Diatomea	0.685	0.010
169	Winter	Gravel	Diatomea	0.680	0.015
161	Winter	Gravel	Diatomea	0.663	0.015
125	Winter	Gravel	Diatomea	0.659	0.005

117	Winter	Gravel	Diatomea	0.655	0.025
98	Winter	Gravel	Diatomea	0.654	0.020
114	Winter	Gravel	Diatomea	0.636	0.005
106	Winter	Gravel	Diatomea	0.632	0.040
244	Winter	Gravel	Diatomea	0.628	0.020
1	Winter	Gravel	Diatomea	0.625	0.020
247	Winter	Gravel	Diatomea	0.623	0.025
157	Winter	Gravel	Diatomea	0.617	0.005
96	Winter	Gravel	Diatomea	0.604	0.030
100	Winter	Gravel	Diatomea	0.597	0.030
243	Winter	Gravel	Diatomea	0.592	0.020
166	Winter	Gravel	Diatomea	0.588	0.005
171	Winter	Gravel	Diatomea	0.570	0.020
119	Winter	Gravel	Diatomea	0.564	0.035
109	Winter	Gravel	Diatomea	0.528	0.035
64	Winter	Gravel	Diatomea	0.500	0.005
159	Winter	Gravel	Diatomea	0.496	0.030
145	Winter	Gravel	Diatomea	0.488	0.035
67	Winter	Gravel	Diatomea	0.471	0.005
132	Winter	Gravel	Diatomea	0.471	0.005
248	Winter	Gravel	Diatomea	0.465	0.020
659	Winter	Gravel	Fungi	1.000	0.005
884	Winter	Gravel	Fungi	1.000	0.005
380	Winter	Gravel	Fungi	0.894	0.005
876	Winter	Gravel	Fungi	0.879	0.005
666	Winter	Gravel	Fungi	0.877	0.005
284	Winter	Gravel	Fungi	0.868	0.005

15	Winter	Gravel	Fungi	0.866	0.020
16	Winter	Gravel	Fungi	0.866	0.015
21	Winter	Gravel	Fungi	0.866	0.015
23	Winter	Gravel	Fungi	0.866	0.020
309	Winter	Gravel	Fungi	0.866	0.020
337	Winter	Gravel	Fungi	0.866	0.015
411	Winter	Gravel	Fungi	0.866	0.020
667	Winter	Gravel	Fungi	0.866	0.020
856	Winter	Gravel	Fungi	0.866	0.020
863	Winter	Gravel	Fungi	0.866	0.020
285	Winter	Gravel	Fungi	0.779	0.005
664	Winter	Gravel	Fungi	0.777	0.015
648	Winter	Gravel	Fungi	0.775	0.010
13	Winter	Gravel	Fungi	0.773	0.020
502	Winter	Gravel	Fungi	0.764	0.020
537	Winter	Gravel	Fungi	0.762	0.020
29	Winter	Gravel	Fungi	0.762	0.020
524	Winter	Gravel	Fungi	0.760	0.020
345	Winter	Gravel	Fungi	0.759	0.010
549	Winter	Gravel	Fungi	0.755	0.035
27	Winter	Gravel	Fungi	0.748	0.035
372	Winter	Gravel	Fungi	0.746	0.005
322	Winter	Gravel	Fungi	0.740	0.035
882	Winter	Gravel	Fungi	0.737	0.010
602	Winter	Gravel	Fungi	0.733	0.040
656	Winter	Gravel	Fungi	0.733	0.025
651	Winter	Gravel	Fungi	0.721	0.015

406	Winter	Gravel	Fungi	0.715	0.035
314	Winter	Gravel	Fungi	0.712	0.040
377	Winter	Gravel	Fungi	0.706	0.015
545	Winter	Gravel	Fungi	0.706	0.025
522	Winter	Gravel	Fungi	0.700	0.005
383	Winter	Gravel	Fungi	0.693	0.035
327	Winter	Gravel	Fungi	0.692	0.010
565	Winter	Gravel	Fungi	0.689	0.025
17	Winter	Gravel	Fungi	0.688	0.005
375	Winter	Gravel	Fungi	0.684	0.025
861	Winter	Gravel	Fungi	0.683	0.035
896	Winter	Gravel	Fungi	0.683	0.035
339	Winter	Gravel	Fungi	0.674	0.035
889	Winter	Gravel	Fungi	0.664	0.015
898	Winter	Gravel	Fungi	0.656	0.040
414	Winter	Gravel	Fungi	0.656	0.015
536	Winter	Gravel	Fungi	0.653	0.030
288	Winter	Gravel	Fungi	0.645	0.030
498	Winter	Gravel	Fungi	0.634	0.005
368	Winter	Gravel	Fungi	0.630	0.035
529	Winter	Gravel	Fungi	0.613	0.010
408	Winter	Gravel	Fungi	0.603	0.025
10	Winter	Gravel	Fungi	0.584	0.005
394	Winter	Gravel	Fungi	0.573	0.005
880	Winter	Gravel	Fungi	0.567	0.005
530	Winter	Gravel	Fungi	0.551	0.030
895	Winter	Gravel	Fungi	0.543	0.020

344	Winter	Gravel	Fungi	0.533	0.005
2	Winter	Gravel	Fungi	0.530	0.025
197	Winter	Gravel	Others	1.000	0.005
734	Winter	Gravel	Others	1.000	0.005
722	Winter	Gravel	Others	0.968	0.005
180	Winter	Gravel	Others	0.866	0.015
185	Winter	Gravel	Others	0.866	0.020
202	Winter	Gravel	Others	0.866	0.020
212	Winter	Gravel	Others	0.866	0.020
253	Winter	Gravel	Others	0.866	0.020
915	Winter	Gravel	Others	0.866	0.020
923	Winter	Gravel	Others	0.866	0.010
740	Winter	Gravel	Others	0.782	0.005
178	Winter	Gravel	Others	0.782	0.020
200	Winter	Gravel	Others	0.780	0.005
95	Winter	Gravel	Others	0.769	0.005
682	Winter	Gravel	Others	0.767	0.045
693	Winter	Gravel	Others	0.756	0.020
182	Winter	Gravel	Others	0.751	0.035
254	Winter	Gravel	Others	0.745	0.025
695	Winter	Gravel	Others	0.744	0.045
269	Winter	Gravel	Others	0.735	0.030
211	Winter	Gravel	Others	0.730	0.015
360	Winter	Gravel	Others	0.722	0.010
727	Winter	Gravel	Others	0.706	0.045
744	Winter	Gravel	Others	0.689	0.035
187	Winter	Gravel	Others	0.685	0.010

263	Winter	Gravel	Others	0.675	0.035
678	Winter	Gravel	Others	0.616	0.045
257	Winter	Gravel	Others	0.577	0.010
819	Winter	Grass	Cercozoa	0.749	0.025
435	Winter	Grass	Cercozoa	0.749	0.025
579	Winter	Grass	Cercozoa	0.728	0.040
480	Winter	Grass	Cercozoa	0.720	0.020
805	Winter	Grass	Cercozoa	0.686	0.020
824	Winter	Grass	Cercozoa	0.681	0.025
820	Winter	Grass	Cercozoa	0.639	0.010
634	Winter	Grass	Cercozoa	0.637	0.035
836	Winter	Grass	Cercozoa	0.537	0.025
77	Winter	Grass	Chrysophycaea	0.866	0.005
85	Winter	Grass	Chrysophycaea	0.747	0.010
86	Winter	Grass	Chrysophycaea	0.639	0.040
173	Winter	Grass	Chrysophycaea	0.572	0.045
673	Winter	Grass	Ciliophora	0.771	0.015
767	Winter	Grass	Ciliophora	0.750	0.020
675	Winter	Grass	Ciliophora	0.750	0.020
105	Winter	Grass	Diatomea	0.675	0.030
490	Winter	Grass	Fungi	0.866	0.010
510	Winter	Grass	Fungi	0.783	0.005
503	Winter	Grass	Fungi	0.764	0.010
410	Winter	Grass	Fungi	0.750	0.015
330	Winter	Grass	Fungi	0.743	0.030
589	Winter	Grass	Fungi	0.704	0.010
555	Winter	Grass	Fungi	0.694	0.010

279	Winter	Grass	Fungi	0.684	0.025
566	Winter	Grass	Fungi	0.657	0.035
497	Winter	Grass	Fungi	0.605	0.015
331	Winter	Grass	Fungi	0.592	0.030
804	Winter	Grass	Fungi	0.583	0.005
73	Winter	Grass	Others	0.866	0.005
215	Winter	Grass	Others	0.866	0.010
214	Winter	Grass	Others	0.764	0.010
900	Winter	Grass	Others	0.762	0.005
731	Winter	Grass	Others	0.735	0.035
188	Winter	Grass	Others	0.696	0.010
927	Winter	Grass	Others	0.624	0.010
224	Winter	Grass	Others	0.596	0.020
801	Winter	Willow_bush	Cercozoa	0.692	0.040
294	Winter	Willow_bush	Cercozoa	0.598	0.045
439	Winter	Willow_bush	Cercozoa	0.596	0.035
474	Winter	Willow_bush	Cercozoa	0.515	0.040
746	Winter	Willow_bush	Ciliophora	0.684	0.040
281	Winter	Willow_bush	Fungi	0.866	0.030
275	Winter	Willow_bush	Fungi	0.741	0.035
559	Winter	Willow_bush	Fungi	0.498	0.020
192	Winter	Willow_bush	Others	0.482	0.035
903	Winter	Willow_bush	Others	0.455	0.010
931	Winter	Willow_bush	Peronosporomycetes	0.636	0.030
49	Winter	Willow_bush	Peronosporomycetes	0.600	0.045
750	Winter	Mixed_forest	Ciliophora	0.591	0.045
168	Winter	Mixed_forest	Diatomea	0.685	0.025

495	Winter	Mixed_forest	Fungi	0.738	0.015
455	Winter	Willow_forest	Cercozoa	0.866	0.030
606	Winter	Willow_forest	Fungi	0.866	0.030
507	Winter	Willow_forest	Fungi	0.850	0.005
421	Winter	Willow_forest	Fungi	0.722	0.035
358	Winter	Willow_forest	Fungi	0.659	0.005
772	Winter	Pasture	Cercozoa	0.774	0.020
813	Winter	Pasture	Cercozoa	0.773	0.020
466	Winter	Pasture	Cercozoa	0.747	0.040
833	Winter	Pasture	Cercozoa	0.635	0.020
814	Winter	Pasture	Cercozoa	0.611	0.035
83	Winter	Pasture	Chrysophycaea	0.734	0.005
759	Winter	Pasture	Ciliophora	0.757	0.045
391	Winter	Pasture	Fungi	0.693	0.045
691	Winter	Pasture	Others	0.734	0.040
626	Winter	Pasture	Others	0.607	0.040
45	Winter	Pasture	Peronosporomycetes	1.000	0.005
40	Winter	Pasture	Peronosporomycetes	0.866	0.025

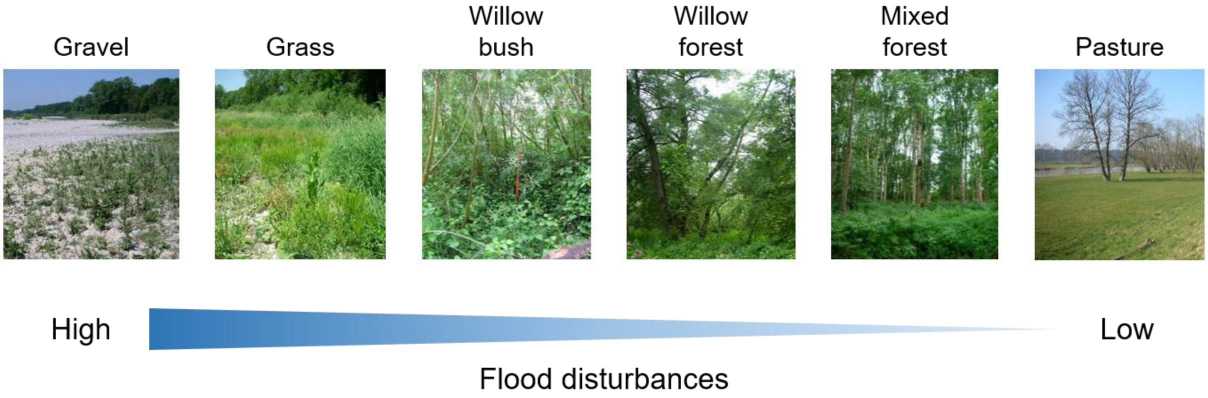


Fig. S1. Illustration of the selected habitats in a Swiss lowland floodplain (River Thur). Habitats are sorted from left to right along a gradient of decreasing flood disturbance.

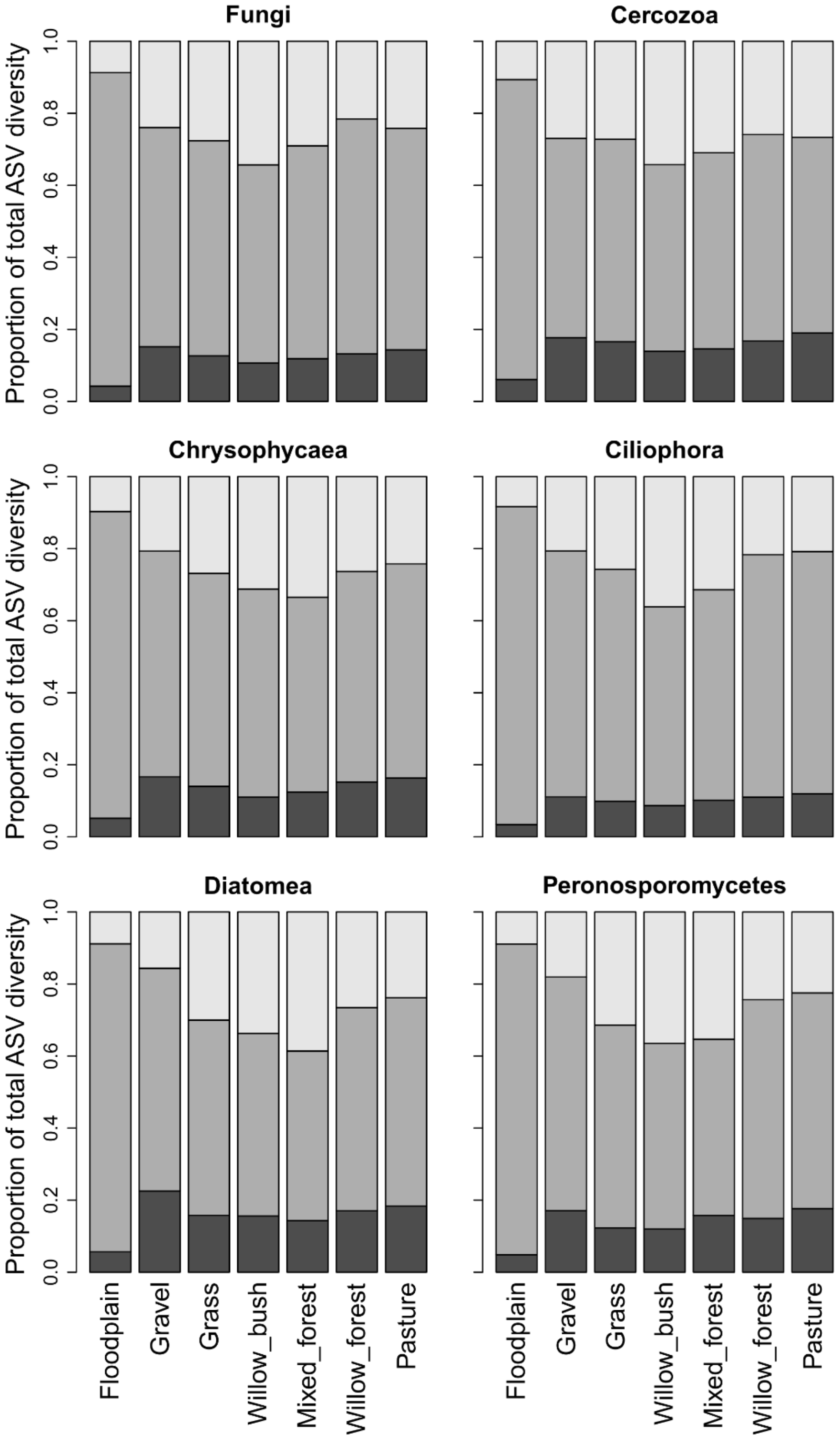


Fig. S2. Spatiotemporal turnover of soil microbial eukaryote taxa (ASV - amplicon sequence variants) in a Swiss lowland floodplain. Partitioning of total diversity (γ) into local diversity (α), temporal species turnover (β_T), and spatial species turnover (β_S) per habitat ($\gamma = \alpha + \beta_T + \beta_S$) and per taxonomic group. This analysis shows a higher spatial than temporal turnover of all groups of soil microbial eukaryotic taxa both at the floodplain scale and within habitats.

Figure 1

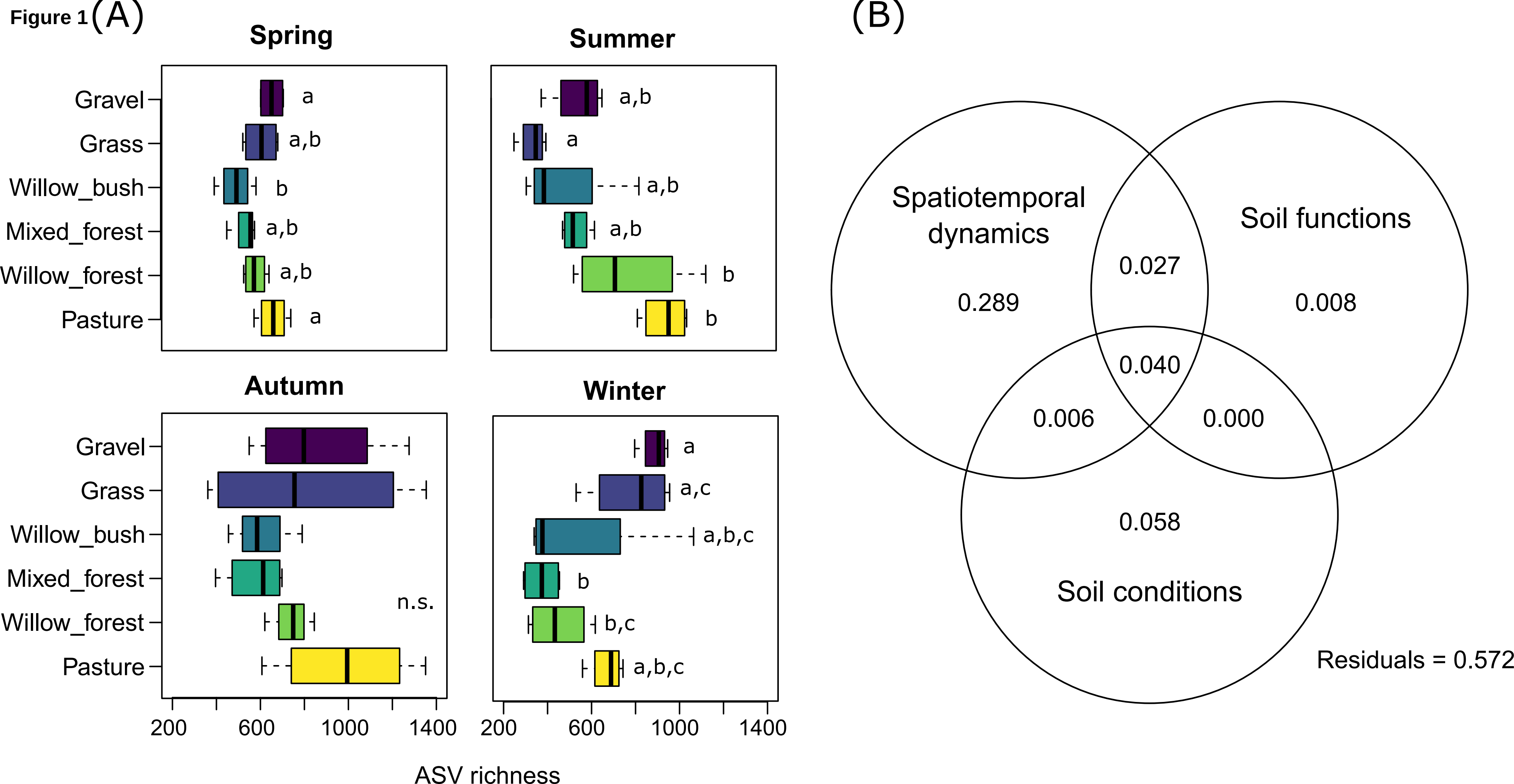

(A)
Spring
Summer
Autumn
Winter
Gravel
Grass
Willow_bush
Mixed_forest
Willow_forest
Pasture
a
a,b
b
a,b
a,b
a
a,b
a
a,b
a,b
b
b
n.s.
a
a,c
a,b,c
b
b,c
a,b,c
200
600
1000
1400
ASV richness
(B)
Spatiotemporal dynamics
Soil functions
Soil conditions
0.289
0.027
0.008
0.040
0.006
0.000
0.058
Residuals = 0.572

Figure 2

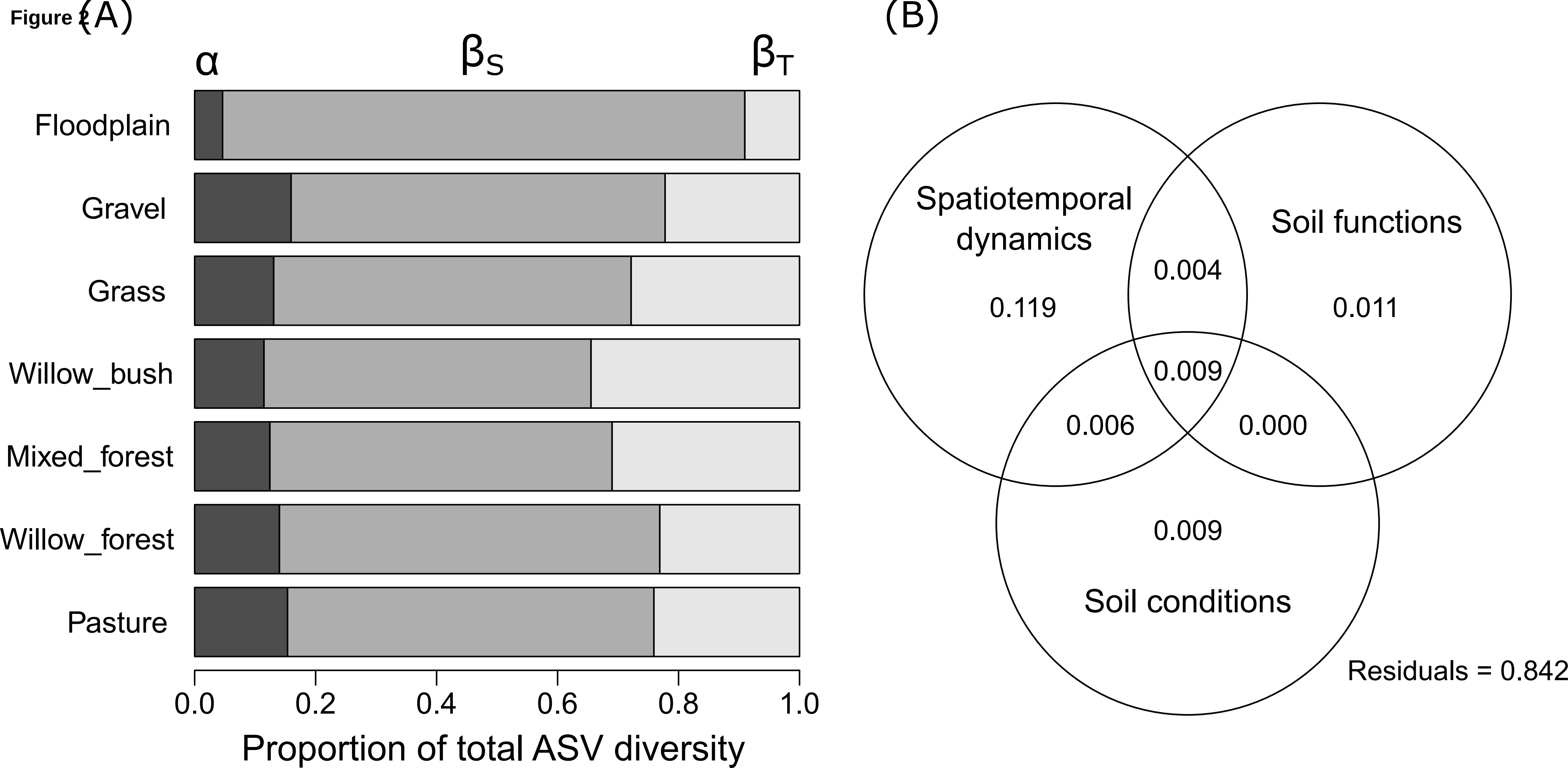
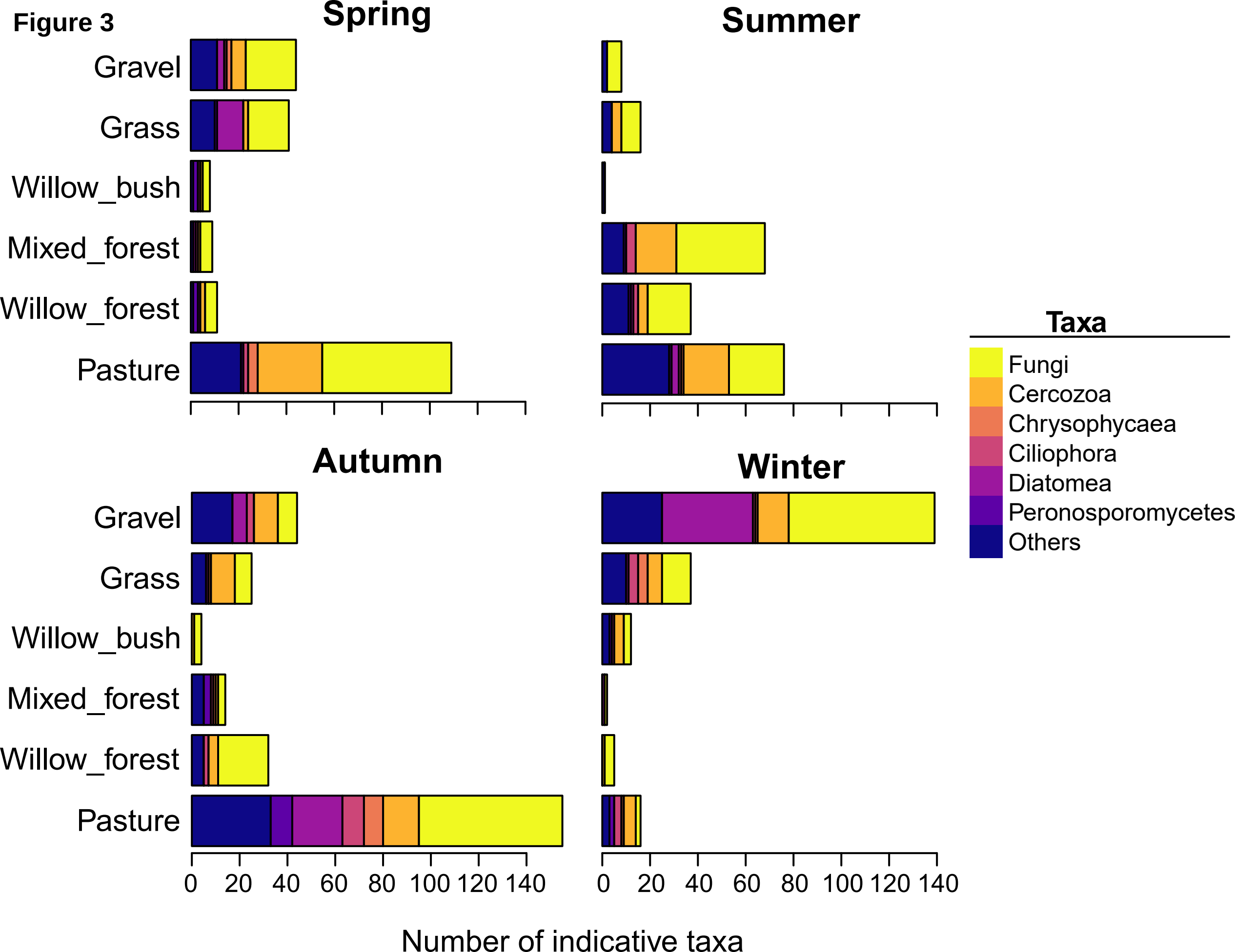

(A)
α
β_S
β_T
Floodplain
Gravel
Grass
Willow_bush
Mixed_forest
Willow_forest
Pasture
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of total ASV diversity
(B)
Spatiotemporal dynamics
Soil functions
Soil conditions
0.119
0.004
0.011
0.009
0.006
0.000
0.009
Residuals = 0.842

Figure 3



Spring
Summer
Autumn
Winter
Gravel
Grass
Willow_bush
Mixed_forest
Willow_forest
Pasture
Taxa
Fungi
Cercozoa
Chrysophycaea
Ciliophora
Diatomea
Peronosporomycetes
Others
0
20
40
60
80
100
120
140
Number of indicative taxa