



# *Microbial communities in local and transplanted soils along a latitudinal gradient*

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1 **Microbial communities in local and transplanted soils along a latitudinal gradient**

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23 **ABSTRACT**

24 Factors shaping community structure of soil microbiota have been intensively studied;  
25 however, the pattern in community composition and structure of soil microbiota at large  
26 geographical scales and factors regulating its metabolic activity remains poorly understood.  
27 Here, we used a field transplantation experiments to investigate the effects of substrate and  
28 climatic conditions on basal soil respiration, microbial biomass C and diversity of soil  
29 microbiota by comparing local and transplanted soils along a latitudinal gradient. Soil samples  
30 collected in April 2008 at donor site (Sokolov, Czech Republic) in Central Europe were gamma-  
31 ray sterilized and transplanted to receptor sites in Europe and the USA in May and early June  
32 2008. Soil samples were taken in June 2009 after one year of exposure and immediately  
33 prepared for laboratory analysis. Basal soil respiration in local soils increased from 22 to 42 mg  
34 CO<sub>2</sub>-C kg<sup>-1</sup> h<sup>-1</sup> with latitude while basal soil respiration in transplanted soils decreased with  
35 latitude from 32 to 19 mg CO<sub>2</sub>-C kg<sup>-1</sup> h<sup>-1</sup>. The microbial biomass C in both transplanted and  
36 local soils decreased with latitude. Content of fungal and bacterial phospholipid fatty acids  
37 increased nearly twice with latitude in local soils. Shannon diversity index of fungal community  
38 decreased from 2.5 to 1.2 along the latitudinal gradient in transplanted soils while local soils  
39 increased from 0.9 to 2.4 with latitude. Based on our results, microbial activity is driven mainly  
40 by changes of the soil substrate along latitudinal and climatic gradients while microbial biomass  
41 is driven more by global climatic factors itself. The diversity of soil microbial communities is  
42 mostly affected by latitudinal and climatic factors while community structure is mostly shaped  
43 by substrate quality.

44 **Keywords:** Soil microbiota; PLFA; microbial biomass C; microbial diversity; climatic  
45 gradient; DNA sequencing

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## 48 **1. Introduction**

49 Soil microbiota (bacteria and fungi) play crucial roles in nutrient cycling (Fierer, 2017), the  
50 maintenance of soil fertility (Ramirez et al., 2010) and soil carbon sequestration (Trivedi et al.,  
51 2013). In addition, soil bacteria and fungi have both direct and indirect effects on the health of  
52 plants and animals in terrestrial ecosystems (Bardgett and van der Putten, 2014; Xu et al., 2015).  
53 Therefore, it is not surprising that the investigation of factors shaping soil microbial  
54 communities has become the Holy Grail in recent microbial ecology (Bardgett and van der  
55 Putten, 2014; Fierer, 2017).

56         Recent progress of instrumental analytical methods such as analysis of phospholipid  
57 fatty acids (PLFA) (Oravecz et al., 2004) or advanced molecular methods such as sequencing  
58 of environmental DNA (Caporaso et al., 2011) allow us more detailed insight into composition  
59 and structure of soil microbiota. For example, content of phospholipid fatty acid provides  
60 reliable information about relative abundance of living organisms (Oravecz et al., 2004) while  
61 DNA methods provide information about total diversity of soil microbiota at finer taxonomic  
62 levels (Caporaso et al., 2011). Synthesis of modern analytical methods such as PLFA or DNA  
63 sequencing with standard laboratory techniques, for example basal soil respiration or microbial  
64 biomass C provide us detailed view on functioning and diversity of soil microbial communities.

65         Recognized major drivers of microbial communities are temperature (Zhou et al.,  
66 2016), precipitation (de Vries et al., 2013; Evans and Wallenstein, 2014) and also various  
67 characteristics of the soil substrate (Birkhofer et al., 2012; Häkkinen et al., 2010; Rousk et al.,  
68 2010; Selonen and Setälä, 2015). For example, Lauber et al. (2009) showed pH as a main  
69 predictor of the relative abundance of soil bacterial communities across various biomes. In  
70 contrast, study of Zhou et al. (2016) showed temperature as a main driver of microbial diversity  
71 in soil ecosystem at larger geographical scale. In addition, study of Fierer, (2017) indicate soil

72 organic carbon as a key factor shaping diversity and structure of soil microbial communities  
73 worldwide.

74         Although the effect of soil physical and chemical soil properties shaping soil microbial  
75 communities at local scales is well known, it is often unclear how the composition and activity  
76 of microbial communities correlate with these key ecological factors (pH, moisture,  
77 temperature) along latitudinal gradient. The traditional concept in microbial ecology postulates  
78 that “everything is everywhere, but the environment selects” (Barberán et al., 2014a; de Wit  
79 and Bouvier, 2006). This principle is a useful basis for the study of biogeography and the  
80 structures of natural communities (Dequiedt et al., 2011).

81         Recent findings suggest that the composition and structure of microbial communities  
82 are shaped by factors related to operating at large scales, such as climate (Delgado-Baquerizo  
83 et al., 2017; Dequiedt et al., 2011) and/or to local edaphic characteristics such as soil pH  
84 (Birkhofer et al., 2012; Rousk et al., 2010, 2009) or litter quality (Prober et al., 2015; Wardle  
85 et al., 2004). However, datasets comparing effect of local (e.g. soil pH) and global factors (e.g.  
86 temperature, precipitation) affecting soil microbiota along large geographical gradients as well  
87 as effect of these factors on metabolic activity of soil microbiota (e.g. basal soil respiration)  
88 remains underestimated (Lazzaro et al., 2011; Rui et al., 2015; Sun et al., 2014; Vanhala et al.,  
89 2011).

90         To address this question, we established field transplantation experiment to explore the  
91 role of local soil condition (pH) and global factors (precipitation, temperature) on the biomass  
92 (microbial biomass C), structure (based on DNA and PLFA) and activity (basal soil respiration)  
93 of soil microbial communities. We transplanted sterilized soil from Central Europe (Czech  
94 Republic) along a latitudinal gradient in Europe (Finland, United Kingdom, Czech Republic  
95 and Greece) and North America (Illinois, USA). We hypothesize that if soil microbiota in

96 transplanted soil is more similar to the local soils at donor site, then local soil factors are the  
97 primary determinants of microbial communities; by contrast, if the transplanted soil is more  
98 similar to the local soil at receptor site, then large-scale drivers (temperature, precipitation) are  
99 the most important.

## 100 **2. Material and methods**

### 101 **2.1. Sampling sites**

102 The soil used in this experiment was obtained from the forefield of an open-cast mine Jiří near  
103 the town of Sokolov in the Czech Republic. The entire area of the Jiří mine forefield was  
104 formerly part of an agricultural landscape. This agricultural landscape was abandoned 30-40  
105 years ago. At present, this area is covered by a mixture of grasslands and open woodlands  
106 dominated by birch (*Betula pendula*) and aspen (*Populus tremula*) on loamy cambisol soils  
107 (Holec and Frouz, 2005; Lukešová, 1993). The soil was sampled from grassland accompanied  
108 by *P. tremula* and *B. pendula* in April 2008 using a soil corer (6 cm in diameter). Soil was taken  
109 to the depth of 10 cm after the removal of vegetation from 10 sampling sites. Samples were  
110 pooled into one composite sample weighing about 20 kg. The soil was sieved through a 2 mm  
111 mesh to remove roots, branches and other visible plant remains and soil animals. The soil was  
112 homogenized and packed in 0.5 kg portions in Ziploc bags and then sterilized with a 40-kGy  
113 dose of gamma radiation (Frouz et al., 2016). The efficiency of the sterilization was tested by  
114 inoculating of soil suspension on Malt extract agar media, where no microbes were present after  
115 incubation (Frouz et al., 2016).

### 116 **2.2. Experimental design**

117 The sterilized soil was then transported in sealed bags to six receptor sites (including the  
118 original donor site) located on a south-north gradient across Europe and in the USA (Table 1).  
119 Selection of plant community for our study was critical. In most of the receptor sites considered

120 in our study semi-natural forest and grasslands form most of the landscape (Häkkinen et al.,  
121 2010). There is known that these two types of habitat differ in microbial community biomass  
122 composition and activity (Fierer et al., 2012; Lauber et al., 2009). For that reasons we choose  
123 in each acceptor site habitat that was mixture of grassland and trees or woody vegetation. At  
124 the receptor sites, the soil was placed into sterilized plastic pots (12 cm in diameter; 10 cm high)  
125 during the last week of May and early June 2008. The pots were placed into the soil so that the  
126 rim of the pots was about 3 cm above the soil surface to prevent the soil in the pots being  
127 affected by the vegetation cover. Vegetation cover at each receptor sites has been removed  
128 under the pot and in 5 cm around. Nine pots were placed at each receptor site as well as at the  
129 donor site. The pots were perforated at the bottom to allow water exchange. Three locations  
130 were used at each site. The distance between the pots at one location was approximately 1  
131 meter. A brief description of all the sites is summarized in Table 1. After one year of exposure  
132 (June 2009), all the pots from all receptor and donor sites were collected and the soil in the pots  
133 was gently placed into Ziplock bags. At the same time, local soil was collected from soil surface  
134 layer 0-10 cm about 1 m from the pots as a control. Several pots at sampling locations in the  
135 Czech Republic, USA and Greece were damaged by fire and wild boars, so only undestroyed  
136 pots were taken. The samples were kept at a temperature similar to that at their sampling sites  
137 and shipped back to the laboratory for soil analysis. The local soil samples were sieved through  
138 a 2 mm mesh to remove roots, branches and other visible plant remains and soil animals. All  
139 laboratory analyses of soil properties were done within one week after sample collection.  
140 Transplanted soil samples at various receptor sites did not show any significant differences in  
141 soil pH and texture after one year of exposure. Soil samples for basal soil respiration and  
142 microbial biomass C were stored at 4 °C and soil samples for PLFA and DNA extraction were  
143 freeze dried and stored in a freezer at -80 °C.

### 144 ***2.3. Measurement of basal soil respiration and microbial biomass C***



145 Basal soil respiration was measured using the traditional incubation method. Soil (10 g) was  
146 enclosed in airtight bottles. Each bottle was equipped with a small container with NaOH and  
147 incubated at 20 °C for one week. Carbon dioxide (CO<sub>2</sub>) released from the soil was trapped in 3  
148 ml of 0.5 M NaOH and then quantified by titration with 0.5 M HCl after addition of BaCl<sub>2</sub>  
149 (Jenkinson and Powlson, 1976). The amount of CO<sub>2</sub> was expressed as mg CO<sub>2</sub>-C kg<sup>-1</sup> h<sup>-1</sup>. The  
150 same bottles without soil were used to assess CO<sub>2</sub> trapping during incubation (from air closed  
151 in vials) and during handling. The microbial biomass C was determined by the chloroform  
152 fumigation–extraction method (Vance et al., 1987). Fumigated and non-fumigated soil samples  
153 (5 g) were shaken in glass bottles with 0.5 M K<sub>2</sub>SO<sub>4</sub> solution (40 ml) for 45 min and then C  
154 content in the filtrates was determined by dichromate digestion. The microbial biomass C was  
155 obtained by subtraction of fumigated and non-fumigated samples multiplied by extraction  
156 coefficient. The microbial biomass C was expressed as mg kg<sup>-1</sup> soil.

#### 157 ***2.4. Extraction and analysis of phospholipid fatty acid (PLFA)***

158 Phospholipid fatty acid (PLFA) analysis were extracted by a chloroform-methanol–phosphate  
159 buffer from one gram of freeze-dried soil. LiChrolut Si-60 solid-phase extraction cartridges  
160 (Merck, Whitehouse Station, NJ) were used to separate the phospholipid fraction (Oravecz et  
161 al., 2004) from liquid sample. Phospholipid fractions were subjected to mild alkaline  
162 methanolysis (Frostegard et al., 2011; Oravecz et al., 2004). Gas chromatography-mass  
163 spectrometry (GC-MS) was used for the analysis of free methyl esters of phospholipid fatty  
164 acids (450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA, USA). The GC  
165 instrument was equipped with a split/splitless injector and a DB-5MS column (J&W Scientific,  
166 Folstom, CA, 60 m, 0.25 mm i.d., 0.25 µm film thickness) was used for separation.

167 The temperature program started at 60 °C and was held for 1 min in splitless mode. Then  
168 the splitter was opened and the oven heated to 160 °C at a rate of 25 °C min<sup>-1</sup>. The second  
169 temperature ramp was up to 280 °C at a rate of 2.5 °C min<sup>-1</sup>, this temperature being maintained

170 for 10 min. The solvent delay time was set to 8 min. The transfer line temperature was set to  
171 280 °C. Mass spectra were recorded under electron impact at 70 eV, mass range 50–350 amu.  
172 Methylated fatty acids were identified according to their mass spectra and quantified using their  
173 individual chemical standards obtained from Sigma-Aldrich, Prague, Czech Republic and  
174 Matreya LLC, Pleasant Gap, PA, USA. Fungi (eukaryotic) were quantified based on 18:2 $\omega$ 6,9  
175 content while bacteria were quantified as the sum of i14:0, i15:0, a15:0, i16:0, 16:1 $\omega$ 7,  
176 16:1 $\omega$ 9, 10Me-16:0, i17:0, a17:0, cy17:0, 10Me-17:0, 18:1 $\omega$ 7, 18:1 $\omega$ 9, 10Me-18:0 and cy19:0,  
177 (Šnajdr et al., 2008).

## 178 ***2.5. DNA extraction and 454 sequencing analysis***

179 Genomic DNA was extracted from soil samples using the Fast DNA Spin kit for soil DNA  
180 extraction (MP Biolabs, Solon, OH, USA) according to the manufacturer's instruction and then  
181 amplified by the PCR method (Větrovský and Baldrian, 2013). To amplify the V4–V5  
182 hypervariable regions of the 16S rRNA and ITS1, ITS4 regions of 18S rRNA genes for  
183 pyrosequencing, universal bacterial primers 519F (50-CAGCMGCCGCGGTAATWC-30) and  
184 926R (50 CCGTCAATTCMTTTRAGTT-30) (Caporaso et al., 2011) and fungal ITS1 and ITS4  
185 (Větrovský and Baldrian, 2013) were used in the PCR. The first amplification step used  
186 bacterial 519F and 926R as well as fungal ITS1 and ITS4 specific primers to amplify the  
187 bacterial 16S rRNA gene and the internal transcribed spacer (ITS) region of the fungal 18S  
188 rRNA gene. Each DNA sample was purified using the Wizard SV Gel and PCR Clean-Up  
189 System (Promega, Madison, WI, USA). The purified DNA concentration was determined using  
190 ND1000 (NanoDrop, Wilmington, DE, USA).

191 In the second amplification step, fusion primers were arranged for tag-encoded 454-  
192 Titanium pyrosequencing: Different barcode sequences were added to the 50 end of the forward  
193 primer separated by a trinucleotide spacer. The Titanium A adaptor was also used (Roche,  
194 Basel, Switzerland). The PCR products were purified using the MinElute PCR Purification Kit

195 (Qiagen, Hilden, Germany) and quantified using a NanoDrop 1000 device (NanoDrop) and the  
196 Quant-iT Picogreen dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). Purified amplicons  
197 were used for the subsequent emulsion PCR (emPCR Kit Lib-L, Roche, Basel, Switzerland),  
198 the products of which were sequenced on a GS Junior platform (Roche) in accordance with the  
199 manufacturer's instructions.

200 Bacterial and fungal sequences were processed with the QIIME 1.6.0 software package  
201 (Caporaso et al., 2010). Quality filtering steps were performed to trim off barcodes and primers  
202 from the raw sequences and to remove sequences that were less than 200 nt long, had  
203 homopolymers longer than 6 nt, and that had a quality score greater than 20 nt. Denoising was  
204 performed as described by Reeder et Knight (2010). QIIME's implementation of the OTU  
205 pipeline script (Edgar et al., 2011) was applied for chimera checking and OTU picking.  
206 Microbial BLAST databases of bacterial 16S rRNA as well as the ITS1 and ITS4 regions were  
207 used as reference databases for the detection of bacterial and fungal chimeric sequences.  
208 Resulting chimera-free reads were clustered into OTUs based on their sequence similarity at  
209 97%. Representative sequences of each OTU were aligned using MUSCLE (Edgar, 2004) and  
210 used to assign OTUs to taxonomic groups. The BLAST database was used to taxonomically  
211 classify the bacterial and fungal sequences. Raw sequences of the bacterial 16S r RNA gene as  
212 well as the ITS1 and ITS4 regions of the 18S rRNA gene are stored in the European Nucleotide  
213 archive (<http://www.ebi.ac.uk/ena/data/view/PRJEB23248>).

## 214 ***2.6. Statistical analysis***

215 Residues were checked by Shapiro-Wilk test and Komolgorov-Smirnov test respectively.  
216 Residues full-filed the assumptions of normality and homoscedasticity for multiple comparison  
217 tests. Filtering of the raw OTU table, the OTU richness, Shannon index (based on number of  
218 OTUs), relative abundances of bacterial and fungal taxa as well as permuted MANOVA  
219 analysis were performed using the 'Phyloseq' packages (McMurdie and Holmes, 2013, 2012).

220 Linear regression was used to show significant effect of latitudinal gradient on basal soil  
221 respiration, microbial biomass C, content of bacterial and fungal PLFA and microbial diversity  
222 (based on DNA sequencing). Principal coordinates analysis (PCoA) of weighted UniFrac  
223 distance were used to evaluate the overall structural change of soil prokaryotic communities  
224 and was performed using the ‘Phyloseq’ R package (Lozupone and Knight, 2005; McMurdie  
225 and Holmes, 2013, 2012). The effect of environmental factors on relative abundance of bacterial  
226 and fungal phyla were tested by two-way ANOVA followed by Tukey–Kramer Multiple  
227 Comparison Test using basic statistics in R package. Regression tree analyses were conducted  
228 using the ‘rpart’ R package (CP value set at 0.01) to determine which environmental factors  
229 explained the deviance of bacterial and fungal biomass (Breiman, 1984).

### 230 **3. Results**

#### 231 ***3.1. Basal soil respiration and microbial biomass C***

232 Linear regression model showed significantly higher basal soil respiration for local soils in  
233 comparison with transplanted soils (Fig. 1A). Additionally, basal soil respiration in local soils  
234 significantly increased 22 to 42 mg CO<sub>2</sub>-C kg<sup>-1</sup> h<sup>-1</sup> with latitude while basal soil respiration in  
235 transplanted soils decreased from 32 to 19 mg CO<sub>2</sub>-C kg<sup>-1</sup> h<sup>-1</sup> significantly with latitude (Fig.  
236 1A). In contrast, no statistically significant differences in microbial biomass C were detected  
237 between local and transplanted soils. The microbial biomass C in transplanted soils as well as  
238 in local soils significantly decreased with latitude (Fig. 1B).

#### 239 ***3.2. Fungal and bacterial PLFA***

240 Fungal PLFA showed higher overall content than bacterial PLFA. Linear regression model  
241 showed significant differences in content of both fungal and bacterial PLFA between  
242 transplanted and local soils along the latitudinal gradient. Fungal PLFA content in local soils  
243 significantly increased along the latitudinal gradient while transplanted soils did not show any

244 significant changes along the latitudinal gradient (Fig. 1C). As with fungal PLFA, bacterial  
245 PLFA content in local soils increased significantly along the latitudinal gradient (Fig. 1D). In  
246 contrast, bacterial PLFA content in transplanted soils showed marginal variation with the  
247 latitudinal gradient. Bacterial and fungal PLFA content in local soils was significantly higher  
248 than in transplanted soils (Fig. 1C, D). To identify the most influential climatic (temperature,  
249 precipitation, latitude) and soil factors (pH) among various site locations, correlations between  
250 environmental factors (data shown in Table 1) and the fungal and bacterial PLFA content were  
251 determined using regression tree analysis (Fig. 2A, B). The regression tree analysis unveiled  
252 precipitation as most influential environmental factors determining bacterial community, while  
253 fungal community was mostly affected by latitude (Fig. 2A, B).

### 254 ***3.3. Diversity, structure and composition of microbial community***

255 In total, we identified 2918 bacterial and 707 fungal OTUs (with 97% accuracy) whose relative  
256 frequency exceeded 0.01%. Shannon diversity index of fungal community decreased  
257 significantly from 2.5 to 1.2 along the latitudinal gradient in transplanted soils while local soils  
258 increased from 0.9 to 2.4 with latitude (Fig 1E). In contrast, Shannon index of bacterial  
259 community did not show any significant pattern between local and transplanted soils along the  
260 latitudinal gradient (Fig 1F).

261 Permuted multivariate analysis of variance showed significant changes in the structure  
262 of soil bacterial and fungal communities based on a weighted UniFrac distance matrix across  
263 various receptor sites. Principal coordinates analysis (PCoA) showed clear changes in the  
264 structure of both bacterial and fungal communities at the various receptor sites (Fig 3A, B).  
265 Furthermore, the resulting PCoA diagram (Fig 3A, B) well illustrates significant changes in  
266 bacterial community structure between local and transplanted soils. By contrast, our results do

267 not indicate any overall differences in fungal community structure between local soils and  
268 transplanted soils.

269 We identified five fungal phyla in both local and transplanted soils from different sites  
270 along various latitudes (Fig. 4A). Two-way ANOVA showed significant changes in relative  
271 abundances of *Ascomycota*, *Basidiomycota* and *Glomeromycota* at various receptor sites  
272 ( $F=4.45$ ;  $p<0.001$ ;  $df=5$ ) as well as between local and transplanted soils ( $F=5.6$ ;  $p<0.001$ ;  $df=1$ ).  
273 Other phyla did not show any significant differences between receptor sites as well as between  
274 local and transplanted soils. Transplanted soils showed higher relative abundance of phylum  
275 *Ascomycota*, *Basidiomycota* and *Glomeromycota* than those from local soils. By contrast, five  
276 bacterial phyla differed significantly in soils taken from various donor and receptor sites (Fig  
277 4B). Soils transplanted to Finland exhibited greater relative abundances of *Acidobacteria*,  
278 *Actinobacteria*, *Bacteroidetes*, *Gemmatimonadetes* and *Proteobacteria*. *Proteobacteria* had the  
279 highest relative abundance in transplanted soil.

#### 280 **4. Discussion**

281 The increase in microbial respiration observed in local soils but not in transplanted soils  
282 suggests that soil respiration is driven more by local soil conditions. We hypothesize that  
283 increase in local soils may be mainly due to the amount and quality of soil organic matter, which  
284 may, however, be indirectly affected by climatic factors (Delgado-Baquerizo et al., 2017;  
285 García-Palacios et al., 2013; Prober et al., 2015). This effect may correspond with well-known  
286 latitudinal changes in plant traits with changing climatic conditions and consequently with  
287 changes in litter quality (García-Palacios et al., 2013; McGill et al., 2006; Reich and Oleksyn,  
288 2004). In contrast, decreasing of basal soil respiration in transplanted soils may correspond  
289 with climatic factors such as temperature and precipitation which in turn affecting metabolic  
290 activity of soil microbial communities (Zhou et al., 2016).

291 In contrast to microbial respiration, microbial biomass C did not show any significant  
292 changes between local and transplanted soils. This fact indicates that the effect of global  
293 climatic factors is more pronounced in this case than the effect of local soil conditions. We  
294 found decreasing microbial biomass C in soils from various sites along the latitudinal gradient.  
295 Here we should underline that microbial biomass C includes the biomass of all microscopic  
296 organisms in the soil, not only of bacteria and fungi, but also of protozoans and microscopic  
297 metazoans (Schmitt and Glaser, 2011). We hypothesize, carbon resides in the vegetation and  
298 soil at lower latitudes for a shorter time than at higher latitude due interaction of metabolic  
299 activity of soil microbes with temperature (Carvalhais et al., 2014; Zhou et al., 2016).

300 The increase in relative abundance of bacteria and fungi (based on PLFA content) along  
301 latitudinal gradient as well as microbial respiration observed in local soils but not in  
302 transplanted soils suggests that these characteristics of the soil microbiota are driven more by  
303 local soil conditions than global factors, which may, however, be affected indirectly by the  
304 effect of climatic factors on soil chemistry (Birkhofer et al., 2012; García-Palacios et al., 2013).  
305 Also, our regression tree analysis singled out precipitation as the main factor controlling content  
306 of bacterial PLFAs. Fungal PLFAs content was mostly affected by latitudinal changes, which  
307 partly corroborates the study of Tedersoo et al. (2014), which identified latitude as the main  
308 factor controlling fungal communities.

309 The observed increases in relative abundance of bacteria and fungi (PLFA) with  
310 increasing latitude are probably influenced by increased total carbon in soil (Wang et al., 2012).  
311 These results correspond to other similar studies done worldwide (Liu et al., 2008; Wang et al.,  
312 2012). This finding indicates that global factors, namely climatic factors strongly affect  
313 microbial communities directly via precipitation (Yao et al., 2017) and temperature (Zhou et  
314 al., 2016) or indirectly via the effect of the climate on the quality of leaf litter, which in turn  
315 plays a key role in shaping the soil biota community (Delgado-Baquerizo et al., 2017; Frouz et

316 al., 2013; Wardle et al., 2004). One may also argue that after one year, a microbial community  
317 is still developing and that it would be interesting to follow its development for a longer period.  
318 However, after a longer period, conditions might change in such a way that it would become  
319 difficult to tell whether what is followed is the development of the microbial community per se  
320 or its response to temporal soil changes, as transplanted soil is likely to increasingly resemble  
321 local soil over time.

322         We found a decreased Shannon index of fungal communities with increasing latitude.  
323 This pattern corroborates general patterns described for aboveground communities (Gaston,  
324 2000; Ricklefs, 2004). We expect that interaction of temperature with metabolism shaping all  
325 biological processes and having a strong impact on ecological patterns and processes (Okie et  
326 al., 2015; Zhou et al., 2016). In our study, however, this was true only for transplanted soils,  
327 whereas local soils showed increased diversity of soil fungal community. This may be caused  
328 by the fact that communities of transplanted soils were still under development and responding  
329 to colonization potential and major environmental drivers. In more mature local soils, their  
330 diversity can be more sensitive to heterogeneity of the soil environment, which provides  
331 enormous potential for niche partitioning, thus allowing high levels of local biodiversity (Dini-  
332 Andreote et al., 2014; Fierer, 2017).

333         We agree with study of Treseder (2014) showing that phylogenetically older phyla  
334 prefer lower latitudes with warmer and wetter conditions than younger phyla, which prefer  
335 colder and drier climates. This hypothesis may also explain the higher diversity of microbial  
336 communities at lower latitudes observed in the current study. We suggest that the dominance  
337 and wider occurrence of bacterial communities could be explained by the fact that bacteria are  
338 considered phylogenetically older organisms than fungi (Treseder et al., 2014). We agree that  
339 exposure time affects the composition and structure of microbial communities. We used soil



340 samples deposited at receptor sites for one year. We hypothesize that spatio-temporal changes  
341 take place in microbial communities at large temporal scales (Dini-Andreote et al., 2014).

342 Furthermore, we expect, that fungal communities and, in general, the taxa involved in  
343 the fungal decomposition pathway (such as fungal-feeding nematodes) prefer lower  
344 temperatures and are more tolerant to higher soil moisture levels (Bhusal et al., 2015). The  
345 weighted UniFrac distance between communities – a measure of beta diversity (Lozupone and  
346 Knight, 2005) – suggests that sites with similar latitudes are more similar regardless of their  
347 actual geographic distance. This is true for both local and transplanted soils in our study. This  
348 finding stands in agreement with other similar studies (Fierer et al., 2012; Lauber et al., 2009)  
349 that consider edaphic factors (e.g. the parent rock, soil pH, moisture, etc.) as well as  
350 aboveground communities as the main drivers of beta diversity. For example, Lauber et al.  
351 (2009) showed a disproportion of beta diversity between acidic and alkaline soil across various  
352 biomes. By contrast, Prober et al. (2015) showed a positive interaction between the composition  
353 of aboveground communities and fungal communities in soils.

354 Finally, our results have revealed significant variation in alpha as well as beta diversity  
355 of soil microbes among various receptor sites. Our results did not show any overall difference  
356 between local and transplanted soils when all sites were evaluated together. This is probably a  
357 result of high variation among sites, which mask differences between local and transplanted  
358 soils. We speculate that variation in microbial diversity results from random events such as the  
359 birth, death, immigration and emigration of soil microbes, as has recently been proposed in the  
360 literature (Dini-Andreote et al., 2015; Lee et al., 2013; Zhou et al., 2014).

361 However, we found significant differences between local and transplanted soils at  
362 individual receptor sites; for example, in Finland and Greece the transplanted soils significantly  
363 differed from the local ones. Similar studies with transplanted soil blocks, such as that of Castro

364 et al. (2010), report changes in the relative abundances and composition of fungal communities  
365 to be shaped by the precipitation regime and temperature. Study of Rui et al. (2015) showed  
366 that transplanted soil bacterial communities became more similar to those at their receptor sites  
367 and more different from those at their donor sites. However, that study considered soil  
368 transplantation along an elevation gradient at a regional scale and considered bacterial  
369 communities only.

370 Our results do not indicate any clear pattern of bacterial diversity at various donor and  
371 receptor sites. In agreement with recent studies (Barberán et al., 2014b), we suggest that bacteria  
372 are ubiquitous across the diversity of habitats. In addition, our results indicate that  
373 Proteobacteria have the highest relative abundance in transplanted soils. We hypothesize that  
374 Proteobacteria dominate in transplanted sterile soil because the group is made up of fast-  
375 growing taxa (Fierer et al., 2007). We suggest that fast growing bacteria indicate increased  
376 growth in habitats with a higher amount of available nutrients such as sterilized soils containing  
377 dead cells and dead organic matter. Similar pattern was shown also for soil fungal community  
378 showing increased relative abundance of *Ascomycetes*, *Basidiomycetes* and *Glomeromycota* in  
379 transplanted soils. This indicate that sterilized soils promotes better conditions for fungal  
380 growth via released nutrient and available niches. Additionally, we found higher relative  
381 abundance of soil fungi in boreal soils (Finland), showing that forest soils promote good  
382 conditions for fungal growth as was shown in previous studies (e. g. Voříšková et al., 2011).

## 383 **5. Conclusion**

384 An increase in basal soil respiration in local but not in transplanted soils suggests that microbial  
385 activity is driven mainly by changes of the soil substrate along latitudinal and climatic gradients.  
386 The decreasing values of the microbial biomass C with latitude suggests that this parameter is  
387 driven by global climatic factors. Differences between microbial biomass C and PLFA may be

388 explained by increases in deposited nutrients in cells, resulting in a larger body size of microbes  
389 at sites situated at higher latitudes. The observed increase in bacterial and fungal PLFA seems  
390 to be driven by latitudinal changes in substrate quality. The alpha diversity of soil fungal  
391 communities is mostly affected by latitudinal and climatic factors whereas their beta diversity  
392 (community structure) is mostly shaped by substrate quality.

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### Figures captions:

Fig. 1. Basal soil respiration (A), microbial biomass C (B), fungal (C) and bacterial (D) PLFA concentration, Shannon index of soil fungal (E) and bacterial (F) community in local and transplanted soil distributed along latitudinal gradient. Linear regression model.

Fig. 2. Regression tree analysis depicting the main factors for the bacterial (A) and fungal (B) PLFA concentration in local and transplanted soil distributed at different sites along the climatic gradient.

Fig. 3. Principal coordinates analysis of weighted UniFrac distance matrix fungal (A) and bacterial (B) communities in local and transplanted soil distributed at different sites along the climatic gradient. Permuted MANOVA (Fungi): Site ( $F_{5,90}=2.236$ ,  $p=0.001$ ), Treatment ( $F_{1,54}=1.215$ ,  $p=0.172$ ), Site\*Treatment ( $F_{11,198}=1.26$ ,  $p=0.017$ ). Permuted MANOVA (Bacteria): Site ( $F_{5,90}=1.415$ ,  $p=0.047$ ), Treatment ( $F_{1,54}=1.512$ ,  $p=0.027$ ), Site\*Treatment ( $F_{11,198}=0.817$ ,  $p=0.62$ ).

Fig. 4. Relative abundance of fungal (A) and bacterial (B) phyla in local and transplanted soils distributed across various sites along the climatic gradient. Asterisk indicates a statistical significant difference (\* $p<0.05$ ; \*\* $p<0.01$ ; \*\*\* $p<0.001$ ). There were no transplanted sites for Sokolov. Bars represent SE.



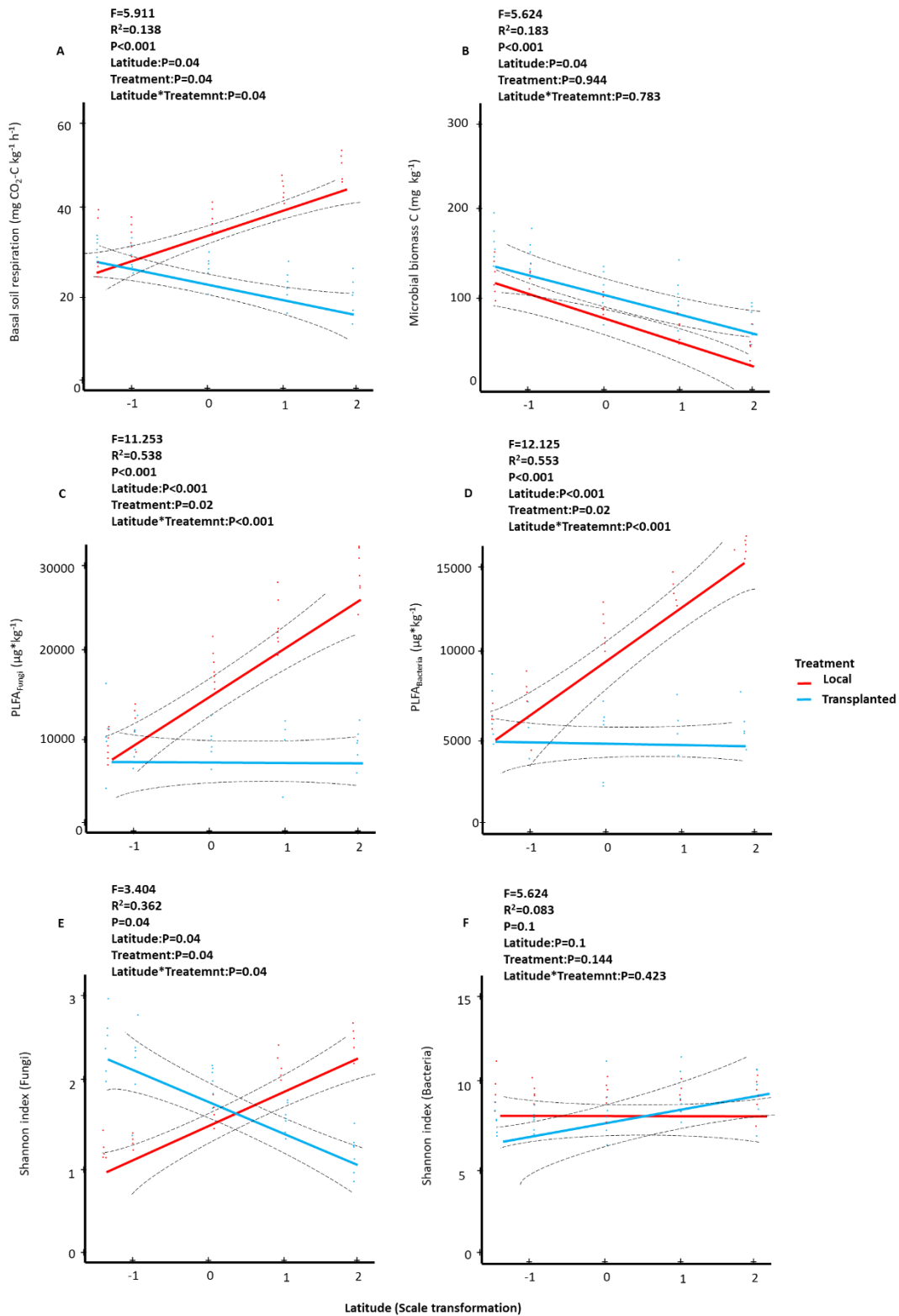


Fig. 1

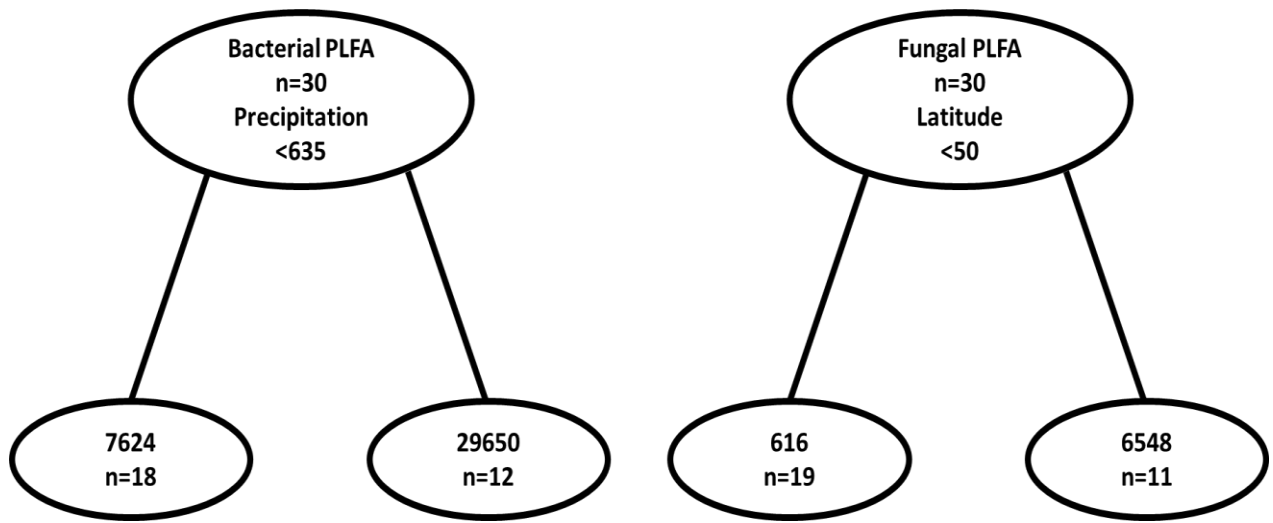


Fig. 2.

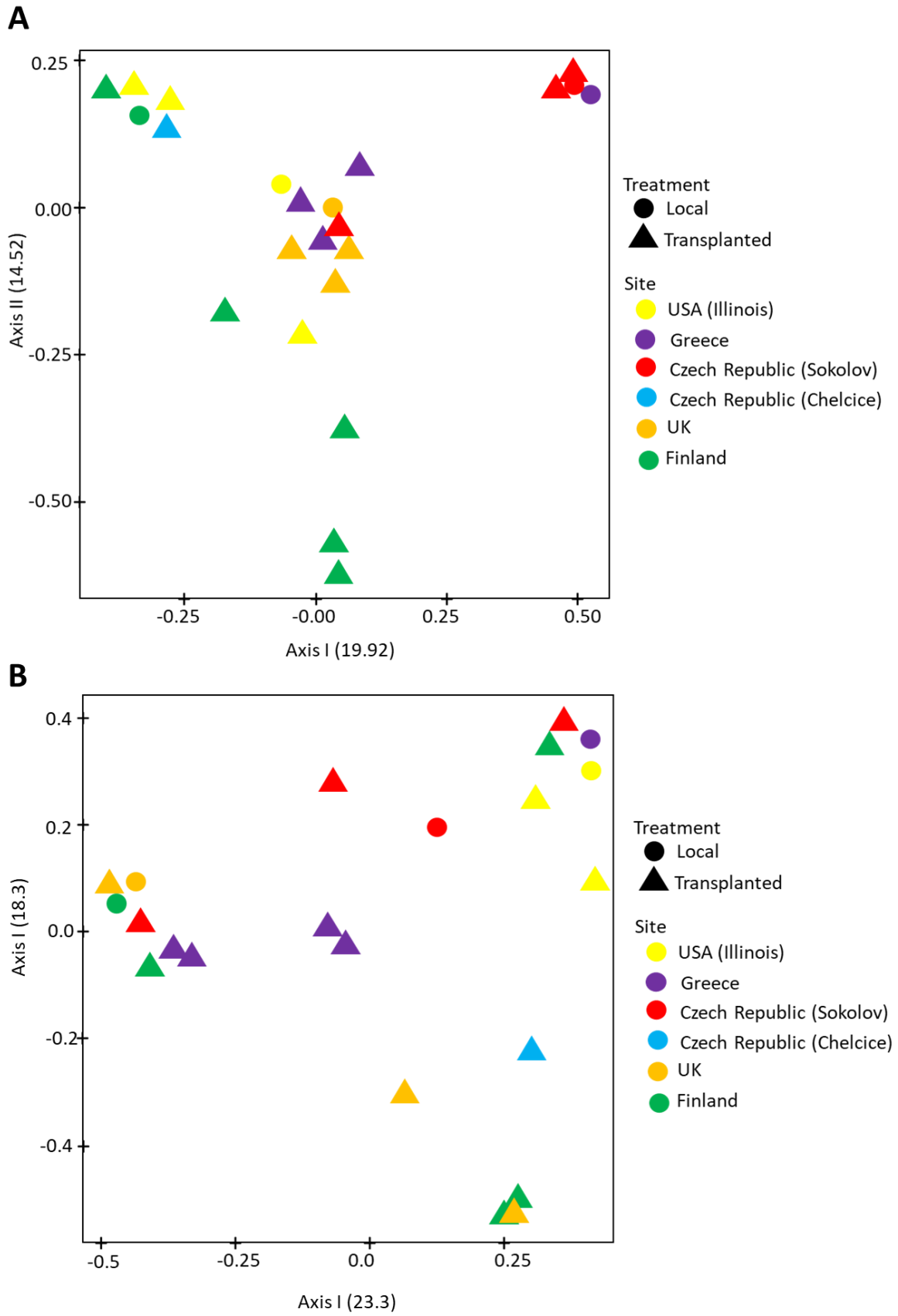


Fig. 3.

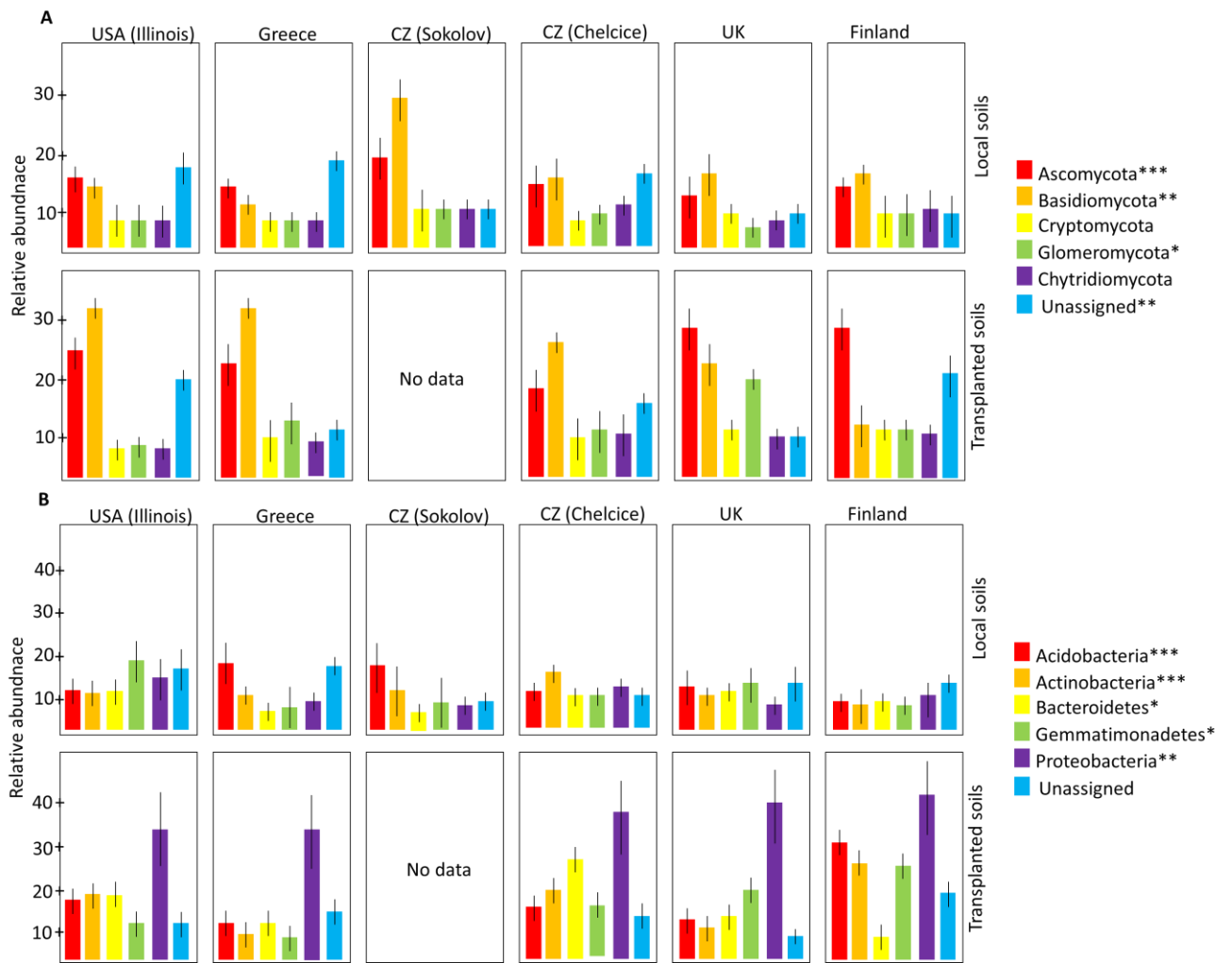


Fig. 4.

Table 1: Study sites and environmental data for the transplantation experiment. The Sokolov (Czech Republic) site serves as soil donor as well as receptor site; all the other sites were receptors of the soil from Sokolov.

Country	Latitude	Longitude	Texture	Soil pH	Content of C (%)	C:N ratio	Annual Temperature	Annual precipitation (mm)	Ecosystem type	Reference
USA (Illinois)	38°56'51.7"N	87°13'04.4"W	Silty Loam	6.5	2.2	13.7	13	1035	Open deciduous forest	(Frouz et al., 2013)
Greece	40°43'48.8"N	22°57'02.5"E	Loam	8.6	3.7	17.6	15.9	455	Pasture with trees	(Bhusal et al., 2015)
Czech Republic	50°12'10.54"N	12°38'13.25"E	Loam	6.5	5	11.9	7.5	579	Grassland with trees	(Holec and Frouz, 2005)
Czech Republic	50°12'14.8"N	12°38'13.8"E	Loam	5.3	2.2	9.16	7.3	605	Grassland with trees	(Lukešová, 1993)
UK	51°38'37.2"N	0°38'43.8"W	Loam	7.22	3.7	9.4	11.1	621	Pasture with trees	(de Vries et al., 2013)
Finland	60°59'04.0"N	25°38'38.9"E	Loamy sand	4.5	25.4	25.6	3.9	647	Open spruce forest	(Häkkinen et al., 2010; Selonen and Setälä, 2015)