1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1 **Cover page for *Journal of Plant Nutrition and Soil Science***

2

3 **text pages:** 12

4 **tables:** 3

5 **figures:** 3

6

7 **running title (≤ 12 words):**

8 Microbial phosphorus in soils influenced by chemical properties, land use, and biodiversity

9

10 **Corresponding author:**

11 Yvonne Oelmann

12 Geoecology, University of Tübingen, Rümelinstr. 19-23, 72070 Tübingen, Germany

13 Email: yvonne.oelmann@uni-tuebingen.de

14 phone: + 49 7071 29 72398

15 fax: + 49 7071 29 5378

16

17

This document is the accepted manuscript version of the following article:
Sorkau, E., Boch, S., Boeddinghaus, R. S., Bonkowski, M., Fischer, M.,
Kandeler, E., ... Oelmann, Y. (2018). The role of soil chemical properties, land
use and plant diversity for microbial phosphorus in forest and grassland
soils. *Journal of Plant Nutrition and Soil Science*, 181(2), 185-197.
<https://doi.org/10.1002/jpln.201700082>

Title

The role of soil chemical properties, land use and plant diversity for microbial phosphorus in forest and grassland soils

Authors

Elisabeth Sorkau¹, Steffen Boch², Runa S. Boeddinghaus³, Michael Bonkowski⁴, Markus Fischer⁵, Ellen Kandeler³, Valentin H. Klaus⁶, Till Kleinebecker⁶, Sven Marhan³, Jörg Müller⁷, Daniel Prati⁵, Ingo Schöning⁸, Marion Schrumpp⁸, Jan Weinert⁴, Yvonne Oelmann^{1*}

¹Geoecology, University of Tübingen, Rümelinstr. 19-23, 72070 Tübingen, Germany

²Department of Biodiversity and Conservation Biology, Ecosystem Dynamics, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf

³Institute of Soil Science and Land Evaluation, Department of Soil Biology, University of Hohenheim, Emil-Wolff-Str. 27, 70593 Stuttgart, Germany

⁴Terrestrial Ecology, Institute of Zoology, University of Cologne, Zùlpicher Str. 47b, 50674 Köln, Germany

⁵Institut of Plant Sciences and Botanical Garden, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

⁶Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany

⁷Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 1, 14469 Potsdam, Germany

⁸Department for Biogeochemical Processes, Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745 Jena, Germany

Keywords (4 – 6)

age class forest, unmanaged forest, land-use intensity, meadow, pasture, microbes

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

43 **Abstract**

44 Management intensity modifies soil properties, e. g. organic carbon (C_{org}) concentrations and soil pH
45 with potential feedbacks on plant diversity. These changes might influence microbial P
46 concentrations (P_{mic}) in soil representing an important component of the P cycle. Our objectives were
47 to elucidate whether abiotic and biotic variables controlling P_{mic} concentrations in soil are the same
48 for forests and grasslands, and to assess the effect of region and management on P_{mic} concentrations
49 in forest and grassland soils as mediated by the controlling variables. In three regions of Germany,
50 Schwäbische Alb, Hanich-Dün, and Schorfheide-Chorin, we studied forest and grassland plots (each
51 $n = 150$) differing in plant diversity and land-use intensity. In contrast to controls of microbial
52 biomass carbon (C_{mic}), P_{mic} was strongly influenced by soil pH, which in turn affected phosphorus (P)
53 availability and thus microbial P uptake in forest and grassland soils. Furthermore, P_{mic}
54 concentrations in forest and grassland soils increased with increasing plant diversity. Using structural
55 equation models, we could show that soil C_{org} is the profound driver of plant diversity effects on P_{mic}
56 in grasslands. For both forest and grassland, we found regional differences in P_{mic} attributable to
57 differing environmental conditions (pH, soil moisture). Forest management and tree species showed
58 no effect on P_{mic} due to a lack of effects on controlling variables (e. g. C_{org}). We also did not find
59 management effects in grassland soils which might be caused by either compensation of differently
60 directed effects across sites or by legacy effects of former fertilization constraining the relevance of
61 actual practices. We conclude that variables controlling P_{mic} or C_{mic} in soil differ in part and that
62 regional differences in controlling variables are more important for P_{mic} in soil than those induced by
63 management.

1 Introduction

In recent years, it has become apparent that phosphorus (P) limitation of primary producers and soil microorganisms is much more widespread in terrestrial ecosystems than previously thought (*Elser et al., 2007; Vitousek et al., 2010*). Anthropogenic nitrogen (N) inputs due to combustion of fossil fuels and N-based fertilizers may further shift terrestrial systems towards P-limitation (*Holland et al., 2005*).

The importance of soil microbial biomass P (P_{mic}) in the P cycle was emphasized by several studies (*Chen et al., 2000; Oberson and Joner, 2005; Richardson and Simpson, 2011; Turner et al., 2013*). However, the understanding of environmental conditions as drivers of P_{mic} in soil is still in its fledgling stage. Only a few variables suspected to control P_{mic} in soil have been included in the studies published so far and these did not consider the influence of plants. First, organic carbon (C_{org}) concentrations correlated with P_{mic} concentrations in forests and grasslands (*Joergensen et al., 1995; Stutter et al., 2015*). This is probably related to the role of C_{org} as ultimate energy source of heterotrophic soil organisms constraining the growth of microorganisms (*Wardle, 1992*). Second, *Liebisch et al. (2014)* found increasing P_{mic} concentrations with increasing soil moisture in a grassland fertilization trial which is in line with a positive effect of soil moisture on microbial biomass carbon (C_{mic}) concentrations in soil in a meta-analysis (*Wardle, 1998*). Third, *Liebisch et al. (2014)* found highest P_{mic} concentrations in soils with high pH (6.8). This effect might derive from the strong pH control of $H_2PO_4^-/HPO_4^{2-}$ ion concentrations in soil solution serving as the pool of P readily available for uptake by soil microorganisms. Fourth, total P concentrations in soil have been shown to be decisive for P_{mic} concentrations in forest soils under beech (*Joergensen et al., 1995*). In addition, as microbes form part of the P cycle, they are likely to be linked to other P fractions in soil (*Tate, 1984; Tate et al., 1991; Khan and Joergensen, 2012*). This is because microbes can act as a source and sink of P while being involved in transformation reactions of organic P (P_o) and inorganic P (P_i) fractions in soil (*Tate, 1984; Brookes, 2001; Griffiths et al., 2012; Burns et al., 2013*). Finally, plants might influence some of these controlling variables thereby also exerting an effect on P_{mic} in soil. In artificial

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

92 grasslands and established forests, it has been shown that increasing plant diversity leads to
93 increased C_{org} stocks likely due to increased above- and belowground litter input (*Fornara* and
94 *Tilman*, 2008; *Steinbeiss et al.*, 2008; *Gamfeldt et al.*, 2013; *Lange et al.*, 2015). Whereas previous
95 studies focused on a smaller set of land-use types and environmental factors driving P_{mic} storage in
96 microorganisms, we are the first to use a larger data basis is required for generalizing these results
97 and potentially uncover environmental conditions controlling P_{mic} in soil that have not yet been
98 accounted for in the above-mentioned studies (C : N ratios and P fractions in soil). Recently
99 developed statistical tools such as structural equation models (SEM) allow to separate direct from
100 indirect effects of such large data sets based on linear regressions (*Grace et al.*, 2012).
101 If P_{mic} concentrations are studied under different climatic conditions, e. g. precipitation feeding back
102 on soil moisture and other controls (parent rock material, soil pH, P fractions in soil, C_{org} , and plant
103 diversity) we hypothesize differences in P_{mic} among regions. Regional differences might be further
104 reinforced by land use and the associated management. In forests, one component of management
105 is associated with the selected tree species or mixtures and accordingly different harvest intervals.
106 Tree species influence soil properties such as pH and C : N ratios thereby potentially affecting P_{mic}
107 concentrations in soil. Because tree species might well have been planted according to tree species
108 performance, e. g. coniferous trees at sites with low soil pH, cause and effect are difficult to
109 disentangle in established, non-natural ecosystems. Nevertheless, the above-mentioned correlations
110 remain. To the best of our knowledge, only one study has been published so far on tree species
111 effects on P_{mic} concentrations in soil. In this study, two Mediterranean oak species resulted in
112 different P_{mic} concentrations in soil (*Aponte et al.*, 2013).
113 In grasslands, management affects P_{mic} concentrations in soil via fertilizer inputs potentially
114 associated with indirect effects, such as changes in soil pH and subsequent availability of P. In
115 agriculture, the most common P containing fertilizers are inorganic fertilizers (produced from rock
116 phosphates), manure or composts (*Ayaga et al.*, 2006) which increase substrate availability for
117 microorganisms. Another management option in grasslands is grazing. Reduced grazing (and

fertilization) intensity increased microbially-mediated processes resulting in microbial immobilization of scarce nutrients including P (*Stutter et al.*, 2015). Therefore, increased P_{mic} concentrations can be expected for low management intensity. But the opposite might also be true, i. e. high management intensity in terms of grazing and fertilization associated with high P_{mic} concentrations in soil. This might be caused by positive effects of fertilization (as reasoned above) combined with the ability of microorganisms to accumulate P as polyphosphates in situations of “luxury P supply” (*Condrón et al.*, 2005).

The main objectives of our study were (1) to elucidate whether abiotic and biotic variables controlling P_{mic} concentrations in soil are the same for forests and grasslands, and (2) to assess the effect of region and management on P_{mic} concentrations in forest and grassland soils as mediated by the controlling variables.

We hypothesized that

- i) C_{org} concentrations, soil moisture as well as soil pH, soil C : N ratios, and P fractions control P_{mic} concentrations in soil with plant diversity exerting an additional effect in forests and grasslands;
- ii) regions with high annual precipitation, high C_{org} concentrations in soil, and high soil pH will be characterized by highest P_{mic} concentrations in soil (ALB > HAI, SCH);
- iii) in forests, P_{mic} concentrations in soil will decrease with increasing land-use intensity as high land-use intensity is associated with coniferous stands (low soil pH, high C : N ratios of litter); in grassland soils, P_{mic} concentrations increase with increasing land-use intensity due to fertilization.

2 Material and methods

2.1 Study regions

Our study is part of the project “Biodiversity Exploratories” (www.biodiversity-exploratories.de) in which the influence of land-use type, land-use intensity, and biodiversity on ecosystem functioning is assessed (*Fischer et al.*, 2010). The project includes plots in three study regions in Germany differing in land-use intensity and biodiversity: Schwäbische Alb (ALB), Hainich-Dün (HAI), and Schorfheide-

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

144 Chorin (SCH). Each region (Table 1) comprises of 50 plots in grassland and 50 plots in forests resulting
145 in a total number of 300 plots. Plots in each region have been used continuously by farmers and
146 foresters for many years (Fischer et al., 2010). The oldest known land-use forms are meadows in ALB
147 established in 1817 whereas in HAI and SCH arable land was converted to grassland in the 1980s and
148 1990s at the latest (personal communication Jan Thiele, University of Münster).

149

150 **2.2 Forest and grassland management**

151 In both forests and grasslands, plots were selected to cover a wide range of land-use types typical for
152 large parts of Central Europe. Forest plots are classified as unmanaged forest ($n = 22$), age class forest
153 ($n = 119$), and selection cutting ($n = 9$). Age class forests have an even-aged stand structure due to
154 harvests at 80 to 120-year intervals. Selection forests are uneven-aged deciduous stands, dominated
155 by European beech, in which single or small groups of trees were harvested selectively. The forest in
156 the ALB and HAI are dominated by European beech [*Fagus sylvatica* L.] (ALB: $n = 38$; HAI: $n = 46$) and
157 Norway spruce [*Picea abies* (L.) Karst] (ALB: $n = 12$; HAI: $n = 4$). In the studied forests in SCH European
158 beech ($n = 21$), sessile oak [*Quercus petraea* Liebl.] and/or English oak [*Quercus robur* L.] ($n = 7$), and
159 Scots pine [*Pinus sylvestris* L.] ($n = 22$) are the dominating tree species.

160 Grassland types are grasses, herbs and legumes. The experimental plots are either fertilized ($n = 63$)
161 or non-fertilized ($n = 87$) and further classified into the land-use types meadow (grasslands mown
162 one to three times per year, $n = 47$), mown pasture (grasslands mown and grazed within the same
163 year, $n = 42$), and pasture (grasslands grazed by different livestock at different intensities, $n = 61$).
164 The fertilization of P comprises application of organic fertilizers (e. g. liquid manure) and mineral-
165 fertilizer application. Average fertilizer application rates to fertilized grasslands during the last
166 vegetation period were $11 [\pm 2.6] \text{ kg P ha}^{-1}$, $4 [\pm 1.2] \text{ kg P ha}^{-1}$, and $5 [\pm 2.2] \text{ kg P ha}^{-1}$ in ALB, HAI and
167 SCH, respectively (Alt et al., 2011). In addition to fertilization differences in mowing frequency
168 (number of cuts per year) and grazing intensity (livestock units $\times$ grazing days $\text{ha}^{-1} \text{ year}^{-1}$) were
169 included.

170

171 2.3 Soil sampling

172 Soil samples (grassland: $n = 150$; forest: $n = 150$) were taken with soil corers (50 mm $\emptyset$, Eijelkamp,
173 Giesenbeck, The Netherlands) in May 2011. Samples were taken in a short time interval of three
174 weeks to avoid possible P release from microbial biomass enhanced by drying-rewetting and trophic
175 interactions of microflora and microfauna due to weather conditions (Cole et al., 1978). This time
176 frame also reduced potential seasonal effects on P_{mic} (Regan et al., 2014) given that samples were
177 collected in three regions. For each plot we used a mixed soil sample of 14 cores (0–10 cm soil
178 depth) collected along two transects (40 m long in forests, 20 m long in grasslands) per plot. As a
179 standard procedure for the coordinated soil sampling campaign, organic layers were removed prior
180 to mineral soil sampling at forest sites. We are aware that this procedure results in an
181 underestimation of P_{mic} concentrations, but it facilitates the comparison between grasslands and
182 forests as we relied on mineral soil samples only. Soil samples were sieved (< 2 mm) to remove
183 stones and roots to minimize the influence of living plant tissue (McLaughlin and Alston, 1987). To
184 avoid quantitative and qualitative changes in microbial biomass we used fresh soil samples for soil
185 biological analyses (stored at 4 °C). Further soil chemical analyses were performed on air-dried soil
186 samples.

187

188 2.4 Soil analyses

189 For analysing soil water content an aliquot of soil was dried to a constant weight at 105°C arriving at
190 a “dry” sample weight. The weight of the moist and dry soil was recorded and the percentage water
191 per dry soil calculated (Gardner, 1986). To determine P_{mic} we used a combination of methods by
192 Kouno et al. (1995) and McLaughlin et al. (1986). The underlying principle is to lyse microbial cells of
193 a field-fresh soil sample by fumigation yielding the sum of P originating from microbial cells and of P
194 extracted from the soil matrix. The latter pool can be subtracted from this sum by analysing P
195 concentrations of a non-fumigated sample. Thus, the difference between the fumigated and non-

fumigated sample represents P originating from lysed microbial cells. However, a proportion of P released during fumigation and extraction is removed from the solution by sorption and/or precipitation. To account for this loss, the difference between fumigated and non-fumigated samples has to be corrected. This is achieved by a third treatment in which a known concentration of P is added to a non-fumigated sample ("P spike"). In all three treatments, we used resin stripes (anion exchange membranes, product code: 551642S VWR, Bruchsal, Germany) to extract P from solution. Resin stripes were conditioned using 0.5 M NaHCO₃ (pH = 8.5). For each sample three aliquots of moist soil equalling 2 g of dry soil were weighed into 50 ml polyethylene tubes and 30 ml distilled water (H₂O_{dest}) was added to each tube. The first aliquot was fumigated with 1 ml liquid hexanol (fumigated aliquot). Only H₂O_{dest} was added to the second aliquot (non-fumigated aliquot) whereas in addition 1 ml of 20 µg P ml⁻¹ (as dissolved KH₂PO₄) was added to the third aliquot (P spike). The samples were horizontally shaken for 16 hours with bicarbonate resin membrane strips. Afterwards, the resin stripes were removed from the soils suspension, rinsed with H₂O_{dest} to remove adhering soil, and transferred to new tubes. After that, 30 ml 0.1 M sodium chloride/hydrochloric acid was added and the resin stripes were shaken again for two hours to desorb P. To correct for sorption of P released during fumigation in the calculation of hexanol P (P_{hex}), we used a sorption curve between non-fumigated and P spiked aliquots (Bünemann et al., 2008). Phosphorus concentrations in the fumigated sample are a function of microbial P (P_{hex}) which are (i) modified depending on the extent of sorption/precipitation (slope *a*), and (ii) shifted along the y axis depending on P extracted from the soil matrix in the non-fumigated aliquot (y axis intercept *b*; Equ. 1).

$$P(\text{fumigated aliquot}) = a \cdot \text{microbial P}(P_{\text{hex}}) + b \quad (\text{Equ. 1})$$

Equation 1 can be rearranged to solve for microbial P (Equ. 2):

$$\text{microbial P}(P_{\text{hex}}) = \frac{P(\text{fumigated aliquot}) - b}{a} \quad (\text{Equ. 2})$$

The slope *a* is calculated as follows (Equ. 3):

$$a = \frac{P(P \text{ spike}) - P(\text{non-fumigated aliquot})}{P_{\text{mass}}(P \text{ spike})} \quad (\text{Equ. 3})$$

221 The y axis intercept b is equal to P concentrations in the non-fumigated aliquot. In accordance with
222 *Oberson and Joner* (2005) and *Bünemann et al.* (2008) we did not use a transformation factor for the
223 calculated P_{hex} concentrations and used P_{mic} synonymously for P_{hex} . We used hexanol instead of
224 chloroform, because it is just as effective as chloroform with less hazardous nature (*McLaughlin et*
225 *al.*, 1986). Noteworthy, *Bergkemper et al.* (2016) reported lower P_{mic} concentrations of hexanol
226 fumigation as compared to chloroform fumigation calling for cautious comparisons among different
227 fumigation agents. Studies by *Bünemann et al.* (2004) showed that neither the P concentration nor
228 the specific activity of ^{33}P in resin-P were not affected by the presence of hexanol during extraction
229 and that the addition of the plant residue (e. g., roots) did not represent a source of error for the
230 determination of P_{mic} by hexanol fumigation of soils.

231 Soil microbial biomass carbon (C_{mic}) and nitrogen (N_{mic}) were determined using the chloroform
232 fumigation extraction method (*Vance et al.*, 1987). In brief, 10 g soil subsamples were fumigated with
233 chloroform for 24 h and then extracted with 40 ml 0.5 M K_2SO_4 on a horizontal shaker for 30 min at
234 250 rpm and centrifuged for 30 min at 4400 g. A second sample remained non-fumigated, but was
235 treated identically. Carbon (C) and N in supernatants were measured with a DOC/TN-analyser (Multi
236 N/C 2100S, Analytik Jena, Jena, Germany). Carbon and N content of the unfumigated samples were
237 deducted from the fumigated samples to calculate the microbial share of C and N.

238 Phosphorus occurs in soils in various forms: $\text{H}_2\text{PO}_4^-/\text{HPO}_4^{2-}$ ions in soil solution and adsorbed to
239 mineral surfaces (labile: $\text{NaHCO}_3\text{-P}$), P more strongly sorbed to iron and aluminium oxides
240 (moderately labile: NaOH-P), P bound in calcium phosphates (stable: HCl-P) and occluded P, e. g.
241 spatially separated from P transformation reactions in secondary minerals such as pedogenic oxides
242 (stable: $\text{H}_2\text{SO}_4\text{-P}$) (*Cross and Schlesinger*, 1995; *Hedley et al.*, 1982; *Negassa and Leinweber*, 2009). For
243 P fractions in soil, we used data published by *Alt et al.* (2011). Because of inaccessibility of some sites
244 (e. g. because of extraordinarily high soil moisture), for P fraction measurements some of the
245 300 sites in total could not be sampled resulting in a reduced data set (forest $n = 131$, grassland
246 $n = 110$; *Alt et al.*, 2011). Different P fractions of 0.5 g air-dried soil samples were measured after a

1
2
3 247 method described by *Hedley* et al. (1982) modified by *Kuo* (1996). The first fraction extracted with
4
5 248 anion exchange resins ("resin-P") was not analyzed separately but is included in the NaHCO_3 -
6
7 249 extractable fraction. The further sequential extraction scheme had four steps (NaHCO_3 -P, NaOH -P,
8
9 250 HCl -P, H_2SO_4 -P). First, 20 ml 0.5 M NaHCO_3 (pH = 8.5) was added to the sample and the suspension
10
11 251 was shaken for 30 min, decanted, and filtrated. Second, 30 ml 0.1 M NaOH was added to the
12
13 252 remaining soil followed by shaking for 16 h, decantation and filtration. Third, the remaining soil was
14
15 253 mixed with 0.1 M HCl , heated in a water bath (80 °C, 30 min) and cooled down (1 h) followed again
16
17 254 by decantation and filtration. Fourth, the residual soil mass was stored overnight in a porcelain
18
19 255 crucible in a muffle furnace at 550 °C to destroy all organic material. Thereafter, 20 ml 0.5 M H_2SO_4
20
21 256 was added and the suspension was shaken for 16 h, decanted, and filtrated. The decanted solution of
22
23 257 each step was analysed for P concentrations. All P_i contents were analysed using the ammonium
24
25 258 molybdate-ascorbic acid blue method described by *Murphy* and *Riley* (1962) and measured with a
26
27 259 continuous flow analyser (CFA, AA3, XY2, Seal-Analytic, Norderstedt, Germany) at $\lambda = 660$ nm. Total
28
29 260 dissolved P in NaHCO_3 -extract and NaOH -extract was measured with an Inductively Coupled
30
31 261 Plasma/Optical Emission Spectrometry (ICP-OES, PerkinElmer Optima 5300 DV, S10 auto sampler,
32
33 262 $\lambda = 213.617$ nm). For the labile and moderately fractions (NaHCO_3 -P, NaOH -P), P_o was calculated by
34
35 263 subtracting P_i from total dissolved P concentrations in the extracts. In addition to the individual
36
37 264 fractions, inorganic P in the labile and moderately labile fraction was calculated as the sum of
38
39 265 $\text{NaHCO}_3\text{-P}_i$ and NaOH-P_i ($\Sigma \text{NaHCO}_3\text{-P}_i + \text{NaOH-P}_i$) and organic P in the labile and moderately labile
40
41 266 fraction as the sum of $\text{NaHCO}_3\text{-P}_o$ and NaOH-P_o ($\Sigma \text{NaHCO}_3\text{-P}_o + \text{NaOH-P}_o$). Total P concentrations
42
43 267 represent the sum of all P fractions. The soil pH was measured using 0.01 M calcium chloride and a
44
45 268 soil : solution ratio of 1:2.5. To analyse total C and total N contents of soils, subsamples were ground
46
47 269 in a ball mill to homogenize the material. Total C and N concentrations were then determined by dry
48
49 270 combustion in an elemental analyzer (VarioMax CN analyzer, Elementar Analysensysteme GmbH,
50
51 271 Hanau, Germany). Similarly, inorganic C was measured with the same analyzer after ignition of C_{org} at
52
53
54
55
56
57
58
59
60

1
2
3 272 a temperature of 450 °C for 16 h (Solly et al., 2014). Then C_{org} was calculated as the difference
4
5 273 between total and inorganic C.
6

7 274

9 275 **2.5 Vegetation**

10
11 276 Plant diversity was measured as number of vascular plant species. In 2009, we sampled vascular
12
13 277 plants in all plots. In grasslands, we conducted this survey once between mid-May and end-of-June in
14
15 278 an area of 4 m × 4 m (Socher et al., 2012), when the vegetation was developed best and the
16
17 279 meadows were not mown yet. In forests, the vegetation changes strongly during the seasons with
18
19 280 high abundances of early flowering geophytes in spring to high abundances of later flowering species
20
21 281 in summer. To account for these differences and sample the total plot diversity, we recorded the
22
23 282 vegetation of all plots in two surveys in spring (April) and late summer (June – July) of the same year,
24
25 283 in an area of 20 m × 20 m. To assess the total plant diversity per plot, we then combined the spring
26
27 284 and summer records (Boch et al., 2013).
28
29
30

31 285 32 33 286 **2.6 Statistical analyses**

34
35 287 Results within the text are shown as mean [± standard deviation] if not specified otherwise. To test
36
37 288 for significant differences in mean P_{mic} concentrations among regions and land-use types, we used an
38
39 289 analysis of variance with *Tukey* Post Hoc tests. Correlations among variables were studied using
40
41 290 *Pearson's* rank correlations. To disentangle complex interactions among variables controlling P_{mic} in
42
43 291 grassland and forest soils and to overcome limitations associated with bivariate correlations we used
44
45 292 structural equation models (Grace et al., 2012). We structured different models to check for the
46
47 293 direct and indirect effect on P_{mic} and disentangle between driving factor C_{org} (Model 1: C_{org}
48
49 294 influencing P_{mic} and plant diversity) and plant diversity (Model 2: plant diversity influencing P_{mic} and
50
51 295 C_{org}), respectively. As evaluation criterion for model quality we used probability level and root mean
52
53 296 square error of approximation (RMSEA). To reduce the number of abiotic variables for the SEM we
54
55 297 used a principal component analysis (PCA) with varimax rotation. We checked whether the
56
57
58
59
60

1
2
3 298 prerequisites for a PCA were met by Bartlett's Test of Sphericity (Bartlett *P*) and the Kaiser-Meyer-
4
5 299 Olkin index (KMO) (*Abdi and Williams, 2010*). We set the threshold for meaningful components to
6
7 300 Eigenvalues > 1. Thereafter, we identified those variables that were most important within one
8
9 301 component and thus, can be considered representative of other variables in the same component. As
10
11 302 selection criterion, the highest loading of the variables in the components was used. For P_{mic}
12
13 303 concentrations, we had to remove some outliers calculated after *Grubbs* and *Beck* (1972) from the
14
15 304 data set (number of outliers: ALB: grassland = 2, forest = 2; HAI: grassland = 4, forest = 3; SCH:
16
17 305 grassland = 4, forest = 12).
18
19
20
21
22
23

24 307 **3 Results**

25 308 **3.1 Forests**

26 309 Across all forest soils, P_{mic} concentrations increased with increasing concentrations of $NaOH-P_o$,
27
28 310 $\Sigma NaHCO_3-P_o + NaOH-P_o$, $HCl-P$, H_2SO_4-P , total P, total N, C_{org} , C_{mic} , N_{mic} concentrations, as well as pH
29
30 311 and plant diversity, and decreased with increasing $NaHCO_3-P_i$, $NaHCO_3-P_o$ concentrations, C : N ratio
31
32 312 and $C_{mic} : N_{mic}$ ratio (Table 2). Microbial P concentrations correlated significantly positively with soil
33
34 313 moisture and clay contents (Table 2). At the same time, soil moisture was higher in fine-textured soils
35
36 314 (Table S1). The ratios of $C_{mic} : P_{mic}$ ranged from 5 to 213 with an average of 22 (median = 16). With
37
38 315 increasing plant diversity, $NaHCO_3-P_i$ concentrations and $C_{mic} : P_{mic}$ ratios decreased ($r = -0.19$ and -
39
40 316 0.27 , respectively; $P < 0.05$). The three regions differed in their overall P_{mic} concentrations in the
41
42 317 order $ALB > HAI > SCH$ (Figure 1a). Separated according to region, neither forest management
43
44 318 influenced P_{mic} concentrations significantly nor did tree species ($P > 0.05$; Table 3). For forests, the
45
46 319 prerequisites for a PCA to reduce the number of variables in a SEM were fulfilled (KMO = 0.40,
47
48 320 Bartlett $P < 0.001$). The PCA resulted in three components explaining 78.9 % of the variance in the
49
50 321 data. Based on the highest loading in each component, we selected the following variables: total N
51
52 322 concentrations (Component 1; loading 0.91), $NaHCO_3-P_i$ concentrations (Component 2; loading 0.90),
53
54 323 $NaOH-P_i$ (Component 3; loading 0.94). If data sets of grasslands and forests were merged, the PCA
55
56
57
58
59
60

identified two further influential variables, i. e. C_{org} concentrations (loading 0.91) and soil pH (loading 0.85). Because of similar loadings (and a close bivariate correlation between total N and C_{org} concentrations; $r = 0.98$, $P < 0.001$) and the desired consistency for grassland and forest SEMs, we replaced total N concentrations by C_{org} concentrations in the final model. We used two SEMs treating plant diversity either as a response variable (depending among others on C_{org} concentrations, Model 1; Figure S1) or as a variable controlling C_{org} concentrations (Figure S2). For forest soils, SEMs could not be adequately fitted to P_{mic} concentrations as probability levels < 0.02 and RMSEA > 0.3 indicated major deviations between data and models if regions were analysed separately (Supplementary Table S2, Figure S1, Figure S2). The one exception was the SCH characterized by a better fit between data and model, which however did not include paths significantly explaining P_{mic} concentrations. If all regions were analysed together (ALL), the deviation between data and model was smaller (Supplementary Table S2). In both models, paths including plant diversity were significant.

336

3.2 Grasslands

Overall, P_{mic} increased with increasing pH, concentrations of $NaOH-P_o$, total P, $\Sigma NaHCO_3-P_o + NaOH-P_o$, N_{mic} , total N, C_{mic} , C_{org} , and plant diversity and decreased with increasing $NaHCO_3-P_i$ concentrations (Table 2). P_{mic} concentrations were related to soil moisture and clay contents (Table 2) while soil moisture was higher in fine-textured soils (Table S1). In grassland soils, we measured a mean $C_{mic} : P_{mic}$ ratio of 14 (median = 12) with a range of 2 to 118. With increasing plant diversity, $NaHCO_3-P_i$ and $C_{mic} : P_{mic}$ ratio decreased ($r = -0.62$ and -0.24 , respectively; $P < 0.01$). Mean concentrations of P_{mic} in grassland soils of the three different regions followed the same order as in forest soils: $ALB > HAI \geq SCH$ (Figure 1b). Microbial P concentrations among management types showed high variability (range in meadows: 11.6 to 105.8 mg kg⁻¹, mown pastures: 19.1 to 114.1 mg kg⁻¹, pastures: 6.1 to 103.0 mg kg⁻¹) but were not significantly different. Phosphorus fertilization rates were low (see Chapter 2.2) and there were also no significant differences in P_{mic} concentrations between fertilized (55.4 [± 3.2] mg kg⁻¹) and non-fertilized soils (51.6 [± 3.0] mg kg⁻¹) in

1
2
3 350 general (specified to exploratory: Table 3). In addition, we found no influence of cutting frequency on
4
5 351 P_{mic} concentrations (0 cut/year: 49.3 [± 3.2] mg kg⁻¹, 1 cut/year: 55.2 [± 4.6] mg kg⁻¹, 2 cuts/year:
6
7 352 60.5 [± 4.6] mg kg⁻¹, 3 cuts/year: 47.6 [± 7.1] mg kg⁻¹) (specified to exploratory: Table 3).
8
9 353 For grasslands, the prerequisites for a PCA to reduce the number of variables in a SEM were fulfilled
10
11 354 (KMO = 0.26, Bartlett $P < 0.001$). The PCA resulted in three components explaining 69.4 % of the
12
13 355 variance in the data. Based on the highest loading in each component, we selected the following
14
15 356 variables: NaOH-P_i (Component 1; loading 0.81), HCl-P (Component 2; loading 0.90), NaHCO₃-P_i
16
17 357 concentrations (Component 3; loading -0.81). We replaced HCl-P concentrations by the variable with
18
19 358 the second-highest loading in Component 2, i. e. total P concentrations (loading 0.84). The SEM thus
20
21 359 included the same variables as described above for forests. Most of the SEMs showed an adequate fit
22
23 360 between data and model (Table S2) with a mean explained variance of P_{mic} of 34 % (median = 26 %)
24
25 361 for Model 1 (Figure 2) and 25 % (median = 20 %) for Model 2 (Figure 3). For the models across all
26
27 362 regions (ALL: Figs 2, 3), we found a significant influence of plant diversity on P_{mic} concentrations in
28
29 363 soils. If the regions were analysed individually, however, this direct effect of plant diversity was no
30
31 364 longer significant (ALB, HAI, SCH: Figs. 2, 3). For Model 1 in which plant diversity was considered as
32
33 365 dependent on C_{org} concentrations and in case of ALL, ALB, and HAI (Figure 2), C_{org} concentrations in
34
35 366 soil were related to both, plant diversity and P_{mic} concentrations in soil. However, plant diversity was
36
37 367 related indirectly to P_{mic} concentrations as i) there was no significant direct path if regions were
38
39 368 analysed individually, and ii) plant diversity significantly explained a proportion of variance in C_{org}
40
41 369 concentrations which itself was an important explanatory variable of P_{mic} concentrations (Figures 2,
42
43 370 3).
44
45 371

50 372 **4 Discussion**

52 373 **4.1 Variables controlling P_{mic} concentrations in soil**

54 374 Variables controlling P_{mic} concentrations in soil were suspected to be partly identical to those driving
55
56 375 C_{mic} concentrations in soil. Indeed, for both forests and grasslands, soil moisture, C_{org} concentrations,

pH, and total P controlled P_{mic} concentrations partly corroborating findings on factors driving C_{mic} concentrations in soil (Wardle, 1992, 1998; Joergensen et al., 1995). Reviews on controls of microbial biomass confirm the positive effect of soil moisture (up to a threshold) on microbial biomass (Wardle, 1992) likely because microbes need water for their metabolism. However, this relationship not necessarily is universal because site-specific properties such as e.g., microbivory might play a role as well (Wardle, 1992). Our results highlight the importance of soil moisture for P_{mic} concentrations. Increasing soil moisture results in an increasing diffusivity of P enhancing the uptake by microbes and plants (Lambers et al., 2006). In our study, soil moisture was related inversely to soil texture (Table S1). Therefore, variability in soil moisture among sites was caused by soil texture and in addition very likely by preceding weather conditions. Because of the covariation between soil moisture and soil texture, we found a relationship between soil texture and P_{mic} concentrations as well (Table 2). Because of the experimental design (highest moisture linked to finest texture and lowest soil moisture linked to coarsest texture), we were not able to tease apart the effects of the two variables. In line with the effect of C_{org} , phospholipid fatty acids (forest site: Herold et al., 2014b) and enzyme activities (grassland site: Boeddinghaus et al., 2015) were mainly related to C_{org} concentrations. Soil pH effects were as strong as those of C_{org} concentrations (Table 2). Microorganisms take up P in the form of $H_2PO_4^-$ ions and the ion concentration in solution is controlled among others by the pH-dependent solubility product of P-containing minerals (Brookins, 1988). Therefore, soil pH acts as a control of P availability in soil in turn influencing the possibility of P uptake by microorganisms. In addition, labile P_i concentrations were negatively related to P_{mic} concentrations in soil (Table 2). This indicates P immobilization in microbial biomass, suggesting P_{mic} to act as a sink rather than a source of plant-available P in our study. Interestingly, relationships between P fractions and P_{mic} concentrations in soil were closer in forests as compared to grasslands (Table 2). In conjunction with higher P_{mic} concentrations (Figure 1), this might be indicative of higher microbial turnover and thus, higher contribution of microbial processes to P cycling in grasslands as compared to forests. A strong microbial contribution to P cycling was suggested for extensively used grasslands by Stutter et al.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

(2015) as well. Another difference between forest and grassland soils was related to N. In forests and grasslands, total N concentrations in soil explained 86 % and 48 % of the variation in P_{mic} concentrations, respectively (Table 2). Though one must keep the collinearity of C_{org} and total N concentrations in soil in mind, the greater relevance of N for microbial biomass (C_{mic}) in forests was already suggested by *Wardle* (1992, 1998). Based on our results the prominent role of N in forest soils is transferable to P_{mic} concentrations. Soil C : N ratios correlated significantly with P_{mic} concentrations in forest soils which was not the case for grasslands (Table 2) with a smaller range in soil C : N ratios as compared to forest soils (range in forests and grasslands, 11.1 to 26.3 and 9.0 to 14.6, respectively). In conclusion, we could accept our hypothesis namely that C_{org} concentrations and soil moisture influence P_{mic} concentrations in forest and grassland soils. In addition, soil pH was a strong control of P_{mic} concentrations in both systems. Finally, total N concentrations, soil C : N ratios, and P fractions (except for NaOH- P_i) were particularly decisive for P_{mic} concentrations in forest soils.

In forest soils, P_{mic} concentrations increased with an increasing plant diversity (Table 2) while the relationship for grassland was marginally non-significant ($r=0.14$, $P=0.09$). The different SEMs (Model 1 and Model 2) revealed, however, that the relationship between plant diversity and P_{mic} resulted from simultaneous and positive relationships of C_{org} concentrations on both plant diversity and P_{mic} in grassland soils. However, this applied for mineral soil types in ALB and HAI only as high C_{org} concentrations in soil associated with organic soil types such as fens in SCH (*Herold et al., 2014c*) revealed no link between plant diversity and C_{org} or P_{mic} concentrations in grassland soil. For the mineral soil types in the ALB and HAI, we suggest that the effect of plant species diversity on P_{mic} concentrations is generated by an increase in resource availability, such as OM deposition by dead plant roots and microorganisms (*Lange et al., 2015*), rather than a direct causal effect of plant diversity on P_{mic} . Increased OM accumulation under diverse plant mixtures was proven based on a plant diversity experiment in grassland sites with random species selection for mixture compositions (*Steinbeiss et al., 2008*). Increased C_{org} concentrations in soil concomitantly increased soil microbial

biomass/ P_{mic} and activity in diverse mixtures (Eisenhauer et al., 2010; Hacker et al., 2015; Lange et al., 2015). Furthermore, a higher leaf area index associated with higher plant diversity resulted in higher soil moisture in the top soil layer (Lange et al., 2014) favoring higher P_{mic} concentrations in soil as was shown in our study. Our results suggest that the positive relationship between OM accumulation and plant diversity might be transferable from artificial grassland mixtures to established grasslands thus, confirming our hypothesis that plant diversity has an effect on P_{mic} concentrations in addition to soil properties.

4.2 Regional differences and management effects

In general, P_{mic} concentrations were higher in grassland than in forest soils (Figure 1). This is in line with the results of Chen et al. (2003) and Yeates and Sagar (1998), who studied P_{mic} in mineral soils in forests and grasslands in New Zealand. One explanation might relate to the increased rhizosphere space that can be colonized by microbes. In line, Solly et al. (2014) found that grassland have higher fine root biomass, higher root turnover and higher rates of root decomposition compared to forest soils for our study site. Another explanation for low P_{mic} concentrations in forest plots may be the strong stratification of microbial colonization with soil depth, i. e. the well-developed organic litter layers on the soil surface contain higher P_{mic} concentrations than the mineral soil (Chen et al., 2003; Joergensen and Scheu, 1999). Though we did not measure P_{mic} in the organic layer, the fact that plant-available P_i concentrations were 6 to more than 20 times higher in the organic layer than in mineral soil (Zavišić et al. 2016) might serve as a corroboration of this stratification. Finally, differences in C_{org} concentrations between forests and grasslands could underly differences in P_{mic} concentrations (C_{org} – grasslands: $72.19 [\pm 64.17] \text{ mg kg}^{-1}$, forests: $39.51 [\pm 20.11] \text{ mg kg}^{-1}$). This was corroborated if analyzed per region as there were significant differences in both, P_{mic} and C_{org} concentrations between forests and grasslands in the HAI and SCH, but not in the ALB (in addition see Baumann et al., 2016). Organic C and clay content in forest and grassland sites increased in the order SCH < HAI < ALB, a similar ranking was found for enzyme activities involved in the P cycle in

1
2
3 454 forest soils (*Herold et al.*, 2014a). Microbial P concentrations were highest in ALB for both forest and
4
5 455 grassland soils (Figure 2). This trend corresponds to the results of total phospholipid fatty acids in
6
7 456 grassland soils by *Herold et al.* (2014b). Higher P_{mic} concentrations of the ALB might be explained by a
8
9 457 combination of finer soil texture and higher annual precipitation, thus increasing soil moisture
10
11 458 compared with the two other regions (ALB: 37.8 [± 5.5] %, HAI: 32.2 [± 4.8] %, SCH: 23.7 [± 13.2] %). In
12
13 459 addition to the reasoning provided in Chapter 4.1, fine-textured soils are known to harbor more
14
15 460 microbial biomass than coarse-textured soils (*Naveed et al.* 2016). Additionally, the ALB (followed by
16
17 461 HAI) is characterized by i) higher P_o and total P concentrations, and ii) higher soil pH in grassland and
18
19 462 forest soils as compared to SCH (*Alt et al.*, 2011). Therefore, we could confirm our hypothesis on
20
21 463 region-specific P_{mic} concentrations in soil which are caused by differences in environmental
22
23 464 conditions among regions (C_{org} as substrate availability for microorganism metabolism, pH, soil
24
25 465 moisture).
26
27
28 466 Analysing the three regions separately, neither tree species nor management (managed versus near-
29
30 467 natural, Table 3) had significant effects on P_{mic} concentrations in forest soils. This might be caused by
31
32 468 the fact that variables identified as controlling P_{mic} concentrations (see Chapter 4.1) did not show an
33
34 469 effect either. For our study sites, no differences in C_{org} storage were observed in the density fractions
35
36 470 among dominant tree species (*Herold et al.* 2014c). In addition, soil pH was not different between
37
38 471 coniferous and broadleaved stands (data not shown; $P > 0.05$). This might be caused by
39
40 472 management, e. g. in HAI spruce stands remained where the thickness of the Loess layer was greater
41
42 473 as compared to stands that were reforested with beech. However, another factor identified as
43
44 474 controlling P_{mic} concentrations in soil (see Chapter 4.1) differed between coniferous and broadleaved
45
46 475 stands: the C : N ratio in mineral soil as an indicator of substrate quality and thus, microbial
47
48 476 colonisation (data not shown: difference between spruce and beech 0.9 – 1.5 (ALB and HAI) and
49
50 477 between pine and beech/oak 3.1 – 4.9 (SCH); $P < 0.05$). We infer that the important role of pH for
51
52 478 P_{mic} concentrations in soil overruled other less important drivers and prevented the occurrence of
53
54 479 tree species effects. This reasoning is corroborated by the study of *Aponte et al.* (2013) where tree
55
56
57
58
59
60

species effects (*Quercus canariensis* versus *Quercus suber*) on P_{mic} concentrations in soil went along with differences in soil pH. Furthermore, we analysed mineral soil, but not the organic layer. Particularly in the organic layer, microbial properties (C_{mic} , N_{mic} , $C_{mic} : C_{org}$ ratio, $N_{mic} : \text{total N}$ ratio) were affected by the presence of coniferous tree species resulting from differences in litter C : N ratios and pH (Bauhus et al., 1998; Zhong and Makeschin, 2006; Smolander and Kitunen, 2011). In contrast, effects of tree species on mineral soil (e. g. pH, C_{mic}) were less pronounced or even absent (Bauhus et al., 1998; Zhong and Makeschin, 2006). Zhong and Makeschin (2006) attributed the discrepancy between the organic layer and the mineral soil to the limited spatial extension of tree species effects in mineral soil which would have required a focus on the uppermost mineral soil (e. g. 0 – 3 cm). The same reasoning might apply to P_{mic} concentrations in our samples which – identical with the study of Zhong and Makeschin (2006) – were collected at a depth of 0 – 10 cm. In summary, we cannot unambiguously reject our hypotheses on tree-species/land-use intensity effects on P_{mic} concentrations in forest soils.

In accordance with results from forest soils, we found no effect of land-use types (pasture, mown pasture, meadow) or management measures (fertilization, cutting) on P_{mic} concentrations in grassland soils. For grassland sites land-use intensity affected the spatial structure of enzymes (Berner et al., 2011), but the influence on microbial biomass was not as large as expected and the individual site characteristic were more important (Boeddinghaus et al., 2015). In contrast to pronounced land-use effects such as grazing in subtropical grasslands (Wang et al., 2006; Devi et al., 2014) plants might regrow rapidly after animal browsing under temperate climate conditions. As a result, the proportion of bare area prone to erosion is restricted and the reduction of microbial biomass and accordingly, P_{mic} , by loss of soil due to erosion is minimized. Bristow and Jarvis (1991) found no difference between C_{mic} concentrations in grassland swards that were either grazed or cut (the latter associated with removal of the harvested material). They speculated that the lacking effect of reduced OM input into soil might be due to the fact that microbes in permanent grassland do not respond to small shifts in C_{org} availability in soil – an explanation that we consider reasonable

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

506 given the generally high soil OM concentrations in grassland ecosystems. Similarly, we found no
507 effect of fertilization on P_{mic} concentrations which contrasts with the study by *Liebisch et al. (2014)*.
508 In established ecosystems such as those we studied with long-lasting history of land use, current
509 information on P fertilization rates might have limited relevance. Particularly for total P
510 concentrations as one important driver of P_{mic} concentrations, legacy effects of former land use have
511 to be taken into account (*Smits et al., 2008; MacDonald et al., 2012*). Therefore, not actual but
512 aggregated fertilization rates over the last decades might better explain P_{mic} concentrations in
513 grassland soils. Regrettably, such information is hardly available at all or if so associated with high
514 uncertainties. Concluding, we have to reject our hypothesis of a positive effect of land-use intensity
515 and fertilization on P_{mic} concentrations in soil.

516
517 **5. Conclusions**

518 Microbial P concentrations in soil differed among study regions. This effect may well be explained by
519 different environmental conditions (pH, soil moisture, substrate availability for microorganism
520 metabolism). In addition, P_{mic} concentrations were closely related to substrate availability (especially
521 C_{org}) in both, forest and grassland soils. Despite management effects on P fractions in soil and a
522 relationship between selected P fractions and P_{mic} concentrations in soil, P_{mic} was found to be
523 insensitive to forest and grassland management measures.

524
525 **Acknowledgements**

526 We thank the managers of the three Exploratories, Kirsten Reichel-Jung, Swen Renner, Katrin
527 Hartwich, Sonja Gockel, Kerstin Wiesner, and Martin Gorke for their work in maintaining the plot and
528 project infrastructure; Christiane Fischer and Simone Pfeiffer for giving support through the central
529 office, Michael Owonibi for managing the central data base, and Markus Fischer, Eduard Linsenmair,
530 Dominik Hessenmöller, Jens Nieschulze, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser,
531 and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We

thank Ulli Bange, Theresa Klötzung, and Doreen Berner for laboratory work and Fabian Alt and all other members of the joint sampling campaign in May 2011 for their help. The work has been (partly) funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (DFG-Oe516/1-2). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

538

539 **References**

- 540 *Abdi, H., Williams, L. J. (2010): Principal component analysis. WIREs Comp. Stat. 2, 433-459.*
- 541 *Alt, F., Oelmann, Y., Herold, N., Schrumpf, M., Wilcke, W. (2011): Phosphorus partitioning in grassland*
542 *and forest soils of Germany as related to land-use type, management intensity, and land use-*
543 *related pH. J. Plant Nutr. Soil Sci. 174, 195-209.*
- 544 *Aponte, C., Garcia, L. V., Maranon, T. (2013): Tree species effects on nutrient cycling and soil biota: A*
545 *feedback mechanism favouring species coexistence. Forest Ecol. Managem. 309, 36-46.*
- 546 *Ayaga, G., Todd, A., Brookes, P. C. (2006): Enhanced biological cycling of phosphorus increases its*
547 *availability to crops in low-input sub-Saharan farming systems. Soil Biol. Biochem. 38, 81-90.*
- 548 *Bauhus, J., Paré, D., Côté, L. (1998): Effects of tree species, stand age and soil type on soil microbial*
549 *biomass and its activity in a southern boreal forest. Soil Biol. Biochem. 30, 1077-1089.*
- 550 *Baumann, K., Schöning, I., Schrumpf, M., Ellerbrock, R. H., Leinweber, P. (2016): Rapid assessment of*
551 *soil organic matter: Soil color analysis and Fourier transform infrared spectroscopy.*
552 *Geoderma 278, 49.*
- 553 *Berner, D., Marhan, S., Keil, D., Poll, C., Schützenmeister, A., Piepho, H.-P., Kandeler, E. (2011): Land-*
554 *use intensity modifies spatial distribution and function of soil microorganisms in grasslands.*
555 *Pedobiologia 54, 341-351.*
- 556 *Bergkemper, F., Bünemann, E. K., Hauenstein, S., Heuck, C., Kandeler, E., Krüger, J., Marhan, S.,*
557 *Mészáros, É., Nassal, D., Nassal, P., Oelmann, Y., Pistocchi, C., Schlöter, M., Spohn, M.,*

1
2
3 558 Talkner, U., Zederer, D. P., Schulz, S. (2016): An inter-laboratory comparison of gaseous and
4
5 559 liquid fumigation based methods for measuring microbial phosphorus (Pmic) in forest soils
6
7 560 with differing P stocks. *J. Microbiol. Methods* 128, 66-68.Boch, S., Prati, D., Müller, J., Socher,
8
9 561 S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E. K. V.,
10
11 562 Linsenmair, K. E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.-D., Seilwinder, C., Weisser,
12
13 563 W. W., Wells, K., Fischer, M. (2013): High plant species richness indicates management-
14
15 564 related disturbances rather than the conservation status of forests. *Basic Appl. Ecol.* 14, 496-
16
17 565 505.
18
19
20 566 Boeddinghaus, R. S., Nunan, N., Berner, D., Marhan, S., Kandeler, E. (2015): Do general spatial
21
22 567 relationships for microbial biomass and soil enzyme activities exist in temperate grassland
23
24 568 soils? *Soil Biol. Biochem.* 88, 430-440.
25
26 569 Bristow, A. W., Jarvis, S. C. (1991): Effects of grazing and nitrogen fertiliser on the soil microbial
27
28 570 biomass under permanent pasture. *J. Sci. Food Agric.* 54, 9-21.
29
30
31 571 Brookes, P. (2001): The Soil Microbial Biomass: Concept, Measurement and Applications in Soil
32
33 572 Ecosystem Research. *Microb. Environ.* 16, 131-140.
34
35 573 Brookins, D. G. (1988): Eh-pH diagrams for Geochemistry. Springer, New York.
36
37 574 Bünemann, E. K., Marschner, P., Smernik, R. J., Conyers, M., McNeill, A. M. (2008): Soil organic
38
39 575 phosphorus and microbial community composition as affected by 26 years of different
40
41 576 management strategies. *Biol. Fertil. Soils* 44, 717-726.
42
43
44 577 Bünemann, E. K., Steinebrunner, F., Smithson, P. C., Frossard, E., Oberson, A. (2004): Phosphorus
45
46 578 dynamics in a highly weathered soil as revealed by isotopic labeling techniques. *Soil Sci. Soc.*
47
48 579 *Am. J.* 68, 1645-1655.
49
50 580 Burns, R. G., DeForest, J. L., Marxsen, J., Sinsabaugh, R. L., Stromberger, M. E., Wallenstein, M. D.,
51
52 581 Weintraub, M. N., Zoppini, A. (2013): Soil enzymes in a changing environment: Current
53
54 582 knowledge and future directions. *Soil Biol. Biochem.* 58, 216-234.
55
56
57
58
59
60

- 583 Chen, C. R., Condon, L. M., Davis, M. R., Sherlock, R. R. (2003): Seasonal changes in soil phosphorus
584 and associated microbial properties under adjacent grassland and forest in New Zealand. *For.*
585 *Ecol. Manage.* 177, 539-557.
- 586 Chen, G. C., He, Z. L., Huang, C. Y. (2000): Microbial biomass phosphorus and its significance in
587 predicting phosphorus availability in red soils. *Commun. in Soil Sci. Plant Anal.* 31, 655-667.
- 588 Cole, C. V., Elliott, L. F., Hunt, H. W., Coleman, D. C. (1978): Trophic interactions in soils as they affect
589 energy and nutrient dynamics. V. Phosphorus transformations. *Microb. Ecol.* 4, 381-387.
- 590 Condon, L. M., Turner, B. L., Cade-Menun, B. J. (2005): Chemistry and Dynamics of Soil Organic
591 Phosphorus. In Sims, T. J., Sharpley, A. N.: Phosphorus: Agriculture and the Environment.
592 ASA, CSSA, SSSA: Madison, WI, 87-121.
- 593 Cross, A. F., Schlesinger, W. H. (1995): A literature review and evaluation of the Hedley fractionation:
594 Applications to the biogeochemical cycle of soil phosphorus in natural ecosystems.
595 *Geoderma* 64, 197-214.
- 596 Devi, T. I., Yadava, P. S., Garkoti, S. C. (2014): Cattle grazing influences soil microbial biomass in sub-
597 tropical grassland ecosystems at Nambol, Manipur, northeast India. *Tropical Ecol.* 55, 195-
598 206.
- 599 Eisenhauer, N., Beßler, H., Engels, C., Gleixner, G., Habekost, M., Milcu, A., Partsch, S., Sabais, A. C.
600 W., Scherber, C., Steinbeiss, S., Weigelt, A., Weisser, W. W., Scheu, S. (2010): Plant diversity
601 effects on soil microorganisms support the singular hypothesis. *Ecology* 91, 485-496.
- 602 Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T.,
603 Seabloom, E. W., Shurin, J. B., Smith, J. E. (2007): Global analysis of nitrogen and phosphorus
604 limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.*
605 10, 1135-1142.
- 606 Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J.,
607 Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E. K.
608 V., Linsenmair, K. E., Schulze, E.-D., Weisser, W. W. (2010): Implementing large-scale and

1
2
3 609 long-term functional biodiversity research: The Biodiversity Exploratories. *Basic Appl. Ecol.*
4
5 610 11, 473-485.
6
7 611 Fornara, D. A., Tilman, D. (2008): Plant functional composition influences rates of soil carbon and
8
9 612 nitrogen accumulation. *J. Ecol.* 96, 314-322.
10
11 613 Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Froberg,
12
13 614 M., Stendahl, J., Philipson, C. D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H.,
14
15 615 Moberg, F., Moen, J., Bengtsson, J. (2013): Higher levels of multiple ecosystem services are
16
17 616 found in forests with more tree species. *Nat. Commun.* 4, 1340.
18
19
20 617 Gardner, W. H. (1986): Water Content. In Klute, A.: Methods of Soil Analysis Part 1. Physical and
21
22 618 Mineralogical Methods. American Society of Agronomy: Madison, Wisconsin (USA), 493-544.
23
24 619 Grace, J. B., Schoolmaster, D. R., Guntenspergen, G. R., Little, A. M., Mitchell, B. R., Miller, K. M.,
25
26 620 Schweiger, E. W. (2012): Guidelines for a graphtheoretic implementation of structural
27
28 621 equation modeling. *Ecosphere* 3, 1-44.
29
30
31 622 Griffiths, B. S., Spilles, A., Bonkowski, M. (2012): C:N:P stoichiometry and nutrient limitation of the
32
33 623 soil microbial biomass in a grazed grassland site under experimental P limitation or excess.
34
35 624 *Ecol. Proc.* 1, e6.
36
37 625 Grubbs, F. E., Beck, G. (1972): Extension of Sample Sizes and Percentage Points for Significance Tests
38
39 626 of Outlying Observations. *Technometrics* 14, 847-854.
40
41 627 Hacker, N., Ebeling, A., Gessler, A., Gleixner, G., González Macé, O., de Kroon, H., Lange, M.,
42
43 628 Mommer, L., Eisenhauer, N., Ravenek, J., Scheu, S., Weigelt, A., Wagg, C., Wilcke, W.,
44
45 629 Oelmann, Y. (2015): Plant diversity shapes microbe-rhizosphere effects on P mobilisation
46
47 630 from organic matter in soil. *Ecol. Lett.* 18, 1356-1365.
48
49
50 631 Hedley, M. J., Stewart, J. W. B., Chauhan, B. S. (1982): Changes in Inorganic and Organic Soil
51
52 632 Phosphorus Induced by Cultivation Practices and by Laboratory Incubations. *Soil Sci. Soc. Am.*
53
54 633 *J.* 46, 970-976.
55
56
57
58
59
60

- 634 Herold, N., Schöning, I., Berner, D., Haslwimmer, H., Kandeler, E., Michalzik, B., Schrumpf, M. (2014a):
635 Vertical gradients of potential enzyme activities in soil profiles of European beech, Norway
636 spruce and Scots pine dominated forest sites. *Pedobiologia* 57, 181-189.
- 637 Herold, N., Schöning, I., Gutknecht, J., Alt, F., Boch, S., Müller, J., Oelmann, Y., Socher, S. A., Wilcke,
638 W., Wubet, T., Schrumpf, M. (2014b): Soil property and management effects on grassland
639 microbial communities across a latitudinal gradient in Germany. *Appl. Soil Ecol.* 73, 41-50.
- 640 Herold, N., Schöning, I., Michalzik, B., Trumbore, S., Schrumpf, M. (2014c): Controls on soil carbon
641 storage and turnover in German landscapes. *Biogeochem.* 119, 435-451.
- 642 Holland, E. A., Braswell, B. H., Sulzman, J., Lamarque, J.-F. (2005): Nitrogen deposition onto the
643 United States and western Europe: Synthesis of observations and models. *Ecol. Appl.* 15, 38-
644 57.
- 645 Joergensen, R. G., Kübler, H., Meyer, B., Walters, V. (1995): Microbial biomass phosphorus in soils of
646 beech (*Fagus sylvatica* L.) forests. *Biol. Fertil. Soils* 19, 215-219.
- 647 Joergensen, R. G., Scheu, S. (1999): Response of soil microorganisms to the addition of carbon,
648 nitrogen and phosphorus in a forest Rendzina. *Soil Biol. Biochem.* 31, 859-866.
- 649 Khan, K. S., Joergensen, R. G. (2012): Relationships between P fractions and the microbial biomass in
650 soils under different land use management. *Geoderma* 173-174, 271-281.
- 651 Kouno, K., Tuchiya, Y., Ando, T. (1995): Measurement of soil microbial biomass phosphorus by an
652 anion-exchange membrane method. *Soil Biol. Biochem.* 27, 1353-1357.
- 653 Kuo, S. (1996): Phosphorus. In Sparks, D. L., Page, A. L., Helmke, P. A., Loeppert, R., Soltanpour, P. N.,
654 Tabatabai, M. A., Johnston, A. E., Sumner, M. E.: *Methods of Soil Analysis. Part 3 - Chemical*
655 *Methods.* Soil Science Society of America: Madison, Wisconsin, 869-919.
- 656 Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J., Veneklaas, E. J. (2006): Root structure and
657 functioning for efficient acquisition of phosphorus: Matching morphological and
658 physiological traits. *Ann. Bot.* 98, 693-713.

1
2
3 659 Lange, M., Eisenhauer, N., Sierra, C. A., Bessler, H., Engels, C., Griffiths, R. I., Mellado-Vázquez, P. G.,
4
5 660 Malik, A. A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B. C., Trumbore, S. E., Gleixner, G.
6
7 661 (2015): Plant diversity increases soil microbial activity and soil carbon storage. *Nat. Commun.*
8
9 662 6.
10
11 663 Lange, M., Habekost, M., Eisenhauer, N., Roscher, C., Bessler, H., Engels, C., Oelmann, Y., Scheu, S.,
12
13 664 Wilcke, W., Schulze, E.-D., Gleixner, G. (2014): Biotic and Abiotic Properties Mediating Plant
14
15 665 Diversity Effects on Soil Microbial Communities in an Experimental Grassland. *PLoS ONE* 9,
16
17 666 e96182.
18
19
20 667 Liebisch, F., Keller, F., Huguenin-Elie, O., Frossard, E., Oberson, A., Bünemann, E. K. (2014): Seasonal
21
22 668 dynamics and turnover of microbial phosphorus in a permanent grassland *Biol. Fertil. Soils* 50,
23
24 669 465-475.
25
26 670 MacDonald, G. K., Bennett, E. M., Taranu, Z. E. (2012): The influence of time, soil characteristics, and
27
28 671 land-use history on soil phosphorus legacies: a global meta-analysis. *Global Change Biol.* 18,
29
30 672 1904-1917.
31
32
33 673 McLaughlin, M. J., Alston, A. M. (1987): Transformations and movement of P in the rhizosphere. *Plant*
34
35 674 *Soil* 97, 391-399.
36
37 675 McLaughlin, M. J., Alston, A. M., Martin, J. K. (1986): Measurement of phosphorus in the soil
38
39 676 microbial biomass: A modified procedure for field soils. *Soil Biol. Biochem.* 18, 437-443.
40
41 677 Murphy, J., Riley, J. P. (1962): A modified single solution method for the determination of phosphate
42
43 678 in natural waters. *Anal. Chim. Acta* 27, 31-36.
44
45
46 679 Naveed, M., Herath L., Moldrup, P., Arthur, E., Nicolaisen, M., Norgaard, T., Ferré, T. P. A., de Jonge, L.
47
48 680 W. (2016): Spatial variability of microbial richness and diversity and relationships with soil
49
50 681 organic carbon, texture and structure across an agricultural field. *Appl. Soil Ecol.* 103, 44-55.
51
52 682 Negassa, W., Leinweber, P. (2009): How does the Hedley sequential phosphorus fractionation reflect
53
54 683 impacts of land use and management on soil phosphorus: A review. *J. Plant Nutr. Soil Sci.*
55
56 684 172, 305-325.
57
58
59
60

- Oberson, A., Jöner, E. J. (2005): Microbial Turnover of Phosphorus in Soil. In Turner, B. L., Frossard, E., Baldwin, D. S.: Organic Phosphorus in the Environment. CABI Publishing: Cambridge, 133-164.
- Regan, K. M., Nunan, N., Boeddinghaus, R. S., Baumgartner, V., Berner, D., Boch, S., Oelmann, Y., Overmann, J., Prati, D., Schlöter, M., Schmitt, B., Sorkau, E., Steffens, M., Kandeler, E., Marhan, S. (2014): Seasonal controls on grassland microbial biogeography: Are they governed by plants, abiotic properties or both? *Soil Biol. Biochem.* 71, 21-30.
- Richardson, A. E., Simpson, R. J. (2011): Soil Microorganisms Mediating Phosphorus Availability. *Plant Physiol.* 156, 989-996.
- Smits, N. A. C., Willems, J. H., Bobbink, R. (2008): Long-term after-effects of fertilisation on the restoration of calcareous grasslands. *Appl. Veg. Sci.* 11, 279-292.
- Smolander, A., Kitunen, V. (2011): Comparison of tree species effects on microbial C and N transformations and dissolved organic matter properties in the organic layer of boreal forests. *Appl. Soil Ecol.* 49, 224-233.
- Socher, S. A., Prati, D., Boch, S., Müller, J., Klaus, V. H., Hölzel, N., Fischer, M. (2012): Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J. Ecol.* 100, 1391-1399.
- Solly, E. F., Schöning, I., Boch, S., Kandeler, E., Marhan, S., Michalzik, B., Müller, J., Zscheischler, J., Trumbore, S. E., Schrumpf, M. (2014): Factors controlling decomposition rates of fine root litter in temperate forests and grasslands. *Plant Soil* 382, 203-218.
- Steinbeiss, S., Beßler, H., Engels, C., Temperton, V. M., Buchmann, N., Roscher, C., Kreutziger, Y., Baade, J., Habekost, M., Gleixner, G. (2008): Plant diversity positively affects short-term soil carbon storage in experimental grasslands. *Glob. Change Biol.* 14, 2937-2949.
- Stutter, M. I., Shand, C. A., George, T. S., Blackwell, M. S. A., Dixon, L., Bol, R., MacKay, R. L., Richardson, A. E., Condron, L. M., Haygarth, P. M. (2015): Land use and soil factors affecting accumulation of phosphorus species in temperate soils. *Geoderma* 257-258, 29-39.

1
2
3 711 Tate, K. R. (1984): The biological transformation of P in soil. *Plant Soil* 76, 245-256.
4
5 712 Tate, K. R., Speir, T. W., Ross, D. J., Parfitt, R. L., Whale, K. N., Cowling, J. C. (1991): Temporal
6
7 713 variations in some plant and soil P pools in two pasture soils of widely different P fertility
8
9 714 status. *Plant Soil* 132, 219-232.
10
11 715 Turner, B. L., Lambers, H., Condron, L. M., Cramer, M. D., Leake, J. R., Richardson, A. E., Smith, S. E.
12
13 716 (2013): Soil microbial biomass and the fate of phosphorus during long-term ecosystem
14
15 717 development. *Plant Soil* 367, 225-234.
16
17
18 718 Vance, E. D., Brookes, P. C., Jenkinson, D. S. (1987): An extraction method for measuring soil microbial
19
20 719 biomass C. *Soil Biol. Biochem.* 19, 703-707.
21
22 720 Vitousek, P. M., Porder, S., Houlton, B. Z., Chadwick, O. A. (2010): Terrestrial phosphorus limitation:
23
24 721 mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* 20, 5-15.
25
26 722 Wang, K. H., McSorley, R., Bohlen, P., Gathumbi, S. M. (2006): Cattle grazing increases microbial
27
28 723 biomass and alters soil nematode communities in subtropical pastures. *Soil Biol. Biochem.* 38,
29
30 724 1956-1965.
31
32
33 725 Wardle, D. A. (1992): A comparative assessment of factor which influence microbial biomass carbon
34
35 726 and nitrogen levels in soil. *Biol. Rev.* 67, 321-358.
36
37 727 Wardle, D. A. (1998): Controls of temporal variability of the soil microbial biomass: A global-scale
38
39 728 synthesis. *Soil Biol. Biochem.* 30, 1627-1637.
40
41
42 729 Yeates, G. W., Saggiar, S. (1998): Comparison of soil microbial properties and fauna under tussock-
43
44 730 grassland and pine plantation. *J. Roy. Soc. New Zeal.* 28, 523-535.
45
46 731 Zavišić, A., Nassal, P., Yang, N., Heuck, C., Spohn, M., Marhan, S., Pena, R., Kandeler, E., Polle, A.
47
48 732 (2016): Phosphorus availabilities in beech (*Fagus sylvatica* L.) forests impose habitat filtering
49
50 733 on ectomycorrhizal communities and impact tree nutrition. *Soil Biol. Biochem.* 98, 127-137.
51
52 734 Zhong, Z., Makeschin, F. (2006): Differences of soil microbial biomass and nitrogen transformation
53
54 735 under two forest types in central Germany. *Plant Soil* 283, 287-297.
55
56
57 736
58
59
60

Table 1: Main geographical and environmental characteristics of the study regions (*Fischer et al.*, 2010).

region	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
abbreviation	ALB	HAI	SCH
located in Germany	south-west	central	north-east
altitude	460 – 860 m a.s.l.	258 – 550 m a.s.l.	3 – 140 m a.s.l.
mean temperature	6 – 7 °C	6.5 – 8 °C	8 – 8.5 °C
mean precipitation	700 – 1,000 mm	500 – 800 mm	500 – 600 mm
parent material	calcareous bedrocks with karst phenomena	calcareous bedrocks of Triassic limestone covered by loess	glacial till covered with glacio-fluvial or Aeolian sand
soil texture	rich in clay	loamy or clayey	sandy loam to pure sand
soil type	Cambisols, Leptosols	Cambisols, Stagnosols, Vertisols, Luvisols	Histosols, Luvisols, Gleysols, Albeluvisols, Cambisols, Regosols, Podzols
main tree species	beech, spruce	beech, spruce	beech, oak, pine
land-use type	<i>grassland</i> : meadow (<i>n</i> = 22), mown pasture (<i>n</i> = 9), pasture (<i>n</i> = 19) <i>forest</i> : age class forest (<i>n</i> = 46), unmanaged forest (<i>n</i> = 4)	<i>grassland</i> : meadow (<i>n</i> = 7), mown pasture (<i>n</i> = 23), pasture (<i>n</i> = 20) <i>forest</i> : age class forest (<i>n</i> = 28), unmanaged forest (<i>n</i> = 13), selection cutting (<i>n</i> = 9)	<i>grassland</i> : meadow (<i>n</i> = 18), mown pasture (<i>n</i> = 10), pasture (<i>n</i> = 22) <i>forest</i> : age class forest (<i>n</i> = 45), unmanaged forest (<i>n</i> = 5)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

740 Table 2: Relationship of different biotic and abiotic variables to P_{mic} in forest and grassland soils
741 (r = *Pearsons's* rank correlation, n = sample size; ns = not significant, * $P < 0.05$ ** $P < 0.01$,
742 *** $P < 0.001$).

land-use type		forest soils		grassland soils	
variable		r	n	r	n
abiotic	clay	0.83***	133	0.33***	140
	medium silt	0.33***	133	0.29**	140
	medium sand	-0.58***	133	-0.38***	140
	soil moisture (10 cm below surface)	0.80***	133	0.54***	140
	NaHCO ₃ -P _i	-0.37***	117	-0.38***	108
	NaHCO ₃ -P _o	-0.51***	117	ns	108
	NaOH-P _i	ns	117	ns	108
	NaOH-P _o	0.57***	117	0.38***	108
	HCl-P	0.71***	117	0.22 *	108
	H ₂ SO ₄ -P	0.71***	117	0.22 *	108
	Σ NaHCO ₃ -P _i + NaOH-P _i	ns	117	ns	108
	Σ NaHCO ₃ -P _o + NaOH-P _o	0.48***	117	0.48**	108
	total P	0.72***	117	0.28**	108
	pH	0.72***	118	0.30***	131
	C _{org}	0.65***	133	0.44***	140
	total N	0.86***	133	0.48***	140
	C : N	-0.55***	133	ns	140
biotic	N _{mic}	0.71***	132	0.57***	140
	C _{mic}	0.86***	132	0.63***	140
	C _{mic} : N _{mic}	-0.26**	132	ns	140
	plant diversity	0.45***	132	ns	140

743

744

Table 3: Mean [$\pm$ standard deviation] of Pmic concentrations differentiated to land use and region (in mg kg⁻¹; na = not available, different letters present significant differences within the exploratory [$P < 0.05$]).

	land-use type	region					
		Schwäbische Alb		Hainich-Dün		Schorfheide-Chorin	
Forest soils	tree species						
	beech	53.6[$\pm$ 18.6]	a	22.2[$\pm$ 9.7]	a	4.7[$\pm$ 2.7]	b
	spruce	48.7[$\pm$ 19.7]	a	29.9[$\pm$ 8.6]	a	na	
	oak	na		na		4.8[$\pm$ 1.4]	ab
	pine	na		na		7.2[$\pm$ 2.9]	a
	management						
	age class forest	51.2[$\pm$ 18.8]	a	24.6[$\pm$ 10.7]	a	5.8[$\pm$ 2.9]	a
	unmanaged forest	66.0[$\pm$ 13.3]	a	24.5[$\pm$ 8.9]	ab	6.7[$\pm$ 3.7]	a
	selection cutting	na		15.6[$\pm$ 2.7]	b	na	
	fertilization						
Grassland soils	yes	63.4[$\pm$ 24.1]	a	49.7[$\pm$ 24.2]	a	46.0[$\pm$ 26.5]	a
	no	66.3[$\pm$ 20.7]	a	52.7[$\pm$ 14.7]	a	42.7[$\pm$ 32.0]	a
	management						
	meadow	64.2[$\pm$ 23.7]	a	44.2[$\pm$ 25.1]	a	53.1[$\pm$ 29.3]	a
	mown pasture	64.6[$\pm$ 25.7]	a	52.9[$\pm$ 22.0]	a	52.2[$\pm$ 35.5]	a
	pasture	65.1[$\pm$ 21.0]	a	52.0[$\pm$ 15.6]	a	31.3[$\pm$ 26.3]	a
	number of cuts per year						
	0	66.1[$\pm$ 21.0]	a	52.6[$\pm$ 14.8]	a	31.3[$\pm$ 26.3]	a
	1	70.5[$\pm$ 22.5]	a	54.1[$\pm$ 25.4]	a	46.7[$\pm$ 35.2]	a
	2	64.8[$\pm$ 25.6]	a	39.6[$\pm$ 8.5]	a	60.0[$\pm$ 25.1]	a
	3	51.7[$\pm$ 18.9]	a	26.3[$\pm$ 5.1]	a	58.7[$\pm$ 30.2]	a

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure captions

Figure 1: Mean concentrations of P_{mic} in a) forest and b) grassland soils from three exploratory regions in Germany (ALB = Schwäbische Alb, HAI = Hainich-Dün, SCH = Schorfheide-Chorin; error bars represent standard errors; different letters represent significant differences [$P < 0.05$]).

Figure 2: Structural equation model 1 of the relationships between different abiotic controlling factors, plant diversity (diversity) and P_{mic} in grassland sites for ALL (all three regions together, RMSEA = 0.081), ALB (Schwäbische Alb, RMSEA < 0.001), HAI (Hainich-Dün, RMSEA < 0.001) and SCH (Schorfheide-Chorin, RMSEA < 0.001). In this model, plant diversity is considered as response variable i.e., depending on organic C (C_{org}) concentrations. The percentage of explained variance of the variable is given in brackets. Numbers next to arrows represent standardized path coefficients. Path lines: bold lines = $P < 0.05$; thin lines = $P \geq 0.05$; solid line = positive path coefficient; dashed line = negative path coefficient.

Figure 3: Structural equation model 2 of the relationships between different abiotic controlling factors, plant diversity (diversity) and P_{mic} in grassland sites with plant diversity as driving factor for ALL (all three regions together, RMSEA = 0.271), ALB (Schwäbische Alb, RMSEA < 0.001), HAI (Hainich-Dün, RMSEA = 0.180), and SCH (Schorfheide-Chorin, RMSEA < 0.001). In this model, plant diversity is considered as independent variable i.e., controlling both organic C (C_{org}) and P_{mic} concentrations. The percentage of explained variance of the variable is given in brackets. Numbers next to arrows represent standardized path coefficients. Path lines: bold lines = $P < 0.05$; thin lines = $P \geq 0.05$; solid line = positive path coefficient; dashed line = negative path coefficient.

Figure 1:

Figure 2:

Figure 3: