

1 Biological Sciences/ Environmental Sciences

2 **Soil food web properties explain ecosystem services across European land**
3 **use systems**

4 Short title: soil food webs explain ecosystem services

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51

52 **Abstract**

53 Intensive land use reduces the diversity and abundance of many soil biota, with
54 consequences for the processes that they govern and the ecosystem services that these
55 processes underpin. Relationships between soil biota and ecosystem processes have
56 mostly been found in laboratory experiments, and rarely in the field. Here, we quantified,
57 across four countries of contrasting climatic and soil conditions in Europe, how
58 differences in soil food web composition resulting from land use systems (intensive
59 wheat rotation, extensive rotation, and permanent grassland) influence the functioning of
60 soils and the ecosystem services they deliver. Intensive wheat rotation consistently
61 reduced the biomass of all components of the soil food web across all countries. Soil food
62 web properties strongly and consistently predicted processes of C and N cycling across
63 land use systems and geographic locations, and were a better predictor of these processes
64 than was land use. Carbon loss increased with soil food web properties that correlated
65 with soil C content, such as earthworm biomass and fungal/bacterial energy channel ratio,
66 and were greatest in permanent grassland. In contrast, processes of N cycling were
67 explained by soil food web properties independent of land use, such as arbuscular
68 mycorrhizal fungi and bacterial channel biomass. Our quantification of the contribution
69 of soil organisms to processes of C and N cycling across land use systems and geographic
70 locations shows that soil biota need to be included in C and N cycling models, and
71 highlights the need to conserve and map soil biodiversity across the world.

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74 **Introduction**

75 Soils are of central importance for delivering ecosystem services such as food production
76 and climate mitigation. These services strongly depend on carbon (C) sequestration and
77 nutrient cycling, processes that are governed by soil biota. Increasing demand for the
78 production of food, fiber and biofuel has resulted in intensification of agricultural
79 production, which reduces soil organic matter content (1) and the biomass and diversity
80 of most soil biota (2), with consequent impacts on processes of C and nutrient cycling.
81 Specifically, land use-induced shifts towards more bacterial-dominated microbial
82 communities have been linked to increased nitrogen (N) losses (3-5) and reduced C
83 sequestration (6). Conversely, fungal-dominated microbial communities, which are
84 common in less intensively managed land use systems, are linked to more conservative
85 nutrient cycling and greater storage of C (5, 7, 8). Although soil microbes are the primary
86 actors in C and N cycling, their biomass and activity is greatly influenced by higher
87 trophic levels of the soil food web. For instance, animals that consume micro-organisms
88 can stimulate rates of nutrient mineralization (9) and plant productivity (10), whereas
89 bioturbators, such as earthworms, can further increase nutrient availability for plants (11),
90 although they can also increase N₂O emissions from soil (12).

91 Although there is evidence from field studies that soil microbial communities are
92 linked to ecosystem functioning (13, 14), most studies on relationships between soil
93 fauna and ecosystem function have been done in controlled (microcosm) experiments
94 (15). As a result, our understanding of the functional importance of different groups of
95 soil biota, and the connections between them (the soil food web) in the field is limited,

96 and it is not known how changes in soil food web structure across contrasting locations
97 and land use systems impact on ecosystem functioning. There is some evidence to
98 suggest that the role of the soil food webs relative to abiotic factors in regulating
99 ecosystem functions will vary across geographical locations and environmental gradients
100 (16). Moreover, differences in land use have been shown to affect the resistance and the
101 resilience of soil food webs to simulated drought, with consequences for processes of C
102 and N cycling (17). Therefore, quantifying general relationships between soil biota and
103 processes of C and N cycling is of pivotal importance for predicting how these processes
104 will be affected by global change.

105 Our aim was to quantify, across geographically contrasting locations in Europe,
106 how changes in soil food web composition resulting from land use systems influence the
107 ecosystem services that they deliver. We hypothesized that, across European land use
108 systems, processes of C and N cycling are explained by soil food web properties, on top
109 of variation explained by other factors such as land use and soil physical and chemical
110 properties. Specifically, we hypothesized that: (i) more intensive land use consistently
111 reduces the biomass of soil fungi and their consumers and increases the dominance of
112 bacteria and their consumers (i.e., decrease the fungal/bacterial (F/B) channel ratio); and
113 (ii) a shift towards greater dominance of bacteria and their consumers (i.e., decreasing
114 fungal/bacterial channel ratio) increases rates of C and N cycling and loss.

115 To test these hypotheses, we measured C and N fluxes at 60 sites in four European
116 countries (Sweden, United Kingdom, Czech Republic, and Greece), distributed across
117 five locations in each country, and representing either intensive annual crop rotation
118 (high intensity or H), extensive rotation including legumes or ley (medium intensity or

119 M), and permanent grassland (low intensity or L). Measurements included potential N
120 mineralization, which is a measure of the release of N for plant uptake, and losses of N
121 and C from soil, both as gases and in drainage waters. Gaseous emissions from
122 agricultural soils, as N₂O, CO₂, and CH₄, contribute significantly to global warming and
123 atmospheric pollution (18), and leaching of C and N in drainage waters contributes to
124 eutrophication of ground and surface water (19). We also quantified the biomass of key
125 functional groups in the soil food web, including fungi and bacteria, protozoa, nematodes,
126 earthworms, Enchytraeids, mites, and collembolans. To relate the structure of the soil
127 food web to C and N fluxes, we calculated traditional soil food web properties, such as
128 the number of feeding groups in the food web. In addition, to test our hypothesis that land
129 use will alter the relative importance of the fungal and bacterial energy channels, we
130 calculated measures based on the fungal, bacterial, and root energy channels
131 (Supplementary Methods).

132 Soil food webs and their corresponding C and N fluxes are likely to be affected by
133 factors such as land use, soil properties, and the spatial structure of sampling sites. To
134 determine whether soil food web characteristics explained a unique proportion of
135 variation in ecosystem services, and to deduce meaningful relationships between soil
136 food web properties and C and N fluxes, we also accounted for variation caused by the
137 spatial structure of the sites (which can be caused by autocorrelation between values of
138 the response variable, or by underlying factors such as climate and geology), land use,
139 and soil properties. We accounted for spatial autocorrelation in the measured variables by
140 calculating spatial filters using principal coordinates of neighbor matrices (20), and we
141 used a hierarchical modeling approach that has previously been used to explain

142 landscape-scale variation in soil microbial communities on the basis of climatic factors,
143 soil properties, and plant traits (21) (Methods and Supplementary Methods).

144

145 **Results and discussion**

146 Across all four countries, soil food web structure was strongly influenced by land use
147 (Table S1, S2). The number of feeding groups, the total biomass of the soil food web, and
148 the biomass of the fungal, bacterial, and root energy channel (which consists of
149 arbuscular mycorrhizal fungi (AMF), root-feeding fauna, and their predators) were all
150 lower under the medium and high intensity land use categories relative to the low
151 intensity category (Table S1). The biomass of many individual feeding groups of soil
152 biota was lower under these more intensive land uses (Table S2). These results indicate
153 that, across contrasting sites in Europe, land use intensification consistently reduces the
154 biomass of all components of the soil food web. However, in contrast to our hypothesis,
155 land use intensification did not influence the ratio of fungal to bacterial biomass, or the
156 ratio of fungal energy channel to bacterial energy channel biomass in any of the countries
157 sampled. Instead, land use intensification equally reduced the biomass of most feeding
158 groups in the soil food web. However, the biomass of the groups that are part of the root
159 energy channel was reduced more than that of the organisms of the fungal and bacterial
160 energy channel together (the detritus energy channel, Table S1). This can be explained by
161 the effect of tillage, which was included in the medium and high intensity land use forms,
162 and disrupts root associated organisms and their consumers (8, 22).

163 All our models explaining processes of C and N cycling included one or more soil
164 food web measures, indicating that relationships between soil biota and ecosystem

165 functioning are surprisingly consistent across contrasting sites in Europe (Table 1, 2). In
166 four out of six models, land use was not included as an explanatory variable, which
167 indicates that soil food web properties are better predictors of processes of C and N
168 cycling than land use. This might be because within our three broad land use categories,
169 more subtle differences in management might have impacted on soil food web structure,
170 which in turn affected ecosystem processes. The inclusion of spatial filters in all final
171 models illustrates the importance of accounting for the spatial structure of sampling sites
172 across this scale (Table 1, 2), and shows that C and N fluxes varied both among and
173 within European regions. Still, only the model for potential N mineralization included an
174 interaction term between a soil food web property (namely bacterial energy channel
175 biomass) and a spatial filter (Filter 3), indicating that the relationship between bacterial
176 energy channel biomass and N mineralization was dependent on geographical location
177 (Table 1, Box 1). For all other models, the relationship between soil food web properties
178 and the process of C or N cycling was independent of location.

179 In line with our second hypothesis, across all 60 European farmland sites, the
180 biomass of the bacterial energy channel was positively related to rates of N
181 mineralization (Fig. 1, Table 1). Interestingly, although the bacterial energy channel was
182 reduced by intensive land use, N mineralization was not affected by land use (Fig. S1),
183 suggesting that the relationship between the bacterial energy channel and N
184 mineralization was independent of land use. Field studies have shown that fungal-based
185 soil food webs have lower N-leaching losses from soil (5, 23) and lower rates of N
186 mineralization (24). In laboratory studies, greater bacterial abundance has been linked to
187 increased rates of N mineralization, and the presence of bacterial-feeders in soil has often

188 been shown to increase rates of N mineralization, both indirectly through stimulating
189 bacterial activity, and directly through excreting N compounds (9, 25, 26). However, our
190 study is the first to show that N mineralization rates increase with greater biomass of the
191 entire bacterial decomposition channel. This suggests that the intensification-induced
192 reduction in bacterial channel biomass might increase the dependency on mineral
193 fertilizer.

194 Mineralization of N can turn into a disservice when N supply is too high for crop
195 uptake, and excess N is washed away in drainage waters, or lost to the atmosphere
196 through denitrification (27). Across all sites, leaching of N was strongly explained by the
197 biomass of two functional groups, which together accounted for more than half of the
198 variation explained by the full model (Table S3). Nitrogen leaching increased with
199 greater biomass of bacterial-feeding nematodes (Table 1, Fig. 1), which is in line with our
200 hypothesis, and with the stimulating effect of bacterial grazers on N mineralization. In
201 addition, we found that N leaching decreased with increasing biomass of AMF across all
202 sites. Laboratory studies have shown that AMF reduce leaching of N and phosphorus (P)
203 (28), but we are not aware of such a relationship being detected in the field, as we show
204 here. Surprisingly, N leaching was not affected by land use across sites (Fig. S1), which
205 shows that its relationship with AMF is independent of the impact of land use on AMF.

206 Production of N₂O – a product of the denitrification process in soil –decreased
207 across all locations with increasing biomass of flagellates, a group of protozoa that are
208 part of the bacterial energy channel (Table 1). A mechanistic link between protozoa and
209 N₂O production has never been reported before. Since protozoa are aquatic organisms,
210 this correlation probably reflects that denitrification predominantly occurs in anoxic

211 zones in the soil (12). Although N₂O emission is generally strongly affected by
212 agricultural management (29), we did not find a link with land use here (Fig. S1).

213 Across all sites, we found that the three land use types were all methane sinks, and
214 the intensive rotation and permanent grassland were stronger methane sinks than the
215 extensive rotation. Legumes were included in the extensive rotation in three of the four
216 countries (Fig. S1, Table S4-S7) and have been shown to reduce the strength of the
217 methane sink in grasslands (30). Methane consumption also decreased with decreasing
218 fungal/bacterial biomass ratio and increasing biomass of bacteria (Table 2), which
219 suggests that the decrease in bacterial biomass as a result of land use intensification, as
220 was found here, might affect the abundance of methanotrophs, for example via an
221 increase in nitrifiers at the expense of methanotrophs (31).

222 Production of CO₂ measured *in situ* is a measure of soil heterotrophic activity and
223 root respiration, and forms a pathway of C loss from soil. Production of CO₂ was greatest
224 in the permanent grassland (Fig. S1), which is consistent with these soils having the
225 greatest C content (Table S4-S7). Production of CO₂ was also positively related to the
226 biomass of earthworms, which were most abundant in the permanent grassland (Table
227 S2). Several field-based experiments have shown significant impacts of earthworms on C
228 and N cycling (12), but evidence for impacts of earthworms on respiration in the field is
229 scarce. In addition, and in contrast to our hypothesis, CO₂ production increased with
230 greater importance of the fungal energy channel (greater F/B channel ratio, Table 2, Fig.
231 1), a relationship that was independent of land use. Fungal-dominated soil food webs are
232 thought to be more efficient in their C use, although evidence is limited (6). The positive
233 relationship found here between the fungal decomposition pathway and CO₂ production

234 might be a consequence of the fact that C-rich soils are generally fungal-dominated (5);
235 consistent with this, we found a positive relationship between biomass of the fungal
236 energy channel and soil organic C (Table S1). However, a greater CO₂ production does
237 not necessarily mean a greater loss of soil C, given that soil C content is determined by
238 the balance between C loss by respiration and C gain by photosynthesis.

239 Similar to CO₂ production, leaching of DOC was greatest from permanent
240 grassland across all sites (Table 2). In addition, DOC leaching increased with the biomass
241 of fungal-feeding collembolans and bacterial-feeding nematodes. This might be a
242 consequence of the greater biomass of the fungal energy channel with greater soil C
243 stocks (Table S1), although the biomass of fungal-feeding collembolans itself was not
244 related to soil organic C (Table S2). The link between DOC leaching and fungal-feeding
245 collembolans suggests that this functional group might be a sensitive indicator for
246 changes in labile C availability. In addition, labile C constitutes an easily decomposable
247 food source for microbes, which might stimulate microbial growth and increase the
248 biomass of bacterial and fungal grazers through bottom-up effects (32).

249 In sum, we found strong and consistent impacts of land use on the structure of soil
250 food webs across land use systems in four climatically different regions in Europe; land
251 use intensification reduced the abundance of most functional groups of soil organisms. In
252 turn, soil food web properties strongly influenced processes of C and N cycling, and these
253 relationships were consistent across land use types and sampling locations. The predictive
254 power of soil food web structure or functional groups varied between the processes
255 measured, but was of equal importance as abiotic factors (Table S3). While relationships
256 between soil food web properties and processes of C cycling were mostly related to land

257 use intensity, relationship with N cycling processes were not. In all cases, soil food web
258 properties were better predictors of processes of C and N cycling than land use. Although
259 ultimately correlative, the relationships we found between bacterial-feeding animals,
260 AMF, and earthworms, and C and N cycling are in line with results from mechanistic
261 experiments (e.g. 9, 12, 28). Therefore, our results strongly suggest that including soil
262 food web parameters will enhance the predictive capacity of C and N cycling models.

263 Process-based C and N cycling models require detailed input information that is
264 often not available on regional scales (33), and general relationships between soil food
265 web properties and processes of C and N cycling have the potential to simplify these
266 models. Although more validation is needed, for example within the countries and soil
267 types sampled, the simple relationships between earthworms and CO₂ production, or
268 between AMF abundance and N leaching, might help parameterize C cycling and
269 ecosystem service models such as ORCHIDEE-STICS (34) and MOSES (35). Moreover,
270 explicitly incorporating soil food web properties and their response to land use and
271 climate change (17) in Dynamic Global Vegetation Models (DGVM's) might improve
272 predictions of climate change impacts on terrestrial ecosystem functions and their
273 feedbacks to climate change (36). Finally, there is an urgent need to identify and evaluate
274 indicators for soil-based ecosystem services (37). The quantitative relationships between
275 simple soil food web measures and ecosystem services demonstrated in our analysis
276 could be used to assess soil-based ecosystem services, such as N leaching from soil.
277 Although the relationships revealed by our analysis require further validation, they are an
278 important first step toward quantifying general relationships between soil food web
279 properties and ecosystem processes in the field. Soil biodiversity is under threat by a

280 range of pressures, but remains severely understudied (38); our results explicitly quantify
281 the contribution of soil organisms to processes of C and N cycling across a wide range of
282 management and environmental conditions, and thus warrant efforts to conserve and map
283 soil biodiversity across the world.

284

285 **Materials and Methods**

286 **Field sites and sampling**

287 We selected four countries across Europe; Sweden, United Kingdom, Czech Republic,
288 and Greece. In each country sampling was done at five locations, each with three
289 managements: intensive rotation (high intensity or H), extensive rotation (medium
290 intensity or M), and permanent grassland (low intensity or L). This nested design resulted
291 in 60 sampling sites (4 countries \times 5 farms \times 3 managements). Between May and July
292 2009, in each site, two 1m² plots were randomly selected, and for each soil nutrient,
293 microbial and faunal analysis separate, replicate soil cores (5cm diam., 10 cm depth)
294 were taken from each plot and kept cool (4 °C) until analysis (see below). Gas samples
295 were taken *in situ*: in each plot, a 10-cm inner diameter collar consisting of a PVC
296 cylinder was pushed 5 cm into the soil. After this, a 5-cm-high PVC lid was fitted into a
297 butyl rubber lined groove in each collar. An eight-ml gas sample was taken immediately,
298 and 30 min after attaching the lids. See Tables S3-S6 for climate data of sampling regions
299 and for details on soil properties and management.

300

301 **Soil analyses**

302 Total soil C and N were analysed on air dried soil with a Leco CNS-2000 analyzer, and
303 total organic C was measured in a Primacs^{SLC} TOC Analyzer on dried (100 °C) soil. Soil
304 pH and gravimetric moisture content were determined using standard methods. Water
305 holding capacity was determined by placing saturated undisturbed soil cores on a suction
306 pressure plate, and after drying at 105°C, bulk density was calculated. All soil, food web,
307 and nutrient flux measures were expressed per m², except potential N mineralization.

308

309 **C and N fluxes**

310 Gas samples were analysed for CO₂, N₂O, and methane as described in Priemé and
311 Christensen (39). Soil leachates were obtained and analysed for concentrations of
312 inorganic N and dissolved organic carbon (DOC) and total N, as described by De Vries et
313 al. (5). Potential N mineralization was assessed by incubating a 5g soil sample at 60%
314 WHC for 1 and 3 weeks at 25°C, extracting with KCl and analysing inorganic N. The net
315 amount of inorganic N mineralized in two weeks was calculated as the difference in
316 inorganic N between week 3 and week 1.

317

318 **Food web analyses**

319 Phospholipid fatty acids (PLFAs) were extracted from 3 g of soil according to Frostegård
320 et al. (40). The PLFAs 15:0, i15:0, a15:0, i16:0, 16:0 ω 9, i17:0, a17:0, cy17:0, 18:1 ω 7 and
321 cy19:0 were used as markers of bacterial biomass (40). The amount of PLFA 18:2 ω 6 was
322 used as marker of non-mycorrhizal fungal biomass and the neutral lipid fatty acid
323 (NLFA) 16:1 ω 5 as a marker for arbuscular mycorrhizal fungi (AMF) (41). Fatty acids
324 were converted into biomass C using the following factors: bacterial biomass 363.6 nmol

325 PLFA = 1 mg carbon (40). Fungal biomass: 11.8 nmol PLFA = 1 mg carbon (42), AMF
326 biomass: 1.047 nmol NLFA = 1 μ g carbon (41). Protozoa numbers were estimated using
327 a modified most probable number method, and enchytraeid worms were extracted from
328 intact soil core samples using wet funnels. Nematodes were extracted from a 150 ml
329 sample with the modified Cobb's sieving and decanting method (43), and soil mesofauna
330 were extracted from undisturbed samples using Tullgren funnels. Nematodes were
331 identified to the genus level and allocated to trophic groups, Collembola, Acari and
332 Oribatida were determined to species level. For more information on food web analyses
333 and biomass calculations see Supplementary Methods.

334

335 **Statistical analysis**

336 We generated statistical models for each ecosystem service, using spatial filters,
337 soil properties, land use, and soil food web characteristics. We used linear mixed effects
338 models with a farm level random effect term to account for the clustering of fields in
339 sampling locations. Analysis was conducted using the lme function of R version 2.11.1
340 (R Development Core Team 2009). Model selection followed the hierarchical procedure
341 used by De Vries et al. (21). In short, the order in which variables were added to linear
342 mixed effects models followed a hypothesized sequence of controls, being such that
343 variables added later in the modeling process are unlikely to affect those added earlier.
344 The first terms added to the models were spatial filters, after which we sequentially added
345 soil properties, land use, soil C and N contents, and finally soil food web properties.
346 Models were selected based on Akaike's Information Criterion (AIC), and true
347 significance of retained terms was assessed by a chi-squared likelihood ratio deletion test

348 (LRTs). For detailed information on the modeling procedure see Supplementary
349 Methods.

350

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357

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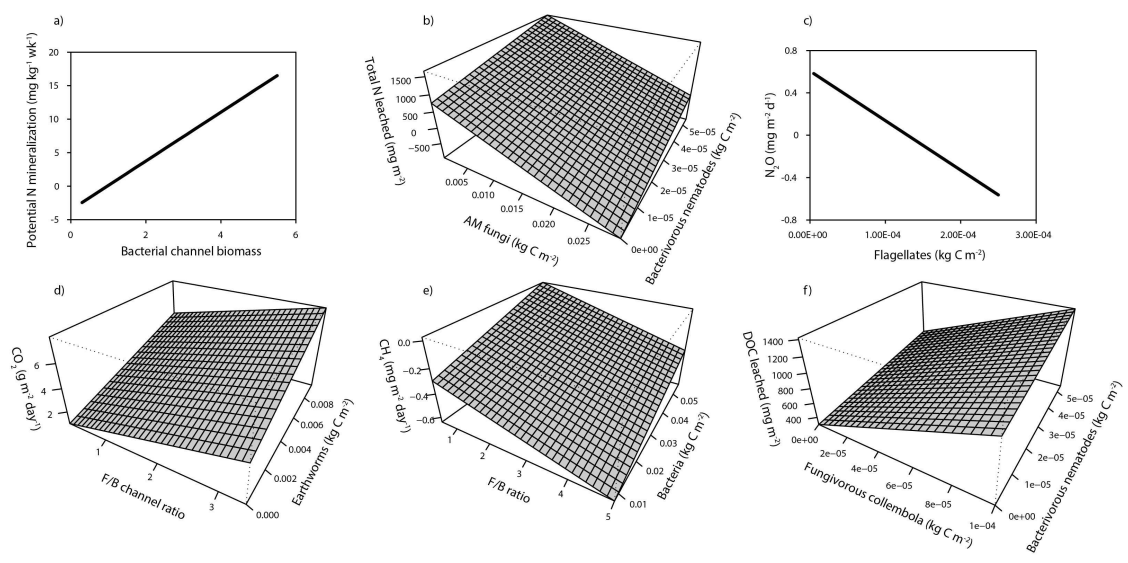
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471 **Figure legends**

472 Figure 1. Fitted relationships between ecosystem services and soil food web properties.
473 Variables that were included in the models, but not shown in the graphs (see Table 1 and
474 2), were kept constant at their mean value in the dataset. a) Potential N mineralization
475 explained by standardized biomass of the bacterial energy channel; b) total N leached
476 explained by AMF biomass and biomass of bacterivorous nematodes; c) N₂O production
477 explained by biomass of flagellates; d) CO₂ production explained by F/B channel ratio
478 and earthworm biomass; e) CH₄ production explained by F/B ratio and bacterial biomass
479 (relationship shown is for intensive wheat rotation and permanent grassland; for
480 extensive rotation CH₄ production increases with 0.17 mg m⁻² d⁻¹, see Table 2); and f)
481 DOC leached from soil explained by fungivorous collembolans and bacterivorous
482 nematodes (relationship shown is for intensive wheat rotation and extensive rotation; for
483 permanent grassland DOC leaching increases with 1317 mg m⁻², see Table 2).
484



485

486 Fig 1

487 Table 1. Selected models for potential N mineralization, total N leached, and N₂O production. For each N cycling process, the best
 488 explaining model is shown, with intercept, parameters and their parameter value (within each category of parameters), and *P*-value as
 489 obtained by an L-ratio deletion test (Supplementary Methods). For interpretation of the models see Box 1.

	<i>Potential N mineralization</i>		<i>Total N leached</i>		<i>N₂O</i>	
	Parameter value	<i>P</i>	Parameter value	<i>P</i>	Parameter value	<i>P</i>
Intercept	-17.33	0.0096	774	<0.0001	0.606	0.0009
Spatial filters	+224.7*Filter3	<0.0001	-1932*Filter2	0.0004	-2.445*Filter5	0.0054
Soil physical properties	+65.7*moist	<0.0001				
	-752.2*Filter3*moist	<0.0001				
Land use						
N and C stocks						
Soil food web structure	+3.64*pathbact	0.0074				
	-38.2*Filter3*pathbact	0.0027				
Biomass of individual functional groups			-60114*AM fungi	0.004	-4678*flagellates	0.0196
			+16357441* bacnem	0.024		
Model R-squared	0.45		0.34		0.17	

490 Abbreviations: moist = moisture content, pathbact = standardized biomass of the bacterial energy channel, bacnem = biomass of
 491 bacterial-feeding nematodes.
 492

493 Table 2. Selected models for CO₂ production, CH₄ production, and DOC leached. For each C cycling process, the best explaining
 494 model is shown, with intercept, parameters and their parameter value (within each category of parameters), and *P*-value as obtained by
 495 an L-ratio deletion test (Supplementary Methods). For interpretation of the models see Box 1.

	<i>CO₂</i>		<i>CH₄</i>		<i>DOC leached</i>	
	Parameter value	<i>P</i>	Parameter value	<i>P</i>	Parameter value	<i>P</i>
Intercept	0.74	0.033	-0.27	0.044	296	<0.0001
Spatial filters	-5.17*Filter2	0.0003			-658*Filter2 -230*Filter4	0.001 0.28
Soil physical properties						
Land use			-0.08*L +0.17*M	0.0078	+326*L -1317*Filter4*L	<0.0001 0.0001
N and C stocks						
Soil food web structure	+1.0*pathFB	0.0003	-0.08*F/B ratio	0.046		
Biomass of individual functional groups	+400*worms	<0.0001	+6.65*bacteria	0.049	+8106164*fungcoll +5798305*bacnem	<0.0001 0.017
Model R-squared	0.53		0.24		0.77	

496 Abbreviations: L = low intensity permanent grassland, M = medium intensity rotation including legume, pathFB = fungal-to-bacterial
 497 energy channel biomass ratio, F/B ratio = fungal-to-bacterial biomass ratio, worms = earthworm biomass, fungcoll = biomass of
 498 fungal-feeding Collembola, bacnem = biomass of bacterial-feeding nematodes.

499

Box 1. Interpretation of predictive models for processes of C and N cycling.

Models obtained through model selection of linear mixed effects models can be used to predict processes of C and N cycling within the locations and land use systems sampled. All our models follow the general structure of $y = a + p_1 * x_1 + p_2 * x_2 + p_i * x_i$ in which a is the intercept, p_1 is the parameter value for predictor x_1 , p_2 is the parameter value for predictor x_2 , and p_i is the parameter value for predictor x_i . For example, according to our selected model, CO_2 production (in $\text{g m}^{-2} \text{ day}^{-1}$) equals $0.74 - 5.17 * \text{Filter2} + 1.0 * \text{pathFB} + 400 * \text{worms}$ (Table 2). This can be interpreted as an increase in CO_2 production of $1 \text{ g m}^{-2} \text{ day}^{-1}$ when the ratio of standardised fungal energy channel to standardised bacterial energy channel increases with one unit, but note that the F/B channel ratio ranges from 0.2 to 3.4 across all sampling locations. Similarly, CO_2 production would increase with $400 \text{ g m}^{-2} \text{ day}^{-1}$ when earthworm biomass increases with 1 kg C m^{-2} , which ranges from 0 to $0.0095 \text{ kg C m}^{-2}$ in our dataset. However, CO_2 production decreases with $5.17 \text{ g m}^{-2} \text{ day}^{-1}$ when values for spatial filter 2, which account for variation between countries, increase with 1 unit. Spatial filter 2 ranges from -0.2104 in Sweden (average value for Sweden is -0.2088) to 0.1257 in the UK (average value for the UK is 0.1254). This means that CO_2 production is, on average, $1.72 \text{ g m}^{-2} \text{ day}^{-1}$ higher in Sweden than in the UK.

The model for potential N mineralization is more complicated, but can be interpreted in the same way. Potential N mineralization (in $\text{mg kg}^{-1} \text{ wk}^{-1}$) equals $-17.33 + 224.7 * \text{Filter3} + 65.7 * \text{moist} - 752.2 * \text{Filter3} * \text{moist} + 3.65 * \text{pathbact} - 38.2 * \text{Filter3} * \text{pathbact}$ (Table 1). This means that N mineralization increases with $3.64 \text{ mg kg}^{-1} \text{ wk}^{-1}$ when the standardized bacterial energy channel biomass (which ranges from 0.3 to 4.7) increases with one unit; however, this increase depends on spatial filter 3 (model interaction term $-38.2 * \text{Filter3} * \text{pathbact}$), which accounts for spatial variation within Czech Republic. Since spatial filter 3 is negative and ranges from -0.322 to -0.047 in Czech Republic, whereas it is positive and relatively constant (from 0.068 to 0.072) in the three other countries, this results in a stronger positive relationship between bacterial energy channel biomass and potential N mineralization in Czech Republic than in Greece, Sweden, and the UK.

For all models, the intercept represents the value of the predicted process when all predictive parameters approach zero. However, the model intercept does not represent the minimum value of the predicted process: although soil food web parameters can have values of zero, they cannot be negative, however, the spatial filters we calculated can have positive as well as negative values.

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