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# 1 **Soil community assembly varies across body sizes in a tropical forest**

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32

## 33 **ABSTRACT**

34 The relative influence of deterministic niche-based (i.e. abiotic conditions, biotic interactions)  
35 and stochastic-distance dependent neutral processes (i.e. demography, dispersal) in shaping  
36 communities has been extensively studied for various organisms, but is far less explored  
37 jointly across the tree of life, in particular in soil environments. Here, using a thorough DNA-  
38 based census of the whole soil biota in a large tropical forest plot, we show that soil  
39 aluminium, topography, and plant species identity are all important drivers of soil richness  
40 and community composition. Body size emerges as an important feature of the comparative  
41 ecology of the different taxa at the studied spatial scale, with microorganisms being more  
42 importantly controlled by environmental factors, while soil mesofauna rather display random  
43 spatial distribution. We infer that niche-based processes contribute differently to community  
44 assembly across trophic levels due to spatial scaling. Body size could hence help better  
45 quantifying important properties of multitrophic assemblages.

46

## 47 **INTRODUCTION**

48 Over a century of documenting patterns of diversity has shown that niche-related,  
49 demographic, dispersal and evolutionary processes are all important determinants of  
50 ecological communities<sup>1-3</sup>. However, their relative contribution across spatial scales and  
51 organisms remains less well known<sup>2,4</sup>, especially when it comes to the soil biota.

52 Soils are structurally complex environments<sup>5</sup>. They are often described as the “poor  
53 man's tropical rainforest”<sup>6</sup> due to the large and elusive diversity of organisms they harbour<sup>7</sup>.  
54 Amplicon-based DNA analysis of environmental samples, or metabarcoding<sup>8</sup> has recently  
55 enabled unravelling novel macroecological patterns for soil fauna, nematodes, bacteria, fungi,  
56 protists, and archaea across biomes and habitats<sup>7,9-11</sup>. These patterns often co-vary with  
57 environmental conditions such as pH and nutrient quality/availability. They also depend on

58 plant cover due to trophic and mutualistic/pathogenic interactions<sup>12-14</sup>, but this relationship  
59 appears context-dependent<sup>15-17</sup>. Also, dispersal limitation or stochastic processes have been  
60 unveiled in e.g. fungi or meiofauna<sup>10,18,19</sup>, although other studies reported the predominance  
61 of niche determinism<sup>11,20</sup>.

62 Much of the difficulty in drawing general conclusions about soil community assembly  
63 lies in that studies often focus on single taxonomic groups (but see<sup>17,20-22</sup>) or consider different  
64 spatial scales. In addition, soil organisms harbour large differences in life-history traits; in  
65 particular their body size, whose spans six orders of magnitude (0.1  $\mu\text{m}$  to 10  $\text{cm}^7$ ). This  
66 property has important consequences for community assembly because organisms of different  
67 body size are ruled by contrasting metabolic and demographic processes<sup>23,24</sup>. Dispersal of  
68 microorganisms is mediated by external agents and is assumed to occur across large spatial  
69 distances. This, together with their large population size and short generation time, would  
70 limit local extinction and ecological drift, resulting in a homogeneous global microbial  
71 species pool<sup>20,25</sup>. However, microorganisms are also more responsive to small-scale changes  
72 in resources, subtle variations that may not be perceived by larger organisms<sup>24,26,27</sup>. Hence,  
73 microbial communities are often reported to be dominated by niche-based processes<sup>25</sup>. In  
74 contrast, larger organisms (e.g. mesofauna) are thought to be limited in their ability to  
75 disperse and have longer reproduction times. They are hence more prone to ecological drift  
76 and could display spatial aggregation patterns irrespective of environmental conditions (<sup>28</sup> and  
77 references within). This has enormous consequences for the spatial scaling of soil biodiversity  
78 and the major biogeochemical cycles and ecosystem services they sustain<sup>7,12,14</sup>. However,  
79 existing knowledge on the scaling of soil communities across body sizes is based entirely on  
80 meta-analyses<sup>14,26,27</sup> and is therefore indirect. This hampers our ability to predict the future of  
81 this important biological component<sup>29,30</sup>.

82           In order to assess the processes governing soil community assemblages, we combined  
83 an extensive characterization of abiotic and plant cover conditions with a comprehensive  
84 survey of soil biodiversity using DNA metabarcoding in a large tropical forest plot, where  
85 samples were collected every ten meters. We sought to (i) determine which factor, both  
86 abiotic (e.g. soil chemistry) and biotic (plant diversity, identity), influence soil communities  
87 composition, (ii) evaluate the relative importance of niche-based versus neutral processes in  
88 shaping these communities and (iii) determine how these effects depend on taxon body size.  
89 We predicted that in communities of small-bodied organisms, niche based-processes would be  
90 more important relative to larger organisms, which would display spatial aggregation patterns  
91 that are consistent with neutrality.

92

## 93 **RESULTS**

94 We found a total of 2,502 archaeal, 19,101 bacterial, and 11,470 eukaryotic OTUs within the  
95 12-ha plot (Table 1). Many of these OTUs were rare (relative abundance < 0.1%) and  
96 accounted for  $36 \pm 10$  % (SD values here and after) of archaea OTUs,  $86 \pm 2$  % of bacterial  
97 OTUs, and  $80 \pm 6$  % of eukaryotic OTUs. Bacterial OTUs identified at the phylum level (88%  
98 of OTUs, 94% of reads) corresponded mainly to Actinobacteria, Alphaproteobacteria, and  
99 Acidobacteria. Identified eukaryotic OTUs (51% of OTUs, 70% of reads) belonged to fungi  
100 (mainly Agaricomycetes, Glomeromycetes and Orbiliomycetes; Supplementary Table 1),  
101 arthropods (mainly termites, mites and springtails) and annelids (Oligochaeta). Plants  
102 represented only 2% of all OTUs (10 % of reads). For Archaea, the identified OTUs (3% of  
103 OTUs, 64% of reads) corresponded to Nitrososphaeria and Methanomicrobia. Figure 2  
104 illustrates the spatial variation in local diversity for the focal taxonomic groups. The pairwise  
105 correlation of these spatial patterns, both in terms of OTU diversity and compositional

106 turnover, was moderate to low ( $|r| < 0.7$ ) and showed low or no correlation with  
107 plant ones (Supplementary Table 2-3).

108 The full RDA models, i.e. including abiotic, plant and spatial descriptors, explained 3-  
109 13% of the variation in OTU composition across the 19 focal taxonomic groups (Fig. 3,  
110 Supplementary Table 4). Spatial total effects contributed for  $77 \pm 9$  % of the total explained  
111 variation. Half of the spatial variation was explained by spatially structured abiotic conditions  
112 (Fig. 1, Supplementary Table 5), in particular, soil aluminium and topographic variables (i.e.  
113 elevation, convexity and wetness) or plant characteristics. They correlated negatively with the  
114 OTU diversity of most unicellular taxonomic groups for soil aluminium and of several  
115 bacterial groups and worms for topographic variables (Supplementary Fig. 1-2). The other  
116 half of the spatial variation corresponded to pure spatial effects ( $41 \pm 15$ % of the total  
117 explained variation). Only  $7 \pm 2$  % of the total explained variation was due to pure abiotic  
118 effects.

119 Plant total effects also explained a significant fraction of the explained variation ( $28 \pm$   
120  $11$  %, Fig. 3) and the plant pure effects were more important than pure abiotic ones in most  
121 cases ( $13 \pm 8$  % of the total explained variation, Supplementary Table 4). The identity of the  
122 dominant plant genera in soil samples as detected with the plant DNA marker was the best  
123 plant predictors. These variables included 66 different dominant plant genera, 42 of which  
124 were unambiguously identified. With OTU diversity instead of OTU composition, 4 to 46%  
125 of the variation was explained and the relative importance of plant, abiotic and spatial factors  
126 was similar to what observed above (Supplementary Table 6, Supplementary Fig. 3).

127 Across taxonomic groups, we found a negative relationship between dispersal unit size  
128 and the fraction of variation in OTU composition explained by the environmental variables,  
129 spatially structured or not (Fig. 4). This relationship held when the full variation or pure  
130 abiotic effects were considered alone (Pearson's  $r = -0.58$  and  $-0.51$  respectively,  $p < 0.05$ ).

131 We did not observe such a relationship when performing the analysis on OTU diversity  
132 (Supplementary Figure 4).

133

## 134 **DISCUSSION**

135         Several recent reviews have emphasized the impressive development of publications  
136 using high-throughput sequencing to describe the diversity in soils to the extent that it may  
137 shift research effort away from fundamental questions in soil ecology and evolutionary  
138 biology<sup>13,31</sup>. They emphasize the focus on single taxonomic groups (mainly bacteria/fungi)  
139 and the limited consideration for the biotic and abiotic environment at relevant spatial scales  
140 are major obstacles to a mechanistic understanding of the processes regulating soil diversity  
141 and functioning. This study is an attempt to address these limits, combining assessment of  
142 environmental conditions with patterns of soil diversity across the tree of life at relatively  
143 reduced spatial scales. We provide evidence for spatial scaling rules across soil taxonomic  
144 groups and discuss the general implications of our findings for the assembly of soil  
145 communities.

146         In the spirit of classical community ecology, we sought to understand the spatial  
147 distribution of taxonomic groups using environmental and geographical variables. Although  
148 the spatial patterns of soil communities differed widely amongst clades, they were all related  
149 to several abiotic and biotic factors, albeit to a varying magnitude. This suggests that niche  
150 processes always contribute to the community assembly of soil taxa at the studied spatial  
151 scale, irrespective of the taxon.

152         We found total aluminium content to be an important predictor of microbial (i.e.  
153 prokaryotes, protists) and nematodes communities. In addition, our study plot is an oxisol  
154 with a  $\text{pH} \leq 5$ , conditions at which the toxic trivalent Al cation ( $\text{Al}^{3+}$ ) predominates over the  
155 other forms<sup>32</sup>.  $\text{Al}^{3+}$  competes with other nutrients, inhibits transport, and binds to DNA, ATP



156 or cell walls<sup>32</sup>, as do other metallic ions<sup>33</sup>. In addition, aluminium abundance strongly  
157 correlated with that of many other metals (e.g. Ti, Cu, Zn, Cd and Pb, Supplementary Table  
158 4). We hence interpret the lower microbial diversity in Al-rich sites by its toxicity or that of  
159 co-varying metals, as suggested for soil tropical microbes<sup>16</sup>. Also, high metal concentration  
160 immobilizes nutrients that are essential for plant/microbial growth and protects organic matter  
161 from biological degradation<sup>34</sup>. This may explain why total N, C and P contents, which were  
162 typical of tropical soils (Methods), were poor predictors of soil diversity. These measures  
163 probably do not reflect their bioavailability. High metal conditions likely recruit microbial  
164 taxa able to accumulate Al or to exudate organic acids and enzymes to immobilize Al and  
165 increase P solubilisation<sup>33,34</sup>. Because soil Al correlates negatively with soil pH (see  
166 Methods), our results are also consistent with the decrease of microbial diversity as soil pH  
167 decreases repeatedly observed<sup>16,20</sup>. Soil metal content may hence provide a mechanistic  
168 understanding of the pervasive soil-pH – microbial diversity relationship, and should be more  
169 often considered in addition to other classical measurements.

170 Topographic variables were also important predictors of OTU composition for many  
171 taxonomic groups. They co-vary with many soil properties (e.g. water availability,  
172 biogeochemical processes) and most likely reflect meso-habitat heterogeneity. As such, they  
173 are often used to predict tropical tree distributions (e.g.<sup>35</sup>) and could be useful to model soil  
174 communities. In particular, topographic variables are closely related to soil moisture, and  
175 were the most important predictors of OTU diversity of flat/earthworms, known for their  
176 sensitivity to this parameter<sup>36,37</sup>, and of some bacterial groups, such as Deltaproteobacteria, an  
177 anaerobic clade highly dependent on water availability<sup>38</sup>. This observation generalizes  
178 previous findings for soil bacteria<sup>39</sup> or animals<sup>40</sup> in tropical environments. We also retrieved  
179 high arthropod:earthworm reads abundance ratios consistent with biomass of these groups  
180 reported for the dry season<sup>36</sup>, a time where the topographic control in soil humidity is highest

181 and where earthworms migrate deeper into the soil. Accordingly, the arthropod:earthworm  
182 reads abundance ratios was lower in a pilot experiment conducted during the wet season.  
183 Seasonal dynamics of soil communities should have important implications for  
184 biogeochemical cycles, and may be directly impacted by the forecasted increased frequency  
185 of Amazonian droughts<sup>41</sup>.

186 Our environmental parameters further included plant species distribution inferred from  
187 DNA metabarcoding. Within our samples, we expected that plant DNA presence relates  
188 directly to the quantity/quality of litter or roots exudates<sup>26</sup>, which is poorly controlled by plant  
189 diversity/community turnover *per se*<sup>42</sup>. In agreement with this expectation, we found that the  
190 locally dominant plant genera influenced the community composition of most focal  
191 taxonomic groups (previously termed the “tree identity effect”<sup>7,17</sup>). Neotropical trees species  
192 indeed greatly differ in the quantity, quality and chemistry of their litter<sup>43</sup> and this may hold  
193 true for the chemical composition of their root exudates, their influence on soil physical  
194 structure or their involvement in specific mutualistic/trophic interactions. This result hence  
195 calls for a more mechanistic interpretation of plant-soil interactions<sup>13,14</sup>.

196 The pervasive contribution of niche-based processes found here echoes previous meta-  
197 analyses<sup>44,45</sup>. However, environmental variables explained little variation, whether alone or  
198 combined with spatial variables. Previous studies on various soil taxonomic groups reported  
199 soil moisture, cation exchange capacity, nutrient or organic matter availability/quality to co-  
200 vary with community composition<sup>11,17,20,37</sup>. Although we have characterized the  
201 environmental conditions to the best of our ability, we did not quantify directly these  
202 important predictors. These often display strong spatial structures in tropical soils<sup>16,35</sup> and  
203 hence potentially contributed to the pure spatial effects observed here. We may also have  
204 neglected parameters acting at fine spatial scales, which, together with the high number of  
205 samples considered, most likely contribute to the amount of unexplained variance found for

206 all taxa. For instance, we did not quantify soil microstructure, which is important in  
207 explaining the small-scale distribution of microbial organisms and water moisture<sup>26,31</sup>, nor did  
208 we quantify the geometry of roots as could be imaged by e.g. neutron tomography<sup>5</sup>. We also  
209 did not considered soil organisms interactions. These parameters do exhibit considerable fine-  
210 scale spatial heterogeneity and might explain the apparent idiosyncrasy of each sample. We  
211 might therefore underestimate the contribution of niche-based processes, but expect this to be  
212 consistent across the studied soil taxa.

213 A major problem in attempts to explain patterns of biodiversity is the difficulty of  
214 observing ecological processes at the precise scale at which they manifest themselves<sup>4</sup>. Soils  
215 are complex media where ecological processes operate at a hierarchy of scales, and any  
216 attempt to interpret them should carefully examine the spatial scale of study and the grain of  
217 the sampling unit<sup>5,26,27,31</sup>.

218 For instance, we found no correlation between the species diversity/composition of  
219 plants and that of our focal taxonomic groups, contrary to previous reports<sup>15,46</sup>. We interpret  
220 this discrepancy as a problem of size and sampling grain. Previous analyses were based on  
221 sampling units of typically 20 to 30 m on a side where several soil samples were pooled and  
222 compared with aboveground floristic surveys. At this scale, local plant community  
223 composition averages over confounding environmental conditions. Our sampling unit was a  
224 local soil core of ca. 15 g from which we inferred both local soil richness and plants. Thus, we  
225 were able to relate the co-presence of microbial cells and plant cells at the centimetric scale<sup>13</sup>.  
226 This allowed us to observe the “tree identity effect” reported above. Recently, Barberan et al.  
227 (2015)<sup>16</sup> reported that the strength of plant-microbial diversity relationship decreased with  
228 decreasing sizes of sampling units and vanished at the scale of the sampling point. Our results  
229 confirm these findings and extend them to the whole soil biota. Hence, soil biodiversity  
230 cannot be inferred from plant floristic patterns at the field scale. As we did not find strong

231 similarities between the spatial patterning of the soil taxonomic groups, we confirm that this  
232 conclusion extends to any inference of soil biodiversity patterns from one or few taxa<sup>21</sup>.

233         Such differences can be explained by strong among-clade differences in body size.  
234 Indeed, a striking result from our analysis was that the amount of variation in diversity or  
235 composition explained by environmental variables decreased significantly and linearly with  
236 increasing propagule size across taxonomic groups.

237         The smallest body-size category includes bacteria, which was primarily explained by  
238 environmental factors, owing to the clear environmental gradient at our site. This is in  
239 agreement with the view that niche-based processes dominate bacterial community  
240 assembly<sup>25</sup>. Micro-eukaryotes displayed an intermediate amount of explained variation,  
241 suggesting niche filtering is less important for these groups than for bacteria. This generalizes  
242 previous comparisons of bacteria and fungi community assembly<sup>22</sup>. Whether it is due to  
243 longer generation time, lower dispersal ability or broader resources distribution remains to be  
244 determined. In fungi, the mycelium can spread across heterogeneous environments and the  
245 apparent distribution of fungi may be less related to environmental conditions at the scale of  
246 observation. Archaea and certain bacterial groups (i.e. Firmicutes and Bacteroidetes)  
247 displayed similar features. These groups are of low abundance in soils or associated with  
248 termites<sup>9,16,20,47</sup>, which suggests that they have smaller population sizes in soils or dispersal  
249 rates similar to those of macroorganisms, and could be hence more prone to ecological drift.

250         On the other hand, the OTUs corresponding to large-bodied organisms, i.e. arthropods,  
251 annelids and flatworms, had a random spatial distribution. Soil mesofauna assembly may  
252 hence be rather determined by neutral processes at the scale of our 12 ha plot and grain  
253 studied. However, pure spatial variation, which is usually indicative of dispersal limitation,  
254 was less important for this group than for microbes, which contrasts with previous reports<sup>28,44</sup>.  
255 We explain this result by the minimal distance between sampling points, 10 m, which was the

256 result of a compromise between spatial resolution and sampling effort. It may have been  
257 insufficient to detect spatial aggregates for soil mesofauna, which usually displays spatial  
258 aggregation below 10 m<sup>19,26,37</sup>. This roughly corresponds to the horizontal distance  
259 earthworms can disperse per year. Alternative sampling strategies should be hence considered  
260 for multi-taxa assessments at the studied spatial scale. Still, studies using a finer sampling  
261 grain suggest these aggregates to seldom covary with environmental factors and to most likely  
262 result from stochastic processes<sup>19,37</sup>. On the opposite end of the range, niche-based  
263 community patterns emerge at scales larger than 12-ha where soils properties are highly  
264 distinct in tropical trees<sup>35</sup> or mesofauna<sup>40,48</sup>.

265         This observation is in line with Levin's argument on the problem of scales<sup>4</sup>. For a  
266 unique studied area and sampling grain, we considered patterns of diversity at a multitude of  
267 spatial scales across the studied taxa owing to their body size; with large-scale patterns (i.e.  
268 microbes) being more predictable than fine-scale ones (i.e. mesofauna). This result further  
269 points to an interesting juncture between two fields of ecological theory that have heretofore  
270 been loosely connected, namely the role of body size in explaining the scaling rules of  
271 metabolism<sup>23</sup> and that of environment and dispersal in explaining the assembly of ecological  
272 communities<sup>2</sup>. In that light the fact that small-bodied organisms are more influenced by  
273 environmental conditions, while large-bodied organisms display neutral assembly is  
274 consistent with the main predictions of macroecology<sup>2</sup> and soil science<sup>26,27</sup>. Our finding of a  
275 log-linear relationship between the contribution of niche-based processes in community  
276 assembly and propagule size generalizes previous empirical observations in freshwater  
277 ecosystems (<sup>28</sup> and references within). Although other important biological features also likely  
278 explain the differences of spatial distribution between soil organisms (e.g. clonal/sexual  
279 reproduction, mutualistic/pathogenic interactions, transport that is active, mediated by  
280 animals, by water or wind), the body size trait constitutes an operational parameter that cuts

281 across the tree of life. It is indicative of the way organisms perceive – or move across –  
282 space<sup>3,24,26,27</sup> and of their trophic status in its broadest sense<sup>29</sup>. Hence, our result provides  
283 empirical evidence of spatial scaling rules across the soil food web.

284 The recent explosion of DNA-based studies has considerably increased our knowledge  
285 on the taxonomic, genetic and functional diversity of soil organisms<sup>7</sup>, but has so far provided  
286 limited understanding of the mechanisms shaping soil biodiversity<sup>31</sup>. We do believe that  
287 quantifying soil biodiversity using amplicon-based techniques is a useful endeavour. It is  
288 increasingly obvious that important properties of multitrophic systems, e.g. species richness,  
289 distribution and extinction rates, cannot be easily retrieved from one or a small set of  
290 surrogate taxa (this study, <sup>21,30</sup>). Co-occurrences multitrophic networks can now be  
291 reconstructed using such DNA-based approaches<sup>49</sup>, and these approaches hold great promises  
292 in assessing soil ecological networks properties at spatial and temporal scales that have been  
293 heretofore inconceivable. Our results show that accounting for body size differences helps  
294 unravel spatial patterns in such complex communities and, combined with DNA-based  
295 approaches, could improve predictive models of soil food webs.

296

## 297 **METHODS**

### 298 ***Study site and sampling***

299 The study site is located at the Nouragues Ecological Research Station, in the lowland  
300 rain forest of French Guiana (latitude: 4° 4' 28" N, longitude: 52° 40' 45" W). Rainfall is 2861  
301 mm.y<sup>-1</sup> (average 1992-2012), with a two-month dry season (< 100 mm.month<sup>-1</sup>), from late  
302 August to early November, and a shorter dry season in March. Our sampling campaign was  
303 conducted November 7-20, 2012, towards the end of the dry season, which lasted from early  
304 September to late November. Cumulated rainfall during the 60 days preceding the sampling

305 session was 134 mm, with 44 days without rain, and over 90% of the rainfall concentrated in  
306 seven days.

307 We surveyed a 12-ha (300 x 400 m) plot established in 1992. This plot extends on a  
308 gentle slope between a ridge and a small creek<sup>50</sup>. The 5,640 trees occurring in the plot  
309 (diameter at breast  $\geq$  10 cm) belong to over 600 species, with the two dominant species  
310 accounting each for only 2.3% of individuals<sup>51</sup>. Sand and clay fractions are about 40% each in  
311 the soil top 10 cm. The parent material is Caribbean granite. Soil edaphic conditions are  
312 typical of tropical oxisols, with an acidic pH (pH = 5.0) and low exchangeable cation content  
313 (ECEC = 3.5 cmolc.kg<sup>-1</sup>). The C:N and N:P ratios are typical of tropical forests<sup>52</sup>  
314 (median=13.4 and 40.5 respectively).

315 We sampled the plot following a regular grid scheme with a 10-m mesh, excluding  
316 bordering points, hence resulting in a total of 1,132 sampling points. At each point, 50-100g  
317 soil cores were collected with an auger at ~10 cm depth, excluding the organic horizon. We  
318 did so because the organic and mineral horizons harbor different arthropods and microbial  
319 communities<sup>53,54</sup>. Lumping together these compartments may hence complicate the  
320 interpretation of the spatial distribution of certain soil clades. Consequently, we focused on  
321 the surface soil layer, which it is the most biogeochemically active in the mineral horizon<sup>55</sup>.  
322 The soil cores were stored and sealed in sterile plastic bags after collection and transported to  
323 the field station laboratory. Extracellular DNA was extracted from 15 g of soil per soil core as  
324 described previously<sup>56,57</sup> within 4 hours after sample collection to prevent from microbial  
325 growth. DNA was extracted twice for each soil core, and the remaining soil material was  
326 dried and stored for analytical chemistry analyses.

### 327 ***Molecular analyses***

328 Soil biodiversity was surveyed through DNA metabarcoding using four DNA markers,  
329 with primers targeting three in hypervariable regions of the *ssu* rRNA gene in Archaea (this

330 study), Bacteria<sup>58</sup> and Eukaryota<sup>59</sup> domains respectively (see Supplementary Table 7) and a  
331 plastid DNA marker (P6 loop of the trnL intron<sup>60</sup>) to characterize the plant composition at the  
332 scale of the sampling point. The universal primers do not present particular amplification  
333 biases (see Supplementary Material for a detailed description of primer similarity with  
334 priming sites across phyla).

335 We conducted duplicated PCRs for each marker and each DNA extract, hence  
336 representing a total of 18,112 independent PCRs. To discriminate PCR products after  
337 sequencing, forward and reverse primers were tagged with a combination of two different 8-  
338 nucleotide labels. Each PCR reaction was performed in a total volume of 20  $\mu$ l and comprised  
339 10  $\mu$ l of AmpliTaq Gold® Master Mix (Life Technologies, Carlsbad, CA, USA), 0.25  $\mu$ M of  
340 each primer, 3.2 $\mu$ g of BSA (Roche Diagnostic, Basel, Switzerland), and 2  $\mu$ l DNA template  
341 that was 10-fold diluted to reduce PCR inhibition by humic substances. Thermocycling  
342 conditions are shown in Appendix S1. All PCR products were then purified using a  
343 MinElute<sup>TM</sup> PCR purification kit (Qiagen, Hilden, Germany). For each marker, PCR products  
344 were distributed into 4 different sequencing libraries, which were pooled and loaded on up to  
345 7 Illumina sequencing lanes, depending on the marker and sequencing platform used  
346 (Supplementary Table 7), using the paired-end sequencing technology. To control for  
347 potential contaminants<sup>61</sup> and false positive caused by tag-switching events<sup>62</sup>, the sequenced  
348 multiplexes comprised extractions/PCR blank controls, as well as unused tag combinations.

### 349 ***Sequence analyses and curation***

350 The ca. 10<sup>9</sup> sequencing reads produced were curated using the OBITools package<sup>63</sup>  
351 and R scripts ([www.r-project.org](http://www.r-project.org)).

352 We first assembled paired-end reads and assigned them to their respective samples and  
353 taxonomic groups on the basis of the tags and primer sequences, by allowing 2 and 0  
354 mismatches on primers and tags, respectively. Reads were dereplicated, and low-quality



355 sequences excluded (i.e. shorter than 7, 13, 50 and 100 nt for the plant, eukaryota, archaea and  
356 bacterial markers, respectively; containing “Ns”; and singletons). We then clustered the  
357 remaining unique sequences into operational taxonomic units (OTUs), as follows. We  
358 computed pairwise dissimilarities between sequences (i.e. the number of mismatches, allowed  
359 to be 0-3) using the Sumatra algorithm<sup>64</sup>, then we formed OTUs using the Infomap  
360 community detection algorithm<sup>65</sup>. We excluded OTUs represented by a single sequence  
361 because PCR/sequencing almost always produce at least one error on amplified fragments.  
362 The true sequence of an OTU was assumed to be the most abundant one in the cluster.

363 OTUs were assigned a taxonomic clade with the ecotag program of the OBITools  
364 package. Since this algorithm requires full-length barcodes as reference, we constructed a set  
365 of reference databases for each marker by running in silico PCRs with the primer pairs used  
366 here (Supplementary Table 7). This was done with the ecoPCR program<sup>66</sup> by using Genbank  
367 (release 197; <ftp://ftp.ncbi.nlm.nih.gov/genbank>) and the MOTHUR-formatted SILVA  
368 database (release 119; [http://www.mothur.org/wiki/Silva\\_reference\\_files](http://www.mothur.org/wiki/Silva_reference_files)) as sequence  
369 template. We here only considered references with unambiguous taxonomic annotation at the  
370 order level. We also used a reference database of tropical plants occurring at the study site,  
371 built with the plant primers, so as to improve plant OTU identification (available in <sup>56</sup> and the  
372 Dryad Digital Repository, doi:10.5061/dryad.1qt12). At the end of this analysis, we had two  
373 taxonomic assignments for each OTU. We gave priority to assignments from SILVA or our  
374 local plant database when the similarity between the query and its best match was > 98%. We  
375 did so because the SILVA and our local plant databases yield taxonomic annotations that are  
376 more reliable than those from Genbank. Otherwise, the taxonomic assignment yielding the  
377 highest similarity score was kept. Paired-end reads were assembled, assigned to their  
378 respective samples/marker and dereplicated. Low-quality sequences were excluded; the

379 remaining ones were clustered into operational taxonomic units (OTUs) and assigned a  
380 taxonomic clade.

381 We paid particular attention to minimize PCR/sequencing errors, contaminant and  
382 false positive sequences as well as potential non-functional PCRs by using several  
383 conservative quality criteria. First, we assumed that OTUs peaking in abundance in the  
384 negative controls were a contaminant. Any OTU with a best-match similarity in any reference  
385 database below  $< \text{ca. } 75\%$  was considered as a chimera or highly degraded sequence. Any  
386 OTU that did not fall into the clade targeted by the primer pair was also excluded. Finally, we  
387 also curated the dataset from false positives caused by tag-switching events. This  
388 phenomenon is suspected to occur during the preparation of the sequencing library and  
389 translates into low abundance “contaminant OTUs” in samples coming from other samples  
390 that were part of the amplicons multiplex. To remove them, we considered each OTU  
391 separately and set to 0 any abundance representing  $< 0.03\%$  of the total OTU abundance in  
392 the entire dataset, similarly to <sup>62</sup>. This abundance threshold was found to be the one for which  
393 most OTUs with unused tag combinations could be removed from the dataset.

394 Verifying the success of our 18,000 PCRs was not possible. Therefore, we used the  
395 PCR replicates to filter out potential non-functional PCR reactions, i.e. containing low  
396 amounts of reads or high amounts of contaminants or false positives that could not be filtered  
397 out with the process described above. First, for each sample we defined an average  
398 community (hereafter centroid) by averaging OTUs counts of the four PCR replicates.  
399 Second, we compared the distribution of dissimilarities (as defined by Euclidean distances) of  
400 PCR replicates with their respective centroid (hereafter  $d_w$ ) against the distribution of pairwise  
401 dissimilarities between all centroids (hereafter  $d_b$ ). As we expect  $d_w < d_b$ , we defined the  
402 intersection of  $d_w$  and  $d_b$  distribution curves as the dissimilarity level above which a PCR  
403 replicate is too distant from its centroid to be reliable. Any PCR above this threshold was

404 excluded from the analysis. This process was repeated iteratively until no more PCR were  
405 removed from the dataset. If a sample was represented by only one PCR product, then it was  
406 excluded during the iterative process. At the end of this procedure, the remaining PCR  
407 replicates were summed for each sample. See Supplementary Table 8 for raw and curated  
408 datasets statistics.

409 Finally, the sequencing depth of each sample was standardized for each marker by  
410 randomly resampling a number of reads equal to the first quartile of read number across  
411 samples. Although such procedure has been recently questioned<sup>67</sup>, the data loss caused by  
412 rarefaction is minimal when the subsampling size well covers the sample diversity, as it is the  
413 case here. It had therefore no or weak effects on the dataset characteristics and the retrieve  
414 patterns of diversity (Supplementary Fig. 5). Raw and curated sequencing data as well as  
415 associated metadata are available on the Dryad Digital Repository under the accession XXX.

#### 416 ***Focus taxonomic groups and body size***

417 Within the Eukaryota and Bacteria domains, we distinguished groups on the basis of  
418 their taxonomic affiliation at the phylum level (Table 1). We did so because broadly defined  
419 functional traits such as body size and trophic categories are relatively well conserved within  
420 phyla<sup>38,68</sup>. We restricted our analysis to the most abundant phyla (i.e. representing  $\geq 1\%$  of the  
421 total bacterial or eukaryotic OTU diversity). Archaea were analysed as a single group due to  
422 imprecise taxonomic assignments.

423 Body size classes were defined as the size of the dispersal unit (propagule), rather than  
424 that of the mature individual: in some taxa, like fungi, mature bodies may extend over large  
425 areas through mycelium growth (i.e. the vegetative part of fungi). The intraspecific variability  
426 of these mature forms besides vary from 1 to 2 orders of magnitude<sup>69</sup>. This makes it difficult  
427 to decide on an effective definition of a ‘body’. In contrast, spore size is more stable and  
428 proportional to the reproduction rate and to the fructification size of certain fungal groups<sup>69,70</sup>.

429 This definition also cuts across the domains of life as it corresponds to average cell size for  
430 unicellular organisms (i.e. archaea, bacteria and protists) and average body size of adults for  
431 the soil meiofauna. For fungi, we used their spore size, as the operational definition of body  
432 size<sup>18</sup>. Body sizes were inferred from<sup>71</sup> for bacterial cells, from<sup>72,73</sup> for fungal propagules, and  
433 from<sup>68</sup> for the other groups (Table 1).

#### 434 ***Environmental parameters***

435 *Soil chemistry and airborne lidar.* Total content in soil chemical elements was assessed on  
436 one soil sample in two (i.e. every 20 meters). Soils were ground and attacked by hydrochloric  
437 and nitric acid. Major element concentration was measured by inductively coupled plasma  
438 optical-emission spectroscopy (ICP-OES). Carbon and nitrogen concentration was measured  
439 by a CHN elemental analyzer (NA 2100 Protein, CE Instruments). All other chemical  
440 elements were quantified by ICP-MS. In total, our dataset included 55 elemental  
441 concentrations, which were krigged using an exponential variogram model so as to obtain  
442 values for all the points of the initial sampling design. This analysis was conducted with the  
443 *sp* (<http://rspatial.r-forge.r-project.org/>) and *gstat* (<http://gstat.r-forge.r-project.org/>) R  
444 packages. Despite soil pH is a common predictor of soil microbes<sup>74</sup>, we did not assess this  
445 parameter here. Soil pH is indeed well known to correlate negatively with soil total  
446 aluminium, in both temperate<sup>75</sup> and tropical soils<sup>76</sup>. Because tropical soils are Al-rich,  
447 conditions that are extreme for the soil biota<sup>34</sup>, we believe this variable to be more relevant in  
448 our study plot than soil pH *per se*, as the latter results from mixed biochemical/chemical  
449 pathways and hence provides a poor mechanistic explanation of the processes shaping soil  
450 communities. Airborne lidar data were obtained previously<sup>77,78</sup> and were used here to retrieve  
451 a 1-m<sup>2</sup> digital elevation model (DEM), from which we derived slope, light penetration, and  
452 topographic wetness indices (see Supplementary Methods).

453 *Plants*. We used several plant-related variables to explain soil community assembly. The first  
454 corresponded to the canopy closure derived from the lidar data. The other corresponded to  
455 plant diversity (Shannon index) and the identity of the three most dominant plant genera in  
456 each soil sample as inferred from the plant metabarcoding dataset. Dominant plant genera  
457 represented on average  $70 \pm 15\%$  of the plant reads in each sample, which provides a good  
458 description of the local plant community composition. Sampling points for which we did not  
459 obtained any plant sequences (330 of the 1,132) were redrawn by a multinomial resampling of  
460 reads from neighboring points. This approach is reasonable because tree roots influence is  
461 detectable up to 20 m from their corresponding stems in tropical forests<sup>16</sup>.

#### 462 ***Statistical analyses***

463 To disentangle the relative importance of niche-based and neutral processes in the  
464 assembly of soil communities, we used variation partitioning and redundancy analysis  
465 (RDA<sup>44,79</sup>) on each focus taxonomic group. We used RDA because preliminary analyses  
466 indicated a linear relationship between soil diversity/community distribution and explanatory  
467 variables. First, we Hellinger-transformed OTU tables to down-weight rare OTUs, as these  
468 may be artifactual, as well as to preserves the Euclidean distance among sites<sup>80</sup>. Next, we  
469 constructed three parsimonious models by applying a forward selection procedure. This  
470 avoids inflating the amount of explained variance and Type I error<sup>81</sup>.

471 A first model corresponded to RDAs including soil chemistry and lidar-derived data.  
472 The second corresponded to RDAs including plant explanatory variables (Fig. 1,  
473 Supplementary Table 9). For these two models, explanatory variables were preselected to  
474 reduce multicollinearity ( $|\text{Pearson's } r| \geq 0.7$ , Supplementary Fig. 6) and normalized with a  
475 Box-Cox transformation to meet the normality assumption. The third model was a spatial  
476 RDA using spatial eigenvectors as explanatory variables, derived from a Principal  
477 Components of Neighbours Matrices (PCNM) approach<sup>82</sup>. These represent spatial structures

478 at different spatial scales that allow modelling the spatial structure of community composition  
479 variation. To further reduce inflation of  $R^2$  statistics caused by the PCNM analyses<sup>83</sup>, we  
480 preselected PCNM eigenvectors prior the forward selection procedure. These corresponded to  
481 eigenvectors explaining significantly ( $p \leq 0.02$ ) the variability in the biological response, as  
482 assessed though partial canonical redundancy analysis (pRDA). This pre-selection was  
483 performed for each studied clade independently. Geographic coordinates were also included  
484 in the model to account for possible linear trends along the study area<sup>82</sup>.

485 Abiotic, plant and spatial models were then combined into a single, “full” RDA  
486 model, which was subjected to variation partitioning. This analysis decomposes the variance  
487 of community composition explained either by abiotic, plant or spatial variables alone as well  
488 their combined effects. The contribution of pure environmental vs. spatial effects in the  
489 variation of community composition is usually considered to be indicative of the relative  
490 importance of niche-base processes vs. dispersal limitation in the community assembly<sup>44,79</sup>,  
491 provided that the environmental context is well characterized and that neutral processes are  
492 not correlated with the environment. Significance of the total RDA models and pure effects  
493 were determined with 1,000 Monte-Carlo permutations. We here only report  $R^2_{\text{adj}}$  statistics,  
494 which are less inflated when the numbers of explanatory variables is high<sup>[84]</sup>. To further  
495 identify the environmental parameters that were spatially structured in our plot, each PCNM  
496 eigenvector was regressed against the set of plant and abiotic variables using pRDA.

497 To test an effect of body size on community assembly patterns, we compared it with  
498 the amount of variance explained by the full model and each pure effect using a Pearson  
499 product-moment correlation test. Finally, we repeated the whole analysis by considering OTU  
500 diversity as a response variable. OTU diversity was calculated as the exponential of the  
501 Shannon entropy, an effective number of species<sup>85</sup> that is less sensitive to rare OTUs. All  
502 analyses were conducted with the vegan R package (<http://vegan.r-forge.r-project.org/>).

503 **Data availability**

504 Raw and curated sequencing data as well as associated metadata and codes are available on  
505 the Dryad Digital Repository (XXX provided upon manuscript acceptance).

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700 **Author contributions**

701 L.Z., E.C., P.T. and J.C. conceived the study. L.Z, P.T., H.S., A.B, M.D.B, P.G., L.G., C.G.C,  
702 A.I., M.R.M, G.R., E.C and J.C. contributed to the fieldwork and/or to DNA extractions. P.T.,  
703 A.B., A.I. and D.R. conducted the laboratory work to produce the metabarcoding data. J.V.  
704 and C.Z. performed the chemical analyses. B.T. provided the LiDAR data. L.Z. did the  
705 bioinformatics and statistical analyses with the help of V.S., F.B., E.C, W.T. and J.C. The  
706 manuscript was written by L.Z. and J.C. with input from all co-authors.

707 **Competing interests**

708 L.G. and P.T. are co-inventors of patents related to the gh primers and the use of the P6 loop  
709 of the chloroplast *trnL* (UAA) intron for plant identification using degraded template DNA.  
710 These patents only restrict commercial applications and have no impact on the use of this  
711 locus by academic researchers.

712

713 **Figures and Tables**

714 **Table 1. Soil biota characteristics in the 12 ha plot.** Relative abundances were calculated

715 for each marker separately and correspond to the % of reads of each clade. Richness values

716 correspond to the number of OTUs (mean  $\pm$  SD for values per sample). Diversity values

717 correspond to the effective number of OTUs (exponential Shannon diversity index; mean  $\pm$

718 SD for values per sample). Occupancy corresponds to the averaged proportion of samples

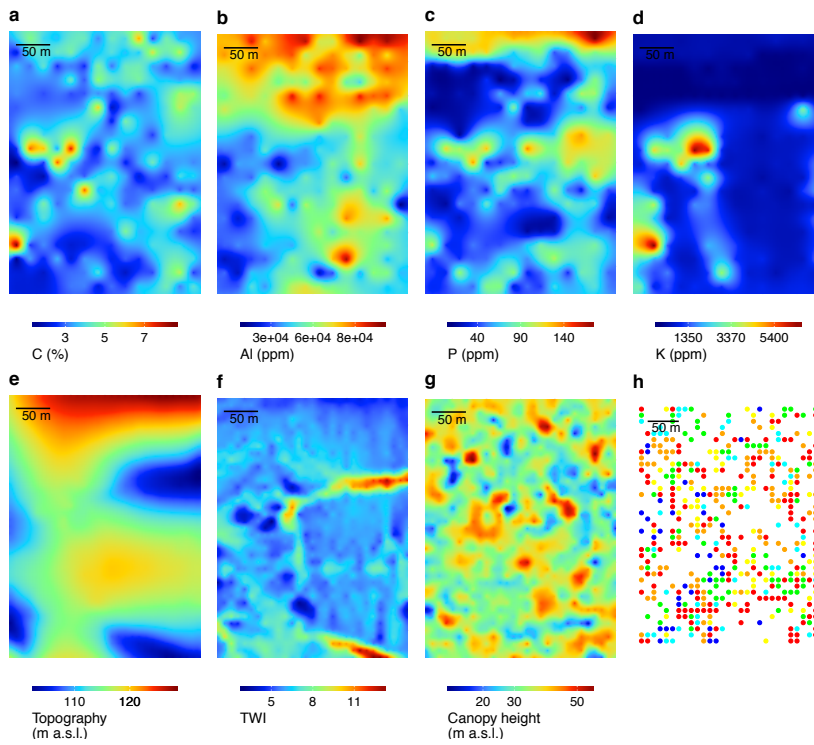
719 where an OTU is detected ( $\pm$  SD). NA: not applicable.

Clade	Total rel. abundance (%)	Total Richness (per sample)	Total Diversity (per sample)	OTU occupancy (%)	Propagule size (m)
Archaea	NA	2,502 (43 $\pm$ 30)	30 (9 $\pm$ 8)	1.707 $\pm$ 6.197	0.5e <sup>-6</sup>
Bacteria	NA	19,101 (1,391 $\pm$ 232)	885 (453 $\pm$ 102)	7.281 $\pm$ 16.379	NA
<i>Acidobacteria</i>	19.81	1,601 (231 $\pm$ 46)	132 (80 $\pm$ 32)	14.42 $\pm$ 22.686	0.5e <sup>-6</sup>
<i>Actinobacteria</i>	20.578	1,696 (167 $\pm$ 37)	86 (54 $\pm$ 13)	9.869 $\pm$ 20.329	5e <sup>-6</sup>
<i>Bacteroidetes</i>	1.023	767 (31 $\pm$ 12)	97 (22 $\pm$ 8)	4.088 $\pm$ 11.389	0.5e <sup>-6</sup>
<i>Chloroflexi</i>	5.22	2,147 (136 $\pm$ 48)	268 (73 $\pm$ 29)	6.341 $\pm$ 12.358	1e-6
<i>Firmicutes</i>	2.658	873 (19 $\pm$ 6)	4 (3 $\pm$ 2)	2.147 $\pm$ 8.048	1e-6
<i>Alphaproteobacteria</i>	19.865	3,234 (303 $\pm$ 57)	242 (129 $\pm$ 25)	9.373 $\pm$ 19.381	0.5e <sup>-6</sup>
<i>Betaproteobacteria</i>	3.469	482 (45 $\pm$ 13)	24 (14 $\pm$ 7)	9.392 $\pm$ 19.023	5e <sup>-6</sup>
<i>Deltaproteobacteria</i>	4.364	1,357 (75 $\pm$ 31)	73 (34 $\pm$ 15)	5.513 $\pm$ 14.073	0.5e <sup>-6</sup>
<i>Gammaproteobacteria</i>	8.589	888 (72 $\pm$ 11)	30 (21 $\pm$ 5)	8.109 $\pm$ 19.47	5e <sup>-6</sup>
<i>Verrucomicrobia</i>	4.989	353 (51 $\pm$ 12)	33 (22 $\pm$ 5)	14.357 $\pm$ 24.53	0.5e <sup>-6</sup>
Eukaryota	NA	11,470 (475 $\pm$ 137)	228 (51 $\pm$ 23)	4.138 $\pm$ 11.113	NA
<i>Ascomycota</i>	3.486	317 (25 $\pm$ 9)	22 (8 $\pm$ 3)	7.813 $\pm$ 15.365	100e <sup>-6</sup>
<i>Basidiomycota</i>	16.941	387 (31 $\pm$ 8)	44 (8 $\pm$ 4)	7.911 $\pm$ 16.184	10e <sup>-6</sup>
<i>Glomeromycota</i>	1.078	38 (7 $\pm$ 2)	8 (5 $\pm$ 1)	19.431 $\pm$ 28.548	200e <sup>-6</sup>
<i>Annelida</i>	6.623	49 (8 $\pm$ 3)	6 (3 $\pm$ 1)	17.182 $\pm$ 23.828	20e <sup>-3</sup>
<i>Arthropoda</i>	17.648	1,777 (63 $\pm$ 21)	91 (15 $\pm$ 7)	3.569 $\pm$ 9.393	10e <sup>-3</sup>
<i>Nematoda</i>	0.469	359 (9 $\pm$ 5)	35 (6 $\pm$ 2)	2.64 $\pm$ 7.257	100e <sup>-6</sup>
<i>Platyhelminthes</i>	0.538	117 (4 $\pm$ 3)	15 (3 $\pm$ 1)	3.361 $\pm$ 9.778	20e <sup>-3</sup>
<i>Protists</i>	1.947	1,610 (53 $\pm$ 40)	126 (27 $\pm$ 18)	3.29 $\pm$ 8.488	100e <sup>-6</sup>

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722 **Figure 1. Maps of environmental characteristics in the 12 ha plot. a-d)** Soil content in  
723 Carbon, Aluminium, Phosphorous and Potassium. **e)** site topography, **f)** soil wetness (TWI  
724 index, unitless) and **g)** canopy height as inferred from LiDAR data. **h)** Distribution of the  
725 most dominant plant genus found in each soil sample as inferred from the plant molecular  
726 dataset. Only the six most frequent dominant genera are shown: red: Apocynoideae; orange:  
727 Andira; yellow: Ingeae; green: Brosimum; lightblue: Sapotaceae; blue: Drypetes. x/y axes are  
728 not shown for representation purposes and range between 10-290 and 10-390 meters  
729 respectively.

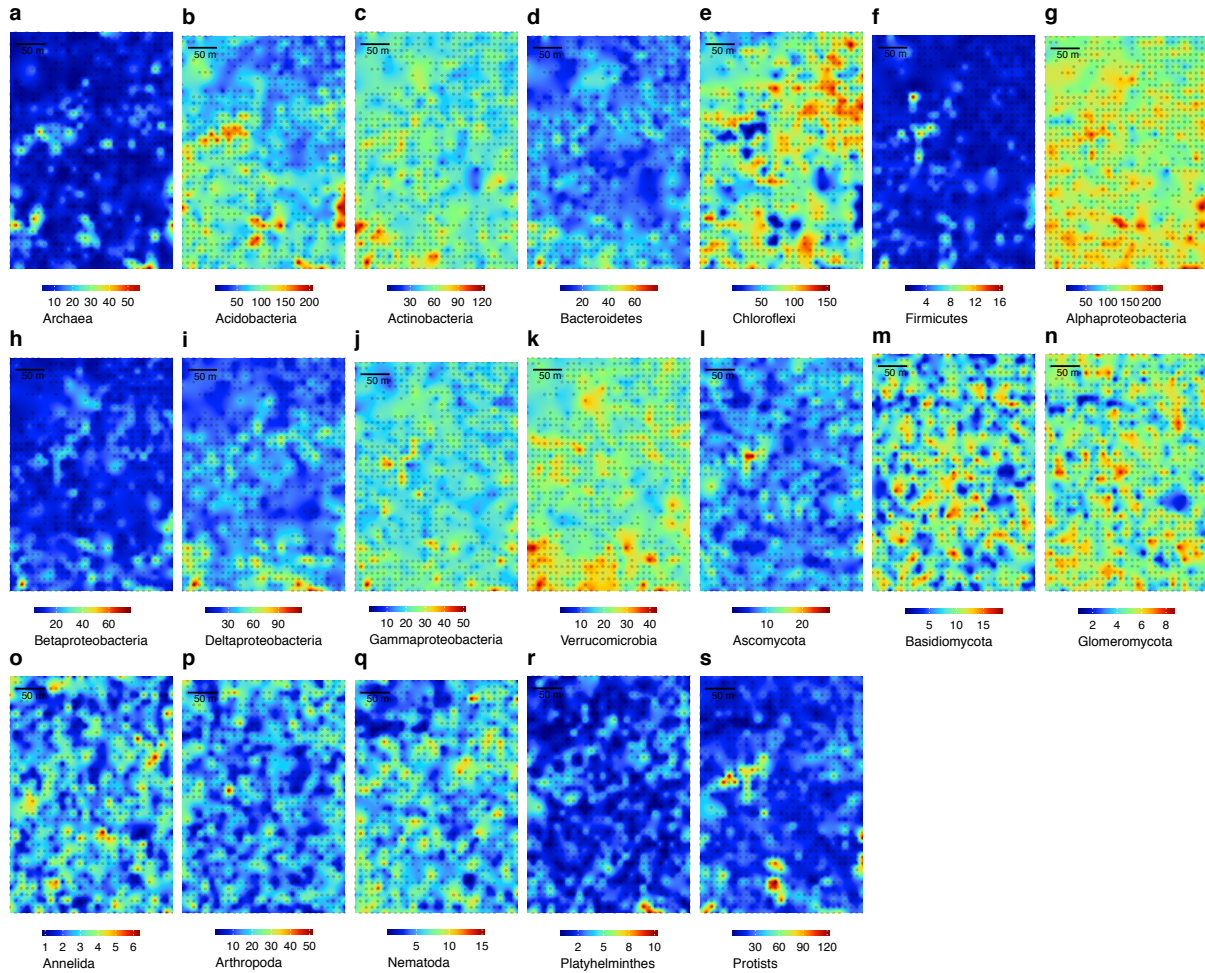


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732 **Figure 2. Spatial distribution of OTU diversity per focal clade.** The colour scale is  
733 expressed as effective numbers of OTUs (exponential Shannon diversity index) for archaea  
734 (a), bacterial clades (b-k) and eukaryotic clades (l-s). Maps were obtained by ordinary  
735 kriging. Grey dots represent the samples available for each clade.

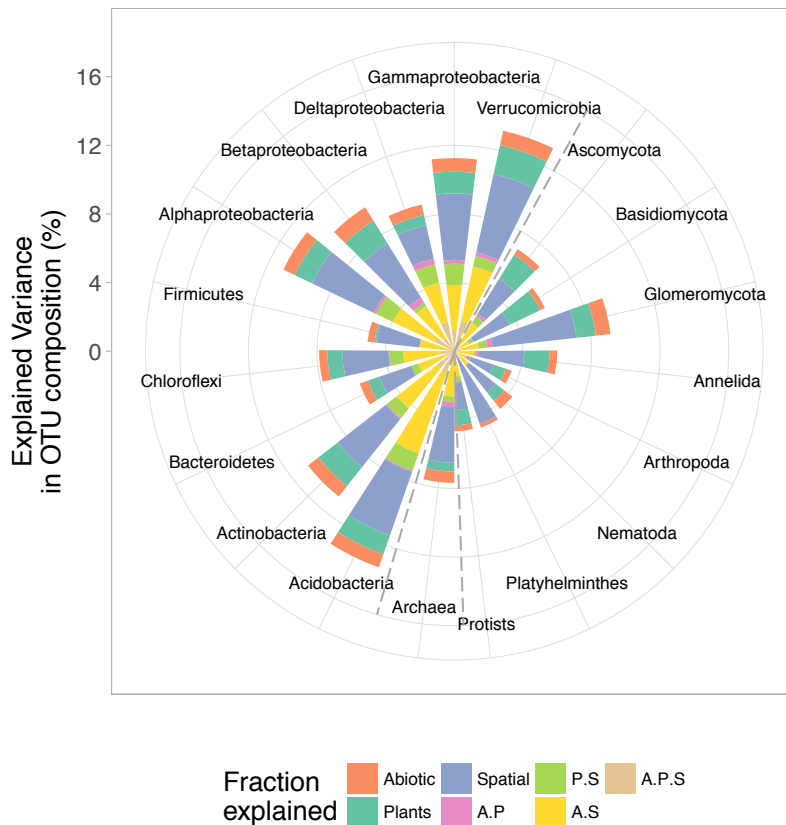


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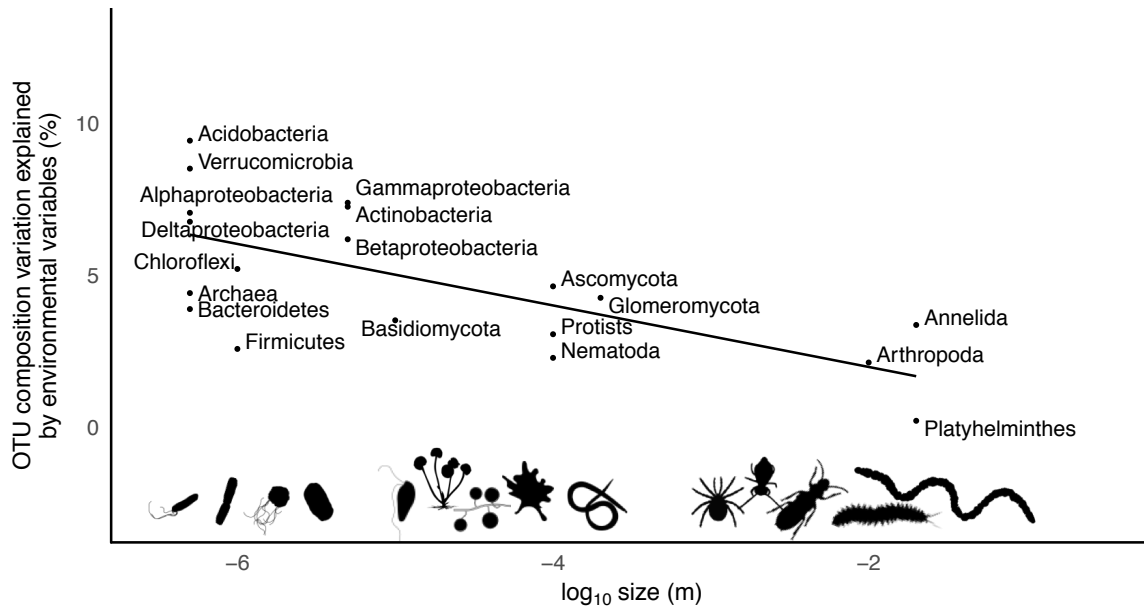
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738 **Figure 3. Variation partitioning of OTU composition in each focus taxonomic group.**

739 Variations of OTU composition are partitioned into pure (i.e. abiotic (A), plant (P) or spatial  
740 (S)) and shared components (A.P, P.S, A.S and A.P.S). The corresponding  $R^2_{adj}$  statistics are  
741 reported. See Supplementary Table 4 for corresponding  $R^2_{adj}$  values and their significance (for  
742 pure components and full models only, shared components not testable).



745 **Figure 4. Variation of OTU composition explained by environmental variables**  
746 **according to organism propagule size.** The variation ( $R^2_{adj}$  statistics) includes pure plants  
747 and abiotic effects as well as their combined effect with spatial variables. The negative  
748 relationship between organism propagule size and the variance explained by environmental  
749 effects is significant (Pearson's  $r = -0.67$ ,  $p = 0.002$ ).



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