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Mylène Hugoni, Naoise Nunan, Jean Thioulouse, Audrey Dubost, Danis Abrouk, et al.. Small-Scale Variability in Bacterial Community Structure in Different Soil Types. *Microbial ecology*, 2021, 82 (2), pp.470-483. 10.1007/s00248-020-01660-0 . hal-03763569

**HAL Id: hal-03763569**

**<https://cnrs.hal.science/hal-03763569v1>**

Submitted on 1 Sep 2022

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Mylène Hugoni, Naoise Nunan, Jean Thioulouse, Audrey Dubost, Danis Abrouk, et al.. Small-Scale Variability in Bacterial Community Structure in Different Soil Types. Microbial ecology, Springer Verlag, 2021, 10.1007/s00248-020-01660-0 . hal-03224926

**HAL Id: hal-03224926**

**<https://hal-cnrs.archives-ouvertes.fr/hal-03224926>**

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1 **Small scale variability in bacterial communities structure in different soil**  
2 **types**

3  
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22  
23 **Keywords:** Bacterial diversity / Community structure / Soil / Spatial scale / Ecological  
24 strategies

26 **Abstract**

27 Microbial spatial distribution has mostly been studied at field to global scales (*i.e.* ecosystem  
28 scales). However, the spatial organization at small scales (*i.e.* centimeter to millimeter scales),  
29 which can help improve our understanding of the impacts of spatial communities structure on  
30 microbial functioning, has received comparatively little attention. Previous work has shown  
31 that small scale spatial structure exists in soil microbial communities, but these studies have not  
32 compared soils from geographically distant locations. Nor have they utilized community  
33 ecology approaches, such as the core and satellite hypothesis and/or abundance-occupancy  
34 relationships, often used in macro-ecology, to improve the description of the spatial  
35 organization of communities. In the present work, we focused on bacterial diversity  
36 (*i.e.* 16SrRNA gene sequencing) occurring in micro-samples from a variety of locations with  
37 different pedo-climatic histories (*i.e.* from semi-arid, alpine and temperate climates) and  
38 physicochemical properties. The forms of ecological spatial relationships in bacterial  
39 communities (*i.e.* occupancy-frequency and abundance-occupancy) and taxa distributions (*i.e.*  
40 habitat generalists and specialists) were investigated. The results showed that bacterial  
41 composition differed in the four soils at the small scale. Moreover, one soil presented a satellite  
42 mode distribution whereas the three others presented bimodal distributions. Interestingly,  
43 numerous core taxa were present in the four soils among which 8 OTUs were common to the  
44 four sites. These results confirm that analyses of the small-scale spatial distribution are  
45 necessary to understand consequent functional processes taking place in soils, affecting thus  
46 ecosystem functioning.

47

48

49

## 50 **1. Introduction**

51 Microbial diversity is central to soil ecosystem functioning and the ecosystem services soils  
52 deliver, as microbial communities are involved in many biogeochemical processes and their  
53 various interactions may affect these activities [1–3]. Despite this fundamental role, we still do  
54 not have a full understanding of the processes underpinning the emergence and maintenance of  
55 soil microbial diversity. Hubbell (2001) defined biodiversity as being synonymous with species  
56 richness and relative species abundance in space and time, where relative species abundance  
57 refers to the commonness or rarity of a species in relation to others, in a given community. The  
58 question of what makes a species common or rare has long been of empirical and theoretical  
59 interest in community ecology [4]. Despite a growing number of surveys interested in rare and  
60 core microbial communities, only a few recent studies have targeted bacterial spatial  
61 distributions, in a range of different ecosystems, such as water, guts, soil or even the surface of  
62 stone [5–9]. These studies have highlighted the fact the “rare biosphere” is constituted of a  
63 myriad of species. The rare communities are of interest as they may be of functional  
64 significance: it has been shown that rare taxa are a resource pool for responding to  
65 environmental changes [10], maintaining species diversity [11], and promoting functional  
66 redundancy [12]. Other studies conducted on aquatic ecosystems at a global scale have shown  
67 the presence of a rich and diverse rare biosphere among Archaea and Bacteria [13, 14]. Hugoni  
68 *et al.* (2013) reported that the rare archaeal biosphere in the ocean should not solely be  
69 characterized as a seed bank of dormant cells; rather, it is a complex association of indigenous  
70 and itinerant cell types of different origins and with different fates that might contribute to  
71 microbial interaction networks and metabolic processes in the environment.

72 Although these have yielded a host of information at larger scales, microbial  
73 distribution patterns and their consequences for ecosystem functioning are far less documented  
74 at small scales [15–17], especially in soils. However, it is clear that cell-to-cell, cell-substrate

75 and cell-substratum interactions that all take place at small scales, are likely to have significant  
76 effects on overall processes [18, 19]. Previous studies have attempted to study bacterial  
77 communities and soil properties at sub-millimeter scales, in different contexts as different soil  
78 aggregate size classes, aggregate surfaces vs interiors, various soil fractions, or different soil  
79 pore distributions [20–25]. These studies, using several methods such as fingerprinting [21],  
80 clone libraries [24], pyrosequencing [20, 22, 25] or particulate organic matter characterization  
81 (POM) [23] suggested that microaggregates represent micro-environments that select specific  
82 bacterial lineages [26]. In order to evaluate the regulatory role of such interactions, the problem  
83 of spatial patterns and scale needs to be addressed and models derived from the community  
84 ecology of macro-organisms might give the tools to understand small-scale microbial  
85 biodiversity.

86         The analysis of how biodiversity is distributed across space has employed various  
87 spatial approaches in community ecology, based on habitat generalists and specialists [27, 28],  
88 and on the core-satellite hypothesis [29, 30]. Classifying species into habitat generalists and  
89 specialists is the first step toward examining the underlying biological and ecological factors  
90 leading to the differential distribution of species among habitats [31]. Habitat generalists are  
91 defined as broadly distributed microbial taxa whereas specialists are rare taxa that can be locally  
92 abundant [28, 32]. The “core-satellite hypothesis” (or “Hanski’s hypothesis”) proposes that  
93 species fall into one of two categories: “core” species, which are widespread and locally  
94 abundant, and “satellite” species consisting mostly of rare species that are present in a limited  
95 number of sites and at low abundances [29, 30]. Core and satellite taxa are classically identified  
96 to predict communities’ occupancy-frequency distributions (with occupancy defined as the  
97 percentage of samples in which a taxon is present and frequency defined as the percentage of  
98 taxa found for each occupancy). This characterization of communities’ ecology in terms of  
99 spatial distribution often showed a bimodal distribution (*i.e.* most species are present in either

100 most patches or only a small number of patches). In contrast, generalists and specialists refer to  
101 the ability of a taxon to tolerate a range of habitats by considering the spatial distribution of  
102 taxa. Previous work focusing on soil bacteria at the small scale showed that a occupancy-  
103 frequency relationship was detectable at this small scale, following Hanski's core-satellite  
104 hypothesis [8]. This work was done using microarray and 454 pyrosequencing data, using  
105 samples of a few milligrams taken along a 22 cm long transect at one cm intervals. Here, we  
106 extend this study to include a range of soils and use Illumina sequencing in order to derive an  
107 more in depth analysis of the distribution of individual taxa. We chose to include a number of  
108 soils with different abiotic properties because it is known that these properties influence the  
109 composition and distribution of microbial communities.

110 Other works have attempted to identify which environmental variables shape microbial  
111 diversity. Indeed, previous work reported a relationships between microbial distributions and  
112 abiotic variables [33–35] and aimed to determine the main spatial community driver at a larger  
113 scale.

114 The objective of this study was to investigate in different soils, at the small scale (from  
115 1cm to 1m intervals and about 100 to 500mg weight) whether (1) soil bacterial communities  
116 exhibit spatial structures and, if so, whether (2) these structures varied among soils from  
117 different environments. We used Hanski's hypothesis (the core and satellite hypothesis) to  
118 structure the analysis. The four soils that were used in the study were from four pedo-climatic  
119 situations and from three different regions: two Alpine polygonal soils (one from the centers  
120 and the other from the sides of polygons), a soil from the Rhône area and a Sahel soil. Bacterial  
121 diversity analyses, evaluated using a 16S rRNA gene metabarcoding approach, were carried  
122 out. Community ecology approaches were used to assess the spatial structures using occupancy-  
123 frequency distribution patterns (*i.e.* core or satellite mode distributions) and abundance-  
124 occupancy relationships (abundance being calculated as the average percent presence of a taxon

125 in samples). An in-depth analysis of bacterial OTU spatial distribution patterns was conducted  
126 by studying core taxa (defined as OTUs present in 100% of the micro-samples for a considered  
127 soil) and satellite taxa (defined as present in only 1 micro-sample for a considered soil, these  
128 satellite taxa were therefore spatially rare taxa). Moreover, in order to gain a better  
129 understanding of the ecological strategies employed by the taxa with regard to their habitat, we  
130 classified them according to their distribution across micro-samples (generalist taxa defined as  
131 broadly distributed bacterial taxa and specialists taxa were satellite taxa with more than 0.1%  
132 of sequences per micro-sample).

133

## 134 **2. Materials and Methods**

### 135 ***2.1. Soil sampling***

136 Soils were sampled in regions presenting four pedo-climatic combinations in three geographic  
137 locations: La Vanoise (Van), a loamy polygonal soil under alpine climate, sampled in the center  
138 of polygons (Van\_PC) and from the sides of polygons (Van\_PS) (polygons being typical  
139 structures retrieved in soil that experience freezing and thawing alternately); La Dombes (LD),  
140 a silty loam soil under temperate climate and Grande Muraille Verte (GMV), a sandy soil in a  
141 semi-arid climate.

142 Thirty nine micro-samples were collected at La Vanoise (col de la Laysse, La Vanoise,  
143 France, 2200m altitude, N 45° 27' 19.56'', L 6° 51' 54.12''), characterized by an average  
144 temperature in the summer of 5.3°C and an annual rainfall of 637mm. Seventeen micro-samples  
145 were collected in Van\_PC and 22 micro-samples were collected in Van\_PS in September 2013  
146 and September 2014 to take into account the soil convection movements typical of this type of  
147 soil with polygons (Supplementary Table 1 [36]). Twenty-two LD soil micro-samples were  
148 collected in an undisturbed agricultural soil in September 2013 (Saint André de Corcy, Ain,  
149 France, 45° 51' 04.7'' N 4° 57' 30.5'') characterized by an average annual min-max



150 temperatures of 8.1°C-16.9°C and annual rain of 832mm. Finally, twenty soil micro-samples  
151 were collected in September 2014 in a Savanna soil (Widou, Grande Muraille Verte, Senegal,  
152 15°58.549'N 15°17.221'W). Maximum and minimum temperatures are 36.9°C and 20.5°C,  
153 respectively, and the annual rainfall is 300mm.

154 The sampling procedure for the Van\_PC, Van\_PS and LD soils proceeded as follows:  
155 soil cores, 1cm diameter and 2cm depth, were taken with a corer along a longitudinal transect,  
156 with 1cm to 10m lags, 0.2 to 10m long (Supplementary Table 2). The top 1mm of the cores  
157 (sample depth named “a”) and a 1 mm thick slice underneath (sample depth named “b”) were  
158 cut with a scalpel blade. The soil water content allowed the sample to remain intact. Samples  
159 were freeze-dried and stored at -80°C for DNA extraction. Two-centimeter depth core was an  
160 intermediary size to sample in the field and to bring it back to lab and subsample the final  
161 sample (*i.e.* the micro-sample) with spatial coordinate. Slice *a* was analyzed systematically and  
162 slice *b* was taken in case there was a need to verify data.

163 In La Vanoise, micro-samples were collected along two 10m transects with lags from  
164 1cm to 1m, to ensure that the sampling covered several polygons, from the centers (Van\_PC,  
165 yellow coloured) and sides of polygons (Van\_PS, brown colored), respectively (Supplementary  
166 Table 2). Micro-sample weights were 119 mg on average (min 70mg - max 288mg) for Van\_PS  
167 and 129 mg on average (from 120 to 150 mg) for Van\_PC.

168 In LD, the micro-samples were collected 1cm lags along a 20m transect, from an area  
169 at the edge of a maize field that had not been ploughed for at least 10 years. Micro-sample  
170 weights were 100mg on average (77 to 144 mg).

171 For the GMV soil, the sampling procedure 1m lags along to a 20m transect, needed to  
172 be adapted as it is a sandy soil and we could not proceed with cores. As the soil was very sandy,  
173 10g of soil were sampled every meter at 20 spots in the field and then subsampled in the  
174 laboratory (250 to 500 mg), lyophilized and stored at -80°C for DNA extraction.

175 Soil physicochemical characteristics (texture, pH, organic carbon, organic matter, C/N,  
176 assimilable P, K, Ca, Mg) were measured by CESAR (Centre Scientifique Agricole Regional,  
177 Ceyzeriat, France, <http://www.labo-cesar.com>) on pooled micro-samples from Van\_PC,  
178 Van\_PS, GMV and LD to get average characteristics of the site (Supplementary Table 1) using  
179 a standard methods that followed the AFNOR French standard (AFNOR, 2004).

180

## 181 **2.2. DNA extraction**

182 DNA extraction from micro-samples was performed following Michelland *et al.* (2016).  
183 Briefly, soil micro-samples were suspended ( $1 \text{ g mL}^{-1}$ ) in PBS (pH=8) and centrifuged at 5,700g  
184 for 1 min. The pellet was suspended in 1 mL washing solution ( $50 \text{ mmol L}^{-1}$  Tris-HCl pH = 7.7,  
185  $25 \text{ mmol L}^{-1}$  EDTA, 0.1 % SDS, 0.1 % PVP,  $\text{H}_2\text{O}$ ) and centrifuged at 5700g for 1min. The pellet  
186 was then suspended in  $35 \mu\text{L}$  lysis solution ( $50 \text{ mmol L}^{-1}$  Tris-HCl, pH = 8,  $25 \text{ mmol L}^{-1}$  EDTA,  
187 3% SDS, 1.2% PVP) and microwaved at 600-700W for 45s (Orsini and Romano-Spica, 2001).  
188 Four hundred microliters of extraction solution ( $10 \text{ mmol L}^{-1}$  Tris HCl, pH =8,  $1 \text{ mmol L}^{-1}$   
189 EDTA,  $0.3 \text{ mol L}^{-1}$  sodium acetate, 1.2% PVP), pre-heated ( $75^\circ\text{C}$ ), were then added before  
190 extraction with one volume phenol-choloroform-isoamylic alcohol (25:24:1) and centrifugated  
191 for 10min at 13,000rpm. One volume of chloroform was then added, the solution centrifuged  
192 for 5min at 13,000rpm, and the aqueous phase was retained. Ten percent of the total volume of  
193 sodium acetate 3M (pH 5) and 2 volumes of cold absolute ethanol were added and, after cooling  
194 on ice for 20min, the micro-samples were centrifuged for 30min at 13,000rpm and  $4^\circ\text{C}$ . The  
195 supernatant was then discarded and the DNA pellets were washed with EtOH 70% and  
196 resuspended in  $20 \mu\text{L}$  water.

197

## 198 **2.3. Illumina sequencing and sequence processing**

199 Amplification of the bacterial V4 region of the 16S rRNA genes was performed using the  
200 universal primers 515F/806R . High-throughput sequencing was carried out after a multiplexing  
201 step using a MiSeq 2x300bp PE technology (MR DNA lab, [www.mrdnalab.com](http://www.mrdnalab.com), Shallowater,  
202 TX, USA).

203 According to the MR DNA analysis pipeline (MR DNA, Shallowater, TX, USA), paired-  
204 end sequences were merged and denoising procedures, that consisted in discarding reads  
205 containing ambiguous bases (N) or reads that were outside the range of expected length (*i.e.*  
206 <150bp), were carried out using Uchime [37]. The remaining sequences were clustered at a  
207 97% similarity threshold [38] with Usearch [39]. Chimeras were detected using Uchime [37]  
208 and removed from the dataset. Final OTUs were taxonomically affiliated using BLASTn  
209 against a cured database derived from Greengenes, RDPII and NCBI ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov),  
210 <http://rdp.cme.msu.edu>) [40].

211 Singletons were removed from the dataset. In order to compare micro-samples and to  
212 retain the largest possible number of micro-samples, a random resampling normalization step  
213 at a depth of 5474 sequences per sample was carried out. It should be noted that this procedure  
214 resulted in the exclusion of 1 sample from the Van\_PC and 3 samples from the GMV soils as  
215 they did not contain 5474 sequences (Table 1).

216 The sequencing data of the LD soil have been published in Michelland *et al.* (2016) and  
217 the dataset is available under the accession number PRJEB14534 in the SRA database. Data for  
218 other soils have been deposited under the following accession number ERP016178 at EBI.

219

#### 220 ***2.4. Statistical analyses***

221 The soil parameters (Supplementary Table 1, parameters in column) were analyzed by a  
222 standardized PCA. Standardization was needed because of the differences in parameter units.  
223 The data table was transformed to row percentages (row sums = 1) before doing the PCA, to

224 reduce the impact of the high sequence count variability among OTUs in the soil micro-  
225 samples.

226 The table of diversity data (OTUs in columns) was analyzed by a PCoA on the Jaccard  
227 distance matrix.

228 Computations were performed with the ade4 package [41] for the R Statistical Software  
229 (R Core Team, 2019).

230

### 231 **3. Results**

#### 232 ***3.1. Physico-chemical characteristics and bacterial diversity***

233 Rarefaction curves indicated that the sequencing effort was sufficient to describe bacterial  
234 diversity in Van\_PC and GMV soils while in Van\_PS and LD, some samples do not appear to  
235 have reached an asymptote (Supplementary Figure 1). Moreover, it showed that bacterial  
236 richness in the Van\_PC micro-samples was more variable than in the other soils  
237 (Supplementary Figure 1). There were 418 OTUs common to the four soils, equivalent to  
238 16.54% of the total richness (Figure 1A).

239 The PCA ordination, based on the physical and chemical properties of the soils (texture,  
240 pH, organic carbon, organic matter, C/N, assimilable P, K, Ca, Mg, Supplementary Table 1), is  
241 shown in Figure 2A. The percentage variability explained by axes 1 and 2 was 59% and 27%,  
242 respectively. There was a clear separation among the soils, the LD soil being related to coarse  
243 silt (Csi), K and assimilable P, the GMV soil related to coarse sand, the Van\_PC soil to high  
244 C/N ratios, and the Van\_PS soil to clay and total nitrogen. Both La Vanoise soils (i.e. Van\_PC  
245 and Van\_PS soils) were associated with high fine silt, OM, Mg, Ca contents. The pH of the La  
246 Vanoise soils was close to or above 8 (Supplementary Table 1).

247 The PCoA ordination graph of bacterial diversity data is shown in Figure 2B. The first  
248 two axes account for 11% and 9% of the total variability. This analysis highlighted that GMV  
249 and LD soils exhibited lower intra-diversity compared to Van\_PC and Van\_PS soils. On the

250 first axis, GMV and LD soils were distinguished from the Van\_PC and Van\_PS soils while on  
251 the second axis, GMV and LD soils were distinguished.

252

### 253 **3.2. Abundance-occupancy and occupancy-frequency relationships**

254 The abundance-occupancy diagrams for each soil showed a positive relationship between the  
255 OTU average relative abundances in micro-samples and the proportion of micro-samples in  
256 which they were found (Figure 3). The patterns in the occupancy-frequency diagrams were  
257 different however (Figure 4). The distribution in Van\_PC was unimodal with a satellite mode  
258 (a large proportion of taxa occupied only one micro-sample), as highlighted by the ratio of  
259  $\text{OTUs}_{\text{number}_{\text{core}}} \text{ over } \text{OTUs}_{\text{number}_{\text{satellite}}}$  equal to 0.027. Van\_PS, GMV and LD presented  
260 bimodal distributions with  $\text{number}_{\text{core}} \text{ OTUs} : \text{number}_{\text{satellite}} \text{ OTUs}$  ratios of 0.301, 0.323 and 0.571,  
261 respectively. Interestingly, compared to Van\_PC, Van\_PS and GMV, a smaller proportion of  
262 the taxa that were limited to a small number of micro-samples associated with a larger  
263 proportion of taxa were present in all micro-samples is characteristic of the LD soil (*i.e.* ratio  
264 of  $\text{OTUs}_{\text{number}_{\text{core}}} \text{ over } \text{OTUs}_{\text{number}_{\text{satellite}}}$  of 0.571). Van\_PS, GMV and LD core taxa  
265 number are always important, 105, 86 and 155 respectively but they were less numerous than  
266 the satellite taxa. The average abundances (*i.e.* % of sequences) of satellite OTUs in micro-  
267 samples were higher in Van\_PC soil than in Van\_PS, GMV and LD soils (Table 1), whereas  
268 the average abundances of core OTUs in Van\_PC soil (*i.e.* 21.72%) were much lower compared  
269 to other soils (80.96%, 78.80% and 82.78% for Van\_PS, GMV and LD soils, respectively,  
270 Table 1). Core OTUs in Van\_PC soil exhibited the lowest frequency compared to the other soils  
271 (7.65, 9.11 and 12.86% for Van\_PS, GMV and LD soils, respectively, Table 1), while satellite  
272 OTUs frequency in Van\_PC soil was the highest (*i.e.* 36.80%) compared to the other soils  
273 (25.34, 28.18 and 22.49% for Van\_PS, GMV and LD soils, respectively, Table 1).

274 The PCoA ordination based on OTU patterns, which explained 11 and 9% of total variability  
275 on the first and second axes, respectively, separated soils with positive coordinates for LD and  
276 Van\_PS soils and negative coordinates for GMV and Van\_PC. Moreover, on the second axis  
277 (Figure 2B) it separated LD and GMV. Moreover, the PCoA ordination based on OTU patterns  
278 separated the four soils as the PCA ordination of the physico-chemical properties did (Figure  
279 2). Thus, the spatial distribution type, which separates Van\_PC (satellite mode) from Van\_PS,  
280 GMV and LD (bimodal), presents a typology that is different from the typology of soil physico-  
281 chemical characteristics and to the typology based on diversity. The first axis of soil PCA  
282 (which explains 59% total variability, Figure 2A) separates GMV and LD soils from Van\_PS  
283 and Van\_PC. This corresponds to the opposition between semi-arid sandy soil of GMV and  
284 organic matter rich soils from La Vanoise while LD is “positioned” by coarse silt. The second  
285 axis (27% explained variability) separates LD and Van\_PS from Van\_PC and GMV. The  
286 community spatial distribution type may thus be driven by a combination of factors different  
287 from the ones driving diversity, thus bringing more information about the soil function.

288

### 289 ***3.3. Composition of core and satellite bacterial communities***

290 Taxonomic investigations, at the phylum\_class level (representing > 2% of sequence  
291 abundance) on satellite and core OTUs, revealed that some classes, as *Actinobacteria*,  
292 *Alphaproteobacteria* and *Betaproteobacteria*, were ubiquitous (Figure 5). *Actinobacteria* were  
293 more abundant among GMV and LD core OTUs than among satellite OTUs, and  
294 *Deltaproteobacteria* were less abundant among core taxa in GMV and LD than among satellite  
295 taxa. Globally, Bacilli and Clostridia represented, on average, 10.2 and 0.7% of all sequences,  
296 respectively, in the satellite taxa of the four soils, but only 4.1 and 2.8 %, on average, in the  
297 core taxa (to be noted that Bacilli were enriched in GMV core OTUs representing 13.9% of  
298 sequences).

299 Core and satellite taxa in bacterial families that accounted for > 2% of the sequences  
300 were also analyzed (Table 2). Among those 52 families, 28 were specific to core taxa while 14  
301 families were specific of satellite taxa (Table 2). The core specific families represented 65.9,  
302 43.3, 44.3 and 33.4% of core taxa sequences in Van\_PC, Van\_PS, GMV and LD, respectively,  
303 while the satellite-specific families represented 40.2, 14.2, 19.3 and 7.5% of satellite taxa  
304 sequences in Van\_PC, Van\_PS, GMV and LD, respectively.

305 Among the core taxa of the four soils (357 OTUs in total), only 2.2% (*i.e.* 8 OTUs) were  
306 common to all of them (Figure 1B): *Acidimicrobiales* spp. (affiliated with Actinobacteria),  
307 *Azospira* spp. (affiliated with Betaproteobacteria, Rhodocyclales order), *Flexibacter* spp.  
308 (affiliated with Bacteroidetes, Cytophagales order), *Gemmatimonas* spp. (affiliated with  
309 Gemmatimonadetes), *Nitrosococcus* spp. (affiliated with Gammaproteobacteria, Chromatiales  
310 order), *Rubrobacter* spp (affiliated with Actinobacteria, Rubrobacterales order), *Sphaerobacter*  
311 *thermophilus* (affiliated with Chloroflexi, Sphaerobacterales order), *Sphingomonas* spp.  
312 (affiliated with Alphaproteobacteria, Sphingomonadales order). Moreover, Van\_PS, GMV and  
313 LD soils had 9.2%, 9.5% and 23.2% specific core taxa, respectively, whereas Van\_PC  
314 presented no specific core taxa (Table 1, Figure 1B). Relatively to common taxa retrieved in  
315 the four soils (*i.e.* 418 OTUs, Figure 1A), core OTUs in Van\_PC which is satellite mode  
316 represented 2.4% of OTUs and in bimodal soils, Van\_PS, GMV and LD soil it represented  
317 24.1, 15.6% and 28.7% of OTUs respectively (Table 1).

318 In the same way, among the 1288 OTUs constituting the satellite taxa retrieved in the  
319 four soils (Figure 1C), only 2 OTUs were common to the four soils (*i.e.* 0.16% of OTUs):  
320 *Ancalomicrobium adetum* (affiliated with Alphaproteobacteria, Rhizobiales order) and  
321 *Nonomuraea terrinata* (affiliated with Actinobacteria, Actinomycetales order). Moreover,  
322 Van\_PC, Van\_PS, GMV and LD soils had 20.3%, 17.6, 13.9 and 14.4% specific satellite taxa,  
323 respectively (Table 1, Figure 1C). Relatively to common taxa retrieved in the four soils (*i.e.*

324 418 OTUs, Figure 1A), satellite OTUs in Van\_PC, Van\_PS, GMV and LD represented 11.2,  
325 3.8, 18.9 and 8.4% of OTUs, respectively (Table 1).

326

### 327 ***3.4. Bacterial ecological strategy at the small scale: habitat generalists and specialists***

328 Concerning generalists, among core taxa retrieved in the four studied soils (*i.e.* 229 OTUs),  
329 34.7% were common to at least two soils, 20.2% common to at least 3 soils and only 3.5%  
330 common to the four soils (Figure 1B).

331 Fifty-three specialist OTUs were found in Van\_PC, representing 4.8% of the total richness in  
332 Van\_PC (Table 1). To be noted that in Van\_PC, 45.3% of specialist taxa belonged to  
333 Proteobacteria and 15.1% belonged to Actinobacteria. In GMV, 9 OTUs were considered  
334 specialist, whilst there were 2 in Van\_PS and only 1 in LD (Table 1). Interestingly, specialists  
335 OTUs in LD and GMV are specific to these soils while one specialist OTU was common to  
336 Van-PC and Van\_PS soils.

337

## 338 **4. Discussion**

339 We use a community ecology approach, drawn from the study of macroorganisms, was  
340 used to investigate bacterial community spatial distributions at the micro-scale across four  
341 different soils. The micro-sampling (few hundred milligrams: from 100 to 500mg) was carried  
342 out on undisturbed soil so as to take the spatial distribution of taxa in the micro-samples into  
343 account (within and between micro-samples). The analysis of bacterial diversity data combined  
344 with soil micro sampling suggested that bacteria can be classified in each soil as core or satellite  
345 taxa, depending on their distribution at the small scale.

346

### 347 ***4.1. Spatial distribution patterns***



348 The separation of the soils on the two PCA and PCoA ordinations, suggests that satellite mode  
349 distribution, retrieved in Van\_PC, is related to coarse sand, high C/N and pH. Unfortunately,  
350 we could not directly correlate bacterial taxa with environmental variables as micro-samples  
351 were too small to perform physico-chemical analyses. To date, quantifying environmental  
352 variables in micro-samples remains a big technical issue which needed to be resolved in further  
353 decades to gain insight into relationships between microbial communities and fine soil physico-  
354 chemical properties. Moreover, other complementary variables could be drivers of community  
355 spatial structure such as bulk density, soil structural heterogeneity, pore size distributions and  
356 connectivity and organic features (i.e. root architecture or soil invertebrate activity).

357 While the existence of a rare microbial biosphere, across different ecosystems, is now  
358 accepted [43, 44], there is no widely accepted definition of rare taxa in the literature. Indeed,  
359 arbitrary relative abundance cut-offs, depending on the study, range from 0.1% to 0.01% [45].  
360 In the present work, conducted at the small scale, we used a spatial definition of rare taxa based  
361 on micro-sample occupancy, where taxa found in only one micro-sample were considered  
362 spatially rare, or satellite taxa [32]). This corresponds to an average relative abundance of  
363 0.027% of the total sequences, when including all micro-samples in this study. Compared to  
364 the definition of Lynch and Neufeld (2015), our percentage of rare taxa identified is quite  
365 conservative. Because rare taxa are substantial contributors to bacterial community ecology  
366 [43, 45], their spatial distribution may be an important factor impacting ecological processes  
367 and thus soil functioning. Studies focusing on spatial ecology of soil bacteria [46] concluded  
368 that the relative importance of the underlying processes contributing to the establishment of  
369 bacterial distributions can change with soil characteristics. More generally, Lindh *et al.* (2017)  
370 suggested that analyses of occupancy-frequency patterns can be a highly valuable approach  
371 allowing the definition of microbial biomes across environmental gradients [7].

372           Although a positive small scale abundance-occupancy relationship has already been  
373 identified in the LD soil [8], this study confirmed this relationship and extended it to three other  
374 soils, suggesting a certain prevalence of the relationship in soil microbial communities. This is  
375 hardly surprising as it is one of the most fundamental patterns in ecology [2]. Moreover, the  
376 bacterial community spatial distributions also conformed to Hanski's core and satellite  
377 hypothesis [29]. However, the present work was conducted in four soils for which samples  
378 differed a bit in the size and/or mass collected as there was a loamy, a silty loam and a sandy  
379 soil that do not allow the strictly same sampling procedure. Soil heterogeneity and thus, the  
380 requirement for different experimental procedures may have an impact on the results.

381           Gleason (1929) showed that quadrats of the most serviceable size should be chosen to  
382 measure frequency distributions of plants, and that the information is obscured or lost if the  
383 quadrats are either too large or too small [47]. The fact that different ecological strategies were  
384 identifiable here suggests that the sample size used was appropriate for the study of bacterial  
385 spatial distributions in soils [16]. Compared to other studies, the present work showed the  
386 relevance of the small scale approach in spite of the very low organism's size to sample size  
387 ratio [48]. Previous studies investigating the type of occupancy-frequency patterns have  
388 suggested that unimodal distributions, that are characterized by an excess of rare, endemic  
389 species, occur more frequently than bimodal distributions [49, 50]. Even when bimodal  
390 distributions are detected, the magnitude of the core mode, representing cosmopolitan species,  
391 is generally smaller than that of the rare species [50]. The three bimodal distributions that we  
392 observed, indicate that it may be a common community spatial distribution of soil bacteria at  
393 the small scale. This suggested that OTUs are either adapted to the majority of micro-habitats  
394 in this soil, or that these OTUs have a high dispersal capabilities favouring the colonization of  
395 empty ecological niches. Indeed, core species are believed to owe their regional commonness  
396 to the rescue effect (*i.e.* reduction in local extinction probability [51]) while satellite species are

397 maintained by the habitat heterogeneity [52]. Cadotte and Lovett-Douste (2007) suggested that,  
398 via the rescue effect, widespread and abundant species should have reduced risk of local  
399 extinction. In their work conducted on trees, different community spatial structures were  
400 observed [53]. Indeed, trees in degraded environments showed a satellite mode distribution,  
401 contrary to the other studied environments. In the Van\_PC soil, the satellite mode distribution  
402 might represent a functional mode (*i.e.* corresponding to a stressful state) as in Cadotte and  
403 Lovett-Douste (2007).

404

#### 405 ***4.2. Bacterial ecological strategies***

406 For some authors, identifying core taxa is the first step in defining a “healthy” community and  
407 predicting community responses to perturbation [54]. Interestingly, it has been suggested that  
408 due to the great microbial diversity among ecosystems, the possibility of any species being  
409 present at high abundance in a large range of samples is low and it is possible that the focus  
410 should instead be on higher taxonomic levels or on functional genes [55]. The results presented  
411 here are in accordance with this theory as only a few core OTUs are common to the four soils.  
412 However, when considering the commonness in only two or three soils, their richness increases,  
413 suggesting a patchy distribution rather than a ubiquitous one.

414

415

416

#### 417 **5. Conclusions**

418 There is an increasing recognition that interactions within bacterial communities can have an  
419 impact on community functioning [56, 57]. In this contribution we have shown that the types  
420 of small-scale distributions of bacterial communities vary across soils with different physico-  
421 chemical features. This suggests that the type and range of interactions that might be expected  
422 to occur within microbial communities are likely to vary depending on the pedo-climatic

423 context. We have shown that one soil presented a core mode, another presented a satellite mode  
424 and the three others presented bimodal distributions. We also identify among bacterial richness  
425 retrieved in those four soils micro-samples that up to 13% can be classified as core taxa, that  
426 could be responsible for the stability of soil bacterial communities. Thus the considering of  
427 microbial spatial distribution, that could play a major ecological role, should further improve  
428 predictions and modelling on diversity modification risks, on soil bio-conservation and  
429 epidemiology.

### 430 **Conflicts of interest**

431 The authors declare that they have no known competing financial interests or personal  
432 relationships that could have appeared to influence the work reported in this paper.

433

### 434 **Funding**

435 This work was cofunded by the EC2CO MicrobiEn AO2012- 779949 'Les communautés  
436 bactériennes dans les sols extrêmes: les paramètres de leur structure et leur composition' and  
437 the Labex DRIIHM, French program "Investissements d'Avenir" (ANR-11-LABX-0010)  
438 which is managed by the ANR. We thank La Vanoise National Parc for soil sampling  
439 authorization.

440

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598 **Figures and Tables Legends**

599 **Figure 1.** Venn Diagrams presenting the shared and specific OTUs (A) detected in the four  
600 soils, (B) among core OTUs and (C) among satellite OTUs.

601 **Figure 2.** PCA map of soils characteristics (A) and PCoA map of bacterial diversity (B) for  
602 LD, GMV, Van\_PC, Van\_PS soils. On Figure 2A, arrows correspond to the four soil samples  
603 and labels to the soil physico-chemical parameters. On Figure 2B, the position of ellipse centers  
604 are given by the means of the coordinates of micro-samples on the two axes of the factor map  
605 for each soil sample origins (LD, GMV, Van\_PC and Van\_PS). The width and height of ellipses  
606 are given by the variance of the coordinates of the micro-samples on the two axes and the ellipse  
607 slope is equal to their covariance.

608 **Figure 3.** Relationship between relative abundance (average percentage taxa presence in micro-  
609 samples) and occupancy (percentage of micro-samples in which each taxa is present) in  
610 Van\_PC, Van\_PS, LD and GMV soils.

611 **Figure 4.** Occupancy-frequency relationship for Van\_PC, Van\_PS, LD and GMV soils.  
612 Frequency is expressed as the percent taxa found for each possible occupancy.

613 **Figure 5.** Distribution of bacterial classes representing more than 2% of total taxa in core and  
614 satellite taxa, in Van\_PC, Van\_PS, LD and GMV soils.

615

616 **Table 1.** Sequence analyses for Van\_PC, Van\_PS, LD and GMV soils: sample number, raw  
617 sequence number and normalization threshold. Detailed analyses of core and satellite taxa:  
618 OTUs number, sequences percentage, frequency, average abundance. Detailed analyses of  
619 ecological strategies: specific core OTUs percentage, percentage of core OTUs found in  
620 common taxa and number of specialist OTUs.



621 **Table 2.** Distribution of bacterial families representing more than 2% of sequences in at least  
622 one of the condition (core or satellite of each site). The ten most abundant families per  
623 conditions were highlighted in grey.

624 **Supplementary Figure 1.** Rarefaction curves for Van\_PC, Van\_PS, LD and GMV soils, using  
625 the normalized datasets (*i.e.* 5474 sequences).

626 **Supplementary Table 1.** Physico-chemical characteristics of Van\_PC, Van\_PS, LD and GMV  
627 soils. The unit is g.kg<sup>-1</sup> except for pH and C/N ratio.

628 **Supplementary Table 2.** La Vanoise soil sampling: Distances between micro-samples (cores)  
629 in Van\_PC and in Van\_PS starting from an initial point, named 0 m. Micro-samples were taken  
630 along two transects 10 cm apart, in September 2013 and September 2014. Results obtained on  
631 all micro-samples were gathered as no difference could be shown between the two sampling  
632 dates. Micro-samples named “a” corresponded to the top 1 mm of the cores and sample “b”  
633 corresponded to the 1 to 2 mm below sample “a”. “b\*”: in two cases, a second core was taken  
634 beside core “b”, at the same distance from the origin.

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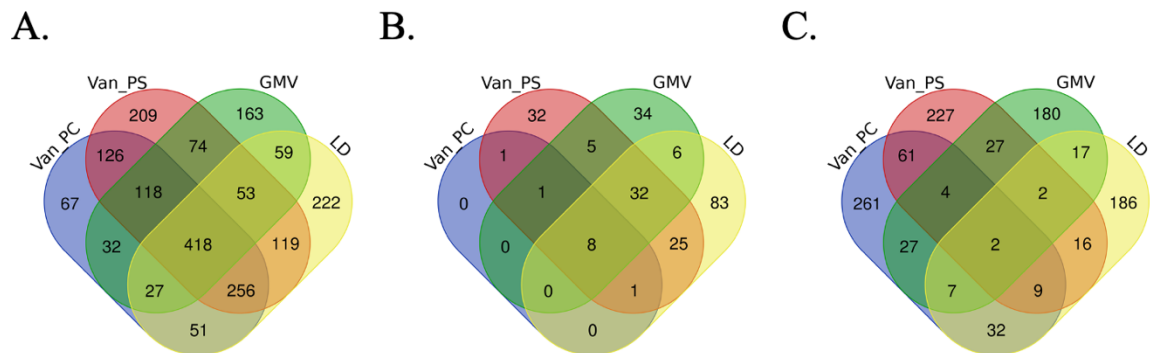
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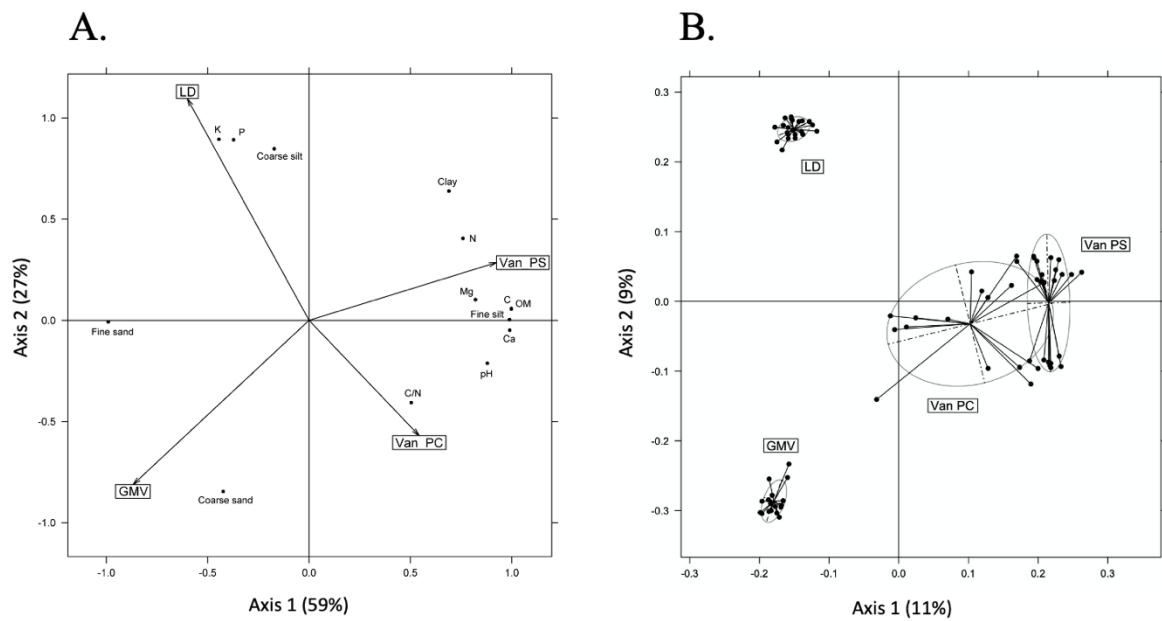
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652 **Figure 1.** Venn Diagrams presenting the shared and specific OTUs (A) detected in the four  
 653 soils, (B) among core OTUs and (C) among satellite OTUs.

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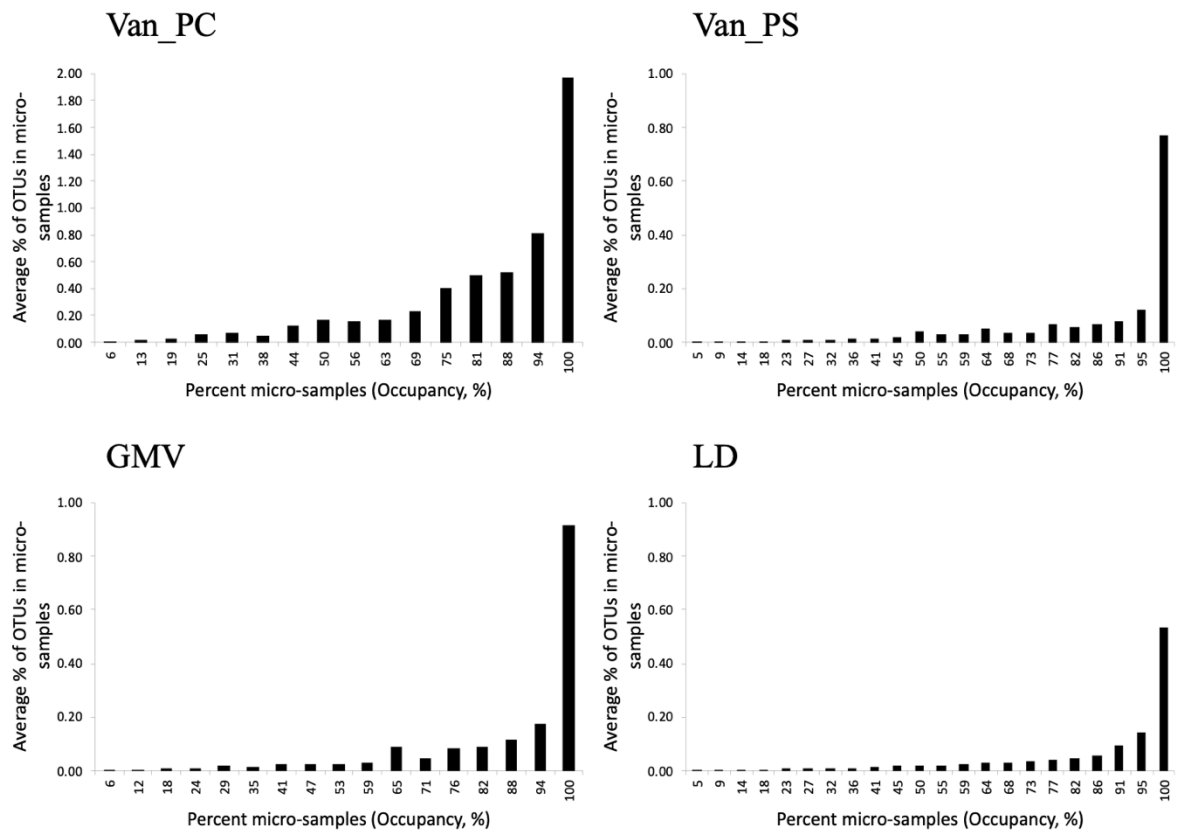
659 **Figure 2.** PCA map of soils characteristics (A) and PCoA map of bacterial diversity (B) for  
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 663 for each soil sample origins (LD, GMV, Van\_PC and Van\_PS). The width and height of ellipses  
 664 are given by the variance of the coordinates of the micro-samples on the two axes and the ellipse  
 665 slope is equal to their covariance.

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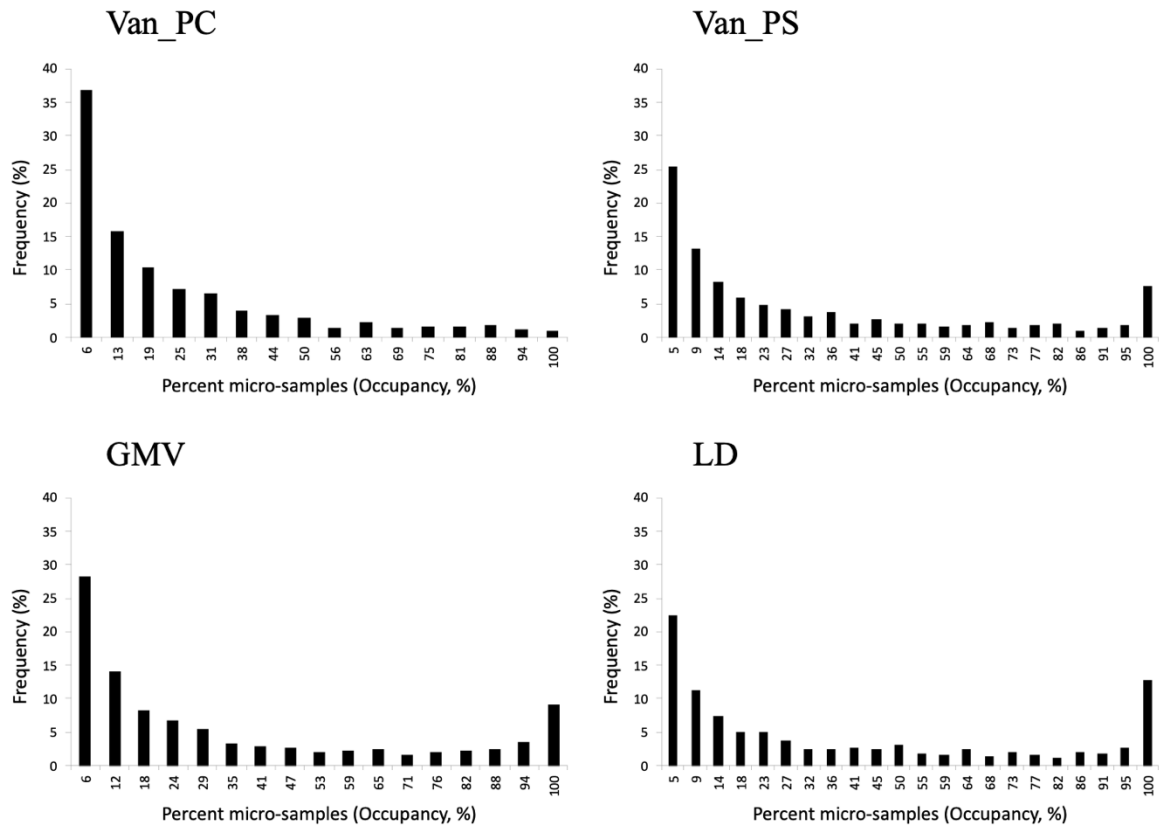
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671 **Figure 3.** Relationship between relative abundance (average percentage taxa presence in micro-  
 672 samples) and occupancy (percentage of micro-samples in which each taxa is present) in  
 673 Van\_PC, Van\_PS, LD and GMV soils.

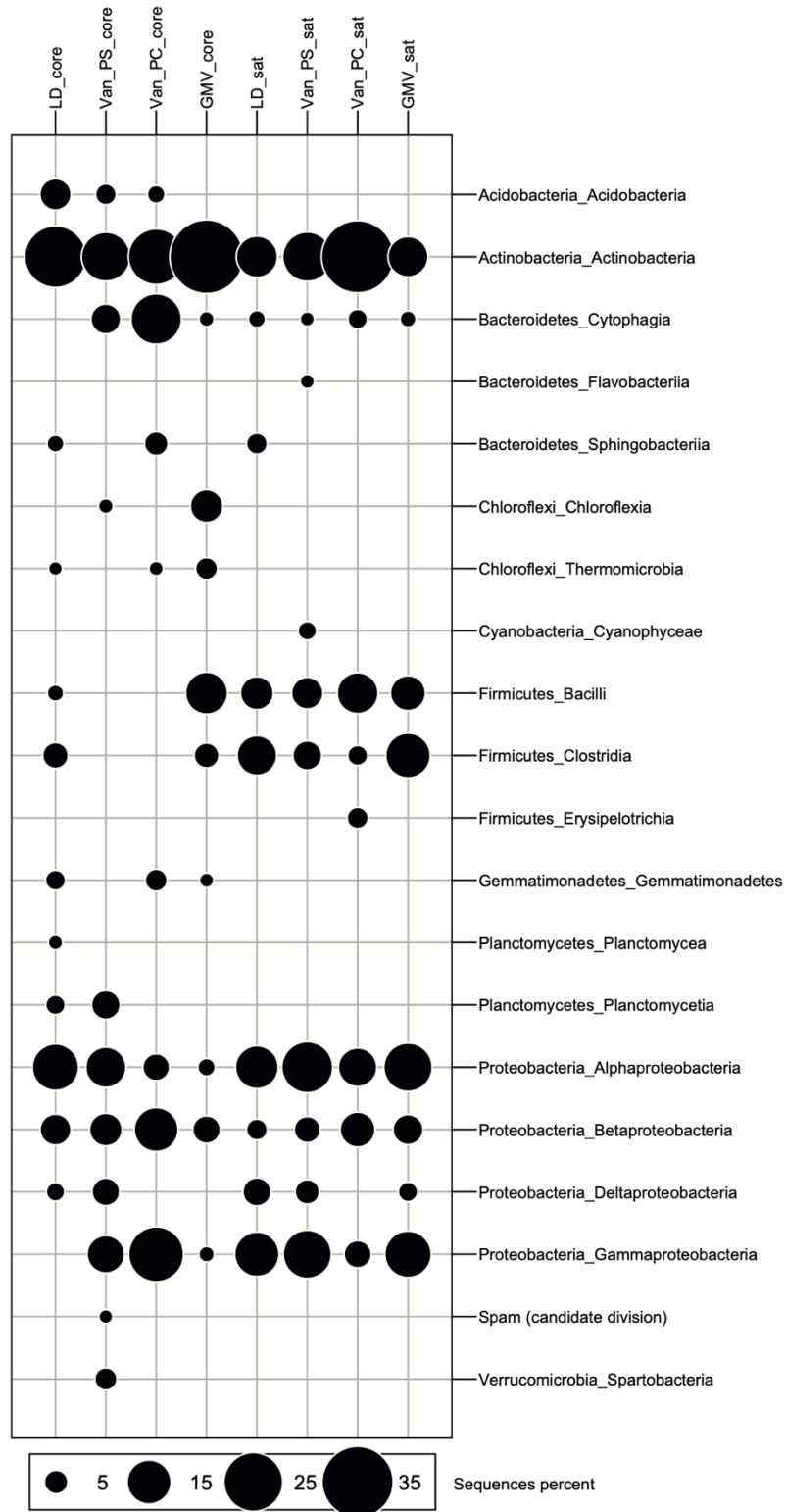
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676 **Figure 4.** Occupancy-frequency relationship for Van\_PC, Van\_PS, LD and GMV soils.

677 Frequency is expressed as the percent taxa found for each possible occupancy.



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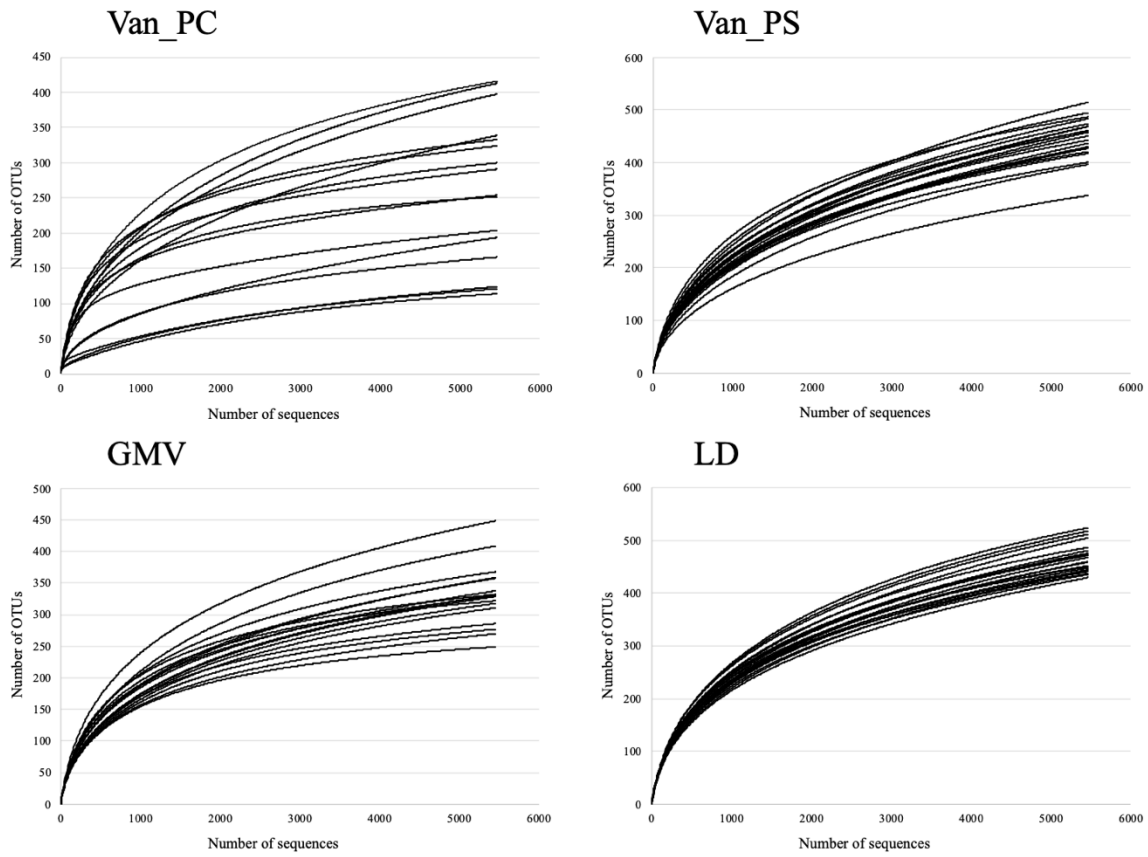
679 **Figure 5.** Distribution of bacterial classes representing more than 2% of total taxa in core and  
 680 satellite taxa, in Van\_PC, Van\_PS, LD and GMV soils.

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686 **Supplementary Figure 1.** Rarefaction curves for Van\_PC, Van\_PS, LD and GMV soils, using

687 the normalized datasets (*i.e.* 5474 sequences).

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695 **Supplementary Table 1.** Physico-chemical characteristics of Van\_PC, Van\_PS, LD and GMV  
 696 soils. The unit is g.kg<sup>-1</sup> except for pH and C/N ratio.

	LD	Van_PS	Van_PC	GMV
Coarse sand	40	127	179	437
Fine sand	392	115	140	476
Coarse silt	337	105	149	38
Fine silt	124	483	458	13
Clay	107	170	74	35
pH	6.82	7.77	8.41	6.61
Organic C	9.1	40.6	30.3	1.9
Organic matter	15.6	69.9	52.2	3.4
Total N	0.9	2.9	0.7	0.2
C/N	10	13	45	9
Assimilable P	0.261	0.032	0.013	0
K	0.138	0.056	0.015	0.044
Ca	1.94	9.54	9.1	0.33
Mg	0.055	0.62	0.174	0.084

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698 **Supplementary Table 2.** La Vanoise soil sampling: Distances between micro-samples (cores)  
 699 in Van\_PC and in Van\_PS starting from an initial point, named 0 m. Micro-samples were taken  
 700 along two transects 10 cm apart, in September 2013 and September 2014. Results obtained on  
 701 all micro-samples were gathered as no difference could be shown between the two sampling  
 702 dates. Micro-samples named “a” corresponded to the top 1 mm of the cores and sample “b”  
 703 corresponded to the 1 to 2 mm below sample “a”. “b\*”: in two cases, a second core was taken  
 704 beside core “b”, at the same distance from the origin.

Van_PC (17 samples)	Distance, meter												
	0 m	0.3 m	0.6 m	0.9 m	1.2 m	1.5 m	1.8 m	2.1 m	2.4 m	2.7 m	3 m	3.3 m	
September 2013		a, b	b, b*					b	b	b		b	
September 2014		a, b, b*	b	b	b	b	b				b		
Van_PS (22 samples)	0 m	0.32 m	1 m	2 m	2.5 m	3 m	3.5 m	4 m	4.5 m	5 m	7 m	9 m	10 m
September 2013	b		b				b	b	b	b	b	b	
September 2014	a, b	a, b	b	b	b	b	b	b	b	b	b		b

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