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► To cite this version:

Guille Peguero, Miquel Ferrín, Jordi Sardans, Erik Verbruggen, Irene Ramírez-Rojas, et al.. Decay of similarity across tropical forest communities: integrating spatial distance with soil nutrients. Ecology, inPress, 10.6084/m9.figshare.16615873.v1 . hal-03411548

HAL Id: hal-03411548

<https://hal.science/hal-03411548>

Submitted on 2 Nov 2021

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1 Running head: Similarity decay in tropical forests

2 Decay of similarity across tropical forest communities: integrating spatial
3 distance with soil nutrients

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27 **OPEN RESEARCH:** All data and code supporting the analyses and figures contained
28 in this contribution are available in the Figshare repository:

29 <https://doi.org/10.6084/m9.figshare.16615873.v1>

30

31 **ABSTRACT**

32 Understanding the mechanisms that drive the change of biotic assemblages over space
33 and time is the main quest of community ecology. Assessing the relative importance of
34 dispersal and environmental species selection in a range of organismic sizes and
35 motilities has been a fruitful strategy. A consensus for whether spatial and
36 environmental distances operate similarly across spatial scales and taxa, however, has
37 yet to emerge. We used censuses of four major groups of organisms (soil bacteria and
38 fungi, ground insects and trees) at two observational scales (1-m² sampling point vs
39 2500-m² plots) in a topographically standardized sampling design replicated in two
40 tropical rainforests with contrasting relationships between spatial distance and nutrient
41 availability. We modeled the decay of assemblage similarity for each taxon set and site
42 to assess the relative contributions of spatial distance and nutrient availability distance
43 and evaluated the potentially structuring effect of tree composition over all other taxa.
44 Similarity of nutrient content in the litter and topsoil had a stronger and more consistent
45 selective effect than did dispersal limitation, particularly for bacteria, fungi and trees at
46 the plot level. Ground insects, the only group assessed with the capacity of active
47 dispersal, had the highest species turnover and the flattest non-significant distance-
48 decay relationship, suggesting that neither dispersal limitation nor nutrient availability
49 were fundamental drivers of their community assembly at this scale of analysis. Only
50 the fungal communities at one of our study sites were clearly coordinated with tree
51 composition. Spatial distance at the smallest scale was more important than nutrient
52 selection for the bacteria, fungi and insects. The lower initial similarity and the
53 moderate variation in composition identified by these distance-decay models, however,
54 suggested that the effects of stochastic sampling were important at this smaller spatial
55 scale. Our results highlight the importance of nutrients as one of the main

56 environmental drivers of rainforest communities irrespective of organismic or propagule
57 size and how the overriding effect of the analytical scale influences the interpretation,
58 leading to the perception of a greater importance of dispersal limitation and ecological
59 drift over selection associated with environmental niches at decreasing observational
60 scales.

61 **Key words:** community assembly, dispersion, environmental filtering, French Guiana,
62 metabarcoding, nutrients, scale-dependency, soil biodiversity

63 **INTRODUCTION**

64 The central quest of community ecology is to elucidate the mechanisms that drive the
65 change of species assemblages over space and time (Vellend 2017). A recurrent pattern
66 identified in such inquiries is the nearly universal decay of similarity between
67 assemblages with the increase in the spatial or environmental distance separating them
68 (Nekola and White 1999). This macroecological pattern has been found in a broad
69 variety of organisms, from bacteria and fungi to plants and animals (Condit et al. 2002,
70 Green et al. 2004, Novotny et al. 2007, Bahram et al. 2013). Whether this pattern
71 emerges from the same mechanisms of community assembly across the entire range of
72 organismic size remains an open debate due to the paucity of studies simultaneously
73 studying multiple co-occurring taxonomic groups. A few attempts to do so have found
74 mixed and sometimes conflicting results usually dependent on their specific ecological
75 contexts (Beisner et al. 2006, Soininen et al. 2007, Bryant et al. 2008, Astorga et al.
76 2012, Zinger et al. 2019, Vleminckx et al. 2019, Luan et al. 2020). Moreover, many
77 patterns of biodiversity are scale-dependent and thus vary with the sampling grain (i.e.
78 the area of the observation unit) and extent (Nekola and McGill 2014, Chase et al.
79 2018). However, the scale-dependency of distance-decay patterns is seldom analyzed,
80 hence hindering the interpretation of the contrasting results gathered to date (Nekola and

81 McGill 2014). This prevents drawing general conclusions about the relative importance
82 of the different mechanisms of community assembly and of the scaling of these
83 processes into biogeographic patterns.

84 A recent conceptual synthesis (Vellend 2017) identified four high-level processes
85 driving the structure and composition of ecological communities: the movement of
86 organisms (dispersal), random or stochastic changes in the abundances of species (drift),
87 deterministic differences in fitness between individuals of different species due to their
88 biotic or abiotic context (selection) and the evolution of populations into new species
89 that operates over larger spatiotemporal scales than does local community assembly
90 (speciation). The decreasing form of the distance-decay relationship has usually been
91 associated with dispersal limitation and environmental selection (Nekola and White
92 1999) In the first case, the decay of similarity between assemblages with increasing
93 spatial distance would be explained by the reduction of the probability of species
94 reaching more distant localities due to their limited dispersal ability (Condit et al. 2002,
95 Gómez-Rodríguez and Baselga 2018). Alternatively, the decay of similarity with spatial
96 distance would derive from similar biotic and abiotic properties in closer localities. The
97 environment would thereby broadly select species based on their ecological niches,
98 making assemblages more dissimilar when biotic and abiotic conditions are more
99 different (Tuomisto et al. 2003, Astorga et al. 2012, Gómez-Rodríguez and Baselga
100 2018). The relative importance of dispersal limitation and environmental selection has
101 thus usually been assessed by measuring how well spatial or multivariate environmental
102 distances account for the dissimilarity between assemblages (Tuomisto et al. 2003,
103 Astorga et al. 2012, Gómez-Rodríguez and Baselga 2018). Nevertheless, environmental
104 conditions are often spatially autocorrelated, which confounds the effect of these
105 assembly mechanisms and hampers assessing their relative importance with current

106 statistical techniques (e.g. simple and partial Mantel tests; Guillot and Rousset 2013,
107 Legendre et al. 2015). A simple alternative is to specifically design spatially
108 standardized samplings for sites that vary in the level of co-variation between the spatial
109 distance separating plots and their environmental features, and then to compare the
110 strength of the distance-decay relationships for multiple taxonomic groups assuming
111 that their dispersal abilities are constant in these contrasting scenarios.

112 Variation in distance-decay relationships among taxonomic groups may arise from basic
113 biological properties such as differences in dispersal ability or traits associated with
114 their environmental sensitivity (Nekola and White 1999, Soininen et al. 2007). Yet,
115 there is no consensus regarding the relative importance of dispersal limitation versus
116 environmental selection across the range of body size from micro to macroorganisms.
117 For instance, the small size of microbial propagules, along with large populations and
118 short generation times, are thought to lead to homogeneous regional species pools from
119 which local communities are assembled by environmental selection (Martiny et al.
120 2006). This view, however, has been recently challenged by findings suggesting that the
121 community assembly of small organisms such as bacteria would be more influenced by
122 dispersal limitation than by environmental selection (Luan et al. 2020). Microorganisms
123 are mostly passive dispersers and at least some groups like fungi have shown variable
124 degrees of dispersal limitation and sometimes even a strong co-variation with plant
125 community composition (Peay et al. 2010, Bahram et al. 2013, Powell et al. 2015,
126 Tedersoo et al. 2016, Vleminckx et al. 2019). By contrast, macroorganisms should
127 generally have higher initial similarities and steeper distance-decay relationships
128 compared to microorganisms, presumably due to lower mobility and responsiveness to
129 fine-scale environmental variation (Soininen et al. 2007). Dispersal limitation may
130 accordingly be the main determinant of beetle similarity at a biogeographic scale in

131 Europe (Gómez-Rodríguez and Baselga 2018). Low levels of species turnover,
132 however, have been reported for herbivorous insects in tropical rainforests, suggesting
133 that dispersal limitation does not have a substantial role in community assembly from
134 local to regional scales in these diverse ecosystems (Novotny et al. 2007). The
135 compositions of plant and insect communities may also be strongly correlated at a
136 landscape level (Zhang et al. 2016), but a comprehensive study at a smaller spatial scale
137 found that ecological drift, not dispersal or environmental selection, may be the only
138 detectable driver of the otherwise highly stochastic assemblages of soil arthropods in
139 tropical rainforests (Zinger et al. 2019). As with microorganisms, it is likely that these
140 disparities between studies may be related to the spatial scale at which communities are
141 analyzed, since how distinct assembly processes structure community types is
142 fundamentally dependent on the sampling grain and extent at which communities are
143 investigated (Chase et al. 2018, Zinger et al. 2019, Luan et al. 2020). This complex
144 scenario therefore illustrates the need for more research if we are to understand whether
145 the processes linking local community assembly with biogeographic patterns differ
146 between the most common types of organisms.

147 Tropical rainforests are an ideal setting to conduct intertaxonomic and cross-site
148 comparisons of distance-decay patterns, because we can find high levels of species
149 richness and turnover associated with high levels of environmental heterogeneity at very
150 small spatial scales of a few hundred meters (Jucker et al. 2018). Since climate, soil
151 parent material and geologic time are largely constant at a landscape level, topography
152 emerges as the main driver of environmental variability in these ecosystems (Weintraub
153 et al. 2015). Topographic features such as slope and ruggedness influence the
154 hydrologic regime and thereby also soil weathering, mineralogy and texture.
155 Accordingly, topography ultimately determine the content and availability of key

156 nutrients such as N and P (Weintraub et al. 2015), which strongly affect the
157 composition, structure and dynamics of tree communities (John et al. 2007, Grau et al.
158 2017, Jucker et al. 2018, Soong et al. 2020). Tree communities may in turn co-
159 determine the composition of other associated taxonomic groups, as suggested by their
160 sometimes coupled spatial distributions (Peay et al. 2013, Zhang et al. 2016, Zinger et
161 al. 2019, Vleminckx et al. 2019). The content of main soil elements and ratios correlate
162 with many relevant environmental features such as soil texture, pH, organic matter and
163 water storage, and thus are major ecological factors and reliable multivariate proxies of
164 environmental heterogeneity.

165 Here, we assessed the relative importance of dispersal limitation and environmental
166 selection to the assembly of communities of soil bacteria, fungi, ground insects and
167 trees. We analyzed their distance-decay patterns across a spatially standardized system
168 of twelve 0.25-ha plots, each containing 3–5 sampling points, thus providing two nested
169 scales. This analysis was replicated at two tropical rainforest sites in French Guiana, one
170 for which the nutrient environment was completely uncorrelated with the spatial
171 distance among plots, while the other exhibited some correlation, hence providing a
172 unique naturally controlled opportunity to tease apart spatial vs. environmental effects.
173 We assessed the co-variation of community similarity patterns with spatial distances or
174 environmental dissimilarity based on the concentrations and ratios of 21 macro- and
175 micronutrients in the topsoil and organic horizons. We expected greater environmental
176 selection effects for microorganisms, and higher dispersal limitation for
177 macroorganisms with passive motility (e.g. trees). We likewise expected higher initial
178 similarities and faster distance-decay rates for trees and ground insects compared with
179 fungi and bacteria. We also evaluated the potential coupling between communities of
180 trees, the main structuring organisms in rainforests and thus a kind of environmental

181 selection agent, with the composition of ground insects, soil bacteria and fungi. Finally,
182 we also assessed if shifting the observational unit from plot to sampling point modified
183 the patterns of distance decay.

184 **MATERIALS AND METHODS**

185 **Study sites**

186 This study was conducted in two primary tropical rainforests in French Guiana in the
187 research stations of Paracou (05°16'38"N, 52°55'38"W) and Nouragues (04°04'53"N,
188 52°41'13"W). Both sites share the same tropical climate, with a wet season from
189 December to June and a dry season from August to November. Mean annual
190 precipitation and temperature are similar at Paracou and Nouragues (3102 mm and 25.7
191 °C vs 3000 mm and 25.2 °C, respectively). The bedrock is Precambrian schist at
192 Paracou and Caribbean granite and gneiss at Nouragues. Acrisols dominated at both
193 sites, but with higher sand content and more extractable N and P in the soil at the
194 bottom of hills and clayey minerals (e.g. kaolinite) and oxides increasing toward the
195 tops, where total nutrient and micronutrient concentrations are highest (Van
196 Langenhove 2020). We established 12 plots of 0.25 ha at each site stratified by three
197 topographic positions to account for this heterogeneity: at the top, slope and bottom of
198 hills. We set a central 20-m quadrat in each plot where we marked and geolocated five
199 evenly spaced sampling points around which we focused our measurements. This
200 design thus contained between 72 and 120 sampling points (2 sites × 3 topographic
201 positions × 4 replicate plots per position × 3-5 sampling points in each plot).

202 **Nutrient variables**

203 We assessed the environmental similarity between the plots and sampling points by
204 compiling data for 21 variables describing the total nutrient concentrations and ratios in

205 soil and litter compartments. We collected three randomized soil cores (4 cm in
206 diameter and 15 cm in length) at each sampling point. These three cores were combined
207 as a single composite sample, forming one sample per sampling point. Litter samples
208 for nutrient analysis were collected at each sampling point within a randomly placed
209 PVC square of 20 cm². We then determined the concentrations of nutrients (C, N, P, K,
210 Ca, Mg and Na) in the litter and soil pools for each sampling point using inductively
211 coupled plasma mass spectrometry (ICP-MS Agilent 7500; Thermo Fisher Scientific,
212 Germany) and also by inductively coupled plasma optical emission spectrometry (iCAP
213 6300 Duo; Thermo Fisher Scientific, Germany)(see Urbina et al. 2021 for further
214 methodological details). The concentration of available P in the soil was determined
215 using both the Olsen and Bray methods. We also derived some nutrient ratios (C:N, C:P
216 and N:P) due to their relevance to nutrient cycling (Peguero et al. 2019).

217 **Taxa sampling**

218 We sampled the communities of soil bacteria and fungi, ground insects and trees at the
219 end of the dry season in 2015. All trees with a diameter at breast height >10 cm within
220 the 0.25-ha plots were mapped, tagged and identified to species or genus using
221 herbarium vouchers with the help of local botanical experts. The communities of ground
222 insects were sampled from the litter surrounding three sampling points per plot. We
223 collected all litter inside four randomly placed 0.25-m² PVC frames and sifted it
224 through a 0.7-cm mesh Winkler bag, manually catching all escaping macrofauna. The
225 sifted litter was hung in Moczarsky traps for 48 h and then carefully inspected for any
226 remaining specimens. The bulk ground insect communities were stored in 70% ethanol.
227 These samples included specimens from Class Insecta and Class Entognatha, i.e.
228 subphylum Hexapoda, but are referred as insects for simplicity. Soil cores were
229 extracted for all five sampling points per plot for collecting soil bacteria and fungi, and

230 a 1-g aliquot of fresh topsoil was tagged, set inside a sealed plastic bag, immediately
231 stored in liquid nitrogen to prevent microbial growth and frozen until lyophilized in the
232 laboratory.

233 **Molecular analyses**

234 The communities of soil bacteria, fungi and ground insects were molecularly
235 characterized to delimit species-level taxa or operational taxonomic units (OTU) using
236 DNA metabarcoding. See Appendix S1: Section S1.1 Molecular Analyses for detailed
237 information of the procedures.

238 **Data analyses**

239 All data handling, visualization and statistical analyses were carried out using R v4.0.0
240 (R Core Team 2020). We first assessed the correlation between the spatial distance
241 separating two plots with their environmental dissimilarity based on the concentrations
242 and ratios of 21 macro- and micronutrients in the topsoil and organic horizons (hereafter
243 referred as nutrient distance). Spatial distance was calculated as the Euclidean distance
244 separating the coordinates of each plot in meters. Nutrient distance was also calculated
245 as Euclidean distance, but with all nutrient variables previously standardized to z-
246 scores. We then built a simple general linear model (GLM), with nutrient dissimilarity
247 between plots as a function of their spatial distance, with site as a fixed-effects term and
248 its interaction with spatial distance to detect potential differences between and within
249 sites in the nutrient-space correlation.

250 We calculated the alpha and gamma richness (i.e. the number of species or OTUs at the
251 plot level and the regional pool, respectively) for each sampled community and site, and
252 we drew their rarefaction curves using the iNEXT package (Hsieh et al. 2016) to
253 evaluate the sampling coverage prior to rarefaction. We partitioned total β -diversity

254 (Sørensen index) of each community into its turnover (Simpson index) and nestedness
255 components for each site separately using the betapart package (Baselga and Orme
256 2012). The turnover component of β -diversity corresponds to the replacement of species
257 between sites, whereas nestedness accounts for species-poor sites resembling subsets of
258 assemblages found at richer sites. By partitioning β -diversity we quantify the
259 compositional dissimilarities between plots and between points, thus exploring the
260 species distribution across assemblages, accounting for all potential drivers, and going
261 beyond their relationship to spatial and nutrient distances.

262 Although it is a debated matter, metabarcoding data may not provide reliable
263 quantitative estimates of the original relative abundances (Lamb et al. 2019). So, to
264 avoid any potentially misleading effect, for each community type we used
265 presence/absence matrices for building the distance-decay models (Gómez-Rodríguez
266 and Baselga 2018). We ran these distance-decay models with mean and median rarefied
267 community data sets in addition to observed nonrarefied data to control for biases in
268 sampling intensity, thereby providing a series of sensitivity analyses. We calculated
269 Simpson's index of assemblage similarity between plots and between sampling points
270 for each taxon group and site as: $(1 - \beta_{sim} = a/[a + \min(b, c)])$, where a is the number
271 of species or OTUs present in both plots, and b and c are the numbers of species unique
272 to one or the other plot as defined in the package betapart (Baselga and Orme 2012). We
273 then assessed the relationship between pairwise similarity and spatial or nutrient
274 distance by fitting a negative exponential or power-law function (i.e. the two main
275 forms describing the decay in similarity; Nekola and White 1999, Nekola and McGill
276 2014) using the *decay.model* function of the betapart package, which adjusts a GLM
277 with similarity as a response variable and a distance matrix as a predictor with log link

278 and Gaussian error (Gómez-Rodríguez and Baselga 2018). See Appendix S1: Section
279 S1.2 Data Analyses for further details.

280 **RESULTS**

281 The relationship between the spatial distance among plots and the similarity of their
282 nutrient concentrations and ratios differed at our two sites (interaction between site and
283 spatial distance: $df = 128$, $F = 14.8$, $P < 0.001$, Figure 1). Spatial distance was not
284 correlated with nutrient distance at Paracou, so nearby plots did not necessarily have a
285 similar nutrient environment ($df = 64$, $F = 2.6$, $P > 0.05$). At Nouragues, however, the
286 further the distance between two plots, the greater the dissimilarity in their nutrient
287 concentration in the litter and topsoil. Only 40% of the variation in nutrient
288 concentration at Nouragues was due to spatial distance ($df = 64$, $F = 42.4$, $P < 0.001$),
289 thus stressing the high heterogeneity of biogeochemical processes operating at small
290 scales at both sites. The same analysis performed at the smallest observational scale
291 available reinforced this finding, indicating that spatial distances between sampling
292 points at Paracou were not correlated with the nutrient similarity ($df = 1768$, $F = 78.2$, P
293 > 0.05 , Appendix S1: Figure S1) and that only 19% of the variation in overall nutrient
294 concentration at Nouragues was explained by the spatial distance between sampling
295 points ($df = 1768$, $F = 431.1$, $P < 0.001$, Appendix S1: Figure S1). The distribution of
296 specific nutrients across the topographic levels differed between sites (Appendix S1:
297 Table S1 and S2), even though the ranges of spatial extent and nutrient content were
298 similar at Paracou and Nouragues (Appendix S1: Figures S3 and S4).

299 We found global totals of 627 tree species and 3512, 6794 and 12268 OTUs for ground
300 insects, bacteria and fungi, respectively (Table 1). Local species richness differed
301 significantly between sites, with the plots at Paracou having more OTUs for all taxa
302 except tree species ($df = 22$ and $P < 0.01$ for all groups, see Appendix S1: Table S3 for

303 extended outputs). Evenness patterns, however, were highly similar between sites and
304 for all community types (Appendix S1: Figure S5). Mean Sørensen β -diversity for all
305 communities was 0.85 ± 0.05 , and its partitioning indicated that species turnover was
306 the main component compared to nestedness (96.7 vs 3.3% for averages in turnover and
307 nestedness components across taxa, respectively). This pattern was consistent at both
308 sites and for all communities (Appendix S1: Figure S2). However, total β -diversity
309 differed greatly between taxa. Ground insect assemblages had the highest β -diversity,
310 followed by fungi, trees and bacteria. This ranking was consistent among sites and was
311 not related with any biological property of each community, such as organism,
312 propagule or community sizes, or with their γ or α richness (Table 1).

313 The analysis of the patterns of decay of similarity indicated that the effect of spatial
314 distance differed among sites, taxa and scales. All taxa but bacteria had significantly
315 lower similarities with increasing spatial distance between plots at Nouragues ($df = 64$,
316 $P < 0.05$, Appendix S1: Table S4), and only fungal communities exhibited such a
317 pattern at Paracou ($df = 64$, $t = 3.449$, $P < 0.01$, Figure 2). The slope of the distance-
318 decay at Nouragues was more negative for the communities of trees and ground insects,
319 despite exhibiting a greater variability when compared with fungi and bacteria (Figure
320 2a). Bacterial communities had the highest pairwise similarities and an almost flat
321 response with increasing distance among plots at both sites. Our analysis of bacterial,
322 fungal and ground insect data at the level of sampling point, the smallest observational
323 unit available, found that the values of initial similarities substantially decreased in all
324 groups (Figure 4 and Appendix S1: Figure S6), indicating that compositional variability
325 was high within the plots. The similarity between sampling points within a plot, i.e.
326 separated by only 15–20 m, was notably lower than aggregated communities between
327 plots, at distances averaging about 60 m (Figure 3). All three groups had a significant

328 decaying relationship with spatial distance at both sites at the smallest scale of analysis
329 ($df = 1429$, $P < 0.01$, Appendix S1: Table S5), although the slope and the explanatory
330 power of the models was generally lower than when using data aggregated to plot level.
331 The models of similarity decay with nutrient distance at the plot level indicated that the
332 filtering effect of the environment was greater and more consistent than spatial distance
333 at both sites and across community types. All taxa at Nouragues had a significant decay
334 of assemblage similarity, with increasing differences in nutrient concentrations between
335 plots, albeit this relationship was weak for ground insects (Figure 4, $t = 1.884$, $P = 0.05$,
336 $Pseudo-R^2 = 0.05$; Appendix S1: Table S4). All taxa at Paracou except insects had the
337 same pattern of decay, which was particularly strong for fungi ($df = 64$, $t = 3.449$, $P <$
338 0.01 , $Pseudo-R^2 = 0.26$). Even the more homogeneous bacterial communities
339 significantly correlated with nutrients at both sites (Figure 4, $df = 1429$, $P < 0.01$,
340 $Pseudo-R^2 = 0.13$). By contrast, the distance-decay models obtained for bacteria, fungi
341 and insects were similar at the sampling point scale (Appendix S1: Table S5) and
342 exhibited lower initial similarity values and explanatory power than at the plot level,
343 although the effect of nutrient condition was still significant for the bacterial and fungal
344 communities at both sites ($df = 1429$, $P < 0.01$, Appendix S1: Figures S7). Finally, the
345 relationship between the similarity of the tree communities with the similarity of
346 bacterial, fungal and insect communities was variable (Appendix S1: Figure S8). Fungal
347 assemblages were strongly coordinated with the composition of the tree community, but
348 only at Paracou ($df = 64$, $t = 3.449$, $P < 0.01$, $Pseudo-R^2 = 0.24$, Appendix S1: Table
349 S4), and insects had a statistically marginal relationship at Nouragues ($df = 64$, $t =$
350 2.295 , $P = 0.06$, $Pseudo-R^2 = 0.05$).

351 The comparison of the amount of variance explained by our distance-decay models
352 reasserted that the spatial distance at the plot level was generally less important than

353 nutrients in accounting for the composition of the communities (Appendix S1: Figure
354 S9). This finding was particularly clear for bacteria because spatial distance had no
355 effect, while >10% of their compositional similarity was due to nutrient differences
356 between plots. Importantly, the explanatory power reached by the same models at
357 sampling point level was lower (Appendix S1: Figure S10). Additionally, the sensitivity
358 analyses done with median rarefied community data sets and observed non rarefied data
359 yielded qualitatively identical results (Appendix S1: Table S6-S9) indicating that
360 differences in sampling intensity between taxa were not relevant.

361 **DISCUSSION**

362 There is an open debate about whether micro- and macroorganisms communities are
363 assembled based on the same mechanisms and if these mechanisms operate equally
364 across spatial scales in all kinds of organisms (Soininen et al. 2007, Nekola and McGill
365 2014, Shade et al. 2018). Our results indicated that trees, soil bacteria and fungi have
366 largely similar distance-decay patterns, with soil nutrient concentrations exerting a
367 stronger control than dispersal limitation over the assembly of these communities in
368 tropical rainforests. The large range of sizes of organisms and propagules did not lead to
369 fundamental differences between micro- and macroorganisms. Insects, the only group
370 assessed that has active dispersal capacity, had the highest species turnover and the
371 flattest, mostly nonsignificant, distance-decay relationships. These results suggest that
372 neither dispersal limitation nor nutrient availability were important drivers of their
373 community assembly, at least at the scales of our analyses. At the smallest observational
374 unit of our study, we found by contrast a greater weight of dispersal limitation. The
375 lower initial similarity and the small amount of variation explained by most of these
376 distance-decay models, however, suggest that stochastic sampling effects, not dispersal
377 limitation, are important for bacteria, fungi and insects at this finer spatial scale (Nekola

378 and McGill 2014). Our study highlights the direct role of nutrient supply capacity or its
379 ability to capture additional environmental factors that drive the assembly of rainforest
380 communities. And in addition, we show that the structuring effect of these nutrients is
381 independent of the propagule size and local or regional richness of particular groups of
382 organisms. Our study also emphasizes how the overriding effect of analytical scale may
383 strongly influence the interpretation of data. This ultimately leads to the perception of a
384 greater importance of dispersal limitation and ecological drift than niche-related
385 environmental selection with decreasing observational scales (Chase 2014).

386 The communities of soil bacteria analyzed at the plot level supported the widely
387 accepted view eloquently synthesized in the Baas-Becking hypothesis: “everything is
388 everywhere but the environment selects” (Martiny et al. 2006). A recent study at the
389 global scale has partly challenged this view (Luan et al. 2020). Nonetheless, several
390 previous studies with a smaller geographic scope have reported that bacterial taxa-area
391 relationships were mainly driven by environmental heterogeneity rather than dispersal
392 limitation (Horner-Devine et al. 2004, Powell et al. 2015). The small size of bacterial
393 propagules is assumed to be associated with a high mobility, which along with large
394 populations and short generation times should lead to homogeneous regional pools of
395 taxa. The environment would then filter the species of bacteria that are best adapted to
396 the local conditions (Martiny et al. 2006). The resulting mechanism, commonly referred
397 as species sorting in metacommunity theory, has been successfully applied to describe
398 the contrasting assemblage dynamics of bacterial specialists and generalists, which are
399 respectively more and less influenced by the environment (Leibold et al. 2004, Székely
400 and Langenheder 2014). Soil pH and C and N content are key factors controlling the
401 distribution of soil bacteria (Fierer and Jackson 2006). In tropical forests they are also
402 particularly limited by P, whose availability is linked with pH, which also depends on

403 topography and soil texture (Camenzind et al. 2018). Our results therefore support the
404 conclusion that in tropical forests, soil nutrients are the main driver of bacterial
405 communities, which are not dispersal-limited at the scale of our study. Thus, bacteria
406 may achieve an effective long-distance passive dispersal via wind, air-driven particles,
407 surface and underground runoffs, and also through animal phoresis (Lindström and
408 Langenheder 2012).

409 We expected to find similar patterns between fungi and bacteria due to their shared
410 biological features, but instead found that fungi were more dispersal-limited than
411 bacteria. This finding agrees with previous research also reporting dispersal limitation
412 in fungi, which may need the mediation of active vectors such as soil fauna to enhance
413 the dispersion of their spores (Peay et al. 2010, Bahram et al. 2013, Powell et al. 2015).
414 Actually, most fungi do not have aboveground fruiting bodies and while every
415 bacterium might be a propagule in itself for filamentous fungi this is not the case.
416 Environmental selection was yet a strong driver of fungal communities in our study.
417 The structuring force of soil nutrients over fungal communities may nevertheless differ
418 depending on the location with reports of contrasting results even within the same
419 ecosystem and study site (Tedersoo et al. 2016). Likewise, our finding of context-
420 dependency also in the relationship between the tree and soil fungi supports the view
421 that the drivers of fungal communities may vary among sites but also across lineages,
422 depending on whether their trophic strategy imply strong bonds with plants or not (Peay
423 et al. 2013, Tedersoo et al. 2016). The simultaneous control of fungi by spatial and
424 nutrient distances, and indirectly by the composition of tree species, thus hinder our
425 ability to determine the relative contributions of dispersion and environmental selection
426 either related with soil nutrients or tree identities.

427 Arthropods, as macroorganisms, are hypothesized to have a low mobility and sensitivity
428 to fine-scale environmental variation (Soininen et al. 2007). Accordingly, dispersal
429 limitation have been suggested to be preponderant over environmental selection in the
430 assembly of communities of freshwater crustaceans and terrestrial beetles analyzed from
431 a watershed to a continental scale (Beisner et al. 2006, Gómez-Rodríguez and Baselga
432 2018). Nevertheless, a broad study documented low levels of β -diversity for
433 herbivorous insects from highly diverse tropical forests, suggesting that dispersal
434 limitation did not have a substantial role in community assembly from local to regional
435 scales (up to 500-1000 km) (Novotny et al. 2007). In addition, the compositions of plant
436 and insect communities can be strongly correlated (Zhang et al. 2016). Our results for
437 insects demonstrated very high species turnover and mostly non significant distance-
438 decay relationships with spatial, nutrient or tree-composition distances. Our findings
439 hence apparently disagree with all these previous studies by indicating that neither
440 dispersal limitation nor environmental selection are important drivers of the community
441 assembly of ground insects, at least at the smallest observational scale of our analyses (1
442 m²). This difference is consistent with a comprehensive study at a single site but with a
443 very high spatial resolution, which similarly documented that ecological drift without
444 dispersal limitation was prominent in the assembly of soil arthropod communities in a
445 tropical rainforest (Zinger et al. 2019).

446 Our analyses also provide cues that decreasing the observational scale may lead to the
447 perception of a greater influence of drift processes that could be due only to stochastic
448 sampling effects (Chase 2014, Nekola and McGill 2014). Insect communities in tropical
449 forests are extremely diverse and complex, with high levels of taxonomic and functional
450 turnover even at small spatial scales (Lamarre et al. 2016). Insects are all active
451 dispersers but their dispersal capacity is variable even within taxonomic orders

452 (Novotny et al. 2007, Gómez-Rodríguez and Baselga 2018). Accordingly, the
453 communities of oribatid mites from forest canopies, whose species usually have a high
454 dispersal capacity, show a lower spatial structure and are more influenced by specific
455 environmental features than the communities of ground-dwelling oribatids, which
456 present a greater dispersal limitation (Lindo and Winchester 2009). In addition, the
457 trophic niches of ground insects are likewise equally diverse, ranging from detritivores,
458 potentially prone to be influenced by nutrient availability, to predators and parasites
459 whose abundances are likely independent of environmental constraints such as soil
460 nutrients or the tree species growing above. Thus, the relative influence of dispersal
461 limitation and environmental selection within such an ecologically variable group is
462 also a function of traits (e.g. dispersal capacity, life-history strategy, trophic niche) other
463 than only body or propagule size (Astorga et al. 2012, Gómez-Rodríguez and Baselga
464 2018). Altogether, this makes insects a particularly challenging group and studies with a
465 narrower taxonomic focus but embracing these functional differences among lineages
466 could help to untangle the relative importance of the different assembly mechanisms.

467 We expected that nutrient selection and dispersal limitation would simultaneously affect
468 the assembly of tree communities (Tuomisto et al. 2003, John et al. 2007). Accordingly,
469 we found a significant effect of nutrient availability at both sites, although the effect of
470 nutrients was moderate. The relationship between tree communities and soil nutrient
471 stocks in tropical forests has long been known to be bidirectional. Nutrients select tree
472 species thus driving assemblage composition, while tree species also modulate nutrient
473 availability through their inputs as litter and root exudates and their belowground
474 symbiotic interactions influence the dynamics of organic matter decomposition (John et
475 al. 2007). Our results for dispersal limitation, however, were mixed being significant
476 only at Nouragues. About 87.7% of the species at Nouragues depend on faunal vectors

477 to disperse their seeds (Charles-Dominique 2001), and similar levels of zoochory are
478 expected for Paracou. Predicting the influence of faunal vectors on tree communities
479 requires knowing the status of the local community of seed dispersers (Gelmi-Candusso
480 et al. 2017). The contrast in dispersal limitation between sites could thus be due more to
481 variation in the composition, structure and behavior of the local community of
482 dispersers rather than to differences in the tree species attributes. Anyhow, nutrient
483 concentrations at Nouragues were significantly correlated with spatial distances, so this
484 effect of dispersal limitation also likely involved masked environmental selection.

485 Integrating different scales in the analyses illustrated how dispersal limitation and
486 nutrient-based selection influence varied not only across taxa but also depending on the
487 area of the observational unit (Nekola and McGill 2014, Chase et al. 2018). The large
488 residual variance of our models was similar to previous studies using similar approaches
489 (Beisner et al. 2006, Astorga et al. 2012, Zinger et al. 2019) but also emphasizes the
490 many unidentified predictors we still need to take into account. Other abiotic soil
491 properties such as moisture, pH or toxic elements like Aluminum (Zinger et al. 2019),
492 and biotic interactions, are only assessable through detailed studies sustained over
493 relevant time periods (Vellend 2017), may be important. Hence, further research ideally
494 including functional traits for as many lineages as possible within different co-occurring
495 taxonomic groups, could help us to elucidate which part of this unexplained variation is
496 truly ecological drift (Zinger et al. 2019, Luan et al. 2020), and which part is due to
497 selection exerted by these unidentified abiotic and biotic factors.

498 **ACKNOWLEDGEMENTS**

499 This research was supported by the Spanish Government grant PID2019-110521GB-
500 I00, the European Research Council Synergy grant ERC-2013-SyG 610028-
501 IMBALANCE-P, and the Catalan Government grant SGR 2017-1005. We thank the

502 staff of the Nouragues (USR mixte LEEISA, CNRS, Cayenne) and Paracou (UMR
503 Ecofog, CIRAD, INRA, Kourou) research stations. Both facilities received support
504 from “Investissement d’Avenir” grants provided by the Agence Nationale de la
505 Recherche (CEBA: ANR-10-LABX- 25-01, ANAEE-France: ANR-11-INBS-0001).
506 We thank Vincent Freycon for the identification and characterization of each
507 topographical position and Pascal Petronelli for the botanical determination.

508 **AUTHOR CONTRIBUTIONS**

509 G.P., M.F., J.P. and I.A.J. designed the study. G.P., O.G., E.V., I.R., L.V.L., J.M., A.I.,
510 D.A., A.G-G., J.Ll., O.M. and R.O. conducted the field and laboratory work and
511 contributed data. G.P. and M.F. analyzed the data. J.S., L.Z., J.M., J.O. and A.R.
512 provided useful ideas for the analyses and interpretation. G.P. and M.F. wrote the first
513 draft of the manuscript, with substantial inputs from J.P., and all other authors
514 contributed to revisions.

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665

666 **TABLE 1**

Table 1. Characteristics of the communities at each site.					
Taxon	Dispersal mode	Propagule size (μm)	Richness (γ)	Site	Richness (α)
Bacteria	Passive	10^{-1} –1	6794	Nouragues	1245 ± 59
				Paracou	1267 ± 26
Fungi	Passive	1– 10^2	12268	Nouragues	991 ± 47
				Paracou	1171 ± 23
Insects	Active	10^3 – 10^4	3512	Nouragues	276 ± 22
				Paracou	333 ± 20
Trees	Passive	10^3 – 10^5	627	Nouragues	41 ± 4
				Paracou	35 ± 3
<p>Gamma richness is the total number of either tree species or molecularly delimited operational taxonomic units (OTUs) of bacteria, fungi and insects. Alpha richness is the mean number of OTUs or species at the plot level with all sampling units combined, at Nouragues and Paracou (French Guiana).</p>					

667

668 **FIGURES**

669 **Figure 1.** Relationship between pairwise spatial distances among plots and their
670 corresponding similarity of nutrient environment at the two study sites, Nouragues and
671 Paracou (French Guiana). Nutrient-based environmental distances are scaled Euclidean
672 distances of elemental concentrations (C, N, P, K, Mg, Ca and Na) and the ratios of the
673 main macronutrients (C:N, C:P and N:P) in the litter and soil stocks at the plot level (see
674 Methods for further details). The interaction between site and the covariate spatial
675 distance was tested using a general linear model. The site-specific equations and
676 coefficients of determination (R^2) for the relationship between spatial and nutrient
677 distances were calculated with separate linear models for each site. R^2 represents the
678 amount of nutrient variability explained by the spatial distance between plots.

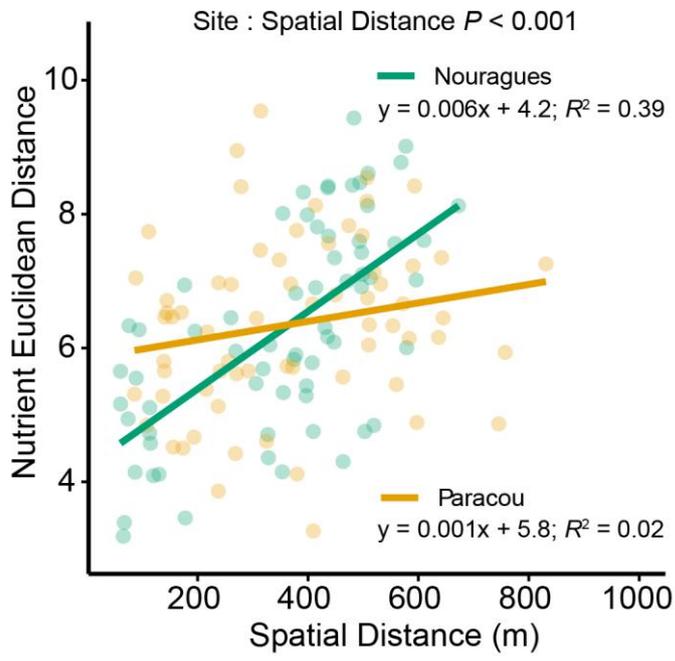
679 **Figure 2.** Patterns of decay of similarity across spatial distances and bootstrapped
680 distribution of their slope for each community at Nouragues (a) and Paracou (b). Dots
681 represent pairs of plots, and lines are their fitted negative exponential functions. **, $P <$
682 0.01; *, $P < 0.05$; •, $0.05 < P < 0.10$ and n.s., $P \geq 0.10$.

683 **Figure 3.** Differences in initial similarity across spatial scales of analysis. Initial
684 similarity distributions from bootstrapping the distance-decay models to estimate their
685 intercepts, i.e. the similarity between assemblages at the minimum distance. Point
686 represents the 1-m² sampling points within the 0.25-ha plots. Minimum distance is <10
687 m between points and >50 between plots. The initial similarity of all taxonomic groups
688 differed significantly ($P < 0.001$) at both sites, depending on the scale of analysis based
689 on the linear models (visit Appendix S1 Table S10 for models' outputs).

690 **Figure 4.** Patterns of decay of similarity across nutrient distances and bootstrapped
691 distribution of their slope for each community at Nouragues (a) and Paracou (b). Dots

692 represent pairs of plots, and lines are their fitted negative exponential functions. **, $P <$
693 0.01; *, $P < 0.05$; •, $0.05 < P < 0.10$ and n.s., $P \geq 0.10$.

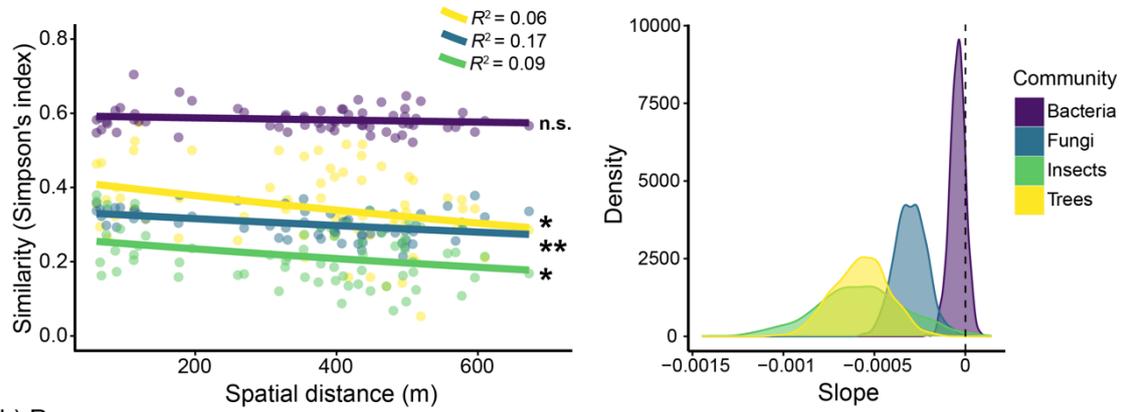
694 FIGURE 1



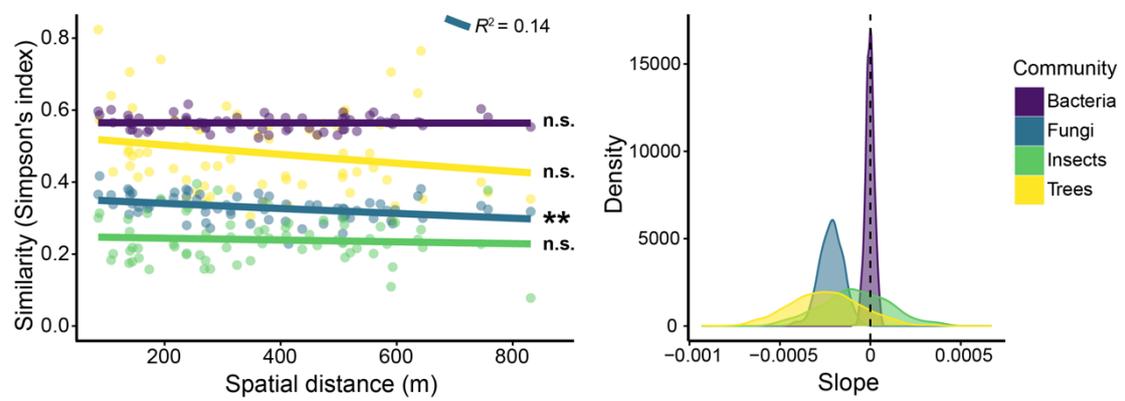
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696

a) Nouragues



b) Paracou

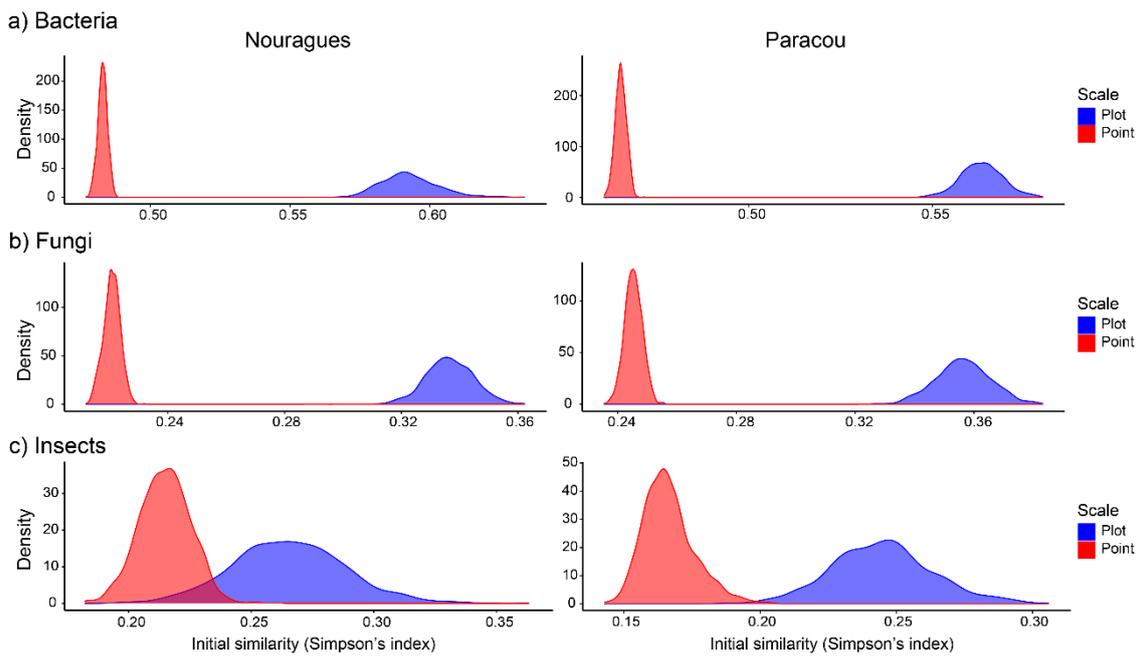


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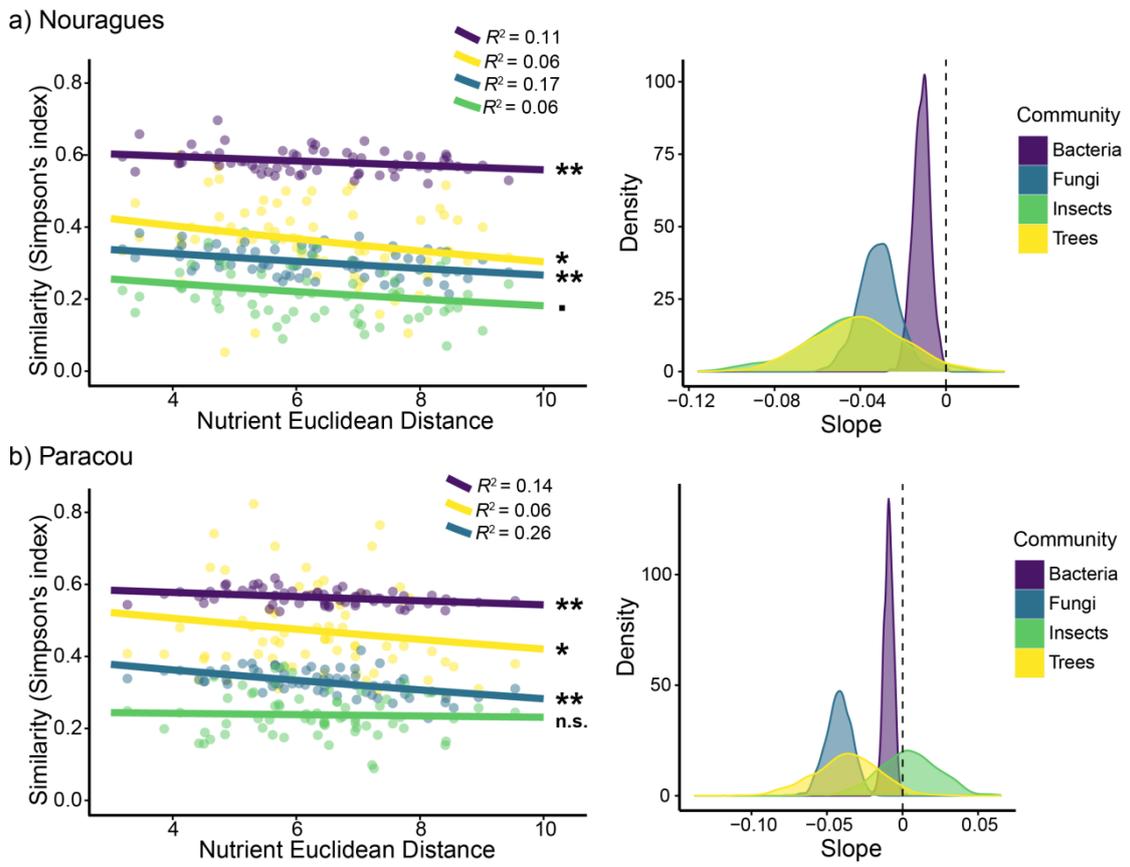
700

701 FIGURE 3



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706