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

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Abstract. Understanding the mechanisms that drive the change of biotic assemblages over space and time is the main quest of community ecology. Assessing the relative importance of dispersal and environmental species selection in a range of organismic sizes and motilities has been a fruitful strategy. A consensus for whether spatial and environmental distances operate similarly across spatial scales and taxa, however, has yet to emerge. We used censuses of four major groups of organisms (soil bacteria, fungi, ground insects, and trees) at two observation scales (1-m^2 sampling point vs. 2,500-m^2 plots) in a topographically standardized sampling design replicated in two tropical rainforests with contrasting relationships between spatial distance and nutrient availability. We modeled the decay of assemblage similarity for each taxon set and site to assess the relative contributions of spatial distance and nutrient availability distance. Then, we evaluated the potentially structuring effect of tree composition over all other taxa. The similarity of nutrient content in the litter and topsoil had a stronger and more consistent selective effect than did dispersal limitation, particularly for bacteria, fungi, and trees at the plot level. Ground insects, the only group assessed with the capacity of active dispersal, had the highest species turnover and the flattest nonsignificant distance–decay relationship, suggesting that neither dispersal limitation nor nutrient availability were fundamental drivers of their community assembly at this scale of analysis. Only the fungal communities at one of our study sites were clearly coordinated with tree composition. The spatial distance at the smallest scale was more important than nutrient selection for the bacteria, fungi, and insects. The lower initial similarity and the moderate variation in composition identified by these distance-decay models, however, suggested that the effects of stochastic sampling were important at this smaller spatial scale. Our results highlight the importance of nutrients as one of the main environmental drivers of rainforest communities irrespective of organismic or propagule size and how the overriding effect of the analytical scale influences the interpretation, leading to the perception of greater importance of dispersal limitation and ecological drift over selection associated with environmental niches at decreasing observation scales.

Key words: community assembly; dispersion; environmental filtering; French Guiana; metabarcoding; nutrients; scale-dependency; soil biodiversity.

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INTRODUCTION

The central quest of community ecology is to elucidate the mechanisms that drive the change of species assemblages over space and time (Vellend 2017). A recurrent pattern identified in such inquiries is the nearly universal decay of similarity between assemblages with the increase in the spatial or environmental distance separating them (Nekola and White 1999). This macroecological pattern has been found in a broad variety of organisms, from bacteria and fungi to plants and animals (Condit et al. 2002, Green et al. 2004, Novotny et al. 2007, Bahram et al. 2013). Whether this pattern emerges from the same mechanisms of community assembly across the entire range of organismic size remains an open debate due to the paucity of research on multiple co-occurring taxonomic groups. A few attempts to do so have found mixed and sometimes conflicting results, generally dependent on their specific ecological contexts (Beisner et al. 2006, Soininen et al. 2007, Bryant et al. 2008, Astorga et al. 2012, Vleminckx et al. 2019, Zinger et al. 2019, Luan et al. 2020). Moreover, many patterns of biodiversity are scale-dependent and vary with the grain sampling (i.e., the area of the observation unit) and extent (Nekola and McGill 2014, Chase et al. 2018). However, the scale-dependency of distance-decay patterns is rarely analyzed, hence hindering the interpretation of the contrasting results gathered to date (Nekola and McGill 2014). This prevents drawing general conclusions about the relative importance of the different mechanisms of community assembly and the scaling of these processes into biogeographic patterns.

A recent conceptual synthesis (Vellend 2017) identified four high-level processes driving the structure and composition of ecological communities. These processes are the movement of organisms (dispersal), random or stochastic changes in the abundances of species (drift), deterministic differences in fitness between individuals of different species due to their biotic or abiotic context (selection), and the evolution of populations into new species that operates over larger spatio-temporal scales than does local community assembly (speciation). Generally, the decreasing form of the distance–decay relationship has been associated with dispersal limitation and environmental selection (Nekola and White 1999). In the first case, the decay of similarity between assemblages with increasing spatial distance would be explained by the reduction of the probability of species reaching more distant localities because of their limited dispersal ability (Condit et al. 2002, Gómez-Rodríguez and Baselga 2018). Alternatively, the decay of similarity with spatial distance would derive from similar biotic and abiotic properties in closer localities. The environment would thereby broadly select species based on their ecological niches, making assemblages more dissimilar when biotic and abiotic conditions are more different (Tuomisto et al. 2003, Astorga et al. 2012, Gómez-Rodríguez and Baselga 2018). Generally, the relative importance of dispersal limitation and environmental selection has been assessed by measuring how well spatial or multivariate environmental distances account for the dissimilarity between assemblages (Tuomisto et al. 2003, Astorga et al. 2012, Gómez-Rodríguez and Baselga 2018). Nevertheless, environmental conditions are often spatially autocorrelated, which confounds the effect of these assembly mechanisms and hampers assessing their relative importance with current statistical techniques (e.g., simple and partial Mantel tests; Guillot and Rousset 2013, Legendre et al. 2015). A simple alternative is to specifically design spatially standardized samplings for sites that vary in the level of co-variation between the spatial distance separating plots and their environmental features, and compare the strength of the distance–decay relationships for multiple taxonomic groups assuming that their dispersal abilities are constant in these contrasting scenarios.

Variation in distance–decay relationships among taxonomic groups may arise from basic biological properties such as differences in dispersal ability or traits associated with their environmental sensitivity (Nekola and White 1999, Soininen et al. 2007). Yet, there is no consensus regarding the relative importance of dispersal limitation versus environmental selection across the range of body size from micro- to macroorganisms. For instance, the small size of microbial propagules, along with large populations and short generation times, are thought to lead to homogeneous regional species pools from which local communities are assembled by environmental selection (Martiny et al. 2006). However, this view has been recently challenged by findings suggesting that the community assembly of small organisms such as bacteria would be more influenced by dispersal limitation than by environmental selection (Luan et al. 2020). Microorganisms are mostly passive dispersers. However, some groups like fungi have shown varying degrees of dispersal limitation and sometimes even a strong co-variation with plant community composition (Peay et al. 2010, Bahram et al. 2013, Powell et al. 2015, Tedersoo et al. 2016, Vleminckx et al. 2019). By contrast, macroorganisms should generally have higher initial similarities and steeper distance–decay relationships compared to microorganisms, probably due to lower mobility and responsiveness to fine-scale environmental variation (Soininen et al. 2007). Accordingly, dispersal limitation may be the main determinant of beetle similarity at a biogeographic scale in Europe (Gómez-Rodríguez and Baselga 2018). Low levels of species turnover, however, have been reported for herbivorous insects in tropical rainforests, suggesting that dispersal limitation does not have a substantial role in community assembly from local to regional scales in these diverse ecosystems (Novotny et al. 2007). The compositions of plant and insect communities may also be strongly correlated at a landscape level (Zhang et al. 2016), but a comprehensive study at a smaller spatial scale found that ecological drift, not dispersal or environmental selection, may be the only detectable driver of the otherwise highly stochastic assemblages of soil arthropods in tropical rainforests (Zinger et al. 2019). As with microorganisms, it is expected that these disparities between studies may be related to the spatial scale at which communities are analyzed, since how distinct assembly processes help in structuring community types is fundamentally dependent on the sampling grain and extent at which communities are investigated (Chase et al. 2018, Zinger et al. 2019, Luan et al. 2020). This complex scenario illustrates the need for more research to understand whether the processes linking local community assembly with biogeographic patterns differ between the most common types of organisms.

We can find high levels of species richness and turnover associated with high levels of environmental heterogeneity at very small spatial scales of a few hundred meters (Jucker et al. 2018). Therefore, tropical rainforests are an ideal setting to conduct intertaxonomic and cross-site comparisons of distance-decay patterns. Since climate, soil parent material, and geological time are largely constant at a landscape level, topography emerges as the main driver of environmental variability in these ecosystems (Weintraub et al. 2015). Topographic features (e.g., slope and ruggedness) influence the hydrologic regime; thereby, influence soil weathering, mineralogy, and texture. Eventually, topography determines the content and availability of key nutrients such as N and P (Weintraub et al. 2015), which strongly affect the composition, structure, and dynamics of tree communities (John et al. 2007, Grau et al. 2017, Jucker et al. 2018, Soong et al. 2020). Tree communities may in turn codetermine the composition of other associated taxonomic groups, as suggested by their sometimes coupled spatial distributions (Peay et al. 2013, Zhang et al. 2016, Vleminckx et al. 2019, Zinger et al. 2019). The content of main soil elements and ratios correlate with many relevant environmental features (e.g., soil texture, pH of soil, organic matter, and water storage). Thus, these are main ecological factors and reliable multivariate proxies of environmental heterogeneity.

Here, we assessed the relative importance of dispersal limitation and environmental selection to the assembly of communities of soil bacteria, fungi, ground insects, and trees. We analyzed their distance-decay patterns across a spatially standardized system of twelve 0.25-ha plots, each containing 3–5 sampling points; thus, provide two nested scales. This analysis was replicated at two tropical rainforest sites in French Guiana; one for which the nutrient environment was completely uncorrelated with the spatial distance among plots, while the other exhibited some correlation and provide a unique naturally controlled opportunity to tease apart spatial vs. environmental effects. We assessed the co-variation of community similarity patterns with spatial distances or environmental dissimilarity based on the concentrations and ratios of 21 macro- and micronutrients in the topsoil and organic horizons. We expected greater environmental selection effects for microorganisms and higher dispersal limitation for macroorganisms with passive motility (e.g., trees). Likewise, we expected higher initial similarities and faster distance-decay rates for trees and ground insects in comparison to fungi and bacteria. Furthermore, we evaluated the potential coupling between communities of trees, the main structuring organisms in rainforests, and a kind of environmental selection agent, with the composition of ground insects, soil bacteria, and fungi. Finally, we also assessed if shifting the observation unit (or statistical unit) from plot to sampling point modified the patterns of distance decay or not.

Materials and Methods

Study sites

This study was conducted in two primary tropical rainforests in French Guiana in the research stations of Paracou (05°16′38″N, 52°55′38″W) and Nouragues (04°04′53″N, 52°41′13″W). Both sites share the same tropical climate, with a wet season from December to June and a dry season from August to November. Mean annual precipitation and temperature are similar at Paracou (3,102 mm and 25.7°C) and Nouragues (3,000 mm and 25.2°C). The bedrock is Precambrian schist at Paracou, and Caribbean granite and gneiss at Nouragues. Acrisols dominated at both sites, but with higher sand content and more extractable N and P in the soil at the bottom of hills and clayey minerals (e.g., kaolinite) and oxides increasing toward the tops, where total concentrations of nutrient and micronutrient are highest (Van Langenhove 2020). We established 12 plots of 0.25 ha at each site stratified by three topographic positions to account for this heterogeneity: at the top, slope, and bottom of hills. We set a central 20-m quadrat in each plot, where we marked and geolocated five evenly spaced sampling points around which we focused our measurements. Thus, this design contained between 72 and 120 sampling points (2 sites × 3 topographic positions × 4 replicate plots per position × 3–5 sampling points in each plot).

Nutrient variables

We assessed the environmental similarity between the plots and the sampling points by compiling data for 21 variables describing the total nutrient concentrations and ratios in soil and litter compartments. We collected three randomized soil cores (4 cm in diameter and 15 cm in length) at each sampling point. These three cores were combined as a single composite sample, forming one sample per sampling point. Litter samples for nutrient analysis were collected at each sampling point within a randomly placed PVC square of 20 cm^2. Then, we determined the concentrations of nutrients (C, N, P, K, Ca, Mg, and Na) in the litter and soil pools for each sampling point using inductively coupled plasma mass spectrometry (ICP-MS Agilent 7500; Thermo Fisher Scientific, Waltham, MA, USA) and by inductively coupled plasma optical emission spectrometry (iCAP 6300 Duo; Thermo Fisher Scientific, Germany; see Urbina et al. 2021 for further methodological details). The concentration of available P in the soil was determined using both the Olsen and Bray methods. We also derived some nutrient ratios (C:N, C:P, and N:P) because of their relevance to nutrient cycling (Peguero et al. 2019).

Taxa sampling

We sampled the communities of soil bacteria and fungi, ground insects, and trees at the end of the dry season in 2015. All trees with a diameter at breast height >10 cm within the 0.25-ha plots were mapped, tagged, and identified to species or genus using herbarium vouchers with the help of local botanical experts. The communities of ground insects were sampled from the litter surrounding three sampling points per plot. We collected all litter inside four randomly placed 0.25-m^2 PVC frames and sifted the litter through a 0.7-cm mesh Winkler bag, manually catching all escaping macrofauna. The sifted litter was hung in Moczarsky traps for 48 h and then carefully inspected for any remaining specimens. The bulk ground insect communities were stored in 70% ethanol. These samples included specimens from classes Insecta and Entognatha belong to subphylum Hexapoda, but are referred to as insects for simplicity. Soil cores were extracted for all five sampling points per plot for collecting soil bacteria and fungi, and a 1-g aliquot of fresh topsoil was tagged, set inside a sealed plastic bag, immediately stored in liquid nitrogen to prevent microbial growth, and frozen until lyophilized in the laboratory.

Molecular analyses

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

Data analyses

All data handling, visualization, and statistical analyses were carried out using R version 4.0.0 (R Core Team 2020). We first assessed the correlation between spatial distance separating two plots with their environmental dissimilarity based on the concentrations and ratios of 21 macro- and micronutrients in the topsoil and organic horizons (hereafter referred to as nutrient distance). Spatial distance was calculated as the Euclidean distance separating the coordinates of each plot in meters. Nutrient distance was also calculated as Euclidean distance, but with all nutrient variables previously standardized to z-scores (or standard score). Then, we built a simple general linear model (GLM), with nutrient dissimilarity between plots as a function of their spatial distance, with site as a fixed-effects term and its interaction with spatial distance to detect potential differences between and within sites in the nutrient−space correlation.

We calculated the alpha and gamma richness (i.e., the number of species or OTUs at the plot level and the regional pool, respectively) for each sampled community and site. Then, we drew their rarefaction curves using the iNEXT package in R (Hsieh et al. 2016) to evaluate the sampling coverage prior to rarefaction. We partitioned the total β-diversity (Sørensen index) of each community into its turnover (Simpson diversity index) and nestedness components for each site separately by using the betapart package (Baselga and Orme 2012). The turnover component of β-diversity corresponds to the replacement of species between sites, whereas nestedness component accounts for species-poor sites resembling subsets of assemblages found at richer sites. By partitioning β-diversity, we quantify the compositional dissimilarities between plots and between points; thus, exploring the species distribution across assemblages, accounting for all potential drivers, and going beyond their relationship to spatial and nutrient distances.

Although it is a debated matter, metabarcoding data may not provide reliable quantitative estimates of the original relative abundances (Lamb et al. 2019). So, we used presence/absence matrices for building the distance-decay models for each community type in order to avoid any potentially misleading effect (Gómez-Rodríguez and Baselga 2018). We ran these distance-decay models with mean and median rarefied community data sets in addition to observed nonrarefied data to control biases in sampling intensity, thereby providing a series of sensitivity analyses. We calculated Simpson's index of assemblage similarity between plots and between sampling points for each taxon group and site as: ($1–\beta\text{sim} = a/[a + \min(b, c)]$), where a is the number of species or OTUs present in both plots, and b and c are the numbers of species unique to one or the other plot as defined in the betapart package (Baselga and Orme 2012). Then, we assessed the relationship between pairwise similarity and spatial or nutrient distance by fitting a negative exponential or power-law function (i.e., the two main forms describing the decay of similarity; Nekola and White 1999, Nekola and McGill 2014) using the *decay.model* function of the betapart package, which adjusts a GLM with similarity as a response variable and a distance matrix as a predictor with log link and Gaussian law of errors (Gómez-Rodríguez and Baselga 2018). See Appendix S1: Section S1.2 Data Analyses for further details.

RESULTS

The relationship between the spatial distance among plots and the similarity of their nutrient concentrations and ratios differed at our two sites (interaction between site and spatial distance: df = 128, $F = 14.8$, $P < 0.001$; Fig. 1). Spatial distance was not correlated with nutrient distance at Paracou, so nearby plots did not necessarily have a similar nutrient environment (df = 64, $F = 2.6$, $P > 0.05$). However, at Nouragues, the further the distance between two plots, the greater the dissimilarity in their nutrient concentration in the litter and topsoil. Only 40% of the variation in nutrient concentration at Nouragues was due to spatial distance (df = 64, $F = 42.4$, $P < 0.001$); thus, this highlights the high heterogeneity of biogeochemical processes operating at small scales at both sites. The same analysis performed at the smallest observation scale available reinforced this finding, indicating that spatial distances between sampling points at Paracou were not correlated with the nutrient similarity (df = 1768, $F = 78.2$, $P > 0.05$; Appendix S1: Fig. S1). According to this analysis, only 19% of the variation in overall nutrient concentration at Nouragues was explained by the spatial distance between sampling points (df = 1768, $F = 431.1$, $P < 0.001$; Appendix S1: Fig. S1). The distribution of specific nutrients across the topographic levels differed between sites (Appendix S1: Tables S1, S2), even though the ranges of spatial extent and nutrient content were similar at Paracou and Nouragues (Appendix S1: Figs. S3, S4).

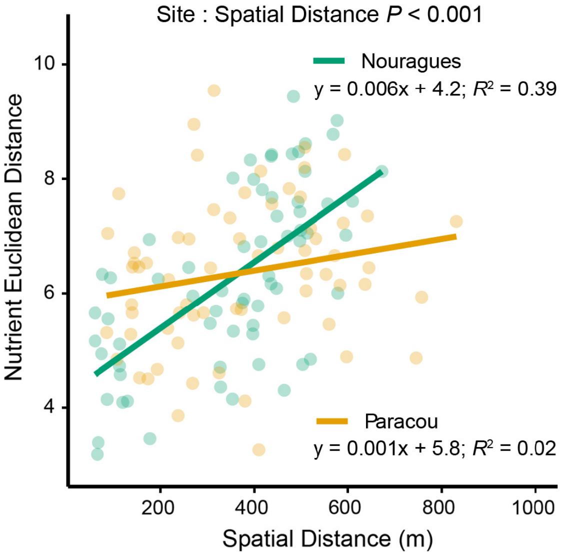


FIG. 1. Relationship between pairwise spatial distances among plots and their corresponding similarity of nutrient environment at the two study sites, Nouragues and Paracou (French Guiana). Nutrient-based environmental distances are scaled Euclidean distances of elemental concentrations (C, N, P, K,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

We found global totals of 627 tree species and 3,512, 6,794, and 12,268 OTUs for ground insects, bacteria, and fungi, respectively (Table 1). Local species richness differed significantly between sites, with the plots at Paracou having more OTUs for all taxa except tree species (df = 22 and $P < 0.01$ for all groups; see Appendix S1: Table S3 for extended outputs). However, evenness patterns were highly similar between sites and for all community types (Appendix S1: Fig. S5). Mean Sørensen β-diversity for all communities was 0.85 ± 0.05, and its partitioning indicated that species turnover was the main component compared to nestedness (96.7% vs. 3.3% for averages in turnover and nestedness components across taxa, respectively). This pattern was consistent at both sites and for all communities (Appendix S1: Fig. S2). However, total β-diversity differed greatly between taxa. Ground insect assemblages had the highest β-diversity, followed by fungi, trees, and bacteria. This ranking was consistent among sites and was not related to any biological property of each community, such as organism, propagule, or community sizes, or with their gamma or alpha richness (Table 1).

The analysis of the patterns of decay of similarity indicated that the effect of spatial distance differed among sites, taxa, and scales. Except bacteria, all species in taxa had significantly lower similarities with increasing spatial distance between plots at Nouragues (df = 64, $P < 0.05$; Appendix S1: Table S4), and only fungal communities exhibited such a pattern at Paracou (df = 64, $t = 3.449$, $P < 0.01$; Fig. 2). The slope of the distance–decay relationship at Nouragues was more negative for the communities of trees and ground insects, despite exhibiting a greater variability when compared with fungi and bacteria (Fig. 2a). Bacterial communities had the highest pairwise similarities and an almost flat response with increasing distance among plots at both sites. Our analysis of bacterial, fungal, and ground insect data at the level of sampling point (i.e., the smallest observation unit available) found that the values of initial similarities substantially decreased in all groups (Fig. 4, Appendix S1: Fig. S6), indicating that compositional variability was high within the plots. The similarity between sampling points within a plot (when the points are separated by only 15–20 m) was notably lower than the aggregated communities between plots, at distances averaging about 60 m (Fig. 3). All three groups had a significant decaying relationship with spatial distance at both sites at the smallest scale of analysis (df = 1429, $P < 0.01$; Appendix S1: Table S5). Yet, the slope and the explanatory power of these models at the smallest scale of analysis were generally lower than those using data aggregated to plot level.

The models of similarity decay with nutrient distance at the plot level indicated that the filtering effect of the environment was greater and more consistent than the spatial distance at both sites and across community types. All taxa at Nouragues had a significant decay of assemblage similarity, with increasing differences in

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

Notes: 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).

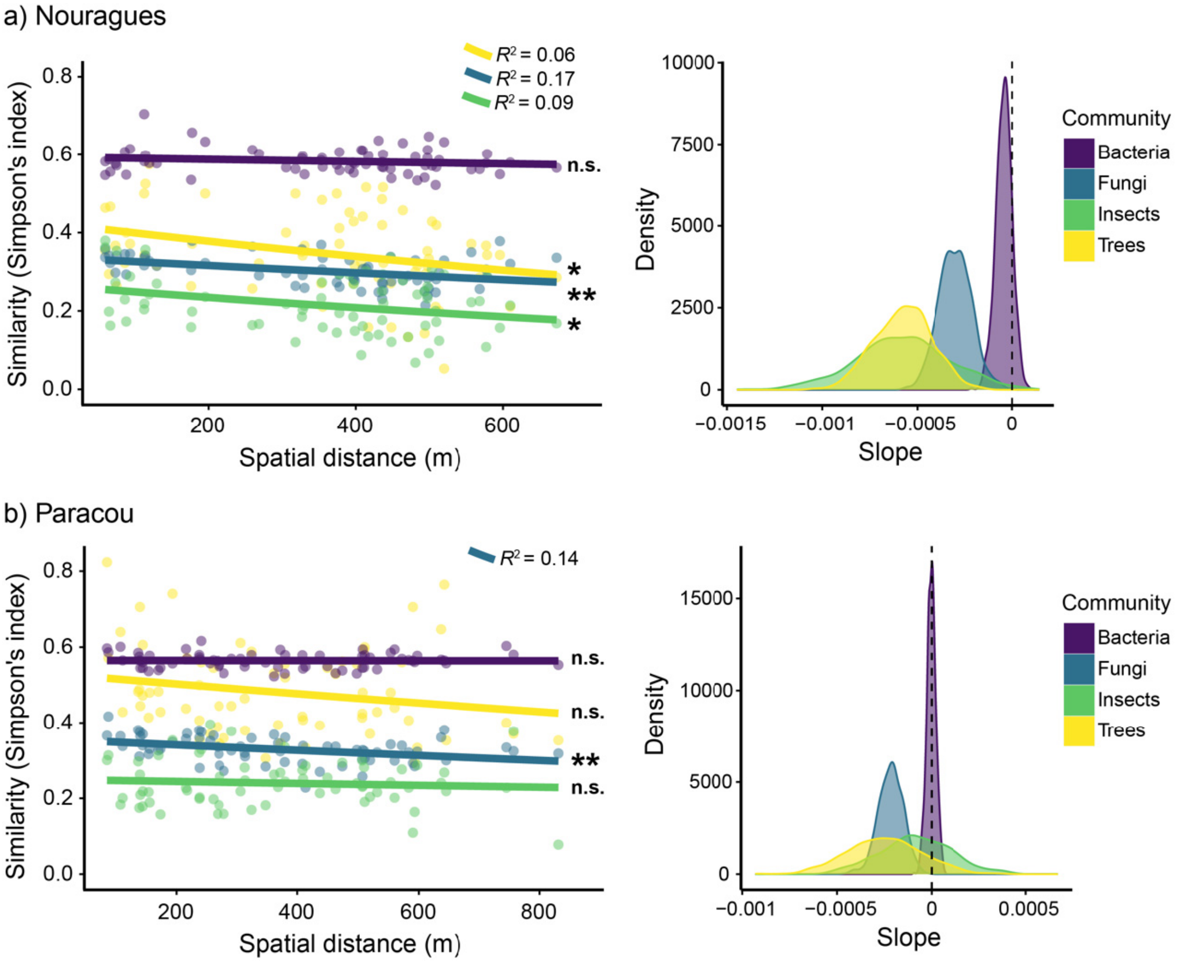


FIG. 2. Patterns of decay of similarity across spatial distances and bootstrapped distribution of their slopes for each community at (a) Nouragues and (a) Paracou. Dots represent pairs of plots, and lines are their fitted negative exponential functions. ∗∗, $P < 0.01$; ∗, $P < 0.05$; •, $0.05 < P < 0.10$;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

nutrient concentrations between plots; albeit this relationship was weak for ground insects (Fig. 4; $t = 1.884$, $P = 0.05$, Pseudo-$R^2 = 0.05$; Appendix S1: Table S4). All taxa at Paracou except insects had the same pattern of decay, which was particularly strong for fungi (df = 64, $t = 3.449$, $P < 0.01$, Pseudo-$R^2 = 0.26$). Even the more homogeneous bacterial communities significantly correlated with nutrients at both sites (df = 1429, $P < 0.01$, Pseudo-$R^2 = 0.13$; Fig. 4;). By contrast, the distance-decay models

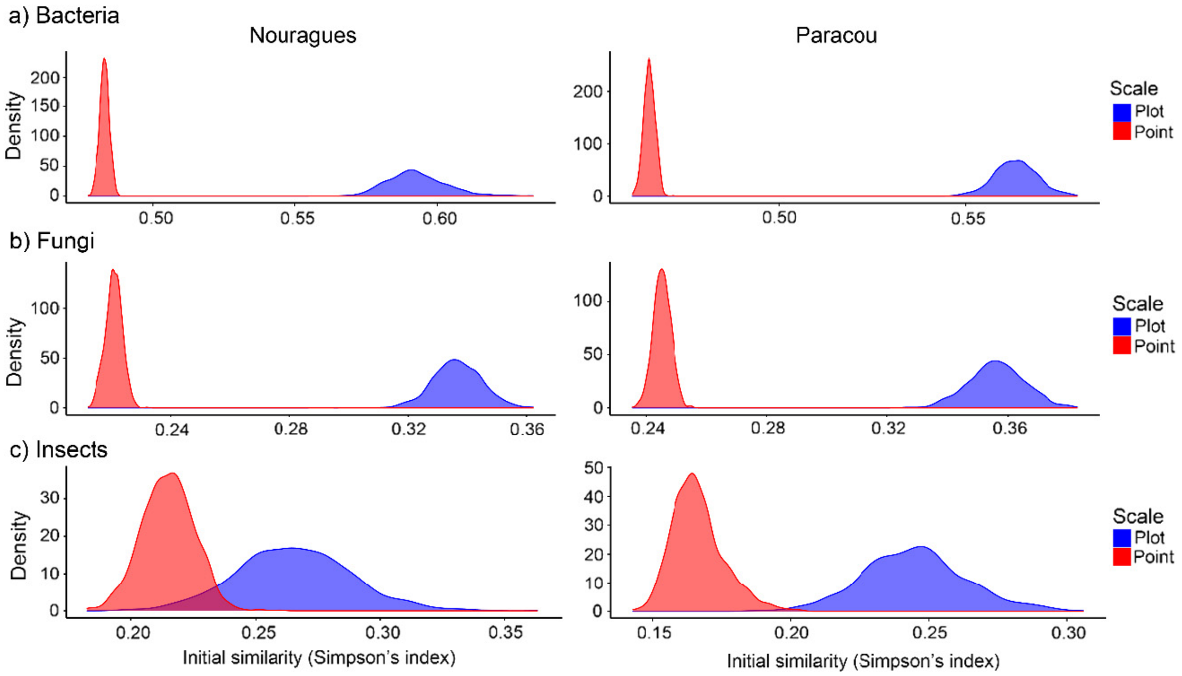


FIG. 3. Differences in initial similarity across spatial scales of analysis. Initial similarity distributions from bootstrapping the distance-decay models to estimate their intercepts, (i.e., the similarity between assemblages at the minimum distance). Point represents the 1-m^2 sampling points within the 0.25-ha plots. Minimum distance is <10 m between points and >50 between plots. The initial similarity of all taxonomic groups differed significantly (P < 0.001) at both sites, depending on the scale of analysis based on the linear models (visit Appendix S1 Table S10 for models' outputs).

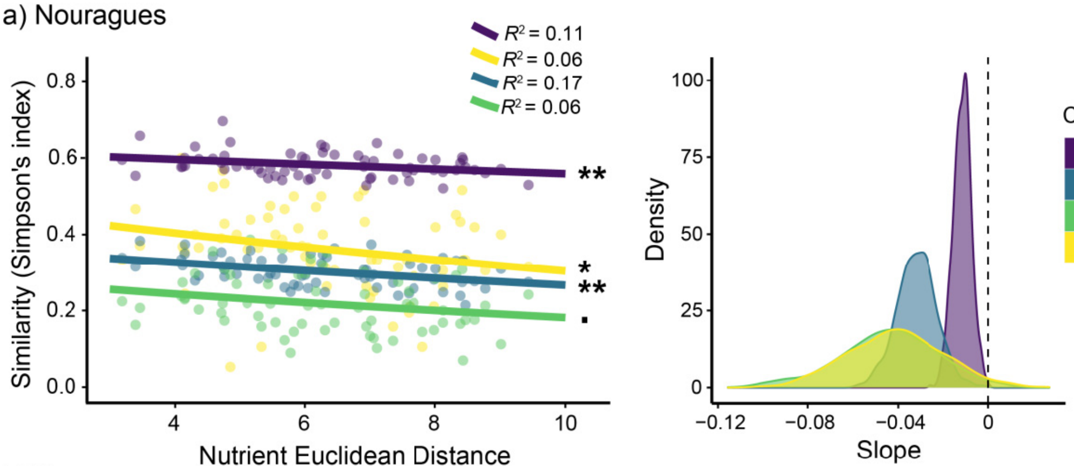
obtained for bacteria, fungi, and insects were similar at the sampling point scale (Appendix S1: Table S5) and exhibited lower initial similarity values and explanatory power than at the plot level, although the effect of nutrient condition was still significant for the bacterial and fungal communities at both sites (df = 1429, P < 0.01; Appendix S1: Fig. S7). Finally, the relationship between the similarity of the tree communities with the similarity of bacterial, fungal, and insect communities was variable (Appendix S1: Fig. S8). Fungal assemblages were strongly coordinated with the composition of the tree community, but only at Paracou (df = 64, t = 3.449, P < 0.01, Pseudo-R^2 = 0.24; Appendix S1: Table S4), whereas insects had a statistically marginal relationship at Nouragues (df = 64, t = 2.295, P = 0.06, Pseudo-R^2 = 0.05).

The comparison of the amount of variance explained by our distance-decay models reasserted that the spatial distance at the plot level was generally less important than nutrients in accounting for the composition of the communities (Appendix S1: Fig. S9). This finding was particularly clear for bacteria because spatial distance had no effect, while >10% of their compositional similarity was due to nutrient differences between plots. Importantly, the explanatory power reached by the same models at the sampling point level was lower (Appendix S1: Fig. S10). Additionally, the sensitivity analyses done with median rarefied community data sets and observed nonrarefied data yielded qualitatively identical results (Appendix S1: Tables S6–S9) indicating that differences in sampling intensity between taxa were not relevant.

DISCUSSION

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

a) Nouragues



b) Paracou

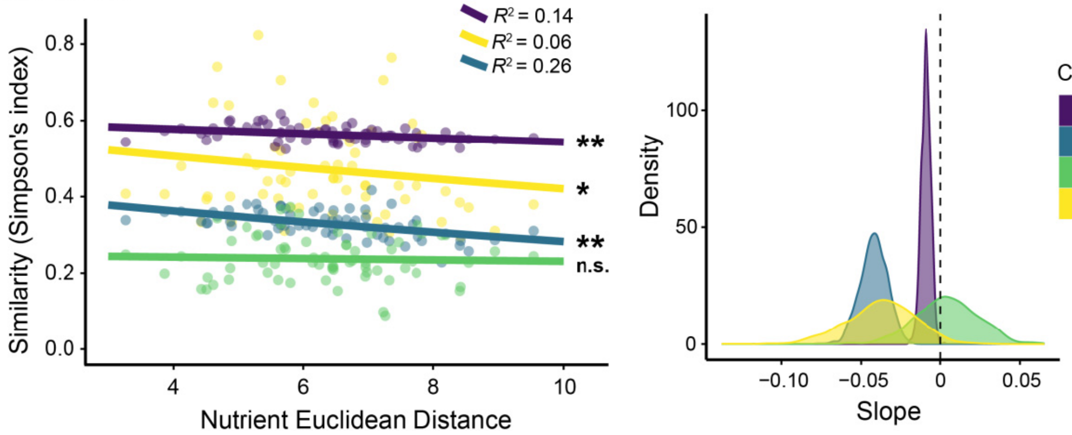


FIG. 4. Patterns of decay of similarity across nutrient distances and bootstrapped distribution of their slope for each community at (a) Nouragues and (b) Paracou. Dots represent pairs of plots, and lines are their fitted negative exponential functions. ∗∗, $P < 0.01$; ∗, $P < 0.05$; •, $0.05 < P < 0.10$; and n.s., $P \geq 0.10$.

distance-decay models, however, suggest that stochastic sampling effects, not dispersal limitation, are important for bacteria, fungi, and insects at this finer spatial scale (Nekola and McGill 2014). Our study highlights the direct role of nutrient supply capacity or its ability to capture additional environmental factors that drive the assembly of rainforest communities. Moreover, we show that the structuring effect of these nutrients is independent of the propagule size and local or regional richness of particular groups of organisms. Our study also emphasizes how the overriding effect of analytical scale may strongly influence the interpretation of data. This ultimately leads to the perception of a greater importance of dispersal limitation and ecological drift than niche-related environmental selection with decreasing observation scales (Chase 2014).

The communities of soil bacteria analyzed at the plot level supported the widely accepted view eloquently synthesized in the Baas-Becking hypothesis: “everything is everywhere but the environment selects” (Martiny et al. 2006). A recent study at the global scale has partly challenged this view (Luan et al. 2020). Nonetheless, several previous studies with a smaller geographic scope have reported that bacterial taxa–area relationships were mainly driven by environmental heterogeneity rather than dispersal limitation (Horner-Devine et al. 2004, Powell et al. 2015). The small size of bacterial propagules is assumed to be associated with a high mobility, which along with large populations and short generation times should lead to homogeneous regional pools of taxa. The environment would then filter the species of bacteria that are best adapted to the local conditions (Martiny et al. 2006). The resulting mechanism, commonly referred to as species sorting in metacommunity theory, has been successfully applied to describe the contrasting assemblage dynamics of bacterial specialists and generalists, which are more and less influenced by the environment (Leibold et al. 2004, Székely and Langenheder 2014). Soil pH and C and N content are the key factors controlling the distribution of soil bacteria (Fierer and Jackson 2006). In tropical forests, they are also particularly limited by P, whose availability is linked with pH, which also depends on topography and soil texture (Camenzind et al. 2018). Therefore, our results support the conclusion that in tropical forests, soil nutrients are the main drivers of bacterial communities, which are not dispersal-limited at the scale of our study. Thus, bacteria may achieve an effective long-distance passive dispersal via wind, air-driven particles, surface and underground runoffs, and also through animal phoresis (Lindström and Langenheder 2012).

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

Arthropods, as macroorganisms, are hypothesized to have low mobility and sensitivity to fine-scale environment variation (Soininen et al. 2007). Accordingly, dispersal limitation has been suggested to be preponderant over environmental selection in the assembly of communities of freshwater crustaceans and terrestrial beetles analyzed from a watershed to a continental scale (Beisner et al. 2006, Gómez-Rodríguez and Baselga 2018). Nevertheless, a broad study documented low levels of β-diversity for herbivorous insects from highly diverse tropical forests suggests that dispersal limitation did not have a substantial role in community assembly from local to regional scales (up to 500–1,000 km) (Novotny et al. 2007). Moreover, the compositions of plant and insect communities can be strongly correlated (Zhang et al. 2016). Our results for insects demonstrated very high species turnover and mostly nonsignificant distance−decay relationships with spatial, nutrient, or tree-composition distances. Hence, our findings apparently disagree with all these previous studies by indicating that neither dispersal limitation nor environmental selection are important drivers of the community assembly of ground insects, at least at the smallest observation scale of our analyses (1-m^2 scale). This difference is consistent with a comprehensive study at a single site but with a very high spatial resolution, which similarly documented that ecological drift without dispersal limitation was prominent in the assembly of soil arthropod communities in a tropical rainforest (Zinger et al. 2019).

Our analyses also provide clues that decreasing the observation scale may lead to the perception of a greater influence of drift processes that could be due only to stochastic sampling effects (Chase 2014, Nekola and McGill 2014). Insect communities in tropical forests are extremely diverse and complex, with high levels of taxonomic and functional turnover even at small spatial scales (Lamarre et al. 2016). Insects are all active dispersers, but their dispersal capacity is variable even within taxonomic orders (Novotny et al. 2007, Gómez-Rodríguez and Baselga 2018). Accordingly, the communities of oribatid mites from forest canopies, whose species usually have a high dispersal capacity, show a lower spatial structure and are more influenced by specific environmental features than the communities of ground-dwelling oribatids, which present a greater dispersal limitation (Lindo and Winchester 2009). Moreover, the trophic niches of ground insects are likewise equally diverse, ranging from detritivores (potentially prone to be influenced by nutrient availability) to predators and parasites whose abundances are likely independent of environmental constraints such as soil nutrients or the tree species growing above. Thus, the relative influence of dispersal limitation and environmental selection within such an ecologically variable group is also a function of traits (e.g., dispersal capacity, life-history strategy, trophic niche) other than body or propagule size (Astorga et al. 2012, Gómez-Rodríguez and Baselga 2018). Altogether, this makes insects a particularly challenging group and studies with a narrower taxonomic focus. However, embracing these functional differences among lineages could help to untangle the relative importance of the different assembly mechanisms.

We expected that nutrient selection and dispersal limitation would simultaneously affect the assembly of tree communities (Tuomisto et al. 2003, John et al. 2007). Although the effect of nutrients was moderate, we found a significant effect of nutrient availability at both sites. The relationship between tree communities and soil nutrient stocks in tropical forests has long been known to be bidirectional. Nutrients select tree species, thus driving assemblage composition, while tree species also modulate nutrient availability through their inputs as litter and root exudates and their belowground symbiotic interactions influence the dynamics of organic matter decomposition (John et al. 2007). However, our results for dispersal limitation were mixed, being significant only at Nouragues. About 87.7% of the species at Nouragues depend on faunal vectors to disperse their seeds (Charles-Dominique 2001), and similar levels of zoochory are expected for Paracou. To predict the influence of faunal vectors on tree communities, we need to know the status of the local community of seed dispersers (Gelmi-Candusso et al. 2017). So, the contrast in dispersal limitation between sites could be due more to variation in the composition, structure, and behavior of the local community of dispersers rather than due to differences in the tree species attributes. Anyhow, nutrient concentrations at Nouragues were significantly correlated with spatial distances. So, this effect of dispersal limitation also likely involved masked environmental selection.

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

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3599/suppinfo

Open research

All data and code (Peguero and Ferrin 2021) supporting the analyses and figures contained in this contribution are available in Figshare: https://doi.org/10.6084/m9.figshare.16615873.v1