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What drives study-dependent differences in distance-decay relationships of microbial communities?

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Running title: Meta-Analysis of Microbial Distance-Decay Relationships

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Abstract

Aim: Ecological communities that exist closer together in space are generally more compositionally similar than those far apart, as defined by the distance-decay of similarity relationship. However, recent research has revealed substantial variability in the distance-decay relationships of microbial communities between studies of different taxonomic groups, ecosystems, spatial scales, as well as between those using different molecular methodologies (e.g. high-throughput sequencing versus molecular fingerprinting). Here, we test how these factors influence the strength of microbial distance-decay relationships, to draw generalisations about how microbial β-diversity scales with space.

Location: Global.

Time period: Studies published between 2005-2019 (inclusive).

Major taxa studied: Bacteria, Archaea, and microbial Eukarya.

Methods: We conducted a meta-analysis of microbial distance-decay relationships, using the Mantel correlation coefficient as a measure of the strength of distance-decay relationships. Our final dataset consisted of 452 data points, varying in environmental/ecological context or methodological approaches, and used linear models to test the effects of each variable.

Results: Both ecological and methodological factors had significant impacts on the strength of microbial distance-decay relationships. Specifically, the strength of these relationships varied between environments and habitats, with soils showing significantly weaker distance-decay relationships than other habitats, whilst increasing spatial extents had no effect. Methodological factors such as sequencing depth were positively related to the strength of distance-decay relationships, and choice of dissimilarity metric was also

important, with phylogenetic metrics generally giving weaker distance-decay relationships than binary or abundance-based indices.

Main conclusions: We conclude that widely studied microbial biogeographic patterns, such as the distance-decay relationship, vary by ecological context but are primarily distorted by methodological choices. Consequently, we suggest that by linking methodological approaches appropriately to the ecological context of a study, we can progress towards generalisable biogeographic relationships in microbial ecology.

Introduction

The distance-decay of community similarity is one of the most widely studied relationships in macroecology (Nekola & White, 1999; Soininen *et al.*, 2007). This relationship quantifies the decrease in compositional similarity (β-diversity) between communities with increasing geographic distance separating them, and demonstrates that nearby communities are more similar to each other than distantly-separated communities. Distance-decay relationships arise through several different, but often interacting ecological and evolutionary processes, and consequently ecologists have extensively debated the underlying mechanisms that generate such patterns (Nekola & White, 1999; Soininen *et al.*, 2007; Hanson *et al.*, 2012). Spatial structuring of the environment can lead to distance-decay relationships, as communities close together in space are likely to experience more similar environmental conditions, and thus contain more similar communities than those situated in different environmental conditions. Dispersal limitation can also lead to distance-decay relationships by limiting the connectivity between communities, meaning that communities closer together in space will share more species through localised dispersal than those further apart.

Distance-decay relationships are well documented in a multitude of plant and animal communities (e.g. multiple taxa - Soininen *et al.*, 2007; urban plants - Sorte *et al.*, 2008; multiple aquatic taxa - Astorga *et al.*, 2012; tropical amphibians - Basham *et al.*, 2019). Yet, these relationships are of particular interest to microbial ecologists as microorganisms were assumed to have ubiquitous distributions for several reasons. Firstly, their small size facilitates passive dispersal over large geographic distances by vectors such as wind, bio-aerosolization, ocean currents or migrating animals (Bisson *et al.*, 2007; Favet *et al.*, 2013; Joung *et al.*, 2017; Vašutová *et al.*, 2019), thus potentially overcoming dispersal limitation as a contributing factor to microbial community composition. Additionally, microorganisms often maintain high population densities in the environment leading to

dispersal by “mass effects”, whereby high dispersal rates from areas of increased population density maintain populations in less optimal environments (Shmida & Wilson, 1985), helping them to overcome the constraints of spatially-structured environmental gradients. Finally, some microorganisms are able to enter dormant states, whether as vegetative cells or as cysts or spores (Locey *et al.*, 2020), allowing them to survive and disperse through suboptimal environments, simultaneously enhancing their dispersive abilities, and reducing the influence of spatially-structured environmental gradients (Low-Décarie *et al.*, 2016). Combined, these traits theoretically lower microbial β-diversity by increasing the amount of shared species between distant communities, in turn leading to weaker distance-decay relationships compared to macroorganisms. However, empirical tests of microbial distance-decay relationships have yielded mixed results. Many studies have detected little or no evidence of distance-decay relationships in microbial communities (Hazard *et al.*, 2013; Kivlin *et al.*, 2014), whilst others report relationships of varying strengths, across a range of spatial extents, study systems, and taxa (Dumbrell *et al.*, 2010; Martiny *et al.*, 2011; Clark *et al.*, 2017). Thus, despite hundreds of empirical studies, the generality of spatial patterns in microbial communities remains unclear, and we are no closer to understanding whether variability in the spatial scaling relationships of microbial β-diversity originates from ecological or methodological sources.

Variation in microbial distance-decay relationships could be due to different environmental or ecological contexts in studies. Here, we consider environmental context as the variability in the physico-chemical environment (e.g. temperature, pH, topology), and ecological context as the total suite of species present and their interactions. The study systems commonly of interest to microbial ecologists vary in terms of connectivity, which may facilitate or hinder dispersal between communities, thus leading to weaker or stronger distance-decay relationships, respectively. In well connected systems where dispersal is more feasible, such as oceanic waters, distance-decay relationships should be weaker than systems in which

dispersal is limited, such as host-associated systems or soil systems, where distance-decay relationships are weaker in deeper soil horizons (Li *et al.*, 2020). Moreover, study systems differ in the spatially structured environmental gradients and heterogeneity they support. Sediments and soils for example, can support strong environmental gradients over distances of a few meters (Dumbrell *et al.*, 2010), and can be highly heterogeneous at the millimeter scale (Vos *et al.*, 2013), strengthening distance-decay relationships. Additionally, different study taxa are likely to yield variable distance-decay relationships because they differ in traits that are linked to dispersal efficacy. For example, small cells disperse more efficiently over long distances (Wilkinson, 2001; Wilkinson *et al.*, 2012; Norros *et al.*, 2014), thus organisms with larger cell sizes, such as microbial Eukarya, should be more strongly dispersal limited than those with small cell sizes, such as Bacteria (although this may not be true for all taxa e.g. see Kivlin, 2020). Finally, it is known that spatial extent can influence our perception of ecological relationships, which may contribute to variable distance-decay relationships (Steinbauer *et al.*, 2012). Studies incorporating larger spatial extents may find stronger distance-decay relationships as they are more likely to incorporate spatial scales at which taxa are dispersal limited and/or at which environmental conditions become spatially structured (Martiny *et al.*, 2011).

Whilst the context in which a study was undertaken may contribute to variability in microbial distance-decay relationships, so too could different methodologies. Technological advances have yielded new insight into the structure and functioning of development of environmental microbial communities (Clark *et al.*, 2018). However, rapid turnover in molecular methodologies means that our perception of microbial β-diversity patterns integrates methods that vary substantially in both coverage (ability to detect a greater proportion of the community in a given sample) and resolution (ability to resolve closely related taxa) (Muyzer, 1999; Glenn, 2011). Early methods such as clone library sequencing and community fingerprinting methods (e.g. denaturing gradient gel electrophoresis (DGGE), terminal

restriction fragment length polymorphism (TRFLP), or phospholipid fatty acid (PLFA) analysis) are limited in their ability to detect rare taxa (Bartram *et al.*, 2011), undoubtedly missing rare taxa (Low-Décarie *et al.*, 2016). In turn, this could reduce the detected β-diversity, inflating estimated community similarity and weakening distance-decay relationships (Hanson *et al.*, 2012). In contrast, high-throughput sequencing (HTS) platforms (also frequently referred to as next-generation sequencing (NGS)) can deliver sequencing depths of tens or even hundreds of thousands of sequences per sample (Caporaso *et al.*, 2012), thus improving both community coverage (the detected proportion of a given community), and allowing more samples to be examined in a single study (sample coverage). Consequently, variation in the ability of molecular methods to resolve closely related taxa, and to detect rare taxa can be an additional source of variability in microbial β-diversity, which by extension can either weaken or strengthen microbial distance-decay relationships.

In addition to the molecular methods, the choice of analytical methods, such as similarity metric, can influence distance-decay relationships. The similarity of communities varies according to the identity and abundance of the species present, their phylogenetic relationships, and by external factors such as varying sample sizes. Thus, similarity metrics that vary by one or more of these characteristics would likely result in contrasting distance-decay relationships (Chao *et al.*, 2005; Barwell *et al.*, 2015). For example, phylogenetic indices would be expected to yield weaker distance-decay relationships than other metrics, because communities that have no species in common can still be highly phylogenetically similar if the species share many branches of a phylogenetic tree, thus reducing the decay of similarity over geographic distance (Bryant *et al.*, 2008). On the other hand, quantitative indices compare not only the composition of species present, but also their abundance in each community, reflecting finer-scale changes in community structure,

and thus should result in stronger distance-decay relationships by providing an additional axis (species abundances) by which communities can differ.

Here, to disentangle the effects of both contextual (e.g. spatial extent, taxon, or ecosystem) and methodological (e.g. means of identifying/differentiating taxa, or similarity metric) variables on microbial distance-decay relationships, we undertook a meta-analysis to test the following specific hypotheses:

- H_1 Bacteria and Archaea will show weaker distance-decay relationships than micro-eukaryotic taxa due to their smaller size and higher population densities in most environments.
- H_2 Environments that are able to maintain steep physicochemical gradients, such as sediments and soils, will have stronger distance-decay relationships than those such as seawater or air, where environmental gradients are more diffuse.
- H_3 Spatial extent will be positively related to the strength of the distance-decay relationship as, at large spatial scales, increased dispersal limitation and environmental heterogeneity will decrease the variance in community similarity at a given spatial distance, resulting in stronger distance-decay relationships.
- H_4 High-throughput sequencing methods will yield stronger distance-decay relationships due to: a) their ability to resolve closely related taxa, b) their greater community coverage (e.g. number of sequences per sample, or number of individuals counted per sample), and/or c) their greater sample coverage.
- H_5 Phylogenetic similarity metrics (e.g. Unifrac, beta nearest taxon index) will result in weaker distance-decay relationships than other metrics as communities can be phylogenetically similar, yet different at fine taxonomic resolutions, whilst quantitative metrics (e.g. Bray-Curtis, Hellinger, Euclidean) will yield the strongest as they reflect changes in both species composition and abundance.

Methods

Meta-Analysis

In order to test our hypotheses, we first gathered available data on microbial distance-decay relationships via a systematic literature search. To do this, five search terms were selected to detect relevant studies (Table 1). All literature searches were conducted using the Web of Science search portal on 18/04/2020, and all results published between 1900-2019 (inclusive) were retained. To further filter the dataset to studies suitable for testing our hypotheses, search results were downloaded and manually screened using the "metagear" (Lajeunesse, 2016) package in R (version 3.4.1; R Core Team, 2019). Here, suitable studies were those that tested the relationship between community similarity and geographic distance in microbial communities, and not studies of "macroorganisms", or studies of strain-level genetic distance (e.g. using multi-locus sequence typing). Furthermore, studies that did not test distance-decay relationships using Mantel correlation, or that used only partial Mantel tests, were also discarded. We did not identify any potentially suitable studies that were published prior to 1967, the year the Mantel test was described (Mantel, 1967), and the earliest suitable study was published in 2005.

Table 1. Details of Web of Science search terms, and the number of results for each search.

Search	Search Term	Number of results
1	TS = (biogeograph*) AND TS = (bacteria* OR archaea* OR microb* OR microorganism*)	2907
2	TS = (macroecolog*) AND TS = (bacteria* OR archaea* OR microb* OR microorganism*)	136
3	TS = ("everything is everywhere") AND TS = (bacteria* OR archaea* OR microb* OR microorganism*)	66
4	TS = ("geographic distance") AND TS = (bacteria* OR archaea* OR microb* OR microorganism*)	220

5	TS = ("distance decay") AND TS = (bacteria* OR archaea* OR microb* OR microorganism*)	186

From these studies, we extracted Mantel correlation coefficients (*r*) as an effect-size measure for each distance-decay relationship. The Mantel test is a permutation-based method used to test for correlation between two distance matrices, or in the context of this study, community (dis)similarity and geographic distance. The Mantel test statistic is an ideal measure of effect size for use in meta-analytical frameworks for several reasons. Firstly, the Mantel correlation test is the most frequently used method for testing distance-decay relationships in microbial ecology (Franklin & Mills, 2007; Ramette, 2007). Secondly, as the Mantel coefficient is a standardised correlation coefficient (i.e. is bound by -1 and 1), it provides an easily interpretable and comparable measure of effect size (Harrison, 2012).

We ensured all Mantel correlation coefficients reflected correlations between geographic distance and community dissimilarity, rather than similarity, by multiplying correlation coefficients by -1 where necessary (so that positive values indicate a typical distance-decay relationship). Partial Mantel statistics (which test for correlation between two matrices whilst controlling for a third) were excluded as they are influenced by other variables included in the test, and are therefore not easily comparable between studies. All Mantel correlation coefficients were transformed to *z*-scores using Fisher's *z* transformation, as recommended by Rosenberg *et al.* (2013). All subsequent statistical analyses were conducted on the transformed *z*-scores, whilst original Mantel correlation coefficients were used to make figures, for ease of interpretation.

In order to test our hypotheses, several variables relating to the context and methodology of each distance-decay relationship were recorded. Details of these variables are described in Box 1.

Box 1. Details of the explanatory variables extracted from each study.

Resolution
Each distance-decay relationship was categorised into either high-resolution (high-throughput or Sanger sequencing), low resolution (molecular e.g. ARISA, TRFLP, DGGE, PhyloChip, PLFA), or low resolution (morphological), based on the method's ability to distinguish between closely related organisms.

Community Coverage
This refers to the sequencing depth in sequencing-based studies, or number of individuals counted in morphology-based studies, per sample. For sequencing studies, we recorded the number of sequences after rarefaction, or if this was not given, the average number of sequences per sample. As there is no comparable measure of coverage for fingerprinting studies, we excluded them from analyses of community coverage.

Sample Coverage
Sample coverage refers to the sample size (e.g. number of communities/samples) of each distance-decay relationship.

Dissimilarity Index
The dissimilarity index used to calculate each distance-decay relationship. Recorded dissimilarity indices were then categorised as quantitative (Bray-Curtis, Horn-Morisita, Euclidean, Hellinger, Theta), qualitative (Jaccard, Raup-Crick, Sørensen, Simpson, βsim), or phylogenetic (weighted or unweighted Unifrac, Rao, β-mean nearest taxon distance, β-mean pairwise distance).

Correlation Type
Studies were categorised according to the type of correlation coefficient used in the analysis distance-decay relationship (e.g. Spearman's or Pearson's correlation coefficient). The correlation type was only recorded if the type of correlation coefficient was explicitly mentioned.

Study Taxon
Each distance-decay relationship was binned into the following broad taxonomic categories based on the taxonomy of the focal organisms (Archaea, Bacteria, Fungi, or other microbial Eukarya), or combination of these categories if a relationship was based on multiple taxa (for example due to using sequencing primers that detect both Archaea and Bacteria). Fungi grouped separately from other micro-Eukaryotes due to their distinct reproductive strategy (e.g. spore-production) and the fact the they are frequently targeted using distinct molecular approaches (e.g. via taxon-specific primer sets), in contrast to most other studies of micro-Eukarya.

Spatial Extent
This is the maximum distance separating communities in km. If this was not stated in text or provided in supplementary material (e.g. in a geographic distance matrix), it was calculated from given geographic coordinates, estimated from a plot of the distance-decay relationship, or estimated from scaled maps.

Environment
We broadly categorised distance-decay relationships based on the type of environment (agriculture, air, aquifer, coastal wetlands/intertidal, desert, dune, forest, glacier, grassland, lake, marine, coastal marshes, mine, river, snow, urban) within which they were

sampled. Whilst these categories are not mutually exclusive, we categorised each study based on which environment best represented the environmental context in which each study was undertaken. For studies on lakes, we also recorded whether relationships originated from a single lake, or across multiple lakes.

Habitat
The type of environmental material that the sampled communities occupied. We categorised distance-decay relationships as: air, host-associated, sediment, snow, soil, water.

Statistical Analyses

In order to determine whether distance-decay relationships varied between categorical variables (as in hypotheses 1, 2, 4, and 5), we used ANOVA tests. In tests where significant differences between groups were found, Tukey's Honest Significant Difference (HSD) tests were used to determine which groups were different. Linear mixed-effect models were used to test relationships between the strength of distance-decay relationships and continuous variables such as spatial extent and community coverage, using a random intercept to account for heteroscedasticity due to some studies contributing multiple relationships. The variables spatial extent and community coverage were initially $\log_{10}$ transformed to aid model fitting, as they spanned several orders of magnitude. To compare the overall influence of ecological vs methodological factors on microbial distance-decay relationships, we compared two full models (including all relevant variables) using AIC scores, on a subset of the data for which all variables were successfully recorded. We report the results of all null hypothesis tests in terms of statistical "clarity" rather than "significance", in line with recommendations from Dushoff *et al.* (2019)

Results

Our Web of Science searches resulted in 2,982 unique search results. Manual screening of the abstracts yielded 951 studies that were deemed to be potentially suitable for use in this analysis. A total of 452 Mantel correlation coefficients were successfully obtained from 187

studies represented in 61 journals (Fig. S1). Reported Mantel correlation coefficients ranged from -0.33 to 0.95, with a mean of 0.27 (std. error = 0.011), whilst a summary of the variables collected is shown in Table 2.

Table 2. Summary of collected data. For categorical variables, the number of individual distance-decay relationships in each category are shown, whereas minima, maxima, median and mean values are shown for continuous variables. Detailed descriptions of each variable are found in Box 1, and raw data can be found in Table S1.

Ecological variables		Methodological variables	
Variable	Summary	Variable	Summary
Study taxon	Archaea: *n* = 26 Bacteria: *n* = 238 Eukarya: *n* = 67 Fungi: *n* = 93 Archaea + Bacteria: *n* = 17 Bacteria + Eukarya: *n* = 3 Bacteria + Fungi: *n* = 6 All: *n* = 2	Resolution	High: *n* = 345 Intermediate: *n* = 84 Low: *n* = 23
Spatial extent (km)	Min = 0.0001 Mean = 1,543 Median = 220 Max = 18,700 NA = 15	Community coverage (number of individuals/ sequences)	Min = 8 Mean = 217,357 Median = 1,257 Max = 34,192,561 NA = 115
Environment type	Agriculture: *n* = 16 Air: *n* = 13 Aquifer: *n* = 1 Coastal: *n* = 8 Desert: *n* = 4 Dune: *n* = 1 Forest: *n* = 76 Glacier: *n* = 5 Grassland: *n* = 96 Lake: *n* = 76 Marine: *n* = 88 Marsh: *n* = 3 Mine: *n* = 1 River: *n* = 57 Snow: *n* = 3 Urban: *n* = 4	Dissimilarity index	β-MNTD: *n* = 13 β-MPD: *n* = 1 β-sim: *n* = 4 Bray-Curtis: *n* = 218 Bray-Curtis$_{Sim}$: *n* = 3 Bray-Curtis$_{Nes}$: *n* = 1 Canberra: *n* = 1 Euclidean: *n* = 9 Hellinger: *n* = 4 Jaccard: *n* = 49 Mash: *n* = 2 Morisita-Horn: *n* = 4 Rao: *n* = 2 Raup-Crick: *n* = 19 Simpson: *n* = 2 Sorensen: *n* = 42 Theta: *n* = 1

			Unweighted Unifrac: *n* = 17 Weighted Unifrac: *n* = 59 NA: *n* = 1
Habitat type	Air: *n* = 16 Host: *n* = 75 Sediment: *n* = 78 Snow: *n* = 3 Soil: *n* = 141 Water: *n* = 137 NA: *n* = 2	Correlation type	Pearson: *n* = 62 Spearman: *n* = 86 NA: *n* = 304
		Sample coverage (Number of samples)	Min = 4 Mean = 52.88 Median = 25 Max = 1,010 NA = 1

Influence of Context on the Distance-Decay Relationship

In order to determine whether contextual factors can influence the strength of distance-decay relationships, the influence of ecological factors including study taxa, study system, and spatial scale were tested. Within the dataset, the most commonly studied taxa were Bacteria (*n* = 238), followed by Fungi (*n* = 93), other microbial Eukaryotes (*n* = 67), and Archaea (*n* = 26). We found no clear differences in the strength of distance-decay relationships between these taxa ($F_{5,\ 441}$ = 0.99, *P* = 0.43), although distance-decay relationships incorporating bacterial and fungal communities showed the weakest relationships, albeit only from six studies (Fig. 1).

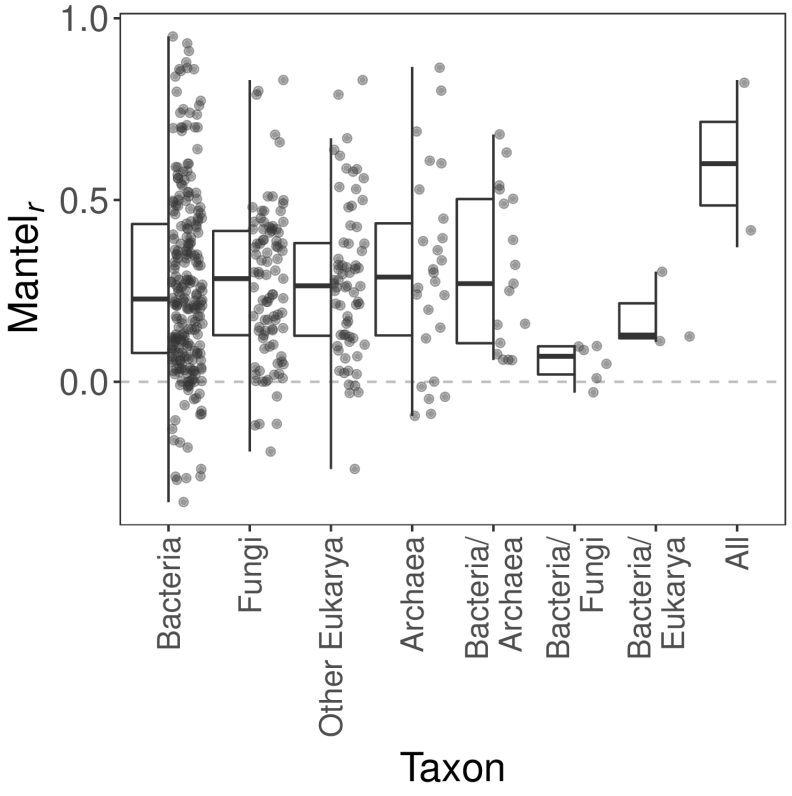

Figure 1. The strength (Mantel$_r$) of distance-decay relationships based on different study taxa. A larger Mantel$_r$ value indicates a stronger distance-decay relationship. The "All" category consists of studies that incorporated all microbial taxonomic groups, whilst combined categories (e.g. Bacteria/Archaea) incorporate communities from multiple taxonomic groups (e.g. bacterial and archaeal communities).

The distance-decay relationships in our dataset originated from 16 different environments. Of these, five were represented by three, or fewer, distance-decay relationships, and so were excluded from further analyses (marsh; n = 3, snow; n = 3, dune, mine, aquifer; n = 1). The most frequently studied environments were grasslands (n = 96), marine (n = 88), and lakes and forests (n = 76 for both). We found clear differences in the strength of distance-decay relationships between environments (Fig. 2A; $F_{10,\ 432}$ = 3.187, P < 0.001). Specifically, and perhaps counter-intuitively, grassland-based studies had weaker distance-decay relationships than those from aquatic environments such as lakes, rivers, or

the marine environment (|coef| > 0.17, $P < 0.05$ for all comparisons). Urban environments, which included built environments such as sewers and indoor air, also produced weak distance-decay relationships, although with only four data points, this difference was not statistically clear ($P > 0.43$ for all comparisons). We also found no difference in the strength of distance-decay relationships between studies conducted in single lakes compared to those incorporating multiple lakes ($F_{1, 74} = 0.11$, $P = 0.74$), despite the average spatial extent of multiple-lake studies being approximately 32-fold greater than that of single-lake studies (Fig. S2).

A more detailed analysis of the interaction between environment type and habitat revealed that, whilst environments ($F_{9, 420} = 3.29$, $P < 0.001$) and habitat ($F_{3, 420} = 6.65$, $P < 0.001$) differ from each other, their interaction was not statistically significant ($F_{4, 420} = 1.93$, $P = 0.10$). In fact, within environments, only marine host-associated and marine water-based distance-decay relationships were clearly different from each other (Fig. 2B), with host-associated communities showing significantly stronger distance-decay relationships (coef = 0.35, $P < 0.001$).

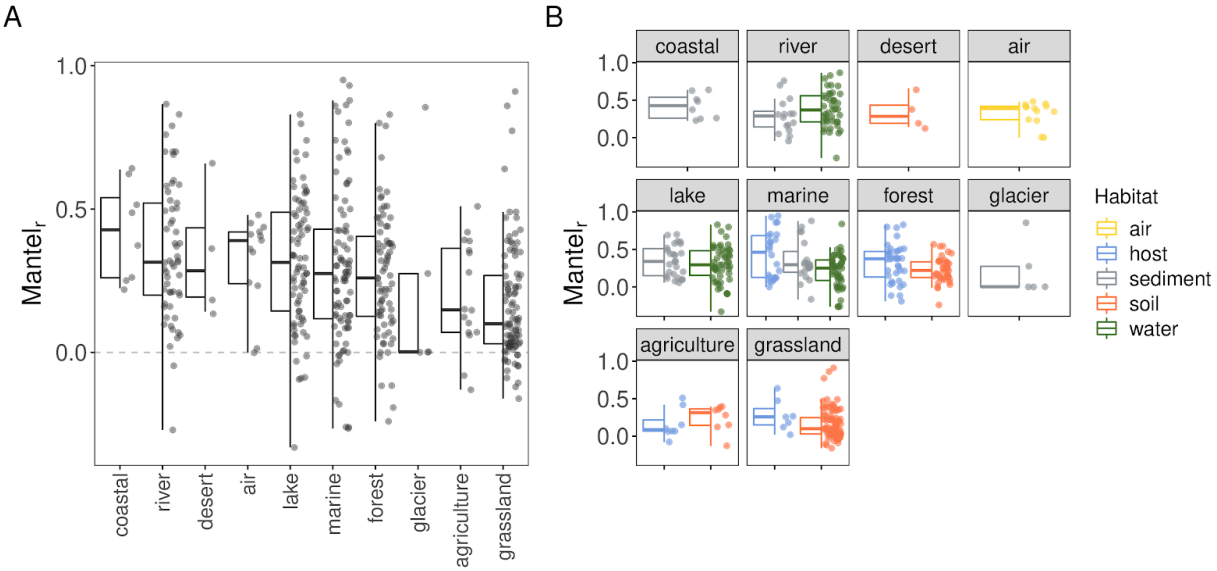

Figure 2. Variation in Mantel correlation coefficients of distance-decay relationships between different environments (A) and habitat types (B). Environment categories are arranged from strongest to weakest mean distance-decay relationship.

The spatial extents of recorded distance-decay relationships ranged from 10 cm to more than 18,000 km, and minimal spatial extents varied notably across environments and habitats, with terrestrial and soil-based studies often conducted over smaller spatial scales (Fig. S3). After accounting for differences between studies, we found no evidence of a statistically clear relationship between the spatial extent of a study and the strength of the observed distance-decay relationship (coef = 0.02, marginal R^2 = 0.020, t = 1.58, P = 0.11). Finally, as larger spatial scale studies might also incorporate greater sampling coverage, we tested for collinearity between the spatial scale of a study and the sampling coverage, but found no correlation between these variables (ρ = 0.06, P = 0.19).

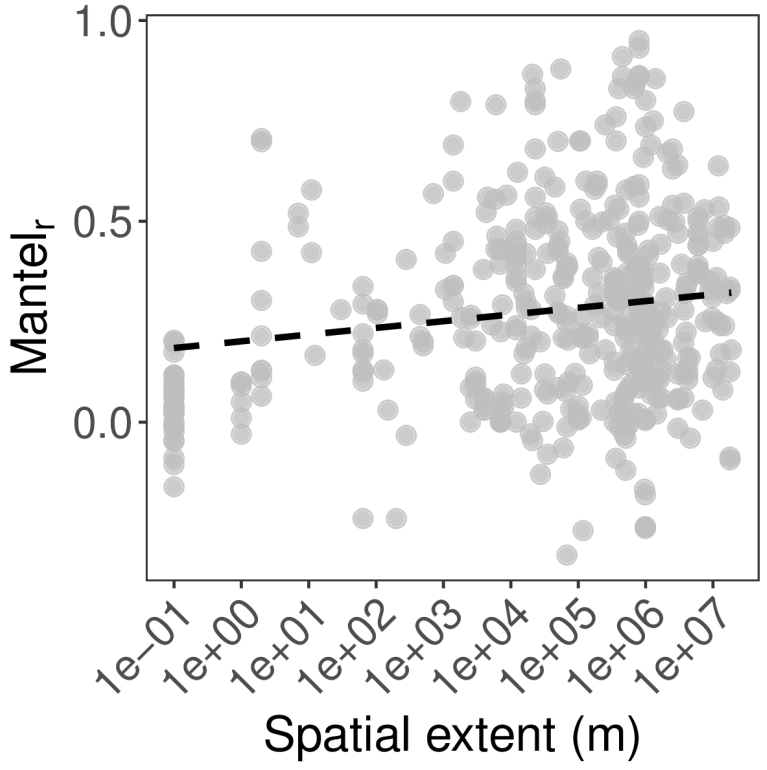

Figure 3. The relationship between spatial extent and the Mantel correlation coefficient of microbial distance-decay relationships. The dashed line represents the fit of a mixed-effects model between the $\log_{10}$ of spatial extent and Mantel correlation coefficient, with a study-dependent random intercept.

Influence of Methodological Factors on the Distance-Decay Relationship

We grouped community characterisation methods according to their ability to distinguish between closely related taxa. There were no clear differences in the strength of distance-decay relationships between different resolution methods ($F_{2, 449} = 0.562$, $P = 0.57$), nor were there clear differences between different molecular methods (Fig. S4, $F_{7, 437} = 1.97$, $P = 0.06$), considering only those methods that had >4 distance-decay relationships across the entire dataset (excluding Ion Torrent; n = 4, phylo-chip; n = 2, and Pac-Bio; n = 1).

Whilst we observed no differences in distance-decay relationships between different resolution methods, after accounting for study-dependent differences, we found a positive relationship between ($\log_{10}$) community coverage and the strength of microbial distance-decay relationships (Fig. 4A; $n = 337$, conditional $R^2 = 0.57$, coef = 0.06, $t = 2.73$, $P < 0.01$), although the marginal effect of community coverage was weak (marginal $R^2 = 0.04$).

The logistics of multiplexing samples on high-throughput sequencing runs means that there is often a trade-off between the community coverage and sampling coverage of a study. However, we found no evidence of negative correlation between these two factors (Pearson's $\rho = -0.03$, $P = 0.54$). Nor did we detect any clear relationship between the number of samples ($\log_{10}$ sample coverage) and the strength of distance-decay relationships, even after accounting for study-specific differences with a mixed effects model (Fig. 4B; $n = 451$, coef = -0.06, marginal $R^2 = 0.01$, $t = -1.40$, $P = 0.16$).

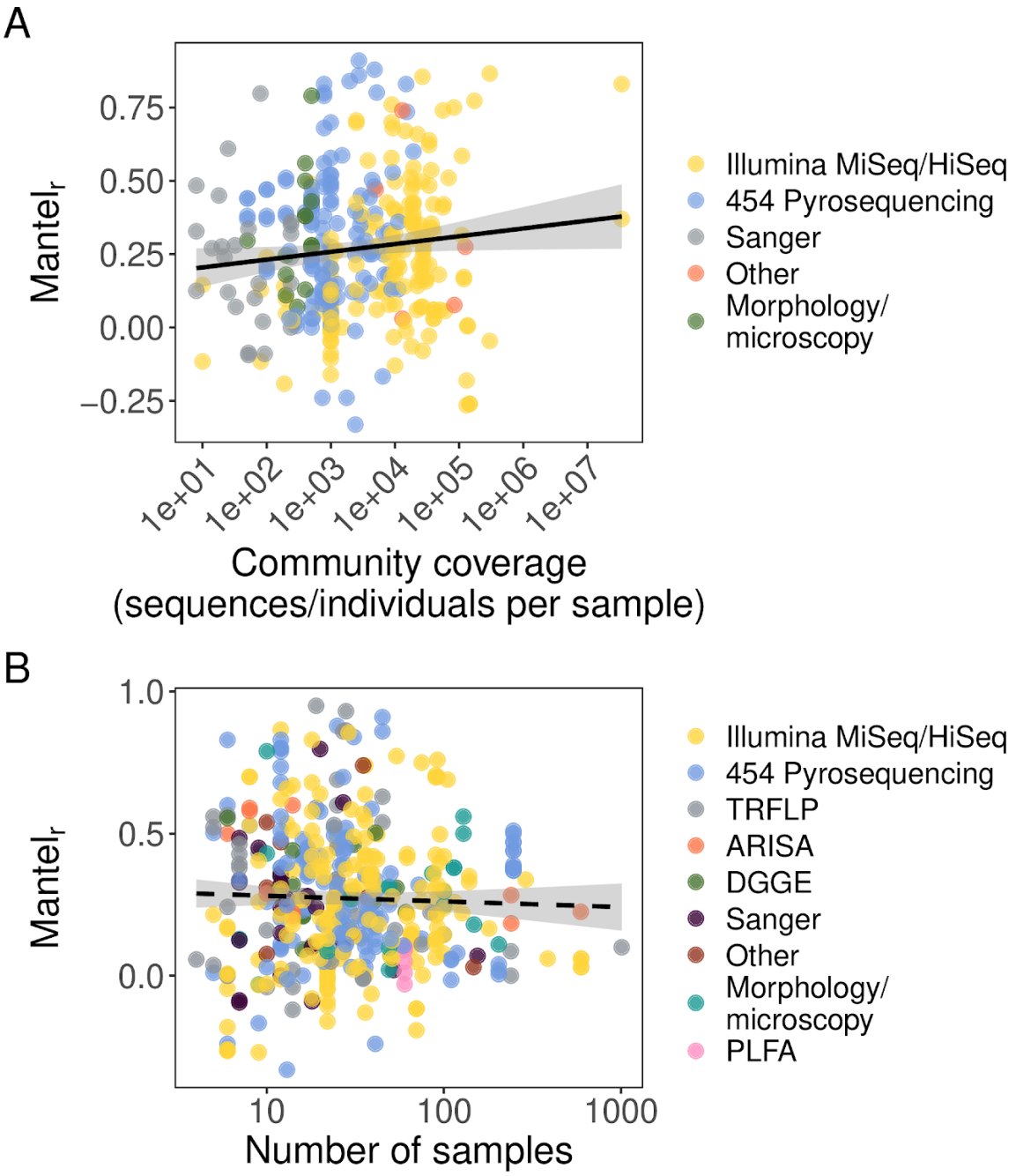

Figure 4. The relationship between the strength of microbial distance-decay relationships (Mantel$_r$) and A) community coverage, quantified as the number of sequences or individuals counted per sample, and B) sample coverage, quantified as the number of individual samples used to construct distance-decay relationships. Points are individual Mantel correlation coefficients, coloured by the molecular technique used to characterise the

microbial community. Solid lines indicate statistically significant relationships ($P < 0.05$), whilst dashed lines indicate non-significant relationships ($P > 0.05$), and shaded grey ribbons represent 95% confidence intervals. Abbreviated molecular methods in the legend are defined as follows (TRFLP = Terminal Restriction Fragment Length Polymorphism; ARISA = Automated Ribosomal Intergenic Spacer Analysis; DGGE = Denaturing Gradient Gel Electrophoresis; PLFA = Phospholipid Fatty Acid analysis; Sanger = Sanger sequencing of cloned phylogenetically informative genes).

Choice of similarity index also had a clear impact on the strength of microbial distance-decay relationships. As well as recording the specific similarity index used, we categorised indices into types (binary, abundance, or phylogenetic) to test for broad differences in distance-decay relationships. We analysed the nested interaction between similarity index and index type, and found no clear differences between different index types (Fig. 5A; $F_{2, 424} = 1.48$, P = 0.23). However, the interaction between index type and similarity index was significant ($F_{7, 424} = 7.20$, P 0.001). Post-hoc analysis revealed differences between similarity indices within and between index types (Fig. 5B). Distance-decay relationships based on the Raup-Crick index were weaker than those based on either Sørensen (coef = -0.38, P < 0.01) or unweighted Unifrac indices (coef = -0.44, P < 0.01), whilst those based on weighted Unifrac were weaker than both Sørensen (coef = -0.29, P < 0.001) and unweighted Unifrac (coef = -0.35 P < 0.05). Finally, most studies did not explicitly state the correlation type used to generate each Mantel test ($n = 304$), but of those that did, Spearman's correlation coefficient was more frequently used ($n = 86$) than Pearson's ($n = 62$). We found no clear difference in the strength of microbial distance-decay relationships using these two methods ($F_{1, 146} = 2.47$, $P = 0.12$).

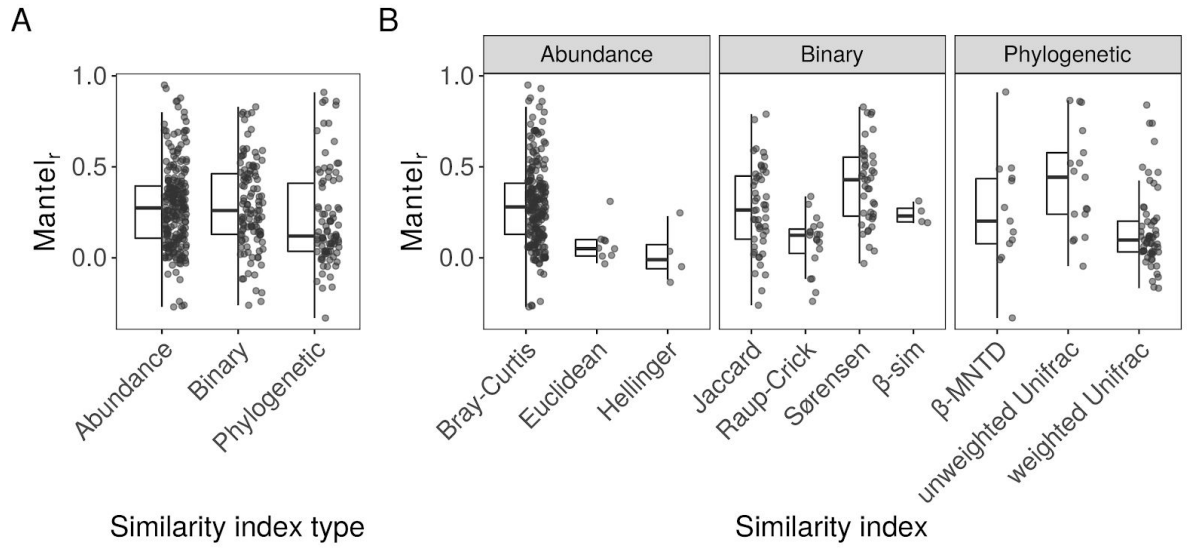

Figure 5. Variation in the strength of microbial distance-decay relationships (*Mantel$_r$*) calculated with different similarity index types (A), or individual indices (B). Only indices with four or more distance-decay relationships were plotted for clarity.

Comparison of Contextual and Methodological Variables

In order to determine whether eco-environmental context or methodological factors better explain the strength of microbial distance decay relationship, we specified two models, with variables from these two categories, using a subset of the original data for which values were obtained for all variables (n = 323). Each model had four variables, and used similar degrees of freedom (context model df = 26, methodological model df = 27). The methodological model outperformed the contextual model in terms of both AIC (Akaike Information Criterion) and R^2 measures of model performance (Table 3). Notably, neither model explained a high proportion of the variance, although both AIC and likelihood ratio tests supported both models over a null (intercept only) model.

Table 3. Comparison of models specified using either contextual, or methodological variables. Akaike Information Criterion (AIC) and adjusted R^2 quantify the likelihood and fit of a model relative to the number of predictor variables, respectively.

Model	AIC	Adj-R^2	Likelihood ratio comparison to null (intercept only) model			
			ΔAIC	Sum of squares	F (df)	*P* value
Contextual	146.89	0.11	-13.69	5.34	2.61	< 0.001
Methodological	134.11	0.14	-26.46	6.47	3.17 (25)	< 0.001

Discussion

Previous research into the spatial ecology of microbial communities has not yielded a consistent distance-decay relationship. Our meta-analysis of 452 microbial distance-decay relationships suggests that the reasons for this lack of consistency are two-fold. Firstly, the differing contexts within which studies are conducted contribute variability to reported distance-decay relationships. In particular, we found that differing study systems were associated with variation in microbial distance-decay relationships. Secondly, methodological differences between studies, including dissimilarity index, data resolution, and sample coverage, all significantly affected observed distance-decay relationships. A central tenet of macroecology is the search for universal patterns and relationships; our results suggest generalisable relationships may only emerge when methodological approaches are appropriately coupled to ecological context.

Our comparison of distance-decay relationships between different study systems revealed that agricultural and especially grassland-based studies had weaker relationships than studies of other environments. Within these environments, soils were by far the most

frequently studied habitat, and we initially expected that, as soils maintain strong physicochemical gradients over small vertical and horizontal spatial scales (e.g. Dumbrell *et al.*, 2010), that these distance-decay relationships would be stronger than in other environments or habitats. It is possible that the environmental gradients present in soils do not change linearly over geographic distance, for example if similar environmental conditions are patchily distributed. Alternatively, soil microorganisms may be able to disperse more effectively than previously thought, perhaps via association with other soil organisms (e.g. bacterial migration along fungal hyphae; Warmink *et al.*, 2011), migratory species such as birds (Bisson *et al.*, 2007), wind blown soil particles (Favet *et al.*, 2013), or via bioaerosols (Joung *et al.*, 2017). The depth profile over which soil samples integrate may also play a role in obscuring distance-decay relationships, as surface soils show stronger distance-decay relationships than deeper ones, likely due to the greater intensity of dispersing propagules entering the surface (Li *et al.*, 2020). Furthermore, soils harbour extensive microbial "seed banks" of dormant organisms and/or relic DNA that could weaken the distance-decay relationship (Lennon & Jones, 2011; Carini *et al.*, 2016; Lennon *et al.*, 2018). Dormant cells and relic DNA are not subject to environmental selection yet, are routinely detected in molecular community assays, likely diminishing the perceived effects of spatially-structured environmental selection on microbial communities (Locey *et al.*, 2020). Thus, in habitats such as soils, distinguishing dormant from active cells could result in stronger distance-decay relationships than those recorded previously, although evidence of the same effect on distance-decay slopes is mixed (Meyer *et al.*, 2018; Locey *et al.*, 2020). The extent to which this phenomenon plays a role in other environments is also unclear.

Originally, we expected the weakest distance-decay relationships to occur in connected aquatic environments such as rivers, oceans, or within single lakes, as the movement of water may provide an effective dispersal mechanism, homogenising microbial communities over larger spatial and environmental distances. In contrast, we found that aquatic

communities actually showed stronger distance-decay relationships. Soininen *et al.* (2007) recorded similar distance-decay rates between terrestrial, marine and aquatic ecosystems, showing that context-dependent distance-decay relationships may be a feature of microbial communities. We also found that the strength of distance-decay relationships was not different in studies based on single, or multiple, lakes, despite the difference in spatial extents of these studies. Lakes act as habitat islands within a terrestrial matrix and so dispersal limitation and environmental heterogeneity should be greater across multiple lakes than within a single lake, resulting in stronger distance-decay relationships in multi-lake studies. One explanation is that catchment-scale environmental parameters such as geology may homogenise environmental conditions across multiple lakes, meaning that environmental distances are similar within and between lakes. Alternatively, other biogeographic processes such as mass effects may homogenise communities between hydrologically connected lakes (Lindström & Bergström, 2004), especially where lakes are of different sizes (Reche *et al.*, 2005). Host-associated communities showed relatively strong, but variable distance-decay relationships. We suggest that this is caused jointly by the ecology of the host species, in combination with the degree of host-specificity with the associated microbiome. For example, if the host is not dispersal limited, and associates with a large variety of microorganisms, then the distance-decay relationship may be relatively weaker than those of either dispersal-limited hosts, or highly specific associated microbiomes.

The scale-dependence of various biogeographical relationships is well studied (Hillebrand, 2004; Bissett *et al.*, 2010; Martiny *et al.*, 2011; Soininen *et al.*, 2011), albeit with contrasting results. Soininen *et al.* (2011) reported that distance-decay relationships of various microbial communities were generally steeper over greater spatial extents, whilst our results suggest that increasing spatial extent does not significantly increase the strength of distance-decay relationships. As we analysed distance-decay strength rather than

steepness, our results are not necessarily contradictory. A strong distance-decay relationship occurs when, at a given spatial distance, all pairs of communities are equally dissimilar to one another, whereas a steep distance-decay occurs when communities separated by different distances are highly dissimilar to each other. We initially expected that spatial extent might alter the strength of distance-decay relationships as, at greater distances, decreased dispersal and increased environmental heterogeneity should reduce the variance in compositional similarity between pairs of communities (at a given distance). Instead, it could be that the spatial configuration or connectivity of the communities could be more important than spatial extent *per se*. For example, at a given spatial distance, some pairs of communities could be linked by dispersal and others not, increasing the variation in community similarity at each distance, and weakening the distance-decay relationship. In practice, this could occur in lake systems where at a certain geographic distance, some pairs of communities fall within the same lake and some in different lakes or when long-distance dispersal vectors link some pairs of communities separated by large distances, but not others, as has been proposed for halophilic microbial communities dispersing on migratory birds for example (Clark *et al.*, 2017; Kemp *et al.*, 2018). Furthermore, we observed that the minimum spatial extents differed according to the environment they were conducted in. Studies from terrestrial environments (e.g. grasslands and forests) or those based on soils generally incorporated smaller spatial extents than those based on aquatic systems (with the exception of some host-associated marine studies) or on habitats such as water or air. This could be due to the logistics of sampling at small scales. For example, sampling planktonic microbial communities at small (centimeters to meters) scales could be confounded by mixing caused by the sampling process or by tidal movements of water. Additionally, since many studies analysing microbial distance-decay relationships aimed to discern between environmental and spatial effects on microbial communities, it may be widely assumed that aquatic environments are more homogenous and/or that microorganisms are not dispersal

limited at these scales compared to more physically stable environments such as soils or sediments.

Distance-decay relationships are frequently interpreted as evidence for neutral community assembly processes such as dispersal limitation, in the microbial literature. Across microbial taxa, cell size is a trait thought to influence dispersal efficacy (Wilkinson, 2001; Wilkinson *et al.*, 2012; Zinger *et al.*, 2019), and so larger microorganisms such as micro-Eukarya should show stronger distance-decay relationships than smaller microorganisms such as Bacteria or Archaea. However, we found no evidence for this, suggesting that phylogenetically structured traits such as cell size may be less important compared to other contextual and methodological factors, or that the broad domain-level classification used here does not sufficiently capture different microbial cell sizes. As discussed previously, distance-decay relationships can arise from spatially autocorrelated environmental gradients as well as dispersal limitation (Nekola & White, 1999). Therefore, the lack of differences in biogeographic patterns observed at the domain level may be the result of a trade-off between dispersal-related processes and environmental filtering. For instance, bacterial distance-decay relationships may be less strongly influenced by dispersal than environmental filtering, and vice versa for Eukarya. Consequently, these influences may balance out at broad taxonomic levels, resulting in similar biogeographic patterns at the domain level.

In comparison to contextual factors, methodological factors were found to have a greater influence on microbial distance-decay relationships. The development of molecular methods, including high-throughput sequencing platforms, has vastly improved our ability to characterise microbial communities (Roesch *et al.*, 2007; Caporaso *et al.*, 2012). However, these methods differ in their resolution, community coverage, and ability to multiplex large numbers of samples, all of which we hypothesised could strengthen or weaken

distance-decay relationships by altering our estimation of microbial β-diversity. In contrast, we observed only a weak relationship between the strength of distance-decay relationships and community coverage, and no clear effects of different resolution methods, or the number of samples, suggesting that molecular methodology may not play as large a role in determining microbial biogeographic patterns as previously thought.

The ability to resolve closely related taxa has previously been found to be an important determinant of our ability to detect biogeographical patterns, as such patterns may only emerge when taxa are defined at sufficiently high resolution (Hanson *et al.*, 2012). Yet, other studies show that bioinformatically altering taxonomic resolution frequently has little effect on microbial biogeographic patterns. For example, increasing the similarity threshold at which operational taxonomic units are defined is thought to be equivalent to increasing the taxonomic resolution (Callahan *et al.*, 2017). Yet, empirical biogeographic relationships often appear robust to such manipulation, in a variety of taxa and ecosystems (Clark *et al.*, 2017; Glassman & Martiny, 2018; Meyer *et al.*, 2018), supporting our finding that resolution may not be important. Perhaps most molecular methodologies operate above resolutions at which biogeographic patterns begin to change, or more worryingly, perhaps we are still studying microbial biogeography at too low a resolution.

Aside from resolution, another important variable related to molecular methodology is community coverage. One of the few universal patterns that appears to hold true for most microbial communities is the “long-tailed” species abundance-distributions (Dumbrell *et al.*, 2010; Shoemaker *et al.*, 2017; Maček *et al.*, 2019), which is caused by the majority of microorganisms in a community being rare. The rarer taxa in microbial communities also tend to be the least widespread (Clark *et al.*, 2017; Lindh *et al.*, 2017; Meyer *et al.*, 2018; Shade & Stopnisek, 2019) and thus, only detecting the more abundant, widespread organisms would overestimate compositional similarity across communities, and

consequently, weaken distance-decay relationships due to the lower rate of turnover (Meyer *et al.*, 2018). Perhaps of more concern is that even with existing sequencing platforms, our surveys of environmental microbial communities still miss taxa that are vanishingly rare in the environment, such as extremophiles that persist in non-extreme habitats (Low-Décarie *et al.*, 2016). The ability of common species to reflect ecological patterns of the wider community is debated (Galand *et al.*, 2009; Heino & Soininen, 2010; van Dorst *et al.*, 2014) and is linked to a wider debate on the ecological importance of rare species that is far beyond the scope of this work (e.g. Gaston, 2012). However, rare microorganisms are well known to be of critical importance in the context of environmental perturbations (Shade *et al.*, 2014; Low-Décarie *et al.*, 2016) and in providing ecosystem processes (e.g. sulfate-reduction in peat soils, Hausmann *et al.*, 2016; and anaerobic ammonia-oxidation in river sediments Lansdown *et al.*, 2016) and as a result, ignoring them may further distance biogeographic patterns from ecosystem-level processes.

Against expectation, we observed no clear differences in distance-decay relationships using different similarity metric types, and differences between specific metrics were minimal. Distance-decay relationships based on the weighted Unifrac distance and the Raup-Crick index were weaker than those based on other metrics. The Raup-Crick index is less influenced by concurrent changes in species richness between communities, and as such is a more pure reflection of shifts in β-diversity (Chase *et al.*, 2011). Consequently, by removing the potentially confounding effects of richness differences, the Raup-Crick index will likely result in more variable estimates of similarity between communities, which would lead to weaker distance-decay relationships.

Phylogenetic metrics, such as Unifrac, cluster communities at a lower resolution, as two communities can be closely genetically related, yet distinct at fine taxonomic resolutions (e.g. species or strain-level). For example, Bryant *et al.* (2008) found that Unifrac similarity

was approximately three times higher than the compositional similarity of the same set of bacterial communities. Further, phylogenetic metrics may be inappropriate in less phylogenetically diverse environments (e.g. extreme systems) where phylogenetic diversity can be largely constrained to one taxon (e.g. the haloarchaea in hypersaline environments), leaving few "phylogenetic degrees of freedom" left to separate communities (Fukuyama, 2019). However, this does not account for the observed difference between weighted and unweighted versions of the Unifrac index, the former of which accounts for species' relative abundance data, whilst the latter is binary (presence/absence based). A criticism of the weighted Unifrac index is that too much weight is placed on abundant taxa (Chen *et al.*, 2012). As abundant species are generally more widespread, placing too much weight on abundant taxa would have the effect of making communities appear artificially similar, exacerbating the effects of using a phylogenetic metric. As we observed no difference between binary and abundance-based compositional indices, the differences observed with weighted Unifrac appear to be the result of combining phylogenetic and weighted indices. We therefore suggest that weighted phylogenetic metrics may underestimate microbial biogeographic patterns, unless appropriate weight is given to rare and abundant taxa (Chen *et al.*, 2012).

Our analysis of 452 microbial distance-decay relationships also revealed the overwhelming preference of microbial ecologists to use classic dissimilarity indices such as the Bray-Curtis (n = 218), Jaccard (n = 49), Sørensen (n = 42) indices. These choices undoubtedly reflect a wider trend in ecology as a whole, however, it is pertinent to draw attention to more recently developed metrics that may be more appropriate given the properties of microbial datasets and the hypotheses being tested. Biotic interactions are drivers of microbial β-diversity (Hanson *et al.*, 2012), yet classic dissimilarity metrics do not account for co-occurrence information in communities. To this end, a new family of metrics described by Schmidt *et al.* (2017) include information on the average interactions of the taxa present, thus providing a

novel approach to integrating co-occurrence data into distance-decay relationships. Microbiome sequencing data also have several characteristics that may be problematic in the analysis of community (dis)similarities. For example, the non-biological variance of sample sizes in sequence datasets can result in statistical artefacts that confound biogeographic relationships (Baselga, 2007). Here, modifications made to some classic indices by Chao *et al.* (2005) reduce the sensitivity of these indices to variable sample sizes by accounting for unobserved species, thus reducing the need for post-sequencing normalisation of sample sizes (McMurdie & Holmes, 2014). Furthermore, "fuzzy logic"-based similarity indices are able to reduce the impact of false-absences or -presences on estimates of β-diversity, which is beneficial for microbial ecology studies where rarefaction may induce false-absences, and taxonomic assignment errors or contamination may lead to false-presences. Additionally, most high-throughput sequence datasets are compositional. Compositionality occurs as the arbitrary total number of sequences per sample imposed by the sequencing machine causes species counts (abundances) to be dependent on each other (e.g. if species A increases in abundance, species B and C will appear relatively less abundant, even if their absolute abundance hasn't changed). Binary indices should be suitable as occurrences (presence/absences) are not affected by compositionality, unless increases in the abundance of one or more species cause others to drop below the detection limit, in which case fuzzy indices may be appropriate. Alternatively, metrics such as the Aitchison distance perform well when appropriate (centered log-ratio) transformations are applied to counts (Gloor *et al.*, 2017), or recently developed metrics such as the Rank Bias Overlap index show promise for analysing similarity between communities based on species abundance ranks (Webber *et al.*, 2010). Finally, many similarity metrics have been shown to merge compositional turnover (replacement of species) and nestedness (whereby communities are subsets of one another), thereby blurring the contribution of distinct ecological processes to total community (dis)similarity. To combat this, modified versions of

classic indices such as Jaccard, Sorensen, and Bray-Curtis have been developed, allowing the partitioning of community similarity metrics into their turnover and nestedness components (Baselga, 2010; Podani & Schmera, 2011). We echo the call of Green and Bohannan (2006) for microbial ecologists to exercise more care in their choice of dissimilarity metrics, especially as many of these new metrics are implemented in popular and freely accessible software, such as R (e.g. Baselga and Orme, 2012).

Overall, our analyses revealed that methodological factors explain more variation in microbial distance-decay relationships than ecological context, but that both sets of factors alter our perception of this biogeographic pattern. Given the importance of methodological factors in determining the strength of microbial biogeographic patterns, it is intuitive to recommend standardising approaches across studies in order to minimise the statistical signals associated with methodological variance. However, our results show variance due to differing ecological contexts would still hinder drawing generalisable relationships across studies. Instead, we suggest that tailoring methodological choices towards specific ecological contexts may enhance generalisable relationships in microbial ecology. For instance, in searching for consistent relationships between ocean waters and terrestrial soils, it would be unrealistic to sample both at the same spatial grain and extent, as the heterogeneity in the physicochemical environment, and dispersal processes of their microbial communities, are fundamentally different. Similarly, we should not necessarily expect the relationships between soils and river sediments to be comparable, as microorganisms in soils can feasibly disperse in any direction, whereas in rivers or streams dispersal would be largely constrained by flow direction. Consequently, tailoring methodological approaches, such as the sampling design and/or (geographical) distance measure, to better reflect the environmental heterogeneity and dispersal dynamics between contrasting ecological contexts may enable us to negotiate the hierarchy of interacting factors that obscure macroecological patterns in microbial communities.

Conclusions

Our meta-analysis of >450 microbial distance-decay relationships revealed that factors related to the eco-environmental context within which a study was conducted, as well as the methodology of the study, jointly influence quantification of this classic biogeographic pattern. Against expectation, factors related to molecular methodology had relatively little effect on distance-decay relationships, whilst choice of dissimilarity metric was more important, highlighting that even after using robust, modern molecular methods, analytical choices have the power to obscure or enhance biogeographic patterns. We detected clear relationships between microbial distance-decay relationships and various contextual and methodological variables, yet combining these variables explained only a modest amount of variation in our dataset. This lack of explanatory power indicates that microbial biogeographic patterns depend on a number of contextual variables beyond those analysed here. In future, we suggest that microbial ecologists should place greater emphasis on quantifying habitat connectivity to better understand the dispersal processes that lead to spatial patterns such as the distance-decay relationship. Additionally, we recommend that experiment designs and data-collection strategies should be replicated spatially, taxonomically, temporally, or any combination therein where possible (e.g. Meyer *et al.*, 2018; Alzarhani *et al.*, 2019; Zinger *et al.*, 2019), facilitating a more generalised understanding of the variation in spatial microbial community patterns. The question of whether microbial communities show spatial patterns such as distance-decay relationships should be laid to rest; disentangling the web of ecological and environmental drivers that shape these patterns is the next challenge in microbial biogeography.

Data Availability Statement

Full raw data analysed in this manuscript are provided in Table S1. Full raw data and R code used in this manuscript will be uploaded to the Dryad data repository upon acceptance of this article.

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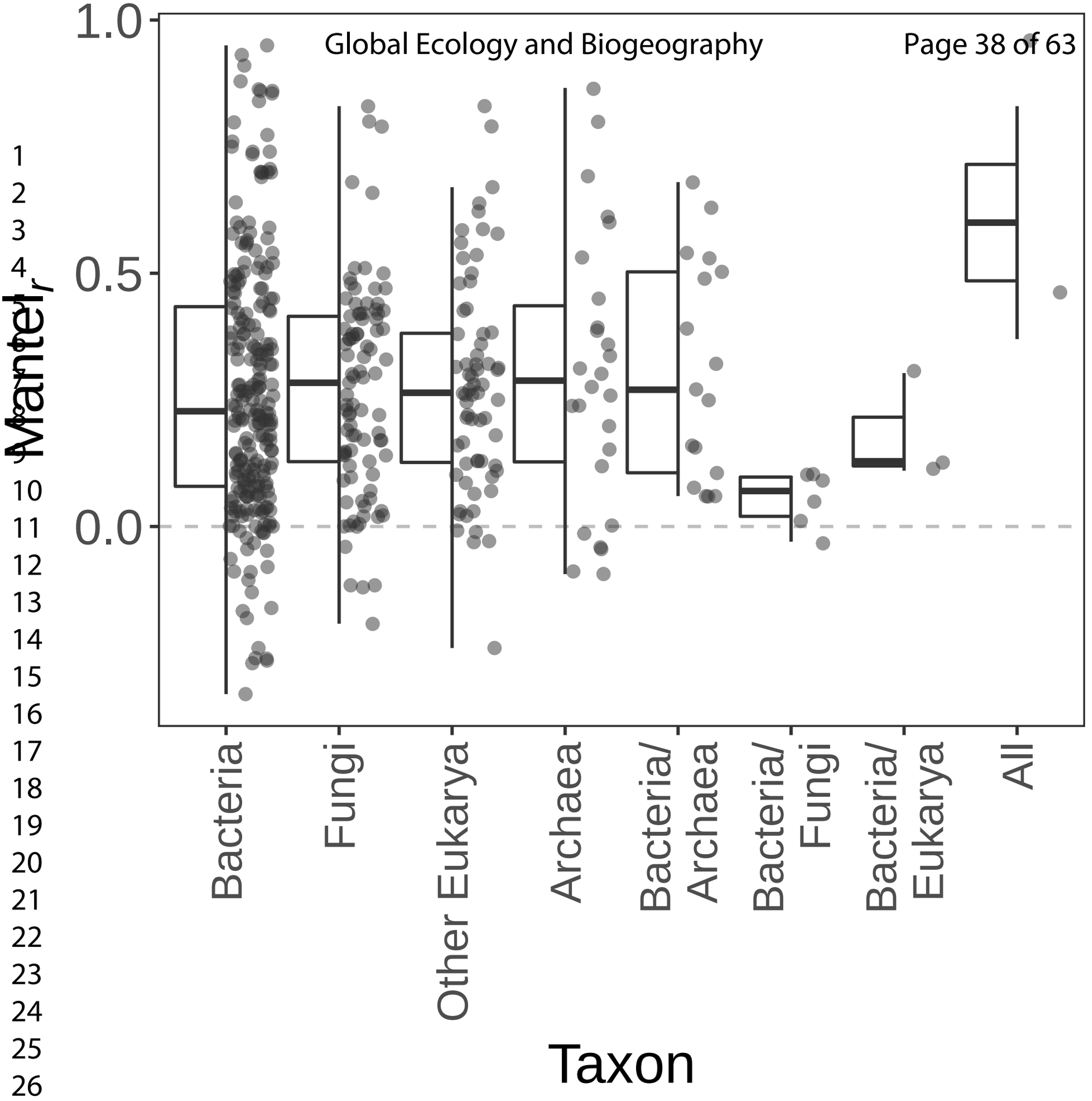
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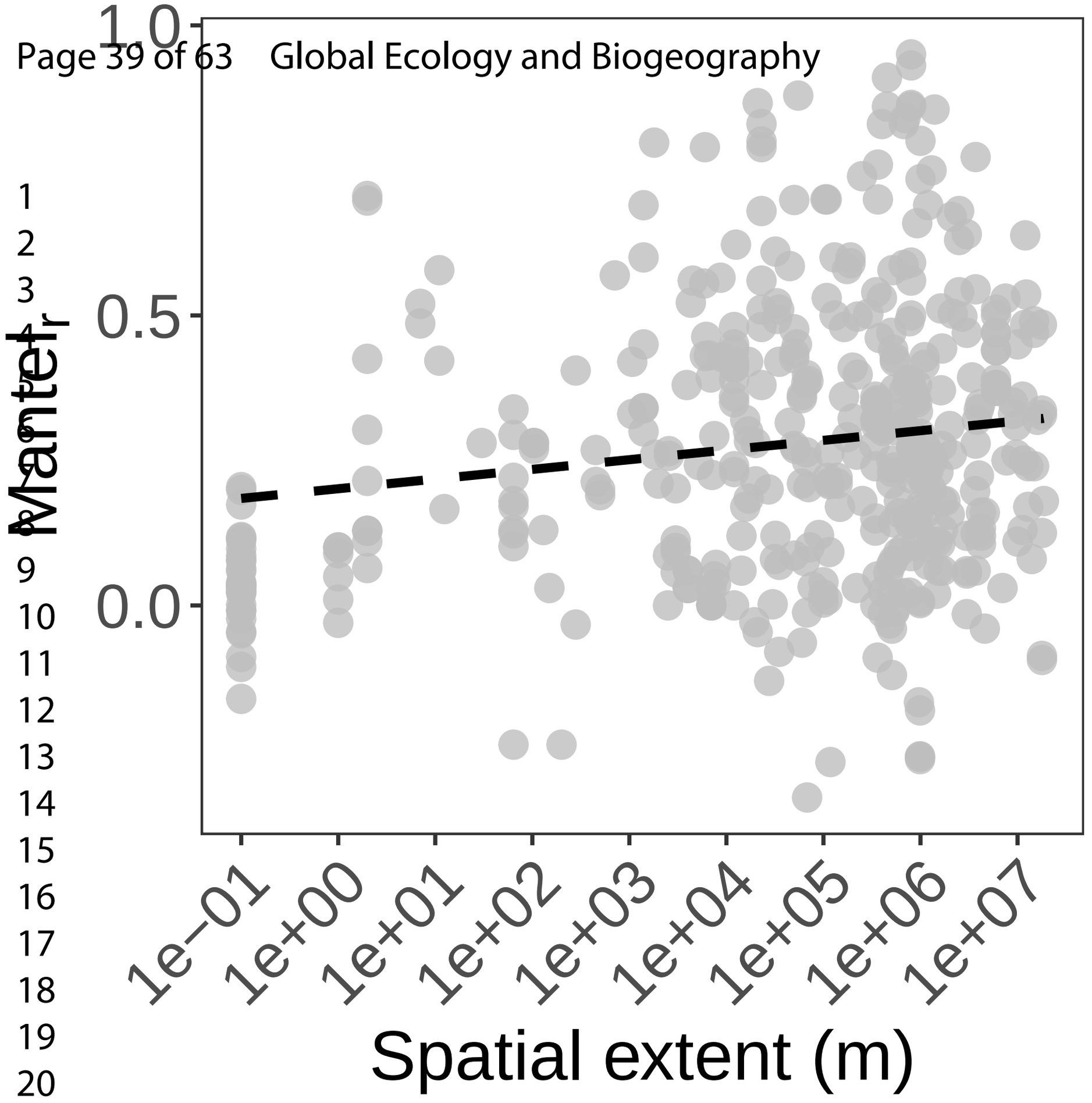
Bacteria
Fungi
Other Eukarya
Archaea
Bacteria/ Archaea
Bacteria/ Fungi
Bacteria/ Eukarya
All
Taxon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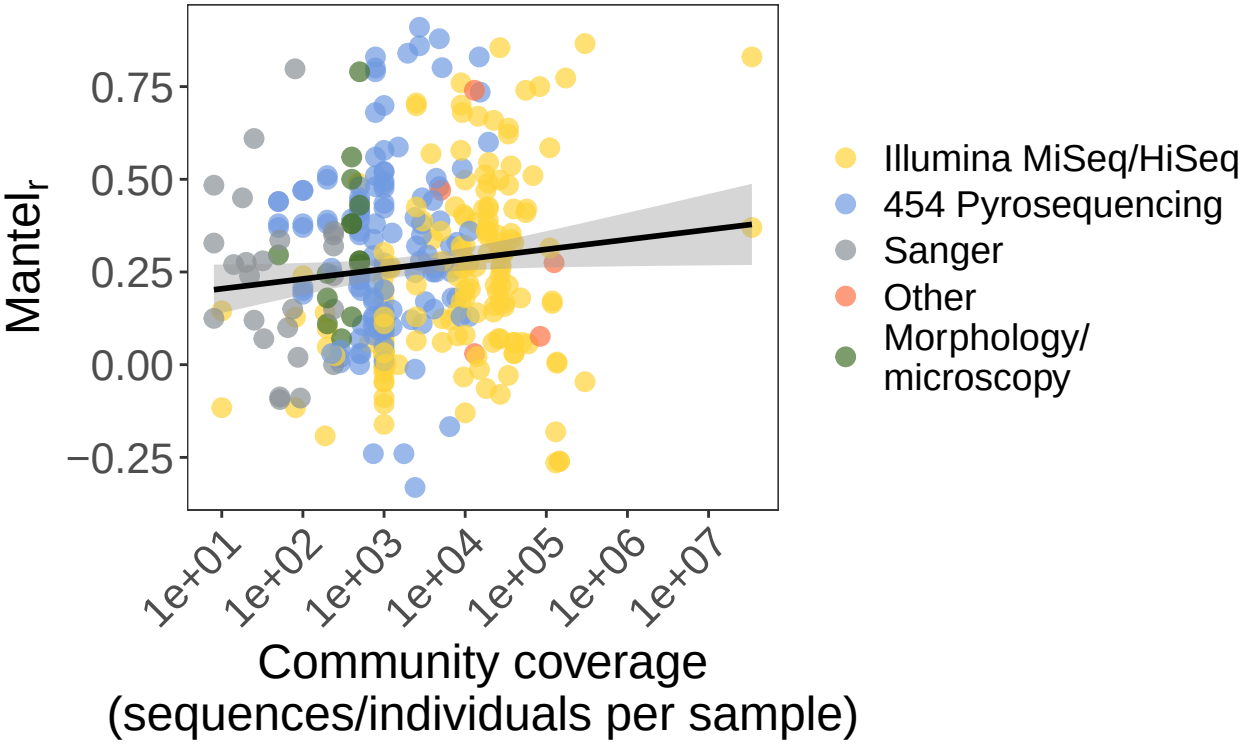
1e+06
1e+07
Spatial extent (m)

A


Mantel$_r$
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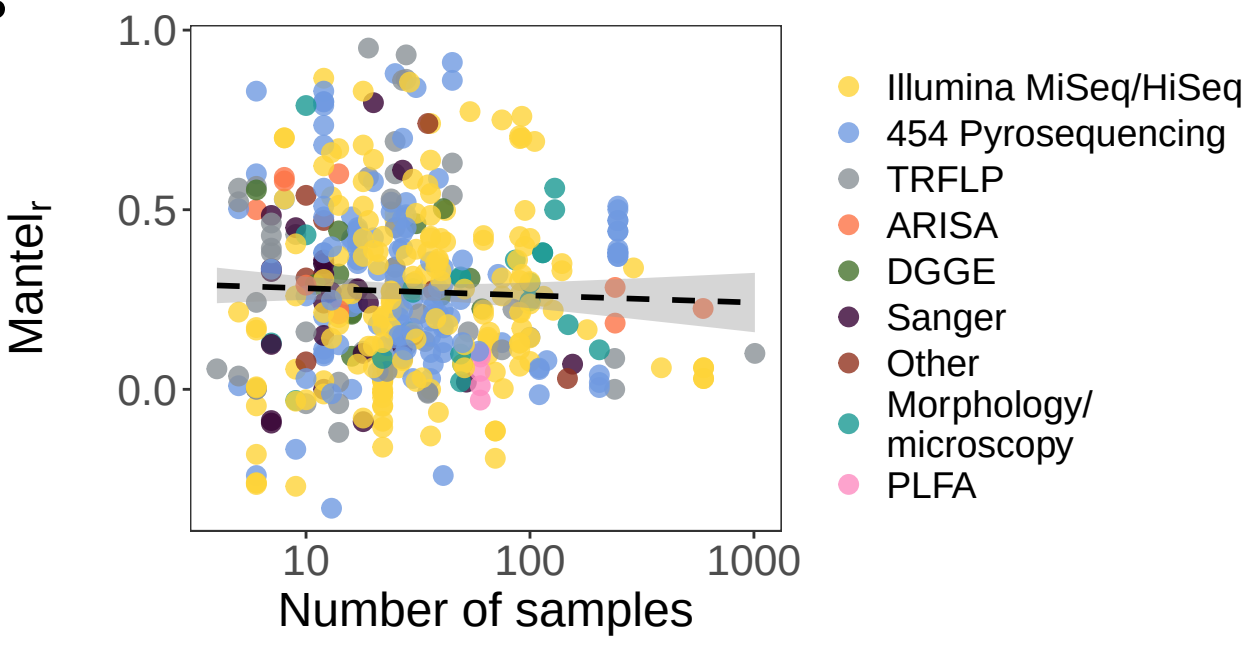
0.50
0.25
0.00
−0.25
1e+01
1e+02
1e+03
1e+04
1e+05
1e+06
1e+07
Community coverage
(sequences/individuals per sample)
Illumina MiSeq/HiSeq
454 Pyrosequencing
Sanger
Other
Morphology/
microscopy

B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10
100
1000
Number of samples
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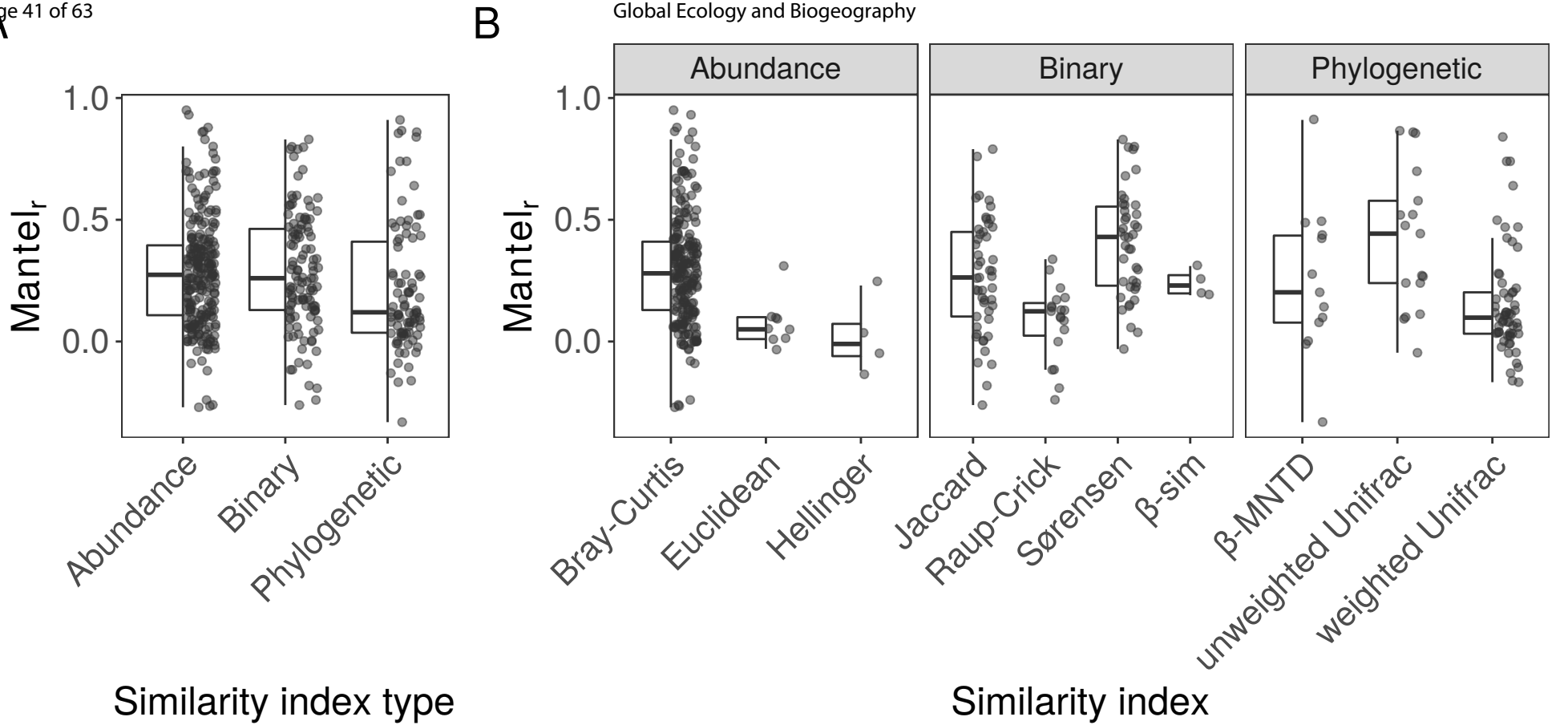
TRFLP
ARISA
DGGE
Sanger
Other
Morphology/
microscopy
PLFA


A
B
Mantel$_r$
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0.5
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Abundance
Binary
Phylogenetic
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Euclidean
Hellinger
Jaccard
Raup-Crick
Sørensen
β-sim
β-MNTD
unweighted Unifrac
weighted Unifrac
Similarity index

Supplementary Information

Title: What drives study-dependent differences in distance-decay relationships of microbial communities?

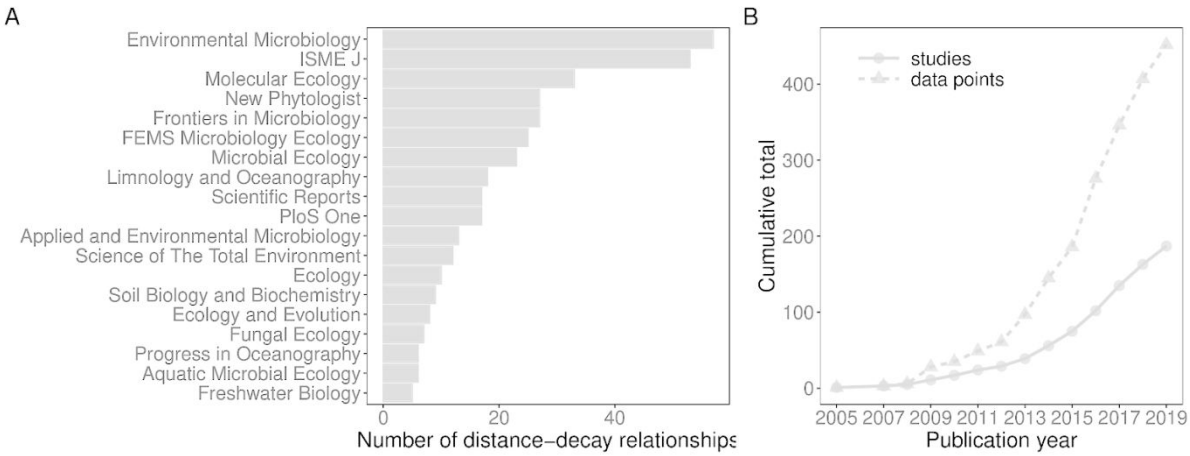

Figure S1. (A) The number of distance-decay relationships obtained from each journal. Only journals with five or more distance-decay relationships are shown for clarity. (B) The cumulative total of suitable studies (circles) and distance-decay relationships (triangles) according to publication year.

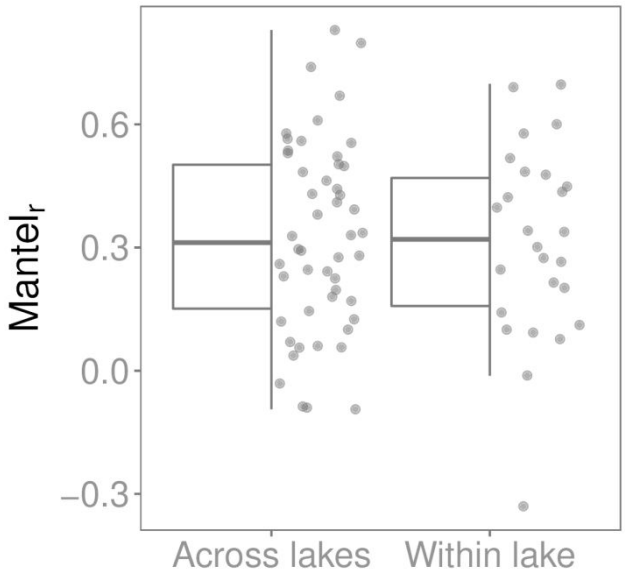

Figure S2. A comparison of the strength of microbial distance-decay relationships from studies conducted within single lakes compared to those across multiple lakes.

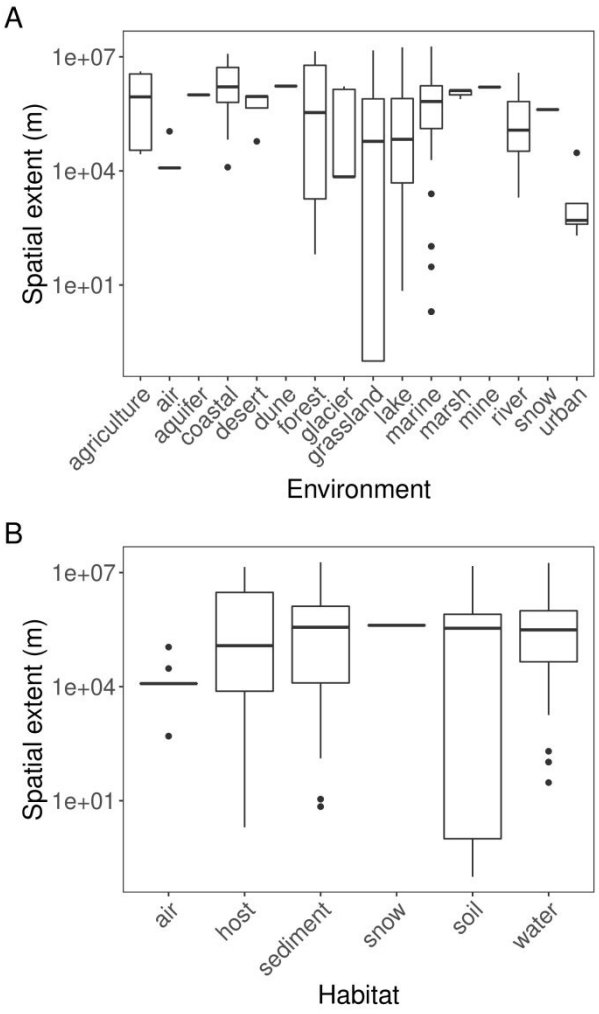

Figure S3. A comparison of the spatial extents of distance-decay relationships across environments and habitats. Note that the y-axis is plotted on a $\log_{10}$ scale for clarity.

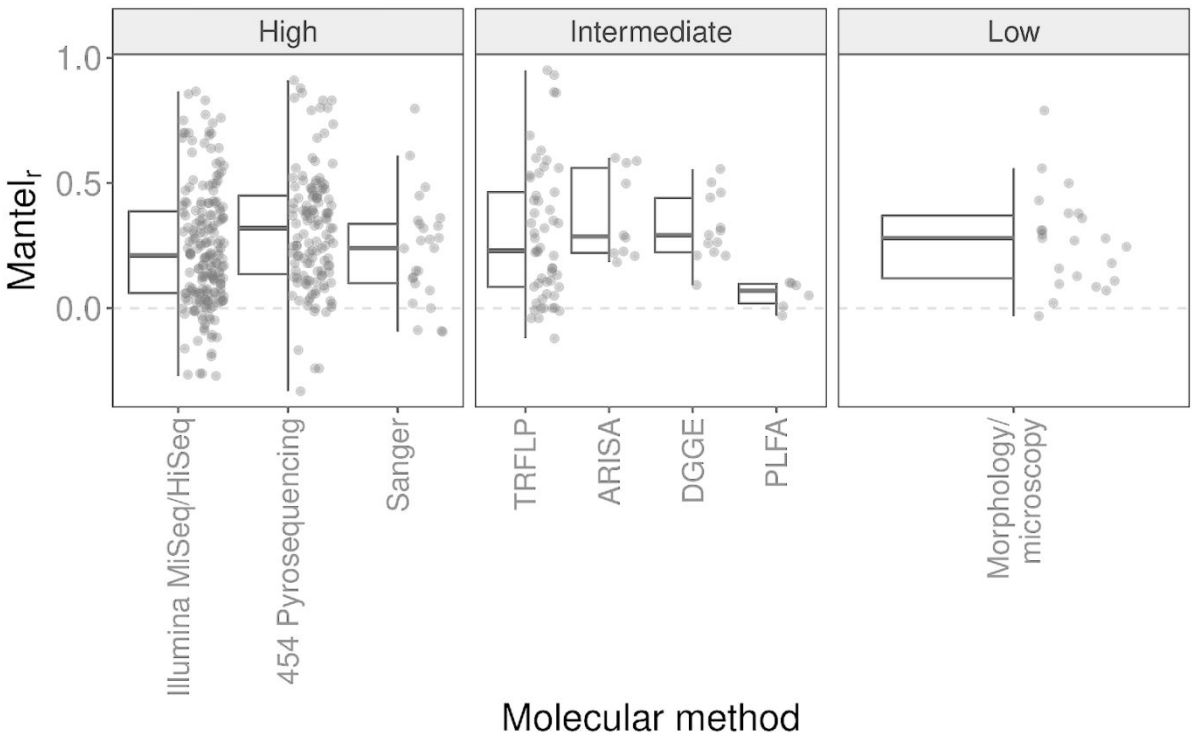

Figure S4. Mantel correlation coefficients of distance-decay relationships where the microbial community was characterised using molecular or morphological methods of varying resolution. High Mantel correlation coefficients indicate a stronger distance-decay relationship. Abbreviated molecular techniques are defined as follows: (TRFLP = Terminal Restriction Fragment Length Polymorphism; ARISA = Automated Ribosomal Intergenic Spacer Analysis; DGGE = Denaturing Gradient Gel Electrophoresis; PLFA = PhosphoLipid Fatty Acid analysis).

Table S1. Metadata extracted from each study confirmed to be suitable for inclusion in this study. Data will be deposited to the Dryad data repository upon acceptance of this manuscript.

Table S2. Full details of all statistical results obtained. For categoric variables, likelihood ratio tests were used to assess the statistical significance of variables, and post-hoc Tukey HSD tests to identify significantly different groups. For continuous variables, Wald tests were used to assess the statistical significance of variables.

Model	Covariate	Coefficient	Test-statistic	Degrees of freedom (used, residual)	Explained variation	P-value

~ taxon	Taxon	NA	F = 0.99	5, 441	R^2 = 0.01	0.43
~ environment	Environment	NA	*F* = 3.1872	10, 432	R^2 = 0.07	< 0.001
~ environment * habitat	Environment	NA	*F* = 3.29	9, 420	R^2 = 0.12	< 0.001
	Habitat	NA	*F* = 6.65	3, 420		< 0.001
	Environment * Habitat	NA	*F* = 1.93	4, 420		0.10
~ within/between lakes	within_lake	NA	*F* = 0.11	1, 74	R^2 = < 0.01	0.743
~ (random intercept | study) + $\log_{10}$(scale)	$\log_{10}$(scale)	0.29	*T* = 8.47	1, 435	*Marginal* R^2 = 0.02 Conditional R^2 = 0.48	< 0.0001
	Intercept	0.02	*T* = 1.58			0.11
~ resolution	Resolution	NA	*F* = 0.56	2, 449	<0.01	0.57
~ method	Method	NA	*F* = 1.97	7, 437	0.03	0.06
~ (random intercept | study) + $\log_{10}$(community coverage)	Community coverage	0.06	*T = 2.73*	1, 337	*Marginal* R^2 = 0.04 Conditional R^2 = 0.57	< 0.01
	Intercept	0.13	*T* = 1.55			0.12
~ similarity index	Similarity index	NA	*F* = 7.24	9, 424	R^2 = 0.13	< 0.001
~ correlation type	Correlation type	NA	*F* = 2.47	1, 146	R^2 = 0.02	0.12

title	year	journal	method	markerGen	nSamples	seqDepth	simIndex	otuDefinitio
Plant divers	2017	Soil Biology	illumina		290	4000	bray	0.97
The differer	2017	Catena	pyrosequer	16S	45	2735	u_unifrac	0.97
The differer	2017	Catena	pyrosequer	16S	45	2735	betaMNTD	0.97
Bacterial D	2017	Microbial E	pyrosequer	16S	75	11248	bray	0.97
Similar com	2017	Limnology a	pyrosequer	16S	21	7909	bray	0.97
Similar com	2017	Limnology a	pyrosequer	16S	21	7909	bray	0.97
Latitudinal v	2017	Marine Eco	TRFLP	16S	45	NA	bray	band
Latitudinal v	2017	Marine Eco	TRFLP	16S	45	NA	bray	band
Latitudinal v	2017	Marine Eco	illumina	16S	18	9226	bray	97
Temporal a	2017	PloS One	pyrosequer	16S	6	19358	bray	97
Temporal a	2017	PloS One	ARISA	ITS	6	NA	bray	band
Regional va	2016	Scientific R	illumina	16S	34	10000	bray	97
Microbial eu	2016	Environmer	DGGE	18S	40	NA	bray	band
Microbial eu	2016	Environmer	illumina	18S	14	14437	bray	NA
Decoupling	2016	Science	illumina	metagenom	139	24644	bray	0.99
Decoupling	2016	Science	illumina	metagenom	139	24644	bray	0.99
Geographic	2016	Frontiers in	pyrosequer	16S	27	400	bray	0.97
Forest area	2016	Ecology	pyrosequer	28S	36	500	bray	0.97
Forest area	2016	Ecology	illumina	ITS	36	1500	bray	0.97
Diversity, B	2016	Frontiers in	pyrosequer	16S	9	6442	w_unifrac	0.97
The local e	2016	Environmer	sanger	ITS	52	87	Horn-moris	0.97
Biogeograp	2016	FEMS Micr	TRFLP	16S	18	NA	bray	band
Biogeograp	2016	FEMS Micr	TRFLP	16S	34	NA	bray	band
Biogeograp	2016	FEMS Micr	TRFLP	16S	53	NA	bray	band
Biogeograp	2016	FEMS Micr	TRFLP	16S	28	NA	bray	band
Taxon inter	2016	Molecular E	Ion Torrent	16S	37	124582	bray	0.97
Biogeograp	2016	Frontiers in	illumina	16S	115	7300	bray	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	70	200	Raup-Crick	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	70	10	Raup-Crick	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	70	81	Raup-Crick	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	70	188	Raup-Crick	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	65	200	Raup-Crick	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	65	10	Raup-Crick	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	65	81	Raup-Crick	0.97
Ectomycorr	2016	Molecular E	illumina	ITS	65	188	Raup-Crick	0.97
Interactions	2016	ISME	illumina	16S	386	50323	bray	0.97
Patterns an	2016	ISME	pyrosequer	18S	28	4783	bray	1
Patterns an	2016	ISME	morphology	NA	86	NA	bray	NA
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmer	illumina	16S	22	1000	w_unifrac	0.97

Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Spatial scal	2016	Environmei	illumina	16S	22	1000	w_unifrac	0.97
Fungal com	2016	Scientific R	pyrosequer	ITS	30	3433	bray	0.97
Microbial eu	2016	Molecular E	illumina	18S	13	36744	sorensen	1
Bacterial cc	2016	Environmei	pyrosequer	16S	12	2900	bray	0.97
Bacterial cc	2016	Environmei	pyrosequer	16S	12	2900	bray	0.97
Biogeograp	2016	Microbial E	illumina	16S	91	27719	theta	0.97
Biogeograp	2016	Microbial E	illumina	16S	91	27719	jaccard	0.97
Salinity sha	2016	Scientific R	illumina	16S	9	60000	bray	0.97
Contrasting	2016	New Phytol	illumina	16S	26	660	bray	0.97
Contrasting	2016	New Phytol	illumina	ITS	26	970	bray	0.98
Diversity ar	2016	PloS One	pyrosequer	16S	27	6883	jaccard	0.97
Archaeal ar	2016	PloS One	TRFLP	16S	239	NA	Raup-Crick	band
Archaeal ar	2016	PloS One	TRFLP	16S	239	NA	Raup-Crick	band
Decoupled	2016	Environmei	illumina	16S	75	83008	bray	0.97
Decoupled	2016	Environmei	TRFLP	dsrA	75	NA	bray	band
The roles o	2016	Hydrobiolo	morpholog	NA	204	200	bray	NA
Scale-depe	2015	FEMS Micr	illumina	16S	54	173260	bray	0.97
Environmei	2015	Journal of F	morpholog	NA	29	NA	bray	NA
Spatiotemp	2015	Applied Mic	DGGE	16S	16	NA	jaccard	band
Spatiotemp	2015	Applied Mic	DGGE	16S	16	NA	jaccard	band
Spatiotemp	2015	Applied Mic	DGGE	18S	16	NA	jaccard	band
Spatiotemp	2015	Applied Mic	DGGE	18S	16	NA	jaccard	band
Depth shap	2015	Environmei	pyrosequer	18S	39	1500	sorensen	0.97
Bacterial bi	2015	Environmei	illumina	16S	95	10000	w_unifrac	0.97
Bacterial bi	2015	Environmei	illumina	16S	95	10000	jaccard	0.97
Soil bacteri	2015	Environmei	Pac-Bio	16S	12	5000	w_unifrac	0.95
Quantifying	2015	ISME	pyrosequer	26S	36	1257	jaccard	0.98
Quantifying	2015	ISME	pyrosequer	26S	36	1257	jaccard	0.98
Quantifying	2015	ISME	pyrosequer	26S	36	1257	jaccard	0.98
The biogeo	2015	ISME	illumina	16S	42	26322	bray	0.97
Biogeograp	2015	Microbial E	illumina	16S	12	300000	u_unifrac	0.98
Biogeograp	2015	Microbial E	illumina	16S	6	300000	u_unifrac	0.98
Quantifying	2015	Environmei	DGGE	16S	31	NA	jaccard	band
Bacterial ar	2015	Microbial E	pyrosequer	16S	12	5192	bray	0.97
Bacterial ar	2015	Microbial E	pyrosequer	16S	12	15320	bray	0.97
Seasonal c	2014	Soil Biolog	plfa	NA	60	NA	euclidean	band
Seasonal c	2014	Soil Biolog	plfa	NA	60	NA	euclidean	band
Seasonal c	2014	Soil Biolog	plfa	NA	60	NA	euclidean	band
Seasonal c	2014	Soil Biolog	plfa	NA	60	NA	euclidean	band
Seasonal c	2014	Soil Biolog	plfa	NA	60	NA	euclidean	band
Seasonal c	2014	Soil Biolog	plfa	NA	60	NA	euclidean	band
A continent	2015	New Phytol	pyrosequer	ITS	247	50	sorensen	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247	50	bray	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247	50	Morisita-ho	0.95

A continent	2015	New Phytol	pyrosequer	ITS	247		50	jaccard	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		100	sorensen	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		100	bray	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		100	Morisita-ho	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		100	jaccard	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		200	sorensen	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		200	bray	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		200	Morisita-ho	0.95
A continent	2015	New Phytol	pyrosequer	ITS	247		200	jaccard	0.95
Catchment-	2015	ISME	pyrosequer	16S	23		2179	bray	NA
Biogeograp	2015	Aquatic Mic	pyrosequer	16S	37		500	bray	0.97
Biogeograp	2015	Aquatic Mic	pyrosequer	16S	37		500	bray	0.85
Aquatic bac	2015	Internationa	sanger	16S	20		80	sorensen	0.97
Testing the	2015	Aquatic Mic	morphology	NA	50		300	bray	NA
Bacterial ar	2015	Aquatic Mic	pyrosequer	16S	8		9200	bray	0.97
Plant divers	2015	Ecology Le	illumina	16S	25		100	bray	0.97
Plant divers	2015	Ecology Le	illumina	16S	25		18000	bray	0.97
Plant divers	2015	Ecology Le	illumina	ITS	25		485	bray	0.97
Environmer	2014	Fungal Eco	pyrosequer	18S	21		1000	euclidean	0.97
Environmer	2014	Fungal Eco	pyrosequer	18S	5		1000	euclidean	0.97
A phylogen	2014	Molecular E	sanger	16S	18		65	u_unifrac	0.97
Biogeograp	2014	Proceeding	illumina	16S	596		40000	bray	0.97
Biogeograp	2014	Proceeding	illumina	16S	596		40000	jaccard	0.97
Biogeograp	2014	Proceeding	illumina	18S	596		40000	bray	0.97
Biogeograp	2014	Proceeding	illumina	18S	596		40000	jaccard	0.97
Distance-D	2014	PloS One	TRFLP	16S	25	NA		sorensen	band
Distance-D	2014	PloS One	TRFLP	mcrA	25	NA		sorensen	band
Distance-D	2014	PloS One	TRFLP	16S	25	NA		sorensen	band
Distance-D	2014	PloS One	TRFLP	16S	25	NA		bray	band
Distance-D	2014	PloS One	TRFLP	mcrA	25	NA		bray	band
Distance-D	2014	PloS One	TRFLP	16S	25	NA		bray	band
Spore dispe	2014	New Phytol	pyrosequer	ITS	16		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	16		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	16		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	16		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	16		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	17		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	17		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	17		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	17		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	17		500	bray	0.97
Spore dispe	2014	New Phytol	pyrosequer	ITS	17		500	bray	0.97
Soil fungal	2014	Molecular E	pyrosequer	ITS	204		289	jaccard	NA
Soil fungal	2014	Molecular E	pyrosequer	ITS	204		289	betaMNTD	NA
Soil fungal	2014	Molecular E	pyrosequer	ITS	204		289	betaMPD	NA
Spatial Sca	2014	Microbial E	pyrosequer	16S	30		520	bray	0.97
Spatial Sca	2014	Microbial E	pyrosequer	16S	26		520	bray	0.97
SSU rDNA	2014	PloS One	TRFLP	18S	35	NA		bray	band
SSU rDNA	2014	PloS One	TRFLP	18S	35	NA		bray	band
Pyrosequer	2014	Journal of A	pyrosequer	16S	6		1759	bray	0.97
Neotropical	2014	Environmer	pyrosequer	16S	5		4400	jaccard	0.97
Diversity ar	2014	Applied an	pyrosequer	16S	49		4000	bray	0.97
The spatial	2014	Ecology	TRFLP	16S	16	NA		bray	band
Drivers sha	2014	Molecular E	pyrosequer	16S	30		4346	bray	0.97
Differentiati	2014	Environmer	sanger	mcrA	27		25	w_unifrac	1

Differentiati	2014	Environmer	sanger	mcrA	27		25	bray		1
Biogeograp	2014	Applied an	pyrosequer	16S	25		4800	bray		0.97
Host rules:	2013	FEMS Micr	TRFLP	16S	28	NA		bray	band	
Host rules:	2013	FEMS Micr	TRFLP	16S	28	NA		bray	band	
Host rules:	2013	FEMS Micr	TRFLP	16S	27	NA		bray	band	
Host rules:	2013	FEMS Micr	TRFLP	16S	27	NA		bray	band	
Host rules:	2013	FEMS Micr	TRFLP	16S	19	NA		bray	band	
Host rules:	2013	FEMS Micr	TRFLP	16S	19	NA		bray	band	
Environmer	2013	Ecosphere	TRFLP	16S	32	NA		bray	band	
Dispersal ir	2013	ISME	pyrosequer	ITS	44		100	beta_sim		0.97
Dispersal ir	2013	ISME	pyrosequer	ITS	36		100	beta_sim		0.97
The biogeo	2013	ISME	DGGE	ITS	61	NA		NA	band	
Phylogenet	2013	ISME	pyrosequer	16S	12		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	12		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	27		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	27		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	20		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	28		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	24		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	25		1000	u_unifrac		0.97
Phylogenet	2013	ISME	pyrosequer	16S	12		1000	betaMNTD		0.97
Phylogenet	2013	ISME	pyrosequer	16S	12		1000	betaMNTD		0.97
Phylogenet	2013	ISME	pyrosequer	16S	27		1000	betaMNTD		0.97
Phylogenet	2013	ISME	pyrosequer	16S	27		1000	betaMNTD		0.97
Phylogenet	2013	ISME	pyrosequer	16S	20		1000	betaMNTD		0.97
Phylogenet	2013	ISME	pyrosequer	16S	28		1000	betaMNTD		0.97
Phylogenet	2013	ISME	pyrosequer	16S	24		1000	betaMNTD		0.97
Phylogenet	2013	ISME	pyrosequer	16S	25		1000	betaMNTD		0.97
Geographic	2013	FEMS Micr	TRFLP	18S	24	NA		bray	band	
Geographic	2013	FEMS Micr	pyrosequer	18S	6		14890	bray		0.95
Biogeograp	2013	ISME	pyrosequer	16S	39		2800	bray		0.97
Contempor	2013	ISME	pyrosequer	16S	59		540	w_unifrac		0.97
Microbial bi	2013	Aquatic Mic	DGGE	16S	14	NA		bray	band	
Microbial bi	2013	Aquatic Mic	DGGE	18S	14	NA		bray	band	
Distance D	2013	PloS One	morphology	NA	114		400	bray	NA	
Distance D	2013	PloS One	morphology	NA	129		400	bray	NA	
Distance D	2013	PloS One	morphology	NA	114		400	simpson	NA	
Distance D	2013	PloS One	morphology	NA	129		400	simpson	NA	
Geographic	2012	Environmer	pyrosequer	16S	17		4000	u_unifrac		0.97
Dispersal li	2012	Ecology an	TRFLP	16S	12	NA		bray	band	
Dispersal li	2012	Ecology an	TRFLP	16S	12	NA		bray	band	
Dispersal li	2012	Ecology an	sanger	16S	12		239	u_unifrac		0.97
Dispersal li	2012	Ecology an	sanger	16S	12		239	bray		0.9
Dispersal li	2012	Ecology an	sanger	16S	12		239	bray		0.93
Dispersal li	2012	Ecology an	sanger	16S	12		239	bray		0.95
Dispersal li	2012	Ecology an	sanger	16S	12		239	bray		0.97
Dispersal li	2012	Ecology an	sanger	16S	12		239	bray		0.99
Bacterial as	2012	Biogeoscie	pyrosequer	16S	16		6687	bray		0.97
Biogeograp	2011	Molecular E	pyrosequer	16S	31		1959	w_unifrac		0.97
Ecology an	2012	Frontiers in	TRFLP	16S	84	NA		bray	band	
Bacterial cc	2011	Freshwater	DGGE	16S	41	NA		jaccard	band	
The bacteri	2011	Environmer	TRFLP	16S	1010	NA		bray	band	
Disentangli	2011	Limnology a	morphology	NA	100		200	sorensen	NA	
Disentangli	2011	Limnology a	morphology	NA	100		50	sorensen	NA	
Disentangli	2011	Limnology a	TRFLP	16S	100	NA		sorensen	band	
Metacomm	2011	Ecology	TRFLP	16S	14	NA		hellinger	band	

Metacomm	2011	Ecology	TRFLP	ITS	14	NA		hellinger	band	
Metacomm	2011	Ecology	TRFLP	16S	14	NA		hellinger	band	
Metacomm	2011	Ecology	TRFLP	ITS	14	NA		hellinger	band	
Possible int	2011	ISME	TRFLP	16S	6	NA		bray	band	
Possible int	2011	ISME	TRFLP	16S	6	NA		bray	band	
Possible int	2011	ISME	TRFLP	16S	6	NA		bray	band	
Evidence o	2010	Ecology	sanger	ITS	155		33	bray		0.97
The ecolog	2010	Environmer	pyrosequer	16S	119		750	w_unifrac		0.97
Community	2010	Freshwater	sanger	amoA	17		20	w_unifrac		0.98
Life history	2010	Molecular E	phylochip	16S	10	NA		bray	NA	
Life history	2010	Molecular E	phylochip	16S	10	NA		bray	NA	
Biogeograp	2010	Journal of E	morphology	NA	7		400	sorensen	NA	
Microbial B	2009	Applied and	sanger	16S	7		52	jaccard		0.99
Microbial B	2009	Applied and	sanger	16S	7		52	jaccard		0.97
Microbial B	2009	Applied and	sanger	16S	7		52	jaccard		0.95
Microbial B	2009	Applied and	sanger	16S	7		8	jaccard		0.99
Microbial B	2009	Applied and	sanger	16S	7		8	jaccard		0.97
Microbial B	2009	Applied and	sanger	16S	7		8	jaccard		0.95
Relationshi	2009	Journal of F	morphology	NA	9	NA		sorensen	NA	
Biogeograp	2009	Environmer	ARISA	16S	593	NA		sorensen	band	
Bar-Coded	2009	Applied and	pyrosequer	16S	39		484	bray	NA	
Contrasting	2009	Limnology a	TRFLP	16S	7	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	9	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	4	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	7	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	6	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	5	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	14	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	5	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	7	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	7	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	6	NA		sorensen	band	
Contrasting	2009	Limnology a	TRFLP	16S	5	NA		sorensen	band	
Bacterial co	2009	Freshwater	DGGE	16S	6	NA		jaccard	band	
Relationshi	2008	Microbial E	TRFLP	16S	10	NA		jaccard	band	
Relationshi	2008	Microbial E	TRFLP	16S	10	NA		jaccard	band	
Water mass	2008	Limnology a	DGGE	18S	54	NA		euclidean	band	
Phylogenet	2007	Applied and	sanger	16S	18		93	bray		0.99
Environmer	2007	Ecology	TRFLP	16S	23	NA		bray	band	
Does ecosy	2005	Ecology	DGGE	16S	11	NA		jaccard	band	
Large varia	2016	ISME	pyrosequer	18S	25		6625	bray		0.97
Microhabita	2015	FEMS Micr	illumina	16S	33		1000	w_unifrac		0.97
Methanoge	2012	Biogeocher	sanger	16S	30		75	sorensen		0.97
Environmer	2011	Microbial E	sanger	nifH	13		14	rao		0.99
[FeFe]-hydı	2010	ISME	sanger	hydA	9		18	rao	NA	
Phyllospher	2016	Microbial E	pyrosequer	ITS	12		784	sorensen		0.9
Phyllospher	2016	Microbial E	pyrosequer	ITS	12		784	sorensen		0.95
Phyllospher	2016	Microbial E	pyrosequer	ITS	12		784	sorensen		0.97
Phyllospher	2016	Microbial E	pyrosequer	ITS	12		784	sorensen		0.99
Phyllospher	2016	Microbial E	pyrosequer	16S	12		784	sorensen		0.9
Phyllospher	2016	Microbial E	pyrosequer	16S	12		784	sorensen		0.95
Phyllospher	2016	Microbial E	pyrosequer	16S	12		784	sorensen		0.97
Phyllospher	2016	Microbial E	pyrosequer	16S	12		784	sorensen		0.99
Stochastic (	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97
Stochastic (	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97
Stochastic (	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97

Stochastic	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97
Stochastic	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97
Stochastic	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97
Stochastic	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97
Stochastic	2016	ISME	pyrosequer	ITS	14		738	Raup-Crick		0.97
Stochastic	2016	ISME	pyrosequer	ITS	41		738	Raup-Crick		0.97
Eutrophicat	2014	Freshwater	morphology	NA	10		500	jaccard	NA	
Eutrophicat	2014	Freshwater	morphology	NA	10		500	jaccard	NA	
High diaton	2019	Marine Bio	morphology	NA	30		500	bray	NA	
High diaton	2019	Marine Bio	morphology	NA	30		500	bray	NA	
High diaton	2019	Marine Bio	morphology	NA	30		500	bray	NA	
Microbial di	2019	Freshwater	illumina	16S	36		55890	w_unifrac		0.97
Microbial di	2019	Freshwater	illumina	16S	42		55890	w_unifrac		0.97
The local e	2019	Catena	illumina	ITS	24		27000	bray		0.97
The local e	2019	Catena	illumina	ITS	24		27000	u_unifrac		0.97
Depth and	2019	Science of	illumina	16S	20		22000	bray		0.97
Depth and	2019	Science of	illumina	18S	20		6600	bray		0.99
Diversity Di	2019	Frontiers in	illumina	18S	21		13595	bray		0.97
Diversity Di	2019	Frontiers in	illumina	18S	15		13595	bray		0.97
Ammonia C	2019	Applied and	sanger	amoA	19		22	w_unifrac		0.95
Ammonia C	2019	Applied and	sanger	amoA	17		32	w_unifrac		0.95
Stochastic	2019	Microbiome	illumina	18S	30		110394	bray		0.97
Stochastic	2019	Microbiome	illumina	18S	30		110394	bray		0.97
Integrated	2019	Frontiers in	illumina	18S	22		7532	bray		0.97
Integrated	2019	Frontiers in	morphology	NA	22	NA		bray	NA	
Not by Sali	2019	Soil Scienc	illumina	ITS	31		30000	bray		0.97
Microbiota	2019	Internationa	Ion Torrent	16S	10		84144	bray		0.94
Large-scale	2019	Microbiolog	illumina	16S	35	NA		bray		0.97
Biogeograp	2019	Science of	illumina	16S	24		11020	bray		0.97
Biogeograp	2019	Science of	illumina	16S	24		11020	w_unifrac		0.97
Biogeograp	2019	Science of	illumina	16S	24		11020	u_unifrac		0.97
Functional	2019	Frontiers in	illumina	18S	180		30890	bray		0.97
On-Site An	2019	Applied and	Ion Torrent	16S	147		13051	bray		0.98
Upland Soil	2019	Science of	illumina	pmoA	30		30381	bray		0.82
Community	2019	Water	illumina	16S	100		16854	bray		0.97
Community	2019	Water	illumina	18S	100		28993	bray		0.97
Phosphorus	2019	FEMS Micr	illumina	16S	9		9563	bray		0.97
Phosphorus	2019	FEMS Micr	illumina	16S	9		9563	bray		0.97
Microbial E	2019	Microbial E	illumina	16S	12		15000	bray		0.97
Microbial E	2019	Microbial E	illumina	ITS	12		9000	bray		0.97
Microbial E	2019	Microbial E	illumina	ITS	12		250	bray		0.97
Historical F	2019	Frontiers in	pyrosequer	16S	10		226	jaccard		0.97
Historical F	2019	Frontiers in	pyrosequer	16S	10		226	bray		0.97
Molecular c	2019	Acta Ocear	pyrosequer	18S	37		100	bray		0.97
Distinct bio	2018	Science of	illumina	16S	50		25571	bray		0.97
How bacter	2018	Molecular E	illumina	16S	105	NA		bray		0.97
Influence o	2018	Scientific R	pyrosequer	ITS	7	NA		bray		0.97
THE EFFE	2018	Journal of F	pyrosequer	rbcL	72		2515	bray	NA	
Multiple pro	2018	Scientific R	illumina	16S	92		8918	bray		0.97
Multiple pro	2018	Scientific R	illumina	16S	92		8918	bray		0.97
Multiple pro	2018	Scientific R	illumina	16S	92		8918	jaccard		0.97
Multiple pro	2018	Scientific R	illumina	16S	92		8918	jaccard		0.97
Association	2018	Ecography	morphology	NA	49	NA		bray	NA	
Association	2018	Ecography	morphology	NA	49	NA		jaccard	NA	
Association	2018	Ecography	morphology	NA	49	NA		bray	NA	
Association	2018	Ecography	morphology	NA	49	NA		jaccard	NA	

Co-occurre	2018	Microbes a	illumina	16S	8	NA	bray		0.97
Co-occurre	2018	Microbes a	illumina	16S	9	NA	bray		0.97
Soil bacteri	2018	Applied Soi	illumina	16S	100	8047	bray		0.97
Soil bacteri	2018	Applied Soi	illumina	16S	100	8047	w_unifrac		0.97
Soil bacteri	2018	Applied Soi	illumina	16S	100	8047	betaMNTD		0.97
Biogeograp	2018	Science of	illumina	16S	51	5209	bray		0.97
Biogeograp	2018	Science of	illumina	16S	51	5209	bray		0.97
Biogeograp	2018	Science of	illumina	16S	51	5209	bray		0.97
Vertical and	2018	Scientific R	illumina	16S	6	135317	bray		0.97
Vertical and	2018	Scientific R	illumina	16S	6	145541	bray		0.97
Vertical and	2018	Scientific R	illumina	16S	6	118482	bray		0.97
Vertical and	2018	Scientific R	illumina	16S	6	130664	bray		0.97
Vertical and	2018	Scientific R	illumina	16S	6	135317	jaccard		0.97
Vertical and	2018	Scientific R	illumina	16S	6	145541	jaccard		0.97
Vertical and	2018	Scientific R	illumina	16S	6	118482	jaccard		0.97
Vertical and	2018	Scientific R	illumina	16S	6	130664	jaccard		0.97
Why do mic	2018	ISME	illumina	16S	35	3790	canberra		0.97
Plant growt	2018	Land Degra	illumina	16S	21	18844	bray		0.97
Ecological a	2018	Oecologia	morphology	NA	148	200	sorensen	NA	
Biogeograp	2018	Applied and	pyrosequer	16S	50	8887	bray		0.987
Biogeograp	2018	Applied and	pyrosequer	16S	50	11273	bray		0.987
Environmer	2018	Scientific R	pyrosequer	ITS	30	3229	sorensen		0.97
Ammonia-C	2018	Frontiers in	pyrosequer	amoA	26	4900	w_unifrac		0.85
Ammonia-C	2018	Frontiers in	pyrosequer	amoA	26	4100	w_unifrac		0.85
Contrasting	2018	Journal of M	illumina	16S	8	NA	bray		0.97
Contrasting	2018	Journal of M	illumina	16S	8	NA	bray		0.97
Facultative	2018	New Phytol	illumina	ITS	43	48363	bray		0.97
The diversit	2018	Environmer	illumina	18S	36	34239	bray		0.97
The diversit	2018	Environmer	illumina	18S	36	34239	bray		0.97
Distribution	2018	PeerJ	illumina	16S	14	10000	w_unifrac		0.97
Soil organic	2018	Functional	illumina	16S	36	19460	bray		0.97
Impact of E	2018	Internationa	illumina	16S	20	NA	w_unifrac		0.97
Highlighting	2018	Molecular E	illumina	ITS	36	19317	bray		0.97
Highlighting	2018	Molecular E	illumina	ITS	36	19317	bray		0.97
Highlighting	2018	Molecular E	illumina	ITS	28	19317	bray		0.97
Highlighting	2018	Molecular E	illumina	ITS	40	19317	bray		0.97
Patterns an	2017	Frontiers in	illumina	18S	9	9513	bray		0.97
Linking bac	2017	Progress in	ARISA	ISR	10	NA	jaccard	NA	
Linking bac	2017	Progress in	ARISA	ISR	8	NA	jaccard	NA	
Linking bac	2017	Progress in	ARISA	ISR	14	NA	jaccard	NA	
Linking bac	2017	Progress in	ARISA	ISR	8	NA	jaccard	NA	
Linking bac	2017	Progress in	ARISA	ISR	14	NA	jaccard	NA	
Linking bac	2017	Progress in	ARISA	ISR	14	NA	jaccard	NA	
Is microbial	2017	Environmer	illumina	ITS	18	57346	bray		0.97
Is microbial	2017	Environmer	illumina	ITS	18	68490	bray		0.97
Is microbial	2017	Environmer	illumina	16S	17	27106	bray		0.97
Is microbial	2017	Environmer	illumina	16S	18	27106	bray		0.97
Deep nirS a	2017	Environmer	Ion Torrent	nirS	35	13000	w_unifrac		0.88
Elevation, s	2017	Fungal Eco	pyrosequer	ITS	27	NA	bray		0.97
Elevation, s	2017	Fungal Eco	pyrosequer	ITS	27	NA	bray		0.97
Distinct sea	2017	Fungal Eco	pyrosequer	18S	27	880	bray		0.99
Biogeograp	2017	Global Eco	illumina	16S	75	27554	beta_sim		0.97
Biogeograp	2017	Global Eco	illumina	16S	75	26578	beta_sim		0.99
Rhizospher	2017	Journal of E	illumina	ITS	19	NA	w_unifrac		0.97
Rhizospher	2017	Journal of E	illumina	ITS	19	NA	w_unifrac		0.97
Distinct mic	2017	Molecular E	illumina	ITS	31	14000	bray		0.97

Distinct mic	2017	Molecular E	illumina	16S		31		19300	bray	0.97
Distinct mic	2017	Molecular E	illumina	ITS		31		14000	bray	0.97
Distinct mic	2017	Molecular E	illumina	16S		31		19300	bray	0.97
Environmer	2017	Molecular E	illumina	ITS		40		39721	bray	0.97
Environmer	2017	Molecular E	illumina	ITS		40		39721	jaccard	0.97
The Patterr	2017	Frontiers in	illumina	ITS		62	NA		bray	0.97
The Patterr	2017	Frontiers in	illumina	16S		62	NA		bray	0.97
The Patterr	2017	Frontiers in	illumina	ITS		62	NA		beta_bray	0.97
The Patterr	2017	Frontiers in	illumina	16S		62	NA		beta_bray	0.97
Patterns an	2017	Frontiers in	illumina	18S		12		33996	bray	0.97
Patterns an	2017	Frontiers in	illumina	18S		12		33996	bray	0.97
Patterns an	2017	Frontiers in	illumina	18S		10		33996	bray	0.97
City-scale c	2017	Microbiome	illumina	18S		76		1058	jaccard	0.97
Climate cor	2017	FEMS Micr	illumina	16S		88		5000	bray	0.97
Microbial di	2017	FEMS Micr	illumina	16S		36		10000	w_unifrac	0.97
Microbial di	2017	FEMS Micr	illumina	16S		14		10000	w_unifrac	0.97
Microbial di	2017	FEMS Micr	illumina	16S		27		10000	w_unifrac	0.97
Biogeograp	2017	Molecular E	illumina	16S		38		36920	bray	0.97
Biogeograp	2017	Molecular E	illumina	16S		38		36920	bray	0.97
Relative rol	2017	Fungal Eco	ARISA	ITS		240	NA		bray	NA
Relative rol	2017	Fungal Eco	ARISA	ITS		240	NA		bray	NA
Transition b	2017	Environmer	illumina	18S		24	61	774	sorensen	1
Distance de	2017	Environmer	illumina	ITS		127	NA		bray	0.95
Ecological S	2017	Frontiers in	pyrosequer	ITS		36		4184	bray	0.97
Biogeograp	2017	FEMS Micr	illumina	16S		29		26800	u_unifrac	0.97
Land scale	2017	Environmer	illumina	16S		14	NA		bray	0.97
Land scale	2017	Environmer	illumina	arsM		14		17434	bray	0.97
Geographic	2017	Genes and	pyrosequer	16S		28		2951	jaccard	0.97
Geographic	2017	Genes and	pyrosequer	16S		28		2951	w_unifrac	0.97
High taxonc	2017	Nature Eco	illumina	16S		22	NA		bray	0.99
Distinct Bio	2017	mSystems	pyrosequer	16S		110	NA		bray	0.97
Distinct Bio	2017	mSystems	pyrosequer	16S		110	NA		bray	0.97
Distinct Bio	2017	mSystems	pyrosequer	18S		110	NA		bray	0.97
Fungal com	2017	Soil Biology	illumina	ITS		13		22466	bray	0.97
Fungal com	2017	Soil Biology	illumina	ITS		13		22466	bray	0.97
Floral organ	2019	Molecular E	illumina	16S		16		1200	bray	0.97
Floral organ	2019	Molecular E	illumina	16S	NA			1200	bray	0.97
Environmer	2019	Science of	illumina	16S		20		11612	bray	0.97
Environmer	2019	Science of	illumina	ITS		20		3018	bray	0.97
Abundant a	2018	Frontiers in	illumina	16S		66		22938	bray	0.97
Ecological p	2018	Water Res	illumina	16S		5		23429	bray	NA
Benthic Alg	2018	Frontiers in	illumina	23S		18		8843	bray	0.97
Phylum-Lev	2018	Geomicrob	illumina	16S		38		24805	bray	0.97
Community	2017	FEMS Micr	pyrosequer	16S		13		2411	betaMNTD	0.97
Community	2017	FEMS Micr	pyrosequer	16S		13		2411	betaMNTD	0.97
Community	2017	FEMS Micr	pyrosequer	16S		13		2411	bray	0.97
Community	2017	FEMS Micr	pyrosequer	16S		13		2411	bray	0.97
Soil Proper	2019	Frontiers in	illumina	16S		39		18182	bray	0.97
Soil Proper	2019	Frontiers in	illumina	16S		39		18182	beta_bray	0.97
Soil Proper	2019	Frontiers in	illumina	16S		39		18182	nes_bray	0.97
Intensive al	2019	Environmer	illumina	metagenon		18	34192561		Mash	NA
Intensive al	2019	Environmer	illumina	metagenon		18	34192561		Mash	NA
Highly struc	2018	ISME	illumina	16S		90		2500	sorensen	0.97
Highly struc	2018	ISME	illumina	UPA		90		2500	sorensen	0.97
Highly struc	2018	ISME	illumina	tufA		90		1000	sorensen	0.98
Highly struc	2018	ISME	illumina	16S		90		2500	bray	0.97

Highly struc	2018	ISME	illumina	UPA	90	2500	bray	0.97
Highly struc	2018	ISME	illumina	tufA	90	1000	bray	0.98
Highly struc	2018	ISME	illumina	16S	90	2500	w_unifrac	0.97
Highly struc	2018	ISME	illumina	UPA	90	2500	w_unifrac	0.97
Highly struc	2018	ISME	illumina	tufA	90	1000	w_unifrac	0.98

taxa	habitat	environmer	within_lake	spatialExte	mantelR	pValue	correlation
fungi	soil	grassland	NA	4000	0.338	0.001	NA
bacteria	soil	grassland	NA	451	0.86	0.001	NA
bacteria	soil	grassland	NA	451	0.91	0.001	NA
bacteria	soil	dune	NA	1700	0.13	0.35	pearson
bacteria	water	lake	across	600	0.18	0.001	spearman
bacteria	water	lake	across	600	0.33	0.001	spearman
Bac_arch	host	marine	NA	2500	0.63	0.001	NA
Bac_arch	host	marine	NA	2500	0.54	0.001	NA
Bac_arch	host	marine	NA	2500	0.68	0.001	NA
bacteria	host	marine	NA	130	0.6	0.01	spearman
bacteria	host	marine	NA	130	0.5	0.01	spearman
Bac_arch	sediment	marine	NA	200	0.322	0.001	pearson
eukarya	water	lake	across	2100	0.26	0.002	NA
eukarya	water	lake	across	2100	0.67	0.003	NA
bacteria	water	marine	NA	9000	0.35	0.004	spearman
bacteria	water	marine	NA	9000	0.33	0.001	spearman
archaea	soil	agriculture	NA	3400	0.3931	0.001	NA
fungi	host	forest	NA	7	0.03	0.23	NA
fungi	host	forest	NA	7	0	0.56	NA
bacteria	sediment	marine	NA	964	-0.167	0.726	NA
fungi	host	grassland	NA	1450	0.02	0.32	NA
bacteria	water	marine	NA	4200	0.106	0.161	NA
bacteria	water	marine	NA	4200	0.133	0.028	NA
bacteria	host	marine	NA	4200	0.16	0.001	NA
bacteria	host	marine	NA	4200	0.12	0.015	NA
bacteria	sediment	glacier	NA	1664	0.275	0.001	NA
bacteria	soil	forest	NA	NA	0.259	0.001	pearson
fungi	host	forest	NA	NA	0.048	0.301	NA
fungi	host	forest	NA	NA	-0.116	0.834	NA
fungi	host	forest	NA	NA	-0.116	0.832	NA
fungi	host	forest	NA	NA	-0.192	0.947	NA
fungi	soil	forest	NA	NA	0.097	0.177	NA
fungi	soil	forest	NA	NA	0.145	0.155	NA
fungi	soil	forest	NA	NA	0.128	0.151	NA
fungi	soil	forest	NA	NA	0.14	0.116	NA
bacteria	water	lake	across	1700	0.06	0.1	NA
eukarya	water	marine	NA	163	0.48	0.01	pearson
eukarya	water	marine	NA	163	0.36	0.01	pearson
bacteria	soil	grassland	NA	0.0001	-0.009	0.912	NA
bacteria	soil	grassland	NA	0.0001	0.199	0.011	NA
bacteria	soil	grassland	NA	0.0001	0.001	0.995	NA
bacteria	soil	grassland	NA	0.0001	0.023	0.779	NA
bacteria	soil	grassland	NA	0.0001	-0.009	0.904	NA
bacteria	soil	grassland	NA	0.0001	-0.048	0.568	NA
bacteria	soil	grassland	NA	0.0001	0.204	0.008	NA
bacteria	soil	grassland	NA	0.0001	0.034	0.644	NA
bacteria	soil	grassland	NA	0.0001	0.079	0.407	NA
bacteria	soil	grassland	NA	0.0001	0.112	0.198	NA
bacteria	soil	grassland	NA	0.0001	0.036	0.649	NA
bacteria	soil	grassland	NA	0.0001	0.116	0.159	NA
bacteria	soil	grassland	NA	0.0001	-0.089	0.31	NA
bacteria	soil	grassland	NA	0.0001	0.032	0.703	NA
bacteria	soil	grassland	NA	0.0001	0.027	0.858	NA
bacteria	soil	grassland	NA	0.0001	0.034	0.666	NA
bacteria	soil	grassland	NA	0.0001	0.059	0.498	NA

bacteria	soil	grassland	NA	0.0001	0.098	0.261	NA
bacteria	soil	grassland	NA	0.0001	0.063	0.428	NA
bacteria	soil	grassland	NA	0.0001	0.021	0.819	NA
bacteria	soil	grassland	NA	0.0001	-0.106	0.166	NA
bacteria	soil	grassland	NA	0.0001	-0.045	0.602	NA
bacteria	soil	grassland	NA	0.0001	0.086	0.334	NA
bacteria	soil	grassland	NA	0.0001	0.174	0.016	NA
bacteria	soil	grassland	NA	0.0001	-0.023	0.79	NA
bacteria	soil	grassland	NA	0.0001	0.038	0.598	NA
bacteria	soil	grassland	NA	0.0001	0.039	0.649	NA
bacteria	soil	grassland	NA	0.0001	0.076	0.4	NA
bacteria	soil	grassland	NA	0.0001	0.118	0.223	NA
bacteria	soil	grassland	NA	0.0001	-0.161	0.072	NA
fungi	sediment	marine	NA	997.47	0.2959	0.001	NA
eukarya	water	lake	across	12270	0.536	0.00002	NA
bacteria	soil	grassland	NA	923	0.35	0.004	NA
bacteria	soil	grassland	NA	923	0.38	0.002	NA
bacteria	host	forest	NA	0.45	0.213	0.001	NA
bacteria	host	forest	NA	0.45	0.268	0.001	NA
bacteria	sediment	lake	across	467	0.056	NA	NA
bacteria	soil	grassland	NA	1530	0.06	NA	NA
fungi	soil	grassland	NA	1530	0.23	0.002	NA
bacteria	sediment	marine	NA	18700	0.18	0.017	spearman
bacteria	host	marine	NA	2.5	0.086	0.01	spearman
archaea	host	marine	NA	2.5	0	NA	spearman
bacteria	sediment	marsh	NA	1300	0.75	0.001	NA
bacteria	sediment	marsh	NA	1300	0.11	0.001	NA
eukarya	water	marine	NA	1500	0.11	NA	spearman
bacteria	soil	grassland	NA	3700	0.773	0.001	pearson
eukarya	water	river	NA	1150	0.16	0.005	NA
bacteria	water	river	NA	115	0.092	0.315	NA
bacteria	water	river	NA	115	0.209	0.022	NA
eukarya	water	river	NA	115	0.212	0.02	NA
eukarya	water	river	NA	115	0.263	0.004	NA
eukarya	sediment	marine	NA	670	0.587	0.001	NA
bacteria	water	marine	NA	225	0.498	0.001	NA
bacteria	water	marine	NA	225	0.398	0.001	NA
bacteria	soil	forest	NA	500	0.47	0.01	NA
fungi	host	agriculture	NA	885.49	########	0.1114	NA
fungi	host	agriculture	NA	885.49	########	0.0502	NA
fungi	soil	agriculture	NA	885.49	########	0.0006	NA
bacteria	water	lake	across	2700	0.498	0.01	spearman
archaea	water	river	NA	21	0.866	0.001	NA
archaea	sediment	river	NA	21	-0.046	NA	NA
bacteria	water	river	NA	380	0.461	0.001	NA
archaea	sediment	marine	NA	1000	0.801	0.001	NA
bacteria	sediment	marine	NA	1000	0.735	0.001	NA
bac_fungi	soil	grassland	NA	0.001	0.1	0.05	pearson
bac_fungi	soil	grassland	NA	0.001	0.05	NA	pearson
bac_fungi	soil	grassland	NA	0.001	-0.03	NA	pearson
bac_fungi	soil	grassland	NA	0.001	0.09	0.05	pearson
bac_fungi	soil	grassland	NA	0.001	0.01	NA	pearson
bac_fungi	soil	grassland	NA	0.001	0.1	0.05	pearson
fungi	host	forest	NA	6000	0.44	0.001	NA
fungi	host	forest	NA	6000	0.38	0.001	NA
fungi	host	forest	NA	6000	0.37	0.001	NA

fungi	host	forest	NA	6000	0.44	0.001	NA
fungi	host	forest	NA	6000	0.47	0.001	NA
fungi	host	forest	NA	6000	0.38	0.001	NA
fungi	host	forest	NA	6000	0.37	0.001	NA
fungi	host	forest	NA	6000	0.47	0.001	NA
fungi	host	forest	NA	6000	0.5	0.001	NA
fungi	host	forest	NA	6000	0.39	0.001	NA
fungi	host	forest	NA	6000	0.38	0.001	NA
fungi	host	forest	NA	6000	0.51	0.001	NA
bacteria	water	river	NA	90	0.1214	0.048	NA
bacteria	water	lake	across	1200	0.23	0.001	NA
bacteria	water	lake	across	1200	0.07	0.019	NA
bacteria	water	lake	across	1.8	0.7979	0.04117	pearson
eukarya	water	river	NA	500	0.07	0.446	NA
Bac_arch	water	marine	NA	7500	0.529	0.1	spearman
archaea	soil	grassland	NA	14800	0.24	0.021	spearman
bacteria	soil	grassland	NA	14800	0.47	0.001	spearman
fungi	soil	grassland	NA	14800	0.49	0.001	spearman
fungi	soil	grassland	NA	360	0.05	0.87	NA
fungi	air	air	NA	110	0.01	0.36	NA
bacteria	water	lake	across	72	0.1	0.31	NA
Bac_arch	soil	grassland	NA	4	0.06	0.001	spearman
Bac_arch	soil	grassland	NA	4	0.06	0.001	spearman
eukarya	soil	grassland	NA	4	0.03	0.02	spearman
eukarya	soil	grassland	NA	4	0.03	0.025	spearman
archaea	sediment	lake	within	1.4	0.45	0.03	NA
archaea	sediment	lake	within	1.4	0.6	0.001	NA
bacteria	sediment	lake	within	1.4	0.34	0.006	NA
archaea	sediment	lake	within	1.4	0.3	0.005	NA
archaea	sediment	lake	within	1.4	0.69	0.001	NA
bacteria	sediment	lake	within	1.4	0.34	0.006	NA
fungi	air	air	NA	12	0	0.51	NA
fungi	air	air	NA	12	0.23	0.04	NA
fungi	air	air	NA	12	0.41	0.04	NA
fungi	air	air	NA	12	0.48	0.01	NA
fungi	air	air	NA	12	0.42	0.04	NA
fungi	air	air	NA	12	0.24	0.08	NA
fungi	air	air	NA	12	0.39	0.01	NA
fungi	air	air	NA	12	0.35	0.03	NA
fungi	air	air	NA	12	0.41	0.03	NA
fungi	air	air	NA	12	0.36	0.02	NA
fungi	air	air	NA	12	0.44	0	NA
fungi	air	air	NA	12	0.45	0.02	NA
fungi	soil	grassland	NA	100	0.019	0.22	pearson
fungi	soil	grassland	NA	100	0.005	0.577	pearson
fungi	soil	grassland	NA	100	0.04	0.12	pearson
bacteria	soil	forest	NA	0.15	0.03	0.05	spearman
bacteria	soil	forest	NA	1300	0.2	NA	spearman
eukarya	water	marine	NA	540	-0.011	NA	NA
eukarya	water	marine	NA	540	-0.008	NA	NA
bacteria	water	urban	NA	0.2	-0.24	0.175	NA
Bac_arch	water	river	NA	290	0.50273	0.05	NA
Bac_arch	sediment	coastal	NA	1350	0.25	0.001	NA
bacteria	water	marine	NA	0.03	0.28	0.01	pearson
bacteria	water	marine	NA	500	0.2497	0.01	NA
archaea	sediment	lake	across	32	0.12	0.14	NA

archaea	sediment	lake	across	32	0.61	0.001	NA
bacteria	sediment	marine	NA	55	0.879	0.001	NA
bacteria	host	marine	NA	800	0.863	NA	NA
bacteria	host	marine	NA	800	0.931	NA	NA
bacteria	host	marine	NA	800	0.085	NA	NA
bacteria	host	marine	NA	800	0.86	NA	NA
bacteria	host	marine	NA	800	0.95	NA	NA
bacteria	host	marine	NA	800	0.591	NA	NA
bacteria	soil	desert	NA	60	0.21	0.006	NA
fungi	air	urban	NA	0.5	0.2	0.001	NA
fungi	air	urban	NA	0.5	0.19	0.003	NA
fungi	sediment	coastal	NA	4000	0.224	0.003	pearson
bacteria	sediment	lake	within	3	0.093	NA	spearman
bacteria	sediment	lake	within	3	0.112	NA	spearman
bacteria	sediment	lake	within	50	0.699	0.001	spearman
bacteria	water	lake	within	50	0.476	0.01	spearman
bacteria	sediment	lake	within	0.011	0.578	0.05	spearman
bacteria	sediment	lake	within	0.007	0.52	0.001	spearman
bacteria	sediment	river	NA	33	0.521	0.01	spearman
bacteria	sediment	lake	within	850	0.267	NA	spearman
bacteria	sediment	lake	within	3	0.099	NA	spearman
bacteria	sediment	lake	within	3	0.202	NA	spearman
bacteria	sediment	lake	within	50	0.435	0.001	spearman
bacteria	water	lake	within	50	0.275	0.01	spearman
bacteria	sediment	lake	within	0.011	0.422	0.001	spearman
bacteria	sediment	lake	within	0.007	0.486	0.001	spearman
bacteria	water	river	NA	33	0.494	0.001	spearman
bacteria	sediment	lake	within	850	0.143	NA	spearman
eukarya	water	lake	across	400	0.53	0.01	NA
eukarya	water	lake	across	400	0.83	0.05	NA
bacteria	water	lake	across	20	0.28	0.001	spearman
Bac_arch	NA	mine	NA	1600	0.106	0.072	spearman
bacteria	water	marine	NA	523	0.441	0.003	NA
eukarya	water	marine	NA	523	0.321	0.013	NA
eukarya	water	river	NA	800	0.38	0.001	NA
eukarya	water	river	NA	800	0.56	0.001	NA
eukarya	water	river	NA	800	0.38	0.001	NA
eukarya	water	river	NA	800	0.5	0.001	NA
bacteria	sediment	lake	across	1670	0.443	0.03	NA
bacteria	soil	forest	NA	343	0.35	0.022	spearman
bacteria	soil	forest	NA	343	0.32	0.027	spearman
bacteria	soil	forest	NA	343	0.24	0.064	spearman
bacteria	soil	forest	NA	343	0	0.479	spearman
bacteria	soil	forest	NA	343	0.15	0.186	spearman
bacteria	soil	forest	NA	343	0.36	0.043	spearman
bacteria	soil	forest	NA	343	0.35	0.036	spearman
bacteria	soil	forest	NA	343	0.32	0.031	spearman
bacteria	water	marine	NA	7700	0.25	0.04	NA
bacteria	water	marine	NA	700	0.84	0.0001	NA
bacteria	NA	aquifer	NA	1000	0.223	0.001	NA
bacteria	water	lake	across	2150	0.503	0.0001	NA
bacteria	soil	grassland	NA	1200	0.1	0.001	pearson
eukarya	water	lake	across	800	0.246	0.001	pearson
eukarya	water	lake	across	800	0.296	0.001	pearson
bacteria	water	lake	across	800	0.145	0.001	pearson
bacteria	soil	grassland	NA	508	0.23	0.007	NA

fungi	soil	grassland	NA	508	-0.12	NA		NA
bacteria	soil	grassland	NA	508	0.02		0.41	NA
fungi	soil	grassland	NA	508	-0.04	NA		NA
bacteria	sediment	glacier	NA	7	0.001		0.007	NA
bacteria	sediment	glacier	NA	7	0		0.392	NA
bacteria	sediment	glacier	NA	7	0.002		0.169	NA
fungi	host	forest	NA	7.8	0.07		0.001	NA
bacteria	host	forest	NA	14000	0.08		0.5	NA
archaea	water	lake	across	333.52	0.276		0.017	NA
bacteria	soil	forest	NA	350	0.54		0.007	NA
bacteria	soil	forest	NA	350	0.31		0.02	NA
eukarya	water	marine	NA	342	0.129		0.614	NA
archaea	water	lake	across	17845.5	0.336		0.116	NA
archaea	water	lake	across	17845.5	-0.094		0.473	NA
archaea	water	lake	across	17845.5	-0.087		0.486	NA
bacteria	water	lake	across	17845.5	0.125		0.166	NA
bacteria	water	lake	across	17845.5	0.484		0.0016	NA
bacteria	water	lake	across	17845.5	0.328		0.002	NA
eukarya	water	lake	across	480	-0.031		0.437	NA
bacteria	soil	grassland	NA	NA	0.225		0.001	NA
bacteria	water	river	NA	2	0.21		0.0001	NA
bacteria	water	lake	across	6.9	0.393		0.01	NA
bacteria	water	lake	across	6.6	0.431		0.05	NA
bacteria	water	lake	across	3	0.057	NA		NA
bacteria	water	lake	across	3.9	0.38		0.001	NA
bacteria	water	lake	across	8.7	0.565		0.01	NA
bacteria	water	lake	across	7.8	0.037	NA		NA
bacteria	water	lake	across	7.1	0.225		0.05	NA
bacteria	water	lake	across	4.5	0.56		0.01	NA
bacteria	water	lake	across	9.1	0.428		0.01	NA
bacteria	water	lake	across	6.2	0.463		0.05	NA
bacteria	water	lake	across	5.2	0.242	NA		NA
bacteria	water	lake	across	4.3	0.522		0.001	NA
bacteria	water	lake	across	5.9	0.555		0.032	NA
archaea	water	marine	NA	4600	-0.04		0.7939	spearman
bacteria	water	marine	NA	4600	0.16		0.3512	spearman
eukarya	water	marine	NA	2000	0.30932		0.019	NA
bacteria	water	lake	across	362	-0.09	NA		NA
bacteria	sediment	river	NA	7.5	0.05	NA		spearman
bacteria	water	lake	across	7.5	0.292		0.025	NA
eukarya	water	marine	NA	16000	0.32		0.001	pearson
bacteria	host	forest	NA	77.5	0.032		0.28	pearson
archaea	soil	marsh	NA	775	0.15		0.67	NA
Bac_arch	sediment	river	NA	51.56	0.27		0.01	NA
bacteria	sediment	river	NA	53.3	0.45		0.01	NA
fungi	host	forest	NA	23	0.83		0.001	pearson
fungi	host	forest	NA	23	0.8		0.01	pearson
fungi	host	forest	NA	23	0.79		0.001	pearson
fungi	host	forest	NA	23	0.68		0.001	pearson
bacteria	host	forest	NA	23	0.38		0.01	pearson
bacteria	host	forest	NA	23	0.48		0.01	pearson
bacteria	host	forest	NA	23	0.51		0.01	pearson
bacteria	host	forest	NA	23	0.56		0.001	pearson
eukarya	soil	forest	NA	0.064	0.338		0.05	NA
eukarya	soil	forest	NA	0.064	-0.24	NA		NA
fungi	soil	forest	NA	0.064	0.171		0.05	NA

eukarya	soil	forest	NA	0.064	0.22	0.05	NA
eukarya	soil	forest	NA	0.064	0.13	NA	NA
fungi	soil	forest	NA	0.064	0.18	0.05	NA
eukarya	soil	forest	NA	0.064	0.102	NA	NA
eukarya	soil	forest	NA	0.064	0.124	NA	NA
fungi	soil	forest	NA	0.064	0.294	0.05	NA
eukarya	water	river	NA	6	0.43	0.01	NA
eukarya	water	river	NA	6	0.79	0.001	NA
eukarya	water	marine	NA	0.104	0.27	0.001	NA
eukarya	water	marine	NA	0.104	0.28	0.001	NA
eukarya	water	marine	NA	0.104	0.28	0.001	NA
bacteria	water	lake	across	250	0.74	0.001	NA
bacteria	water	lake	across	200	0.41	0.001	NA
fungi	soil	forest	NA	12900	0.17	0.001	NA
fungi	soil	forest	NA	12900	0.24	0.001	NA
Bac_arch	water	river	NA	14.3	0.06	0.31	NA
eukarya	water	river	NA	14.3	0.12	0.07	NA
eukarya	water	marine	NA	66.48	0.383	0.001	spearman
eukarya	sediment	coastal	NA	66.48	0.264	0.007	spearman
archaea	water	river	NA	1100	0.24	0.02	pearson
bacteria	water	river	NA	1100	0.28	0.04	pearson
eukarya	water	river	NA	45	0.315	0.001	spearman
eukarya	water	river	NA	45	0.585	0.001	spearman
eukarya	water	marine	NA	50	0.426	0.001	NA
eukarya	water	marine	NA	50	0.086	0.242	NA
fungi	soil	grassland	NA	406.98	0.301	0.001	NA
Bac_arch	sediment	lake	within	64.35844	0.0764	0.2525	NA
bacteria	soil	grassland	NA	737	0.383	0.001	NA
bacteria	soil	grassland	NA	800	0.274	0.001	NA
bacteria	soil	grassland	NA	800	0.219	0.001	NA
bacteria	soil	grassland	NA	800	0.271	0.001	NA
eukarya	soil	grassland	NA	0.0124	0.1661	0.0001	spearman
bacteria	water	marine	NA	7000	0.03	NA	NA
Bac_arch	soil	grassland	NA	2000	0.1567	0.046	NA
bacteria	water	river	NA	16.75	0.42	0.01	NA
eukarya	water	river	NA	16.75	0.3	0.01	NA
bacteria	soil	grassland	NA	0.28	0.405	0.056	NA
bacteria	soil	grassland	NA	0.28	-0.033	0.504	NA
bacteria	snow	snow	NA	410	-0.013	0.438	pearson
fungi	snow	snow	NA	410	0.306	0.033	pearson
eukarya	snow	snow	NA	410	0.024	0.281	pearson
bacteria	sediment	marine	NA	220	0.26	NA	spearman
bacteria	sediment	marine	NA	220	0.03	NA	spearman
eukarya	sediment	marine	NA	500	0.21	0.001	NA
bacteria	host	agriculture	NA	NA	0.07	NA	spearman
bacteria	water	river	NA	1200	0.69	0.01	NA
fungi	water	river	NA	940	0.3343	0.001	NA
eukarya	sediment	river	NA	3816.9	0.32	0.001	pearson
bacteria	sediment	river	NA	15.63357	0.32	0.04	pearson
bacteria	sediment	river	NA	364.114	0.7	0.002	pearson
bacteria	sediment	river	NA	15.63357	0.17	0.22	pearson
bacteria	sediment	river	NA	364.114	0.76	0.001	pearson
eukarya	sediment	river	NA	667.6188	0.098	0.074	spearman
eukarya	sediment	river	NA	667.6188	0.021	0.336	spearman
eukarya	sediment	river	NA	667.6188	0.31	0.001	spearman
eukarya	sediment	river	NA	667.6188	0.313	0.001	spearman

bacteria	water	river	NA	105	0.7	0.01	NA	
bacteria	water	river	NA	118	-0.27	NA	NA	
bacteria	soil	grassland	NA	524.5567	0.2376	0.001	spearman	
bacteria	soil	grassland	NA	524.5567	0.1432	0.001	spearman	
bacteria	soil	grassland	NA	524.5567	0.07761	0.015	spearman	
bacteria	soil	agriculture	NA	3700	0.279	0.001	NA	
bacteria	soil	agriculture	NA	3700	0.124	0.055	NA	
bacteria	host	agriculture	NA	3700	0.06	0.201	NA	
bacteria	water	marine	NA	989	0.007	0.978	pearson	
bacteria	water	marine	NA	989	-0.26	0.35	pearson	
bacteria	water	marine	NA	989	0.165	0.557	pearson	
bacteria	water	marine	NA	989	-0.265	0.34	pearson	
bacteria	water	marine	NA	989	0.004	0.987	pearson	
bacteria	water	marine	NA	989	-0.261	0.348	pearson	
bacteria	water	marine	NA	989	0.172	0.539	pearson	
bacteria	water	marine	NA	989	-0.181	0.519	pearson	
bacteria	soil	forest	NA	########	0.569	0.001	NA	
bacteria	soil	agriculture	NA	4129.6	0.347	0.05	spearman	
eukarya	sediment	grassland	NA	1673.871	0.18	0.001	NA	
bacteria	sediment	marine	NA	11250.7	0.13	0.0001	pearson	
archaea	sediment	marine	NA	11250.7	0.36	0.0001	pearson	
fungi	sediment	lake	across	148	0.17	0.014	NA	
archaea	soil	agriculture	NA	740.6049	0.388	0.001	spearman	
bacteria	soil	agriculture	NA	740.6049	0.15	0.007	spearman	
archaea	water	river	NA	108	0.53	NA	NA	
bacteria	water	river	NA	108	0.7	0.01	NA	
fungi	host	grassland	NA	1804.736	0.18	0.001	NA	
eukarya	sediment	coastal	NA	12000	0.638	0.01	pearson	
eukarya	sediment	coastal	NA	12000	0.484	0.01	pearson	
bacteria	water	marine	NA	251.9414	0.18	NA	spearman	
bacteria	soil	forest	NA	3700	0.545	0.001	NA	
bacteria	host	grassland	NA	3000	0.64	0.01	NA	
fungi	water	marine	NA	544.152	0.421	0.001	NA	
fungi	water	marine	NA	544.152	0.426		NA	
fungi	water	marine	NA	544.152	0.373		NA	
fungi	sediment	marine	NA	544.152	0.302	0.002	NA	
eukarya	water	marine	NA	1300	0.26	0.13	NA	
bacteria	water	river	NA	175	0.29	NA	NA	
bacteria	water	river	NA	175	0.58	0.05	NA	
bacteria	water	river	NA	140	0.22	0.05	NA	
bacteria	water	river	NA	190	0.59	0.005	NA	
bacteria	water	river	NA	190	0.6	0.0005	NA	
bacteria	water	river	NA	140	0.21	NA	NA	
fungi	host	agriculture	NA	35	0.42	0.007	spearman	
fungi	host	agriculture	NA	35	0.51	0.001	spearman	
bacteria	host	agriculture	NA	35	0.07	0.27	spearman	
bacteria	host	agriculture	NA	35	-0.08	0.61	spearman	
bacteria	sediment	marine	NA	NA	0.74	0.001	pearson	
fungi	host	forest	NA	NA	0.15	0.013	NA	
fungi	host	forest	NA	NA	0.22	0.002	NA	
fungi	sediment	marine	NA	590	0.091	0.085	NA	
archaea	sediment	marine	NA	9714.929	0.26	0.001	spearman	
archaea	sediment	marine	NA	9714.929	0.31	0.001	spearman	
fungi	host	grassland	NA	3000	0.47	0.01	NA	
fungi	host	grassland	NA	3000	0.12	0.18	NA	
fungi	soil	grassland	NA	771.278	0.022	0.63	NA	

Bac_arch	soil	grassland	NA	771.278	0.49	0.001	NA
fungi	soil	grassland	NA	771.278	0.14	0.008	NA
Bac_arch	soil	grassland	NA	771.278	0.39	0.001	NA
fungi	soil	forest	NA	1.070612	0.33	0.01	NA
fungi	soil	forest	NA	1.070612	0.42	0.01	NA
fungi	soil	grassland	NA	1100	0.428	0.0001	NA
bacteria	soil	grassland	NA	1100	0.221	0.0001	NA
fungi	soil	grassland	NA	1100	0.415	0.0001	NA
bacteria	soil	grassland	NA	1100	0.209	0.0001	NA
eukarya	water	marine	NA	19.95401	0.214	0.085	spearman
eukarya	sediment	coastal	NA	12.54235	0.622	0.001	spearman
eukarya	water	marine	NA	19.39535	-0.029	0.85	spearman
fungi	air	urban	NA	30	0.002	0.4	NA
bacteria	soil	desert	NA	888	0.36	0.001	NA
bacteria	soil	agriculture	NA	27.54095	-0.13	NA	NA
bacteria	sediment	river	NA	27.23884	0.2	NA	NA
bacteria	water	river	NA	31.57764	0.08	NA	NA
bacteria	soil	grassland	NA	360	0.3381	0.01	spearman
bacteria	soil	grassland	NA	360	0.3539	0.01	spearman
fungi	host	forest	NA	17.06215	0.2837	0.001	NA
fungi	host	forest	NA	16.95822	0.1843	0.001	NA
eukarya	sediment	marine	NA	11626.09	0.25	0.001	NA
fungi	host	forest	NA	110	0.22	0.001	NA
fungi	soil	forest	NA	1.840173	0.26	0.003	NA
bacteria	sediment	glacier	NA	1396.279	0.855	0.001	pearson
bacteria	sediment	coastal	NA	1624.666	0.371	0.001	pearson
bacteria	sediment	coastal	NA	1624.666	0.512	0.001	pearson
bacteria	soil	forest	NA	10000	0.45	0.0001	NA
bacteria	soil	forest	NA	10000	0.11	0.204	NA
bacteria	sediment	forest	NA	0.13	0.13	0.09	spearman
bacteria	soil	forest	NA	3000	0.059	0.012	NA
archaea	soil	forest	NA	3000	-0.015	0.657	NA
fungi	soil	forest	NA	3000	0.055	0.051	NA
fungi	soil	desert	NA	925	0.142	0.181	NA
fungi	soil	desert	NA	925	0.659	0.001	NA
bacteria	host	grassland	NA	2.55474	0.266	0.038	NA
bacteria	host	grassland	NA	2.55474	0.258	0.032	NA
bacteria	soil	grassland	NA	70	0.204	0.017	NA
fungi	soil	grassland	NA	70	0.387	0.002	NA
Bac_arch	sediment	river	NA	610	0.159	0.001	NA
bacteria	water	lake	within	NA	0.215	NA	pearson
eukarya	sediment	lake	across	514	0.578	0.001	spearman
archaea	sediment	lake	across	3656	0.197	0.001	pearson
bacteria	water	lake	within	67.85	-0.3311	NA	spearman
bacteria	water	lake	within	67.85	-0.0122	NA	spearman
bacteria	water	lake	within	67.85	0.2482	0.0285	spearman
bacteria	water	lake	within	67.85	0.3969	0.0003	spearman
bacteria	soil	grassland	NA	60	0.3574	0.0001	NA
bacteria	soil	grassland	NA	60	0.3626	0.0001	NA
bacteria	soil	grassland	NA	60	-0.0642	NA	NA
all	water	river	NA	674	0.83	0.001	pearson
all	water	river	NA	674	0.37	0.1	pearson
bacteria	host	marine	NA	0.00199	0.7059	0.0001	NA
eukarya	host	marine	NA	0.00199	0.2147	0.1072	NA
bac_euk	host	marine	NA	0.00199	0.3029	0.0543	NA
bacteria	host	marine	NA	0.00199	0.698	0.0002	NA

eukarya	host	marine	NA	0.00199	0.1289	0.2247	NA
bac_euk	host	marine	NA	0.00199	0.1102	0.2611	NA
bacteria	host	marine	NA	0.00199	0.4252	0.0128	NA
eukarya	host	marine	NA	0.00199	0.0644	0.3428	NA
bac_euk	host	marine	NA	0.00199	0.1286	0.2345	NA