

Distance decay of plant and fungal communities at the mesotopographical scale of the Arctic tundra

Shota Masumoto

masumoto.shota@gmail.com

University of Tsukuba

Ryo Kitagawa

Forestry and Forest Products Research Institute

Ryo Kaneko

National Institute of Polar Research

Keita Nishizawa

the University of Tokyo

Shunsuke Matsuoka

Kyoto University

Masaki Uchida

National Institute of Polar Research

Akira S. Mori

the University of Tokyo

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Abstract

Distance decay of biological community similarity occurs at global and local scales. Although fine-scale environmental heterogeneity and stress-tolerant organisms likely promote distance decay at local scales in Arctic tundra ecosystems, these dynamics have not been fully tested. Here, community data were obtained for plants and fungi from 216 plots, including along slope gradients, at the Pond Inlet on northern Baffin Island. Beta diversity was calculated between plots resampled in systematic combinations, and variations with geographic distance and environmental heterogeneity were assessed. Our results showed that distance decay occurred at a local scale. However, the mechanisms underlying differences in distance decay varied between sites and taxa. Specifically, distance decay at the mid-slope section was caused by niche-based mechanisms underlying the increasing environmental heterogeneity with spatial extent. While the predictors of distance decay differed among taxa between the top and bottom sites, plant community composition was more strongly influenced by dispersal limitation than that of the fungal community. Moreover, the distance decay tendency disappeared for combinations of plots with different topography, suggesting that distance decay was not a dominant effect across the study area. Our results suggest that the effects of topography and distance decay on communities in the slope direction and horizontal direction, respectively, may interfere with each other, thereby making the effects less observable. The spatial dependence of community dissimilarity, even within a few meters to kilometers, should be considered when designing studies aimed at capturing the community structure in tundra ecosystems.

Introduction

Biological community similarity reflects site-to-site variations in local species composition within a given region and provides insights into the processes that drive community assembly (Cadotte 2006; Chase and Myers 2011; Tatsumi et al. 2021) and its functional consequences (Mori et al. 2018). Community similarity typically decreases with an increase in geographical distance (Nekola and White 1999; Soininen et al. 2007), and this distance decay can be explained via three main factors: topographic barriers, environmental heterogeneity, and dispersal limitations (Soininen et al. 2007). Distance decay caused by topographic barriers indicates that community similarity decreases sharply in landscapes with major dispersal barriers compared to those with open and homogeneous geographic characteristics. Thus, topographic barriers are often adapted to interpret distance decay at relatively large geographic scales (Garcillán and Ezcurra 2003). On the other hand, the scale at which environmental heterogeneity and dispersal limitations occur is more difficult to define. Distance decay due to environmental heterogeneity is observed when environmental heterogeneity increases with spatial distance. Distance decay caused by dispersal limitations implies that such limitations make the community composition more similar at closer sites, even when topographical and environmental factors are homogeneous. Therefore, distance decay based on these two factors theoretically varies depending on the spatial grain (size of the sampling unit), environmental heterogeneity within the study ecosystem, or the body size and dispersal ability of the target organism (Nekola and White 1999; Soininen et al. 2007). The two factors differ in the underlying processes: environmental heterogeneity

can be attributed to a niche-based community process (deterministic process), whereas dispersal limitations are supported by neutral theory (stochastic process). Thus, the two factors should be considered separately when interpreting the community assembly rule, and their contribution rates vary depending on the site scale, environment, and taxonomic group.

Many studies on terrestrial ecosystems have examined distance decay patterns from tropical forests to tundra regions (Nekola and White 1999; Condit et al. 2002; Tuomisto et al. 2003; Gilbert and Lechowicz 2004; Qian et al. 2005; Lenoir et al. 2012). Almost all of these studies were carried out at relatively large spatial scales, such as the continental scale, while only a few studies investigated the distance decay of small-scale community assemblages or the relative contributions of spatial or environmental factors to such communities (Bahram et al. 2016; Cacciatori et al. 2020; Azovsky et al. 2022). Meta-analyses by Soininen et al. (2007) showed that distance decay occurs at smaller scales at higher latitudes, which seems to contradict the results of global observations. For example, the existence of common circumpolar plants in the Arctic region generates similar regional vegetation (Walker et al. 2005), which may indicate that there is no dispersal limitation over a very long-time scale. Moreover, such a pattern would be detected when the survey grain size is 10–100 km², such as for a survey using remote sensing. In the fine scale, distance decay may occur in the Arctic because of the tundra microclimate due to environmental heterogeneity. In stressful ecosystems such as the Arctic, deterministic processes are predicted to have a more predominant effect on community assemblages than in ecosystems at lower latitudes (Myers et al. 2013). Indeed, the species composition of tundra vegetation can vary significantly at small scales and is influenced by mesotopography or microclimate. For example, mesotopography by periglacial processes or the patchy distribution of permafrost causes drastic vegetation changes in small areas (Vetaas 1997; Walker et al. 2008) by strongly restricting plant activity (Chapin 1987, Suvanto et al. 2014). These microenvironments and their responsiveness to tundra species contribute to the distribution of a fine mosaic of communities at the landscape level (Bliss and Matveyeva 1992; Walker et al. 2008). Another reason for distance decay in the Arctic is that tundra plants are typical stress-tolerant resource-allocating species (Grime 1979) that show a small dwarf form and slow growth rate (Chapin and Shaver 1985). Some of these species have lower reproductive value, such as seed production (Bliss 1958). These features reduce the subsequent spatial spread of established individuals, indicating that stochastic processes may drive distance decay in tundra ecosystems. A comparison of the rates of deterministic and stochastic processes along a latitudinal gradient showed a tendency for stochastic factors to dominate at high latitudes after weakening from low to mid-latitudes (Nishizawa et al. 2022).

Those previous studies suggest that distance decay may occur even at a fine scale (e.g., ecosystems that share the same regional species pool) in tundra ecosystem and is dependent on both environmental heterogeneity and geographical distance. However, trend of distance decay will change depending on taxonomic group, biome, site scale and so on (Nekola and McGill 2014). Although the theoretical principles established through meta-analysis can be used to identify interesting trends, its ability to infer processes is poor because the inferences are based on studies with different aims and sample sizes that were treated with a uniform statistical method. Moreover, few data points are available at high latitudes in the Arctic region. To verify the occurrence and mechanisms of distance decay in tundra

ecosystems, systematic survey site designs are needed that allow for comparisons of community composition across various spatial scales and have the ability to include or exclude environmental heterogeneity. Simultaneously investigating taxonomic groups with differing dispersal ability could also provide important clues regarding the scale dependence of distance decay and the contribution of its mechanisms. Explicitly addressing patterns of distance decay at a small scale could provide insights on a number of major research themes in the Arctic ecology. For example, such work could provide valuable data for vegetation surveys on the effect of primary succession or the microenvironment (Walker 2000; Walker and Del Moral 2003) because ecologists often establish study plots by distance from a glacier terminus or along a slope gradient (Bardgett et al. 2005; Masumoto et al. 2023). Therefore, the geographical distance between study plots must be correlated with the gradient of the observed environmental changes. In such cases, distance decay would become another cause of community variations in addition to the gradient we want to observe. Considering the contribution of geographical distance on Arctic community assembly and underlying mechanisms may provide important fundamental information for highlighting other ecological effects.

In this study, we aimed to demonstrate (1) whether distance decay is also observed at small spatial scales in tundra ecosystems and (2) whether such decay is driven by environmental heterogeneity or dispersal limitations (i.e., deterministic or stochastic processes). Accordingly, we established study plots with systematic intervals at a tundra site that includes a slope gradient. The design allowed us to generate various combinations of soil conditions and geographical distances within a range of several kilometers. We also assess the differences in distance decay and its drivers between taxonomic groups by comparing plant and soil fungal communities. By clarifying where distance decay is likely to appear and the processes that drive it, we sought to generate fundamental and important insights for assessing community assemblages in tundra ecosystems.

Materials and Methods

Study site and plot establishment

Our study sites were located near the Pond Inlet (72 °39 N, 78 °03 W) in the northern region of Baffin Island, Canada (Fig. 1A). The mean summer (June–August) temperature and precipitation between 1991 and 2020 were 6.4°C and 35.6 mm, respectively (ECCC 2025). The sedimentary bedrock is dated to the Mesozoic and Tertiary (Jackson and Morgan 1978). The vegetation is mostly a mix of tundra plant communities (graminoids, sedges, and prostrate shrubs) in mesic soils and wetlands or on exposed rocks (Walker et al. 2005; Olthof et al. 2015).

From July to August 2018, we established nine 42 m line transects at three sites on the top, middle, and bottom of a hill (hereinafter “Top”, “Mid,” and “Bot,” respectively), as shown Fig. 1A and B. In the Arctic tundra, entirely different landscapes are often observed along the slopes of a valley because the soil and microclimate (e.g., snowmelt or wind) conditions of each location are completely different. Our study site also showed a higher proportion of bare ground at the Top site and increased vegetation

development toward Bot. Stable dry heath tundra vegetation in Top was dominated by *Cassiope tetragona* and *Dryas integrifolia*, and wet tussock vegetation in Bot was dominated by graminoids, such as *Eriophorum* spp. and *Carex* spp. An intermediate type between that in Top and Bot was found in Mid. The elevations of each site range from 90 to 110 m (Bot), 100 to 120 m (Mid), and 120 to 130 m (Top), and the differences between sites were 10 to 20 m. All transects ran parallel to the topographic contour lines, and we established 1 × 1 m quadrats at 6 m intervals for a total of 216 quadrats (8 quadrats × 9 transects × 3 sites).

Field and laboratory measurements

The presence and absence of all vascular plant species were recorded within each quadrat, and the soil water content (%) was measured at three random locations within each quadrat using a soil moisture sensor (HH2, DeltaT Devices Ltd, Cambridge, UK) and then averaged. From the same locations, we collected approximately 20 g of soil samples from the O–A horizons (soil layers with a high percentage of organic matter) after removing slightly decomposed litter, including the Oi horizon (top of the organic surface layer with subdivisions of fresh, undecomposed plant debris). Those sample were obtained from 0 to 10 cm using a trowel, which were sieved to eliminate root tissue.

The samples were transported to the laboratory to measure abiotic environmental factors. Specifically, the soil pH, electrical conductivity (Ec; mS/cm), and ratio of soil carbon (C; mg C/g soil) to nitrogen (N; mg N/g soil) were measured in the soil sampled from each quadrat. The pH and Ec values of dry-sampled soil in water (soil/water weight ratio of 1:5) were measured using pH and Ec meters (Twin pH and Twin Ec, Horiba Ltd., Kyoto, Japan), respectively. The C and N concentrations in the sampled soil were measured using a CN analyzer (Sumigraph NCH-22F, Sumika Chemical Analysis Service, Tokyo, Japan). We also used fresh soil (0.5 g) sampled from the same site to estimate the fungal community structure based on a DNA analysis. The soil sample for DNA analysis was collected into 2 ml tubes containing RNAlater (Qiagen, UK) using a sterilized spoon, which was stored below 0°C until DNA analysis. The vegetation and soil environmental factor dataset was deposited in The Arctic Data Archive System (ADS, <https://ads.nipr.ac.jp/>) under accession number A20161228-001.

DNA extraction, polymerase chain reaction, and DNA sequencing

To characterize the fungal community structure, we analyzed fungal sequences in the soil samples from all quadrats by sequencing large subunit (LSU) ribosomal RNA (rRNA) genes using a MiSeq sequencer (Illumina, San Diego, CA, USA). Genomic DNA was extracted using a FastDNA SPIN Kit for Soil (MP Biomedicals, Santa Ana, CA, USA). We amplified the partial LSU rRNA gene sequence regions using the primers LR22R and LR3 (Mueller et al. 2016), with Illumina overhang adaptor sequences attached to their 5' ends. As per Illumina's protocols (Illumina n.d.), we performed polymerase chain reaction (PCR) amplification of the LSU rRNA gene with the following thermal cycling program: initial denaturation at 98°C for 30 s; 22 cycles of denaturation at 98°C for 15 s, annealing at 64°C for 15 s, and extension at

72°C for 15 s; and a final extension at 72°C for 1 min. We performed reactions in triplicate to amplify sequences with Illumina overhang adaptors, and amplicons were pooled before the index PCR assay using a Nextera XT Index Kit (Illumina). Genomic DNA was purified using an Agencourt AMPure XP (Beckman Coulter Genomics, CA, USA). The resulting DNA was mixed with Phi X control DNA at a ratio of 75:25, and this mixture was used as a template for paired-end sequencing using a MiSeq Reagent Kit v3 (600 cycles) and MiSeq Desktop Sequencer.

Data processing of LSU rRNA genes

Bioinformatics and data analyses were performed as described by Matsuoka et al. (2019). For raw MiSeq reads, we merged the forward and reverse sequences. The sequences were assembled using the Claident pipeline (ver. 0.2.2018.05.29) (Tanabe 2019). First, potential chimeric sequences and sequencing errors were removed using UCHIME (Edgar et al. 2011) and the algorithm in CDHIT-OTU (Li et al. 2012), respectively. The remaining sequences (30007440 reads; mean 138923 ± 34568 reads per sample, $n = 216$) were assembled at a threshold similarity of 97% (Mueller et al. 2016), and the resulting consensus sequences represented molecular operational taxonomic units (OTUs). After removing singletons, we generated an OTU table (i.e., a matrix of OTUs and samples with sequence reads for each cell entry). For each OTU, we conducted taxonomic identification based on the query-centric auto-k-nearest-neighbor (QCaute) method (Tanabe and Toju 2013) using the National Center for Biotechnology Information (NCBI) database and the lowest common ancestor algorithm (Huson et al. 2007) using Claident software. Differences in the sequencing depth of individual samples affect the number of OTUs retrieved, often leading to an underestimation of OTU richness in samples with low sequence reads. Hence, we examined rarefaction curves depicting OTU numbers in sequence reads and calculated the coverage-based rarefied OTU richness to standardize the effect of sequencing depth (Chao and Jost 2012). For the statistical analyses described below, we used only the presence/absence (more than one sequence was defined as presence) data of the OTUs that belonged to the kingdom "Fungi". Datasets from the high-throughput sequencing of LSU genes were submitted to the NCBI Sequence Read Archive under accession number PRJNA541059 (<http://trace.ddbj.nig.ac.jp/dra/index.html>).

Statistical analysis

The following statistical analyses were performed using R ver. 3.6.1 (R Core Team 2019).

Principal component analysis for soil environmental features

Principal component analysis (PCA) was performed to summarize the soil environmental factors and their changes among the sampled quadrats. Five abiotic environmental variables (water content, EC, pH, carbon content, and nitrogen content) were standardized for the analysis. We performed log transformations of some variables (EC, carbon content, and nitrogen content) to achieve a normal

distribution. The obtained synthetic axes were used in subsequent analyses as factors to explain plant and fungal diversity.

Scale-dependent plot “resampling”

To demonstrate the scale dependence of the beta diversity of the plant and fungal communities, we resampled three plots within or across site, at different spatial scales (Fig. S1). Here, our aim is to calculate beta-diversity (β) using the following formula via a data set of the three plots.

$$\beta = \frac{\gamma}{\bar{\alpha}}$$

where, γ is total species richness of the three plots and $\bar{\alpha}$ is average of species richness of each three plots.

To create data sets belonging to the same site, all plots within a site (72 plot in total) were randomly divided into four groups of 18 plots each. Then, two additional plots to be paired with the initial plot were selected based on the following spatial scale, and a total of three plot sets were formed. Group 1 (ScaleSS): two plots neighboring the initial plot were sampled within the same transect. If the initial plot was located at the end of a transect, then the two closest plots within the same transect were sampled. Group 2 (ScaleS): two additional plots were randomly sampled from the same transects. Group 3 (scale M): two additional plots were sampled within a block, including the initial plot. Group 4 (scale L): two plots were randomly sampled from all plots in the same site. At each scale, 18 sets of plots were resampled with repetition (allowing for duplication).

Compared with resampling designs within the same site, we also conducted alternative resampling to confirm the scale dependence of communities containing different sites (see Fig. S1). For the smallest scale (scale SS), we sampled three plots with the same Transect and Plot number from different sites (e.g., Plot 3 of transect 4 on Top, Mid, and Bot). For the other scales (scales S, M, and L), we sampled two additional plots from different sites, which was similar to the resampling process of the same site. At scale S, we randomly sampled plots from different sites but with the same transect number. At scale M, we sampled plots from different sites belonging to the same block. At scale L, we sampled plots from different sites across the study site. We obtained 72 sets of plots for each resampling scale.

For each plot set obtained by the resampling, we calculated the beta diversity of plants and fungi. Furthermore, by using the same plot set, the average Euclidean and Gower distances between plots were calculated to evaluate geographical distance and environmental heterogeneity respectively.

Community dissimilarities and its predictive factors

To evaluate the dissimilarity in plant and fungal composition, we calculated the Sørensen dissimilarity index for all plot combinations. We also determined the geographical distance and environmental heterogeneity of the plots using the Euclidean distance and Gower distance, respectively. Dissimilarity or distance variables were determined based on the Mantel test or variation partitioning analysis. To consider situations with and without the effect of mesotopography, analyses were performed using four types of datasets, including a dataset for each of the three sites and an overall datasets for all sites. These tests were conducted using the vegan package in R.

To confirm the factors that predict community dissimilarity, we performed the Mantel test to examine the correlation between plant or fungal dissimilarity (as object variables) and geographical or environmental distance (as explanatory variables). In addition, two partial Mantel tests were performed to assess the correlation between (i) plant dissimilarity or (ii) fungal dissimilarity and environmental distance, while controlling for the partial effect of geographical distance. Here, the partial Mantel tests analyzed whether environmental heterogeneity caused by factors other than distance decay explained the community dissimilarity caused by factors other than distance decay.

To focus on the factors underlying distance decay (i.e., geographical distance or environmental heterogeneity depending on spatial differences), we conducted variation partitioning analysis. Models were constructed using spatial variables extracted based on the principal components of neighbor matrices (PCNMs, Borcard et al. 2004). The PCNM analysis produced a set of orthogonal variables derived from the geographical coordinates of the sampling locations (position of sampling squares). We used the PCNM vectors to represent spatial variability and overall environmental dataset to represent environmental variability. For the four site-type datasets, we performed variation partitioning by calculating the adjusted R^2 values for each fraction (Peres-Neto et al. 2006).

Additional analysis for community assemblage in Mid

We conducted an additional analysis using a dataset across sites because the resampling analysis showed that the beta diversity did not change with across site resampling while variation partitioning showed that environmental distance has a greater effect on the Mid plots (see Figs. 3 and 4). To demonstrate the vertical variation in slope of the community dissimilarities, we calculated the pairwise Sørensen similarity of plant and fungal communities between the Top and Mid plots or between the Mid and Bot plots. Each pair consisted of the same plot and transect number for each site. The Euclidean distance between the geographical position and Gower distance of environmental factors was also calculated for the same pair. Therefore, we obtained datasets consisting of 72 pairs of dissimilarities in each of Top-Mid site (TM pairs) and Mid-Bot site (MB pairs). Then, linear mixed models were established using the TM and MB paired datasets, which consist of the pairwise similarities of plants or fungi as object variables and geographic distance and environmental heterogeneity as explanatory variables, with the type of pair (TM or MB pair) as a random effect.

Results

Soil environment features

In the PCA across all plots (Fig. 1C), PC1 exhibited high negative loadings for soil EC, carbon contents, and nitrogen content and accounted for 57.2% of the total variance. Therefore, this component represented the development of organic soil with a higher enrichment of these abiotic variables along the slope. PC2 had high loadings for water content and pH and accounted for 28.2% of the total variation in soil physicochemistry. Therefore, this component represented the change in these abiotic variables along the slope gradient. PC3 showed high loadings for water content and pH; however, the trend was different from that in PC2. Specifically, PC3 showed positive loadings for water content but negative loadings for pH, whereas PC2 showed negative loadings for both water content and pH. These three PCA axes accounted for 95.1% of the total variance.

Distance decay of beta diversity and environmental heterogeneity

The beta diversity of the community increased with the size of the resampling scale when resampling was performed within site (Fig. 2). This trend was similar for both plants and fungi regardless of the differences between sites. Beta diversity and geographical distance were correlated between plots in a dataset (Fig. 3). Furthermore, environmental heterogeneity also increased with the geographical distance between plots, meaning that spatial autocorrelation occurred based on environmental conditions (Fig. 3).

For resampling across sites, none of the variables except geographic distance showed differences with the resampling scale (Fig. 2); moreover, beta diversity was not correlated with geographic distance (Fig. 3). In summary, distance decay was not detectable.

Community similarities and predictive factors

The Mantel analysis showed that both geographical and environmental distance significantly affected community dissimilarity. Geographical distance significantly predicted both plant and fungal dissimilarities at all sites, while environmental distance did not significantly predict plant dissimilarity of the Bot and Top plots or fungal dissimilarity of the Bot plots (Table 1). In the partial Mantel tests, in which community dissimilarity and environmental distance controlled for the partial effect of geographical distance, a similar trend was shown.

Table 1

Correlation coefficient and p-value of the Mantel and partial Mantel test correlations of pairwise Sørensen dissimilarity (plant species or fungal OUT) with geographical distance and environmental heterogeneity. Statistics correspond to partial Mantel tests controlling the differences in geographical distance. The significant and non-significant correlations are shown as black and gray letters, respectively ($P < 0.05$).

	For Plant						For Fungi					
	vs Spa.		vs Env.		vs Env. partial out space		vs Spa.		vs Env.		vs Env. partial out space	
ALL	0.08	***	0.11	***	0.10	***	0.09	***	0.26	***	0.25	***
Top	0.16	***	-0.04	n.s.	-0.04	n.s.	0.09	*	0.24	***	0.24	***
Mid	0.33	***	0.17	***	0.14	***	0.19	***	0.27	***	0.25	***
Bot	0.18	***	-0.01	n.s.	-0.04	n.s.	0.08	*	0.07	n.s.	0.06	n.s.

Figure 4 shows the results of the variation partitioning analysis. The two factors underlying distance decay (i.e., pure geographical factor and environmental factor varying with spatial distance) are illustrated as the blue and green effects in Fig. 4. The results indicate that plants are more influenced by the pure geographical factor than fungi. Additionally, the contribution of environmental heterogeneity was greater at the Top site than at the other sites. Furthermore, the environmental effect was greater at the Mid site than at the other sites (as detailed in the next paragraph).

Analysis for community assemblage in Mid

In Fig. 5A and B, we plot the similarity values by subtracting the dissimilarity of the MB pair from the dissimilarity of the TM pair. Thus, if the value was positive, then the community composition of the Mid site was more similar to that of the Top site; conversely, if the value was negative, then the community composition of the Mid site was more similar to that of the Bot site. The differential dissimilarity values varied across transects and taxa, and trends were not observed for different transects or taxa. The linear mixed model for pairwise similarities between the Mid and other sites showed a correlation with geological distance and environmental heterogeneity (Table S1). In particular, the relation of plant dissimilarity and environmental heterogeneity was significant.

Discussion

Slope and scale dependence of community composition

PCA confirmed that the two main environmental gradients were from the top of the hill to the bottom. Specifically, soil organic matter and moisture content were poor at the top of the hill and became richer downhill (Fig. 1C). Such environmental gradients and community assemblages are typically observed along slopes in tundra ecosystems (Berry 1987; Vetaas 1997; Zumsteg et al. 2013). This could be due to

water or nutrient gradients depending on the mesotopography (Rastetter et al. 2004) and physio-climatic influences, such as permafrost distribution and wind exposure (Williams and Smith 1989; Vetaas 1994).

The beta diversity and environmental heterogeneity of the resampled plots within sites showed that similar decay occurred with geographical distance between plots (Figs. 2 and 3). On the other hand, if a vertical change in the slope was included in the resampling, then the magnitude of similarity did not change despite the scale widening horizontally. Such results indicate that the effect of distance decay on community assembly is present but not dominant in the ecosystem that includes a slope gradient; moreover, environmental change along slope had a stronger ability explain the effects at this site. Community composition is known to respond to micro-environmental changes depending on the topography of the tundra (Berry 1987; Jónsdóttir et al. 1999; Masumoto et al. 2023), which is consistent with the findings of this study. However, since we aimed to focus on changes in community composition with distance decay, we mainly discuss the case without the influence of topography in the following section.

Distance decay due to environmental heterogeneity

Within the same site where topographic effects were eliminated, the effect of spatial distance became apparent, which led to an increase in community beta diversity with distance (i.e., distance decay). As shown in Fig. 3, geographical distance significantly increased both plant and fungal beta diversity at each site, although the correlation coefficient was larger at the Mid site. For the Mid site, variation partitioning analysis revealed that environmental factors had a higher explanatory power for community composition compared with the other sites, and the additional analysis showed that vertical slope effects caused considerable variation in the community composition (see Fig. 5). The species composition of tundra vegetation can vary significantly at small scales and is influenced by the mesotopography, patchy permafrost distribution, or microclimate (Vetaas 1997; Walker et al. 2008). Our results suggested that in Mid, the environment became more heterogeneous by horizontal resampling and environmental variations between plots caused by spatial expansion were more influenced by topography than community dissimilarity. In other words, deterministic processes due to environmental factors that vary spatially cause distance decay.

A comparison of the Top and Bot sites showed that in the Top sites, which have a harsher environment, both plant and fungal beta diversity responded more sensitively to geographical distance (Fig. 3). The correlation between geographical distance and environmental heterogeneity was relatively small at the Top site (Fig. 2, lower panel). However, the variation partitioning analysis indicated that the environmental contribution to the community composition was high at the Top site. This suggests that the species at the Top site would be more sensitive to environmental niche partitioning. Previous studies have found that the contribution rate of deterministic factors to community assemblage is higher than that of stochastic factors in stressful environments, which is influenced by species characteristics (Chase 2007; Guo et al. 2014). We confirmed the different species composition between the Top and Bot sites, with stable dry heath tundra vegetation dominated by *Cassiope tetragona* and *Dryas integrifolia* at the Top and wet tussock vegetation dominated by graminoids, such as *Eriophorum* spp. and *Carex* spp.,

at the Bot. Such species differences would enhance the deterministic contribution to distance decay, even if within a small spatial range

Distance decay due to dispersal limitation

A comparison of the results for the plant and fungal communities revealed that although distance decay occurred in both communities, the mechanisms underlying the influence may differ. Specifically, geographical distance had a stronger effect on plants than fungi, which would reflect differences in dispersal limitations between taxonomic groups. Tundra plants are typical stress-tolerant resource-allocating species (Grime 1979), meaning that they have slow growth rates (Chapin and Shaver 1985) and lower reproduction rates (Bliss 1958). Moreover, tundra plants tend to colonize via rhizome growth rather than seed dispersal. Thus, for the same regional species pool, we may observe distance decay due to dispersion limitation over a short period and within a specific location. In contrast, previous studies have shown that geographical distance has a lower contribution to fungal communities (Bahram et al. 2016), moreover bacterial community even in the Arctic (Malard et al. 2019), indicating that their higher dispersal ability contributes to lower distance decay owing to stochastic processes (Clark et al. 2021). Note that the spatial grain (size of the sampling unit) differs between plants and fungi. When the spatial grain increases, the correlation between beta diversity and the environment weakens (Nekola and White 1999; Soininen et al. 2007). Because the grain size between plants (1 m²) and fungi (0.5 g) could not be compared in this study, performing further comparisons of the results of the two taxa directly may lead to errors.

Additionally, the contribution of geographical distance to the fungal community decreased in the Top habitat. These results mean that fungal dispersal limitation was weakened, and niche-based process was enhanced under harsh environmental conditions. The fungal trait variation may explain the trend as the mechanism. In tundra dry heath communities, such as at the Top site, lichens often become predominant, and those distributions were affected by ground condition or vascular plants existence. In such situation, the fungal community composition varies based on functional turnover at the local scale (Masumoto et al. 2023). However, previous studies have not reported such a relationship between these fungal traits and distance decay, and whether such effects can be observed in fungi with inherently weak dispersal limitation remains unclear. As another possible reason for this trend, the soil fungal community is known to be influenced by the plant community due to their symbiotic relationships (Prober et al. 2015). If the correlation between fungal and plant community is enhanced along environmental harshness, the niche-based mechanism of fungi also would more appear along environmental gradients.

Conclusion and Implications

Although distance decay occurred in the Arctic tundra ecosystem, it was not a dominant factor underlying the community structure in the study area. This seems reasonable for the ecosystem, which presented heterogeneous mesotopography and a maximum extent of 3 km. However, distance decay was observed at such a fine scale if the mesotopography was excluded. To the best of our knowledge, the present study is the first to explicitly address distance decay patterns on a small scale, and our

results suggest that distance decay is driven not only by the environmental heterogeneity of the tundra ecosystem but also by stochastic mechanisms based on the lower mobility of tundra plants. Moreover, they showed that the driver changes depending on environmental gradient or different taxon. Our study supported previous studies in which the distance decay of several taxa within community assemblages at a small scale was found to be driven by both spatial and environmental factors (Bahram et al. 2016; Cacciatori et al. 2020; Azovsky et al. 2022).

Such spatial variations may also complicate the interactions between community composition and its predictors when discussing the effect of target factors on community similarity. Indeed, in our study, the slope effect and distance decay canceled each other out. A few meters to kilometers is the typical distance between multiple survey plots set up by ecologists for treatments or repetitions in the field. Our results revealed that distance decay can occur at such a fine scale, which suggests that environmental factors and geographical distances between plots should be measured on a plot-by-plot basis whenever possible. Validating the effects of geographical distance or miniscule environmental conditions between sampling sites is important when considering tundra community assemblages, even if community diversity is tested under distinct geohistorical conditions, such as primary succession or topography.

Declarations

Competing Interests:

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

Author Contribution

S Masumoto, AS Mori and M Uchida conceived and designed the study. S Masumoto, R Kitagawa, R Kaneko, and K Nishizawa conducted the field research and experiments. S Matsuoka contributed to processing the DNA data. S Masumoto analyzed data. S Masumoto prepared the manuscript. All authors have read and approved the final manuscript.

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Data Availability

The vegetation and soil environmental factor dataset was deposited in The Arctic Data Archive System (ADS, <https://ads.nipr.ac.jp/>) under accession number A20161228-001. Datasets from the high-throughput sequencing of LSU genes were submitted to the NCBI Sequence Read Archive under accession number PRJNA541059 (<http://trace.ddbj.nig.ac.jp/dra/index.html>).

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Figures

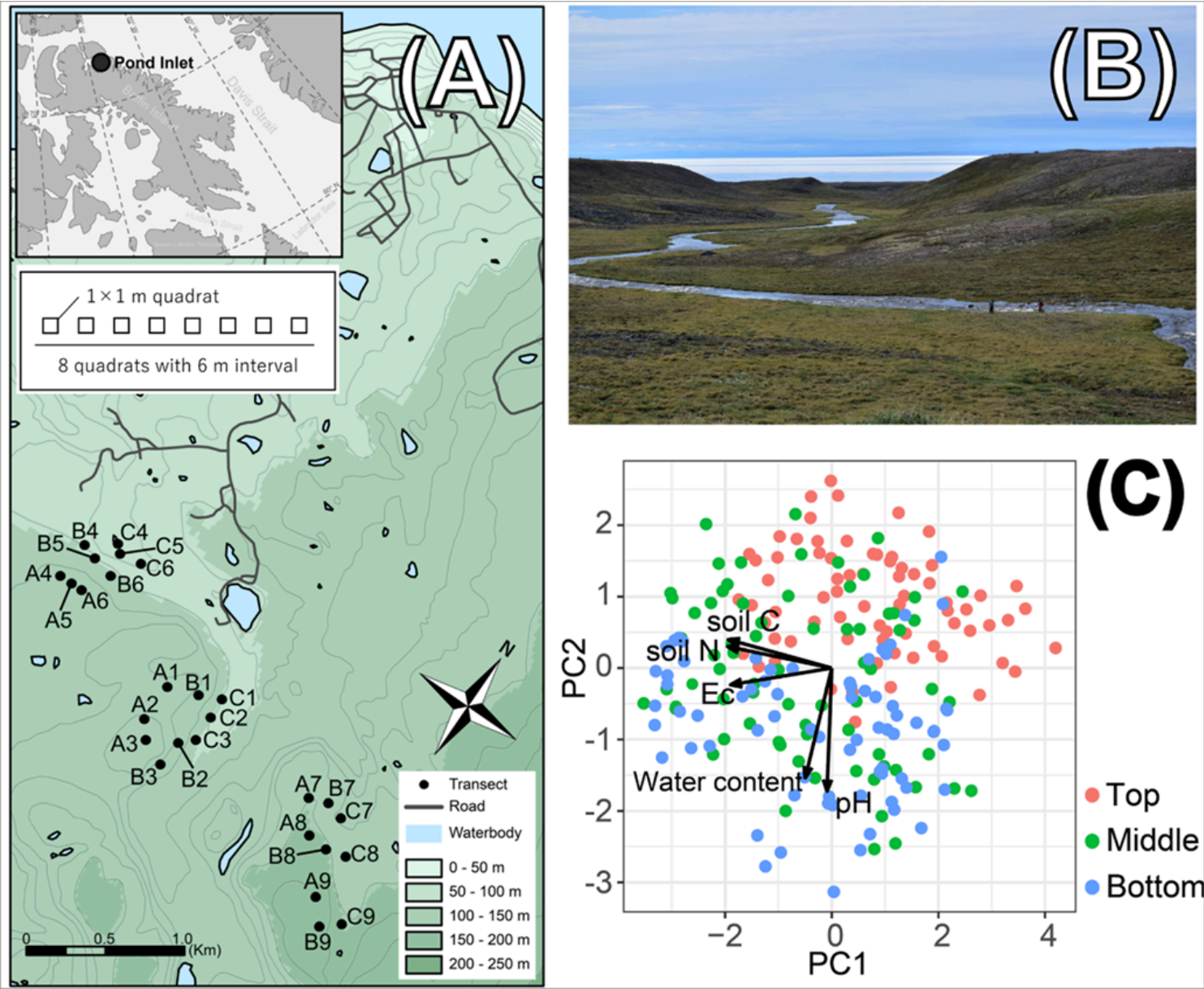


Figure 1

Study site location (A) and landscape (B). Principal component analysis of soil environmental factors showed a gradual change in stress intensity from the bottom to the top of a hill (C).

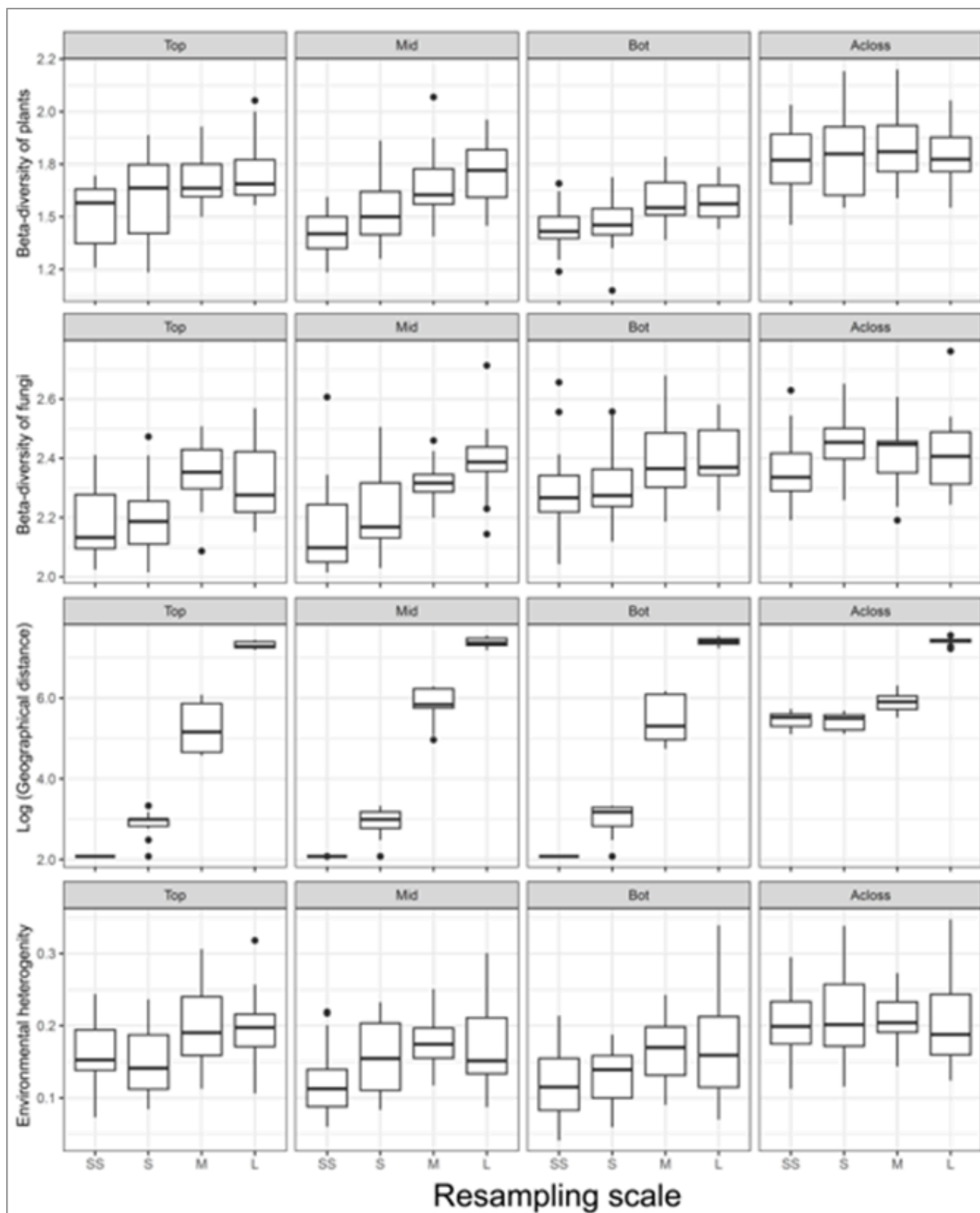


Figure 2

Differences in beta diversity of plants and fungi, geographical distance, and environmental heterogeneity depending on the resampling scale. Resampling was conducted within sites and across sites.

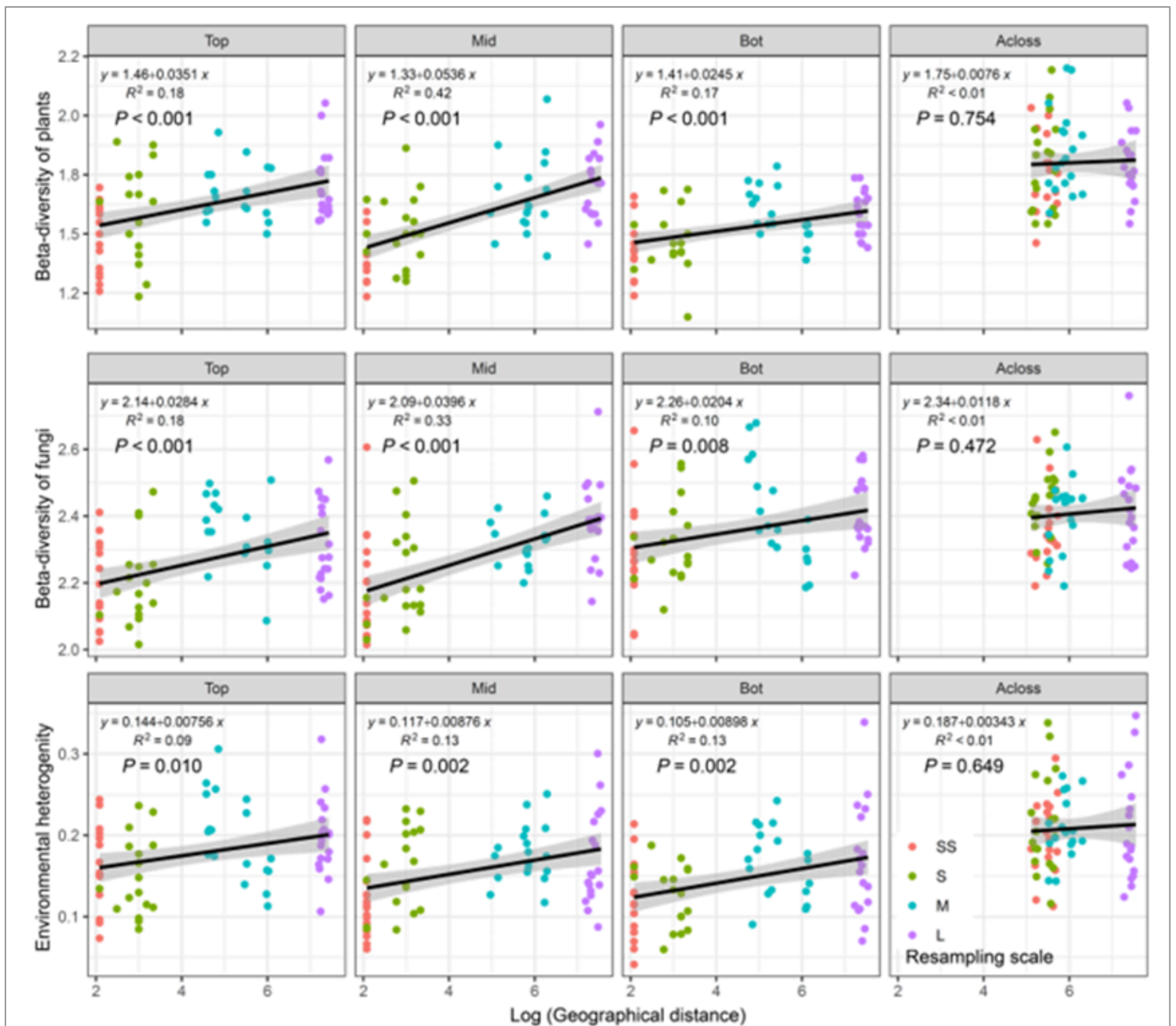


Figure 3

Correlations of plant diversity, fungal diversity, or environmental heterogeneity with geographical distance using the resampling data set. Resampling was conducted within sites and across the sites.

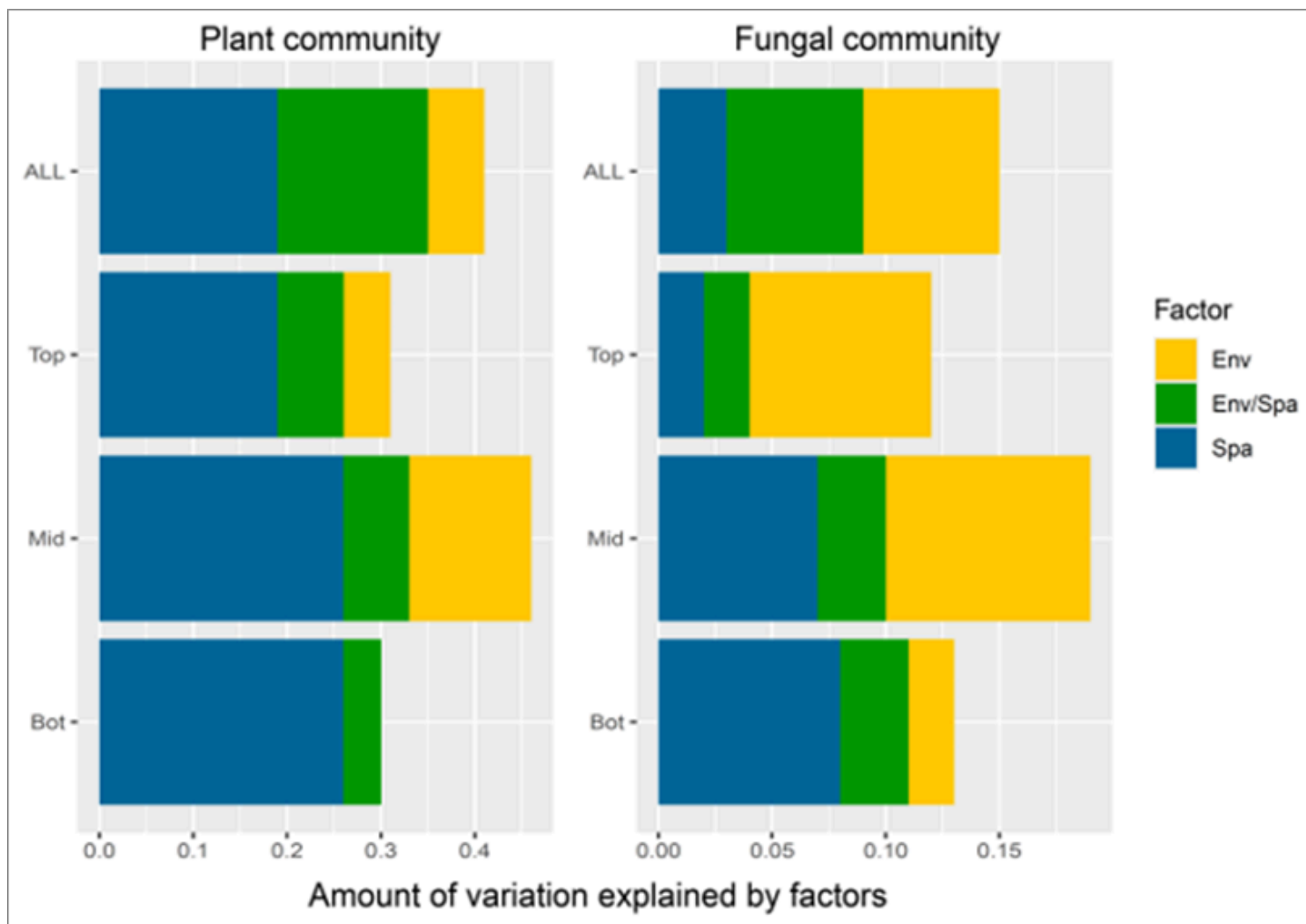


Figure 4

Bar plot of the relative independent contribution of predictors by variation partitioning analysis. Each color bar indicates the pure effects of space (blue), shared effects of space and environment (green), and pure effects of environment (yellow). The total value of the blue and green parts represents the contribution for distance decay on community structure. The pure effects of space are interpreted as a result of dispersal limitation, while the shared effects suggest a niche-based community formation by environmental factors.

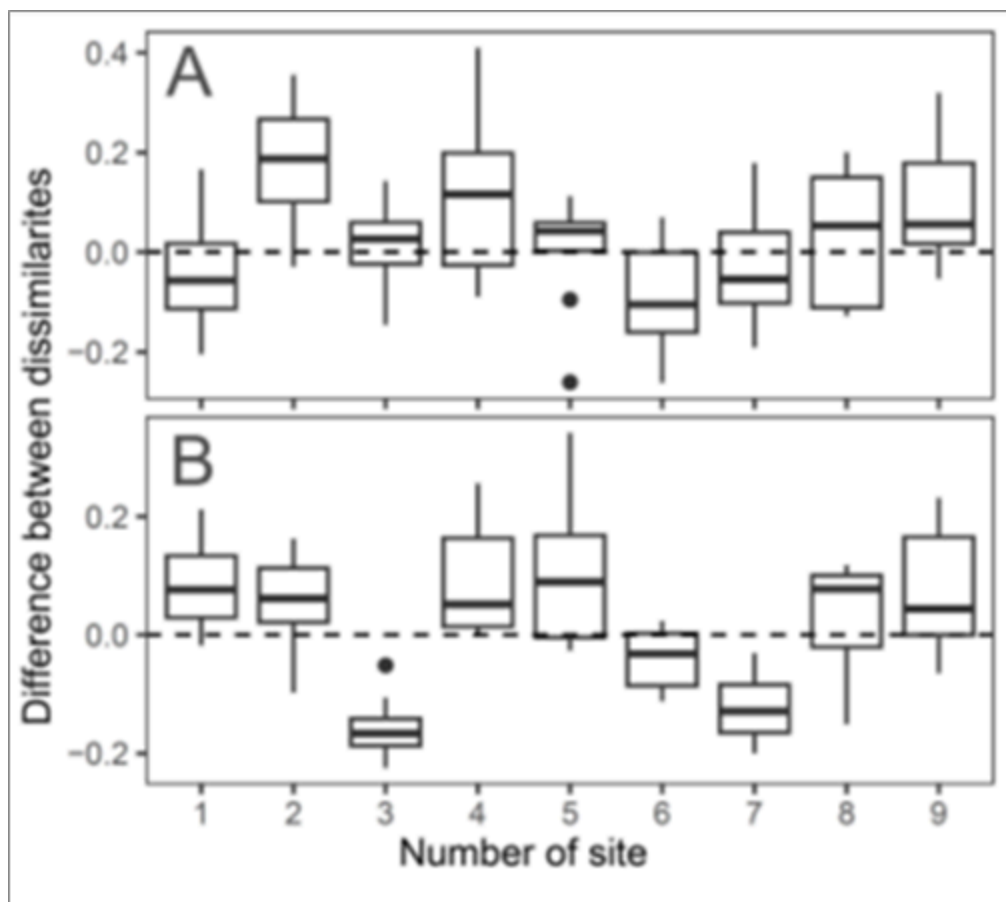


Figure 5

Similarity values were determined by subtracting the similarity of plants (A) and fungi (B) between the Mid-h and Bot-h plots from the similarity between the Top-h and Mid-h plots. The value is positive if the composition in Mid-h is more similar to that of Top-h than Bot-h. The value is indicated for each transect.

Supplementary Files

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