



Cross-taxon congruence of aquatic microbial communities across geological ages in Iceland: Stochastic and deterministic processes

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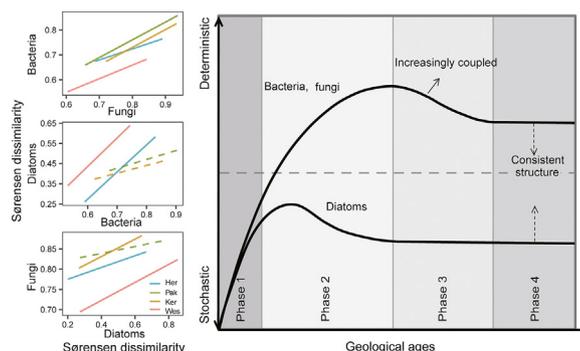
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HIGHLIGHTS

- Bacteria and fungi have a similar geological trend in beta diversity.
- Microbial beta diversity shows strongest cross-taxon congruence in oldest region.
- Deterministic processes dominate bacteria and fungi, but stochasticity for diatoms.
- We show a four-phase conceptual model in ecological processes across geological ages.

GRAPHICAL ABSTRACT



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ABSTRACT

Biotic groups usually have nonrandom cross-taxon relationships in their biodiversity or compositions across sites, but it is poorly known how such congruence varies across long-term ecosystem development, and what are the ecological processes underlying biodiversity patterns. Here, we examined the cross-taxon congruence in diversity and compositions of bacteria, fungi and diatoms in streams from four regions with different geological ages in Iceland, and further studied their community assembly processes. Bacteria and fungi showed contrasting trends in alpha and gamma diversities across geological ages, while their beta diversity patterns were consistent, being the lowest in the oldest region. The three taxonomic groups had the strongest cross-taxon congruence of beta diversity in the oldest region, while the weakest for intermediate-aged regions. Although environmental variables played important roles in shaping their congruence, biotic interaction had nonnegligible influences. Deterministic processes, being dominant for bacteria and fungi, had the highest relative influence in intermediate-aged regions, whereas diatoms showed higher stochasticity. We proposed a four-phase conceptual model to show how the balance of deterministic and stochastic processes changes across geological ages. Taken together, our results provide an advanced understanding of cross-taxon congruence and community assembly processes for aquatic communities over long-term periods of geological age.

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1. Introduction

Understanding the mechanisms that underlie spatiotemporal patterns of species biodiversity is a major challenge in microbial ecology.

Different groups of taxa usually have nonrandom biodiversity or composition relationships across space and time, a phenomenon known as cross-taxon congruence (Toranza and Arim, 2010; Ozkan et al., 2014; Westgate et al., 2014). Strong congruence may result from species interactions and similar responses to the same or intercorrelated environmental factors (Gaston, 1996; Cabra-García et al., 2012; Tisseuil et al., 2013; Schalkwyk et al., 2019b). The establishment of one biotic group at sites may promote the occurrence (or extinction if groups of species are competing) of another group, which is essential for shaping diversity (Grover, 1994; Longumuir et al., 2007). Recent studies show congruence in species richness among taxa is scale dependent with stronger association at larger spatial scales (Wolters et al., 2006; Burrascano et al., 2018; Vilmi et al., 2020), while remarkably little is known about the temporal variations in the relationships among different organisms (Ozkan et al., 2014). We might expect cross-taxon congruence to differ in response to variations in abiotic (Johnson and Hering, 2010; Corte et al., 2017) and biotic (Englund et al., 2009; Greve et al., 2012) properties during long-term ecosystem development. In addition, even though most studies have reported strong cross-taxon congruence, the underlying causes remain poorly understood (Orwin et al., 2006; Ozkan et al., 2014; Schalkwyk et al., 2019a). Thus, cross-taxon congruence over long-term periods, such as geological ages, is important for understanding the underlying processes that drive the shift of microbial communities.

Geological ages offer a great opportunity to assess the shifts in cross-taxon congruence and ecological processes of community compositions over long-term periods. Communities diversify over time, and the scales vary from seasonal and successional to long-term geological time (Margalef, 1963). The older the geological age of a habitat type, the greater the opportunity for speciation in the past, therefore, the more species that could adapt to this habitat type (Zobel, 1992; Borges and Brown, 1999). However, biological communities across geological time scales are rarely investigated because they require extensive investigations over space and time (Zaitsev et al., 2012). For macroorganisms, regional geological age provides time for species evolution and diversification (Lososová et al., 2015; Tanzler et al., 2016) and is one of the dominant factors shaping species diversity (Willis, 1922; Fischer, 1960; Eriksson, 1993). For instance, in the Netherlands, geological age drives the spatial patterns of oribatid mite community diversity and compositions (Zaitsev et al., 2012). However, microbial biodiversity is rarely considered across geological ages possibly because of short life cycle and high dispersal ability. For instance, it is unclear whether microbial diversity and community compositions become more coupled among taxa with stronger environmental selection and trophic interactions across geological ages. Such studies of microbial ecological processes would be essential to understand the mechanisms that underlie patterns of species biodiversity over long-term periods.

Biodiversity is simultaneously shaped by two types of ecological processes, namely deterministic and stochastic processes (Chase and Myers, 2011; Nemergut et al., 2013; Dini-Andreote et al., 2015). The deterministic processes include abiotic selection and species interactions (Chesson, 2000; Fargione et al., 2003; Stegen et al., 2012), suggesting that organisms are densely clustered at the local optimum of each niche. In contrast, the stochastic processes are driven by dispersal limitation, random changes in births and deaths and mass effects (Ofiteru et al., 2010; Wang et al., 2013). From long-term perspectives, neutral evolution hypothesizes that all organisms have an equal opportunity of occupying a niche, but biodiversity changes with random events (Shi et al., 2018). Ecological succession can be assessed across space and time to understand the mechanisms in governing processes of community assembly (Fierer et al., 2010), and the relative importance of deterministic and stochastic processes in microbial communities is time dependent (Ferrenberg et al., 2013; Zhou et al., 2014). Previous literature that focused on microbial ecological processes in soil ecosystems have shown the shifts in stochastic and deterministic balance along soil chronosequences due to changes of soil chemistry and organic

matters (Dini-Andreote et al., 2015). Most studies focus on community assembly along soil chronosequences (Turner et al., 2019) and receding glaciers (Tripathi et al., 2018), while it is unclear how microbial communities and the balance of their deterministic and stochastic processes vary across geological ages, particularly among multiple trophic groups including producers and decomposers (Vass et al., 2019).

Here, we studied the biodiversity and community compositions of three stream microbial groups, that is bacteria, fungi and diatoms that have different trophic positions, from four regions with different geological ages in Iceland. Iceland provides a discrete geological time series for investigating changes in communities and their cross-taxon congruence. This is because Icelandic landmass is considered to be mostly the product of a hotspot located at a divergent plate boundary, which has different ages of rocks and unusual volcano types (Sturkell et al., 2006). Moreover, subaerial exposure of the active spreading segments allows detailed geologic mapping and age determination for the products of individual eruptions (Sinton et al., 2005). Specifically, we focused on three aims. First, we assessed the alpha, beta and gamma patterns of the three microbial taxonomic groups in the four regions. Second, we evaluated their cross-taxon congruence in terms of species richness and beta diversity, and further explored the influential factors for the beta diversity of microbial communities. Third, we investigated the changes in the relative influences of stochastic and deterministic processes for the three groups across four regions with different geological ages. Due to the suppression of biological competition at the end of successional stages (Jackson et al., 2001) and similar response of organisms to environmental factors (Ozkan et al., 2014), we expected the strongest cross-taxon congruence to occur among taxa in the region with the oldest geological age. We further hypothesized that the deterministic processes played relatively stronger roles in the older regions because of the strong environmental filtering and biotic interactions in selecting microbial communities adapted well to local habitats (Zhou et al., 2014; Dini-Andreote et al., 2015).

2. Material and methodology

2.1. Study region

The Iceland basalt plateau is situated at the junction of two large submarine physiographic structures, the Mid-Atlantic Ridge and the Greenland Iceland Faeroe Ridge (Thordarson and Larsen, 2007). We obtained samples from four regions spanning from the southwestern to central parts of Iceland, that is, Herðubreið (65°10'43.2" N, 16°20'42" W), Þakgil (63°31'49.6"N, 18°53'19.6"W), Kerlingarfjöll (64°37'37.8" N, 19°15'42"W) and Westfjords (65°40'N, 22°30'W) (Fig. 1). These regions vary in two major ways regarding geological processes (Table S2), which may affect species extinction and colonization, soil succession and relevant ecosystem development, and finally microbial biodiversity and ecosystem functions (Hu et al., 2020). First, the ages of rocks are a major geological factor in Iceland, with maximum geological ages of 16 Ma (Watkins and Walker, 1977; McDougall et al., 1984). The maximum age is 10,000 years in Þakgil. Herðubreið and Kerlingarfjöll have similar ages of less than 0.8 Ma, whereas Westfjords is between 3.3 and 16 Ma (Thordarson and Larsen, 2007). Second, volcanic systems are another main geological feature (Gudmundsson, 2000; Thordarson and Larsen, 2007). Most surface soils derive from volcanic ash on the original shield surface, and local communities are destroyed and repeat recolonization due to frequent volcanism.

Here, we focused on the main volcanoes, which can influence the geological features of the four regions (Fig. 1, Tables S3, S4). Herðubreið is located around Askja, which is a late Pleistocene to Holocene volcanic center in the middle of the Eastern Rift-Zone of Iceland. Both Krafla and Askja volcano eruptions can influence the geological age of Herðubreið. The last eruption of Krafla occurred in 1984 (Tryggvason, 1986; Harrils et al., 1995), the lava flows cover an area of approximately 24 km² (Gönlvold, 1987) and the total length of the discontinuous volcanic

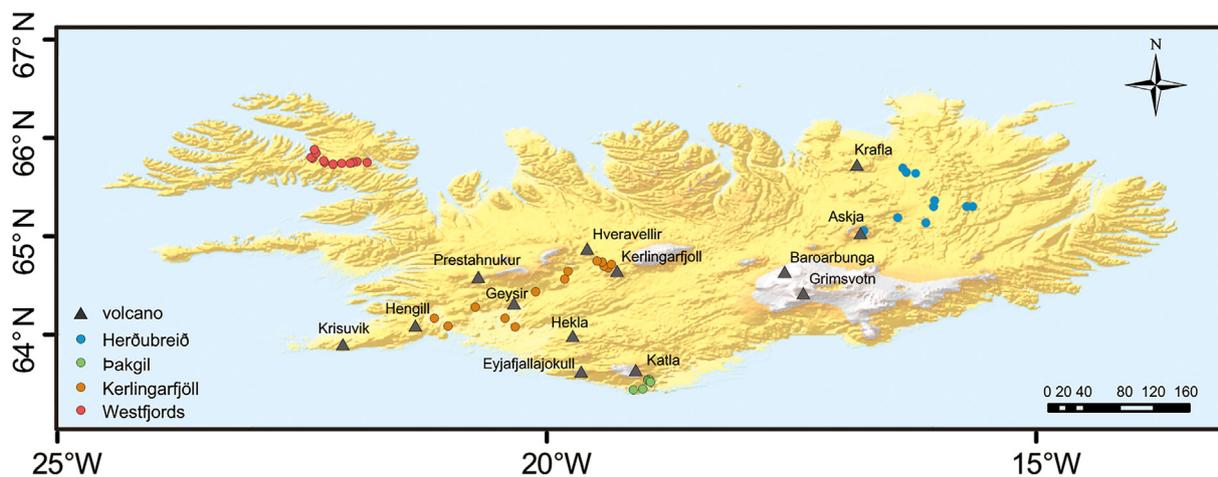


Fig. 1. Distribution of study sites in Iceland. The study area was located in four regions spanning from the southwestern to central parts of Iceland. From the four regions, that is, Herðubreið, Þakgil, Kerlingarfjöll and Westfjords, we collected 13, 9, 11 and 12 biological samples, respectively. Herðubreið is the youngest geological region, followed by Þakgil, Kerlingarfjöll and Westfjords. The dots indicate the sampling sites, and triangles represent the main volcanoes, that can influence the geological features of the four regions.

fissure is 8.5 km (Harrils et al., 1995). The Askja volcanic system, located in North Iceland, experienced its last eruption in 1964 with an 11 km² lava area (Thorarinsson and Sigvaldason, 1962) and a large eruption in 1874–1876 producing globally dispersed ash that was recorded in Scandinavia (Sigvaldason, 2002; Hartley and Thordarson, 2013). This had a fatal impact on the biological communities in Herðubreið. In Þakgil, the region is mainly affected by the Katla volcano, which is one of the most active volcanoes in Iceland (Óladóttir et al., 2018), and is dominated by subglacial phreatomagmatic eruptions (Óladóttir et al., 2007). Katla experienced a large volcano eruption in 1918 (Tómasson, 1996; Duller et al., 2014), which caused a massive glacial outburst flood and produced huge amounts of ash. Kerlingarfjöll is close to the Hveravellir, Geysir, Prestahnjúkur, and Hengill volcanoes, the last eruptions of which date back to 7550 BCE. Kerlingarfjöll may also be influenced by the Hekla volcano, which underwent five eruptions in 1970–2000 (Gudmundsson et al., 1992; Tryggvason, 1994; Ólafsdóttir et al., 2002), but the lava did not reach the region due to the position of associated fissure swarm. Compared to the other three regions, Westfjords is the oldest, and less likely to be affected by volcanoes. Thus, by synthesizing the two geological processes and their impacts on biological communities, we regarded Herðubreið as the youngest due to the new coverage of magma and tephra layers, followed by Þakgil, Kerlingarfjöll and Westfjords.

From the four regions, we studied bacteria, fungi and diatoms from 45 streams along elevational gradients in August 2016 (Fig. 1). In total, we collected 13, 9, 11 and 12 biological samples from Herðubreið, Þakgil, Kerlingarfjöll and Westfjords, respectively, by following previous procedures (Wang et al., 2011). Briefly, each study site was divided into five or ten cross-sections, depending on the stream width. We randomly selected ten stones from riffle or run habitats along these transects and scraped off biofilms of stones for subsamples from a predefined area (~9 cm²) using a toothbrush for diatoms and a sterilized sponge for bacteria and fungi. These subsamples were then pooled into a composite sample for each site. Samples for bacteria and fungi analysis were frozen at -18 °C immediately after sampling. The water samples were collected simultaneously and preserved at -18 °C until chemical analyses could be conducted.

Several important environmental characteristics were measured at each site by following previous procedures (Wang et al., 2017). We logged the latitude, longitude and elevation by using a GPS unit and then measured water conductivity, temperature and pH. The shading (% canopy cover) was measured at ten locations in evenly spaced cross-channel transects covering the whole study section. We obtained depth, width, substratum particle size and current velocity at ten random locations along the same transects. For water samples, total organic

carbon (TOC) was measured by high-temperature oxidation with a Shimadzu TOC analyzer (model 5000; Tokyo, Japan). Total phosphorus (TP, $\mu\text{mol L}^{-1}$) and total nitrogen (TN, $\mu\text{mol L}^{-1}$) were analyzed by peroxodi-sulphate oxidation and the spectrophotometric method (Jin and Tu, 1990). TN or TP is a combination of all the forms of inorganic and organic nitrogen or phosphorus, respectively (Lane et al., 1999). Ammonium (NH_4^+), nitrate plus nitrite (NO_x^-), nitrite (NO_2^-) and phosphate (PO_4^{3-}) were measured using a continuous flow analyzer (Skalar SA 1000, Breda, The Netherlands).

2.2. Community analyses

Community analyses for bacteria, fungi and diatoms were performed mostly according to previous studies (Wang et al., 2017). Briefly, bacterial DNA was extracted from biofilm using a phenol chloroform method (Zhou et al., 1996). 16S rRNA genes were amplified in triplicate using bacterial universal primers [515F, 5'-GTGCCAGCMGCCGCGGTAA-3' and 806R, 5'-GGACTACHVGGGTWTCTAAT-3'] target the V4 region. For fungi, ITS2 region was targeted using the primers: gITS7F, 5'-GTGARTCATCGARTCTTTG-3' and ITS4R, 5'-TCCTCCGCTTATTGATATGC-3'. Further, positive PCR products were confirmed by agarose gel electrophoresis. We combined and quantified PCR products of triplicate reactions with PicoGreen (Eugene, OR, USA), and PCR products from samples to be sequenced were pooled at equal molality to maximize the even-sequencing efforts for all samples. The pooled mixture was purified with a QIAquick Gel Extraction Kit (QIAGEN Sciences, Germantown, MD, USA) and was re-quantified with PicoGreen. Sample libraries for sequencing were prepared according to the MiSeq Reagent Kit Preparation Guide (Illumina, San Diego, CA, USA), then sequenced on the Illumina MiSeq platform. The sequence with the average Phred quality score lower than 25 within a 4 bp sliding window was trimmed using Trimmomatic v0.39 (Bolger et al., 2014) and the resulting reads shorter than 250 bp were discarded. Then, paired-end sequences from MiSeq were joined using FLASH with the minimum overlap 10 bp (Magoc and Salzberg, 2011). Chimeric sequences were removed using de novo chimera detection with USEARCH (Edgar, 2010).

For bacteria, the clustering and selection of operational taxonomic units (OTUs) and taxonomy assignment were achieved using the script 'pick_open_reference_otus.py' in QIIME v1.9.1 (Caporaso et al., 2010b). Operational taxonomic units (OTUs) were clustered at 97% similarity with the seed-based uclust algorithm (Edgar, 2010). Then chimeras were re-moved via UCHIME against ChimeraSlayer reference database in the Broad Microbiome Utilities using PyNAST (Caporaso et al., 2010a). For fungi, the clustering of OTUs was the same as for bacteria. To avoid the effect of variation in abundance or sampling intensity on

biodiversity, the bacterial and fungal sequences were rarefied at 10,000 and 12,000 sequences, respectively.

Diatom samples at each site were identically treated in the laboratory. The diatom frustules of organic material were cleaned by wet combustion with hydrogen 3-EV peroxide. We mounted these cleaned diatoms in Naphrax and then identified and counted 500 frustules per sample using phase-contrast light microscopy (magnification 1000). All diatoms were identified at the species level according to standard European and North American references (Krammer and Lange-Bertalot, 1986-1991; Lavoie & Hamilton, 2008; Metzeltin et al., 2009).

2.3. Statistical analyses

First, we compared multiple facets of biodiversity for bacteria, fungi and diatoms in four regions with different geological ages in Iceland, such as the diversity of alpha (species richness), beta, gamma and the community compositions. We used species richness as our primary measure of alpha diversity and calculated the gamma diversity and beta diversity for the three groups in the four regions, where gamma diversity is measured as total species richness in a region. The beta diversity was calculated for microbial communities using the Sørensen dissimilarity index (Baselga, 2010) based on the presence-absence data, which is because the binary forms of the beta-diversity component indices is more suitable for large spatial or geographical studies than abundance-based data (Legendre, 2014), and the vast majority of explicit studies of beta diversity have focused on presence or absence of species (Koleff et al., 2003). Differences of alpha diversity between geological ages were assessed by Tukey's honest significant differences tests. We performed the permutational multivariate analysis of variance (PERMANOVA) and multivariate pairwise comparisons in beta diversity to test for significant differences in community composition between regions. We further ordinated each taxonomic group by non-metric multidimensional scaling (nMDS) to investigate the relationships between compositions of ecological communities and geological ages.

Second, we studied the cross-taxon congruence in species richness and community compositions among the three groups with Pearson correlation and Mantel tests (9999 permutations) in the four regions, respectively. For the congruence in community composition, we considered beta diversity partitioning components, that is total beta diversity, species turnover and nestedness (Baselga, 2010). This method requires the calculation for each region of three different dissimilarity matrices based on species composition matrix as follows: (1) the total pairwise beta diversity is measured using the Sørensen dissimilarity index between two communities; (2) species turnover is considered the Simpson dissimilarity; and (3) species nestedness dissimilarity can be estimated by subtracting the turnover effect from the total beta diversity.

Third, to quantify the relative importance of the environmental and spatial variables on the three beta indices for bacteria, fungi and diatoms, we used multiple regression on matrices (MRM) for distance matrices approach (Legendre et al., 1994). Prior to the statistical analyses, all environmental variables were z-score standardized (i.e., mean = 0, SD = 1), then we excluded the variables with high correlation coefficients (Pearson's $r > 0.7$). NO_2^- and NO_3^- were highly correlated with TN (Pearson's $r = 0.79, 0.71$), PO_4^{3-} was highly correlated with TP (Pearson's $r = 0.84$), thus, NO_2^- , NO_3^- and PO_4^{3-} were excluded from further analyses because total nutrient concentrations are better preserved in remote field conditions. A Euclidean distance matrix was calculated for other variables. For spatial distance, we converted geographic latitude and longitude coordinates to kilometer-based grid coordinates, and the pairwise spatial distances were then estimated using the Euclidean distance. Finally, the partial regression coefficients of these variables in the model were calculated and their significance was tested through 9999 permutations (Martiny et al., 2011).

Fourth, we examined the relationships between spatial distance and beta diversity metrics (that is, the total beta diversity, species turnover

and nestedness) with Mantel test (9999 permutations) for the three taxonomic groups across geological ages.

Finally, we used a classic null model approach based on the Raup-Crick metric of beta diversity (β_{RC}) following Chase et al. (2011) method to estimate the relative importance of different community assembly processes for bacteria, fungi and diatoms. Since regional species pool includes those species that can possibly colonize a given site within a reasonable time period, we defined the regional species pool in our Raup-Crick null model as the observed communities in each region. β_{RC} uses a randomization approach to estimate the probability that the expected number of shared species between any two communities is greater than their observed number of shared species. It is impossible for us to distinguish detailed community assembly processes combining both β_{RC} and phylogenetic beta diversity (Chase and Myers, 2011; Stegen et al., 2015) because we lacked phylogenetic information of diatoms. Comparison of β_{RC} provided a guide to whether deterministic processes had occurred during the community assemblages: The values of $0.95 < \beta_{RC} < 1$ and $-1 < \beta_{RC} < -0.95$ indicate that the communities were either less similar or more similar than expected by chance, and values of $-0.95 < \beta_{RC} < 0.95$ represent no difference in the observed similarity from the null expectation. The β_{RC} metric was converted to a binary number to identify the relative importance of the deterministic and stochastic processes. Pairwise comparisons of communities were given the value 0 when $-0.95 < \beta_{RC} < 0.95$, and otherwise were assigned the value 1. The proportions of the two ecological processes were estimated as the ratio between the sum of all corresponding pairwise tests (comparisons with values equal to 0 or 1) and the total number of possible pairwise comparisons. For instance, the relative contribution of deterministic processes was estimated as the ratio between the number of values 1 and the total numbers of values 1 and 0. Furthermore, we performed variation partitioning analyses (Anderson and Gribble, 1998; Legendre and Legendre, 2012) to reveal the influence of environmental and spatial variables on community composition with Hellinger-transformation. The spatial structures among sites were modeled by principal coordinates of neighbor matrix analysis (Borcard and Legendre, 2002; Legendre et al., 2013), which generates multiple spatial variables that model spatial structures at different spatial scales. These spatial variables were used as explanatory variables in the analyses. The environmental variables were the same as those in the MRM model, and the significant variables were selected by forward selection against the community compositions with 9999 permutations for all three taxa.

All above statistical analyses were done with *betapart* V1.5.1 (Baselga and Orme, 2012), *vegan* V2.5-6 (Oksanen et al., 2013), *SpatialEpi* V1.2.3 (Kim and Wakefield, 2010), *ecodist* V2.0.1 (Goslee and Urban, 2007), and *packfor* V0.0-8 (Dray et al., 2009) in R Core Team (Core et al., 2014).

3. Results

3.1. Alpha, beta and gamma diversity

In the four regions of different geological ages, there were clear variations in the alpha, beta, and gamma diversity and the community composition for bacteria, fungi and diatoms (Fig. 2). For alpha and gamma diversities, bacteria showed increasing patterns across geological ages, except for the oldest region Westfjords, although differences were not significant for alpha diversity (Fig. 2a, d, S1). In contrast, fungi reached a minimum in the intermediate-aged region Þakgil, with a maximum in the oldest region ($P < 0.05$, Fig. 2b, e, S1). The alpha and gamma diversities of diatoms were initially high in the youngest region, decreasing to a minimum in the intermediate-aged region (Fig. 2c, f). For community compositions, there were significant differences among the four regions (PERMANOVA, $P < 0.05$, Table S1). The beta diversity increased across geological ages for bacteria and fungi, except for the oldest region, where it reached its minimum (Fig. 2g, h, S2). However, there was no obvious change in diatom beta diversity (Fig. 2i).

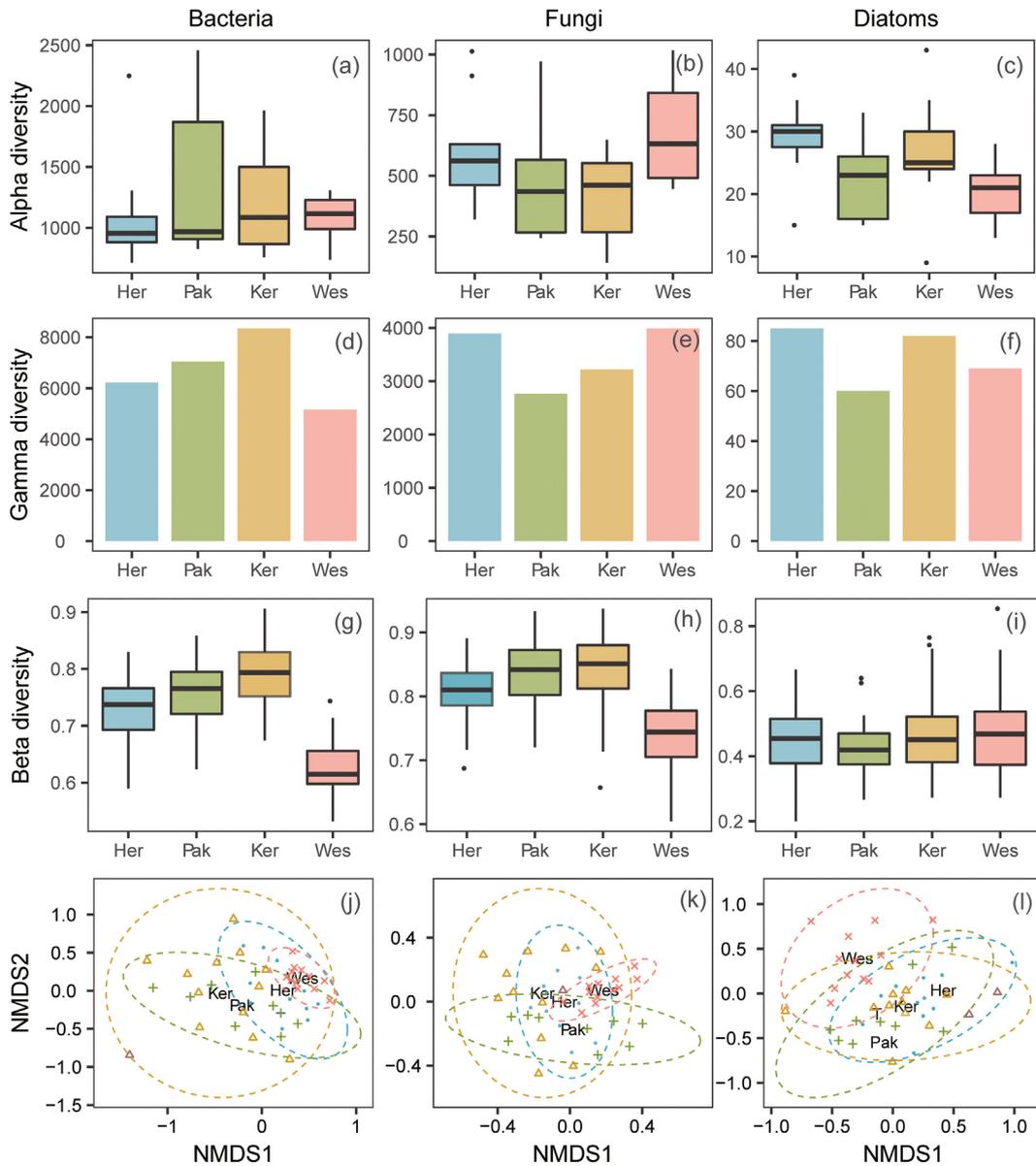


Fig. 2. The alpha, beta and gamma diversity and community compositions in four regions with different geological ages in Iceland, that is Herðubreifð (Her), Þakgil (Pak), Kerlingarfjöll (Ker), and Westfjords (Wes). Herðubreifð is the youngest geological region, followed by Þakgil, Kerlingarfjöll and Westfjords. For the alpha and beta diversity of each taxonomic groups, the boxes contain all values within the 25th and 75th percentiles, the whiskers extend to 150% of the interquartile range from the box, and outliers are represented by dots. For community compositions, non-metric multidimensional scaling plot of the three assemblages, grouped by region (indicated by colour and shape) (j-l). This plot illustrates that the communities in the oldest region were more similar than the communities in younger regions for bacteria and fungi, which is supported by their similar trends of beta diversity (g-i, upper panels).

Similar patterns in beta diversity were consistent with the nMDS plots of the community compositions for the three taxonomic groups, which is especially true for bacteria and fungi showing the strongest clustering in the oldest region (Fig. 2j-l). Furthermore, for the mean beta diversity of the three taxonomic groups, fungi showed the highest values from 0.74 to 0.85, and diatoms had the lowest values from 0.43–0.48. Similar trends were found for abundance-based dissimilarity of bacteria and fungi across geological ages, while diatoms reached a maximum in the intermediate-aged region (Figs. S3, S4), which is contrary to the results of beta diversity based on abundance-based dissimilarity.

3.2. Extent of cross-taxon congruence and drivers of community dissimilarity

The cross-taxon congruence regarding total beta diversity and species turnover was the strongest in the oldest region, evidenced by their significantly ($P < 0.05$) positive relationships (Table 1, Fig. S5).

For instance, bacteria and diatoms showed a significant ($P < 0.05$) correlation for total beta diversity or species turnover with Mantel r of 0.53 and 0.45 in the oldest region, respectively. Such a strong relationship was also found for alpha diversity with a Pearson coefficient of 0.71 ($P < 0.01$). The relationship between bacteria and fungi increased in older regions with Mantel r from 0.26 to 0.70 for the total beta diversity and species turnover. In the youngest region, there was a marginally significant ($r = 0.58$, $P = 0.06$) relationship between bacteria and diatoms in species richness, and the correlations among total beta diversity of the three taxonomic groups were all significant, with Mantel r of 0.34–0.66 ($P < 0.05$).

In multiple regression model, environmental factors were pivotal ($P < 0.05$) for total beta diversity and species turnover of the three groups (Fig. 3). For these two beta indices of bacteria ($R^2 = 0.31$, 0.34 respectively) (Table 1), pH contributed the largest partial regression coefficient ($b = 0.33$, 0.37, respectively, $P = 0.001$), followed by elevation, temperature and NH_4^+ (Fig. 3a, d). However, pH ($b = 0.23$, $P < 0.01$) and

Table 1

The correlations among bacteria, fungi and diatoms regarding species richness and community dissimilarities in the four regions. The Pearson correlation was used for species richness among the three taxonomic groups. For community dissimilarity, we included total beta diversity and its two components, that is species turnover and nestedness, and used Mantel test to examine the correlations.

Biodiversity		Pearson r or Mantel r			
		Herðubreið	Þakgil	Kerlingarfjöll	Westfjords
Alpha	Bacteria-Fungi	0.09	0.76*	-0.35	0.09
	Bacteria-Diatoms	0.58+	-0.06	0.19	0.71**
	Fungi-Diatoms	0.29	0.03	0.00	-0.21
Total beta	Bacteria-Fungi	0.34*	0.63*	0.69**	0.70**
	Bacteria-Diatoms	0.66**	0.24	0.21	0.53**
	Fungi-Diatoms	0.39*	0.39*	0.19	0.46*
Turnover	Bacteria-Fungi	0.26*	0.62**	0.46*	0.62**
	Bacteria-Diatoms	0.21	0.38*	0.05	0.45*
	Fungi-Diatoms	0.46*	0.22	0.11	0.35*
Nestedness	Bacteria-Fungi	-0.13	0.36*	0.03	0.03
	Bacteria-Diatoms	0.00	-0.07	-0.15	0.43*
	Fungi-Diatoms	0.03	0.05	0.00	-0.15

Significance levels: +, $P \leq 0.07$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

NH_4^+ ($b = -0.26, P < 0.01$) were the most important for total beta diversity and species turnover of fungi, respectively (Fig. 3b, e). For diatoms, TOC was the strongest predictor ($b = 0.30-0.33, P = 0.001$) in explaining the variations of total beta diversity and species turnover (Fig. 3c, f). In addition, spatial variables ($b = 0.10-0.14, P \leq 0.063$) were important for total beta diversity and species turnover of fungi and diatoms. However, environmental and spatial variables were not significant for nestedness of the three groups (Fig. 3g-i).

3.3. Patterns of community structure across geological ages

Null model analyses showed that there were time-dependent changes in the relative influences of stochastic and deterministic processes across geological ages (Fig. 4, left panel). For bacteria and fungi, communities were mainly structured by deterministic processes, with the relative contribution of deterministic processes exceeding 67% and 52%, respectively, while diatoms showed a stronger stochasticity, with

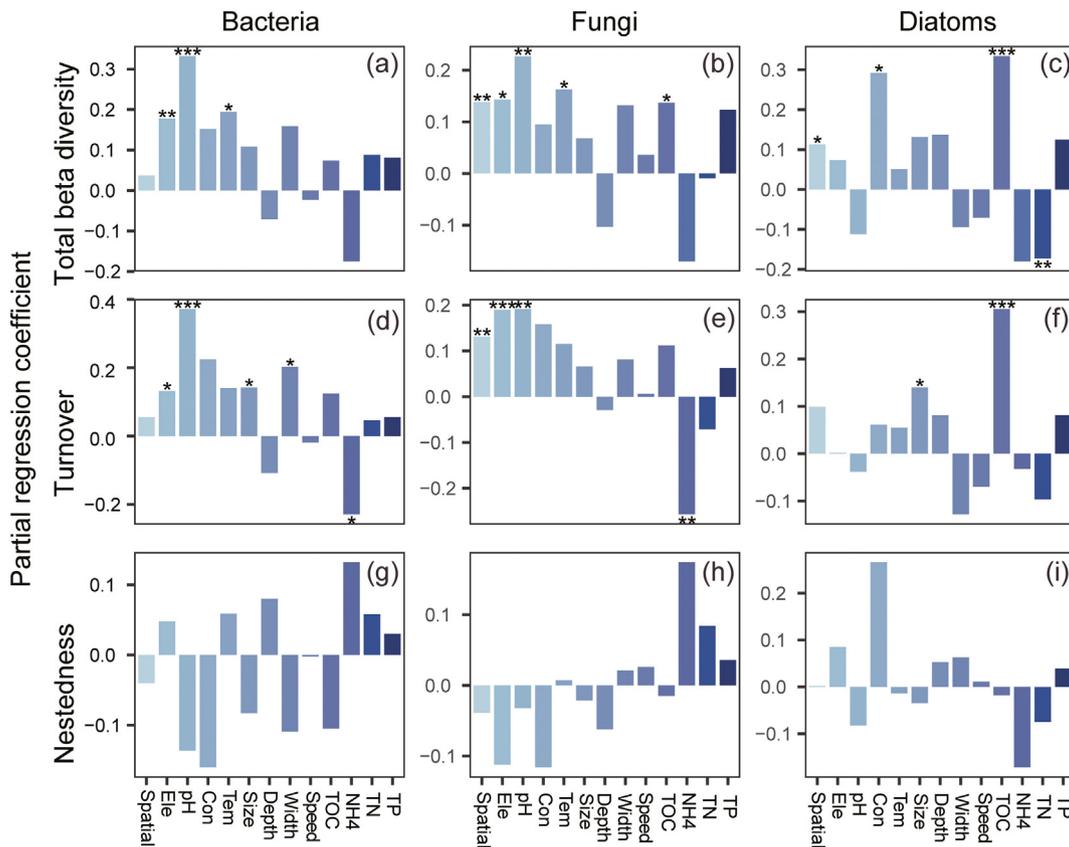


Fig. 3. The relative importance of the environmental and spatial variables on beta diversity components for bacteria, fungi and diatoms based on multiple regression models of distance matrices. We considered total beta diversity (a-c) and its partitioning components, that is species turnover (d-f) and nestedness (g-i). For spatial distance, we converted geographic latitude and longitude coordinates to kilometer-based grid coordinates, and the pairwise spatial distances (Spatial) were then estimated using the Euclidean distance. For environmental variables, we included elevation (Ele), water conductivity (Con), pH, temperature (Tem), substratum particle size (Size), water depth (Depth), stream width (Width), current speed (Speed), total organic carbon (TOC), the concentrations of NH_4^+ (NH4), total nitrogen (TN), and total phosphorus (TP). The significance of variables was assessed with 9999 permutation test. *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

the relative contribution of deterministic processes less than 39%. The relative influence of deterministic processes was stronger for bacteria and fungi at the intermediate ages (e.g., Þakgil and Kerlingarfjöll). However, the stochasticity increased towards older regions for diatoms, with the relative contribution of deterministic processes decreasing from 38.18% to 28.79%.

Consistent with null model results, the variation partitioning analyses for bacteria and fungi showed that a higher proportion of variation in community composition could be explained by abiotic environmental variables, whereas the pure effects of spatial factors were important in the youngest region (Fig. 4, right panel). More precisely, pure environmental effects explained 0–16.24% of the variation in bacterial and fungal community compositions. The pure spatial effects accounted for 5.01–15.20% of the variation in their communities in the youngest region (Herðubreið) and 0.93–2.44% in the oldest region (Westfjords). For diatoms, most of the explained proportions were linked to pure effects of environmental (5.03–27.59%) and spatial (0.88–10.31%) variables in the four regions (Fig. 4, right panel).

For the three taxonomic groups, total beta diversity and species turnover were significantly ($P < 0.05$) positively related to the spatial distance in the youngest and oldest regions (Table 2, Fig. S6). Such distance-decay relationships were the strongest in the youngest region, followed by those in the oldest region. For instance, the Mantel r between total beta diversity or species turnover and spatial distance ranged from 0.39 to 0.50 in the youngest region and 0.21–0.37 in the oldest region. Interestingly, bacterial nestedness was significantly spatially structured in an intermediate-aged region (e.g., Þakgil, $r = 0.16$, $P < 0.05$).

4. Discussion

Cross-taxon congruence has been given considerable attention in recent ecological, biogeographical and conservation studies (Heino et al., 2009; Rooney et al., 2015), but it is unclear how such biotic relationships vary with long-term ecosystem development (Ozkan et al., 2014). To the best of our knowledge, this is the first study to reveal the cross-taxon congruence among multiple microbial groups and their community assembly

Table 2

Mantel tests for the correlations between the community dissimilarity (total beta diversity, species turnover, and nestedness) and the spatial distance for bacteria, fungi and diatoms in the four regions.

	Beta diversity	Herðubreið	Þakgil	Kerlingarfjöll	Westfjords
Bacteria	Total beta	0.50*	0.12	0.14	0.21⁺
	Turnover	0.39*	−0.04	−0.02	0.22⁺
	Nestedness	0.04	0.16*	0.26	−0.05
Fungi	Total beta	0.39*	− 0.01*	0.26	0.37*
	Turnover	0.44*	− 0.09*	0.27	0.37*
	Nestedness	−0.21	0.12	−0.12	−0.13
Diatoms	Total beta	0.41*	−0.14	0.13	0.31*
	Turnover	0.50*	− 0.22*	0.26	0.27*
	Nestedness	−0.24	0.12	−0.12	0.14

Significance levels: ⁺, $P \leq 0.07$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

processes across regions with different geological ages. Here, we found that bacteria and fungi showed contrasting trends in alpha or gamma diversities across regions with different geological ages, but their beta diversity patterns were consistent, being the lowest in the oldest region. The total beta diversity or species turnover showed the strongest cross-taxon congruence in the oldest region for the three taxonomic groups, and were increasingly coupled towards older geological ages in bacteria and fungi. Deterministic processes, dominant for bacteria and fungi, had the highest relative influence in the intermediate-aged regions, whereas diatoms showed higher stochasticity.

4.1. Biodiversity patterns across geological ages

There were clear variations in alpha, beta and gamma diversity in bacteria, fungi and diatoms across the regions with different geological ages, the patterns of which have been rarely reported for microbes so far. Bacterial alpha and gamma diversities peaked in the intermediate-aged region, which is consistent with the maximum species number in intermediate ages of dynamic community assembly for macroorganisms, such as spiders (Gillespie, 2004) and soil arthropods (Gruner, 2007). However, the trends of fungal alpha and gamma diversities reached a

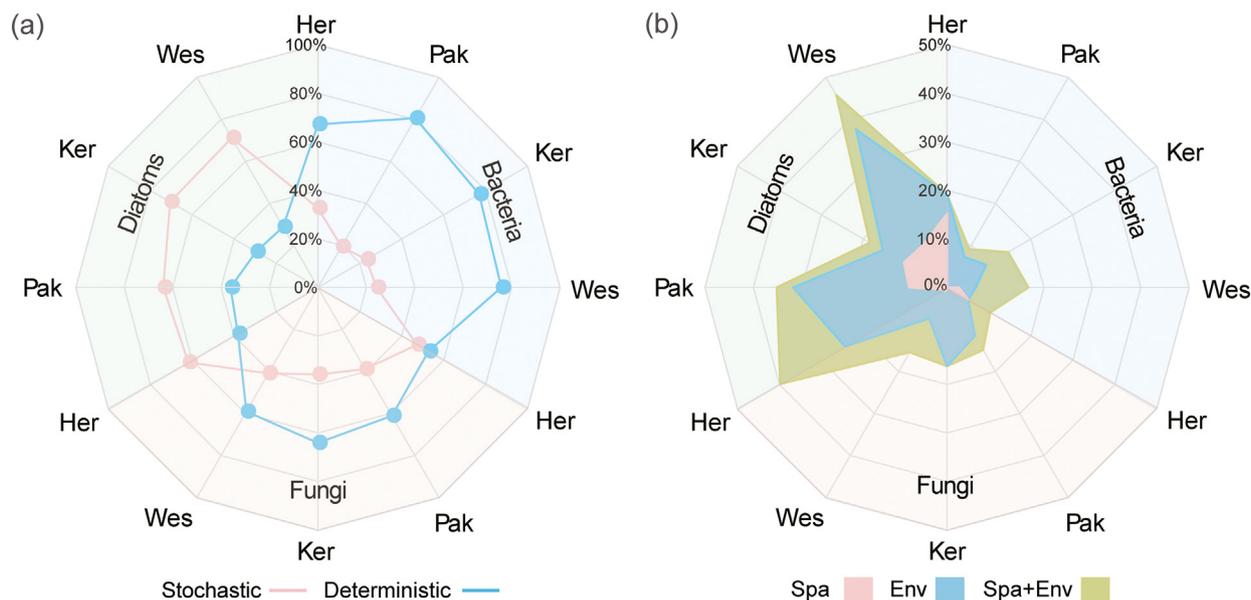


Fig. 4. The relative importance of deterministic or stochastic processes for bacteria, fungi and diatoms in four regions with different geological ages. The four regions are Herðubreið (Her), Þakgil (Pak), Kerlingarfjöll (Ker), and Westfjords (Wes). For geological ages, we regarded Herðubreið as the youngest, followed by Þakgil, Kerlingarfjöll and Westfjords. The left panel shows the relative influence of two ecological processes for the three taxonomic groups across geological ages in null model approach based on the Raup-Crick metric of beta-diversity following the Chase et al. (2011) algorithm. The right panel illustrates the proportions of variations in community composition explained by environmental and spatial variables based on variation partitioning analyses. Env and Spa: the pure variation explained by environmental and spatial variables, respectively; Spa+Env: the joint effects of these variables.

minimum in the intermediate-aged region, which disagrees with earlier findings of increasing (Shi et al., 2018) or decreasing (Albornoz et al., 2016) fungal diversity along soil chronosequences. With regard to beta diversity, it increased both for bacteria and fungi across regions with different geological ages, except for the oldest region with a minimum value, while there were no obvious changes for diatom beta diversity. As succession proceeds, such high variations in beta diversities of bacteria and fungi may be associated with an increase in deterministic processes, although high beta diversity also likely resulted from dispersal limitation and stochastic ecological drift (Chase, 2007, 2010). Our findings support the idea that species richness and community compositions are affected by geological age, which is also revealed in macroorganisms, such as trigonopterus weevils (Tanzler et al., 2016) and mites (Zaitsev et al., 2012). Even if microbes evolve fast and show high dispersal ability, their communities can still show imprints of historical events (Vyverman et al., 2007). Geological processes can influence local environment and soil types (Borges and Brown, 1999) through weathering and erosion, and then affect the distribution patterns of biodiversity and compositions (Hu et al., 2020). Thus, geological ages explain at least partly the environmental differences among regions due to the effect of geological processes, which then affect water quality and finally biotic communities. Furthermore, among the three groups, the mean beta diversity of fungi was the highest, whereas diatoms showed the lowest mean beta diversity, which is consistent with previous studies showing lower beta diversity in autotrophs than organisms higher up the food web (Orwin et al., 2006). Such contrasting patterns in alpha, beta or gamma diversity among the three groups might be because of their different adaptive strategic responses to extrinsic environments (Png et al., 2018), and differences in ecological features, such as trophic position (Kolomiytsev and Poddubnaya, 2018).

4.2. Cross-taxon congruence for biodiversity across geological ages

We found a strong cross-taxon congruence for alpha or beta diversities among the three taxonomic groups in the youngest and oldest regions, especially for the latter. In other words, the three taxonomic groups appear to be in a consistent stage in the youngest region, but become decoupled in the intermediate-aged regions, and finally form the most consistent structure in the oldest region. For instance, the three taxonomic groups showed significant relationships among their total beta diversity or species turnover in the oldest region, in contrast to the increased decoupling of prokaryotic and eukaryotic communities in the older stages of ecosystem development in soils (Turner et al., 2019). The strong cross-taxon congruence in the youngest regions could occur because of random effects (Gaston, 2000), and then as succession proceeds, the increased competition for resources among organisms may lessen the congruence between different groups (Toranza and Arim, 2010). In the oldest region, the strongest cross-taxon congruence may be due to the suppression of biological competition at the end of successional stages (Jackson et al., 2001) and similar response of organisms to environmental factors (Ozkan et al., 2014). In addition, we note that the level of cross-taxon congruence may depend on diversity indicators used, such as species richness and beta diversity partitioning components (Su et al., 2004; Gioria et al., 2011; Schalkwyk et al., 2019b), which can influence the predictive power of cross-taxon congruence. This phenomena may be because they behave differently in space and time and are possibly driven by different ecological and biogeographical processes (Kessler et al., 2009; Wang et al., 2012). Our results suggest the measures of beta diversity are better at revealing the congruence among different assemblages than alpha diversity, such as species richness (Barlow et al., 2007; Kessler et al., 2009; Vilmi et al., 2020). Nonetheless, we encourage future studies to consider multiple biodiversity metrics to reveal a reliable view of cross-taxon congruence.

The observed biodiversity congruence in the oldest region is probably attributable to the strong and stable environmental selection at the

end of successional stages (Dini-Andreote et al., 2015), including species-to-species associations and abiotic habitat filtering. Between-species associations, such as biotic interactions and trophic relations, play important roles in shaping the congruence of species diversity and community composition over long-term periods (Ozkan et al., 2014; Schalkwyk et al., 2019b). The interactions can promote species diversity through community assembly processes, which is supported by significant correlations for species richness or beta diversity between bacteria and diatoms in the youngest and oldest regions. For instance, the abundance and community structure of bacteria greatly depend on the growth, species identities and physiological status of algae (Goedkoop et al., 1997; Grossart et al., 2005), and the colonization of algae could provide an enriched microenvironment to support high bacterial growth rates (Murray et al., 1986; Gardes et al., 2011). For bacteria and fungi, the congruence of their total beta diversity or species turnover was increasingly coupled towards older regions, which is consistent with their similar patterns of beta diversity across geological ages. Bacteria and fungi play significant roles in organic matter degradation, but their contributions vary across detrital types and among habitats in streams (Sinsabaugh and Findlay, 1995). Fungi mainly degrade the large size classes of particulate material (Heino et al., 2014), while bacteria dominate in finer particulate matter (Findlay et al., 2002), and are able to utilize residual organic matter degraded by fungi. Thus, the congruence of bacteria and fungi may be due to their complex biotic interactions (Leibold and McPeck, 2006b), such as mutualism, which could promote the coexistence of trophically similar species in highly structured food webs.

Additionally, abiotic environmental variables can influence cross-taxon congruence in biodiversity (Englund et al., 2009; Burrascano et al., 2018). Deterministic and stochastic processes could promote the congruence of ecologically similar or equivalent species (Leibold and McPeck, 2006b). A positive correlation of species richness or beta diversity between bacteria and fungi might be observed because they covary with the similar environmental variables (Ozkan et al., 2014; Rapacciolo et al., 2019). Environmental factors have a strong influence on the biodiversity, distribution of microbial communities, and thereby affect community succession processes through time (van der Gast et al., 2008; Dini-Andreote et al., 2015; Giam and Olden, 2016). For bacteria and fungi, pH was important for affecting their total beta diversity and species turnover, followed by elevation, temperature and NH_4^+ . Extreme pH conditions could impose stricter restrictions on microbial communities, exert strong environmental selective pressures, and lead to community assembly more clustered through deterministic processes (Tripathi et al., 2018). Moreover, water temperature is a major environmental factor that drives the temporal variation in composition of macroorganisms (Brown and Milner, 2012) and microorganisms (Gu et al., 2020) in streams and lakes, and regulates the development of organisms (Hullar et al., 2006), such as microbial population growth and activity (Kim et al., 2014). The similar effects of environments, such as pH and temperature, may cause strong cross-taxon congruence in the total beta diversity or species turnover between bacteria and fungi. For diatoms, TOC was the strongest predictor in explaining the variations of total beta diversity and species turnover, which is line with the finding that community structure of benthic diatoms is related to TOC in lagoons of the Po River Delta, and high TOC can stimulate algal development (Cibic et al., 2019). This may indicate the influence of nutrient concentrations on diatom aggregation.

4.3. Stochastic and deterministic processes underlying community assembly

Finally, we assessed the relative importance of deterministic and stochastic processes to community assembly of bacteria, fungi and diatoms. For bacteria and fungi, communities were mainly affected by deterministic processes, which was further supported by the fact that the pure effects of environmental factors were higher than those of

spatial variables for the two groups in the four regions, except for the youngest region. Similar microbial ecological processes can be found in other habitats, such as rivers (Graham et al., 2017) and desert environments (Caruso et al., 2011). For instance, soil bacterial communities are governed by deterministic processes in Fynbos, South Africa (Moroenyane et al., 2016). However, fungal communities of soils in Scotland exhibit high stochasticity via dispersal limitation and stochastic demographics (Powell et al., 2015). The contrasting results may be due to the substantially different habitat contexts: Compared with soil microbes, microbial communities in streams are more disturbed by ambient environmental variations, such as water movement, and these communities have higher dispersal ability. For diatoms, however, stochasticity had a stronger influence. These contrasting results between bacteria or fungi and diatoms may be due to their different trophic positions or different methods used to reveal the community compositions. Compared to microscopic, molecular techniques more sensitively distinguish morphologically similar species.

Furthermore, our analyses revealed a predictable time-dependent variation in the relative importance of deterministic and stochastic processes across geological ages. The main geological feature in Iceland is volcanic systems, and large-scale volcanic eruptions can lead to the widespread extinction of living things, loss of original soil conditions (Chen et al., 2020) and disruption of terrestrial and aquatic ecosystems (Van Eaton et al., 2013). The lava flow and ash deposits produced in the process create the original land surface (Yoshitake et al., 2012). Microorganisms are among the first re-colonizers in the initially sterile surface (Guo et al., 2014; Kim et al., 2018), since then, plants and animals begin to re-colonize and mobilize nutrients, which together contribute to early community succession and ecosystem development process (Ooum, 1969; Zeglin et al., 2016). In the youngest region, there were the strongest relationships between their total beta diversity or species turnover and spatial distance for bacteria and fungi. Random events, such as stochastic differences among taxa in births, deaths and migration, can influence nearby community compositions, leading to a distance-decay pattern (Hanson et al., 2012). As succession proceeds, deterministic processes may become increasingly important as resource competition and depletion drive the development of communities (Jackson et al., 2001; Chase, 2010; Fierer et al., 2010), which is consistent with previous studies showing a progressively increasing tendency in the relative importance of deterministic processes for bacteria over 105 years (Dini-Andreote et al., 2015). Further, the impact of deterministic processes slightly declined for the three groups, which is supported by that the total beta diversity or species turnover of the three groups showed marginally significant correlations with spatial distance. In later succession stages, environment becomes less harsh, and every community effectively utilizes a variety of nutrient resources in habitats, such as available carbon sources (Jackson et al., 2001). Furthermore, the relatively stable environments are associated with stochasticity (Chase, 2007) and allow species to move towards specialization with a simultaneous narrowing of their ecological niches, which in turn reduces niche overlap (Kolomytsev and Poddubnaya, 2018).

Therefore, we propose a conceptual model to predict the shifts in stochastic and deterministic processes across geological ages (Fig. 5). Specifically, we hypothesize that there are four phases with distinct scenarios in community assembly across geological ages (Fig. 5).

(1) Stochastic processes strongly influence microbial community assembly in initial community establishment. At the initial stage of community establishment, there are large random differences in births, deaths and immigration among taxa and weak competition for space and resources, and thus, stochasticity prevails (Sigler and Zeyer, 2002; Leibold and McPeck, 2006a; Ferrenberg et al., 2013). (2) The importance of deterministic processes progressively increases due to strong environmental filtering and interspecific interactions, while two opposing scenarios subsequently emerge between bacteria or fungi and diatoms due to their different trophic positions or feedback dynamics (Reynolds et al., 2003). For bacteria and fungi, the relative importance

of deterministic processes continues to increase, while it shows a transitory peak for diatoms and then decreases, stochastic processes dominate diatom community assembly. (3) Over a longer period, the role of deterministic processes marginally decreases for bacteria and fungi, whereas a dynamic balance emerges between deterministic and stochastic processes for diatoms. This may be because communities are more mature with ages and not that affected by environment or other species like in earlier phases. (4) A stable balance between the two ecological processes is maintained due to stable environment over long-term periods, and the three taxonomic groups finally form the most consistent structure.

Compared to previous studies (e.g., Dini-Andreote et al., 2015), our findings have important implications regarding community assembly processes over long-term geological periods. First, we characterized the shifts in the two ecological processes over longer time scales, and the maximum geological ages of Iceland date to 16 Ma. Second, we focused on multitrophic microbial groups, including bacteria, fungi and diatoms, and found two different scenarios among the three groups regarding the shifts in deterministic and stochastic processes over long-term geological periods. Finally, the three taxonomic groups all showed a marginal decrease in the relative importance of deterministic processes in later succession stages, which is rarely reported.

Nevertheless, there are two caveats for the interpretation of our results. First, the different spatial distances of the four regions sampled may influence the relationship between spatial distance and beta diversity. For example, the correlation between geographic distance and bacterial community similarity varies among the local, regional and continental scales in salt marsh sediments, and the average similarity between two samples tends to decrease with larger distances (Martiny et al., 2011). We argue however that our results from these four regions are still comparable due to their relatively similar environmental variations at local scales (Figs. S7, S8, Table 5). There was no distinct cluster pattern for environmental variables among the four regions by principal component analysis (Fig. S7), and detailed environmental parameters at each site was provided in the supplementary tables (Tables S3, S4). Second, there are only three microbial groups studied in the streams from four regions in Iceland showing different geological ages due to volcanic activity. Further studies are encouraged to evaluate the generality of current conceptual model of community assembly processes over long-term geological periods with more taxonomic groups in more geographical regions.

5. Conclusions

Overall, this study aimed to reveal that the cross-taxon congruence of microbial communities and the underlying ecological processes of community assembly vary over long-term periods of geological age. Our data supported the hypothesis that the strongest cross-taxon congruence occur among taxa in the region with the oldest geological age. In particular, such congruence between bacteria and fungi increased towards older geological ages. Biotic associations and environmental variables were important for the level of cross-taxon congruence in the total beta diversity and species turnover of the three studied taxonomic groups. In addition, our hypothesis that relatively stronger roles for deterministic processes occur in the older regions was not the case. Deterministic processes, being dominant for bacterial and fungal assemblages, had the highest relative influence in the intermediate-aged regions, whereas diatoms showed overall higher stochasticity. We further proposed a four-phase conceptual model to depict the shifts of balance in deterministic and stochastic processes across geological ages. It is worth noting that there were two different scenarios between bacteria or fungi and diatoms regarding the shifts in deterministic and stochastic processes over long-term geological periods. Further detailed studies are encouraged to investigate multiple microbial community assembly processes and the underlying mechanism over long-time periods.

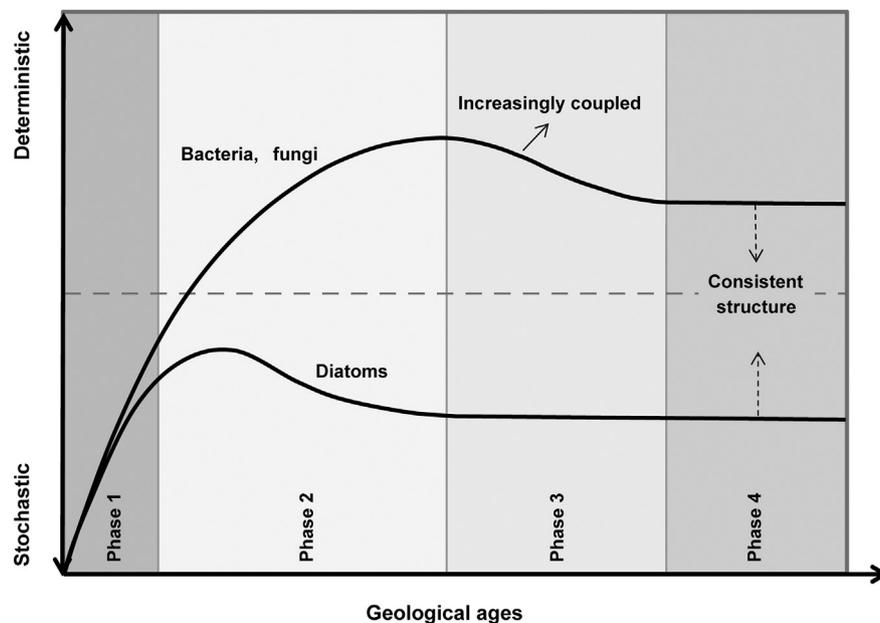


Fig. 5. Conceptual model showing four phases of community assembly across geological ages. (1) Stochastic processes strongly influence the microbial community assembly in initial community establishment. (2) The importance of deterministic processes progressively increases, while two different scenarios subsequently emerge among the three groups. For instance, the relative importance of deterministic processes continues to increase for bacteria and fungi, whereas shows a transitory peak for diatoms and then decrease, stochastic processes dominate diatom community assembly. (3) The influence of deterministic processes marginally decreases for bacteria and fungi, while a dynamic balance emerges between deterministic and stochastic process for diatoms. (4) Stable environment leads to dynamic balance between the two ecological processes, and the three taxonomic groups finally form the most consistent structure.

Declaration of competing interest

The authors declare no conflict of interest.

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Data accessibility

The bacteria and fungi sequences were deposited in NCBI Short Read Archive under accession number PRJNA603626.

CRediT authorship contribution statement

JW conceived the idea. JW and FP collected the samples and provided physicochemical and biological data. JS and VT provided diatom data. WZ performed statistical analyses. WZ wrote the first draft of the manuscript. WZ and JW finished the manuscript with the contributions from other co-authors. All authors contributed to the intellectual development of this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.145103>.

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