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Stream diatom community assembly processes in islands and continents: A global perspective

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Abstract

Aim: Understanding the roles of deterministic and stochastic processes in community assembly is essential for gaining insights into the biogeographical patterns of biodiversity. However, the way community assembly processes operate is still not fully understood, especially in oceanic islands. In this study, we examine the importance of assembly processes in shaping diatom communities in islands and continents, while also investigating the influence of climate and local water chemistry variables on species distributions.

Location: Global.

Taxon: Stream benthic diatoms.

Methods: We used diatom datasets from five continents and 19 islands and applied beta diversity analyses with a null model approach and hierarchical joint species distribution modelling. To facilitate comparisons with continents, we used continental area equivalents (CAEs), which represent continental subsets with comparable areas and the same number of study sites as their corresponding islands counterparts.

Results: We found that homogeneous selection (i.e., communities being more similar than the random expectation) was the dominant assembly process within islands whereas stochastic processes tended to be more important within continents. In addition, assembly processes were influenced by study scale and island isolation. Climatic variables showed a greater influence on species distribution than local factors.

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However, in islands, local environmental variables had a greater impact on the distributions of unique taxa as opposed to non-unique taxa.

Main Conclusions: We observed that the assembly processes of diatom communities were complex and influenced by a combination of deterministic and stochastic forces, which varied across spatial scales. In islands, there was no universal pattern of assembly processes, given that their influence depends on abiotic conditions such as area, isolation, and environmental heterogeneity. In addition, the sensitivity of species occurring uniquely in islands to local environmental variables suggests that they are perhaps less vulnerable to climatic changes but may be more influenced by changes in local physicochemistry.

KEYWORDS

beta diversity, climate, community assembly, freshwater diatoms, Island biogeography, streams

1 | INTRODUCTION

Biological communities are shaped by a combination of deterministic and stochastic factors, which are frequently referred to as community assembly processes (Chase & Myers, 2011). Deterministic processes encompass non-random ecological processes such as environmental filtering and biotic interactions (Stegen et al., 2012). Such deterministic processes can lead to either similar (homogeneous selection) or dissimilar (heterogeneous selection) species composition depending, for example, on study scale and dispersal limitation of species (Chase et al., 2011; Ning et al., 2020). In contrast, stochastic processes include demographic stochasticity, such as random dispersal, births and deaths (ecological drift) (Vellend, 2016; Vellend et al., 2014), and environmental stochasticity due to random environmental fluctuations (Lande, 1993; Shoemaker et al., 2020).

Recently, multiple studies have investigated the community assembly processes in different ecosystems and taxa in order to define their relative importance in controlling biodiversity. Studies found that the extent to which communities are shaped by deterministic and/or stochastic processes depends on several fundamental factors. Firstly, their balance may be affected by organismal body size. However, the evidence so far is conflicting because either stochastic (Farjalla et al., 2012; Logares et al., 2018; Roguet et al., 2015; Soininen et al., 2013; Vilmi et al., 2021) or deterministic factors (Pound et al., 2019; Powell et al., 2015; Soininen, 2023) may play a more prominent role in structuring the communities of smaller organisms, such as the microorganisms studied here. The second factor is ecosystem type, whereby taxa in lotic systems, the focus of our study, may often exhibit stochastic distributions due to physical disturbance, unlike taxa in other aquatic systems (Soininen, 2014; Soininen et al., 2013). Thirdly, as spatial scale increases, stochastic factors typically become more prevalent in structuring biological communities due to stronger dispersal limitation at larger, biogeographical scales (Soininen, 2023).

Understanding the interplay between deterministic and stochastic processes is critical for drawing conclusions about species

biogeography. In this regard, islands where species distribution and diversity are strongly influenced by isolation and area with impact on dispersal and extinction, respectively (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007), provide exceptional natural laboratories (Whittaker et al., 2017) to investigate the community assembly processes. However, despite advances in island biogeography, the relative roles of deterministic and stochastic processes in structuring island communities are still not well understood, given that both environmental filtering (Jamoneau et al., 2022; Teittinen & Soininen, 2015; Burns et al., 2010) and dispersal limitation (Verleyen et al., 2021) have been reported as the dominant process. Furthermore, it is still unclear if filtering results in homogenous or heterogeneous selection in islands.

Another important question regarding the environmental control of communities is whether climatic or local environmental variables have a greater overall impact on explaining the community variability than the local environmental variables or vice versa. Typically, climatic variables show remarkable variation mostly at broad scales while physico-chemical factors may vary across spatial scales. Recent studies found that climatic variables have a greater influence on species distribution than local factors, and this effect is likely more pronounced at broader scales (Gillard et al., 2020; Pajunen et al., 2016; Potapova & Charles, 2002; Pound et al., 2021). To our knowledge, no study has examined this issue simultaneously in island and continental communities at least for microorganisms. This question is, however, of great interest because when compared to continental climates, island climates are often considered anomalous due to strong oceanic influence (Whittaker & Fernández-Palacios, 2007). Therefore, climate may affect species distributions differently in islands than continents within the same geographic area. In addition, identifying the key climatic and local factors that influence the species distributions would be highly relevant for our understanding of how island communities, and especially species unique to islands (i.e., not occurring in continents) might be altered by global change. Although island species with narrow distributions may occupy only a small fraction of their climatic niche and not be

immediately affected by climate change, these species could still be vulnerable to other kinds of environmental change (Thomas, 2010). Particularly, in recent decades, we have seen a significant increase in exposure and vulnerability of island species to climate-related hazards, often attributed to a combination of factors, such as accelerated sea level rise and other anthropogenic factors (Becker et al., 2012; Duvat et al., 2017).

Using null model approaches (Chase et al., 2011) and hierarchical joint species distribution modelling (Ovaskainen et al., 2017), we investigated stream diatom community assembly processes globally in islands with different level of isolation vs. continents and whether communities are subject to homogeneous or heterogeneous selection by environment. We also identified key environmental drivers of species occurrence in islands and continents, putting special emphasis on disentangling the roles of climate and local water chemistry variables in driving species distributions.

2 | MATERIALS AND METHODS

2.1 | Diatom and environmental data

In this study, we used the stream community and environmental data from Jamoneau et al. (2022), who investigated diatom species richness patterns in islands and continents globally. These data consist of benthic (epilithic and epiphytic) diatoms collected from a total of 19 islands and six continental areas covering 5440 sites in total (Table 1). The procedures for sampling, counting, and identifying diatoms are described in detail in Jamoneau et al. (2022). While sampling aimed to comprehensively cover entire islands, this was not feasible in certain cases due to the absence of suitable stream sites. Some continental regions such as the USA, France, and most of Finland were thoroughly sampled. However, in places like Africa and China, sampling was less extensive. Diatoms were sampled from stony substrates or macrophytes, processed with acid or hydrogen peroxide, and enumerated in counts of approximately 400 to 700 valves per sample. Most of the diatoms were identified to species level, with less than 5% being identified only to genus level. The OMNIDIA database (Lecointe et al., 1993) was used to standardize the taxonomy across the different datasets.

Physico-chemical data collection was conducted up to two months prior to the diatom sampling and included altitude (m.a.s.l.), conductivity ($\mu\text{S cm}^{-1}$), pH, and slope for each sampling site. Climate data were extracted from WorldClim 1.4 database at 0.5-minute resolution (Hijmans et al., 2005) and included mean annual precipitation (mm), seasonality in precipitation (%), mean annual temperature ($^{\circ}\text{C}$), and temperature seasonality (i.e., standard deviation of monthly mean temperatures). Although often found as an important factor for diatoms (Soininen, 2007), we did not include total phosphorus (TP) in our analyses because TP values were not available for Ireland, Kenya, and New Zealand. In addition, our exploratory analyses with distance-based Redundancy Analysis indicated that TP had only a low importance (i.e., adjusted R^2 increased only by 0.3% after

TABLE 1 Dataset descriptions for each mainland and island regions examined in this study.

Datasets	Sampling years	No. of sites	Isolation
<i>Continents</i>			
China	2008–2013	257	
Finland	1986–2001	196	
France	1992–2009	2717	
French Guiana	2007–2018	132	
Kenya	2016	61	
USA	1993–2009	1201	
<i>Islands</i>			
Corsica	1997–2009	31	23
Cyprus	2018	36	27
Guadeloupe	2009–2013	61	33
Iceland	2016	45	65
Ireland	2018	175	29
Hawaii	2017	11	109
Kauai	2017	10	113
La Réunion	2010	55	73
Madeira	2015 and 2020	67	66
Majorca	2008	18	32
Martinique	2009–2013	71	42
Mayotte	2015	39	47
New Caledonia	2012	61	88
North New Zealand	2006	48	88
Oahu	2017	28	109
Possession island	1997–1998	10	83
São Miguel	2012	15	77
Sardinia	2020–2021	30	32
South New Zealand	2006	56	86

Note: Isolation is measured by the index developed by Dahl (1991).

adding TP) for explaining diatom distribution in European sites and even lower importance in other geographical regions. In addition, variance partitioning analyses, which considered the fixed effects and random levels defined for joint species distribution analyses (see Section 2.3 for further details), indicated that TP had only a minimal contribution to the data variance. It showed some significance only in the European and American islands, explaining 5% and 8% of the total explained variance (100%), respectively.

2.2 | Geographical divisions and continental area equivalents (CAEs)

For conducting beta diversity analyses (see below), it is crucial to characterize diatom species pools as realistically as possible. In this regard, Chase et al. (2011) noted that a suitable regional species pool might consist of those species capable of colonizing a given location

in a reasonable period of time. Based on this reasoning, we grouped our data into five geographical divisions corresponding to the five major geographical areas from which the data originated (i.e., America, Europe, Africa, China, and Pacific). We assumed that most diatom species might be able to disperse among localities within each division due to the high dispersal capacity of diatoms. However, we acknowledge that this assumption may not hold for many other organisms with more limited dispersal capabilities. These five divisions were delineated as follows (Figure 1): (1) America division comprised data from the Guadeloupe, Hawaii, Kauai, Martinique, and Oahu islands, and the continental data from French Guiana and USA; (2) Europe division comprised island data from Corsica, Cyprus, Iceland, Ireland, Madeira, Majorca, São Miguel, and Sardinia, and continental data from Finland and France; (3) Africa division was composed of island data from La Réunion, Mayotte, and Possession islands, and continental data from Kenya; (4) China division only consisted of continental data from China; and finally (5) Pacific division had island data from New Caledonia, North New Zealand, and South New Zealand (Figure 1). Then, ANOSIM analysis was performed to evaluate whether differences in diatom community composition among the five divisions were significantly higher than within them. ANOSIM confirmed that diatom communities differed significantly among the divisions (p value=0.02). However, the relatively low R statistic (0.21) indicated that the among-division differences were

modest. This was not surprising, given the relatively similar composition of communities in some well-separated regions, especially North America and Europe (see Figure S1), as recognized previously (Soininen et al., 2016). It must be noted that defining species pools by dividing our dataset into fixed geographical regions constitutes an arbitrary decision that might affect the conclusions drawn about community assemblage processes. In this context, probabilistic methods, such as those developed by Karger et al. (2016), represent alternative approaches to defining species pools while avoiding arbitrary decisions. However, they are not suitable for the purpose of our study because the beta diversity indices we applied are based on presence-absence data (see Section 2.3), which make probabilistic (continuous) values unsuitable for this type of analysis. In addition, the method developed by Karger et al. (2016) requires prior knowledge of specific dispersal rates, which are context-dependent and not known for diatom species.

To facilitate the corresponding analyses in islands and continents, we used the continental area equivalents (CAEs) as a basis for analyses in continents. They represent subsets of a given continent that are similar in area and contain the same number of study sites as corresponding islands (Jamoneau et al., 2022). Briefly, CAEs were formed by a total of 15 sites, except for CAEs corresponding to islands with fewer than 15 sampling sites. These CAEs-island pairs were as follows: Kenia – Possession island (11 sites), USA – Hawaii

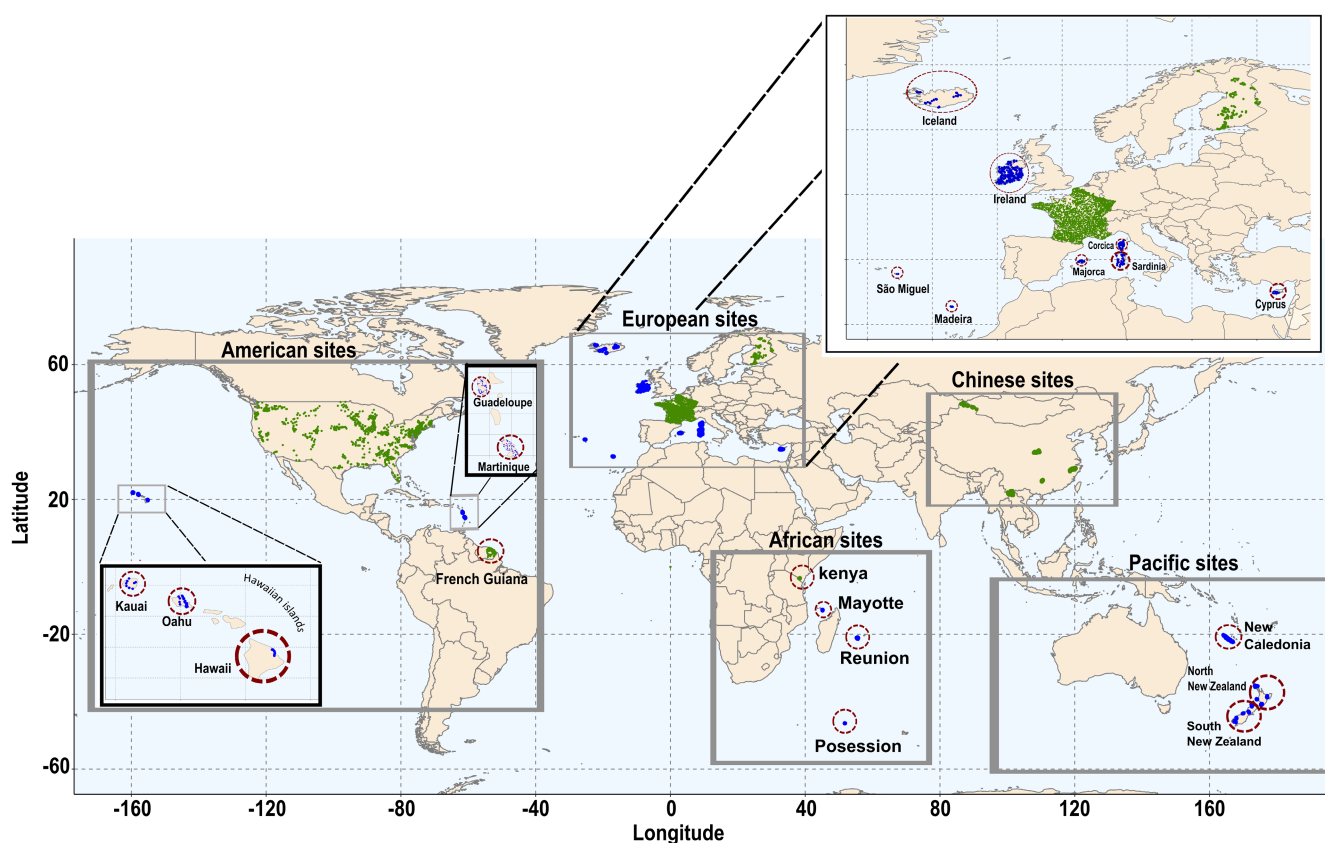


FIGURE 1 Global location of sample sites in this study. Grey squares indicate the five major geographical divisions (American sites; European sites; African sites; Chinese sites; and Pacific sites). Sites from continental area equivalents are coloured in green and those from islands are in blue.

(12 sites), USA – Kauai (11 sites), French Guiana – Hawaii (12 sites), and French Guiana – Kauai (11 sites). In addition, the island data were subsampled by pulling 15 samples at random except for Possession Island, Hawaii and Kauai, which were not randomized due to their smaller sample size. Out of the total number of 833 CAEs generated by Jamoneau et al. (2022), in this study we use only 448 CAEs as this was the number corresponding to the continental-island pair data from America, Europe, and Africa datasets (note that for China and Pacific datasets, there were no CAEs data as these datasets exclusively comprised continental and island data, respectively). In addition, area of island and CAEs, and island isolation data were extracted from Jamoneau et al. (2022). In particular, island isolation was computed using the isolation index of Dahl. This index is based on the distances between islands, archipelagos, and the nearest continent to quantify how isolated an island is from larger land masses (Dahl, 1991; Gillespie et al., 2008).

2.3 | Data analyses

To investigate diatom community assembly processes in islands and continents, we calculated a matrix of modified Raup-Crick beta diversity indices (β_{RC}) derived from the pair-wise Jaccard distance of diatom presence-absence (RC.pc function from the R icamp package [Ning et al., 2020]). Briefly, this index is calculated with a null model procedure following Chase et al. (2011) that re-frames the original β_{RC} to where the sign and magnitude together describe the strength of determinism/stochasticity as well as the tendency of two sites to share more or less species than expected (retaining the original bounds of the Raup-Crick index: $-1 \leq \beta_{RC} \leq 1$). In this sense, and following Chase et al. (2011) and Stegen et al. (2013), β_{RC} values ≥ 0.95 and β_{RC} values ≤ -0.95 were interpreted as significant departures from the expected degree of turnover when a stochastic process acts alone. Thus, β_{RC} values ≤ -0.95 indicate both strong deterministic assembly and greater similarity than expected by chance, suggesting homogeneous selection by the environment. In contrast, we interpreted that β_{RC} values ≥ 0.95 suggest strong deterministic assembly but with greater dissimilarity than expected by chance, which points to heterogeneous selection, e.g., due to environmental heterogeneity or competition. Finally, β_{RC} values less than $|0.95|$ indicate stochastic community assembly with their positive and negative values respectively interpreted as dissimilarity and similarity. The underlying null models to generate the β_{RC} values were ran with 999 randomizations, and we implemented Wilcoxon test to evaluate if β_{RC} values differed between islands and continents. For this, we studied beta diversity for each geographical division at two scales: (1) within-island and within-CAE beta diversity and (2) across-island and across-CAE beta diversity. Overall, we also analysed the Spearman correlation between island isolation and islands' beta diversity, as well as the correlation between the convex hull area of islands and CAEs and their beta diversity.

Despite our efforts to harmonize diatom taxonomic names across data sets, we admit that somewhat subjective decisions in

species identification by different analysts may affect the community dissimilarities between the data sets. This is especially true for endemic and rare taxa for which only limited taxonomic information is currently available. Therefore, to determine whether similar conclusions could be drawn when using species and genus levels, we calculated Raup-Crick beta diversity indices also using genus-level data.

Next, to assess how environmental factors influence diatom occurrence in islands and continents, we applied Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017), a recently developed hierarchical joint species distribution modelling (JSDM) method. We built two set of models, one for islands (m_{isl}) and one for continents (m_{cont}) separately for each geographical division. Hence, the total number of models were eight ($m_{isl-America}$, $m_{isl-Europe}$, $m_{isl-Africa}$, $m_{isl-Pacific}$, $m_{cont-America}$, $m_{cont-Europe}$, $m_{cont-Africa}$, $m_{cont-China}$). To compare the effects of environmental factors on diatoms that are exclusive to islands or continents (i.e., unique species) versus diatoms that occur in both islands and continents (i.e., non-unique species), we computed the model twice. One set of models considered taxa that were detected exclusively in continents (560 taxa) or islands (219 taxa), while the other set included taxa that were present in both continents and islands (610 taxa).

All models followed a binomial distribution (probit link function) and were fitted with the same environmental variables (altitude, conductivity, pH, slope, annual precipitation, annual temperature, precipitation seasonality, and temperature seasonality). Response variables included diatom presence-absence data. For non-unique species models, taxa with less than four occurrences were excluded for improving the model performance. For unique species models, all taxa were considered even if they had fewer than four occurrences to maintain similar site number for the regions. This was done to avoid potential biases in the conclusions due to the smaller number of taxa.

To account for spatial autocorrelation, we included a spatially explicit random effect (i.e., site location) using the nearest-neighbour Gaussian process (NNGP) spatial technique (Tikhonov et al., 2020). Furthermore, and in order to account for any possible influence that the definition of CAEs may have on explaining diatom occurrence, an additional random effect was included at the level of CAEs (i.e., CAE identity).

The first 20,000 iterations were removed as burn-in and the remaining were thinned by 2 to yield 20,000 posterior samples per chain. In the case of $m_{cont-Europe}$ models, the first 2000 and 12,000 iterations were discarded as burn-in and the remaining were also thinned by 2 to yield 2000 and 12,000 posterior samples per chain.

The convergence of the models was evaluated through examination of the Gelman and Rubin's convergence diagnostic (potential scale reduction factor, Gelman & Rubin, 1992) and the explanatory power was assessed by taxon-specific $T_{jur} R^2$ (T_{jur} , 2009) and AUC (Pearce & Ferrier, 2000) applying the HMSC framework with the default prior distributions (Ovaskainen & Abrego, 2020). Following Ovaskainen et al. (2017), variance partitioning (examined as the respective R^2 variance components attributed to the fixed and random

effects of the HMSC models) was performed to disentangle the role of environmental variables and random effects in shaping diatom communities.

3 | RESULTS

3.1 | Beta diversity

Within islands, 60.77% of island sites had βRC values ≤ -0.95 , while within CAEs, the corresponding value was only 34.73%, indicating that globally, homogeneous selection affected a higher proportion of sites in islands than in continents. Nevertheless, homogeneous selection was the main assembly process within CAEs in Europe and America (Figure 2). Stochastic influence, on the other hand, was particularly strong for Sardinia, Cyprus, China, Ireland, and Kenya (Figure S2), as in these regions more than 70% of βRC values ranged between -0.95 and 0.95 (Figure 2). When βRC values were compared for islands vs. continents for three divisions, mainland areas in America, Europe, and Africa had significantly different βRC values than islands (Wilcoxon test $W = 2.10^6$, $p < 0.05$) (Figure 3a).

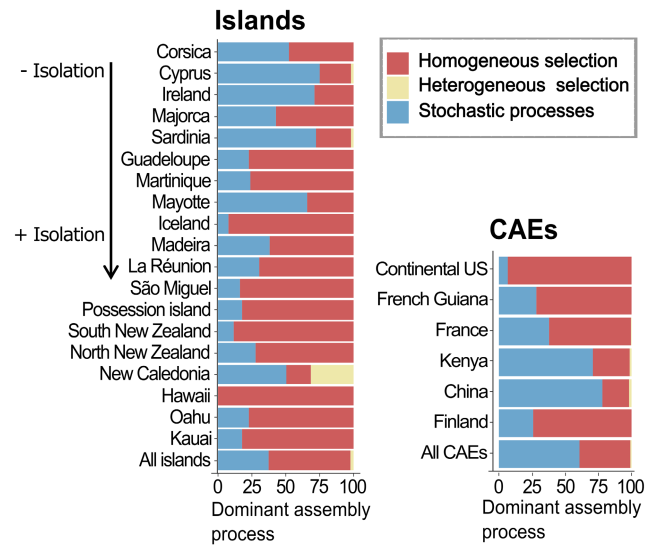
Among CAEs and among islands belonging to the same geographical division, most of the sites from both CAEs and islands (62.8% and 76.2%, respectively) had $-0.95 < \beta RC < 0.95$ suggesting that stochastic processes dominated community assembly at this scale in both CAEs and islands (Figure 2). While stochasticity was the dominant assembly process in most island ecosystems, African islands were characterized by heterogeneous selection, and Pacific islands exhibited a combination of homogeneous and heterogeneous selection that was at a roughly similar level as stochasticity (Figure 2). Overall, homogeneous selection was the second strongest force among CAEs in America, Europe, and Africa and its contribution ranged from 28.4% to 67.3% (Figure 2). When examining βRC values of the three divisions (mainland areas from America, Europe, and Africa) between islands and continents, CAEs showed overall significantly (Wilcoxon test $W = 2.10^{11}$, $p < 0.001$) more negative βRC values than islands in America, Europe, and Africa (Figure 3b).

A significant negative correlation ($p < 0.01$, Spearman's $Rho = -0.24$) was found between the log-transformed convex hull area of European CAEs and the proportion of sites within CAEs that were subjected to homogeneous selection. In contrast, a positive correlation ($p < 0.01$, Spearman's $Rho = 0.20$) was found between the convex hull area of European CAEs and the proportion of sites within CAEs subjected to stochasticity. Similar trends were found between the transformed area of the convex hull of the islands and their beta diversity, but the correlations were not statistically significant.

We also found a positive correlation between island isolation and the proportion of sites subjected to homogeneous selection within islands ($p < 0.05$, Spearman's $Rho = 0.56$) and a negative correlation between island isolation and the proportion of sites subjected to stochasticity ($p < 0.01$, Spearman's $Rho = -0.66$) (Figure S3).

When beta diversity was analysed using genus-level data, results were overall similar to the species-level results with the only

(a) Within CAEs and islands



(b) Among CAEs and islands

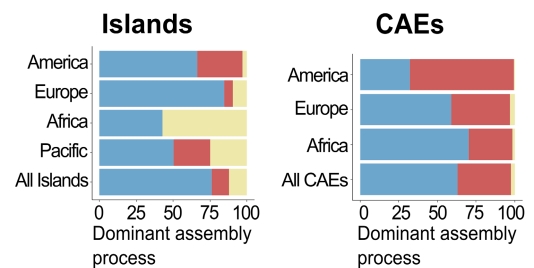


FIGURE 2 Percent of sites that were subjected to strong homogenous selection ($\beta RC \leq -0.95$), heterogenous ($\beta RC \geq 0.95$) selection, and stochasticity ($-0.95 \leq \beta RC \leq 0.95$) for the analyses performed within islands (ordered by the level of isolation) and continental area equivalents (CAEs) (a) and among islands and CAEs (b). Note that for the China dataset, there was no CAEs data as this dataset exclusively comprised continental data.

discrepancies being the Pacific islands and Africa, where stochasticity was the dominant force both within and across islands and CAEs (Figure S4). In addition, island isolation and community assembly processes showed similar trends for genus-level data as species-level data, but the correlations were not statistically significant (Figure S5).

3.2 | HMSCs results

The Gelman and Rubin's potential scale reduction factor for all the models was < 1.2 , indicating good convergence for all the models (Table 2). Furthermore, the models demonstrated acceptable fit as evidenced by their discriminatory and explanatory powers. For example, all models showed mean AUC values greater than 0.9. In addition, mean Tjur R^2 among models ranged between 0.08 and 0.77, with half of the models showing mean Tjur R^2 greater than 0.31. Models based on continental communities from America, Europe,

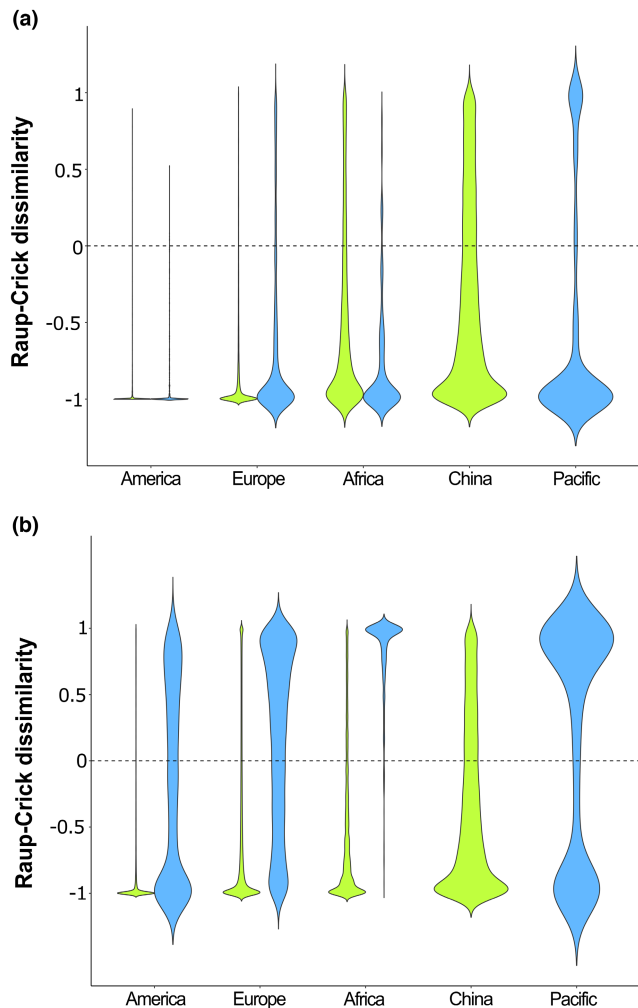


FIGURE 3 Violin plots of the Raup-Crick beta diversity index (β_{RC}) (a) within islands (in blue) and continental area equivalents (CAEs) (in green) and (b) among islands and CAEs for all five geographical divisions.

and Africa showed lower explanatory power than the respective models based on island data, except in the case of European models based on non-unique taxa. In particular, the American models showed the greatest differences in explanatory power, with models based on continental diatoms exhibiting much greater explanatory power than models based on island communities (Table 2).

Variance partition indicated that diatom distributions were influenced mostly by climatic factors for islands and continents for all divisions, except for continental communities in Europe where random effect was the most important variable (Figure 4). Particularly, mean annual temperature was identified as the most important variable for both non-unique continental and island diatoms for Africa and island diatoms for Europe, as well as for continental communities from the Pacific (Figure S6).

In contrast, local factors had a minor impact on diatom distributions, except for altitude and conductivity. Altitude played an important role for continental diatoms in Africa and China, as well as for unique taxa from African islands and diatoms from American

islands. On the other hand, conductivity showed a considerable influence on diatoms from China and European islands (Figure S6).

When focusing on taxa unique to islands, local environmental variables had a greater relative impact on their distributions, compared to non-unique species. This pattern was especially pronounced in Africa and Europe, where altitude and conductivity showed the highest increase in the proportion of explained variance (Figure S6). In continents, the same pattern was only found for China.

4 | DISCUSSION

Our findings indicate that diatom community assembly in islands and continents is influenced by a combination of deterministic and stochastic forces and their balance varies with spatial scale. Importantly, we found differences in how assembly processes act within islands and continents (i.e., using CAEs data). Globally, our results showed that homogeneous selection dominated the assembly process within islands, followed by stochastic processes, whereas stochastic processes tended to be more important within continents, followed by homogeneous selection. We further discovered that at larger scales (i.e., among islands and CAEs), the influence of stochasticity increased being the dominant process in most of the surveyed regions. In addition, our results provided evidence that stochasticity increased with the area of European CAEs, while homogeneous selection decreased with area. Although we observed a similar trend in islands, this correlation was not statistically significant.

Overall, these findings agree with previous diatom studies in mainland, showing that stochastic processes become more prominent at larger scales (Soininen et al., 2004). The most likely reason for such a finding is that stochasticity stems partly from dispersal processes (Ossysek et al., 2023), with dispersal limitation being more prevalent at larger scales (Keck et al., 2018; Soininen, 2023). However, the high rates of stochasticity within CAEs observed in some areas may be related to smaller-scale dispersal limitation associated with local dispersal barriers (e.g., mountains) (Keck et al., 2018). Similarly, the higher stochasticity observed among islands may suggest that only part of the species was able to disperse among them, as evidenced by the only moderate percent of shared taxa among some of the islands. But at the same time, environmental conditions were sufficiently homogeneous to select similar communities within islands. Interestingly, these results contrasted to what has been found for other microbes where homogeneous selection had a strong effect among islands but stochastic factors were more important within freshwater islands (Wang et al., 2020).

It must be noted that in both islands and continents, the relative importance of different assembly processes was not uniform across all the regions surveyed. Rather, there was considerable between-region variation in the assembly processes, and it is thus difficult to predict whether communities in a particular region are primarily shaped by stochastic processes or environmental selection. Nonetheless, our results suggest that the prevalence of

TABLE 2 Gelman and Rubin's convergence diagnostic and explanatory power of all models built using Hierarchical Modelling of Species Communities.

Model	Species included	Potential scale reduction factor		Mean explanatory/discriminatory power	
		Mean point estimate	Upper credible interval	Tjur R^2	AUC
$m_{\text{cont-America}}$	Non-unique	1.07	1.17	0.77	0.99
$m_{\text{isl-America}}$	Non-unique	1.00	1.00	0.29	0.91
$m_{\text{cont-Europe}}$	Non-unique	1.07	1.19	0.19	0.94
$m_{\text{isl-Europe}}$	Non-unique	1.00	1.00	0.22	0.91
$m_{\text{cont-Africa}}$	Non-unique	1.02	1.06	0.44	0.96
$m_{\text{isl-Africa}}$	Non-unique	1.00	1.00	0.39	0.91
$m_{\text{cont-China}}$	Non-unique	1.00	1.00	0.19	0.96
$m_{\text{isl-Pacific}}$	Non-unique	1.00	1.00	0.32	0.92
$m_{\text{cont-America}}$	Unique	1.06	1.15	0.63	0.99
$m_{\text{isl-America}}$	Unique	1.00	1.00	0.22	0.96
$m_{\text{cont-Europe}}$	Unique	1.04	1.12	0.38	0.99
$m_{\text{isl-Europe}}$	Unique	1.00	1.00	0.16	0.97
$m_{\text{cont-Africa}}$	Unique	1.00	1.01	0.35	0.98
$m_{\text{isl-Africa}}$	Unique	1.00	1.00	0.33	0.97
$m_{\text{cont-China}}$	Unique	1.00	1.00	0.08	0.96
$m_{\text{isl-Pacific}}$	Unique	1.00	1.01	0.26	0.97

Note: Discriminatory and explanatory power were assessed by computing the area under the curve (AUC) and the taxa-specific Tjur R^2 .

one process over the other is somewhat correlated with the level of island isolation. Specifically, homogenous selection appears to be more pronounced within isolated islands. In our data set, the Hawaiian Islands were the most isolated and displayed within island β RC values smaller than -0.95 . This suggested that, within islands, communities were highly similar because of shared environmental filters, especially climatic variables, as shown by HMSC models. However, it can be expected that dispersal limitation plays a dominant role within extremely isolated islands, as found by Verleyen et al. (2021). Therefore, the observed pattern of diatom community assembly in isolated islands could most probably stem from the combined effect of environmental filtering and dispersal limitation, similar to what has been observed for bacteria communities in isolated lakes in Antarctica (Logares et al., 2018).

Conversely, in less isolated islands (mostly European islands), stochasticity may result from a diverging history of colonization from a common source and subsequent extinctions. Indeed, nearby islands, e.g., Corsica and Sardinia, share only around 28% of taxa (Figure S1). Furthermore, HMSC model for European islands showed the lowest explanatory power among island models, reinforcing the idea that environmental filtering may be less important than stochastic factors. This is surprising, as European islands showed the highest environmental heterogeneity, which should typically have a strong impact on species distribution (Langenheder & Lindström, 2019). One reason could be that these environmental variations do not greatly influence diatom

composition, as the HMSC results suggest. In essence, these findings indicate that perhaps no universal pattern can be discerned about island community assembly processes acting on a global scale, but rather that the degree to which these processes operate in freshwater diatom communities is highly dependent on abiotic conditions, such as area, isolation, and environmental heterogeneity.

We found that climatic variables were the most important environmental factors explaining diatom occurrence in both continents and islands, which is consistent with previous mainland studies (Pajunen et al., 2016; Potapova & Charles, 2002; Pound et al., 2021). However, we may have not fully assessed the role of local variables because some physicochemical variables, potentially important for freshwater diatoms, such as substrate composition, nutrient levels, current velocity, and colour (Castro et al., 2019; Dalu et al., 2017; Pajunen et al., 2016; Passy, 2001; Soininen et al., 2004), were missing from our global analysis. On the other hand, the highest explanatory power of climatic variables for insular diatoms indicates that climate models may provide a robust approach to track and predict changes in diatom distribution due to changes in climate. Furthermore, the greater sensitivity to local environmental variables of species found only in islands and not in continents (i.e., observed for European and African insular communities) implies that species with more restricted distributions may be less vulnerable to changes in climate but more at risk from changes in local physicochemistry. However, further research based on molecular and trait diatom data

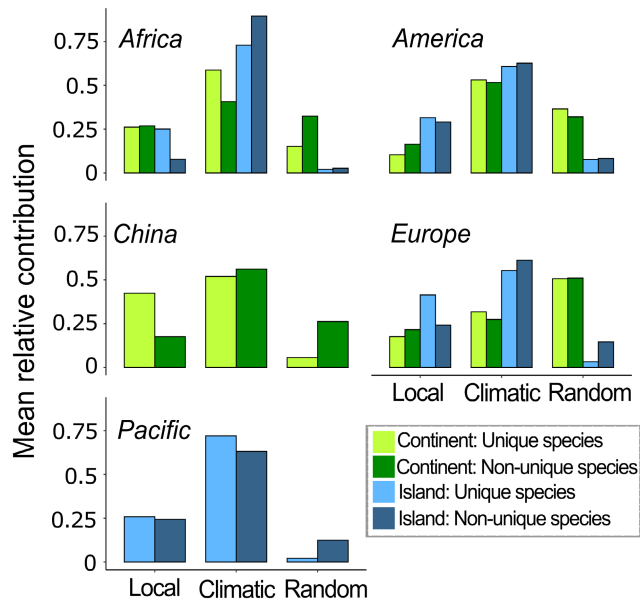


FIGURE 4 Variance partitioning resulting from the Hierarchical Modelling of Species Communities performed for each of the five different geographical divisions for unique species and non-unique species. The bar diagrams represent the average relative importance of the local (altitude, conductivity, pH, and slope), climatic (annual precipitation, annual temperature, precipitation seasonality, and temperature seasonality), and random factors (geographic coordinates and CAE identity).

might provide a more comprehensive understanding of how insular diatoms interact with their environment and how they may be affected by future changes in climate and/or other environmental variables.

In conclusion, we found that diatom community assembly processes vary between islands and continents but also with spatial scale. Within islands, homogeneous selection dominated the assembly followed by stochastic processes, whereas within continental areas, stochastic processes tended to be more important. Moreover, stochasticity increased with study scale most probably due to stronger dispersal limitation. Overall, species distribution was mostly driven by climatic variables, which may reflect partly the lack of some potentially influential local variables. We think these results are highly useful for a better understanding of how freshwater algal communities are shaped by environmental factors in fragmented ecosystems under global change.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Data on the presence or absence of diatom species for all island and continental sites, along with the corresponding environmental data for these sites, can be accessed at the following link: <https://doi.org/10.57745/ZPBSLT>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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