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A Global Comparison of Stream Diatom Beta Diversity on Islands Versus Continents Across Scales

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ABSTRACT

Aim: To evaluate the patterns of stream diatom beta diversity in islands versus continents across scales, to relate community similarities with spatial and environmental distances and to investigate the role of island characteristics in shaping insular diatom beta diversity.

Location: Africa, America, Europe and the Pacific.

Time Period: Present.

Major Taxa Studied: Stream diatoms.

Methods: We compared diatom beta diversity between islands and continents at large scales (within biogeographic regions) in two study regions (America and Europe) and at small scales (within islands/equivalent areas in continents) in three regions (Africa, America and Europe) partitioning beta diversity into turnover and nestedness components. We used a partial Mantel test

and distance–decay curves to assess how diatom beta diversity on islands and continents is affected by spatial and environmental distances. Finally, using island data from all four regions, we evaluated the relationship between island beta diversity and island latitude, area, age and isolation using linear models.

Results: At large scales, mean dissimilarities were higher on islands than in continents in Europe but lower in America. At smaller scales, the differences varied mostly depending on island isolation. Beta diversity was mainly caused by species turnover. Partial Mantel test and distance–decay curves revealed that spatial and environmental distances shaped diatom beta diversity at large, but not at small scales. Moreover, diatom beta diversity on islands was affected by island latitude, age and isolation, but not by island area.

Main Conclusions: Diatom beta diversity on islands versus continents and its responses to spatial and environmental factors are scale and region dependent. Incomplete colonisation, evolutionary processes and environmental filtering likely contribute to insular beta diversity, which further varies with island latitude, age and isolation. This study sheds new light on beta diversity of microorganisms on islands and suggests that beta diversity should be explicitly considered in island biogeographical research.

1 | Introduction

Exploring the factors contributing to biodiversity on islands has been a central theme of biogeography for centuries. Influential theories have elucidated that island species richness is a product of colonisation, speciation and extinction, whose effects are determined by island attributes, such as size, isolation and age (MacArthur and Wilson 1967; Fattorini 2010; Lomolino 2000; Whittaker et al. 2008). For example, colonisation typically increases with island area and decreases with isolation (Helmus, Mahler, and Losos 2014), and speciation occurs more frequently on isolated islands and extinction peaks on small and isolated islands (Kisel and Barraclough 2010). Comparisons of islands and continents further demonstrated that area is a more important factor for species living on islands than in continents (MacArthur and Wilson 1967; Winegardner et al. 2012; but see Jamoneau et al. 2022). With respect to age, older islands have had not only longer time for colonisation and speciation but also longer time for extinctions (Borregaard et al. 2017) due to island erosion.

The variation in species composition between sites (i.e., beta diversity) on islands has been the subject of numerous studies over time (e.g., Kadmon and Pulliam 1993), and particularly in recent years (Astorga et al. 2014; Carvalho and Cardoso 2014; Fattorini 2010; Palmeirim et al. 2018; Si, Baselga, and Ding 2015; Valli et al. 2019; Wu et al. 2017; Zhao et al. 2021). These studies found that island latitude, area, age, isolation and environmental heterogeneity are important factors shaping island beta diversity. Thus, island attributes constrain not only species richness and community composition but also beta diversity. A reasonable expectation is that similar to mainland (Soininen, McDonald, and Hillebrand 2007; Qian 2009; Qian et al. 2013), beta diversity on insular systems (both, between and within islands) would decrease with latitude because higher latitudes harbour fewer species with less restricted distributions. However, beta diversity decline with latitude appears to be, in part, context dependent across some taxa and ecosystems (Zhang et al. 2020). Island area may increase within-island beta diversity as larger islands contain more habitats and therefore can maintain different types of species (Ricklefs and Lovette 1999). Additionally, within-island beta diversity is potentially influenced by island age as intermediate-aged and older islands likely contain more phylogenetically variable species than younger islands (although older islands may undergo erosion and species loss). Finally, isolation

may decrease within-island beta diversity since good dispersers, with the ability to colonise isolated islands, can also disperse throughout the island. Thus, high isolation would result in low beta diversity due to biotic homogenisation within islands. Age and isolation are generally meaningful only for islands (although island-like systems can occur on continents naturally, e.g., mountaintops or isolated lakes). Given that these island properties are likely to strongly impact beta diversity, it is to be expected that island beta diversity may differ from beta diversity on continental equivalents. Nonetheless, both the extent to which beta diversity depends on island attributes and how beta diversity differs from similar-sized areas in continents (i.e., on continental area equivalents, CAE; Jamoneau et al. 2022) remain poorly understood, particularly at a global scale (but see König, Weigelt, and Kreft 2017).

The study of beta-diversity patterns and their underlying processes is important for a better understanding of the causes of spatial variation of biodiversity (Anderson et al. 2011). The relationship between similarity in species composition between pairwise sites and the spatial or environmental distance between them, that is, distance–decay of similarity (Nekola and White 1999), may uncover the roles of dispersal limitation and species sorting in shaping beta diversity (Gómez-Rodríguez and Baselga 2018; Graco-Roza et al. 2022; Verleyen et al. 2009). Distance–decay patterns can be modelled with parametric functions, and the form and parameters of these functions may be related to species range size, dispersal ability or niche breadth (Martín-Devasa et al. 2022; Nekola and White 1999; Soininen, McDonald, and Hillebrand 2007). Moreover, beta-diversity partitioning (Baselga 2010) reveals if observed compositional differences between sites are due to species replacement (turnover), which typically is the larger component of beta diversity (Soininen, Heino, and Wang 2018), or nested differences in species richness due to ordered species loss (nestedness) (Baselga 2010; Baselga and Leprieur 2015). Beta-diversity partitioning is particularly illuminating on islands, as it allows for testing in a straightforward manner the effects of latitude, area, age and isolation on species replacement versus species loss (Carvalho and Cardoso 2014; Wu et al. 2017; Zhao et al. 2021).

Spatial and environmental distances among sites and island attributes are not the only factors affecting beta diversity, as beta diversity also varies with spatial scale (Barton et al. 2013; Steinbauer

et al. 2012). Beta diversity tends to increase with study scale (i.e., extent), probably because dispersal limitation and environmental variation increase with scale (Soininen, Heino, and Wang 2018). Overall, the relative importance of dispersal limitation and species sorting along environmental gradients varies with scale, such that dispersal limitation has a stronger effect at broader scales, while species sorting tends to dominate at intermediate scales (Heino et al. 2015). Since both dispersal limitation and environmental heterogeneity increase beta diversity, we predict higher beta diversity at intermediate-to-large scales than at small scales. At small spatial scales, beta diversity may be low due to mass effect (i.e., efficient dispersal from favourable to unfavourable habitats) that homogenises communities and due to lower environmental heterogeneity (Heino et al. 2015).

For beta-diversity studies, microorganisms, specifically freshwater diatoms are one of the most appealing taxa (Wetzel et al. 2012). Diatoms are one of the most studied and abundant primary producer groups in streams (Jyrkänkallio-Mikkola, Heino, and Soininen 2016). They are particularly interesting due to their presence in all aquatic ecosystems, high diversity and variety of life forms, differing in dispersal capacity and environmental preferences (Rimet and Bouchez 2011; Soininen 2007). This facilitates assessing the effects of dispersal limitation versus environmental conditions on diatom biodiversity across scales. However, we are just beginning to understand how diatoms respond to environmental and spatial drivers on islands as opposed to continents (Jamoneau et al. 2022; Pérez-Burillo et al. 2023). For example, Jamoneau et al. (2022) revealed a steeper slope of diatom species–area relationship in continents than on islands. Pérez-Burillo et al. (2023) demonstrated that diatom community assembly was mainly driven by environmental filtering on islands but stochasticity in continents. Nevertheless, the responses of diatom beta diversity to environmental and spatial processes on islands versus continents remain largely unknown.

Using a global stream diatom dataset, first, we evaluate whether diatom beta-diversity patterns vary between islands and continents across scales. Specifically, we assess (i) whether diatom beta diversity is higher on islands or equivalent continental areas within biogeographic regions (hereafter called a large study scale) and (ii) within-islands or within-continental areas (hereafter called a small study scale). Our first hypothesis (H$_1$) is that beta diversity is higher on islands compared to continents at large study scales because islands are more isolated than continental areas and have a greater proportion of unique species, which increases beta diversity (Stuart, Losos, and Algar 2012). At small study scales, the level of beta diversity on islands shows context dependency and likely depends on factors such as latitude, gamma diversity, age, isolation and environmental heterogeneity (e.g., Fattorini 2010; Liu et al. 2018).

We further investigate whether differences in community composition on islands and equivalent continental areas are mainly caused by species turnover or nestedness. Our second hypothesis (H$_2$) is that the turnover is the main component of beta diversity on both islands and in continents, as typically found across a wide range of biotic communities (Jamoneau et al. 2018; Soininen, Heino, and Wang 2018). This is mostly because turnover measures changes in species composition between sites,

which is driven by factors affecting communities broadly, such as environmental and spatial gradients (Soininen, Heino, and Wang 2018). In contrast, nestedness is dominant only under specific circumstances such as passive sampling, nested habitats and selective extinctions or selective colonisation (Dobrovolski et al. 2012; Ulrich, Almeida-Neto, and Gotelli 2009).

We then examine the relationships between pairwise community similarities and spatial and environmental distances on islands versus equivalent continental areas at large and small study scales using a distance–decay approach. Our third hypothesis (H$_3$) is that spatial and environmental distances are important factors shaping diatom community composition at large study scales due to dispersal limitation and environmental heterogeneity, while at a small study scale, weak dispersal limitation and lower environmental heterogeneity result in small effects of spatial and environmental distances (Heino et al. 2015) on both islands and in continents.

Finally, we investigate how diatom beta diversity within islands is related to island attributes, namely latitude, island area, age and isolation. Our fourth hypothesis is as follows: (H$_{4a}$) beta diversity decreases with latitude (Qian 2009; Qian et al. 2013); (H$_{4b}$) larger islands have higher beta diversity because of higher environmental heterogeneity and stronger dispersal limitation (Whittaker and Fernández-Palacios 2007); (H$_{4c}$) older islands have had more time for species to colonise and evolve leading to more heterogeneous communities and higher beta diversity, although lower extinction rates may cause intermediate age islands communities to be even more heterogeneous (Borges and Brown 1999; Fattorini 2010); and (H$_{4d}$) isolated islands have morphologically and ecologically more similar species than less isolated islands and thus, lower beta diversity within islands as only a small part of the species pool (i.e., the best dispersers) can colonise isolated islands and disperse throughout them, homogenising the communities (Carvalho and Cardoso 2014; Whittaker and Fernández-Palacios 2007).

2 | Material and Methods

2.1 | Diatom Distribution Data and Environmental Variables

Presence–absence data for diatoms from 19 islands and five continental areas (5183 sites in total) were obtained from Jamoneau et al. (2022). Following Pérez-Burillo et al.'s (2023) classification, territories were divided into four biogeographic regions: American region (1), comprising the islands of Guadeloupe (Gu), Hawaii (Ha), Kauai (Ka), Martinique (Ma) and Oahu (Oa), and the continental territories of French Guiana and the United States; European region (2), comprising the islands of Corsica (Co), Cyprus (Cy), Iceland (Ic), Ireland (Ir), Madeira (Md), Majorca (Mj), Sardinia (Sa) and São Miguel (Sm), and the continental territories of Finland and France; African region (3), encompassing the islands of La Réunion (Re), Mayotte (My) and Possession (Po), and continental territory of Kenya (Ke); and Pacific region (4), composed of the islands from New Caledonia (Nc), North New Zealand (Nz) and South New Zealand (Sz) (Figure 1). Despite the lack of an equivalent continental area, we included the data of the Pacific region as one of our main
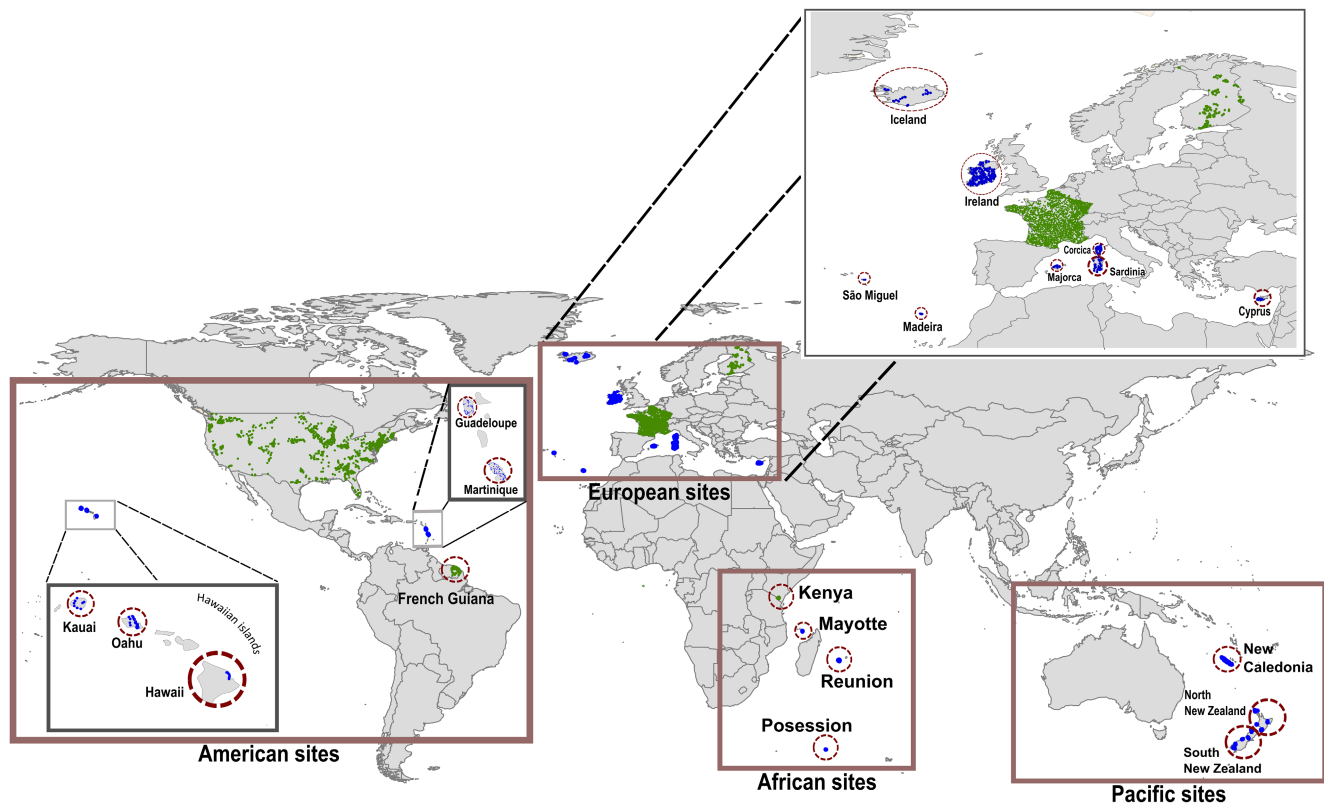
FIGURE 1 | Map of all sampling locations included in this study. Grey squares indicate the four geographical divisions considered (American, European, African and Pacific). Blue dots correspond to island sites, whereas green dots correspond to continents. Map adapted from Pérez-Burillo et al. (2023).

goals was to assess how island attributes are related to diatom beta diversity.

The procedures for sampling, counting and identifying diatoms are described in detail in Jamoneau et al. (2022). In brief, diatoms were sampled from stony substrates or macrophytes and processed with hydrogen peroxide. They were then enumerated in counts of approximately 400–700 valves per sample, which allows reliable estimates of total diversity and has only a marginal impact on richness estimations (Jamoneau et al. 2022). Note that in the present paper, we do not investigate richness patterns but beta diversity. Diatoms were identified mostly to species level and only < 5% of the valves were identified to genus but were still included in the analyses. The OMNIDIA database (Lecointe, Coste, and Prygiel 1993) was used to standardise the taxonomy across the different datasets. For each sampling site, we had environmental data for altitude (metres above the sea level), conductivity ($\mu S \cdot cm^{-1}$), pH, slope and climate. Climate data were extracted from the WorldClim database at 0.5-min resolution (Hijmans et al. 2005), including mean annual precipitation (mm), seasonality in precipitation (%), mean annual temperature (°C) and temperature seasonality (i.e., standard deviation of monthly mean temperatures).

2.2 | Continental Area Equivalents

For a meaningful comparison of islands and continents, which differ greatly in area, we used continental area equivalents

(CAEs) (Jamoneau et al. 2022). A CAE is defined as a subset of a given continent with a similar area and the same number of study sites (15) as a corresponding island. They were calculated by first computing the geographical distance between each island centroid and its sampling sites and then, considering each sampled site from a continent as a potential centroid, finding a set of at least 15 study sites that equals the spatial distance structure between the centroid and sampling points from the corresponding island with a 5 km error margin for each computed distance (Jamoneau et al. 2022). Each CAE could theoretically have between 15 and the total number of sampled sites on the corresponding island, but for achieving a comparable sampling effort, we selected CAEs with a total of 15 sites, except for CAEs corresponding to Possession Island, Hawaii and Kauai, which had, respectively, 11, 11 and 12 sites due to a lower number of sampled sites. Thus, in each CAE–island pair, we randomly pulled 15 samples from each, except for Possession Island, Kauai and Hawaii where we used all the sampled sites. Here, we analysed only the CAEs corresponding to the continental–island pair data within biogeographic regions, that is, CAEs whose equivalent islands are in the same biogeographic region. Moreover, to avoid pseudoreplication, we selected only CAEs separated by a distance of at least twice the mean distance between centroids and their corresponding sites. Consequently, a total of 448 CAEs were included in the analyses. For the Pacific Region, no CAEs were available. Finally, data on island sampled area, island age (determined from the literature, Appendix S1) and island isolation were obtained from Jamoneau et al. (2022). Island isolation was computed with Dahl index, which is based on the sum of

square root distances to the nearest equivalent or larger island, the nearest island group or archipelago, or the nearest continent (Dahl 1991).

2.3 | Beta-Diversity Measures

To assess whether beta diversity on islands and in continents, at both large and small study scales, is caused by species turnover or nestedness and whether the level of beta diversity varies between islands and continents, we computed three different pairwise dissimilarity indices. Sorensen index (β_{sor}), which quantifies the total dissimilarity between sites; Simpson index (β_{sim}), which quantifies the dissimilarity between sites due to species turnover; and nestedness-resultant index (β_{sne}), which quantifies the differences between sites in terms of species richness caused by nested species composition between sites (Baselga 2010). The indices were computed using the function *beta. pair* of the R package *betapart* (Baselga et al. 2023; Baselga and Orme 2012). For comparison, we also computed beta-diversity partitioning using Podani's approach (Podani and Schmera 2011; Schmera and Podani 2011). This method divides total beta diversity (Sorensen index) into its replacement (Brepl) and richness difference (Brich) components using relativised species replacement and relativised richness difference (Schmera and Podani 2011). To do so, we used the function *beta* of the *BAT* package (Cardoso et al. 2024). Implementing both Baselga's and Podani's beta-diversity partitioning approaches limits potential biases in the estimates of beta diversity.

First, at a large study scale (within biogeographic regions), we computed the pairwise similarity between all selected sites from all islands within a region. The CAEs for the African region were excluded from the analyses at a large study scale as the longest distances between sites in Kenya were notably smaller than the longest distances among African islands. To obtain a comparable beta-diversity measure in the CAEs, we randomly selected one analogous CAE for each island within the same biogeographic region (Europe or America), obtaining a set of CAEs 'representing' all islands and computed the pairwise similarity between all their sites. We repeated this step 100 times to ensure adequate capturing of the variation in beta diversity in continents. In each iteration, sampling was performed with replacement to ensure that all CAEs representing one island are picked with the same probability (so none of them is overrepresented) avoiding bias in the beta diversity computation. We used the Kruskal–Wallis test to assess if the differences in dissimilarities between islands and CAEs were significant as our results did not meet the normality and heteroscedasticity requirements for a parametric test. We computed the β_{ratio} (β_{sim}/β_{sor}) to assess the relative importance of turnover and nestedness on each pairwise comparison (Dobrovolski et al. 2012). If $\beta_{ratio} > 0.5$, turnover is predominant, whereas $\beta_{ratio} < 0.5$ indicates that nestedness predominates.

To assess the relationships between spatial distance and environmental distance, and diatom community composition change on islands and in CAEs, we first used a partial Mantel test to evaluate the correlation of spatial and environmental distances with community dissimilarity, after, respectively, the effects of environmental and spatial distances had been accounted for. Partial

Mantel test was computed using the function *mantel. partial* of the *vegan* package (Oksanen et al. 2022). Then, we generated and modelled spatial and environmental distance–decay curves. To do so, we converted dissimilarity to similarity by subtracting dissimilarity index from 1 ($1 - \beta_{sim}$) and then regressed the pairwise similarities between sites on islands and CAEs over the spatial and environmental distances between the corresponding sites. Spatial distance was computed as the geodesic distance between the study sites using the function *geodist* of the R package *geodist* (Padgham and Sumner 2020). The geodesic distances were used as diatoms frequently dispersed passively via air, not only via water routes.

We analysed environmental variables, measured across all island or CAE sites within a biogeographic region, with a principal component analysis (PCA) using a correlation matrix due to the different scales of the variables, and the first two PC axes were retained (100% explained variance). Then, we calculated the environmental distance between sites as the Euclidean distance between their respective PCA scores. Distance and environmental–decay curves were fitted with linear, power law, negative exponential and Gompertz models to study the relationship of community similarity with spatial and environmental distances (Martín-Devasa et al. 2022; Nekola and McGill 2014), using the function *lm* for linear models and *nlsLM* of the package minpack.lm (Elzhov et al. 2016) for nonlinear models. The goodness of fit of each model was assessed using pseudo-r^2 [$1 -$ deviance (model)/deviance (null model)].

We used the pseudo-r^2 to compare the amount of variation in diatom community composition explained by spatial and environmental distances between islands and CAEs. First, for each region, we obtained the pseudo-r^2 for between-islands spatial and environmental distance–decay models. Second, for each region, we randomly selected one CAE equivalent to each island in that region (as in the previous analysis), computed the distance and environmental–decay models and obtained the corresponding pseudo-r^2. Then, we repeated this step 200 times (obtaining 200 values of pseudo-r^2). This way we could estimate the empirical distribution of variance in community composition explained by spatial and environmental distances between islands and between CAEs. Third, using these empirical distributions, we assessed the probability of both variables explaining more variation in species composition on islands than on CAEs, applying a proportion test with the function *prop. test* to test if that probability is significantly different from 0.5 (a probability = 0.5 would represent that the effects of spatial and environmental distances are the same on islands and CAEs). We used this 200 CAEs resample for the partial Mantel test, computing the mean r value and the proportion of significant correlations found in the resamples (number of resamples with $p < 0.05$).

Second, at a small study scale (within island or CAE), the same procedures as explained above were used to evaluate the differences in beta diversity between islands and CAEs and the contribution of turnover and nestedness. However, this time, the pairwise dissimilarity was only computed within islands and compared to the mean pairwise dissimilarities within the set of all corresponding CAEs. We also used the Kruskal–Wallis test to assess the significance of the differences in dissimilarity between islands and CAEs. Similarly, to assess the effects of spatial

and environmental distances at small scale, we computed pseudo-r^2 of the within-islands spatial and environmental distance–decay models. Then, using the pseudo-r^2 of all corresponding CAE distance–decay models, we obtained the empirical distribution of explained variance by spatial and environmental distances in continents.

Finally, to evaluate how beta diversity responds to mean latitude (mean latitude of the study sites on each island), island sampled area (for each island, the area that was sampled, i.e., the size of the polygon including all sample sites), island age and island isolation on, we computed multiple-site Sorensen (β_{SOR}), Simpson (β_{SIM}) and nestedness-resultant (β_{SNE}) indices for each island using the function *beta.multi* from the *betapart* package. This allowed the overall dissimilarity, turnover and nestedness of each island to be expressed as a single dissimilarity value that can be related to island attributes. As in the previous analyses, the indices were computed using 15 sites per island (all sites for islands with < 15 sampling sites) to obtain standardised results. We performed linear regressions to assess the relationship between each index (dependent variable) and island attributes (predictors), considering in all cases a normal error distribution. To obtain the best possible model, we carried out a variable selection with the function *dredge* from the *MuMIn* package (Bartoń 2023), which indicates the best variable combination based on the AICc (Akaike information criterion corrected for small sample sizes) considering all possible independent variables combinations [16 in this case including the model with just an intercept (null model)]. The model with the lowest AICc

was selected. In addition, we accounted for the potential effect of biogeographical regions over the relation between island beta diversity and their attributes. To do so we fitted a linear mixed model specifying bioregions as a random effect using the function *lmer* from the *lme4* package (Bates et al. 2015). Then, we tested the significance of the bioregion effect (significance of the random variable in the model) with a restricted likelihood ratio test (RLRT) using the *exactRLRT* function from the *RLRsim* package (Scheipl, Greven, and Kuechenhoff 2008).

As our data come from different sources and were counted by different specialists, they may be affected by some subjective decisions in species-level identifications. To ensure the accuracy of our results, we repeated the data analyses after classifying diatoms into genus, as genus-level identifications are less prone to subjectivity.

3 | Results

At a large study scale, mean dissimilarities were significantly ($p < 0.05$) higher on islands than in CAEs for the European region but significantly lower on islands than in CAEs for the American region (Figure 2, Table 1 and Table S1) only partially supporting our hypothesis (H_1). While differences in species turnover were greater on European islands, nestedness tended to be greater in CAEs. In the American region, turnover was greater on CAEs and nestedness on islands (Figure 2, Table 1 and Table S1). As hypothesised (H_2), turnover was the main
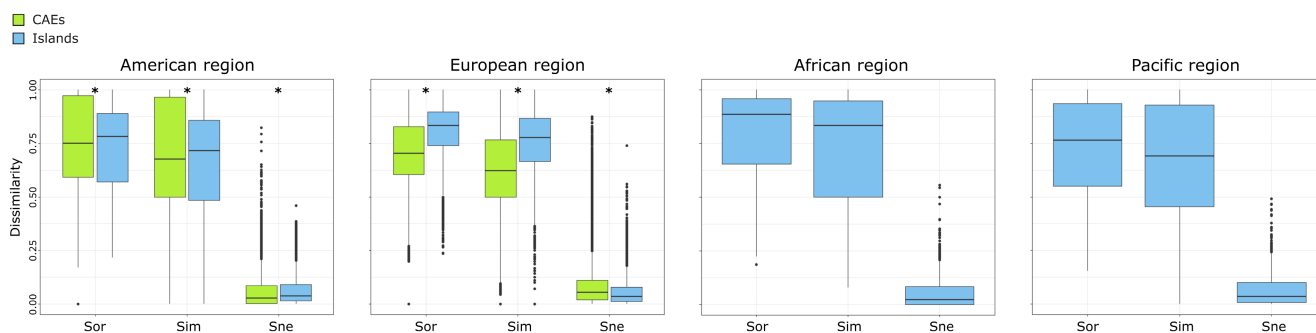

FIGURE 2 | Boxplots of the within-biogeographic regions (i.e., large study scale) pairwise dissimilarities computed with Baselga's approach for islands (blue) and continental area equivalents (CAEs, for America and Europe) (green). Sor, Sorensen index (total dissimilarity); Sim, Simpson index (turnover); Sne, nestedness resultant index (nestedness). Asterisks indicate significant differences in mean dissimilarities (note that medians but not means are represented in the boxplots).

TABLE 1 | Mean (±sd) dissimilarities computed using Baselga's approach with Sorensen (Sor, total), Simpson (Sim, turnover) and nestedness resultant (Sne, nestedness) indices for the within-biogeographic regions (large study scale) comparisons for islands and continental area equivalents (CAEs).

Region	Sor		Sim		Sne	
	CAEs	Islands	CAEs	Islands	CAEs	Islands
American	**0.759 ± 0.213**	**0.730 ± 0.181**	**0.703 ± 0.251**	**0.667 ± 0.216**	**0.056 ± 0.071**	**0.063 ± 0.069**
European	**0.711 ± 0.145**	**0.807 ± 0.130**	**0.632 ± 0.177**	**0.749 ± 0.164**	**0.079 ± 0.082**	**0.058 ± 0.069**
African	—	0.795 ± 0.212	—	0.738 ± 0.261	—	0.056 ± 0.082
Pacific	—	0.735 ± 0.206	—	0.669 ± 0.254	—	0.066 ± 0.080

Note: Significant differences (Kruskal–Wallis *p*-value < 0.05) are marked in bold.

cause of compositional differences between diatom communities among islands and among CAEs. In contrast, nestedness had overall only a small contribution to total beta diversity for both Baselga's and Podani's indices, although Podani's approach estimated higher nestedness values (richness differences) (Figure 2, Figure S1, Table 1 and Table S1). The β_{ratio} was < 0.5 in 1%–4% (Baselga's approach) and 12%–15% (Podani's approach) of the pairwise comparisons for islands, and in 1%–2% (Baselga's approach) and 11%–16% (Podani's approach) of the pairwise comparisons for CAEs across the two regions.

At a smaller study scale, turnover was also the main cause of compositional differences between sites (both Baselga's and Podani's approaches). Nestedness was predominant (β_{ratio} < 0.5) in 2%–13% (Baselga's approach) and 8%–34% (Podani's approach) of the pairwise comparisons for islands and in 1%–6% (Baselga's approach) and 13%–26% (Podani's approach) of the comparisons for CAEs. When comparing the level of within-island and within-CAEs dissimilarities, the results were variable. On isolated islands (e.g., Hawaii or São Miguel), dissimilarities tended to be lower than the associated CAEs, whereas less isolated islands (e.g., Corsica or Cyprus) had greater dissimilarities than associated CAEs (Figures S2, S3, Table 2 and Table S2). These differences were, in most

cases, significant (Kruskal–Wallis p-value < 0.05), except for nestedness, which tended to be similar between islands and continents (Table 2 and Table S2).

On islands at a large study scale, both spatial and environmental distances generated substantial similarity decays, as hypothesised (H_3). However, spatial distance better explained the differences in species composition than environmental distances (higher pseudo-r^2, Figure 3a,b). Partial Mantel test showed that the correlation of spatial distance with compositional similarity on islands was equal to or greater than this in CAEs, whereas the correlation of environmental distance with compositional similarity was greater in CAEs than on islands (Table 3). Moreover, the partial Mantel test correlations were stronger for spatial distance than for environmental distance on islands.

Distance–decay models revealed that the amount of variation in species composition explained by spatial distance varied among the biogeographic regions. For the American region, the amount of explained variation was equal between islands and continents, while in the European region, the spatial effect was greater in CAEs than on islands (Figure 3c and Table 3). Environmental distances had greater effects on species composition on continents than on islands (Figure 3c and Table 3).

TABLE 2 | Mean (±sd) dissimilarity computed using Baselga's approach with Sorensen (Sor, total), Simpson (Sim, turnover) and nestedness resultant (Sne, nestedness) indices for the within-islands and within-continental area equivalents (CAEs) (i.e., small study scale) comparisons for each island/CAE.

Region		Sor CAEs	Sor Islands	Sim CAEs	Sim Islands	Sne CAEs	Sne Islands
American	Gu	0.611 ± 0.168	0.585 ± 0.158	0.517 ± 0.174	0.486 ± 0.158	0.093 ± 0.078	0.099 ± 0.081
	Ha	**0.551 ± 0.162**	**0.441 ± 0.084**	**0.465 ± 0.166**	**0.334 ± 0.109**	0.086 ± 0.067	0.106 ± 0.077
	Ka	**0.576 ± 0.145**	**0.521 ± 0.126**	0.465 ± 0.155	0.425 ± 0.158	0.111 ± 0.101	0.095 ± 0.076
	Ma	0.575 ± 0.131	0.588 ± 0.131	0.483 ± 0.137	0.514 ± 0.159	**0.092 ± 0.080**	**0.074 ± 0.068**
	Oa	0.543 ± 0.129	0.544 ± 0.134	0.453 ± 0.140	0.447 ± 0.155	0.090 ± 0.071	0.097 ± 0.099
European	Co	**0.604 ± 0.128**	**0.673 ± 0.135**	**0.514 ± 0.144**	**0.557 ± 0.165**	**0.090 ± 0.085**	**0.116 ± 0.108**
	Cy	**0.610 ± 0.135**	**0.751 ± 0.142**	**0.522 ± 0.150**	**0.675 ± 0.186**	**0.087 ± 0.086**	**0.082 ± 0.080**
	Ic	**0.622 ± 0.130**	**0.472 ± 0.115**	**0.531 ± 0.151**	**0.369 ± 0.116**	0.091 ± 0.090	0.103 ± 0.090
	Ir	**0.634 ± 0.137**	**0.679 ± 0.117**	**0.542 ± 0.162**	**0.597 ± 0.143**	0.092 ± 0.091	0.082 ± 0.081
	Md	0.597 ± 0.127	0.584 ± 0.115	**0.499 ± 0.145**	**0.523 ± 0.136**	**0.098 ± 0.091**	**0.061 ± 0.053**
	Mj	**0.594 ± 0.124**	**0.646 ± 0.131**	**0.490 ± 0.142**	**0.568 ± 0.157**	**0.104 ± 0.095**	**0.078 ± 0.069**
	Sa	**0.622 ± 0.131**	**0.702 ± 0.161**	**0.535 ± 0.149**	**0.623 ± 0.165**	0.087 ± 0.082	0.080 ± 0.085
	Sm	**0.594 ± 0.122**	**0.504 ± 0.136**	**0.490 ± 0.140**	**0.364 ± 0.117**	**0.104 ± 0.099**	**0.140 ± 0.123**
African	My	**0.587 ± 0.124**	**0.619 ± 0.144**	0.501 ± 0.132	0.498 ± 0.159	**0.086 ± 0.072**	**0.121 ± 0.111**
	Po	**0.578 ± 0.119**	**0.435 ± 0.136**	**0.491 ± 0.128**	**0.326 ± 0.105**	0.087 ± 0.072	0.109 ± 0.120
	Re	**0.602 ± 0.129**	**0.501 ± 0.137**	**0.521 ± 0.139**	**0.376 ± 0.163**	**0.082 ± 0.067**	**0.126 ± 0.096**
Pacific	Nc	—	0.781 ± 0.196	—	0.719 ± 0.243	—	0.061 ± 0.097
	Nz	—	0.557 ± 0.126	—	0.447 ± 0.162	—	0.110 ± 0.094
	Sz	—	0.507 ± 0.089	—	0.400 ± 0.121	—	0.107 ± 0.083

Note: Significant differences (Kruskal–Wallis p-value < 0.05) are marked in bold. For island abbreviations, see the main text (2. Material and Methods).
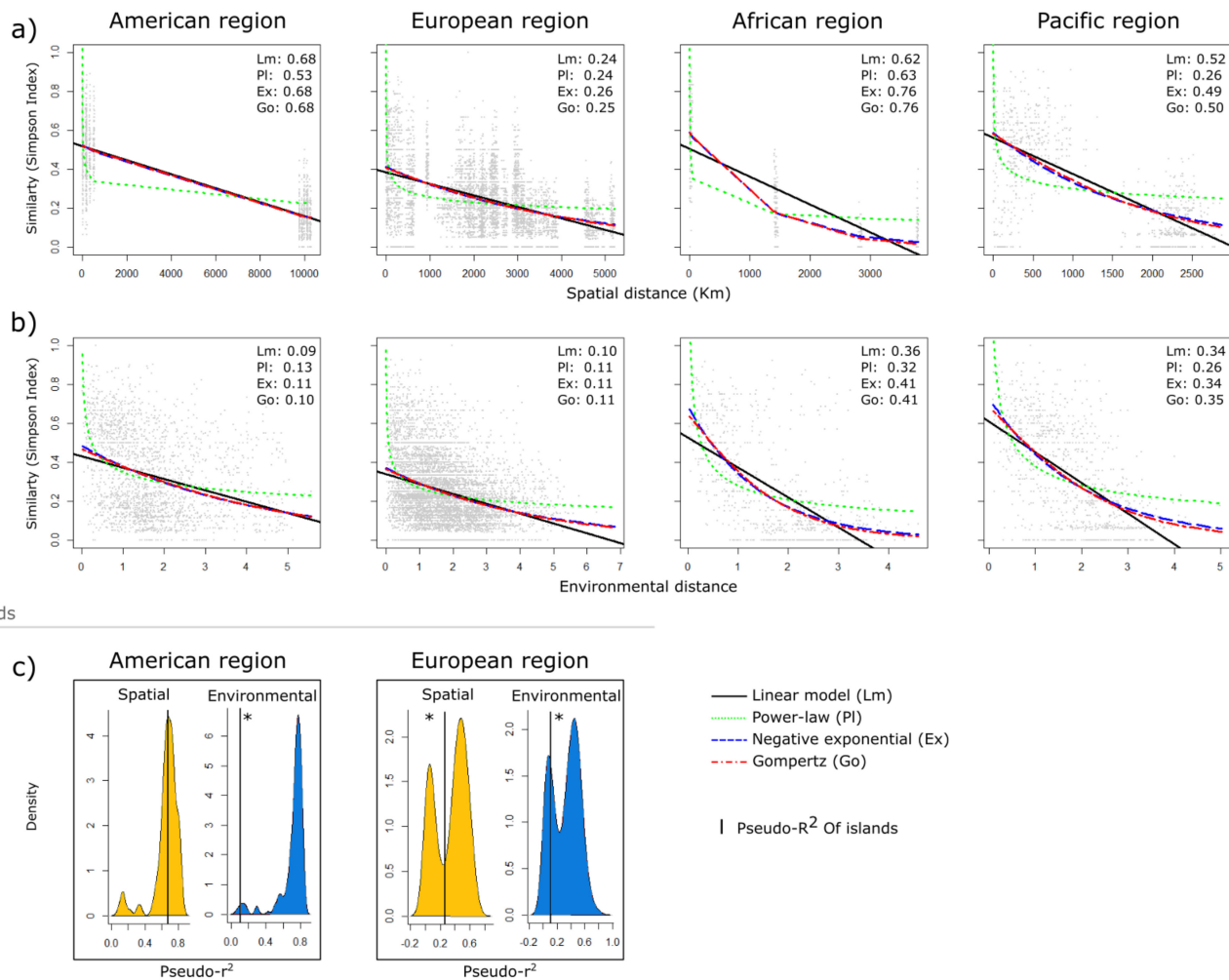
FIGURE 3 | (a) Spatial distance–decay among islands for the four biogeographic regions. (b) Environmental distance–decay among islands for the four biogeographic regions. In each figure, the pseudo-R^2 values for each model are represented. (c) Density of the pseudo-r^2 of the spatial and environmental distance–decay models (negative exponential function) for the continental area equivalents' resamples (America and Europe), indicating the pseudo-r^2 of the exponential models for the islands in the same region. Significant differences are indicated with an asterisk.

Agreeing with Hypothesis H_3 at small study scales, spatial distance had little effect on community composition (pseudo-r^2 between 0.01 and 0.11) in CAEs and on islands, except for Oahu (pseudo-$r^2 = 0.19$; Table S3). Environmental distances also contributed little to explain the compositional differences among communities within CAEs and islands (pseudo-r^2 between 0.00 and 0.21), except for Kawaii and Ireland (pseudo-r^2 0.50 and 0.28, respectively, Table S3). When compared with CAEs, the effects of spatial distance on diatom community composition were weaker within islands, with only two cases in which the pseudo-r^2 for islands was significantly > 50% of the pseudo-r^2 for the corresponding CAEs (Table S3). With respect to environmental distances, in seven of 16 cases (there are no comparisons for the three islands of the Pacific region), the pseudo-r^2 for islands was greater than the median pseudo-r^2 for the corresponding CAEs (Table S3), but only in five of these cases this difference was significant.

When assessing the relationship between island attributes (island mean latitude, island area, island age and island isolation) and multiple site dissimilarities (β_{SOR}, β_{SIM} and β_{SNE}), the best

model according to AICc included mean latitude, isolation and age of the islands for β_{SOR} and β_{SIM}, but mean latitude and age for β_{SNE}. No effects of biogeographic region were observed (RLRT p-value > 0.2 in all cases). For β_{SOR} ($R^2 = 0.729$, $F_{3,15} = 13.47$, $p < 0.01$), island mean latitude had a positive effect, opposite to our Hypothesis H_{4a} (Table 4 and Figure 4a). However, island age had a positive effect and isolation had a negative effect on β_{SOR} (Table 4 and Figure 4b,c), as we hypothesised (H_{4c} and H_{4d}). Notably, a similar relationship was found for β_{SIM} ($R^2 = 0.745$, $F_{3,15} = 14.63$, $p < 0.001$), in which island latitude and age both had a positive effect, whereas isolation had a negative effect (Table 4). β_{SNE} ($R^2 = 0.522$, $F_{2,16} = 8.74$, $p < 0.01$) had opposite relationships with island attributes as island mean latitude and age both had a negative effect on nestedness (Table 4). The same relation emerged with the pairwise total dissimilarities that multiple site total dissimilarities (Figure 4a–c).

Generally similar results were obtained when the analyses were repeated at a genus level (Figures S4–S8 and Tables S4–S9). The principal difference was that the genus-level dissimilarities were lower than species dissimilarities, but the comparison of

TABLE 3 | Partial Mantel test results for the effects of spatial distances controlling for environmental distances and environmental distances controlling for spatial effects on islands and continental area equivalents (CAEs) at large scale.

	Spatial distance	Environmental distance
Islands		
American region	$r = 0.821; p < 0.001$	$r = 0.266; p = 0.001$
European region	$r = 0.407; p < 0.001$	$r = 0.060; p = 0.080$
African region	$r = 0.649; p < 0.001$	$r = 0.169; p = 0.004$
Pacific region	$r = 0.570; p < 0.001$	$r = 0.250; p = 0.003$
Continents		
American region	$\mu(r) = 0.239$; significance % = 79.5	$\mu(r) = 0.340$; significance % = 87.5
European region	$\mu(r) = 0.226$; significance % = 93.5	$\mu(r) = 0.225$; significance % = 96.5
African region	$\mu(r) = 0.190$; significance % = 76.0	$\mu(r) = 0.235$; significance % = 92.0
Pacific region	—	—

Note: For CAEs, mean r values [$\mu(r)$] and the percentage of significant correlations between community similarity and spatial or environmental distances in 200 resamples.

TABLE 4 | Results of the multiple linear models for the relation between multiple-site dissimilarity and island attributes (latitude, age and isolation) chosen by corrected Akaike information criterion (AICc).

	Latitude	Age	Isolation
β_{SOR}	0.0007; $p = 0.015$	0.0031; $p = 0.001$	−0.0008; $p = 0.004$
β_{SIM}	0.0011; $p = 0.005$	0.0044; $p < 0.001$	−0.0010; $p = 0.005$
β_{SNE}	−0.0005; $p = 0.001$	−0.0014; $p = 0.003$	—

Abbreviations: β_{SIM}, Simpson index (turnover); β_{SNE}, nestedness resultant index (nestedness); β_{SOR}: Sorensen index (total dissimilarity).

beta diversity between islands and CAEs and the relationship between beta diversity and island attributes remained generally the same.

4 | Discussion

Our results showed that the patterns of island versus continental diatom beta diversity varied between study regions. At large study scales, beta diversity was generally higher on islands than in CAEs in the European region, but higher in CAEs than on islands in the American region. At smaller study scales, the patterns varied too, and island beta diversity largely depended on island isolation. Turnover was the principal component of beta diversity in all cases. Partial Mantel tests and distance–decay curves suggested that dispersal limitation and species sorting likely shape diatom beta diversity at a large, but not at small scales on both islands and in CAEs. Overall, all three components of diatom beta diversity on islands largely depended on island attributes, namely island latitude, age and isolation but not on area.

In the European region, the greater beta diversity observed on islands compared to CAEs at large study scales (within biogeographic regions) probably stems from greater spatial distances and lower connectivity (due to large marine areas between islands) between islands resulting in stronger dispersal limitation for freshwater diatoms (Soininen, Heino, and Wang 2018), as we hypothesised (H_1). Additionally, the number of unique species found on islands may also increase beta diversity among them (Stuart, Losos, and Algar 2012). However, contrary to Hypothesis H_1, in the American region, we found higher beta diversity among CAEs than among islands, which could have originated from greater environmental heterogeneity and distinct evolutionary history in the considered continental areas from both North and South America (the United States and French Guyana).

At smaller study scales (within islands and CAEs), the differences in beta diversity between islands and their corresponding CAEs were possibly the result of differential dispersal and historical processes. Thus, the higher beta diversity of less isolated islands compared to corresponding CAEs may be due to random colonisation of these islands by species with diverse dispersal capacities and subsequent speciation. These islands are also large continental fragments, that is, Corsica, Sardinia, Majorca, Ireland and Cyprus, where extinction is expected to be low and vicariance events could have happened, further contributing to higher beta diversity (MacArthur and Wilson 1967; Tracy and George 1992; Whittaker and Fernández-Palacios 2007).

In contrast, the lower beta diversity of more isolated islands than corresponding CAEs can be explained by dispersal limitation, whereby only species with high dispersal ability reach and then spread throughout these islands (Whittaker and Fernández-Palacios 2007), especially if environmental constraints are weak or a mass effect is taking place. Therefore, isolated islands may have experienced the so-called 'incomplete colonisation', the colonisation of a newly available territory by only a portion of the available species pool. This process was described in continents in the context of postglacial recolonisation of northern territories from the southern species pool (e.g., Gómez-Rodríguez and Baselga 2018; Hortal et al. 2011; Schuldt et al. 2009). In some
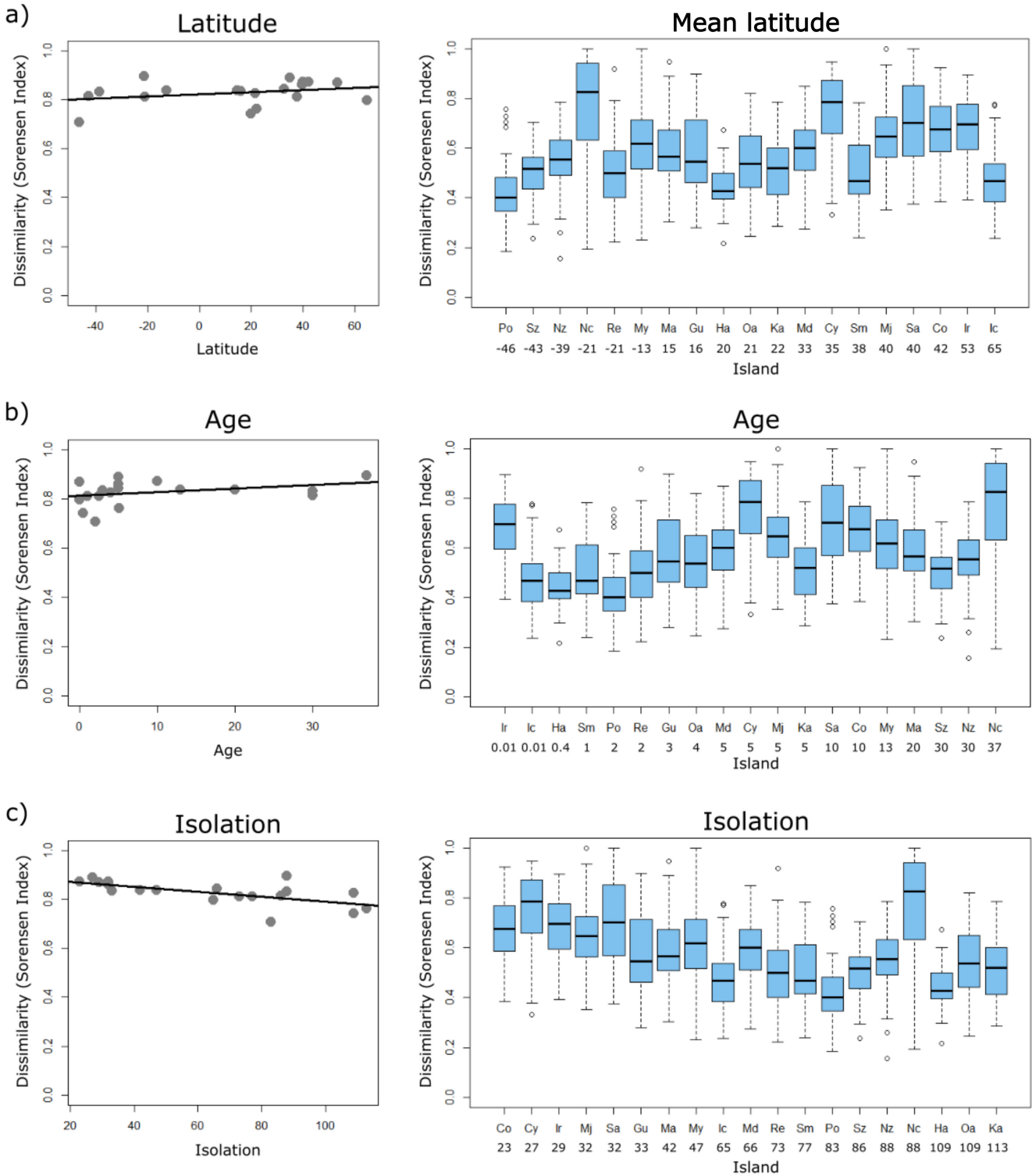
FIGURE 4 | (a) Relationship between total multiple-site dissimilarity (multiple-site Sorensen index) of islands and their (a) mean latitude, (b) age and (c) isolation. Mean latitude was measured in degrees, age in million years and isolation, as Dahl index. For island abbreviations, see the main text (2. Material and Methods).

species groups, only good dispersers could colonise northern territories, causing incomplete recolonisation with a subsequent effect on beta diversity among regions (Gómez-Rodríguez and Baselga 2018). This process has been proposed as an explanation for the differences in distance–decay between oceanic islands, continental islands and continents (König, Weigelt, and

Kreft 2017; Gómez-Rodríguez and Baselga 2018). Moreover, incomplete colonisation could be linked with disharmony in island biota. Disharmony, that is, the over- or underrepresentation of certain biological groups on oceanic islands compared with the continental species pool (Carlquist 1965), is mainly produced by dispersal filtering, as only the highly motile species

in continental species pool can colonise the most isolated islands (Carlquist 1966, 1974; König et al. 2021; Taylor et al. 2019; Whittaker and Fernández-Palacios 2007). Thus, incomplete colonisation could be understood as one of the major probable processes underlying oceanic islands' disharmonic biotas. The finding of more homogeneous selection (i.e., sites are more similar in species composition than expected by chance) in diatoms on more isolated islands (Pérez-Burillo et al. 2023) is consistent with incomplete colonisation in our study system.

Agreeing with our Hypothesis (H_2), beta diversity in CAEs and islands was mostly due to species turnover at both large and small study scales. At a large scale, high turnover was likely caused by the great spatial distances and environmental heterogeneity within biogeographical regions. At a small scale, community composition is typically shaped by local environmental conditions, known to be very influential for diatom communities (Soininen 2007) and biotic interactions (García-Girón et al. 2020), which together may have led to species sorting and an increase in species turnover between sites.

The distance–decay curves showed not only a strong spatial distance effect but also a notable environmental effect on diatom community similarity at large study scales for both islands and CAEs, which agrees with our Hypothesis (H_3) and previous literature (Keck, Franc, and Kahlert 2018; Soininen 2023). The results of the partial Mantel test also showed that both spatial and environmental variables underlie diatom community composition on islands and CAEs at large scales (with the spatial effect being stronger). While the spatial and environmental dependence of diatom composition in continents was previously noted globally (Soininen et al. 2016), here we report for the first time similar dependence on islands globally. When we compared the spatial and environmental effects between islands and continents at large study scales, we observed a significantly higher spatial effect in CAEs but only in the European region, and a significantly higher environmental effect in both the American and European regions. With respect to the spatial effect, the nonsignificant differences between islands and CAEs may be due to a similar level of dispersal limitation, given that both islands and CAEs spanned vast areas (maximum distance between sites was 10,294 km for islands and 8199 km for CAEs). In Europe, on the other hand, spatial distances among islands were much greater than among CAEs (maximum distance between sites was 5217 km for islands and 3225 km for CAEs), producing a stronger spatial effect on islands. With respect to the environmental effect, diatom composition was significantly more strongly controlled by the environment in CAEs than on islands, which is likely due to the greater environmental heterogeneity in the studied continental areas compared to islands (Jamoneau et al. 2022). At small study scales, we detected only weak spatial and environmental effects on diatom composition on both islands and CAEs, which could have resulted from efficient dispersal and more limited environmental variability (Gómez-Rodríguez and Baselga 2018; Winegardner et al. 2012). It is also possible that some unmeasured environmental variables shape diatom species distributions as diatoms typically respond to a wide range of environmental variables (Soininen 2004, 2007).

Our results failed to support hypothesis and H_{4a}, given that insular diatom beta diversity increased with island mean latitude. This is opposite to observations of most other organisms, whose beta diversity generally decreased with latitude (Qian 2009; Qian et al. 2013; Rodríguez and Arita 2004; Soininen, McDonald, and Hillebrand 2007) or showed no response (Mruzek et al. 2022). Surprisingly, area was not included in the best model explaining diatom beta diversity in our analysis, disagreeing with our Hypothesis H_{4b}. Weak area effects on beta diversity have also been reported in other microorganisms, such as arbuscular mycorrhizal fungi (Davison et al. 2018). A possible explanation could be that other variables, for example, isolation or latitude, are counteracting the area effects, but the absence of island species–area relationship (Jamoneau et al. 2022) and the flat distance–decay curves point to stochastic causes. As hypothesised (H_{4c}), island age positively affected beta diversity, likely because species had more time to colonise older islands and diversify (Badano et al. 2005; Borges and Brown 1999) and have likely passed through more environmental and ecological filters (Hui et al. 2013), making species composition more dissimilar among sites. Consistent with Hypothesis H_{4d}, island isolation increased beta diversity, which could be related to incomplete colonisation, as explained above. It should be stressed that New Caledonia differs from the general pattern (it has higher beta diversity than expected), probably because of its great number of endemic species (Moser, Lange-Bertalot, and Metzeltin 1998). When analysing beta-diversity components separately, the turnover component had the same relationship with island attributes as total beta diversity, whereas nestedness had the opposite relationship. The same negative relationship between beta diversity components has been shown in other studies for continents (Jamoneau et al. 2018; Soininen, Heino, and Wang 2018). Our results show that it also applies to islands.

In conclusion, diatom beta diversity on islands and how it compares with beta diversity in continents are scale and region dependent. Additionally, insular beta diversity varies with island attributes (latitude, age and isolation) and is mainly caused by species turnover. Incomplete colonisation, efficient dispersal, evolutionary factors and environmental filtering are possible causes of the differences in beta diversity between islands and equivalent continental areas. As a result of these processes, spatial and environmental distances affect diatom composition at a large scale but have negligible effects at a smaller scale. The emerging new knowledge about the patterns and drivers of island beta diversity is fundamental to understanding how biodiversity is structured in insular systems. Similarly to species richness, the role of island characteristics in shaping beta diversity should be included in island biogeography theory and studied further for multiple taxonomic groups.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The script and data used to perform this study are available as supplementary material. The raw data (same as in Jamoneau et al. 2022 and Pérez-Burillo et al. 2023) are available 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.