



Environmental and stochastic processes drive diatom taxonomic and functional temporal beta diversity

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ABSTRACT: Studying patterns of biodiversity is central to ecological research. Temporal beta diversity, i.e. the change in community composition over time, has emerged as a promising study field during the last decades. Following global climatic change, understanding the consequences of environmental alterations on temporal community composition has become increasingly important. We examined patterns and drivers of temporal beta diversity and whether the temporal variation in community composition is related to temporal environmental variation among 9 coastal diatom communities sampled 12 times at a ca. 10 d interval. We applied a temporal beta diversity index (TBI) decomposed into gains and losses to quantify changes in taxonomic and functional community similarity through time, and for environmental variables to determine temporal change in local abiotic conditions. We assessed environmental and spatial drivers of temporal community change by regression models and partitioned variation in the community composition according to sampling day by distance-based redundancy analyses. Taxonomic TBI was higher than functional TBI, characterized by sharper changes in species gains and losses. Taxonomic TBI was explained by site location, whereas functional TBI had a linkage with both spatial and environmental variables. Environmental TBI was significantly related to taxonomic TBI only. The sites significantly differing in taxonomic or functional TBI did not coincide with those with a significantly different environmental TBI between the sites. The communities were probably structured by both environmental variation and random stochastic processes, creating unpredictability in the TBI. Our results highlight the importance of rapid environmental alterations in shaping temporal beta diversity within dynamic coastal communities.

KEY WORDS: Loss · Gain · Similarity · Algae · Rock pool · Trait

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1. INTRODUCTION

Biodiversity patterns have been at the center of ecological research for decades, and the quantification of beta diversity forms one of the most fundamental issues in biogeography and ecology (Carvalho et al. 2012). Much of the preceding research about biotic communities has concentrated on spatial beta diversity, i.e. variation in species composition between sites (Whittaker 1960), while traditionally, lesser attention has been paid to the temporal aspect of community change, i.e. temporal beta diversity (Magurran et al. 2019).

In aquatic ecosystems, temporal beta diversity has received far less attention in comparison with other ecosystem types (Cook et al. 2018). Following global climatic change, understanding the cascading consequences of climate-driven shifts in biodiversity has become increasingly important, particularly in dynamic coastal ecosystems under continuous environmental perturbations (Crabot et al. 2020, Buckley et al. 2021). Temporal turnover describes the unidirectional change in community composition from one point in time to another. Through simultaneous gains and losses, species are replaced or persist in a community because of environmental, spatial, biotic, or

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historical constraints (Shimadzu et al. 2015). The effects of environmental change on taxonomic community composition are not necessarily translated into similar changes in functional composition, and vice versa (Villéger et al. 2012). Thus, as a valuable tool for widening the dimensions of traditional taxonomy-based biodiversity research, functional diversity estimators routinely complement taxonomic measures in ecology (Mammola et al. 2021).

Following the tentatively growing interest in temporal beta diversity, statistical tools have been introduced for monitoring species' compositional shifts over time (Magurran et al. 2019). The temporal beta diversity index (TBI) was recently developed to measure temporal differences in community composition among sites at 2 separate points in time (Legendre 2019). The index — applicable to both taxonomic and functional community data — measures the degree to which communities are differentiated from each other in time, ranging from 0 (no temporal differentiation) to 1 (complete temporal differentiation) to identify sites experiencing exceptional changes in community composition (Legendre 2019). For measuring directional change in community composition, which is often neglected in temporal beta diversity studies, TBI allows the partitioning of site-specific total dissimilarity into 2 additive components, gains and losses, according to species or traits gained and lost over time (Schmera et al. 2022). For assessing the drivers of community change at a given location, TBI can further be assessed for environmental variables to test whether changes in temporal beta diversity are driven by temporal changes in the local environment or random stochastic processes (Magurran & Henderson 2010, Baselga et al. 2015). Despite the emerging interest in patterns of temporal beta diversity in various types of natural communities (reviewed in Buckley et al. 2021), studies incorporating TBI on marine biota by both taxonomic and trait-based approaches are still rare (but see Virta et al. 2020, Paquette et al. 2022).

Being strongly responsive to environmental changes, microalgal diatoms (Bacillariophyceae) are at the lowest biological level to exhibit temporal changes in taxonomic and functional composition (Soininen 2007). Small, spatially isolated, and environmentally heterogeneous granitic rock pools comprising diverse biota exhibit a naturally dynamic transitional habitat at the marine–freshwater interface for testing the influence of environmental filtering on taxonomic and functional microbial diversity through time (Blaustein & Schwartz 2001, Srivastava et al. 2004). With data of high temporal resolution sampled across a 5 mo period from 9 coastal rock pools, we aimed to investi-

gate (1) how taxonomic and functional temporal beta diversity (partitioned into loss and gain components) covary, (2) which environmental variables best explain taxonomic and functional temporal beta diversity, and (3) how temporal beta diversity is related to temporal environmental variation.

2. MATERIALS AND METHODS

2.1. Field sampling

We sampled 9 brackish-water, isolated rock pools 12 times ($N = 108$) at roughly 10 d intervals (with the exception of 21 days between the 9th and 10th sampling days) in May–September 2019 on a granitic outcrop in Pihlajasaari Island (66° 68' N, 38° 40' E), ca. 2 km south of Helsinki on the coast of the northern Baltic Sea (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m742p059_supp.pdf). In the study area, tidal influence is virtually absent, and changes in sea level are caused predominantly by wind and differences in air pressure (Pajunen & Pajunen 2007). Despite varying size and shape, the studied pools share a similar geology and basin structure mostly covered by a thin sediment layer, and the boulders and pebbles within them are likely of the same geological origin. The pools were unshaded by vegetation and mainly rainfall-fed; the pools closest to the sea were occasionally influenced by direct inflows and salty splashes from the sea. Pool nutrient enrichment was likely mostly of biological origin, caused by decaying organism remains and faunal excretions (Brendonck et al. 2016).

We measured water pH, conductivity, and temperature *in situ* with a YSI Professional Plus field meter. We measured pool morphometrics (i.e. maximum depth, length, and width), and pool area was approximated by multiplying pool length by pool width. We collected a 0.5 l water sample from each pool preserved at 4°C for the determination of total P (Finnish Standards Association 2004) and total N (Finnish Standards Association 1998) concentrations and a nutrient supply (i.e. N:P) ratio. We determined pool location by latitude and longitude with a GPS and measured distance from the sea and mean isolation as a mean Euclidean distance (i.e. the mean distance to 5 closest pools; Vanschoenwinkel et al. 2007) on an aerial photograph.

2.2. Taxonomic data

We sampled benthic diatoms following standard methodology (European Committee for Standardiza-

tion 2003) by collecting 10 subsamples (ca. 25 cm²) from each pool bottom, using a toothbrush to brush material into a plastic container filled with pool water. We combined the accumulated diatom suspension as a single composite sample in a plastic test tube in the field. The bottom of the 2 largest pools (Pools 6 and 9) was unreachable; therefore, only the pool walls were sampled, deep enough to ensure the frustules were permanently submerged. Between each sampling, the toothbrush was rinsed in pool water to remove attached cells and reduce contamination and taxonomical bias between the samples (Kelly et al. 1998).

We preserved the samples in 98% ethanol at 4°C until treatment with 30% H₂O₂ to remove organic material and then mounted them on slides with Naphrax. A minimum of 500 valves per slide were counted and identified to the lowest taxonomic level possible (mostly species level) with a light microscope (1000-fold magnification) following Krammer & Lange-Bertalot (1986–1991), Snoeijs (1993), Snoeijs & Vilbaste (1994), Snoeijs & Potapova (1995), and Snoeijs & Kasperovicienė (1996). From the 14 most sparsely celled slides from Pools 1, 5–6, and 8–9, less than 500 valves (<100 from 5 of the slides with a minimum of 18) could be counted. We created a binomial site–species matrix based on species presence–absence after the count abundances.

2.3. Functional data

We classified the diatom species into 21 functional groups. We first divided the species into 5 size classes based on their biovolume (determined by cell length, width, thickness, and shape) and 14 life-form categories based on their morphological adaptations (i.e. cell motility, posture, and type of adhesion) to physical and chemical disturbance following Rimet & Bouchez (2012). Any taxon with various successive life forms was classified into multiple life-form categories (Berthon et al. 2011).

We further divided the species into 4 ecological guilds according to their preferences for nutrient concentration and physical disturbance after Passy (2007) and Rimet & Bouchez (2012): high profile (the upper benthic layer in nutrient-rich, weakly disturbed habitats), low profile (in highly disturbed and oligotrophic habitats in the base of the benthos), motile (nutrient-tolerant taxa with low tolerance for physical disturbance—but physically capable of selecting a suitable habitat, thus only marginally affected by disturbance and resource limitation), and planktic guild

(species morphologically adapted to lentic, less turbulent environments prone to sedimentation).

Finally, we separated between acid-tolerant (acidobiontic or acidophilous species with pH optimum of <7 in Van Dam et al. 1994) and nitrogen-fixing species (members of the genus *Epithemia* capable of fixing atmospheric nitrogen by cyanobacterial endosymbionts) (Soininen et al. 2016). We created a binomial site–trait matrix in which each species belonging to a given guild was given a value of 1; otherwise, the value was set to 0. Most species were characterized by multiple traits and belonged to more than one guild.

2.4. Statistical analyses

To account for temporal change in the explanatory variables (other than pool coordinates, isolation, and distance to the sea), we subtracted each variable's site-specific value of an earlier sampling day from that of the proceeding sampling day for each consecutive sampling day pair ($n = 11$) and used these as model covariates (expressed with the sign ' Δ ') in our analyses (except for counting environmental TBI based on the original environmental data). We calculated Spearman's rank correlation coefficients and variation inflation factors with a threshold value of 3.0 (Zuur et al. 2010) and examined temporal and spatial patterns in the data with co-plots to detect statistical dependence between the variables. Hence, Δ total N, Δ length, Δ width, latitude, longitude, and a 12-level categorical variable for sampling day were excluded from the statistical analyses (although sampling day was used as the only explanatory variable in the ordination analyses as described below). We further assessed temporal autocorrelation for the environmental variables with an autocorrelation function (ACF) correlogram with 20 lags.

We first quantified the TBI (Legendre 2019) to measure temporal beta diversity within the rock pool communities. We applied the Sørensen dissimilarity coefficient for the taxonomic and functional presence–absence data, respectively, with 9999 permutations to examine whether a species assemblage at a given site had changed exceptionally between each of the 12 sampling days, by first repeating the analysis for each consequent sampling day pair (i.e. 1–10, 11–21, ..., 110–119; $n = 99$) and then for the entire sampling period (i.e. 1–119, $N = 108$). We decomposed total taxonomic and functional TBIs (hereafter TBI_{Tax} and TBI_{Func}, respectively) into loss and gain components to assess the direction and significance of change in community composition through time; i.e.

whether the studied communities had lost or gained species or traits between the consecutive sampling days.

To examine whether the communities with a significant change in TBI_{Tax} or TBI_{Func} were also experiencing significant changes in environmental conditions, we assessed environmental TBI (hereafter TBI_{Env}) by applying Euclidean distance for *a priori* standardized environmental data with non-negative, equally weighted variables (Legendre 2019). For all TBI indices, we used p-values of paired *t*-tests and corrected for multiple testing to express the significance of the temporal change in community composition.

We used linear regression models with a beta error distribution (Ferrari & Cribari-Neto 2004) to examine the factors best explaining variation in TBI_{Tax} and TBI_{Func} . We first fit all models both with and without a 9-level random factor for the study site (Wood 2006) to account for possible spatial dependence in the data. Due to high model complexity and low variance in the grouping factor for the study site (results not shown), we decided to use generalized linear models (GLMs; McCullagh & Nelder 1983) with only the fixed effect part, without any random structure. We further applied a beta regression model to investigate whether variation in TBI_{Tax} and TBI_{Func} could be explained by variation in TBI_{Env} . Due to an overall better model fit, we chose to use the sampling site as a random intercept and TBI_{Env} as a fixed term, as in generalized linear mixed models (GLMMs; Zuur et al. 2009). Since possible temporal dependence in the data was linked to the variable sampling day that models within- rather than between-group dependence when applied as a random factor in a GLMM (Zuur et al. 2009), we did not include this 12-level categorical covariate in the random structure (or in the fixed part due to collinearity with the other covariates) of our regression models.

Prior to running the regression models, all continuous covariates were standardized. Since the beta distribution can only deal with values larger than 0, we added a constant (with the formula $[x \times (N - 1) + 0.5] / N$) to TBI_{Func} with a few values equaling 0.0. We used quadratic terms for the explanatory variables with a unimodal relationship with the response variables; otherwise, only first-level terms were used. The covariates were removed from the full models by a backward stepwise method, and the model with the lowest Akaike information criterion value (Akaike 1973) was considered the best. The explanatory power of the covariates in the reduced regression models was assessed by the likelihood ratio test and either pseudo- R^2 (for the

GLMs) or Nakagawa's R^2 (for the GLMMs; Nakagawa & Schielzeth 2013); the statistical significance of the variables was based on Pearson's chi-squared test.

The regression models were validated following the protocol proposed by Zuur & Ieno (2016). We assessed model independence by plotting the residuals against the fitted values and against the covariates both included in and excluded from each of our models. We checked the significance of any non-linear pattern between the model residuals and a covariate with generalized additive models (Hastie & Tibshirani 1990). We assessed spatial independence of the residuals by Moran's *I* (Moran 1950) with 5 distance classes and Bonferroni-corrected p-values for the correlation coefficients (Legendre & Legendre 2012); for detecting temporal autocorrelation, we used ACF correlograms with 20 lags.

Lastly, we applied a distance-based redundancy analysis (dbRDA; Legendre & Anderson 1999) to partition variation in the taxonomic and functional community composition, according to sampling day ($N = 108$). We used the square-rooted Sørensen dissimilarity matrix as an input in a principal coordinate analysis (Gower 1966); the resulting matrix was then used as a response variable in a dbRDA, constrained by a 12-level factor representing the consecutive sampling days. The statistical significance of the explanatory variable and ordination axes was assessed using an *F*-test with 999 permutations.

All statistical analyses were conducted in R v.3.6.2 (R Core Team 2022), using R source code provided in Zuur et al. (2009), primarily with packages 'adespatial' (Dray et al. 2021), 'betareg' (Cribari-Neto & Zeileis 2010), 'glmmTMB' (Brooks et al. 2017), and 'vegan' (Oksanen et al. 2019).

3. RESULTS

Most of the total of 299 detected species (including subspecies; per-pool range: 10–62, mean: 26) of 78 genera were classified as non-colonials (81.4%), mobile (75.1%), and motile (45.5%), with the most abundant taxa being *Nitzschia microcephala* (37.9%), *Achnanthydium minutissimum* (9.3%), and *Navicula perminuta* (6.1%).

The rock pools were generally small (mean area: $<7 \text{ m}^2$) and shallow ($<0.5 \text{ m}$ deep), with a large range in overall Δ conductivity ($|2\text{--}20\,780| \mu\text{S cm}^{-1}$) and Δ total P ($|0.2\text{--}1095| \mu\text{g l}^{-1}$) (Table S1). The pools followed clear gradients in water conductivity ($r_s = -0.38$, $p < 0.0001$), pool area ($r_s = 0.45$, $p < 0.0001$), and

depth ($r_s = 0.55$, $p < 0.0001$) along increasing distance to the sea, and in water pH ($r_s = 0.26$, $p = 0.006$), conductivity ($r_s = 0.44$, $p < 0.0001$), and depth ($r_s = -0.27$) with increasing pool isolation. Δ Temperature ($r_s = -0.46$) and Δ depth ($r_s = 0.21$, $p = 0.040$) were significantly associated with sampling day, while temporal variation in various physicochemical variables scaled significantly with Δ depth and Δ area. Significant temporal autocorrelation for several lags was found for water pH, conductivity, and temperature (Fig. S2). TBI_{Tax} was significantly related to both TBI_{Func} ($r_s = 0.37$, $p < 0.001$) and TBI_{Env} ($r_s = -0.43$, $p < 0.0001$). TBI_{Tax} and TBI_{Env} were further related to pool distance from the sea ($r_s = 0.32$, $p < 0.001$ and -0.34 , $p < 0.001$, respectively), while TBI_{Func} was correlated with Δ temperature ($r_s = -0.22$, $p = 0.029$) and pool isolation ($r_s = -0.32$, $p = 0.002$), and TBI_{Env} was correlated with sampling site ($r_s = -0.22$, $p = 0.029$) (Table S2).

The TBI_{Tax} was considerably high (range: 0.23–0.68; mean: 0.44), practically always exceeding TBI_{Func} (range: 0.0–0.24; mean: 0.08) (Table S3). Mean TBI_{Tax} was highest in Pool 1 and lowest in Pool 2, and mean TBI_{Func} was highest in Pool 6 and lowest in Pool 8. The highest TBI_{Tax} was recorded in Pool 1 between sampling days 8 and 9, and the highest TBI_{Func} was in Pool 6 between sampling days 7 and 8, both characterized by a significant change in total dissimilarity; at the lowest, TBI_{Tax} was in Pool 4 between sampling days 11 and 12, and TBI_{Func} was in Pools 2 and 8 between sampling days 1–2 and 4–5, respectively. At the minimum, the taxonomic composition on the last sampling day was only 23% (mean: 0.37), similar to that on the first day in Pool 1, whereas in Pool 5, up to 100% similarity (mean: 0.92) was observed for the functional community composition considering the entire study period (i.e. Days 1–119); however, these long-term changes in total dissimilarity were non-significant.

Overall, mean TBI and its components (i.e. losses and gains) were rather similar yet consistently higher for TBI_{Tax} than for TBI_{Func} . Both mean TBI_{Tax} (range: 0.4–0.49) and mean TBI_{Func} (range: 0.07–0.12) peaked between sampling days 8 and 9, followed by a downward trend toward the end of the study period (Fig. 1). The loss component slightly dominated changes in both mean TBI_{Tax} and TBI_{Func} . For mean TBI_{Tax} , the direction of overall change regardless of

site was significantly negative between sampling days 1 and 2; for mean TBI_{Func} , the direction of change was significantly negative from sampling days 1 to 2 and positive from days 9–10. For TBI_{Tax} , temporal and within-pool variability was always higher than for TBI_{Func} (Fig. S3). At the site level, maximum gains nearly equaled maximum losses for both TBI_{Tax} and TBI_{Func} . Species gains dominated significant changes in TBI_{Tax} in Pools 1 (characterized by the highest gains of 0.64) and 5 between sampling days 8–9 and 4–5, respectively; in Pool 9, the maximum species losses (0.62) outweighed gains between sampling days 5 and 6. For TBI_{Func} , significant dominance of gains (with a recorded maximum of 0.18) was found for Pool 6 between sampling days 7 and 8 (Table S3).

The majority of the 9 pools — especially Pools 2 and 3 — were characterized by notable changes in the physicochemical variables and in TBI_{Env} . However, for Pool 1, the environmental variability was minimal. A significant increase in TBI_{Env} up to the recorded maximum (7.43) was found for Pool 2 between sampling days 8–9 and 9–10, and for Pool 3 between sampling days 4 and 5; the lowest TBI_{Env} (1.09) was found in Pool 5 between sampling days 9 and 10 (Table S3).

According to the best approximating regression models, variation in both TBI_{Tax} and TBI_{Func} was significantly (TBI_{Tax} $p < 0.05$, TBI_{Func} $p = 0.003$) explained by a negative unimodal relationship with pool isolation, and either a concave-up (for TBI_{Tax} ; $p < 0.001$), or a

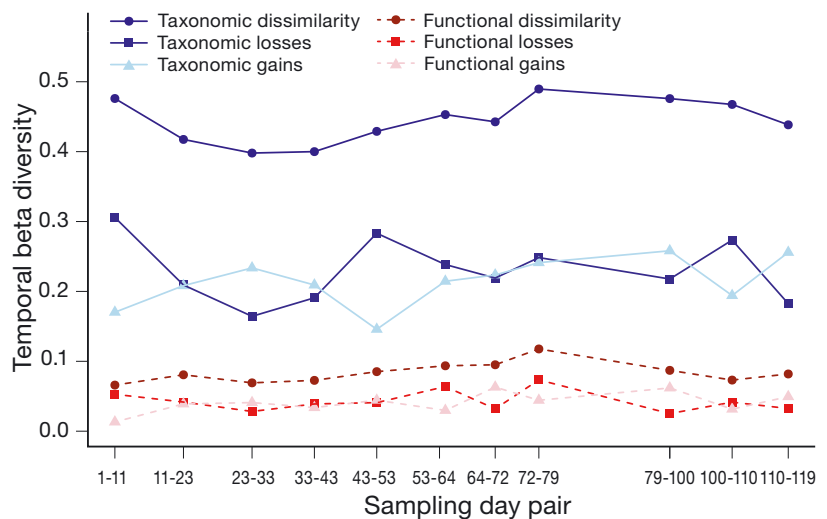


Fig. 1. Mean change in community dissimilarity, expressed as temporal beta diversity, for the taxonomic and functional presence-absence data across the 9 sites between the 11 sampling day pairs. Sampling days are numbered with running numbers from 1 to 119. Shown is the mean total dissimilarity partitioned into mean losses and gains. Note the irregular interval between the sampling day pairs

concave-down (for TBI_{Func} ; $p = 0.034$) relationship with pool distance to the sea. TBI_{Func} was further linearly related to $\Delta N:P$ ratio ($p = 0.021$), Δ conductivity ($p = 0.006$), and Δ temperature ($p = 0.04$) and negatively unimodally to Δ area ($p = 0.035$) (Fig. 2, Table 1). For both GLMs, significant temporal autocorrelation was found for one lag (Fig. S4). The

GLMMs showed a significant negative ($p < 0.001$) relationship between TBI_{Env} and TBI_{Tax} ; for TBI_{Func} , no significant relationship with TBI_{Env} was found (Fig. 3, Table 2).

In the dbRDA, sampling day was significant ($p < 0.05$) in explaining 11 and 13% of the temporal variation in taxonomic and functional community compo-

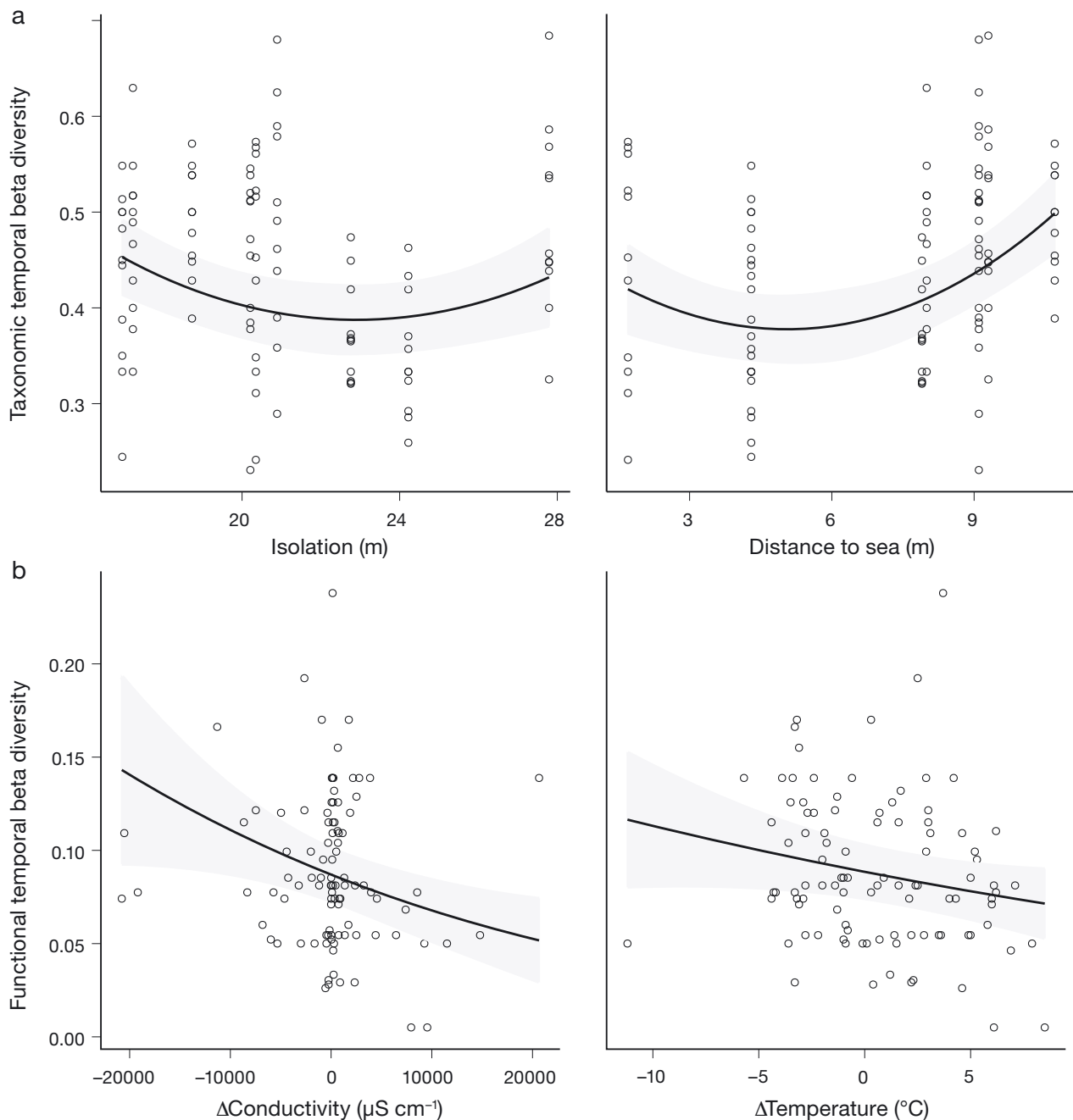


Fig. 2. Generalized linear model fit for (a) taxonomic and (b) functional temporal beta diversity indices. Shown is the model fit for selected statistically significant ($p < 0.05$) covariates explaining variation in the response variable, including a fitted Loess smoothing curve with 95% confidence intervals (gray shading). Hollow circles: observed relationship between the response variable and the covariates ($N = 99$)

Table 1. Generalized linear model for the taxonomic (TBI_{Tax}) and functional (TBI_{Func}) temporal beta diversity indices, explained by temporal change in the environmental variables between the 12 sampling days. Quadratic terms (coefficients marked with ²) were used for the explanatory variables with a unimodal relationship with the response variables. Model selection was based on the Akaike information criterion (AIC); pseudo- R^2 was attained by re-fitting the reduced model with the 'betareg' function. Statistical significance of the covariates is based on the likelihood ratio test (LRT); * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Model	Coefficient	Estimate	SE	df	LRT	Pr(>Chi)	AIC	Pseudo- R^2
TBI_{Tax}	(Intercept)	-0.43078	0.07203				-185.8	0.18
	Isolation	-0.09440	0.04342	1	4.6027	0.03192*		
	Isolation ²	0.08270	0.03475	1	5.4991	0.01903*		
	Distance to sea	0.18503	0.04790	1	13.9834	0.00018***		
	Distance to sea ²	0.12525	0.04618	1	7.0752	0.00782**		
TBI_{Func}	(Intercept)	-2.34832	0.08693				-379.2	0.36
	Total P	0.08557	0.05092	1	2.7631	0.09646		
	N:P	0.11438	0.04814	1	5.3140	0.02116*		
	Conductivity	-0.15320	0.05325	1	7.6018	0.00583**		
	Temperature	-0.09906	0.04751	1	4.2322	0.03966*		
	Area	-0.01347	0.03856	1	0.1204	0.72865		
	Area ²	0.02676	0.01201	1	4.4261	0.03539*		
	Isolation	-0.16111	0.05167	1	8.8823	0.00288**		
	Isolation	0.06245	0.04022	1	2.3373	0.12631		
	Distance to sea	0.06371	0.05433	1	1.3462	0.24594		
	Distance to sea ²	-0.12019	0.05726	1	4.4895	0.03410*		

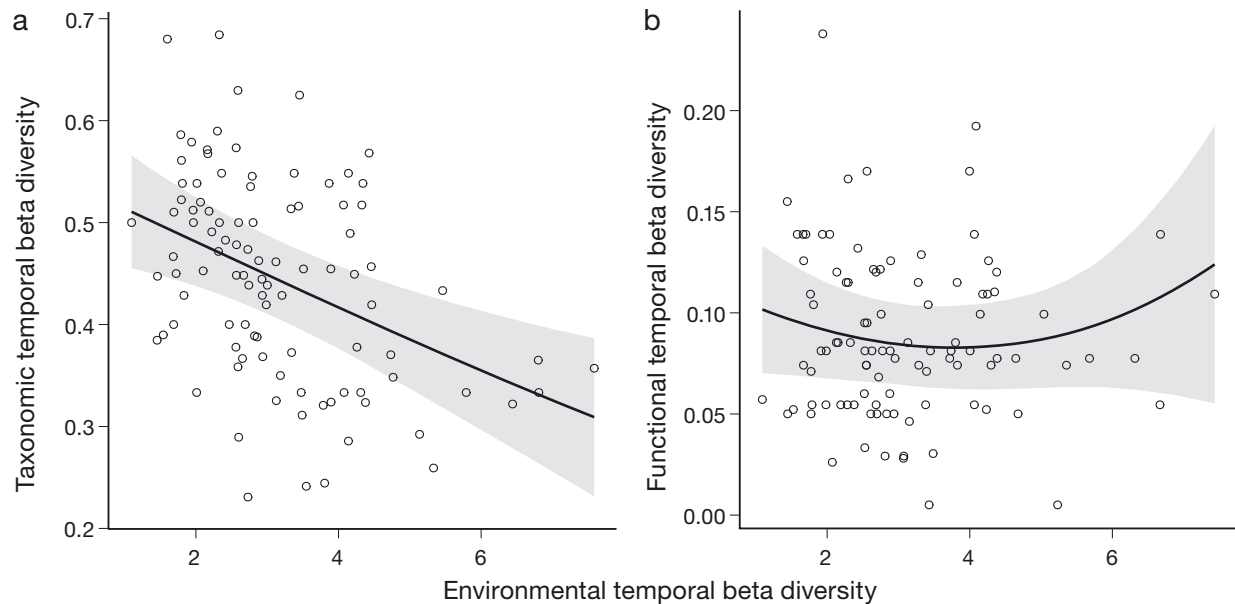


Fig. 3. Generalized linear mixed model fit for (a) taxonomic and (b) functional temporal beta diversity indices, explained by environmental temporal beta diversity index. Shown is the model fit for the environmental temporal beta diversity index explaining variation in the response variables for an average site, including a fitted Loess smoothing curve with 95% confidence interval (gray shading). Hollow circles: observed relationship between the response variable and the covariate ($N = 99$)

sition, respectively (Table S4). The first sampling day was distinctive in taxonomic composition, as were sampling days 7–9 and 10–12; the rest of the taxonomic and all functional communities were more uniformly located in the ordination space in relation to each other, with little temporal variation across the studied pools (Fig. 4).

4. DISCUSSION

4.1. Taxonomic versus functional temporal beta diversity

The studied communities were characterized by relatively high temporal differentiation and sharp

Table 2. Generalized linear mixed models for the taxonomic (TBI_{Tax}) and functional (TBI_{Func}) temporal beta diversity indices, explained by the environmental temporal beta diversity index (TBI_{Env}). Quadratic term (TBI_{Env}^2) was used for the explanatory variable with a unimodal relationship with the response variable. Model selection was based on the Akaike information criterion (AIC); the explanatory power of the entire model and the fixed effects was assessed by conditional (R^2_c) and marginal (R^2_m) Nakagawa's R^2 values, respectively. The statistical significance of the covariates is based on the likelihood ratio test (LRT); * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Model	Coefficient	Estimate	SE	df	LRT	Pr(>Chi)	AIC	R^2_c	R^2_m
TBI_{Tax}	(Intercept)	-0.22586	0.03819				-189.7	0.78	0.75
	TBI_{Env}	-0.16632	0.04747	1	11.9280	0.00055***			
TBI_{Func}	(Intercept)	-2.41605	0.10020				-358.0	0.28	0.03
	TBI_{Env}	-0.05560	0.06470	1	0.7313	0.39250			
	TBI_{Env}^2	0.05233	0.03245	1	2.3746	0.12330			

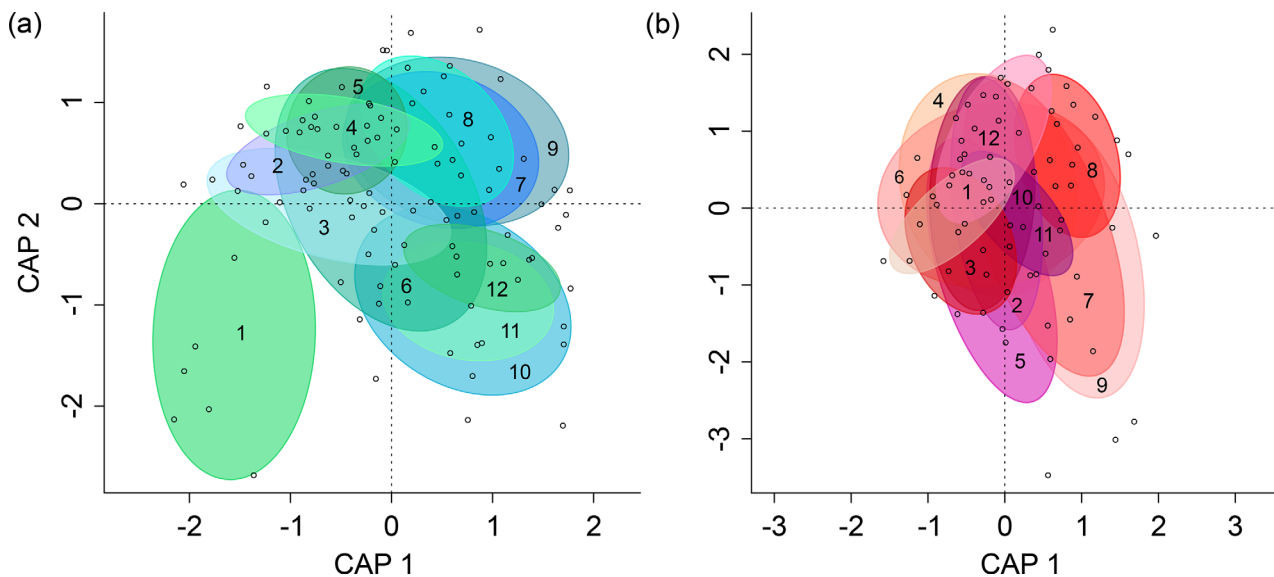


Fig. 4. Canonical ordination plot obtained by the distance-based redundancy analysis for the Sorensen dissimilarity index calculated for the (a) taxonomic and (b) functional data from the 9 sites, constrained by a factor representing the 12 sampling days. The colored ellipses cover 60% of the sites (hollow circles; $N = 108$) of each sampling day (numbered 1–12)

alterations in taxonomic composition, with up to 70% of the species replaced from one time point to the other. Most of this replacement was non-significant and due to species loss. Despite similar patterns with TBI_{Tax} , mean and total TBI_{Func} were lower and more stable over time. Similar patterns in temporal beta diversity have emerged for other taxa and habitats (e.g. Villéger et al. 2012, Virta et al. 2020, Paquette et al. 2022), referring to taxonomically diverse yet functionally complementary species. This functional redundancy, associated with unstable taxonomic composition, resulted in the low functional diversity change indicative of weak functional response to environmental disturbance through time (Boersma et

al. 2014). Typical of harsh habitats, taxa replacements largely cover few functionally similar, temporally dominant traits, buffering against the taxonomic variability (Villéger et al. 2012, Crabot et al. 2020). Thus, rapid shifts in taxonomic diversity may not affect trait diversity in functionally redundant communities (Cadotte et al. 2011).

4.2. Taxonomic and functional TBI versus environmental variables

The TBI_{Env} scaled significantly with TBI_{Tax} in the GLMM while having no relationship with TBI_{Func} . How-

ever, several pool physicochemical variables performed well in explaining TBI_{Func} in the GLM, as TBI_{Func} was highest in pools with variable areas, decreasing water conductivity and temperature, and an increasing N:P ratio, indicative of functional adaptations toward shifting physicochemistry, lower water temperatures nearer the sea, or alternating water volume (Boersma et al. 2014, Camara et al. 2021). In contrast, TBI_{Tax} was predominantly associated with pool location. This agrees with studies relating taxonomic diversity more strongly with spatial than environmental gradients in response to local dispersal processes (Erős et al. 2009), whereas the linkage between environmental variation and functional diversity has been better captured by trait-based methods (Mouillot et al. 2013, Stenger-Kovács et al. 2020). Through functional traits covering polyphyletic groups of species sharing similar ecological preferences, species keep pace with local environmental changes (Zhang et al. 2019). However, changes in taxonomic composition do not necessarily involve concomitant changes in functional configuration: although these 2 metrics may covary to some extent, they may differ in their drivers (Zhang et al. 2019, Aarnio & Soininen 2021).

4.3. Taxonomic and functional TBI versus spatial variables

Both TBI_{Tax} and TBI_{Func} scaled negatively unimodally with pool isolation. According to the theory of island biogeography (MacArthur & Wilson 1967), temporal variation in community composition depends on species gained and lost through time. In the least isolated pools, the constant inflow of species and traits likely maintains temporal instability in the communities connected by stronger passive dispersal, whereas in the most isolated pools, the compensation of taxonomic or functional losses by new colonizers is hindered by their weaker accessibility (Borthagaray et al. 2023). At intermediate isolation, instead, the distance between neighboring sites is probably short enough not to restrict immigration in high quantities yet far enough to prevent most sporadic appearances of the temporally rarest taxa, maintaining low TBI_{Tax} and TBI_{Func} . In frequently disturbed habitats, such as our pool communities, such stochastic dispersal-related processes may have profound effects on beta diversity (Vanschoenwinkel et al. 2013).

The explanation above could also apply to the U-shaped relationship between TBI_{Tax} and pool distance from the sea. The pools nearest the shore were often

in direct contact with the sea through salty inflows, promoting passive dispersal. Thus, the aggregation of species from the sea likely prevents temporal taxonomic homogenization, as species are occasionally present in several pools yet largely absent from all pools (Adler 2004). Contrastingly, the pools farthest from the sea lose species at a rate higher than immigration of new species, increasing their TBI_{Tax} . These views are partly supported by a significant negative correlation between pool isolation and functional gains, and a significant positive correlation between pool distance from the sea and taxonomic losses in our study system. The peaking TBI_{Func} halfway inland likely stems from the negative correlation between water conductivity and pool distance from the sea. Coastal diatoms are greatly impacted by water conductivity (Virta et al. 2020, Teittinen et al. 2021). At intermediate conductivities in transition from mostly marine to freshwater pools, a wider salinity gradient may enable the survival of different functional groups either adapted to certain salinities or occasionally expanding their niche over suboptimal conditions, adding to the TBI_{Func} of these weakly saline pools (Schröder et al. 2015). At the opposite ends of the distance gradient, several species may perform similar ecological functions adapted to these conductivity extremes, impeding functional temporal turnover due to redundant traits (Baselga et al. 2015, Camara et al. 2021). Previous studies have shown that taxonomic and functional diatom diversity scales significantly with distance to the shore among correspondingly local-scale rock pool communities (Aarnio & Soininen 2021, Teittinen et al. 2021).

4.4. Taxonomic and functional TBI versus environmental TBI

At the site level, a significant increase in TBI_{Tax} was mostly attributable to temporarily sharply peaking species gains or losses, while a moderate increase in gains affected significant changes in TBI_{Func} values. However, the pools with a significant change in either TBI_{Tax} or TBI_{Func} did not coincide with the pools of exceptional environmental change at any point in time. Contrastingly, the sites with significant environmental change showed only moderate, non-significant changes in TBI_{Tax} and TBI_{Func} . Similar results have emerged in studies examining the link between TBI and environmental change, with sites of low temporal diversity dissociated with trends in the abiotic environment (Galvanese et al. 2022). However, significant gains in TBI_{Tax} and TBI_{Func}

appeared to be associated with steep temporary declines in water conductivity and pool area, whereas the dominance of species losses for TBI_{Tax} seemed to be linked to expanded pool area and a generally stable environment. Overall, the pools with significant and the most abrupt change in TBI_{Env} had variable water physicochemistry (i.e. nutrient concentrations, conductivity, and pH).

The observed significant negative relationship between TBI_{Env} and TBI_{Tax} further contrasts with studies reporting higher beta diversity in habitats with high environmental heterogeneity (Astorga et al. 2014). This is partly supported by the weak covariance between TBI_{Tax} and the temporal gradient. Habitat heterogeneity is maintained by spatiotemporal variation in the abiotic environment. These environmental disturbances drive local community dynamics and species composition by maintaining a temporal mosaic of abiotic resources (Myers et al. 2015). Strong environmental variability may thus increase biotic diversity by favoring opportunistic species with temporally divergent niches, preventing competitive exclusions and temporal dominance by generalists (Anderies & Beisner 2000, Shurin 2007).

However, severe disturbances may also homogenize communities, resulting in lower beta diversity (Hawkins et al. 2015). For example, significant changes in resource supply may reduce temporal beta diversity by filtering out species with a lowered resistance toward extreme environmental conditions (Lamy et al. 2015). In our pools, the taxonomic composition converged over time according to the dbRDA results, supporting the idea of the homogenizing effect of environmental disturbances. Recent aquatic studies found similar signs of decreasing temporal beta diversity despite environmental heterogeneity (Lopes et al. 2017, Lindholm et al. 2021). Diatom diversity is strongly influenced by spatiotemporal environmental oscillations (Verleyen et al. 2009). In small and shallow rock pools, the buffering capacity against physicochemical disturbances is often low (Jocque et al. 2010). Thus, short-term environmental variation may have significant and temporally varying effects on diatom diversity, as, e.g. the local microclimate such as wind, precipitation, and air temperature may directly affect water depth, wave exposure, desiccation, and other physicochemical conditions (Dethier 1984). For coastal microbial communities, strikingly fast turnover rates have been discovered due to sharp transitions in environmental variability (Wu et al. 2016, Martin-Platero et al. 2018).

We found site-specific temporal trends but no systematic change in overall community composition or

environmental dissimilarity. In other aquatic ecosystems, environmental disturbances have been similarly linked with rapid site-level compositional shifts masked by the overall temporal beta diversity pattern (Cereghetti & Altermatt 2023). Regardless of pronounced site-specific shifts in gains and losses, species replacements were moderate, resembling that observed for other aquatic communities (Lindholm et al. 2021). Despite the observed overall balance between species gains and losses, these minor changes may result in notable differences in community dissimilarity over a longer timescale. Disturbed habitats with high environmental autocorrelation tend to exhibit higher short-term than long-term biotic instability, introducing randomness to turnover (Korhonen et al. 2010, Crabot et al. 2020). Thus, although the studied communities showed temporal differences in TBI_{Tax} and TBI_{Func} on a scale of individual pools and between subsequent points in time, the causes remain uncertain. While our models found factors influencing TBI_{Tax} and TBI_{Func} , we could not link temporal beta diversity to a single factor — more so, random stochastic community events likely acted in concert with environmental variability in filtering species into the local communities (Baselga et al. 2015).

We acknowledge that our pool communities were sampled over a limited time span, mostly during the summer season characterized by fast seasonal successive changes in the microalgal communities, which likely contributed to the taxonomic and functional diversity. Increasing UV radiation and temperature during the summer enhance benthic primary productivity and biomass accumulation through intensified photosynthetic activity in the microphytobenthos (Serôdio & Catarino 1999). Accounting for this seasonality by extending the sampling period into earlier spring and later autumn might have resulted in more pronounced temporal differences across the studied communities, depending on the season and the current biomass accumulation rate. We also note that biotic interactions were not considered in this study, yet herbivory and competition are known to structure rock pool communities (Jocque et al. 2010). Short-lived diatoms also exhibit delayed responses to fluctuating water physicochemistry: thus, environmental perturbations may alter local biota in a lagged manner that may not be observed through snapshot sampling (Buckley et al. 2021). Moreover, seasonality and excessively general or partly correlated functional guilds (e.g. colonial and high profile) may have influenced TBI_{Func} (Villéger et al. 2008, Ricotta et al. 2021, Zhang et al. 2021).

5. CONCLUSIONS

We applied TBI to study taxonomic and functional differentiation along with environmental variation within 9 rock pool communities sampled 12 times over a 5 mo period on a coastal rocky outcrop. We found significant site-specific temporal turnover but no clear trend in overall temporal beta diversity. TBI_{Tax} was occasionally high, always outweighing TBI_{Func} . While the indices were successfully explained by different environmental factors in the regression models, only TBI_{Tax} was significantly related to TBI_{Env} . The pools with significant TBI_{Env} did not, however, coincide with the pools experiencing significant TBI_{Tax} or TBI_{Func} . Thus, we conclude that temporal changes in our pool communities were probably driven by rapid environmental oscillations such as short-term microclimatic variations together with random stochastic processes, resulting in inconsistency to the observed patterns in temporal beta diversity. As most temporal community research still relies on short time series with few temporal replicates, especially for microorganisms, future studies should preferably consider finer temporal scales and longer time series to understand the effects of rapid environmental alterations and stochastic processes across highly dynamic microbial communities (Dornelas et al. 2013, Baselga et al. 2015, Buckley et al. 2021).

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