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Research

Drivers of global pre-industrial patterns of species turnover in planktonic foraminifera

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Anthropogenic climate change is altering global biogeographical patterns. However, it remains difficult to quantify how bioregions are changing because pre-industrial records of species distributions are rare. Marine microfossils, such as planktonic foraminifera, are preserved in seafloor sediments and allow the quantification of bioregions in the past. Using a recently compiled data set of pre-industrial species composition of planktonic foraminifera in 3802 worldwide seafloor sediments, we employed multivariate and statistical model-based approaches to study spatial turnover in order to 1) quantify planktonic foraminifera bioregions and 2) understand the environmental drivers of species turnover. Four latitudinally banded bioregions emerge from the global assemblage data. The polar and temperate bioregions are bi-hemispheric, supporting the idea that planktonic foraminifera species are not limited by dispersal. The equatorial bioregion shows complex longitudinal patterns and overlaps in sea surface temperature (SST) range with the tropical bioregion. Compositional-turnover models (Bayesian bootstrap generalised dissimilarity models) identify SST as the strongest driver of species turnover. The turnover rate is constant across most of the SST gradient, showing no SST threshold values with rapid shifts in species composition, but decelerates above 25°C, suggesting SST is less predictive of species composition in warmer waters. Other environmental predictors affect species turnover non-linearly, and their importance differs across regions. In the Pacific ocean, net primary productivity below 500 mgC m^{-2} day^{-1} drives fast compositional change. Water depth values below 3000 m (which affect calcareous microfossil preservation) increasingly drive changes in species composition among death assemblages in the Pacific and Indian oceans. Together, our results suggest that the dynamics of planktonic foraminifera bioregions are expected to be highly responsive to climate change; however, at lower latitudes, environmental drivers other than SST may affect these dynamics.

Keywords: beta diversity, faunal provinces, macroecology, marine biogeography, microfossils, zooplankton

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Introduction

Species are responding to anthropogenic climate change in different ways, by expanding or contracting their distributions or by locally adapting to the new conditions. Thus, the species composition of local communities is changing through time (Burrows et al. 2019) and, as a consequence, global biogeographical patterns are being reshaped. Global trends in biodiversity change have been increasingly studied, for example, by analysing how local assemblages change through time (Antão et al. 2020) or by comparing locations facing different pressures (Purvis et al. 2018). However, the dynamics of biogeographical regions (bioregions) are seldom studied because they rely on the observation of species' geographical ranges in the past.

Microfossils, such as the calcareous planktonic foraminifera, allow for the study of global biogeographical patterns through time (Lazarus 2011, Yasuhara et al. 2020a). Such fossils occur in the oceans worldwide, and accumulate on the seafloor over time, creating layers of preserved biomineralised structures (e.g. microscopic shells or tests). These layers are sampled using sediment cores: the top layers of the core (coretops) recover younger assemblages, while deeper layers recover older, fossil assemblages. Because of slow sedimentation rates in the open ocean, the coretop assemblages of planktonic foraminifera represent pre-industrial assemblage composition (Jonkers et al. 2019). These pre-industrial, death assemblages (sampled in seafloor sediments) have been shown to differ in species composition from their living counterparts (sampled in the water column) (Jonkers et al. 2019). Although this observed change in species composition could be a result of temporal scaling effects (Kidwell and Tomasovych 2013), it is consistent with historical changes in temperature (Jonkers et al. 2019), suggesting that planktonic foraminifera species are shifting their geographical ranges as a response to anthropogenic climate change. However, although global bioregions of planktonic foraminifera are likely being re-shaped, we still lack an understanding of the patterns and drivers of their pre-industrial biogeography.

Assemblages of planktonic foraminifera deposited on the ocean floor have been widely sampled around the world due to their importance for palaeoceanography and palaeoclimatology (Kucera 2007). These assemblage data have been recently compiled into an exceptional standardised database (Siccha and Kucera 2017), ideal for the study of global, pre-industrial biogeographical patterns in planktonic foraminifera. Such data allow for statistical biogeographic characterisations, which are valuable tools for understanding species distributions and managing marine biodiversity (Woolley et al. 2020). Biogeographic studies of microfossils are particularly important for the study of the long-term temporal dynamics of bioregions. Global bioregions (i.e. faunal provinces) of planktonic foraminifera have been described in pre-industrial and ice-age times (Bé and Tolderlund 1971, Moore Jr. et al. 1981). However, these studies used less comprehensive assemblage data and non-reproducible methods to define the bioregions. Moreover, their bioregions were either based on hydrographical conditions instead of assemblage data (Bé and Tolderlund 1971), or included other groups (e.g. radiolaria) decreasing the taxonomic consistency of the study (Moore Jr et al. 1981). Thus, a statistical quantification of planktonic foraminifera bioregions based on global assemblage data is yet to be undertaken.

Bioregions can be quantified based on how species composition changes through space (Hill et al. 2020). Understanding how this spatial turnover (i.e. beta diversity) relates to environmental gradients informs us about the drivers of global biogeographical patterns. Despite the importance of planktonic foraminifera to palaeoclimate reconstructions, only one study, Morey et al. (2005), has explored the relationships between global assemblage composition and multiple environmental variables. Using canonical correspondence analysis (CCA) and data from the Atlantic and Pacific oceans, Morey et al. (2005) found that sea surface temperature was the main predictor of planktonic foraminifera assemblage composition, but other variables such as salinity and ocean productivity were also important. Ordination-based methods such as the CCA assume a constant rate of species turnover across environmental gradients, which is often not the case (Ferrier et al. 2007). Generalised dissimilarity models (GDMs) account for variation in the rate of turnover along environmental variables (Ferrier et al. 2007) and can further inform us about the uncertainty related to the estimated relationships between species turnover and environmental variables (Woolley et al. 2017). Thus, compositional-turnover models such as GDMs provide a robust way to analyse large-scale drivers of global biogeographical patterns.

Here, we quantify the pre-industrial biogeographical patterns of planktonic foraminifera and model the environmental drivers of their spatial variation in assemblage composition. We applied compositional-turnover models globally and within the Atlantic, Pacific and Indian oceans separately, because ocean basins differ in their geological history and environmental gradients. We tested the following hypotheses: 1) community composition changes discontinuously in space, allowing the quantification of bioregions of planktonic foraminifera; 2) the spatial variation in species composition is explained by multiple environmental variables (e.g. temperature, nutrients, salinity) and 3) the rate of species turnover changes across these environmental gradients.

Methods

Species' relative abundance data

To calculate compositional turnover globally, we used data on the relative abundance of planktonic foraminifera species from the ForCenS database, which is a curated database of 4205 marine samples from the surface of sediment cores (coretops) (Siccha and Kucera 2017). The age of these coretop assemblages was estimated based on sedimentation rate and bioturbation depth, yielding mean ages of centuries to millennia, which warrant the use of these coretop samples as

a pre-industrial baseline (Jonkers et al. 2019). The sampling methodology in the ForCenS database is standardised and consists of counting around 300 specimens larger than 150 µm in each sample. All individuals are identified to species level based on the morphology of their shells/tests (i.e. morphospecies), and species' relative abundances are recorded as a percentage. The samples are geo-referenced; when samples had identical coordinates (303 samples out of 4205), we randomly selected one of them and removed the others. Additionally, we removed samples that did not differentiate between pair of species, namely *Globorotalia menardii* and *Globorotalia tumida*, *Globigerinoides ruber* pink and white, and *Turborotalita humilis* and *Berggrenia pumilio*. With these restrictions, the data set we used consists of 3802 unique sites of relative abundances of 41 planktonic foraminifera species distributed across the globe.

Compositional turnover

We quantified species turnover based on pairwise compositional dissimilarity between all 3802 sites, using the R package *vegan* (Oksanen et al. 2019). We selected dissimilarity metrics that capture two different aspects of turnover (Jost et al. 2011): 1) the Sorensen dissimilarity (Sorensen 1948), based on presence–absence data, is the probability that two randomly sampled species from two assemblages do not belong to any of the shared species between the assemblages; 2) the Morisita–Horn dissimilarity (Morisita 1959), based on abundance data, is the probability that two randomly sampled individuals from two assemblages do not belong to the same species. The values of both metrics vary between 0 (identical communities) and 1 (completely distinct communities). We compared these two metrics to assess the effect of taking species abundances into account when analysing global turnover patterns. Additionally, we compared the Morisita–Horn metric to the commonly used Bray–Curtis metric (Bray and Curtis 1957). Both show similar results (Supporting information), thus we discuss the Morisita–Horn metric only.

Environmental variables

To model compositional turnover as a function of environment, we compiled data on sea surface temperature (SST) mean and standard deviation, net primary production, concentrations of phosphate, nitrate and dissolved oxygen, salinity and water depth. To assess the influence of species dispersal in assemblage composition, we used the geographical distance between sites as a predictor in the compositional-turnover models. The shortest distance between sites was calculated considering only seaways (excluding land).

SST is known to be a major correlate of planktonic foraminifera assemblage composition (Morey et al. 2005) and richness patterns (Rutherford et al. 1999, Fenton et al. 2016). We retrieved sea surface temperature (SST) data from the Extended Reconstructed Sea Surface Temperature (ERSST ver. 5; Huang et al. 2017) from 1854 to 1899, to get estimates of the annual mean and the standard deviation of historical SST. We also ran the compositional-turnover models using modern SST data (1985–2017) from the World Ocean Atlas 2018 (WOA18; Locarnini et al. 2018), and the results were almost identical (Supporting information).

Net primary production (NPP), used here as a proxy for nutrient availability, is also likely to affect the assemblage composition of planktonic foraminifera, given that species have different trophic strategies (Takagi et al. 2019). However, historical data on NPP is not available, and model reconstructions of NPP yield different outputs (Fu et al. 2016). Other proxies for nutrient availability such as phosphate and nitrate are also not available for pre-industrial periods. Currently, anthropogenic marine nutrient pollution affects a minor area of the global open ocean, having a greater effect on coastal regions (< 200 m depth) (Halpern et al. 2008), where planktonic foraminifera do not occur. Therefore, we retrieved annual mean values of NPP from the Ocean Productivity project (<www.science.oregonstate.edu/ocean.productivity/>), using the standard VGPM algorithm (Behrenfeld and Falkowski 1997), which extends the furthest back in time (1997). Annual mean values of phosphate and nitrate concentrations (at the surface) were retrieved from the WOA18 database (Garcia et al. 2018b).

Annual mean values of dissolved oxygen (at 100 m depth) and salinity were also retrieved from the WOA18 database (Garcia et al. 2018a, Zweng et al. 2018). Data on salinity extended back to 1955–1964, so we retrieved data from this decade. For each site of the species composition data, we matched its spatial coordinates to the nearest grid point of each environmental variable, based on the shortest geographical distance using the World Geodetic System of 1984 (WGS 84) and the R package *geosphere* (Hijmans 2015).

Water depth values were taken directly from the ForCenS database and were expected to influence species composition of death assemblages because of calcite dissolution at the deep seafloor. Dissolution is related to the carbonate saturation in the seawater, and species have different susceptibility to it depending on the structure and thickness of their shells (Berger 1970).

Quantifying bioregions

To determine the planktonic foraminifera bioregions, we used 1) hierarchical clustering (UPGMA method) and 2) non-metric multidimensional scaling (NMDS), both based on the Morisita–Horn metric. We quantified the optimum number of clusters (bioregions) based on the Silhouette method, which retrieved the same optimum number of clusters as the method minimising the total within sum-of-squares per number of clusters (Supporting information). We then assigned each site to its bioregion (cluster) to plot a world map and the two-dimensional NMDS.

After determining the bioregions, we related them to their environment by modelling the presence and absence of each cluster along the studied environmental gradients (Hill et al. 2020). We ran a generalised additive model (GAM) on each cluster separately, setting the response

variable for each community assemblage sample to 0 (absence of the given cluster) or 1 (presence of the given cluster) and the environmental variables as explanatory variables. We used the R package *mgcv* (Wood 2020) to fit the GAM models with a binomial family, logit link function and a maximum of three knots. We removed predictors that were strongly correlated to avoid issues with co-linearity of covariates in the model, namely dissolved oxygen and nitrate (Supporting information). We used the remaining six environmental predictors for the analyses: SST mean and standard deviation, salinity, NPP, phosphate and water depth (Supporting information).

Compositional-turnover models

To assess what drives global compositional turnover of planktonic foraminifera, we modelled turnover as a function of environmental predictors using Bayesian bootstrap generalised dissimilarity models (Ferrier et al. 2007, Woolley et al. 2017). Strongly correlated predictors were removed and, in total, six environmental variables were used for the analyses (as in the GAM analysis) plus the geographical distance between sites (Supporting information). Generalised dissimilarity models (GDM) are based on generalised linear models and use a negative exponential link function to transform the response variable (i.e. the dissimilarity metric), which has values constrained between 0 and 1. GDM relates the change in species composition to environmental or spatial gradients via monotonic I-spline functions. The monotonic assumption means that as environmental or geographical distances increase, communities can only become more dissimilar. The sum of the fitted I-spline functions shows the relationship between the observed species turnover and the given environmental predictor (partial effect plots). The maximum height of each curve shows the relative contribution (magnitude) of each predictor in explaining overall turnover. The I-spline functions also give information on the rate of turnover along the gradient of each predictor. Linearity or non-linearity is assessed as the shape of the I-splines curve and its derivative. Acceleration (or levelling-off) of the rate of turnover along the environmental gradient shows where in the gradient most (or least) of the change in species composition occurs.

Model-based likelihoods calculated on dissimilarities can be misleading due to the correlation between site pairs and their unknown probability distribution. Thus, model selection based on the log-likelihood (such as R^2, or Akaike or Bayesian information criteria) can be unreliable (Warton et al. 2012, Woolley et al. 2017). Bayesian bootstrap GDM (BBGDM) attempts to relate the underlying model back to the amount of data observed (i.e. measured species abundances), rather than the number of dissimilarities used in the model (Woolley et al. 2017). BBGDM characterises the uncertainty around each predictor using Bayesian bootstrapping and provides confidence intervals for the parameters estimates. Important predictors will be ones with larger magnitudes (height of the sum of I-splines) and smaller confidence intervals.

Typically, GDM performs significance testing using random matrix permutations (Fitzpatrick et al. 2013). This procedure tests if the predictors explaining the variance are significant compared to a null hypothesis, but it does not account for the inflated degrees of freedom in the dissimilarities (Woolley et al. 2017). Following Woolley et al. (2017), we used a Wald-like test to select the subset of environmental parameters that significantly explain the observed compositional turnover.

In total, we ran five BBGDMs with 100 bootstraps: two global models each with a different dissimilarity metric (presence–absence-based: Sorensen; abundance-based: Morisita–Horn) and one model for the Atlantic, the Pacific and the Indian ocean basins, using the Morisita–Horn metric. We used the R packages *gdm* (Fitzpatrick et al. 2020) and *bbgdm* (Woolley et al. 2015) to run the BBGDMs. All data visualisation and analyses were conducted in R ver. 4.0.2 (<www.r-project.org>). Additionally, we used *ggplot2* (Wickham 2016), *oce* (Kelley and Richards 2020) and *viridis* (Garnier 2018) for the graphical representation of the analyses.

Results

Bioregions

The clustering analysis of global compositional dissimilarity resulted in four bioregions (Fig. 1), based on a parsimonious selection of the number of groups (Supporting information). The four bioregions are latitudinally distributed, characterised by the bi-hemispheric temperate and polar zones separated by the continuous equatorial and tropical zones. Given the distribution of samples, the equatorial bioregion occurs mostly between −13° and 18° latitude, the tropical bioregion includes the subtropics and occurs between −30° and 35°, the temperate zone occurs between −50° and −21° in the Southern Hemisphere and 15° and 65° in the Northern Hemisphere, and the polar zone between −63° and −43° and 42° and 81° latitude (Supporting information).

Bioregions show different patterns across and within ocean basins (Fig. 1). The equatorial zone is extensive in the Pacific Ocean but less present in the Atlantic Ocean. The Atlantic and the Pacific oceans show equatorward deflections of the temperate bioregions in the eastern boundary currents. These regions also show high local turnover, with a mix of polar, temperate and equatorial assemblages off the Chilean coast (Humboldt current) and a mix of temperate, tropical and equatorial assemblages off the south-west coast of Africa (Benguela current). Other regions of high local turnover are the upwelling zones in the north-west coast of Africa and southeast Asia. Our bioregional map broadly matches the planktonic foraminifera map of Bé and Tolderlund (1971). However, the equatorial bioregion overlaps with the tropical and emerges distinctively in the Pacific Ocean, plus the transitional zone characterised by *Globoconella inflata* in Bé and Tolderlund (1971) is merged with our temperate bioregion.

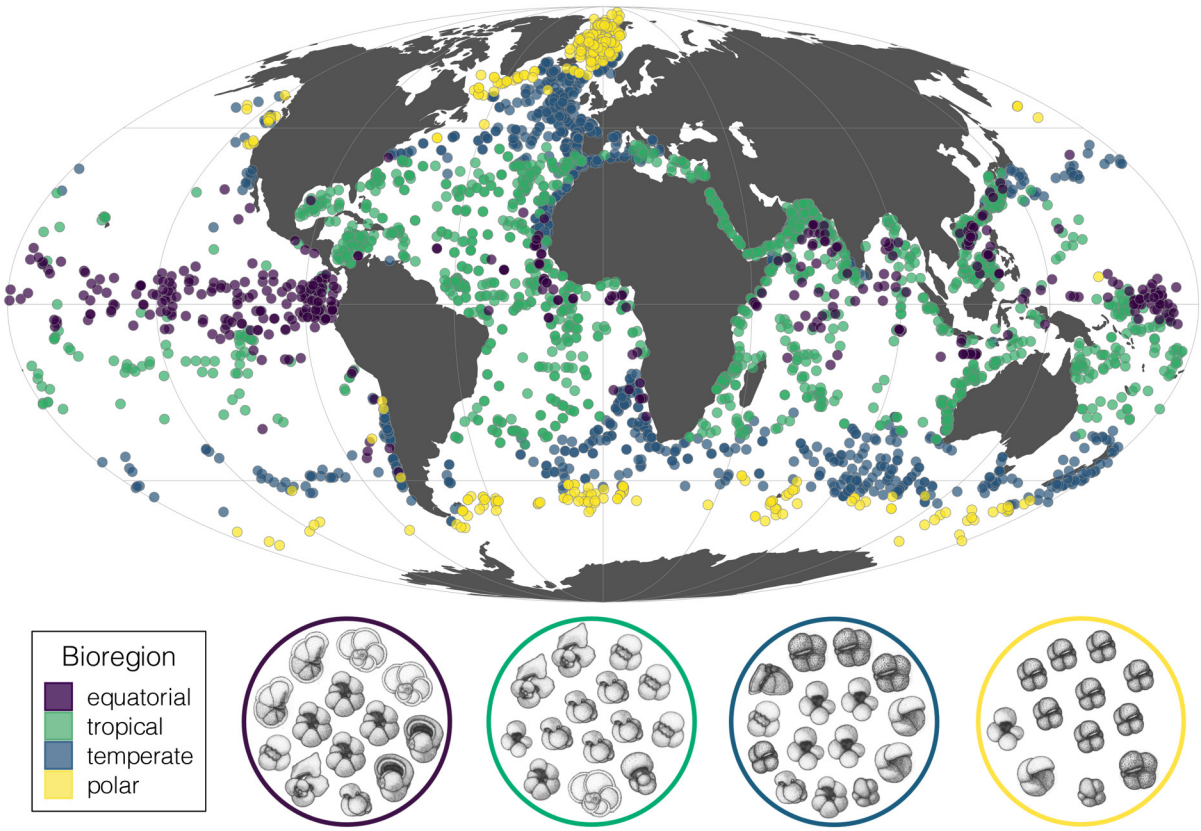

Figure 1. Bioregions of planktonic foraminifera based on assemblage data from ocean-floor surface sediments (pre-industrial period). The map shows the 3802 sites coloured by bioregions (defined based on the clustering analysis): polar 348 sites, temperate 1179, tropical 1837 and equatorial 438 sites. Assemblages show the averaged relative abundances of species within each bioregion. Drawings from Parker (1962); reproduced with permission.

The bioregions are composed of different species (Fig. 2). The polar zone is dominated by one species, *Neogloboquadrina pachyderma* (on average 75% relative abundance), and the temperate zone by *Globigerina bulloides* (24%), *Neogloboquadrina incompta* (22%) and *G. inflata* (17%). The tropical zone contains *G. ruber* white (28%), *Globigerinita glutinata* (13%) and *Trilobatus sacculifer* (12%), and the equatorial zone *Neogloboquadrina dutertrei* (30%), *Pulleniatina obliquiloculata* (15%), *G. menardii* (13%) and *G. tumida* (13%).

The bioregions can be distinguished via non-metric multidimensional scaling (NMDS) based on abundance data (Fig. 3a); however, overlap among bioregions is large when considering presence–absence data (Supporting information). Within bioregions, assemblage composition is not homogeneous (Fig. 3b). The equatorial bioregion has the lowest average similarity between sites; this heterogeneity can also be seen in the clustering dendrogram (Supporting information), as the equatorial zone diverges earlier into sub-groups than the other zones. Regarding the total number of species, the tropical bioregion is the richest, followed by the equatorial and temperate regions and, lastly, the species-poor polar region (Fig. 4). In the Pacific Ocean, however, the richness of the equatorial bioregion reaches low values, comparable to the polar region.

The patterns of bioregion occurrence along SST show how the polar, temperate and tropical bioregions are distinctively distributed along this gradient (Fig. 3c). The temperate zone shows the largest SST range, and the equatorial and tropical bioregion overlap in SST range. Besides SST, the occurrence of the equatorial bioregion is also related to low phosphate concentration, low salinity and deep waters (Supporting information). All environmental variables contribute to the occurrence of the tropical bioregion (Supporting information). This bioregion contains more oligotrophic waters than the other bioregions in terms of NPP and phosphate concentration, but it also includes sites with high NPP in upwelling zones (Supporting information). Higher salinity and low seasonality (SST standard deviation) also characterise the tropical bioregion (Supporting information). The temperate bioregion occurs in regions with marked seasonality and dominates the waters with NPP values between 800 and 2000 mgC m^{-2} day^{-1} and intermediate values of phosphate concentration (around 0.8 µmol kg^{-1})(Supporting information). The polar bioregion is characterised by high-latitude patterns: low SST values, low seasonality, low salinity and high phosphate concentration (Supporting information).

Predictors of species' turnover

Mean annual sea surface temperature (SST) is the main predictor of planktonic foraminifera compositional dissimilarity

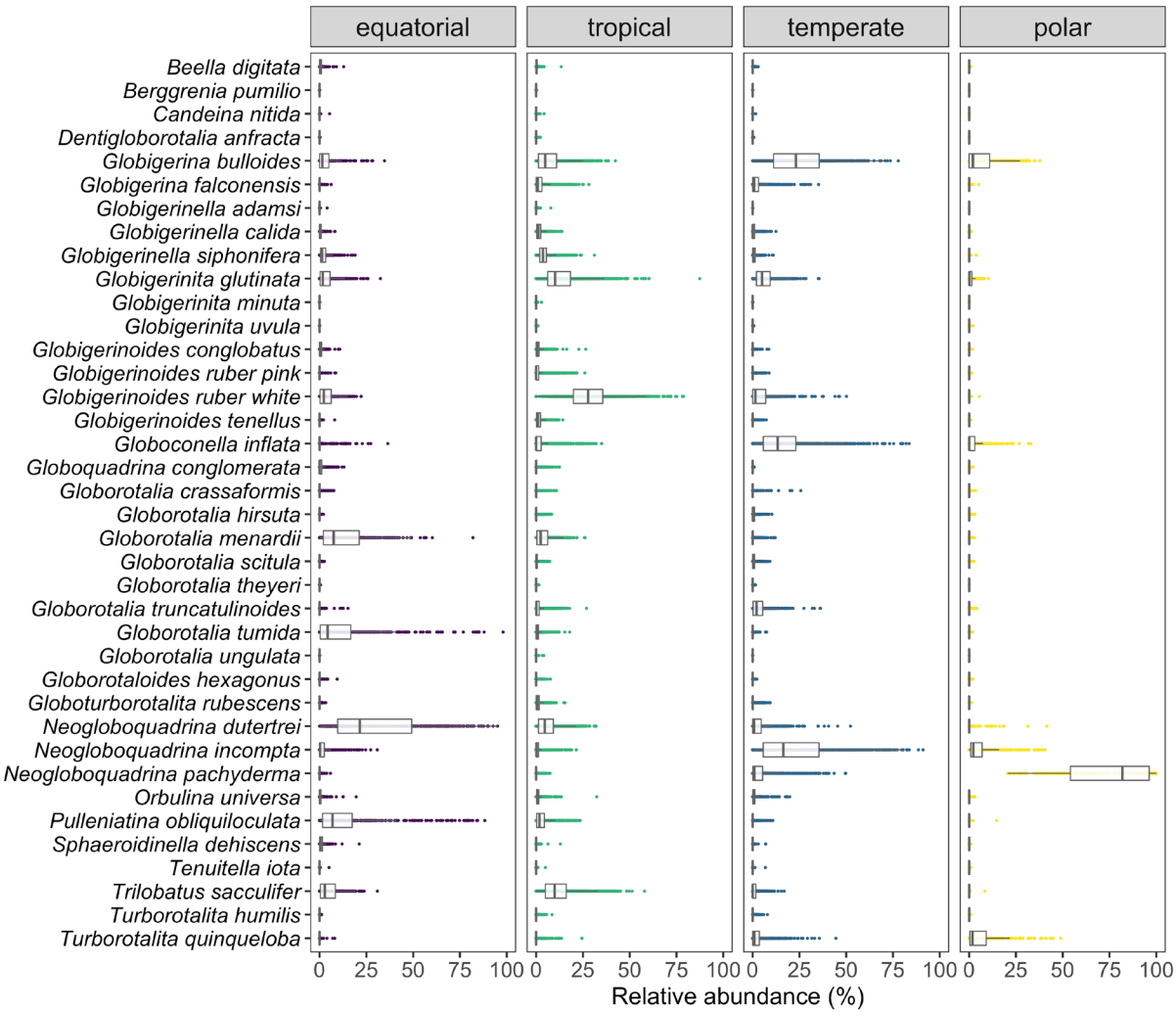

Figure 2. Relative abundances of species within each bioregion, following the taxonomy of Siccha and Kucera (2017).

globally (Fig. 5). The rate of abundance-based compositional change along the SST gradient is mostly linear, but decelerates in the tropics, for SST values above 25°C (Fig. 5a, black line). The presence–absence-based species turnover changes non-linearly along the SST gradient, showing less compositional change for SST values above 15°C (Fig. 5a, red line). The change in species turnover across the SST gradient can also be seen in the derivative plots of the I-splines functions (Supporting information). When conducting the analyses within oceans, SST remains the main predictor of turnover, particularly in the Atlantic Ocean (Fig. 5b).

Other environmental variables explain some, but overall less, global compositional change than SST and show non-linear relationships with species turnover (Fig. 5, Supporting information). Globally, NPP and phosphate concentration show higher association with abundance- than presence–absence-based turnover (Fig. 5a), which suggest that ocean productivity contributes more to shifts in species abundances than species' occurrence. Salinity affects species turnover as much as NPP and, although it shows a significant effect, it has a wider confidence interval than NPP meaning a more uncertain relationship with turnover (Fig. 5a). In the Indian ocean, phosphate is a more important predictor than NPP but phosphate correlates strongly with SST in this ocean (Pearson correlation: −0.74, $p < 0.001$); the rate of turnover accelerates for salinity values above 36 units (Fig. 5b; Supporting information), characteristic of the Red Sea (Siccha et al. 2009). In the Pacific and Indian oceans, the rate of turnover greatly accelerates below 2500–3000 m depth (Fig. 5b, Supporting information). In the Pacific Ocean, water depth explains almost as much compositional variation as SST and turnover is faster at NPP values below 500 mgC m^{-2} day^{-1} (Fig. 5; Supporting information). Geographical distance shows a weak contribution to global turnover, but it is significant in the Pacific Ocean (Fig. 5b).

Discussion

Our global analysis of species turnover of planktonic foraminifera preserved in pre-industrial sediments resulted in four, latitudinally banded bioregions (Fig. 1), similar to the

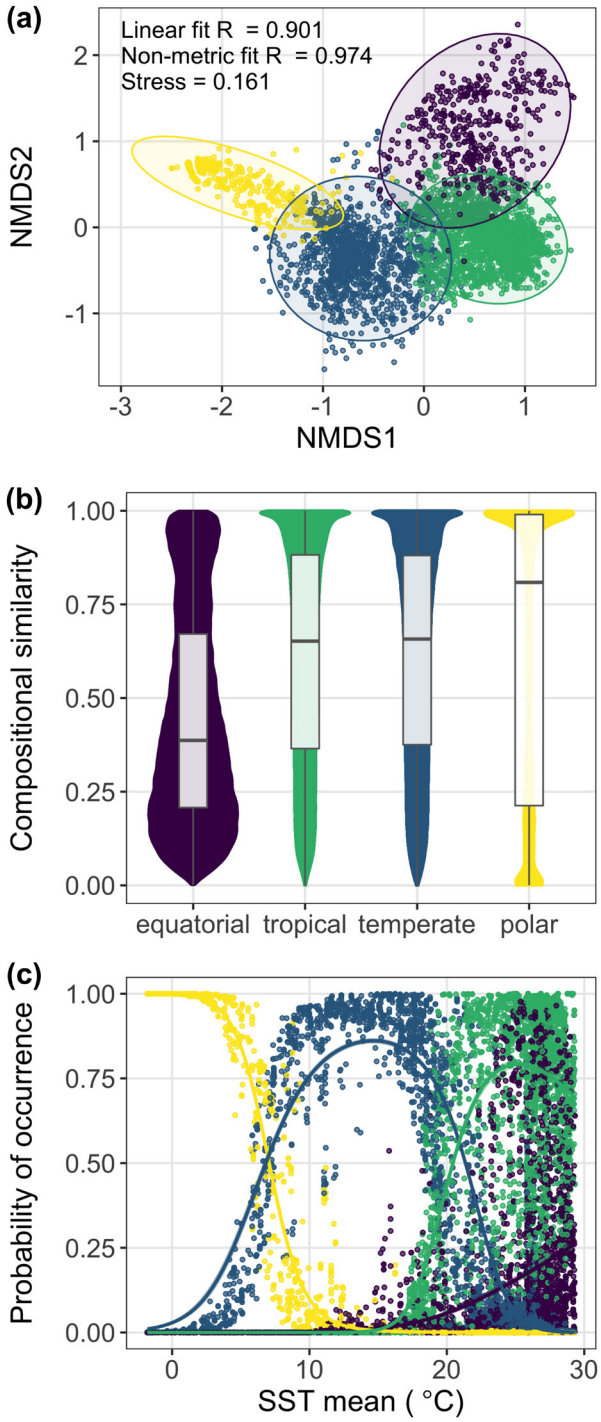

Figure 3. (a) Non-metric multidimensional scaling (NMDS, two-dimensional) coloured by bioregion based on abundance-based dissimilarities (Morisita–Horn metric). (b) Pairwise compositional similarity of sites within each bioregion (Morisita–Horn metric). Values of 1 mean that assemblages are identical (share all species in equal proportions), and value 0 means assemblages are completely dissimilar (share no species). (c) Probability of occurrence of each bioregion along sea surface temperature (SST, annual mean), predicted by the generalised additive models (GAM). The dots represent the individual samples and their predicted probability of occurrence in each bioregion given the GAM fit.

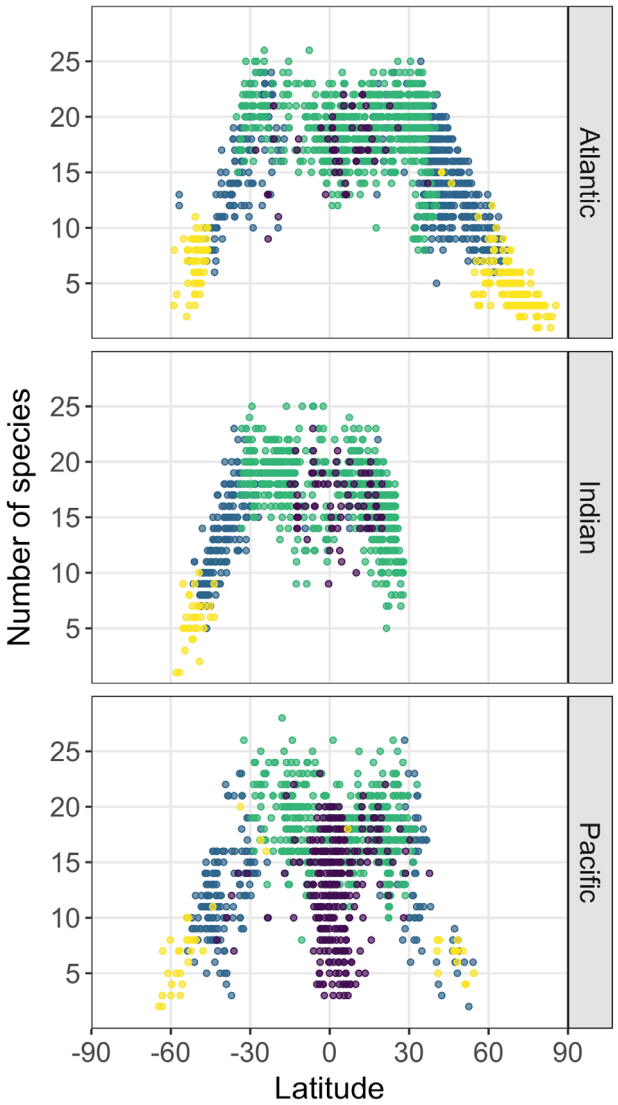

Figure 4. Latitudinal richness gradient per ocean basin, coloured by the four bioregions (purple equatorial, green tropical, blue temperate and yellow polar).

pelagic provinces of the world (Longhurst 2010, Lazarus 2011, Spalding et al. 2012) and the open-ocean surface biome map (Fay and McKinley 2014). The bioregions span all ocean basins, and the temperate and polar zones are bihemispheric, with all species occurring in both hemispheres. Thus, similar communities emerge in environmentally similar regions, even when these regions are in different ocean basins and/or hemispheres. This pattern, added to the fact that geographical distance was not a strong predictor of species turnover (Fig. 5), indicates that planktonic foraminifera species are not limited by dispersal and suggests that this group has the ability to overcome constraints on global dispersal set by local natural selection (Ward et al. 2021). However, planktonic foraminifera assemblages may still be limited by dispersal at shorter time scales, as opposed to the centennial to millennial time scales analysed in this study. Whether the observed biogeographical patterns also

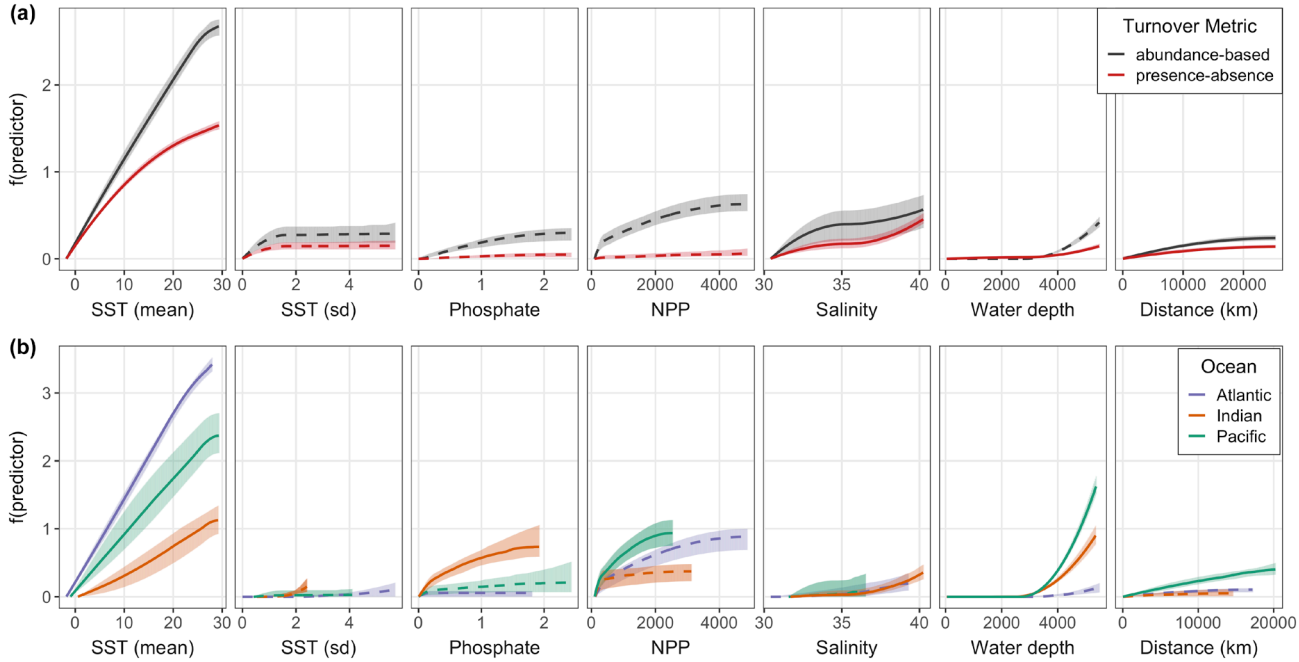

Figure 5. Partial response plots of Bayesian bootstrap generalised dissimilarity modelling (BBGDM) for planktonic foraminifera coretop data. x-axis: environmental gradient; y-axis: BBGDM spline function (see Methods). The maximum height attained on the y-axis indicates the relative importance of the predictor to overall compositional dissimilarity. For example, if the total sum of I-splines of temperature exceeds that of salinity by a factor of 2, then half of the temperature gradient explains the same amount of turnover than the full gradient of salinity. The shape of the spline function shows the rate of compositional change along the environmental gradient: straight lines reveal linear, and curved lines reveal non-linear, relationship between species turnover and the given predictor. Lines are the BBGDM median estimate, solid lines indicate significant relationships and dashed lines non-significant relationships (see Supporting information); the shading is the 95% confidence interval for BBGDM variance. (a) Global model; abundance-based metric (black line): Morisita–Horn; presence–absence-based metric (red line): Sorensen. (b) Model per ocean basin (Atlantic, Pacific and Indian oceans), based on the abundance-based metric (Morisita–Horn).

persist at shorter timescales or with genetic analyses remains to be tested.

Marine biogeography can also show complex longitudinal patterns (Longhurst 2010, Spalding et al. 2012, Proud et al. 2017, Sutton et al. 2017). Such complexity in planktonic foraminifera biogeography can be partially reproduced if we increase the number of optimal clusters. Considering five clusters instead of four, the polar, temperate and tropical bioregions remain identical but the western equatorial Pacific breaks from the equatorial zone and emerges as a new bioregion (Supporting information). This heterogeneous longitudinal pattern is consistent with former planktonic foraminifera studies in the North Pacific (Coulbourn et al. 1980, Taylor et al. 2018) and can explain why geographical distance is a significant, albeit weak, predictor of species turnover in this ocean (Fig. 5b). The equatorial zone can also be seen as a less integrated bioregion given it contains the lowest compositional similarity of all bioregions (Fig. 3b) and that it continues to subdivide longitudinally into more bioregions as we increase the number of clusters (Supporting information). Thus, the polar, temperate and tropical bioregions of planktonic foraminifera show a marked latitudinal pattern and are more homogeneous when compared to the equatorial bioregion, which shows heterogeneous longitudinal patterns within and across ocean basins.

The latitudinally banded bioregions found in our study reflect the strong relationship between SST and species composition in planktonic foraminifera (Fig. 3c, Morey et al. 2005). Indeed, SST is the best predictor of their global spatial turnover (Fig. 5). The abundance-based turnover rate is constant across most of the SST gradient (Fig. 5a, black line), suggesting that species' abundances change relatively evenly with SST change, without any major compositional shifts for particular SST threshold values. Thus, the dynamics of planktonic foraminifera bioregions are expected to be at pace with global warming. Since the thermal niches of planktonic foraminifera seem to be static throughout glacial–interglacial climate change (Antell et al. 2021), species will likely track climate change by colonising newly suitable habitats and/or going locally extinct, instead of adapting to new local conditions. As the oceans get warmer, the polar bioregion is expected to contract and the temperate and tropical bioregions to expand to higher – and to contract in lower – latitudes, resulting in increases in richness at higher latitudes (Antão et al. 2020) and decreases in richness around the equator (Yasuhara et al. 2020b).

The rate of abundance-based turnover is constant across most of the SST gradient; however, it decelerates for SST values above 25°C (Fig. 5a–b; Supporting information).

This pattern is stronger when considering presence–absence of species: the turnover rate levels off for SST values above 15°C (Fig. 5a, red line). This deceleration in turnover rates in warmer SST gradients could be a result of the large decline in richness from the tropical to the polar oceans (i.e. latitudinal richness gradient), which is strong in the Atlantic and Indian oceans but weaker in the Pacific Ocean (Fig. 4). To explore this hypothesis, we decomposed the presence–absence-based turnover into species replacement and nestedness (the latter captures in part richness differences between sites; Baselga 2010) and re-ran the compositional-turnover models. The results suggest that the deceleration in turnover rates in warmer waters is related to latitudinal richness differences in the Atlantic Ocean but not in the Pacific and Indian oceans (Supporting information). Thus, the deceleration in turnover rates for higher SST values in the Pacific and Indian oceans is probably related to the longitudinal patterns in the equatorial zone, where there is small SST change but large compositional change (Supporting information). In these oceans, the weaker relationship between species compositional change and SST change can lead to an underestimation of warmer SST values in palaeoclimate reconstructions (Mix et al. 1999, Morey et al. 2005).

We found no SST thresholds values where species composition rapidly shifts, but community composition changes discontinuously in space, as seen in the clustering and NMDS analyses (Fig. 1, 3a). This apparent contradiction can be explained by the fact that global thermal gradients are non-linear across space. Thus, species distribution across space and latitude does not directly translate into species distribution across SST gradients (Tomašovỳch et al. 2015). Moreover, bioregional boundaries can be gradual instead of discrete as a result of widespread distribution of species (O'Hara et al. 2011) or time-averaging in sedimentary assemblages (Kidwell and Tomasovych 2013). Regions that experience higher temporal variability in environmental variables, such as boundaries where ocean fronts meet, will experience higher temporal variability in community composition. Over time, this variability can generate mixed (e.g. tropical/temperate) sedimentary assemblages and smooth bioregional boundaries, blurring discontinuous breaks in the turnover rate along the SST gradient.

Although other processes not captured by our models can cause bioregion delineation (e.g. ocean currents and/or historical contingency; Fukami 2015, Richter et al. 2020), salinity, net primary productivity (NPP) and water depth contribute to planktonic foraminifera bioregionalisation (Supporting information). This contribution is less predictable than SST, as these variables relate differently to turnover across oceans and also show non-linear relationships with the turnover rate (Fig. 5). NPP contributes to species turnover particularly in the Pacific Ocean and at low values characteristic of the equatorial upwelling zone (Fig. 5, Supporting information). This Pacific upwelling zone creates a latitudinal and longitudinal gradient from oligotrophic to productive waters, possibly contributing to the observed shift from tropical to equatorial assemblages (Fig. 1) and to the longitudinal heterogeneity in species composition within the equatorial bioregion (Supporting information; Taylor et al. 2018).

Water depth also greatly contributes to species composition in the Pacific Ocean (Fig. 5b), suggesting that shell preservation influences species composition of planktonic foraminifera death assemblages. The equatorial zone occurs in deeper waters (Supporting information) and has high relative abundances of large, thick-shelled species such as *G. tumida* and *P. obliquiloculata* (Fig. 2), known to be less susceptible to dissolution (Berger 1970). Although Morey et al. (2005) and Taylor et al. (2018) concluded there is no significant effect of dissolution in planktonic foraminifera biogeographical patterns, Morey et al. (2005) did not consider non-linear relationships (which is evidently the case for water depth; Fig. 5b) and Taylor et al. (2018) transect did not reach the Pacific equatorial zone. Thus, our results suggest that dissolution also influences species composition of planktonic foraminifera and hint at an equatorial assemblage with mixed biological and fossil preservation signals. As the uptake of anthropogenic carbon dioxide acidifies the ocean, deep-sea calcite dissolution will increase (Sulpis et al. 2018) and intensify preservational signals in planktonic foraminifera sedimentary assemblages.

Preservational biases in assemblage composition blur ecological and physiological relationships between assemblage composition and environmental variables and influence palaeo-environmental reconstructions based on microfossils assemblages (Parker and Berger 1971, Coulbourn et al. 1980). The time-averaging of assemblages in seafloor sediments can also obscure ecological signals of species distributions, because individuals that died over centuries or even millenia are pulled together into a single sampling unit (death assemblages). Such time-averaging can be advantageous for biogeographical studies because it averages out seasonal and interannual fluctuations as well as stochastic populational dynamics. However, it can also significantly change the composition of the fossil assemblages when compared to the living assemblage, depending on the dispersal capability of the studied group and the environmental (and associated community) volatility of a given location (Kidwell and Tomasovych 2013). Planktonic foraminifera species have a high dispersal capability (this study), thus time-averaging likely has a strong impact on their spatial diversity patterns observed in seafloor sediments. The expected change related to time averaging is a decrease in the spatial variation of species composition (Kidwell and Tomasovych 2013), which could explain why we found only four global bioregions and why comparisons of assemblages sampled in the water column and in seafloor sediments can show different species composition (Jonkers et al. 2019).

In conclusion, we showed that pre-industrial, spatial variation in species composition of planktonic foraminifera is strongly related to SST variation. The constant rate of turnover across the global SST gradient found in our study suggests that changes in SST are expected to generate proportional, and therefore predictable, changes in local species composition. However, to use the pre-industrial baseline of planktonic

foraminifera communities to predict future responses to climate change, we need to not only understand how differences between living and death assemblages relate to environmental change (Jonkers et al. 2019) but also quantify how much of the diversity patterns observed in seafloor sediments are a result of taphonomic biases (Kidwell 2013). This way, we can leverage the potential of microfossils as windows into long-term baselines of the pelagic ecosystem and better predict the response of this ecosystem to future climate change.

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Author contributions

Marina C. Rillo: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Software (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Skipton Woolley**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Software (equal); Visualization (supporting); Writing – review and editing (supporting). **Helmut Hillebrand**: Conceptualization (supporting); Funding acquisition (lead); Investigation (supporting); Writing – review and editing (supporting).

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Data availability statement

Data and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.xpnvx0kgt> (Rillo et al. 2021).

Supporting information

Any supporting information associated with this article is available from the online version.

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