Received: 6 May 2019 | Revised: 10 July 2019 | Accepted: 19 July 2019

DOI: 10.1111/geb.13000

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology WILEY

On the mismatch in the strength of competition among fossil and modern species of planktonic Foraminifera

Marina C. Rillo[1,2] | Mauro T. C. Sugawara[3] | Brenno Cabella[4] | Lukas Jonkers[2] | Ulrike K. Baranowski[5] | Michal Kučera[2] | Thomas H. G. Ezard[1]

[1]Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton, United Kingdom

[2]Center for Marine Environmental Sciences, University of Bremen, Bremen, Germany

[3]Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada

[4]Instituto de Física Teórica, Universidade Estadual de São Paulo, Sao Paulo, Brazil

[5]School of Geography, Earth and Environmental Science, University of Birmingham, Birmingham, United Kingdom

Correspondence
Marina C. Rillo, Institute for Chemistry and Biology of Marine Environments, University Oldenburg, Schleusenstrasse 1, Wilhelmshaven 26382, Germany.
Email: marina.rillo@evobio.eu

Funding information
Natural Environment Research Council, Grant/Award Number: NE/J018163/1 and NE/P019269/1; German Academic Exchange Service London, Grant/Award Number: DAAD 2016/17 (57210260); Graduate School of the National Oceanography Centre Southampton

Editor: Derek Tittensor

Abstract

Aim: Many clades display the macroevolutionary pattern of a negative relationship between standing diversity and diversification rates. Competition among species has been proposed as the main mechanism that explains this pattern. However, we currently lack empirical insight into how the effects of individual-level ecological interactions scale up to affect species diversification. Here, we investigate a clade that shows evidence for negative diversity-dependent diversification in the fossil record and test whether the clade's modern communities show a corresponding signal of interspecific competition.

Location: World's oceans.

Time period: Holocene.

Major taxa studied: Planktonic Foraminifera (Rhizaria).

Methods: We explore spatial and temporal ecological patterns expected under interspecific competition. Firstly, we use a community phylogenetics approach to test for signs of local competitive exclusion among ecologically similar species (defined as closely related or of similar shell sizes) by combining species relative abundances in seafloor sediments. Secondly, we analyse whether population abundances of co-occurring species covary negatively through time using sediment trap time-series spanning 1–12 years.

Results: The great majority of the assemblages are indistinguishable from randomly assembled communities, showing no significant spatial co-occurrence patterns regarding phylogeny or size similarity. Through time, most species pairs correlated positively, indicating synchronous rather than compensatory population dynamics.

Main conclusions: We found no detectable evidence for interspecific competition structuring extant planktonic Foraminifera communities. Species co-occurrences and population dynamics are likely regulated by the abiotic environment and/or distantly related species, rather than intra-clade density-dependent processes. This interpretation contradicts the idea that competition drives the clade's macroevolutionary dynamics. One way to better integrate community ecology and macroevolution is to

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2019 The Authors. Global Ecology and Biogeography published by John Wiley & Sons Ltd

consider that diversification dynamics are influenced by groups that interact ecologically even when distantly related.

KEYWORDS

community ecology, community phylogenetics, diversity dependent diversification, interspecific competition, macroevolution, microfossils, time-series analysis, zooplankton

1 | INTRODUCTION

Ecological interactions play an important role in shaping the diversity of life across space and time. By interacting with each other, individuals change the dynamics of their populations and communities. Population dynamics, in turn, influence species' abundances and geographical ranges, which affect species' diversification rates (i.e., the balance between speciation and extinction rates) (Harnik, 2011; Jablonski, 2017). However, the resulting net effect of ecological interactions on species' diversification might not correspond to the fitness effects at the individual level. For example, positive interactions such as mutualism can have a negative effect on diversification, and negative interactions such as predation (for the prey) and parasitism (for the host) can enhance diversification (Jablonski, 2008a; Yoder & Nuismer, 2010). How individual-level interactions scale up to affect species' diversification remains a topic that has received scant attention (Jablonski, 2017), and we currently lack understanding of how congruent or discordant these effects are across ecological and geological time scales (Harmon et al. 2019; Weber, Wagner, Best, Harmon, & Matthews, 2017).

Competition among species has, by definition, a negative effect on the fitness of the interacting individuals. Yet, interspecific competition can affect species' diversification positively, by promoting niche partitioning and character displacement (Bailey, Dettman, Rainey, & Kassen, 2013; Meyer & Kassen, 2007) or negatively by driving species to extinction due to niche overlap (Bengtsson, 1989). Within macroevolutionary research, interspecific competition has often been proposed to have a consistent negative effect across ecological and geological time scales, generating the pattern of a negative relationship between species diversity and diversification rates (Rabosky, 2013). This negative diversity-dependent diversification (DDD) pattern is thought to reflect how increases in species richness suppress diversification rates due to increased extinction or because opportunities for speciation become reduced once niches are filled, whereas decreases in species richness promote diversification because of weaker competitive interactions (Rabosky, 2013).

Many clades have been shown to display the negative DDD pattern (Etienne et al., 2011; Ezard, Aze, Pearson, & Purvis, 2011; Phillimore & Price, 2008; Pires, Silvestro, & Quental, 2017; Rabosky, 2013). Although most of these studies evoke interspecific competition to explain the observed macroevolutionary pattern, they do not explicitly test for it. Such an explicit test is difficult to perform, as it requires not only a sufficiently well-preserved fossil record to assess the deep-time individual- or population-level fitness responses to ecological interactions, but also an actual fossilized interaction proxy, both of which are rare (but see Liow, Martino, Voje, Rust, & Taylor, 2016). An alternative approach to test whether the negative DDD pattern is a result of upward causation from competition among individuals is to contrast macroevolutionary and present-day community ecology dynamics (Voje, Holen, Liow, & Stenseth, 2015; Weber et al., 2017). This approach involves investigating whether the ecological interactions among most (if not all) extant species of a clade (clade-wide) support interspecific competition, and are thus consistent with the clade's observed DDD pattern. To our knowledge, none of the clades that have shown the negative DDD pattern have been studied in a clade-wide community ecology framework.

Planktonic Foraminifera (PF) represent a useful model system for integrating macroevolution and community ecology (Yasuhara, Tittensor, Hillebrand, & Worm, 2017). They are marine unicellular zooplankton that produce calcium carbonate shells, which accumulate on the seafloor building up a remarkably complete fossil record (Ezard et al., 2011; Schiebel, 2002). The PF fossil record of the last 66 million years shows a negative DDD pattern (Figure 1), either by analysing the phylogenetic tree structure (Etienne et al., 2011), or considering biotic and abiotic correlates of diversification (Ezard et al., 2011), or using nonlinear ecological models of alternative modes of competition (Ezard & Purvis, 2016). These ecological models suggest that although abiotic factors affect the dynamics of PF diversification, their diversification is driven by compensatory contest competition (Ezard & Purvis, 2016), which is analogous to a populational logistic growth where resource availability is limited and only successful individuals get the amount of resource they require (Hassell, 1975).

While competition among PF species likely affected their diversification dynamics (Etienne et al., 2011; Ezard et al., 2011; Ezard & Purvis, 2016), we do not know if (or how) species compete today. PF are difficult to culture because they do not reproduce under laboratory conditions (Hemleben, Spindler, & Anderson, 1989), hindering our understanding of their population dynamics and ecological interactions. Globally, there are 47 extant PF species (Siccha & Kucera, 2017), occurring in low densities when compared to other eukaryotic groups (Keeling & del Campo, 2017). PF prey on other plankton groups (e.g., phytoplankton, ciliates and copepods), and several species host photosymbionts (Hemleben et al., 1989; Takagi et al., 2019); however, we currently lack understanding of the role of ecological interactions in shaping extant PF diversity. Assessing if extant PF species compete is valuable not only to bridge macroevolution and community ecology, but also to improve ecological models used

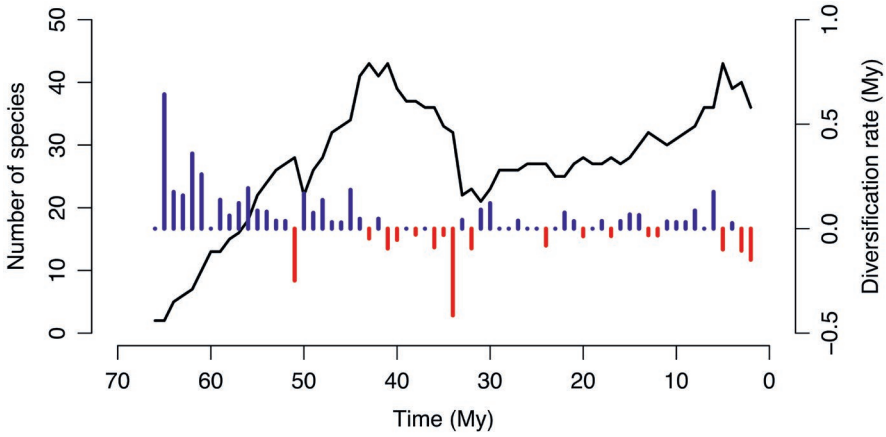

FIGURE 1 Bounded diversification pattern observed in the planktonic Foraminifera fossil record. Number of species (black line) through geological time in millions of years (My) ago, zero represents the present. The coloured bars represent the diversification rate per million-year time bin, calculated by dividing the number of new and extinct species per bin (Ezard et al., 2011). Blue bars represent positive diversification rates, while red bars represent negative rates. We removed the most recent time bin to avoid the pull of the present effect (i.e., species not having had time to go extinct yet). We used the Aze et al. (2011) lineage phylogeny of macroperforate Cenozoic planktonic Foraminifera for this figure

in palaeoceanographic reconstructions, as these models assume that PF compete without explicitly testing for it (e.g., Fraile, Schulz, Mulitza, & Kucera, 2008; Lombard et al., 2011).

Here, we integrate PF abundance data globally in space and through time to investigate whether ecological signatures are expressed consistently across macroecological and macroevolutionary scales (Figure 2). The temporal scale we study ranges from weeks (sediment trap data) to millennia (coretop data). We explore two community-level patterns expected under interspecific competition: local competitive exclusion (spatial pattern) and compensatory dynamics (temporal pattern). When resources are limiting, ecologically similar species (e.g., similar size or diet) are expected to compete more intensely, and ultimately exclude one another from the local community (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Webb, Ackerly, McPeek, & Donoghue, 2002). Thus, we expect competitive exclusion to lead to the spatial segregation of ecologically similar species, resulting in overdispersed local communities (Cavender-Bares et al., 2009; Pearse, Purvis, Cavender-Bares, & Helmus, 2014; Webb et al., 2002). Yet if competing species coexist, population sizes of competitors are expected to show a negative relationship

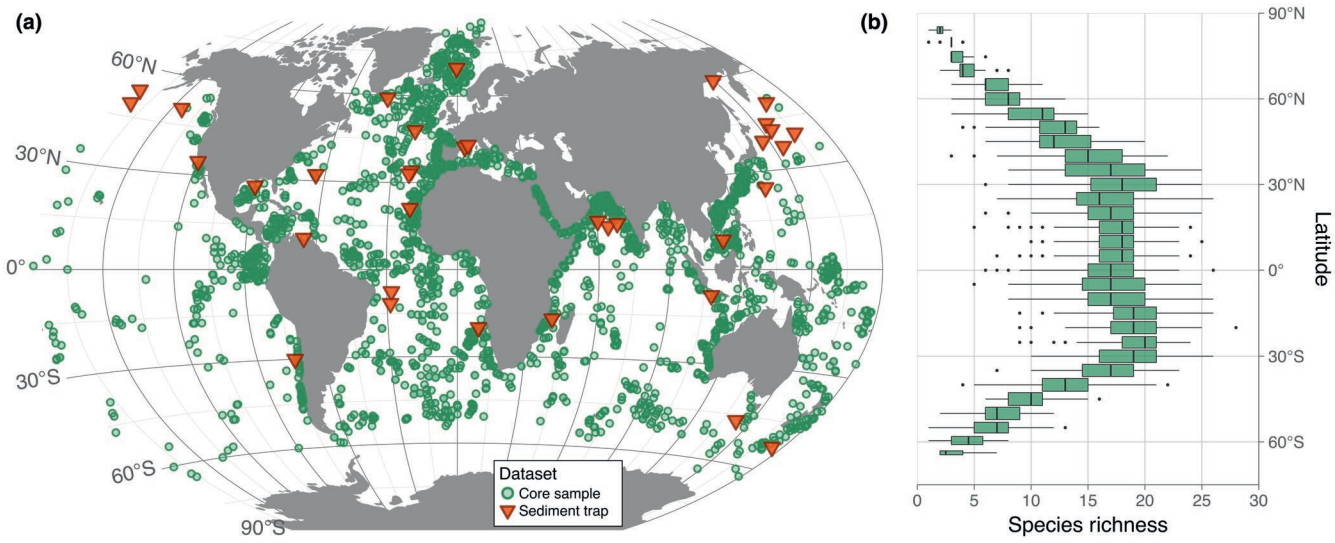

FIGURE 2 (a) Map of modern planktonic Foraminifera (PF) abundance data. Green dots, spatial data: 3,053 ocean-floor coretop samples, each with data on relative abundance of all the species present in the sample (usually larger than 150 μm; Siccha & Kucera, 2017). Orange triangles, temporal data: 35 sediment traps, each with data on abundance (shell flux) time series of PF species. Not all species were identified in the sediment trap samples. In total there are 370 population time series available (Supporting Information Table S2). (b) Latitudinal richness gradient of PF for each 5° bin, based on coretop samples with richness equal to or greater than two species

through time (compensatory dynamics; Houlahan et al., 2007). Thus, we expect that, depending on the strength of interspecific competition, ecologically similar species will either show complete local competitive exclusion, or population abundances will covary negatively through time. If ecological interactions have a consistent effect across geological and current ecological time scales, we expect competition among PF species to play a key role in structuring their modern communities.

2 | MATERIAL AND METHODS

We used two types of observational data: spatial data from 3,053 coretop samples and temporal data from 35 sediment traps (370 time series of population abundances in total) (Figures 2 and 3). We performed two distinct and independent analyses for each data type: spatial data were analysed using a community phylogenetics approach, considering random assembly null models. Temporal data were analysed by pairwise correlation of time series, considering a null model of species' annual seasonality. All analyses were conducted using R (version 3.3.3, R Core Team, 2017).

2.1 | Spatial data

Ocean-floor sediment samples are recovered using core sampling (Figure 3); the coretop represents the most recent (surface) sediment. Because there is no precise estimate of local sedimentation rate in most sampled sites, core samples hold information on species relative abundances (relative to the sampled assemblage, as all individuals are identified) rather than absolute abundances. Coretop samples represent time-averaged assemblages on the order of hundreds to thousands of years depending on local sedimentation and bioturbation rates (Jonkers, Hillebrand, & Kucera, 2019). Such time-averaged assemblages have the advantage of averaging out seasonal and inter-annual fluctuations in abundance that might blur macroecological patterns (Fenton, Pearson, Jones, & Purvis, 2016).

We used relative abundance data from the ForCenS database, which is a curated database, taxonomically harmonized and treated for sampling inconsistencies (Siccha & Kucera, 2017). Sites deeper than 3,500 m in the Pacific and Indian oceans and 4,500 m elsewhere were excluded to minimize the effects of calcium carbonate dissolution on assemblage composition (Tittensor et al., 2010). We also removed samples that only contained one species and those that did not differentiate between the species *Globorotalia menardii* and *Globorotalia tumida*; *Globigerinoides ruber* pink and white; or *Turborotalita humilis* and *Berggrenia pumilio*. With these restrictions, the data we analysed consisted of 3,053 unique sites of relative abundances of 41 PF species distributed across the globe (Figure 2a).

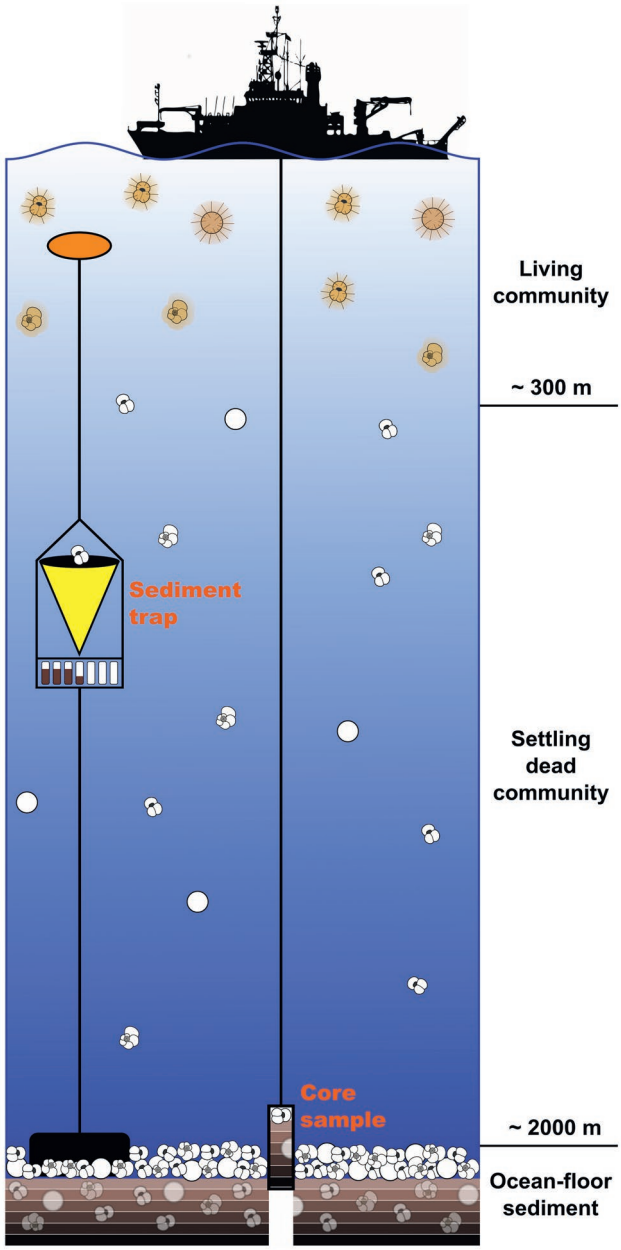

FIGURE 3 Schematic figure showing the two different types of data used in our analyses: sediment traps (temporal data) provide a virtually continuous time series of settling, dead planktonic Foraminifera shells. An upward-facing funnel (yellow triangle) directs sinking particulate material towards a sampling bottle. At pre-determined time intervals, a new sampling bottle is shifted into position. Core samples (spatial data) are a cylindrical section of the ocean floor sediment obtained by coring with a hollow tube. The top of the core (coretop) contains the most recently settled particles, and down core samples contain older, fossil material. The ship silhouette represents the German Research Vessel *Meteor*

2.2 | Temporal data

Sediment traps consist of an upward-facing funnel that directs sinking particulate material towards a sampling bottle (Figure 3), providing a time series of settling PF shells (expressed as flux: number of shells per square metre per day). We used data collected globally from 35 sediment traps (Figure 2a and Supporting Information Table S2) including 37 PF species, in total 370 time series of population

shell fluxes (11 species per trap on average). We used the sediment traps selected by Jonkers and Kucera (2015), who harmonized the taxonomy on these samples. The total duration of the sampling ranged from a minimum of 1 to 12 years (mean 3.4 years), and the mean length of the time series was 59 samples. Sampling intervals (resolution) varied between four and 58 days (mean 18 days). For more information, see Supporting Information Table S2 and Jonkers and Kucera (2015).

Shell fluxes represent the settling of dead individuals and indirectly represent the population abundance in the water column (Jonkers & Kucera, 2015). PF have a short life span (typically 1 month; Hemleben et al., 1989), thus shell fluxes are likely to be a good proxy of population abundance (standing stock). The comparison of shell fluxes between different species makes the underlying assumption that species have similar life spans and settling time, which is reasonable given the average sampling resolution. As we expect competition to affect individuals' mortality, the dynamics of settling dead individuals are assumed to represent the dynamics of competition among living individuals.

2.3 | Ecological similarity data

We use three different measures to capture ecological similarity between species: phylogenetic relatedness, species' average size and presence or absence of photosymbionts. Phylogenetic relatedness can be used as a proxy for ecological similarity between species under the assumption of niche conservatism (Cavender-Bares et al., 2009; Wiens et al., 2010). PF are divided into two monophyletic groups, microperforates and macroperforates (Aurahs et al., 2009). We used the Aze et al. (2011) Cenozoic phylogeny of macroperforate species as a basis to obtain phylogenetic relationships among extant PF. Following the taxonomic standardization of Siccha and Kucera (2017), we updated the taxon names in the Aze et al. (2011) phylogeny, removed synonyms and added newly recognized species (Supporting Information Figure S1). The final phylogeny includes 33 species (Supporting Information Figure S1); the 14 species not present in the phylogeny (e.g., microperforates) were excluded from the phylogenetic analysis.

We used similarity between species' average sizes as an alternative proxy for ecological similarity, because zooplankton body size is a functional trait related to physiological and ecological processes (Litchman, Ohman, & Kiørboe, 2013; Sauterey, Ward, Rault, Bowler, & Claessen, 2017). We estimated average size of 36 PF species, by compiling shell diameter data of 2,774 individuals from three different datasets (Baranowski, 2013; Rillo, Miller, Kucera, & Ezard, 2019; Weinkauf, Kunze, Waniek, & Kucera, 2016; Supporting Information Table S1). Although there is high intraspecific size variation within species, size differences among species are evident (Supporting Information Figure S2) and assumed to represent species-level niche differences. The 11 species for which no size data are available were excluded from the size analysis.

Many PF species are known to exhibit photosymbiosis (Hemleben et al., 1989; Takagi et al., 2019). Symbiont-bearing PF mostly live in tropical to subtropical oligotrophic waters (Bé & Hutson, 1977). Thus, photosymbiosis seems to be a successful ecological strategy in nutrient-limited environments, possibly allowing for greater flexibility in resource acquisition for growth and reproduction (Takagi et al., 2019). We use presence or absence of symbionts (symbiotic strategy), recently measured for 30 species (Takagi et al., 2019), as a third proxy for ecological similarity between species. We considered species that display low to high intensity of photosymbiosis as phototrophs (19 species) and no photoactivity as heterotrophs (11 species), following Takagi et al. (2019). The 17 species not included in the Takagi et al. (2019) study were excluded from the photosymbiosis analysis.

2.4 | Community phylogenetics analysis (spatial data)

To test for competitive exclusion in the spatial data, we use a community phylogenetics approach and the *picante* R package (version 1.6–2; Kembel et al., 2010). We test if species coexisting in a local community are more or less ecologically similar (clustered or overdispersed, respectively) than what would be expected given a random assembly process (null model). Overdispersed communities are predicted to emerge because of intense competition among ecologically similar species for limiting resources, whereas clustered communities contain species that share similar traits, hypothetically related to environmental tolerances (Cavender-Bares et al., 2009; Pearse et al., 2014; Webb et al., 2002).

We assessed the ecological similarity of species in the community given a species-by-species distance matrix (cophenetic distance, i.e., divergence time, for the phylogenetic tree and Euclidean distance for the species' average sizes). We assume that closely related species share more traits (niche conservatism) and therefore compete more strongly than distantly related species. Similarly, we also assume species of similar sizes compete more strongly.

For each of the 3,053 PF assemblages in the spatial data (Figure 2a), we calculated two community dispersion metrics: the mean pairwise distance (MPD) and the mean nearest (taxon) distance (MNTD), both calculated given the species-by-species distance matrices, and weighted by the abundance of each species in the local community. MPD is the average distance between all species in the assemblage and thus takes into account clade-wide patterns. MNTD is the average distance between each species and its nearest neighbour in the distance matrix, representing local patterns in the phylogeny or trait space.

To test if the observed MPD and MNTD values differ significantly from the values that would be expected under a random assembly process, we generated null models of community assembly. If species are equivalent (neutral dynamics), we expect communities to be composed of a random subset of species capable of colonizing the local community (i.e., the source pool; Pearse et al., 2014; Webb et al., 2002). Our source pool includes all extant PF species, because the ranges of all but two species cover every ocean basin (Bé & Tolderlund, 1971). Thus, we assume in the null models that species

can reach all oceanographic regions in the world. If there are local community assembly processes (competitive exclusion and environmental tolerances), the species' local establishment will be different from the random subset, because the local fitness of species differ (i.e., species are not equivalent).

We tested two random assembly models: 'taxa', which shuffles the species-by-species distance matrix, and tests if the observed communities show phylogenetic or size structure; 'richness', which shuffles the species' abundances in the sample (holding the richness constant), and tests if community structure could have been generated by randomly drawing species from the source pool (Kembel et al., 2010). We ran each null model 100 times, then standardized the observed MPD and MNTD values with respect to the expected values and standard deviations of the null distributions (standardized effect size), generating the net relatedness index (NRI) and the nearest taxon index (NTI), respectively. Positive values of NRI and NTI indicate clustered assemblages (environmental filters), whereas negative values of NRI and NTI indicate overdispersed assemblages (competitive exclusion). We used a statistical significance level of 1% to avoid false positives given the large number of samples (3,053 assemblages). Additionally, we retrieved annual mean sea-surface temperature (SST) for each of the 3,053 assemblages from the World Ocean Atlas 2013 (Locarnini et al., 2013) to assess the relationship between SST and community patterns.

2.5 | Time-series analysis (temporal data)

If two species compete in the local community, we expect that increases in the abundance of one species should have a negative impact on the abundance of the other species, generating a negative correlation of abundances through time. To test for such compensatory dynamics in the temporal data, we calculated the correlation between the differentiated time series (i.e., first differences) of co-occurring species pairs (sampled in the same sediment trap). We used the nonparametric Kendall rank correlation, which makes no assumption on the underlying pairwise distribution. In total, 2,303 correlations were calculated and analysed regarding ecological similarity between species pairs (i.e., phylogenetic relatedness, average sizes or symbiotic strategy).

PF species' abundances (fluxes) vary seasonally in response to SST and primary productivity (Jonkers & Kucera, 2015). When correlating these abundance time series, similar seasonal cycles can yield strong positive correlations even if species compete within their seasonal peaks. In order to correct for this bias, we built a null model assuming a seasonal cycle with a 1-year period, but allowing each species to have any number of abundance peaks within the year. This flexibility of species seasonality is consistent with observations that the same species can display unimodal or bimodal yearly abundance patterns depending on the regional oceanographic setting (Jonkers & Kucera, 2015). Thus, for each observed time series (i.e., each species in each sediment trap) we obtained a smoothing spline, which calculates the average abundance of the species for each day of the year, resulting in a yearly averaged series (spline series; Supporting Information Figure S7), without having to enforce an a priori fixed annual seasonality. The smoothing spline parameter λ was estimated using the generalized cross-validation (GCV) method (Craven & Wahba, 1978), which finds the optimum parameter value by minimizing the mean squared error of the fitting (also used in generalized additive models). The mean error of the spline fitting is larger for time series of shorter length (number of samples) and shorter duration (number of years) (Supporting Information Figure S8), but not in a way that qualitatively affected our results.

To generate the seasonality null model, we calculated the residuals between the observed time series and its spline series (Supporting Information Figure S7). We then randomized these residuals and added them to the spline series. This procedure was repeated 100 times, to produce a set of surrogate time series with the same seasonality as the observed time series, but with random departures from it. For each species pair, we calculated the Kendall rank correlation coefficient between their surrogate series, resulting in a null distribution of 100 correlations for each co-occurring species pair (Supporting Information Figure S7). We report the standardized effect size (SES), which is the observed correlation standardized with respect to the null distribution. We compared the observed correlation with its null distribution for significance, and used a statistical significance level of 1% because of the large number of comparisons.

The residuals between the observed series and the spline series quantify the deviation of the observed abundances from the average annual abundance pattern. Thus, to calculate inter-annual variation in abundances, we correlated the residual series of all co-occurring species pairs within sediments traps that were sampled for longer than 2 years (21 traps in total, Supporting Information Table S2). A positive average correlation of residuals within the sediment trap indicates synchronous inter-annual variation in species abundances.

3 | RESULTS

3.1 | Community phylogenetics (spatial data)

Out of the 3,053 PF assemblages studied, only two differ significantly from random assembly processes (Figure 4), that is, a negligible proportion of the studied assemblages. The majority of NRI and NTI values are positive, indicating a trend towards phylogenetic and size clustering in the PF assemblages. As there is no qualitative difference between the results of the 'richness' and 'taxa' null models (Supporting Information Figure S3), we discuss only the former.

Using phylogeny as an ecological proxy, NRI values never reach below two standard deviations of the null distributions (i.e., the value of −2, Figure 4a), not supporting competitive exclusion of close relatives. NTI values, however, show a trend towards negative values in assemblages between 5 and 12 °C, reaching values below −2 (Figure 4c). These assemblages have, on average, seven species and are dominated by *Globigerina bulloides* and *Neogloboquadrina incompta* or *N. pachyderma*. These species come from two distantly related PF subclades, so the phylogenetic distance between coexisting

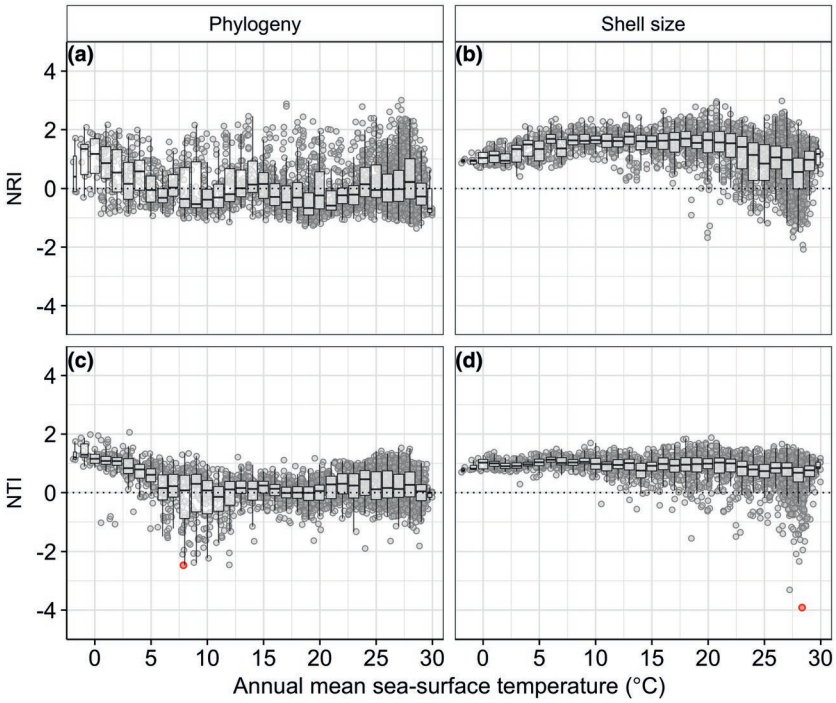

FIGURE 4 Spatial data: most planktonic Foraminifera assemblages are indistinguishable from randomly assembled communities. Values show the net relatedness index (NRI) and nearest taxon index (NTI) calculated for 3,053 coretop assemblages, plotted against annual mean sea-surface temperature on each site, boxplots binned by 1 °C. (a) and (c) were calculated based on the phylogenetic distance among co-occurring species; (b) and (d) were calculated based on the shell size differences among co-occurring species. Grey dots show non-significant NRI or NTI values, the two red dots show significant negative values (overdispersed). No values were significantly positive (clustered). Significance level 1%, based on 100 runs of the null model 'richness'

individuals in the community is mostly high (overdispersed). The opposite is observed for the polar assemblages (0 °C), which are dominated by *N. pachyderma* (average relative abundance of 97%) and show a non-significant tendency for positive NTI values (environmental filters; Figure 4c).

Dispersion metrics based on species' size differences show either no or one overdispersed assemblages (Figure 4b,d, respectively). This single overdispersed assemblage has a remarkably low NTI value (around −4) and high relative abundance of the large species *Globorotalia menardii* (37%, Supporting Information Figure S6). In general, there is a tendency for negative, but not significant, NRI and NTI values at high SST (25–30 °C, Figure 4b,d), suggesting large size disparity. In fact, these tropical assemblages contain species of large average sizes (Supporting Information Figure S5), which is consistent with the known trend of increasing assemblage size towards the tropics (Schmidt, Renaud, Bollmann, Schiebel, & Thierstein, 2004).

3.2 | Time series (temporal data)

Out of the 2,303 standardized correlations, 634 differ significantly from the seasonality null model, of which 588 are positive and 46 negative. As such, even without correction for multiple testing, we find only 2% of the correlations to conform to the expected competition scenario. All sediment traps show median positive standardized correlations (Figure 5), indicating that population dynamics within communities are mostly synchronous. The correlations between the differentiated time series are similar to the standardized correlations (Supporting Information Figure S9), and not discussed further.

Standardized correlations are positive between both closely and distantly related species pairs (Figure 6a), and show highest positive values between species of similar sizes (Figure 6b). Moreover, species pairs with the same symbiotic strategy, that is, both hosting symbionts (phototrophs) or not (heterotrophs), show similar correlation patterns when compared to species pairs with opposite symbiotic strategies (heterotrophs and phototrophs; Figure 6c). Species also have synchronous dynamics across years (inter-annual variation), as the residuals of observed time series minus spline series correlate positively in the sediments traps (Supporting Information Figures S7 and S10).

4 | DISCUSSION

4.1 | Spatial patterns

Our community phylogenetics analysis of 3,053 assemblages revealed that PF co-occurrence patterns are indistinguishable from neutral assembly processes (Figure 4). The sediment samples used in this analysis are globally distributed (Figure 2a) and, importantly, contain data on relative abundance of species instead of presence and absence. Competitive exclusion over broad spatial extents is known to be a slow process (Yackulic, 2017) and particularly difficult to observe in the highly dynamical marine systems

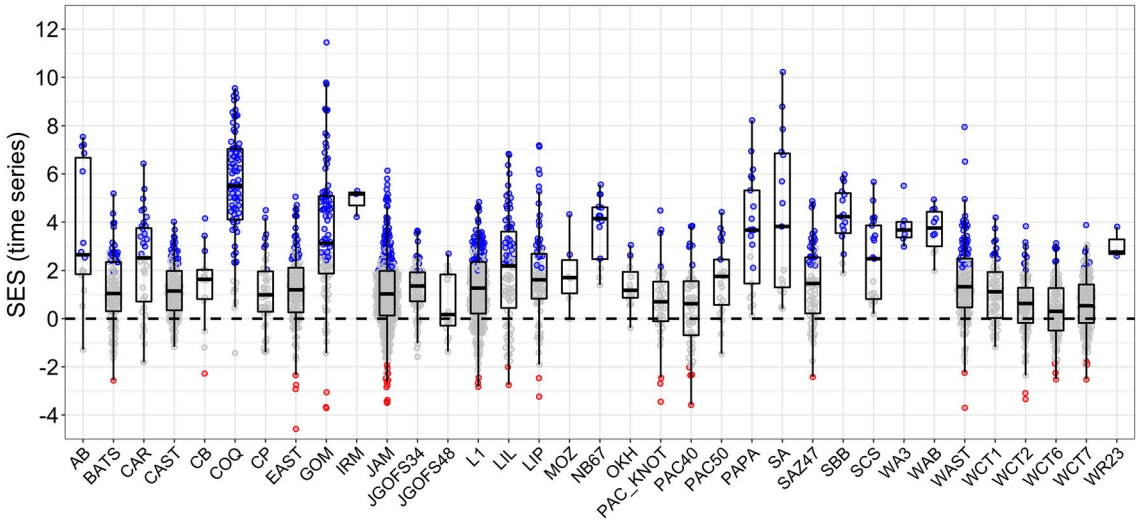

FIGURE 5 Temporal data: most sediment traps show non-significant or positive correlations between planktonic Foraminifera population dynamics. Values show pairwise time-series correlations of species abundances (2,303 in total) plotted by sediment trap (see Supporting Information Table S2 for sediment trap name abbreviation). Grey dots show non-significant, blue significant positive, red significant negative standardized size effect (SES) values, based on the seasonality null model and significance level of 1%

(Clayton, Dutkiewicz, Jahn, & Follows, 2013). However, by considering species local abundance, competitive exclusion need not have gone to completion. Overdispersed communities can emerge when ecologically similar species still coexist but have disparate abundances (Ulrich & Gotelli, 2010). Yet overdispersion was observed only in two assemblages (Figure 4), indicating that if competitive exclusion is happening in these communities, it leaves no phylogenetic or morphological signal in the seafloor sediments.

We observed no global significant relationship between the NTI and NRI values and SST (Figure 4), although PF show a clear latitudinal diversity gradient (Figure 2b). When considering a significance level of 5% (instead of 1%), NTI and NRI values regarding phylogenetic distance remain the same; however, regarding size differences, many significant clustered communities emerge (Supporting Information Figure S4). These clustered communities occur across the SST range, with no clear SST pattern; instead, they show a relationship with the local relative abundance of the species *Globorotalia menardii* and *Globorotalia tumida*. These disproportionately large species (Supporting Information Figure S2) bias the NTI and NRI metrics: when they are absent or in low abundances, communities are clustered (Supporting Information Figure S6). This bias in the PF co-occurrence patterns due to only two species suggests that our community phylogenetics analysis is limited by the low number of extant PF species.

The dichotomy of competition versus environmental filtering, pervasive in community phylogenetic approaches, is oversimplified (Cadotte & Tucker, 2017). Competition can instead reinforce co-occurrence of ecologically similar species, giving rise to clustered communities identical to those expected under environmental filtering (Mayfield & Levine, 2010). However, the fact that we observe no significant clustering or overdispersed patterns suggests that these plankton communities are influenced by neutral processes, such as dispersal and stochastic extinction (Rosindell, Hubbell, & Etienne, 2011). Indeed, dispersal assembly mechanisms have been shown to prevail over niche-assembly mechanisms for the past 30 million years of PF evolution (Allen & Gillooly, 2006), but the lack of support for competition found in our study does not necessarily indicate that PF dynamics are neutral. Other non-neutral mechanisms such as symbiosis, predation and competition with other groups can drive PF community assembly and need to be further investigated.

4.2 | Temporal patterns

The time-averaging of seafloor sediment samples (Jonkers et al., 2019) added to the complex spatio-temporal dynamics of the marine environment can mask local patterns that emerge from ecological interactions (Clayton et al., 2013; McGillicuddy, 2016). Therefore, we also investigated high-resolution time-series to test for competition among PF species. Previous sediment trap studies have shown that PF abundances (measured as shell flux) change synchronously through time largely in response to changes in temperature and food availability (Jonkers & Kucera, 2015; Marchant, Hebbeln, Giglio, Coloma, & Gonzalez, 2004; Marchant, Hebbeln, & Wefer, 1998; Northcote & Neil, 2005; Poore, Tedesco, & Spear, 2013; Rigual-Hernandez, Sierro, Barcena, Flores, & Heussner, 2012; Tedesco & Thunell, 2003; Wan, Jian, Cheng, Qiao, & Wang, 2010). However, other studies have shown that species abundance peaks can occur sequentially (Deuser & Ross, 1989; Jonkers et al., 2010; Jonkers, Heuven, Zahn, & Peeters, 2013) or be inversely related (Kincaid et al., 2000; Kuroyanagi, Kawahata, Nishi, & Honda, 2002; Mohiuddin, Nishimura, Tanaka, & Shimamoto, 2002; Rigual-Hernandez et al., 2012), suggesting that species have different ecological preferences. Species with opposite abundance patterns during the year are expected to exhibit low correlation values, whereas species with

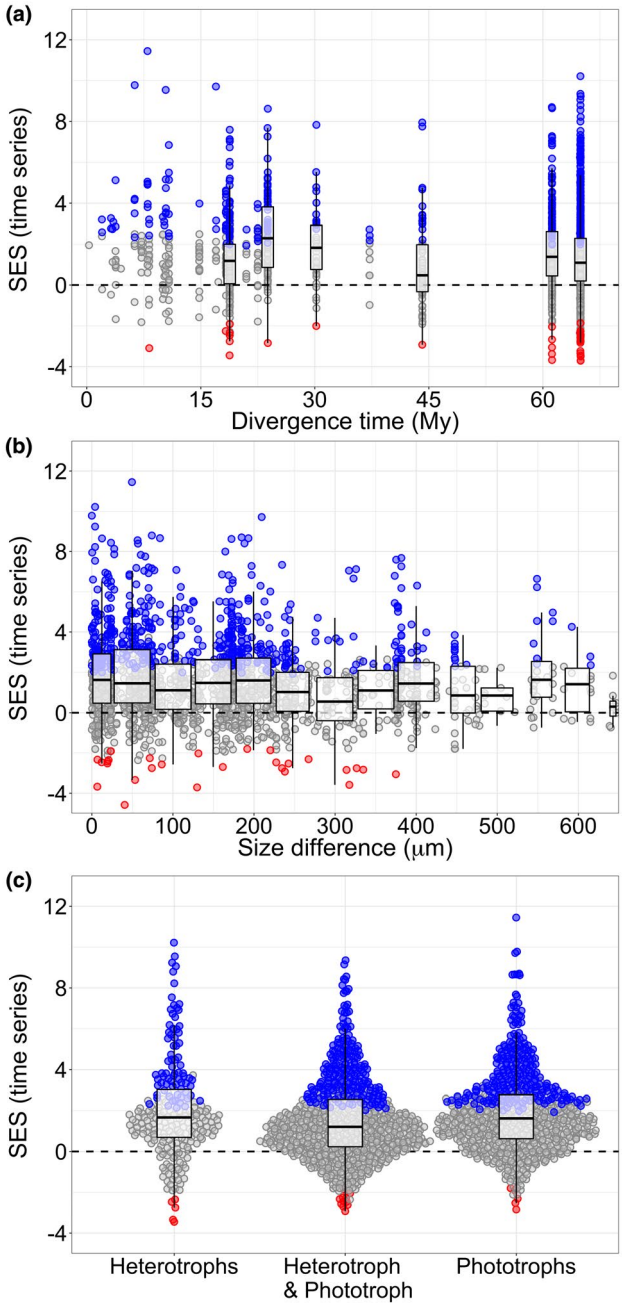

FIGURE 6 Temporal data: most planktonic Foraminifera species display seasonal and synchronized population dynamics. Values show pairwise time-series correlations of species abundances plotted against (a) the phylogenetic distance between species in millions of years (My) (1,843 pairwise correlations in total), boxplots represent divergence times with more than 40 species pairs; (b) the shell size difference between species (1,801 pairwise correlations), binned by 50 μm; (c) the photosymbiotic strategy of the species pair (1,721 pairwise correlations): both species do not host symbionts (heterotrophs), one species does not host symbionts and the other does (heterotroph & phototroph), or both species host symbionts (phototrophs). Grey dots show non-significant, blue significant positive, red significant negative standardized size effect (SES) values, based on the null seasonality model and significance level of 1%

sequential abundance peaks (compensatory dynamics) should correlate negatively through time. Here, we show that the dynamics of PF abundances are largely explained by annual seasonality: 72% of the pairwise correlations did not differ significantly from our seasonality null model. The remaining significant correlations were predominantly positive (93%), indicating synchronous population dynamics. This pattern was consistent across sediment traps with different sampling durations (Figure 5 and Supporting Information Table S2) and across years (Supporting Information Figure S10). Moreover, species with similar ecologies did not correlate more negatively than other species pairs (Figure 6), as would be expected if they were partitioning the resource through time. Therefore, PF population dynamics seems to be influenced by external factors such as the abiotic environment and/or abundance of other distantly related plankton groups, rather than intra-clade density-dependent processes.

PF species might have different vertical niches and thus live in parapatry in the water column (Hemleben et al., 1989; Rebotim et al., 2017), yet they would still fall within the same sediment trap or core-top sample, and thus be observed as co-occurring species in our analyses. Species' vertical niches have been shown to cover a wide range of depths and to overlap considerably (Rebotim et al., 2017), making it difficult to define consistent depth habitats of species for all samples analysed here. Nevertheless, symbiont-bearing species are limited to the surface euphotic zone for the optimum maintenance of their photosynthetic algae (Bé, Spero, & Anderson, 1982; Takagi et al., 2019). Assuming that photosymbiosis is a reasonable proxy for depth habitat, symbiont-bearing species did not show stronger compensatory dynamics than species with different symbiotic strategies (Figure 6c), supporting our results at an admittedly coarse depth habitat classification.

4.3 | Mismatch between macroevolutionary and community dynamics

The fossil record suggests that the diversification dynamics of PF are strongly regulated by competition among species (Ezard et al., 2011; Ezard & Purvis, 2016). However, we found no evidence of interspecific competition shaping spatial or temporal diversity patterns of extant PF. The global and clade-wide scales of our ecological analysis are comparable in scope to macroevolutionary analysis, yet these analyses differ markedly in temporal and taxonomic scales (Harmon et al. 2019). The PF fossil record showed evidence for competition when analysed at the species level (taxon counts) over millions of years (Ezard & Purvis, 2016). Here, we tested for competition among species at the population level and at shorter time scales, ranging from weeks up to a few thousands of years. While PF population dynamics could potentially show different emergent patterns when analysed over million-year time spans, interspecific competition operates at the individual level and requires population overlap in space and time, also as a diversity-dependent diversification process (Marshall & Quental, 2016). Moreover, the nested hierarchy of organizational levels (individuals, populations, species) implies

that dynamics at higher levels should always propagate downwards (Jablonski, 2008b). Thus, if a clade's diversification is limited by competition among species, this mechanism should be observable at the population level and ecological time scales.

It could be that interspecific competition limited PF diversification throughout the Cenozoic (Ezard & Purvis, 2016), but species are not competing at present because they are below the clade's carrying capacity (Rabosky, 2013). In fact, a total of seven PF species went extinct in the past 5 million years, and the clade is currently in a negative diversification phase (Figure 1; Aze et al., 2011). If the niche space was saturated, then the extinction of these species would have released the competitive pressure by making niche space available. Nevertheless, we would still expect extant species to show niche partitioning and evidence for interspecific competition across space and/or ecological time, which we did not observe in our competition proxies. The macroevolutionary compensatory dynamics proposed by Ezard and Purvis (2016) leads to the hypothesis that empty niche space is filled by species occupying similar niches (incumbency advantages). Thus, we could expect that species that are ecologically similar to the recently extinct species expanded their niche by increasing in abundance and/or biogeographical range, compensating for the extinction of their competitors. This hypothesis remains to be tested in the PF fossil record.

Alternative mechanisms could generate the DDD pattern, without the need to evoke interspecific competition and niche partitioning. In a model where speciation and extinction rates emerge from population dynamics, Wang, Chen, Fang, and Pacala (2013) showed that the average speciation rate of a clade declines over time because species' abundances decrease at speciation. In this model, lineages with high speciation rates have the disadvantage of having high extinctions because of low population size (see also Harnik, 2011). Thus, a positive correlation between speciation and extinction rates naturally emerges (the macroevolutionary trade-off; Jablonski, 2017), which is also observed in the macroperforate PF fossil record (Supporting Information Figure S11).

The geography of diversification might also play a crucial role in the emergence of DDD patterns (Moen & Morlon, 2014). During allopatric speciation, cladogenesis not only reduces species' abundances but also species' biogeographical ranges. Larger ranges are more likely to experience the emergence of geographical or oceanographical barriers. Thus, as diversification proceeds, ranges are subdivided and per-species rates of speciation decline, generating the DDD pattern without competition among species (Moen & Morlon, 2014; Pigot, Phillimore, Owens, & Orme, 2010). PF have the ability to disperse long distances, evidenced by genetic and fossil data (Darling et al., 2000; Sexton & Norris, 2008). This high dispersal suggests that it may be difficult to geographically isolate pelagic populations for extended periods of time, a key component in allopatric speciation models. In fact, the PF fossil record has shown cases of sympatric speciation (Lazarus, Hilbrecht, Spencer-Cervato, & Thierstein, 1995; Pearson, Shackleton, & Hall, 1997), questioning the use of purely allopatric speciation models (e.g., Pigot & Etienne, 2015). Nevertheless, PF genetic studies revealed phylogeographical patterns of allopatry (Darling, Kucera, & Wade, 2007; De Vargas, Norris, Zaninetti, Gibb, & Pawlowski, 1999; Weiner et al., 2014), suggesting that ocean circulation and directional flow create dynamical barriers to populations. Moreover, species' abundances and geographical ranges might interact in a negative way, and rare but widespread species (e.g., globorotaliids) might experience oceanographical gene-flow barriers more often than abundant species. Genetic data provide new perspectives for speciation modes in the plankton, and could reveal PF ecological interactions at other organizational levels (Alizon, Kucera, & Jansen, 2008; Aurahs, Treis, Darling, & Kucera, 2011; Darling, Kucera, Wade, von Langen & Pak, 2003).

Overall, our results suggest that PF species are not competing in the modern oceans, which is consistent with the known low densities of PF in the water column (Keeling & del Campo, 2017; Schiebel & Hemleben, 2005). Abiotic factors such as SST have been shown to affect PF diversity patterns in space and time (Fenton et al., 2016; Jonkers & Kucera, 2015; Yasuhara, Hunt, Dowsett, Robinson, & Stoll, 2012), as well as their diversification dynamics (Ezard et al., 2011; Ezard & Purvis, 2016). However, phytoplankton abundance also plays an important role in PF population dynamics (Jonkers & Kucera, 2015), but their effect on PF diversification has not been explored. To further understand the processes governing biodiversity dynamics, we need to include species that are coupled ecologically, even when belonging to distantly related clades (Marshall & Quental, 2016). By defining the species pool of macroevolutionary dynamics ecologically rather than only phylogenetically, we can potentially elucidate the mismatch found in our study.

ACKNOWLEDGMENTS

We thank all the researchers who have made their data openly available; Isabel S. Fenton, Daniela Schmidt, Phillip Fenberg, and two anonymous reviewers for insightful comments on the manuscript; James Rosindel, Rampal Etienne, Rachel Germain and Mathias Pires for helpful discussions about the project.

AUTHOR CONTRIBUTION

M.R. designed the research, performed the analyses, wrote the manuscript and led the revisions. B.C. participated in the time-series analysis. U.B. provided shell size data. M.K. participated in the design of the research and interpretation of the results. M.S., L.J. and T.E. participated in the interpretation of the results and critically reviewed the manuscript. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available and previously published: refer to Siccha and Kucera (2017) for core-top abundance data; Supporting Information Table S2 for time-series data; Aze et al. (2011) for phylogeny; Baranowski (2013); Weinkauf et al. (2016); Rillo et al. (2019) for shell size data; Takagi et al. (2019) for symbiosis data. The R code used to produce the analyses and figures is available at https://github.com/mcrillo/Rillo-competition-forams.git.

ORCID

Marina C. Rillo https://orcid.org/0000-0002-2471-0002
Mauro T. C. Sugawara https://orcid.org/0000-0003-0403-8586
Brenno Cabella https://orcid.org/0000-0003-2214-645X
Lukas Jonkers https://orcid.org/0000-0002-0253-2639
Ulrike K. Baranowski https://orcid.org/0000-0003-3177-5936
Michal Kučera https://orcid.org/0000-0002-7817-9018
Thomas H. G. Ezard https://orcid.org/0000-0001-8305-6605

REFERENCES

Alizon, S., Kucera, M., & Jansen, V. A. (2008). Competition between cryptic species explains variations in rates of lineage evolution. *Proceedings of the National Academy of Sciences USA*, *105*, 12382–12386. https://doi.org/10.1073/pnas.0805039105

Allen, A. P., & Gillooly, J. F. (2006). Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecology Letters*, *9*, 947–954. https://doi.org/10.1111/j.1461-0248.2006.00946.x

Aurahs, R., Goker, M., Grimm, G. W., Hemleben, V., Hemleben, C., Schiebel, R., & Kucera, M. (2009). Using the multiple analysis approach to reconstruct phylogenetic relationships among planktonic Foraminifera from highly divergent and length-polymorphic SSU rDNA sequences. *Bioinformatics and Biology Insights*, *3*, 155–177. https://doi.org/10.4137/BBI.S3334

Aurahs, R., Treis, Y., Darling, K., & Kucera, M. (2011). A revised taxonomic and phylogenetic concept for the planktonic foraminifer species *Globigerinoides ruber* based on molecular and morphometric evidence. *Marine Micropaleontology*, *79*, 1–14. https://doi.org/10.1016/j.marmicro.2010.12.001

Aze, T., Ezard, T. H., Purvis, A., Coxall, H. K., Stewart, D. R., Wade, B. S., & Pearson, P. N. (2011). A phylogeny of Cenozoic macroperforate planktonic foraminifera from fossil data. *Biological Reviews*, *86*, 900–927. https://doi.org/10.1111/j.1469-185X.2011.00178.x

Bailey, S. F., Dettman, J. R., Rainey, P. B., & Kassen, R. (2013). Competition both drives and impedes diversification in a model adaptive radiation. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131253. https://doi.org/10.1098/rspb.2013.1253

Baranowski, U. K. (2013). *Phylogenetic significance of test morphology and ultrastructure in Recent planktonic Foraminifera inferred from cladistic analyses* (MSc thesis). Eberhard Karls University, Tübingen. https://doi.org/10.1594/PANGAEA.901825

Bé, A. W. H., & Hutson, W. H. (1977). Ecology of planktonic foraminifera and biogeographic patterns of life and fossil assemblages in the Indian Ocean. *Micropaleontology*, *23*, 369–414. https://doi.org/10.2307/1485406

Bé, A. W. H., Spero, H. J., & Anderson, O. R. (1982). Effects of symbiont elimination and reinfection on the life processes of the planktonic foraminifer *Globigerinoides sacculifer*. *Marine Biology*, *70*, 73–86. https://doi.org/10.1007/BF00397298

Bé, A. W. H., & Tolderlund, D. S. (1971). Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans. In B. M. Funnell & W. R. Riedel (Eds.), *The micropaleontology of oceans* (pp. 105–149). Cambridge, UK: Cambridge University Press.

Bengtsson, J. (1989). Interspecific competition increases local extinction rate in a metapopulation system. *Nature*, *340*, 713. https://doi.org/10.1038/340713a0

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology and Evolution*, *32*, 429–437. https://doi.org/10.1016/j.tree.2017.03.004

Cavender-Bares, J., Kozak, K. H., Fine, P. V., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*, 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Clayton, S., Dutkiewicz, S., Jahn, O., & Follows, M. J. (2013). Dispersal, eddies, and the diversity of marine phytoplankton. *Limnology and Oceanography: Fluids and Environments*, *3*, 182–197. https://doi.org/10.1215/21573689-2373515

Craven, P., & Wahba, G. (1978). Smoothing noisy data with spline functions. *Numerische Mathematik*, *31*, 377–403. https://doi.org/10.1007/BF01404567

Darling, K. F., Kucera, M., & Wade, C. M. (2007). Global molecular phylogeography reveals persistent Arctic circumpolar isolation in a marine planktonic protist. *Proceedings of the National Academy of Sciences USA*, *104*, 5002–5007. https://doi.org/10.1073/pnas.0700520104

Darling, K. F., Kucera, M., Wade, C. M., von Langen, P., & Pak, D. (2003). Seasonal distribution of genetic types of planktonic foraminifer morphospecies in the Santa Barbara Channel and its paleoceanographic implications. *Paleoceanography*, *18*, 1–11. https://doi.org/10.1029/2001PA000723

Darling, K. F., Wade, C. M., Stewart, I. A., Kroon, D., Dingle, R., & Brown, A. J. L. (2000). Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers. *Nature*, *405*, 43–47. https://doi.org/10.1038/35011002

De Vargas, C., Norris, R., Zaninetti, L., Gibb, S. W., & Pawlowski, J. (1999). Molecular evidence of cryptic speciation in plank- tonic foraminifers and their relation to oceanic provinces. *Proceedings of the National Academy of Sciences USA*, *96*, 2864–2868. https://doi.org/10.1073/pnas.96.6.2864

Deuser, W., & Ross, E. (1989). Seasonally abundant planktonic foraminifera of the Sargasso Sea; succession, deep-water fluxes, isotopic compositions, and paleoceanographic implications. *Journal of Foraminiferal Research*, *19*, 268–293. https://doi.org/10.2113/gsjfr.19.4.268

Etienne, R. S., Haegeman, B., Stadler, T., Aze, T., Pearson, P. N., Purvis, A., & Phillimore, A. B. (2011). Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1732), 1300–1309. https://doi.org/10.1098/rspb.2011.1439

Ezard, T. H. G., Aze, T., Pearson, P. N., & Purvis, A. (2011). Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science*, *332*, 349–351. https://doi.org/10.1126/science.1203060

Ezard, T. H. G., & Purvis, A. (2016). Environmental changes define ecological limits to species richness and reveal the mode of macroevolutionary competition. *Ecology Letters*, *19*, 899–906. https://doi.org/10.1111/ele.12626

Fenton, I. S., Pearson, P. N., Jones, T. D., & Purvis, A. (2016). Environmental predictors of diversity in Recent planktonic foraminifera as recorded in marine sediments. *PLoS ONE*, *11*, e0165522. https://doi.org/10.1371/journal.pone.0165522

Fraile, I., Schulz, M., Mulitza, S., & Kucera, M. (2008). Predicting the global distribution of planktonic foraminifera using a dynamic ecosystem model. *Biogeosciences*, *5*, 891–911. https://doi.org/10.5194/bg-5-891-2008

Harmon, L. J., Andreazzi, C. S., Débarre, F., Drury, J., Goldberg, E. E., Martins, A. B., … Matthews, B. (2019). Detecting the macroevolutionary signal of species interactions. *Journal of Evolutionary Biology*, *32*(8), 769–782. https://doi.org/10.1111/jeb.13477

Harnik, P. G. (2011). Direct and indirect effects of biological factors on extinction risk in fossil bivalves. *Proceedings of the National Academy of Sciences USA*, *108*, 13594–13599. https://doi.org/10.1073/pnas.1100572108

Hassell, M. P. (1975). Density-dependence in single-species populations. *The Journal of Animal Ecology*, 283–295. https://doi.org/10.2307/3863

Hemleben, C., Spindler, M., & Anderson, O. R. (1989). *Modern planktonic Foraminifera*. New York: Springer-Verlag.

Houlahan, J. E., Currie, D. J., Cottenie, K., Cumming, G. S., Ernest, S. K. M., Findlay, C. S., … Wondzell, S. M. (2007). Compensatory dynamics

are rare in natural ecological communities. *Proceedings of the National Academy of Sciences USA*, *104*, 3273–3277. https://doi.org/10.1073/pnas.0603798104

Jablonski, D. (2008a). Biotic interactions and macroevolution: Extensions and mismatches across scales and levels. *Evolution*, *62*, 715–739. https://doi.org/10.1111/j.1558-5646.2008.00317.x

Jablonski, D. (2008b). Species selection: Theory and data. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 501–524. https://doi.org/10.1146/annurev.ecolsys.39.110707.173510

Jablonski, D. (2017). Approaches to Macroevolution: 2. Sorting of variation, some overarching issues, and general conclusions. *Evolutionary Biology*, *44*, 451–475. https://doi.org/10.1007/s11692-017-9434-7

Jonkers, L., Brummer, G.-J.-A., Peeters, F. J., van Aken, H. M., & De Jong, M. F. (2010) Seasonal stratification, shell flux, and oxygen isotope dynamics of left-coiling *N. pachyderma* and *T. quinqueloba* in the western subpolar North Atlantic. *Paleoceanography and Paleoclimatology*, *25*, 1–13. https://doi.org/10.1029/2009PA001849

Jonkers, L., Hillebrand, H., & Kucera, M. (2019). Global change drives modern plankton communities away from the pre-industrial state. *Nature*, *570*(7761), 372–375. https://doi.org/10.1038/s41586-019-1230-3

Jonkers, L., & Kucera, M. (2015). Global analysis of seasonality in the shell flux of extant planktonic Foraminifera. *Biogeosciences*, *12*, 2207–2226. https://doi.org/10.5194/bg-12-2207-2015

Jonkers, L., van Heuven, S., Zahn, R., & Peeters, F. J. (2013). Seasonal patterns of shell flux, δ^{18}O and δ^{13}C of small and large *N. pachyderma* (s) and *G. bulloides* in the subpolar North Atlantic. *Paleoceanography*, *28*, 164–174. https://doi.org/10.1002/palo.20018

Keeling, P. J., & del Campo, J. (2017). Marine protists are not just big bacteria. *Current Biology*, *27*, R541–R549. https://doi.org/10.1016/j.cub.2017.03.075

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., … Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kincaid, E., Thunell, R. C., Le, J., Lange, C. B., Weinheimer, A. L., & Reid, F. M. (2000). Planktonic foraminiferal fluxes in the Santa Barbara Basin: Response to seasonal and interannual hydrographic changes. *Deep Sea Research Part II: Topical Studies in Oceanography*, *47*, 1157–1176. https://doi.org/10.1016/S0967-0645(99)00140-X

Kuroyanagi, A., Kawahata, H., Nishi, H., & Honda, M. C. (2002). Seasonal changes in planktonic foraminifera in the north- western North Pacific Ocean: Sediment trap experiments from subarctic and subtropical gyres. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*, 5627–5645. https://doi.org/10.1016/S0967-0645(02)00202-3

Lazarus, D., Hilbrecht, H., Spencer-Cervato, C., & Thierstein, H. (1995). Sympatric speciation and phyletic change in *Globorotalia truncatulinoides*. *Paleobiology*, *21*, 28–51. https://doi.org/10.1017/S0094837300013063

Liow, L. H., Di Martino, E., Voje, K. L., Rust, S., & Taylor, P. D. (2016). Interspecific interactions through 2 million years: Are competitive outcomes predictable? *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20160981. https://doi.org/10.1098/rspb.2016.0981

Litchman, E., Ohman, M. D., & Kiørboe, T. (2013). Trait-based approaches to zooplankton communities. *Journal of Plankton Research*, *35*, 473–484. https://doi.org/10.1093/plankt/fbt019

Locarnini, R. A., Mishonov, A. V., Antonov, J. I., Boyer, T. P., Garcia, H. E., Baranova, O. K., … Seidov, D. (2013). World Ocean Atlas 2013, Volume 1: Temperature. *NOAA Atlas NESDIS*, *73*, 1–40. https://doi.org/10.7289/V55X26VD

Lombard, F., Labeyrie, L., Michel, E., Bopp, L., Cortijo, E., Retailleau, S., … Jorissen, F. (2011). Modelling planktic foraminifer growth and distribution using an ecophysiological multi-species approach. *Biogeosciences*, *8*, 853–873. https://doi.org/10.5194/bg-8-853-2011

Marchant, M., Hebbeln, D., Giglio, S., Coloma, C., & Gonzalez, H. E. (2004). Seasonal and interannual variability in the flux of planktic foraminifera in the Humboldt Current System off central Chile (30 S). *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*, 2441–2455. https://doi.org/10.1016/j.dsr2.2004.08.013

Marchant, M., Hebbeln, D., & Wefer, G. (1998). Seasonal flux patterns of planktic foraminifera in the Peru-Chile Current. *Deep Sea Research Part I: Oceanographic Research Papers*, *45*, 1161–1185. https://doi.org/10.1016/S0967-0637(98)00009-0

Marshall, C. R., & Quental, T. B. (2016). The uncertain role of diversity dependence in species diversification and the need to incorporate time–varying carrying capacities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150217. https://doi.org/10.1098/rstb.2015.0217

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, *13*, 1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

McGillicuddy, D. J. Jr (2016). Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale. *Annual Review of Marine Science*, *8*, 125–159. https://doi.org/10.1146/annurev-marine-010814-015606

Meyer, J. R., & Kassen, R. (2007). The effects of competition and predation on diversification in a model adaptive radiation. *Nature*, *446*, 432–435. https://doi.org/10.1038/nature05599

Moen, D., & Morlon, H. (2014). Why does diversification slow down? *Trends in Ecology and Evolution*, *29*, 190–197. https://doi.org/10.1016/j.tree.2014.01.010

Mohiuddin, M. M., Nishimura, A., Tanaka, Y., & Shimamoto, A. (2002). Regional and interannual productivity of biogenic components and planktonic foraminiferal fluxes in the northwestern Pacific Basin. *Marine Micropaleontology*, *45*, 57–82. https://doi.org/10.1016/S0377-8398(01)00045-7

Northcote, L. C., & Neil, H. L. (2005). Seasonal variations in foraminiferal flux in the Southern Ocean, Campbell Plateau, New Zealand. *Marine Micropaleontology*, *56*, 122–137. https://doi.org/10.1016/j.marmicro.2005.05.001

Pearse, W. D., Purvis, A., Cavender-Bares, J., & Helmus, M. R. (2014). Metrics and models of community phylogenetics. In L. Z. Garamszegi (Ed.), *Modern phylogenetic comparative methods and their application in evolutionary biology* (pp. 451–464). Heidelberg, Germany: Springer-Verlag.

Pearson, P. N., Shackleton, N., & Hall, M. (1997). Stable isotopic evidence for the sympatric divergence of *Globigerinoides trilobus* and *Orbulina universa* (planktonic Foraminifera). *Journal of the Geological Society*, *154*, 295–302. https://doi.org/10.1144/gsjgs.154.2.0295

Phillimore, A. B., & Price, T. D. (2008). Density-dependent cladogenesis in birds. *PLoS Biology*, *6*, e71. https://doi.org/10.1371/journal.pbio.0060071

Pigot, A. L., & Etienne, R. S. (2015). A new dynamic null model for phylogenetic community structure. *Ecology Letters*, *18*, 153–163. https://doi.org/10.1111/ele.12395

Pigot, A. L., Phillimore, A. B., Owens, I. P., & Orme, C. D. L. (2010). The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Systematic Biology*, *59*, 660–673. https://doi.org/10.1093/sysbio/syq058

Pires, M. M., Silvestro, D., & Quental, T. B. (2017). Interactions within and between clades shaped the diversification of terrestrial carnivores. *Evolution*, *71*, 1855–1864. https://doi.org/10.1111/evo.13269

Poore, R. Z., Tedesco, K. A., & Spear, J. W. (2013). Seasonal flux and assemblage composition of planktic foraminifers from a sediment-trap study in the Northern Gulf of Mexico. *Journal of Coastal Research*, *63*, 6–19. https://doi.org/10.2112/SI63-002.1

R Core Team. (2017) *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org

Rabosky, D. L. (2013). Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 481–502. https://doi.org/10.1146/annurev-ecolsys-110512-135800

Rebotim, A., Voelker, A. H., Jonkers, L., Waniek, J. J., Meggers, H., Schiebel, R., … Kucera, M. (2017). Factors controlling the depth habitat of planktonic foraminifera in the subtropical eastern North Atlantic. *Biogeosciences*, *14*, 827–859. https://doi.org/10.5194/bg-14-827-2017

Rigual-Hernandez, A. S., Sierro, F. J., Barcena, M. A., Flores, J. A., & Heussner, S. (2012). Seasonal and interannual changes of planktic foraminiferal fluxes in the Gulf of Lions (NW Mediterranean) and their implications for paleoceanographic studies: Two 12-year sediment trap records. *Deep Sea Research Part I: Oceanographic Research Papers*, *66*, 26–40. https://doi.org/10.1016/j.dsr.2012.03.011

Rillo, M. C., Miller, C. G., Kucera, M., & Ezard, T. H. G. (2019). *Supplementary Material: Predictability of intraspecific size variation in extant planktonic foraminifera*. Natural History Museum Data Portal (data.nhm.ac.uk), https://doi.org/10.5519/0056541

Rosindell, J., Hubbell, S. P., & Etienne, R. S. (2011). The unified neutral theory of biodiversity and biogeography at age ten. *Trends in Ecology and Evolution*, *26*, 340–348. https://doi.org/10.1016/j.tree.2011.03.024

Sauterey, B., Ward, B., Rault, J., Bowler, C., & Claessen, D. (2017). The implications of eco-evolutionary processes for the emergence of marine plankton community biogeography. *The American Naturalist*, *190*, 116–130. https://doi.org/10.1086/692067

Schiebel, R. (2002). Planktic foraminiferal sedimentation and the marine calcite budget. *Global Biogeochemical Cycles*, *16*, 1065. https://doi.org/10.1029/2001GB001459

Schiebel, R., & Hemleben, C. (2005). Modern planktic foraminifera. *Paläontologische Zeitschrift*, *79*, 135–148. https://doi.org/10.1007/BF03021758

Schmidt, D. N., Renaud, S., Bollmann, J., Schiebel, R., & Thierstein, H. R. (2004). Size distribution of Holocene planktic foraminifer assemblages: Biogeography, ecology and adaptation. *Marine Micropaleontology*, *50*, 319–338. https://doi.org/10.1016/S0377-8398(03)00098-7

Sexton, P. F., & Norris, R. D. (2008). Dispersal and biogeography of marine plankton: Long-distance dispersal of the foraminifer *Truncorotalia truncatulinoides*. *Geology*, *36*, 899–902. https://doi.org/10.1130/G25232A.1

Siccha, M., & Kucera, M. (2017). ForCenS, a curated database of planktonic foraminifera census counts in marine surface sediment samples. *Scientific Data*, *4*, 170109. https://doi.org/10.1038/sdata.2017.109

Takagi, H., Kimoto, K., Fujiki, T., Saito, H., Schmidt, C., Kucera, M., & Moriya, K. (2019). Characterizing photosymbiosis in modern planktonic foraminifera. *Biogeosciences Discussions* (accepted, in press), *2019*, 1–32. https://doi.org/10.5194/bg-2019-145

Tedesco, K. A., & Thunell, R. C. (2003). Seasonal and interannual variations in planktonic foraminiferal flux and assemblage composition in the Cariaco Basin, Venezuela. *Journal of Foraminiferal Research*, *33*, 192–210. https://doi.org/10.2113/33.3.192

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, *466*, 1098–1101. https://doi.org/10.1038/nature09329

Ulrich, W., & Gotelli, N. J. (2010). Null model analysis of species associations using abundance data. *Ecology*, *91*, 3384–3397. https://doi.org/10.1890/09-2157.1

Voje, K. L., Holen, Ø. H., Liow, L. H., & Stenseth, N. C. (2015). The role of biotic forces in driving macroevolution: Beyond the Red Queen. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20150186. https://doi.org/10.1098/rspb.2015.0186

Wan, S., Jian, Z., Cheng, X., Qiao, P., & Wang, R. (2010). Seasonal variations in planktonic foraminiferal flux and the chemical properties of their shells in the southern South China Sea. *Science China Earth Sciences*, *53*, 1176–1187. https://doi.org/10.1007/s11430-010-4039-3

Wang, S., Chen, A., Fang, J., & Pacala, S. W. (2013). Speciation rates decline through time in individual-based models of speciation and extinction. *The American Naturalist*, *182*, E83–E93. https://doi.org/10.1086/671184

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Weber, M. G., Wagner, C. E., Best, R. J., Harmon, L. J., & Matthews, B. (2017). Evolution in a community context: On integrating ecological interactions and macroevolution. *Trends in Ecology and Evolution*, *32*, 291–304. https://doi.org/10.1016/j.tree.2017.01.003

Weiner, A. K., Weinkauf, M. F., Kurasawa, A., Darling, K. F., Kucera, M., & Grimm, G. W. (2014). Phylogeography of the tropical planktonic foraminifera lineage *Globigerinella* reveals isolation inconsistent with passive dispersal by ocean currents. *PLoS ONE*, *9*, e92148. https://doi.org/10.1371/journal.pone.0092148

Weinkauf, M. F., Kunze, J. G., Waniek, J. J., & Kucera, M. (2016). Seasonal variation in shell calcification of planktonic foraminifera in the NE Atlantic reveals species-specific response to temperature, productivity, and optimum growth conditions. *PLoS ONE*, *11*, e0148363. https://doi.org/10.1371/journal.pone.0148363

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., … Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*, 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Yackulic, C. B. (2017). Competitive exclusion over broad spatial extents is a slow process: Evidence and implications for species distribution modeling. *Ecography*, *40*, 305–313. https://doi.org/10.1111/ecog.02836

Yasuhara, M., Hunt, G., Dowsett, H. J., Robinson, M. M., & Stoll, D. K. (2012). Latitudinal species diversity gradient of marine zooplankton for the last three million years. *Ecology Letters*, *15*, 1174–1179. https://doi.org/10.1111/j.1461-0248.2012.01828.x

Yasuhara, M., Tittensor, D. P., Hillebrand, H., & Worm, B. (2017). Combining marine macroecology and palaeoecology in understanding biodiversity: Microfossils as a model. *Biological Reviews*, *92*, 199–215. https://doi.org/10.1111/brv.12223

Yoder, J. B., & Nuismer, S. L. (2010). When does coevolution promote diversification? *The American Naturalist*, *176*, 802–817. https://doi.org/10.1086/657048

BIOSKETCH

Marina C. Rillo is a biologist interested in community ecology and macroevolution, and developed this research during her PhD studies. She is currently a postdoctoral fellow using microfossils as a model system to investigate biodiversity change across different time scales.

SUPPORTING INFORMATION

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

How to cite this article: Rillo MC, Sugawara MTC, Cabella B, et al. On the mismatch in the strength of competition among fossil and modern species of planktonic Foraminifera. *Global Ecol Biogeogr*. 2019;00:1–13. https://doi.org/10.1111/geb.13000