# How consistent are macroevolutionary and community ecology patterns of interspecific competition?

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**Abstract**

A key ecological mechanism proposed to explain the lack of exponential diversification rates in the fossil record is competition among species. Under such a diversity dependent model, speciation rate declines with increasing standing species richness. However, if interspecific competition is an important driver of long-term evolution, we should expect competition to also structure modern communities. Two community-level patterns would support interspecific competition: (1) if species distributions result from competitive exclusion, we expect a pattern of allopatric species ranges. Alternatively, (2) if species coexist but still compete, we expect a negative correlation among species' abundances through time. We used 35 population-level time-series encompassing 33 of the 47 extant species of the planktonic foraminifera clade. These time-series have mean length of 60 assemblage samples collected globally from sediment traps. We defined species pairs based on shell size and aspect ratio, and expected the most morphologically similar pairs to compete more strongly for resources than two randomly selected ones. Using co-occurrence analysis, we rejected the allopatric species ranges pattern since most species co-occur. Species' abundances correlated more positively than negatively through time and no difference was found between morphologically similar species pairs and other pairs. Restricting analysis to the highest resolution time-series, we used Empirical Dynamical Models (EDM) that seeks to distinguish causality from correlation among species abundances time-series, considering seawater temperature time-series as well. The EDMs showed no causality between species time-series, and species continue to correlate positively even when considering temperature changes. In summary, we found no evidence of within-clade interspecific competition driving planktonic foraminifera population dynamics. There is thus a mismatch between the processes inferred from shorter-term ecological patterns and those inferred from simplistic interpretations of macroevolutionary diversity dependence, especially when models fail to acknowledge that the changing biotic and abiotic environment alters the outcome of interspecific interactions.

# 1 Introduction

The interplay of ecological and evolutionary processes is central to our understanding of biodiversity patterns. This connection is well accepted, but we still lack a powerful theory for how population-level processes scales up to clade-level dynamics, and vice versa [7, 13]. One of the main reason this integration is still missing, is because community ecology and macroevolutionary patterns differ in temporal, spatial and taxonomic scales (Jablonski 2008, Weber 2017 and more refs). Community ecology, on the one hand, focusses on local and regional processes, happening along the life-span of individual organisms (which could range from hours to decades). The community is defined taxonomically as the species that co-occur in space and time, and therefore includes species from distantly related clades, from unicellular bacteria and protists to multicellular funghi, animal and plants. Macroevolution, on the other hand, focusses on processes that affect the diversification of species. The time scale is millions of years, scaled to the "life-span" of species, and the spatial scale encompasses species' ranges, which can be global. Moreover, macroevolution studies usually focus on monophyletic clades, and therefore species that share more recent evolutionary (and are taxonomically closer) when compared to species that live together in a community.

Although community ecology and macroevolution describe and seek to understand patterns at different scales, the processes generating these patterns are fundamentally linked through eco-evolutionary feedbacks. Ecological interactions, which happen at the community scale, are known to shape species' population dynamics (ref), alter natural selection (ref), and impact trait evolution (ref) and lineage diversification (DDD refs and others). Species evolution and diversification, in turn, respond to the changing environment and affect how species interact with the environment and with each other (refs, and more examples). Even knowing that both abiotic and biotic factors play key role in community dynamics and clade diversification, the different scales of the observed patterns makes it hard to test hypothesis relevant to both fields. A promising avenue of research, however, includes contrasting predictions from accepted theories within macroevolution and ecology [12].

Within macroevolution theory, there is the hypothesis that higher levels of diversity tend to suppress rates of diversification (negative diversity-dependence diversification, DDD) (Sepkoski 1978; for a recent debate read: Harmon and Harrison 5 and Rabosky et al. 11). DDD is used to describe both a pattern and a process within macroevolution [10]. As a pattern, DDD describes a clade's bounded diversity trajectory through time (observed in the fossil record: Sepkoski 1978; Ezard 2011, 2016; and inferred from molecular filogenies: refs) and/or a negative relationship between standing taxonomic richness and rates of diversification across a clade's history (Foote 2018, Alroy, Quental). As a process, DDD is usually thought to reflect competition among ecologically similar species and the filling of niche space (refs, but see Moen and Morlon TREE). This mechanism also explains species richness rebounds after mass extinctions events (refs), and has been tested by comparing predictions of the DDD and alternative diversification models, including models in which diversification is a function of temperature and rock sedimentation (Ezard 2016, Silvestro PNAS?, achar mais - ver filogenias molecular)(include Marshall and Quental 2016 somewhere). Although the DDD patterns and models evoke competition among

species, they do not explicitly test it, neither reveal how biotic interactions generated them [7]. Explicitly testing for biotic interactions in the fossil record requires not only a high resolution fossil record (to get closer to temporal scales of community dynamics), but also an actual fossilized interaction proxy, both of which are so rare that until today only one study exists (Liow 2016 PRSB).

To generate more mechanistic models of DDD, we need a better understanding of how and under what geographical and environmental circumstances species affect each others' diversification rates (i.e., speciation minus extinction rates) [13]. Competitive interactions happen at the individual level. By competing with each other, individuals shape the dynamics of their populations and communities. Population dynamics, in turn, is directly linked to species' abundance and geographical range. And both, species' abundance and geographical range, influences species' diversification rates (Harnik 2011 PNAS, more refs). At the community ecology scale, clade-wide interspecific competition is also hard to test, because you would need geographical and temporal data on population abundances of all (or most) species within a clade. Since it is hard to explicitly test for ecological interactions in the fossil record and observe clade-wide community dynamics, the empirical basis for an integration between community ecology and macroevolution theories has thus far been limited (e.g. molluscs; Jablonski et al., 2003, 2013).

Planktonic foraminifera (PF) represent a useful model system for such an integrative research (Yasuhara 2015 Bio Rev). PF are rhizarian protist that build a calcite shell, featuring the most complete fossil record of the Cenozoic Era currently known [9, 3]. Besides their simple morphology grants them a mature taxonomy, and the extant species are confirm by molecular studies (refs), although some morphospecies might encompass more than one genetic distinct type (cryptic species, refs). PF excellent fossil record has been used to test the DDD model. PF speciation rates along the Cenozoic depend on the number of species present at the time, suggesting interspecific competition affects speciation [3]. More recently, [4] showed that the diversification of the PF Cenozoic clade is regulated by competition among species, the strength of which varies through time as a function of environmental change. They invoke niche saturation and competition among species as the underlying mechanisms driving the DDD pattern ,but without explicitly testing for it in the fossil record. Indeed it is yet not possible to test for PF ecological interactions in the fossil record, because of our lack of understanding of their population dynamics and ecology. However, PF species live today as zooplankton in the marine pelagic environment, and their low diversity (46 extant morphospecies) allows a clade-wide study of their community dynamics. We can expect that, if competition is an important process of PF evolution, competition would also be an important ecological interaction among living PF species.

To test for interspecific competition in modern PF asseblages (obs: check use of population, community and assemblage), we analysed PF assemblage data spatially using 4177 assemblage counts around the world's oceans and temporally using 35 time-series collected globally from sediment traps. The essence of interspecific competition is that individuals of one species suffer a reduction in fecundity, growth or survivorship as a result of resource exploitation or interference by individuals of another species [2]. This way, competition among individuals affects the population dynamics of the competing species, and these dynamics then influence the species' distributions and diversification. Two pat-

ters could emerge as ecological effects of interspecific competition: *(i)* species may be eliminated from a habitat by competition from individuals of other species, resulting in a pattern of non-overlapping species' ranges (i.e. allopatry); or, if competing species coexist, *(ii)* individuals of at least one of them suffer reductions in abundance due to the presence of the other, leading to a pattern of negative correlation of abundances through time. Sister species are morphogically similar (Supp Info - phylogenetic signal of shell size), thus we assume sister species pairs are ecologically more similar, and therefore compete more strongly, than randomly chosen species pairs.

EDM paragraph (correlation of time-series does not imply causality).

Here we analyse clade-wide population dynamics of living planktonic foraminifera species using spatial and temporal data to determine how populations of different species interact across their ranges and through ecological time. Given the PF diversity-dependent dynamics in their fossil record [3, 4], we expect interspecific competition to play a key role in structuring modern PF communities.

# 2 Methods

## 2.1 Sediments trap data

Sediments traps consist of an upward-facing funnel that directs sinking organic and inorganic particulate material towards a sampling bottle (Fig. 1). Traps are moored at a specific depth in the water column (usually below the euphotic zone or mixed layer) and anchored to a particular location. Each trap usually contains several collecting bottles to record the changes in sinking flux with time, typically at the resolution of weeks. Therefore, sediment traps provide continuous time series of settling foraminiferal shell fluxes (expressed as number of shells per $m^2$ per day).

Shell fluxes represent the settling of dead foraminifera and are strictly speaking not directly a measure of abundance of foraminifera in the water column [8]. However, given the short life span of foraminifera (typically one month [6]), the fluxes are likely to be a good proxy for populational abundance. Moreover, to be able to compare fluxes of different species, we assume that species have similar life spans. This means that similar fluxes (i.e. species dying synchronously) indicate that species grow and reach different life stages (juvenile, adults) also synchronously.

We used the data of 35 globally distributed moored sediment trap time series (Fig. 2, compiled by Jonkers and Kučera 8). All the traps have duration of at least one year; and traps 36 and 37 were excluded from this study because they contain only one polar species. Further information about each trap (*e.g.* location, resolution, total period of sampling) can be found in Table 1. Figure 3 shows an example of the data gathered by trap no.1 in the North Atlantic.

## 2.2 Co-occurrence of species

To test whether species overlap in their ranges, I simply recorded whether two species were sampled at the same time in the same sediment trap, or whether they were never found together in the same collecting bottle. If species were sampled together at least once, they co-occur (live in sympatry).

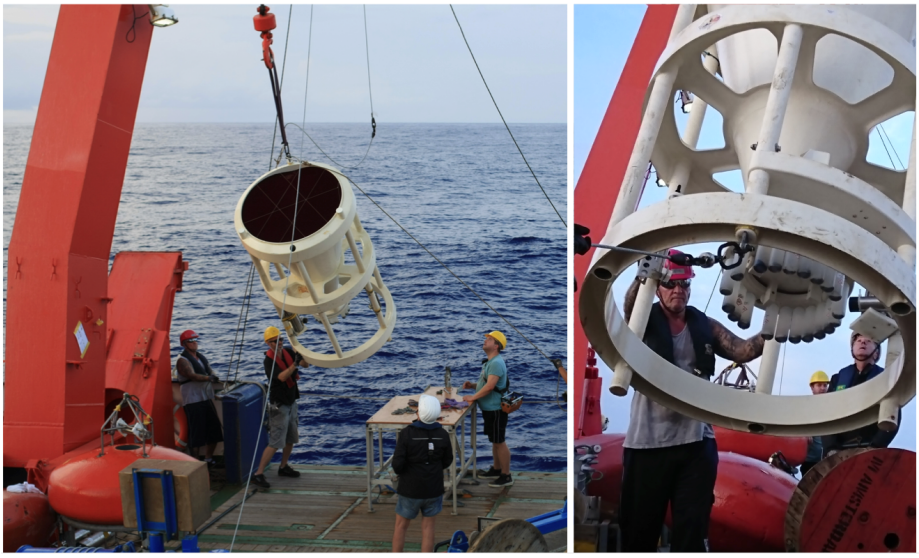

Figure 1: Recovery of sediment trap during the German Research Cruise M140 in the North Atlantic, crew in the *RV* Meteor, August 2017. **Left**: sediment trap has a sampling area of $1m^2$, **Right**: 20 bottles with samples, note the four missing bottles.

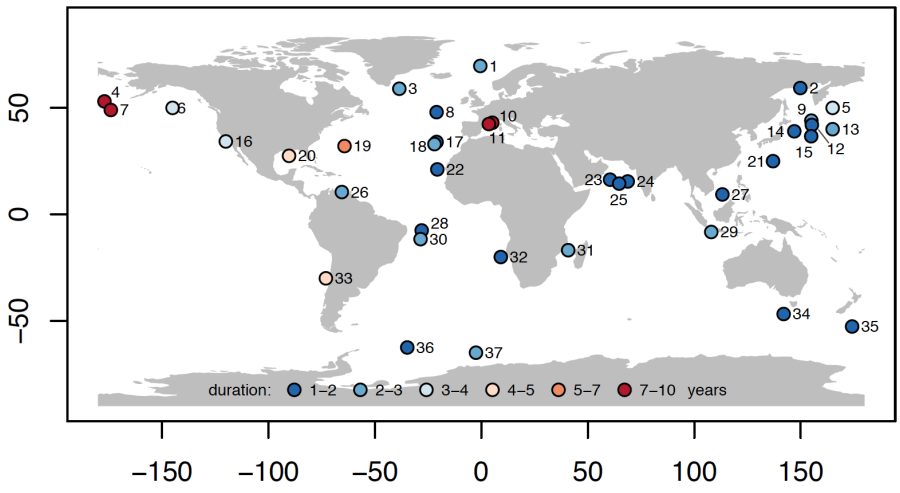


Figure 2: Distribution and total duration of sediment trap time series used in this study. Figure taken from [8]. Traps 36 and 37 were excluded from this study because they contain only one species.

Table 1: Meta-data of sediment traps taken from [8]. Columns: **Trap number** as in Figure 2; **Trap name**; Coordinates (**Lat, Lon**); **resolution**: mean period (in days) that each sample (bottle) in the trap was open; **length days**: total period trap was open (in days); **length years**: total period in years; **length series**: total number of samples collected in each trap (length of the time-series); **from, to**: year interval when trap was active; **all ssp**: whether all species were identified in each trap, "NO" means that just dominant species were picked.

| Trap no. | Trap name | Lat | Lon | resolution days | length days | length years | length series | from | to | all ssp |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | NB67 | 69.69 | -0.47 | 18.20 | 787 | 2.20 | 32 | 1991 | 1993 | YES |
| 2 | OKH | 59.32 | 149.83 | 16.40 | 365 | 1.00 | 21 | 1990 | 1991 | YES |
| 3 | IRM | 59.00 | -38.50 | 16.00 | 1372 | 3.80 | 58 | 2003 | 2007 | NO |
| 4 | AB | 53.05 | -177.00 | 26.90 | 3264 | 8.90 | 105 | 1990 | 1999 | NO |
| 5 | PAC50 | 50.00 | 165.00 | 15.50 | 1287 | 3.50 | 69 | 1997 | 2001 | NO |
| 6 | PAPA | 50.00 | -145.00 | 12.80 | 1437 | 3.90 | 82 | 1982 | 1986 | NO |
| 7 | SA | 49.00 | -174.00 | 26.80 | 3267 | 9.00 | 101 | 1990 | 1999 | NO |
| 8 | JGOFS48 | 48.00 | -21.00 | 12.80 | 377 | 1.00 | 26 | 1989 | 1990 | YES |
| 9 | PACKNOT | 44.00 | 155.00 | 15.40 | 893 | 2.40 | 52 | 1997 | 2000 | NO |
| 10 | LIP | 43.02 | 5.18 | 27.80 | 4457 | 12.20 | 116 | 1993 | 2006 | YES |
| 11 | LIL | 42.41 | 3.54 | 22.50 | 4167 | 11.40 | 151 | 1993 | 2005 | YES |
| 12 | WCT6 | 42.01 | 155.24 | 19.10 | 381 | 1.00 | 19 | 1999 | 2000 | YES |
| 13 | PAC40 | 40.00 | 165.00 | 16.50 | 952 | 2.60 | 44 | 1997 | 2000 | NO |
| 14 | WCT2 | 39.00 | 147.00 | 14.20 | 628 | 1.70 | 40 | 1997 | 1999 | PROB |
| 15 | WCT7 | 36.69 | 154.94 | 18.80 | 375 | 1.00 | 19 | 1999 | 2000 | PROB |
| 16 | SBB | 34.25 | -120.00 | 10.90 | 2144 | 5.90 | 93 | 1993 | 1999 | NO |
| 17 | JGOFS34 | 34.00 | -21.00 | 12.80 | 377 | 1.00 | 26 | 1989 | 1990 | YES |
| 18 | L1 | 33.00 | -22.00 | 21.80 | 767 | 2.10 | 35 | 2002 | 2004 | YES |
| 19 | BATS | 32.08 | -64.25 | 58.60 | 2232 | 6.10 | 31 | 1978 | 1984 | PROB |
| 20 | GOM | 27.50 | -90.30 | 7.30 | 2245 | 6.20 | 238 | 2008 | 2014 | NO |
| 21 | WCT1 | 25.00 | 137.00 | 14.10 | 612 | 1.70 | 37 | 1997 | 1999 | PROB |
| 22 | CB | 21.13 | -20.67 | 17.90 | 753 | 2.10 | 38 | 1989 | 1991 | NO |
| 23 | WAST | 16.32 | 60.47 | 13.30 | 529 | 1.40 | 38 | 1986 | 1987 | YES |
| 24 | EAST | 15.47 | 68.75 | 11.70 | 527 | 1.40 | 38 | 1986 | 1987 | YES |
| 25 | CAST | 14.47 | 64.75 | 12.20 | 516 | 1.40 | 32 | 1986 | 1987 | YES |
| 26 | CAR | 10.50 | -65.50 | 12.40 | 1089 | 3.00 | 75 | 1997 | 1999 | NO |
| 27 | SCS | 9.38 | 113.23 | 29.10 | 663 | 1.80 | 22 | 2004 | 2006 | NO |
| 28 | WA3 | -7.52 | -28.00 | 24.00 | 499 | 1.40 | 20 | 1993 | 1994 | NO |
| 29 | JAM | -8.25 | 108.00 | 16.20 | 983 | 2.70 | 56 | 2000 | 2003 | PROB |
| 30 | WAB | -11.60 | -28.53 | 23.80 | 1001 | 2.70 | 38 | 1997 | 1999 | NO |
| 31 | MOZ | -16.80 | 40.80 | 20.90 | 862 | 2.40 | 39 | 2003 | 2006 | NO |
| 32 | WR23 | -20.00 | 9.16 | 17.70 | 751 | 2.10 | 28 | 1989 | 1991 | NO |
| 33 | COQ | -30.00 | -73.00 | 8.80 | 2679 | 7.30 | 159 | 1994 | 2001 | NO |
| 34 | SAZ47 | -46.75 | 142.00 | 10.60 | 493 | 1.40 | 40 | 1997 | 1999 | PROB |
| 35 | CP | -52.62 | 174.15 | 8.80 | 425 | 1.20 | 42 | 1998 | 1999 | NO |

## 2.3 Correlation of time-series

For the species that did co-occur, we tested whether their changes in abundances are positively or negatively correlated through time. To record the change in species abundances from one time step to the next, we calculated the first differences of each time-series. Additionally, this method reduces the time-series autocorrelation. First differences were not calculated for consecutive samples between which there was a sampling gap of more than 10 days. The reason is that if the sediment trap did not sample for a specific period (*e.g.* a collecting bottle was lost), there was no recording of the abundance flux for that period, and thus the first difference of the two adjacent samples does not record the change in abundance from one time-step to the next.

Next, for each trap, we calculated for each species pair the non-parametric Kendall correlation of the differentiated series (for example, Fig. 3 for trap no.1). This correlation does not rely on any assumptions on the distributions of the time-series (Note: Pearson and Spearman correlations show similar overall results).

Finally, we wanted to see the overall species abundances patterns for all 35 sediment traps, noting that species can behave differently in different environments (sediment traps). For each species pair, we calculated the proportion of significant positive and negative correlations considering the total number of sediment traps they both co-occurred.

## 2.4 Empirical dynamic modelling and convergent cross mapping of the Gulf of Mexico sediment trap

### 2.4.1 Gulf of Mexico sediment trap

The Gulf of Mexico (GoM, 27.5N -90.3E (= 269.7), REF) sediment trap has the best resolution of all the sediment traps compiled by [8]. The resolution is one community sample every 7 days (*i.e.* each sample represents the accumulation of foraminifera shells of the previous week). The total length of the GoM time-series is 238 samples, spanning over 2245 from 14th January 2008 to 8th March 2014.

### 2.4.2 Temperature for the Gulf of Mexico sediment trap

I used the dataset NOAA 1/4o daily Optimum Interpolation Sea Surface Temperature (or daily OISST, AVHRR-Only) [1]. We used the temperature data point of coordinates (lon 269.625 lat 27.625) 15,76 km away from the sediment trap.

I calculated the mean of the daily temperature for each sampling interval. The NOAA dataset has the temperature values in Kelvin, the Celcius column was created subtracting 273.15 from the Kelvin values.

### 2.4.3 Empirical dynamic modelling and convergent cross mapping

Empirical dynamic modelling (EDM) and convergent cross mapping (CCM), R package rEDM.

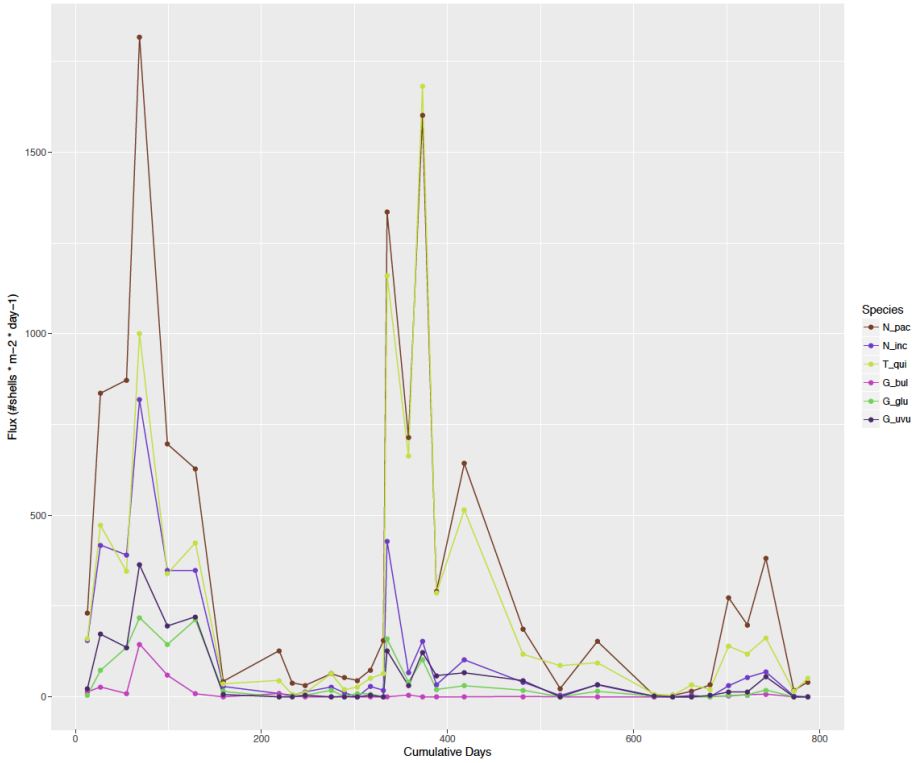


Figure 3: Example of data from trap no.1 (named NB67), colors represent species. This trap was active for 787 days, samples were taken in average every 18.2 days, with a total of 32 samples (Table 1)

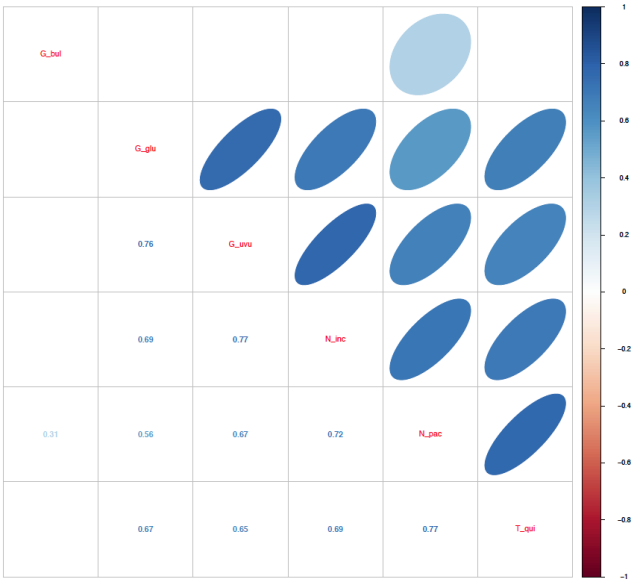


Figure 4: Pair-wise Kendall correlation plot of first differences of time-series from Trap no.1 (NB67, Fig.3). Lower triangular matrix shows the correlation values and upper triangular matrix shows a representation of the correlation in form of elipses. R package corrplot [14].

# 3 Results

## 3.1 Co-occurrence of species

The majority of species co-occur (Fig. 5). The species that often do not co-occur with other species are rare species (*i.e.* present in less than 5% of the samples). PF float passively in the highly-connected pelagic environment, thus we expected most PF species to co-occur.

- How many times and where do species co-occur? Build a co-occurrence matrix based on frequency of co-occurrences (instead of just single-tons 0 and 1 as in Fig 5).
- Strength of the co-occurrence resolution sediment trap (2 months open, everybody co-occurs)
- Take depth habitat into account. Species may fall in the same sediment trap (sympatry here) but actually live in different depths of the water column (and thus in allopatry).
- Take cryptic (genetic) species biogeography into account. Some genetic types show allopatric geographical patterns. Maybe competition acts at this level?

### 3.1.1 Problems

Null model: it is hard to build a null model of plankton spatial distribution, especially taking abundance into account (instead of just presence/absence). Many of the environmental variables covary and ocean currents have to be taken into account.

## 3.2 Correlation of time-series

The majority of the correlations between species pairs were positive (Fig. 6)

- Strength of the correlation  resolution sediment trap (2 months open, everybody co-occurs)
- Calculate correlations of one species against all other species in the community (instead of just pairs of species)
- How do the patterns change when doing this for relative abundances (as in the fossil record)?
- Are the species with higher abundances in the time-series always the same? (are they always the "winners"?)

### 3.2.1 Problems

How to test if this overall positive correlation is not expected due to, for example, phytoplankton seasonality? How to build a null model of abundances time-series? My idea would be to somehow take out the variance explained by environmental data (temperature and primary productivity) and then try to correlate the residuals.

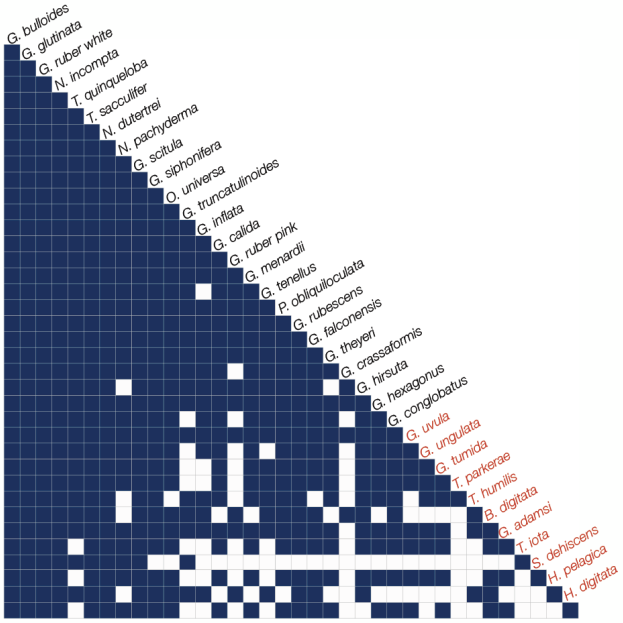


Figure 5: Co-occurrence matrix. In blue: species that co-occurred at least in one samples. The species names are positioned to indicate the columns and rows that represent their pairwise co-occurrence with other species. The matrix is clustered accordingly to the incidence of species on the samples; rarely sampled species are shown in red and were found in less than 5% of the total samples.

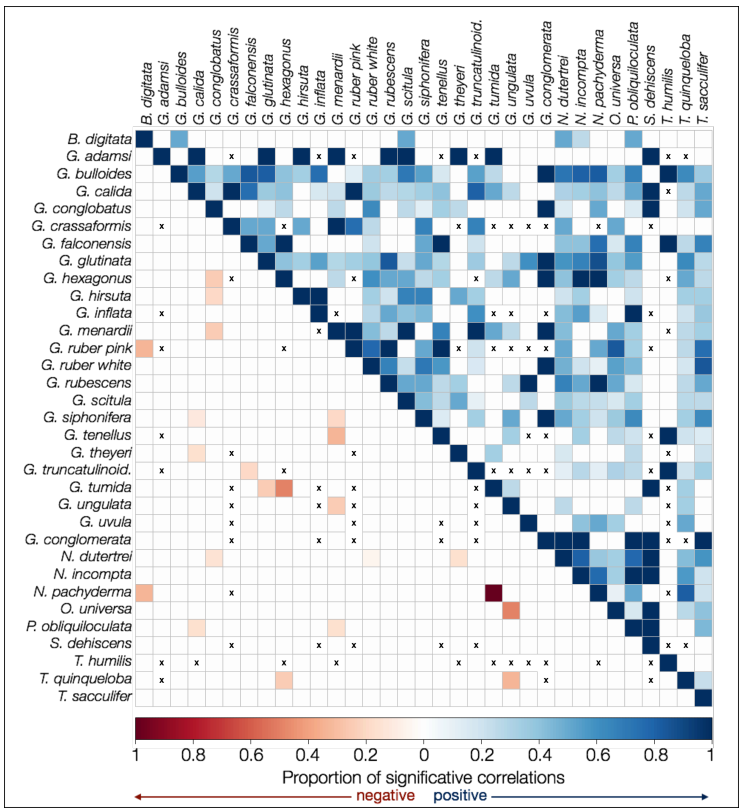


Figure 6: Proportion of significant positive (upper triangle, blue) and negative (lower triangle, red) correlations between first differences of time-series in which both species occur. White squares represent species pairs that co-occur but showed no significant positive and/or negative correlation. The black crosses indicate species pairs that did not co-occur.

# 4 Discussion

We found no evidence for interspecific competition structuring planktonic foraminifera communities. Thus there seems to be a mismatch between the processes inferred from macroevolutionary patterns over deep time and those inferred from ecological patterns observed in a shorter time scale. This means that either macroevolutionary processes are different than the current the ecological processes, or that interspecific competition might not be the mechanism underlying the patterns seen in the fossil record.

Scale problem: competition takes time, competition at ecological scales might generate diversification at evolutionary scales. Intraspecific competition promotes diversification theoretically (Doebeli, adaptive dynamics) and experimentally (Bailet et al. 2013 bacteria, increased richness, increased diversification; check david's intro as well) - what about interspecific competition? Niche partitioning / specialization first step to species diversification Jablonski 2008: competition at the community scale might not have negative impact at the macroevolutionary scale.

A promising avenue of research, however, includes contrasting predictions from relevant theories within ecology and macroevolution, as well as embracing both abiotic and biotic proxies while modelling long-term evolutionary data [12]. Biotic and abiotic affects population dynamics.

An important shortcoming of microfossils, for example compared to molluscs, is insufficient knowledge of their basic biology and natural history. Yet this current weakness is balanced by some distinctive strengths of the microfossils record, such as high abundance, large spatio-temporal coverage, and good taxonomic and temporal resolution (Yasuhara 2015).

Planktonic foraminifera (PF) unique fossil record has been used to test the diversity-dependent diversification model. PF speciation rates along the Cenozoic depend on the number of species present at the time, and decline as the number of species increases (DDD pattern), whereas extinction rate was driven largely by climate [3]. More recently, [4] showed that the diversification of the PF Cenozoic clade is regulated by competition among species, the strength of which varies through time as a function of environmental change. They invoke niche saturation and within-clade interspecific competition as the underlying mechanisms driving the DDD pattern without explicitly testing for it in the fossil record (because it is not possible actually).

A group may have more potential for coexistence among close relatives simply because that lineage has been present in that area for a longer amount of time.

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