Diversity-dependent diversification: but do modern planktonic foraminifera actually compete?

Marina C. Rillo, Lukas Jonkers, Michal Kucera & Thomas Ezard

October 11, 2017

1 Introduction

Macroevolution seeks to understand patterns and processes of species diversification. The fossil record and, more recently, time-calibrated molecular phylogenies are used to characterize the diversification dynamics of clades and to estimate the per-lineage diversification rate (*i.e.* speciation minus extinction rate). However, the inferences that can be drawn from molecular phylogenies are limited, as they include solely living clades and thus lack information about extinct lineages [7]. The fossil record is therefore crucial to access the true diversity trajectories of clades, but unfortunately only few taxa display sufficient taxonomic and temporal resolution to document speciation and extinction along lineages in deep time.

Planktonic foraminifera (PF) are unicellular marine zooplankton with a global distribution and about 45 extant morphospecies [6]. PF build a calcite shell, which rapidly sinks after the death of the organism [6]. Consequently, PF have arguably the most complete fossil record of the Cenozoic Era [6]. This fossil record allows us to investigate in a unique way the processes underlying diversification patterns. In 2011, Ezard and collaborators [2] used the PF fossil record and data from both abiotic (oxygen isotopic composition of deep-sea carbonates) and biotic (species diversity and morphology) proxies to investigate which factor is the strongest driver of changes in speciation and extinction rates. They concluded that speciation rates depend more on the number of species present at the time, and decline as the number of species increases, whereas extinction was driven largely by climate [2]. More recently, Ezard & Purvis [3] 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.

These studies suggest that as the number of species within a region and using a particular set of ecological resources increases, then the opportunity for new species to originate and persist declines (*i.e.* diversity-dependent diversification). They invoke niche saturation and interspecific competition as underlying mechanisms driving macroevolutionary patterns, but they do not explicitly test for them. Indeed, it is yet not possible to observe PF species interactions in the fossil record. However, interspecific competition happens at the community

level, and thus an integration of the field of community ecology and macroevolution brings us closer to a more mechanistic understanding of the processes underlying biodiversity patterns across time and space [9]. A way forward to a theoretical integration of these fields is to contrast observations and predictions from macroevolution and community ecology studies and thus reduce the micro- and macroevolutionary divide [8].

Here we analyse planktonic foraminifera population dynamics from spatial and temporal data to determine how populations of different species interact across their ranges and through ecological time. If competition among species is an important driver of PF evolution [2, 3], we expect that interspecific competition would also be a strong structuring force of modern PF communities. 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 [1]. This competition among individuals affects the population dynamics of the competing species, and these dynamics then influence the species' distributions and diversification. Two patters 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. To test these two predictions, we analysed PF assemblage data spatially and temporally using 35 time-series collected globally from sediment traps.

2 Methods

2.1 Sediments trap data

Sediments traps consist of an upward-facing funnel that directs sinking 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 a resolution of weeks. Therefore, sediment traps provide continuous time series of settling foraminiferal shell fluxes (no. 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 [5]. However, given the short life span of foraminifera (typically one month [4]), 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 [5]. 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

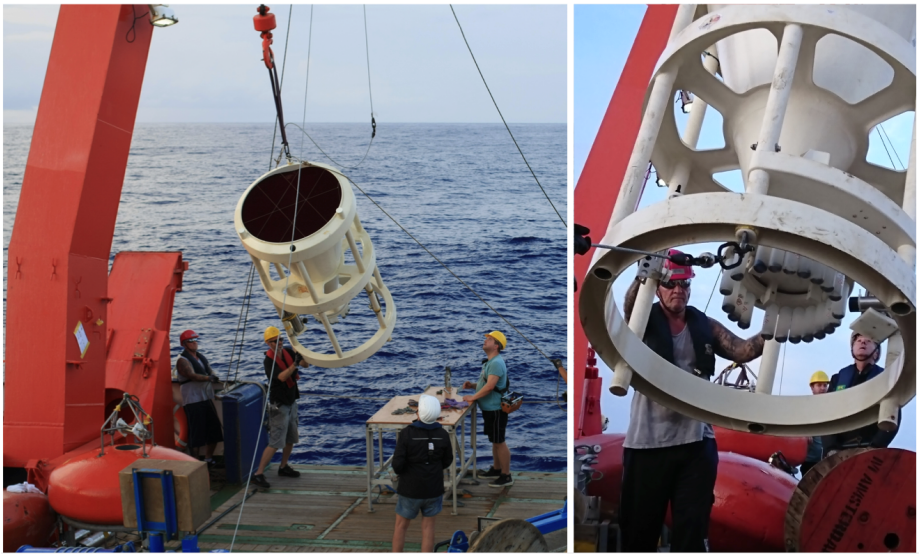

Figure 1: Recovery of sediment trap during the German Research Cruise M140 in the North Atlantic, crew in the *RV* Meteor, August 2017. **Left**: sediment trap has a sampling area of $1m^2$, **Right**: 20 bottles with samples, note the four missing bottles.

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 in the same collecting bottle. If species were sampled together at least once, they co-occur (live in sympatry).

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. First differences were not calculated for 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).

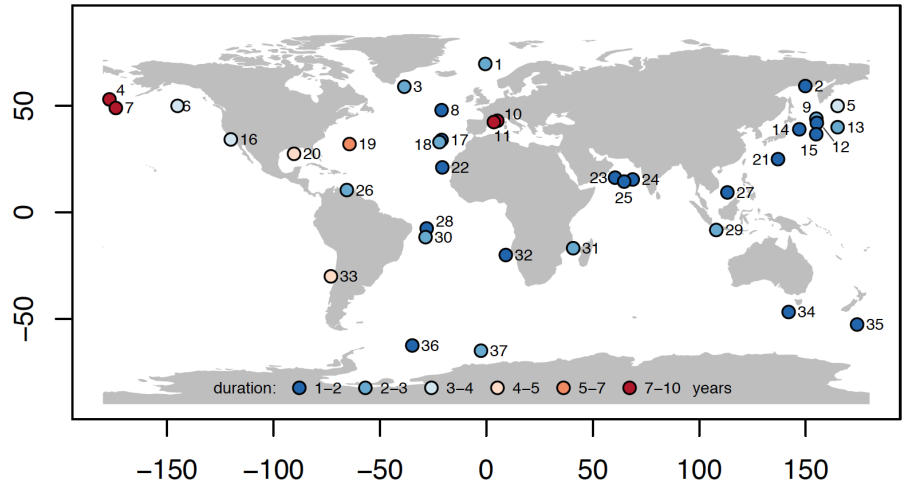

Figure 2: Distribution and total duration of sediment trap time series used in this study. Figure taken from [5]. Traps 36 and 37 were excluded from this study because they contain only one species.

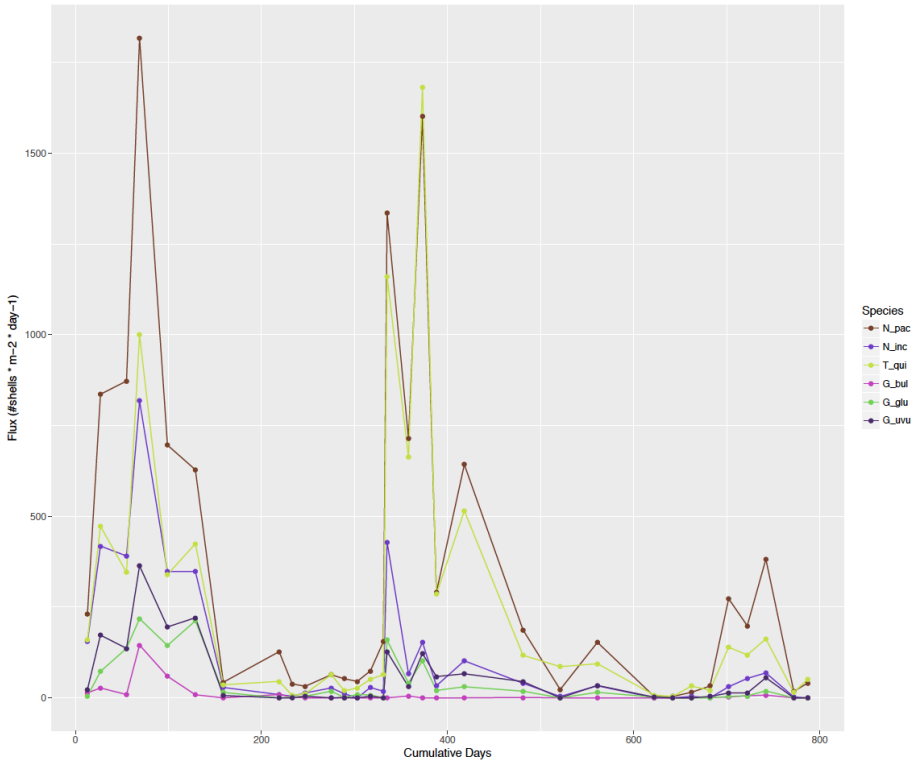

Figure 3: Example of data from trap no.1 (named NB67), colors represent species. This trap was active for 787 days, samples were taken in average every 18.2 days, with a total of 32 samples (Table 1)

Table 1: Meta-data of sediment traps taken from [5]. 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

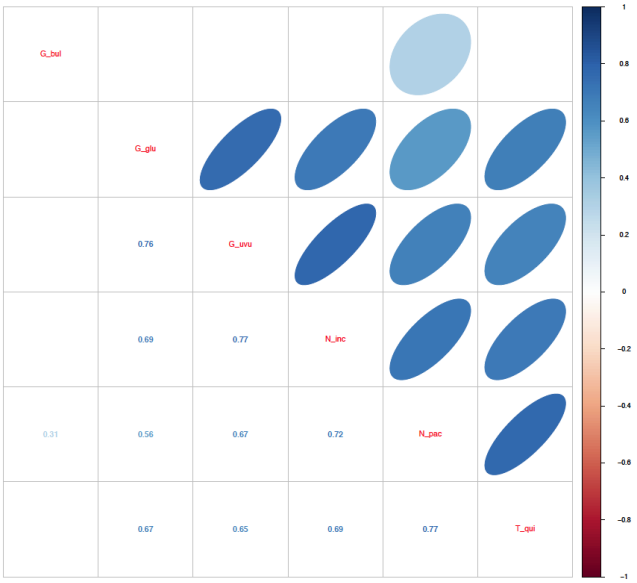

Figure 4: Pair-wise Kendall correlation plot of first differences of time-series from Trap no.1 (NB67, Fig.3). Lower triangular matrix shows the correlation values and upper triangular matrix shows a representation of the correlation in form of elipses. R package corrplot [10].

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.

3 Results and Discussion

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.

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)

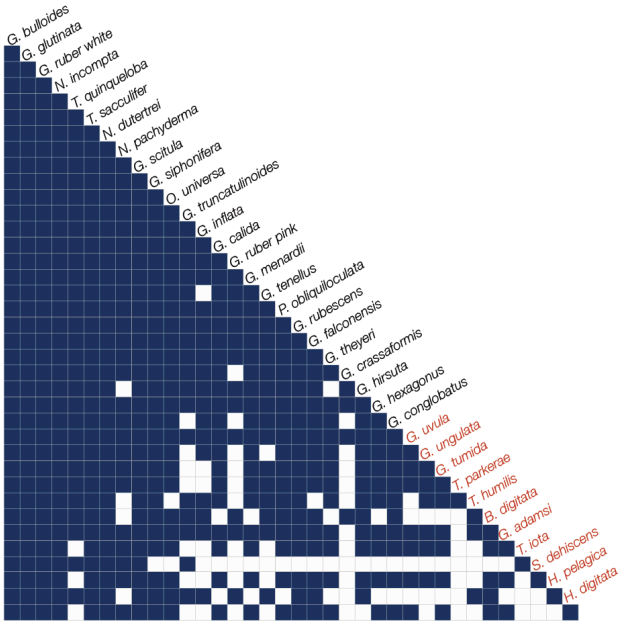

Figure 5: Co-occurrence matrix. In blue: species that co-occurred at least in one samples. The species names are positioned to indicate the columns and rows that represent their pairwise co-occurrence with other species. The matrix is clustered accordingly to the incidence of species on the samples;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

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.

4 Future steps

4.1 Co-occurrence of species

- How many times and where do species co-occur? Build a co-occurrence matrix based on frequency of co-occurrences (instead of just 0 and 1 as in Fig 5).
- 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?

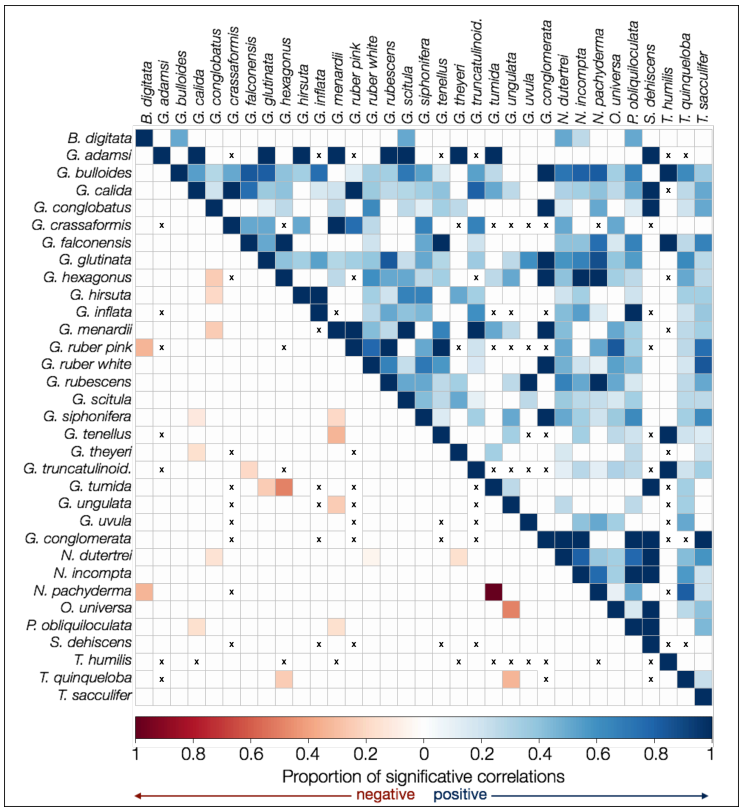

Figure 6: Proportion of significant positive (upper triangle, blue) and negative (lower triangle, red) correlations between first differences of time-series in which both species occur. White squares represent species pairs that co-occur but showed no significant positive and/or negative correlation.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

4.2 Correlation of time-series

- 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"?)

5 Preliminary conclusion

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.

References

[1] M. Begon, C. R. H. Townsend, L. John, R. T. Colin, and L. H. John. *Ecology: from individuals to ecosystems*. Blackwell Publishing, 2006.

[2] T. H. Ezard, T. Aze, P. N. Pearson, and A. Purvis. Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science*, 332(6027):349–351, 2011.

[3] T. H. G. Ezard and A. Purvis. Environmental changes define ecological limits to species richness and reveal the mode of macroevolutionary competition. *Ecology Letters*, 19(8):899–906, 2016.

[4] C. Hemleben, M. Spindler, and O. R. Anderson. *Modern planktonic foraminifera*. Springer-Verlag New York Inc., 1989.

[5] L. Jonkers and M. Kučera. Global analysis of seasonality in the shell flux of extant planktonic foraminifera. *Biogeosciences*, 12(7):2207–2226, 2015.

[6] M. Kučera. Planktonic foraminifera as tracers of past oceanic environments. *Developments in marine geology*, 1:213–262, 2007.

[7] T. B. Quental and C. R. Marshall. Diversity dynamics: molecular phylogenies need the fossil record. *Trends in Ecology & Evolution*, 25(8):434–441, 2010.

[8] K. L. Voje, Ø. H. Holen, L. H. Liow, and N. C. Stenseth. The role of biotic forces in driving macroevolution: beyond the red queen. *Proceedings of the Royal Society B: Biological Sciences*, 282(1808):20150186, 2015.

[9] M. G. Weber, C. E. Wagner, R. J. Best, L. J. Harmon, and B. Matthews. Evolution in a community context: on integrating ecological interactions and macroevolution. *Trends in Ecology & Evolution*, 2017.

[10] T. Wei and V. Simko. *corrplot: Visualization of a Correlation Matrix*, 2016. URL `https://CRAN.R-project.org/package=corrplot`. R package version 0.77.