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

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Planktonic foraminifera fossil record shows negative diversity-dependent diversification

Planktonic foraminifera (PF) are marine unicellular eukaryotes that produce calcium carbonate shells. Upon death, these shells accumulate on the ocean floor, creating a uniquely complete Cenozoic fossil record. PF fossil record has shown a negative diversity-dependent diversification (DDD) pattern, and **competition among species is the main mechanism proposed to explain the DDD pattern** [*1*]. However, it is yet not possible to explicitly test for PF species' interactions in the fossil record.

But do extant planktonic foraminifera species compete?

We expect that, if interspecific competition is an important driver of PF diversification, **competition should also be an important ecological process among living PF species**. There are **48 species of extant PF** [*2*], and none of them reproduce under controlled laboratory conditions. Thus we investigated observation data (Fig.1) to test for patterns that would support competitive interactions among species. We tested **two hypotheses**:

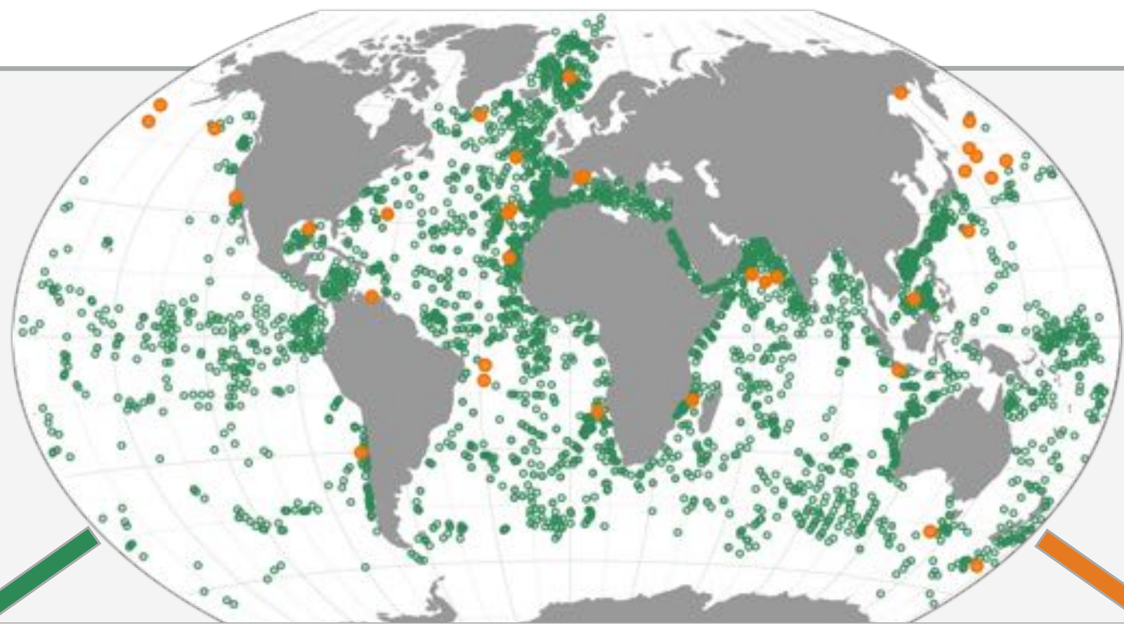

Fig. 1 Map of species abundance data. **Green: 3,886 ocean-floor surface sediments samples** [*3*]. **Orange: 35 sediment traps** [*4*].

Competitive exclusion

If resources are limiting, species with similar ecologies are expected to compete strongly, and ultimately exclude one another from the local community. Thus, we expect competitive exclusion to result in **communities with less ecologically similar species (*i.e.*, overdispersion)** than expected by chance.

Data & Methods

- **3,886** samples of PF relative abundance (Fig.1), including **41 species**
- Two proxies of **ecological similarity: species' shell size** and **phylogenetic distances** [*5*], thus two distance values for each species pair
- For each sample, we calculated the **mean nearest distance** (MND) among species pairs considering local relative abundances [*6*]
- We used two community assembly **null models**: randomised (1) **tree tips** and (2) abundances but fixed sample **richness**
- The observed MNDs were then compared to the null distributions for significance (1% level)

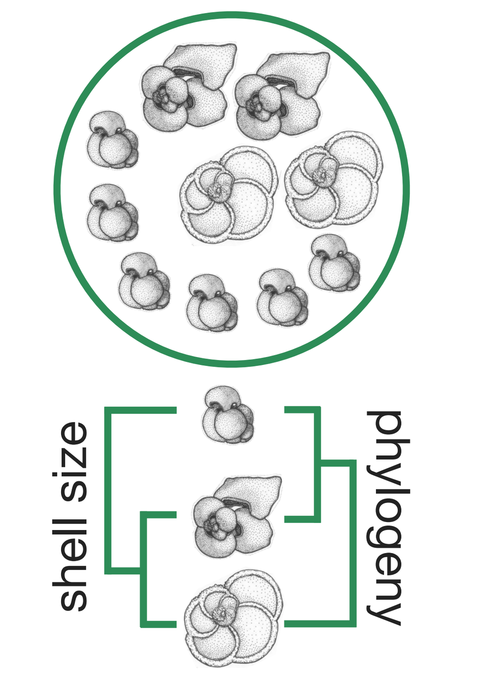

Fig. 2 Top: sample of relative abundances. Bottom: distances between species as to shell size and phylogeny.

Results

None of the communities showed significant overdispersion of shell size or phylogenetic distance among co-occurring species (Fig.4). Twenty communities were clustered regarding shell size, all in the tropical oceans.

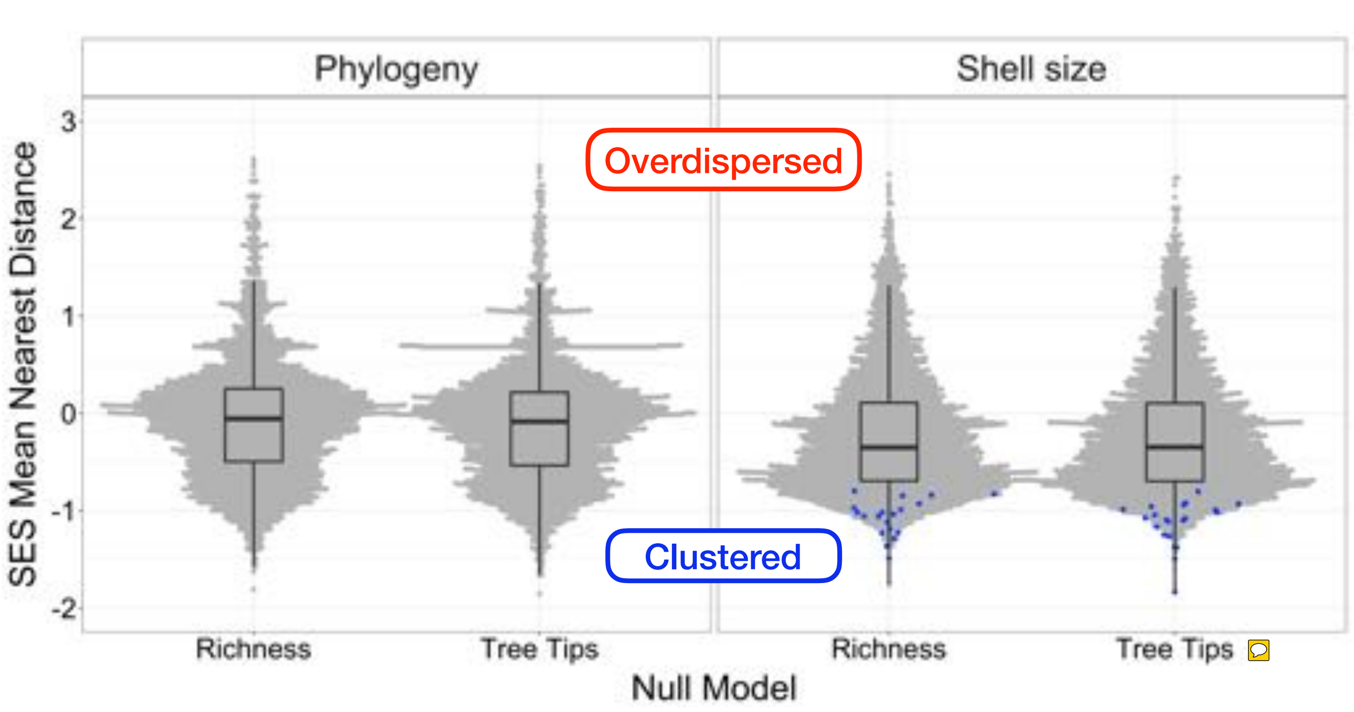

Fig. 4 Standardised Size Effect between each observed MND and the null models. Blue dots represent clustered and grey non-significant SES values.

Compensatory dynamics

If competitive interactions are important in driving fluctuations in abundance in the local community, then changes in the abundance of one species should generally be accompanied by compensatory changes in the abundances of others. Thus, we expect that **species within communities will covary negatively through time.**

Data & Methods

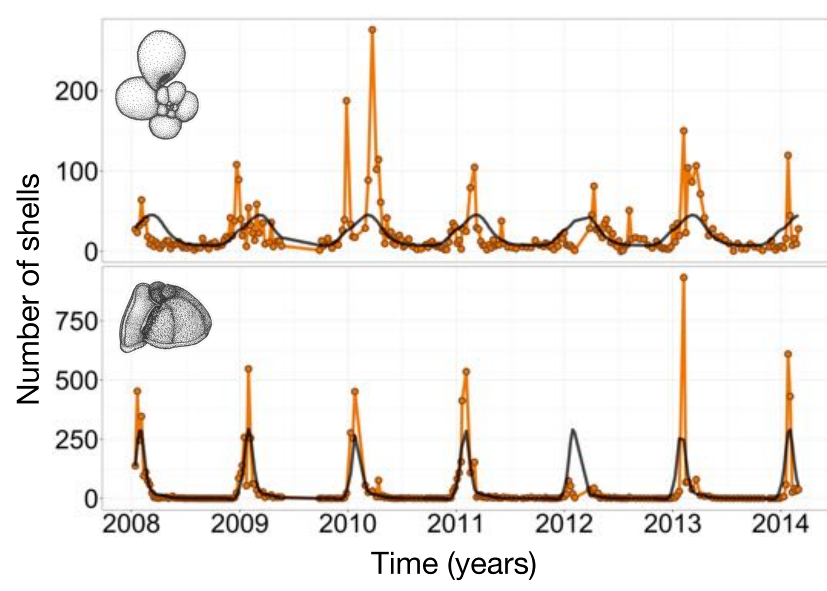

Fig. 3 Example of two time-series in the Gulf of Mexico sediment trap. Number of shells in number/day*m^2. Species: *G. calida* (top) and *G. truncatulinoides* (bottom). **Orange dots and lines: observed data. Black lines: null seasonality model.**

- **35** sites (Fig.1), including **370 abundance time-series** (Fig.3) of **30 species**
- **Null model considering annual seasonality** (Fig.3, black line) Null distribution: randomised and correlated residuals of observed values minus the null model
- We calculated the **Kendall correlation** between **388 co-occurring species pairs** and compared each obs. correlation to its null distribution for significance

Results

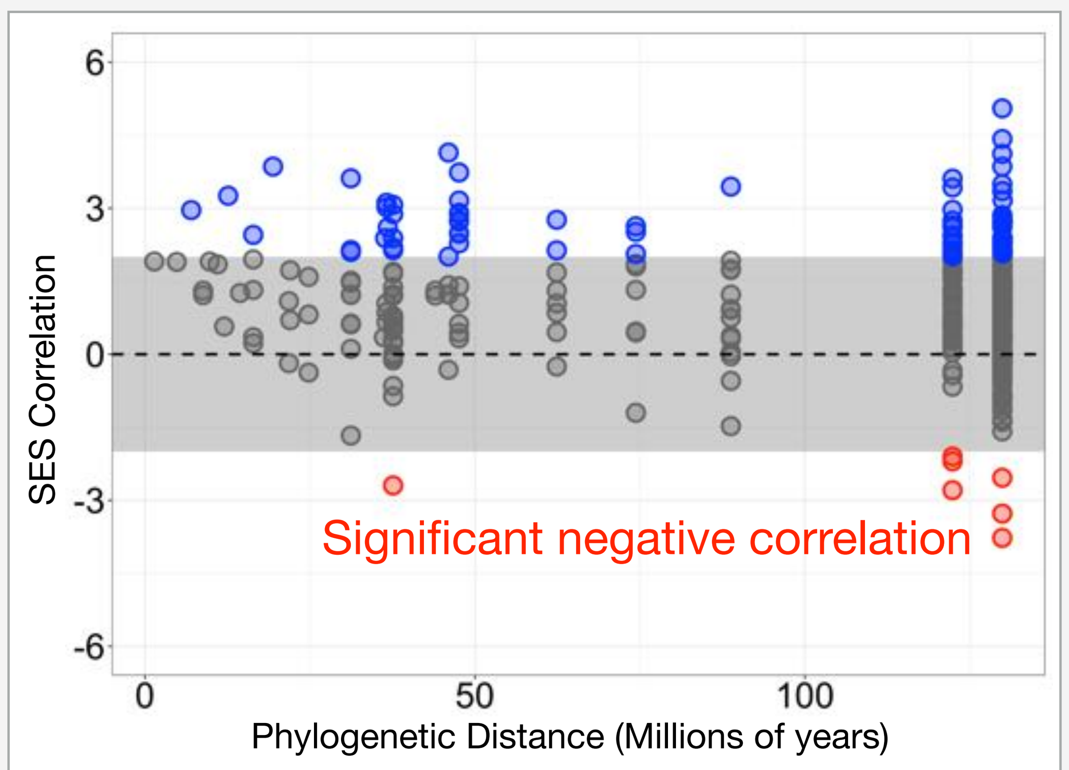

Fig. 5 Standardised Size Effect (SES) between each observed species pair correlation and its null distribution, plotted against the phylogenetic distance of the species pair. **Blue dots represent positive, red negative and grey non-significant SES values.**

- **Only seven species pairs showed significant negative correlation through time**, six of which included distantly related species (Fig.5)
- **92 species pairs showed significant positive correlation** (*i.e.*, synchronised fluctuations in abundances over time)

Conclusions

We found **no evidence for interspecific competition** structuring planktonic foraminifera communities. The abiotic environment and/or species other than PF probably affect PF population dynamics. More generally, **our results indicate that either the processes acting on today's PF communities are different than the ones driving PF macroevolution, or that interspecific competition might not be the main mechanism underlying the patterns seen in the PF fossil record.**

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