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Unravelling macroecological patterns in extant planktonic Foraminifera

by

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Ao meu pai, Marcio Rillo (in memoriam)

Nature, it seems, is more like a jazz ensemble than a symphony orchestra.
(Oswald J. Schmitz, 2018)

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ABSTRACT

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES
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Doctor of Philosophy

UNRAVELLING MACROECOLOGICAL PATTERNS IN EXTANT PLANKTONIC FORAMINIFERA

Marina Costa Rillo

Present-day ecological communities and the deep-time fossil record both inform us about the processes that give rise to, and maintain, diversity of life on Earth. However, these two domains differ in temporal, spatial and taxonomic scales. Integrating these scales remains a major challenge in biodiversity research, mainly because the fossil record gives us an incomplete picture of the extinct communities. Planktonic Foraminifera provide an excellent model system to integrate present and past changes in biodiversity. They are single-celled marine zooplankton that produce calcite shells, yielding a remarkably complete fossil record across millions of years, and are alive today enabling genetic and ecological studies. Their fossil record has been widely used in the fields of stratigraphy and palaeoclimate. However, we have limited knowledge about their ecology, preventing us from fully understanding the evolutionary processes that shaped their diversity through time. The primary objective of this thesis is to improve our understanding of community ecology of extant planktonic Foraminifera species, to enable us to more comprehensively study their fossil record. I created a large image dataset of over 16,000 individuals from a historical museum collection (Chapter 2) and assessed its potential biases (Chapter 3). Using the data gathered from the collection, I investigated the extent to which individuals of the same species vary in shell size (Chapter 4). Size relates to many physiological and ecological characteristics of an organism, thus understanding how it varies within species and across space gives us insights about the function of the species in the ecosystem. Planktonic Foraminifera species greatly differ in how much size variation is explained by environmental (temperature and productivity) and/or ecological (local relative abundance) conditions, suggesting that the known pattern of large size at favourable conditions is not widespread in the group. Next, I explored how planktonic Foraminifera species interact with each other in ecological communities (Chapter 5). Their fossil record suggests that competition among species is an important ecological interaction limiting the number of species that can emerge within the group. I tested whether species are competing today in the oceans, and found no evidence for negative interactions. This result suggests that either the ecological processes acting on communities today are different than the ones driving planktonic Foraminifera evolution, or that competition among species did not shape the patterns we observe in their fossil record. Together, these discoveries extend our current understanding of planktonic Foraminifera biology and highlight the complexity of ecological dynamics. Future work using the planktonic Foraminifera fossil record to understand marine biodiversity changes will require scientific research across different scales as well as considering other interacting plankton groups.

Contents

List of Figures

List of Tables

Declaration of Authorship

I, Marina Costa Rillo, declare that this thesis entitled *Unravelling macroecological patterns in extant planktonic Foraminifera* and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Either none of this work has been published before submission, or parts of this work have been published as: Rillo *et al.* 2016; Rillo *et al.* 2019.

Signed:

Date:

Acknowledgements

The doctoral research is a long journey, in which you know the starting point but seldom know the final destination. This journey is not only academic, but also very personal. Thus, the inspiration and encouragement to pursue a PhD have come from many sources, which I would like to acknowledge here.

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Chapter 1

Introduction

There is a mind-blowing variety of life on Earth. Recent estimates predict that 8.7 million ($\pm$ 1.3 million) eukaryotic species inhabit the Earth today (Mora et al., 2011), and this estimate does not even include the much older and more diverse Archaea and Bacteria domains of life (Hug et al., 2016). It remains a challenge to understand the ecological and evolutionary processes that give rise to and maintain this rich biodiversity. Scientific research is often inclined to seek simple and general explanations for observed patterns (Kinnison et al., 2015). However, ecology and evolution are characterised by complex multilevel processes, and finding general and predictive rules to explain biodiversity has proven difficult (Evans et al., 2012).

Biological systems are subject to many dynamical factors, with each of the factors affecting and sometimes driving the observed patterns. Therefore, one has to consider multiple variables rather than focus on a single one when studying these patterns. This principle, which prevents the development of general rules applicable to different biological systems, was pointed out by Brian McGill as 'multicausality' in his blog post on "Why ecology is hard (and fun)"[1]. To understand what multicausality means in ecology, McGill proposes a simple exercise: try to sketch all the factors affecting the life of an organism. Let us focus on a single-celled calcareous zooplankton in the middle of the ocean. Which factors are affecting the fitness of this individual? These factors can be divided into three broad categories: physical/chemical, physiological and ecological (Fig. 1.1). The "hard (and fun)" part of ecology is to try to calculate the relative contribution of each of these factors to the fitness of this individual, considering that the environmental conditions and the strength of ecological interactions are dynamic, so the relative impact of each varies through time. We definitely do not have a short list of the major causes affecting this individual's life.

Instead of abandoning all hope and claiming nothing generalises beyond an individual system, we can try to deal with this complexity by zooming out of the individual level and looking at biodiversity patterns at large spatial and temporal scales. **Macroecology** comes as a large-scale pattern-oriented approach to seek generality in ecology and unveil the mechanisms underlying the structure and functioning of communities and ecosystems (Marquet, 2009). By statistically describing macro-biodiversity patterns, we can build the empirical foundations from which deductive and prediction-rich ecological and evolutionary hypotheses emerge.

[1] Weblink (accessed in July 2018): https://dynamicecology.wordpress.com

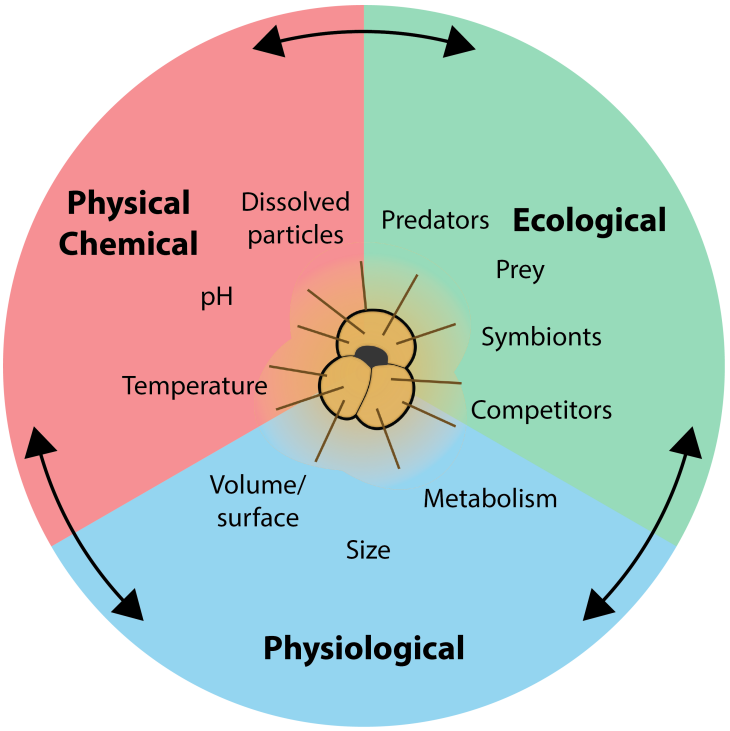

FIGURE 1.1: Factors that can affect the fitness of a single-celled zooplankton. **Physical and chemical** structure of the water column, such as temperature, pressure, pH, salinity and other dissolved particles such as oxygen. **Ecological** factors include interactions such as feeding, which is influenced by availability of prey (e.g., bacteria, phytoplankton or even other zooplankton), symbiosis, competition with other individuals, predation and virus and bacterial infection. The cell's volume to surface ratio, size and metabolic rate influence **physiological** processes vital for its survival. The arrows indicate the feedbacks among these categories. For example, organism size influences the size range of organisms with which this individual interacts ecologically. Temperature directly affects the metabolic rate of the cell. The temperature and pH of the water affects the output of symbionts. In conclusion, it is difficult to establish the main factors influencing the fitness of this individual.

1.1 Macroecology

Macroecological patterns describe how biodiversity varies in space and time (Brown, 1995; Gaston, 2000) and thus include the fields of community ecology, biogeography and phylogeography. Macroecological work is usually concerned with patterns occurring at regional to global scales where experiments are not feasible. One might think that it is difficult to obtain data at such broad scales; however, the last two decades have seen an explosive development and availability of big datasets, such as the Global Biodiversity Information Facility (http://www.gbif.org). Technological advances have also facilitated the digitisation of museum collections, which have played a major role in this so-called 'big data era'.

Many macroecological patterns are currently known, for example: *(i)* species diversity is greatest in the tropics and declines steadily towards the poles (latitudinal diversity gradient; Hillebrand 2004a), *(ii)* widespread species are more abundant (abundance-occupancy relationship; Gaston et al. 2000), *(iii)* species richness found at a site is positively related to the area of the site (species–area relationship; Lomolino 2000), *(iv)* most communities contain a few abundant species and many rare ones (species abundance distributions; McGill et al. 2007). However, all the described macroecological patterns have exceptions (e.g., Wardle et al. 1997; Gaucherel et al. 2018) and can actually be generated by several

different causal pathways (Levins and Lewontin, 1980). Progress in understanding can be advanced by determining the conditions under which a given pattern occurs or not (Vellend, 2016).

Most macroecological patterns have been described on the terrestrial biota, making marine macroecology a relatively new quantitative science (Witman and Roy, 2009; Webb, 2012). Interest in quantifying and understanding large-scale marine diversity patterns has been rapidly increasing over the last two decades, following technological innovations in the fields of engineering and molecular biology (e.g., Danovaro et al. 2014; De Vargas et al. 2015). Macroecological patterns in the oceans can differ to the ones described on land (Webb, 2012). For example, the latitudinal diversity gradient in the oceans shows higher diversity at mid-latitudinal bands instead of in the tropics (Tittensor et al. 2010; Sunagawa et al. 2015), but this pattern may vary depending on the studied group (Roy et al., 2000; Hillebrand, 2004b; Tittensor et al., 2010). Moreover, a longitudinal diversity gradient is observed, where coastal species show maximum diversity in the Western Pacific (Indo-Australian Archipelago; Renema et al. 2008; Tittensor et al. 2010).

The great advantage of studying ecology on such broad scales, is that it emphasises the role of evolutionary and historical processes in shaping present-day biodiversity patterns (Marquet, 2009; Vellend, 2016). By acknowledging that the processes of natural selection, drift, dispersal, and speciation are central in the dynamics of ecological communities (Vellend, 2010; Fritz et al., 2013), macroecology provides a framework to bridge the fields of community ecology and macroevolution. These fields have long differed in temporal, spatial and taxonomic scales (Vellend, 2010; Weber et al., 2017), but together seek to understand the processes generating and maintaining biodiversity.

1.1.1 Community ecology

Community ecology focuses on local and regional processes affecting patterns in the diversity, abundance, and composition of species in ecological communities (Vellend, 2010). Communities can be studied at many different spatial scales and, consequently, be defined in many ways (Vellend, 2016). Therefore, the field of community ecology can include the fields of biogeography, macroecology[2] and paleoecology. Here, I use the definition that an ecological community includes species that directly or indirectly interact, and thus the populations of these species should overlap in space and time (see Vellend 2016). When studied at the macroecological scale, population level processes underlie species level patterns, such as geographic range, population size and density, which, in turn, are known to affect species diversification in deep time (i.e., macroevolution; reviewed in Jablonski 2008b). Therefore, macroecology expands the spatial and temporal scale of community ecology and brings it closer to the field of macroevolution.

[2] I chose to use 'macroecological patterns' instead of 'community ecology patterns' in the title of my thesis because I studied the biogeography of organism size, and community ecology traditionally focuses on number of individuals and abundance instead of morphology.

1.1.2 Macroevolution

Macroevolution focuses on the processes of speciation and extinction acting over long time spans, which created the biodiversity we observe, assembled into ecological communities (Schluter, 2013). In contrast to evolutionary biology fields that focus on genetic changes in populations from one generation to the next (i.e., microevolution), macroevolution zooms out to the tree of life, investigating the diversity at and above the species level, focusing on entire clades (i.e., lineages that share a common ancestry). The temporal scale of macroevolutionary processes is geological time (i.e., millions of years). The spatial scale of macroevolution can be continental (terrestrial; e.g. Pires et al. 2015), provincial (marine; e.g. Renema et al. 2008) or global (e.g., Benson et al. 2014; Rabosky et al. 2018). Finer temporal and spatial scales are usually unattainable. Nevertheless, macroevolution and macroecology share a similar spatial scale, and the processes underlying macroecological patterns are directly linked to macroevolutionary processes (Mittelbach et al., 2007; Schluter and Pennell, 2017; Rabosky et al., 2018).

Macroevolution can be studied using molecular phylogenies of extant species (neontological approach) or the fossil record (palaeontological approach). Molecular phylogenies allow an explicit test of the evolutionary relationships among lineages, whereas the fossil record enables a more direct assessment of how diversity changed through time (i.e., diversity trajectories; Quental and Marshall 2010) and estimation of extinction and speciation rates (Foote, 2000). Integrating both the palaeontological and neontological approaches is the best way to study the dynamics of biodiversity (Quental and Marshall, 2010; Fritz et al., 2013). However, molecular studies on extinct taxa are usually not feasible, and only some traits of certain organisms are preserved in the fossil record. It has been estimated that probably less than 10% of the biota is represented in the fossil record (Forey et al., 2004).

1.1.3 The bridge between community ecology and macroevolution

The coarser temporal and spatial scale of macroevolution and the lack of longer temporal perspective in community ecology have prevented the integration of these two fields (Fritz et al., 2013; Yasuhara et al., 2015). However, ecological interactions, which happen at the community scale, are known to shape species' population dynamics, alter natural selection, and impact trait evolution and lineage diversification (Jablonski, 2008b). Species evolution and diversification, in turn, influence how species interact with the environment and with each other, affecting the dynamics of ecological communities (Fussmann et al., 2007; Schoener, 2011). Thus, eco-evolutionary feedbacks are at the core of the mechanisms generating and maintaining biodiversity, making the disconnection between community ecology and macroevolution artificial.

Besides the different temporal and spatial scales, different taxonomic scales also challenge the integration of macroevolution and community ecology. Community ecology focuses on the population level, studying abundances of interacting species that can belong to distantly related clades. Macroevolution, in turn, focuses on patterns above the species level, studying diversification of species, genera or families, that are usually phylogenetically related. The preservational bias of the fossil record makes the direct analysis of community dynamics in deep time unfeasible for the majority of taxonomic groups (Marshall and Quental, 2016), and thus the connection of population-level ecological processes to macroevolutionary processes impossible.

Few taxonomic groups have palaeontological data at population level and enough temporal and spatial resolution to connect the mechanisms acting on the community to the macroevolutionary scale. Some examples include marine invertebrates (Foote and Sepkoski, 1999) such as ostracodes (Hunt et al., 2017) and bryozoans (Liow et al., 2016), as well as protists such as diatoms, radiolaria, coccolithophores, dinoflagellates and foraminifers (microfossils; reviewed in Yasuhara et al. 2015). Planktonic Foraminifera have the most complete and abundant fossil record currently known (Kucera, 2007; Ezard et al., 2011) and are, therefore, the most promising model system to integrate community ecology and macroevolution (Yasuhara et al., 2015).

1.2 Planktonic Foraminifera

Planktonic Foraminifera are single-celled eukaryotes (protists) that live as zooplankton throughout the world's oceans and produce a calcium carbonate test (or shell; Kucera 2007) around their cells. Upon death, these shells sink to the ocean floor, accumulating in great numbers and building up an exceptionally complete fossil record. Planktonic Foraminifera species have at least an 81% chance of being detected per million year interval (Ezard et al., 2011), making their species-level fossil record at least as complete as the best-preserved genus-level records of marine invertebrates (Foote and Sepkoski, 1999). Such complete information on the diversity trajectory of a clade is rare and, therefore, planktonic Foraminifera are unique for macroevolutionary studies (Ezard et al., 2011; Marshall and Quental, 2016). At the same time, extant species enable genetic and ecological studies, which gives us information of how these organisms live in the modern oceans, and facilitates the connection between communities living today and millions of years ago. However, there is currently insufficient knowledge of planktonic Foraminifera ecology and community dynamics (Yasuhara et al., 2015). It is odd that we know more about the fossil record of dead planktonic Foraminifera than we do of the biology of living ones.

The evolutionary history of planktonic Foraminifera can be traced back in high temporal resolution by using the world wide archive of deep-sea sediment cores, drilled by the Deep Sea Drilling Project (DSDP) and its successors the Ocean Drilling Program (ODP), the Integrated Ocean Drilling Program and the International Ocean Discovery Program (IODP). Not surprisingly, planktonic Foraminifera have wide applications in biostratigraphy, because of their abundant and widely distributed fossil record as well as morphologically distinct, diverse and rapidly-evolving lineages (Wade et al., 2011). Moreover, the calcium carbonate of their shells preserves stable isotopes of sea water molecules, which can be used to reconstruct past ocean surface properties and climatic conditions on Earth (i.e., palaeoceanography and palaeoclimate; Kucera 2007).

1.2.1 Origin and Taxonomy

Foraminifera are an ancient group of protists that first appeared in the fossil record during the Early Cambrian (Culver, 1991), although genetic data suggest that Foraminifera were already part of the Proterozoic biota (Pawlowski et al., 2003). They first appeared in the benthos and expanded into the plankton in the Early Jurassic (Toarcian; Hart et al. 2003).

Planktonic Foraminifera belong to the eukaryotic supergroup Rhizaria, phylum Foraminifera, class Globothalamea, order Rotaliida, and the suborder Globigerinida, following the classification of

Pawlowski et al. (2013). Planktonic Foraminifera are usually divided into four major clades: microperforate non-spinose (Candeinidae), macroperforate non-spinose (Globorotaliidae), macroperforate spinose bilamellar (Globigerinidae) and macroperforate spinose monolamellar (Hastigerinidae). These four clades are supported phylogenetically (Aurahs et al., 2009a; Weiner et al., 2012) and defined morphologically based on characteristics of their shell walls, such as number of calcite layers, size of the pores that perforate the wall, presence of pustules or spines (Hemleben et al., 1989; Kucera, 2007). Some non-spinose species show a sharp ridge, or keel, in the periphery of their shells.

It is still unclear whether microperforates share a common ancestor with the macroperforate clade (Aurahs et al., 2009a). For example, the modern species *Gallitellia vivans* has been shown to have originated from a distinct clade of benthic Foraminifera (Ujiie et al., 2008). Moreover, colonisation of the plankton realm by benthic Foraminifera likely occurred multiple times (Darling et al., 1997; De Vargas et al., 1997; Ujiie et al., 2008; Arenillas and Arz, 2017), suggesting that the Globigerinida is polyphyletic. However, this polyphyly remains to be tested (Pawlowski et al., 2013). Interestingly, tychopelagic Foraminifera (i.e., occupying both the planktonic and benthic realm) have been recently discovered (Darling et al., 2009; Kucera et al., 2017), supporting multiple benthic-planktonic transitions.

In my thesis, I follow the taxonomic nomenclature of the SCOR 138 Working Group[3] of modern planktonic Foraminifera (except in Chapter 2) and, similarly to Siccha and Kucera (2017), incorporate the new genus *Trilobatus* described by Spezzaferri et al. (2015).

1.2.2 Diversity

Traditionally, the diversity of planktonic foraminiferal species has been defined using the morphological species concept (Pearson, 1998; Benton and Pearson, 2001), meaning the diagnosis of species is based on morphological features of their shells (i.e., morphospecies). Molecular analyses of living taxa (using the small subunit 18S of the ribosomal RNA gene) have confirmed the taxonomic classification of extant planktonic Foraminifera morphospecies, but demonstrated that morphospecies can comprise several distinct genetic types (i.e., cryptic species; Darling and Wade 2008; Ujiie and Lipps 2009; Morard et al. 2015, 2018). Some of these cryptic species not only show large genetic distances, but also distinct biogeography and biology (e.g., Huber et al. 1997; De Vargas et al. 1999; Darling et al. 2007; Aurahs et al. 2011; Weiner et al. 2012; Quillevere et al. 2011), questioning the morphological species concept.

The current diversity of extant planktonic Foraminifera is 48 species[3], but depends on the level of cryptic diversity included. Detailed re-examinations of the foraminiferal shell have uncovered diagnostic morphological characteristics that could be used to differentiate extant cryptic species, such as shell wall porosity (Huber et al., 1997; Morard et al., 2009; Weiner et al., 2015), chamber coiling direction (Darling et al., 2006) and chamber shape and/or size (Morard et al., 2009; Aurahs et al., 2011; Weiner et al., 2015). However, morphological differentiation among distinct genetic types has not always been observed: the highly morphologically variable *Trilobatus sacculifer* showed no genetic differentiation among any of the four morphotypes (Andre et al. 2013; for other examples see: Aurahs et al. 2011; Weiner et al. 2012). These examples highlight how the connection between genetic and morphologic variability in planktonic Foraminifera is complex, challenging our understanding of their diversity.

So far, detailed molecular studies can only be undertaken on living Foraminifera species. Thus, we lack an assessment of their cryptic diversity in the fossil record. Adopting the morphological species concept

[3] SCOR WG 138 (accessed in 2018): http://www.eforams.org/

to estimate diversity in the fossil record can be problematic, because morphological change can occur within a single evolving lineage without a corresponding change in diversity (i.e., anagenesis; Simpson 1951). The importance of planktonic Foraminifera in biostratigraphy means that morphological change, even when anagenetic, has been subject to fine-scale splitting to achieve high stratigraphical resolution (Aze et al., 2011). As a consequence, species diversity can be largely overestimated in the fossil record. Recently, the fossil record of Cenozoic macroperforate planktonic Foraminifera has been revised using fine stratigraphic resolution and an underlying ancestor-descendant evolutionary hypothesis (Aze et al., 2011). Morphospecies that were seen to intergrade through time were assigned into a single evolving lineage in the phylogeny, being defined as evolutionary species (Simpson, 1951; Pearson, 1998). This evolutionary lineage phylogeny resulted in a Cenozoic diversity of 210 planktonic Foraminifera macroperforate species (Aze et al., 2011; Ezard and Purvis, 2016), although the relative contribution of anagenetic change to the clade's diversity has been questioned (Strotz and Allen, 2013) and sampling biases in the fossil record were not considered (Lloyd et al., 2012). Cenozoic species occurrence directly extracted from the Neptune Sandbox Berlin database (Lazarus, 1994) have resulted in a diversity estimate of 572 species including macro- and microperforates (Hannisdal et al., 2017).

1.2.3 Physiology and Ecology

Our knowledge about cell biology and ecology of planktonic Foraminifera is remarkably limited. This lack of biological knowledge is due to the fact that they are difficult to cultivate and have never generated a second generation under laboratory conditions (Schiebel and Hemleben, 2017). Thus, in order to study live individuals, it is necessary to sample them from the surface waters in the open ocean either by SCUBA diving and hand-collecting them with a glass jar (e.g., LeKieffre et al. 2018) or using plankton net sampling (e.g., Takagi et al. 2018). The diving method is preferred over collection with a net because it minimises cell damage or death due to contact with the net (Huber et al., 1996). Planktonic Foraminifera occur in low densities (in the order of tenths of individuals per m^3; Schiebel and Hemleben 2005; Meilland et al. 2019). When compared to other eukaryotic groups, planktonic Foraminifera represent less than 0.1% of the plankton abundance in the sunlit ocean (Keeling and del Campo, 2017). This low abundance in the water column complicates their sampling. More generally, no Rhizaria parasite of humans is currently known, so there is little economical importance to sequence Foraminifera genomes (Burki and Keeling, 2014), further hindering our understanding of their biology.

Although we have never observed a full life cycle of planktonic Foraminifera, we know from laboratory studies that they grow by sequential addition of chambers until reproduction, when the gametes are released (gametogenesis) and the cell dies (Be, 1976; Brummer et al., 1986; Hemleben et al., 1989). They can experience drastic morphological changes throughout their ontogeny (Brummer et al., 1986), such as gametogenesis calcification which includes shedding of spines and/or thickening of the shell (Hemleben et al., 1989). Because of their chamber-by-chamber growth, an adult individual retains the its entire ontogenetic history within its shell. Documenting this ontogenetic history using x-ray microscopy has the potential to elucidate the role of developmental constraints in species diversification (Schmidt et al., 2013).

The life of a planktonic foraminifer possibly spans from a few weeks to months and is characterised by a single reproductive episode before death (i.e., semelparity; Hemleben et al. 1989). Planktonic Foraminifera are currently thought to only reproduce sexually, as opposed to the alternating sexual and assexual life cycle of benthic Foraminifera (Parfrey et al., 2008). Therefore, planktonic Foraminifera rely

on very precise spatial and temporal synchrony with each other for the release, encounter and fusion of their gametes in the three-dimensional oceanic pelagic zone. Some species appear to synchronise their reproductive cycle with lunar periodicity (Bijma et al., 1990; Bijma and Hemleben, 1994; Jonkers et al., 2015; Venancio et al., 2016), possibly to maximise chances of fertilisation.

Planktonic Foraminifera are heterotrophic and passively feed using their large reticulate networks of cytoplasm (i.e., rhizopods) to phagocytise their prey. They are omnivorous and prey on other plankton including diatoms, dinoflagellates, ciliates and copepods (Anderson et al., 1979; Spindler et al., 1984; Schiebel and Hemleben, 2017). It has been suggested that spinose species have a more carnivorous diet, whereas non-spinose species tend to be more herbivorous (Schiebel and Hemleben, 2017). Some species of planktonic Foraminifera are photosymbiotic with eukaryotic algae (Schiebel and Hemleben, 2017) or cyanobacteria (Bird et al., 2017). These photosymbiotic species usually occur in tropical-subtropical oligotrophic waters, suggesting photosymbiosis is an ecological strategy to survive in nutrient-limited environments (Be and Hutson, 1977). However, experiments have shown that photosymbiotic species still rely on prey phagocytosis to grow and achieve reproductive maturation, indicating that photosymbiosis can not be the only form of daily nutrition (Takagi et al., 2018).

Because planktonic Foraminifera are difficult to observe in their natural habitat and no population dynamics experiment can be accomplished without reproduction in culture, our knowledge about ecological interactions within and among planktonic Foraminifera species is scant. As a consequence, we currently do not know about selective predators of living planktonic Foraminifera, nor about intra- or interspecific competition. Mathematical models have helped to fill in this knowledge gap (e.g., Lombard et al. 2011; Grigoratou et al. 2019). However, there is enough observational data on species relative abundance on the seafloor (coretops) as well as data on population dynamics through time (sediment traps) that, when analysed under a community ecology framework, can give us insights about the ecological processes regulating planktonic Foraminifera abundance, distribution and community composition. I explore this framework in the next sections as well as throughout my thesis.

1.2.4 Macroecological patterns

Global diversity patterns of planktonic Foraminifera have been widely studied in relation to environmental variables, especially sea surface temperature (SST) (Fig. 1.2). Rutherford et al. (1999) showed that the number of modern planktonic Foraminifera species peaks at intermediate latitudes in all oceans. SST explained nearly 90% of the geographic variation of species richness, and Rutherford et al. (1999) suggested that the underlying mechanism explaining this pattern was vertical niche partitioning dictated by the thermal structure of the water column. The strong relationship between SST and diversity was further confirmed by Tittensor et al. (2010), who studied 13 marine taxa, including planktonic Foraminifera. Tittensor et al. (2010) suggested that higher temperatures increase metabolic rates promoting higher speciation rates, which lead to greater diversity in lower latitudes (metabolic theory of ecology; Brown et al. 2004; Allen et al. 2006). In fact, speciation rates of planktonic Foraminifera calculated over the past 30 million years increase towards the tropics, supporting the metabolic theory hypothesis (Allen et al. 2006; Allen and Gillooly 2006; but see Wei and Kennett 1986). More recently, Fenton et al. (2016b) explored different diversity measures of planktonic Foraminifera assemblages (including species relative abundance and functional diversity) and how these measures relate globally to ten environmental variables. SST was still the variable with the most explanatory power and the vertical structure of the

surface water (i.e., thickness of the mixed layer) did not explain the diversity observed. Moreover, Fenton et al. (2016b) did not find support for the metabolic theory because the relationship between SST and diversity changed across oceans, which would not be expected if temperature has a consistent effect on diversification.

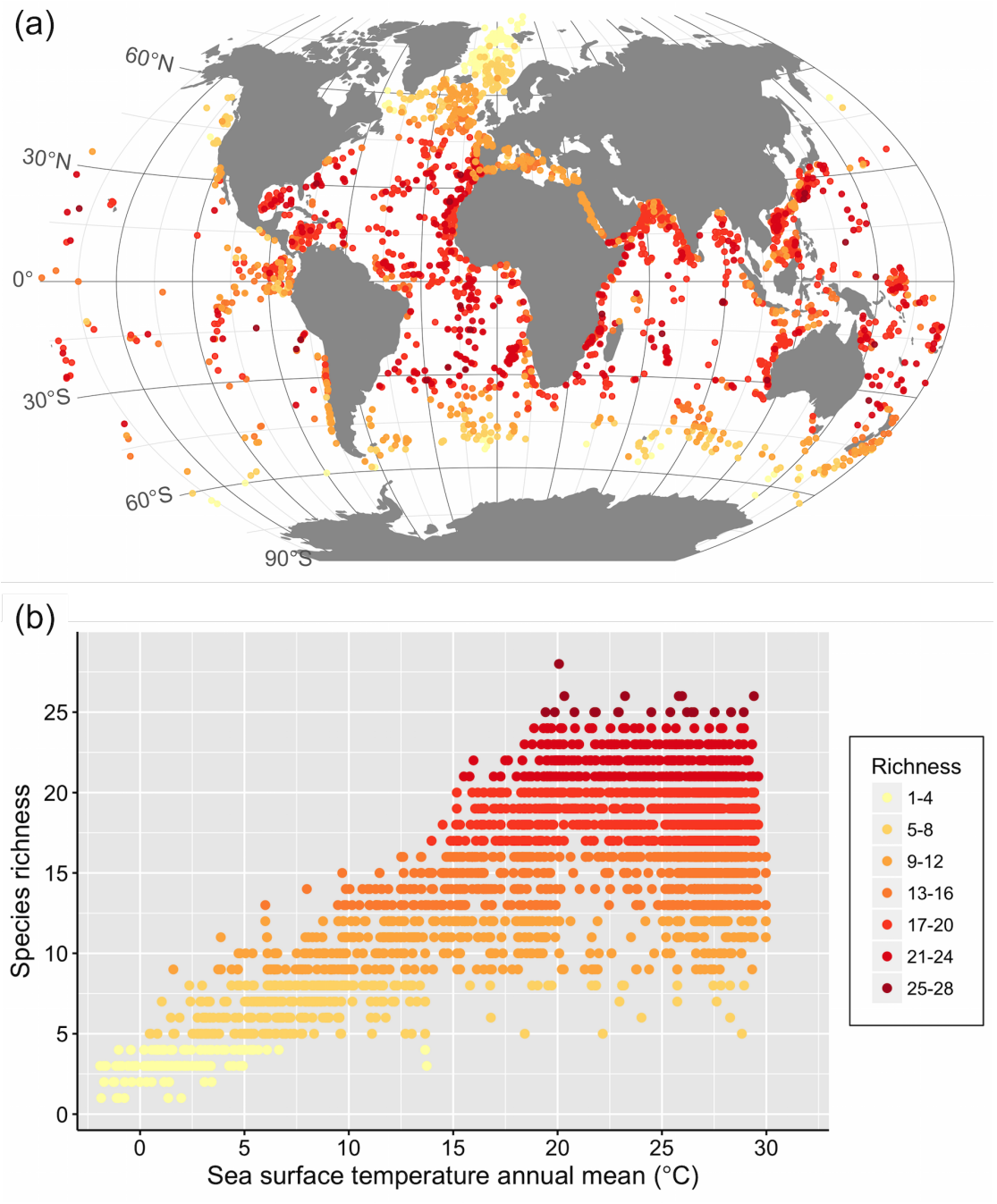

FIGURE 1.2: Species richness of planktonic Foraminifera **(a)** across the globe (latitudinal diversity gradient) and **(b)** as function of annual mean sea surface temperature. Data from Siccha and Kucera (2017) and World Ocean Atlas 2013 (0 meters depth, Locarnini et al. 2013).

Planktonic Foraminifera assemblages show a latitudinal morphological pattern of larger average shell sizes towards the tropics, only interrupted by polar and subtropical fronts and in upwelling areas (Schmidt et al., 2004a). The global two-fold increase in assemblage size from the poles to the tropics correlates with SST and the thermal stratification of the surface water (Schmidt et al., 2004a). The mechanisms generating this morphological pattern could be related to food availability, cell physiology (as higher SST affects metabolic and growth rates) and/or ecology, as larger sizes could be adapted to vertical niches created by the increased stratification of the surface water (Schmidt et al., 2004a). Interestingly, the modern oceans host the largest planktonic Foraminifera of all time (Schmidt et al., 2004b).

Most of these works explored the relationship between planktonic Foraminifera diversity and primary productivity, which concerns the ecological interaction of herbivory (predation). However, to date no research has investigated competitive interactions among planktonic Foraminifera. We currently do not know if they compete, although ecological models developed to aid palaeoceanographic reconstructions generally assume they do (e.g., Kretschmer et al. 2018). It is prohibitively difficult to observe direct ecological interactions among planktonic Foraminifera in the open ocean, but the outcomes of ecological interactions can yield informative evidence that they have occurred. Thus, instead of studying how planktonic Foraminifera abundances change in relation to environmental variables, one can investigate how the changes in their abundances relate to each other. For example, if species occur together in high abundances and are ecologically similar, they are probably adapted to similar environmental conditions, and are not competitively excluding one another. In this way, unravelling community ecology patterns can help us elucidate the role of ecological interactions among planktonic Foraminifera species. I explore these ideas in Chapter 5.

1.2.5 Macroevolutionary patterns

During the approximately 170 million years of evolution, planktonic Foraminifera species diversity had three major peaks (Upper Cretaceous, Eocene, Miocene-Pliocene) and two minima (Cretaceous-Paleogene and Eocene-Oligocene transitions), with several fluctuations within these major events (Cifelli, 1969; Norris, 1991; Fraass et al., 2015). Their diversity never exceeded 100 species (Fraass et al. 2015; or 150 species, using a sub-sampling correction; Lloyd et al. 2012). This noticeable low diversity, especially when compared to the extant diversity of 4000 benthic Foraminifera species (Murray, 2007), is an interesting macroevolutionary pattern, and raises the question of why the Foraminifera tree is so unbalanced?

Many non-exclusive hypotheses can be put forward to explain this macroevolutionary pattern. Benthic Foraminifera lineages are older than planktonic ones and, therefore, have had more time to speciate and accumulate species. Also, the plankton was more severely harmed by the asteroid impact at the Cretaceous-Paleogene (K-Pg) boundary than the benthic realm (Culver, 2003; Thomas, 2007), and planktonic Foraminifera suffered their most extreme extinction event at this boundary (Fraass et al., 2015). Moreover, most of the observed speciation processes involve populations that are in allopatry (i.e., non-overlapping distributions; Coyne and Orr 2004). Geo- or hydrographic barriers block gene flow between populations, which, over time, become reproductively isolated due to random mutations and/or local adaptation. The apparent lack of barriers to gene flow in marine pelagic ecosystems might prevent allopatric divergence of plankton populations (the 'ubiquity hypothesis'; Finlay 2002) and maintain low species diversity. Indeed, benthic Foraminifera species usually have restricted biogeographical ranges

suggesting allopatric processes, whereas planktonic Foraminifera species, which are non-motile and passive dispersers, have extremely broad and overlapping biogeographical distributions (Be and Tolderlund, 1971; Norris, 2000; Kucera, 2007). The planktonic Foraminifera fossil record also support the ubiquity hypothesis, in which their high dispersal capability favours sympatric (i.e., co-occurring populations) over allopatric diversification processes (e.g., Lazarus et al. 1995; Pearson et al. 1997; Sexton and Norris 2008). Sympatric diversification of planktonic Foraminifera probably occurs via shifts in the timing of reproduction (seasonal sympatry) or in the depth habitat of co-occurring populations (depth parapatry; Norris 2000). The surface water stratification can create different depth habitats in the water column, allowing niche partitioning between populations and subsequently speciation by depth parapatry (Norris, 2000).

Present day molecular analyses at macroecological scales can help us elucidate planktonic Foraminifera speciation modes. For example, Weiner et al. (2012) confirmed that genetic types of the species *Hastigerina pelagica* were consistently separated by depth throughout their global range, supporting the depth parapatry hypothesis. Moreover, three species of planktonic Foraminifera exhibit genetic mixing between Arctic and Antarctic populations (Darling et al., 2000), supporting the high inter-oceanic dispersal potential observed in the fossil record (Sexton and Norris, 2008). Transoceanic distributions of genetic types were also found by Ujiie and Lipps (2009). However, at the same time, other global phylogeographical studies have shown that many planktonic Foraminifera species comprise genetic types with different geographical distributions (e.g. De Vargas et al. 1999; Darling et al. 2007; Aurahs et al. 2009b; Weiner et al. 2014; Ujiie and Ishitani 2016), supporting allopatric processes and opposing the ubiquitous dispersal hypothesis. In particular, Darling et al. (2004) combined molecular, biogeographic, fossil, and paleoceanographic data to reconstruct the possible mechanisms driving *Neogloboquadrina pachyderma* diversification. They showed that the onset of the Northern Hemisphere glaciation created oceanographic barriers to the gene flow of the Atlantic Arctic and Antarctic populations (Darling et al., 2004). Thus, allopatric processes driven by ocean circulation can play an important role in planktonic Foraminifera diversification. More generally, Darling et al. (2004) emphasise how palaeontological data are crucial to the understanding of present-day marine biogeographical patterns, and vice versa.

The planktonic Foraminifera fossil record allows a precise estimation of diversification rates in deep time and has been used to understand the relative contribution of biotic and abiotic factors driving macroevolutionary patterns. Traditionally, there is the idea that competition, predation, and other ecological interactions (i.e., biotic factors) shape ecosystems locally and over short time spans, whereas extrinsic, abiotic factors such as climate, oceanographic and tectonic events shape larger-scale patterns regionally and globally across long time scales (Benton, 2009). Planktonic Foraminifera diversification has been shown to be shaped by changes in ocean circulation and climate (e.g., Cifelli 1969; Lipps 1970; Leckie et al. 2002; Peters et al. 2013; Fraass et al. 2015). However, Ezard et al. (2011) showed that the interplay between species ecology (biotic) and climate (abiotic) drives planktonic Foraminifera diversification across the Cenozoic. More specifically, speciation rate was more strongly shaped by standing species diversity than by climate change, whereas the reverse was true for extinction (Ezard et al., 2011).

The relationship between diversification rate and standing diversity (per million year time bin) observed across planktonic Foraminifera macroevolution is negative, supporting a known macroevolutionary pattern termed negative diversity-dependent diversification (DDD; Rabosky 2013). DDD theory sees global diversity increasing up to an equilibrium point, dictated by a limited number of niches available (i.e., macroevolutionary carrying capacity), which regulates species richness (for a recent discussion see: Rabosky et al. 2015; Harmon and Harrison 2015). This DDD pattern is usually thought to reflect competition among species and the filling of niche space (Rabosky 2013, but see Moen and Morlon 2014).

Thus, competition among species seems to play a major role in planktonic Foraminifera diversification (Ezard et al., 2011; Etienne et al., 2011), and their high-resolution fossil record has even enable the test of different competition hypotheses (Ezard and Purvis, 2016). Explicitly testing for competition in the fossil record is difficult, usually because of low taxonomic resolution and small sample sizes. Until today, only one study has investigated species-level competitive interactions directly observable in the fossil record (bryozoans; Liow et al. 2016). The planktonic foraminiferal fossil record does not face the problem of resolution nor sample size; however, there is not enough ecological knowledge to derive hypotheses that would explicitly test for competition in their fossil record. Therefore, studying ecological dynamics of modern planktonic Foraminifera can certainly help us unlock the full ecological potential of their fossil record (Chapter 5).

Besides taxonomic diversification, macroevolutionary patterns can also be described based on morphological evolution. Cope's rule (Cope, 1887; Stanley, 1973), for example, describes an increase in average organism size over time and has been observed in many groups (e.g., Alroy 1998; Hone et al. 2005; Hunt and Roy 2006; Novack-Gottshall and Lanier 2008; Heim et al. 2015). Explanations for average size increase over time usually assume microevolutionary adaptive causes: larger body sizes are under selective advantages because of better resistance to predation, better food exploitation and higher reproductive success (Kingsolver and Pfennig, 2004; Schmidt et al., 2004c; Van Valkenburgh et al., 2004; Hone and Benton, 2005).

Planktonic Foraminifera lineages display the macroevolutionary trend towards increased size (Arnold et al., 1995; Webster and Purvis, 2002). However, speciation events do not occur more often in larger lineages, so it is not clear whether there are selective advantage for large-sized species (Arnold et al., 1995). Planktonic Foraminifera also increased in average assemblage size across the Cenozoic, and this size increase correlates positively with increases in latitudinal and vertical temperature gradients (Schmidt et al., 2004b,c). This correlation indicates an abiotic forcing of the macroevolutionary size increase, possibly related to adaptation to new niches that became available due to increased thermal stratification of the surface water (Schmidt et al., 2004c). Moreover, there is evidence that planktonic Foraminifera species decrease in size before they go extinct (Cordey et al., 1970; Wade and Olsson, 2009; Brombacher et al., 2017a), which suggests that smaller sizes are related to sub-optimal and stressful conditions (but see Weinkauf et al. 2014). On the other hand, the survivors of both the K-Pg and the Eocene-Oligocene extinction events were small sized (and unkeeled) planktonic Foraminifera species (Norris, 1991; Keller and Abramovich, 2009). This demise of large species during mass extinctions suggests that smaller sized species have a selective advantage of reduced extinction rates, possibly because of higher population densities (McKinney, 1997).

Macroecological patterns can help us elucidate whether there are selective advantages for larger (or smaller) sizes in planktonic Foraminifera. If there are selective advantages for larger sizes, the signatures of this mechanism should be evident not only among species, but also among populations within a species. Within a species' range, larger average sizes should be related to optimal conditions whereas smaller average sizes would be found in sub-optimal conditions. This macroecological pattern was observed in modern planktonic Foraminifera species (e.g., Hecht 1976; Schmidt et al. 2004a). In Chapter 4, I further explore within-species size variation in a global scope, which was possible because of the macroecological scope of natural history collections.

1.3 The importance of natural history collections

Natural history collections (NHCs) provide a rich source of data and can contribute to a wide range of studies at taxonomic, population and community levels (Lister and Climate Change Research Group, 2011; Ward, 2012; De La Sancha et al., 2017; Marshall et al., 2018). Conserved in museums and other institutions, NHCs contain the specimens as primary data curated with associated metadata (Schilthuizen et al., 2015). NHCs enable researchers to re-examine the primary data, which is especially important in groups where the taxonomy is in flux (Balke et al., 2013; Schilthuizen et al., 2015). NHCs have become widely used in macroecological and palaeontological studies because of their extensive spatial and temporal coverage, that cannot be replicated by new surveys (Balke et al., 2013; Marshall et al., 2018).

NHCs are particularly important in the assessment of the extent to which humans have impacted the Earth's biota and reshaped biodiversity patterns (Lister and Climate Change Research Group, 2011; Johnson et al., 2011). NHCs samples extend back into previous centuries (i.e., historical samples), which is fundamental for the establishment of a pre-anthropogenic baseline of the state of the Earth's biota (e.g., Roemmich et al. 2012; Ward 2012; Gardner et al. 2014; Penn et al. 2018). NHCs have been used, for example, to assess species biogeographical range shifts (Boakes et al., 2010; Hoeksema et al., 2011) and phenological changes (e.g. flowering time; Robbirt et al. 2011) during the past centuries. Although NHCs likely contain sampling biases, these biases can often be estimated (e.g., Boakes et al. 2010; Ward 2012; Guerin et al. 2018; Chapter 3) and taken into consideration when analysing NHC generated data. At a time when conserving biodiversity is a global priority, NHCs are a window into the natural world before human pressures approached their current intensity and are, therefore, essential to understand current and future biodiversity trends (Johnson et al., 2011).

Despite their importance, NHCs are significantly under-used due to the difficulty of obtaining and analysing data within and across collections (Smith and Blagoderov, 2012; Balke et al., 2013). Digitisation and mobilisation of specimens and associated metadata removes this barrier, making NHCs more accessible for research (Balke et al., 2013). However, digitisation requires considerable work, presenting major technical and organisational challenges when performed on such large scales (Smith and Blagoderov, 2012). In addition, with dwindling resources being made available for the management of museum collections, it is becoming more difficult to obtain funds for routine collection maintenance, let alone digitisation projects (Suarez and Tsutsui, 2004; Gardner et al., 2014; Kemp, 2015; De La Sancha et al., 2017). A recent and rather extreme example of the funding difficulties that natural history museums face was the fire that consumed the Museu Nacional in Rio de Janeiro in September 2018. Despite being the biggest natural history museum in Latin America, the Museu Nacional had no adequate support from the Brazilian government to preserve and digitise its collection. Sadly, much of its archive is now destroyed by the fire and its data permanently lost. It is therefore extremely important for collection managers and researchers to work together, providing new opportunities for funding and collaboration to increase the public and governmental awareness of the relevance and value of NHCs, as well as intensify its digitisation efforts (Ward et al., 2015).

Technological advances and innovative workflows are allowing natural history museums to enter a new age of mass digitisation of NHCs (e.g., Blagoderov et al. 2012; Heerlien et al. 2015; Hudson et al. 2015; Blagoderov et al. 2017). Modern imaging technologies also enable scientists to extract new data from the same specimens (e.g., Schmidt et al. 2013; Cunningham et al. 2014). As digitisation gets faster and cheaper, more governments and institutions are investing in it (Rogers, 2016). NHCs are becoming ever more available online through open-access data portals (Graham et al., 2004), which provide easy access

to NHCs for scientists, students and the public worldwide (Balke et al., 2013). Natural history museums are not only important scientific research institutions, but also one of the most popular, competent, and successful institutions for the transfer of scientific knowledge to the public (Ohl et al., 2014). Through their NHCs and exhibitions, natural history museums all over the world communicate how scientists explore and understand the natural world to the public. Thus, by connecting people to biodiversity research and discovery, natural history museums play a crucial role in inspiring people to protect and conserve the amazing diversity of life that exists on Earth.

1.4 A narrative overview of this thesis

I started my doctoral studies working at the Natural History Museum in London (NHM), to re-discover the forgotten Henry Buckley Collection of Planktonic Foraminifera (Chapter 2). This work was very exciting because I was part of the NHM efforts to digitise NHCs, using their new imaging technologies and innovative workflows. I imaged every slide of the collection and it is fulfilling to realise that anyone from anywhere in the world can now see these specimens online at the NHM Data Portal (https://-doi.org/10.5519/0035055). I also had the chance to participate on public engagement events at the NHM, such as the Science Uncovered and Nature Live.

The Buckley Collection has mainly modern specimens with a wide geographical scope and high intraspecific resolution (i.e., many specimens per species per sample) (Chapter 2). However, little information was available about the methodology used to sample the seafloor sediments and the foraminifers from these sediments. These seafloor sediments were sampled by pioneering marine expeditions such as HMS *Challenger*, when seafloor sampling techniques were elementary. To assess whether these historical samples are representative of surface sediments, I re-sampled untouched bulk sediments that were still in their original glass jars (Fig. 3.4). I compared the species composition of the randomly sampled historical data with the composition extracted from openly available datasets of the Holocene and Last Glacial Maximum, to assess the degree of sediment mixture in the historical samples (Chapter 3).

Buckley amassed his collection rather secretly, because the museum in the 1970s and 80s did not encourage him to study microfossils (Chapter 2). Despite the lack of support, Buckley picked and mounted almost 24,000 specimens, certainly out of passion, with the aim of producing an Atlas of modern planktonic Foraminifera. I used the Buckley Collection to explore how species vary in shell size across their ranges, and also estimated the shell size biases in the collection (Chapter 4). I tested the hypothesis that species are largest where they are most abundant, with this correlation indicating the species' ecological optimum (Hecht, 1976; Schmidt et al., 2004a). This hypothesis is very interesting because shell size is readily measurable in the fossil record, and could potentially inform us about ecological optimum of extinct species and adaptive evolution in deep time. Size could also inform us about the species' cryptic genetic diversity: if two populations of the same species are adapting to different environmental conditions (i.e., adaptive divergence), we could expect to see these populations increasing in size at different environmental optima. Thus, within the biogeographical range of the species, more than one peak in maximum shell size could indicate the beginning of a speciation process that would also be evident when analysing the species' cryptic genetic diversity (Schmidt et al., 2004a). With this idea in mind, I wrote a proposal to work in Bremen for one year with Prof. Michal Kucera and was awarded the Research Grant for Doctoral Candidates from the German Academic Exchange Service (DAAD) to do so.

During my doctoral studies I discovered that, although we communicate science in an objective and linear way (i.e., question, data to answer the question, answer), the *process* of doing science is actually 'branchy' and cloudy[4]. We often have to re-evaluate our questions, hypotheses and expectations. This was the case of my Chapter 4: shell size and abundance did not show the positive relationship that I expected based on the literature. Thus, the project I wrote for the DAAD grant could not be accomplished. However, in Bremen, I had the amazing chance to participate on the FORAMFLUX expedition (RV *Meteor* M140) in August−September 2017 and experience how to sample the plankton with nets and sediment traps. Knowing about available data on species relative abundance in seafloor sediments (coretops) and species population dynamics in the water column (sediment traps), I had the idea that we could test how species' occurrence patterns and dynamics relate to each other. From the fossil record, it seems that competition among species is an important mechanism driving planktonic Foraminifera diversification (Ezard et al., 2011; Ezard and Purvis, 2016), thus I tested in Chapter 5 whether competition is also structuring communities in the modern oceans.

In summary, my thesis examines ecological patterns within and interactions among extant planktonic Foraminifera species. Because of the global scale of the population- and community-level patterns I investigate in this thesis, my work contributes to the field of macroecology. I begin by describing the NHM Henry Buckley Collection of Planktonic Foraminifera with the aim of encouraging the use of NHCs (Chapter 2). I then study historical ocean-floor surface sediments to assess their age biases, i.e., degree of mixing between modern and glacial material (Chapter 3). These historical sediment samples were used by Buckley to create his collection, but could also be used as a pre-1900s reference baseline of the ocean floor environment. The global scope and high intraspecific resolution of the Buckley Collection allowed me to investigate the biogeography of population shell size of nine modern planktonic Foraminifera species (Chapter 4). I then investigate ecological interactions among modern species using a community ecology approach with data from coretop and sediment trap samples (Chapter 5). By deepening our understanding of modern planktonic Foraminifera ecology, we can unlock the unique population-level macroevolutionary dynamics their fossil record provides. I conclude by summarising the implications of my discoveries, discussing their limitations, and suggesting future areas of research (Chapter 6).

[4]Inspired by the TED talk from Uri Alon named "Why Science Demands a Leap into the Unknown"

Chapter 2

The unknown planktonic foraminiferal pioneer Henry A. Buckley and his collection at The Natural History Museum, London

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Abstract:
The Henry Buckley Collection of Planktonic Foraminifera at the Natural History Museum in London (NHMUK) consists of 1665 single-taxon slides housing 23 897 individuals from 203 sites in all the major ocean basins, as well as a vast research library of Scanning Electron Microscope (SEM) photomicrographs. Buckley picked the material from the NHMUK Ocean-Bottom Deposits Collection and also from fresh tow samples. However, his collection remains largely unused as he was discouraged by his managers in the Mineralogy Department from working on or publicizing the collection. Nevertheless, Buckley published pioneering papers on isotopic interpretation of oceanographic and climatic change and was one of the first researchers to investigate foraminiferal wall structure using the SEM technique. Details of the collection and images of each slide are available from the NHMUK Data Portal (http://dx.doi.org/10.5519/0035055). The Buckley Collection and its associated Ocean-Bottom Deposits Collection have great potential for taxon-specific studies as well as geochemical work, and both collections are available on request.

Keywords:
natural history collections, digitisation, open-access, zooplankton, sea-bottom

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Natural history collections provide a rich source of palaeontological data and contribute to a wide range of biostratigraphic studies at taxonomic, population and community levels. Conserved in museums and other institutions, these repositories contain specimens as primary data curated with associated metadata. One such repository is the Henry Buckley Collection of Planktonic Foraminifera held by the Natural History Museum in London (NHMUK). For convenience in this paper, the abbreviation 'NHMUK' is used throughout, even where the original name of the institution was The British Museum (Natural History). Here we present an overview of the Henry Buckley Collection with the aim of promoting the work of Buckley to the micropalaeontological community and to advocate the use of abundant resources like these held in natural history museums.

2.1 Historical Background

The establishment of the Oceanographic Section in the Department of Mineralogy of the NHMUK began with the acquisition, in 1935, of the John Murray Collection. Sir John Murray was one of the naturalists on the voyage of HMS *Challenger* and his collection included many of the zoological, botanical and geological specimens collected during the expedition (Lingwood, 1981). The Marine Deposits of the Murray Collection consist of 9746 marine samples and formed the nucleus of the Ocean-Bottom Deposit (OBD) Collection. The His Egyptian Majesty's Ship *Mabahiss* John Murray Expedition in 1933-34 further enlarged the OBD Collection with samples from the western Indian Ocean, a region that the *Challenger* expedition had not visited. Moreover, the Admiralty (British Royal Navy) continuously supplied the OBD Collection with material collected by its survey ships (Kempe and Buckley, 1987). Today the OBD Collection consists of samples from some 40 000 geographical locations from all of the world's oceans.

The first Keeper of the OBD Collection was Dr John Dugdale Holt Wiseman (1907-91), who worked at the NHMUK until his retirement in 1972 and was Henry A. Buckley's first manager. Henry Alexander Buckley (1939-2002, Fig. 2.3) joined the NHMUK Oceanographic Section in 1961 to curate the OBD Collection. Buckley had a degree in Geology and Zoology from the University of Manchester. He became interested in foraminiferal research through the encouragement of Dr Wiseman (Kempe and Buckley, 1987). During his working years with the OBD Collection, Buckley amassed a large specimen slide collection of planktonic Foraminifera and a research library of SEM photomicrographs for each species that he could recognize morphologically (Fig. 2.1). His initial work focused on the use of planktonic Foraminifera for isotopic interpretation of oceanographic and climatic change (Shackleton et al., 1973). In 1966, Buckley became one

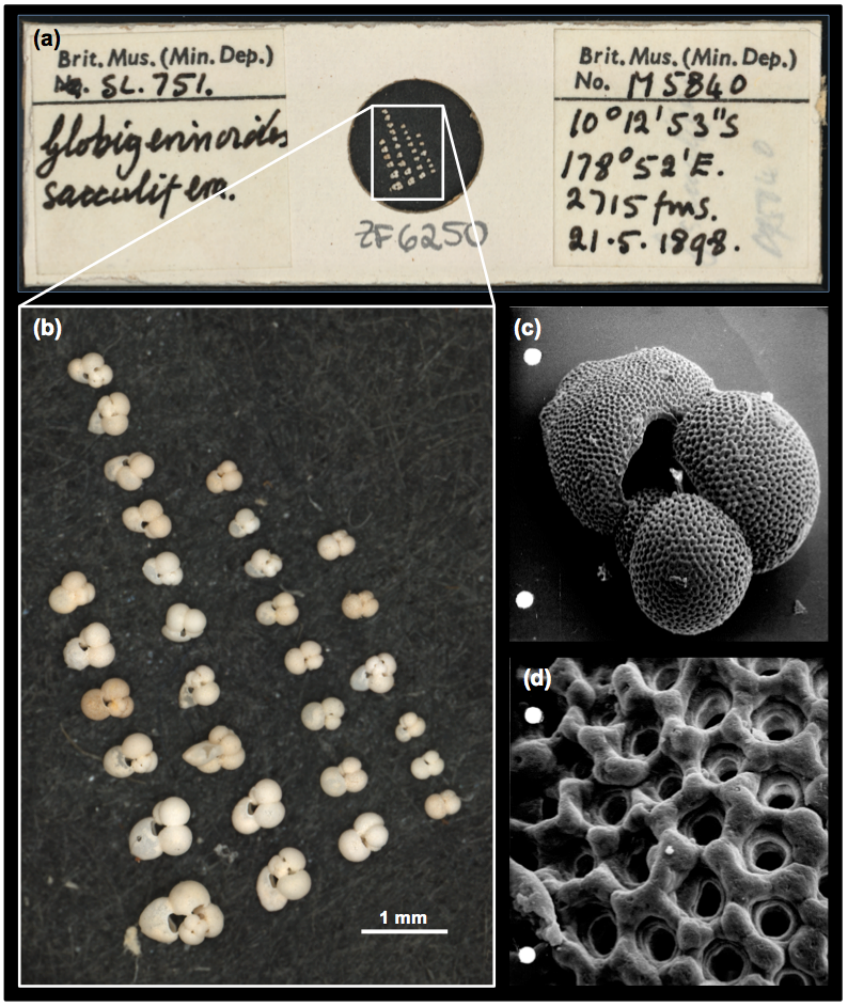

FIGURE 2.1: Example of the contents of the Henry Buckley Collection, NHMUK: **(a)** slide no. ZF6250 with *Trilobatus sacculifer*; **(b)** specimens of the slide no. ZF6250; SEM photomicrographs taken in 1968 of **(c)** *T. sacculifer* x130 magnification; and **(d)** its wall structure x1300 magnification.

of the first scientists to use the SEM technique, when the first SEM (Cambridge Stereoscan Mk II, Fig. 2.4) was purchased by the NHMUK. He used the SEM to examine the wall structure, texture and composition of planktonic Foraminifera tests (Fig. 2.1d), and appreciated the importance of these characteristics for the group's systematics.

Buckley's passion was to produce an *Atlas of Modern Planktonic Foraminifera*. He progressed by refining and augmenting his slide collection with specimens from different deep-sea locations and also fresh tow samples (from 1953 to 1967). Buckley described a new species (*Globorotalia oveyi* Buckley 1973) and used the collection in a series of papers on climate change, glaciation and sapropel formation (Buckley, 1976; Buckley et al., 1982; Buckley and Johnson, 1988). Buckley also published on the formation of minerals such as glauconite (Buckley et al., 1978; Fleet et al., 1980; Buckley et al., 1984; Hall and Buckley, 1991) and the mineralogical composition of sediments

(Buckley et al., 1974; Easton and Buckley, 1979, 1983; Buckley and Woolley, 1990). Despite early encouragement from Dr Wiseman, Buckley was officially discouraged by his later managers at the NHMUK from working on the biology and taxonomy of planktonic Foraminifera for a number of political reasons, and because he was not considered to be a trained micropalaeontologist (Whittaker, pers. comm. 2015). He was never allowed to proceed with his *Atlas*. As a consequence, Buckley is almost unknown within the planktonic foraminiferal community.

2.2 The Henry Buckley Collection of Planktonic Foraminifera

2.2.1 Slide Collection

The Buckley collection includes 1665 slides from 203 geographic sites and contains 23 897 picked and mounted specimens (Table 2.1). Each slide is arranged taxonomically and labelled with geographic coordinates and sampling details (Fig. 2.1a). Of the 203 sites, 79 are represented by plankton tow specimens, 122 from ocean bottom sediments and two from onshore (Fig. 2.2). The collection includes coretop material and also material from various depths within cores. Topotypes from the original type locality include the species *Beella digitata* (Brady, 1879), *Turborotalita quinqueloba* (Natland, 1938), *Globorotaloides hexagonus* (Natland, 1938) and *Neogloboquadrina dutertrei* (d'Orbigny, 1839).

Of the 1665 slides, 1355 contain modern planktonic Foraminifera (Table 2.1) sampled from 181 geographical sites worldwide. In total there are 16 343 modern specimens: 15 355 macroperforate and 988 microperforate (Table 2.2). Buckley mainly used the taxonomy of Parker (1962) and was able to identify 33 morphospecies in the collection, which are well spread throughout the phylogeny of planktonic Foraminifera and cover all recognized ecogroups (Aze et al., 2011).

Only 87 slides (5%) contain identified extinct planktonic Foraminifera species (Table 2.1), corresponding to 21 fossil species and a total of 915 individuals (Table 2.1). These specimens were sampled from 27 geographic sites, mostly concentrated within tropical latitudes of the Atlantic, Pacific and Indian oceans plus the Mediterranean Sea. There are also samples from onshore sites: Bissex Hill nappe on Barbados (Caribbean) and the Saipan Island Limestone (Pacific Ocean) (Fig. 2.2). Several locations contain fossil material derived from multiple depths. The deepest sample was taken from 950 to 953 cm below the seafloor in the Western Central Atlantic Ocean by RV *Vema* in 1959.

Table 2.1: Overview of the slide contents of the Henry Buckley Collection

Content of Slides	No. of Slides	No. of Specimens
Modern macroperforate planktonic Foraminifera	1253	15 355
Modern microperforate planktonic Foraminifera	102	988
Fossil planktonic Foraminifera	87	915
Unidentified Foraminifera	223	6639
Total	**1665**	**23 897**

Table 2.2: Modern specimens of the Henry Buckley Collection. The table shows the species' name (original and revised), ordered by the number of mounted specimens in the slide collection, and the number of geographical sites from which these specimens came.

Species name (original) (Henry A. Buckley)	**Species name (revised)** (Aze et al., 2011) (Spezzaferri et al., 2015)	**Number of specimens**	**Number of sites**
Macroperforate			
Globorotalia menardii	*Menardella menardii*	1,753	75
Globigerina pachyderma	*Neogloboquadrina pachyderma*	1,752	52
Globigerinoides sacculifera	*Trilobatus sacculifer*	1,564	79
Globigerinoides ruber	*Globigerinoides ruber*	1,484	81
Globoquadrina eggeri / Globigerina dutertrei	*Neogloboquadrina dutertrei*	1,054	76
Globorotalia inflata	*Globoconella inflata*	866	36
Globorotalia truncatulinoides	*Truncorotalia truncatulinoides*	861	51
Globigerinella aequilateralis / siphonifera	*Globigerinella siphonifera*	855	75
Globigerinoides conglobatus	*Globigerinoides conglobatus*	774	60
Globigerina bulloides	*Globigerina bulloides*	675	31
Pulleniatina obliquiloculata	*Pulleniatina obliquiloculata*	619	67
Sphaeroidinella dehiscens	*Sphaeroidinella dehiscens*	476	41
Globorotalia crassaformis	*Truncorotalia crassaformis*	311	27
Globigerinoides tenellus	*Globoturborotalita tenella*	308	26
Globorotalia tumida	*Globorotalia tumida*	306	31
Globoquadrina conglomerata	*Globoquadrina conglomerata*	214	28
Globigerina rubescens	*Globoturborotalita rubescens*	200	23
Globorotalia hirsuta	*Hirsutella hirsuta*	179	14
Globorotalia scitula	*Hirsutella scitula*	166	25
Orbulina universa	*Orbulina universa*	162	24
Globigerinita humilis	*Turborotalita humilis*	147	14
Globoquadrina hexagona	*Globorotaloides hexagonus*	142	26
Globigerina calida	*Globigerinella calida*	133	25
Globigerina falconensis	*Globigerina falconensis*	127	13
Globigerina digitata	*Beella digitata*	90	25
Globigerina quinqueloba	*Turborotalita quinqueloba*	77	9
Globigerinoides trilobus	*Trilobatus trilobus*	47	1
Globigerinella adamsi	*Globigerinella adamsi*	13	8
Microperforate			
Globigerinita glutinata	*Globigerinita glutinata*	695	43
Candeina nitida	*Candeina nitida*	221	25
Hastigerina pelagica	*Hastigerina pelagica*	34	12
Globigerinita iota	*Tenuitella iota*	31	5
Globigerinita uvula	*Globigerinita uvula*	7	2
Total		**16 343**	**181**

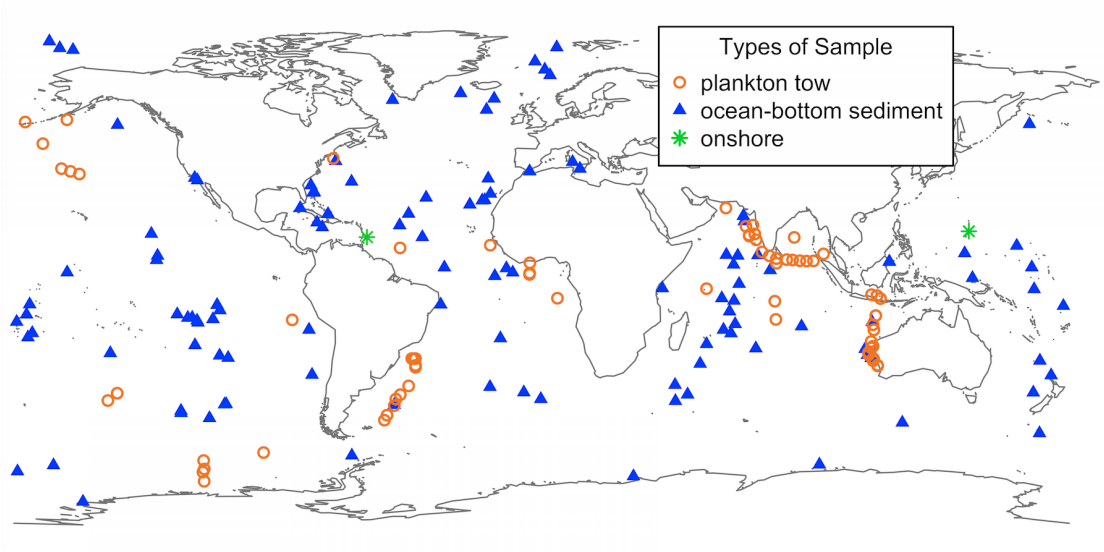

FIGURE 2.2: Map with the sample sites of the Henry Buckley Collection plotted on modern coordinates.

2.2.2 Scanning Electron Microscope Photomicrographs

The Buckley Collection includes 100 files of SEM photomicrographs, arranged by planktonic foraminiferal taxon, plus 23 files of nannofossil images. These files are curated with museum numbers, which allow the access to geographic and cruise information. In total, there are more than 1000 photomicrographs (Fig. 2.1c,d).

2.2.3 Digitisation of the Buckley Slide Collection

In 2015 the collection was entered into a database using information from the slides and derived information from the OBD Collection, such as core length or total sediment mass sampled. Water depth measurements available with the collection were mostly reported in fathoms. We added more precise and repeatable water depth values based on modern bathymetric models using the R *marmap* package (Pante and Simon-Bouhet, 2013; R Core Team, 2017) with five arc-minute resolution. Slides were imaged in the NHMUK Sackler Biodiversity Imaging Laboratory using the Zeiss Axio Zoom V16 microscope and the ZEN software. Images were taken of whole slides and labels at 3.5x magnification (18.43 μm x 18.43 μm per Pixel, Fig. 2.1a) and added to the NHMUK Data Portal. More detailed images of the specimens on each slide were also taken at 25x magnification (2.58 μm x 2.58 μm per Pixel, Fig. 2.1b).

2.3 Future Use of the Collection

The Henry Buckley Collection of Planktonic Foraminifera is available for study as part of the NHMUK Micropalaeontology Collection at South Kensington, London. The OBD Collection, including the original samples studied by Buckley, is located at the NHMUK off-site storage facility and also available on request. Information about each slide of the Buckley Collection can be found on the NHMUK Data Portal. Searching for a particular planktonic foraminiferal taxon is most efficient. To help with locating relevant specimen data, a file of the whole dataset has been deposited on the portal (http://dx.doi.org/10.5519/0035055).

Our ongoing work seeks to understand and quantify possible biases in the Henry Buckley Collection. Sediments from the OBD Collection used by Buckley have been resampled and reprocessed to assess taxonomic bias (systematic misidentification or incomplete representation of the assemblage) and size bias (bias towards picking out larger specimens or larger species). Once this bias analysis is complete, it will be added along with morphometric data to the collection dataset on the NHMUK Data Portal. Both will be discussed fully in future publications.

The Buckley Collection and the OBD Collection include historical sampling events dating back from the 1870s. Destructive sampling is possible for geochemical analyses, which allow the study of the consequences of human impact on the oceans in the intervening period, e.g. ocean acidification (Moy et al., 2009). The global scope of the Buckley Collection and the abundance of modern specimens in many species favour taxon-specific macroecological studies, such as the investigation of what drives the biogeography of size of modern planktonic Foraminifera species.

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FIGURE 2.3: Henry Alexander Buckley organising samples from the Ocean-Bottom Deposits Collection at the Natural History Museum of London (NHMUK). Courtesy of the NHMUK.

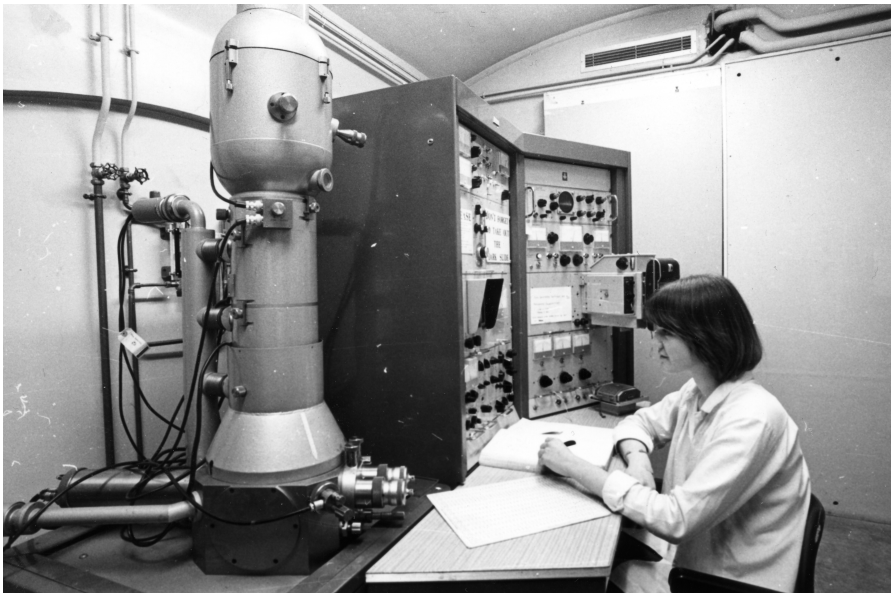

FIGURE 2.4: Scanning electron microscope (SEM) Cambridge Stereoscan Mk II, the first SEM held by the Natural History Museum of London, purchased in April 1966. Courtesy of Dr. Alex Ball.

Chapter 3

Surface sediment samples from early age of seafloor exploration can provide a late 19th century baseline of the marine environment

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Abstract:
Ocean-floor sediment samples collected up to 150 years ago represent an important historical archive to benchmark global changes in the seafloor environment, such as species' range shifts and invasions and pollution trends. Such benchmarking requires that the historical sediment samples represent the state of the environment at, or shortly before, the time of collection. However, early oceanographic expeditions sampled the ocean floor using devices like the sounding tube or a dredge, which potentially disturb the sediment surface and recover a mix of Holocene (surface) and deeper, Pleistocene sediments. Here we use climate-sensitive microfossils as a fast biometric method to assess if historical seafloor samples contain a mixture of modern and glacial sediments. Our assessment is based on comparing the composition of planktonic Foraminifera (PF) assemblages in historical samples with Holocene and Last Glacial Maximum (LGM) global reference datasets. We show that eight out of the nine historical samples contain PF assemblages more similar to the Holocene than to the LGM assemblages, but the comparisons are only significant in two sites where there is high local species' temporal turnover (from the LGM to the Holocene). When analysing temporal turnover globally, we show that upwelling and temperate regions had greatest species turnover, which are areas where our new methodology would be most diagnostic. Our results suggest that sediment samples from historical collections can provide a baseline of the state of marine ecosystems in the late nineteenth century, and thus be used to assess ocean global change trends.

Keywords:
natural history collection (NHC), historical collections, pre-industrial, pre-anthropogenic, beta-diversity, species turnover, global change

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3.1 Introduction

Late nineteenth and early twentieth century oceanographic expeditions set out to explore the vast and then widely unknown deep ocean. The voyage of HMS *Challenger* is a notable example. As she sailed around the globe between 1872−76, researchers mapped for the first time the shape of the ocean basins and described over 4,500 new species of marine life (Manten, 1972). These early expeditions have important historical significance, as they mark the beginning of modern oceanography and stimulated further ocean exploration (Wust, 1964).

From a scientific perspective, the observations and material acquired by these historical expeditions have great potential for global change research (Lister and Climate Change Research Group, 2011; Johnson et al., 2011), as they provide a pre-1900 baseline of the marine environment (e.g., Roemmich et al. 2012; Gleckler et al. 2016). Yet historical seafloor sediment samples remain largely underutilised, because early seafloor sampling techniques involved collecting surficial sediments with instruments like the sounding tube, dredge or even the anchor (Thomson and Murray, 1891). All these instruments can penetrate below the surface and disturb the top layer of the sediment. As a result, such historical sediment samples might contain surface (Holocene) sediments mixed with deeper, glacial material (Hayward and Kawagata, 2005), potentially hindering their use as a historical baseline of the modern marine environment. Coring techniques provide more accurate sediment chronology (e.g., Rohl et al. 2000); however, historical samples represent the seafloor environment as much as 50 years before the earliest core samples collected (Wust, 1964) and, thus, contain sediments without any objects deposited after 1900. These uncontaminated historical samples can be useful for chemical analyses of the seafloor (e.g., pollution trends; Dekov et al. 2010), single-specimen analysis (e.g., Reichart et al. 2003; Wit et al. 2010) and investigations of species range shifts and invasions in the past century (e.g., Hoeksema et al. 2011). Therefore, it is important to assess the degree to which historical sediment samples represent Holocene or mixed-Pleistocene sediments.

One way to assess the degree of glacial mixing in the historical material is to determine its absolute age using the radiocarbon dating technique or glacial material proxies (e.g., Mg/Ca, oxygen isotopes). However, in cases where the extent of mixing is small, the exponentially decaying nature of the radiocarbon analysis can cause an ambiguous dating, and the isotopic analysis would require a large enough number of specimens to correctly represent the extent of the glacial mixing. Here we propose a complimentary method that uses planktonic Foraminifera assemblage composition as a climate-sensitive fingerprint of the sediment age. Planktonic Foraminifera (PF) are single-celled zooplankton that produce calcium carbonate shells and, upon death, accumulate in

great numbers on the ocean floor (Hemleben et al., 1989). PF assemblage composition is sensitive to sea surface temperature (Morey et al., 2005; Fenton et al., 2016b) and its change between glacial and interglacial times has been used to determine the magnitude of glacial ocean cooling (MARGO Project Members, 2009).

In this brief report, we make use of the temperature sensitivity of PF and compare the composition of their assemblages in nine historical (> 100 years old) samples against reference PF assemblages from the Holocene (Siccha and Kucera, 2017) and the Last Glacial Maximum (Kucera et al., 2005a). We test whether it is possible to recover the extent of glacial mixing in historical seafloor sediment samples using PF assemblage composition. This new biometric method contributes to a more multidisciplinary approach to dating historical sediments.

3.2 Material and Methods

3.2.1 Historical samples

Historical samples were retrieved from the Ocean-Bottom Deposits (OBD) Collection held by The Natural History Museum in London. The OBD Collection holds about 40,000 historical samples from the world's oceans (https://doi.org/10.551 9/0096416), including most of the sediment samples collected by HMS *Challenger* and the British Royal Navy survey ships (Kempe and Buckley, 1987). The OBD samples are kept sealed in their original glass jars and tubes (Fig. 3.4) and are usually dry as the result of the long (over 100 years) storage. We selected nine samples collected between 1874 and 1905, chosen to cover different oceans, latitudes and historical marine expeditions (Table 3.1). Half of the amount available in the OBD containers was further split into two equal parts, leaving an archive sample and a sample to be processed. The sample processing consisted of weighing, wet washing over a 63μm sieve and drying in a 60°C oven. The residues were further dry sieved over a 150μm sieve and the coarser fraction was split with a microsplitter as many times as needed to produce a representative aliquot containing around 300 PF shells (see Al-Sabouni et al. 2007). All PF specimens in each of the nine final splits were picked, glued to a micropalaeontology slide and identified under a stereomicroscope to species level, resulting in a total of 2,611 individuals belonging to 31 species (Table 3.1, Table A.1).

TABLE 3.1: Information about the historical sediment samples from the Ocean Bottom Deposits (OBD) Collection at The Natural History Museum, London (NHMUK). Columns: NHMUK John Murray sample number; vessel that collected the sample (HMS stands for Her/His Majesty's Ship); date that the sample was collected; method used for sampling; ocean where the sample was collected; latitude and longitude in decimal degrees; water depth in meters (transformed from fathoms); sampled mass before processing, in grams; number of splits to sample around 300 planktonic Foraminifera (PF) individuals; number of PF individuals identified; number of PF species identified.

Sample	Vessel HMS	Date	Method	Ocean	Lat	Long	Depth	m(g)	N(spl)	N(ind)	N(sp)
M.25	*Challenger*	21/02/1873	Sounding	Atlantic	24.33	-24.47	5011	2.73	5	260	18
M.192	*Challenger*	07/03/1874	Sounding	Indian	-50.02	123.07	3976	0.19	5	318	7
M.284	*Challenger*	11/03/1875	Sounding	Pacific	-0.70	147.00	2012	1.98	7	331	16
M.408	*Challenger*	21/03/1876	Dredge	Atlantic	-21.25	-14.03	3639	9.35	7	265	21
M.3787	*Egeria*	31/10/1887	Sounding	Indian	-19.57	64.63	2869	1.23	5	376	24
M.4080	*Egeria*	26/08/1889	Sounding	Pacific	-15.65	-179.06	2579	2.42	8	300	13
M.5246	*Penguin*	16/04/1891	Sounding	Indian	-26.94	111.18	3676	1.49	5	279	18
M.8780	*Waterwitch*	22/01/1895	Sounding	Indian	-40.45	49.82	3780	1.51	6	177	11
M.7487	*Sealark*	09/11/1905	Sounding	Indian	-7.59	61.48	3758	2.86	8	305	18
Total										2,611	31

3.2.2 Holocene and Last Glacial Maximum data

We tested whether the composition of PF assemblages in the historical samples is more similar to assemblages of the Holocene (last 11,700 years, Walker et al. 2008) or the Last Glacial Maximum (LGM, 21,000 years ago, MARGO Project Members 2009). The Holocene census dataset (i.e., marine surface sediment samples taken by coring methods after 1945) was recently curated and published as the ForCenS dataset, comprising 4,205 assemblage counts from unique sites (Siccha and Kucera, 2017). Three LGM datasets from the MARGO project (Kucera et al., 2005a,b,c; Barrows and Juggins, 2004) were merged following the taxonomic standardisation of Siccha and Kucera (2017). This merged LGM dataset includes 1165 counts from 389 unique sites. Moreover, local estimates of open-ocean sedimentation rates are available for 156 samples in the LGM dataset, and were used to analyse the results.

The assemblage compositions of the nine historical samples were then compared to the samples from the geographically nearest site in the Holocene and LGM datasets (Fig. 3.1A). The distances between sites were calculated using the World Geodetic System of 1984 (WGS84, Hijmans 2015). We then compiled annual mean and standard deviation values of sea surface temperature (SST) from the World Ocean Atlas 2013 (WOA13, 0 meters depth, Locarnini et al. 2013) for each of the 27 sites (historical, Holocene and LGM) to evaluate whether the neighbouring sites are at similar modern SST ranges. Most neighbouring sites had similar SST values except the two most southern samples (Fig. 3.1B). The exceptional Holocene nearest sample neighbouring M.8780 was substituted by the fourth nearest neighbour, 66 km farther but more similar in SST (Fig. 3.1B). The mean distance between our nine sites and their nearest neighbour set was 253 km in the Holocene data and 415 km in the LGM data.

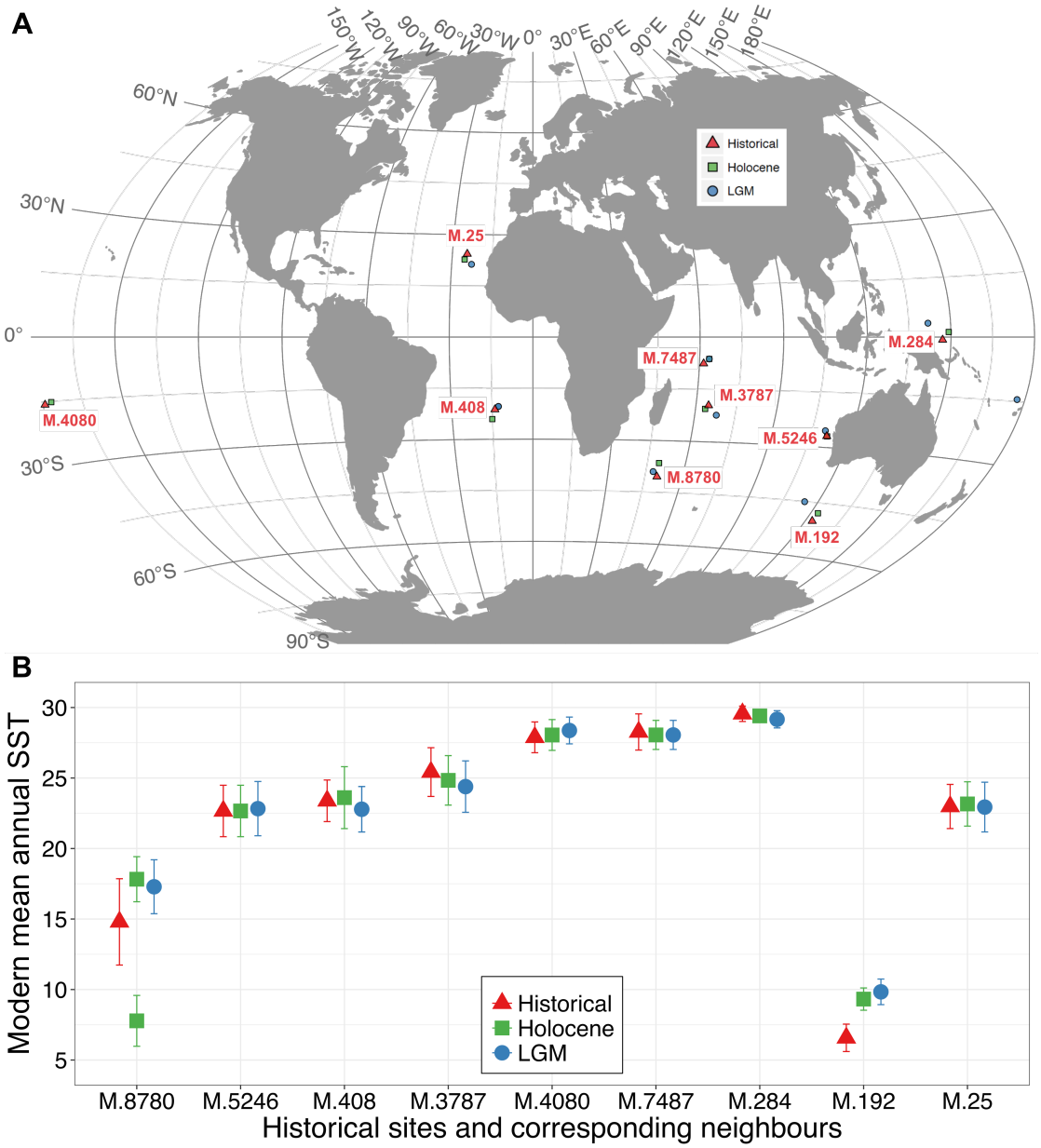

FIGURE 3.1: (A) Map of historical sample sites (red triangles) and corresponding neighbouring sites of the Holocene (green squares, ForCenS database) and Last Glacial Maximum (blue dots, LGM, MARGO datasets). Distances between each historical site and its corresponding Holocene and LGM neighbours can be seen in Tables A.2, A.3, A.4. (B) Modern mean annual sea surface temperature (SST, in degree Celsius) and annual standard deviations (bars) at each studied site (WOA13 data). Note that historical sample M.8780 has two values for the Holocene neighbour. The nearest Holocene neighbour (SST 7.8°C, distance of 374 km) was substituted by the fourth nearest neighbour, which had more similar SST values (17.8°C, distance of 440 km, see map above).

3.2.3 Compositional similarity

Assemblage similarity was expressed using the Morisita-Horn index (Morisita, 1959; Horn, 1966), which is an abundance-based overlap measure that preserves essential properties of similarity measurements (Jost et al., 2011). The Morisita-Horn calculates the compositional similarity by pairwise comparison of the relative abundance of each species, and is robust to under-sampling (i.e., rare species occurrence) (Jost et al., 2011). The index was calculated using the under-sampling bias correction (Chao et al., 2006), bootstrap confidence intervals based on 100 replicates and the R package *SpadeR* (version 0.1.1, Chao et al. 2016).

For each of the nine historical assemblages, we calculated the Morisita-Horn index three times: between *(i)* historical and neighbouring Holocene assemblages, *(ii)* historical and neighbouring LGM assemblages and *(iii)* neighbouring Holocene and LGM assemblages. This third comparison gives us a baseline index value of how much the PF assemblage composition changed locally since the LGM. If historical samples are representative of surface sediments, the similarity index calculated between historical and Holocene samples should be higher than between historical and LGM samples, with non-overlapping confidence intervals. However, if historical samples are a mixture of Holocene and LGM material, confidence intervals of the historical-Holocene and historical-LGM comparisons overlap. Confidence intervals might also overlap if the baseline index value calculated between the neighbouring Holocene and the LGM samples is high. A high baseline value means that the local Holocene and LGM assemblages are similar and thus there is less statistical potential to detect whether a historical sediment is a surface or mixed-glacial sample. To understand where our biometric methodology would be most diagnostic, we compiled a world map of local species' turnover since the LGM, by calculating the Morisita-Horn index for each LGM sample and its nearest Holocene neighbour. Compositional similarity indexes were averaged per site. Distances between the Holocene sites and the 389 LGM sites were calculated using the WGS84, and averaged 52 km (median 1.5 km).

3.3 Results and Discussion

In eight out of the nine samples, the compositional similarity was higher between the historical and Holocene assemblages than between historical and LGM assemblages (Fig. 3.2A). However, non-overlapping confidence intervals were only present in two samples (M.25 and M.5246), inferring a Holocene age for these historical sediments. These two samples also showed the lowest similarities in assemblage composition between neighbouring LGM and Holocene assemblages (i.e., baseline value, grey dots in Fig. 3.2A), meaning that there was a greater change in PF assemblage composition since the LGM in these two locations. The main differences in species compositions were the high relative abundance of *Globigerina bulloides* in the LGM neighbouring sample of M.25, and of *Globoconella inflata* in the LGM neighbouring sample of M.5246 (Tables A.2,A.4).

Compositional similarity index between historical and Holocene samples was always above 0.75, reaching maximum similarity in five samples (Fig. 3.2A). In six samples, the confidence intervals of the three comparisons overlapped, and all the similarity indexes were above 0.75. Since LGM and Holocene PF assemblages showed higher similarity at these six sites, our biometric test is less diagnostic. The historical sample M.8780 showed no overlap between historical-Holocene and Holocene-LGM, but the historical-LGM comparison overlapped with both comparisons, suggesting that either this sample has a mix of Holocene and glacial material, or the SST differences among these neighbouring samples prevents appropriate compositional comparisons (Fig. 3.1B). M.8780 had more *Neogloboquadrina pachyderma* than both the Holocene and LGM neighbours, and had *G. bulloides* abundances above 20%, similar to the LGM neighbour (Table A.2). Moreover, differences in SST among the neighbouring samples of M.192 (Fig. 3.1B) did not seem to influence their compositional similarities (Fig. 3.2A). Finally, the historical sample M.7487 was the only one that showed higher similarity with LGM than Holocene assemblages, indicating possible sediment mixing. The higher relative abundances of *Trilobatus sacculifer*, *N. incompta* and *Globigerinita glutinata* were responsible for this pattern (Table A.4).

The global comparison between the Holocene and the LGM reference datasets shows the magnitude of PF assemblages turnover since the LGM (i.e., temporal beta-diversity, Fig. 3.2B). In general, upwelling (eastern boundary currents and equatorial regions) and temperate sites had greatest species turnover. Our methodology would be most diagnostic in these settings. Open-ocean sedimentation rates available for 156 sites averaged 6.8 centimetres per thousand of years (cm/ky). Therefore, historical sampling devices would have had to penetrate on average 142.8 cm (6.8 cm/ky times 21

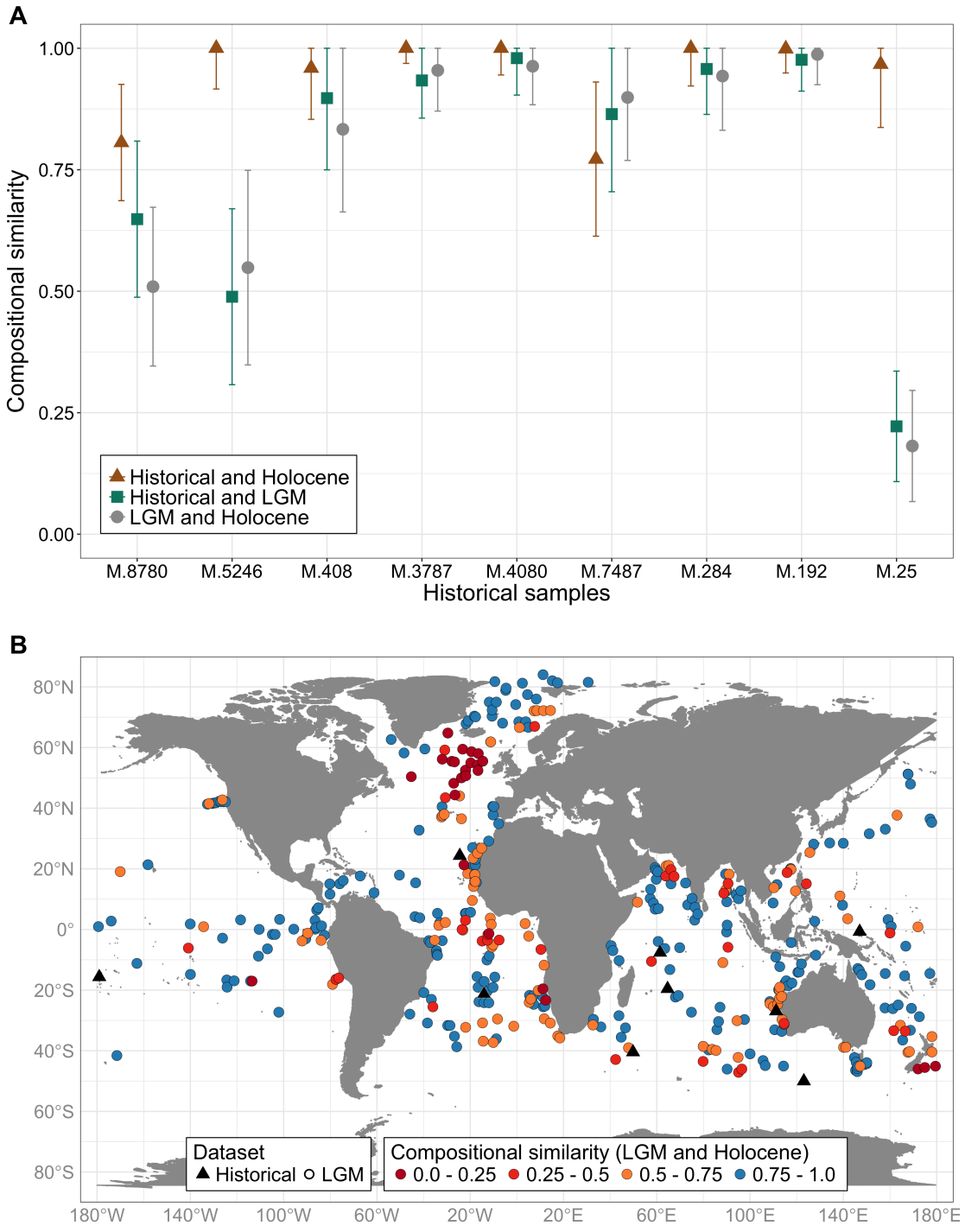

FIGURE 3.2: **(A)** Compositional similarity (Morisita-Horn index) between planktonic foraminiferal assemblages from historical sediment samples and assemblages from surface sediments (Holocene, brown triangle) and from the Last Glacial Maximum (LGM, green squares); and between Holocene and LGM assemblages (grey dots, baseline value of local temporal turnover). 0 means that the two assemblages share no species; 1 means that the same species were present in both samples at statistically indistinguishable proportions. Lines represent confidence intervals based on 100 bootstrap replicates. The x-axis shows the historical sample number (Table 3.1). **(B)** Black triangles: historical samples (nine in total). Coloured dots: LGM samples from 389 sites worldwide. The colours represent the Morisita-Horn similarity index between the LGM sample and its neighbouring Holocene sample (i.e., temporal turnover). Red to orange dots indicate low similarity (i.e., high species turnover), whereas blue dots indicate similar Holocene and LGM planktonic Foraminifera assemblages.

ky) into the sediment to contaminate the surface seafloor sample with glacial material. Nevertheless, comparing sedimentation rates to the compositional similarity between LGM samples and their Holocene neighbours reveals that the greatest temporal turnover in species composition happened at sites of lower sedimentation rates (< 5 cm/ky, Fig. 3.3), where sediment mixing during historical sampling would be most likely. Furthermore, six LGM neighbours of our nine historical samples had local estimates of sedimentation rate, which varied from 1.0 to 3.4 cm/ky (mean 1.8 cm/ky, Tables A.2,A.3,A.4). Thus, considering our historical samples only, depths of 21−71.4 cm into the sediment would have already reached glacial age material. Historical ocean-floor sampling methods potentially disturbed the surface and led to recovery of a mix of Holocene and deeper sediments, especially at sites of lower sedimentation rates. Our biometric method would be most useful at these sites with similar sedimentation settings, which also show the greatest temporal turnover in species composition (Fig. 3.3).

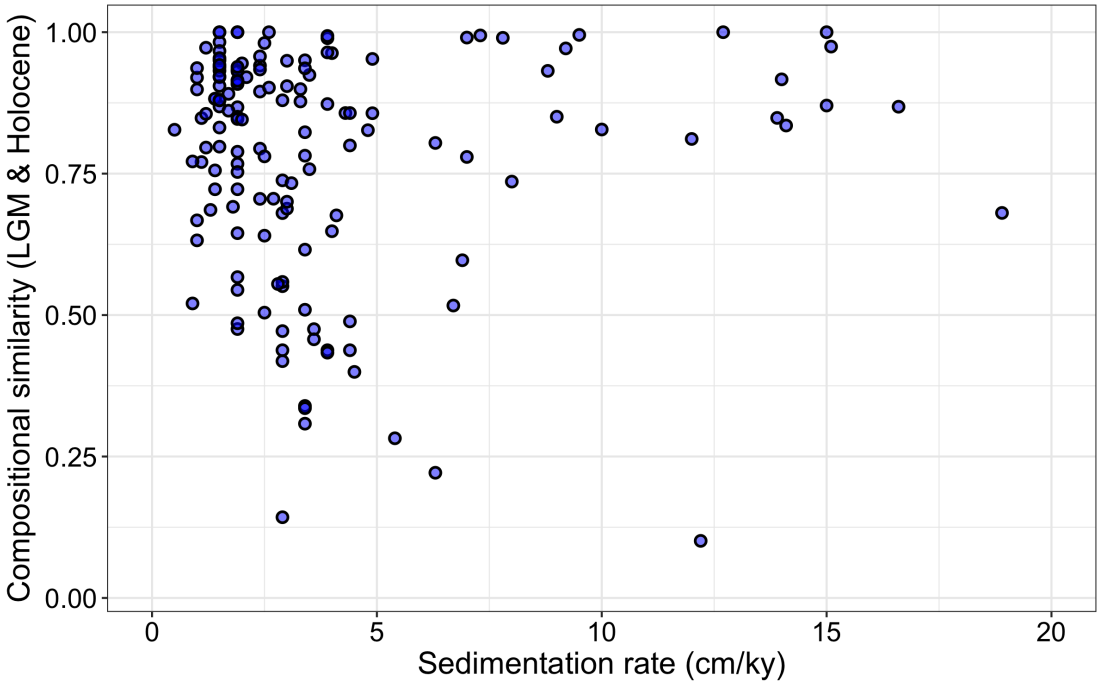

FIGURE 3.3: Compositional similarity (Morisita-Horn index) between planktonic Foraminifera assemblages in the LGM sample and its neighbouring Holocene sample, plotted against local estimates of open-ocean sedimentation rates (centimetres per thousand of years). Low similarity means a greater temporal turnover in the local assemblage composition. In total there are 150 sedimentation rate estimates; six samples with sedimentation rate higher than 20 cm/ky and compositional similarity above 0.75 are not shown.

3.4 Conclusion

Our results indicate that historical ocean-floor sediment samples (collected more than 100 years ago) can represent surface (Holocene) sediments, despite the use of technology not designed to recover undisturbed sediments. Our biometric method relies on the temporal turnover in species occurrence since the LGM. We show that this turnover varies in space making our method particularly suitable for upwelling and temperate areas with low sedimentation rates. The new method allows a non-destructive preliminary assessment of glacial contamination of historical samples. Independent proxy records (e.g., Mg/Ca) and/or radiocarbon dating would be valuable to validate the success of our technique. Ideally, the biometric approach would compliment chemical-based techniques to date historical sediments, aiming for more robust results as multiple alternative lines of evidence are presented. Our results highlight the scientific potential of historical seafloor sediment collections (Table 3.2). As human activities increasingly modify the marine environment, these historical collections contain important information on the pre-1900 state of marine ecosystems.

TABLE 3.2: Historical surface sediments collections

Museum	**Expedition**	**Spatial coverage**	**Period**
Natural History Museum in London	*Challenger*[1]	Atlantic, Antarctic, South Indian, Pacific	1872—76
Muséum National d'histoire Naturelle in Paris	*Travailleur, Talisman*[2]	Atlantic, Mediterranean	1880—83
Museum für Naturkunde in Berlin	German Deep-Sea[3] (*Valdivia*)	Atlantic, Antarctic, Indian, Mediterranean	1898—99

[1] https://www.hmschallenger.net/
[2] https://gallica.bnf.fr/ark:/12148/bpt6k65190274
[3] Keltie (1898); Sandeman (1900)

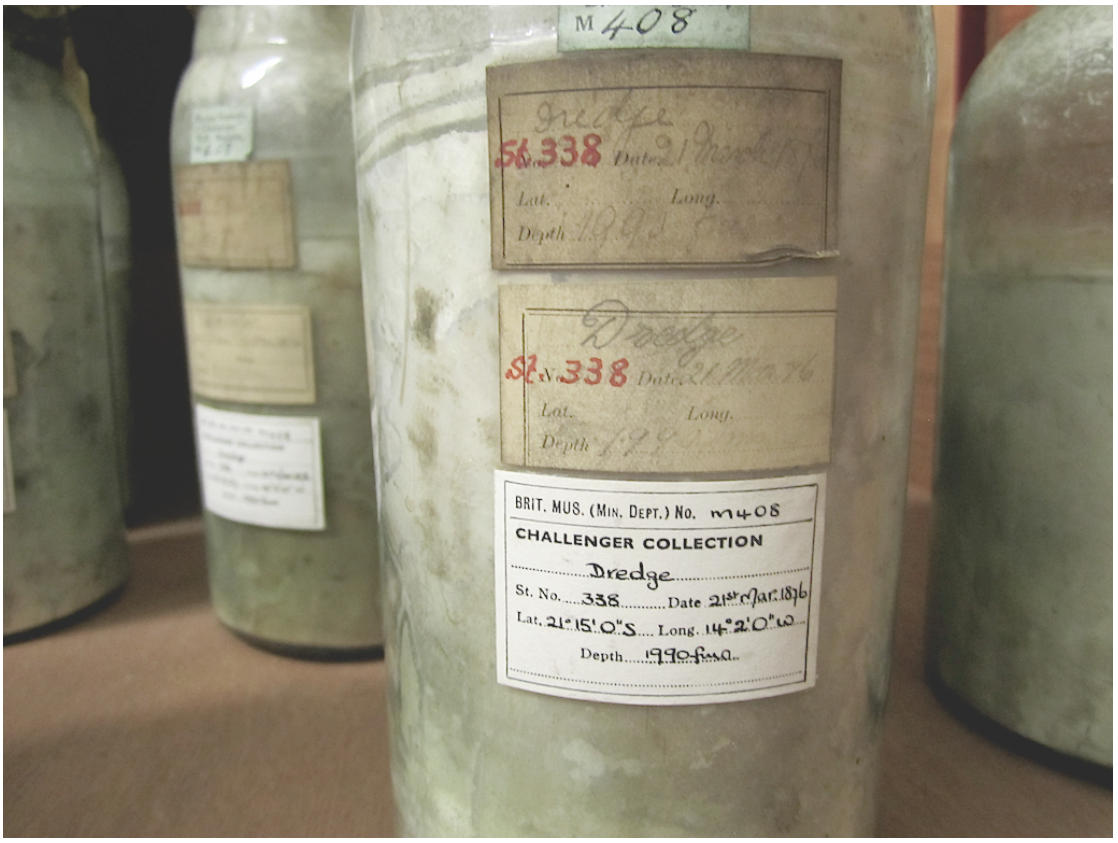

FIGURE 3.4: Ocean-floor sediment sample collected by HMS *Challenger* on the 21^{st} of March of 1876 with a dredge in the South Atlantic, sample number M.408 (see Table 3.1).

Author Contributions All authors designed the research question. MR processed the historical sediments, with input from GM. MR and MK identified all specimens. MR designed and performed the analysis, with input from MK and TE. MR wrote the initial draft, and all authors reviewed and edited the final manuscript.

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Data Availability Statement The data and the R code used to produce this analysis are available from the NHM Data Portal: https://doi.org/10.5519/0001936.

Chapter 4

Biogeographical patterns of intraspecific size variation in extant planktonic Foraminifera

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Abstract:
How plankton organism size varies within species across biogeographical scales is still poorly documented, although evidence has accumulated that intraspecific trait variation affects plankton functions in marine ecosystems. Here, we investigate for the first time at high intraspecific resolution how planktonic Foraminifera species, a ubiquitous zooplankton group, vary in size across the tropical and subtropical oceans of the world. We measured 3817 individuals of nine species in 53 surface sediments and obtained corresponding local values of annual mean sea-surface temperature (SST) and net primary productivity (NPP), as well as local relative abundance of the species. Given former studies, we expected populations to reach largest sizes under optimal environmental conditions, where populations reach highest relative abundances. However, we found that species greatly differ in how much size variation is explained by SST, NPP and/or relative abundance. While some species showed a high predictability of size variation given one single variable (SST for *Trilobatus sacculifer* and *Pulleniatina obliquiloculata*), other species showed either no (*Globigerinoides ruber*, *Neogloboquadrina dutertrei*) or weak (*Globoconella inflata*, *Globorotalia menardii*) relationships between size and the studied variables. SST and NPP combined explained most of the size variation observed in *Globigerinella siphonifera*, *Globorotalia truncatulinoides* and *Globigerinoides conglobatus*. Moreover, the relationship between size and local abundance was weak, contradicting the idea that planktonic Foraminifera species are largest at their environmental optima. By incorporating intraspecific variation and sampling broader geographical ranges compared to previous studies, we conclude that the relationship between planktonic Foraminifera size and SST, NPP and abundance differs among species and is, in general, weaker than previously reported.

Keywords:
biogeography of traits, intraspecific variation, macroecology, size trends, morphometrics, natural history collections (NHC), museum collections

4.1 Introduction

The size structure of plankton communities is an important determinant of the functions they realise in marine ecosystems (Litchman and Klausmeier, 2008; Litchman et al., 2013). However, most studies quantifying the size variation of plankton have focused on size distributions of communities (irrespective of species) or among-species (interspecific) instead of intraspecific, among-individuals variation (Sommer et al., 2017). Intraspecific variation can affect community dynamics as much as interspecific variation (Des Roches et al., 2018), and size variation within plankton species has been shown to influence their responses to environmental change (Mousing et al., 2017). Thus, by ignoring intraspecific variation, we have an incomplete understanding of the functions different plankton species perform in the community. A promising approach to investigate how variation within species corresponds to variation among species is to explore trait distributions biogeographically, i.e., along various environmental gradients, such as temperature or nutrient concentrations (Barton et al., 2013; Litchman et al., 2013).

Planktonic Foraminifera are an interesting group for studying intraspecific size variation across environmental gradients. They are unicellular zooplankton that occur across the world's oceans at low diversities (48 currently recognised species, (Siccha and Kucera, 2017)). They produce calcium carbonate tests (or shells), which upon death, sink and accumulate on the ocean floor. The abundance of their shells preserved in marine sediments allows estimates of population-level size variation on a global biogeographical scale (e.g., Schmidt et al. 2004a). Moreover, these abundant shells play a key role in the ocean carbon cycle (Schiebel, 2002a) and, under good sedimentary conditions, yield a remarkably complete fossil record that allows the quantification of how plankton size varied in response to past climatic changes (Schmidt et al., 2004c; Brombacher et al., 2017a). Thus, planktonic Foraminifera can help us elucidate the role of intraspecific variation in marine ecosystems across space and time; however, a quantification of individual size variation across large biogeographical ranges is missing, hampering our understanding of what controls their within-species size variation.

A planktonic foraminifer grows by sequential addition of chambers until reproduction, when the gametes are released (gametogenesis), the cell dies and the empty shell sinks to the ocean floor (Be, 1976; Hemleben et al., 1989). Modern species vary remarkably in size, from diameters in the order of 0.1 mm (*Berggrenia pumilio*) up to 2.5 mm (*Hastigerina pelagica*; Anderson and Be 1976). Planktonic Foraminifera show a global two-fold increase in average assemblage size from the poles to the tropics, and this increase correlates strongly with sea surface temperature (Schmidt et al., 2004a). This positive size-temperature relationship is opposite to the common pattern of smaller

sizes at higher temperatures observed in other plankton groups (Atkinson et al., 2003; Barton et al., 2013; Sommer et al., 2017). Higher temperatures are known to affect metabolic rates positively, resulting in smaller organisms and faster generation times (Brown et al., 2004; Savage et al., 2004). Planktonic Foraminifera assemblages, however, do not follow this rule (Schmidt et al., 2004a) and the reason might be related to their reproductive strategy. As far as we know, they reproduce only sexually (Hemleben et al., 1989) and thus rely on precise spatial and temporal synchrony with each other to maximise chances of fertilisation in the pelagic environment. Indeed, there appears to be a lunar periodicity to the reproductive cycle of some species (Bijma et al., 1990; Bijma and Hemleben, 1994; Jonkers et al., 2015; Venancio et al., 2016), suggesting that planktonic Foraminifera generation and development time is constrained by their synchronic reproduction. Unfortunately, planktonic Foraminifera have never reproduced in laboratory conditions, thus we have limited knowledge of their reproductive cycle, ecology and population dynamics.

Previous studies have looked at the biogeographical size distribution of planktonic Foraminifera and found that maximum shell size often coincides with maximum relative abundance, and occurs at specific optimum temperatures (optimum-size hypothesis; Kennett 1976; Hecht 1976; Malmgren and Kennett 1976, 1977; Kahn 1981; Schmidt et al. 2004a; Moller et al. 2013; see Be et al. 1973 for an exception). The local abundance of planktonic Foraminifera species is usually estimated by counting dead assemblages from ocean floor sediments (Siccha and Kucera, 2017). Although this methodology often yields species' relative abundances (relative to the co-occurring species in the sample) instead of absolute abundances, relative abundances estimated from marine sediments have the advantage of averaging out short-term fluctuations that might blur macroecological patterns (Fenton et al., 2016b). Most of the studies supporting the optimum-size hypothesis focused on a single oceanic basin, and thus a limited part of each species' biogeographical range (Be et al., 1973; Kennett, 1976; Hecht, 1976; Malmgren and Kennett, 1976, 1977; Kahn, 1981; Moller et al., 2013). The exception is the global study of Schmidt et al. (2004a), who analysed 69 Holocene samples worldwide. Although Schmidt et al. (2004a) were concerned with size variation of whole assemblages instead of within-species variation, they showed that the temperatures at which a species reaches largest size and highest relative abundance coincide, supporting the idea that planktonic Foraminifera species reach largest shell sizes at their environmental (thermal) optima. However, Schmidt et al. (2004a) only taxonomically identified a fraction of their measured individuals, thus a test of the optimum-size hypothesis at high intraspecific resolution and large biogeographical scale is still missing.

Nutrient availability can mediate the temperature-size relationships observed in the

plankton (Peter and Sommer, 2013; Marañón, 2015) and has been shown experimentally to affect planktonic Foraminifera size: more food facilitates faster cell growth and larger final shell size (Be et al., 1981; Takagi et al., 2018). Planktonic Foraminifera are omnivorous, preying on other plankton including diatoms, dinoflagellates, ciliates and copepods (Anderson et al., 1979; Spindler et al., 1984; Schiebel and Hemleben, 2017). Thus, phytoplankton are part of the foraminiferal diet and also attract herbivorous zooplankton, which planktonic Foraminifera also predate (Northcote and Neil, 2005). Thus, within a species's range, we expect planktonic Foraminifera size to increase positively with net primary productivity. Some species of planktonic Foraminifera are photosymbiotic with eukaryotic algae (Hemleben et al., 1989; Takagi et al., 2019). High net primary productivity means that nutrient and light conditions are favourable for photosynthesis, possibly having a direct positive effect on the photosymbionts inside the foraminifers. However, these photosymbiotic species usually occur in tropical-subtropical oligotrophic waters, suggesting photosymbiosis is an ecological strategy to survive in nutrient-limited environments (Be and Hutson, 1977). Nevertheless, experiments have shown that photosymbiosis can not be the only form of daily nutrition to the foraminifer, as symbiotic species still rely on prey phagocytosis to grow and achieve reproductive maturation (Takagi et al., 2018). Thus, symbiotic species might show different relationships between size and net primary productivity when compared to non-symbiotic species, but the expected relationship is not clear, and has not been tested on a biogeographical scale.

Here, we quantify the relationship between planktonic Foraminifera within-species size variation and local sea surface temperature (SST), net primary productivity (NPP) and relative abundance, plus the interaction between SST and NPP. We built a new population-level shell size dataset for nine extant species at a macroecological scale, which included the Pacific, Indian and Atlantic tropical and subtropical oceans. We expect population shell size to *(i)* increase with increasing SST for tropical species and *(ii)* reach largest values at intermediate SST for transitional species (Schmidt et al., 2006). The optimum-size hypothesis also predicts a *(iii)* positive relationship between local population shell size and relative abundances (Hecht, 1976). Lastly, we expect *(iv)* species to reach larger sizes where there are more resources available (i.e., higher NPP). As SST and NPP correlate in the open ocean (Schmidt et al., 2006; Fenton et al., 2016b), they might interact and, thus, jointly predict more of the observed size variation.

4.2 Material and Methods

Our size dataset was extracted from the recently-digitised Henry Buckley Collection of Planktonic Foraminifera (Rillo et al., 2016), held at The Natural History Museum in London, UK (NHMUK). We measured shell area of 3817 individuals from the nine species most commonly represented in the collection across 53 sites worldwide (Fig. 4.1). For each sampled site, we obtained corresponding data on the mean annual values of SST, NPP and relative abundance of each species. All the data visualisation and analyses were performed in the R programming language (version 3.3.3, R Core Team 2017).

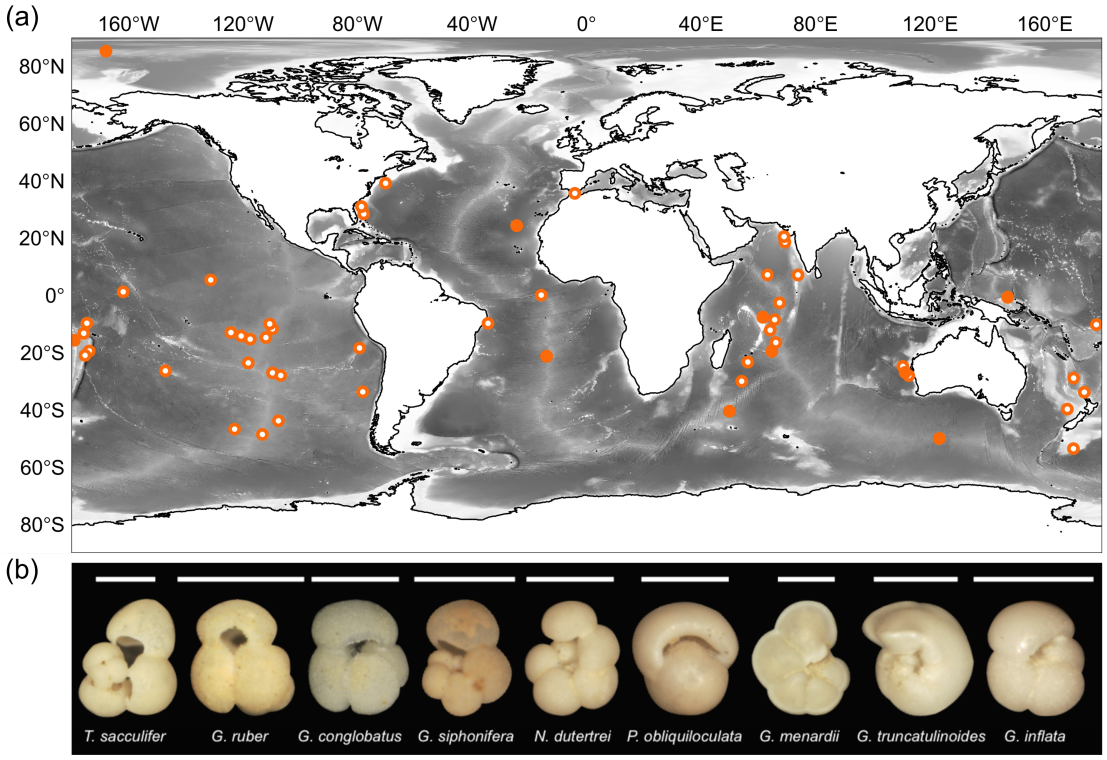

FIGURE 4.1: **(a)** Geographic distribution of the samples used from the Henry Buckley Collection of Planktonic Foraminifera. Each dot on the map includes data on planktonic Foraminifera shell size distributions, and corresponding data on mean annual values of sea surface temperature, net primary productivity and relative abundance. The filled dots represent the ten samples that were used to analyse the biases in the museum collection. The sample above 80°N was used only in the collection bias analysis. Grey colouring represents ocean depth, light grey shallower and dark grey deeper waters (R package *marmap*; (Pante and Simon-Bouhet, 2013). **(b)** A representative specimen from the collection for each species analysed. White bars represent 0.5 mm. From left to right: *Trilobatus sacculifer*, *Globigerinoides ruber*, *Globigerinoides conglobatus*, *Globigerinella siphonifera*, *Neogloboquadrina dutertrei*, *Pulleniatina obliquiloculata*, *Globorotalia menardii*, *Globorotalia truncatulinoides* and *Globoconella inflata*.

4.2.1 Study sites and samples

Henry Buckley sampled 122 marine sediments from the NHMUK Ocean-Bottom Deposits Collection (OBD) to amass the Henry Buckley Collection of Planktonic

Foraminifera (Rillo et al., 2016). Sample processing usually consists of washing the sediment and dry sieving it over a 150μm sieve, then sampling the coarser fraction for planktonic Foraminifera (see Appendix B). From the 122 samples processed by Buckley, we selected those that contained only modern Foraminifera species (Table B.6) within the upper 15 cm of sediment and included at least one of the nine studied species (Fig. 4.1b). This resulted in 53 study sites predominantly in the tropical and subtropical regions of the Pacific, Indian and Atlantic oceans (Fig. 4.1a), which were collected by historical marine expeditions between 1873 and 1965 (Table B.3).

We determined the water depth for each site by matching the collection's reported latitudes and longitudes to the ETOPO1 database hosted at the National Oceanic and Atmospheric Administration website (Amante and Eakins, 2009) using a 2 arc-minute grid resolution (R package *marmap* version 0.9.5; Pante and Simon-Bouhet 2013). Water depth ranged from 746 to 5153 meters below sea level (median 3296 m). Ten of the 53 samples in our dataset come from sediments prone to dissolution (i.e., waters deeper than 4000 meters for newly sedimented foraminifers; Berger and Piper 1972). Dissolution may affect species size distributions, as smaller individuals are more prone to dissolution (Kennett, 1976). We tested if water depth could explain population shell size variation using a linear-mixed effects model with species as a categorical random effect. We found no evidence that water depth is related to the size variation in the data (chi-square test, χ^2 = 1.83, P value = 0.18, Table B.7).

4.2.2 Shell size data

We measured cross-sectional shell area of the nine most abundant planktonic Foraminifera species in the Buckley Collection. Each species has at least 244 specimens in the collection, resulting in 3817 individuals (Table 4.1, 4.2). The specimens of the collection were imaged using a Zeiss Axio Zoom V16 microscope and ZEN software at a resolution of 2.58 μm x 2.58 μm per pixel. Individual size was estimated based on the two-dimensional image of the specimen using the software Image-Pro Premier (version 9.1), which automatically recognises each specimen and measures its shell area. This automated individual recognition is based on the contrast between the white shell and the black background of the slide. However, there was differential fading through the years of slide backgrounds of the Buckley Collection, which impeded the use of the same automated contrast threshold. Thus, the contrast threshold was inspected for each image and, when necessary, altered in order to precisely measure the shell contour of the specimen. Henry Buckley mounted most specimens on the slides in a standard orientation (Fig. 4.1b, Table 4.1); individuals that had a different orientation or dubious taxonomic identification were excluded from the analysis.

Brombacher et al. (2017b) quantified the reproducibility of shell area measurements and concluded that this two-dimensional size metric is highly consistent across slight orientations in mounting orientation. We avoided re-mounting the slides in order to preserve the Buckley Collection.

TABLE 4.1: Overview of the morphometric dataset extracted from the Henry Buckley Collection of Planktonic Foraminifera. Columns: species names; number of individuals measured; number of populations per species (i.e., number of geographical sites per species); species resolution (i.e., median number of individuals per sample); mounting position in the collection (i.e., position in which the individuals of each species were measured).

Species	N(ind)	N(pop)	Resolution	Mounting Position
Trilobatus sacculifer	674	38	15	umbilical or spiral
Globigerinoides ruber	481	39	10	umbilical or spiral
Globigerinoides conglobatus	345	38	8	umbilical
Globigerinella siphonifera	244	37	5	umbilical or spiral
Neogloboquadrina dutertrei	321	30	9	umbilical
Pulleniatina obliquiloculata	295	32	8.5	edge
Globorotalia menardii	665	29	16	umbilical or spiral
Globorotalia truncatulinoides	311	30	8.5	umbilical
Globoconella inflata	481	20	17.5	umbilical
Total	**3817**	**293**		

The Buckley Collection could exhibit a collector effort bias, typically towards larger specimens. To assess this potential bias, we re-sampled ten original bulk sediments from the OBD Collection that Buckley had used to amass his collection (filled dots in Fig. 4.1a, Table B.1). We processed these re-sampled samples (Appendix B), and mounted species-specific slides to extract shell size data in the same way as for the original Buckley Collection (described above). We then compared the shell size distributions between Buckley's samples and our re-samples. This comparison included 2873 individuals - 1824 from re-samples (Table B.1) and 1049 from the Buckley Collection - across 65 populations from 20 species collected from the ten samples. We log-transformed the shell area data and calculated the mean, median, 75^{th} percentile, 95^{th} percentile and maximum value of each population shell size distribution. We then regressed each of these five population metrics of the Buckley Collection against the re-sampled data (e.g., Fig. 4.3b), and calculated the residuals based on the identity function (1:1 or y=x, relationship). The residuals of the regressions are predominantly positive (Fig. 4.3a), indicating that the Buckley Collection has a consistent collector bias towards large specimens.

The mean squared error is lowest for the 95^{th} percentile (Fig. 4.3a), meaning that this metric is the most representative population metric of the Buckley Collection. The robustness of the 95^{th} percentile of size distributions has also been documented by Schmidt et al. (2004a), as it is less sensitive to single outliers than the maximum value, and to representative sampling at the lower end of the size range than the mean and

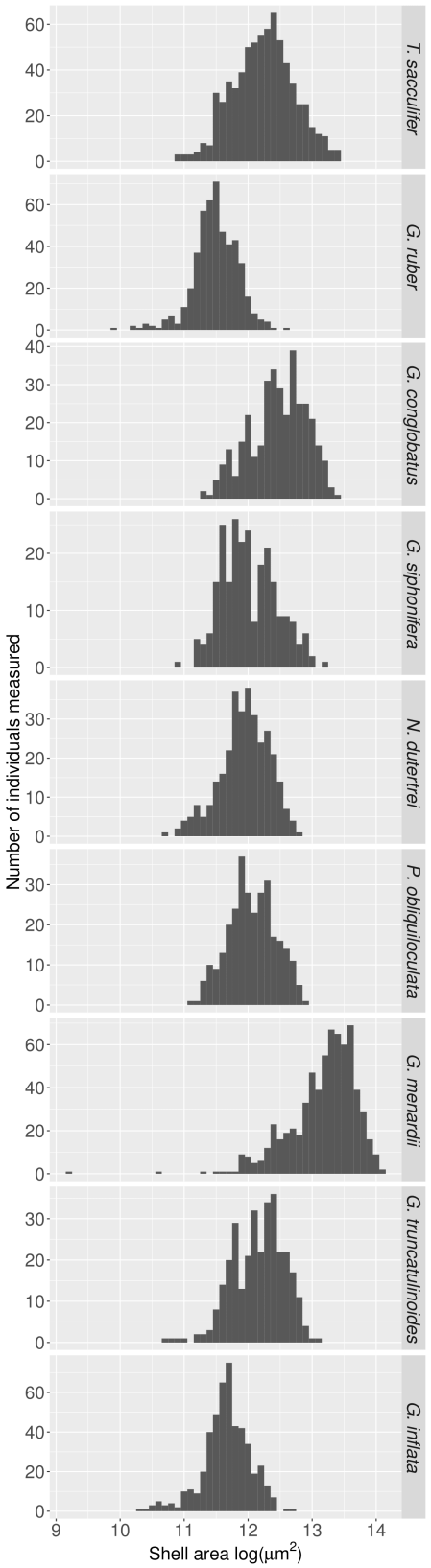

FIGURE 4.2: Shell size histograms (logarithm of the area) for each species of planktonic Foraminifera present in the morphometric dataset. A total of 3817 individuals were measured.

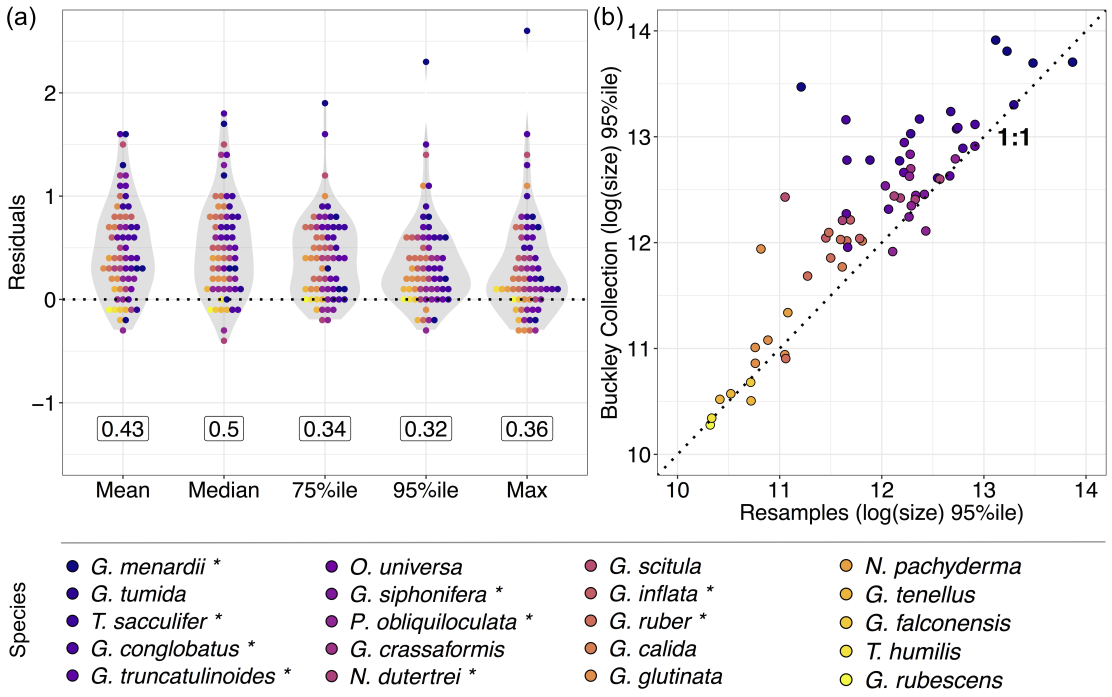

FIGURE 4.3: Bias analysis: difference in shell size distributions between populations of the samples re-sampled by us and of the samples from the Buckley Collection. Species are coloured and ordered by shell size (larger sizes in purple-blue, smaller sizes in orange-yellow); species marked with (∗) were present in the global morphometric dataset (Fig. 4.2). **(a)** Residuals were calculated between the Buckley Collection and the re-sampled samples with respect to the identity function (dotted line), using log-transformed population shell sizes. Numbers indicate mean squared error. **(b)** Plot of the 95^{th} percentile of the log-transformed population shell size distributions from the Buckley Collection against the re-sampled samples, dotted line represents the identity function. See also Appendix B.

median values. Accordingly, in our analyses, we used the 95^{th} percentiles of the population shell size distributions as the dependent variable to investigate what controls planktonic Foraminifera intraspecific shell size variation. As Henry Buckley personally carried out all the sample processing, isolation of foraminiferal specimens and their identification, the collector biases in his collection are likely to be systematic for within-species comparisons.

4.2.3 Sea-surface temperature data

We compiled mean annual values of SST from the World Ocean Atlas 2013 (WOA13, 0 meters depth, Locarnini et al. 2013) for each morphometric sample by matching its unique latitude and longitude coordinates to the nearest WOA13 1° grid point (1° is approximately 111 km at the equator). The distances between the datasets were calculated using the World Geodetic System of 1984 (WGS 84) and R package *geosphere* (version 1.5-7; Hijmans 2015). We used SST data from the earliest decade available in the WOA13 database, resulting in SST data averaged for the years between 1955 and

1964. We chose this time period because the latest historical expedition associated with our morphometric dataset sailed in 1965 (Table B.3).

4.2.4 Net-primary productivity data

We compiled mean annual values of NPP from the Ocean Productivity website (http://www.science.oregonstate.edu/ocean.productivity/). We selected the SeaWiFS estimates (based on the Eppley variation of the VGPM algorithm; Behrenfeld and Falkowski 1997) because they provide the earliest NPP data (starting in late 1997). We matched each morphometric sample coordinate to its nearest NPP sample as described for SST. The median distance between the datasets was 15 km. We considered only full years of NPP data collection, averaging from January 1998 until December 2007.

4.2.5 Relative abundance data

To test for the relationship between population shell size and abundance, we extracted assemblage composition data from the ForCenS database (Siccha and Kucera, 2017). This database is a synthesis of planktonic Foraminifera assemblage counts from surface sediment samples, with 4205 records from unique sites worldwide, each with corresponding information on species' relative abundance. We retrieved species relative abundance data for each morphometric sample by matching its coordinates to its nearest neighbour in the ForCenS database as described for SST. The median distance between the datasets was 106 km.

The spatial arrangement of shells on the seafloor is affected during settling by subsurface currents (Berger and Piper, 1972). Recent models estimate that settling foraminiferal shells can travel a maximum distance of 300 km in regions with large horizontal velocities (e.g., along the equator, in the western boundary currents and in the Southern Ocean; Van Sebille et al. 2015). To account for this post-mortem spatial variation of foraminiferal abundance on the seafloor, we retrieved ForCenS abundance data within a 300 km radius distance of each morphometric sample coordinate, which would be the maximum error according to Van Sebille et al. 2015. We then calculated the median relative abundance of each species based on all ForCenS samples that fell within the 300 km distance of the morphometric sample. The analysis considering all ForCenS samples within a 300 km distance produced consistent results compared to that using the nearest ForCenS sample (Table B.4). Thus, we discuss results given the single nearest ForCenS sample.

4.2.6 Statistical analysis

Effects of SST, NPP and species relative abundance on planktonic Foraminifera size distributions were assessed using linear and quadratic models and a hierarchical model selection framework. For each species, the dependent response variable was the log-transformed size distribution (95^{th} percentile) whereas the independent explanatory variables were the local mean annual SST, NPP and local relative abundances. Linear and quadratic relationships were considered between shell size and SST and NPP, as well as the interaction between SST and NPP. We compared the models through a hierarchical model selection framework: we started all analyses with a null model that included the population shell size as the dependent variable and the regression parameter constant (sample mean). We then added the predictor variable(s) to this model incrementally to see whether the model was improved. Model fit was assessed using Akaike information criterion corrected for small sample size (AICc); models within a difference of two AICc units (i.e., ΔAICc < 2) are equally plausible. Adjusted R squared (R^2_{adj}) were calculated for each model using the R package *rsq* (version 1.0.1; (Zhang, 2017)). Visual inspection of the residual plots did not reveal any obvious deviations from homoscedasticity, except for *G. inflata* (Fig. B.1).

We used the observations in the 53 samples to investigate two species-level patterns: *(i)* the SST at which each species reaches its largest size (95^{th} percentile of the population) and the SST at which each species is most abundant and *(ii)* the relationship between species' maximum size against its maximum relative abundance. These relationships were tested using a standard linear model. We expected to see a tight positive relationship between SST at largest size and SST at highest abundance, as found by Schmidt et al. (2004a).

4.3 Results

Size variation of planktonic Foraminifera is high within- (Fig. 4.4) and among populations (Fig. 4.5). Among adults within the same species, size variation can range over one order of magnitude (e.g., from 150 μm to 1500 μm *Globorotalia menardii*, Fig. 4.2). This high intraspecific variation is differentially explained by SST, NPP and relative abundance across species. When tested alone, SST shows a significant relationship with size in four out of nine species. *T. sacculifer*, *G. siphonifera* and *P. obliquiloculata* increase in size significantly with linear increase of SST, and *G. truncatulinoides* size variation is significantly explained by a quadratic function of SST (Fig. 4.5a). Shell sizes in the other five species do not co-vary significantly with SST. NPP and size variation show a significant positive relationship only in *G. siphonifera* (adjusted R^2 of 24%; Fig. 4.5b). Although not significant, NPP explains a relatively high proportion of the size variation observed within *G. truncatulinoides* (11%, negative relationship) and *G. inflata* (15%, weak positive relationship). Local relative abundance explains less size variation than SST and NPP for all species except *G. menardii* (Fig. 4.5c). *T. sacculifer* also shows a positive relationship between shell size and relative abundance, but weaker than with SST. Note that due to the low relative abundances (below 10%) of *G. conglobatus*, *G. siphonifera* and *G. truncatulinoides*, we do not infer a relationship between size and relative abundance for these species.

SST and NPP correlate (Fig. 4.6), thus their isolated effect on size (Fig. 4.5a,b) might be confounding. For this reason, we considered all variables together in a model selection framework, including the interaction between SST and NPP. The explanatory power of the variables SST, NPP and relative abundance still varies greatly among species (Table 4.2). SST explains 25% and 21% of the intraspecific size variation of *T. sacculifer* and *P. obliquiloculata*, respectively. SST and NPP together reach the highest predictability of size variation: 33% in *G. siphonifera* and 32% in *G. truncatulinoides*. When considering the interaction between SST and NPP, 34% of the size variation in *G. truncatulinoides* and 19% in *G. conglobatus* is explained. NPP alone explains 15% of the size variation of *G. inflata*, although the null model is equally plausible (ΔAICc < 2). *G. menardii* size variation can be predicted by 15% given the additive effect of SST and relative abundance, but the null model is also plausible. Surprisingly, *G. ruber* and *N. dutertrei* size variations are poorly predicted by any of the three variables (see also Fig. 4.5), being best explained by the null model.

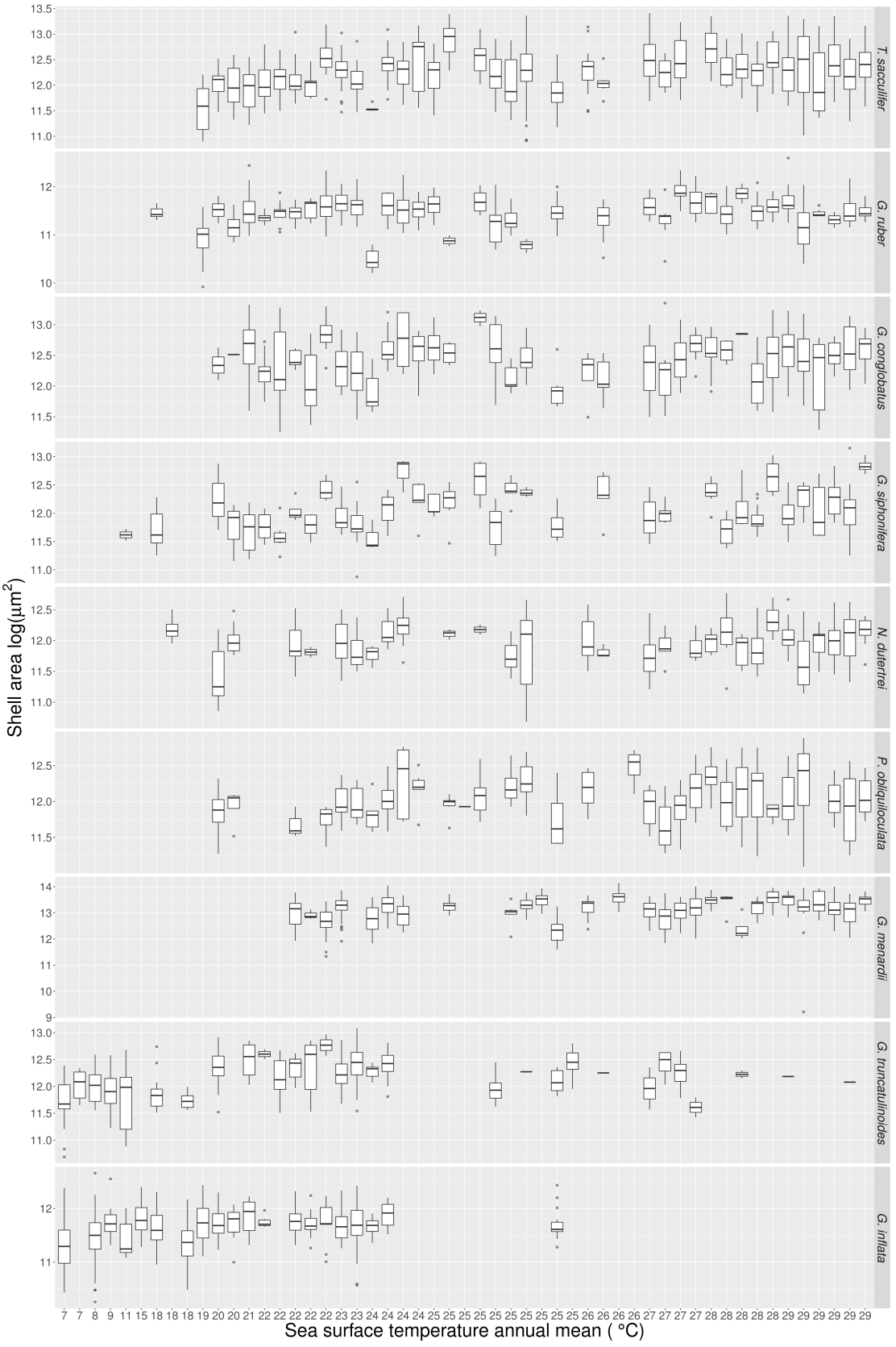

FIGURE 4.4: Boxplots of shell area measurements of each sample for each of the nine planktonic Foraminifera species studied. Samples are ordered by sea-surface temperature; note that the x-axis does not increase linearly.

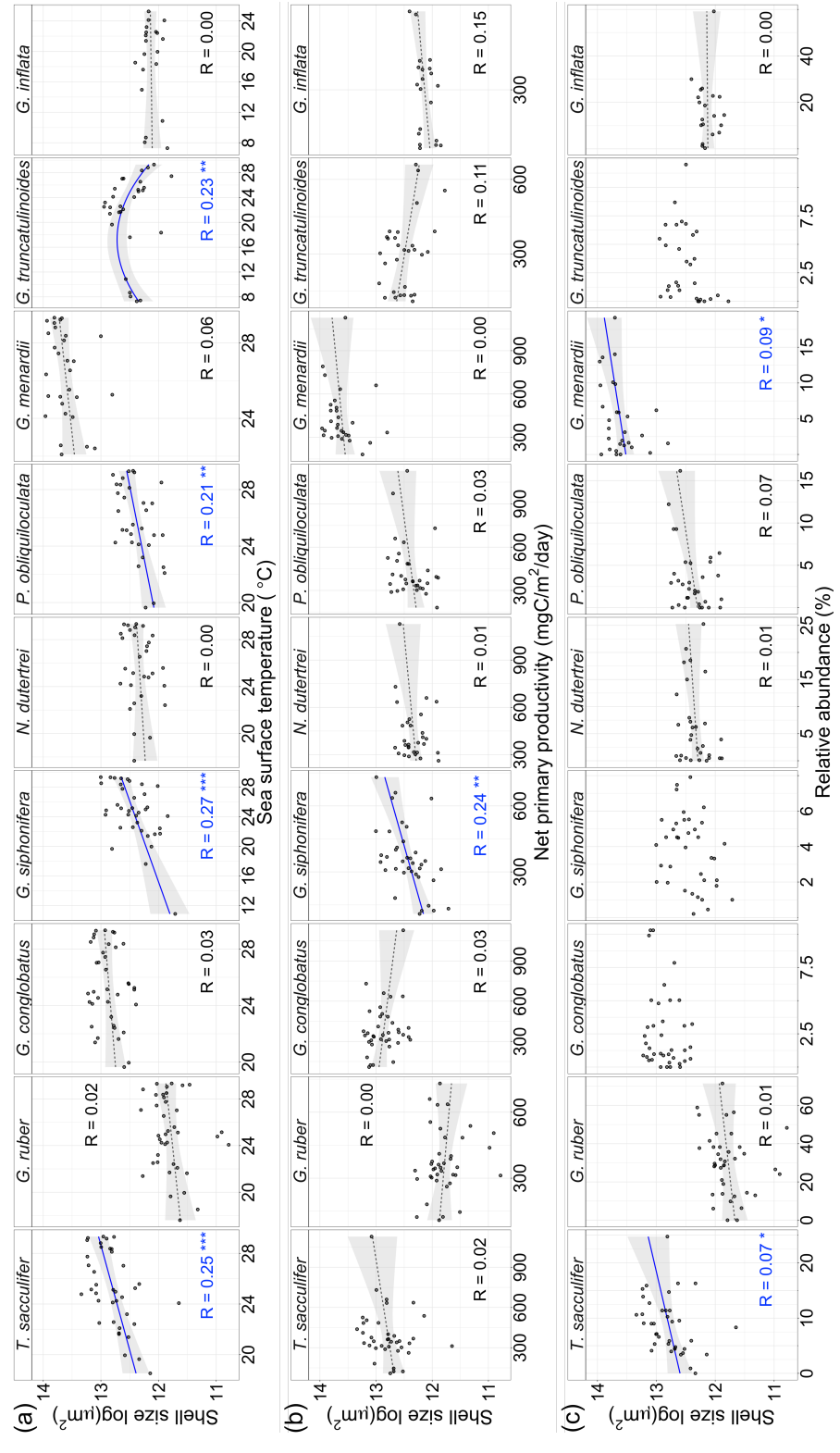

FIGURE 4.5: Logarithm of shell size (represented by the 95th percentile of each population size distribution) as a function of **(a)** annual mean sea-surface temperature, **(b)** annual mean net-primary productivity and **(c)** species' local relative abundance. Solid blue lines show significant relationship whereas dashed grey lines non-significant; grey shades show standard error of the model. Most models are linear, except for the quadratic relationship between *G. truncatulinoides* size and temperature. Due to the low relative abundances (below 10%) of *G. conglobatus*, *G. siphonifera* and *G. truncatulinoides*, we do not infer a relationship between size and relative abundance for these species. The legend in each plot shows the adjusted R squared for each species. Significance codes: *** p$<$0.001; ** p$<$0.01; * p$<$0.05.

TABLE 4.2: Model selection of the linear and quadratic models testing if planktonic Foraminifera shell size (represented by the 95^{th} percentile of each population size distribution) can be predicted by annual mean sea-surface temperature (sst linear effect, sst^2 quadratic effect), annual mean net-primary productivity (npp) and/or species' relative abundance (abund). A model including the interaction between sst and npp (sst : npp) was also considered. Columns: species, explanatory variables, degrees of freedom, log-likelihood, Akaike Information Criterion corrected for small sample size (AICc), AICc difference between models ($\triangle$AICc), model weight, adjusted R squared. All models within two $\triangle$AICc units are shown and equally plausible.

Species	**Expl.Var.**	**df**	**logLik**	**AICc**	**$\triangle$AICc**	**weight**	**R^2_{adj}**
T. sacculifer	sst	3	-7.04	20.79	0.00	0.40	0.25
T. sacculifer	sst^2	4	-6.78	22.78	1.99	0.15	0.24
G. ruber	null	2	-12.45	29.22	0.00	0.18	0.00
G. ruber	sst + npp	4	-10.34	29.85	0.63	0.13	0.05
G. ruber	sst	3	-11.61	29.90	0.67	0.13	0.02
G. ruber	abund	3	-11.76	30.21	0.99	0.11	0.01
G. ruber	npp	3	-12.01	30.70	1.47	0.09	0.00
G. ruber	sst : npp	5	-9.45	30.71	1.49	0.09	0.07
G. conglobatus	sst : npp	5	5.29	1.30	0.00	0.28	0.19
G. conglobatus	sst + npp	4	3.40	2.40	1.10	0.16	0.13
G. conglobatus	sst^2 : npp	6	5.82	3.07	1.77	0.12	0.19
G. siphonifera	sst + npp	4	-2.22	13.69	0.00	0.28	0.33
G. siphonifera	sst	3	-4.24	15.20	1.51	0.13	0.27
G. siphonifera	sst : npp	5	-1.63	15.20	1.52	0.13	0.33
N. dutertrei	null	2	3.59	-2.73	0.00	0.22	0.00
N. dutertrei	npp	3	4.34	-1.76	0.98	0.13	0.01
N. dutertrei	abund	3	4.26	-1.60	1.13	0.12	0.01
N. dutertrei	sst	3	4.12	-1.32	1.41	0.11	0.00
N. dutertrei	sst^2	4	5.25	-0.90	1.83	0.09	0.04
P. obliquiloculata	sst	3	1.89	3.08	0.00	0.31	0.21
P. obliquiloculata	sst + abund	4	2.50	4.47	1.39	0.15	0.22
P. obliquiloculata	sst + npp	4	2.26	4.97	1.89	0.12	0.21
G. menardii	sst + abund	4	-0.43	10.53	0.00	0.23	0.15
G. menardii	abund	3	-2.08	11.11	0.58	0.17	0.09
G. menardii	sst	3	-2.53	12.02	1.50	0.11	0.06
G. menardii	null	2	-3.92	12.29	1.77	0.09	0.00
G. truncatulinoides	sst^2 + npp	5	2.99	6.51	0.00	0.39	0.32
G. truncatulinoides	sst^2 : npp	6	3.88	7.90	1.39	0.19	0.34
G. inflata	npp	3	11.96	-16.41	0.00	0.40	0.15
G. inflata	null	2	9.79	-14.88	1.54	0.19	0.00

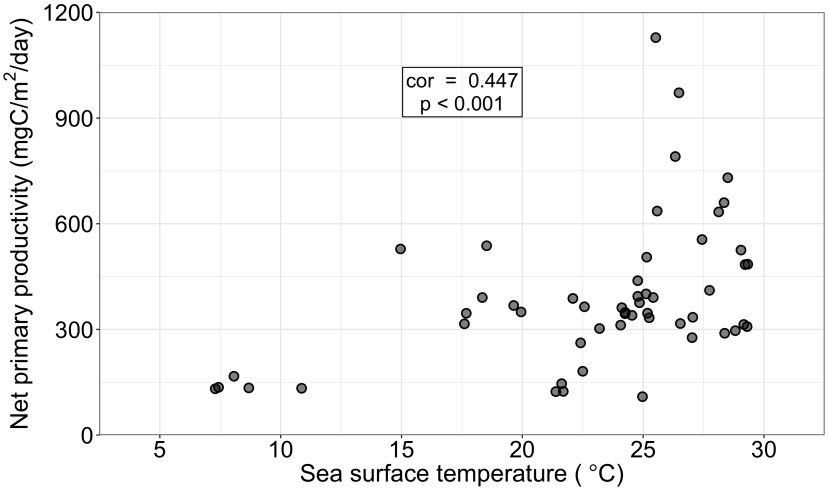

FIGURE 4.6: Relationship between annual mean sea-surface temperature and net-primary productivity for the studied samples, and the corresponding Pearson correlation.

Regarding species-level patterns, we tested the relationship between the SST where each species reaches its largest size and the SST where each species is most abundant (as in Schmidt et al. 2004a). Although our data shows a positive trend, the linear relationship is not significant (R^2 = 0.24, P value = 0.18; Fig. 4.7a). When maximum size and relative abundance are plotted against each other, they show a negative, but not significant trend (Fig. 4.7b). This negative relationship means that abundant species such as *G. ruber* (tropical) and *G. inflata* (transitional) reach smaller maximum sizes when compared to less abundant species, e.g., *G. conglobatus* (tropical) and *G. truncatulinoides* (transitional).

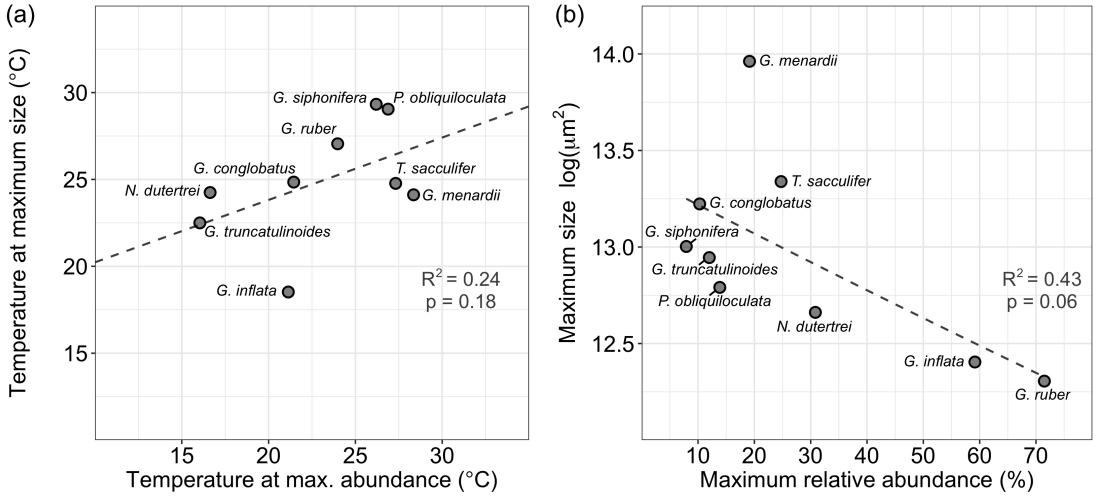

FIGURE 4.7: **(a)** Sea surface temperatures where planktonic Foraminifera species reach maximum shell size and maximum relative abundance in the surface sediments. **(b)** Relationship between maximum shell size (logarithmic scale) and maximum relative abundance of each species. Dashed lines indicate non-significant linear models, with corresponding R squared and P values in grey. Shell size data is calculated from the 95^{th} percentile of each population size distribution. Relative abundance data is calculated as the median relative abundance of all ForCenS samples within 300 km from each morphometric sample (see methods).

4.4 Discussion

Our new morphometric dataset of species-resolved planktonic Foraminifera allowed us to explore the correlates of intraspecific shell size variation at a macroecological scale. We expected planktonic Foraminifera species to be larger at their environmental optima, identified here using sea surface temperature, net primary productivity and species' relative abundances. However, we found that species greatly differed in how much size variation is explained by these variables (Table 4.2). While some species showed a high predictability of size variation in one variable (e.g., SST for *T. sacculifer* and *P. obliquiloculata*), others showed no relationship between size variation and the studied variables (e.g., *G. ruber* and *N. dutertrei*). SST and NPP combined explained most of the size variation observed in our study, predicting more than 30% of the variation within *G. truncatulinoides* and *G. siphonifera*.

When tested alone, SST explained most of the shell size variation within planktonic Foraminifera species; however, only four of the nine studied species showed a significant relationship between size and SST (Fig. 4.5a). The tropical species *T. sacculifer*, *G. siphonifera* and *P. obliquiloculata* showed the expected positive linear relationship between SST and shell size, while the transitional *G. truncatulinoides* showed a quadratic relationship between shell size and SST (Fig. 4.5a). Results for these four species support previous observations that that planktonic Foraminifera species are largest at their thermal optima (Schmidt et al., 2004a). The remaining five species (namely *G. ruber*, *G. conglobatus*, *G. menardii*, *N. dutertrei* and *G. inflata*) showed neither a linear nor quadratic relationship between shell size and SST, indicating that the optimum-size hypothesis does not apply to all planktonic Foraminifera species. Moreover, the local relative abundance of a species was in general a poor predictor of its size variation (Table 4.2, Fig. 4.5c), contrary to the common perception that planktonic Foraminifera species are largest where they are most common (Hecht, 1976).

Six of the nine species studied are obligatory (persistent) photosymbiotic species, namely *G. siphonifera*, *T. sacculifer*, *G. ruber*, *G. conglobatus*, *N. dutertrei* and *G. menardii* (Hemleben et al., 1989; Takagi et al., 2019). Of these, only *G. siphonifera* and *G. conglobatus* size variation was best explained by a model that includes NPP (and SST, Table 4.2), but the relationship between size and NPP differed in sign and significance for these two species: significant positive and non-significant negative, respectively (Fig. 4.5b). Photosymbiosis is an important ecological strategy in nutrient-limited environments (Be and Hutson, 1977; Takagi et al., 2018), but we found weak and conflicting evidence for links between shell size of symbiotic species and open-ocean NPP. The facultative symbiotic species *P. obliquiloculata* and *G. inflata* (Takagi et al., 2019) showed non-significant relationships between size and NPP. And *G. truncatulinoides*, the only

asymbiotic species, included NPP in all the best models explaining its intraspecific size variation (Table 4.2), but the relationship between size and NPP is negative, contrary to the expected if species would grow more when more food is available. More generally, NPP was not a good predictor of size within the mostly photosymbiotic species studied here.

The idea that species are largest at their ecological optima is supported by the strong relationship between the SST at which a species reaches maximum size and the SST at which it reaches maximum relative abundance (Schmidt et al., 2004a). Our species-level comparison showed a positive but, given the limited number and range of species analysed, not significant relationship between SST at maximum size and maximum relative abundance (Fig. 4.7a). The non-significance of our regression is probably due to the absence of sub-polar and polar species in our dataset (e.g., *G. bulloides*, *N. incompta* and *N. pachyderma*), when compared to the data of Schmidt et al. (2004a). If we had included additional cold-water species in our analysis, the species-level relationship between size and abundance of Fig. 4.7a could have been significant. However, this relationship is mostly absent within species (i.e., at population level, Fig. 4.5a,c), indicating that contrasting results may be found when analysing patterns at different organisational levels as well as across different biogeographical scales. Thus, our results emphasise the importance of considering intraspecific variation when analysing macroecological patterns. Further attempts to reconcile the intra- and interspecific processes underlying organism size variation are necessary to bridge discrepancies observed among local, regional and global patterns (Bolnick et al., 2011).

4.4.1 Limitations

The Buckley Collection contains samples from historical expeditions that collected marine sediments using devices such as a dredge, which potentially disturb the ocean floor surface and can recover a mix of Holocene (surface) and deeper, Pleistocene sediments (Rillo et al., 2019a). Although this source of bias is inherent to the Buckley and OBD collections, as they include samples from pioneering marine expeditions such as HMS *Challenger*, it can potentially increase the size variation observed and, consequently, blur biogeographical patterns because of the temporal mixing of samples. To assess this bias, we removed six samples recovered using dredges or grabers (Table B.3) and re-ran the analysis to test if different patterns emerge. Most species' size patterns were unchanged except for *G. conglobatus*, whose best models without dredged samples include the null model, and *G. inflata*, whose best model includes only NPP (and not the null model as before) (Table B.5). Although these changes are significant for

these two species, the general pattern remains: intraspecific size variation in planktonic Foraminifera cannot be explained consistently for all species.

The presence of cryptic genetic diversity could also have contributed to the high intraspecific variation found in our study. Some planktonic Foraminifera species are in fact complexes of lineages, which are genetically independent but morphologically similar (Morard et al., 2015). Cryptic species have been shown to occupy different niches and to be endemic to particular ocean basins (De Vargas et al., 1999; Darling and Wade, 2008; Weiner et al., 2014). So, the macroecological scale of our study likely includes cryptic diversity within our morphologically-defined species. *T. sacculifer* and *G. conglobatus* are the only genetically homogeneous species in our study (Aurahs et al., 2011; Seears et al., 2012; Andre et al., 2013). The other species have been shown to comprise some level of cryptic diversity (De Vargas et al., 1999; Darling and Wade, 2008; Morard et al., 2011; Aurahs et al., 2011; Ujiie et al., 2012; Quillevere et al., 2011; Weiner et al., 2014, 2015), except for *G. menardii*, whose genetic diversity has not yet been determined (Seears et al., 2012). The predictability of size variation in our study does not seem to relate directly to the cryptic diversity of the species: species with strong relationships between size and SST and/or NPP include not only the genetically homogeneous *T. sacculifer* and *G. conglobatus*, but also the genetically diverse *G. siphonifera*, *P. obliquiloculata* and *G. truncatulinoides*. This result suggests that shell growth of these different genetic types likely respond to SST and/or NPP in similar ways.

The weak relationship between size and local relative abundance found in our study could be due to the fact that we used relative abundance data from a different source (the ForCenS database; Siccha and Kucera 2017). We assessed the robustness of our results by testing the optimum-size hypothesis on a more uniform, but smaller, dataset: the ten re-sampled bulk samples used for the bias analysis (Fig. 4.1a; Table B.1). We measured shell sizes and calculated species' relative abundances for each of the ten assemblages, so that the same specimens were used to extract abundance and size data. 65 populations of 20 species were then used to test if population shell size could be predicted by relative abundance using a linear-mixed effect model with species as random effects. The results showed no significant relationship between size variation and relative abundance (chi-square test, χ^2 = 2.18, P value = 0.14, Table B.2), supporting our previous findings using the Buckley Collection data (Table 4.2, Fig. 4.5c).

Potentially the most significant source of uncertainty in the evaluation of the existence of a relationship between size and optimum environmental conditions is the use of relative abundance as an indicator of planktonic Foraminifera ecological (Hecht, 1976) and thermal (Kucera, 2007) optima. Preferably the environmental optimum of a species would be determined by comparing absolute abundances of populations of

the same species independently of the abundances of the other species in the assemblage. When a species is less abundant (or longer-lived) than other species in the local plankton community, its relative abundance in the sediment will be strongly influenced by the more abundant (or shorter-lived) co-occurring species. Moreover, a species can reach high relative abundance because it is better able to tolerate stress than other species. As a result of stress, the abundances of all species will be low, but the most tolerant species will reach high relative abundances. The high relative abundances of *G. ruber* together with the lack of a relationship between shell size and SST, NPP and/or relative abundance (Table 4.2, Fig. 4.5) suggests that this species is able to tolerate stress and, therefore, reach high relative abundance in sub-optimal conditions (Be and Tolderlund, 1971; Schmuker and Schiebel, 2002). Thus, further investigation on the relationship between size and optimal environmental conditions within species should focus on absolute abundances estimates derived from plankton tows and sediment traps (e.g., Beer et al. 2010; Aldridge et al. 2012; Weinkauf et al. 2016), instead of relative abundances in the sediment.

4.5 Conclusion

We tested the hypothesis that planktonic Foraminifera species are largest under optimal environmental conditions (Hecht, 1976; Schmidt et al., 2004a), identified using local SST, NPP and relative abundance of the species. We found that species vary in the predictability of their intraspecific size variation. While *T. sacculifer*, *G. conglobatus*, *G. siphonifera*, *P. obliquiloculata* and *G. truncatulinoides* reach larger sizes at specific environmental conditions, *G. ruber*, *N. dutertrei*, *G. menardii* and *G. inflata* do not show significant relationships between size and the studied environmental and ecological variables. Our results suggest that the prediction of growing bigger at optimal conditions is simplistic to apply to all species. More standardised individual-level studies are necessary to disentangle the mechanisms underlying planktonic Foraminifera biogeographical size distributions.

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Authors contribution MR designed the research question, with input from MK. MR imaged and measured all the individuals, with input from GM. MR and TE designed the statistical analysis. MR performed the analysis and wrote the initial draft. All authors reviewed and edited the manuscript. The authors declare no conflict of interest.

Data Availability Statement The data and the R code used to produce this analysis are available from the NHM Data Portal: https://doi.org/10.5519/0056541. Specimens' images can be found at https://doi.org/10.5519/0035055.

FIGURE 4.8: Washed ocean-floor sediment sample collected by HMS *Challenger* in the South Atlantic (sample number 34991, see Table B.1).

Chapter 5

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

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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 spatial 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 co-vary negatively through time using sediment-trap time series spanning one to 12 years.

Results: The great majority of the assemblages are indistinguishable from randomly assembled communities, showing no significant spatial co-occurrence patterns regarding size similarity or phylogeny. 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 bring community ecology and macroevolution closer together is to consider that diversification dynamics are influenced by groups that interact ecologically even when distantly related.

Keywords:

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

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5.1 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. Positive interactions can have a negative effect on diversification, and negative interactions can enhance diversification (Jablonski, 2008a; Yoder and Nuismer, 2010). For example, predation can actually promote speciation of the prey due to adaptation to divergent predator regimes (Langerhans et al., 2007; Meyer and Kassen, 2007); and mutualism can sometimes lead to increased extinction rate because of the interdependence of the interacting species (Sachs and Simms, 2006). 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 (Weber et al., 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 (Meyer and Kassen, 2007; Bailey et al., 2013) 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 that increases in species number suppress diversification rates due to increased extinction or because opportunities for speciation become reduced once niches are filled, whereas decreases in species number promote diversification because of weaker competitive interactions (Rabosky, 2013).

Many clades have been shown to display the negative DDD pattern, including birds (Phillimore and Price, 2008; Rabosky and Lovette, 2008), mammals (Alroy, 1996), including carnivores (Pires et al., 2017), marine metazoans (Sepkoski, 1978; Alroy, 2008) and marine protists Ezard et al. (2011). Although most of these studies evoke interspecific competition to explain the observed macroevolutionary pattern (Rabosky, 2013), 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 fossilised interaction proxy, both of which are rare (but see Liow et al. 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 et al., 2015; Weber et al., 2017). This approach involves investigating whether the ecological interactions among most (if not all) extant species of a clade (i.e., 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 represent a useful model system for integrating macroevolution and community ecology (Yasuhara et al., 2015). They are unicellular eukaryotes that live as zooplankton in the marine pelagic environment and produce calcium carbonate shells. Upon death, these shells accumulate on the ocean floor building up a remarkably complete fossil record (under adequate sedimentation conditions; Schiebel 2002b; Kucera 2007; Ezard et al. 2011). The planktonic Foraminifera fossil record of the last 66 million years shows a negative DDD pattern (Fig. 5.1) either by analysing phylogenetic tree structure (Etienne et al., 2011), or considering biotic and abiotic correlates of diversification (Ezard et al., 2011), or using non-linear ecological models of alternative modes of competition (Ezard and Purvis, 2016). Using a model selection framework, Ezard and Purvis (2016) show that although abiotic factors affect the dynamics of planktonic Foraminifera diversification, species richness in deep time exhibits strong evidence for regulation by interspecific competition. More specifically, their diversification appears to be driven by compensatory contest competition (Ezard and Purvis, 2016), which is analogous to populational logistic growth where resource availability is limited and only successful individuals get the amount of resource they require (Brannstrom and Sumpter, 2005). At macroevolutionary scales, compensatory contest competition results in species with higher average fitness eventually excluding the lower fitness ones (Ezard and Purvis, 2016). Newly available niches would be filled by species already in similar niches (i.e., incumbency; Ezard and Purvis 2016), invoking niche partitioning and niche conservatism (Wiens et al., 2010).

While competition among planktonic Foraminifera species likely affected the Cenozoic diversification of the group (Ezard et al., 2011; Etienne et al., 2011; Ezard and Purvis, 2016), we currently do not know if (or how) species compete today in the oceans. Planktonic Foraminifera are difficult to cultivate and do not reproduce under laboratory conditions (Hemleben et al., 1989), hindering our understanding of their population dynamics and ecological interactions. Assessing if extant planktonic Foraminifera species compete is valuable not only to bridge macroevolution and community ecology,

but also to improve ecological models used in palaeoceanographic reconstructions, as these models generally assume that planktonic Foraminifera compete without explicitly testing for it (e.g., Fraile et al. 2008; Lombard et al. 2011; Kretschmer et al. 2018). Globally, there are 47 extant planktonic Foraminifera species (Siccha and Kucera, 2017), occurring in low densities (in the order of tenths of individuals per m^3; Schiebel and Hemleben 2005; Meilland et al. 2019). When compared to other eukaryotic groups, planktonic Foraminifera represent less than 0.1% of the plankton abundance in the sunlit ocean (Keeling and del Campo, 2017). Planktonic Foraminifera prey on other plankton groups including phytoplankton, ciliates and copepods (Anderson et al., 1979; Spindler et al., 1984; Hemleben et al., 1989), and several species host photosymbionts (Hemleben et al., 1989; Takagi et al., 2019). Previous works have used observational data to explore the relationship between environmental variables and current diversity patterns of planktonic Foraminifera spatially (Rutherford et al., 1999; Morey et al., 2005; Tittensor et al., 2010; Fenton et al., 2016b) and temporally (Zaric et al., 2005; Jonkers and Kucera, 2015; Weinkauf et al., 2016). These studies suggest that mean annual sea surface temperature (SST) explains the largest portion of the geographical and temporal variation of planktonic Foraminifera extant diversity. However, to our knowledge, no study has explored the role of ecological interactions in shaping their present diversity patterns.

Here, we test if extant planktonic Foraminifera species compete by investigating abundance patterns globally in space and through time (Fig. 5.2a). The temporal scale we studied ranges from weeks (sediment trap data) to centuries (coretop data). We explore two community-level patterns expected under interspecific competition: *(i)* local competitive exclusion (spatial pattern) and *(ii)* compensatory dynamics (temporal pattern). In terms of the former, 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 (Webb et al., 2002). Thus, we expect competitive exclusion to lead to the spatial segregation of ecologically similar species, resulting in overdispersed local communities (i.e., local coexistence of less-ecologically similar species given a random assembly process; Webb et al. 2002; Pearse et al. 2014). The underlying assumption is that the ecological similarity measured among species in a community reflects the biogeographic and ecological processes structuring it (i.e., community assembly processes). On the other hand, if competing species coexist, population sizes are predicted to change as a function of the abundances of co-occurring competitors (e.g., TerHorst 2011; Alzate et al. 2017). Through time, changes in the abundance of one species should be accompanied by compensatory changes in the abundances of other species (i.e., compensatory dynamics; Houlahan et al. 2007).

Thus, we expect that, depending on the strength of the 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 planktonic Foraminifera species to play a key role in structuring their modern communities.

5.2 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) (Fig. 5.2, 5.3). 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).

5.2.1 Spatial data

Ocean-floor sediment samples are recovered using core sampling (Fig. 5.3); the coretop represents the most recent (surface) sediment. Because there is no precise estimate of local sedimentation rate in most sampled sites, core samples typically hold information on species relative abundances (i.e., 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 (Rigual-Hernandez et al., 2012; Jonkers et al., 2019). Such time-averaged assemblages prevent analyses on finer time resolution and might accommodate evolutionary change; however, they have the advantage of averaging out seasonal and inter-annual fluctuations in abundance that might blur macroecological patterns (Fenton et al., 2016b).

We used relative abundance data from the ForCenS database, which is a curated database, taxonomically harmonised and treated for sampling inconsistencies (Siccha and Kucera, 2017). Sites deeper than 3,500 meters in the Pacific and Indian oceans and 4,500 meters elsewhere were excluded to minimise 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 *G. tumida*; *Globigerinoides ruber* pink

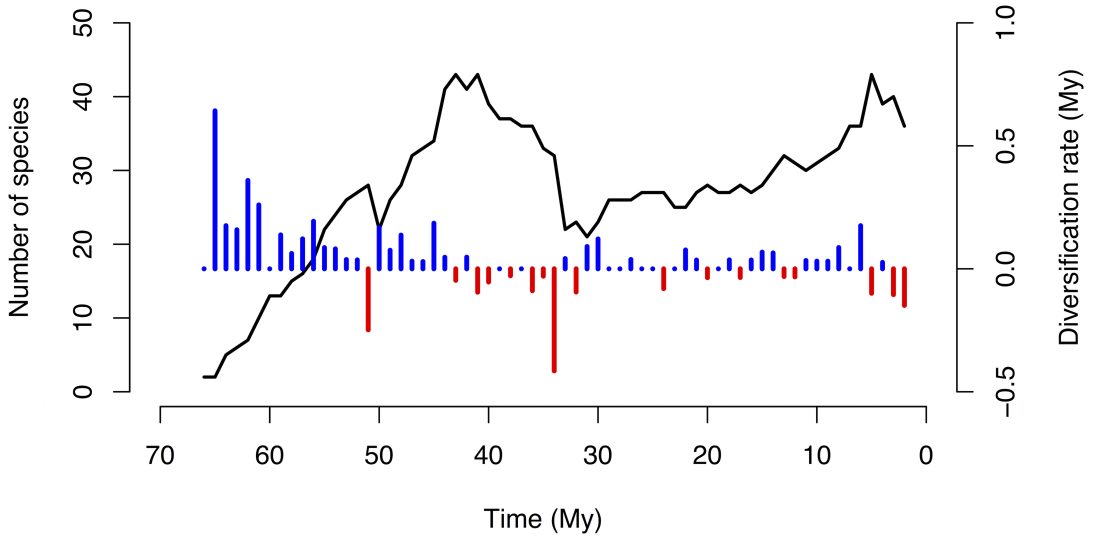

FIGURE 5.1: Bounded diversification pattern observed in the planktonic Foraminifera fossil record. Number of species of planktonic Foraminifera (black line) through geological time in million of years (My) ago, zero represents the present. The coloured bars represent the diversification rate per million 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 from fossil data for this figure.

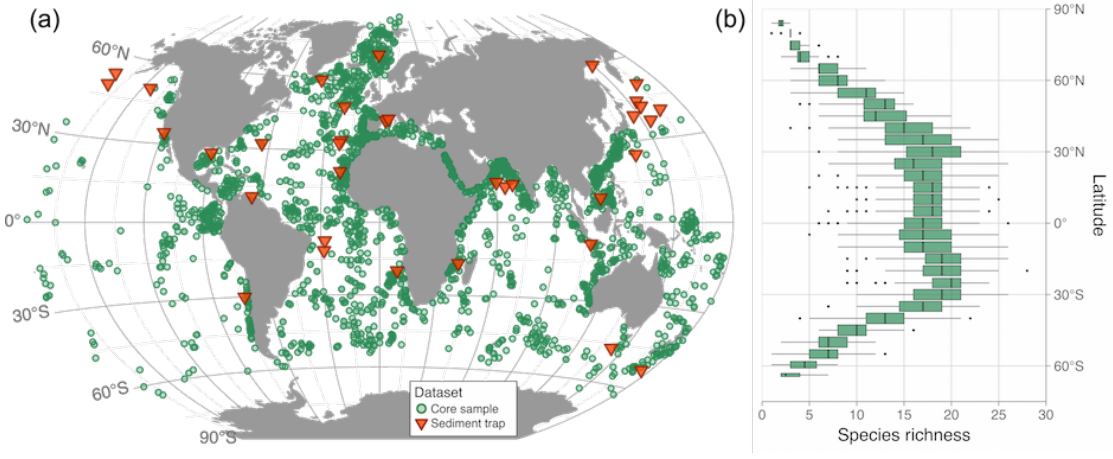

FIGURE 5.2: **(a)** Map of modern planktonic Foraminifera abundance data. **Green dots**, spatial data: 3,053 ocean-floor coretop samples, each with data on relative abundance of all the species present in the sample (usually larger than 150 μm; Siccha and Kucera 2017). **Orange triangles**, temporal data: 35 sediment traps, each with data on abundance (shell flux) time series of planktonic Foraminifera species. Not all species were identified in the sediment traps samples. In total there are 370 population time series available (Table C.2). **(b)** Latitudinal richness gradient of planktonic Foraminifera for each 5° bin, based on coretop samples with richness equal or larger than two species.

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 planktonic Foraminifera species distributed across the globe (Fig. 5.2a).

5.2.2 Temporal data

Sediment traps consist of an upward-facing funnel that directs sinking particulate material towards a sampling bottle (Fig. 5.3), providing a continuous time series of settling planktonic Foraminifera shells (expressed as flux: number of shells per squared-meter per day). We used data collected globally from 35 sediment traps (Fig. 5.2a, Table C.2) including 37 planktonic Foraminifera 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), as they recently harmonised the taxonomy. The total duration of the sampling ranged from a minimum of one up 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 Table C.2 and Jonkers and Kucera (2015).

Shell fluxes represent the settling of dead individuals and indirectly represent the population abundance in the water column (Jonkers and Kucera, 2015). Planktonic Foraminifera have a short life span (typically one 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 (i.e., species dying synchronously are also synchronous in their growth and reproduction) 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.

5.2.3 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 (Cadotte et al., 2008; Wiens et al., 2010; Winter et al., 2013). Planktonic Foraminifera are divided into two monophyletic groups, microperforates and macroperforates (Aurahs et al., 2009a). We used the Aze et al. (2011) Cenozoic phylogeny of macroperforate species as a basis to obtain

phylogenetic relationships among extant planktonic Foraminifera. Following the taxonomic standardisation of Siccha and Kucera (2017), we updated the taxon names in the Aze et al. (2011) phylogeny, removed synonyms and added newly recognised species (Fig. C.1). The final phylogeny includes 33 species (Fig. C.1); 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 size is a functional trait related to individual's physiological and ecological processes (Litchman et al., 2013; Sauterey et al., 2017). We estimated average size of 36 planktonic Foraminifera species, by compiling shell diameter

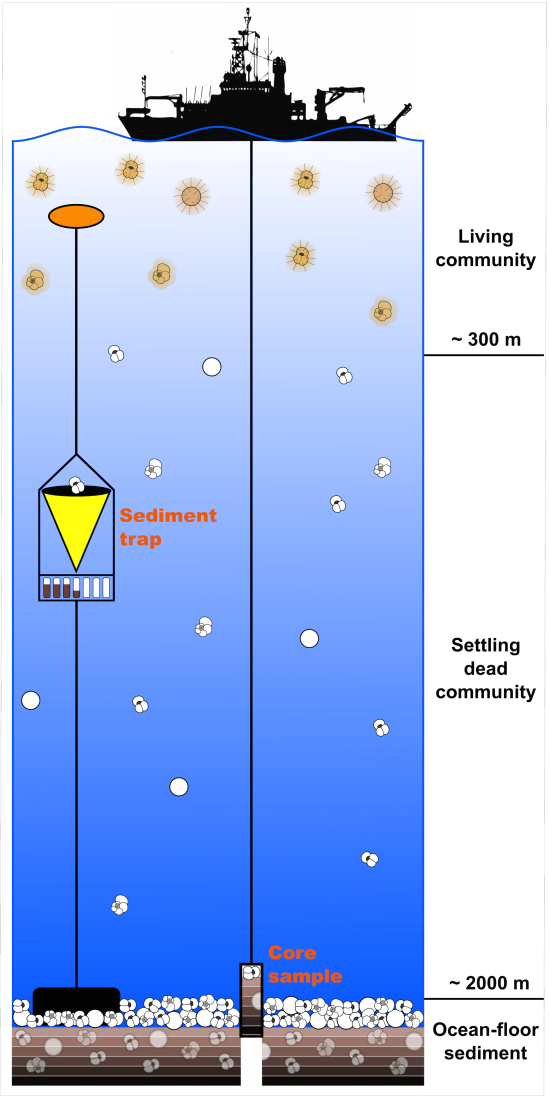

FIGURE 5.3: We used two types of data: **sediment traps** (temporal data) provide a virtually continuous time series of settling, dead planktonic Foraminifera shells. An upward-facing funnel (yellow triangle) directs sinking particulate material towards a sampling bottle. At pre-determined time intervals, 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*.

data of 2774 individuals from three different datasets (Baranowski 2013; Weinkauf et al. 2016; Rillo et al. 2019b; Table C.1). Ideally, size similarity should be estimated based on the sizes of co-occurring individuals rather than the species' average sizes; however, the methods available for community phylogenetic analysis do not allow including biogeographical variation of traits. Although there is high intraspecific size variation within species, size differences among species are evident (Fig. C.2) and assumed to represent species-level differences in niche. The 11 species for which no size data are available were excluded from the morphological analysis.

Many planktonic Foraminifera species are known to exhibit photosymbiosis (Hemleben et al., 1989; Takagi et al., 2019), and mostly live in tropical to subtropical oligotrophic waters (Be and Hutson, 1977). Thus, photosymbiosis seems to be a successful ecological strategy in nutrient-limited waters, 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 photo-activity 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.

5.2.4 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 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 (Webb et al., 2002; Pearse et al., 2014).

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 planktonic Foraminifera assemblages in the spatial data (Fig. 5.2a), we calculated two community dispersion metrics: the mean pairwise distance (MPD) and the mean nearest (taxon) distance (MNTD), both 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 colonising the local community (i.e., the source pool; Webb et al. 2002; Pearse et al. 2014). Our source pool includes all extant planktonic Foraminifera species, because the ranges of all but two species cover every ocean basin (Be and 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 (i.e., competitive exclusion and environmental tolerances), the species' local establishment will be different than 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 standardised the observed MPD and MNTD values with respect to the expected values and standard deviations of the null distributions (standardised 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). The difference between NRI and NTI is that the former accounts for the average (net) distance among all co-occurring species in the assemblage, and the latter accounts for the smallest (nearest) distance between co-occurring species. 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.

5.2.5 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 non-parametric 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).

Planktonic Foraminifera species' abundances (fluxes) vary seasonally in response to SST and primary productivity (Jonkers and 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 one 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 and 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 an yearly-averaged series (spline series; Fig. C.8), without having to enforce an *a priori* fixed annual seasonality. The smoothing spline parameter (λ) was estimated using the generalised cross-validation method (GCV; Craven and Wahba 1978), which finds the optimum λ value by minimising the mean squared error of the fitting (also used in generalised additive models).

To generate the seasonality null model, we calculated the residuals between the observed time series and its spline series (Fig. C.8). We then randomised 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 (Fig. C.8). We report the standardised effect size (SES), which is the observed correlation standardised 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 two years (21 traps in total, Table C.2). A positive average correlation of residuals within the sediment trap indicates synchronous inter-annual variation in species abundances. We also quantified the intra-annual variability of each species is in each sediment trap, by correlating its observed time series with its spline series (Fig. C.8). High positive correlation coefficients indicate that the species has a consistent intra-annual variability (or seasonality) within the given sediment trap.

5.3 Results

5.3.1 Community phylogenetics (spatial data)

Out of the 3,053 planktonic Foraminifera assemblages studied, only two differ significantly from random assembly processes (Fig. 5.4), i.e., 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 seafloor assemblages. As there is no qualitative difference between the results of the 'richness' and 'taxa' null models (Fig. C.3), we discuss only the former. If we consider a significance level of 5%, 190 assemblages show significant size structure (of which 182 are clustered), and 12 assemblages show significant phylogenetic structure (of which 10 are clustered), supporting an environmental filtering scenario.

Using phylogeny as an ecological proxy, NRI values never reach below two standard deviations of the null distributions (i.e., the value of -2, Fig. 5.4a), not supporting competitive exclusion of close relatives. NTI values, however, show a trend towards negative values in assemblages between 5°C and 12°C, reaching values below -2 (Fig. 5.4c). 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 planktonic Foraminifera subclades, so the phylogenetic distance between coexisting 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; Fig. 5.4c).

Dispersion metrics based on species' size differences show either none or one overdispersed assemblages (Fig. 5.4b,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%, Fig C.6). In general, there is a tendency for negative, but not significant, NRI and NTI values at high SST (25-30°C, Fig. 5.4b,d), suggesting large size disparity. In fact, these tropical assemblages have large average community sizes (Fig. C.5), which is consistent with the known trend of increasing assemblage size towards the tropics (Schmidt et al., 2004a).

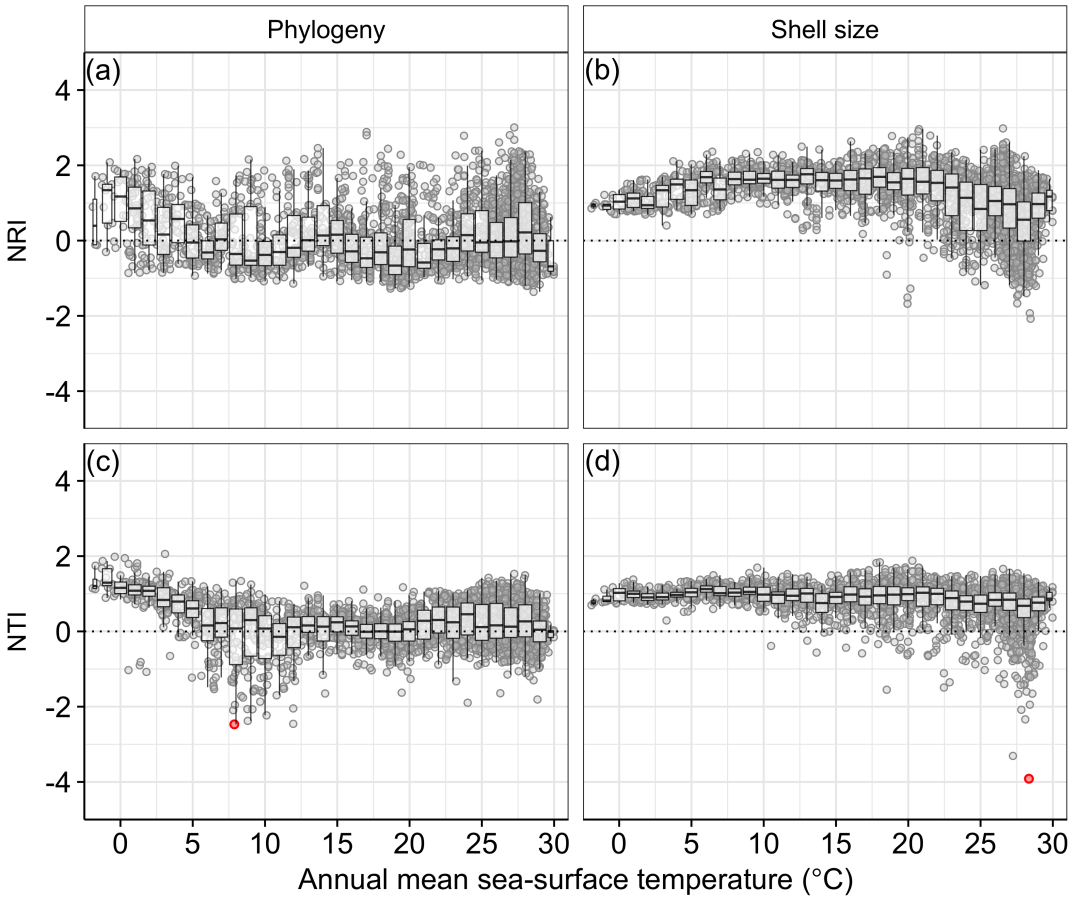

FIGURE 5.4: Spatial data: most planktonic Foraminifera assemblages are indistinguishable from randomly assembled communities. Values show the net relatedness index (NRI) and nearest taxon index (NTI) calculated for 3,053 coretop assemblages of planktonic Foraminifera, plotted against annual mean sea-surface 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'.

5.3.2 Time series (temporal data)

Out of the 2,303 standardised 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. If a significance level of 5% is used instead, 850 time series correlate significantly, of these 794 positively. The correlations between the differentiated time series are similar to the standardised correlations (Fig. C.7). We discuss the results in light of the standardised correlations, because the seasonality null model allows us to explore the inter- and intra-annual variation of species abundances (Fig. C.8).

All sediment traps show median positive standardised correlations (Fig. 5.5), indicating that population dynamics within communities are mostly synchronous. The sediment traps off Coquimbo, central Chile ('COQ'; Marchant et al. 1998, 2004) and in the Gulf of Mexico ('GOM'; Poore et al. 2013; Reynolds and Richey 2016) show remarkably high positive correlations given the large number of co-occurring species (Fig. 5.5). Both of these sediments traps sampled the water column for longer than 6 years, and with high temporal resolution (from one to two weeks per sample).

Standardised correlations are positive between both closely- and distantly-related species pairs (Fig. 5.6a), and show highest positive values between species of similar sizes (Fig. 5.6b). Moreover, species pairs with the same symbiotic strategy, i.e., both hosting symbionts (phototrophs) or not (heterotrophs), show similar correlation patterns when compared to species pairs with opposite symbiotic strategies (heterotrophs and phototrophs; Fig. 5.6c).

Species also have synchronous dynamics across years (i.e., inter-annual variation), as the residuals of observed time series minus spline series correlate positively in the sediments traps (Fig. C.8, C.10). The strength of correlated inter-annual variation does not show a positive trend with the number of years sampled (Fig. C.10). Within years, species show remarkable geographic variation in seasonality (intra-annual variation measured as the correlation of time series and its spline series, Fig. C.9), supporting the patterns found by Jonkers and Kucera (2015).

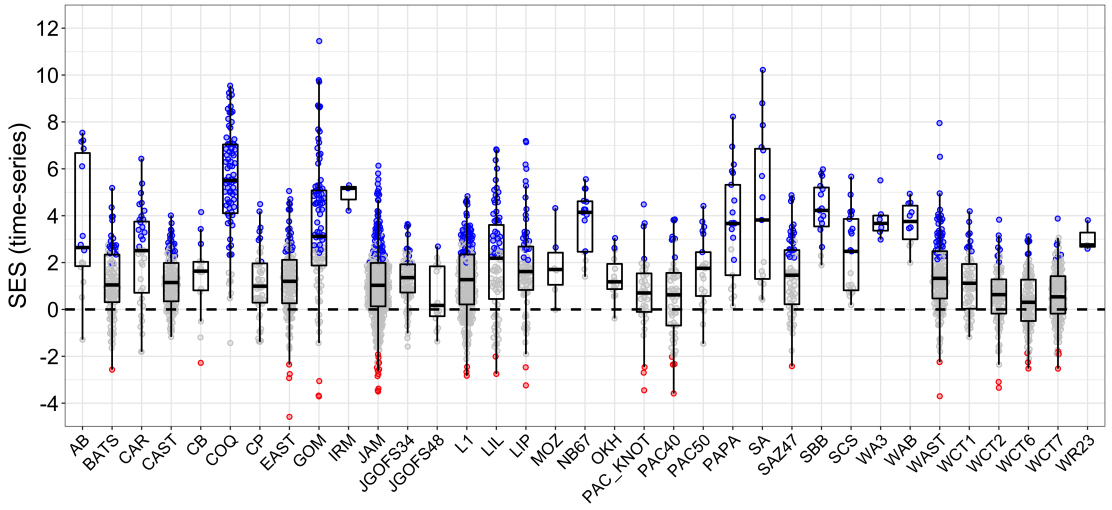

FIGURE 5.5: Temporal data: most sediment traps show non-significant or positive correlations between co-occurring planktonic Foraminifera species. Values show pairwise time-series correlations of species abundances (2,303 in total) plotted by sediment trap (see Table C.2). Grey dots show non-significant, blue significant positive, red significant negative standardised size effect (SES) values, based on the seasonality null model and significance level of 1%.

5.4 Discussion

5.4.1 Spatial patterns

The samples for our community phylogenetics analyses are globally distributed (Fig. 5.2a) 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 and difficult to observe empirically (Yackulic, 2017). 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 and Gotelli, 2010). Overall, our spatial community phylogenetic analyses revealed that planktonic Foraminifera assemblages show co-occurrence pattern that are indistinguishable from neutral assembly processes. Species do not coexist more often with closely- or distantly-related species across space (Fig. 5.4a,c). Thus, if competitive exclusion is happening in these communities, it leaves no phylogenetic signal in the seafloor sediment. Planktonic Foraminifera assemblages also revealed weak co-occurrence patterns regarding species shell size similarity (Fig. 5.4b,d). The few exceptions were potentially leveraged by the presence of the large species *Globorotalia menardii* (Fig. C.6). Taken together, these results suggest that competition among ecologically similar species is not structuring planktonic Foraminifera spatial co-occurrence patterns in seafloor sediments.

The dichotomy of competition versus environmental filtering, pervasive in community phylogenetic approaches, is oversimplified (Cadotte and Tucker, 2017). Competition

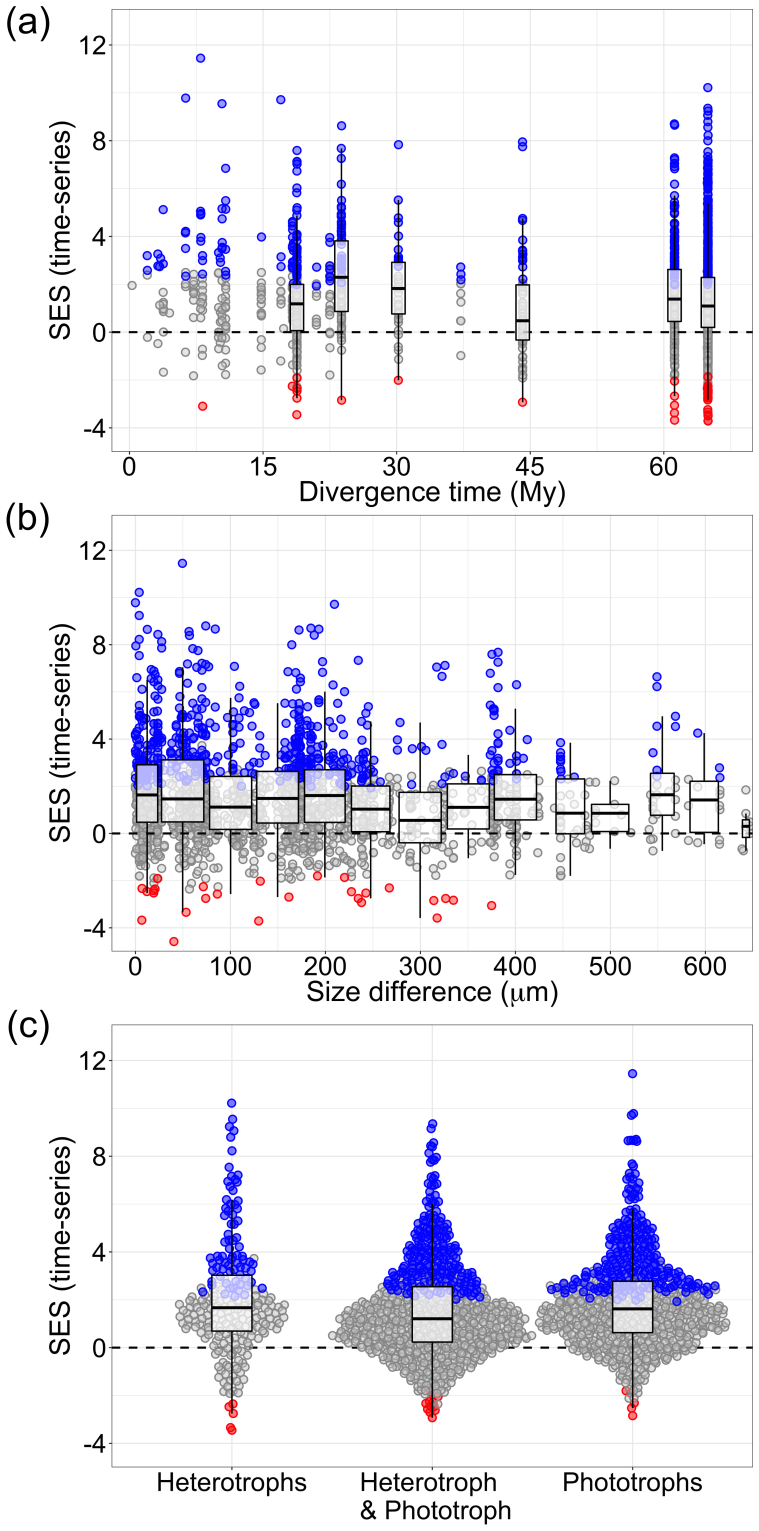

FIGURE 5.6: Temporal data: most planktonic Foraminifera species display seasonal and synchonised population dynamics. Values show pairwise time-series correlations of species abundances plotted against **(a)** the phylogenetic distance between species in million of years (My) (1,843 pairwise correlations in total), boxplots represents divergence times with more than 40 species pairs; **(b)** the shell size difference between species (1,801 correlations), binned by 50μm; **(c)** the photosymbiotic strategy of the species pair (1,721 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 standardised size effect (SES) values, based on the null seasonality model and significance level of 1%.

can instead reinforce co-occurrence of ecologically similar species, giving rise to clustered communities identical to those expected under environmental filtering (Mayfield and Levine, 2010). However, the fact that we observed no significant patterns suggests that these plankton communities are influenced by neutral processes, such as dispersal and stochastic extinction (Hubbell, 2001; Rosindell et al., 2011; Matthews and Whittaker, 2014). Indeed, dispersal–assembly mechanisms have been shown to prevail over niche-assembly mechanisms for the past 30 million years of planktonic Foraminifera evolution (Allen and Gillooly, 2006; Allen and Savage, 2007), and recent work have shown that plankton biogeography can emerge simply by considering body size, spatial heterogeneity and neutral dispersal given oceanographic currents (Sauterey et al., 2017). However, 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.

5.4.2 Temporal patterns

Previous individual sediment-trap studies have shown that planktonic Foraminifera abundances (measured as shell flux) change synchronously through time largely in response to changes in temperature and food availability (Marchant et al., 1998; Tedesco and Thunell, 2003; Marchant et al., 2004; Northcote and Neil, 2005; Wan et al., 2010; Rigual-Hernandez et al., 2012; Poore et al., 2013; Jonkers and Kucera, 2015). However, other studies have shown that although seasonal abundances are related to oceanographic conditions, species abundance peaks can occur sequentially (Deuser and Ross, 1989; Jonkers et al., 2010, 2013) or be inversely related (Kincaid et al., 2000; Kuroyanagi et al., 2002; Mohiuddin et al., 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 sequential abundance peaks (compensatory dynamics) should correlate negatively through time. Here, we analysed sediment trap data globally, and show that the dynamics of planktonic Foraminifera 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 (Fig. 5.5, Table C.2) and across years (Fig. C.10). Therefore, planktonic Foraminifera 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.

Species with similar ecologies (phylogenetically closely related, with similar sizes or same symbiotic strategies) did not correlate more negatively than other species pairs (Fig. 5.6), as would be expected if they were partitioning the resource through time. Purely heterotrophic species correlated largely positively through time (Fig. 5.6c), showing no temporal niche partitioning. Former research has concluded that phytoplankton blooms play an important role in planktonic Foraminifera population dynamics, both directly as part of their diet and symbiosis, and indirectly as it attracts herbivorous zooplankton which are also preyed upon by them (Marchant et al., 1998, 2004; Northcote and Neil, 2005). Our null model accounted for the annual seasonality in species abundances and tested if planktonic Foraminifera species could negatively influence each other within their seasonal abundance peaks. We found no such compensatory dynamics, even in sediment traps with high temporal resolution in terms of days between samples and total number of samples (e.g., 'COQ' and 'GOM' in Fig. 5.5, Table C.2).

Planktonic Foraminifera species might have different vertical niches and thus live in parapatry in the water column (Fairbanks et al., 1982; Hemleben et al., 1989; Rebotim et al., 2017), yet they would still fall within the same the sample of the sediment trap or the coretop, 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 (Be et al., 1982; Takagi et al., 2019). Assuming that photosymbiosis is a reasonable proxy for depth habitat, symbiont-bearing species did not show stronger compensatory dynamics (Fig. 5.6c), supporting our results at an admittedly coarse depth habitat classification.

Planktonic Foraminifera species also showed synchronous dynamics across years (Fig. C.10), indicating that inter-annual variation plays a key role in their population dynamics. Inter-annual variation in assemblage composition and abundance can be partially explained by changes in SST, such as the El Niño (Kincaid et al., 2000; Tedesco and Thunell, 2003; Marchant et al., 2004; Rigual-Hernandez et al., 2012) or the Loop Current in the Gulf of Mexico (Poore et al., 2013) (producing the high positive correlation in the sediment traps 'COQ' and 'GOM'). However, in other cases inter-annual variation is not predicted by SST, and planktonic Foraminifera abundances respond to the dynamics of phytoplankton (Sautter and Thunell, 1989; Sautter and Sancetta, 1992; Rigual-Hernandez et al., 2012) and/or wind forcing (Wan et al., 2010).

5.4.3 Mismatch between macroevolutionary and community dynamics

The fossil record suggests that the diversification dynamics of planktonic Foraminifera are strongly regulated by competition among species (Ezard et al., 2011; Ezard and Purvis, 2016). However, we found no evidence of interspecific competition shaping spatial and temporal diversity patterns of extant planktonic Foraminifera. The global and clade-wide scales of our community ecology analysis are comparable in scope to macroevolutionary analysis, yet these analyses differ markedly in temporal and taxonomic scales. The planktonic Foraminifera fossil record showed evidence for competition when analysed at the species level (taxon counts) over millions of years (Ezard and Purvis, 2016). Here, we tested for competition among species at the population level and in shorter time scales, ranging from weeks up to few thousands of years. While planktonic Foraminifera 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 and Quental, 2016). Moreover, the nested hierarchy of organisational levels (i.e., 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 planktonic Foraminifera diversification throughout the Cenozoic (Ezard and 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 planktonic Foraminifera species went extinct in the past five million years, and the clade is currently in a negative diversification phase (Fig. 5.1; 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 (i.e., 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 planktonic Foraminifera 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 et al. (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 tradeoff; Jablonski 2017).This predicted positive correlation between speciation and extinction rates is observed in the planktonic Foraminifera fossil record (Fig. 5.7), suggesting that population dynamics could potentially explain the observed DDD pattern. Moreover, Wang et al. (2013) neutral model had a limit on the number of individuals which could coexist, but species were equivalent. Thus, total abundance of individuals regulated by a finite resource could create a DDD pattern without species competing for niche space or showing niche differentiation. Our analyses show that planktonic Foraminifera species change their abundance synchronously, suggesting that species have similar niches and also that their total abundance might be regulated by resource availability. Further predictions of the Wang et al. (2013) model could be tested in planktonic Foraminifera, such as the relationship between diversification rates and population abundances.

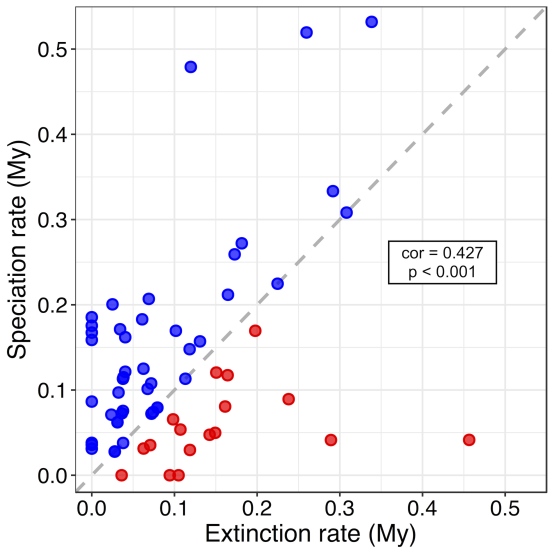

FIGURE 5.7: Positive significant relationship between speciation and extinction rates of planktonic Foraminifera. Rates were calculated using the lineage phylogeny of Cenozoic macroperforate species (Aze et al., 2011) and the methodology of (Ezard and Purvis, 2016) (see Fig. 5.1). Blue dots represent positive diversification rates, while red dots represent negative rates. We removed the first two (oldest) and the last (present) time bins, to avoid outlier effect (i.e., edge effects; see Foote 2000).

The geography of diversification might also play a crucial role in the emergence of DDD patterns (Moen and Morlon, 2014). Allopatric speciation, for example, occurs alongside the splitting of the lineage's distribution in space. In this case, cladogenesis not only reduces species' abundances but also species' biogeographical ranges. Larger ranges are more likely to experience the emergence of geographic or oceanographic barriers. Thus, as diversification proceeds, ranges are subdivided and per-species rates of speciation declines, generating the DDD pattern without niche differentiation among species (Pigot et al., 2010; Moen and Morlon, 2014). Planktonic Foraminifera have the ability to disperse long distances, evidenced by fossil and genetic data (Darling et al., 2000; Sexton and 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. Planktonic Foraminifera fossil record has shown cases of sympatric speciation (Lazarus et al., 1995; Pearson et al., 1997), preventing the use of purely allopatric speciation models. Nevertheless, planktonic Foraminifera genetic studies revealed phylogeographic patterns of allopatry (De Vargas et al., 1999; Darling et al., 2007; 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 oceanographic gene-flow barriers more often than abundant species. Genetic data provide new perspectives for speciation modes in the plankton, and can shed light on planktonic Foraminifera ecological interactions (e.g., Alizon et al. 2008; Aurahs et al. 2011) and the relationships among species' abundances, geographical ranges, genetic diversity and diversification.

Overall, our results suggest that planktonic Foraminifera species are not competing in the modern oceans, which is consistent with the known low densities of planktonic Foraminifera in the water column (Schiebel and Hemleben, 2005; Keeling and del Campo, 2017). Abiotic factors such as SST have been shown to affect current diversity patterns of planktonic Foraminifera in space (Fenton et al., 2016b) and time (Jonkers and Kucera, 2015), as well as their diversification dynamics (Ezard et al., 2011; Ezard and Purvis, 2016). However, phytoplankton abundance also plays an important role in planktonic Foraminifera population dynamics (Jonkers and Kucera, 2015), but their effect on planktonic Foraminifera 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 and Quental, 2016). By defining the species pool of macroevolutionary dynamics ecologically rather than only phylogenetically, we can potentially solve the mismatch found in our study.

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Data accessibility The data that support the findings of this study are openly available and previously published: refer to Siccha and Kucera (2017) for coretop abundance data; Table C.2 for time series data; Aze et al. (2011) for phylogeny; Baranowski (2013); Weinkauf et al. (2016); Rillo et al. (2019b) 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.

Authors 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.

Chapter 6

Conclusion

6.1 Synthesis

Planktonic Foraminifera are an important model system for the empirical integration of spatial and temporal biodiversity dynamics (Yasuhara et al. 2015; Chapter 1). Their remarkably complete fossil record and mature taxonomy allow in-depth investigation of climatic forcing and evolutionary change across geological time scales (Brombacher et al., 2017a), providing a window into community dynamics in deep time (Fenton et al., 2016a) and improving predictions of plankton community responses to future climatic change. However, our basic ecological understanding of the planktonic Foraminifera remains limited and studies addressing ecological questions are still rare, preventing us from fully leveraging the potential of their high-resolution fossil record to elucidate the processes that regulate biodiversity dynamics across geological time. In this thesis, I have contributed to our understanding of modern planktonic Foraminifera ecology by combining a global, macroecological approach with natural history collections (NHCs).

The ecological patterns I described and analysed differed from those expected given our former knowledge of planktonic Foraminifera. Species did not all reach larger sizes under optimal environmental conditions (Chapter 4), suggesting the optimum-size hypothesis (Hecht, 1976; Schmidt et al., 2004a) might be overly simplistic. Instead, different physiological and ecological mechanisms are likely to affect growth patterns in different species. Moreover, we found no evidence for competition among modern planktonic Foraminifera species (Chapter 5), contrary to what has been inferred from their deep time dynamics in the Cenozoic fossil record (Ezard et al., 2011; Ezard and Purvis, 2016). Instead, it seems more likely that planktonic Foraminifera population dynamics, and consequently evolutionary dynamics, are influenced by availability of resources (i.e., phytoplankton abundance), but this hypothesis remains to be tested. The questions posed by the two “negative” results presented in this thesis highlight

the need of more hypothesis-driven research on planktonic Foraminifera biology and ecology.

The use of NHCs to describe ecological patterns can be challenging, as historical samples were not necessarily collected following current methodological expectations. The use of non-uniform sampling protocols has the potential to increase measurement errors, which need to be accounted for (Chapter 4). Nevertheless, museum collections provide repositories of major surveys (Lister and Climate Change Research Group, 2011) usually not achievable within the time frame of a Ph.D. project or research grants. The digitised Buckley Collection (Chapter 2), for example, is now part of the largest public database of modern planktonic Foraminifera images and IDs, available at http://www.endlessforams.org/ and recently published in a collaboration with Pincelli Hull, Allison Yi Hsiang and the Yale Peabody Museum of Natural History (Hsiang et al., 2019). This database will be an important resource for those looking to learn modern planktonic foraminiferal taxonomy and to automate the recognition of species using a machine learning approach (Hsiang et al., 2019). Thus, the aggregation of individual collections into uniformly curated databases facilitates evidence-based investigation of ecological hypotheses (e.g., Salguero-Gómez et al. 2016; Dornelas et al. 2018), allowing the different datasets, each with their own advantages and disadvantages, to become more than the sum of their parts.

6.2 Future directions

There is still much to explore and understand about planktonic Foraminifera ecology and evolution. High-resolution time series coupled with local biotic and abiotic variables can give us further insights into what drives the ecological dynamics in this model system. By understanding which other groups of organisms are ecologically relevant to planktonic Foraminifera communities today, we will then be able to incorporate them into studies using the foraminiferal fossil record. Ecological interactions among species, however, are highly nonlinear in nature (Deyle et al., 2016). Thus, relationships among species temporal dynamics likely vary in intensity and sign through time (Ushio et al., 2018). Recently, a new method has been developed to investigate nonlinear ecological interactions among species using time series data and a dynamical systems approach (Sugihara et al., 2012; Ye et al., 2015; DeAngelis and Yurek, 2015). In the future, this method could be applied to the highest-resolution time series of planktonic Foraminifera to investigate the dynamics of their ecological interactions. Applying such methods to observational data on planktonic Foraminifera will certainly further our ecological knowledge. These methods are likely to provide an important source of

information in this group particularly, where laboratory based experiments are often impractical.

Planktonic foraminifera thermal niches (i.e., thermal tolerances) have been largely estimated based on their relative abundances in the sediment (Kucera, 2007). Species' relative abundances in the local assemblage provide ecological information about the species-rank abundance distribution and species dominance in the local community. However, the interpretation of this relative abundance is complicated by the time-averaged nature of such sediments, meaning it potentially provides little information about the population density of the given species and, consequently, about its niche. As discussed in Chapter 4, a species might reach high relative abundances in the sediment because it is better able to tolerate stress or because it has a shorter life cycle than other species in the community, without necessarily being highly abundant while living in the plankton. Thus, in the future, the estimation of the niche of a species should ideally be determined using absolute abundances of species (e.g., sediment trap data and plankton tow data), instead of relative abundances in the sediment. Where this is not possible, reliable estimates of sedimentation rates and of reworking within sediments (e.g., Chapter 3) are critical for reducing uncertainty in age models and thus producing more accurate estimations of absolute abundances from sediment data.

6.3 Concluding remarks

The planktonic Foraminifera fossil record provides a unique window into how marine biodiversity changed across millions of years, and this evolutionary history is shaped by ecology. Thus understanding the patterns observed in the fossil record requires us to understand the generating ecological processes. Ecological and evolutionary dynamics are complex, because they are influenced by processes occurring at multiple organisational, temporal and spatial scales, challenging our ability to determine which processes are the main drivers of the observed dynamics. In this thesis, I used a macroecological approach to unravel morphological and ecological patterns observed within extant planktonic Foraminifera species operating at scales from weeks to hundreds of years. I focused on a global spatial scale but explored different temporal scales to study their community ecology. Fully comprehending planktonic Foraminifera ecology, and thus unlocking their evolutionary history, will involve scientific research across multiple spatio-temporal scales. Whilst there is already abundant data available on modern planktonic Foraminifera, facilitating such efforts, there are many discoveries yet to be made.

Appendix A

Supplement to Chapter 3

TABLE A.1: Planktonic Foraminifera species counts in the nine historical samples (see Table 3.1). IRN (OBD) stands for the internal registration number of the Ocean-Bottom Deposits collection at the Natural History Museum in London. Individuals were identified to the species level by M. Rillo and M. Kucera together.

Historical samples									
Museum number	M.192	M.8780	M.5246	M.408	M.3787	M.4080	M.7487	M.284	M.25
IRN (OBD)	32657	38482	36053	34991	34671	34993	37148	33668	33286
Latitude	-50.02	-40.45	-26.94	-21.25	-19.57	-15.65	-7.59	-0.70	24.33
Longitude	123.07	49.82	111.18	-14.03	64.63	-179.06	61.48	147	-24.47
Species									
Beella digitata	0	0	0	0	2	1	0	0	0
Berggrenia pumilio	0	0	0	0	0	0	0	0	0
Candeina nitida	0	0	0	0	1	0	0	0	0
Globigerina bulloides	175	38	13	4	2	3	8	28	6
Globigerina falconensis	0	4	11	17	2	6	0	12	0
Globigerinella calida	1	1	6	8	11	15	0	12	3
Globigerinella siphonifera	0	0	5	4	29	10	16	14	2
Globigerinita glutinata	5	5	52	18	24	63	77	65	2
Globigerinoides conglobatus	0	0	1	3	12	8	6	2	2
Globigerinoides ruber pink	0	0	0	11	0	0	0	0	0
Globigerinoides ruber white	0	3	73	84	196	131	53	115	68
Globigerinoides tenellus	0	0	0	20	9	19	0	6	0
Globoconella inflata	96	58	10	31	2	0	0	0	35
Globoquadrina conglomerata	0	0	2	0	1	0	0	1	0
Globorotalia crassaformis	0	0	2	2	1	0	0	0	5
Globorotalia hirsuta	0	0	0	1	0	0	0	0	0
Globorotalia menardii	0	0	37	0	1	0	30	1	23
Globorotalia scitula	0	0	0	2	1	0	5	0	0
Globorotalia theyeri	0	0	0	0	0	0	1	0	0
Globorotalia truncatulinoides	14	10	6	12	3	0	1	0	10
Globorotalia tumida	0	0	0	2	0	0	15	2	7
Globorotalia ungulata	0	0	3	2	2	0	4	0	0
Globorotaloides hexagonus	0	0	0	0	1	0	0	0	0
Globoturborotalita rubescens	0	0	0	3	2	4	4	4	0
Neogloboquadrina dutertrei	0	0	34	1	11	4	21	9	7
Neogloboquadrina incompta	8	17	4	1	0	0	33	10	33
Neogloboquadrina pachyderma	19	38	0	0	0	0	0	0	0
Orbulina universa	0	1	1	6	3	4	0	0	1
Pulleniatina obliquiloculata	0	0	2	3	7	0	16	22	5
Sphaeroidinella dehiscens	0	0	0	0	1	0	1	0	2
Trilobatus sacculifer	0	0	17	30	52	32	13	28	46
Turborotalita humilis	0	0	0	0	0	0	1	0	3
Turborotalita quinqueloba	0	2	0	0	0	0	0	0	0
Total count	318	177	279	265	376	300	305	331	260

TABLE A.2: Relative abundance (in %) of planktonic Foraminifera species in the historical samples M.192, M.8780 and M.5246, and their corresponding neighbouring samples in the Holocene and Last Glacial Maximum reference datasets. Species not shown had 0% abundance in all samples. Local sedimentation rate is given by the LGM datasets (see Methods) and expressed in centimetres per thousand of years.

Sample	Historical	Holocene	LGM	Historical	Holocene	LGM	Historical	Holocene	LGM
Sample/core number	M.192	CLIMAP_0078	E45-078	M.8780	BUFD_1027	RC14-009	M.5246	MARGO_2820	RC11-145
Latitude	-50.02	-47.77	-45.04	-40.45	-36.50	-39.02	-26.94	-26.97	-25.48
Longitude	123.07	123.10	114.35	49.82	49.57	47.88	111.18	111.33	110.02
Distance (km)	0	250.11	857.04	0	440.25	229.83	0	15.42	199.38
Sedimentation rate (cm/ky)			1.5			3.4			1.4
Species									
Beella digitata	0	0	0	0	0.48	0	0	0	0
Globigerina bulloides	55.03	60.71	51.67	21.47	7.88	25.58	4.66	8.85	1.81
Globigerina falconensis	0	0	0	2.26	15.75	0.66	3.94	0.66	3.32
Globigerinella calida	0.31	0	0	0.56	4.06	0	2.15	0	0.30
Globigerinella siphonifera	0	0	0	0	3.34	0.33	1.79	5.53	1.21
Globigerinita glutinata	1.57	1.53	3.67	2.82	3.58	1.99	18.64	19.25	18.73
Globigerinoides conglobatus	0	0	0	0	0	0	0.36	0.33	0.60
Globigerinoides ruber white	0	0	0	1.69	7.64	1.00	26.16	28.10	16.92
Globigerinoides tenellus	0	0	0	0	0	0	0	5.20	0.30
Globoconella inflata	30.19	20.66	17.33	32.77	35.56	11.63	3.58	6.19	47.73
Globoquadrina conglomerata	0	0	0	0	0	0	0.72	0	0
Globorotalia crassaformis	0	0	0.33	0	0	0	0.72	0	0.60
Globorotalia hirsuta	0	0	0	0	1.43	0.66	0	1.00	0
Globorotalia menardii	0	0	0	0	0	0	13.26	9.85	0.30
Globorotalia scitula	0	0	0.33	0	0.48	0	0	0	0
Globorotalia truncatulinoides	4.40	6.12	1.33	5.65	2.86	1.66	2.15	1.66	1.51
Globorotalia ungulata	0	0	0	0	0	0	1.08	0	0
Globoturborotalita rubescens	0	0	0	0	0	0.33	0	0.33	0
Neogloboquadrina dutertrei	0	0	0	0	1.19	1.00	12.19	3.87	3.93
Neogloboquadrina incompta	2.52	3.32	4.67	9.60	10.02	40.53	1.43	1.00	0.91
Neogloboquadrina pachyderma	5.97	6.63	14.33	21.47	0.24	5.65	0	0	0
Orbulina universa	0	0.51	0.33	0.56	0.72	0.33	0.36	0.66	0.60
Pulleniatina obliquiloculata	0	0	0	0	0	0	0.72	1.66	0
Trilobatus sacculifer	0	0	0	0	0.48	0	6.09	5.86	0
Turborotalita humilis	0	0	0.33	0	0	0	0	0	0
Turborotalita quinqueloba	0	0	5.67	1.13	0.24	8.64	0	0	0

TABLE A.3: Relative abundance (in %) of planktonic Foraminifera species in the historical samples M.408, M.3787 and M.4080, and their corresponding neighbouring samples in the Holocene and Last Glacial Maximum reference datasets. Species not shown had 0% abundance in all samples. Local sedimentation rate is given by the LGM datasets (see Methods) and expressed in centimetres per thousand of years.

Sample	Historical	Holocene	LGM	Historical	Holocene	LGM	Historical	Holocene	LGM
Sample/core number	M.408	BUFD_0336	GeoB1417-1	M.3787	CLIMAP_0211	V20-175	M.4080	MARGO_1184	RC13-038
Latitude	-21.25	-24.07	-20.37	-19.57	-20.58	-22.30	-15.65	-15.15	-14.52
Longitude	-14.03	-15.12	-12.71	64.63	63.53	68.00	-179.06	-176.49	177.10
Distance (km)	0	332.71	169.48	0	161.12	463.76	0	281.64	431.21
Sedimentation rate (cm/ky)			NA			1.5			1.9
Species									
Beella digitata	0	2.08	0.38	0.53	0	1.82	0.33	0.10	0.61
Candeina nitida	0	0	0.19	0.27	0.27	0.36	0	0	0
Dentigloborotalia anfracta	0	0	0.32	0	0	0	0	0	0
Globigerina bulloides	1.51	1.33	17.75	0.53	2.73	2.55	1.00	0.50	2.66
Globigerina falconensis	6.42	3.60	2.02	0.53	2.19	0.73	2.00	0.70	1.43
Globigerinella adamsi	0	0	0	0	0	0	0	0.10	0
Globigerinella calida	3.02	2.84	0.78	2.93	1.91	5.84	5.00	4.73	3.89
Globigerinella siphonifera	1.51	5.30	2.48	7.71	2.46	1.82	3.33	4.53	4.09
Globigerinita glutinata	6.79	12.88	8.62	6.38	9.29	18.25	21.00	19.32	31.49
Globigerinoides conglobatus	1.13	0.76	0.89	3.19	0.55	1.82	2.67	5.03	2.45
Globigerinoides ruber pink	4.15	1.33	0.81	0	0	0	0	0	0
Globigerinoides ruber white	31.70	40.15	24.42	52.13	56.56	44.16	43.67	38.23	40.90
Globigerinoides tenellus	7.55	4.55	2.50	2.39	0.55	4.38	6.33	4.02	2.86
Globoconella inflata	11.70	2.08	10.20	0.53	0.82	0.36	0	0	0
Globoquadrina conglomerata	0	0	0	0.27	0	0	0	0	0
Globorotalia crassaformis	0.75	0.38	1.82	0.27	0	0.36	0	0	0.41
Globorotalia hirsuta	0.38	0.57	0	0	0	0.73	0	0	0
Globorotalia menardii	0	2.65	0.04	0.27	0.82	0.73	0	0	0.20
Globorotalia scitula	0.75	1.70	1.81	0.27	1.37	1.09	0	0	0.20
Globorotalia truncatulinoides	4.53	5.49	6.34	0.80	1.37	6.57	0	0.20	0
Globorotalia tumida	0.75	0.38	0.02	0	0.82	0	0	0	1.02
Globorotalia ungulata	0.75	0	0	0.53	0	0	0	0	0
Globorotaloides hexagonus	0	0	0	0.27	0	0	0	0.30	0
Globoturborotalita rubescens	1.13	2.08	4.73	0.53	1.64	3.65	1.33	3.82	1.23
Neogloboquadrina dutertrei	0.38	0.19	0.89	2.93	2.73	1.82	1.33	0.10	2.25
Neogloboquadrina incompta	0.38	0	3.97	0	0.82	0	0	0	0.41
Neogloboquadrina pachyderma	0	0	0	0	0.27	0	0	0	0
Orbulina universa	2.26	3.22	0.96	0.80	2.73	1.46	1.33	2.41	2.66
Pulleniatina obliquiloculata	1.13	0	0	1.86	0	0.36	0	0	0.61
Sphaeroidinella dehiscens	0	0	0	0.27	0.27	0.36	0	0	0
Tenuitella iota	0	0	0.17	0	0	0	0	0	0
Trilobatus sacculifer	11.32	5.30	7.33	13.83	9.56	0	10.67	11.37	0
Turborotalita humilis	0	0	0.35	0	0	0.36	0	0.20	0
Turborotalita quinqueloba	0	0	0.16	0	0	0.36	0	4.33	0.61

TABLE A.4: Relative abundance (in %) of planktonic Foraminifera species in the historical samples M.7487, M.284 and M.25, and their corresponding neighbouring samples in the Holocene and Last Glacial Maximum reference datasets. Species not shown had 0% abundance in all samples. Local sedimentation rate is given by the LGM datasets (see Methods) and expressed in centimetres per thousand of years.

Sample	Historical	Holocene	LGM	Historical.1	Holocene.1	LGM.1	Historical.2	Holocene.2	LGM.2
Sample/core number	M.7487	BUFD_1236	V29-048	M.284	BUFD_0402	KH92-1-5a	M.25	ATL947_0944	V23-100
Latitude	-7.59	-6.27	-6.27	-0.70	1.27	3.53	24.33	22.70	21.30
Longitude	61.48	63.43	63.43	147.00	149.20	141.86	-24.47	-25.33	-22.68
Distance (km)	0	261.13	260.62	0	328.48	740.79	0	202.35	384.21
Sedimentation rate (cm/ky)			1.0			NA			NA
Species									
Beella digitata	0	0.26	1.11	0	0.11	0	0	0.50	0
Candeina nitida	0	0	0	0	0.22	0.50	0	0	0
Globigerina bulloides	2.62	5.03	3.33	8.46	4.20	5.50	2.31	2.30	9.64
Globigerina falconensis	0	0	0	3.63	0.82	1.50	0	0	1.79
Globigerinella calida	0	1.32	3.33	3.63	2.78	0	1.15	0.20	0.30
Globigerinella siphonifera	5.25	4.76	5.56	4.23	5.94	18.50	0.77	2.90	3.78
Globigerinita glutinata	25.25	6.61	9.63	19.64	17.18	25.50	0.77	2.90	0
Globigerinoides conglobatus	1.97	3.44	4.07	0.60	1.42	0.50	0.77	1.80	0
Globigerinoides ruber	0	0	0	0	0	0	0	0.50	0
Globigerinoides white	17.38	24.07	22.22	34.74	28.57	31.00	26.15	15.18	7.36
Globigerinoides tenellus	0	0.26	0.74	1.81	1.42	1.50	0	0.20	0.50
Globoconella inflata	0	0	0	0	0	0	13.46	16.28	0.30
Globoquadrina conglomerata	0	4.76	0.37	0.30	0.87	0	0	0	0
Globorotalia crassaformis	0	0	0.74	0	0.44	0	1.92	1.80	46.42
Globorotalia hirsuta	0	0	0	0	0.11	0	0	0	0
Globorotalia menardii	9.84	14.02	14.44	0.30	2.24	1.75	8.85	13.59	0
Globorotalia scitula	1.64	0.79	1.48	0	0.22	0	0	0.20	0
Globorotalia theyeri	0.33	0	0	0	0	0	0	0	0
Globorotalia truncatulinoides	0.33	0	0	0	0.49	0	3.85	7.89	1.49
Globorotalia tumida	4.92	1.85	1.48	0.60	1.58	1.75	2.69	4.30	0
Globorotalia ungulata	1.31	0	0	0	0	0	0	0	0
Globorotaloides hexagonus	0	3.44	2.22	0	0.11	0	0	0	0
Globoturborotalita rubescens	1.31	0	0.74	1.21	2.29	0.50	0	0	0
Neogloboquadrina dutertrei	6.89	7.94	17.41	2.72	4.74	3.50	2.69	5.69	0
Neogloboquadrina incompta	10.82	0.26	4.44	3.02	0.27	0	12.69	4.80	1.99
Neogloboquadrina pachyderma	0	0	0	0	0.05	0	0	0	5.07
Orbulina universa	0	0.26	1.11	0	0.11	0	0.38	0.20	3.08
Pulleniatina obliquiloculata	5.25	3.17	5.19	6.65	12.21	4.50	1.92	0.70	13.72
Sphaeroidinella dehiscens	0.33	0.79	0.37	0	0.22	0	0.77	0.90	0
Trilobatus sacculifer	4.26	15.87	0	8.46	10.69	3.50	17.69	17.18	3.28
Turborotalita humilis	0.33	0	0	0	0	0	1.15	0	0.99
Turborotalita quinqueloba	0	0	0	0	0	0	0	0	0.30

Appendix B

Supplement to Chapter 4

Museum collection shell size bias analysis

To assess the size bias in the Buckley Collection, we re-sampled ten bulk sediments of the NHMUK Ocean-Bottom Deposits Collection (OBD) Collection, from which the Buckley Collection was created (Fig. 4.1a, Table B.1). Samples were chosen to encompass different oceans, latitudes and marine expeditions; however, the final choice also depended on the availability of bulk sediment samples in the OBD Collection. Half of the amount available in the OBD containers was further split into two equal parts, leaving an archive sample and a sample to be processed. The sample processing consisted of weighing, wet washing over a 63μm sieve and drying in a 60°C oven. The residues were further dry sieved over a 150μm sieve and the coarser fraction was split with a microsplitter as many times as needed to produce a representative aliquot containing around 300 planktonic Foraminifera specimens (see Al-Sabouni et al. 2007). All specimens in each of the nine final splits were identified by MCR and MK under a stereomicroscope to species level, resulting in a total of 2,611 individuals belonging to 31 species (see also Rillo et al. 2019a). We mounted species-specific slides from the re-sampled samples, calculated the relative abundance of each species in each sample, and then extracted shell size data in the same way as for the slides of the Buckley Collection. Only the sizes of species also present in the Buckley Collection samples were measured, resulting in 1824 specimens' shell sizes from 20 species (Table B.1). See section 4.2.2 in the main text for further information.

TABLE B.1: Bias analysis: samples re-sampled from the Ocean-Bottom Deposits (OBD) Collection at the Natural History Museum, London (NHMUK) used in the museum collection size bias analysis. Columns: NHMUK Internal Record Number of the sediment in the OBD Collection; name of the Vessel that collected the sample; latitude (Lat) and longitude (Long) given in decimal degrees; water depth in meters; sampled mass in grams; number of times sediment was split N(splits) to achieve around 300 specimens; number of planktonic Foraminifera specimens N(ind) and species N(ssp) measured in each re-sampled sample. For more information, see Table B.3.

OBD IRN	Vessel	Lat	Long	Depth (m)	Mass (g)	N(splits)	N(ind)	N(ssp)
32657	HMS *Challenger*	-50.02	123.07	-3976	0.19	5	14	1
34991	HMS *Challenger*	-21.25	-14.03	-3740	9.35	7	239	11
33668	HMS *Challenger*	-0.70	147.00	-2213	1.98	7	185	7
33286	HMS *Challenger*	24.33	-24.47	-5153	2.73	5	31	3
34671	HMS *Egeria*	-19.57	64.63	-2708	1.23	5	348	11
34993	HMS *Egeria*	-15.65	-179.06	-2519	2.42	8	262	8
36053	HMS *Penguin*	-26.94	111.18	-3350	1.49	5	230	10
37148	HMS *Sealark*	-7.59	61.48	-3507	2.86	8	222	11
38482	HMS *Waterwitch*	-40.45	49.82	-3780	1.51	6	67	2
14609	*Alpha 6*	85.25	-167.90	-1774	0.57	4	226	1
						TOTAL	1824	20

Linear mixed-effects regression using the bias analysis data

Using the re-sampled populations described above, we tested whether relative abundance variation significantly explains population shell size variation. Since the re-sampled data includes only ten samples (Fig. 4.1a), there is not enough data to run species-specific generalised linear models (GLM). Instead, we used linear mixed-effect models (LMER). The log-transformed 95^{th} percentiles of the population shell size distributions were modelled as the response variable, and the independent fixed effect was the species' relative abundance in the re-sampled sample. Species were modelled as random effects, allowing for random intercepts and slopes (*i.e.*, the intercept and slope of the relationship between shell size and the relative abundance may vary among species). We used the Likelihood Ratio Test (LRT) to compare the likelihood of the fixed effect. We calculated the LRT between the models with and without the effect. Significance of each fixed effect was given through the LRT. Marginal R^2 (R^2_m), which is associated with the fixed effects, was calculated for each LMER model (Barton, 2017).

TABLE B.2: Bias analysis: linear mixed-effects model (LMER, ANOVA) using the re-sampled data, and size variation (log-transformed 95^{th} percentile of the population) as the response variable, species as the random effects (r.e.) and either a null model (H0) or relative abundance (H1) as the explanatory variable. Columns: model explanatory variables (fixed effects), degrees of freedom, Akaike Information Criterion, log-likelihood, model deviance, chi-squared, P value, marginal R squared.

Explanatory variables	df	AIC	logLik	dev	χ^2	P	R^2_m
H0: 1 + r.e.	5	130.20	-60.10	120.20			0.00
H1: (abund) + r.e.	6	130.02	-59.01	118.02	2.18	0.14	0.07

TABLE B.3: Samples from the Henry Buckley Collection of Planktonic Foraminifera at The Natural History Museum, London (NHMUK) used in the morphometric analysis. Columns: NHMUK Internal Record Number of the sediment in the Ocean-Bottom Deposits Collection (OBD IRN); name of the vessel that collected the sample; year the sample was collected; latitude (Lat) and longitude (Long) given in decimal degrees; sea surface temperature (SST) in Celsius degrees; water depth in meters; sampling method used in the historical expedition; depth below the seafloor (Dbsf) sampled in centimetres; number of planktonic Foraminifera specimens N(ind) and species N(ssp) measured at each site.

OBD IRN	Vessel	Year	Lat	Long	SST	Depth(m)	Sampling	Dbsf(cm)	N(ind)	N(ssp)
31945	CS *Britannia*	1899	39.21	-70.24	19.25	-2731	Sounding	surface	65	1
34297	CS *Buccaneer*	1886	-0.03	-15.94	26.30	-3226	Sounding	surface	57	1
30724	HEMS *Mabahiss*	1934	7.19	63.04	28.38	-4346	Core	4-5.5	53	7
35818	HMIMS *Investigator*	1906	20.44	68.84	27.24	-2680	Sounding	surface	56	5
17229	HMNZS *Lachlan*	1955	-33.88	173.83	17.80	-2464	Worsel sampler	surface	106	8
17262	HMNZS *Pukaki*	1957	-53.63	169.87	7.95	-746	Dietz grab	surface	52	2
33286	HMS *Challenger*	1873	24.33	-24.47	23.16	-5153	Sounding	surface	46	1
32657	HMS *Challenger*	1874	-50.02	123.07	9.32	-3976	Sounding	surface	11	1
33668	HMS *Challenger*	1875	-0.70	147.00	29.40	-2213	Sounding	surface	95	7
34607	HMS *Challenger*	1875	-33.70	-78.30	16.79	-3798	Sounding	surface	8	1
34991	HMS *Challenger*	1876	-21.25	-14.03	23.61	-3740	Dredge	surface	181	8
34671	HMS *Egeria*	1887	-19.57	64.63	24.83	-2708	Sounding	surface	66	8
34676	HMS *Egeria*	1887	-23.23	56.30	25.14	-4646	Sounding	surface	73	9
34678	HMS *Egeria*	1887	-29.93	54.10	21.13	-4211	Sounding	surface	63	8
34993	HMS *Egeria*	1889	-15.65	-179.06	28.05	-2519	Sounding	surface	124	8
35238	HMS *Egeria*	1894	7.08	73.80	28.57	-2658	Sounding	surface	66	7
16621	HMS *Enterprise*	1962	30.90	-78.68	26.63	-821	Dredge	surface	35	1
36043	HMS *Penguin*	1891	-28.01	112.46	21.94	-1206	Sounding	surface	189	9
36053	HMS *Penguin*	1891	-26.94	111.18	22.66	-3350	Sounding	surface	203	9
36057	HMS *Penguin*	1891	-24.89	110.39	22.83	-3829	Sounding	surface	193	9
36361	HMS *Penguin*	1896	-10.21	178.01	28.91	-4844	Sounding	surface	123	8
36515	HMS *Penguin*	1897	-9.68	-174.62	28.05	-4057	Sounding	surface	71	6
36683	HMS *Penguin*	1897	1.21	-161.84	27.32	-4634	Sounding	surface	47	8
36704	HMS *Penguin*	1897	-13.17	-175.69	28.05	-3952	Sounding	surface	111	7
37130	HMS *Sealark*	1905	-8.42	65.63	28.35	-3694	Sounding	surface	78	7
37148	HMS *Sealark*	1905	-7.59	61.48	28.06	-3507	Sounding	surface	87	8
37149	HMS *Sealark*	1905	-2.70	67.38	28.95	-3594	Sounding	surface	119	7
37190	HMS *Sealark*	1905	-12.12	64.12	27.16	-3322	Sounding	surface	72	7
37299	HMS *Serpent*	1868	18.63	69.17	27.85	-3261	Sounding	surface	9	1
38482	HMS *Waterwitch*	1895	-40.45	49.82	7.78	-3780	Sounding	surface	39	2
17031	RNZFA *Tui*	1956	-39.77	167.75	16.04	-1137	Dietz grab	surface	71	4
17240	RNZFA *Tui*	1956	-28.88	170.00	22.18	-3021	Dietz grab	surface	165	8
17273	RNZFA *Tui*	1958	-20.95	-175.23	25.66	-869	Cone dredge	surface	40	6
16657	RV *Argo*	1960	-16.42	66.03	26.20	-2810	Core	4-9	60	8
16365	RV *Horizon*	1953	-19.48	-173.73	25.66	-4347	Gravity core	5-10	43	4
16640	RV *Horizon*	1953	-13.09	-124.28	26.67	-3456	Gravity core	4-8	58	7
16641	RV *Horizon*	1953	-14.27	-120.68	25.97	-3617	Gravity core	4-8	41	6
16642	RV *Horizon*	1953	-15.22	-117.51	25.97	-3641	Gravity core	1-4	32	5
16656	RV *Horizon*	1958	-23.61	-118.22	23.98	-3362	Gravity core	7-11	48	5
(1971,O87)	RV *Maria Paolina G*	1970	35.68	-4.08	18.17	-1500	Sphincter core	0-5	40	3
16645	RV *Spencer F. Baird*	1957	5.43	-131.32	27.65	-3415	Gravity core	7-10	51	6
16646	RV *Spencer F. Baird*	1957	-26.32	-147.12	21.85	-2312	Gravity core	3-7	54	6
16647	RV *Spencer F. Baird*	1957	-46.75	-123.00	9.91	-4030	Gravity core	6-11	53	2
16648	RV *Spencer F. Baird*	1957	-48.48	-113.28	8.06	-2677	Gravity core	0-8	41	2
16649	RV *Spencer F. Baird*	1957	-43.72	-107.60	10.99	-3141	Gravity core	3-7	17	3
16370	RV *Spencer F. Baird*	1958	-11.70	-109.72	25.27	-3296	Gravity core	0-3	1	1
16650	RV *Spencer F. Baird*	1958	-18.33	-79.34	20.07	-3157	Gravity core	8-12	49	7
16651	RV *Spencer F. Baird*	1958	-27.93	-106.92	21.45	-3039	Gravity core	8-15	67	6
16652	RV *Spencer F. Baird*	1958	-27.15	-109.83	21.45	-2819	Gravity core	10-14	51	5
16653	RV *Spencer F. Baird*	1958	-14.73	-112.10	24.90	-3034	Gravity core	12-15	69	7
16654	RV *Spencer F. Baird*	1958	-9.88	-110.68	25.26	-2712	Gravity core	5-9	46	7
17162	RV *Vema*	1959	28.40	-77.93	24.89	-1004	Piston core	0-2	136	8
17359	RV *Vema*	1959	-9.75	-34.40	27.14	-4123	Piston core	5-6	86	6

TABLE B.4: Analysis considering ForCenS samples within a 300 km distance: model selection of the linear and quadratic models testing if planktonic Foraminifera shell size (represented by the 95^{th} percentile of each population size distribution) can be predicted by annual mean sea surface temperature (sst linear effect, sst^2 quadratic effect), annual mean net primary productivity (pp) and/or species' relative abundance (abund, calculated as the median relative abundance of all ForCenS samples within a 300 km distance of each morphometric sample). A model including the interaction between sst and pp (sst : pp) was also considered. Columns: species, explanatory variables, degrees of freedom, log-likelihood, Akaike Information Criterion corrected for small sample size, delta AICc between models, model weight, adjusted R squared. All models within 2 delta AICc units are shown.

Species	**Expl.Var.**	**df**	**logLik**	**AICc**	**$\triangle$AICc**	**weight**	**R^2_{adj}**
T. sacculifer	sst	3	-7.04	20.79	0.00	0.38	0.25
T. sacculifer	sst^2	4	-6.78	22.78	1.99	0.14	0.24
G. ruber	null	2	-12.45	29.22	0.00	0.18	0.00
G. ruber	sst + pp	4	-10.34	29.85	0.63	0.13	0.05
G. ruber	sst	3	-11.61	29.90	0.67	0.13	0.02
G. ruber	abund	3	-11.69	30.06	0.84	0.12	0.01
G. ruber	pp	3	-12.01	30.70	1.47	0.09	-0.00
G. ruber	sst : pp	5	-9.45	30.71	1.49	0.08	0.07
G. conglobatus	sst : pp	5	5.29	1.30	0.00	0.27	0.19
G. conglobatus	sst + pp	4	3.40	2.40	1.10	0.16	0.13
G. conglobatus	sst^2 : pp	6	5.82	3.07	1.77	0.11	0.19
G. siphonifera	sst + pp	4	-2.22	13.69	0.00	0.29	0.33
G. siphonifera	sst	3	-4.24	15.20	1.51	0.14	0.27
G. siphonifera	sst : pp	5	-1.63	15.20	1.52	0.14	0.33
N. dutertrei	null	2	3.59	-2.73	0.00	0.22	0.00
N. dutertrei	pp	3	4.34	-1.76	0.98	0.13	0.01
N. dutertrei	abund	3	4.17	-1.42	1.31	0.11	0.00
N. dutertrei	sst	3	4.12	-1.32	1.41	0.11	0.00
N. dutertrei	sst^2	4	5.25	-0.90	1.83	0.09	0.04
P. obliquiloculata	sst	3	1.89	3.08	0.00	0.35	0.21
P. obliquiloculata	sst + pp	4	2.26	4.97	1.89	0.13	0.21
G. menardii	sst	3	-2.53	12.02	0.00	0.18	0.06
G. menardii	sst + abund	4	-1.29	12.26	0.23	0.16	0.10
G. menardii	null	2	-3.92	12.29	0.27	0.16	0.00
G. menardii	abund	3	-3.02	13.01	0.99	0.11	0.02
G. menardii	pp	3	-3.48	13.92	1.90	0.07	-0.01
G. truncatulinoides	sst^2 + pp	5	2.99	6.51	0.00	0.36	0.32
G. truncatulinoides	sst^2 : pp	6	3.88	7.90	1.39	0.18	0.34
G. inflata	pp	3	11.96	-16.41	0.00	0.41	0.15
G. inflata	null	2	9.79	-14.88	1.54	0.19	0.00

TABLE B.5: Analysis excluding historical samples collected by dredging the ocean floor, namely samples collected by HMNZS *Pukaki*, HMS *Challenger* (dredge only), HMS *Enterprise* and RNZFA *Tui* (see Table B.3). Table shows the model selection of the linear and quadratic models testing if planktonic Foraminifera shell size (represented by the 95^{th} percentile of each population size distribution) can be predicted by sea surface temperature annual mean (sst linear effect, sst^2 quadratic effect), net primary productivity annual mean (pp) and/or species' relative abundance (abund, calculated as the nearest ForCenS sample). A model including the interaction between sst and pp (sst : pp) was also considered. Columns: species, explanatory variables, degrees of freedom, log-likelihood, Akaike Information Criterion corrected for small sample size, delta AICc between models, model weight, adjusted R squared. All models within 2 delta AICc units are shown.

Species	**Expl.Var.**	**df**	**logLik**	**AICc**	**$\triangle$AICc**	**weight**	**R^2_{adj}**
T. sacculifer	sst	3	-5.29	17.34	0.00	0.32	0.30
T. sacculifer	sst + pp	4	-4.76	18.81	1.47	0.15	0.30
T. sacculifer	sst2	4	-4.88	19.05	1.71	0.14	0.30
G. ruber	null	2	-12.40	29.16	0.00	0.21	0.00
G. ruber	sst	3	-11.50	29.75	0.60	0.16	0.02
G. ruber	sst + pp	4	-10.53	30.35	1.19	0.12	0.04
G. ruber	abund	3	-11.91	30.57	1.41	0.11	-0.00
G. ruber	pp	3	-12.12	30.98	1.82	0.09	-0.01
G. conglobatus	sst + pp	4	3.71	1.87	0.00	0.15	0.11
G. conglobatus	sst : pp	5	5.06	1.88	0.02	0.15	0.15
G. conglobatus	sst + abund	4	3.48	2.33	0.46	0.12	0.10
G. conglobatus	sst	3	1.93	2.89	1.02	0.09	0.05
G. conglobatus	sst + abund + pp	5	4.36	3.28	1.41	0.07	0.12
G. conglobatus	null	2	0.45	3.45	1.59	0.07	0.00
G. conglobatus	abund	3	1.61	3.54	1.67	0.06	0.03
G. conglobatus	sst2 : pp	6	5.63	3.65	1.78	0.06	0.15
G. siphonifera	sst + pp	4	-2.06	13.51	0.00	0.28	0.35
G. siphonifera	sst	3	-4.09	14.98	1.47	0.13	0.29
G. siphonifera	sst : pp	5	-1.42	14.98	1.47	0.13	0.35
N. dutertrei	pp	3	6.51	-6.06	0.00	0.24	0.07
N. dutertrei	null	2	4.93	-5.40	0.66	0.17	0.00
N. dutertrei	sst	3	5.52	-4.07	1.99	0.09	0.00
P. obliquiloculata	sst	3	2.31	2.28	0.00	0.35	0.18
P. obliquiloculata	sst + abund	4	2.79	3.96	1.68	0.15	0.18
G. menardii	abund	3	-1.68	10.36	0.00	0.23	0.08
G. menardii	sst + abund	4	-0.59	10.92	0.56	0.17	0.11
G. menardii	null	2	-3.34	11.16	0.81	0.15	0.00
G. menardii	sst	3	-2.50	12.00	1.64	0.10	0.02
G. truncatulinoides	sst2 + pp	5	2.16	8.84	0.00	0.24	0.31
G. truncatulinoides	sst2	4	0.47	9.06	0.23	0.21	0.24
G. truncatulinoides	sst2 + abund	5	1.62	9.92	1.08	0.14	0.28
G. inflata	pp	3	11.05	-14.26	0.00	0.57	0.27

List of species

TABLE B.6: List of all modern species present in the seafloor sediment samples of the Buckley Collection. Note that only extant species are present in these samples. Species and genus names were updated to their current names.

Beella digitata	*Berggrenia pumilio*	*Candeina nitida*	*Globigerina bulloides*
Globigerina falconensis	*Globigerinella adamsi*	*Globigerinella calida*	*Globigerinella siphonifera*
Globigerinita glutinata	*Globigerinoides conglobatus*	*Globigerinoides ruber*	*Globoconella inflata*
Globoquadrina conglomerata	*Globorotalia crassaformis*	*Globorotalia hirsuta*	*Globorotalia menardii*
Globorotalia scitula	*Globorotalia truncatulinoides*	*Globorotalia tumida*	*Globorotaloides hexagonus*
Globoturborotalita rubescens	*Globoturborotalita tenella*	*Hastigerina pelagica*	*Neogloboquadrina dutertrei*
Neogloboquadrina pachyderma	*Orbulina universa*	*Pulleniatina obliquiloculata*	*Sphaeroidinella dehiscens*
Tenuitella iota	*Trilobatus sacculifer*	*Turborotalita humilis*	*Turborotalita quinqueloba*

Dissolution results

We carried out a linear-mixed effect model (LMER) using the log-transformed 95^{th} percentile of the population shell size as the response variable, and each sample's water depth as the independent fixed variable (effect) (see depths in Table B.3). Species were modelled as random effects, allowing for random intercepts and slopes, which takes into account interspecific variation on resistance to dissolution. We used Likelihood Ratio Test (LRT) to test for significance of the fixed effect. If dissolution affected our results, we would expect water depth to significantly explain part of the population shell size variation we found. However, the LMER results show that water depth is not a significant explanatory variable of planktonic Foraminifera population shell size variation in our dataset (Table B.7).

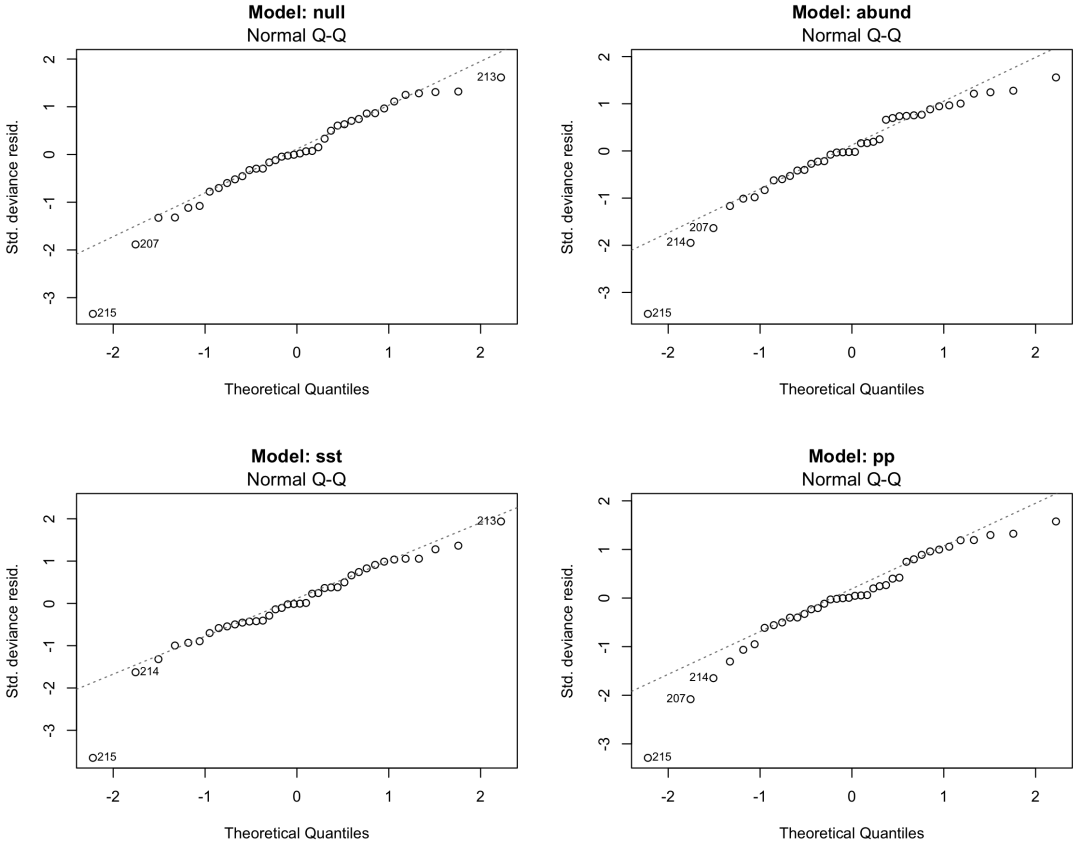
TABLE B.7: Dissolution analysis: linear mixed-effects model (LMER, ANOVA), using size variation (95^{th} percentile of the population) as the response variable, species as the random effects and either a null model (H0) or water depth (H1) as the explanatory variable. Columns: model explanatory variables (fixed effects), degrees of freedom, Akaike Information Criterion, log-likelihood, model deviance, chi-squared, P value, marginal R squared.

Explanatory variables	**df**	**AIC**	**logLik**	**dev**	χ^2	**P**	$\mathbf{R}^2_m$
H0: 1 + r.e.	5	151.19	-70.60	141.19			0.00
H1: (water depth) + r.e.	6	151.36	-69.68	139.36	1.83	0.18	0.00

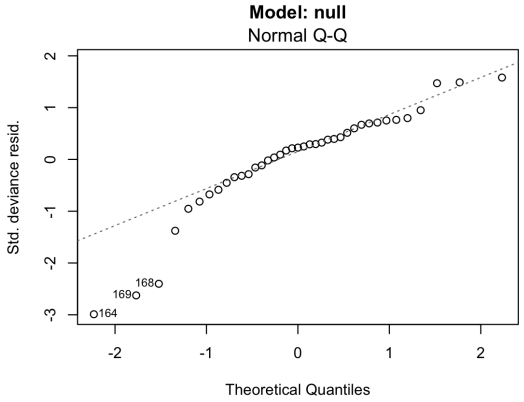
Linear models residual plots

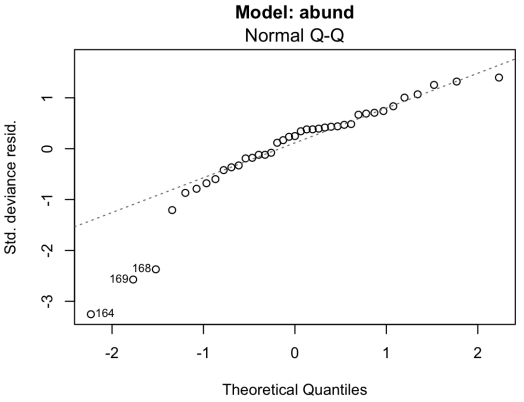
Residual plots of linear models per species. Models: null, abund (relative abundances), sst (mean annual sea surface temperature), and pp (mean annual net primary productivity).

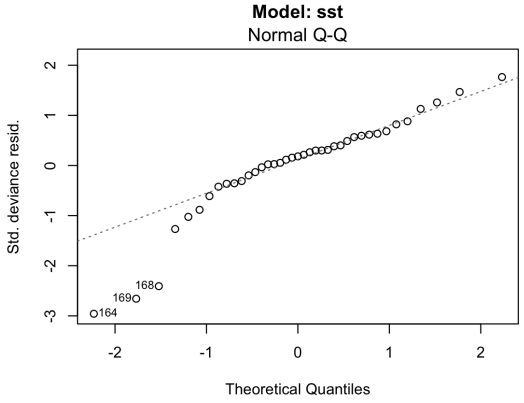
(a) Trilobatus sacculifer

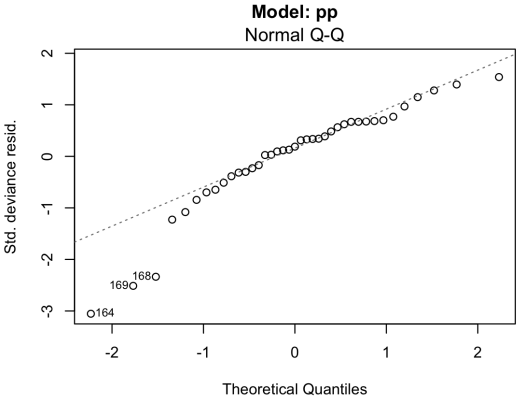


(b) Globigerinoides ruber

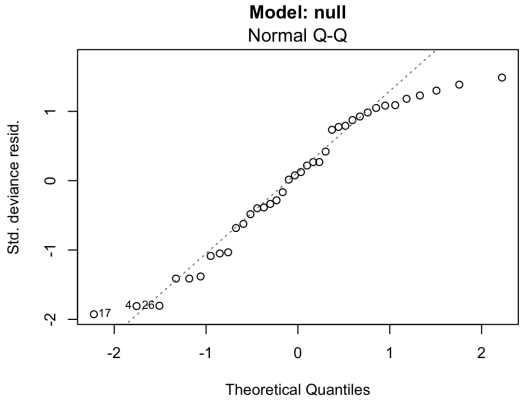


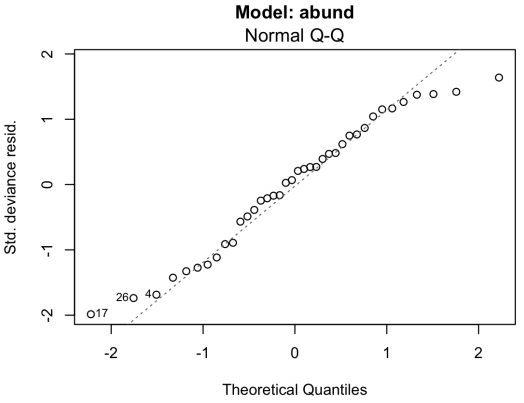


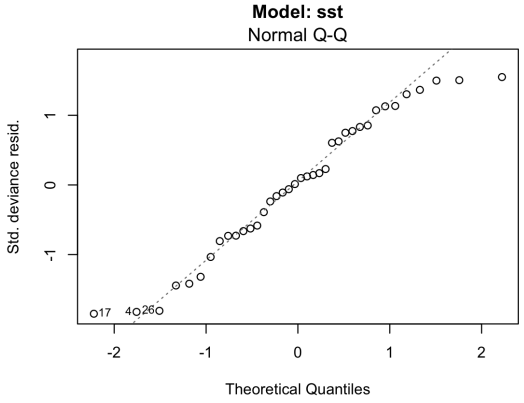


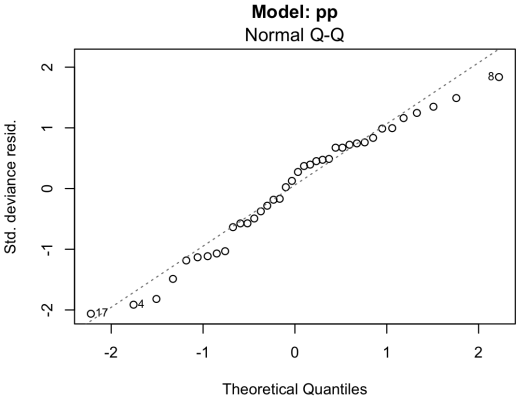


(c) Globigerinoides conglobatus

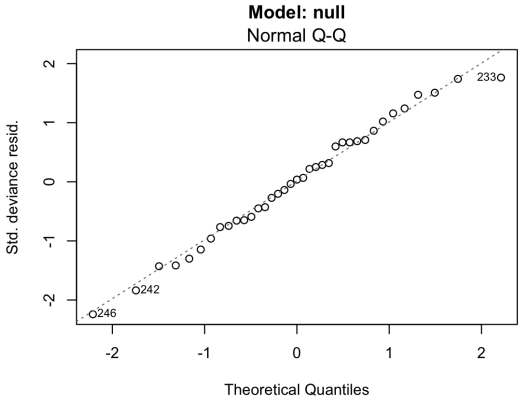


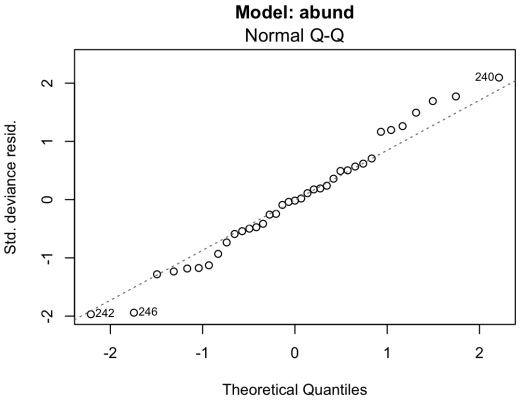


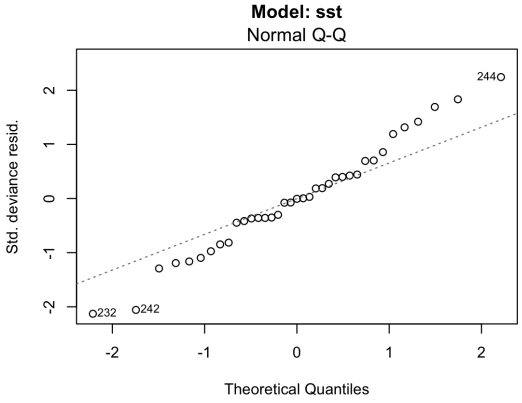


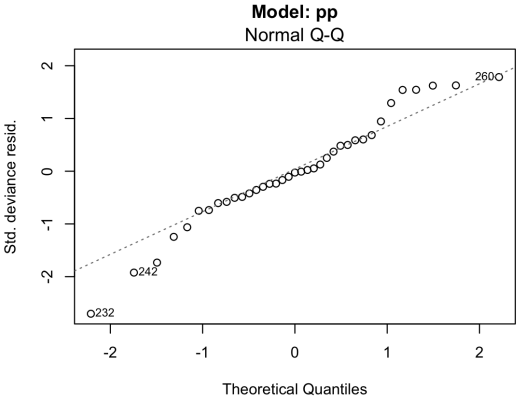


(d) Globigerinella siphonifera

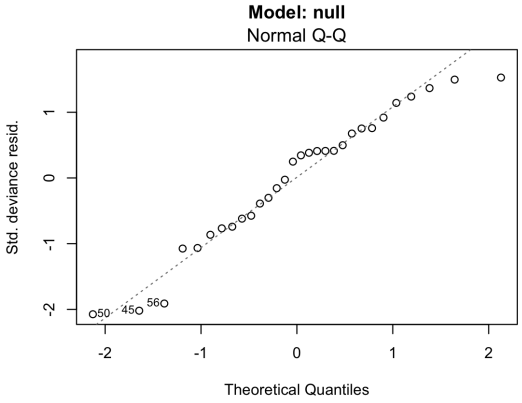


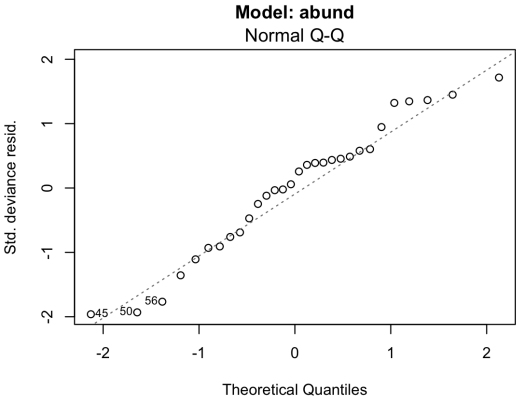


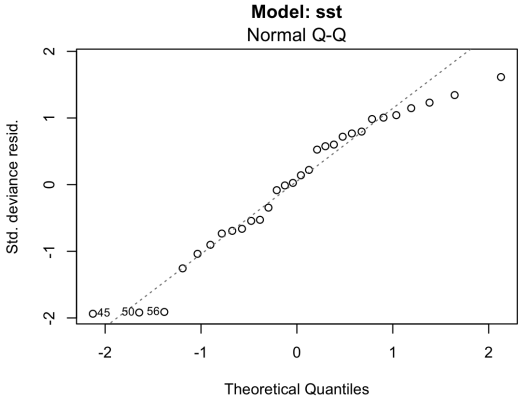


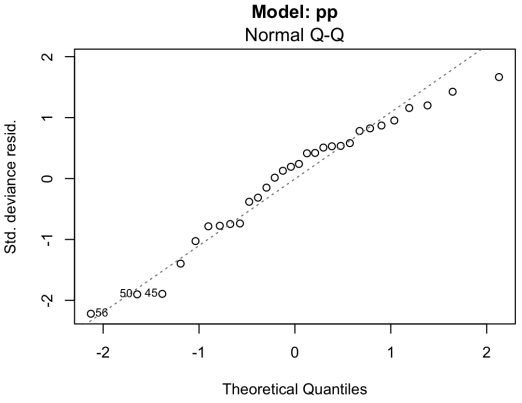


(e) Neogloboquadrina dutertrei

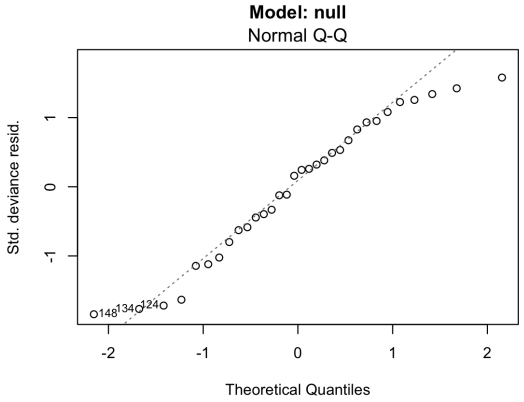


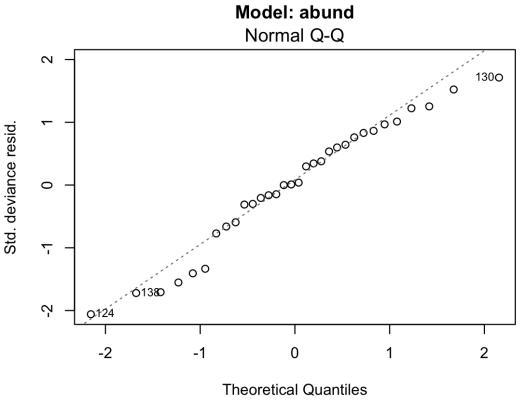


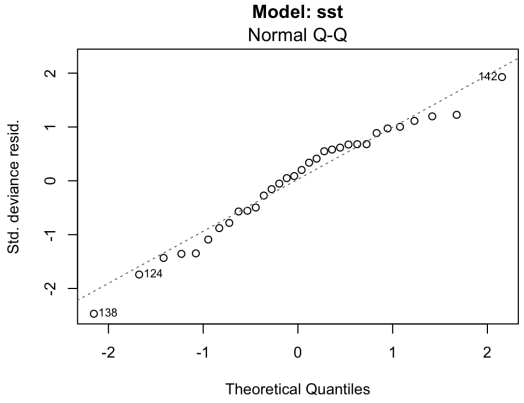


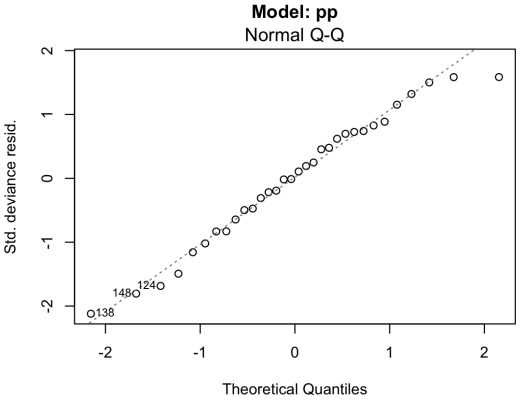


(f) Pulleniatina obliquiloculata

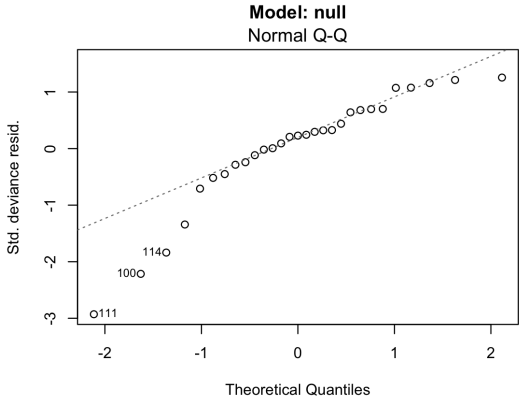


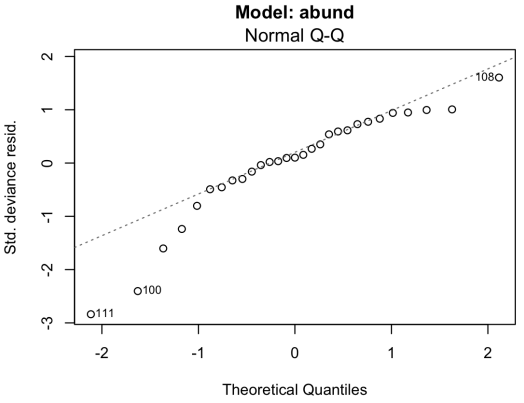


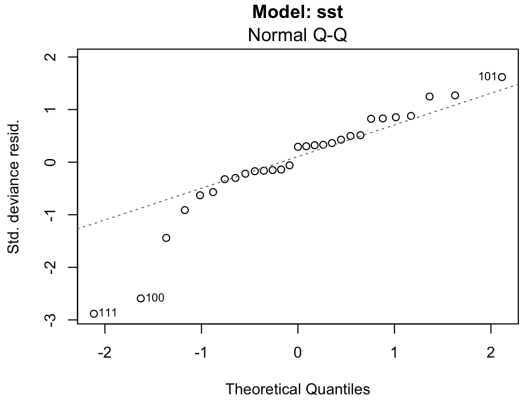


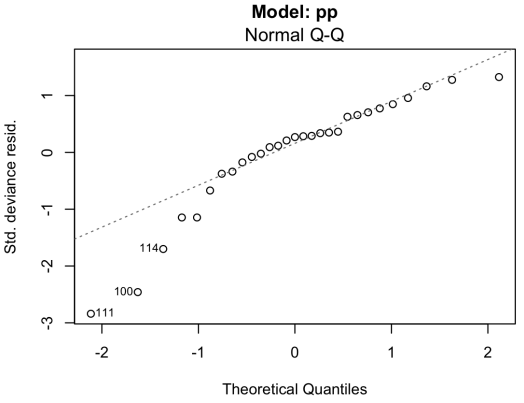


(g) Globorotalia menardii

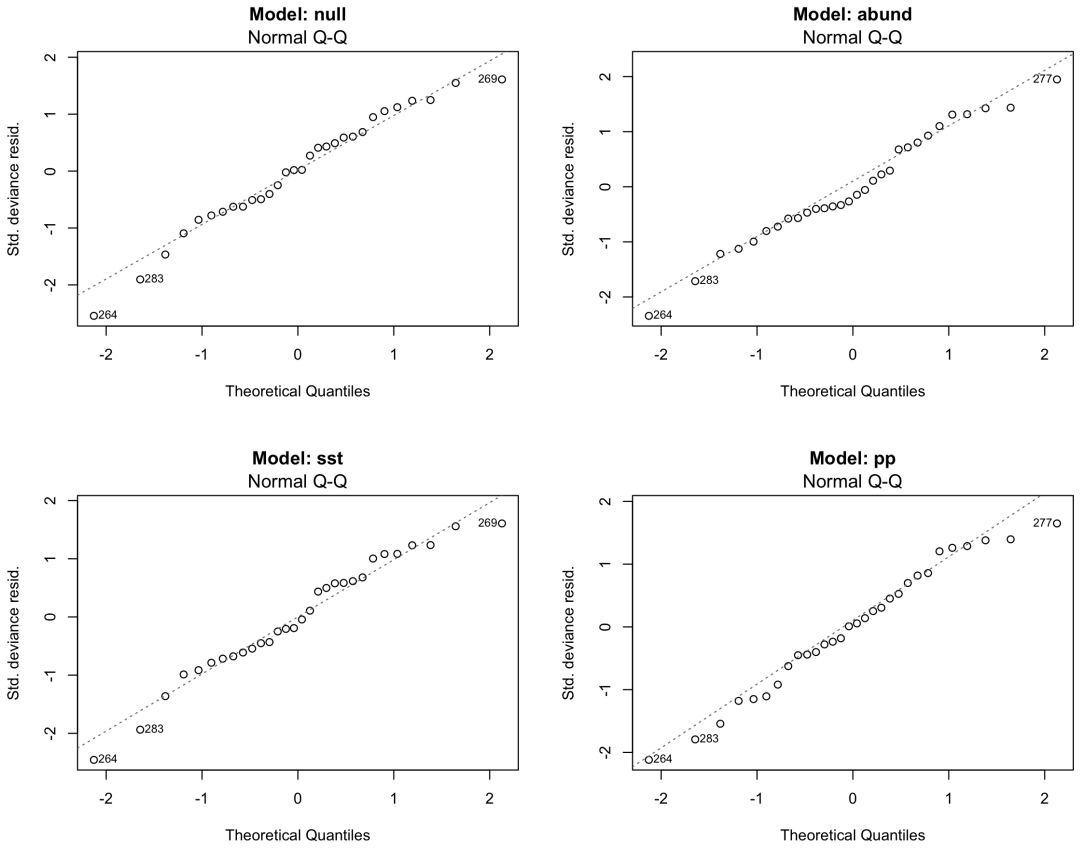








(h) Globorotalia truncatulinoides



(i) Globoconella inflata

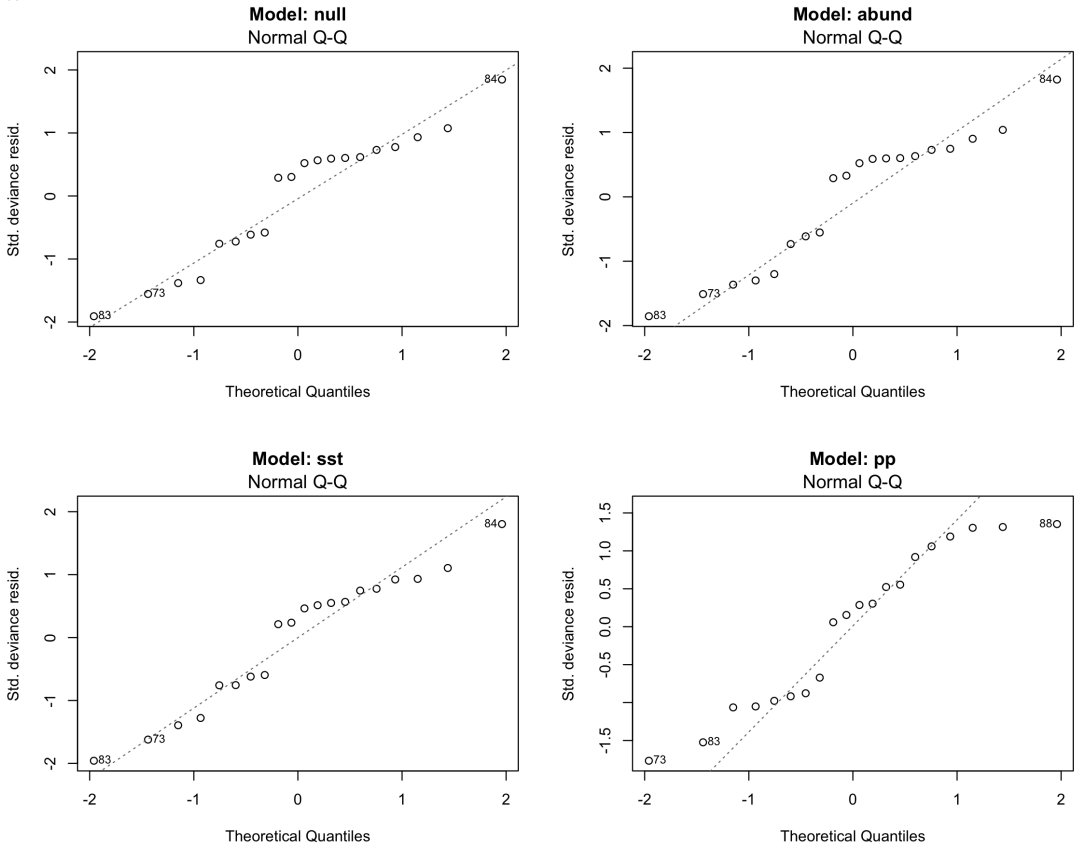


FIGURE B.1: Residual plots of linear models per species. Models: null, abund (relative abundances), sst (mean annual sea surface temperature), and pp (mean annual net primary productivity).

Appendix C

Supplement to Chapter 5

Phylogeny of extant species

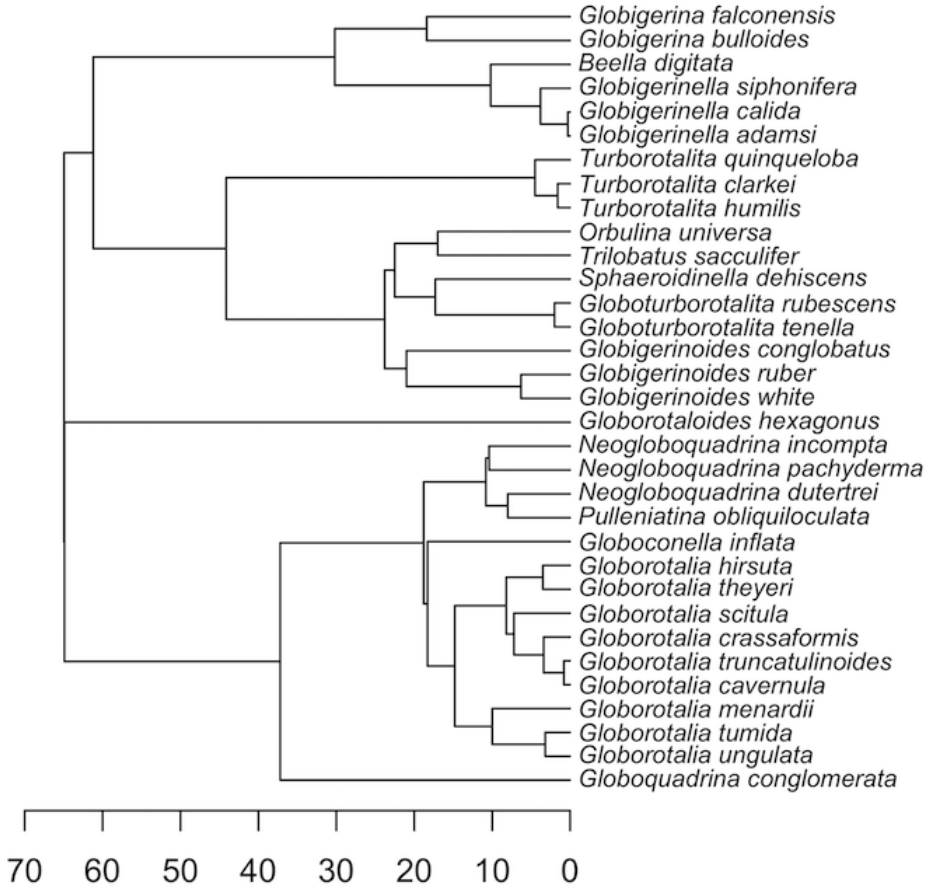


FIGURE C.1: Phylogeny of extant planktonic Foraminifera macroperforate species, modified from Aze et al. (2011).

We modified the Aze et al. (2011) Cenozoic phylogeny of macroperforate planktonic Foraminifera (PF) species, following the taxonomic standardisation of Siccha and Kucera (2017) (Fig. C.1) . More specifically, we split the species *Globigerinoides ruber* into *G. ruber* (pink pigmented) and *G. white* (not pigmented) at 6.3 million years ago (Ma) (Aurahs et al., 2011). We also split the species *Neogloboquadrina pachyderma* into *N. pachyderma* and *N. incompta* at 10.4 Ma (Darling et al., 2006). The main reason for adding these species to the Aze et al. (2011) phylogeny is that they are currently recognised species, with clear morphological differences and population-level coretop and sediment trap data.

Shell size estimates of extant species

In order to build a clade-wide species-level size dataset of extant PF, we used data on 2774 individual shell measurements of 36 species (Table C.1). We extracted data from three different datasets on shell size: [1] Rillo et al. (2019b) (20 species, 1824 individuals), [2] Weinkauf et al. (2016) (2 species, 831 individuals) and [3] Baranowski (2013) (35 species, 118 individuals). These three datasets are openly available online, respectively, at: [1] https://doi.org/10.5519/0056541, [2] https://doi.org/10.1594/PANGAEA.846744 and [3] https://doi.org/10.1594/PANGAEA.901825,. Specimens were collected from seafloor and/or sediment trap samples, and we used shell diameter to represent shell size. The species *Globigerinoides ruber* (white), *G. ruber* (pink) and *G. elongatus* were analysed together as *G. ruber*. For more information about the sampling and the method of measurement, see corresponding references of each dataset.

Shell diameter was measured as the longest shell-axis through the proloculus by Rillo et al. (2019b) and Weinkauf et al. (2016) and from the middle of the last chamber through the proloculus to the opposite side of the test by Baranowski (2013). These two ways of measuring the shell diameter would only differ if the last chamber is smaller than the penultimate chamber, which was not the case for most of the individuals measured by Baranowski (2013).

TABLE C.1: Average size of planktonic Foraminifera species (square-root of shell area). Column: species names; size as shell diameter; number of individuals measured per species; dataset(s) used for the size estimates: [1] Rillo et al. (2019b), [2] Weinkauf et al. (2016), [3] Baranowski (2013).

Species	Size (μm)	N(ind)	Reference
Berggrenia pumilio	92.08	9	[3]
Candeina nitida	418.11	2	[3]
Dentigloborotalia anfracta	166.19	2	[3]
Globigerina bulloides	259.92	193	[2;3]
Globigerina falconensis	262.49	19	[1;3]
Globigerinella calida	320.33	22	[1;3]
Globigerinella siphonifera	440.47	75	[1;3]
Globigerinita glutinata	236.29	233	[1;3]
Globigerinita minuta	129.45	2	[3]
Globigerinita uvula	133.05	3	[3]
Globigerinoides conglobatus	503.56	34	[1;3]
Globigerinoides ruber	255.76	1270	[1;2;3]
Globoconella inflata	314.74	99	[1;3]
Globoquadrina conglomerata	644.71	2	[3]
Globorotalia crassaformis	392.28	9	[1;3]
Globorotalia hirsuta	590.5	3	[3]
Globorotalia menardii	804.75	96	[1;3]
Globorotalia scitula	243.25	9	[1;3]
Globorotalia truncatulinoides	417.32	48	[1;3]
Globorotalia tumida	902.49	8	[1;3]
Globorotaloides hexagonus	424.52	2	[3]
Globoturborotalita rubescens	189.46	7	[1;3]
Globoturborotalita tenella	212.8	51	[1;3]
Neogloboquadrina dutertrei	429.41	80	[1;3]
Neogloboquadrina pachyderma	263.91	226	[1]
Orbulina universa	637.46	8	[1;3]
Orcardia riedeli	130.71	5	[3]
Pulleniatina obliquiloculata	478.9	53	[1;3]
Sphaeroidinella dehiscens	654.56	2	[3]
Tenuitella fleisheri	135.91	3	[3]
Tenuitella iota	111.81	4	[3]
Tenuitella parkerae	149.42	3	[3]
Trilobatus sacculifer	427.96	170	[1;3]
Turborotalita clarkei	131.34	8	[3]
Turborotalita humilis	173.18	12	[1;3]
Turborotalita quinqueloba	189.92	2	[3]

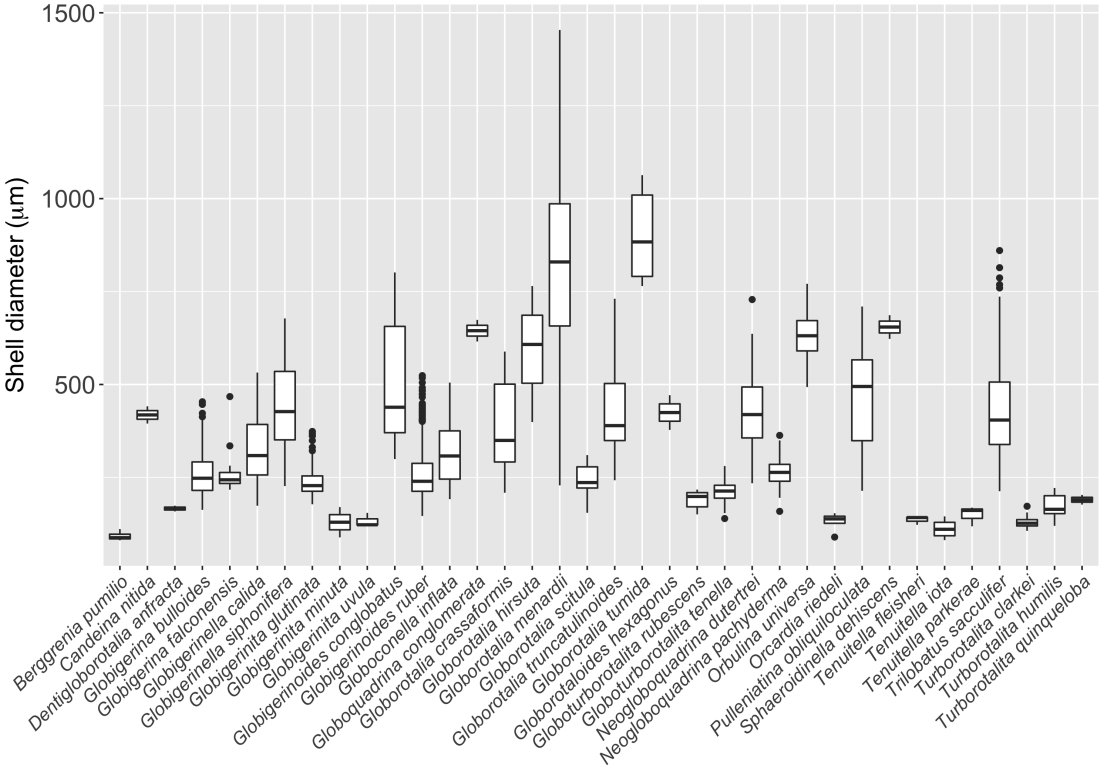


FIGURE C.2: Boxplots of individual shell diameter measurements for each planktonic Foraminifera species. Data from Rillo et al. (2019b); Weinkauf et al. (2016); Baranowski (2013). See also Table C.1.

Community phylogenetics

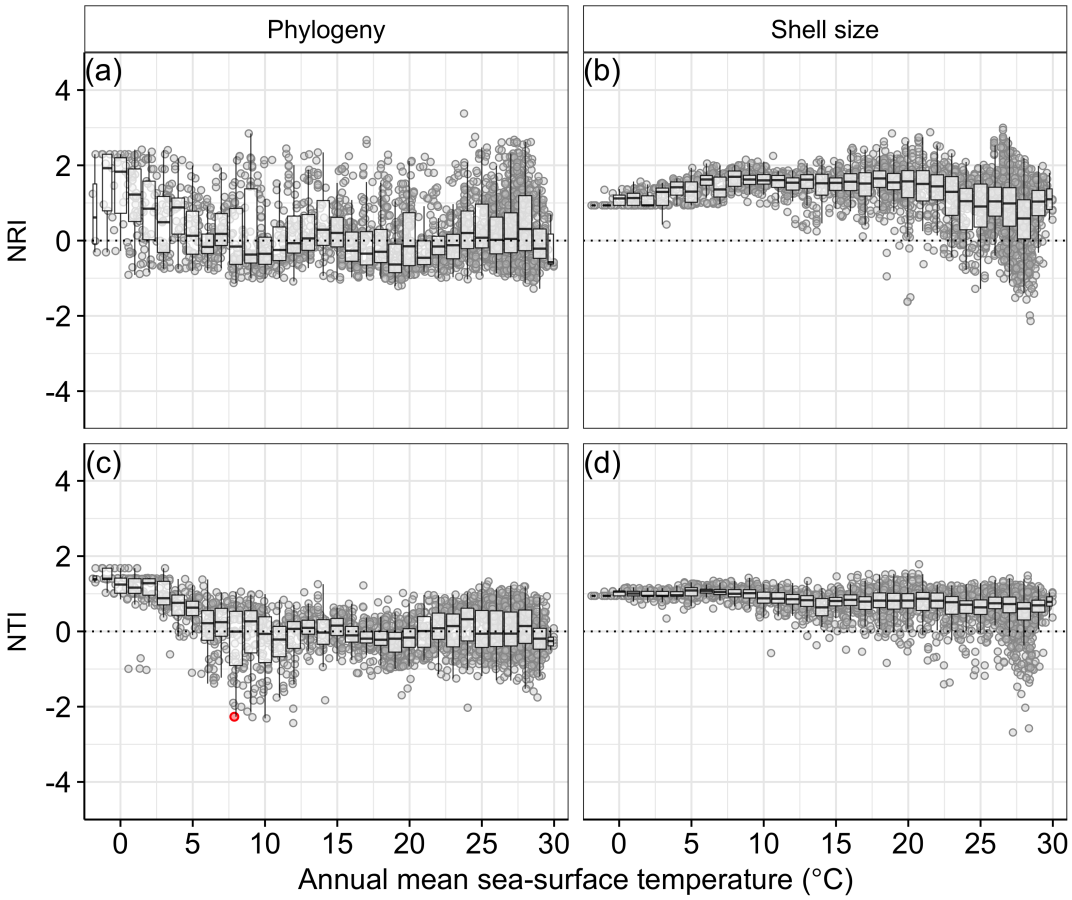


FIGURE C.3: Spatial data: null model 'taxa' shows similar patterns as null model 'richness'. Net relatedness index (NRI) and nearest taxon index (NTI) calculated for 3,053 planktonic Foraminifera coretop assemblages, plotted against sea surface temperature annual mean at each site. **(a)** and **(c)** 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, red significant negative (overdispersed) NRI or NTI values; there are no significant positive values (clustered). Box-plots in black represent the distribution of NRI or NTI for each 1°C. Significance level 1%, based on 100 runs of the null model 'taxa'.

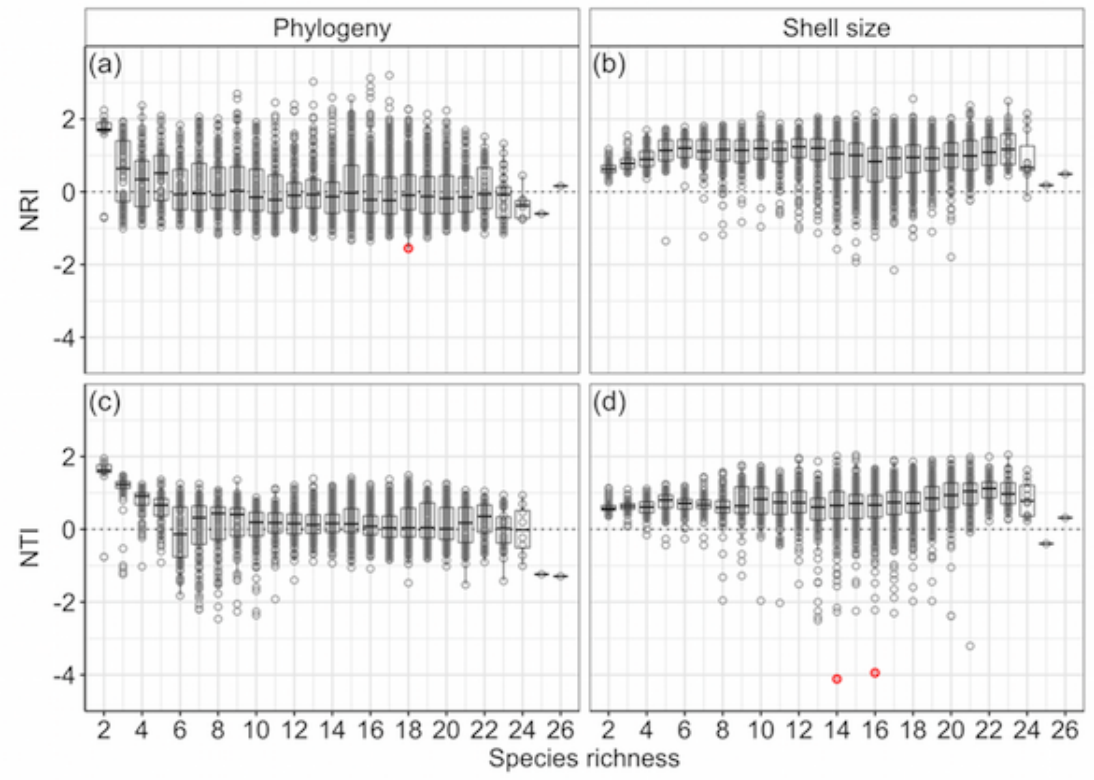


FIGURE C.4: Spatial data: net relatedness index (NRI) and nearest taxon index (NTI) calculated for 3,053 planktonic Foraminifera coretop assemblages, plotted against species richness in each assemblage. **(a)** and **(c)** were calculated based on the phylogenetic distance among co-occurring species. **(b)** and **(d)** were calculated based on the shell size differences among co-occurring species. Grey dots show non-significant, red significant negative (overdispersed) NRI or NTI values; there are no significant positive values (clustered). Significance level 1%, based on 100 runs of the null model 'richness'.

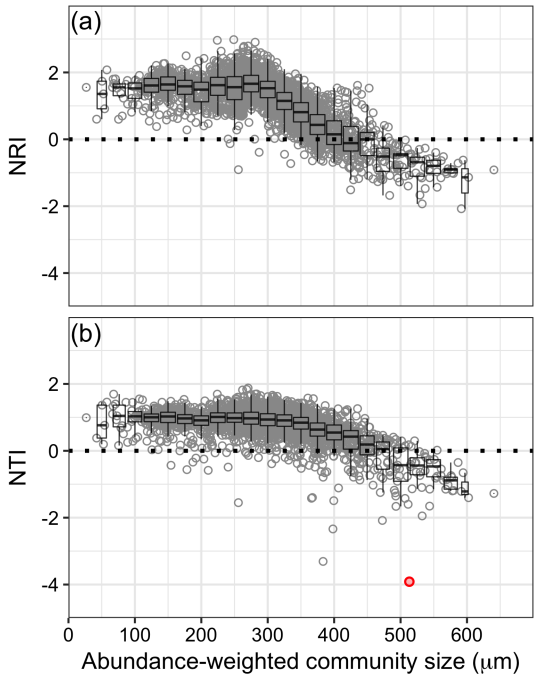


FIGURE C.5: Spatial data: communities of larger average sizes are more overdispersed (more negative index values). Net relatedness index (NRI) and nearest taxon index (NTI) calculated for 3,053 planktonic Foraminifera coretop assemblages, plotted against abundance-weighted community size (based on Table C.1). NRI and NTI were calculated based on the shell size differences among co-occurring species. Grey dots show non-significant, red significant negative (overdispersed) NRI or NTI values; there are no significant positive values (clustered). Box-plots in black represent the distribution of NRI or NTI for each 25μm. Significance level 1%, based on 100 runs of the null model 'richness'.

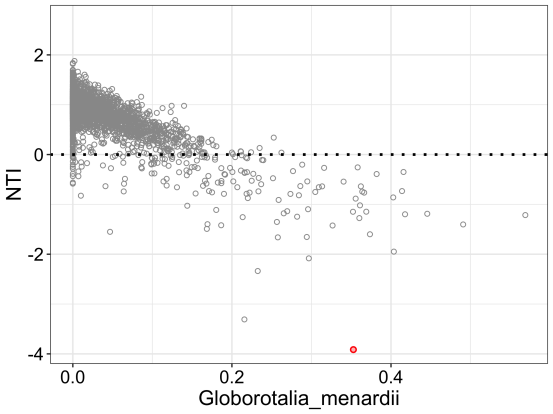


FIGURE C.6: Spatial data: communities with high relative abundances of *Globorotalia menardii* are more overdispersed regarding size similarity among species. Net nearest taxon index (NTI) calculated for 3,053 planktonic Foraminifera coretop assemblages based on the shell size differences among co-occurring species, plotted against the relative abundance of *G. menardii*. Significance level 1%, based on 100 runs of the null model 'richness'. Grey dots show non-significant, red significant negative (overdispersed) values.

Time series analysis

The first differences of the time series calculate the change in species abundances from one time step to the next, and reduces the time-series autocorrelation. First differences were not calculated for consecutive samples between which there was a sampling gap of more than ten 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 true change in abundance from one time step to the next.

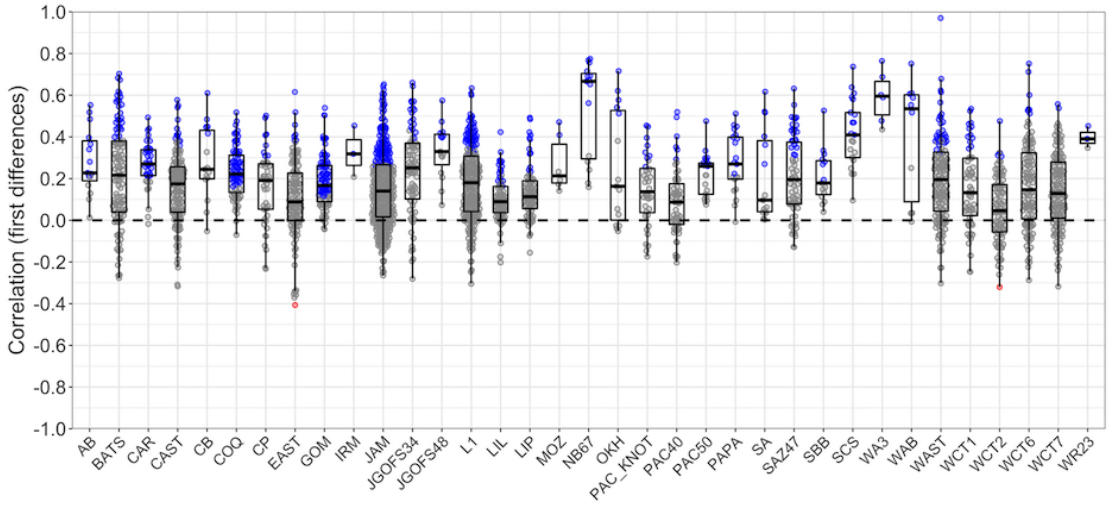


FIGURE C.7: Temporal data, first differences: pairwise Kendall rank correlations of the differentiated time-series of planktonic Foraminifera abundances (2,303 in total) plotted by sediment trap (see Table C.2). Grey dots show non-significant, blue significant positive, red significant negative values; significance level of 1%.

TABLE C.2: Temporal data: meta-data of sediment traps taken from Jonkers and Kucera (2015). Columns: sediment trap name; latitude and longitude given in decimal values; 'L' stands for length of the time series in: years, days and samples (series); 'Res' stands for resolution: average number of days between samples; 'N' is the number of species identified in each sediment trap (i.e., number of time series); depth in which the sediment trap was moored (in meters), asterisk (*) means that the depth changed during the data collection; reference studies that collected the sediment trap data.

Trap name	Latitude	Longitude	L(years)	L(days)	L(series)	Res(days)	N	Depth (m)	References
AB	53.10	-177.00	8.90	3264	105	26.90	6	3198	Asahi and Takahashi (2007)
BATS	32.10	-64.30	6.10	2232	31	58.60	15	3200	Deuser et al. (1981); Deuser and Ross (1989)
CAR	10.50	-65.50	3.00	1089	75	12.40	9		Tedesco and Thunell (2003)
CAST	14.50	64.80	1.40	516	32	12.20	17	732	Curry et al. (1992)
CB	21.10	-20.70	2.10	753	38	17.90	6	3500	Fischer et al. (1996); Zaric et al. (2005)
COQ	-30.00	-73.00	7.30	2679	159	8.80	13	2300*	Marchant et al. (1998, 2004)
CP	-52.60	174.20	1.20	425	42	8.80	10	362*	Northcote and Neil (2005)
EAST	15.50	68.80	1.40	527	38	11.70	16	2790	Curry et al. (1992)
GOM	27.50	-90.30	6.20	2245	238	7.30	14	700	Poore et al. (2013); Reynolds and Richey (2016)
IRM	59.00	-38.50	3.80	1372	58	16.00	3	2750	Jonkers et al. (2010, 2013)
JAM	-8.30	108.00	2.70	983	56	16.20	27	1370*	Mohtadi et al. (2009)
JGOFS34	34.00	-21.00	1.00	377	26	12.80	13	2000	Wolfteich (1994)
JGOFS48	48.00	-21.00	1.00	377	26	12.80	6	2000*	Wolfteich (1994)
L1	33.00	-22.00	2.10	767	35	21.80	22	3000	Storz et al. (2009)
LIL	42.40	3.50	11.40	4167	151	22.50	13	500	Rigual-Hernandez et al. (2012)
LIP	43.00	5.20	12.20	4457	116	27.80	13	500	Rigual-Hernandez et al. (2012)
MOZ	-16.80	40.80	2.40	862	39	20.90	4	2250	Fallet et al. (2010, 2011)
NB67	69.70	-0.50	2.20	787	32	18.20	6	500	Jensen (1998)
OKH	59.30	149.80	1.00	365	21	16.40	6	258	Alderman (1996)
PAC_KNOT	44.00	155.00	2.40	893	52	15.40	9	2957	Kuroyanagi et al. (2002)
PAC40	40.00	165.00	2.60	952	44	16.50	11	2986	Kuroyanagi et al. (2002)
PAC50	50.00	165.00	3.50	1287	69	15.50	7	3260	Kuroyanagi et al. (2002)
PAPA	50.00	-145.00	3.90	1437	82	12.80	7	3800	Sautter and Thunell (1989)
SA	49.00	-174.00	9.00	3267	101	26.80	6	4812	Asahi and Takahashi (2007)
SAZ47	-46.80	142.00	1.40	493	40	10.60	12	3800	King and Howard (2003)
SBB	34.30	-120.00	5.90	2144	93	10.90	6	470*	Darling et al. (2003); Kincaid et al. (2000)
SCS	9.40	113.20	1.80	663	22	29.10	7	720	Wan et al. (2010)
WA3	-7.50	-28.00	1.40	499	20	24.00	4	671	Zaric et al. (2005)
WAB	-11.60	-28.50	2.70	1001	38	23.80	5	710	Zaric et al. (2005)
WAST	16.30	60.50	1.40	529	38	13.30	17	3020	Curry et al. (1992)
WCT1	25.00	137.00	1.70	612	37	14.10	11	917*	Mohiuddin et al. (2002)
WCT2	39.00	147.00	1.70	628	40	14.20	14	1371*	Mohiuddin et al. (2002)
WCT6	42.00	155.20	1.00	381	19	19.10	15	1091	Mohiuddin et al. (2005)
WCT7	36.70	154.90	1.00	375	19	18.80	17	5034	Mohiuddin et al. (2004)
WR23	-20.00	9.20	2.10	751	28	17.70	3	1648	Zaric et al. (2005)

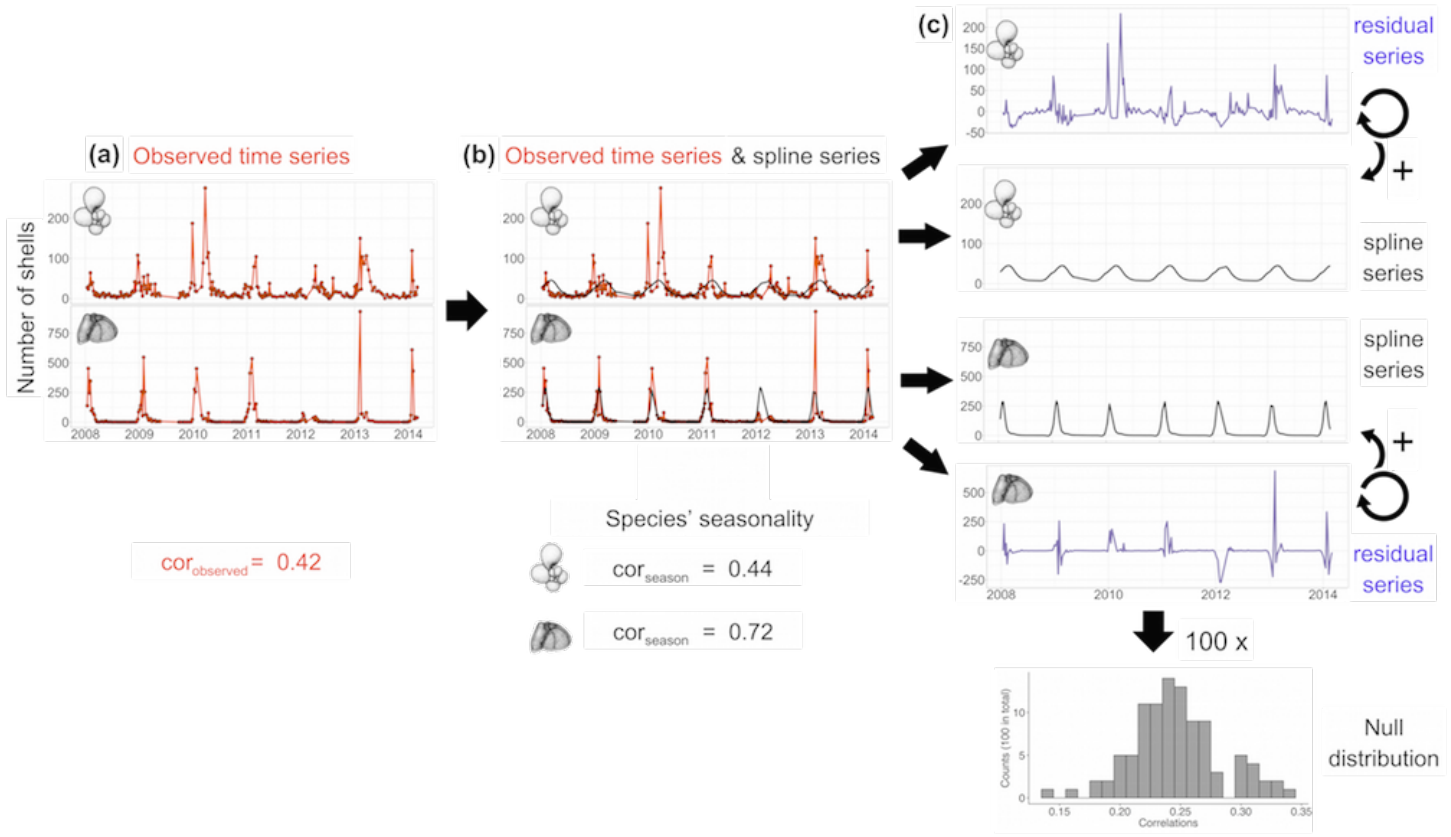


FIGURE C.8: Temporal data: schematic explanation of the time-series analysis. **(a)** Observed time series of two species (orange dots and line), *G. calida* (top) and *G. truncatulinoides* (bottom), in the Gulf of Mexico (GOM) sediment trap (Reynolds and Richey, 2016). Y-axis indicates shell flux (number of shells$*m^{-2}*day^{-1}$), used here as a proxy for absolute abundance; x-axis indicates time in years (2008-2014). The observed correlation between these two species in the GOM is 0.42. **(b)** A smoothing spline calculates an yearly-averaged series, the spline series (black line). The correlation between the observed time series of a species (orange line) and its spline series (black line) indicates how seasonal the species is in the given sediment trap. *G. truncatulinoides*, for example, has a strong annual seasonality in the GOM (cor = 0.72). **(c)** To generate the null distribution of how we expect these two species to correlate given their annual seasonality, we first calculate the residual series for each species (purple line, i.e., the observed time series minus its spline series), shuffle it (indicated by the circle arrow), sum it back to the spline series (indicated by the '+'), and then correlate the two randomised series of the two species. This randomisation is repeated 100 times to yield a null distribution of correlations between these two species in the GOM. The observed correlation (0.42) is then compared to this null distribution for significance. In this example, the observed correlation is significant, as it is greater than the top 1% of the null distribution. Additionally, the residual series show how the species' observed abundances departure from its annual seasonality (spline series). The average correlation of the residuals of all species in the GOM trap gives us a measure of inter-annual variation.

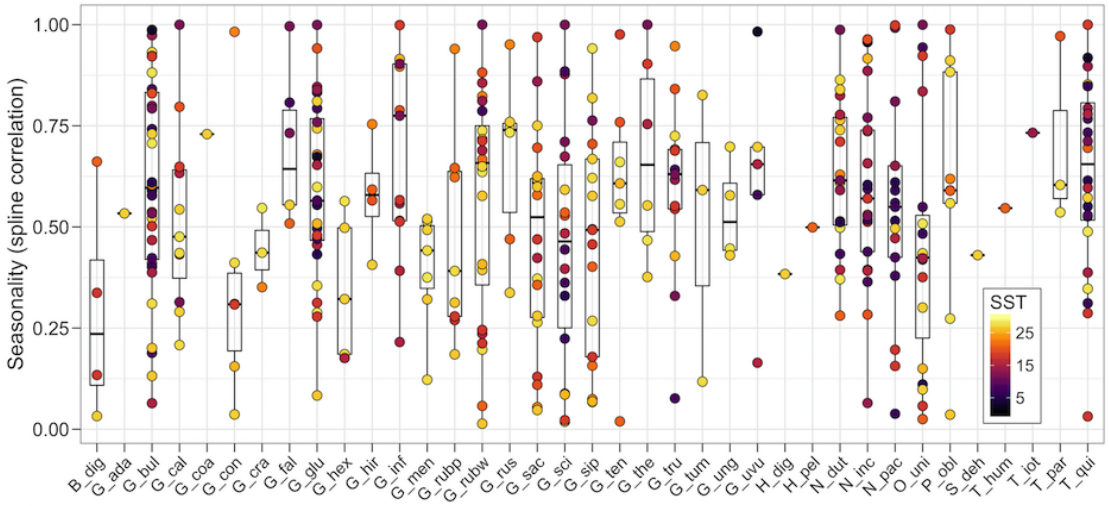


FIGURE C.9: Temporal data: correlation between the observed time-series and its spline-series for each species in each sediment trap, coloured by local mean annual sea-surface temperature (SST) in the trap location, shown for each species (x-axis). Note the high variability in seasonality (i.e., correlation values) within species in different sediment traps.

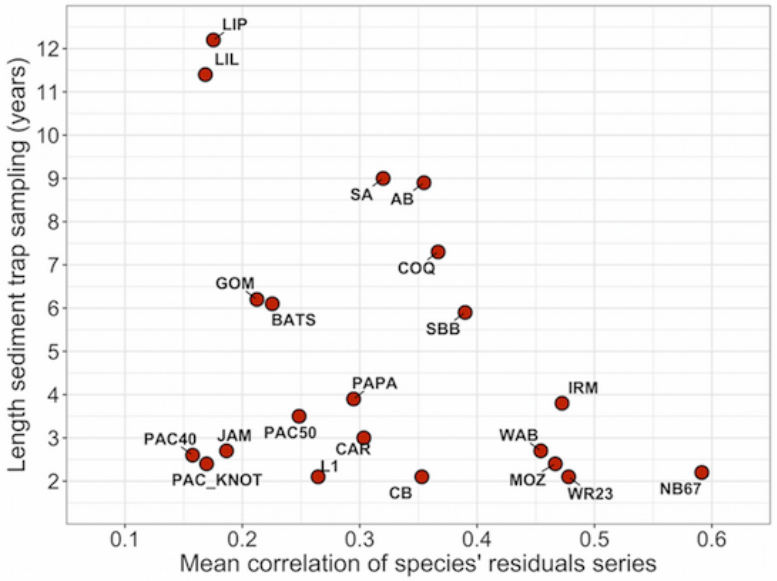


FIGURE C.10: Temporal data, interannual variation within sediment traps: length (in years) of sediment trap sampling as a function of mean correlation among all species' residual-series (i.e., original time-series minus its spline-series, Fig. C.8). The 21 sediments traps shown collected samples for longer than two years (Table C.2).

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