# Ecological modeling of the temperature dependence of cryptic species of planktonic Foraminifera in the Southern Hemisphere

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## ABSTRACT

Cryptic genetic species of planktonic Foraminifera often exhibit narrower biogeographic distributions and ecological preferences than the respective morphospecies. In theory, it should therefore be possible to improve the resolution of the paleoceanographic reconstructions based on sediment assemblages of these species. Here, we use observational data on the latitudinal distribution of 11 genotypes of *Globigerina bulloides* (including a newly described genotype), *Orbulina universa*, *Truncorotalia truncatulinoides* and *Globoconella inflata* in plankton tows from south Indian Ocean to model the relationship between their abundance and the sea surface temperature (SST). We then use this model to assess the potential benefit of knowing the ecological preferences of cryptic species on assemblage-based transfer functions. In doing so, we first apply this model to a database of assemblage counts in 1334 surface sediment samples from the Southern Hemisphere and simulate the expected abundances of individual genotypes in sediment samples. This simulated dataset is used to calibrate three different transfer functions: the Imbrie and Kipp Method, Weighted Averaging Partial Least Squares and Modern Analog Technique. Trials show that such simulated splitting of morphospecies into their respective genotypes leads to a substantial (7 to 25%) overall reduction of the error rates of SST estimates in the calibration dataset. The degree of error rate reduction is sensitive to the increase of taxonomic richness in the simulated assemblages induced by the co-occurrence of genotypes of the same morphospecies. Although the studied species occur across a broad SST range, the largest reduction of error rate by the transfer functions is obtained within the 4 °C to 12 °C SST range, where most of the studied genotypes are found. Our results show that all genotypes are not expected to improve the accuracy of transfer functions at the same level: while integrating cryptic diversity in *G. bulloides*, *T. truncatulinoides* and *G. inflata* clearly improve assemblage-based SST reconstructions, genotypes of *O. universa* have a negligible effect.

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## 1. Introduction

The fossil record of planktonic Foraminifera constitutes one of the most informative archives of paleoceanographic changes. In addition to the development of paleoproxies deduced from the chemical composition of calcite of their shells (e.g., Katz et al., 2010), the use of planktonic Foraminifera in paleoceanography largely revolves around quantitative empirical calibrations between the sea surface temperature (SST) and the relative abundances of morphospecies in surface sediments (e.g., Imbrie and Kipp, 1971; Berger and Gardner, 1975; Hutson, 1977; Malmgren et al., 2001; Kucera et al., 2005). Such environmental transfer functions, when applied to assemblage composition data from fossil samples, allow the reconstruction of ancient

SSTs with an estimated precision matching that of geochemical paleo-thermometers (Katz et al., 2010). The application of these transfer functions relies on the assumption that each of the counted morphospecies of planktonic Foraminifera has a specific relationship to SST that is stable in space and through time.

The discovery of cryptic genetic diversity in planktonic Foraminifera (for a review, see Darling and Wade, 2008) has significant repercussions for the use of all species-specific paleoproxies in this group. Molecular analyses have revealed that most modern morphospecies are composed of a complex of two to seven distinct genotypes, most of them exhibiting a distinct biogeography and/or ecology (Huber et al., 1997; Darling et al., 1999, 2000, 2004, 2006, 2007; de Vargas et al., 1999, 2001, 2002; Stewart et al., 2001; Bauch et al., 2003; Aurahs et al., 2009, 2011; Morard et al., 2009, 2011; Ujiié et al., 2010). This discovery implies that SST reconstructions relying on the morphospecies concept of planktonic Foraminifera are based on aggregates of biogeographically and ecologically distinct genotypes and may contain significant noise (Kucera and Darling, 2002).

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The presence of additional ecological information is potentially beneficial for paleoceanographers, since some of the genotypes within a given morphospecies exhibit peculiar shell characteristics (Huber et al., 1997; de Vargas et al., 2001; Darling et al., 2006; Morard et al., 2009; Aurahs et al., 2011; Quillévéré et al., 2013), making it possible to transfer the biological information acquired through genetic analysis to paleoceanography.

Kucera and Darling (2002) were the first to model the effect of cryptic diversity in planktonic Foraminifera on assemblage-based SST reconstructions. After splitting the morphospecies Globigerina bulloides into three genotypes in the Atlantic Ocean, they showed that the incorporation of the geographic range of each genotype resulted in a substantial decrease in error rate of the transfer functions. The parametrization of genotypes abundances was, however, rather intuitive and the exercise was limited to simulating the effect of splitting a single morphospecies only. Although the additional environmental information carried by the cryptic diversity was promising, a direct integration in transfer functions was limited by the absence of quantitative models allowing recognition of genotypes based on shell morphology. Kucera et al. (2005) chose a by-pass strategy by reducing the potential occurrence of different genotypes with distinct narrower ecological ranges within a given calibration set in developing regional rather than global calibration sets. Unfortunately, this approach allows a limited potential for decreasing error rate in transfer functions because genotypes can co-occur in the same area or are distributed along ecological gradients representing short geographical distances. As a consequence, fossil assemblages are likely a mixture of multiple genotypes even on a small regional scale (Darling et al., 2004; Morard et al., 2009; Aurahs et al., 2009).

In this study, we model the distribution in surface sediments of the cryptic genetic species of four morphospecies (Globigerina bulloides, Orbulina universa, Truncorotalia truncatulinoides, and Globoconella inflata) based on their observed SST preferences along a 30° latitudinal transect in the south Indian Ocean. These four morphospecies were selected because of their geographically extended and recently characterized cryptic diversity (de Vargas et al., 2001; Darling and Wade, 2008; Morard et al., 2009, 2011; Quillévéré et al., 2013). Together with Neogloboquadrina incompta (which displays a single genotype in the Southern Ocean; Darling et al., 2006) and Globigerinoides sacculifer (which is globally genetically homogenous; André et al., 2013), these four morphospecies constitute more than half of the assemblages

recovered from sediments deposited in subtropical to subpolar waters of the Southern Hemisphere (Fig. 1). We first characterize the genetic diversity of G. bulloides along the latitudinal transect in south Indian Ocean. Together with the data published on the same transect on the distribution and abundance of the genotypes of O. universa (Morard et al., 2009), T. truncatulinoides (Quillévéré et al., 2013) and G. inflata (Morard et al., 2011), we use the observed environmental preferences of the cryptic genetic types found within these morphospecies to simulate their abundance in sediments. We then use the simulated dataset to test the effect of cryptic diversity on the skill of three transfer function methods to extract the relationship between SST and foraminiferal counts across the Southern Hemisphere.

## 2. Material

### 2.1. Sample collection

Plankton samples were collected onboard the Marion-Dufresne during the cruise OISO-4 (January–February 2000; Metzl, 2000). The collection transect covers a 30° latitude range in the south Indian Ocean, replicating twice the gradient from subtropical to subpolar waters (Fig. 2, Table 1). Ring net tows (100 μm mesh size) were used between 250 m depth and the sea surface. Because the sampling was not consistently depth-stratified, we ignore for the purpose of this study the vertical dimension. Although Weiner et al. (2012) have recently shown that cryptic genetic types in planktonic Foraminifera can be separated by depth, we believe that none of the species involved in this study is affected by this phenomenon, making it possible to interpret their ecological preferences on the basis of the information from the surface layer, where all these species dwell at least during some time in their life cycle. Of the included species, Truncorotalia truncatulinoides has the largest vertical habitat range, but Ujiié et al. (2010) found no evidence for separation of genetic types in this species by depth.

Following plankton net collection, samples were filtered through a 2 mm sieve and the finer fraction including the planktonic Foraminifera was distributed into plastic Petri-dishes with 0.2 μm filtered sea water. Using a dissecting microscope and a fine brush, Foraminifera were isolated and transferred into smaller Petri-dishes with filtered sea water. At each station and within each morphospecies, as many individuals as possible were collected. Specimens were individually cleaned by
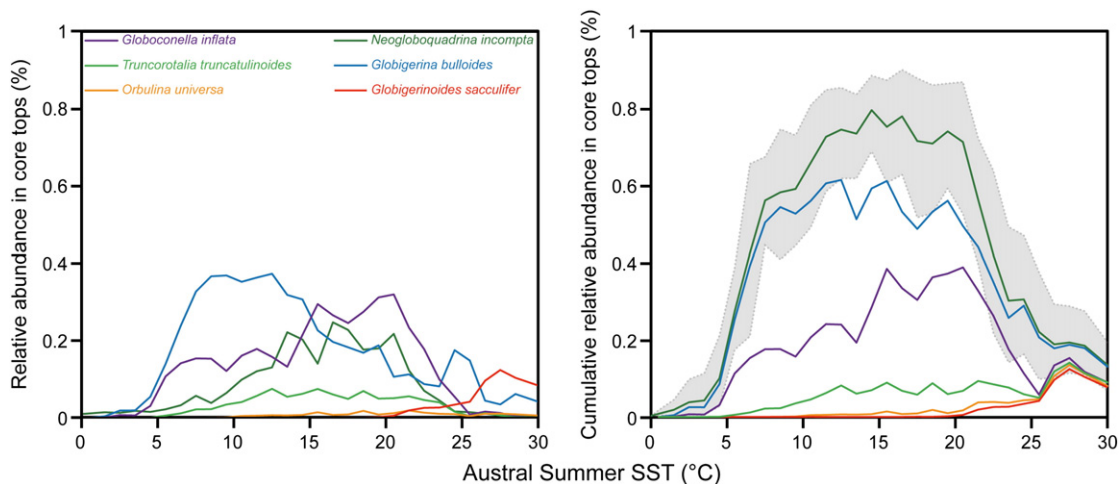


**Fig. 1.** Relative abundances (left) and cumulative relative abundances (right) of Globigerinoides sacculifer, Orbulina universa, Truncorotalia truncatulinoides, Globoconella inflata, Globigerina bulloides and Neogloboquadrina incompta in core tops from the Southern Hemisphere plotted against summer SST at 10-m depth. Thick lines represent mean individual or cumulative abundances of the morphospecies within each 1 °C interval. The gray light area delimited by dotted lines represents the standard deviation of the total cumulative abundances of the six morphospecies together.
Sediment abundance data are from Barrows and Juggins (2005), SST data are from WOA Locarnini et al. (2006).