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Coccolithus pelagicus subsp. *braarudii* morphological plasticity in response to variations in the Canary region upwelling system over the past 250ka

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Abstract. Coccolith size matters on routine identification of calcareous nannofossil species. But morphometry can also be a tool to study their morphological plasticity and adaptations to environmental patterns. Most current studies are limited in extracting morphological plasticity data, with most statistical methods varying from histogram analysis to mixture analysis, or even multistatistical analysis, allowing the identification of morphotypes but with significant assumptions (e.g., normal distribution) on the morphological pattern of the potential different morphotypes within a population. To address this limitation a multivariate statistical morphometrical tool, Integrated Multivariate Morphon Analysis (IMMA), was developed to identify different placolith morphotypes regarding maximum coccolith length and applied to Quaternary GeoB5559-2 samples, using morphometry data of *C. p. braarudii*. The results show that IMMA and morphometry microvariations can be used to extract variations in upwelling intensity and primary productivity, extracting the morphological plasticity of *C. p. braarudii* as a response to primary productivity variations. Thus, IMMA has great potential for studies on the effects of climatic events on coastal upwelling regions during the Quaternary.

1 Introduction

Coccolithophores are commonly subjected to evolutionary studies since they present an almost continuous fossil record since the limit between the Triassic to the Jurassic (Bown et al., 2004), making them ideal tools for biostratigraphy, evolution and palaeoceanographys of the Mesozoic and Cenozoic with many of the taxa appearing during the Cenozoic epochs, still extant (see references in Frada et al., 2010).

Thus, coccolithophores provide plentiful and consistent (micro)fossil data in continuity to extant living data. They have short life cycles rapidly producing numerous generations, an advantage to study their physiology and observe biological adaptations

30   to environmental changes, either in lab cultures (Daniels et al., 2014; Sheward et al., 2014, 2017) or in the water column (Renaud & Klaas, 2001), but a disadvantage for paleontological studies, since morphological responses to environmental changes in such short time intervals need ultra-high resolution sample sets.

Here we'll consider a long-time span taxon plexus commonly referred to as the species *Cocolithus pelagicus* s.l.. *C. pelagicus* s.l. is one of the most interesting taxa that evolved during the Cenozoic. Its fossil record appears since the beginning of the

35   Palaeocene stage and still thrives in present day oceans. This means that due to its genetic plasticity, *C. pelagicus* s.l. managed to survive and adapt to several dramatic changes that occurred since the extinction of the non-avian Dinosaurs (see Zachos et al., 2001, 2008 for a broad discussion on Cenozoic climate events). However, previous works (e.g., Reitan et al., 2012) indicate that its morphology does not reveal major direct influence of long-term climate change, although morphological and palaeogeographical changes are observed in the fossil record. This raises the question at what time scales would climate have

40   an effect, if not on a million-year time scale? This is certainly due to short life cycle/generation time, which would imply, assuming a capable genetic plasticity, adaptations on much shorter time scales.

Although the generation time presents a great challenge for palaeontological evolutionary studies in coccolithophores, the continuous fossil record together with the several extant species are major advantages that advocate this group for evolutionary studies with many extant species having continuous fossil record since distinct Cenozoic epochs.

45   Both the geno- and the phenotype (co-)evolve. In this last case it may include the organism size, in addition or separate from other morphological traits by differential fitness. How a phenotypic character like body size evolves over time and what environmental factors influence phenotypic change are an important question both for Biology and Palaeontology (Reitan et al., 2012) with significant changes between uni and pluricellular organisms. Among the unicellular calcareous nannoplankton the size of *C. pelagicus* s.l. has been demonstrated to present genetically different subspecies, with an extant smaller (*C.*

50   *pelagicus* spp. *pelagicus*) and an intermediate (*C. pelagicus* spp. *braarudii*) form (Saez et al., 2003; Vargas & Probert, 2004). This means that the morphometry on coccolithophores can be used as a proxy of their genetic variability along the fossil record.

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Focusing on morphometrics, both palaeoecology and evolution of coccolithophores can be addressed simultaneously (e.g., Read et al., 2013).

Although morphometry has been widely used in palaeoceanographic studies, discrete empirical nature of usual methodologies,
55 are strongly biased regarding short-term genetic/evolutionary observations, i.e., the fast-evolving plasticity of a certain species to respond/adapt to climate perturbations are very difficult to address. Arising from these limitations, most current studies are limited in extracting morphological plasticity data. Most statistical methods, varying from histogram analysis (e.g., Mattioli et al., 2004; Thibault, 2010) to mixture analysis (e.g., Suchéras-Marx et al., 2010), or even multistatistical analysis (Peti et al., 2021), allow the identification of morphotypes but with significant assumptions (e.g., normal distribution) on the
60 morphological pattern of the potential different morphotypes within a population. To address this limitation a multivariate statistical morphometrical tool (MMA) was developed to identify different placolith morphotypes regarding maximum coccolith length in the Quaternary and applied to Quaternary Northeast Atlantic Offshore *C. pelagicus* s.l. data (Parente et al., 2004; Narciso et al., 2006). The method was then modified to study morphological plasticity on coccolithophores, having been renamed to Integrated Multivariate Morphons Analysis (IMMA), and already used in *C. pelagicus* s.l. data from the Quaternary
65 of the West Coast of Iberia (Prista et al., 2020).

In this work we present the results of applying IMMA to *C. pelagicus* s.l. data from Quaternary samples in the Canary Islands region.

2 Materials and Methodology

The survey was conducted during 1998 aboard the research vessel Meteor as part of the European project CANIGO16 in the
70 submarine mountain slope of Agadir, 31° 38,7'N and 13° 11,2'W (Wefer et al., 1998) (Fig. 1). The hole was performed at a depth of 3178m, with a recovery of 5.85m of sediment, from isotopic stages 1 to 8. Due to the proximity of this site to the upwelling regime of Cape Ghir, climate-induced variations on the palaeoproductivity are reflected in the sediment core (Moreno et al., 2002).

A total of 117 samples were selected from this survey with 5cm equal spacing between samples. Age model was obtained from
75 the correlation between $\delta^{18}O$ data from the sediment and the SPECMAP $\delta^{18}O$ chronological curve (Martinson et al., 1987 in

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Moreno et al., 2002). Samples were dated through a linear interpolation of the corresponding dating to the control points used, which in this case were associated to isotopic events. The final correlation between SPECMAP curve and GeoB5559-2 survey is 0.807, resulting in a mean resolution of 2.4 ka between samples (Moreno et al., 2001) (see age model in supplementary material).

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Figure 1 – Location of Site GeoB5559-2 near the Canary archipelago region (map ESRI ©).

Smear slides were prepared from a speck of ocean sediment and observed under an optical double polarizing petrographic
85 microscope (OLYMPUS BX-40), at x1250 magnification, connected to a digital camera (OLYMPUS DP11) to register placolith images for measurement. For morphometry, 100 placoliths were randomly selected and photographed throughout the slide of each sample, and their distal shield maximum diameters were subsequently digitally evaluated (Narciso et al., 2006).

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A methodological development of the previous Multivariate Morphon Analysis (MMA) (Parente et al., 2004; Narciso et al., 2006) was applied, the Integrated Multivariate Morphon Analysis (IMMA), which extends the computation of a single

90 morphometric matrix to a set of 10 morphometric matrixes by systematically shifting 10 times the 1.0 µm initial morphon tabulations by 0.1 micron each, allowing the definition of morphotypes with a 10 times higher precision, up to 0.1 µm resolution (see Prista et al., 2020). The multivariate statistical analysis (PCA) was carried out using IBM© SPSS© version 23.0 software.

3 Results

IMMA was applied as an exploratory method to all (117) the samples allowing to extract two most significant components

95 representing 73.5% of the total variance, 50.7% for component one (C1) and 22.8% for component two (C2). Three sets of significant morphons were identified, two for C1 and one for C2. According to C1 the limits were determined as [6.9; 12.9[µm for the smaller (sC1) and [14.0; 17.2[µm for the larger (LC1) morphotypes. C2 defined a third (median) morphotype (MC2) with size ranges between [11.5; 15.2[µm.
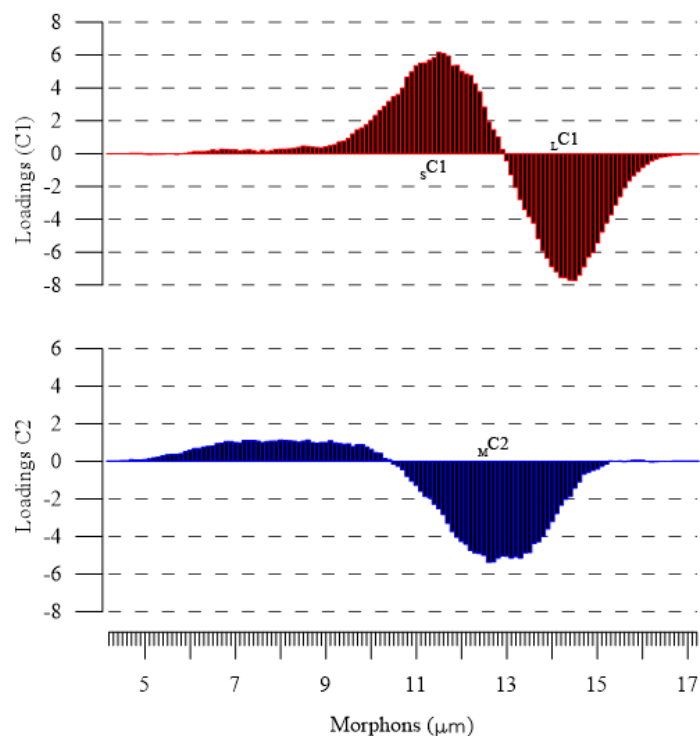

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Figure 2 – IMMA loadings of component one (red bars) and component two (blue bars) applied to GeoB5559-2

According to C1 scores, the smaller morphotype shows a small dominance, being active in 53% of the samples, while along

C2 the morphotype is active in 68% of the samples (Fig. 3).
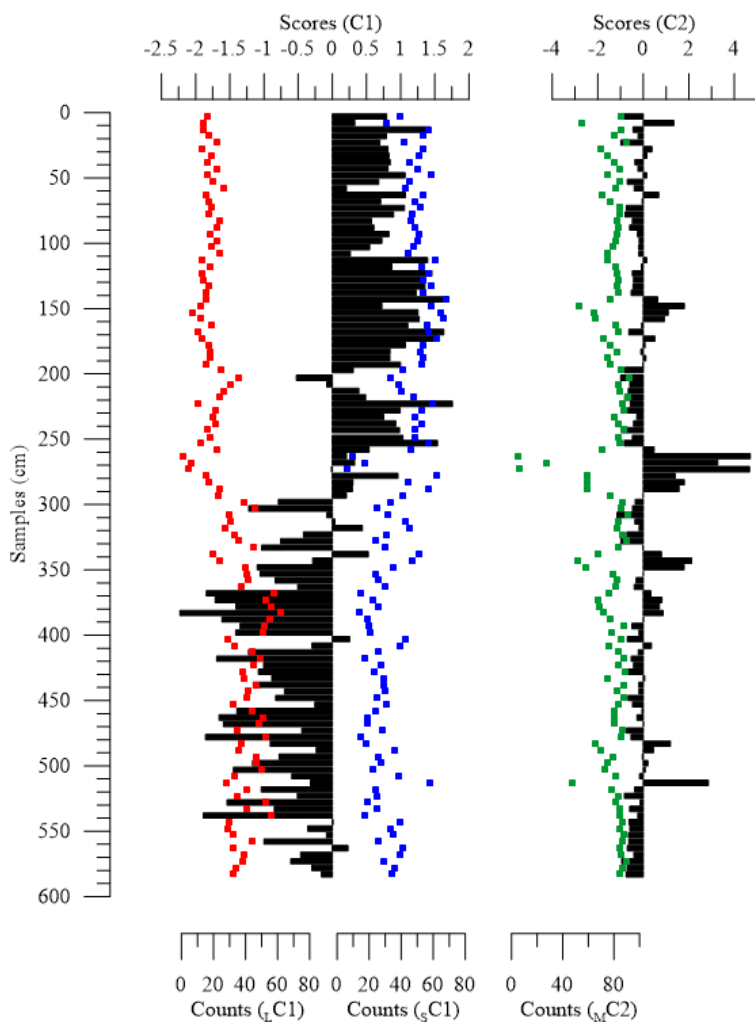
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Figure 3 – Scores and counting's for GeoB5559-2. From left to right: C1 and C2 scores (black bars); Blue dots correspond to

smaller morphotype; red dots to larger morphotype; green dots to median morphotype.

110 Correlation between counting's and scores is high and significant (Table 1), strengthening the PCA results.

Table 1 – Correlation between morphotype counting's and PCA scores.

| Interval (µm)	Morphotype	Correlation with counting's
6.9 – 12.9	$_sC1$	0.88
14.0 – 17.2	$_LC1$	-0.93
11.5 – 15.2	$_MC2$	-0.98

4 Discussion

Site GeoB5559-2 is located near Canary Islands, an eutrophic upwelling region (Barton, 1998; Arístegui et al., 2009; Benazzouz et al., 2014) where only the larger morphotypes, belonging to *Coccolithus pelagicus braarudii*, are expected to be found. The results confirm the presence of this *C. p. braarudii*, with its core size range defined by C2, while C1 shows its variability in size due to palaeoceanographic changes. Since only one morphotype is present, PCA C1 is expected to show its

120 variability. Instead of two or more morphotypes defining the major variance in the data, with only one morphotype it is its variability where most of the data variance is found.

The PCA extracted a third morphotype in C2, which would theoretically be independent of the C1 morphotypes. However, the size range of C2 morphotype and the fact that all morphometric data belongs to *C. p. braarudii* suggests that the variance extracted corresponds to the core size variations of *C. p. braarudii*. The reason why this data variance is extracted in a different

125 component is due to the fact that oscillations on the core size of the morphotype are not obliged to follow the general size tendency of *C. p. braarudii*. Mean resolution is of 2.4 ka, meaning that each sample covers more than 2 ka. The tendency for coccoliths for decreasing or increasing in size do not have to affect equally the variations in the morphons that make up the core size of *C. p. braarudii*. The core size represents 85.8% of all measurements (see supplementary material). Samples showing tendency for lower sizes reflect an interval of nearly 2.5 ka where conditions for reduced coccolith size were frequent.

130   However, the core size continues to exist and in this time interval its much smaller variations do not have to follow the major

tendency.

The region of the Canary Islands is an area of the ocean characterized by the presence of both coastal upwelling and eolian

input from the Sahara/Sahel regions (Nave et al., 2001 and references within). Cape Ghir filament is a quasi-permanent feature,

and its origin is thought to be on the cyclonic relative vorticity injection by the wind-stress curl (Troupin et al., 2012; Sangrà

135   et al., 2015). Filaments at Cape Jubi and between Cape Jubi and Cape Bojador are smaller, show intermittency and are variable

in their location due to their interaction with the eddy field induced by the Canary Islands (Barton et al., 1998, 2004). It has

been proposed that their origin is in the entrainment of upwelled water by such offshore eddy field. Cape Blanc filament is

also a permanent feature, as the Cape Ghir filament (see Fig. 4).
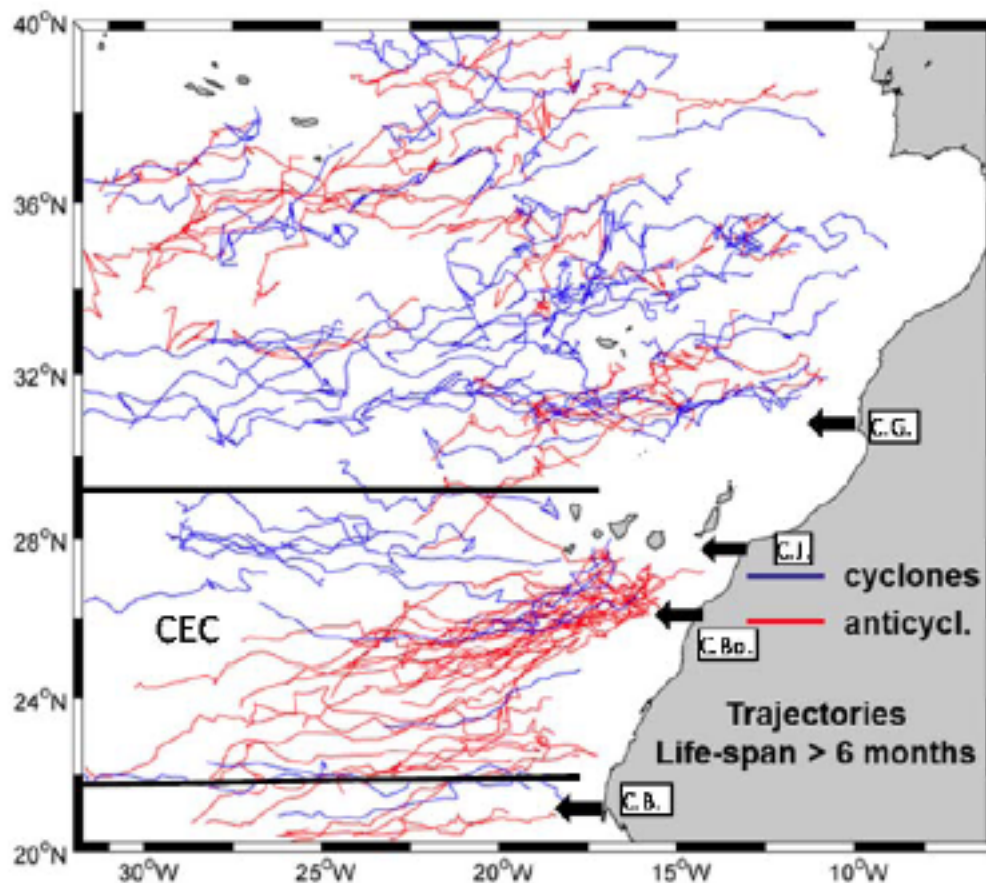
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Figure 4 – Westward-propagating eddy trajectories lasting over 6 months, as obtained from 14 years (1992–2006) of merged altimeter data, showing the Canary Eddy Corridor (CEC) extending from 22°N to 29°N. Black arrows indicate the sites of recurrently observed upwelling filaments. They are located in the region near Cape Ghir (C.G.), near and between Cape Jubi (CJ) and Cape Bojador (C.bo.), and near Cape Blanc (C.B.). Adapted from Sangrà et al. (2009).

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This means that the Canary Islands region is, to some extent, similar to the West coast of Iberia, with an upwelling regime, which in the Spanish archipelago goes from nearly permanent to intermittent, while in West Iberia has a more seasonal character. In fact, these two upwelling regions are often considered part of the same system, the Portuguese-Canary eastern boundary upwelling system (Peliz et al. 2005).

150 However, during Ice the Age ages *C. p. pelagicus* is not found around the Canary Islands like happens further North off West

Iberia. The cooling and ice extent during the last ice age pushed the polar front as far south as North of Iberia (Eynaud et al.,

2009), which forced *C. p. pelagicus* and its oceanographic realm further down till the West coast of the Iberian Peninsula. In

the Canary Islands region increased winds during glacial periods should be expected (see Grousset et al., 1998 for the Last

Glacial Maximum), which would in turn increase upwelling events/strength in the region. If so, this would be observed in the

155 size variability of *C. p. braarudii*, with relatively smaller coccoliths dominating during periods of stronger upwelling (see

Prista et al. 2020).

IMMA C1 extracted two morphotypes, which are interpreted as reflecting the size variability of *C. p. braarudii* in the region.

C2 gives the "normal" size of the morphotype, defined as between 11.5 and 15.2 µm, values that completely agree with extant

C. p. braarudii size range. Since the main morphometric results in the data are attributed only to *C. p. braarudii* as the only

160 taxon present, the first component reflects its morphological plasticity.

C. p. braarudii thus reveals for the Canary region a variation between 6.9 and 17.2µm, which is in good agreement with

morphometric results from culture data that indicate that its size may range from a minimum of 7.87 µm and a maximum of

17.32 µm, with 12.21 µm mean (see Sheward et al., 2017)

4.1 Evidence of *C. p. braarudii* morphological plasticity in the Canary Islands region

165 The upwelling regime of the Canary Islands represents a typical oceanographic regime currently inhabited only by *C. p.*

braarudii since the lower latitude of this site makes it unreachable by the smaller *C. p. pelagicus*, even during glacial times.

The global size histogram (Fig. 5) also suggests the presence of the larger morphotype associated to the subspecies *C. p.*

braarudii, with a residual tail towards small morphons though which, apparently, is out of this subspecies size spectrum.

However, such histogram, although may roughly determine this morphotype size boundaries, is unsuitable to extract size

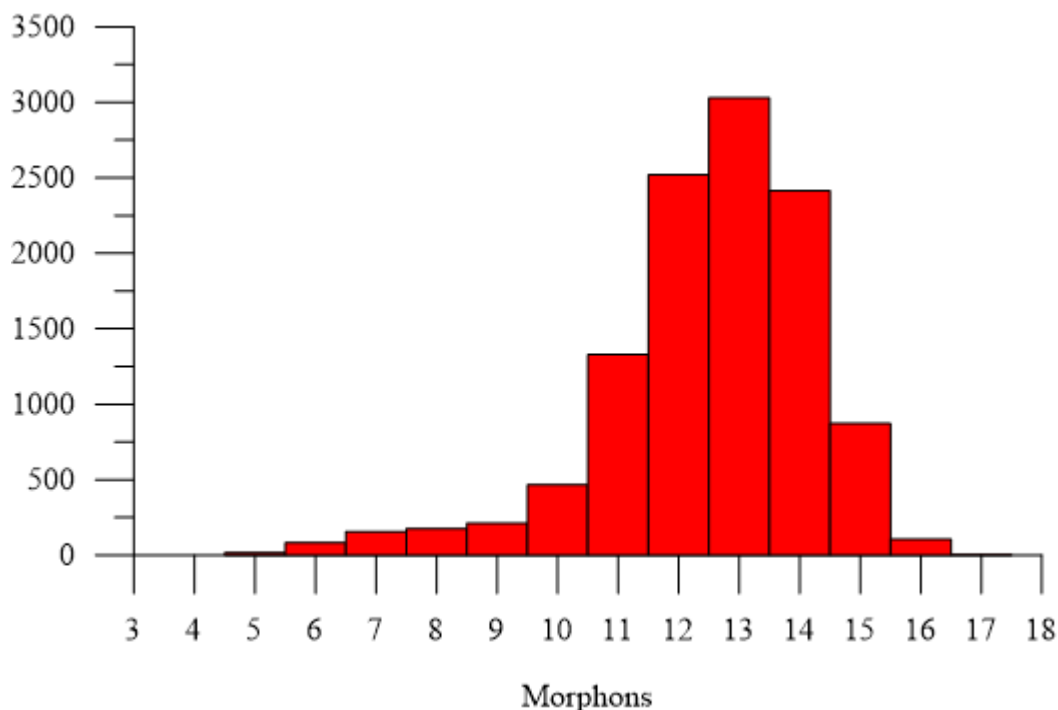170 variations and morphotype behaviour through time.

Figure 5 – Global histogram of GeoB5559-2.

175 Instead, IMMA loadings provides much richer morphometric information. Even when only one subspecies (*C. p. braarudii*)

is present, IMMA allows to extract three morphotypes, the median ($_M$C2) interpreted as reflecting normal (palaeoproductivity)

conditions. In parallel significant changes in size were also detected, reflecting a broader spectrum of palaeoceanographic

conditions operating in the region. In some moments enhanced palaeoproductivity conditions favoured a smaller ($_S$C1) relative

to a larger ($_L$C1) morphotype, and thus these revealed opposing behaviour to each other expressed by their positive and negative

180 loadings, respectively.

An overall broader evolution of *C. p. braarudii* placolith lengths through time can be analysed from the obtained IMMA scores.

The oldest samples, up to 155 ka, are dominated by larger sizes, with an average size above 13 μm. Between 151 ka and 129

ka a transition period is identified, and onwards, with only six exceptions with an average around 13 μm, the mean size of *C.

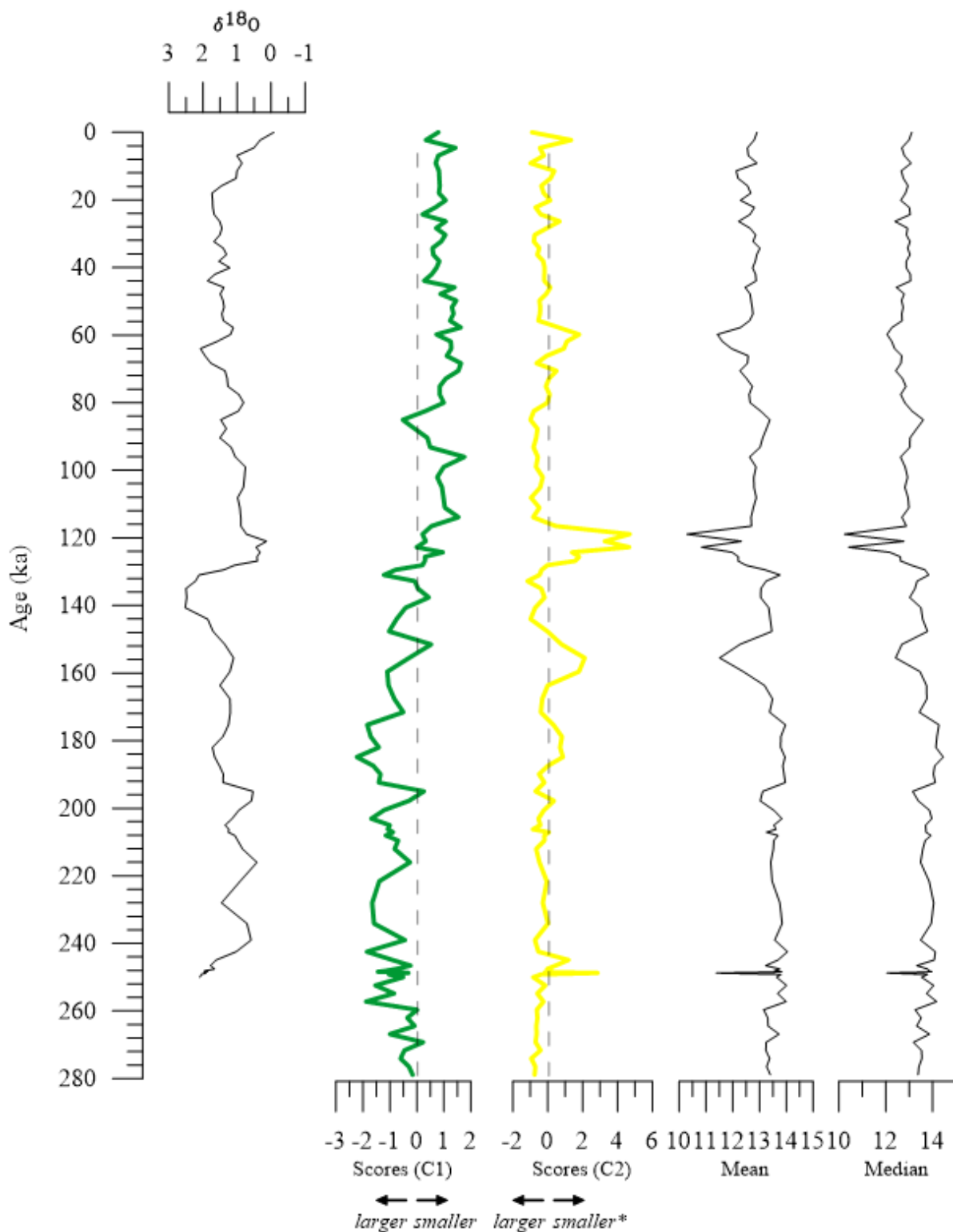p. braarudii* drops to morphon 12 μm or 11 μm (Fig. 6).

Figure 6 – IMMA C1 scores (green), C2 scores (yellow), mean and median of *C. p. braarudii* in site GeoB5559-2. *when C2 scores are positive, although IMMA component loadings are low, they are linked to the presence of smaller specimens.

Moreno et al. (2002) describe the primary productivity in GeoB5559-2 for the last 250 ka. They're results detected strong

190   peaks of increased primary productivity at Terminations I, II and III (~13 ka, ~126 ka, ~245 ka, respectively), and smaller peaks at 36, 60, 107 and 220 ka. Our results also show higher primary productivity at ~246 ka, ~125 ka and ~61 ka. The authors present a very high peak in Ba excess, which they consider a reliable proxy for primary productivity at this site, at 126 ka, in agreement with our findings for the Eemian interglacial, with high primary productivity between ~135 ka and ~128 ka, and again between ~125 ka until ~118 ka. After the Eemian high peaks, our data shows some small peaks in size reduction in

195   different moments of the ones presented by Moreno et al. (2002). However, according to our data, primary productivity from ~115 ka until present was kept relatively high, with low variability. In the work of Moreno et al. (2002), Ba excess presents an increase tendency from 90 ka until 11 ka, with some variability, but keeping above the values presented between 250 ka and 138 ka (exception for 99-83 ka which were slightly lower). During the same period, total organic carbon also shows an increase to levels above the same previous interval, according to the authors. This supports our data, with *C. p. braarudii* reducing its

200   size over the past 250 ka, following the increase in primary productivity.

Stolz and Baumann (2010) analysing ODP site 980 in the North Atlantic observe a peak in coccolithophore numbers on the onset of MIS 5 and another peak at 120 ka, declining afterwards, but keeping above glacial levels. They conclude on coccolithophore assemblages' data that interglacial conditions were frequent at this site up to the next glacial cycle, MIS 4, around 71 ka. This means that conditions in lower latitudes, like the Canary Islands, would probably be more stable, adding

205   the fact that during MIS 5 insolation was never as low as between 240 ka and 150 ka, showing a more stable pattern (see Moreno et al., 2002). Our data suggest a high primary productivity during the Eemian in this region, depicted by the major drop on coccoliths size in samples 273 cm and 263 cm (~122 ka to ~118 ka – see age model Martinson et al., 1987; Moreno et al., 2002) and good conditions during the rest of MIS 5, which were enhanced by less amplitude in insolation variations when compared to the previous period.

210 In fact, there is a tendency towards smaller sizes in the mean size and median of the measurements obtained in this site, which in turn correlate well with IMMA C1 scores that determine the morphotype size variations – towards smaller or larger specimens (Fig. 7).
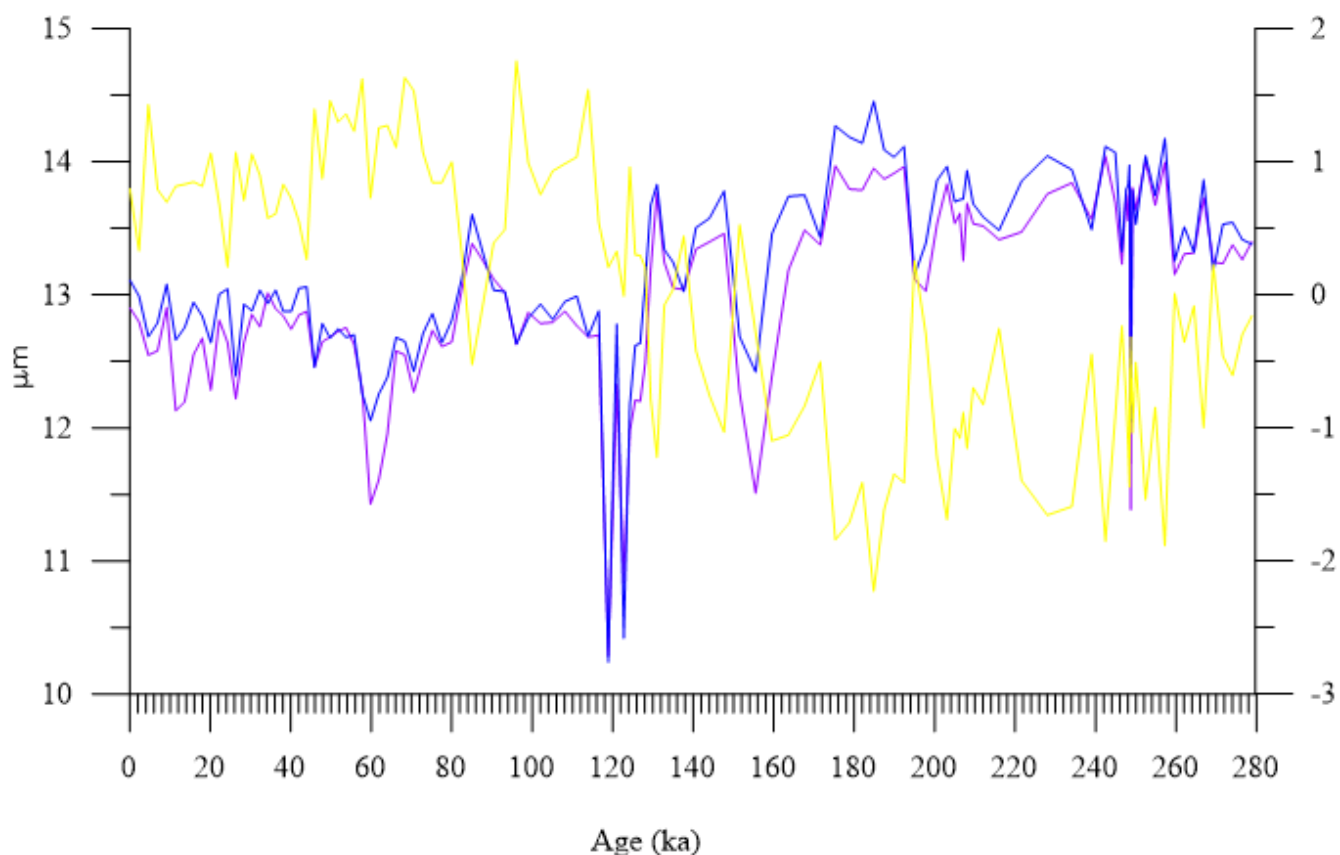

215 Figure 7 – Mean (blue), median (purple) and C1 scores (yellow) of *C. p. braarudii* in site GeoB5559-2.

The peak in low size between samples 158 cm and 148 cm corresponds to a period between ~64 ka and ~59 ka, which is during the MIS 4 glacial period (~71-57 ka) and may be related to induced increased winds by the onset of the last glaciation, boosting both coastal upwelling and eolian input from the Sahara/Sahel regions. The relatively stable and good insolation during MIS

220 3 (see Shackleton et al., 2021) could have been the reason for maintaining conditions for the lower sizes, indicating conditions of good primary productivity, even if lower than the period between 240 ka and 150 ka.
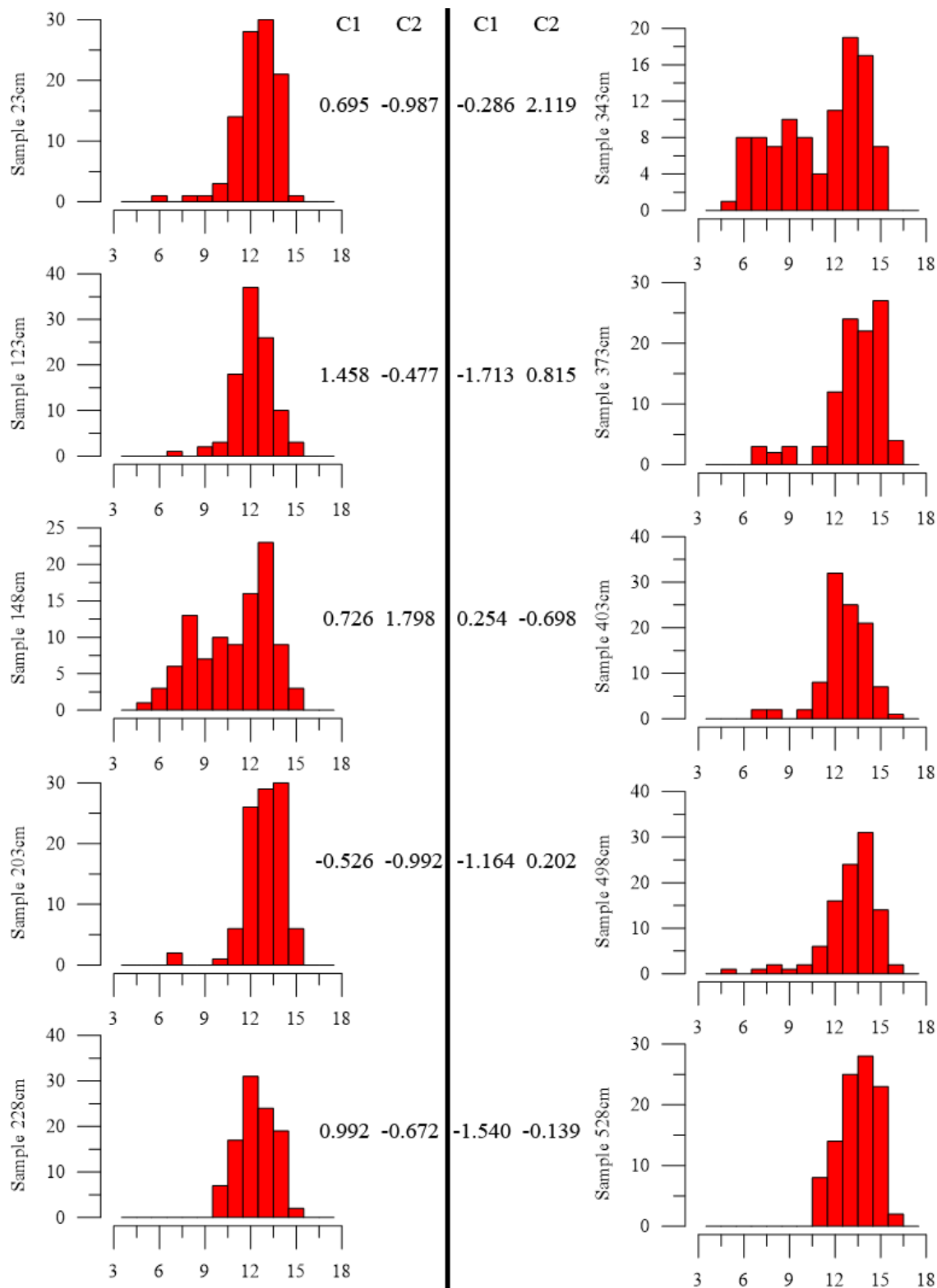
The variation of the mean and median is fairly connected with C1 variability. However, the correlation increases when the two major size drops during the Eemian are removed as eventual outliers (see Fig. 8).
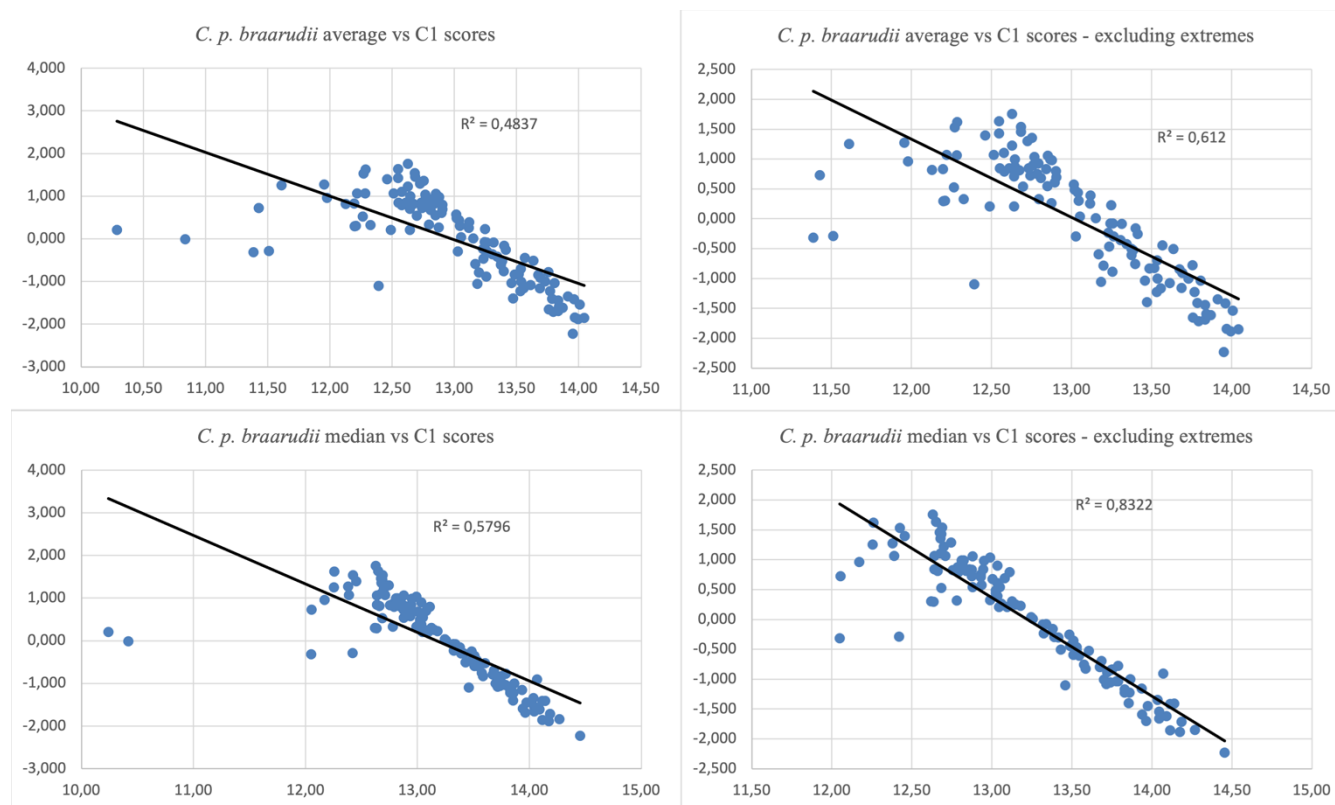
Figure 8 – Scatter plot of the relation between C1 scores with *C. p. braarudii* mean and median in GeoB5559-2 DataSet_1 matrix.

Histograms also show how scores predict size variability and how positive IMMA C2 scores reflect the presence of small coccoliths (Fig. 9). Sample 23 cm has small *C. p. braarudii* coccoliths, as predicted by C1 positive scores. The negative C2 scores define the morphometric data in this sample as characteristic of *C. p. braarudii*, which is supported by the histogram centred in morphons 12 and 13 µm.

	C1	C2	C1	C2
Sample 23cm	0.695	-0.987	-0.286	2.119
Sample 123cm	1.458	-0.477	-1.713	0.815
Sample 148cm	0.726	1.798	0.254	-0.698
Sample 203cm	-0.526	-0.992	-1.164	0.202
Sample 228cm	0.992	-0.672	-1.540	-0.139

235   Figure 9 – Histograms and scores of selected samples from GeoB5559-2.

Sample 123 cm has a high positive IMMA C1 score and morphon 12 µm is dominant, while C2 reflects a *C. p. braarudii*

morphometric characterization. In samples 148 cm and 343 cm the information given by a positive IMMA C2 score is well

visible in the histograms. When C2 is positive lower sizes are more prevalent, and C1 should indicate the dominant morphon

240   of the sample. In the first case C1 score is positive and morphon 8 mm appears with significant relevance. In the second case

C1 score is negative and morphons 13 and 14 µm dominate, with small morphons presenting relevant counting's but with none

standing out.

Samples 203 cm, 228 cm, 373 cm, 403 cm, 498 cm and 528 cm represent the common pattern of these site histograms, which

are characteristic of *C. p. braarudii* populations. C1 scores clearly depict the size variation of the population, with negative

245   scores in samples dominated by morphon 14, morphon 15 in one case, and positive scores in samples dominated by morphon

12.

5 Conclusions

IMMA was applied to a single coccolithophore (*Coccolithus pelagicus braarudii*) to unravel the presence of distinct

morphotypes with increased (up to 0.1 µm) resolution.

250   The most important component extracted (C1) is related to its morphological plasticity expressing the alternate dominance

between a smaller ([6.9; 12.9[µm) and a larger ([14.0; 17.2[µm) morphotype. An increase in (the presence of) the smaller

morphotype is interpreted to reflect the cumulative occurrence of more than average favourable (nutrient available) conditions

(inducing higher reproduction rates) while the dominance of the larger morphotype reflects the prevalence of less favourable

conditions (inducing lower reproduction rates). The lesser relevant C2 is related to the prevalence of median conditions with

255   no clear trend for either extreme but to a mean core size for this subspecies. Thus, *C. p. braarudii* morphometry can be used

to infer the primary productivity, being a reliable proxy for coastal upwelling regions studies, and with great potential for

studies on the effects of climatic events on coastal upwelling regions during the Quaternary.

Future work will be carried out to evaluate the efficacy of IMMA to older periods and, most importantly, to lower time resolutions, which can have a negative impact in extracting morphological plasticity data in short life cycle species.

Acknowledgments

Competing Interests

The authors declare that they have no conflict of interest.

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