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Glacial-interglacial shifts in dominant climate forcing over the last 33 ka in the northern South China Sea

Xueqin Zhao*[1], Shengjie Ye[1], Jiahui Yao[1], Michael E. Meadows[2, 3], Chengyu Weng[4], Yasong Wang[1], Mingxing Zhang[1], Yunping Xu[1]

[1]Shanghai Frontiers Research Center of the Hadal Biosphere, College of Oceanography and Ecological Science, Shanghai Ocean University, Shanghai 201306, China
[2]School of Geography and Ocean Sciences, Nanjing University, Nanjing 210023, China
[3]Department of Environmental & Geographical Science, University of Cape Town, Cape Town 7701, South Africa
[4]State Key Laboratory of Marine Geology, Tongji University, Shanghai, China

Correspondence to: Xueqin Zhao (xqzhao@shou.edu.cn)

Abstract. The northern South China Sea is a critical region for understanding East Asian Monsoon dynamics. However, integrated, multi-proxy records elucidating long-term climatic and vegetation changes in this region remain fragmented, with a notable scarcity of coherent land-ocean interaction data during the Last Glacial Maximum (LGM). This gap has impeded progress in elucidating the mechanisms underpinning monsoon variability and in rigorously evaluating the performance of palaeoclimate models. To address this, we conducted a multi-proxy analysis combining palynological, organic- and inorganic-geochemical methods on a marine sediment core from the northern South China Sea to reconstruct environmental and oceanic dynamics at millennial-scale resolution that spans the last 33 ka. Our results reveal a clear contrast between glacial and interglacial conditions and drivers: the glacial period was characterized by higher sedimentation rates, elevated marine primary productivity, cooler climate, lower humidity and herb-dominated vegetation associated with enhanced fire activity in the adjacent terrestrial ecosystems. Deglaciation was characterized by pronounced warming and reduced productivity, together with increased moisture availability, a shift toward pine-dominated vegetation, minimal fire activity, and reduced fluvial input as the coastline retreated. The overall findings highlight a fundamental transition in climatic controls, from a regime dominated by sea level forcing during the glacial period to one increasingly governed by tropical ocean-atmosphere interactions initiated by early ocean warming during the interglacial.

1 Introduction

Low latitude regions play a critical role in the global climate and its dynamic because they are the seat of the most active moisture and heat exchanges between the atmosphere and the ocean expressed via the monsoon regime. Tropical and subtropical monsoon regions such as East Asia and the South China Sea (SCS) experience the most significant seasonal reversal in wind directions with associated migration of regional intense precipitation (Wang et al., 2017). Monsoon wind and precipitation patterns have changed significantly in the late Quaternary, influenced by gradual changes in insolation and internal interactions among the atmosphere, oceans, land surfaces and Northern Hemisphere ice sheets (An, 2000; Ding et al., 1994; Kissel et al., 2020; Tian et al., 2010; Wang et al., 2001). These changes have affected the climate and land-ocean energy balance of western Pacific marginal basins, whereas the influence and dynamics of the monsoon system remain insufficiently constrained. Investigations of paleoclimate variability have significant value in providing valuable insights into monsoonal dynamics across tectonic, orbital and millennial time scales.

Given the importance of the climate signature during the last Glacial Maximum (LGM, spanning approximately 26.5-19 ka) to climate model validation and testing, new reconstructions of precipitation and vegetation response during the LGM are necessary to resolve inconsistencies and improve model reliability. Marine sediments potentially record the interplay of the East Asian Monsoon, surface and deep oceanic circulation and sea level compared with other terrestrial records (Tian et al., 2004; Wang et al., 1999). The South China Sea is divided into a northern deep basin with isolated, oxygen-poor waters and a

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southern extensive shelf province, a dichotomy fundamentally controlled by a ~2400 m deep sill that restricts deep-water exchange with the open Pacific (Chen and Huang, 1996). Due to its well-preserved sedimentary strata, abundant sediment supply, and relatively high sedimentation rates, the northern SCS is recognized as a key area with strong potential for high-resolution paleoenvironmental reconstructions. Such records can substantially enhance our ability to resolve global and regional climate variability during the Quaternary (Wang et al., 2014). A range of different proxies is preserved in marine sedimentary archives. Pollen evidence, for example, can provide a valuable signal of vegetation evolution on the adjacent continental land mass (Cheng et al., 2023; Luo et al., 2016; Sun et al., 2000a), while microcharcoal particles are widely used in palaeofire reconstruction to infer fire frequency, intensity and vegetation changes, and terrestrial ecosystem response (Conedera et al., 2009). Foraminifera are sensitive to environmental changes, and are widely applied as a paleo-proxy of marine conditions (Haynes, 1981), although the shells of planktonic foraminifera are susceptible to dissolution which may have limitations. Organic walled dinoflagellate cysts (dinocysts), the resting cysts formed during the sexual reproduction process of these taxa, are characterized by resistant organic matter and are also generally well preserved in marine sediments (Dale, 1996; Zonneveld et al., 2013). The well-known correlation of modern dinocyst distribution with distinct physical marine water properties such as sea surface temperature (SST), salinity, nutrients and productivity indicates the value of dinocysts as a proxy in paleoceanographic reconstruction, although current research on dinocysts in the South China Sea remains largely confined to their modern distribution in marine surface sediments (Li et al., 2018a; Li et al., 2020; Li et al., 2023). Fossil dinocyst records in the SCS are scarce (Li et al., 2021; Li et al., 2017).

Given the complementary strengths of different archives, we adopt a multiproxy approach in this study, combining palynological indicators (pollen, spores, microcharcoal, and dinocysts), organic geochemical proxies (TOC and TN), and inorganic geochemical markers (element ratios, $\delta^{13}C$ and $\delta^{18}O$, and Mg/Ca-based SST of planktonic foraminifera) to reconstruct vegetation, fire regimes, sediment sources, ocean productivity, and sea surface temperature. A marine sediment core (SCS-GC-1; Fig. 1a) recovered from the northern SCS was analyzed to reconstruct millennial-scale climate and ocean dynamics over the last 33 ka. The specific aims of this study are: (1) to reconstruct the palaeovegetation and palaeoclimate; (2) to document the evolution of palaeoceanographic conditions; and (3) to clarify the mechanisms governing land-ocean interactions across glacial-interglacial transitions.

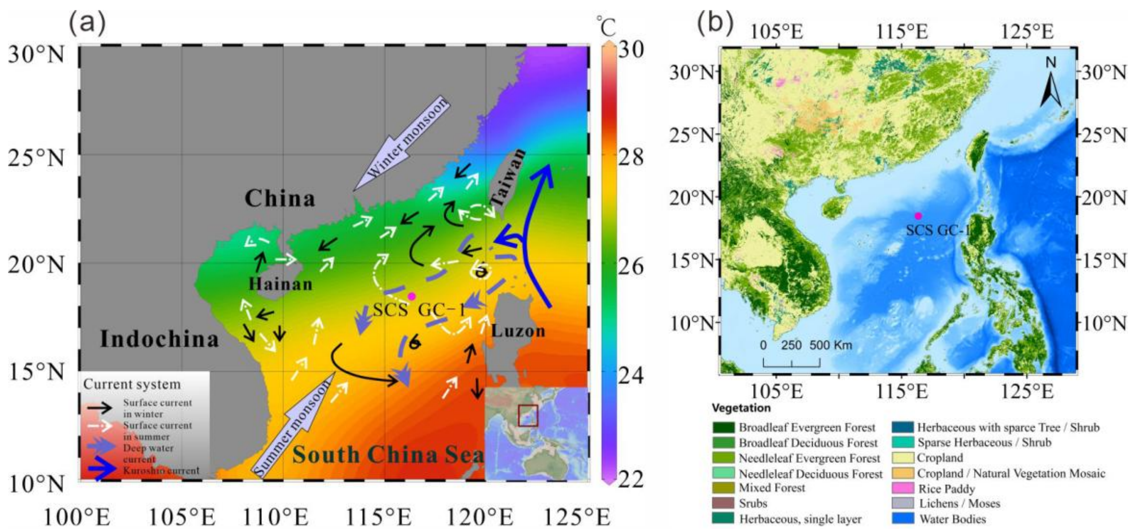

Figure 1: (a) Map of the East Asian monsoon system and ocean circulations with annual modern mean annual sea surface temperature (Data from World Ocean Atlas, 2023) and the location of core SCS GC-1 (red) retrieved from the northern SCS. (b) Map of the distribution of vegetation types in the main areas around the South China Sea retrieved from Stibig et al. (2007) and https://forobs.jrc.ec.europa.eu/products/glc2000/products.php. The black solid line indicates the position of the winter surface current, the white dashed line is the position of the summer surface current, the purple dashed line is the deep current, and the blue solid line is the Kuroshio Current.

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2 Environmental setting

2.1 Atmospheric circulation and climate

The northern SCS experiences a subtropical to tropical climate that is primarily governed by the seasonal East Asian Monsoon system: northeasterly winds prevail during winter (December-February) and southwesterlies dominate in summer (June-August) (Chao et al., 1995; Wang et al., 2017). In winter, decreasing temperatures over the Asian continent lead to the development and intensification of a cold high-pressure system over Inner Mongolia, while the Aleutian Low strengthens over the North Pacific. The resulting continent-ocean pressure gradient drives the East Asian Winter Monsoon (EAWM), transporting cold, dry northeasterly air masses southwards across China into the SCS. In summer, this pattern reverses: the continental system is replaced by the Indian Low, and stronger high-pressure systems develop over the North Pacific and the Australian region, generating the East Asian Summer Monsoon (EASM), which adverts warm, moist-laden air from the ocean onto the Chinese mainland (Liu et al., 2016a).

2.2 Oceanic circulation

Surface currents in the SCS are controlled by seasonal variations in the dominant wind directions related to the EASM and EAWM (Hu et al., 2000), monsoon-topography interactions, and additional influences from wind-stressed eddies. During winter, the EAWM drives a strong southward western boundary current along the Vietnamese and southern Chinese coasts, associated with a basin-scale cyclonic circulation. In contrast, summer circulation is weaker and more complex, with coastal currents generally reversing to flow northward under EASM influence.

The EASM drives distinct northern and southern circulation patterns in the SCS, which form two anticyclonic eddies separated near 12°N by a strong upwelling off Vietnam (Fang et al., 1998). In addition, the region is influenced by the intrusion of warm, saline Kuroshio waters entering through the Luzon strait between Luzon from Taiwan (Huang et al., 2025).

Seasonal variations in marine primary productivity are primarily modulated by the East Asian Monsoon (Liu et al., 2002). During winter, stronger northeasterlies induce eutrophic conditions in the upper euphotic layer, elevating marine primary productivity. In summer, persistent heating of warmer, lower-density surface waters intensifies stratification, leading to oligotrophic conditions and reduced primary productivity (Liu et al., 2002; Zhang et al., 2016).

2.3 Vegetation

Vegetation types on the adjacent continental landmass around the SCS are diverse and reflect regional climate conditions (Luo and Sun, 2013), although they are dominated by tropical and subtropical broadleaved evergreen forests (Fig. 1b) (Stibig et al., 2007). Whereas tropical rain forest vegetation occurs at low altitudes on tropical islands along the southern coast of the Chinese mainland, e.g., Hainan Island, and southern Taiwan Island, tropical monsoon forests are distributed widely throughout the Indochina Peninsula and along the coast of southeastern China. Subtropical evergreen forests are prominent between 24°N and 25°N on southeast-facing hills and on high plateaus (Wang, 1961; Whitmore, 1985). Generally, the abundance of both tropical and subtropical taxa increase gradually towards the south in eastern China, indicating the significance of the north-south temperature gradient (Dai and Weng, 2015; Dai et al., 2015). The vegetation types occurring in southeast and southern China, as well as Taiwan Island, are the main pollen sources of the northern SCS (Dai and Weng, 2011; Sun et al., 1999).

2.4 Sedimentation rates

The SCS receives enormous amounts of terrigenous sediments (ca. 700×10^6 tons/year) every year, mainly during the rainy season in summer. The sediments originate from the erosion/weathering of rocks in the catchment basins particularly from three Asian rivers (the Red River, the Pearl River, and the Mekong River) which are among the largest in the world (Liu et al., 2010; Milliman and Syvitski, 1992). Beyond the river deltas, part of the terrigenous sediments is deposited on the shelves (Zhong et al., 2017), while the rest reaches the open sea where the sediment is transported by the oceanic currents and deposited on the continental slope and in the deep basins (Liu et al., 2013).

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3. Materials and methods

3.1 Materials and chronological analysis

The 305 cm long marine sediment core SCS GC-1 was retrieved from the northern SCS during R/V Songhang (Shanghai Ocean University) cruise in October 2022 (18.47°N, 116.34°E; water depth of 3764 m) (Fig. 1).

Eight accelerator mass spectrometry AMS ^{14}C dates at depths of 20 cm, 45 cm, 65 cm, 90 cm, 107 cm, 133 cm, 203 cm and 275 cm were obtained on mixed planktic foraminiferal (including *Globigerinoides ruber*, *Globigerinoides sacculifer*, *Neogloboquadrina dutertrei*, *Pulleniatina obliquiloculata*, *Orbulina universa*) tests isolated from the core. AMS ^{14}C measurements were carried out on a NEC 0.5Mev ^{14}C AMS (National Electrostatics Corporation, NEC) at Guangzhou Institute of Geochemistry, Chinese Academy of Sciences (GIGCAS).

3.2 X-ray fluorescence (XRF) analysis

The core was non-destructively scanned using the Avaatech XRF Core Scanner at the State Key Laboratory of Marine Geology, Tongji University. The parameters of the Avaatech XRF core scanner were set for 30 s exposure time, three voltage and current conditions with 10 kv and 0.75 mA for Al-Fe, 30 kV and 0.5 mA for Co-Mo, and 50 kV and 0.2 mA for Tc-U. The scanning area was 5 mm (length) × 10 mm (width), and at a scanning time of 30 s. The relative content of each element including Al to Ba which was obtained, is expressed in cps as counts per second.

3.3 TOC and TN analysis

Approximately 1 g of each freeze-dried sample was treated with diluted 3 mol/L HCl for 24 hours at room temperature to remove inorganic carbonates. After the reaction, the samples were repeatedly rinsed with ultrapure water (<18 MΩ·cm) and centrifuged until the supernatant reached a neutral pH. The remaining residue was oven-dried at 60°C, ground and then weighed. The decarbonated samples were analyzed for elemental content using a Vario EL cube elemental analyzer (Elementar, Germany) at the State Key Laboratory of Marine Geology, Tongji University, employing the dry combustion method. Replicate analyses were conducted to ensure data reliability, with average standard deviations of ≤ 0.1 wt% for both TOC and TN measurements.

3.4 Planktonic foraminiferal isotopic and Mg/Ca analysis

The samples were freeze-dried, disaggregated by soaking in water for 1-2 days, then were rinsed repeatedly through a 63 µm sieve to remove organic matter and fine impurities. The rinsed wet samples were then dried at 60°C (approximately 24 h) and passed through a 125 µm and 250 µm sieve, respectively (Schönfeld et al., 2012). *G. ruber* larger than 250 µm size were selected under a microscope. For each sample, clean and intact *G. ruber* (around 30 specimens) were picked and tested using a Finnigan MAT253 Mass Spectrometer. The $\delta^{18}O$ results are reported versus VPDB after calibration with NBS 19. The average test accuracy is ±0.07‰.

For the Mg/Ca analysis, surface dwelling foraminiferal species with smooth-surface individuals of *G. ruber* between 250-350 µm (ca. 0.3 mg) were picked to ensure no obvious contamination or damage, and that the atrioventricular structure was intact (Barker et al., 2003). The analysis was performed on a quadrupole inductively coupled plasma mass spectrometry (ICP-MS). Duplicate measurements of two samples yield an average relative deviation of 0.064 mmol/mol, confirming that analytical uncertainty is minimal and does not materially affect interpretation. Sea surface temperatures were reconstructed following Eq. (1) (Huang et al., 2008):

$$SST=0.5*(\mathrm{Ln}(Mg/Ca/0.3)/0.09+\mathrm{Ln}(Mg/Ca/(0.38-0.02*D))/0.09) \quad (1)$$

Where *SST* represents mean annual sea surface temperature (°C), *Mg/Ca* is the *G. ruber* based Mg/Ca ratio (mmol/mol), *D* is water depth of the core (km).

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3.5 Palynological analysis

In total, 61 samples (mean interval 4 cm) were processed for palynological analysis at Shanghai Ocean University following standard preparation procedures. Samples were treated sequentially with 10% HCl, 40% HF, 30% HCl, sieved with 125 μm and 7 μm meshes, and mounted for microscopic examination. Routine identification was performed under a ZEISS Promostar 3 microscope at 400x magnification, with 1000x used for detailed taxonomic identification. Four *Lycopodium* spore tablets with 10315±845 spores were added to each sample prior to processing to enable calculation of pollen concentration. Pollen taxa were identified using the reference of Tang et al. (2020). At least 300 pollen grains (including terrestrial pollen taxa, sedges and aquatic taxa) were counted for most of the samples. The percentages of pollen taxa were calculated based on the pollen sum, and the percentages of spore taxa were calculated based on pollen and spore sum.

Charcoal particles were identified and counted on the same microscope slides prepared for pollen analysis. Only particles which were black, opaque and angular were considered as charcoal. Particles smaller than 10 μm were not counted due to the risk of false identification (Mooney and Tinner, 2011). More than 1500 charcoal particles (with an average of 3500 particles) were counted for each sample. Two size classes were defined, based on the length of the long axis of each fragment: 10-100 μm is assumed to relate to the regional fire signal and >100 μm to local fire signals (Conedera et al., 2009). Charcoal accumulation rates (particles/cm^2/yr) were calculated by applying the sediment accumulation rates interpolated from the radiocarbon age-depth model. The charcoal accumulation rate is a proxy for burned biomass which can represent changes in the amount of biomass burned or the number of fire occurrences (Aleman et al., 2013).

Organic-walled dinoflagellate cysts (dinocysts) were identified based on Zonneveld et al. (2013), DINOFLAJ3 (Williams et al., 2017), and the online modern dinocyst determination key, viz Zonneveld and Pospelova (2015) and references therein. The percentage of each taxon was calculated based on the total number of dinocysts. All identified dinocyst taxa and their motility affinities are listed in Table S1. In addition to the above content, foraminiferal organic linings, and other non-pollen palynomorphs such as fungal spores were counted. All counts of pollen, microcharcoal and dinocysts as well as other data discussed in this study have been submitted in the Pangaea database (https://pangaea.de) (Felden et al., 2023).

3.6 Statistical analysis

The dinocyst data were analyzed statistically using the CANOCO software (Canonical Community Ordination: version 5) (ter Braak and Smilauer, 2012). The percentage data used for statistical analysis was not transformed. A Detrended Correspondence Analysis (DCA) was first conducted to test the distribution of the dataset (unimodal or linear). The longest gradient of DCA analysis was found to be 1.1 for pollen data and 1.5 for dinocyst data with standard deviations both less than 3, suggesting that the linear model is more suitable. Accordingly, Principal Component Analysis (PCA) was performed to determine the relationship between relative abundances of pollen and dinocyst taxa, respectively. Assemblage zones were determined using the constrained cluster analysis (CONISS) in the TILIA (3.0.1) software (Grimm, 2015), including all counted pollen and dinocyst taxa with the exception of the top two samples in which insufficient dinocysts were found.

4. Results

4.1 Age-depth model

The eight ^{14}C AMS measurements exhibit a systematic increase in radiocarbon age with sediment depth (Table 1). The age-depth model was constructed using the eight AMS ^{14}C measurements in a Bayesian framework implemented in Bacon (Blaauw and Christen, 2011). A prior accumulation rate of 100 yr/cm (shape = 1.5, normal distribution) was applied, with the core divided into 52 depth sections of 5 cm. The default memory parameter was retained. Posterior weighted mean calibrated ages were used to derive linear sedimentation rates. The resulting model indicates a basal age of ~33 ka for core SCS GC-1, with sedimentation rates ranging between 0.005 and 0.013 cm/yr (Figs. 2 and 3a).

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Table 1: AMS ^{14}C measurement for mixed planktonic foraminifera from the core SCS GC-1.

Lab #	Depth (cm)	Material	^{14}C age (yr BP)	Calibrated age median (cal. yr BP)	cal. ^{14}C age (cal. yr BP, ±2σ)
GZ10650	20	mixed species	3420±25	3036	1810-4285
GZ10651	45	mixed species	8005±35	8289	7260-9443
GZ10652	65	mixed species	10055±50	10868	9533-12260
GZ10653	90	mixed species	13090±70	14708	13392-16057
GZ10654	107	mixed species	15950±70	18342	17138-19485
GZ10655	133	mixed species	16000±90	18399	17185-19555
GZ10656	203	mixed species	20540±170	23656	22496-24875
GZ10657	275	mixed species	26700±350	29977	28806-31063

yr BP denote before present (1950 AD); all age data were calibrated using the software Calib.Rev.8.10 (Stuiver and Reimer, 1993) and Marine 20 (Hughen et al., 2004). The standard marine reservoir age with a local modification (ΔR =71±499 yr) in the northern South China Sea was applied (Wan and Jian, 2014).

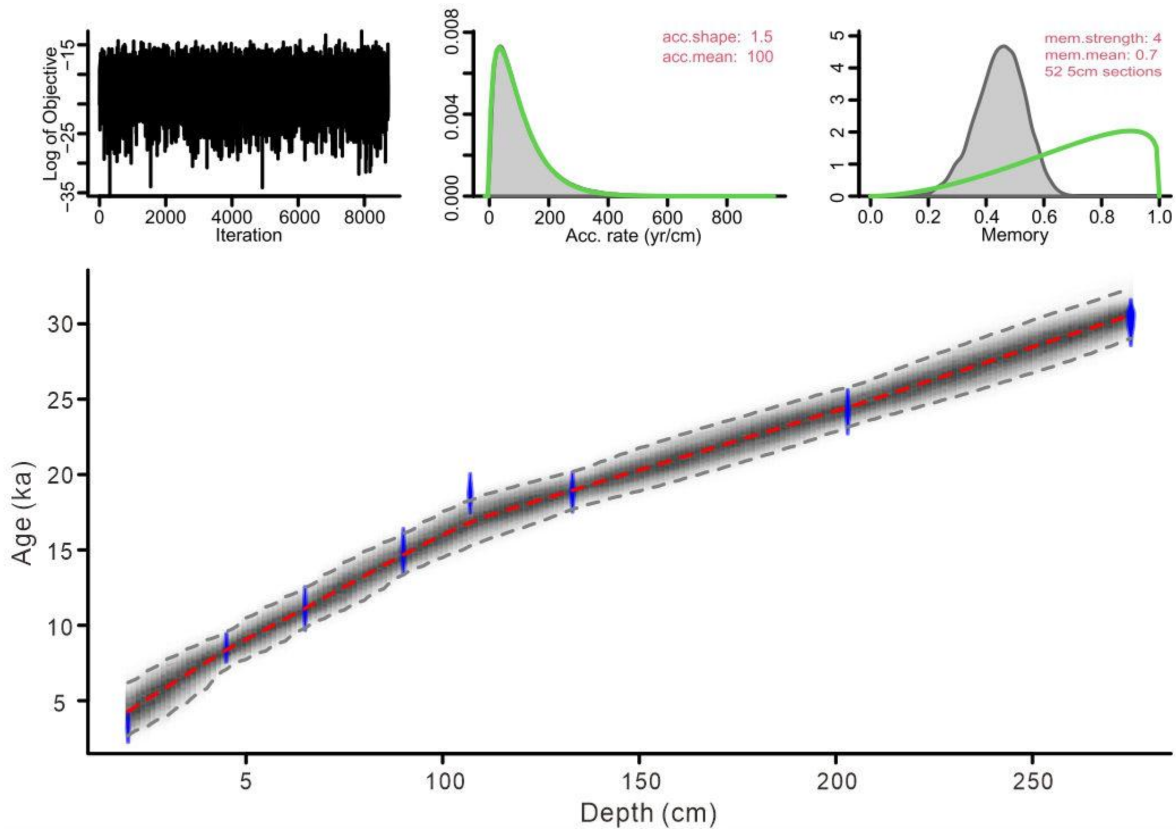

Figure 2: Bayesian age-depth model based on eight AMS ^{14}C dates from core SCS GC-1: the blue areas represent the 95% probability distributions of the calibrated ages; the thin red line shows the weighted mean ages, and the blackish-gray area shows the 95% age-depth relations as modeled by the R software package Bacon 2.2 (Blaauw and Christen, 2011).

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4.2 XRF record

The relative contents of these six elements are found for Fe (5×10^3 -750×10^3 cps, mean = 540×10^3 cps), Ca (0.7×10^3 -650×10^3 cps, mean = 190×10^3 cps), K (1.5×10^3 -166×10^3 cps, mean = 91×10^3 cps), Si (1×10^3 -144×10^3 cps, mean = 71×10^3 cps) followed by Ti (2×10^3 -68×10^3 cps, mean = 41×10^3 cps) and Al (0.5×10^3 -14×10^3 cps, mean = 6×10^3 cps) (Fig. S1). Similar patterns among terrigenous elements Fe, K, Ti, Al and Si were observed together with a clearly opposite pattern of marine origin element Ca. The Ti/Al and K/Al show similar patterns with significant correlation ($r = 0.94$, $P<0.001$) throughout the record (Figs. 3b and 3c), with low values prior to 16 ka and then increase quickly to much higher values after 16 ka with gradually decreasing trend to the end of the record.

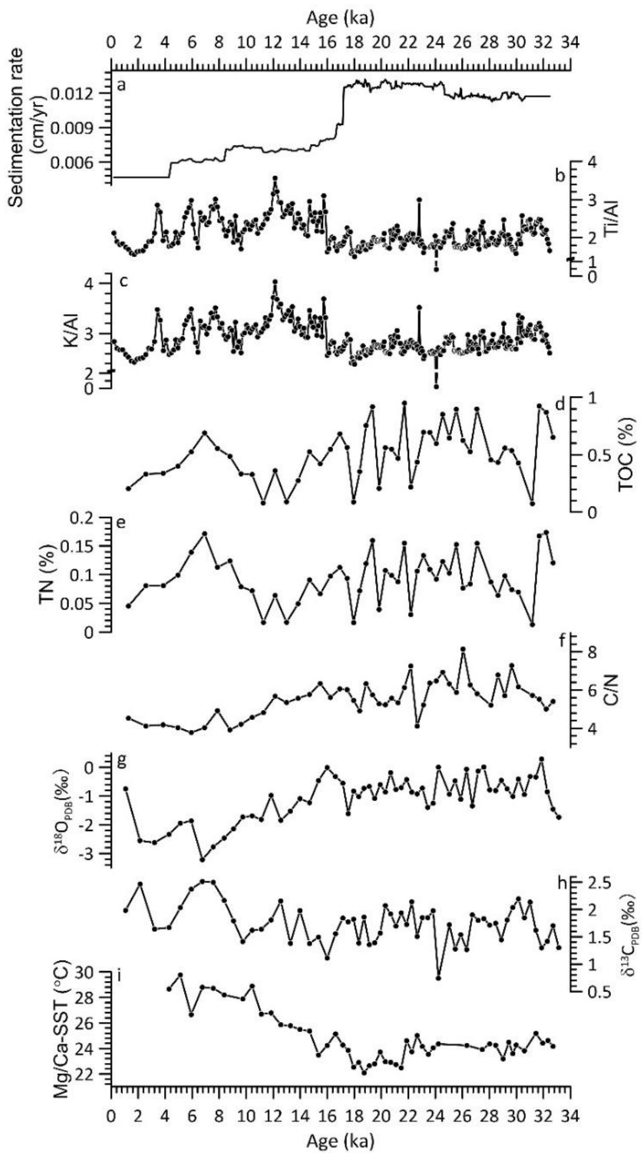

Figure 3: Core SCS GC-1 sedimentation rate (a), major element ratio (b-c), contents of total organic carbon (TOC, d) and nitrogen (TN, e), TOC/TN ratio (f), stable carbon $\delta^{18}O_{VPDB}$ (g) and oxygen $\delta^{18}O_{VPDB}$ (h) isotopes of planktic foraminifera, and Mg/Ca-SST (i).

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4.3 TOC, TN and C/N record

TOC content and the TOC/TN ratio exhibit significant fluctuations throughout the record (Figs. 3d, 3e and 3f). The period prior to 14.7 ka is characterized by high TOC content with low values around 31.2 ka, 22.2 ka, 19.8 ka, 17.9 ka. After 14.7 ka, TOC decreased until 10.4 ka when it increased again to a high level around 6.9 ka followed by a decline trend until the top of the record. Similarly, TOC/TN ratio also exhibits high values prior to 14.7 ka, which then decreased to minimum between 8.8-5.9 ka interrupted by a brief increase around 7.9 ka.

4.4 Planktonic foraminiferal isotopic and Mg/Ca-SST record

The $\delta^{18}O$ values of planktonic foraminifera *G. ruber* shells range from −3.2‰ to 0.3‰ (mean=−1.1‰) with higher values prior to 16 ka, then rapidly decreasing to much lower values (Fig. 3g). The $\delta^{13}C$ values range from 0.7‰ to 2.5‰ (mean=1.7‰) with relatively low values prior to 16 ka (Fig. 3h), there after increasing but with substantial variation.

Mean Mg/Ca-derived SSTs range from 22.1°C to 29.7°C (mean = 24.8°C) across the core (Fig. 3i). Relatively low values (23.2-25.2°C, mean = 24.2°C) occur prior to 21.9 ka, followed by a further decline to the lowest values (22.1-24.6°C, mean = 23.1°C) between 21.9-17.5 ka. After ~15.4 ka, SSTs increase progressively toward the highest values observed in the record (23.5-29.7°C, mean = 26.8°C).

4.5 Palynological record

The complete diagram of pollen, charcoal and dinocyst results are shown in Figs. S2 and S3. Pollen preservation is variable, with particularly high concentrations (390-4100 grains/cm^3; mean = 1200 grains/cm^3) prior to 16.1 ka, and highest concentrations around 25.3-25.0 ka (3300-4100 grains/cm^3; mean = 3700 grains/cm^3) (Fig. 4). Similarly, charcoal exhibits the highest concentrations (36-155×103 particles/cm^3; mean = 83×10^3 particles/cm^3) around 25.3-23.7 ka, decreasing after 15.6 ka, reaching minimum values at the top of the core (9-31×10^3 particles/cm^3; mean = 21×10^3 particles/cm^3) (Fig. 4). Dinocyst concentrations are relatively low, ranging from 7-1600 cysts/cm³ (average of 450 cysts/cm³) with high values of 110-1600 cysts/cm³ (average of 650 cysts/cm³) between 25.6-11.7 ka (Fig. 4). After 11.7 ka, dinocyst concentrations decrease, reaching a minimum at the end of the record.

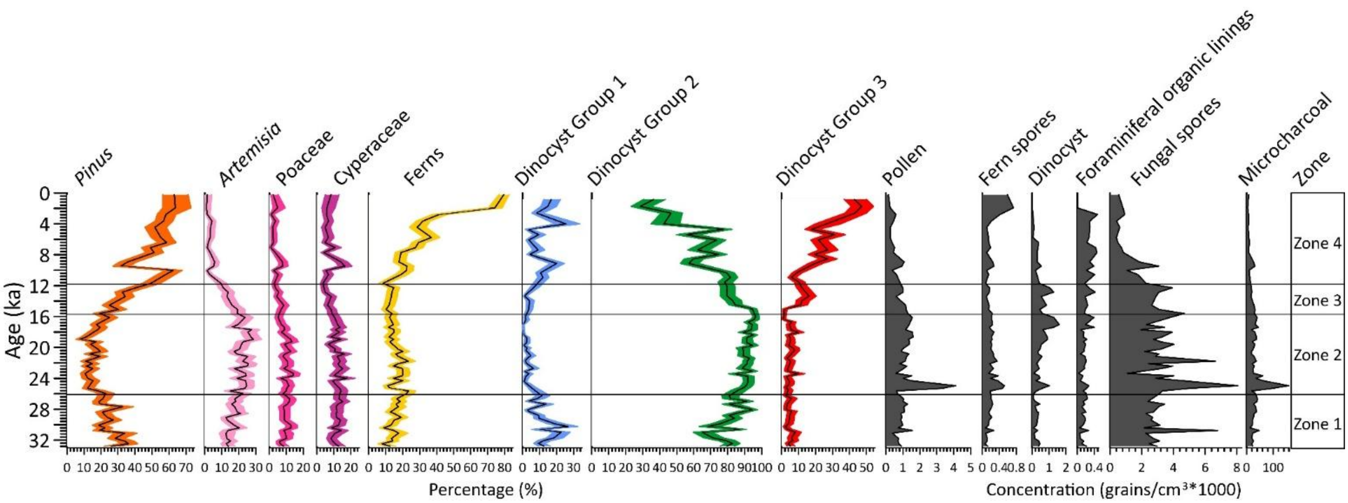

Figure 4: Percentages of dominated pollen taxa, including tree pollen *Pinus*, terrestrial pollen *Artemisia*, Poaceae and Cyperaceae, fern spores, and three dinocyst groups based on principal component analysis (PCA) analysis, concentrations (grains/cm^3*1000) of pollen, fern spores, dinocyst, foraminiferal organic linings, fungal spores and microcharcoal concentration (particles/cm^3*1000).

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According to the PCA results (Fig. 5a), pollen and spore taxa are well-separated based on their associated biomes. Specifically, *Pinus* and fern spore (notably *Hicriopteris)* form a distinct cluster on the positive end of axis 1, while characteristic terrestrial herbs (particularly *Artemisia*, Poaceae and Cyperaceae) are separated along the negative end of axis 2. Three groups of dinocyst taxa can be distinguished based on the PCA results, showing clearly different trends across the record (Fig. 5b). Group 1: *Operculodinium. centrocarpum*, *Impagidinium* spp., *Impagidinium aculeatum*, *Impagidinium patulum*, *Impagidinium paradoxum*, *Impagidinium strialatum*, *Impagidinium* type1; *Bitectatodinium spongium*; Group 2: *Brigantedinium* spp.; Group 3: *Echinidinium* spp., *Echinidinium aculeatum*, *Echinidinium transparantum*, *Selenopemphix nephroides*, *Stellasinium stellatum*; *Selenopemphix quanta*, *Dubridinium* spp., *Operculodinium israelianum*; *Operculodinium* spp., *Lingulodinium machaerophorum*, *Tuberculodinium vancampoae*, *Spiniferites mirabilis*, *Spiniferites* spp.; *Spiniferites bentori*.

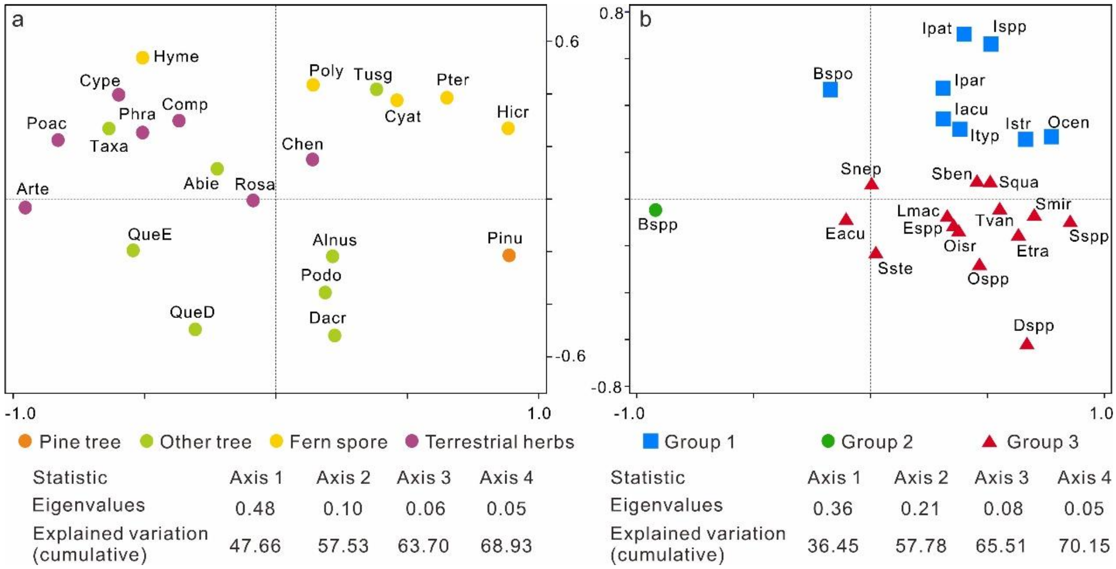

Figure 5: Results of the principal component analysis (PCA) illustrating the ordination of pollen (a) and dinocyst taxa (b) from core SCS GC-1 with colored symbols referring to the groups. For pollen, pine tree (orange): Pinu (*Pinus*); other tree (light green): QueE (*Quercus* evergreen), QueD (*Quercus* decedious), Alnu (*Alnus*), Podo (Podocarpaceae), Dacr (*Dacrycapus*), Taxa (Taxaceae), Abie (*Abies*), Tusg (*Tusga*); fern spores (yellow): Hicr (*Hicriopteris*), Pter (*Pteris*), Cyat (Cyatheaceae), Poly (Polypodiaceae), Hyme (Hymenophyllaceae); terrestrial herbs (purple): Arte (*Artemisia*), Poac (Poaceae), Cype (Cyperaceae), Comp (Compositae), Phra (*Phragmites*), Chen (Chenopodiaceae), Rosa (Rosaceae);. For dinocyst groups, Group 1 (blue): Ocen (*O. centrocarpum*), Ispp (*Impagidinium* spp.), Iacu (*Impagidinium aculeatum*), Ipat (*Impagidinium patulum*), Ipar (*Impagidinium paradoxum*), Istr (*Impagidinium strialatum*), Ityp (*Impagidinium* type1); Bspo (*Bitectatodinium spongium*); Group 2: Bspp (*Brigantedinium* spp.); Group 3: Espp (*Echinidinium* spp.), Eacu (*Echinidinium aculeatum*), Etra (*Echinidinium transparantum*), Snep (*Selenopemphix nephroides*), Sste (*Stellasinium stellatum*); Squa (*Selenopemphix quanta*), Dspp (*Dubridinium* spp.), Oisr (*Operculodinium israelianum*); Ospp (*Operculodinium* spp.), Lmac (*Lingulodinium machaerophorum*), Tvan (*Tuberculodinium vancampoae*), Sben (*Spiniferites bentori*); Smir (*Spiniferites mirabilis*); Sspp (*Spiniferites* spp.).

Based on the variations in percentage and concentration values of pollen, dinocyst and charcoal as well as the CONISS analysis, four zones can be recognized (Fig. S2):

4.5.1 Zone SCS GC-1 1 (301-217cm, 32.8-25.6 ka)

This zone is characterized by relatively high percentages of *Pinus* and *Quercus* (evergreen), while pollen taxa of terrestrial herbs such as *Artemisia*, Poaceae and Cyperaceae as well as fern spores including *Hicriopteris*, Polypodiaceae, Cyathaceae are relatively low (Fig. 4 and Fig. S2). High fungal spore concentrations here coincide with low charcoal concentrations. The

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percentages of heterotrophic taxa *Brigantedinium* spp. (Group 1) increase gradually to the end of this zone, whereas the percentages of autotrophic taxa (Group 2) particularly *Impagidinium* species reach their maximum levels in the record but decline towards the end of this zone (Fig. 4 and Fig. S2). Concentrations of foraminiferal organic linings reach minimum in this zone.

4.5.2 Zone SCS GC-1 2 (217-97 cm, 25.6-15.6 ka)

The percentage of *Pinus* pollen decreases to its lowest values of the entire record. Meanwhile, terrestrial herb taxa, particularly *Artemisia*, increase to their highest levels along with fungal spores. Some fern spore types, including Polypodiaceae, Hymenophyllaceae, Cyatheaceae and *Pteris*, also exhibit relatively high values compared to Zone SCS GC-1 1 (Fig. 4 and Fig. S2). Concentrations of pollen, fern spores and charcoal all reach maximum values, peaking around 25.3-24.3 ka when dinocyst concentrations also exhibit a maximum, along with *Brigantedinium* spp. On the other hand, Group 1 dinocyst taxa are at minimum values in this zone. Concentrations of foraminiferal organic linings remain at low value in this zone.

4.5.3 Zone SCS GC-1 3 (97-69 cm, 15.6-11.7 ka)

This zone is characterized by the rapid increase in *Pinus* pollen, accompanied by a sharp decline in terrestrial herbs, especially *Artemisia*. Concentrations of fungal spores exhibit a declining trend and return to the levels observed in Zone SCS GC-1 1. Concentrations of pollen, fern spores and charcoal also exhibit a declining trend to reach near the lowest levels, whereas dinocyst concentrations remain relatively prominent. However, the percentage of *Brigantedinium* spp. exhibits a decline in this zone, accompanied by a marked increase of Group 3 taxa, including *Dubridinium* spp. and *Echinidinium* spp. Meanwhile, dinocysts in Group 2 achieve relatively high values. Concentrations of foraminiferal organic linings increase gradually from the beginning of this zone.

4.5.4 Zone SCS GC-1 4 (69-0 cm, 11.7 ka-present)

The percentages of *Pinus* pollen reach their highest values of the entire record interrupted around 9.5-9.0 ka by a very marked decline to values close to those of Zone SCS GC-1 1. The abrupt reduction in *Pinus* pollen is also observed in the overall pollen, fungal spore, charcoal concentration, and in terrestrial herb pollen especially. Additionally, this zone is characterized by the increase in fern spores, particularly *Hicriopteris* which exhibits a short, sharp increase around 2.8 ka (Fig. 4 and Fig. S2). The percentage of *Brigantedinium* spp. decreases to the lowest values of the entire record, whereas the percentage of Group 3 dinocyst taxa, along with the concentration of foraminiferal organic linings all reach their highest values.

5. Discussion

5.1 Environmental significance of key proxies

5.1.1 K/Al and Ti/Al

In comparison to single elements, elemental ratios which are insensitive to dilution effects, are more useful as environmental indicators (Govin et al., 2012). Ti is highly enriched in mafic and volcanic rocks, while Al is a major component of most common clay mineral found in all types of weathered continental crust. The SCS is surrounded by diverse geological terrains with distinct Ti/Al ratios originating from different sources such as the Luzon Volcanic Arc (Philippines), Taiwan and other basaltic sources with high Ti/Al, while with low Ti/Al originating from the major continental river systems that drain ancient, weathered landmasses. Thus, Ti/Al can provide a robust picture of terrestrial input and its origin in the complex environment of the SCS. High Ti/Al indicates increased relative input of sediment from a volcanic or mafic source/less chemical, and low Ti/Al indicates increased relative input of sediment from a felsic continental source (e.g., Pearl River, Mekong River) (Hu et al., 2013; Wan et al., 2007). K/Al and Ti/Al records of ODP Site 1143 from the SCS generally show low values during glacial

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periods and high values during interglacial periods, clearly indicating that increase in K/Al and Ti/Al is probably related to wetter conditions and thus the intensified chemical weathering (Clift et al., 2008; Tian et al., 2011; Wei et al., 2004).

5.1.2 Source area and transport of pollen and spores

In the northern SCS sediments, the modern distribution of tree pollen, particularly *Pinus*, shows disproportionately high representation relative to other pollen types. This suggests substantial contributions from south and southeast China, transported primarily by the northeasterly winter monsoon and associated wind-driven currents. While elevated *Pinus* percentages can signal either a strengthened winter monsoon or a cool, humid climate (Luo et al., 2018; Sun et al., 2003), PCA results (Fig. 5a) indicate that this ambiguity can be resolved by incorporating fern spore data. Unlike the wind-dispersed *Pinus* pollen, fern spores are larger, heavier, and primarily transported by river runoff. Their high abundance in sediments therefore signals a proximal source from humid montane forests (e.g., in Taiwan and Southern China), reflecting a humid climate controlled by the EASM (Kaars et al., 2000; Sun et al., 2000b; Wang et al., 2009). Consequently, a simultaneous peak in both *Pinus* pollen and fern spores is incompatible with a scenario of solely strengthened, dry winter winds. Instead, this combined signal robustly indicates a cool and humid climate, where a vigorous EASM delivered high rainfall (promoting fern-rich vegetation and riverine spore transport) while the winter monsoon remained active enough to distribute *Pinus* pollen without dominating the climatic regime. *Artemisia*, Poaceae and Cyperaceae pollen are the main components of terrestrial herbs observed in the core. *Artemisia* spp. is currently widely distributed in temperate grassland and steppe which is associated with cool, semi-arid conditions (Bandara et al., 2023; Sun et al., 2003). Although Poaceae and Cyperaceae pollen indicate a range of different habitats, high percentages of Poaceae pollen in the sediment are suggestive of grassland vegetation, and a high representation of Cyperaceae pollen typically points to a wetland environment(Sun et al., 2003; Wang et al., 2009).

Previous studies have found clear temporal variations in pollen assemblages in the SCS characterized by marked higher pollen concentrations in glacial sediments than in interglacial sediments (Jiwarungrueangkul and Liu, 2021; Sun et al., 2000a; Sun and Luo, 2001; Sun et al., 2003; Zheng and Lei, 1999). On one hand, the large amount of pollen in glacial sediments at the site might be transported by a strengthened northeast winter monsoon from the Asian mainland and Taiwan Island. In contrast, during the last glacial low stand, sea level was 120-150 m lower than today, exposing much of the northern SCS continental shelf and increasing land area by roughly 24×104 km^2 (Chen et al., 2020; Sun et al., 2000a; Wang et al., 2009). The northern SCS would likely receive substantial pollen and spore amounts via wind or water from the exposed continental shelf which was covered by grassland under the prevailing dry and temperate climate of the time (Luo and Sun, 2005; Sun et al., 2003). Typically, during glacial periods, herbaceous vegetation is predominant in the region, whereas during interglacial periods tree and ferns dominate the terrestrial land mass adjacent to the SCS (Sun et al., 2000a; Sun and Luo, 2001). Such glacial-interglacial transitions are driven by changes in climate, or ocean currents, or both. During MIS 2 (21-11.5 ka), *Artemisia* increased again and occupied most of the extensive emerged continental shelf (Sun et al., 2003). Accordingly, the ratio of trees/herb pollen is a valuable indicator of glacial-interglacial cycles along with their associated vegetation and climate conditions.

5.1.3 Dinocysts

Although modern dinocyst distributions are strongly correlated with sea surface conditions such as sea surface temperature, sea surface salinity, nutrient levels and productivity (Dale, 1996; Marret and Zonneveld, 2003; Zonneveld et al., 2024), dinocyst deposition and preservation in marine sediments are affected by various non-ecological, taphonomic factors which may alter the primary dinocyst accumulation in the sediment (Holzwarth et al., 2007). It is therefore crucial to account for these factors before relating the fossil dinocyst record to palaeoenvironmental conditions. Upwelling off west Luzon is driven by the EAWM and intensifies during stronger EAWM phases. This process brings nutrient-rich subsurface waters to the surface, promoting enhanced dinoflagellate production (Yuan et al., 2004b). The Kuroshio Current, which transports warm and high-salinity water into the northern SCS leading to a significant increase in sea surface temperature, is also a significant factor influencing dinoflagellate growth. Additionally, heterotrophic taxa, such as degradation-sensitive species from the *Protoperidinium* genus, are more susceptible to aerobic degradation compared to autotrophic taxa (Holzwarth et al., 2007). This may be influenced by the water oxygen content which may therefore alter dinocyst assemblages before and after sedimentation (Zonneveld et al., 2008). However, the persistent dominance of heterotrophic dinocysts in the record (up to 99%

with mean values of 85%) suggests that selective dissolution of protoperidiniacean species relative to other taxa in the sediments is negligible (Zhao et al., 2017).

Impagidinium cysts as well as *O. centrocarpum* typically indicate open ocean, fully marine settings characterized by low primary productivity, low nutrient levels, and well-oxygenated bottom waters (Zonneveld et al., 2013; Zonneveld and Pospelova, 2015). Modern surface dinocyst distribution in SCS shows that most of *Impagidinium* species, *Nematosphaeropsis labyrinthus* and *Polysphaeridium zoharyi* are positively correlated with water depth. Their highest abundances were observed in the northern slope-deep basin which is influenced by the Kuroshio Current, indicating an open-ocean environment (Li et al., 2020). In the northern Philippine Sea, the predominance of *Impagidinium* taxa from the bottom sediments is also indicative of pelagic and tropical regions (Matsuoka, 1981). During winter, the Kuroshio Current transports high-salinity, low-nutrient waters from the Philippine Sea through the Luzon Strait, which then flows along the continental shelf break, reaching the study area in the northern SCS. This provides further evidence that the increased abundance of Group 1 taxa may reflect typical nutrient-poor open ocean environments. Dinocysts preserved in SCS GC-1 are dominated by *Brigantedinium* spp. (28-96%, mean = 80%), which have also been observed from sediment trap samples in the southwest Taiwan waters of the SCS with high representation ranging from 68% to 91% (Li et al., 2018b). High abundances of *Brigantedinium* spp. are characteristic of increased nutrient supply (Dale, 1996), which has been used as an indicator of primary productivity (Li et al., 2020; Zonneveld et al., 2013). In addition, *Brigantedinium* spp. is usually more abundant near the winter upwelling zone in the South China Sea (Li et al., 2020). Therefore, Group 2 taxa, characterized by the dominance of *Brigantedinium* spp., indicates intensified upwelling conditions with strong terrigenous influence that contrasts with open-ocean oligotrophic conditions indicated by Group 1. The stratigraphic variation of Group 2 cysts (Fig. 6h) displays an inverse relationship with Mg/Ca-SST, supporting the glacial 'high-productivity/low-temperature' paradigm. Group 3 taxa, characterized by dinocysts such as *Echinidinium* spp. and *S. quanta* are typically adapted to fully marine, eutrophic, and highly productive regimes, and are likely indicative of water column stratification and upwelling processes in open ocean environments (Zonneveld et al., 2013).

5.2 Sea level forcing during the LGM

Over the past 33 ka, four different periods have been clearly recognized based on our multiproxy record (Fig. 6): pre-LGM (32.8-25.6 ka), LGM (25.6-15.6 ka), last deglaciation (15.6-11.7 ka) and the Holocene (11.7-present) indicating a distinctive pattern of glacial-interglacial transition. The pre-LGM phase was characterized by higher sedimentation rates (Fig. 3a), cooler SST (Figs. 6c and 6d), higher primary productivity (Figs. 6e and 6h), reduced humidity (Figs. 6f, 6j, 6l and 6m), a predominance of terrestrial herbs (Fig. 6j), and strengthened fire activity (Fig. 6k) which became more pronounced during the LGM.

Previous studies have suggested that elevated charcoal and terrestrial pollen concentrations during the LGM reflect reduced distance to the sediment source associated with the exposure of the northern SCS continental shelf during glacial low stands (Luo and Sun, 2005; Sun et al., 2000a). Our data supports this interpretation: the minimum tree/herb ratio (Fig. 6j) indicates extensive expansion of herbaceous vegetation at the expense of *Pinus* on the exposed shelf surface, which would have supplied abundant fuel, consistent with the high pollen concentrations (Fig. 6k) and the increased abundance of large charcoal particles (>100 μm) (Fig. S3) representing predominantly local fires. Enhanced terrigenous nutrient delivery also appears to have stimulated marine productivity during the LGM. Elevated $\delta^{13}C$ values of planktonic foraminifera (Fig. 6e), increased dinocyst Group 2 and reduced Group 1 (Figs. 6g-h), together with rising TOC/TN (Fig. 6e), all point to strengthened terrestrial nutrient supply. A global compilation further shows that OC accumulation rates during glacial maxima were ~50% higher than interglacial intervals (Cartapanis et al., 2016). The substantially shortened distance between the exposed shelf and the core site (Lambeck et al., 2014) would have facilitated more efficient transfer of terrigenous nutrients to proximal deep-sea areas. The low Ti/Al ratios (Fig. 6f) suggest that this enhanced input originated mainly from felsic continental rivers (e.g., the Pearl River). Although the reduced K/Al (Fig. 6f) and Donge-Hulu cave $\delta^{18}O$ records (Fig. 6l) (Wang et al., 2001; Yuan et al., 2004a) indicate a weakened EASM that would typically suppress fluvial discharge, this appears to have been offset by the markedly closer coastline and the likely persistence of eolian dust transport from the Chinese mainland. The combined effect of these terrestrial nutrient sources would have favoured heterotrophic dinoflagellate production (Smayda and Trainer, 2010), contributing to the observed rise in marine productivity. Independent evidence from the northern SCS similarly links higher

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glacial productivity to intensified winter winds, enhanced water-column mixing, and upwelling, as well as increased land-derived nutrient supply (Li et al., 2008).

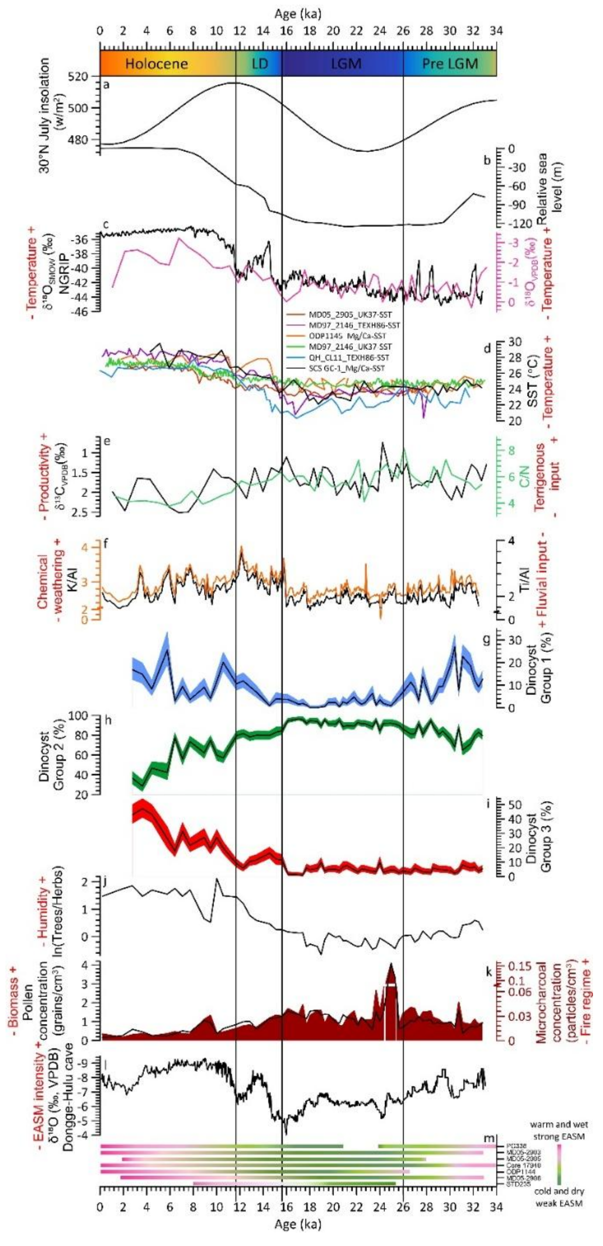

Figure 6: 30°N July insolation (Laskar et al., 2004) (a); relative sea level on the Sunda Shelf, South China Sea (Hanebuth et al., 2000) (b); NGRIP $\delta^{18}O_{SMOW}$ (Andersen et al., 2004) (c, black) and stable oxygen $\delta^{18}O_{VPDB}$ of planktonic foraminifera from SCS GC-1 (c, pink); SST records from MD052905 (Zhou et al., 2012), MD972146 (Lin et al., 2014), ODP1145 (Oppo and Sun, 2005), QHCL11 (Liu et al., 2020) and SCS GC-1 (d); stable carbon $\delta^{13}C_{VPDB}$ of planktonic foraminifera (e, black) and C/N ratio (e, green); major element ratio Ti/Al (f, black) and K/Al (f, orange), percentages of three dinocyst groups (g, h, i); ratio of trees/herbs (j); pollen concentration (k, black) and microcharcoal concentration (k, dark red shading); Dongge-Hulu cave $\delta^{18}O_{PDB}$ (l) (Wang et al., 2001; Yuan et al., 2004a); summary of records indicating climate and potential intensity of

EASM (m) (Sun et al., 2000a; Sun et al., 2000b; Luo and Sun, 2005; Zhou et al., 2012; Xie et al., 2014; Dai and Weng, 2015; Dai et al., 2015a; Yu et al., 2017; Li et al., 2019). Pre LGM: pre Last Glacial Maximum; LGM: Last Glacial Maximum; LD: last deglaciation.

5.3 Dominance of ocean forcing since the last deglaciation

Since the last deglaciation, the northern SCS has experienced a comprehensive environmental transformation characterized by decreasing sedimentation rates, rising SST, declining primary productivity, increased moisture availability, a pronounced expansion of pine forests, and minimal fire activity. A key observation is that SST warming in the northern SCS begins ~1.9 ka earlier than changes recorded by the other proxies (Figs. 6c and 6d) (Andersen et al., 2004; Lin et al., 2014; Liu et al., 2020; Oppo and Sun, 2005; Zhou et al., 2012). This earlier onset corresponds more closely with rising insolation (Fig. 6a) (Laskar et al., 2004) than with sea-level rise (Fig. 6b) (Hanebuth et al., 2000). This implies that, in addition to the well-recognized role of sea-level rise, ocean warming likely acted as an initial trigger for subsequent environmental changes. This effect is especially pronounced in the tropics and is consistent with the concept of tropical ocean-atmosphere forcing (Cheng et al., 2019; Xie et al., 2010).

The mechanisms underlying these changes can be traced through both marine and terrestrial proxies. The rising sea level reduced the extent of the exposed continental shelf, increasing the distance from terrestrial sediment sources to the core site (Luo and Sun, 2005; Sun et al., 2000a). Inundation of the continental shelf created a massive sediment trap in newly formed shallow marine environments, leading to a dramatic reduction in terrigenous material reaching the deep basin (Liu et al., 2003; Wang and Sun, 1994). This is reflected in markedly lower sedimentation rates and increased Ti/Al ratios (Figs. 3a and 6f), indicating reduced terrestrial input. At the same time, shrinkage of the continental shelf area constrains the growth of terrestrial herbs, which were progressively replaced by expanding pine forests and ferns (Figs. 5 and 6j). Relatively high concentrations of foraminiferal organic linings (Fig. 4) also imply that the water depth and the open ocean environments had become suitable for planktonic foraminifera (Tyszka et al., 2021). The synchronous strengthening of the EASM, likely initiated by intensified ocean-atmosphere interactions, is reflected by the rapid negative shift in the Dongge-Hulu Cave $\delta^{18}O$ record (Fig. 6l) (Wang et al., 2001; Yuan et al., 2004a), and is further supported by other paleorecords from the northern SCS (Fig. 6m) (Dai and Weng, 2015; Dai et al., 2015; Li et al., 2019; Luo et al., 2015; Sun et al., 2000a; Sun et al., 2000b; Xie et al., 2014; Yu et al., 2017; Zhou et al., 2012). This further supported the vegetation shift by enhancing regional humidity. The wetter conditions led to a sharp reduction in fire activity, as evidenced by decreased charcoal concentrations (Fig. 6k), while the decline in coprophilous fungal spores (Lee et al., 2022) suggests a corresponding response in herbivore populations to the changing landscape (Fig. 4). Similar conditions with increase in fern spores, decrease in terrestrial herbs and dinocyst concentration were also recorded from 12.5-6.8 ka in the core GLW31D (Li et al., 2017).

Likewise, reduced terrestrial input cannot fully explain the marine environmental changes particularly the decreased primary productivity and shift in dinocyst associations. The early onset of SST warming may have strengthened upper water column stratification, thereby reduced vertical nutrient supply and contributed to the decline in primary productivity. This interpretation is supported by the shift in dinocyst assemblages: Group 2 taxa decreases while Group 3 increases, consistent with more strongly stratified conditions and reduced upwelling relative to the LGM. Periodic peaks in Group 1, particularly around 10.6 ka and 5.8 ka, further point to an enhanced influence of the warm, nutrient-poor Kuroshio Current (Liu et al., 2016b), which would additionally suppress productivity. Independent evidence for strengthened Kuroshio intrusion during the early Holocene is also recorded in core GLW31D from the northern SCS (Li et al., 2021).

Collectively, the multi-proxy dataset shows that deglacial environmental transitions in the northern SCS reflect the combined action and interaction of several forcings rather than a single dominant driver (Fig. 7). Tropical ocean warming initiated the deglacial transition through both direct marine influence and remote atmospheric feedback, triggering a marked shift in dinocyst associations and decreased primary productivity through enhanced water column stratification. This was followed by sea-level rise that reconfigured coastal geography and sediment transport, further reducing terrestrial nutrient input. The superimposed intensification of the EASM then completed the regional shift to humid conditions, driving vegetation succession and suppressing fire activity. This multi-mechanism framework highlights the complex yet coherent response of both marine and terrestrial systems to global climatic changes during the last deglaciation.

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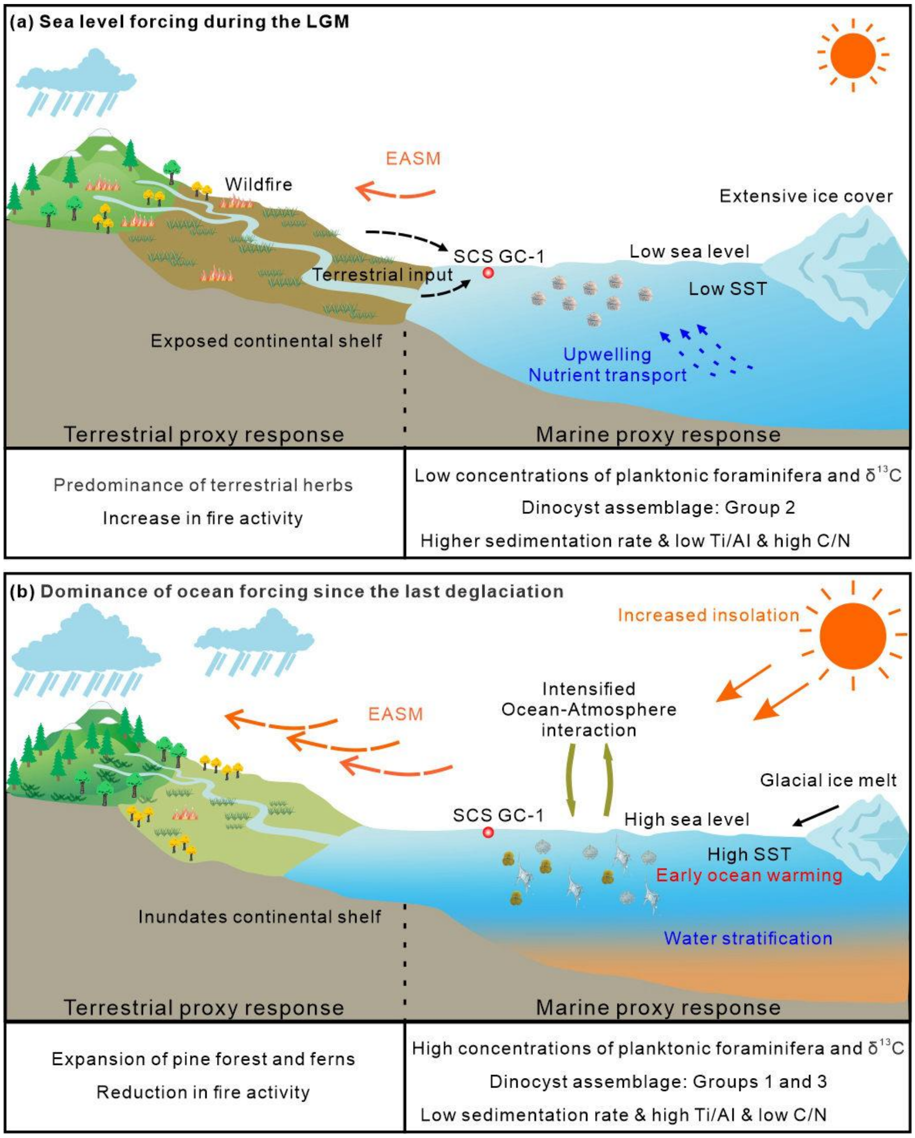

Figure 7: A conceptual framework of driving mechanisms and associated environmental responses during the LGM (a) and since the last deglaciation (b) based on multiproxy record from the core SCS GC-1 in the northern SCS.

6 Conclusions

Our multi-proxy reconstruction from the northern SCS provides a high-resolution record of clear glacial-interglacial climatic and oceanic transitions over the past 33 ka. Four distinct climatic phases are identified, viz. the pre-Last Glacial Maximum (32.8-25.6 ka), Last Glacial Maximum (25.6-15.6 ka), last deglaciation (15.6-11.7 ka) and the Holocene (11.7 ka-present). The glacial intervals (pre-LGM and LGM) were characterized by higher sedimentation rates, cooler SST, higher primary productivity, herb-dominated landscapes, reduced humidity and intensified fire activity. A fundamental regime shift occurred during the last deglaciation, marked by evidently decreasing sedimentation rates, rising SST, declining primary productivity, a pronounced expansion of pine forests, increased moisture availability, and diminished fire activity. The Holocene was

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characterized by a period of relative stability, defined by the lowest sedimentation rates, warmest SST, highest humidity, maximum pine forest coverage and minimal fire disturbance. In summary, the combined evidence reveals that the deglacial environmental changes of the northern SCS were driven by the interplay of multiple forcings including increased insolation, sea-level rise and monsoon intensification, with ocean warming preceding other changes, suggesting the important role of tropical ocean-atmosphere interactions in initiating this transition. This study highlights the value of integrated land-sea proxies in deciphering complex climate interactions and underscores the northern SCS's sensitivity to both high- and low-latitude forcing. Future research employing a spatial network of cores across the SCS will be crucial to better resolve the spatial patterns and teleconnections of these changes.

Author Contributions

Xueqin Zhao: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing – original draft, Writing – review and editing; Shengjie Ye: Investigation, Visualization, Writing – review and editing; Jiahui Yao: Investigation, Formal analysis, Writing – review and editing; Michael Meadows: Validation, Writing – review and editing; Chengyu Weng: Validation, Writing – review and editing; Yasong Wang: Visualization, Writing – review and editing; Mingxing Zhang: Investigation; Yunping Xu: Conceptualization, Writing – review and editing.

Competing Interests

The authors declare that they have no conflict of interest.

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Data Availability

Data used in this study has been submitted in the Pangaea database (https://www.pangaea.de) with specific DOI: https://doi.pangaea.de/10.1594/PANGAEA.987882 for pollen and spore , https://doi.pangaea.de/10.1594/PANGAEA.987861 for organic-walled dinoflagellate cyst, and https://doi.pangaea.de/10.1594/PANGAEA.987870 for microcharcoal.

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