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Physical Sciences - Article

Keywords: Southern Ocean, poleward shift, Southern Hemisphere westerly winds, deglacial rise in CO₂

Posted Date: April 16th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-404786/v1>

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Poleward shift in the Southern Hemisphere westerly winds synchronous with the deglacial rise in CO₂

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The Southern Hemisphere westerly winds strongly influence deep ocean circulation and carbon storage¹. While the westerlies are hypothesised to play a key role in regulating atmospheric CO₂ over glacial-interglacial cycles²⁻⁴, past changes in their position and strength remain poorly constrained⁵⁻⁷. Here, we use a compilation of planktic foraminiferal $\delta^{18}\text{O}$ from across the Southern Ocean and constraints from an ensemble of climate models to reconstruct changes in the westerlies over the last deglaciation. We find a 4.7° (2.9-6.9°, 95% confidence interval) equatorward shift and about a 25% weakening of the westerlies during the Last Glacial Maximum (about 20,000 years ago) relative to the mid-Holocene (about 6,000 years ago). Our reconstruction shows that the poleward shift in the westerlies over deglaciation closely mirrors the rise in atmospheric CO₂. Experiments with a 0.25° resolution ocean-sea-ice-carbon model demonstrate that shifting the westerlies equatorward substantially reduces the overturning rate of the abyssal ocean, leading to a suppression of CO₂ outgassing from the Southern Ocean. Our results establish a central role for the westerly winds in driving the deglacial CO₂ rise, and suggest natural CO₂ outgassing from the Southern Ocean is likely to increase as the westerlies shift poleward due to anthropogenic warming⁸⁻¹⁰.

The Southern Hemisphere westerly winds play a key role in returning deep ocean waters to the surface and thus largely govern the rate at which the deep oceanic reservoirs of heat and carbon communicate with the surface ocean and atmosphere^{1,11}. South of ~47°S the modern westerly winds drive divergent northward Ekman transports in the near-surface ocean that contribute to lift deepwaters and tilt density surfaces¹¹. Although mesoscale eddies work to flatten out the steep isopycnals, the counteraction of the wind-driven circulation by the

40 eddies is incomplete, resulting in a residual circulation which brings macro-nutrient and carbon
41 rich deepwaters to the surface^{1,12}. Due to iron¹³ and light limitation¹⁴ the upwelled nutrients are
42 not completely utilised before buoyancy loss close to the Antarctic continent causes some of
43 the upwelled waters to sink as Antarctic Bottom Water, filling the deep ocean with 'preformed'
44 nutrients¹⁵. This 'leak' in the biological pump, largely caused by the over-supply of nutrients to
45 the surface ocean by the wind-driven upwelling, leads to the hypothesis that changes in the
46 Southern Hemisphere westerly winds could regulate atmospheric CO₂ over glacial-interglacial
47 cycles²⁻⁴. Modelling studies¹⁵⁻¹⁷ indicate a tight coupling between the oceans' preformed
48 nutrient inventory and atmospheric CO₂, while proxy data^{4,18} indicate large changes in nutrient
49 supply to the surface of the Southern Ocean over glacial-interglacial cycles.

50

51 Past changes in the position and strength of the Southern Hemisphere westerly winds
52 are poorly constrained, making it difficult to assess their role in driving past carbon cycle
53 changes. A recent compilation of diverse proxy data⁵ suggested signals of an equatorward
54 shift in the westerlies during the Last Glacial Maximum (LGM, 19-23 ka) relative to the
55 Holocene. However, relating changes in the measured proxies (i.e. terrestrial moisture, marine
56 productivity) back to the position of the westerlies is challenging, both quantitatively and
57 qualitatively, such that even the direction of change during the LGM (i.e. poleward versus
58 equatorward) is debated^{6,7}. Furthermore, while climate models show a relatively clear and
59 consistent signal of an equatorward shift in the Northern Hemisphere near-surface westerlies
60 under glacial forcings¹⁹⁻²¹ in good agreement with proxy data¹⁹, they show little consistency in
61 the magnitude or sign of change in the Southern Hemisphere^{6,20,22}. Ice core data suggest
62 abrupt shifts in the westerlies during the millennial scale atmospheric CO₂ variability of the last
63 glacial period²³, but there is currently very little constraint on how or when the westerlies shifted
64 over the last deglaciation (20 - 10 ka), as atmospheric CO₂ rose by ~90 ppmv²⁴.

65

66 To reconstruct changes in the position of the Southern Hemisphere westerly winds
67 over the last deglaciation we exploit the coupling between the latitude of the maximum zonal
68 wind stress (hereafter referred to as *wind latitude*) and the latitude of the maximum meridional
69 sea surface temperature (SST) gradient (hereafter referred to as *SST front latitude*) in the
70 Southern Ocean (Fig. 1). This two-way coupling arises through the winds' dependence on the
71 atmospheric temperature gradient and through the winds' control on ocean circulation, which
72 together shape the meridional SST profile²⁵⁻²⁷. The position of the peak in westerly wind-speed
73 coincides with the position of the SST front around much of the modern Southern Ocean,
74 except where bathymetric steering of ocean currents causes local decoupling^{25,28} (Fig 1). An
75 ensemble of models from the Paleoclimate Modelling Intercomparison Project (PMIP3 and
76 PMIP4) and Coupled Model Intercomparison Project (CMIP5 and CMIP6) show a tight

77 relationship between the wind latitude and the SST front latitude across pre-industrial, LGM,
78 and 4xCO₂ simulations (Methods; Fig. 1c). This relationship, stemming from large-scale
79 atmosphere-ocean coupling, indicates we can use changes in the SST front latitude to
80 reconstruct past shifts in the wind latitude.

81

82 To track changes in the latitude of the Southern Ocean SST front over the deglaciation
83 we use a basin-wide compilation of $\delta^{18}\text{O}$ in planktic foraminiferal calcite ($\delta^{18}\text{O}_{\text{calcite}}$). Although
84 $\delta^{18}\text{O}_{\text{calcite}}$ is a function of both temperature and the $\delta^{18}\text{O}$ of seawater ($\delta^{18}\text{O}_{\text{water}}$), the effect of
85 temperature is around six times greater than the effect of $\delta^{18}\text{O}_{\text{water}}$ at the basin scale (Extended
86 Data Fig. 1). As no physical mechanism exists to drive such large changes in $\delta^{18}\text{O}_{\text{water}}$ at the
87 basin scale, the meridional pattern of $\delta^{18}\text{O}_{\text{calcite}}$ will always be dominated by temperature
88 (Methods). Meridional profiles of $\delta^{18}\text{O}_{\text{calcite}}$ thus allow us to identify the latitude of the SST front
89 and ultimately that of the westerly winds.

90

91 We compiled existing records of planktic foraminiferal $\delta^{18}\text{O}$ from near-surface dwelling
92 species from core sites across the Southern Ocean and generated new data from the
93 Kerguelen plateau and southeast Pacific, resulting in a dataset of 64 planktic foraminiferal
94 $\delta^{18}\text{O}$ records spanning the last deglaciation (Fig. 1a; Extended Data Figs. 2 and 3; Methods).
95 Meridional shifts in the SST front ($\Delta\text{Lat}_{\text{SST}}$) are calculated by finding the latitudinal shift that
96 minimises the difference between the Holocene $\delta^{18}\text{O}$ profile and the profile at each time step
97 within a 10° latitudinal window that includes the steepest part of the meridional $\delta^{18}\text{O}$ profile¹⁹
98 (Methods; Fig. 1b and Extended Data Figs. 2 and 3). We account for whole ocean changes in
99 $\delta^{18}\text{O}_{\text{water}}$ and the global-mean SST change ($\delta^{18}\text{O}_{\text{ivc-gtc}}$; Fig. 1a; Extended Data Figs. 2 and 3),
100 quantifying uncertainties via bootstrapping and Monte-Carlo simulation (Methods). We
101 compute $\Delta\text{Lat}_{\text{SST}}$ across the entire Southern Ocean, as well as separately in the Indian-Pacific
102 and Atlantic sectors (Fig. 2; Extended Data Fig. 4).

103

104 The data reveal an equatorward shift in the SST front during the LGM (20ka) relative
105 to 10 ka, indicative of an equatorward shift in the westerly winds (Fig. 1b; Extended Data Figs.
106 2 and 3). Mapping the LGM $\delta^{18}\text{O}_{\text{ivc-gtc}}$ anomalies shows a large mid-latitude cooling during the
107 LGM across the Indian and Pacific sectors (Fig. 1a; equivalent to a cooling of 4-5°C beyond
108 the global-mean SST change). Our Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$ reconstruction shows a 4.8° (3.6-
109 6.1° 95% confidence interval [CI]) equatorward shift in the SST front during the LGM relative
110 to 10 ka (Fig. 2c; Extended Data Fig. 4). We perform a 'leave-one-out' analysis of the Indian-
111 Pacific dataset which shows that no single record is contributing more than 5% of the total

112 reconstruction and indicates that Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$ reconstruction primarily reflects a mid-
113 latitude signal (Methods; Extended Data Fig. 4).

114

115 By contrast, we find a slight warming anomaly (relative to the global-mean LGM SST
116 change) at all latitudes in the western Atlantic (Fig. 1), possibly a signal of a weakened Atlantic
117 Meridional Overturning Circulation (AMOC)^{29,30}, and no significant change in the SST front
118 latitude within the Atlantic sector over deglaciation (Extended Data Fig. 4). This result is
119 consistent with strong bathymetric steering of currents in the Atlantic sector²⁸, and the lack of
120 a modelled relationship between the SST front latitude and wind latitude in this sector,
121 particularly in the eastern Atlantic where the vast majority of the mid-latitude cores are located
122 (Fig. 1; Extended Data Fig. 5bc). Although we attribute the lack of change in the SST front
123 latitude within the Atlantic to the modelled decoupling of the westerlies and SST front there
124 (Extended Data Fig. 5bc), we cannot rule out that the westerlies did not shift substantially over
125 deglaciation within the Atlantic.

126

127 We apply the multi-model relationship between the wind latitude and the SST front
128 latitude in the Indian-Pacific sector (Fig. 2; Extended Data Fig. 5a) to our Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$
129 reconstruction and quantify shifts in the zonal-mean wind latitude over the deglaciation
130 ($\Delta\text{Lat}_{\text{wind}}$). A regional subset test demonstrates that our method is able to track shifts in the
131 zonal-mean wind latitude using changes in the latitude of regional SST fronts (Fig. 2;
132 Methods); although different regions yield differing magnitudes of deglacial change in the SST
133 front latitude (Fig. 2b), they yield almost identical time series of the zonal-mean wind latitude
134 (Fig. 2d), given the region-specific multi-model relationship between the two variables (Fig.
135 2c). Measured shifts in the SST front latitude thus provide a robust constraint on the wind
136 latitude. We find a 6.2° ($4.4\text{-}8.4^\circ$ 95% CI) equatorward shift in the wind latitude during the LGM
137 (20 ka) relative to 10 ka (Figs. 2d and 3a). The evolution of the wind latitude over deglaciation
138 closely mirrors, and is highly correlated with, the evolution of atmospheric CO_2 (ref²⁴) (Fig. 3).
139 A lagged correlation suggests changes in the wind latitude may have led the rise in
140 atmospheric CO_2 and global temperature³¹ by a few hundred years during certain intervals
141 over the deglaciation, although difficulties in fully quantifying age uncertainties make this result
142 tentative (Methods; Fig. 3c).

143

144 Extending our analysis to span a longer time interval (22 to 6.5 ka) indicates an early
145 Holocene extremum in the poleward position of the westerlies, followed by a
146 $\sim 1.5^\circ$ equatorward shift in the winds over 10-6.5 ka (Extended Data Fig. 6). Despite the larger
147 uncertainties in the early Holocene reconstruction, it agrees well with the analysis of the full
148 dataset (i.e., 10-20 ka) in the overlapping sections (Extended Data Fig. 6). Our results thus

149 indicate a 4.7° (2.9-6.9° 95% CI) equatorward shift of the westerlies during the LGM (20 ka)
150 relative to the mid Holocene (6.5 ka). Assuming no substantial shift in the westerlies from the
151 mid- to late- Holocene (Methods), the magnitude of the reconstructed wind shift is substantially
152 greater than that predicted by any of the models within the PMIP3/4 ensemble between
153 preindustrial and LGM states (Extended Data Fig. 7). The models show a relationship between
154 the wind latitude and the maximum magnitude of the zonal-mean zonal wind stress (*wind*
155 *strength*; Extended Data Fig. 5e), such that the reconstructed shift in wind latitude also implies
156 a reduction in wind strength of ~25% during the LGM relative to the mid Holocene (Methods;
157 Extended Data Fig. 8).

158

159 The similarity of the changes in wind latitude and atmospheric CO₂ over the
160 deglaciation (Fig. 3) reinforces the hypothesis of their coupling through Southern Ocean
161 circulation and carbon cycling. While modelling studies typically show a consistent increase in
162 oceanic carbon storage following a weakening of the westerlies, the impact of shifts in the
163 latitude of the westerlies is more uncertain^{17,32}. To better understand how changes in the
164 latitude of the westerlies may affect the oceanic overturning circulation and carbon cycle, we
165 performed two experiments with a global ocean-sea-ice-carbon model with 0.25° horizontal
166 resolution^{33,34}: A Control experiment is forced by climatological atmospheric forcing
167 representative of the recent instrumental period. A Perturbed experiment uses the same
168 forcing except for a uniform 4° equatorward shift of the Southern Hemisphere westerlies, with
169 no change in their magnitude (Methods). Both experiments are run for 125 years, starting from
170 the near-equilibrium control state. As the applied wind stress forcing does not include the
171 implied 25% reduction in wind strength (and is smaller than our reconstructed LGM shift) this
172 simulation is not designed to represent our 'best estimate' of LGM Southern Hemisphere wind
173 stress, but rather represents a conservative estimate which enables us to assess the broad
174 impacts of an equatorward shift in the westerlies alone. The 125-year transient response of
175 the system forced by an equatorward shift in the westerlies does not allow quantification of
176 the equilibrium response of the deep ocean nutrient and carbon cycles¹⁷. It nevertheless
177 reveals clear trends in circulation and biogeochemistry which provide an indication of how the
178 rapidly responding Ekman-driven transport reorganizes the residual circulation, allowing us to
179 assess how an equatorward shift in the westerlies may qualitatively impact the carbon cycle
180 on longer timescales.

181

182 We find a complete suppression of CO₂ outgassing south of 60°S in the Perturbed
183 experiment (Fig. 4), with only a partial compensation further north. As such, there is an
184 anomalous uptake of 27 GtC by the Southern Ocean south of 35°S over the course of the
185 Perturbed experiment, equivalent to a CO₂ decrease of 13 ppm (Fig. 4). Deepwater upwelling

186 and surface nutrient and carbon concentrations are substantially reduced south of 60°S (Fig.
187 4), indicating that reduced exposure of nutrient and carbon rich deepwaters in the polar
188 Southern Ocean underpins the simulated carbon cycle response to equatorward-shifted
189 westerlies (Methods). As the winds shift equatorward relative to their modern position,
190 northward Ekman transports become more divergent north of about 60°S, but less divergent
191 south of 60°S (Fig. 4). In our simulation, the effect is a substantial decrease in upwelling within
192 the polar Southern Ocean south of 60°S (Fig. 4) and a pronounced slowdown in the residual
193 circulation of the abyssal ocean globally (Fig. 5), with the largest reduction within the Pacific
194 (Extended Data Fig. 9). The decrease in abyssal overturning results in increased storage of
195 carbon and regenerated nutrients throughout the deep ocean below ~1.5 km, concurrent with
196 a decrease in dissolved oxygen (Fig. 5c; Extended Data Fig. 10). Conversely, we see an
197 increase in upwelling north of 60°S and increased overturning at intermediate depths, such
198 that carbon concentrations decrease in the upper ~1.5 km (Fig. 5c; Extended Data Fig. 10).
199 Hence, although shifting the winds equatorward increases the overall Ekman divergence
200 across the Southern Ocean (Fig. 4b), it focuses the wind's energy away from isopycnals
201 outcropping carbon-rich abyssal waters, toward isopycnals outcropping intermediate waters
202 containing relatively less carbon (Fig. 5b); these changes are synergistic such that the
203 concentration of carbon and nutrients within the intermediate depths decreases as the
204 overturning at these depths spins up. The net effect in the model is an increase in oceanic
205 carbon storage (Fig 5c). In contrast, some previous studies using coarser-resolution models
206 simulated a decrease in oceanic carbon content in response to an equatorward shift in the
207 westerlies^{17,32}. We attribute this difference to the response of the residual circulation in the
208 Southern Ocean, the representation of which should improve at higher resolution^{35,36}.

209
210 Crucially, the reduction in the upwelling of nutrients to the surface of the polar Southern
211 Ocean lowers the preformed nutrient concentration of Antarctic Bottom Water (Fig. 4;
212 Extended Data Fig. 10). Preformed nutrient concentrations also decrease in the upper cell
213 (Methods), such that preformed nutrient concentrations begin to decrease throughout the
214 deep ocean (Extended Data Fig. 10). The simulated circulation changes with equatorward-
215 shifted winds thus imply a substantial long-term increase in the efficiency of the biological
216 pump and decrease in atmospheric CO₂ (Methods; refs^{15,16}). In addition to the overall increase
217 in regenerated nutrients and carbon, the model indicates a redistribution of the regenerated
218 nutrient and carbon pools toward the abyss (Fig. 5c; Extended Data Fig. 10), such that the
219 vertical carbon gradient increases. This implies a further reduction atmospheric CO₂ via
220 carbonate compensation^{16,37} (Methods).

221

222 Despite the 4° equatorward shift in the Southern Hemisphere westerlies being the only
223 perturbation applied, and the short duration of the Perturbed experiment, the sign of the
224 simulated circulation and carbon cycle changes concurs with proxy observations from the
225 LGM of a more sluggish abyssal circulation³⁸, an increase in regenerated nutrients and carbon
226 within the deep ocean^{39–41} and a redistribution of regenerated nutrients and carbon toward the
227 abyss^{39,40,42}, as well as a shoaling of the AMOC²⁹ (Fig. 5; Extended Data Fig. 9). The simulated
228 decrease in nutrient upwelling and export production within the polar Southern Ocean, and
229 the increase further north (Fig. 4; Extended Data Fig. 10), are also in good agreement with
230 LGM proxy data^{3,5,43}.

231

232 The sign of the simulated trends is unlikely to be contingent on the absence of a
233 simulated change in atmospheric temperature or on model approximations such as
234 parameterized eddy effects (Methods). Indeed, the trends directly ensue from changes in
235 Ekman transports—themselves a function only of wind stress and geometry—and their
236 position relative to the underlying bathymetry. The northward shift of the Ekman divergence
237 (Fig. 4b,c) explains the northward shift in upwelling and CO₂ outgassing (Fig. 4d,e; Methods).
238 This shift does not merely draw the overturning northward but shoals the upper cell and
239 weakens the abyssal cell (Fig. 5b; Extended Data Fig. 9). This response stems from the
240 influence of bathymetry on the vertical extent of wind-driven upwelling^{11,44}. Specifically, the
241 presence of a zonally continuous channel at Drake Passage latitudes (56–60°S) above 2 km
242 depth favors deeper waters as the mass replacement for the surface divergence to its
243 south^{11,45}. Displacement of the Ekman divergence from south of 60°S to lower latitudes thus
244 suppresses the privileged upwelling pathway of abyssal waters (> 2 km depth) and instead
245 favors overturning in the upper ocean. Although the representation of surface buoyancy
246 forcing and mesoscale eddies can affect the response of the overturning to changing
247 winds^{12,44}, the simulated slowdown of the abyssal overturning is a robust consequence of its
248 bathymetry-driven sensitivity to Ekman flow in the polar Southern Ocean.

249

250 Our results thus suggest that as the winds shifted poleward through the deglaciation,
251 their ability to lift abyssal waters to the surface increased in approximate proportion to the
252 northward Ekman transport at 60°S. Using the relationship between wind latitude and the
253 zonal-mean wind stress at 60°S within the PMIP/CMIP ensemble (Extended Data Fig. 5d;
254 Extended Data Fig. 8) we estimate that over deglaciation this transport increased from an
255 LGM minimum of around $4 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ to a maximum of $18 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ at 11 ka, before
256 decreasing back to $14 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ by the mid-Holocene (Fig. 6a; Methods). This invigoration
257 of the abyssal overturning over deglaciation would have driven carbon out of the abyssal
258 ocean and back to the intermediate depths, surface, and atmosphere. This concurs with

259 records of deep Pacific oxygen⁴¹ and deep Southern Ocean pH³⁹ which suggest of a loss of
260 regenerated nutrients and carbon from the abyssal ocean over deglaciation (Fig. 6c).
261 Furthermore, a decrease in the global-mean deep-intermediate carbon isotope gradient⁴², and
262 other carbon cycle tracers^{39,46}, suggest the vertical gradient of regenerated nutrients and
263 carbon weakened over deglaciation (Fig. 6b). Finally, records of nutrient utilisation¹⁸ and
264 export production⁴ support an increase in nutrient upwelling to the Southern Ocean's surface
265 over deglaciation, with boron isotope records⁴⁷ demonstrating a concurrent increase in CO₂
266 outgassing from the Southern Ocean. The early Holocene maximum in poleward position of
267 the winds may have led to an overshoot of the oceanic carbon cycle, with enhanced upwelling
268 and CO₂ outgassing persisting until ~6 ka^{4,47}. However, atmospheric CO₂ decreased by ~10
269 ppm from 10 to 6 ka suggesting uptake by another sink, likely the terrestrial biosphere⁴⁸.

270

271 Our findings indicate that shifts in the Southern Hemisphere westerlies are likely to
272 have played a key role in driving the deglacial rise in atmospheric CO₂ (ref³³), and thus may
273 be an important mechanism underlying glacial-interglacial CO₂ variations^{2,3}. Given that
274 atmospheric CO₂ and global temperature may also influence the latitude of the westerly
275 winds⁸⁻¹⁰, a deglacial feedback mechanism has been proposed². The apparent temporal lead
276 of shifts in the westerlies over atmospheric CO₂ and global temperature during certain intervals
277 of the deglaciation indicated by our reconstruction (Fig 3c) suggests that some initial change
278 in the winds, perhaps driven by obliquity^{18,49}, could have initiated a cascade of increasing CO₂,
279 global warming, and poleward shifting winds. The tight coupling demonstrated here between
280 the latitude of the westerlies and atmospheric CO₂ over the last deglaciation, together with the
281 sensitivity of the abyssal circulation and carbon cycle to the latitude of the westerlies in our
282 ocean-sea-ice-carbon model experiments, suggest that future poleward shifts in the position
283 of the westerly winds⁸⁻¹⁰ are likely to drive a positive feedback on anthropogenic warming—
284 via a decrease in the efficiency of the biological pump and an increase in natural CO₂
285 outgassing from the Southern Ocean⁵⁰.

286

287 **Acknowledgements**

288 Some of the collaborations in this study were initiated through the PAGES QUIGS workshop
289 2020. EM received financial support from French-Swedish project on SO VR-349-2012-6278
290 and CNRS-INSU project INDIEN-SUD. RCJW was funded by NSF Grant AGS-1929775. LM
291 acknowledges funding from Australian Research Council grant FT180100606. PS was
292 supported by the Australian Research Council grant FT190100413 and the Australian National
293 Computing Infrastructure. MH acknowledges funding from Australian Research Council grant
294 DP210101650. We acknowledge the World Climate Research Programme's Working Group

295 on Coupled Modelling for the coordination of CMIP and thank the climate modelling groups
296 for producing and making available their model output.

297

298 **Author contributions**

299 WRG, EM, LM and CdL designed the study. EM generated the new $\delta^{18}\text{O}$ data. WRG compiled
300 the $\delta^{18}\text{O}$ data and performed the statistical analysis. RCJW and WRG analysed the coupled
301 climate model output with input from MK. LM and PS conducted the ocean-carbon model
302 simulations and analysed the output with CdL. MH provided an analysis of deep-to-surface
303 transport in the modern ocean to aid interpretation. WRG, CdL and LM developed the
304 interpretation with input from all authors. WRG led the writing of the manuscript. All authors
305 contributed to the preparation of the manuscript.

306

307 **Competing interests**

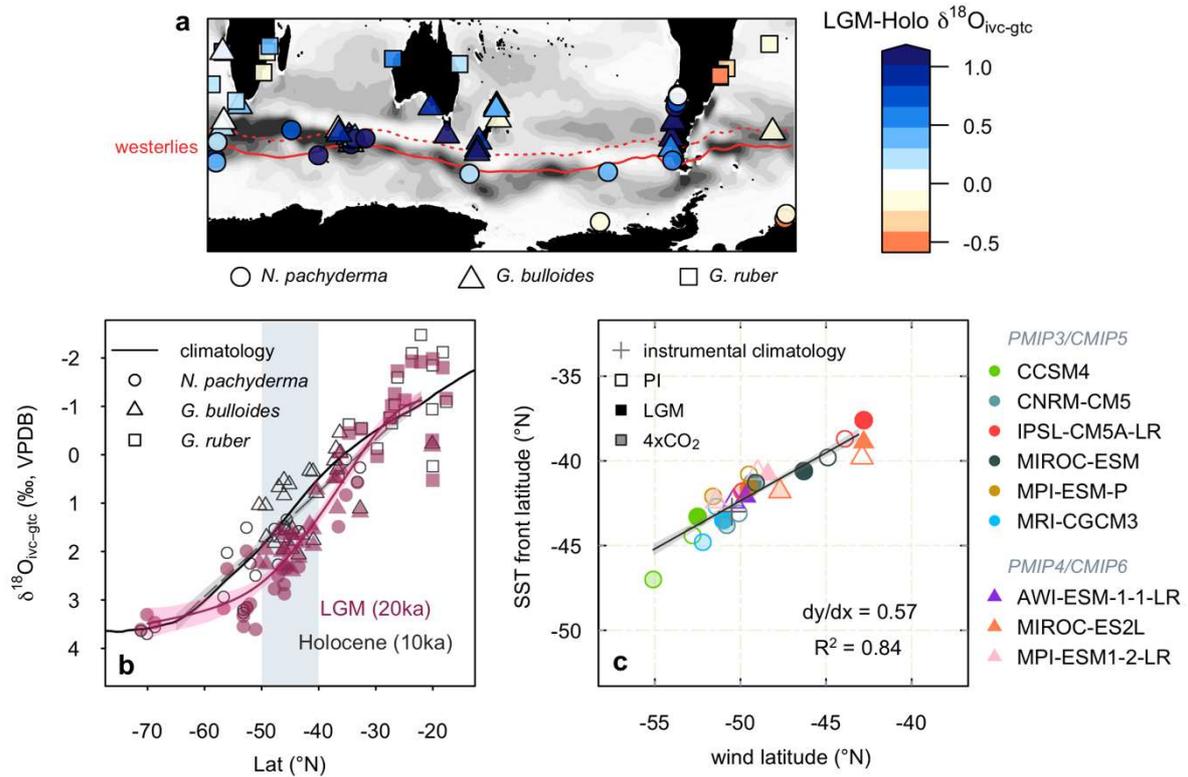
308 The authors declare no competing interests.

309

310 **Correspondence and requests for material** should be addressed to WRG

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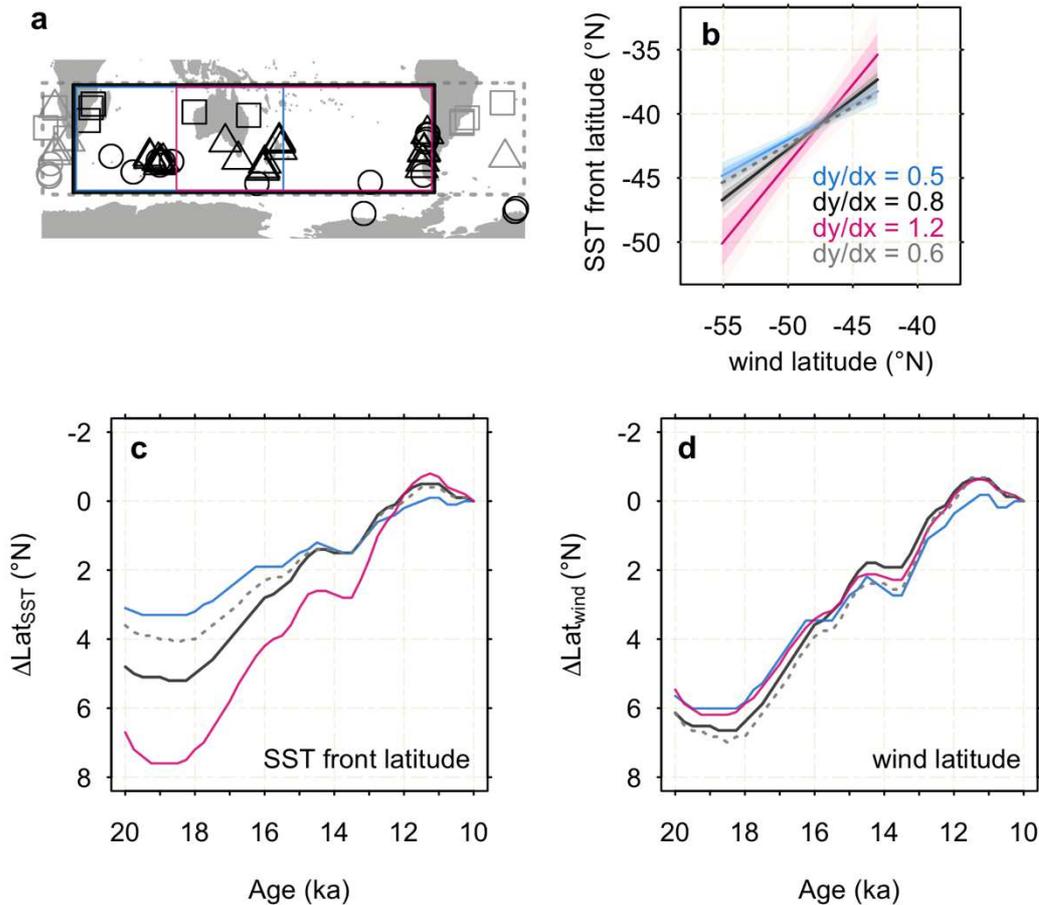


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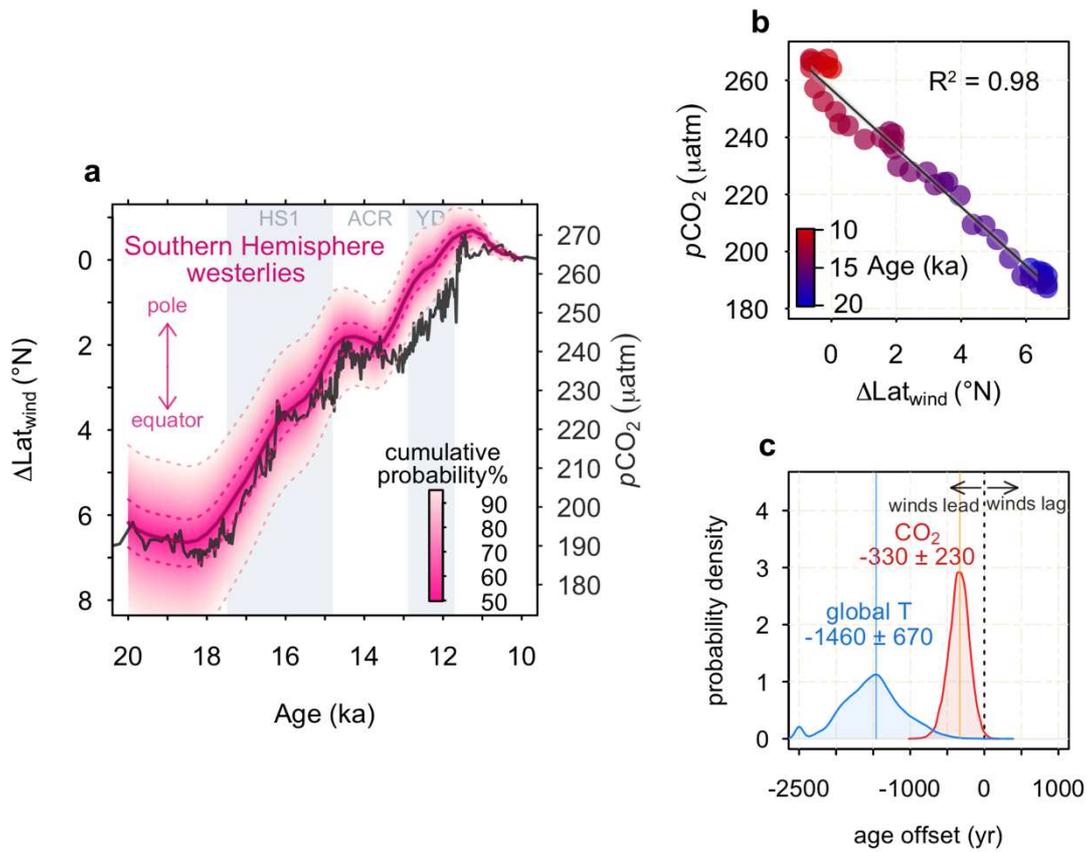
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316 **Fig. 1: $\delta^{18}\text{O}$ data and relationship between wind latitude and SST front latitude in the model**
 317 **ensemble. (a)** LGM-Holocene $\delta^{18}\text{O}_{\text{ivc-gtc}}$ ($\delta^{18}\text{O}_{\text{calcite}}$ corrected for ice volume and global-mean SST
 318 changes; Methods) at the core sites with climatological meridional $\delta^{18}\text{O}$ gradient represented by
 319 background shading (Extended Data Fig. 1; darkest shade represents $0.25\text{‰}/^\circ\text{Lat}$, equivalent to ~ 1
 320 $^\circ\text{C}/^\circ\text{Lat}$). Modern position of maximum westerlies⁵¹ (solid red line) and the estimated LGM position of
 321 the westerlies based on a uniform shift (dashed red line). **(b)** LGM and Holocene $\delta^{18}\text{O}_{\text{ivc-gtc}}$ meridional
 322 profiles. The grey box shows latitudinal window in which $\Delta\text{Lat}_{\text{SST}}$ is calculated (Methods). Symbols on
 323 (a) and (b) distinguish foraminiferal species. **(c)** Relationship between positions of the wind latitude
 324 (latitude of maximum τ_u) and SST front latitude (latitude of maximum $\partial\text{SST}/\partial\text{Lat}$) within the
 325 PMIP3/CMIP5 and PMIP4/CMIP6 ensemble (Methods).



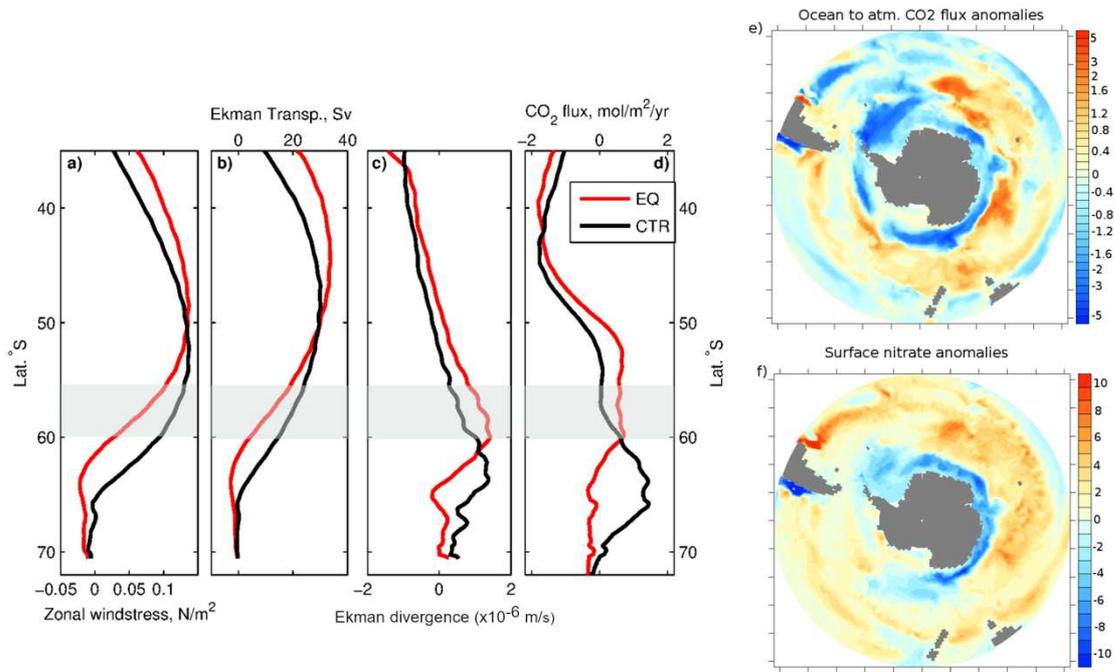
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Fig. 2: SST front and westerly wind changes based on regional subsets (a) Map showing regional subsets of data. Light grey dashed line corresponds to all core sites. Black includes all Indian-Pacific sites, blue has eastern Pacific sites removed, while pink has western Indian sites removed. Note that given the paucity of data from south of 65°S we include Antarctic marginal sites from all sectors in all regional subsets. (b) Relationship between wind latitude (latitude of maximum zonal-mean τ_u) and regional SST front latitude (latitude of maximum $\partial\text{SST}/\partial\text{Lat}$) within the model ensemble. (c) Reconstructed change in SST front latitude ($\Delta\text{Lat}_{\text{SST}}$) within the regional subsets. (d) Reconstructed zonal-mean wind latitude ($\Delta\text{Lat}_{\text{wind}}$) calculated from the regional $\Delta\text{Lat}_{\text{SST}}$ reconstruction (c) and the relationships between regional SST front and zonal-mean wind latitude given in (b).



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Fig. 3: Deglacial shifts in the westerlies and atmospheric CO₂. (a) Deglacial change in the position of the wind latitude ($\Delta\text{Lat}_{\text{wind}}$, lines show the 5th, 32nd, 50th, 68th, and 95th percentiles) and atmospheric CO₂ (ref²⁴) over time. HS1, ACR, and YD are Heinrich Stadial 1, Antarctic Cold Reversal, and Younger-Dryas, respectively. (b) Correlation between $\Delta\text{Lat}_{\text{wind}}$ and atmospheric CO₂ over deglaciation. (c) Lead-lag between changes in $\Delta\text{Lat}_{\text{wind}}$ and changes in atmospheric CO₂ and global temperature³¹ over deglaciation (Methods).



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Fig. 4: Modelled impact of shifted westerlies on Southern Ocean CO₂ outgassing. Zonally averaged (a) zonal wind stress, (b) northward Ekman transport, (c) Ekman divergence and, (d) ocean-atmosphere CO₂ flux (positive flux for ocean outgassing). Black curves correspond to the Control equilibrium state (CTR) and red curves to the average over years 116-126 of the Perturbed experiment (EQ). The grey box on (a-d) indicates the latitude of the Drake Passage (56-60°S). 1 Sv is 10⁶ m³ s⁻¹. Map of (e) ocean-atmosphere CO₂ flux (mol/m²/yr, positive flux for ocean outgassing) and (f) nitrate (mmol/m³, average over upper 149 m depth) anomalies, obtained as difference between Perturbed and Control simulations.

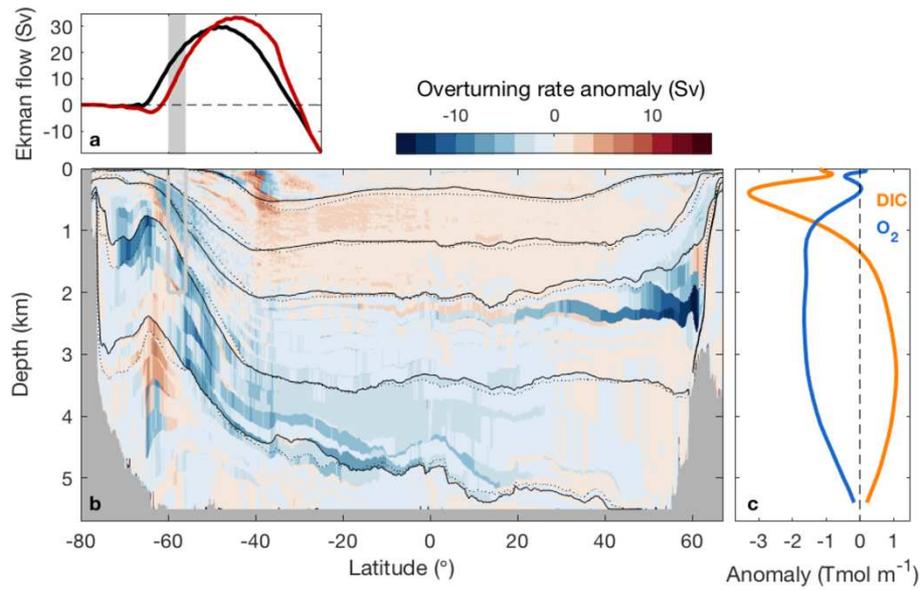
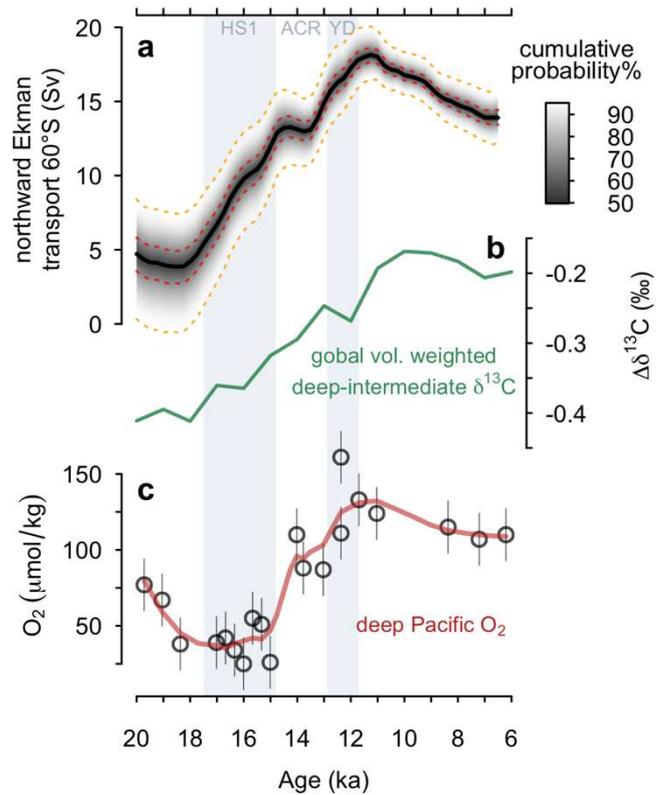


Fig. 5: Modelled impact of shifted westerlies on deep ocean circulation and carbon storage. (a) Northward Ekman transport in the Control (Black) and Perturbed (red) simulations. 1 Sv is $10^6 \text{ m}^3 \text{ s}^{-1}$. **(b)** Global MOC anomaly (Perturbed-Control) after 125 years, normalised for sign such that blue is a decrease in overturning rate and red is an increase. Contours show Control (solid) and Perturbed (dashed) isopycnals **(c)** Dissolved Inorganic Carbon (DIC) and Oxygen anomalies (Perturbed-Control) horizontally integrated globally. Zonally averaged concentration anomalies are shown in Extended Data Fig. 10). Grey box on (a) and (b) indicates the Drake Passage.

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Fig. 6: Deglacial changes in northward Ekman transport at 60°S and deep ocean carbon cycling. (a) Reconstructed change in northward Ekman transport at 60°S over deglaciation (lines show the 5th, 32nd, 50th, 68th, and 95th percentiles). (b) Global volume-weighted deep-intermediate $\delta^{13}\text{C}$ gradient⁴², broadly indicative of the vertical gradient in regenerated nutrients/carbon. (c) O_2 in the deep Pacific⁴¹ (fit with a LOESS smooth), indicative of regenerated carbon storage.

399 **Materials and methods**

400

401 *Planktic foraminiferal $\delta^{18}\text{O}$ records from the Kerguelen plateau and southeast Pacific*

402 We generated new planktic foraminiferal $\delta^{18}\text{O}$ data from sediment cores spanning the last
403 deglaciation located in the mid-latitudes of the Indian and Pacific sectors of the Southern
404 Ocean. We generated new records from two sediment cores retrieved from the Kerguelen
405 Plateau during cruise OSCAR INDIEN-SUD (MD12-3396CQ, -47.73 °N, 87.69 °E; MD12-
406 3401CQ, -44.68°S, 80.39°E). Furthermore, we extended/increased the resolution of two
407 previously published records from cores located on Kerguelen (MD02-2488, -51.07 °N, 67.73
408 °E) and in the southeast Pacific (MD07-3119, -46.08 °N, -76.1 °E). We analysed $\delta^{18}\text{O}$ on either
409 *G. bulloides* or *N. pachyderma* using a GV Isoprime 100 and an OPTIMA, and a Finnigan
410 MAT251 and a $\Delta+$ at CFR/LSCE laboratory. The measurements are reported versus Vienna
411 Pee Dee Belemnite standard (VPDB) defined with respect to the NBS19 standard. The mean
412 external reproducibility (1σ) of carbonate standards is $\pm 0.06\%$ for $\delta^{18}\text{O}$; the different mass
413 spectrometers are regularly inter-calibrated and the data are corrected, depending on the
414 devices, for nonlinearity and the common acid bath. Within this internal calibration, NBS18 is
415 $-23.2\pm 0.2\%$ VPDB for $\delta^{18}\text{O}$ and $-5.0\pm 0.1\%$ VPDB for $\delta^{13}\text{C}$. Age models for all the cores are
416 based on radiocarbon dating, and further details of the age models can be found in ref⁵² for
417 core MD07-3119 and ref⁵³ for core MD12-3396CQ. Reservoir age changes for the Kerguelen
418 area followed recent results by ref⁵³ to establish the age model of core MD12-3401CQ. The
419 new data are provided in Table S1 and are available on Pangaea (*DOI pending*).

420

421 *Southern Ocean planktic foraminiferal $\delta^{18}\text{O}$ compilation*

422 We compiled all available existing $\delta^{18}\text{O}$ records for near-surface dwelling planktic foraminifera
423 species (*G. ruber*, *G. bulloides*, *N. pachyderma*) spanning the last deglaciation (10-20 ka) from
424 across the Southern Ocean (refs⁵⁴⁻⁹⁷). All records are kept on the original age model of
425 publication. The compilation contains 64 deglacial records of planktic foraminiferal $\delta^{18}\text{O}$. All
426 $\delta^{18}\text{O}$ data are given in table Table S1 and are available on Pangaea (*DOI pending*).

427

428 *Using planktic foraminiferal $\delta^{18}\text{O}$ to track the latitude the SST front*

429 Although $\delta^{18}\text{O}_{\text{calcite}}$ is a function of both temperature and $\delta^{18}\text{O}_{\text{water}}$, at the basin scale the effect
430 of temperature dominates over $\delta^{18}\text{O}_{\text{water}}$ (Extended Data Fig. 1). Using the Southern Ocean
431 salinity- $\delta^{18}\text{O}_{\text{water}}$ relationship of ref⁹⁸ a meridional salinity difference of greater than 25 PSU
432 would be required to equal the meridional temperature changes across the basin. As no
433 physical mechanism exists to drive such changes, the meridional pattern of $\delta^{18}\text{O}_{\text{calcite}}$ will
434 always be dominated by temperature, enabling us to use meridional profiles of $\delta^{18}\text{O}_{\text{calcite}}$ to
435 identify the latitude of the SST front¹⁹.

436

437 We quantify changes in the position of the SST front through time ($\Delta\text{Lat}_{\text{SST}}$) from following the
438 method of ref¹⁹. Briefly, we first interpolate the $\delta^{18}\text{O}$ data to 250-year time steps from 20 ka to
439 10 ka using a Generalised Additive Model (GAM)⁹⁹, with the smoothing term determined by
440 restricted maximum likelihood (REML)¹⁰⁰. The reader is referred to ref¹⁰¹ for an overview of
441 GAMs. Only foraminiferal $\delta^{18}\text{O}$ records that span the entire time period of the reconstruction
442 are utilised such that our analysis is always comparing relative changes in the same cores
443 through time. The mean resolution of the individual records over deglaciation is about 1 point

444 per 250 yrs and we only include $\delta^{18}\text{O}_{\text{calcite}}$ records with a minimum of 1 point per 2 ka over the
445 deglaciation.

446

447 We model the $\delta^{18}\text{O}$ data at each time step (first correcting for whole ocean effects, see below)
448 as a function of latitude using a GAM⁹⁹, with the smoothing term determined by restricted
449 maximum likelihood (REML)¹⁰⁰ (Extended Data Figs. 2 and 3). We compute the shift in latitude
450 which minimises the Euclidean distance (L^2) between the GAM fit at each time step relative to
451 10 ka, within a 10° latitude band centred around the steepest part of the Holocene meridional
452 SST/ $\delta^{18}\text{O}_{\text{calcite}}$ profile (-50 to -40°N ; grey box in Fig. 1b and Extended Data Figs. 2 and 3). The
453 10 ka reference time is chosen to maximise the number of records spanning the deglaciation.
454 Our analysis thus tracks changes in the position of the steepest part of meridional SST profile
455 across a 10° latitudinal window, rather than the position of any individual front.

456

457 To minimise changes in the meridional $\delta^{18}\text{O}_{\text{calcite}}$ profile between different time steps that arise
458 from whole-ocean changes rather than local dynamics we correct the $\delta^{18}\text{O}_{\text{calcite}}$ data for the
459 whole ocean change in $\delta^{18}\text{O}_{\text{water}}$ (arising from ice sheet growth/retreat) and the global-mean
460 SST change ($\delta^{18}\text{O}_{\text{ivc-gtc}}$). For the whole-ocean change in $\delta^{18}\text{O}_{\text{water}}$ we scale the LGM-Holocene
461 change of $1 \pm 0.1 \text{‰}$ (2σ) (ref¹⁰²) to the sea level curve of ref¹⁰³. For the global-mean SST
462 change we scale the $-1.7 \pm 1.0 \text{ °C}$ (2σ) area-weighted global-mean LGM-preindustrial change
463 in SST from the PMIP3/4 ensemble (see below) to the global temperature record of ref³¹, using
464 the water-calcite temperature fractionation ($\delta^{18}\text{O}_{\text{calcite-water}}$) of ref¹⁰⁴, which agrees well with the
465 pooled-foraminiferal species sensitivity of ref¹⁰⁵. We propagate all of the uncertainty from these
466 whole-ocean corrections through to our final results (see below). We note these whole-ocean
467 corrections make the reconstructed changes in the position of the winds more conservative;
468 removing the global-mean SST change correction entirely results in an Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$
469 of $\sim 7^\circ$ between 10-20 ka (c.f. $\sim 5^\circ$ including the correction). Furthermore, our leave-one-out
470 analysis shows that our reconstruction is primarily driven by mid-latitude sites, indicating these
471 whole ocean corrections are unlikely to be biasing our results.

472

473 We derive uncertainties via bootstrapping¹⁰⁶ (10,000 iterations), accounting for the age and
474 analytical uncertainties on individual records as well as the uncertainties in the whole-ocean
475 change in $\delta^{18}\text{O}_{\text{water}}$ and the global-mean SST change with Monte-Carlo simulation. We ascribe
476 conservative age uncertainties of ± 1000 years (2σ), and analytical uncertainties of $\pm 0.08 \text{‰}$
477 (2σ) to all planktic foraminiferal $\delta^{18}\text{O}$ records. The R code and data used to perform the
478 analysis is provided on Github (<https://github.com/willyrgray/SOd18O>).

479

480 We repeat the analysis over a longer time period (22-6.5 ka) which necessitates using a
481 smaller subsection of cores and thus results in larger uncertainties (Extended Data Fig. 6).
482 Still, the results show excellent agreement with the complete set of cores (i.e. spanning 10-20
483 ka) (Extended Data Fig. 6), with a ratio of 0.95 during the overlapping interval. We apply this
484 correction to the longer reconstruction, though the correction makes a negligible difference
485 and does not impact our conclusions (Extended Data Fig. 6). Performing the analysis further
486 into the Holocene (22-2.5 ka) results in substantially higher uncertainties due to the lack of
487 cores spanning this interval, but the results suggest the westerlies are relatively stable through
488 the late Holocene (Extended Data Fig. 6), in agreement with qualitative indicators of the
489 winds^{23,107}.

490

491 *Leave-one-out analysis*

492 We perform a jackknife resampling of the dataset to determine the contribution of each planktic
493 foraminiferal $\delta^{18}\text{O}$ record to the Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$ reconstruction. We sequentially remove
494 each record from the dataset, recompute $\Delta\text{Lat}_{\text{SST}}$, and determine the contribution of that record
495 as the time-integrated absolute difference from $\Delta\text{Lat}_{\text{SST}}$ computed using the entire dataset
496 (expressed as a percentage of the absolute cumulative change in $\Delta\text{Lat}_{\text{SST}}$ over deglaciation;
497 Extended Data Fig. 4). This analysis shows that no single record is contributing more than 5%
498 of the total signal, and that the cores with the highest weighting are all located in the mid-
499 latitudes. Thus, we conclude that our reconstruction is primarily tracking a mid-latitude signal.

500

501 *Seasonality of planktic foraminifera*

502 Our approach assumes that any changes in the seasonal bias of foraminifera relating to their
503 habitat preference are small relative to the change in temperature due to the movement of the
504 SST front. The validity of this approach is supported by $\delta^{18}\text{O}$ records measured on species of
505 foraminifera with different temperature/seasonal habitats at the same (or nearby) mid-latitude
506 sites within the compilation. Foraminiferal species with different habitat temperature (and thus
507 seasonal) preferences (*G. bulloides* and *N. pachyderma*, ref ¹⁰⁸) show very similar Holocene-
508 LGM changes (compare circles and triangles on Fig. 1a). Furthermore, the leave-one-out
509 analysis (Extended Data Fig. 4) shows that records of *G. bulloides* and *N. pachyderma* $\delta^{18}\text{O}$
510 (which should have different seasonal biases) are both contributing highly to the $\Delta\text{Lat}_{\text{SST}}$
511 reconstruction. This suggests the impacts of seasonality on the reconstruction are likely to be
512 small. Crucially, the relatively warm temperature preference of *G. bulloides* (the dominant
513 species in the mid-latitudes) means that global SST cooling during the LGM would shift the
514 annual SST distribution further away from its preferred habitat temperature, shifting its
515 seasonal bias further towards the summer and minimising the degree of glacial cooling it
516 records. This would thus make the anomalous mid-latitude cooling we see in the LGM more
517 conservative relative to the annual mean cooling, thus making our reconstruction of changes
518 in the wind latitude more conservative.

519

520 *PMIP3/4 and CMIP5/6 ensemble*

521 We use an ensemble of models from the Paleoclimate Modelling Intercomparison Project
522 (PMIP3¹⁰⁹ and PMIP4^{20,110}) and Coupled Model Intercomparison Project (CMIP5¹¹¹ and
523 CMIP6¹¹²); data available at <https://esgf-node.llnl.gov/projects/esgf-llnl/>. We use all
524 CMIP5/PMIP3 and CMIP6/PMIP4 models for which both SST and zonal surface wind fields
525 are available for the LGM and preindustrial simulations, and also include the 4xCO₂
526 simulations from these models where available. Annual-mean climatologies are calculated
527 from the final 100 years of each simulation and interpolated to a common 2-degree analysis
528 grid.

529

530 To convert the reconstructed changes in the SST front latitude ($\Delta\text{Lat}_{\text{SST}}$) to changes in the
531 latitude of the westerly winds we use the relationship between the SST front latitude and the
532 wind latitude within the ensemble. We calculate the SST front latitude as the latitude of
533 maximum meridional SST gradient ($\partial\text{SST}/\partial\text{Lat}$) in each simulation within a 10° latitudinal
534 averaging window (to emulate the 10° latitudinal window used to calculate $\Delta\text{Lat}_{\text{SST}}$ from the
535 $\delta^{18}\text{O}_{\text{ivc-gtc}}$ data downcore. We do this using zonal-mean SST across the Southern Ocean (Fig.
536 1c) and across regional subsets (Fig. 2; Extended Data Fig. 5). We calculate the wind latitude
537 as the latitude of maximum zonal-mean zonal wind stress (τ_u). We regress the SST front

538 latitude against wind latitude (Fig. 2; Extended Data Fig. 5) and then apply this relationship to
539 our $\Delta\text{Lat}_{\text{SST}}$ reconstruction in order to determine changes in the position of the wind latitude
540 ($\Delta\text{Lat}_{\text{wind}}$), propagating the uncertainty in the relationship through to our final estimates of
541 $\Delta\text{Lat}_{\text{wind}}$ using Monte-Carlo simulation. We exclude the MPI model from the regressions for the
542 Indian-Pacific sector, as this model sits as an outlier from the remainder of the ensemble
543 (however we note the slope between wind latitude and SST front latitude within the MPI model
544 is consistent with the rest of the ensemble). The peculiarity of the MPI model is possibly due
545 to SST biases relating to meridional heat transport in the Indian sector within the model¹¹³,
546 where we find the largest difference relative to the other models. Including the MPI model in
547 the Indian-Pacific sector regression has a negligible effect on our results, slightly increasing
548 the reconstructed change in the wind latitude ($\Delta\text{Lat}_{\text{wind}}$) between 10-20 ka from 6.2° to 6.7°
549 and increasing the uncertainty by 0.5° at the 95% CI. The $\Delta\text{Lat}_{\text{wind}}$ reconstruction is provided
550 in Table S2.

551

552 *Regional subset test*

553 To ascertain that our method is able to track zonal-mean shifts in the wind latitude from
554 changes in the SST front latitude (which is also affected by bathymetry and ocean
555 eddies^{25,28,114}), we perform a regional subset test. We sequentially remove regional subsets of
556 cores from the compilation, re-compute $\Delta\text{Lat}_{\text{SST}}$, and recalculate the relationship between the
557 zonal-mean wind latitude and the regional SST front latitude (Fig. 2). The results demonstrate
558 that the difference in zonal-mean $\Delta\text{Lat}_{\text{wind}}$ reconstructed from the regional subsets is markedly
559 smaller than the difference in $\Delta\text{Lat}_{\text{SST}}$ between the regional subsets. This indicates that (i) the
560 model ensemble and (ii) our method to track the SST front downcore, capture the regional
561 SST front response to zonal-mean shifts in the wind latitude. We can thus confidently apply
562 the relationship observed in the model ensemble to estimate shifts in the zonal-mean latitude
563 of the westerlies using the Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$ reconstruction over deglaciation.

564

565 *Reconstructing peak wind stress*

566 Using our $\Delta\text{Lat}_{\text{wind}}$ reconstruction and the relationship between wind latitude and the
567 magnitude of peak wind stress in the model ensemble (*wind strength*, Extended Data Fig. 5),
568 we estimate changes in the magnitude of peak wind stress over deglaciation (Extended Data
569 Fig. 8). The tendency for the magnitude of peak wind stress to decrease as the winds move
570 equatorward (and vice-versa) has been previously noted^{115,116}. Our reconstructed equatorial
571 shift in the wind latitude implies a weakening of the peak westerlies by 0.034 N m⁻² (about
572 25%) during the LGM relative to the mid Holocene, resulting in a LGM wind strength of 0.106
573 (0.085-0.12, 95% CI) N m⁻², assuming mid-Holocene wind stress is equal to the modern
574 climatology (0.14 N m⁻²; Fig. 4a). This assumption is supported by qualitative tracers of the
575 westerlies^{23,107} which indicate little change between ~6.5 ka and the present day.
576 Furthermore, running our analysis further into the Holocene suggests little change in the
577 position of the winds (Extended Data Fig. 6), although uncertainties are very large given the
578 few core sites that span this interval. Although the shape of the zonal-mean westerly wind
579 profile may have changed together with the latitude and magnitude of its peak, the model
580 ensemble suggests that the meridional wind profile changes little between PI and LGM
581 states; there is a -0.25±7% and 0.5±3.5% ensemble mean change in peak width at 50% and
582 15% peak height, respectively, between LGM and preindustrial. Furthermore, we observe no
583 significant relationship between the wind latitude and the peak width (at either 50% or 15%
584 peak height) within the ensemble, such that we do not expect substantial changes in the

585 shape of the wind profile as the winds shift. The wind strength (max τ_u) reconstruction is
586 provided in Table S2.

587

588 *Reconstructing northward Ekman transport at 60°S*

589 To calculate changes in zonal wind stress at 60°S (60S τ_u) we use the relationship between
590 the wind latitude and the zonal-mean zonal wind stress at 60°S in the model ensemble
591 (Extended Data Fig. 5d), and apply this relationship to our reconstruction of $\Delta\text{Lat}_{\text{wind}}$,
592 propagating through the uncertainty in the relationship (Extended Data Fig. 8). We assume
593 mid-Holocene wind stress equal to the modern climatology (0.09 N m⁻²; Fig. 4a). We calculate
594 northward Ekman transport (Fig. 6a) as the zonal integral of $\tau_u/(\rho_0 * f)$, where ρ_0 is the density
595 of seawater (1027 kg/m³) and f is the Coriolis parameter. The reconstruction of 60S τ_u and
596 northward Ekman transport at 60°S is provided in Table S2. The ensemble shows that the
597 latitude of the peak in zonal wind stress is a better predictor of wind stress at 60°S ($R^2= 0.9$;
598 Extended Data Fig. 5d) than the magnitude of the peak in wind stress ($R^2= 0.7$).

599

600 *Lead-lag analysis*

601 We calculate the lead-lag between the Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$ reconstruction and the change
602 in atmospheric CO₂ (or in global temperature) over deglaciation as the time offset that
603 maximises the correlation between the two time series, broadly following the approach of ref³¹.
604 We account for age uncertainties in the CO₂ record using the typical gas age uncertainty in
605 the WAIS divide ice core over deglaciation¹¹⁷ (± 75 yrs, 1σ). For the age uncertainty in the
606 global mean temperature stack we take the uncertainty in the lag of global temperature over
607 CO₂ (± 340 yrs, 1σ) in ref³¹. To account for age uncertainties in the Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$
608 reconstruction we repeat the lead-lag analysis using each boot strap/Monte-Carlo iteration of
609 the Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$ reconstruction. This approach assumes age uncertainties within the
610 $\delta^{18}\text{O}$ compilation are uncorrelated, which is unlikely to strictly hold given e.g. reservoir age
611 changes (although methodological differences between studies add a source of random
612 'human behavioural' error), but provides a first-order assessment of leads and lags between
613 the different time series. As a sensitivity test, we repeat the lead-lag analysis with CO₂,
614 including varying degrees of 'structural' uncertainty in the Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$
615 reconstruction. This suggests that the lead in the change in the winds over CO₂ is significant
616 at the 95% level until more than ~30% of the age uncertainty is correlated across the
617 compilation. Assuming 100% of the age uncertainty is correlated (i.e. perfect covariance)
618 results in uncertainties of ± 860 yrs (95% CI). To test whether the lead of $\Delta\text{Lat}_{\text{SST}}$ relative to
619 CO₂ holds in the early deglaciation, we repeat this analysis for 20-14 ka (cf. 20-10 ka) and find
620 a lead of 160 yrs (-10 to 330 yrs 95% CI), cf. 330 yrs (100 to 560 yrs 95% CI).

621

622 *Experiments with a 0.25° ocean-sea-ice-carbon model*

623 We use the ocean-sea-ice-carbon model MOM5-SIS-Wombat with a Mercator horizontal
624 resolution of 0.25° (~11 km grid spacing at 65°S), and 50 vertical levels^{33,34}. The model is
625 initialised with modern-day temperature and salinity distributions, and biophysical fields
626 derived from an observation-based climatology (GLODAP v2, 2016)¹¹⁸. The model is then
627 spun-up for 700 years with version 2 of the Coordinated Ocean-ice Reference Experiments
628 (CORE) Normal Year Forcing (NYF) reanalysis data¹¹⁹, representative of a 'normal year'
629 during the recent instrumental period. To study the impact of equatorward shifted southern
630 hemispheric westerlies, a 4° equatorward shift (with no change in magnitude) is applied to the
631 near surface wind speeds between 25°S and 70°S. The perturbation simulation is run for 125

632 years. Given the carbon and nutrient cycles have around an order of magnitude longer time
633 scales in the deep Pacific¹⁷, the perturbation simulation is far from equilibrium, but it does
634 provide a strong indication of the impact on circulation and the carbon cycle. Anomalies are
635 calculated as the difference, averaged over the last 10 years, between the Perturbed
636 experiment and the concomitantly extended Control experiment to remove the influence of
637 linear model drift.

638

639 The model includes a parameterization for the effects of mesoscale eddies, with isopycnal
640 tracer¹²⁰ and thickness¹²¹ diffusivities set to $600 \text{ m}^2 \text{ s}^{-1}$. The meridional overturning circulation
641 (Fig. 5b and Extended Data Fig. 9) includes both resolved and parameterized advection. It is
642 calculated in neutral density¹²² coordinate and reprojected onto the depth coordinate¹²³ in
643 order to eliminate adiabatic recirculations and avoid spurious effects due to vertical inversions
644 in potential density fields.

645

646 As a result of the equatorward shifted winds, the Ekman pumping is suppressed south of 60°S ,
647 and the ACC weakens by 6% (122 Sv instead of 130 Sv). South of 60°S , the surface DIC
648 concentration decreases by 13 mmol/m^3 (Extended Data Fig. 10), thus leading to a surface
649 $\text{pCO}_{2\text{DIC}}$ decrease of 25 ppm, which is partly compensated by a decrease of surface alkalinity
650 of 8.6 mmol/m^3 ($\Delta \text{pCO}_{2\text{alk}} = +14 \text{ ppm}$). A small decrease in surface salinity is
651 compensated by a small increase in SST, so that the solubility contribution to $\text{pCO}_{2\text{sol}}$ is
652 negligible south of 60°S . As a result, the CO_2 outgassing over the polar Southern Ocean (south
653 of 60°S) is completely suppressed (Fig. 4d). On the other hand, the equatorward shift in the
654 westerlies and associated increased Ekman pumping north of 60°S leads to a greater CO_2
655 outgassing in that region. Nevertheless, if integrated over the Southern Ocean (south of 35°S),
656 there is an anomalous uptake of 27 GtC by the Southern Ocean over the course of the
657 Perturbed experiment, equivalent to a CO_2 decrease of 13 ppm. While the model also displays
658 an increase in Southern Ocean sea ice extent in the Perturbed experiment (not shown), likely
659 an impact of the reduction in upwelling of relatively warm deepwaters, the decrease in CO_2
660 flux out of the polar ocean is associated with decreased surface ocean pCO_2 rather than
661 increased air-sea disequilibria. Hence, changes in wind-driven carbon supply, rather than sea
662 ice driven disequilibria, cause the reduction in CO_2 outgassing from the polar Southern Ocean.
663 Furthermore, the CO_2 flux anomalies are largely decoupled from the sea ice anomalies around
664 the basin. Both pCO_2 and CO_2 flux anomalies are, however, clearly linked to changes in
665 Ekman divergence.

666

667 As a result of shifted winds, the strength of the lower overturning cell (maximum stream flow
668 below 2500 m within $20\text{-}50^\circ\text{S}$) weakens by 3 Sv, from 16 to 13 Sv and the mixed layer shoals
669 in the polar Southern Ocean (Fig. 5b; Extended Data Fig. 9). The DIC concentration increases
670 in the Southern Ocean below the sub-surface south of 60°S by about 10 mmol/m^3 , and the
671 slowdown of the lower cell causes DIC to increase throughout the deep ocean below 1.5km
672 (Fig. 5c; Extended Data Fig. 10), even if the magnitude of the increase is small due to the
673 short duration of the experiment. The increase in upwelling between 60°S and 50°S leads to
674 a DIC increase in the upper 2000m depth in that region, but causes the overturning of the
675 upper cell to increase by 6.4 SV (maximum overturning between 500-1000m and $20^\circ\text{S}\text{-}40^\circ\text{S}$;
676 Fig. 5b; Extended Data Fig. 9) which results in a DIC decrease in the intermediate depths
677 throughout the ocean north of 35°S (Fig. 5c; Extended Data Fig. 10). These DIC changes are
678 accompanied by similar changes in remineralised nitrogen, and inverse changes in dissolved
679 O_2 , highlighting the role of changes in oceanic circulation.

680

681 The reduction in upwelling within the polar Southern Ocean causes the preformed nitrate
682 concentration of Antarctic Bottom Water to decrease. This may be enhanced by a shoaling of
683 the polar Southern Ocean mixed layer depth within the simulation (Extended Data Fig. 9),
684 which would reduce light limitation, providing a potential mechanism to further increase the
685 utilisation of the upwelled nutrients¹³. Driven by a reduction in water column mixing due to a
686 shoaling of the mixed layer in deepwater formation regions of the North Atlantic (not shown),
687 the preformed nitrate concentration of the northern end member also decreases. As such, the
688 preformed nitrate concentration begins to decrease throughout the deep ocean, with a 1.3%
689 increase in global mean N^* (N^* = regenerated NO_3 /total NO_3) after 125 years (Extended Data
690 Fig. 10). The short duration of the Perturbed experiment inhibits a full quantification of the CO_2
691 response. However, by extrapolating the initial changes in endmember preformed NO_3 (N_{pre} ,
692 given in mmol/m^3) based on the relative volume of the ocean they represent (V) we can broadly
693 estimate the magnitude of CO_2 change implicated by the initial changes in endmember
694 preformed nitrate.

695

696 We take the Southern Ocean endmember as an average through the water column between
697 $60\text{-}80^\circ\text{S}$, and the North Atlantic endmember as an average through the water column between
698 $60\text{-}70^\circ\text{N}$ in the North Atlantic. In the control run $N_{\text{pre_SO_ctr}} = 22.12$ and $N_{\text{pre_NA_ctr}} = 8.5$.
699 Global mean N_{pre} in the control run ($N_{\text{pre_ctr}}$) is 15.45. Using the global mean and endmember
700 values we calculate the volumetric contribution of the Southern Ocean endmember (V_{SO}) as
701 0.51 and the North Atlantic endmember (V_{NA}) as 0.49. Total nitrate (N_{tot}) is 33.84 mmol/m^3
702 such that globally averaged N^* in the control run is 54%.

703 After 125 years of the Perturbed experiment N_{pre} in both the endmembers decreases:
704 $N_{\text{pre_SO_125}} = 20.31$ and $N_{\text{pre_NA_125}} = 7.3$. Assuming the same volumetric contributions
705 as the control experiment, we calculate the expected change in global mean N_{pre} in the
706 Perturbed run ($N_{\text{pre_EQSH}}$) as,
707 $N_{\text{pre_EQSH}} = V_{\text{SO}} * N_{\text{pre_SO_125}} + V_{\text{NA}} * N_{\text{pre_NA_125}} = 13.9$, equivalent to a globally averaged
708 N^* value of 59%.

709

710 Based on the initial changes in N_{pre} within the endmember regions we would thus expect a
711 global mean N^* increase of $\sim 5\%$ in the Perturbed experiment relative to the Control, once
712 these anomalies had propagated through the deep ocean. Applying the sensitivity of
713 atmospheric CO_2 to global preformed nutrients of ref¹⁵, this increase in N^* within the Perturbed
714 experiment equates to an atmospheric CO_2 decrease of ~ 15 ppm. However, timeseries of the
715 endmember N_{pre} values indicate they are not yet equilibrated and are still decreasing after 125
716 years such that this likely represents a conservative estimate of the increase N^* and
717 associated lowering of CO_2 we would expect if the Perturbed experiment was run to
718 equilibrium.

719

720 Further to this effect, the model indicates a redistribution of the regenerated nutrient and
721 carbon pools from the intermediate depths toward the abyss. The deepening of the
722 regenerated nutrient and carbon pools would drive a further CO_2 decrease via carbonate
723 compensation^{16,37}. The higher DIC content at depth would lower the carbonate ion
724 concentration, increasing CaCO_3 dissolution within the ocean. This in turn would result in a
725 transient increase in alkalinity, lowering atmospheric CO_2 . While the scaling between
726 preformed nutrients and atmospheric CO_2 used above (ref^{37,124}) accounts for a linear
727 approximation of CaCO_3 dissolution following the total increase in regenerated carbon within

728 the ocean, the effect of nutrient deepening is not accounted for by this scaling. Based on the
729 initial changes we see in deep ocean DIC in the model (Extended Data Fig. 10), and the
730 scaling between intermediate-deep DIC and atmospheric CO₂ given in given refs^{37,124} we
731 would thus expect a further substantial decrease in CO₂.

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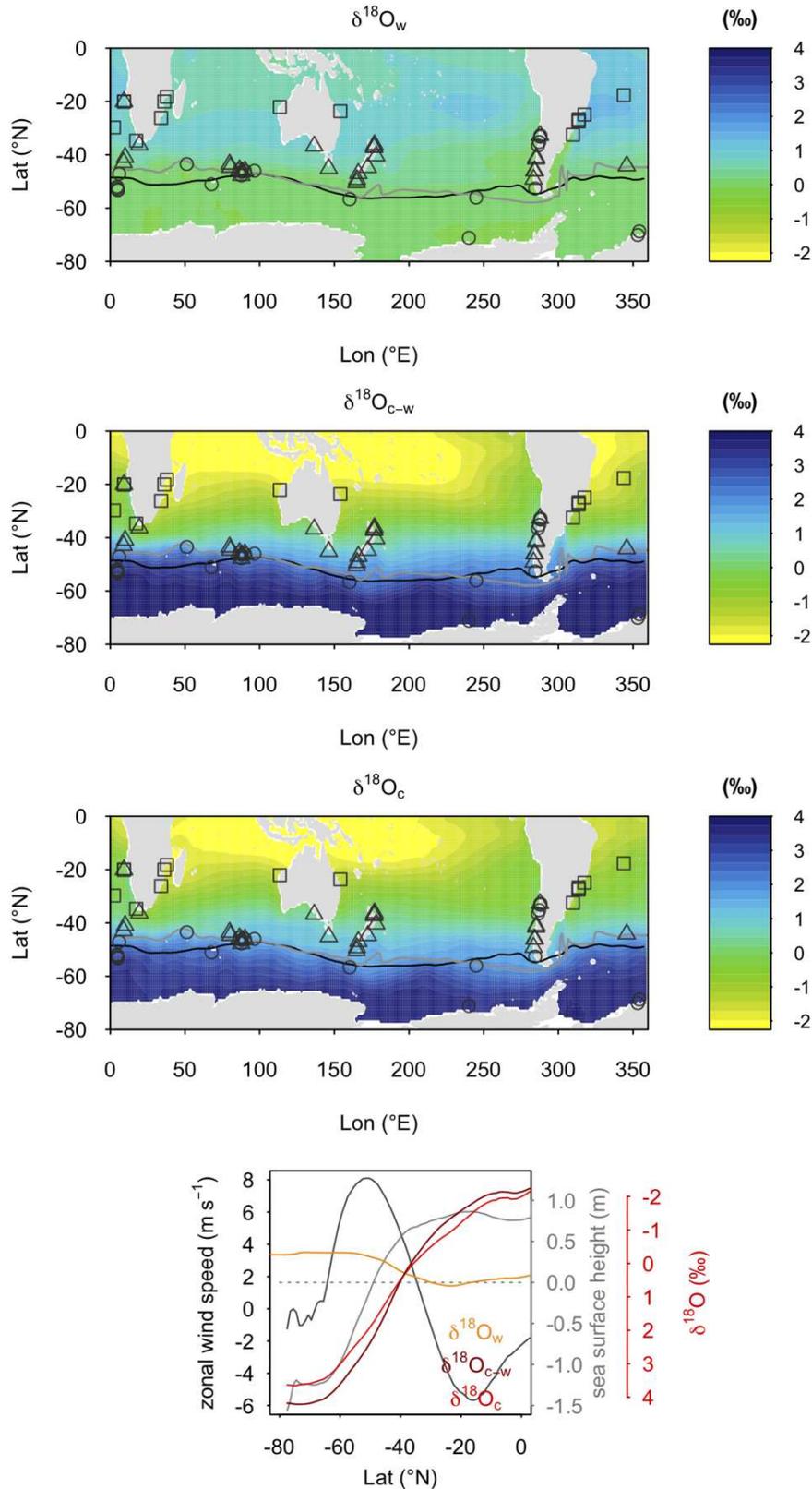
733 **Data availability**

734 The new and compiled $\delta^{18}\text{O}$ data are given in table Table S1 and are available on Pangaea
735 (*DOI pending*). The westerly wind reconstructions generated in this study are given in table
736 Table S2. The PMIP and CMIP data are available from <https://esgf-node.llnl.gov/projects/esgf-llnl/>.

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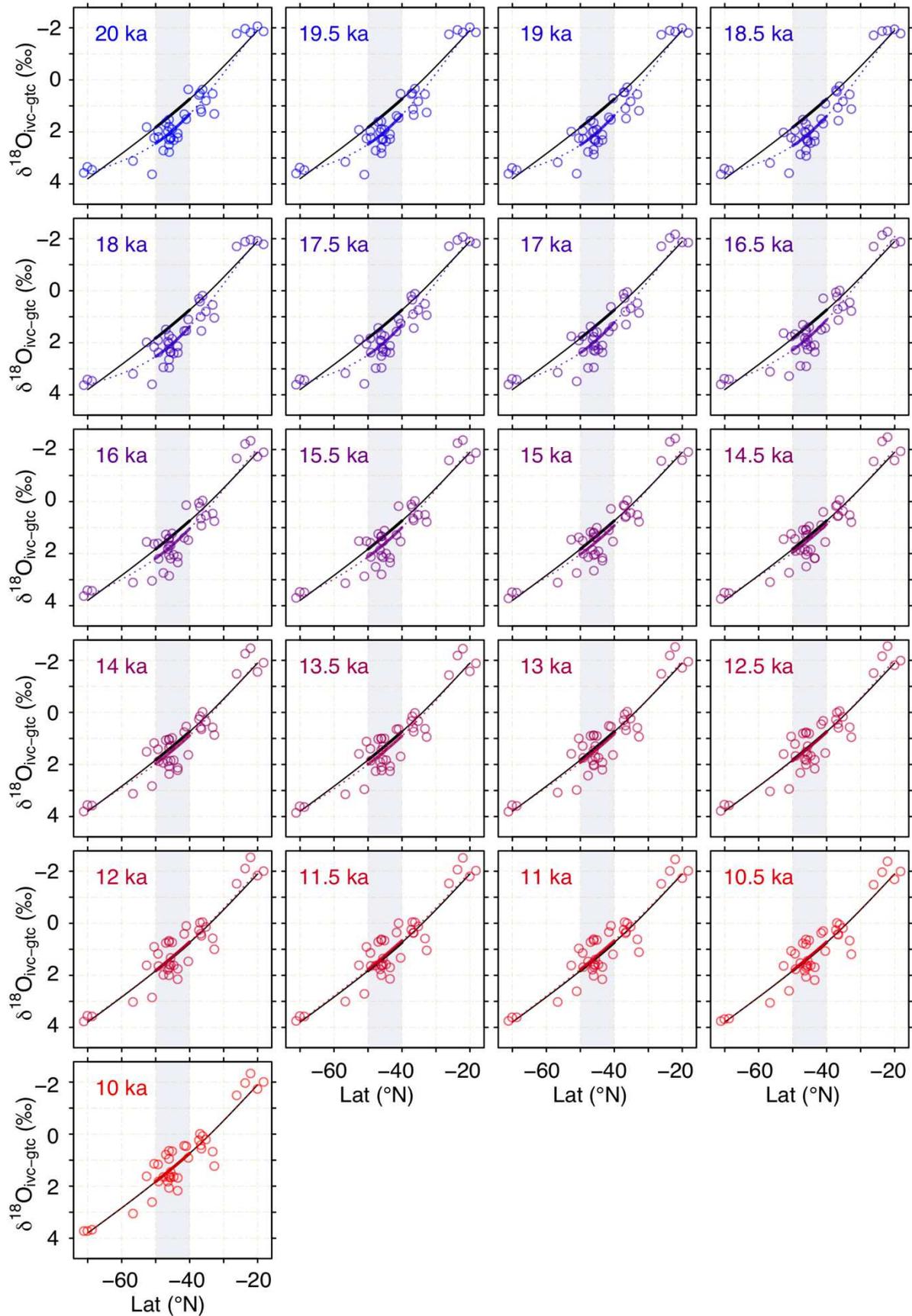
739 **Code availability**

740 The R code and data used to perform the $\Delta\text{Lat}_{\text{SST}}$ analysis is provided on Github
741 (<https://github.com/willyrgray/SOd18O>).



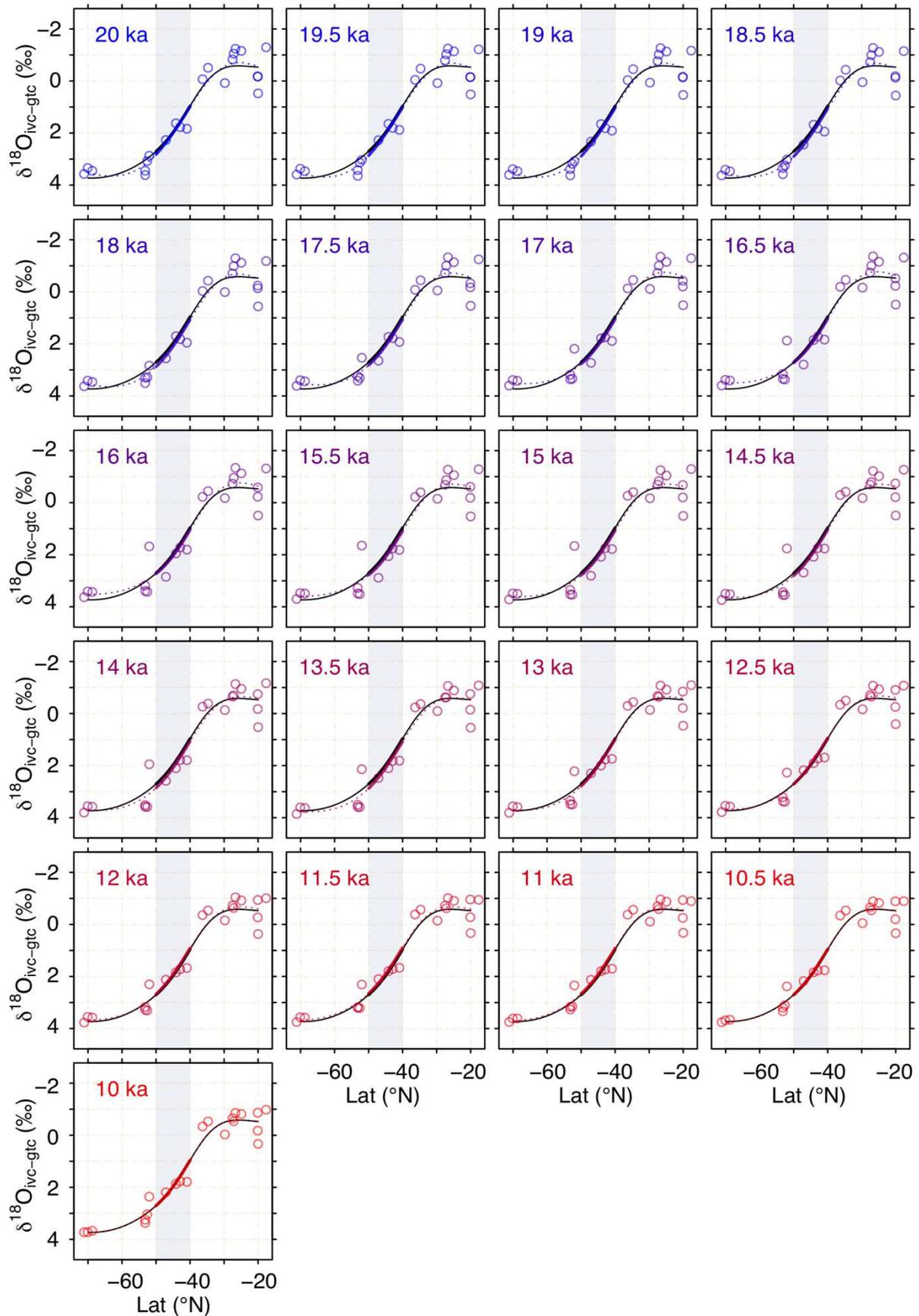
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743 **Extended Data 1. Climatological $\delta^{18}\text{O}$.** Climatological $\delta^{18}\text{O}_{\text{water}}$ (ref⁹⁸), $\delta^{18}\text{O}_{\text{calcite-water}}$ (calculated using
 744 refs^{104,125}), and $\delta^{18}\text{O}_{\text{calcite}}$ (note, colour scale is the same for panels). Symbols show location of core
 745 sites and species of planktic foraminifera (circles = *N. pachyderma*, triangles = *G. bulloides*, squares =
 746 *G. ruber*). Black line shows the position of westerlies as determined by maximum zonal wind speed
 747 (ref⁵¹) and grey line shows zero sea surface height anomaly ref¹²⁶). Zonal-mean climatological
 748 $\delta^{18}\text{O}_{\text{water}}$, $\delta^{18}\text{O}_{\text{calcite-water}}$, and $\delta^{18}\text{O}_{\text{calcite}}$ (as shown on Fig. 1), zonal wind speed, and sea surface height.



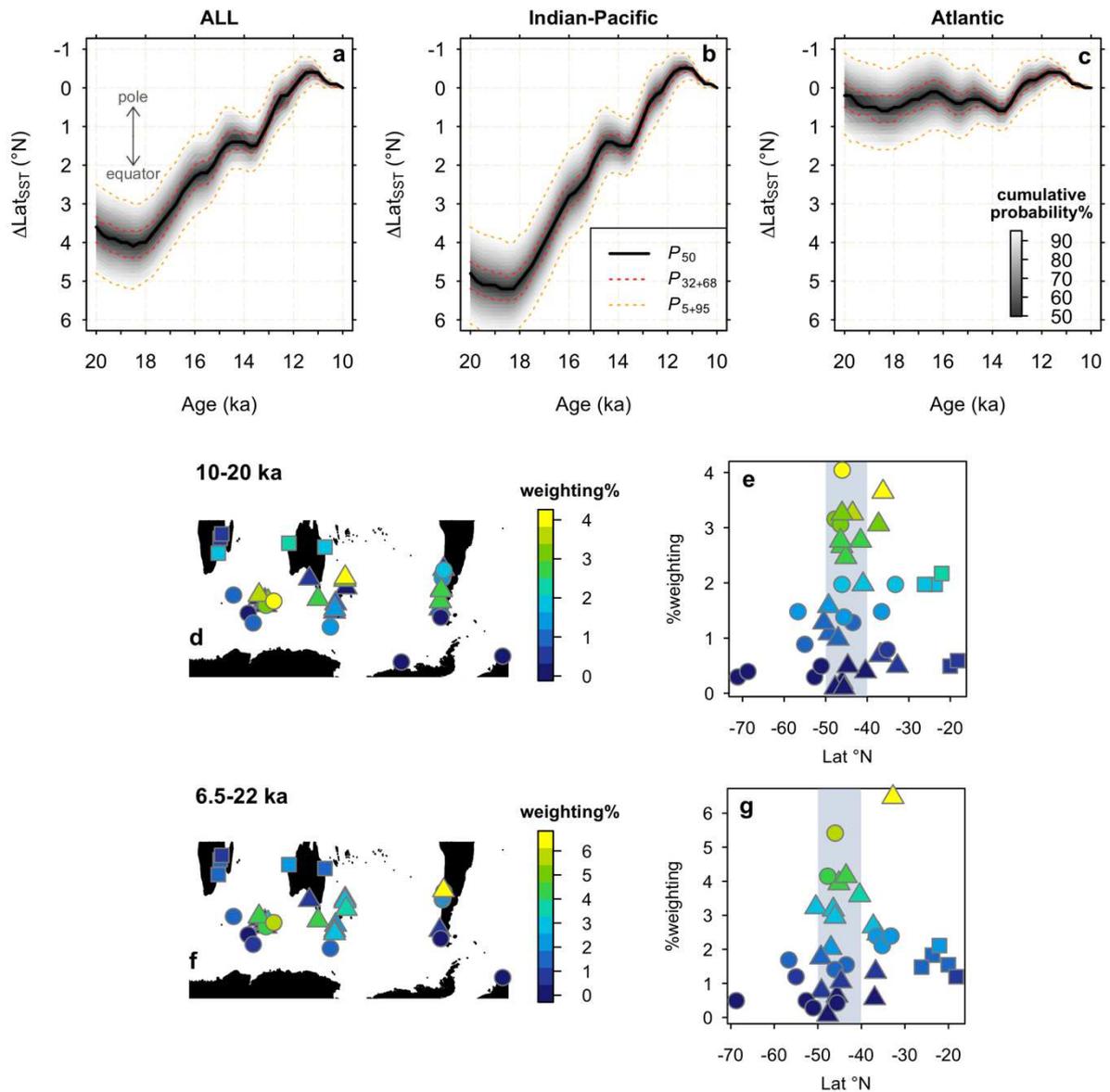
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Extended Data 2. Indian-Pacific meridional $\delta^{18}\text{O}$ profiles. Indian-Pacific meridional $\delta^{18}\text{O}_{\text{IVC-gtc}}$ data with GAM fits at 500-year time steps. The GAM fit at 10 ka is shown in black. The grey box is the window in which $\Delta\text{Lat}_{\text{SST}}$ is calculated and the thick lines show the portion of the curves falling within this window.

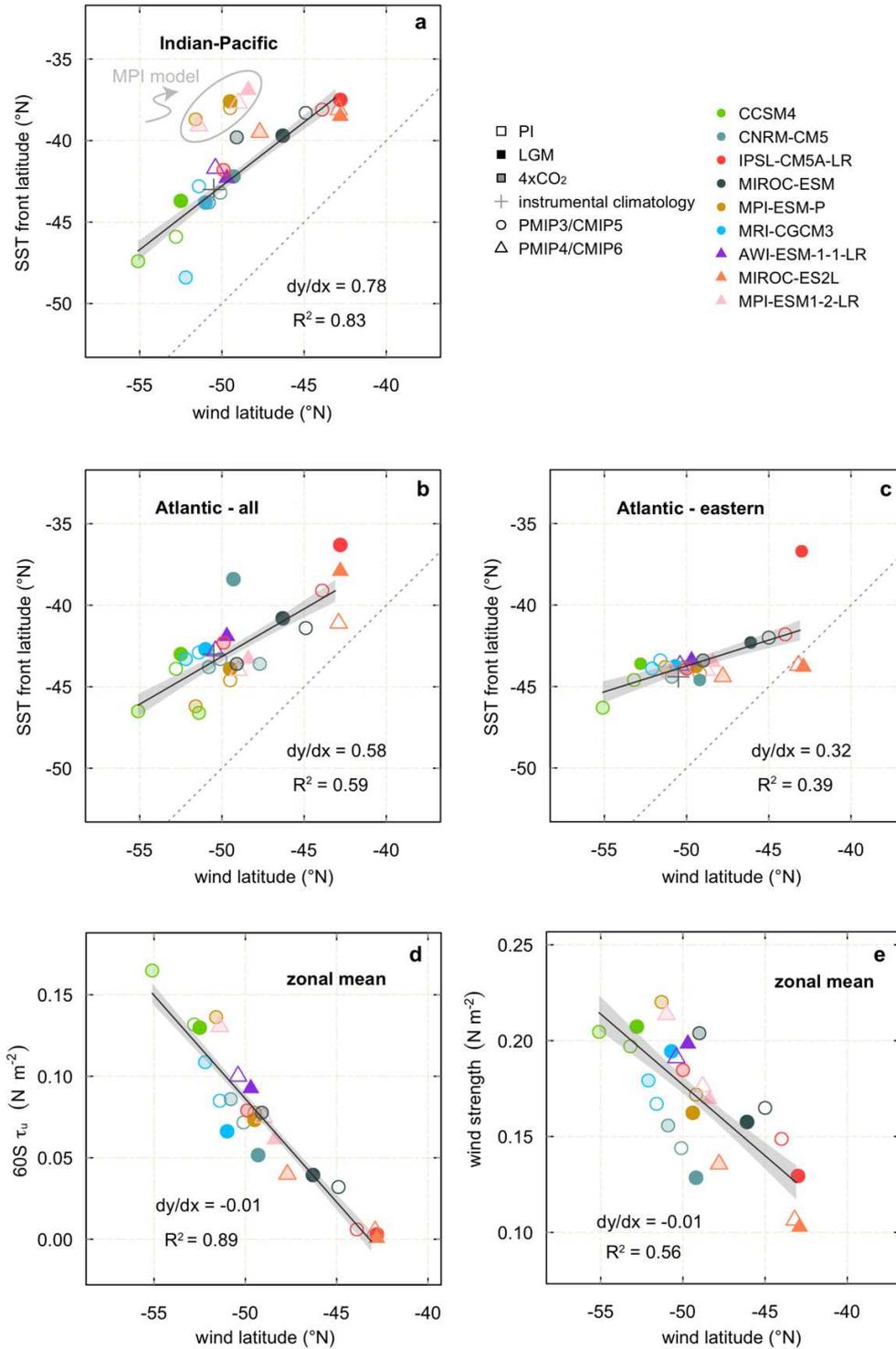


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Extended Data 3. Atlantic meridional $\delta^{18}\text{O}$ profiles. As above, but for the Atlantic.

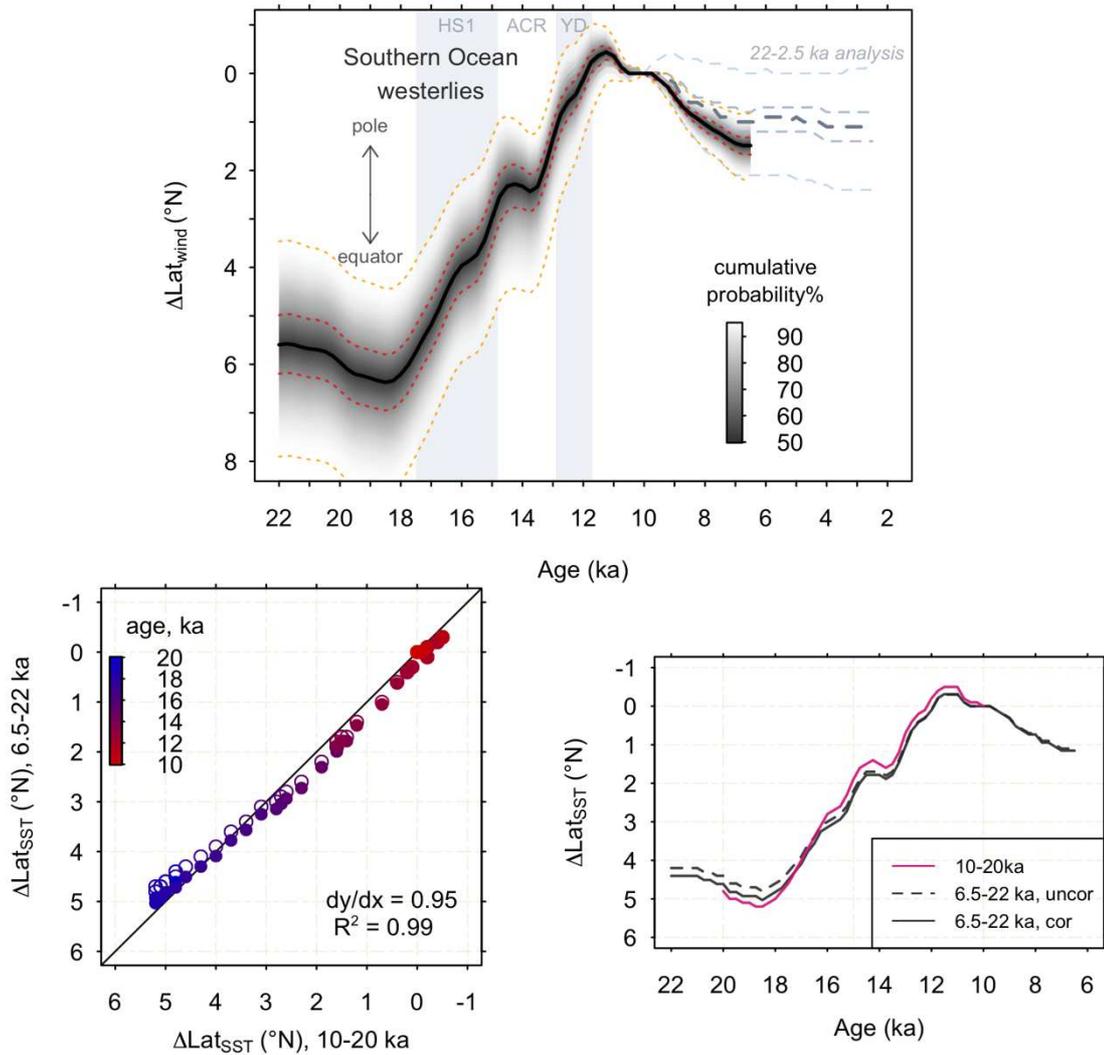


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 758 **Extended Data 4. $\Delta\text{Lat}_{\text{SST}}$ within different sectors and core weightings in the Indian-Pacific**
 759 **sectors.** Change in the SST front latitude ($\Delta\text{Lat}_{\text{SST}}$) from 20-10 ka using (a) all data from across the
 760 Southern Ocean, and in the (b) Indian-Pacific and (c) Atlantic sectors separately. The 5th, 32nd, 50th,
 761 68th, and 95th percentiles are indicated. Contribution of each record to the Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$
 762 reconstruction based on leave-one-out analysis (Methods). (d-e) 10-20 ka reconstruction (f-g) 6.5-22
 763 ka reconstruction. Note Antarctic marginal sites from the Atlantic sector are also included given the
 764 paucity of data from south of 65°S. Symbols distinguish species of planktic foraminifera (circles = *N.*
 765 *pachyderma*, triangles = *G. bulloides*, squares = *G. ruber*).
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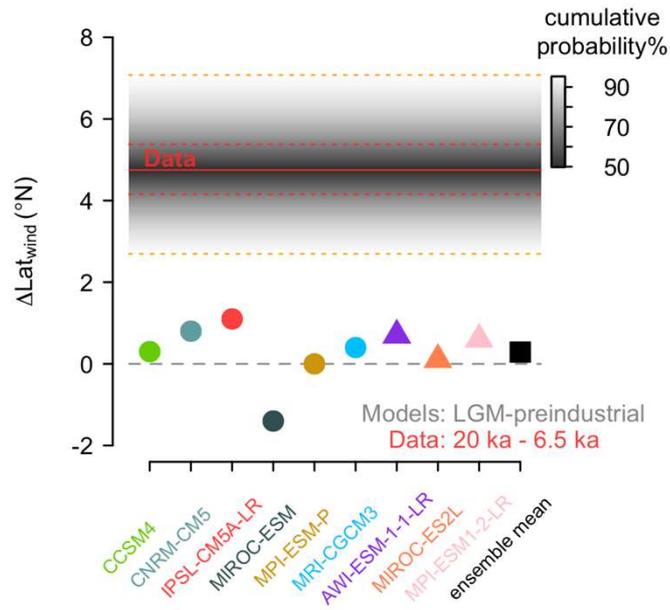
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Extended Data 5. PMIP3/4 and CMIP5/6 ensemble. (a) Relationship between the wind latitude (latitude of maximum zonal-mean τ_u) and SST front latitude (latitude of maximum $\partial\text{SST}/\partial\text{Lat}$, averaged over a 10° latitudinal window) in the model ensemble across the Indian and Pacific sectors. The MPI model sits as an outlier from this the rest of the ensemble, possibly due to known SST temperature biases in the Indian Ocean¹¹³, and is excluded from the regression. Including the MPI model has a negligible impact on our results (Methods). (b) As (a) but for the Atlantic sector. (c) As (a) but for the eastern Atlantic sector, where the vast majority of the mid-latitude sites in the Atlantic are located. (d) Relationship between the wind latitude and zonal-mean wind stress at 60°S ($60\text{S } \tau_u$) in the model ensemble (e) Relationship between the wind latitude and the wind strength (maximum zonal-mean τ_u) in the model ensemble.



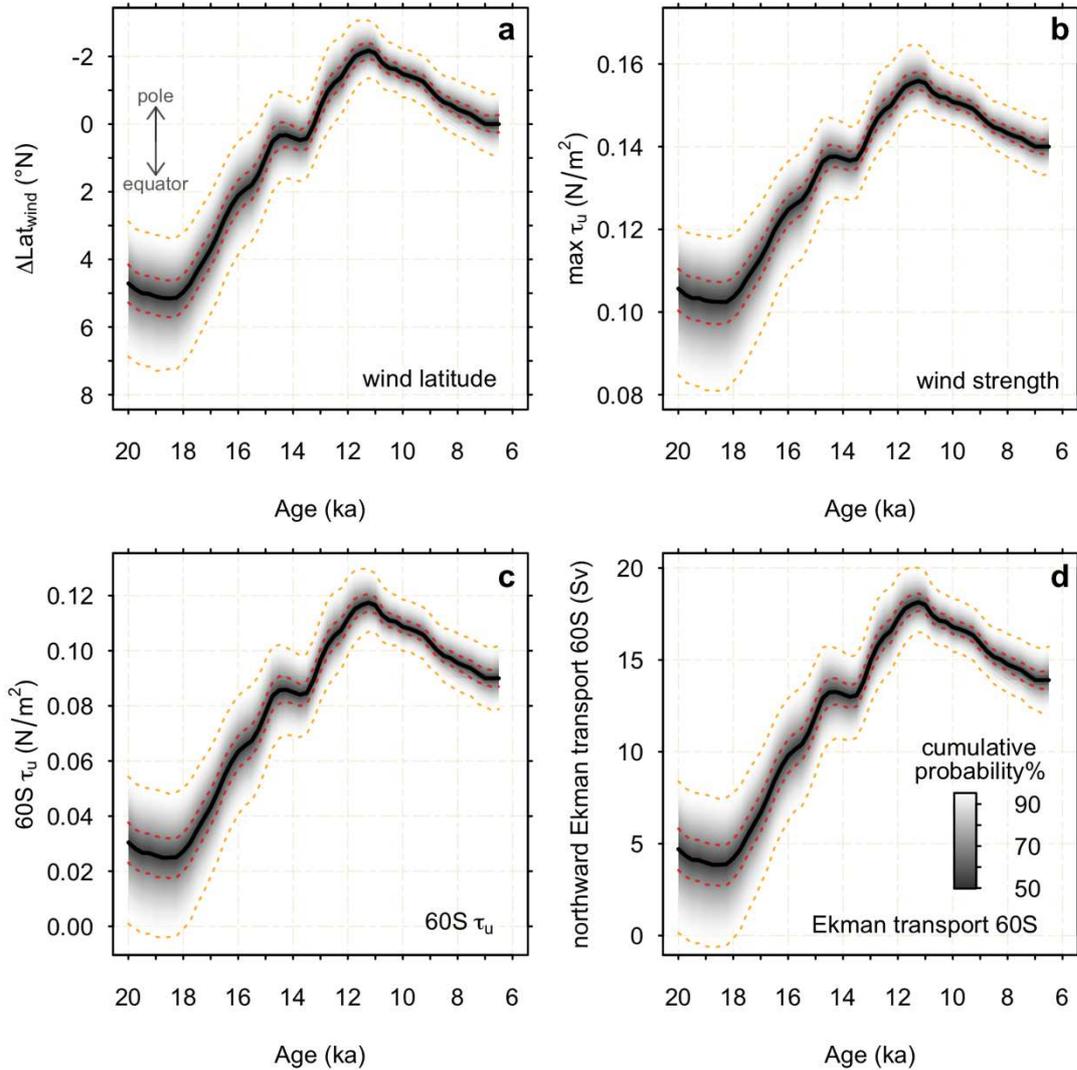
789 **Extended Data 6. 22-6.5 ka analysis. (top)** Changes in the wind latitude ($\Delta\text{Lat}_{\text{wind}}$) from 22-6.5 ka. The
 790 higher uncertainties compared to the 20-10 ka reconstruction is due to the lower number of sites than
 791 span this interval. The 5th, 32nd, 50th, 68th, and 95th percentiles are indicated. The grey dashed line
 792 shows the same analysis extended to 2.5 ka; while the uncertainties are very large due to the limited
 793 number of cores than span this interval, the results indicate little change in the position of the wind
 794 latitude during the Holocene **(bottom)** Comparison of reconstructed Indian-Pacific $\Delta\text{Lat}_{\text{SST}}$ using the
 795 10-20 ka subset and 6.5-22 ka subset of cores. Open circles and the dashed grey curve correspond to
 796 the the 6.5-22 ka reconstruction uncorrected; filled circles and solid grey line correspond to the 6.5-22
 797 ka reconstruction with a 1/0.95 correction applied (see Methods). The pink curve shows the 10-20 ka
 798 reconstruction.
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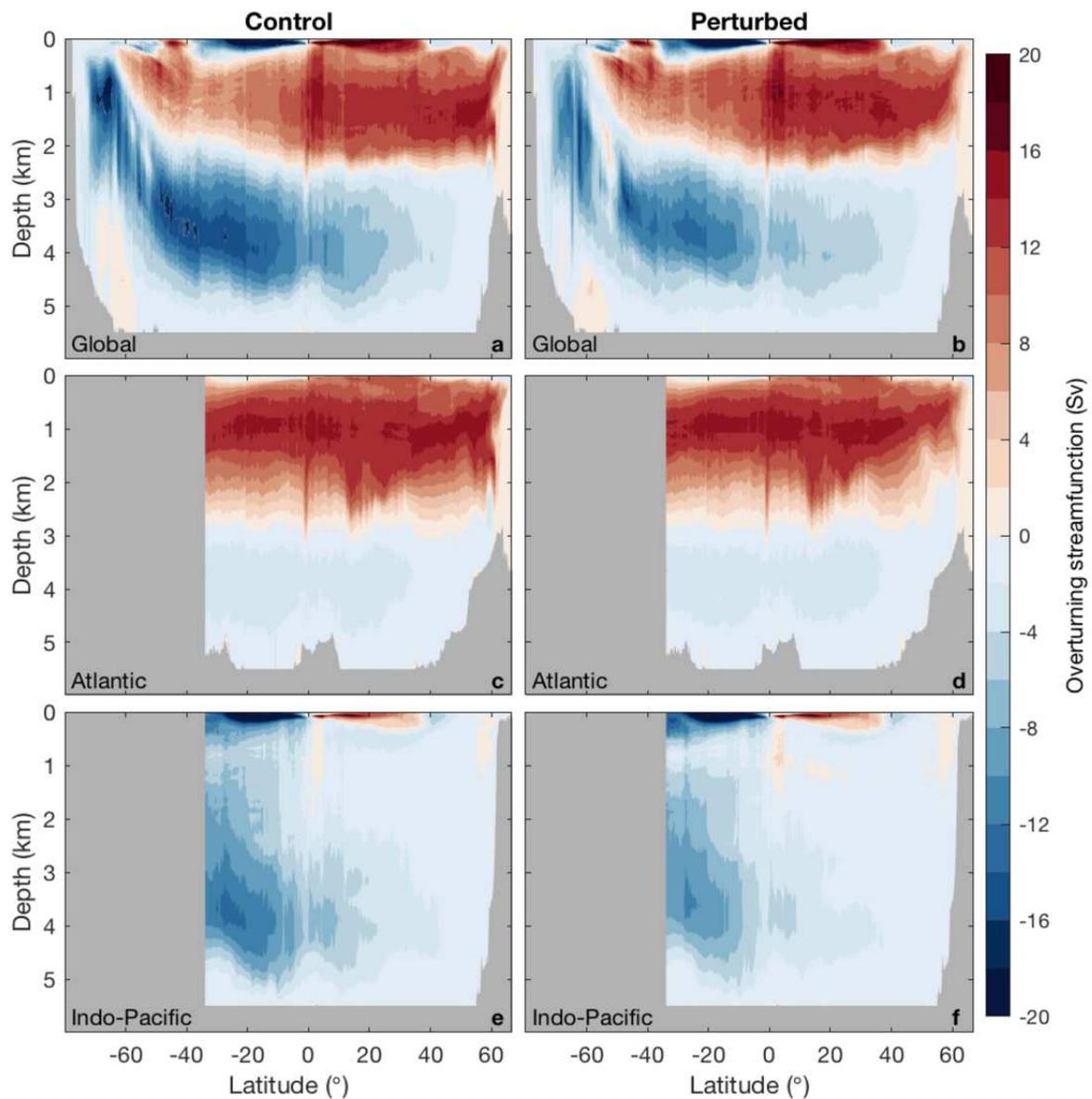
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Extended Data 7. LGM-PI change in the PMIP3/4 ensemble. LGM-PI change in position of maximum zonal-mean zonal wind stress in the PIMP3 (circles) and PMIP4 (triangles) ensemble, compared to the reconstructed change in $\Delta\text{Lat}_{\text{wind}}$ between 20-6.5 ka.



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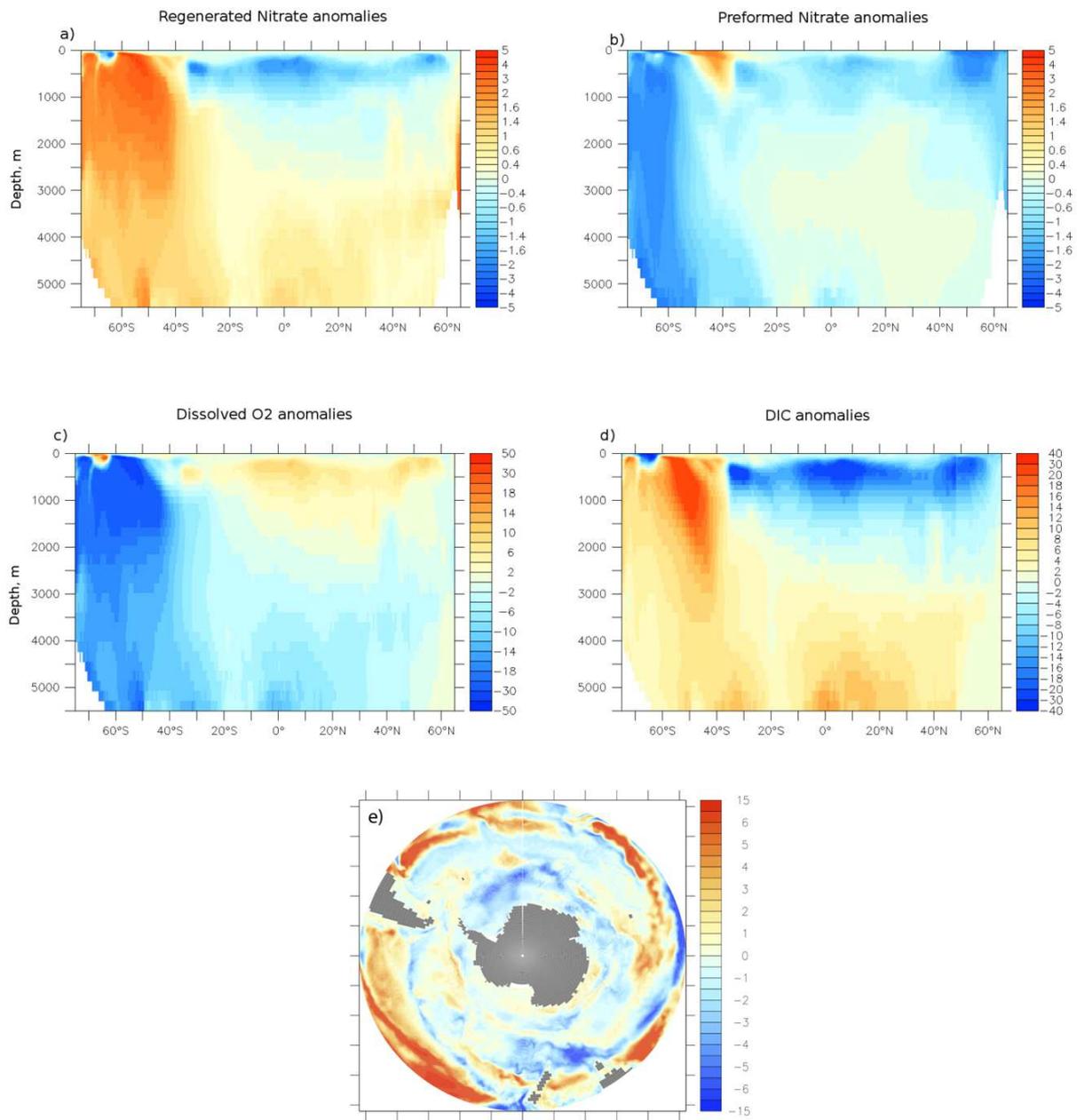
Extended Data 8. Deglacial changes in wind latitude, wind strength, wind stress at 60°S and northward Ekman transport at 60°S. Reconstructed changes in **(a)** the wind latitude ($\Delta\text{Lat}_{\text{wind}}$) **(b)** the wind strength ($\text{max } \tau_u$) **(c)** zonal-mean wind stress at 60°S ($60\text{S } \tau_u$) **(d)** northward Ekman transport at 60°S. (b) and (c) are calculated using the reconstructed changes in wind latitude (a) and the relationships between wind latitude and these parameters in the model ensemble (Extended Data Fig. 5). Northward Ekman transport at 60°S is calculated using zonal wind stress at 60°S (Methods).



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Extended Data 9. MOM5-SIS-Wombat circulation results. (a-f) Meridional overturning streamfunction in the Control (a,c,e) and Perturbed experiments (b,d,f), for the global ocean (a,b), Atlantic (c,d) and Indo-Pacific (e,f) oceans. (g) Zonally averaged mixed layer depth (MLD) in the Control (black) and Perturbed (red) simulations.



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Extended Data 10. MOM5-SIS-Wombat biogeochemical results. Zonally averaged anomalies (Perturbed-Control) in **(a)** regenerated NO₃ (mmol/m³), **(b)** preformed NO₃ (mmol/m³), **(c)** O₂ (mmol/m³), **and (d)** DIC (mmol/m³). **(e)** Vertically integrated (over the upper 149 m) gross phytoplankton production (molC/m²/yr) anomalies (Perturbed-Control).

829 **References**

- 830 1. Marshall, J. & Speer, K. Closure of the meridional overturning circulation through Southern Ocean
831 upwelling. *Nat. Geosci.* **5**, 171–180 (2012).
- 832 2. Toggweiler, J. R., Russell, J. L. & Carson, S. R. Midlatitude westerlies, atmospheric CO₂, and
833 climate change during the ice ages. *Paleoceanography* **21**, (2006).
- 834 3. Sigman, D. M. & Boyle, E. A. Glacial/interglacial variations in atmospheric carbon dioxide. *Nature*
835 **407**, 859–869 (2000).
- 836 4. Anderson, R. F. *et al.* Wind-Driven Upwelling in the Southern Ocean and the Deglacial Rise in
837 Atmospheric CO₂. *Science* **323**, 1443–1448 (2009).
- 838 5. Kohfeld, K. E. *et al.* Southern Hemisphere westerly wind changes during the Last Glacial
839 Maximum: paleo-data synthesis. *Quat. Sci. Rev.* **68**, 76–95 (2013).
- 840 6. Sime, L. C. *et al.* Southern Hemisphere westerly wind changes during the Last Glacial Maximum:
841 model-data comparison. *Quat. Sci. Rev.* **64**, 104–120 (2013).
- 842 7. Sime, L. C. *et al.* Sea ice led to poleward-shifted winds at the Last Glacial Maximum: the
843 influence of state dependency on CMIP5 and PMIP3 models. *Clim. Past* **12**, 2241–2253 (2016).
- 844 8. Yin, J. H. A consistent poleward shift of the storm tracks in simulations of 21st century climate.
845 *Geophys. Res. Lett.* **32**, (2005).
- 846 9. Chen, G., Lu, J. & Frierson, D. M. W. Phase Speed Spectra and the Latitude of Surface
847 Westerlies: Interannual Variability and Global Warming Trend. *J. Clim.* **21**, 5942–5959 (2008).
- 848 10. Goyal, R., Gupta, A. S., Jucker, M. & England, M. H. Historical and Projected Changes in the
849 Southern Hemisphere Surface Westerlies. *Geophys. Res. Lett.* **48**, e2020GL090849 (2021).
- 850 11. Toggweiler, J. R. & Samuels, B. Effect of drake passage on the global thermohaline circulation.
851 *Deep Sea Res. Part Oceanogr. Res. Pap.* **42**, 477–500 (1995).
- 852 12. Abernathy, R., Marshall, J. & Ferreira, D. The Dependence of Southern Ocean Meridional
853 Overturning on Wind Stress. *J. Phys. Oceanogr.* **41**, 2261–2278 (2011).
- 854 13. Martin, J. H., Gordon, R. M. & Fitzwater, S. E. Iron in Antarctic waters. *Nature* **345**, 156–158
855 (1990).
- 856 14. Mitchell, B. G., Brody, E. A., Holm-Hansen, O., McClain, C. & Bishop, J. Light limitation of
857 phytoplankton biomass and macronutrient utilization in the Southern Ocean. *Limnol. Oceanogr.*
858 **36**, 1662–1677 (1991).

- 859 15. Ito, T. & Follows, M. J. Preformed phosphate, soft tissue pump and atmospheric CO₂. *J. Mar.*
860 *Res.* **63**, 813–839 (2005).
- 861 16. Toggweiler, J. R. Variation of atmospheric CO₂ by ventilation of the ocean's deepest water.
862 *Paleoceanography* **14**, 571–588 (1999).
- 863 17. Lauderdale, J. M., Williams, R. G., Munday, D. R. & Marshall, D. P. The impact of Southern
864 Ocean residual upwelling on atmospheric CO₂ on centennial and millennial timescales. *Clim.*
865 *Dyn.* **48**, 1611–1631 (2017).
- 866 18. Ai, X. E. *et al.* Southern Ocean upwelling, Earth's obliquity, and glacial-interglacial atmospheric
867 CO₂ change. *Science* **370**, 1348–1352 (2020).
- 868 19. Gray, W. R. *et al.* Wind-Driven Evolution of the North Pacific Subpolar Gyre Over the Last
869 Deglaciation. *Geophys. Res. Lett.* **47**, e2019GL086328 (2020).
- 870 20. Kageyama, M. *et al.* The PMIP4-CMIP6 Last Glacial Maximum experiments: preliminary results
871 and comparison with the PMIP3-CMIP5 simulations. *Clim. Past Discuss.* 1–37 (2020)
872 doi:<https://doi.org/10.5194/cp-2019-169>.
- 873 21. Li, C. & Battisti, D. S. Reduced Atlantic Storminess during Last Glacial Maximum: Evidence from
874 a Coupled Climate Model. *J. Clim.* **21**, 3561–3579 (2008).
- 875 22. Chavaillaz, Y., Codron, F. & Kageyama, M. Southern westerlies in LGM and future (RCP4.5)
876 climates. *Clim. Past* **9**, 517–524 (2013).
- 877 23. Buizert, C. *et al.* Abrupt ice-age shifts in southern westerly winds and Antarctic climate forced
878 from the north. *Nature* **563**, 681–685 (2018).
- 879 24. Bereiter, B. *et al.* Revision of the EPICA Dome C CO₂ record from 800 to 600 kyr before present.
880 *Geophys. Res. Lett.* **42**, 542–549 (2015).
- 881 25. Dong, S., Sprintall, J. & Gille, S. T. Location of the Antarctic Polar Front from AMSR-E Satellite
882 Sea Surface Temperature Measurements. *J. Phys. Oceanogr.* **36**, 2075–2089 (2006).
- 883 26. Yang, H. *et al.* Tropical Expansion Driven by Poleward Advancing Midlatitude Meridional
884 Temperature Gradients. *J. Geophys. Res. Atmospheres* **125**, e2020JD033158 (2020).
- 885 27. Gnanadesikan, A. & Hallberg, R. W. On the Relationship of the Circumpolar Current to Southern
886 Hemisphere Winds in Coarse-Resolution Ocean Models. *J. Phys. Oceanogr.* **30**, 2013–2034
887 (2000).

- 888 28. Gordon, A. L., Molinelli, E. & Baker, T. Large-scale relative dynamic topography of the Southern
889 Ocean. *J. Geophys. Res. Oceans* **83**, 3023–3032 (1978).
- 890 29. Gherardi, J.-M. *et al.* Glacial-interglacial circulation changes inferred from ²³¹Pa/²³⁰Th
891 sedimentary record in the North Atlantic region. *Paleoceanography* **24**, (2009).
- 892 30. Stocker, T. F. & Johnsen, S. J. A minimum thermodynamic model for the bipolar seesaw.
893 *Paleoceanography* **18**, (2003).
- 894 31. Shakun, J. D. *et al.* Global warming preceded by increasing carbon dioxide concentrations during
895 the last deglaciation. *Nature* **484**, 49–54 (2012).
- 896 32. Gottschalk, J. *et al.* Mechanisms of millennial-scale atmospheric CO₂ change in numerical model
897 simulations. *Quat. Sci. Rev.* **220**, 30–74 (2019).
- 898 33. Menviel, L. *et al.* Southern Hemisphere westerlies as a driver of the early deglacial atmospheric
899 CO₂ rise. *Nat. Commun.* **9**, 2503 (2018).
- 900 34. Hogg, A. M., Spence, P., Saenko, O. A. & Downes, S. M. The Energetics of Southern Ocean
901 Upwelling. *J. Phys. Oceanogr.* **47**, 135–153 (2017).
- 902 35. Spence, P., Saenko, O. A., Eby, M. & Weaver, A. J. The Southern Ocean Overturning:
903 Parameterized versus Permitted Eddies. *J. Phys. Oceanogr.* **39**, 1634–1651 (2009).
- 904 36. Hallberg, R. & Gnanadesikan, A. The Role of Eddies in Determining the Structure and Response
905 of the Wind-Driven Southern Hemisphere Overturning: Results from the Modeling Eddies in the
906 Southern Ocean (MESO) Project. *J. Phys. Oceanogr.* **36**, 2232–2252 (2006).
- 907 37. Boyle, E. A. Vertical oceanic nutrient fractionation and glacial/interglacial CO₂ cycles. *Nature*
908 **331**, 55–56 (1988).
- 909 38. Du, J., Haley, B. A. & Mix, A. C. Evolution of the Global Overturning Circulation since the Last
910 Glacial Maximum based on marine authigenic neodymium isotopes. *Quat. Sci. Rev.* **241**, 106396
911 (2020).
- 912 39. Rae, J. W. B. *et al.* CO₂ storage and release in the deep Southern Ocean on millennial to
913 centennial timescales. *Nature* **562**, 569–573 (2018).
- 914 40. Jaccard, S. L. & Galbraith, E. D. Large climate-driven changes of oceanic oxygen concentrations
915 during the last deglaciation. *Nat. Geosci.* **5**, 151–156 (2012).
- 916 41. Hoogakker, B. A. A. *et al.* Glacial expansion of oxygen-depleted seawater in the eastern tropical
917 Pacific. *Nature* **562**, 410–413 (2018).

- 918 42. Peterson, C. D. & Lisiecki, L. E. Deglacial carbon cycle changes observed in a compilation of 127
919 benthic $\delta^{13}\text{C}$ time series (20–6 ka). *Clim. Past* **14**, 1229–1252 (2018).
- 920 43. Jaccard, S. L. *et al.* Two Modes of Change in Southern Ocean Productivity Over the Past Million
921 Years. *Science* **339**, 1419–1423 (2013).
- 922 44. Bishop, S. P. *et al.* Southern Ocean Overturning Compensation in an Eddy-Resolving Climate
923 Simulation. *J. Phys. Oceanogr.* **46**, 1575–1592 (2016).
- 924 45. Dufour, C. O. *et al.* Role of Mesoscale Eddies in Cross-Frontal Transport of Heat and
925 Biogeochemical Tracers in the Southern Ocean. *J. Phys. Oceanogr.* **45**, 3057–3081 (2015).
- 926 46. Burke, A. & Robinson, L. F. The Southern Ocean’s Role in Carbon Exchange During the Last
927 Deglaciation. *Science* **335**, 557–561 (2012).
- 928 47. Martínez-Botí, M. A. *et al.* Boron isotope evidence for oceanic carbon dioxide leakage during the
929 last deglaciation. *Nature* **518**, 219–222 (2015).
- 930 48. Menviel, L. & Joos, F. Toward explaining the Holocene carbon dioxide and carbon isotope
931 records: Results from transient ocean carbon cycle-climate simulations. *Paleoceanography* **27**,
932 (2012).
- 933 49. Fogwill, C. J., Turney, C. S. M., Hutchinson, D. K., Taschetto, A. S. & England, M. H. Obliquity
934 Control On Southern Hemisphere Climate During The Last Glacial. *Sci. Rep.* **5**, 11673 (2015).
- 935 50. Gruber, N., Landschützer, P. & Lovenduski, N. S. The Variable Southern Ocean Carbon Sink.
936 *Annu. Rev. Mar. Sci.* **11**, 159–186 (2019).
- 937 51. Kalnay, E. *et al.* The NCEP/NCAR 40-Year Reanalysis Project. *Bull. Am. Meteorol. Soc.* **77**, 437–
938 472 (1996).
- 939 52. Haddam, N. A., Michel, E., Siani, G., Licari, L. & Dewilde, F. Ventilation and Expansion of
940 Intermediate and Deep Waters in the Southeast Pacific During the Last Termination.
941 *Paleoceanogr. Paleoclimatology* **35**, e2019PA003743 (2020).
- 942 53. Gottschalk, J. *et al.* Glacial heterogeneity in Southern Ocean carbon storage abated by fast South
943 Indian deglacial carbon release. *Nat. Commun.* **11**, 6192 (2020).
- 944 54. Sarin, M. *et al.* Changes in East Atlantic Deepwater Circulation over the last 30,000 years:
945 Eight time slice reconstructions. *Paleoceanography* **9**, 209–267 (1994).

- 946 55. Wang, Y. V. *et al.* Northern and southern hemisphere controls on seasonal sea surface
947 temperatures in the Indian Ocean during the last deglaciation. *Paleoceanography* **28**, 619–632
948 (2013).
- 949 56. Stuut, J.-B. W. *et al.* A 300-kyr record of aridity and wind strength in southwestern Africa:
950 inferences from grain-size distributions of sediments on Walvis Ridge, SE Atlantic. *Mar. Geol.*
951 **180**, 221–233 (2002).
- 952 57. Levi, C. *et al.* Low-latitude hydrological cycle and rapid climate changes during the last
953 deglaciation. *Geochem. Geophys. Geosystems* **8**, (2007).
- 954 58. Schneider, R. R., Müller, P. J. & Ruhland, G. Late Quaternary surface circulation in the east
955 equatorial South Atlantic: Evidence from Alkenone sea surface temperatures. *Paleoceanography*
956 **10**, 197–219 (1995).
- 957 59. Stuut, J.-B. W. *et al.* A 5.3-Million-Year History of Monsoonal Precipitation in Northwestern
958 Australia. *Geophys. Res. Lett.* **46**, 6946–6954 (2019).
- 959 60. Bostock, H. C., Opdyke, B. N., Gagan, M. K. & Fifield, L. K. Carbon isotope evidence for changes
960 in Antarctic Intermediate Water circulation and ocean ventilation in the southwest Pacific during
961 the last deglaciation. *Paleoceanography* **19**, (2004).
- 962 61. Santos, T. P. *et al.* Prolonged warming of the Brazil Current precedes deglaciations. *Earth Planet.*
963 *Sci. Lett.* **463**, 1–12 (2017).
- 964 62. Caley, T. *et al.* High-latitude obliquity as a dominant forcing in the Agulhas current system. *Clim.*
965 *Past* **7**, 1285–1296 (2011).
- 966 63. Portilho-Ramos, R. C. *et al.* Methane release from the southern Brazilian margin during the last
967 glacial. *Sci. Rep.* **8**, 5948 (2018).
- 968 64. Pereira, L. S., Arz, H. W., Pätzold, J. & Portilho-Ramos, R. C. Productivity Evolution in the South
969 Brazilian Bight During the Last 40,000 Years. *Paleoceanogr. Paleoclimatology* **33**, 1339–1356
970 (2018).
- 971 65. Carlson, A. E. *et al.* Subtropical Atlantic salinity variability and Atlantic meridional circulation
972 during the last deglaciation. *Geology* **36**, 991–994 (2008).
- 973 66. Scussolini, P. & Peeters, F. J. C. A record of the last 460 thousand years of upper ocean
974 stratification from the central Walvis Ridge, South Atlantic. *Paleoceanography* **28**, 426–439
975 (2013).

- 976 67. Chiessi, C. M. *et al.* Variability of the Brazil Current during the late Holocene. *Palaeogeogr.*
977 *Palaeoclimatol. Palaeoecol.* **415**, 28–36 (2014).
- 978 68. Winn, K. Carbon and oxygen isotope ratios on planktonic foraminifera in subtropical Southeast
979 Pacific core GIK17747-2. 333 data points (2013) doi:10.1594/PANGAEA.815877.
- 980 69. Mohtadi, M. *et al.* Deglacial pattern of circulation and marine productivity in the upwelling region
981 off central-south Chile. *Earth Planet. Sci. Lett.* **272**, 221–230 (2008).
- 982 70. Dyez, K. A., Zahn, R. & Hall, I. R. Multicentennial Agulhas leakage variability and links to North
983 Atlantic climate during the past 80,000 years. *Paleoceanography* **29**, 1238–1248 (2014).
- 984 71. Schiraldi, B., Sikes, E. L., Elmore, A. C., Cook, M. S. & Rose, K. A. Southwest Pacific subtropics
985 responded to last deglacial warming with changes in shallow water sources. *Paleoceanography*
986 **29**, 595–611 (2014).
- 987 72. Martínez-Méndez, G. *et al.* Contrasting multiproxy reconstructions of surface ocean hydrography
988 in the Agulhas Corridor and implications for the Agulhas Leakage during the last 345,000 years.
989 *Paleoceanography* **25**, (2010).
- 990 73. Calvo, E., Pelejero, C., Deckker, P. D. & Logan, G. A. Antarctic deglacial pattern in a 30 kyr
991 record of sea surface temperature offshore South Australia. *Geophys. Res. Lett.* **34**, (2007).
- 992 74. Nelson, C. S., Hendy, I. L., Neil, H. L., Hendy, C. H. & Weaver, P. P. E. Last glacial jetting of cold
993 waters through the Subtropical Convergence zone in the Southwest Pacific off eastern New
994 Zealand, and some geological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **156**, 103–
995 121 (2000).
- 996 75. Gottschalk, J. *et al.* Past Carbonate Preservation Events in the Deep Southeast Atlantic Ocean
997 (Cape Basin) and Their Implications for Atlantic Overturning Dynamics and Marine Carbon
998 Cycling. *Paleoceanogr. Paleoclimatology* **33**, 643–663 (2018).
- 999 76. Lamy, F. *et al.* Antarctic Timing of Surface Water Changes off Chile and Patagonian Ice Sheet
1000 Response. *Science* **304**, 1959–1962 (2004).
- 1001 77. Haddam, N. A. *et al.* Changes in latitudinal sea surface temperature gradients along the Southern
1002 Chilean margin since the last glacial. *Quat. Sci. Rev.* **194**, 62–76 (2018).
- 1003 78. Hodell, D. A., Venz, K. A., Charles, C. D. & Ninnemann, U. S. Pleistocene vertical carbon isotope
1004 and carbonate gradients in the South Atlantic sector of the Southern Ocean. *Geochem. Geophys.*
1005 *Geosystems* **4**, 1–19 (2003).

- 1006 79. Pichon, J.-J. *et al.* Surface water temperature changes in the high latitudes of the southern
1007 hemisphere over the Last Glacial-Interglacial Cycle. *Paleoceanography* **7**, 289–318 (1992).
- 1008 80. Rickaby, R. E. M. & Elderfield, H. Planktonic foraminiferal Cd/Ca: Paleonutrients or
1009 paleotemperature? *Paleoceanography* **14**, 293–303 (1999).
- 1010 81. Gottschalk, J., Skinner, L. C. & Waelbroeck, C. Contribution of seasonal sub-Antarctic surface
1011 water variability to millennial-scale changes in atmospheric CO₂ over the last deglaciation and
1012 Marine Isotope Stage 3. *Earth Planet. Sci. Lett.* **411**, 87–99 (2015).
- 1013 82. Sikes, E. L. *et al.* Southern Ocean seasonal temperature and Subtropical Front movement on the
1014 South Tasman Rise in the late Quaternary. *Paleoceanography* **24**, (2009).
- 1015 83. Sicre, M. A. *et al.* Mid-latitude Southern Indian Ocean response to Northern Hemisphere Heinrich
1016 events. *Earth Planet. Sci. Lett.* **240**, 724–731 (2005).
- 1017 84. Labeyrie, L. *et al.* Hydrographic changes of the Southern Ocean (southeast Indian Sector) Over
1018 the last 230 kyr. *Paleoceanography* **11**, 57–76 (1996).
- 1019 85. Govin, A. *et al.* Evidence for northward expansion of Antarctic Bottom Water mass in the
1020 Southern Ocean during the last glacial inception. *Paleoceanography* **24**, (2009).
- 1021 86. Bostock, H. C., Hayward, B. W., Neil, H. L., Sabaa, A. T. & Scott, G. H. Changes in the position of
1022 the Subtropical Front south of New Zealand since the last glacial period. *Paleoceanography* **30**,
1023 824–844 (2015).
- 1024 87. Hodell, D. A., Charles, C. D. & Ninnemann, U. S. Comparison of interglacial stages in the South
1025 Atlantic sector of the southern ocean for the past 450 kyr: implications for Marine Isotope Stage
1026 (MIS) 11. *Glob. Planet. Change* **24**, 7–26 (2000).
- 1027 88. Charles, C. D., Froelich, P. N., Zibello, M. A., Mortlock, R. A. & Morley, J. J. Biogenic opal in
1028 Southern Ocean sediments over the last 450,000 years: Implications for surface water chemistry
1029 and circulation. *Paleoceanography* **6**, 697–728 (1991).
- 1030 89. *Use of Proxies in Paleoceanography: Examples from the South Atlantic.* (Springer-Verlag, 1999).
1031 doi:10.1007/978-3-642-58646-0.
- 1032 90. Caniupán, M. *et al.* Millennial-scale sea surface temperature and Patagonian Ice Sheet changes
1033 off southernmost Chile (53°S) over the past ~60 kyr. *Paleoceanography* **26**, (2011).
- 1034 91. Hasenfratz, A. P. *et al.* The residence time of Southern Ocean surface waters and the 100,000-
1035 year ice age cycle. *Science* **363**, 1080–1084 (2019).

- 1036 92. *Proceedings of the Ocean Drilling Program, 177 Scientific Results*. vol. 177 (Ocean Drilling
1037 Program, 2003).
- 1038 93. Mashiotta, T. A., Lea, D. W. & Spero, H. J. Glacial–interglacial changes in Subantarctic sea
1039 surface temperature and $\delta^{18}\text{O}$ -water using foraminiferal Mg. *Earth Planet. Sci. Lett.* **170**, 417–
1040 432 (1999).
- 1041 94. Crosta, X., Sturm, A., Armand, L. & Pichon, J.-J. Late Quaternary sea ice history in the Indian
1042 sector of the Southern Ocean as recorded by diatom assemblages. *Mar. Micropaleontol.* **50**,
1043 209–223 (2004).
- 1044 95. *Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change:
1045 Quantitative Approaches in Paleoceanography*. (Springer-Verlag, 1994). doi:10.1007/978-3-642-
1046 78737-9.
- 1047 96. Grobe, H. & Mackensen, A. Late Quaternary climatic cycles as recorded in sediments from the
1048 Antarctic continental margin. in *Antarctic Research Series* (eds. Kennett, J. P. & Warkne, D. A.)
1049 vol. 56 349–376 (American Geophysical Union, 1992).
- 1050 97. Lu, Z. *et al.* Oxygen depletion recorded in upper waters of the glacial Southern Ocean. *Nat.*
1051 *Commun.* **7**, 11146 (2016).
- 1052 98. LeGrande, A. N. & Schmidt, G. A. Global gridded data set of the oxygen isotopic composition in
1053 seawater. *Geophys. Res. Lett.* **33**, L12604 (2006).
- 1054 99. Wood, S. N. Fast stable restricted maximum likelihood and marginal likelihood estimation of
1055 semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* **73**, 3–36
1056 (2011).
- 1057 100. Wood, S. N., Pya, N. & Säfken, B. Smoothing Parameter and Model Selection for General
1058 Smooth Models. *J. Am. Stat. Assoc.* **111**, 1548–1563 (2016).
- 1059 101. Simpson, G. L. Modelling Palaeoecological Time Series Using Generalised Additive Models.
1060 *Front. Ecol. Evol.* **6**, (2018).
- 1061 102. Schrag, D. P. *et al.* The oxygen isotopic composition of seawater during the Last Glacial
1062 Maximum. *Quat. Sci. Rev.* **21**, 331–342 (2002).
- 1063 103. Lambeck, K., Rouby, H., Purcell, A., Sun, Y. & Sambridge, M. Sea level and global ice
1064 volumes from the Last Glacial Maximum to the Holocene. *Proc. Natl. Acad. Sci.* **111**, 15296–
1065 15303 (2014).

- 1066 104. Kim, S.-T. & O'Neil, J. R. Equilibrium and nonequilibrium oxygen isotope effects in synthetic
1067 carbonates. *Geochim. Cosmochim. Acta* **61**, 3461–3475 (1997).
- 1068 105. Malevich, S. B., Vetter, L. & Tierney, J. E. Global Core Top Calibration of $\delta^{18}\text{O}$ in Planktic
1069 Foraminifera to Sea Surface Temperature. *Paleoceanogr. Paleoclimatology* **34**, 1292–1315
1070 (2019).
- 1071 106. Efron, B. Bootstrap Methods: Another Look at the Jackknife. *Ann. Stat.* **7**, 1–26 (1979).
- 1072 107. Saunders, K. M. *et al.* Holocene dynamics of the Southern Hemisphere westerly winds and
1073 possible links to CO₂ outgassing. *Nat. Geosci.* **11**, 650–655 (2018).
- 1074 108. Lombard, F. *et al.* Modelling planktic foraminifer growth and distribution using an
1075 ecophysiological multi-species approach. *Biogeosciences* **8**, 853–873 (2011).
- 1076 109. Braconnot, P. *et al.* Evaluation of climate models using palaeoclimatic data. *Nat. Clim.*
1077 *Change* **2**, 417–424 (2012).
- 1078 110. Kageyama, M. *et al.* The PMIP4 contribution to CMIP6 – Part 1: Overview and over-arching
1079 analysis plan. *Geosci. Model Dev.* **11**, 1033–1057 (2018).
- 1080 111. Taylor, K. E., Stouffer, R. J. & Meehl, G. A. An Overview of CMIP5 and the Experiment
1081 Design. *Bull. Am. Meteorol. Soc.* **93**, 485–498 (2012).
- 1082 112. Eyring, V. *et al.* Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6)
1083 experimental design and organization. *Geosci. Model Dev.* **9**, 1937–1958 (2016).
- 1084 113. Fathrio, I. *et al.* Assessment of western Indian Ocean SST bias of CMIP5 models. *J.*
1085 *Geophys. Res. Oceans* **122**, 3123–3140 (2017).
- 1086 114. Chapman, C. C., Lea, M.-A., Meyer, A., Sallée, J.-B. & Hindell, M. Defining Southern Ocean
1087 fronts and their influence on biological and physical processes in a changing climate. *Nat. Clim.*
1088 *Change* **10**, 209–219 (2020).
- 1089 115. Barnes, E. A. & Polvani, L. Response of the Midlatitude Jets, and of Their Variability, to
1090 Increased Greenhouse Gases in the CMIP5 Models. *J. Clim.* **26**, 7117–7135 (2013).
- 1091 116. McGraw, M. C. & Barnes, E. A. Seasonal Sensitivity of the Eddy-Driven Jet to Tropospheric
1092 Heating in an Idealized AGCM. *J. Clim.* **29**, 5223–5240 (2016).
- 1093 117. Sigl, M. *et al.* The WAIS Divide deep ice core WD2014 chronology – Part 2: Annual-layer
1094 counting (0–31 ka BP). *Clim. Past* **12**, 769–786 (2016).

- 1095 118. Olsen, A. *et al.* The Global Ocean Data Analysis Project version 2 (GLODAPv2) – an
1096 internally consistent data product for the world ocean. *Earth Syst. Sci. Data* **8**, 297–323 (2016).
- 1097 119. Griffies, S. M. *et al.* Coordinated Ocean-ice Reference Experiments (COREs). *Ocean Model.*
1098 **26**, 1–46 (2009).
- 1099 120. Redi, M. H. Oceanic Isopycnal Mixing by Coordinate Rotation. *J. Phys. Oceanogr.* **12**, 1154–
1100 1154 (1982).
- 1101 121. Gent, P. R. & McWilliams, J. C. Isopycnal Mixing in Ocean Circulation Models. *J. Phys.*
1102 *Oceanogr.* **20**, 150–155 (1990).
- 1103 122. Jackett, D. & McDougall, T. A Neutral Density Variable for the World’s Oceans. (1997)
1104 doi:10.1175/1520-0485(1997)027<0237:ANDVFT>2.0.CO;2.
- 1105 123. Zika, J. D., England, M. H. & Sijp, W. P. The Ocean Circulation in Thermohaline Coordinates.
1106 *J. Phys. Oceanogr.* **42**, 708–724 (2012).
- 1107 124. Boyle, E. A. The role of vertical chemical fractionation in controlling late Quaternary
1108 atmospheric carbon dioxide. *J. Geophys. Res. Oceans* **93**, 15701–15714 (1988).
- 1109 125. Boyer, T. P. *et al.* World ocean database 2013. (2013) doi:10.7289/V5NZ85MT.
- 1110 126. AVISO: Satellite derived Sea Surface Height above Geoid | NCAR - Climate Data Guide.
1111 [https://climatedataguide.ucar.edu/climate-data/aviso-satellite-derived-sea-surface-height-above-](https://climatedataguide.ucar.edu/climate-data/aviso-satellite-derived-sea-surface-height-above-geoid)
1112 [geoid.](https://climatedataguide.ucar.edu/climate-data/aviso-satellite-derived-sea-surface-height-above-geoid)

Figures

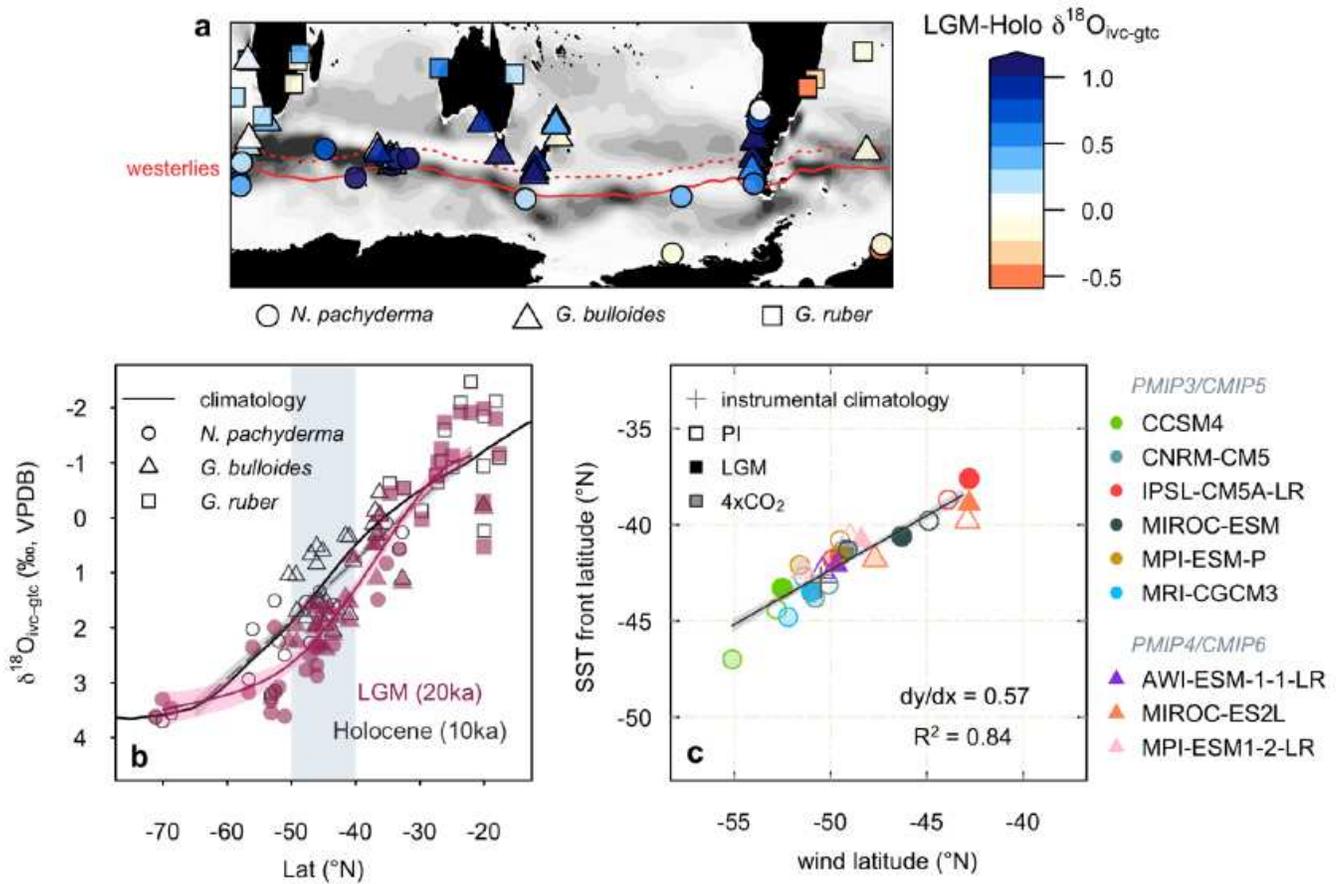


Figure 1

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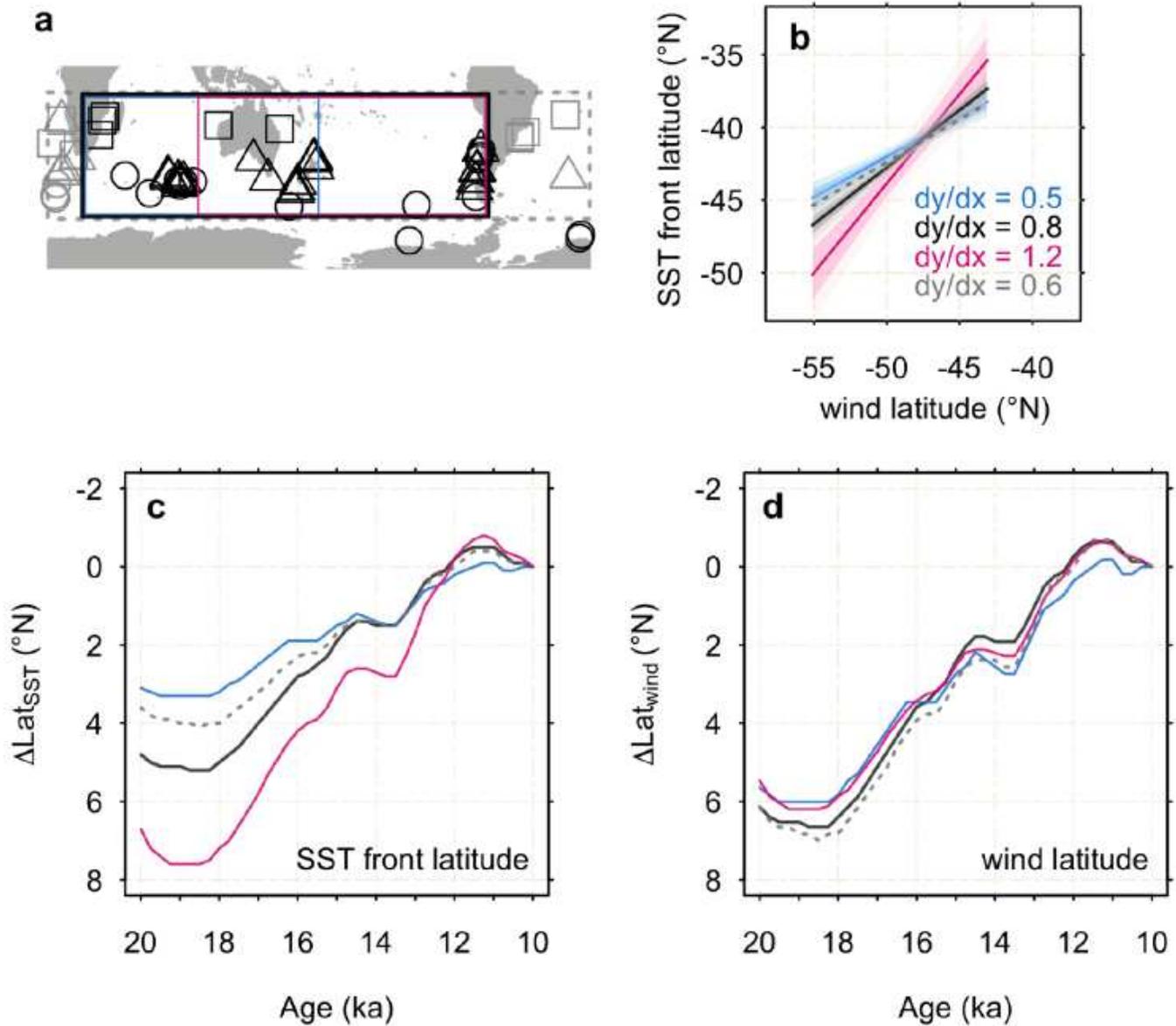


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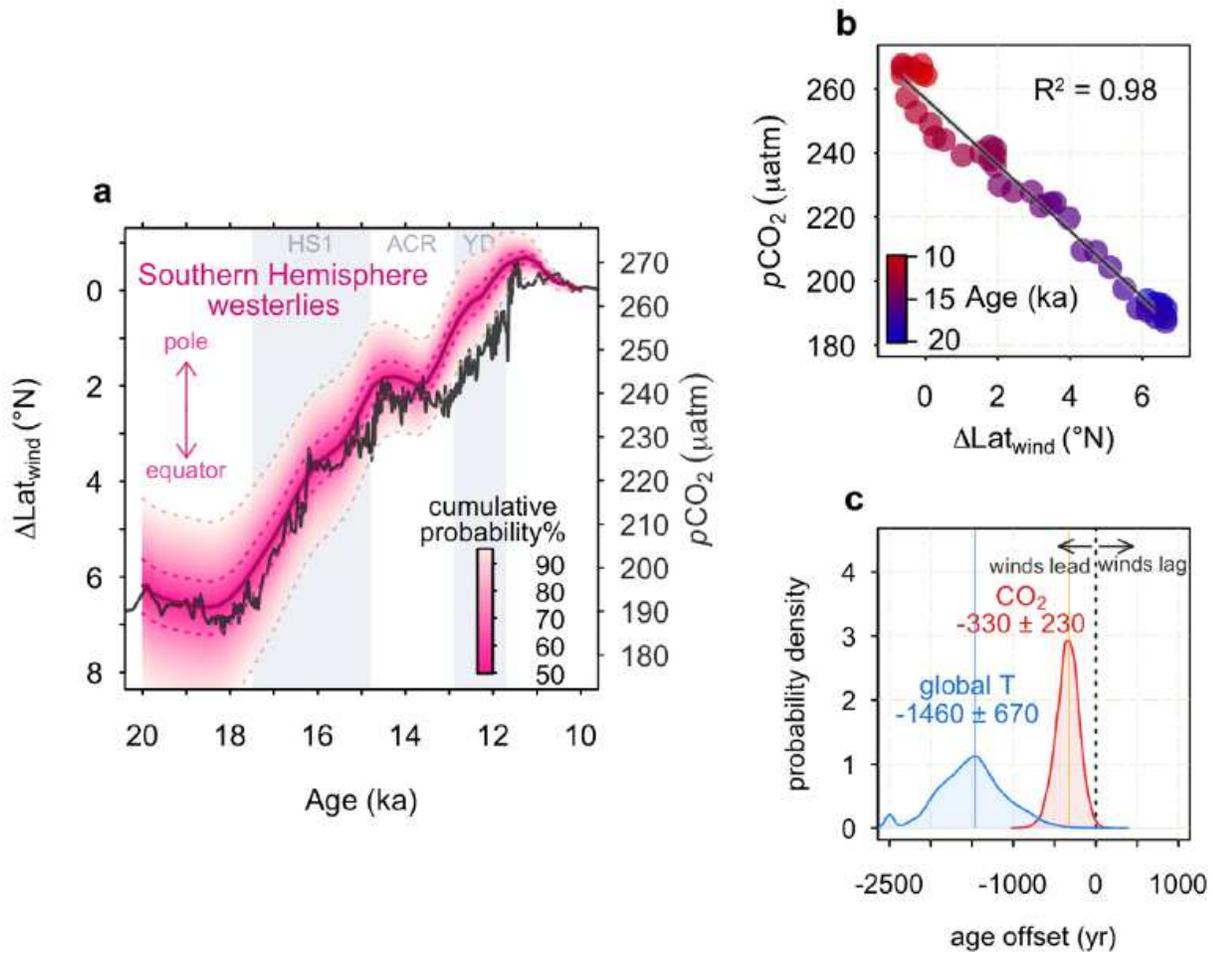


Figure 3

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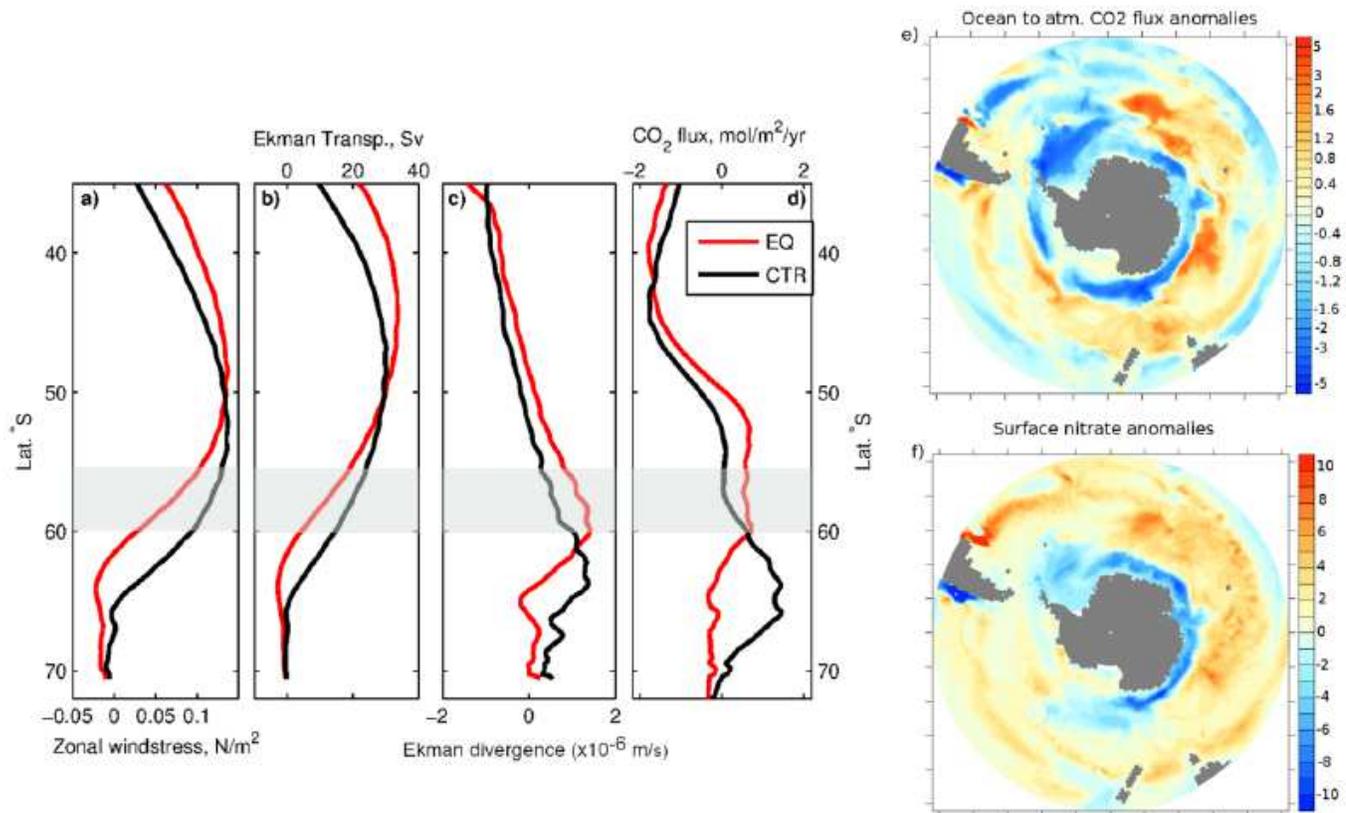


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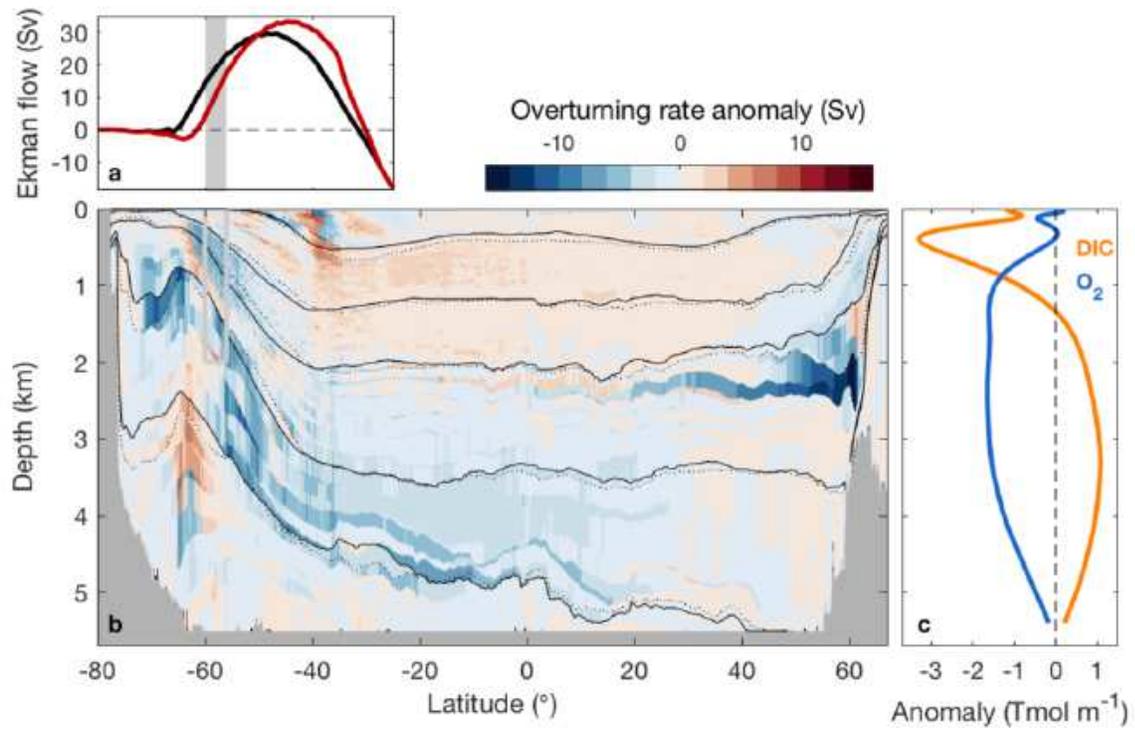


Figure 5

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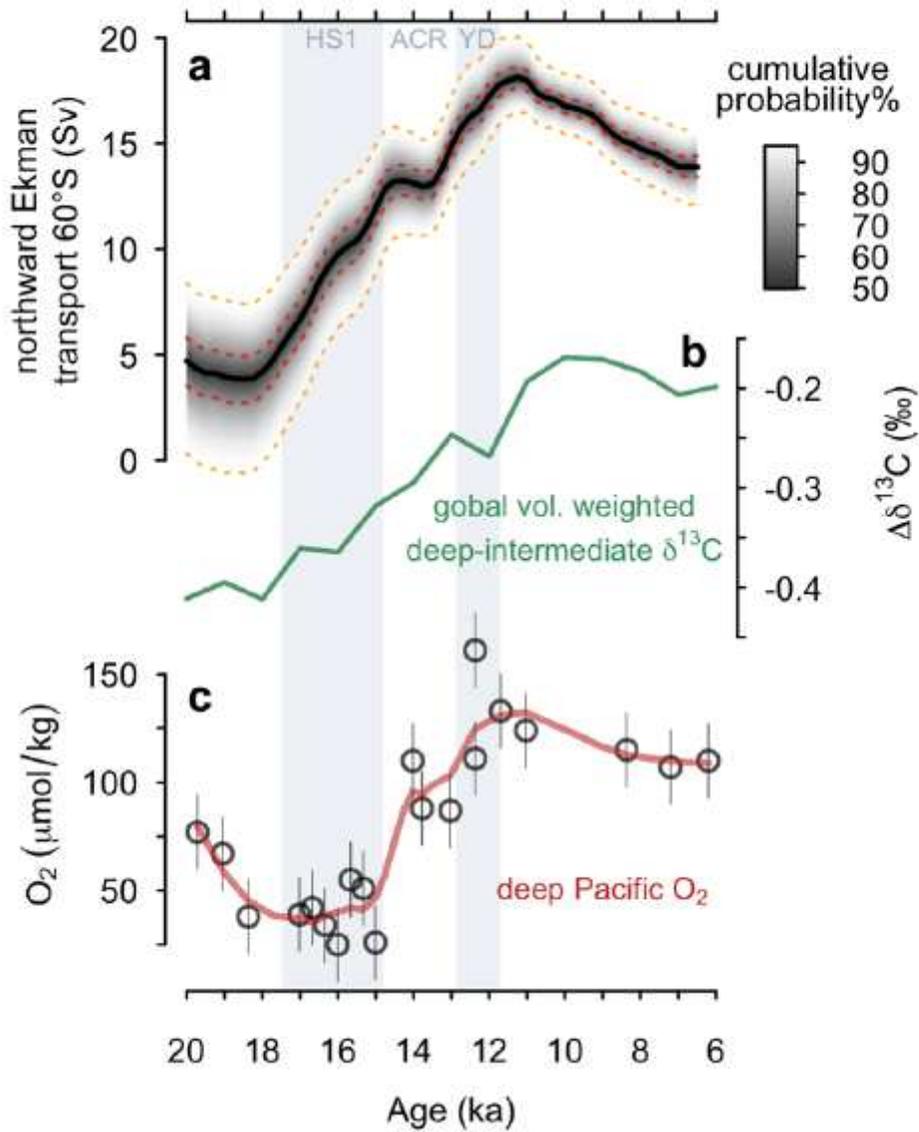


Figure 6

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