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Fig. 2. Frequency distributions showing the number of changes required to describe the covariation of fungal lineage with season. Observed distributions are based on trees in the posterior probability distribution from Bayesian analysis (observed) and distribution of randomly generated trees from MacClade (random). Dashed lines indicate the 95% lower confidence limit for the randomized data. (A) Comparison of winter and spring communities (P > 0.05; not significant). (B) Comparison of spring and summer communities (P <0.001).



Nevertheless, the presence of previously unknown, higher order lineages of fungi in tundra soils suggests that the cold, snow-covered soils may be an underappreciated repository of biological diversity.

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# Synchroneity of Tropical and High-Latitude Atlantic Temperatures over the Last Glacial Termination

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A high-resolution western tropical Atlantic sea surface temperature (SST) record from the Cariaco Basin on the northern Venezuelan shelf, based on Mg/Ca values in surface-dwelling planktonic foraminifera, reveals that changes in SST over the last glacial termination are synchronous, within  $\pm$  30 to  $\pm$ 90 years, with the Greenland Ice Sheet Project 2 air temperature proxy record and atmospheric methane record. The most prominent deglacial event in the Cariaco record occurred during the Younger Dryas time interval, when SSTs dropped by 3° to 4°C. A rapid southward shift in the atmospheric intertropical convergence zone could account for the synchroneity of tropical temperature, atmospheric methane, and high-latitude changes during the Younger Dryas.

Ice core gas records (1, 2) demonstrate that the atmospheric concentration of methane, which is thought to be dominantly derived from tropical wetlands (3, 4), rose and fell within decades of the Greenland deglacial warming and cooling events (5, 6). Because the atmosphere integrates globally, the methane signal suggests that a large part of the terrestrial tropics responded in kind with North Atlantic changes (3). Proxy temperature records from tropical ice cores also show a deglacial signal similar to the Greenland records, although dating issues and local effects complicate interpre-

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Materials and Methods Figs. S1 and S2 References

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tation of the observed signals (7). Evidence for a thermal response in tropical surface waters during the Younger Dryas (YD) chronozone, the most prominent of the deglacial events, is more ambiguous; highresolution Pacific sea surface temperature (SST) records show either a small ( $<1^{\circ}$ C) cooling (8) or no response (9), whereas a record from the Tobago Basin in the southeastern Caribbean indicates what has been interpreted as an antiphased response (10), with a small warming during the YD.

The Cariaco Basin, on the northern Venezuelan shelf, is a unique repository of tropical paleoclimate records (11-17). The combination of shallow sills (<150 m), permanent anoxia below ~300 m, and high sedimentation rates (0.3 to > 1 mm/year) has produced nearly continuous, annually laminated, unbioturbated sediments for the past 14,700 years (12–14). The presence of annual varves in the deglacial portion of the Cariaco sequence makes it possible to develop an independent chronology that can be directly compared to ice core records (18, 19).

Today, the Cariaco Basin has two distinct seasons: a cool dry season in (boreal) late winter, when the northeasterly trades are directly overhead and coastal upwelling and high productivity dominate; and a warm wet season in late summer, when the intertropical convergence zone (ITCZ) is

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directly overhead and rainfall reaches its maximum (13, 20). The annual migration of the ITCZ, from its southernmost position in winter to its northerly position in summer, has a marked impact on SST, rainfall, primary productivity, and sediment properties, and the annual cycle of light-colored biogenic input in winter and dark-colored detrital input in summer is what leads to the formation of distinct varves in Cariaco Basin sediments (13). Past changes in Cariaco Basin sediment light reflectance (grayscale) and composition have been correlated with high-latitude climate events (13, 14, 16, 18, 19), and previous studies have hypothesized that shifts in the mean position of the ITCZ can explain the observed changes (12, 16, 17). The development of a deglacial temperature record for Cariaco enables a direct test of this hypothesis.

We have generated a detailed Mg/Ca record for the surface-dwelling planktonic foraminifer *Globigerinoides ruber*, white variety (predominantly), from piston core PL07-39PC (10°42.00'N, 64°56.50'W, 790 m), which spans the past 25,000 years before the present (yr B.P.) and has a detailed oxygen isotope record and radiocarbon chronology, as well as grayscale correlations (13-15, 21) (Fig. 1). Previous work indicates that *G. ruber* is the most

Fig. 1. Climate proxy data from Cariaco Basin core PL07-39PC (10°42.00'N, 64°56. 50'W, 790 m). The Mg/Ca record is from planktonic foraminifera G. ruber, white variety, with the pink variety analyzed when sample abundances were limited (see supporting online material). Each point is the average of one to five replicates; the pooled SD of all replicate analyses (df = 155)was ±0.16 mmom/ mol (±4%) (21). Oxygen isotope data are from G. ruber, white variety (15). Sedimentary grayscale data are from (14). The gap between 165 and 192 cm is due to a turbidite (15). Core PL07-39PC has nearly conlaminations tinuous from 0 to 630 cm; the transition to bioturbated sediments occurs at the Bølling transition. ‰, V-PDB, per mil, Vienna Pee Dee belemnite scale.

representative species for reconstructing warm and/or annual conditions (15), because it has a nearly uniform annual occurrence (20). Mean Mg/Ca values in PL07-39PC range from a maximum of ~4.5 mmol/mol in the early Holocene and Bølling/Allerød (B/A) intervals to a minimum of  $\sim$ 3 mmol/mol in the early part of the YD and in the last glacial maximum (LGM) interval (19,000 to 23,000 yr B.P.). The high end of the measured Mg/Ca values is typical of the values found for the late Holocene in well-preserved tropical sediments (22) and is similar to Mg/Ca levels in G. ruber shells from Caribbean plankton tows (23).

The Mg/Ca record shows three sharp, steplike transitions through the deglaciation (Fig. 1). The *G. ruber*  $\delta^{18}$ O record generated on the same sample intervals shows many similarities to the Mg/Ca record, but it is dominated by a longer period signal, which primarily reflects the influence of slowly changing continental ice volume but also local salinity changes (*15*). Comparison of the Mg/Ca record with the grayscale record from PL07-39PC indicates that these two proxies are in phase over the large climate transitions, with light biogenic-rich intervals corresponding to low (cold) Mg/Ca values.



Foraminifera shells from the Cariaco Basin are superbly preserved because of the high carbonate ion content of Caribbean thermocline waters entering the basin, an observation supported by the presence of aragonitic pteropods throughout the PL07-39PC sequence. Therefore, G. ruber Mg/Ca values are converted to temperature using the surface projected calibration of Dekens et al. (22), which has been independently corroborated by sediment trap data (24):  $SST = \ln(Mg/Ca/0.38)/0.09$ . Applying this calibration to Mg/Ca from the top 10 cm yields an SST of  $26.6^{\circ} \pm 0.2^{\circ}$ C (the error is the SD of SSTs from 0 to 10 cm), which is slightly higher than the  ${\sim}26^\circ C$  modern mean annual SST in the Cariaco Basin (13). A calendar time scale, derived from the available radiocarbon ages (15) and by matching the grayscale record of 39PC to core 56PC, which has been placed on a varve chronology (18, 19), provides the chronological framework for the proxy SST record (21) (Fig. 2 and table S2).

Cariaco SST indicates a LGM cooling relative to the youngest samples (300 to 550 yr B.P.) of  $2.6^\circ \pm 0.5^\circ$ C (the compound error includes the SD of core-top and LGM samples) (Fig. 2). The glacial level of cooling in Cariaco agrees with the growing consensus for a 2.5° to 3.0°C cooling of the glacial tropics (8-10) and also agrees with a previous estimate of 3° to 4°C LGM cooling of Cariaco surface waters based on comparison of surface and deep planktonic oxygen isotope records (15) (SOM text). Both the early Holocene interval between 10,000 and 8000 yr B.P., with an average of  $27.1^{\circ} \pm 0.5^{\circ}$ C, and the B/A interval, with an average of  $26.9^\circ \pm 0.8^\circ$ C, are recorded as similar to, or slightly warmer than, modern conditions. The SST record also shows a differentiation between the early YD before 12,300 yr B.P.  $(23.4^{\circ} \pm 0.5^{\circ}C)$  and the late YD (24.3°  $\pm$  0.4°C), as well as between the colder LGM (23.9°  $\pm$  0.5°C) and the late glacial interval between 19,000 and 15,000 yr B.P. (24.7°  $\pm$  0.5°C). During the late glacial interval, there is a subtle transition at  $\sim 16,000$  years to slightly cooler  $(\sim 0.5^{\circ}C)$  SST that lasted until the prominent Bølling transition at ~14,600 yr B.P. This cool interval probably occurs within the Heinrich layer 1 (H1) time interval, which manifested itself as a very prominent cold interval between 17,500 and 15,000 yr B.P. in the subtropical northeast North Atlantic (25). During the full time interval corresponding to H1, however, Cariaco SSTs are statistically indistinguishable from their average during the late glacial, suggesting that H1 was not marked by cooling in the tropical Atlantic.

Comparison of the Cariaco SST record to the layer-counted Greenland Ice Sheet Project 2 (GISP2) ice core  $\delta^{18}$ O (proxy temperature) record (Fig. 2) reveals that the timing of the three rapid transitions that characterized the last glacial termination (the Bølling onset and the YD onset and termination), as judged by the midpoints of the Cariaco SST and GISP2  $\delta^{18}$ O records (26), are synchronous within the present age model and sample resolution (table S3). Some of the smaller features, such as the cold event that punctuates the Bølling at ~14,020 yr B.P. in GISP2 (13,990 ± 65 yr B.P. in Cariaco SST) and the Preboreal cooling at ~11,340 yr B.P. in GISP2  $(11,140 \pm 120 \text{ yr B.P. in Cariaco SST}),$ also appear to have correlatives in the Cariaco SST record. The Cariaco and GISP2 records clearly differ in some aspects, most markedly during the late B/A, during which the Cariaco SST record remains relatively elevated (~27°C), whereas the GISP2  $\delta^{18}$ O record indicates a progressive cooling. Comparison of Cariaco SST to absolutedated speleothem  $\delta^{18}O$  records from Hulu Cave in subtropical China also indicates that the deglacial transitions are synchronous within error (27) (table S3).

Because of the postulated link between atmospheric methane levels and the tropics (3-5), it is useful to make a comparison to the GISP2 methane record over the last glacial termination (1, 2) (Fig. 3C). Comparison of the timing of the transitions (table S3) indicates that the midpoints of the Cariaco SST and methane records are synchronous within estimated age errors [the exact timing of the methane changes depends on how gas ages are determined (5, 6)]. The records reveal a drop in SST  $(\sim 1^{\circ}C)$  and methane that might correspond to the Preboreal Oscillation (3); the methane drop occurs at  $\sim 11,330$  yr B.P. in the GISP2 chronology and ~11,140 yr B.P. in the Cariaco SST record, but the grayscale chronology in this part of PL07-39PC is uncertain (21). During the B/A chronozone, SST and CH4 remain elevated, as also inferred for summer East Asian monsoon precipitation (27), in contrast to the progressive cooling indicated by the Greenland air temperature proxy record (Fig. 3). During the B/A, methane concentrations and interpolar gradients indicate that tropical sources outweighed northern sources by  $\sim 3:1$ (3, 4). The observation of sustained warmth in the Cariaco record throughout the B/A, which would have fostered conditions for methane emissions in tropical wetlands (3), provides a potential explanation for the dominance of tropical methane emissions at this time. Alternatively, if some portion of the methane signal is due to methane clathrate degassing (28), then the similarity of Cariaco SST to the methane record might indicate a tropical climate impact on clathrate stability.

How can changes in the global climate system during deglaciation account for the similarity between the GISP2 records and the Cariaco SST and grayscale records? Previously observed faunal and grayscale correlations have been explained by invoking an atmospheric connection via the sensitivity of trade wind-driven upwelling in Cariaco to meridional temperature gradients, as mediated by North Atlantic temperatures (11, 14, 29). But the rapid shifts in SST in the Cariaco Basin are unlikely to represent a response to upwelling alone; first, the SST record is derived from G. ruber, which has nearly uniform annual distribution today and is not strongly associated with upwelling episodes under present conditions (20). In addition, the G. ruber SST record bears little relation to Globigerina bulloides abundance patterns in PL07-39PC, which are interpreted as an upwelling indicator (11, 12, 15, 20, 29). Second, the strong warming observed in the B/A time interval of the Cariaco SST record does not have a counterpart in an open Caribbean SST record from the Tobago Basin (10), which lies 430 km NE of Cariaco. Because warmer coastal conditions cannot be explained by upwelling, they must reflect an atmospheric forcing that was either subdued or alternatively not recorded at the Tobago site. Finally, the similarity between the Cariaco SST and the GISP2 methane record suggests that the temperature history of Cariaco is represen-

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that account for changing tropical methane emission over the deglaciation. Shifts in the mean position of the ITCZ over the tropical Americas during the deglaciation could explain the deglacial oscillations between warm and wet versus cold and dry conditions in Cariaco (16, 17). During the YD stadial, which stands out in all the records as the most dramatic climate reversal (Fig. 3), Cariaco returned to cold dry (17) conditions, and the thickness of the light laminae during this time interval reach their maximum (14), suggesting that the seasonal length of wind-driven upwelling and high productivity, which today is limited to late winter (13, 20), might have been significantly longer. A southward shift of the ITCZ during the YD is

tative of those parts of the terrestrial tropics



Fig. 2. Comparison of the Cariaco SST record, calculated using SST = ln (Mg/Ca/0.38)/0.09 (22, 24), with the GISP2  $\delta^{18}$ O (26) and GISP2 and Greenland Ice Core Project (GRIP) methane records (1, 2) over the past 25,000 years. The modern annual temperature at the Cariaco site is estimated at ~26°C, with an annual cycle of ~22° to 28°C (12, 13, 20). Chronology for the Cariaco record is based on calibrated radiocarbon dates and grayscale wiggle matching (supporting online material) and is independent of the GISP2 time scale. ppbV, parts per billion by volume; V-SMOW. Vienna standard mean ocean water scale; PB = Preboreal; GL = glacial.

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Fig. 3. Blowup of the deglacial portion of the records shown in Fig. 2. The midpoints of the three major transitions in the Cariaco SST record are as follows: Bølling onset, 14,650 ± 90 yr B.P.; YD onset, 12,820 ± 30 yr B.P.; YD termination, 11,490 ± 70 yr B.P. (table S3). Over the Bølling transition, methane gas ages derived from the thermal diffusion signature in nitrogen and argon isotopes are significantly younger (~150 years) than displayed here (3, 5). The methane reversal in the Preboreal time interval takes place at  $\sim$ 11,330 yr <sup>'</sup>B.P. in the GISP2 chronology and at  $\sim$  11,140 yr B.P. in the Cariaco SST record. But given the uncertainty in the , chronology Cariaco for this interval (21), the two events could be synchronous.



supported by records from Lake Titicaca  $(\sim 16^{\circ} \text{ to } 17.50^{\circ}\text{S}, 68.5^{\circ} \text{ to } 70^{\circ}\text{W})$ , which indicate maximum lake levels during this time period (30); by a reduction in meridional SST gradients in the eastern equatorial Pacific (31); and by modeling studies that suggest that meltwater input to the North Atlantic and associated thermohaline circulation collapse would be accompanied by a southward ITCZ shift and consequent cooling and drying of the Venezuelan coast (32, 33). The YD is also the time interval in which it is inferred that tropical methane sources dropped back nearly to their previously low glacial levels (3, 4), perhaps reflecting the cooling and drying of the tropical regions that were north of the ITCZ at this time.

A key question that emerges is whether the rapid shifts in the ITCZ implied by the Cariaco data were a passive response to changes in the Laurentide Ice Sheet (11) or were an active tropical feedback to highlatitude changes. The timing of deglacial SST changes in Cariaco, which was synchronous within  $\pm 30$  to  $\pm 90$  years with that of changes in Greenland air temperature, points to an active role, via changes in atmospheric convection (30) and/or water-

vapor transport (16), for the tropical Americas in deglacial climate change. High-resolution records from the western tropical Pacific indicate that there was a prominent increase in salinity (as indicated by  $\delta^{18}$ O values) during the YD (8, 9), which likely reflects a decrease in summer East Asian monsoon intensity, as supported by records from Hulu Cave in subtropical China (27). Some climatologists regard the Asian monsoon as a manifestation of the seasonal migration of the ITCZ (34). We speculate that the synchroneity between deglacial shifts observed in the Cariaco record, the records of East Asian monsoon intensity, the atmospheric methane signal, and Greenland air temperature is caused by rapid shifts in the mean position of the ITCZ during deglaciation.

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#### Supporting Online Material

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