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Future tales from ancient reefs: fundamental differences between Last Interglacial and modern coral reef community changes on the island of Curaçao (lower Caribbean)

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2 **Abstract**

3 Coral reefs have experienced widespread and accelerated decline in the last decades,
4 that was driven by a combination of global and local anthropogenic stressors. To
5 contextualize these changes, we compared the composition of coral reef communities
6 on Curaçao between 1973 and 2023 with that of corals preserved in fossil reefs from
7 the Last Interglacial period (128–116 ka), the last geological period of the Earth’s
8 history when global climate was warmer than pre-industrial. These fossil reefs,
9 exposed along the island’s leeward coast, provide a multi-millennial baseline of
10 ecological variability. Our analyses show that the ecological transformation observed
11 on modern reefs over the past five decades exceeds the magnitude and persistence of
12 community variability maintained for more than 12,000 years during the Last
13 Interglacial. This unprecedented transformation, likely driven by accelerating
14 anthropogenic impacts, marks an ecological shift unmatched in the long-term history
15 of Caribbean reef systems and may represent a striking signal of coral community
16 change in the Anthropocene.

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21 **Keywords:** Coral reef decline; Last Interglacial; Paleoecology; Caribbean reefs

2 Coral reefs are among the most diverse marine ecosystems, supporting millions of
3 people through services such as tourism, food security, and coastal protection¹⁻⁴. A
4 combination of global, e.g., ocean warming and acidification⁶ and local, e.g.,
5 overfishing and pollution⁷ stressors led global coral cover to decline by 50% between
6 1957 and 2007, and mass coral bleaching events and climate-driven disturbances have
7 further accelerated the loss of coral cover worldwide^{8,9}. These trends have been
8 particularly severe in the Caribbean, where local pressures such as disease outbreaks,
9 e.g., black- and white-band disease, hurricane impacts, nutrient enrichment, and the
10 overharvesting of herbivores, have intensified the effects of global change and
11 accelerated regional reef degradation.

12 Although the global decline of coral reefs is well documented, it remains unclear how
13 recent changes compare to those that happened in the geological past. Are the losses
14 observed over the past few decades truly without precedent, or do they echo patterns
15 seen during earlier periods of environmental stress?

16 The geological record provides a means of evaluating whether recent reef degradation
17 exceeds the range of natural variability. Fossil reefs, particularly from the Pleistocene,
18 can serve as ecological baselines against which modern reef assemblages can be
19 compared¹⁰⁻¹². The Last Interglacial (LIG, 128–116 ka) represents the most recent
20 period in Earth's history with global atmospheric temperatures exceeding pre-
21 industrial values (~1°C), smaller polar ice sheets, and sea levels several meters higher
22 (3-7m) than today¹³⁻¹⁵. Understanding how coral reefs responded to such conditions
23 may provide critical context for interpreting the magnitude and significance of recent
24 ecological change.

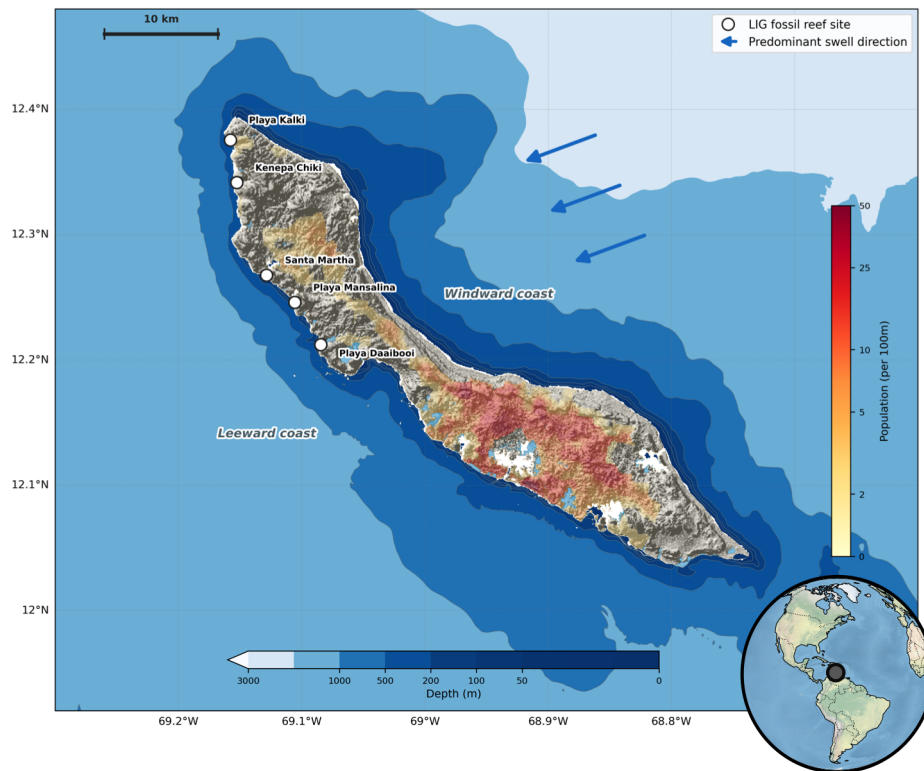
25 The island of Curaçao, in the southern Caribbean offers a unique opportunity to
26 compare modern and fossil reef dynamics^{11,16}. Along its coast, well-preserved LIG
27 reef stratigraphic sequences are exposed in erosional gullies and cliff faces¹⁷⁻²⁰,
28 providing a stratigraphically ordered, high-resolution record of coral community
29 composition and structure. These outcrops allow the reconstruction of ecological
30 change across early, middle, and late phases of the LIG. In parallel, Curaçao's modern
31 reefs are comprehensively surveyed, with quantitative ecological data available
32 starting from 1973. Together, these datasets create a natural laboratory for evaluating
33 whether the recent reef degradation exceeds the bounds of natural variability.

34 In this work, we present findings from an extensive palaeoecological survey of Last
35 Interglacial (LIG, 128-116 ka) coral reefs on the leeward coast of Curaçao, an area
36 sheltered from high wave energy. We compare changes in shallow reef (10 m depth)
37 coral cover and community composition observed over the past five decades with
38 fossil coral assemblages preserved in growth position from the early, middle, and late
39 phases of the LIG. By integrating these data with Southern Caribbean paleoclimatic
40 records, we show that although LIG reefs were subject to natural fluctuations in sea
41 level, temperature, and salinity, they did not exhibit the persistent community
42 restructuring or severe coral loss seen on modern reefs. Our results therefore point to

2 a form of reef ecosystem change without precedent in the late Quaternary history of
3 the southern Caribbean, likely driven by pervasive and lasting human impacts
4 defining the Anthropocene.

5 Modern and LIG reefs in Curaçao

6 We analyzed data from quantitative ecological surveys conducted between 1973 and
7 2023 on Curaçao's shallow coral reefs at 10 m depth (Figure 1). In 1973, coral cover
8 exceeded 60%, with large *Orbicella* spp. colonies dominating the benthic community
9 (Figure 2 A, B). Over the following three decades, coral cover declined steadily to
10 ~20%, corresponding to an annual loss rate of 1.4% (Figure 2 A, C). This initial
11 decline coincided with the outbreak of white-band disease, which decimated
12 *Acropora* populations across the Caribbean^{21,22}, and with the mass mortality of the
13 herbivorous sea urchin *Diadema antillarum*, leading to reduced grazing pressure and
14 macroalgal overgrowth on Curaçaoan reefs²³.

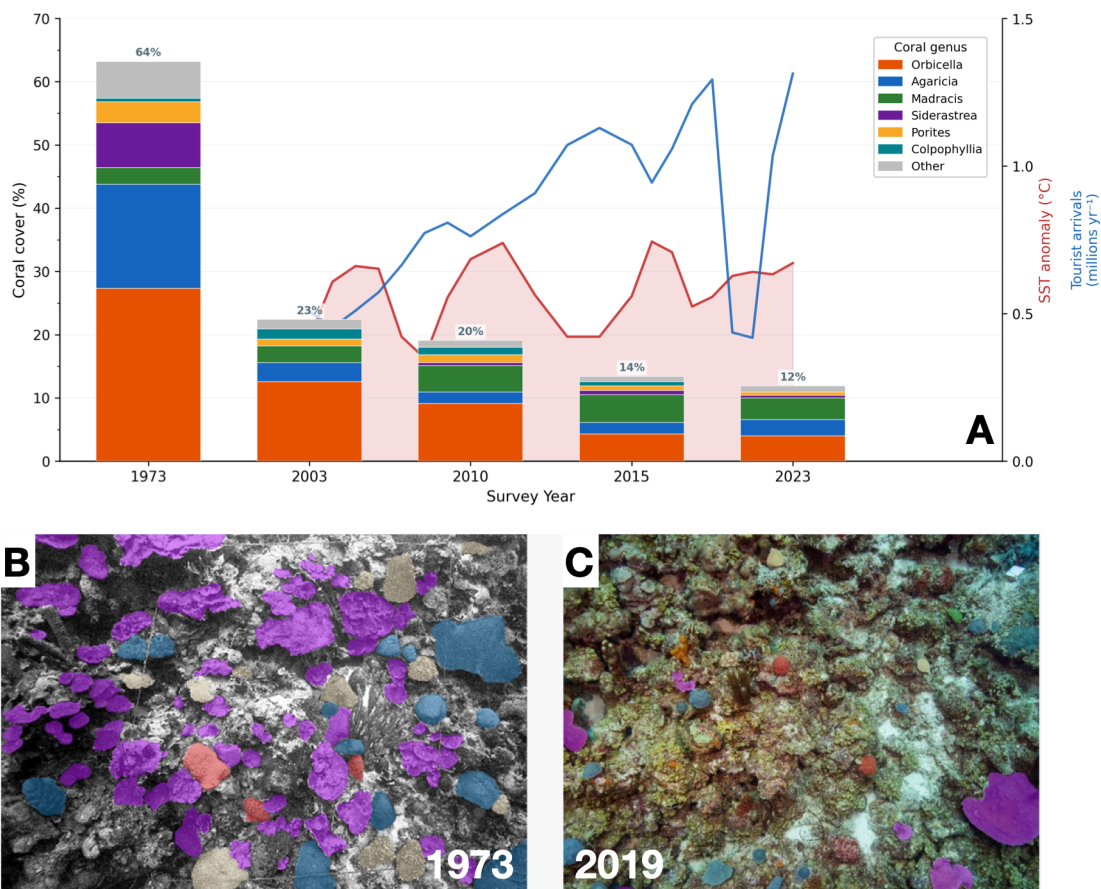


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16 **Figure 1.** Study area map of Curaçao. White circles indicate Last Interglacial (LIG) fossil reef survey
17 sites along the leeward coast; the red star marks the modern reef monitoring site. Ocean bathymetry
18 derived from the Global Multi-Resolution Topography (GMRT) synthesis, with depth contours at 50,
19 100, 200, 500, and 1000 m. Population density (persons per 100 m pixel) from WorldPop is overlaid on
20 land. Blue arrows indicate the predominant swell direction driven by the easterly trade winds.

21 While disease and herbivore loss initiated the decline, mounting anthropogenic
22 pressures likely amplified its severity. Although the island's population remained
23 relatively stable²⁴, the number of tourist arrivals more than tripled between 1995 and
24 2019, reaching 1.29 million annual visitors²⁵ (Figure 2 A). Coastal development and

2 the discharge of insufficiently treated sewage, particularly near urban centers ²⁶, likely
 3 contributed to eutrophication and localized reef degradation. Concurrently, the effects
 4 of global climate change intensified the pressure on Curaçao’s reefs. Marine
 5 heatwaves triggered coral bleaching events in 1987, 1990, 1995, and 1998 ²⁷, while
 6 several hurricanes and tropical storms including Lenny (1999), Ivan (2004), and Omar
 7 (2008), inflicted direct physical damage on reef structures ²⁸. After 2003, coral cover
 8 continued to decline, albeit at a slower pace of 0.6% per year (Figure 2 A), with
 9 another severe bleaching event in 2010, causing a 1% loss of live coral cover in only a
 10 few months ²⁷. Although overall community composition remained relatively stable,
 11 average colony size decreased (Figure 2 B,C) due to the loss of large *Orbicella* spp.
 12 colonies ²⁹.



13

14 **Figure 2.** Temporal changes in coral reef community structure and environmental drivers on the shallow reefs of
 15 Curaçao (10 m depth), 1973–2023. **A)** Genus-level coral cover (%) as stacked bars, with superimposed annual sea
 16 surface temperature (SST) anomaly (°C; NOAA ERSSTv5, baseline 1973–2022, red line) and tourist arrivals
 17 (millions yr⁻¹; Curaçao Tourist Board, blue line). **B)** and **C)** visual examples of hard coral cover in 1973 and 2019
 18 of the same photo quadrat on Curaçao. Colors indicate different coral genera (images taken by Bak and Meesters).

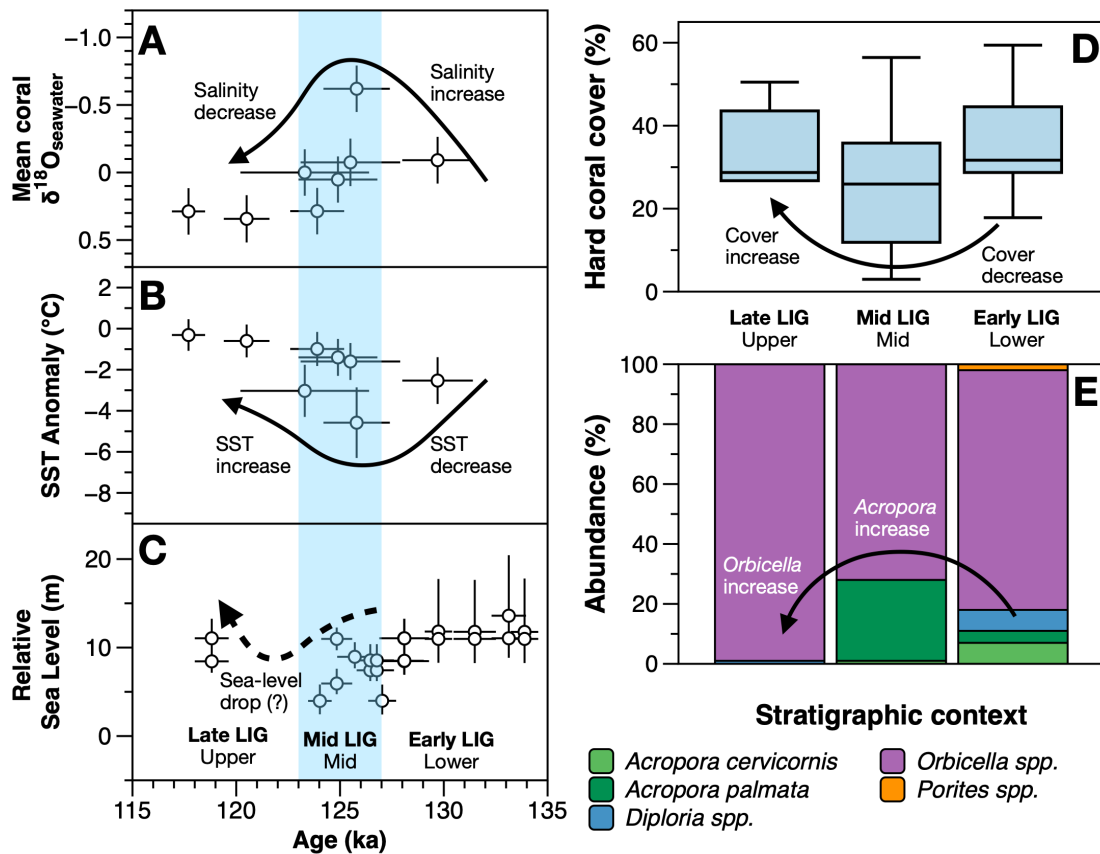
19 To evaluate whether ecological changes comparable to those on modern reefs
 20 occurred in the geological past, we turn to the fossil record. The fossil reef outcrops in
 21 Curaçao expose stratigraphically ordered reef frameworks, with older reef structures
 22 at the base and younger sequences toward the top, corresponding to the early, middle,
 23 and late phases of the Last Interglacial (LIG, 128–116 ka), a period characterized by
 24 global temperatures and sea levels equal to or exceeding present-day conditions.

2 Hard coral cover averaged 26.4% during the early LIG, declined slightly to 23.7% in
3 the mid-LIG, and rose again to 28.7% in the late LIG (Figure 3 D). These millennial-
4 scale fluctuations were modest in magnitude and accompanied by reversible shifts in
5 community composition. Notably, the mid-LIG was marked by a transient increase in
6 *Acropora palmata* abundance and a decline in *Orbicella* spp., followed by a return to
7 *Orbicella*-dominated assemblages in the late LIG (Figure 3 E).

8 These community shifts occurred against a backdrop of regional environmental
9 fluctuations during the Last Interglacial, as documented in previous studies ³⁰⁻³².
10 Strontium/calcium-derived sea surface temperature (SST) reconstructions from
11 *Diploria* corals on neighboring Bonaire indicate that SSTs were slightly cooler than
12 present at the onset of the interglacial (~128 ka)^{30,32}, followed by a sharp thermal drop
13 of 2.1 ± 0.7 °C around 126 ka, and a rapid return to modern-like conditions thereafter
14 ³¹ (Figure 3 B). The same proxies suggest that while temperature seasonality during
15 the early and late LIG was comparable to modern values, it was notably amplified
16 between 126 and 124 ka ³². Salinity reconstructions from the same corals indicate a
17 temporary freshwater pulse around 125.8 ka, followed by increasing salinity toward
18 the end of the interglacial ³¹ (Figure 3 A).

19 Sea-level variability during the LIG may have also influenced reef development on
20 Curaçao. While local sea level in the southern Caribbean was likely shaped by glacial
21 isostatic adjustment and rose gradually throughout the interglacial, stratigraphic
22 evidence from Curaçao's reef terraces suggests minor internal sea-level fluctuations
23 (Figure 3 C). These may align with a brief global sea-level fall of approximately 1 m
24 recorded in the Bahamas around 124–125 ka, possibly linked to asynchronous melting
25 of Northern and Southern Hemisphere ice sheets ^{33,34}. Although wind and wave
26 energy reconstructions for the LIG remain sparse, climate model simulations centered
27 at 127 ka indicate weaker trade winds in the Southern Caribbean ³⁵ but more favorable
28 conditions for tropical cyclone genesis across the broader Caribbean basin ³⁶. These
29 fluctuations in sea level and storm dynamics may have contributed to mid-LIG shifts
30 in coral community composition observed in the fossil record.

31 Despite these climatic and oceanographic fluctuations, the LIG coral communities on
32 Curaçao exhibited only moderate and reversible ecological responses. During the
33 mid-LIG, a shift in community composition occurred, with a temporary increase in
34 *Acropora palmata* coinciding with reduced *Orbicella* spp. cover (Figure 3 E). This
35 transition may reflect opportunistic colonization by *A. palmata* following storm
36 disturbances, consistent with its known capacity to proliferate via fragmentation.
37 However, this shift did not result in sustained coral loss. As environmental conditions
38 stabilized toward the end of the interglacial, coral cover increased (Figure 3 D), and
39 *Orbicella* spp. once again dominated the reef framework. Overall, LIG reef
40 communities displayed resilience to regional environmental variability, maintaining
41 ecological structure over millennial timescales.



2

3 **Figure 3.** Mean coral $\delta^{18}O_{\text{seawater}}$ for Bonaire corals³¹ using the Sr/Ca - SST relationship of -0.066 ³⁷ and
 4 corresponding coral $\delta^{18}O$ - SST relationship of $-0.196\text{‰ per }^{\circ}\text{C}$ ³⁷. B) Mean coral Sr/Ca - SST anomaly for
 5 Bonaire corals³¹ calculated using the same annual mean Sr/Ca - SST used in A). Interpretations of oscillations in
 6 A) and B) are based on the discussions in Brocas et al.^{31,32}. C) Sea-level index points^{17,38-40} for the Northern part
 7 of the island of Curaçao, filtered to avoid inclusion of sites with differential tectonic uplift. Horizontal error bars in
 8 A-C represent 2-sigma age errors, while vertical error bars represent 1-sigma errors. D) Whisker plots of hard
 9 coral cover across the 5 sites on Curaçao surveyed and three stages of LIG reef growth indicated in (E). E)
 10 Community abundance at each stage of LIG reef growth, focusing on the main hard coral constituents of each
 11 stage.

12 Discussion and conclusions

13 The ecological trajectories of fossil and modern reefs on the leeward side of Curaçao
 14 provide a long-term perspective on the range of coral reef responses to environmental
 15 change. Over the course of the LIG, coral communities in this area responded to
 16 environmental variability, (including shifts in temperature, salinity, sea level, and
 17 possibly storm activity) with moderate changes in composition and structure that
 18 proved reversible over millennial timescales. Coral cover remained relatively stable,
 19 and community dominance by *Orbicella* spp. re-emerged as conditions stabilized. By
 20 contrast, the past five decades have seen a dramatic and sustained decline in coral
 21 cover, affecting multiple taxa and lacking any clear signs of recovery or functional
 22 reorganization. This contrast highlights a rate and persistence of reef degradation that
 23 exceeds the ecological variability observed under natural climate forcing during the
 24 Last Interglacial.

2 The mid-LIG shift from long-lived, slow-growing *Orbicella* spp. to fast-growing
3 *Acropora palmata* suggests that ancient coral communities were capable of adjusting
4 to environmental stress through changes in dominant functional groups and life
5 history strategies. This transition, from a K-selected generalist (*Orbicella* spp.) to an
6 r-selected opportunist (*Acropora palmata*), is consistent with ecological theory
7 predicting increased opportunism under disturbance regimes. Importantly, this shift
8 was temporary: as conditions stabilized later in the interglacial, *Orbicella* spp.
9 regained dominance and coral cover rebounded. In contrast, the trajectory of modern
10 reefs shows no comparable capacity for reorganization. Since the 1970s, coral cover
11 decline has been broad-based, marked by the loss of large colonies, reduced coral
12 size, and persistent mortality across taxa, with little evidence of adaptive restructuring
13 or recovery ²⁹.

14 It is worth highlighting that comparisons between modern and fossil reef records are
15 inherently constrained by methodological limitations, which must be considered when
16 interpreting differences among periods. Fossil data lack the temporal resolution of
17 modern ecological monitoring and are subject to preservation bias, including the
18 inability to distinguish live from dead coral or detect short-lived ecological
19 overgrowths. However, such constraints generally act to dampen or obscure evidence
20 of ecological disturbance rather than exaggerate it, making the fossil record a
21 conservative baseline for comparison. Moreover, the fossil record provides a unique
22 and necessary window into the long-term dynamics of coral reef communities, one
23 that is inaccessible through short-term ecological studies alone ¹².

24 Building on this long-term perspective, our analysis of LIG reef sequences on
25 Curaçao reveals no evidence of sustained coral loss or persistent community collapse,
26 despite pronounced climatic variability during that period. Although LIG reefs
27 experienced fluctuations in temperature, sea level, and oceanographic conditions,
28 these changes were accompanied by moderate and reversible ecological shifts rather
29 than enduring structural decline. In striking contrast, the scale and rate of degradation
30 observed on Curaçao's modern reefs—characterized by sharp, island-wide coral loss
31 within just five decades—have no clear analogue over at least the past 120,000 years.

32 The rapid, island-wide collapse we document in Curaçao represents more than an
33 ecological regime shift; it may also carry stratigraphic significance. A synchronous
34 breakdown of reef-building communities at this scale is likely to leave a durable
35 imprint in the island's carbonate archive, preserving evidence of an abrupt and
36 unprecedented reorganization of reef ecosystems. In this sense, the transformation of
37 Curaçao's reefs may not only define a biological turning point but also constitute a
38 geological signal. With no comparable disruption evident in the Late Quaternary
39 record, modern reef degradation strengthens the case that coral reef collapse could
40 form a lasting stratigraphic marker of the Anthropocene.

2 **Methods**

3 **Modern coral reef data**

4 The data on the historical evolution of modern reefs was obtained from several
5 different sources. Data for 1973 were gathered from the PhD thesis of Nagelkerken
6 (1979) (9 sites, % cover, as original per site data was lost). Data for 2003 was
7 compiled by K. Vermonden ⁴¹ (island-wide average, 9 sites). Data for 2010 was
8 compiled by M.J.A. Vermeij (CARMABI, unpublished data, island wide average, 21
9 sites). The 2015 dataset was compiled by the Waitt Institute (145 sites, the same
10 dataset used in Sandin et al ⁴²) using the Global Coral Reef Monitoring Network
11 (GCRMN) recommended methodology for surveying Caribbean reef communities ⁴³.
12 The 2023 dataset was compiled by UvA/CARMABI (122 sites using the GCRMN
13 methodology).

14 **LIG coral reef data**

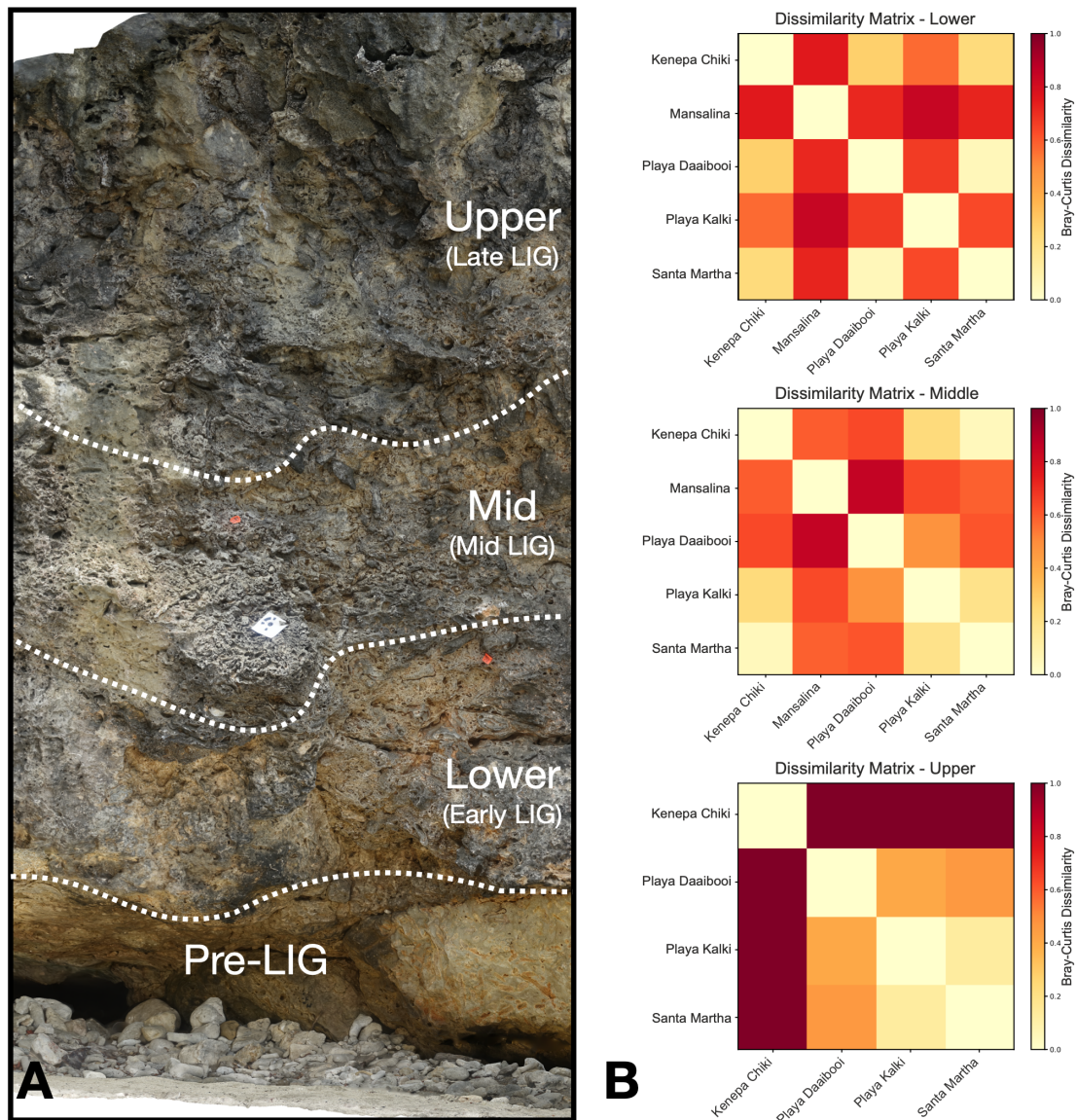
15 We surveyed 5 sites where fossil reefs are exposed above sea level on the leeward
16 coast of Curaçao. To capture and analyze the entire exposed LIG reef sequence at
17 each outcrop, land-based Structure from Motion/Multi-View Stereo (SfM/MVS)
18 surveys were conducted (see example in Figure 4 A). Using a 20.1-megapixel Sony
19 DSC-RX100M3 camera (8.8 mm focal length and resolution of 5472 x 3648 pixels)
20 mounted on a collapsible pole, around 750 photos were collected per site. At least six
21 ground control points (GCPs) were evenly distributed within each outcrop for
22 georeferencing purposes. Positions and elevations of each GCP were then measured
23 using an Emlid Reach RS2+ dual-band dGNSS receiver (Rover). Meanwhile, a
24 second Emlid Reach RS2+ receiver (Base) recorded a daily continuous static base
25 station log from atop the CARMABI Research Station (12.122527 N, -68.968600 E).
26 Following data collection, sketches of significant ecological and lithological
27 components were made for later reference.

28 Post-processing of dGNSS data began by correcting the Base data using the online
29 Canadian Spatial Reference System Precise Point Positioning (CSRS-PPP) tool
30 provided by Natural Resources Canada (NRCan). Using the corrected Base position
31 and elevation, Rover survey logs were then post-processed using Emlid Studio Stop
32 and Go (©Emlid Tech Kft., v. 1.3). Resulting GCP positions were then converted
33 from WGS84 ellipsoidal height to EGM08 orthometric height and the root-mean
34 squares of all associated errors were calculated (see Supplementary Material for raw
35 and processed dGNSS data). Next, digital twins of each site were created using the
36 SfM/MVS software Agisoft Metashape Professional edition (version 2.1.0 build
37 17532). Within each model, the above-mentioned post-processed GCPs were then
38 manually identified. Once constructed, high-resolution orthomosaics (< 1.5 mm/pix)
39 were then exported.

40 To extract paleoecological data from different parts of each outcrop captured via the
41 digital twins, we subdivided each model into a maximum of three synchronously
42 occurring reef subunits (lower, middle, and upper). While time-averaging is of

2 concern when drawing ecological data from fossil reefs ^{44,45}, we made a concerted
3 effort to circumvent this by basing the subunits on relative elevation to the LIG coral
4 reef terrace top as well as stratigraphic context. To further better constrain time-
5 averaging and add replicability, three 10-m point intercept transects (PITs) were
6 plotted horizontally with a vertical spacing of 50 cm around the vertical midpoint of
7 each subunit. In total nine PITs were selected per outcrop and, depending on outcrop
8 dimensions and exposure, additional sets of PITs were collected at different sections
9 of the outcrop and treated as additional sub-sites. Drawing on the experience of
10 previous paleoecological surveys, we utilized a PIT interval of 10 cm to achieve the
11 most reliable ecological data ^{10,46,47}. PIT data was extracted from the scaled
12 orthomosaics in QGIS (v. 3.34.4-Prizren), where interval points were classified
13 following a tiered scheme down to the genus level. Care was taken to only classify in-
14 growth position coral colonies as 'live colonies'. Final site-specific, paleo benthic
15 coverage was then calculated across each subunit by taking the average of
16 classifications for each subunit (lower, middle, and upper).

17 Following benthic coverage derivation, dissimilarity was calculated across each site
18 and respective subunit using Bray-Curtis dissimilarity ⁴⁸ of the square-root
19 normalized genus abundance data (Figure 4 B). We then analyzed the dissimilarity
20 within ages using a permutation test (n=10,000). The resulting p-values: lower
21 (0.9824), middle (0.8823), and upper (0.8338) strongly support our field observations
22 that there are 3 distinct phases of coral growth within the leeward LIG reefs of
23 Curaçao. In order to assess the effect of stratigraphic age on the shift in hard coral
24 cover, we fitted a Linear Mixed-Effects (LMM) model using the glmmTMB package
25 in R (v. 4.4.3) ⁴⁹. The model included stratigraphic age as a fixed effect and
26 incorporated site as a random intercept to account for spatial variations across sites.
27 None of the predictors included in the LMME were collinear with one another. Model
28 validation diagnostics plots were obtained via the DHARMA package ⁵⁰. Model
29 residuals against fitted values showed homogeneity and no additional variance
30 structure was added to the model.



2

3 **Figure 4.** A) Excerpt of the digital twin of the LIG fossil reef at Playa Daaibooi. B) Dissimilarity matrices
 4 between the surveyed sites for the Lower, Mid, and Upper LIG. Kenepa Chiki serves as the one outlier in the
 5 upper record as it is dominated by a thick *A. cervicornis* rubble lay and has no in-growth position corals present.

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7 **Author contributions**

8 AR, PTB, and BM wrote the manuscript, based on an original idea conceived by AR
9 and EM. AH and MV provided data on historical coral reef patterns on Curaçao. AR,
10 PTB, YCE, SB, GS, GS, DC, and PS participated in the survey of fossil sites. PTB
11 analyzed the fossil reef data with guidance from CW and SB. All authors contributed
12 to the manuscript, revised it through multiple rounds, and approved the final version.
13 ChatGPT (OpenAI) was used to support the refinement of narrative structure, clarity
14 of expression, and adherence to journal formatting guidelines. All content generated
15 with its assistance was critically reviewed and revised by the authors.

16 **Conflict of interest**

17 The authors declare no conflict of interests

18 **Data availability**

19 All data is available in Zenodo at this link: <https://doi.org/10.5281/zenodo.15570498>

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