

Large-scale climate variability and marine heatwaves increase harmful algal bloom events along global coastlines

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Abstract

Climate change is reshaping coastal harmful algal blooms (HABs), yet how climate processes shape them remains poorly understood. We constructed a 1990–2025 country–year panel of coastal countries integrating country-level coastal exposure to ENSO, marine heatwaves (MHWs), HAB events and 13 environmental variables. Poisson pseudo-maximum-likelihood models showed that ENSO exposure had a modest linear relationship with HAB event counts, while MHW frequency exhibited a U-shaped nonlinear relationship. Probit models showed nonlinear associations of both climate variables with HAB occurrence probability, which rose increasingly rapidly at high MHW frequencies. The MHW–HAB relationship varied with the concurrent ENSO phase, strengthening during El Niño but weakening or reversing during La Niña. Spatial heterogeneity was strongest at the basin level, with El Niño affecting more basins than La Niña. At high latitudes, warm and cold ENSO phases had opposing effects, with a particularly strong positive La Niña effect. Sea surface height and iron strengthened MHW effects, while salinity and sea surface height moderated El Niño and La Niña effects, respectively. These findings establish a multiscale framework in which ENSO provides the large-scale climatic background for HAB events, whereas MHW frequency captures the key thermal stress of repeated heat extremes rather than transient local warming.

Introduction

ENSO, the dominant mode of large-scale climate variability, reshapes regional ocean conditions through atmosphere–ocean teleconnections¹, whereas marine heatwaves manifest as anomalous warming of regional seas and are often accompanied by changes in upper-ocean stratification and mixing². Together, these processes influence coastal ecosystems worldwide³. Under persistent disturbance from both climate processes, the frequency and spatial extent of harmful algal blooms (HABs) in coastal areas worldwide have expanded rapidly^{4,5}. According to the Harmful Algal Event Database (HAEDAT), only 430 HAB events had been reported worldwide before 1990, whereas more than 13,640 additional events were reported over the subsequent three decades⁶, representing a 32-fold increase. Their distribution has extended beyond traditionally warm waters into cold-water regions⁷. HABs alone cause an estimated US\$8 billion in direct losses to marine fisheries each year⁷, while their combined threats to aquatic ecosystems, coastal tourism and human health are more difficult to quantify^{8–10}.

Previous HAB research has focused on freshwater systems such as inland lakes and rivers^{11,12}, as well as local coastal waters, including estuaries, recurrent red-tide hotspots and aquaculture-intensive areas^{13,14}. However, discussions of climate drivers have largely been confined to regional thermal stressors such as long-term ocean warming and marine heatwaves^{15,16}, with limited consideration of the broader context of large-scale climate variability, particularly ENSO. This missing perspective makes current findings strongly region-dependent and difficult to generalize across global coastal systems. Existing case studies show that the effects of warming on HABs are not uniform. Gobler et al. showed that long-term ocean warming has expanded the thermally suitable habitat of toxic algae in parts of the North Pacific and North Atlantic and lengthened potential bloom seasons¹⁷. An analysis of more than 1.2 million satellite images from 2003 to 2022 found that floating algal blooms had expanded significantly across multiple ocean regions and suggested ocean warming and eutrophication as possible drivers¹⁸. By contrast, phytoplankton biomass declined by approximately 50% during marine heatwaves in four eastern-boundary upwelling systems, including the California and Benguela systems¹⁹. Thus, the relationship between local warming and HABs exhibits pronounced regional heterogeneity. Fundamentally, HAB formation depends not only on seawater temperature but also on nutrient supply, stratification, upwelling, runoff and circulation-driven transport^{20,21}, whose interannual variability is broadly modulated by large-scale climate variability²². Therefore, global coastal HAB events should be examined within a multiscale framework that integrates large-scale climate variability and regional thermal extremes.

Previous studies have often simplified the response of HABs to climate disturbances as a linear relationship; nonlinear associations remain largely qualitative^{11,23} and have not been tested empirically at the global scale. Mechanistically, ENSO shapes conditions for algal proliferation by altering seawater temperature, runoff, upwelling and nutrient transport, but strong climate anomalies may also suppress algal development by disrupting nutrient supply and abruptly restructuring water-column structure^{22,24}. Similarly, algae have physiological thermal optima: moderate warming promotes proliferation, whereas sustained exceedance of thermal thresholds can constrain growth and reproduction through declining dissolved oxygen, nutrient depletion and disrupted stratification^{24,25}. When ENSO and marine heatwaves coincide, multiple ecological and hydrological processes may reinforce or offset one another, thereby shaping nonlinear and spatially heterogeneous responses of global coastal HABs.

Here, we constructed a 1990–2025 country–year panel of coastal nations, using the continental shelf within the 200-m isobath of each country's exclusive economic zone as the study area. ENSO exposure was characterized by the sensitivity of coastal sea-surface temperature anomalies in each country to the Niño3.4 index (Fig. 1a). Marine heatwave exposure was derived from daily NOAA OISST sea-surface temperature data and measured as annual MHW frequency, MHW days and cumulative intensity (Fig. 1b–d). HAB events were obtained from HAEDAT and characterized using cumulative event counts (Fig. 1e) and occurrence probability (Fig. 1f). Figure 1g,h shows the temporal trajectories of the climate indicators and HAB events, respectively. Empirically, we first used PPML and Probit models controlling for country and year fixed effects and differences in observation effort to test linear, nonlinear and interactive relationships of ENSO and marine heatwaves with HAB event counts and occurrence probability. Second, we identified spatial heterogeneity across ocean basins, climate zones and long-term warming backgrounds. Third, we incorporated 13 marine environmental indicators spanning biogeochemical conditions, physicochemical properties and ocean dynamics to test how they modulate climate–HAB relationships. Finally, we assessed robustness using alternative control variables and by excluding observations from the COVID-19 period.

Climate effects on HAB events: a linear positive ENSO association and nonlinear perturbations dominated by MHW frequency

The two climate processes exhibited distinct relationships with HAB events. ENSO had a stable linear association. A one-standard-deviation increase in country-level coastal ENSO exposure was associated with a 14.1% increase in the expected number of reported HAB events ($p = 0.039$; Fig. 2a), consistently accounting for overall variation in HAB event counts worldwide. By contrast, none of the three marine heatwave metrics exhibited a stable average linear association. PPML models including quadratic terms showed a significant nonlinear relationship between MHW frequency and HAB event counts ($p = 0.003$; Fig. 2b), with a characteristic U-shaped response²⁶. HAB event counts reached a minimum at an annual mean of approximately 3.3 heatwaves and then increased continuously as MHW frequency rose.

Nonlinear climate responses of HAB occurrence probability: a gradual ENSO response and ENSO-dependent MHW effects

Probit models showed a significant but gradual U-shaped relationship between ENSO exposure and HAB occurrence probability ($\beta = 0.0105$, $p < 0.001$; Fig. 3a). HAB occurrence probability was relatively low at intermediate ENSO exposure and increased slowly at high exposure. MHW frequency showed a more pronounced nonlinear association ($\beta = 0.0462$, $p = 0.065$; Fig. 3b). At average and intermediate frequencies, thermal stress remained below the triggering threshold and HAB occurrence probability was low; when heatwaves reached the high-frequency range, the probability increased sharply. These results suggest that marine heatwaves do not induce HAB outbreaks through a gradual cumulative process, but instead trigger a step-like increase in occurrence probability when extreme heatwaves recur frequently^{27,28}.

More importantly, the nonlinear influence of MHWs on HAB occurrence depended strongly on the concurrent ENSO background^{29,30}. Joint significance tests showed that the linear and quadratic interaction terms of ENSO with MHW frequency and cumulative intensity were significant (MHW frequency, $p = 0.030$; MHW cumulative intensity, $p < 0.001$), confirming that ENSO variability reshapes the nonlinear relationship between regional thermal stress and HAB occurrence probability.

Specifically, as ENSO exposure increased, the effect of MHWs on HAB occurrence probability shifted markedly in the positive direction (Fig. 3c,d). At low ENSO exposure, HAB occurrence probability declined as MHW frequency increased³. As ENSO exposure rose, this negative relationship gradually weakened and, at high ENSO exposure, gave way to a nonlinear pattern with a sharp rise at high MHW frequencies (joint test, $p = 0.030$). Increasing ENSO exposure similarly altered the response to MHW cumulative intensity. At low ENSO exposure, occurrence probability declined continuously with cumulative intensity; at high ENSO exposure, the relationship became inverted U-shaped, with the highest occurrence probabilities at moderate-to-high cumulative intensity (joint test, $p < 0.001$). Phase-specific models further showed that El Niño significantly strengthened the positive relationship between MHW frequency and HAB occurrence probability³¹, whereas the relationship remained largely flat during neutral phases (Fig. 3f). Whether regional marine heatwaves induce HAB occurrence therefore depends not only on the heatwaves themselves, but also on threshold constraints and phase modulation imposed by the concurrent large-scale ENSO background.

Spatial heterogeneity in the effects of ENSO and MHWs on HAB events

Spatial heterogeneity in the relationship between ENSO and HAB event counts was strongest across ocean basins, followed by climate zones, and showed pronounced phase asymmetry (Fig. 4a,c). At the basin level, between-group differences in the effects of El Niño and La Niña were substantially larger than those for the continuous ENSO index ($\Delta\beta = 3.00, 1.98$ and 0.48 , respectively), with El Niño showing the strongest cross-basin differentiation³². Specifically, El Niño was significantly negatively associated with HAB event counts in semi-enclosed marginal seas such as the Red Sea–Persian Gulf and Baltic Sea–North Sea, but positively associated with counts in more open basins such as the Atlantic–Caribbean. Robust La Niña effects occurred in only a few basins. Differences among climate zones were weaker but showed a clear latitudinal pattern: HAB events in subpolar and polar waters responded significantly to both the continuous ENSO index and its warm and cold phases, with a negative El Niño effect and a positive La Niña effect. Only El Niño showed a stable positive effect in temperate waters, whereas only the continuous ENSO index had a weak effect in tropical waters. Coefficient differences among SST-warming regimes were also small ($\Delta\beta < 0.41$). El Niño had a significant positive effect in the low-warming group, whereas only the continuous ENSO index had a significant positive effect in the moderate-warming group.

For MHWs, the relationship with HAB event counts also exhibited the strongest spatial heterogeneity at the ocean-basin scale (Fig. 4b,d), with broadly similar between-group effect ranges for the three MHW metrics (Fig. 4d). In the Pacific, only MHW frequency had a robust positive association with HAB event counts ($\text{FDR } q < 0.10$). In the Indian Ocean, MHW days and cumulative intensity both had significant negative associations, and MHW days were also significantly negatively associated with event counts in the Red Sea–Persian Gulf. Background warming further altered the direction of the effects of persistent heat exposure, with MHW days and cumulative intensity showing marginal positive effects in regions of moderate long-term SST warming, but marginal negative effects in regions of high long-term warming.

Environmental conditions modulate the effects of ENSO and MHWs on HAB events

Regional environmental conditions significantly modulated the direction and strength of climate effects on HAB event counts. Analyses of interactions between the climate indicators and 13 environmental variables (including chlorophyll, water clarity, nutrients, iron, dissolved oxygen, surface-current speed and sea-surface height) showed that the positive effect of MHW frequency on HAB event counts was significantly stronger at higher sea-surface height ($\beta_{\text{int}} = 0.246$, $q = 0.010$) and higher iron concentrations ($\beta_{\text{int}} = 0.438$, $q = 0.018$)³³, but weakened or even reversed at low sea-surface height or under iron limitation (Fig. 5a,b). Similarly, Higher salinity strengthened the effect of El Niño on HAB event counts ($\beta_{\text{int}} = 0.178$, $q < 0.001$; Fig. 5c). In contrast, sea-surface height modulated the La Niña effect in the opposite direction: low sea-surface height amplified it, whereas high sea-surface height weakened and ultimately reversed it into an inhibitory effect ($\beta_{\text{int}} = -0.321$, $q = 0.005$; Fig. 5d).

These interaction effects differed markedly among ocean basins. To identify the environmental factors that dominated this modulation within each basin, we selected the climate-disturbance–environment interaction with the strongest statistical effect in each basin (Fig. 5e). First, nutrient supply and hydrodynamic conditions jointly regulated responses in the Atlantic–Caribbean. Higher Fe and Si strengthened the effects of MHW frequency and the continuous ENSO index, respectively³⁴, whereas higher Speed and SSH strengthened the La Niña effect. Second, in the Indian Ocean, environmental factors predominantly modulated MHW effects. Higher O₂ and PO₄ strengthened the MHW-frequency effect, and a deeper MLD strengthened the effect of MHW days, whereas Si and SSH weakened the effects of MHW days and frequency, respectively³⁵. Third, environmental modulation of the El Niño effect was most prominent in the Mediterranean–Black Sea: pH, PO₄ and Si strengthened the effect, whereas ZSD and MLD weakened it³⁶. For MHW frequency, O₂ strengthened the effect, whereas salinity weakened it³⁸. Fourth, robust interactions in the Pacific were concentrated in Chl, ZSD and Fe, which positively modulated the effects of El Niño, MHW days and cumulative intensity, respectively. Fifth, the only robust interaction in the Baltic Sea–North Sea was a negative interaction between Si and La Niña. This may reflect the dominance of eutrophication, freshwater inputs and strong seasonality in this semi-enclosed shallow sea, which can obscure interactions between climate disturbances and individual environmental factors. Sixth, the Red Sea–Persian Gulf showed multiple forms of environmental modulation centred on ENSO signals. O₂ and PO₄ strengthened the El Niño effect, pH and salinity weakened it, and a deeper MLD further amplified the relationship between the continuous ENSO index and HAB event counts³⁷.

Robustness tests using alternative controls for observation effort and a pre-pandemic sample

We conducted two sets of robustness tests. First, we replaced the country-level observation-effort indicator in the baseline models with the number of scientific and technical journal articles from the WDI and the number of publications across all subject areas from SCImago, thereby controlling for the influence of national research output on the capacity to detect, record and report HAB events. Second, using the same model specifications, we re-estimated the models after excluding observations from the COVID-19 pandemic period (2020 onward) to remove potential interference from disruptions to monitoring, reporting delays and abnormal human activity. Neither test changed the main conclusions (Table 1), confirming the robustness of the results.

Table 1
Robustness tests: alternative control variable sets and pre-pandemic subsample regressions

Observation and models	OBIS full	OBIS pre	WDI full	WDI pre	Scimago full	Scimago pre
ENSO annual count	0.1316 (0.039)	0.1021 (0.065)	0.1096 (0.001)	0.0803 (0.067)	0.1095 (0.010)	0.0848 (0.046)
MHW frequency linear count	0.0979 (0.422)	-0.0481 (0.338)	0.0493 (0.513)	-0.0733 (0.085)	0.0531 (0.570)	-0.0718 (0.088)
MHW frequency count nonlinearity	0.2106 (0.003)	0.0382 (0.424)	0.1859 (< 0.001)	0.0830 (0.006)	0.1988 (< 0.001)	0.0813 (0.011)
MHW frequency high-tail slope	1.4534 (< 0.001)	0.4133 (0.022)	1.2154 (< 0.001)	0.5393 (< 0.001)	1.3435 (< 0.001)	0.5345 (0.001)
MHW frequency occurrence nonlinearity	0.0462 (0.065)	0.0466 (0.072)	0.0553 (0.038)	0.0451 (0.114)	0.0507 (0.060)	0.0497 (0.088)
ENSO occurrence nonlinearity	0.0105 (< 0.001)	0.0138 (< 0.001)	0.0094 (0.011)	0.0120 (0.001)	0.0086 (0.017)	0.0126 (0.001)
ENSO positive-count association	0.1225 (0.057)	0.0933 (0.101)	0.0865 (0.032)	0.0647 (0.159)	0.0987 (0.025)	0.0698 (0.119)
Note: All models in Table 1 include country and year fixed effects. Coefficients are reported with p values in parentheses, and standard errors are clustered by country. OBIS denotes observation effort; WDI denotes the number of scientific and technical journal articles; SCImago denotes the number of publications across all subject areas; full denotes the full 1990–2025 sample; and pre denotes the pre-COVID-19 sample for 1990–2019.						

Discussion

We developed a multiscale analytical framework to examine climate effects on HAB events and found that ENSO and MHWs exhibited distinct patterns of association (Figs. 2 and 3). ENSO had a stable positive average association with annual HAB event counts, but only a small nonlinear relationship with HAB occurrence probability. This suggests that ENSO primarily acts as a large-scale climatic background, persistently altering regional environmental conditions conducive to HAB formation and accumulation, though this influence is relatively mild. Previous studies have shown that ENSO teleconnections can transmit tropical Pacific signals to remote coastal ecosystems by altering seawater temperature, wind fields, coastal circulation and nutrient transport, producing phytoplankton responses with pronounced regional differences²⁴. By contrast, MHWs lacked a stable global-average linear association but clearly altered HAB occurrence probability at high frequencies and under specific ENSO backgrounds, indicating strong nonlinearity and background dependence³⁰. As ENSO exposure increased, the relationship between MHW frequency and HAB occurrence probability shifted from negative or flat to a rapid increase in the high-frequency range. Observational studies have likewise shown that anomalous warming can expand environmentally suitable conditions for harmful algae²⁹.

Strong ENSO phase differentiation across ocean basins (Fig. 4) indicates that ENSO teleconnection signals are substantially filtered by basin configuration. Specifically, El Niño was associated with fewer HAB events in semi-enclosed marginal seas, such as the Red Sea–Persian Gulf and Baltic Sea–North Sea, but with more events in relatively open basins such as the Atlantic–Caribbean. This contrast may arise because exchanges between semi-enclosed marginal seas and the open ocean are restricted, making their temperature, salinity, stratification and nutrient conditions more strongly governed by the combined effects of local winds and river inputs. Thus, the same ENSO phase may produce responses that differ substantially from those in open basins. Previous studies have shown that more open

basins may respond more directly to large-scale anomalies in wind stress, thermocline structure and currents induced by El Niño, thereby altering nutrient transport and phytoplankton growth and accumulation³⁸. By comparison, the effective influence of La Niña contracted sharply, with robust effects confined to a few smaller basins. This narrower influence may arise from intrinsic asymmetry between the warm and cold ENSO phases: El Niño warm anomalies are generally stronger and extend farther eastward, inducing broader and more coherent anomalies in convection, winds and ocean circulation, whereas La Niña anomalies are displaced farther westward and their remote effects are more readily modulated by background circulation, basin boundaries and local processes³⁹.

Differences in ENSO effects among climate zones were comparatively weaker but showed clear latitudinal differentiation (Fig. 4). HAB events in subpolar and polar waters responded significantly to both the continuous ENSO index and its warm and cold phases, but the phase effects were strongly asymmetric: El Niño significantly reduced HAB events, whereas La Niña significantly increased them. This pattern may reflect contrasting effects of warm and cold phases on high-latitude winds, sea-ice cover and upper-ocean mixing⁴². For example, central-Pacific El Niño events can cool the Canada Basin in summer and increase sea-ice cover, thereby shortening the window for algal growth⁴⁰. La Niña produces the opposite response, revealing a long-overlooked pathway through which meridional ENSO teleconnections modulate sea ice and stratification and create conditions for the expansion of HABs into cold waters. Tropical waters responded only weakly to the continuous ENSO index, while neither warm nor cold phases had significant effects. Strong thermal stratification in the tropics may restrict nutrient transport from depth to the surface, leaving phytoplankton growth in many low-latitude open waters persistently constrained by low surface nutrient concentrations^{13,41}, thereby weakening average phase effects at the climate-zone scale.

Differences in MHW effects among ocean basins (Fig. 4) suggest that recurrent thermal anomalies and persistent cumulative heat stress correspond to distinct ecological processes. In the Pacific, frequent heatwaves may shorten recovery windows, repeatedly reinforce upper-ocean stability and disrupt nutrient resupply, creating a competitive advantage for thermally tolerant or opportunistic harmful algae⁴⁵. By contrast, the Indian Ocean and Red Sea–Persian Gulf have high background temperatures, and some areas also experience persistent strong stratification and nutrient limitation. In these environments, longer-duration or higher-cumulative-intensity heat exposure may exceed the thermal optima of some harmful algae and further restrict nutrient supply to surface waters, shifting the effect on HAB events from enhancement to suppression. Consistent with this threshold interpretation, MHW days and cumulative intensity had marginal positive associations with HAB event counts in regions with moderate long-term SST warming, but marginal negative associations in regions with high long-term warming. This suggests that background warming may shift MHW effects on HAB events from thermal enhancement to thermal stress⁴⁶.

Local environmental conditions modulated and amplified both climate signals (Fig. 5). First, nutrients and trace elements imposed resource thresholds. Iron determines whether MHW-induced warming can overcome metabolic constraints and translate into proliferation³⁴. Nitrogen, phosphorus and other nutrients can relieve resource limitation, increase potential phytoplankton biomass and amplify responses to climate disturbances. Silicate may reshape climate effects on HAB events by altering competition between diatoms and non-siliceous phytoplankton. In waters dominated by diatom–dinoflagellate competition, an adequate supply of dissolved silicon helps maintain the competitive advantage of diatoms⁴². This offers a possible ecological explanation for the negative Si interactions identified in the Indian Ocean and Baltic Sea–North Sea: higher Si supply may weaken the response of some non-siliceous harmful algae to climate disturbances. Second, physicochemical conditions such as salinity, pH and dissolved oxygen may reshape climate–HAB relationships through physiological tolerance and community filtering. Salinity directly affects osmoregulation and habitat suitability in microalgae, and culture experiments show that harmful algal species and strains have distinct salinity optima and tolerance limits⁴³. The directions of modulation by pH and O₂ varied markedly among ocean basins. Third, hydrodynamic conditions acted as physical filters. Higher sea-surface height enhanced

water-column stratification and residence time, amplifying the positive effects of marine heatwaves; lower sea-surface height and stronger currents weakened positive climate effects through upwelling-driven renewal and advective dilution³⁵. Mixed-layer depth and water clarity jointly governed the light–nutrient balance, buffering or constraining the effects of climate signals on bloom dynamics.

This study reveals the multiscale response mechanisms through which climate change drives coastal HAB events. ENSO modulates the regional climatic background through teleconnections, while marine heatwaves are superimposed as transient disturbances; together, they reshape the occurrence and intensity of HAB events. The global-average linear association with ENSO was particularly pronounced, and El Niño affected a substantially broader area than La Niña. Further analysis of thermal mechanisms revealed that the critical determinant of HAB outbreaks was not the intensity of individual heatwaves, but the repeated thermal stress captured by MHW frequency. This finding advances beyond previous studies that treated heat intensity as a single driver and provides insights for routine coastal HAB monitoring and climate-hazard early warning.

Methods

Study area and variable definitions

We defined each national coastal analysis unit as the intersection of the country's exclusive economic zone (EEZ) with shallow continental-shelf waters inside the 200-m isobath, and area-weighted climate and environmental indicators within these units⁴⁴.

HAB event data were obtained from the HAEDAT⁶, aggregated by year and country, with overseas territories assigned to their sovereign states. Because the probability that a HAB event is reported may depend on a country's monitoring network, sampling intensity and research attention, the baseline models included $\log(OBIS_{it} + 1)$, the logarithm of the number of records in the Ocean Biodiversity Information System (OBIS). OBIS is an open database that compiles global records of marine species occurrences and was used to control for differences in observation effort at the country–year level⁴⁵. In the robustness tests, the number of scientific and technical journal articles from the World Bank and the number of publications across all subject areas from SCImago were used as alternative indicators of national monitoring capacity⁴⁵.

Marine heatwave metrics were derived from daily sea-surface temperature data in NOAA's Optimum Interpolation Sea Surface Temperature (OISST) product from 1982 onward^{46,47}. Following the definition and calculation method of Hobday et al.⁴⁸, we derived MHW days, MHW frequency (number of events) and cumulative intensity (°C d), and then aggregated these metrics using coastal-area weights.

We defined country-level coastal ENSO exposure, classification of El Niño and La Niña phases. The monthly Niño3.4 index was first aggregated to a calendar-year mean, N_t , and country-level mean annual coastal SST anomalies, $SSTA_{it}$, over the full OISST period were used to estimate the country-specific ENSO teleconnection loading, l_i :

$$SSTA_{it} = \alpha_i + l_i N_t + \epsilon_{it}$$

1

Country-level coastal ENSO exposure was defined as $ENSO_{it} = l_i N_t$. Using monthly Niño3.4 anomalies from NOAA ERSSTv6, we reconstructed El Niño and La Niña phases following the historical Oceanic Niño Index (ONI) event-identification criteria of NOAA/CPC⁴⁹. A complete event was defined as an ONI anomaly reaching the corresponding threshold for at least five consecutive overlapping three-month windows. For year t , windows were assigned to years

according to their central month. The ONI_m magnitudes of windows belonging to complete El Niño and La Niña events were then summed separately for each year and divided by 12, yielding annual exposure metrics that captured both event intensity and within-year duration. Country–year phase exposure was obtained by multiplying annual phase exposure by the country-specific loading l_i . To place El Niño and La Niña exposure on a comparable scale, both phase exposures were scaled by the sample standard deviation of the signed exposure difference, $E_{it}^{El} - E_{it}^{La}$, and entered jointly into the regression model, and set to zero in neutral years. Because ENSO phases represent globally synchronous shocks, global phase indicators are absorbed by year fixed effects. Phase effects were therefore identified primarily from cross-country variation in exposure generated jointly by global ENSO event intensity and country-specific ENSO teleconnection loadings.

Long-term SST trends were calculated from the 0.25° monthly NOAA OISST v2.1 product⁵⁰. For each ocean grid cell, a linear trend was estimated by ordinary least squares over a 120-month rolling window ending in the target year and converted to °C decade⁻¹. Grid-cell–year observations were retained only when at least 96 months were valid, then area-weighted according to their actual intersection with the study area to obtain country–year coastal trends, $TrendSST_{it}$, which were standardized within the estimation sample.

Environmental conditions were characterized using indicators of biogeochemistry, physicochemical properties and ocean dynamics. Biogeochemical and physicochemical variables included chlorophyll a (Chl), Secchi depth (ZSD), iron (Fe), dissolved oxygen (O₂), nitrate (NO₃), pH, phosphate (PO₄), silicate (Si) and salinity (SSS)⁵⁷. Physical and dynamical variables included photosynthetically active radiation (PAR), sea-surface height (SSH), mixed-layer depth (MLD) and current speed (Speed)³⁰. Current speed was calculated from eastward (uo) and northward (vo) current velocities. All variables followed the same country-assignment rules as HABs, MHWs and ENSO. For data with a vertical dimension, we selected the valid layer closest to the sea surface. Monthly gridded data were first area-weighted over the actual marine area within each national coastal study unit and then averaged by country and year. Owing to limitations in data coverage, the common analysis period was 1998–2025.

Variable standardization and model specification

Because ENSO exposure and the MHW metrics differ substantially in their units and ranges, all continuous climate variables were z-standardized within the actual estimation sample for each model to improve coefficient comparability, except for the observation-effort indicator and the El Niño and La Niña phase exposures, which were scaled using a common standard deviation.

First, our baseline specification used a Poisson pseudo-maximum-likelihood (PPML) model with country and year fixed effects⁵⁸. HAB event counts are non-negative count data containing many zero values; PPML retains zero observations directly and does not require the conditional variance to equal the conditional mean. The baseline regressions, heterogeneity analyses, moderator analyses and robustness tests all used this PPML framework. The model was specified as:

$$\mathbb{E}(Y_{it} \mid \mathbf{Z}_{it}) = \exp(\beta C_{it}^z + \gamma O_{it} + \mu_i + \delta_t)$$

2

where Y_{it} denotes the number of HAB events reported by country i in year t , C_{it}^z denotes climate exposure, $\log(OBIS_{it} + 1)$ controls for marine observation effort at the country–year level, and μ_i and δ_t denote country and year fixed effects, respectively.

To allow for possible nonlinear relationships of ENSO and MHWs with HAB event counts, we further included linear and quadratic terms for each climate indicator in the baseline PPML model:

$$\mathbb{E}(Y_{it} | \mathbf{Z}_{it}) = \exp \left(\beta_1 C_{it}^z + \beta_2 (C_{it}^z)^2 + \gamma O_{it} + \mu_i + \delta_t \right)$$

3

Nonlinearity was evaluated using a two-sided test of β_2 and the predicted response curve. Curves show average marginal predictions over the observed sample, with 95% confidence intervals.

Second, we used Probit models to examine the effects of the climate indicators on HAB occurrence probability⁵⁹. The dependent variable was redefined as a binary indicator equal to 1 when at least one HAB event was reported in a country–year and 0 otherwise. To allow for nonlinear and interactive relationships of ENSO and MHWs with HAB occurrence probability, the Probit models included quadratic and interaction terms:

$$Pr(D_{it} = 1 | \text{\textcolor{red}{\texttt{varvec}}}Z_{it}) = \Phi \left[\beta_1 C_{it}^z + \gamma O_{it} + \mu_i + \delta_t \right]$$

4

$$Pr(D_{it} = 1 | Z_{it}) = \Phi \left[\beta_1 C_{it} + \beta_2 C_{it}^2 + \gamma O_{it} + \mu_i + \delta_t \right]$$

5

$$Pr(D_{it} = 1 | Z_{it}) = \Phi \left[\beta_E E_{it} + \beta_H H_{it} + \theta_1 (E_{it} \times H_{it}) + \gamma O_{it} + \mu_i + \delta_t \right]$$

6

$$Pr(D_{it} = 1 | Z_{it}) = \Phi \left[\beta_E E_{it} + \beta_{H1} H_{it} + \beta_{H2} H_{it}^2 + \theta_1 (E_{it} \times H_{it}) + \theta_2 (E_{it} \times H_{it}^2) + \gamma O_{it} + \mu_i + \delta_t \right]$$

7

where E_{it} denotes standardized ENSO exposure and H_{it} denotes the standardized MHW metric.

Third, to identify spatial and background-dependent differences in the climate–HAB event count relationship, we pre-specified heterogeneity analyses across ocean basins⁴⁵, climate zones⁵¹ and rolling 10-year SST-warming backgrounds⁵². Between-group differences were tested using interaction models fitted to the full sample. For the categorical grouping variable G_i , the model was:

$$\lambda_{it} = \exp \left[\sum_{g=1, \dots, G} \beta_g C_{it}^z 1(G_i = g) + \gamma O_{it} + \mu_i + \delta_t \right]$$

8

where β_G denotes the relationship of climate exposure with HAB event counts in region type g . A joint Wald test of the null hypothesis $H_0 : \beta_1 = \dots = \beta_G$ was used to determine whether climate effects differed systematically among regions. The Benjamini–Hochberg procedure was used to control the false discovery rate (FDR) across multiple interaction tests.

Fourth, to test whether local environmental conditions modulated the climate–HAB event count relationship, we conducted moderator analyses for each environmental variable M_{it}^k . Within the complete common-observation

sample, climate and environmental variables were standardized separately within the sample before estimating how environmental conditions modulated the climate–HAB relationship:

$$\lambda_{it} = \exp \left(\beta C_{it}^z + \theta M_{it}^{k,z} + \psi C_{it}^z M_{it}^{k,z} + \gamma O_{it} + \mu_i + \delta_t \right)$$

9

where ψ measures the extent to which a climate effect changes with environmental conditions. Regression results were subjected to separate FDR corrections, and a joint Wald test of $H_0 : \psi_{El} = \psi_{La} = 0$ was used to assess the overall evidence that each environmental variable modulated the effects of the climate indicators on HAB event counts.

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Figures

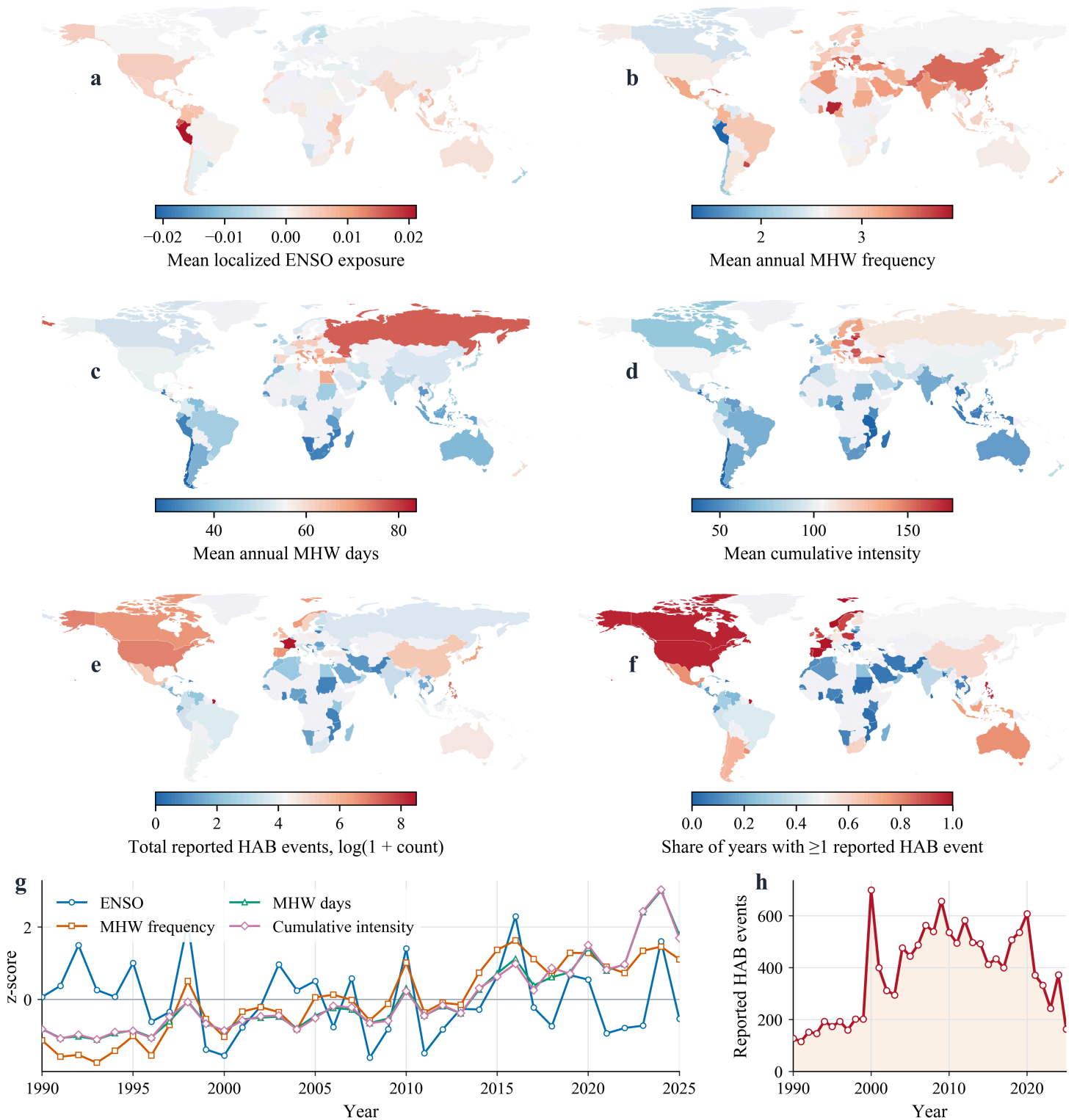


Figure 1

Coastal climate exposure and reported HAB risk. a, ENSO exposure; b, MHW frequency; c, MHW cumulative intensity; d, MHW days; e, Total reported HAB events from 1990 to 2025, shown as $\log(1 + \text{count})$; f, Share of years with at least one reported HAB event; g, Annual standardized trajectories of ENSO exposure, MHW frequency, days and cumulative intensity. All climate-exposure variables are expressed as z-scores to allow comparison across metrics. h, Annual total number of reported HAB events.

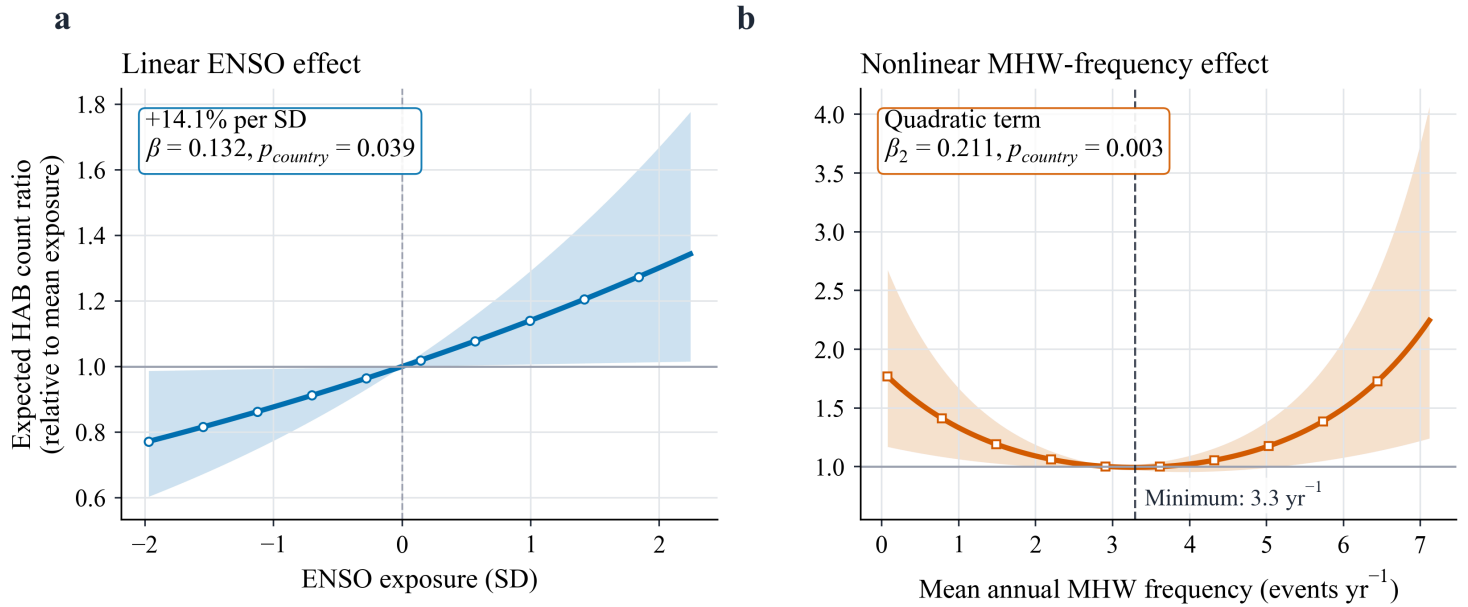


Figure 2

Average climate effects on reported HABs counts. Baseline linear and nonlinear PPML models controlling for country and year fixed effects and differences in observation effort were used to estimate the average effects of the two climate factors. a, Linear relationship between country-level coastal ENSO exposure and reported HAB event counts. b, Nonlinear relationship between annual mean MHW frequency and reported HAB event counts. Shading indicates 95% confidence intervals.

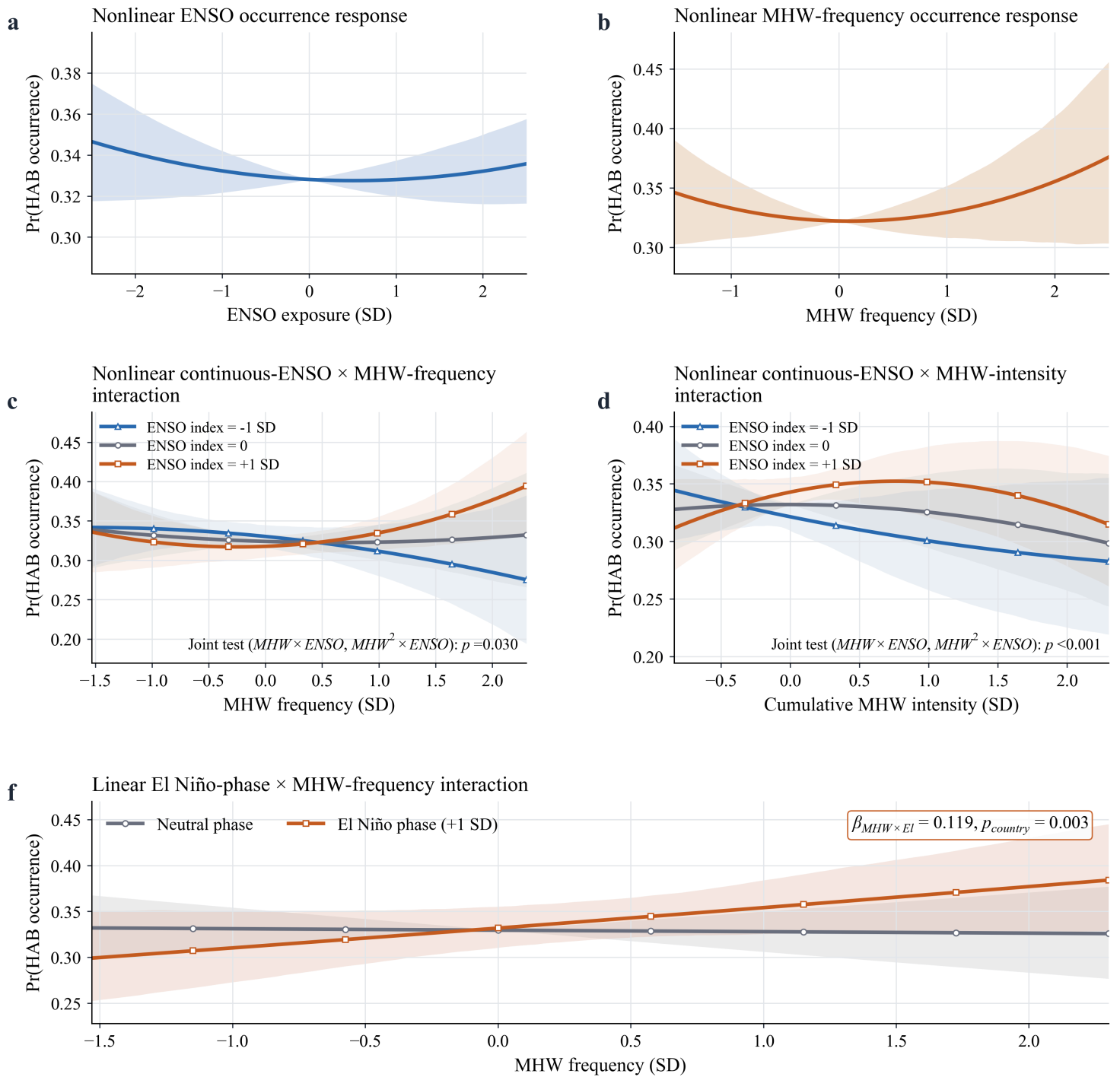


Figure 3

HABs occurrence probability climate responses. Probit models controlling for country and year fixed effects and differences in observation effort were used to identify nonlinear and interactive responses to the two climate factors. The y-axis represents the predicted probability of at least one reported HAB event at the country-year level. All climate exposure variables are standardized, with the x-axis expressed in standard-deviation units. a, Nonlinear effect of ENSO exposure on HAB occurrence probability. b, Nonlinear effect of MHW frequency exposure on HAB occurrence probability. c–d, Nonlinear interactions between ENSO exposure and MHW frequency (c) and MHW cumulative intensity (d); different colored curves indicate ENSO exposure fixed at -1 SD, 0 and +1 SD. f, Linear interaction between ENSO phase and MHW frequency. Shaded areas indicate 95% confidence intervals.

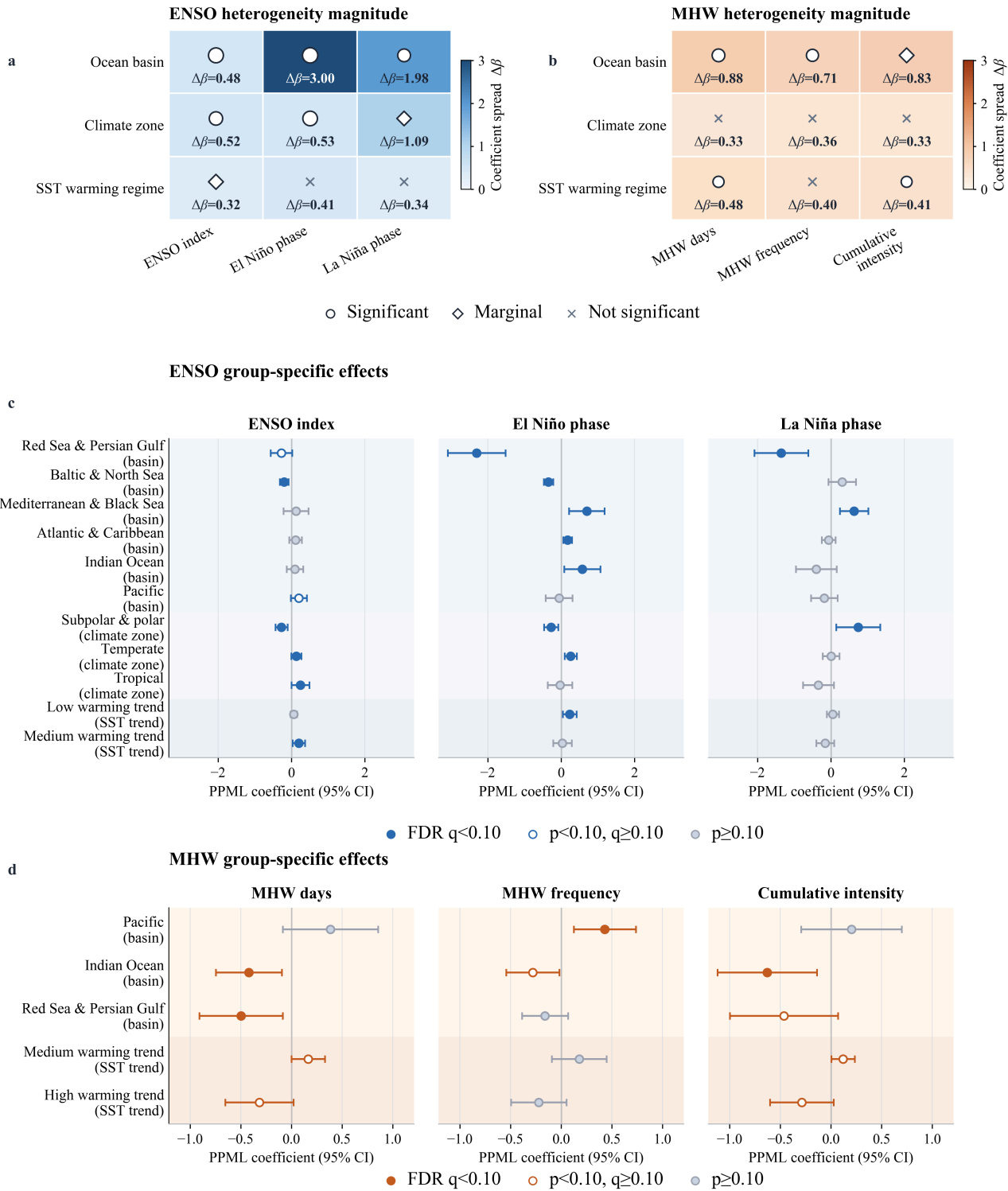
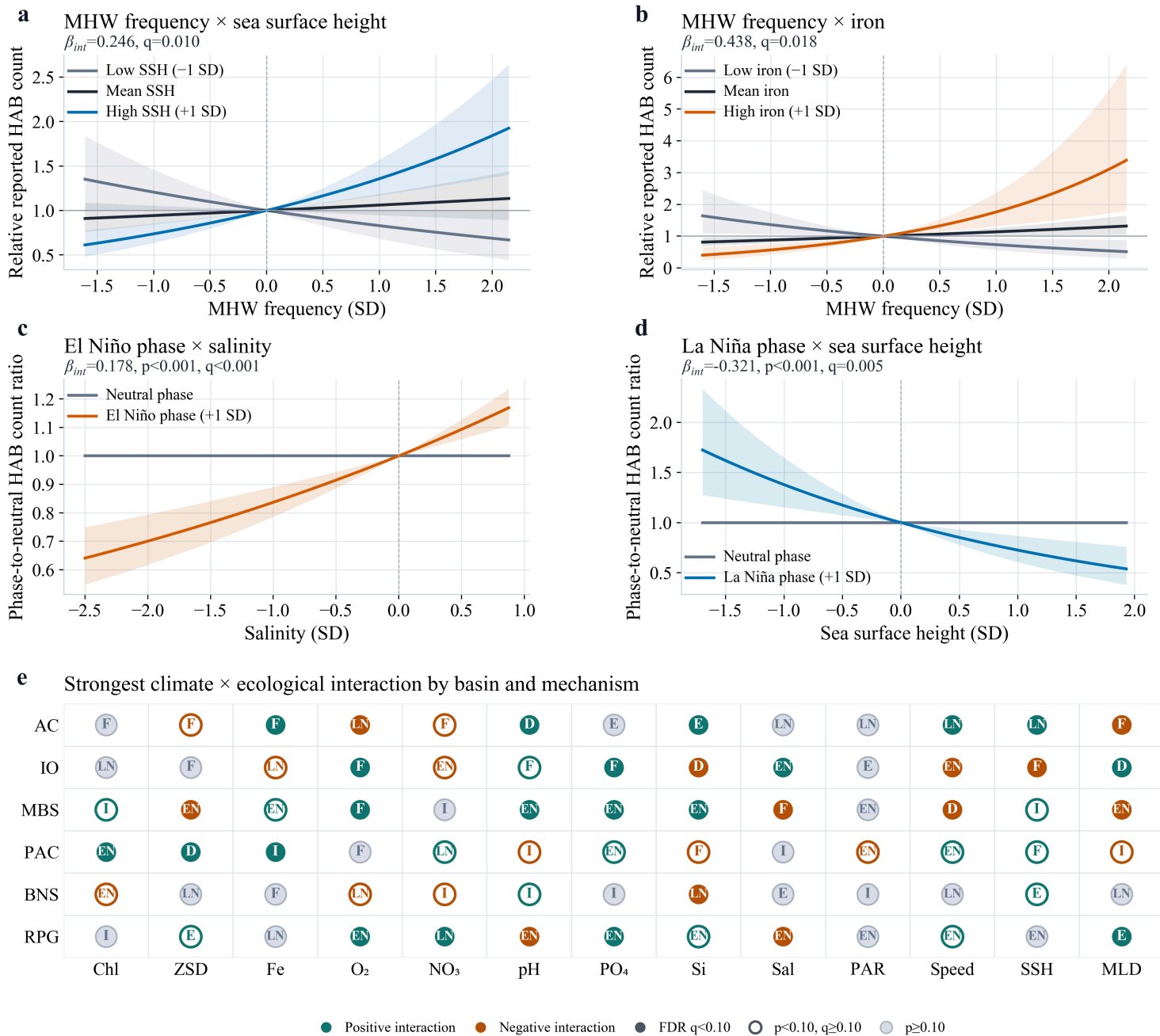


Figure 4

Spatial heterogeneity. PPML models controlling for country and year fixed effects and differences in observation effort, together with between-group coefficient heterogeneity tests and FDR correction for multiple testing, were used to identify spatial heterogeneity in the effects of the two climate factors on reported HAB event counts. a, ENSO heterogeneity tests across long-term SST warming regime, ocean basin and climate zone; b, MHW heterogeneity tests across long-term SST warming regime, ocean basin, climate zone; c-d, representative group effects estimated from interaction models.



Y-axis basin abbreviations: AC=Atlantic & Caribbean; IO=Indian Ocean; MBS=Mediterranean & Black Sea; PAC=Pacific; BNS=Baltic & North Sea; RPG=Red Sea & Persian Gulf.

Codes: E=continuous ENSO; EN=El Niño phase; LN=La Niña phase; D=MHW days; F=MHW frequency; I=MHW cumulative intensity.

Figure 5

Environmental modulation of climate–HAB associations. PPML models controlling for country and year fixed effects and differences in observation effort used interaction terms to identify how environmental factors modulated the effects of climate factors on reported HAB event counts. a,b, Environmental modulation of MHW effects. c,d, Environmental modulation of the effects of different ENSO phases. e, Leading environmental moderators in different ocean basins.