communications earth & environment

ARTICLE

https://doi.org/10.1038/s43247-023-00946-8 OPEN

Different environmental response strategies in sympatric corals from Pacific Islands

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Coral reefs are severely threatened by global and local environmental changes. However, susceptibility to perturbations and subsequent mortality varies among coral species. In this study, we tested the contribution of genetic and environmental conditions to coral's phenotypic response in *Pocillopora* spp. and *Porites* spp. sampled together at a large ecological and temporal scale throughout the Pacific Ocean. We assessed coral phenotype signatures using a multi-biomarker approach (animal and symbiont biomasses, protein carbonylation and ubiquitination and total antioxidant capacities). In both genera, we highlighted a strong anticorrelation between the redox state and the animal and symbiont biomasses. In addition, *Pocillopora* exhibited high phenotypic plasticity, responding to various environmental variables such as temperature, nutrients, phosphate, and carbonate chemistry. In contrast, *Porites* displayed more robust phenotypes influenced by both genetics and past climate events. In conclusion, co-located coral species display different phenotypic response strategies that are influenced by different environmental conditions.

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Climate change is expected to significantly increase the occurrence of cold and warm ocean sea-surface temperature extremes[1,2] that have already been well documented in the Pacific Ocean[3,4]. Accentuated by direct anthropogenic stressors due to local pollution and overfishing, climate change will have devastating consequences on marine organisms. Among them, reef-building corals are highly vulnerable to environmental changes, experiencing repeated mass coral bleaching (loss of the intracellular photosynthetic protist symbionts belonging to the Symbiodiniaceae family), which have already led to substantial coral mortalities over large spatial scales[2].

However, susceptibility to environmental changes, and subsequent bleaching that may lead to mortality, vary among coral species[5,6], but also within species[7]. Consequently, the surviving species will play a key role for coral reef resilience in a changing climate[8]. In these last decades, monitoring of reefs over the world has allowed to identify several species able to persist after perturbations and therefore considered today as winner species[7,9,10]. Among them, two groups of corals have been identified:[11] (i) massive and long-living species (as *Porites* species) persisting during the environmental perturbations and considered highly stress-tolerant and (ii) 'weedy' species (as *Pocillopora* species), with fast growth and reproduction allowing a rapid recolonisation of the environment after stress. However, predictive models of global change forecast increasingly drastic and rapid climate changes that species have never experienced before and consequently make it difficult to predict who will be the future winners. It is therefore still imperative to know which coral species may have the adaptive potential and innate resilience to survive the disturbances of the Anthropocene for conservation and restoration purposes[12].

The response of coral species to the environment has been attributed to different factors as, for example, the host genetic background[13–15], specific holobiont composition (the combination of different host species with one or multiple Symbiodiniaceae and bacterial lineages)[16–19], nutrient supply[20–22], ocean deoxygenation[23,24] and/or preconditioning to past repeated environmental changes[25–27]. However, the contribution of each of these factors to the coral susceptibility remains unclear, as the extent to which it is conserved within a coral genus, or within diverse Scleractinia corals living in sympatry in a broad range of environmental conditions.

To predict the ability of coral species to respond to stress, it is necessary to define the coral phenotype with pertinent traits. The search of relevant, sensitive and quantifiable biomarkers of coral traits remains a key goal[28]. The coral phenotypic response is an unconstrained notion mainly due to their intrinsically morphological plasticity linked to environment-induced skeleton changes[29] and to their photoacclimation capacity that induced significant colour changes by modifying their cellular pigments and/or their symbiont population contents[30,31]. As corals can strongly depend on the high-energy products of their algal symbionts, those acclimation processes are essential for trophic equilibrium[32]. In addition, environmental perturbations (especially variations in temperature) induce in extreme cases bleached coral phenotypes which reflect symbiotic homeostasis breakdown[33]. To prevent bleaching, corals could then have (i) specific host-symbiont genotypes as specific adaptation to the local environment, or (ii) display a large spectrum of phenotypic plasticity. The latter allows the emergence of diverse physiological states from a unique genotype, in response to the environmental conditions[12]. Several studies performed under controlled laboratory or field conditions have identified biomarkers as indicators/proxy of coral physiological states. Among them, biomarkers of the trophic coral state, as polyp tissue thickness and/or the hosted symbiont density, have been linked to coral sensitivity to environmental perturbations and reflected the existing nutrient intake by the coral[34–37]. In addition indicators of intracellular redox state modification (as protein carbonylation and oxidative scavenging capacities) or more general damage signature as the protein ubiquitination, have been validated reflecting imbalances between reactive oxygen species overproduction and antioxidant defences during environmental stress[38–46]. Accordingly, one consequence of this imbalance was the disruption of the cnidarian–Symbiodiniaceae association. However, to what extent the diverse biomarker signatures reflect an inherited and genotypically fixed character or diverse coral response to specific environmental factors is not clear.

Hence, a large coral sampling was carried out, at an unprecedented ecological scale throughout the Pacific Ocean during the Tara Pacific expedition 2016–2018[47]. In this study, we assessed the biological response to the environment from 321 colonies from 11 islands (across East-West and South-North gradients from the coasts of Panama to Micronesia) of two emblematic coral-species complexes with different morphologies and lifestyles, *Pocillopora* spp. and *Porites* spp.. *Pocillopora* species consist mostly of branched morphotypes, fast-growing and with a moderate lifespan of some decades[11,48]. *Pocillopora* species display flexibility towards Symbiodiniaceae, with the ability to harbour diverse species of *Symbiodinium*, *Cladocopium* or *Durisdinium* genera[49–54]. In contrast, even if they are found in sympatry with *Pocillopora*, *Porites* species display contrasted characteristics. *Porites* species consist mostly of massive corals, with slow growth and long lifespan (several centuries)[48,55], with a strict symbiont fidelity to the genus *Cladocopium*, specifically with subclade C15 in the Indo-Pacific[18,52].

In this study, we questioned whether visually healthy colonies, from two reef-building corals, co-located in the same wide range of habitats, showed common or divergent phenotypic signatures in response to identical environmental variations. Our first objective was to test the ability of quantitative and reliable biomarkers to define different physiological states for healthy corals, and subsequently establish interpretive coral phenotypic signatures. We used multiple physiological biomarkers at a macroscopic scale (quantification of animal and symbiont biomasses to assess polyp tissue thickness and symbiont density) and at a cellular scale (evaluation of the redox state by quantifying protein carbonylation, protein ubiquitination and total antioxidant capacities). Our second objective was to test, by a comparative approach between the two coral genera, to what extent these diverse physiological traits reflect genetic relatedness (in the coral host and its symbionts) and/or environmental correlations. For this purpose, a holistic integration of those signatures with putative explanatory parameters (as host, symbiont and microbiome diversities and environmental variables), collected during the Tara Pacific expedition, was performed.

Results

Distinct coral biomarker profiles across the Pacific Ocean. To obtain a physiological/phenotype profiling of *Porites* and *Pocillopora* colonies collected in reefs of different Pacific Ocean islands, we measured five different biomarkers revealing diverse trophic (animal and symbiont biomasses) and redox states (protein carbonylation, ubiquitination and Total Oxidant Scavenging Capacity—TOSC). The comparison of the different biomarkers across the 11 islands and within the two genera, revealed a heterogeneous pattern both among islands and among species (Figs. 1 and 2).

For *Pocillopora*, animal biomass was high in the first three islands and then declined to a minimal mean in Moorea Island which presented around three times less proteins compared to

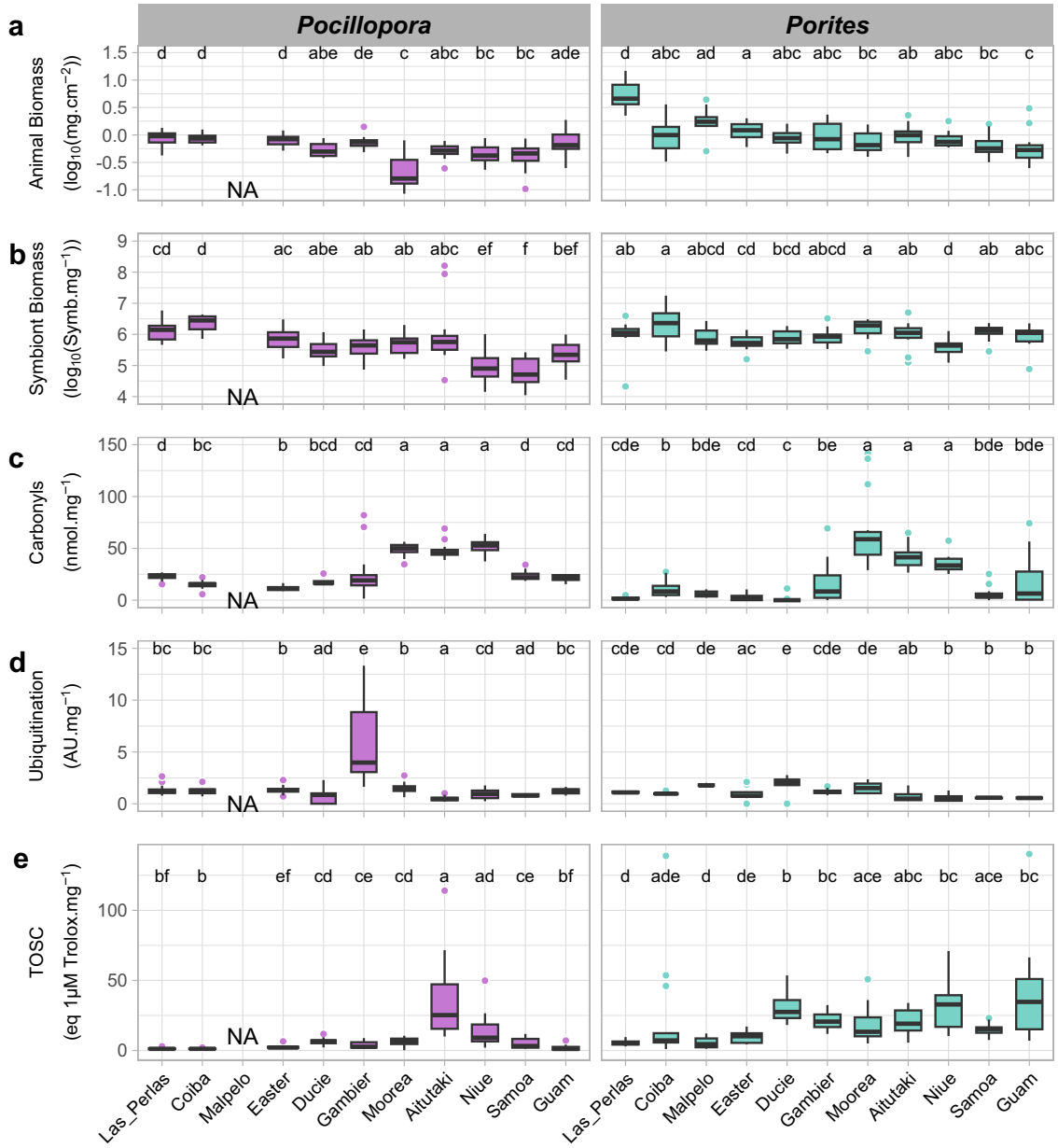

Fig. 1 Biomarker assays of coral colonies in the function of Pacific island origins. Variability of the biomarkers measured in *Pocillopora* (purple-pink) and *Porites* (cyan) genera and in function of sampled islands. **a** Animal biomass assay. **b** Symbiont biomass assay (normalised by mg of protein). **c** Protein carbonylation. **d** Protein ubiquitination. **e** Antioxidant capacity. The boxes represent the 1st and the 3rd quartiles around the median (horizontal black bar). Outlier points are plotted individually (dots). Statistically significant differences among the islands within the two genera have been tested by a Kruskall–Wallis' test and a Dunn's test as post hoc. The identical letter above boxplots indicates no statistically significant differences. NA: not applicable as no *Pocillopora* samples were available for Malpelo. Island coordinates and dates are indicated in Supplementary Table S8.

eastern colonies or to Guam (Fig. 1a). For *Porites*, we observed an eightfold reduction comparing colonies from Las Perlas to Guam colonies (Fig. 1a). Thanks to the identification of the coral species[56,57] (five species within *Pocillopora* and three species in *Porites*), we could assess the species specificity of this phenotype within each genus. Figure 2a shows that despite some statistically significant differences among *Pocillopora* species, no species-specific animal biomass signature was identified. In contrast, all three *Porites* species identified in our sample showed a statistically significant species-specific pattern for animal biomass.

Symbiont biomass normalised per milligram of protein was highest in Eastern Pacific for *Pocillopora* colonies (specifically for colonies from Panama islands, Las Perlas and Coiba) and lowest in Niue and Samoa islands (10- to 20-fold lower, respectively; Fig. 1b). *Porites* colonies harboured a more homogenous symbiont biomass even if Niue showed a lower symbiont content (Fig. 1b). Very similar trends were observed following a tissue surface normalisation (Supplementary Fig. S1a). The comparison of symbiont biomass in respect to host lineages showed a higher symbiont content of *Pocillopora* species 4 (highly frequent in the Eastern Pacific) and in *Porites* species 3 (present in the Central Pacific) (Fig. 2b and Supplementary Fig. S1b). Due to the strong correlation measured between the two symbiont biomass datasets (Supplementary Fig. S2), we hence conserved only symbiont biomass normalised per milligram of protein for the following analyses.

For both genera, carbonyl content was higher in the three central islands of the transect, Moorea, Aitutaki and Niue (Fig. 1c). For example, in these three islands, the coral colonies of

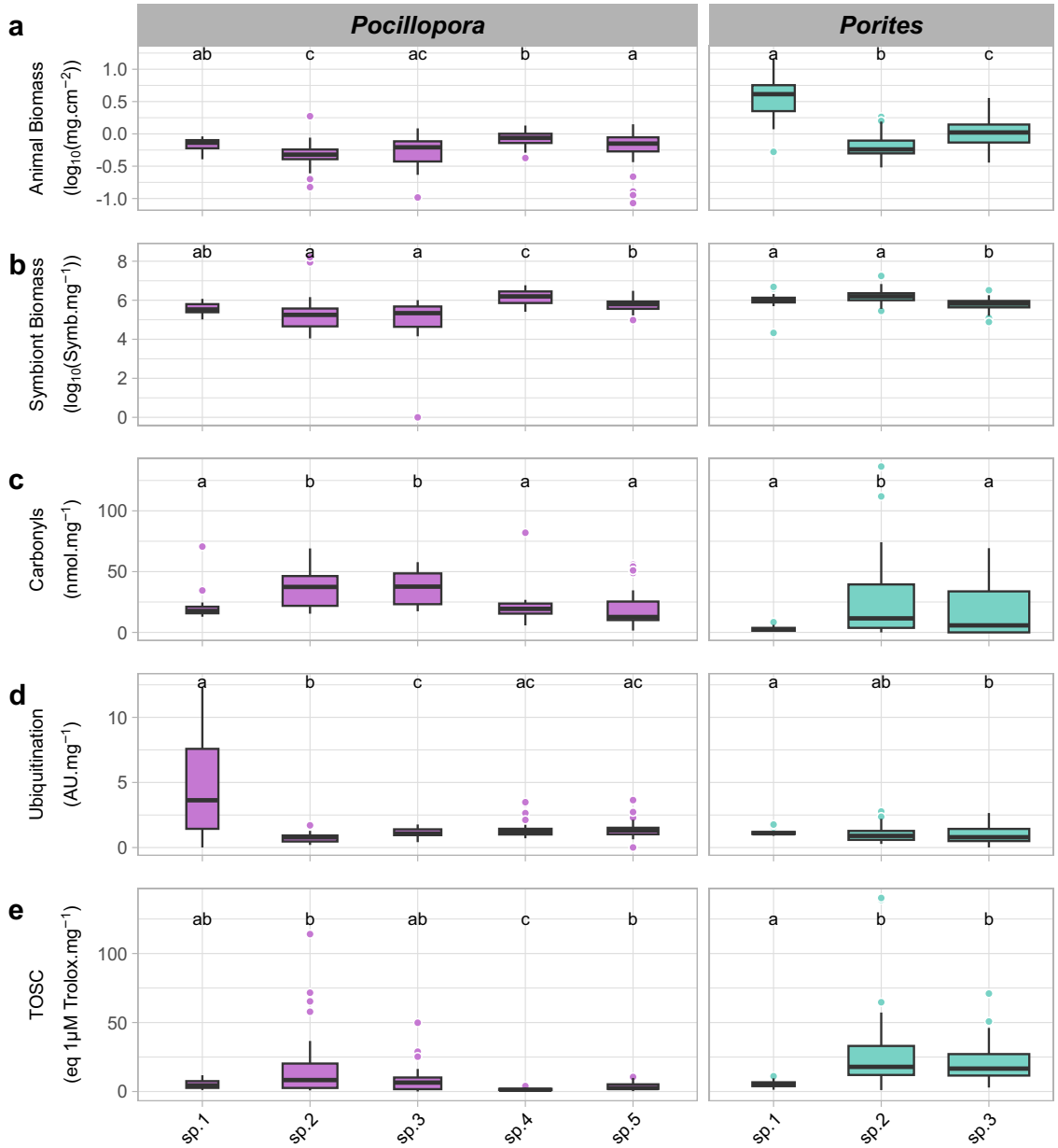

Fig. 2 Biomarker assays of coral colonies in the function of coral species. Variability of the biomarkers measured among species within *Pocillopora* (purple-pink) and within *Porites* (cyan) genera (**a**) Animal biomass assay. **b** Symbiont biomass assay (normalised by mg of protein). **c** Protein carbonylation. **d** Protein ubiquitination. **e** Antioxidant capacity. The coral-species attribution is detailed in Table 3. The boxes represent the 1st and the 3rd quartiles around the median (horizontal black bar). Outlier points are plotted individually (dots). Statistically significant differences among the species within the two genera have been tested by a Kruskall–Wallis' test and a Dunn's test as post hoc. Identical letters above boxplots indicate no statistically significant differences. Species distributions and lineages are indicated in Supplementary Fig. S6 and Table 3.

Pocillopora and *Porites* respectively presented carbonyl content means of two- to eightfold higher than the colonies from the East Pacific Ocean. The comparison of carbonyl content in respect to host lineages (Fig. 2c) showed that despite differences among the *Pocillopora* species, no species-specific response on protein carbonyl was measured. Contrastingly, the *Porites* species 2 (present in Central Pacific) had higher carbonyl content than the other two Porites species.

With regard to the protein ubiquitination biomarker, the analyses showed a high specific content of ubiquitinated proteins in *Pocillopora* from Gambier, with a median more than three-time higher than elsewhere and with a statistically significant variation among the sampled colonies (Fig. 1d). Although less pronounced, a low specific amount of ubiquitinated proteins was also observed in *Porites* colonies from Niue, Samoa and Guam (Fig. 1d). No species specificity was observed for this marker within either genera (Fig. 2d).

For *Pocillopora*, the colonies from the two Panama, Easter and Guam islands had the lowest TOSC values. Contrastingly, Aitutaki colonies harboured maximal TOSC values, with around 20 times more antioxidant capacities (Fig. 1e). For *Porites*, TOSC values were more homogenous with a slight increase along the transect line (Guam colonies presented a sevenfold increase of TOSC compared to Las Perlas). The comparison of TOSC in respect to host lineages revealed a species-specific reduced amount of TOSC on *Pocillopora* species 4 and *Porites* species 1 (Fig. 2e), although this species was only found in Eastern Pacific islands.

Island- and species-specific coral phenotypic signatures. We then used a multimarker approach using the five biomarkers to establish phenotype signatures for each colony and compared them in respect to the genus, species and islands of origin. A first PERMANOVA analysis testing the genus affiliation shows different phenotypic profiles (P value = 0.0001) with greater phenotypic dispersion of *Pocillopora* phenotype than *Porites* (P value = 0.001) visible in Supplementary Table S1 and Supplementary Fig. S3. We have therefore analysed more in detail the *Pocillopora* and *Porites* signatures independently, using principal component analysis (PCA) and PERMANOVA tests. The PCA of *Pocillopora* biomarker signatures revealed the gradual distribution of the phenotypes along the first axis (Fig. 3a), mostly driven by both biomasses and carbonyls (Fig. 3b and Supplementary Table S2). For *Porites*, the phenotypes were less spread into the PCA space but dispersed more homogeneously along the two first axes (Fig. 3c), due to a stronger independence between animal biomass and symbiont biomass (Fig. 3d and Supplementary Table S2) than in *Pocillopora*.

The statistical partition of the phenotypic signatures by geographic origin or by coral species has been tested for both genera by PERMANOVA (Table 1 and Fig. 4). For *Pocillopora*, the colonies from the eastern and the western islands displayed statistically different phenotypes (Fig. 4 and Supplementary Table S3). *Pocillopora* colonies from Las Perlas and Coiba had a strong phenotypic differentiation with high biomasses and low redox state. In addition, the results show some phenotypic dissimilarity among *Pocillopora* species: with the often sympatric species 4 and 5 different from species 1 and from the other sympatric pair the species 2 and 3 (Fig. 4 and Supplementary Table S4). The *Porites* phenotypes were less structured by geographical regions, but few islands appeared as one-off pairwise differentiation (as Niue or Coiba; Fig. 4 and Supplementary Table S5). Only *Porites* species 3 had statistically different phenotypes from the two other species (Fig. 4 and Supplementary Table S6).

To test the influence, on the global phenotype signature, of the island or species origins but also the associated microorganism diversity (testing separately the Symbiodiniaceae and the microbiome diversities), we performed a variation partition analysis. To avoid any bias, we considered only coral colonies from islands containing more than one coral species per genus. The analysis confirmed a main effect of the geographical origin on the variance of the diverse phenotypic signature for *Pocillopora* (Fig. 5a) and

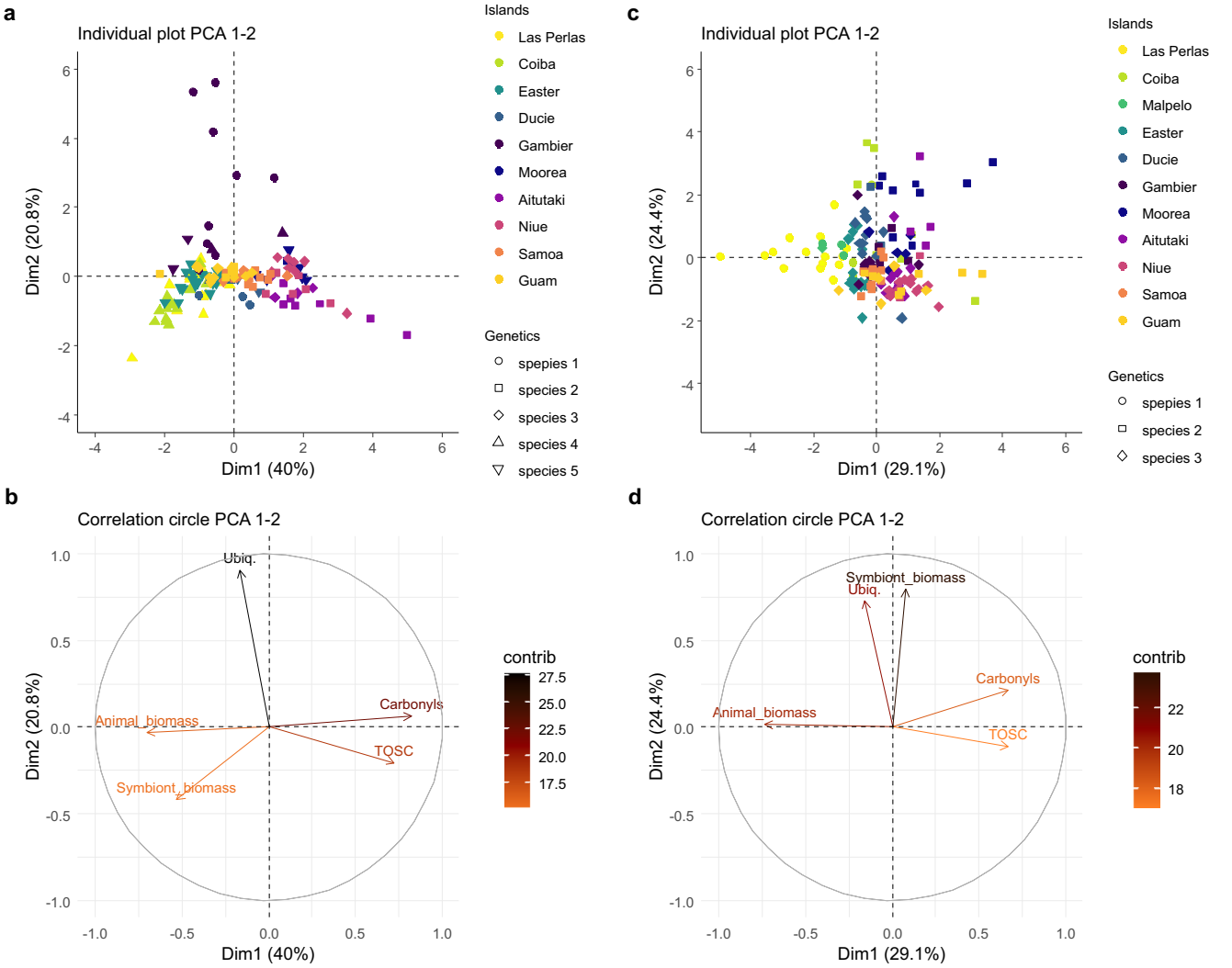

Fig. 3 Principal component analysis of coral phenotypic signatures. PCA on biomarkers data from *Pocillopora* spp. **a**, **b** and *Porites* spp. **c**, **d** The dispersion of the phenotypic signatures (defined by the five measured biomarkers) are shown in (**a**, **c**), where the colours represent the island origin, and the shapes represent the species. The importance of each biomarker explaining the PCA distribution of data is shown with correlation circles in (**c**, **d**), where the colour scale is the contribution of each biomarker to the plotted PCA dimensions.

Table 1 Phenotypes partitioning PERMANOVA test.

	Df	Sums of squares	Mean squares	F model	R^2	Pr (>F)
Pocillopora						
Species	4	7.494	1.8735	14.212	0.27171	5.00E-05
Islands	9	3.7204	0.41338	3.1359	0.13489	5.00E-05
Species x Islands	5	1.0751	0.21502	1.6311	0.03898	0.067
Residuals	116	15.2917	0.13182		0.55442	
Total	134	27.5812			1	
Porites						
Species	2	3.0816	1.54082	20.0167	0.19312	1.00E-04
Islands	10	2.3537	0.23537	3.0576	0.1475	0.0002
Species x Islands	6	0.6689	0.11148	1.4482	0.04192	0.1404
Residuals	128	9.853	0.07698		0.61747	
Total	146	15.9572			1	

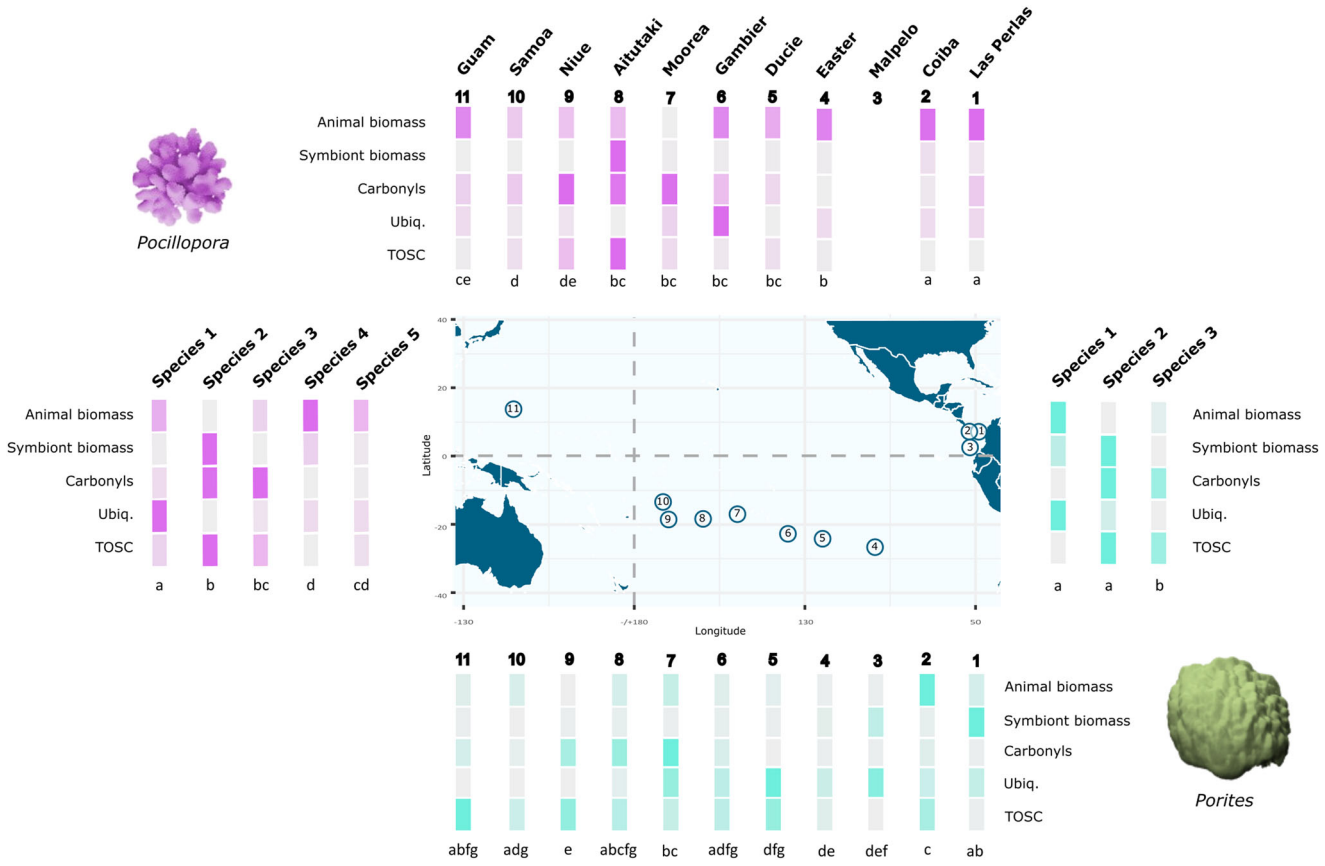

Fig. 4 Distribution of phenotypic signatures across corals and islands. The phenotypic signature of *Pocillopora* (purple-pink) and *Porites* (cyan) colonies by biomarker is represented by scaled average values (from grey: the minimum value; to *genus colour*: the maximum value) used here as an illustrative barcode-like phenotypic signature. The letters associated to the barcodes are the groups of statistical significance based on pairwise PERMANOVAs (Supplementary Tables S3 and S5 for island comparisons; Supplementary Tables S4 and S6 for species comparisons within *Pocillopora* and *Porites* genera, respectively). The same letter indicates no statistically significant difference.

Porites (Fig. 5b). For *Porites*, the coral species seemed to be an additional explanatory factor. A complementary Mantel's test performed within each species did not reveal any correlation between the genetic distance and the coral phenotype (Supplementary Fig. S4). On the other hand, the associated microorganism diversity was a marginal driver of the coral phenotypes, compared to the variance explained by the partition into islands.

Differing coral sensitivities to environmental conditions. Because the phenotypes of both genera were demonstrated to be influenced mainly by the geographical origin of the corals, we identified putative drivers, by exploring the correlations between biomarkers and several environmental variables, collected during the Tara Pacific expedition or recovered by historical temperature data extracted from satellite imagery (see details in material and methods). Using sPLS (sparse Partial Least Squares method), we identified clusters based on similar correlations between biomarker data and environmental variables, and found that the two coral genera did not show the same clustering of these data.

For *Pocillopora*, the 20 variables most correlated with the studied biomarkers were included in all environmental categories (for

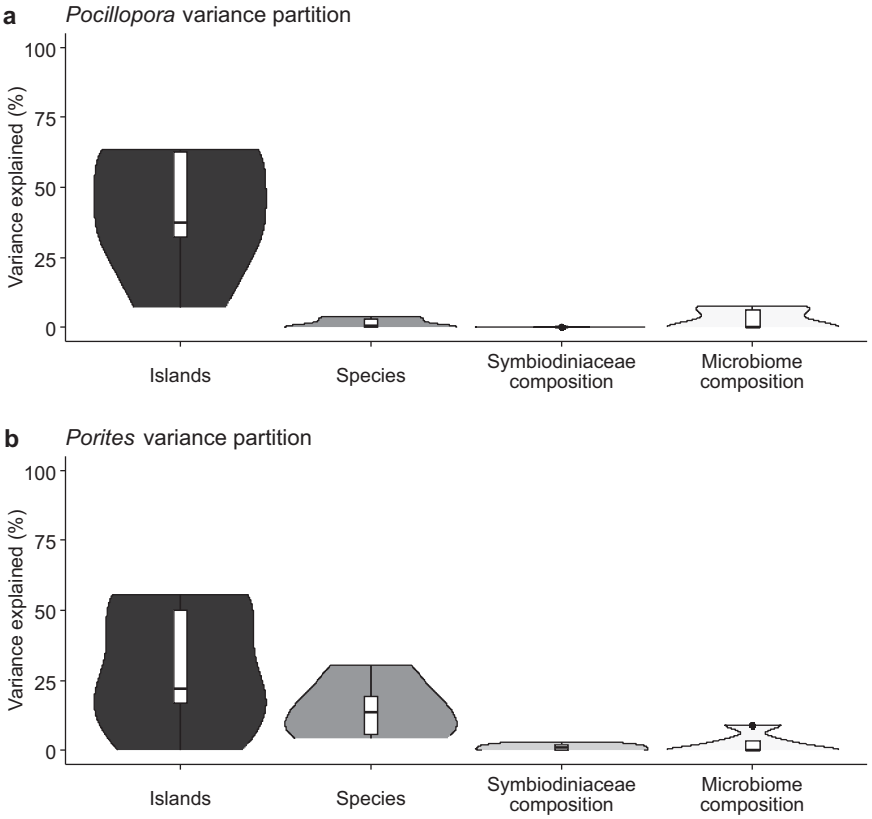

Fig. 5 Variance partition of coral phenotypic signatures. Proportion of the variance explained by the different partitions of the *Pocillopora* (**a**) and *Porites* (**b**) phenotypic signatures (defined by the five measured biomarkers): island of origin (black), host species (grey), Symbiodiniaceae composition (light grey) or the microbiome composition (white). The white boxes represent the 1st and the 3rd quartiles around the median (horizontal black bar). Outlier points are plotted individually (black dots). The shaded surface of each violin displays the distribution of the data.

details, see 'Methods') and structured in two clusters (Fig. 6a and Table 2). Among the first cluster, characterised by strong correlation with antioxidant capacity and protein carbonylation, we identified three biological variables (C_Bio_086, C_Bio_092, C_Bio_094; corresponding respectively to high content on chlorophyll, nanoplankton and total Eukaryotes analysed in the seawater); five physico-chemical variables measured the sampling days (C_Phy_081, C_Phy_090, C_Phy_099, C_Phy_100 and C_Phy_101; corresponding respectively to high oxygen, turbidity, pH, silica content and sun exposure duration, Table 2); three climate variables (the sea surface temperature of the sampling day, recent cold temperature anomaly and past cold sea surface temperature anomalies, respectively C_Cli_084, R_Cli_045 and H_Cli_009). Among the second cluster, characterised by high biomasses and low redox state, we identified one dynamics variable (the sea surface height; C_Dyn_077), three contemporary physico-chemistry variables (C_Phy_083, C_Phy_096, C_Phy_098; corresponding respectively to high carbon dioxide content, total alkalinity, phosphate concentration) and three historical climate variables (H_Cli_013, H_Cli_015, H_Cli_029, H_Cli_071; corresponding to high intensity of sea surface temperature deviations, recent heatwaves episodes and short recovery time after recent cold waves). In *Pocillopora*, all those variables displayed strong correlation (between −0.66 and 0.57) with the biomarkers, except for protein ubiquitination, whose correlations never reached the 0.3 fixed threshold. For all correlated environmental variables, two main biomarker clusters were also observed showing anti-correlation between TOSC and carbonyl content biomarkers versus animal and symbiont biomass biomarkers.

On the other hand for *Porites*, the 34 most correlated environmental variables with the biomarkers, belonged mainly on historical climatological variables and were more weakly correlated (around −0.55 and 0.5, Fig. 6b) than what we observed in *Pocillopora*. In *Porites*, the most correlated variables were clustered in three groups (Fig. 6b and Table 2). A first cluster grouped the sea surface height (C_Dyn_077) and historical seawater temperature anomalies linked to minimal recorded seawater temperature (H_Cli_001), cold waves (in frequency and duration, respectively H_Cli_060, H_Cli_065) but also to the recovery time after heat wave (H_Cli_043, H_Cli_044). In the second cluster, we identified biomarker correlations with three physico-chemistry variables (corresponding to high oxygen, turbidity and sun exposure duration; C_Phy_081, C_Phy_090, and C_Phy_101) and 11 historical climate variables depicting recurrent past and recent seawater cold temperature anomalies (H_Cli_047, H_Cli_048, R_Cli_049, H_Cli_052, H_Cli_073) and strong past fluctuation of seawater temperatures (H_Cli_004, H_Cli_012, H_Cli_013, H_Cli_014, H_Cli_015, H_Cli_019). Finally, a third cluster grouped only climate variables linked with past and recent heatwaves events (H_Cli_020, H_Cli_021, H_Cli_025, H_Cli_026, H_Cli_027, H_Cli_028, R_Cli_029, H_Cli_030, H_Cli_031, H_Cli_032, H_Cli_033, H_Cli_035, H_Cli_037, H_Cli_039). In *Porites*, we also observed anti-correlation between TOSC and carbonyl content biomarkers versus animal biomass. However, contrasting with *Pocillopora* results, animal and symbiont biomasses did not correlate in the same way with the variables. In addition, even when the protein ubiquitination content of *Porites* passed the sPLS filters and showed correlations with the environment variables, the correlation values were far weaker.

Although the intensity of the correlations between biomarkers and environmental variables and the type of environmental

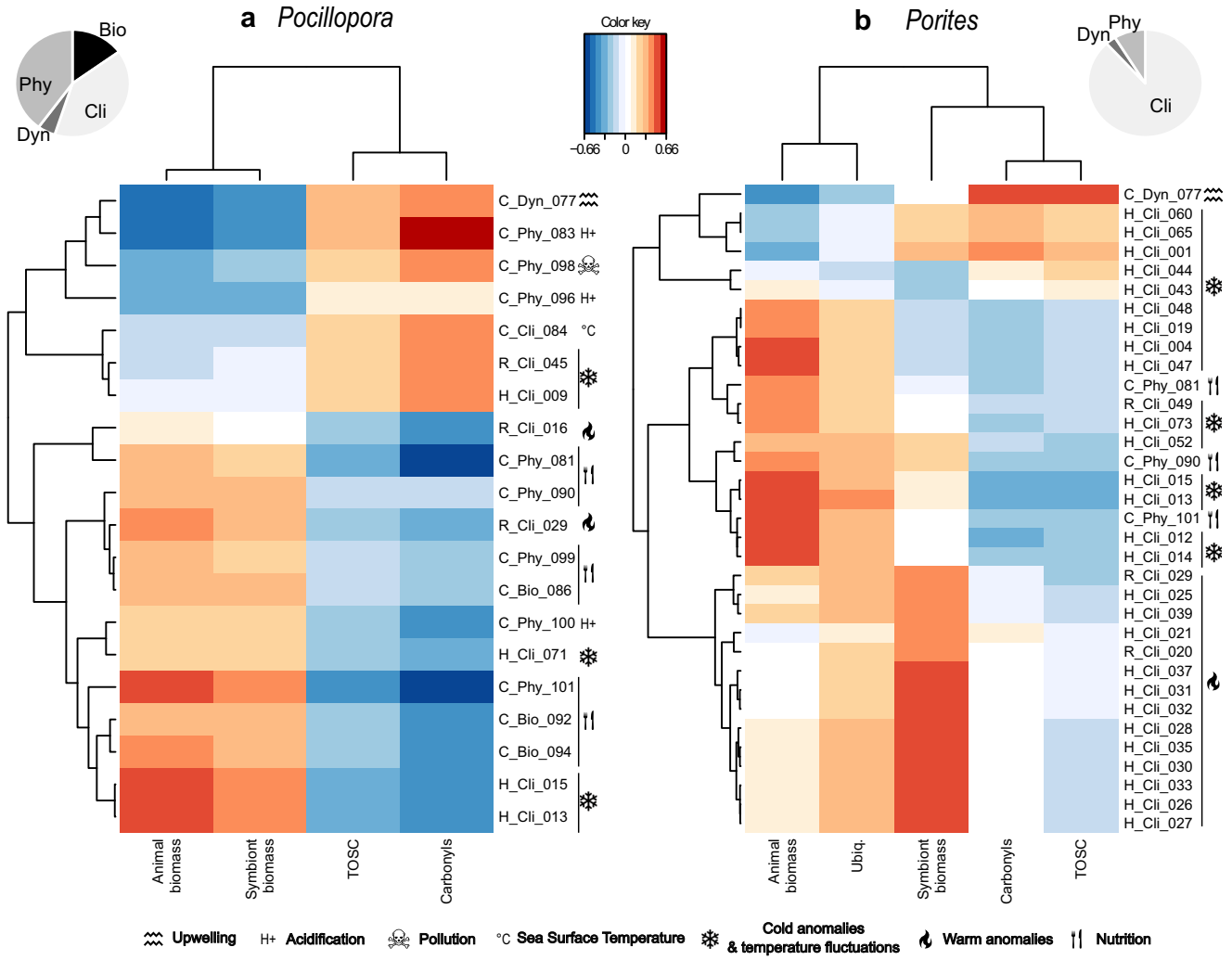

Fig. 6 Sparse partial least squares (sPLS) regression of the coral biomarkers and the environment variables. Correlations among *Pocillopora* (**a**) or *Porites* (**b**) biomarkers and the environment data are represented with a classification of the environmental data by grey shades and with 3-letters code (from darker to lighter: Biological data (Bio); Hydro- and Aerodynamics data (Dyn); Physico-chemical data (Phy); and Climatic data (Cli)). In addition, environmental data are also identified as historical (H), recent (R) and contemporary to the sampling (C). Finally, an interpretation of these environmental variables is proposed in Table 2, and displayed by a symbol code present on the bottom of the figure. The corresponding original variable names are available in Supplementary Table S9. The correlation coefficient values are given by the central colour key, and only biomarkers or environmental variables with an absolute coefficient value higher than 0.3 are displayed (leaving the lower values blank). In the top, left and right are represented by pie charts of the proportion of environmental variables correlated with at least one biomarker for *Pocillopora* and *Porites,* respectively.

variables mostly depended on the genus, 7 environmental variables were common to *Pocillopora* and *Porites* (Fig. 7a) and concerned the sun exposition duration (C_Phy_101) and O_2 concentration (C_Phy_081), frequency of recent (R_Cli_029) and historical sea temperature anomalies (H_Cli_013, H_Cli_015), the sea surface height (C_Dyn_077), and the turbidity (C_Phy_090). Comparing the correlation pattern of these biomarkers (Fig. 7b–e and Supplementary Table S7), the animal biomass (Fig. 7b) appeared to be the biomarker that responded most similarly in the analysed *Pocillopora* and *Porites*.

Discussion

Characterising multiple biomarker variations in the widespread and co-occurring *Pocillopora* and *Porites* species in the Pacific Ocean, we identified diverse phenotypes, reflecting discrete physiological states. In addition, comparing their phenotypic signatures, we highlighted two different strategies of environmental response that could be synthesised as 'the Oak and the Reed' strategies. Indeed, those two genera respond to the environment by a contrasting gradient of phenotypic plasticity. *Porites* exhibited more robust phenotypes (with limited changes in physiological traits) mainly influenced by past climate events while *Pocillopora* harboured a greater phenotypic plasticity responding to a large variety of environmental variables.

In this study, we validated the use of five different biomarkers, never measured in combination at such large species and geographic scales, to determine the phenotypic profiling of coral colonies. The analysis of the diverse phenotypes corroborated in both genera a significant and strong anti-correlation between the animal biomass, and to a lesser extent the symbiont biomass, with the redox state. A coral with thick tissue and high symbiont density hence presents a low redox state with reduced oxidative damage and reduced activation of antioxidant defences.

Previous studies have observed that variations of coral tissue thickness and symbiont density could be as well species-specific, related to seasonality, geography or environmental perturbations[34–37,58,59] and/or considered to be a proxy of the trophic state of the colony[58]. In addition, high tissue thickness

Table 2 Summary of the association between coral phenotypes and environments.

Genera	Environmental variables	Environment description	Coral phenotypic signatures
Pocillopora	**C_Dyn_077**, C_Phy_083, C_Phy_096, C_Phy_098, H_Cli_009, R_Cli_045, C_Cli_084	-· **Upwelling (Sea Surface Height)** -· Acidification (Carbon dioxide, pH, Alkalinity) -· Pollution (Inorganic Phosphate) -· Climate anomalies (Severe Past and Recent Cold Anomalies)	>High Redox state >Low Biomasses
	C_Bio_086, C_Bio_092, C_Bio_094, **C_Phy_081, C_Phy_090**, C_Phy_099, C_Phy_100, **C_Phy_101, H_Cli_013, H_Cli_015, R_Cli_029**, H_Cli_071	-· Phyto- and Zooplankton richness (Chlorophyll, Nanophytoplankton, TotalEukaryot, **Turbidity (KD_{490})**, Biogenic Silica ($SiOH_4$), **Oxygen, Sun**) -· Climate anomalies **(sea surface temperature deviation, Recent Heatwaves**, Past Heat Anomalies, Short resilient time after cold waves)	>Low Redox state >High Biomasses
Porites	**C_Dyn_077**, H_Cli_001, H_Cli_043, H_Cli_044, H_Cli_060, H_Cli_065	-· **Upwelling (Sea Surface Height)** -· Severe Cold Past Anomalies (maximal frequency of cold anomalies, maximal length of cold days, minimal sea surface temperature)	>High Redox state >Low Animal Biomass
	C_Phy_081, C_Phy_090, C_Phy_101, H_Cli_004, H_Cli_012, **H_Cli_013**, H_Cli_014, **H_Cli_015**, H_Cli_019, H_Cli_047, H_Cli_048, R_Cli_049, H_Cli_052, H_Cli_073	-· Nutrient richness **(Turbidity (KD_{490}), Oxygen, Sun)** -· Climate anomalies (recurrent Past and Recent Cold Anomalies and high fluctuation of seawater temperature)	>Low Redox state >High Animal Biomasses
	H_Cli_020, H_Cli_021, H_Cli_025, H_Cli_026, H_Cli_027, H_Cli_028, **R_Cli_029**, H_Cli_030, H_Cli_031, H_Cli_032, H_Cli_033, H_Cli_035, H_Cli_037, H_Cli_039	-· **Recent** and past heatwaves	>Low Redox state >High Symbiont Biomasses

In bold, the environmental variables displaying same correlation for *Pocillopora*'s and *Porites*' biomarkers. The original environmental variable names are available in Supplementary Table S9.

would be characteristic of stress-tolerant species with high survival rates after bleaching[7,60]. Taking into account those considerations, our results from a large geographic and species scale show that coral colonies with high animal and symbiont biomasses present a resistant phenotype, less susceptible to stressors.

The redox baseline of corals can reflect host or symbiont specificities[61,62] and/or environmental perturbations that are responsible for reactive oxygen species overproduction in coral tissues, which in turn activates antioxidant systems preventing cellular damages[63]. The extended ability of corals to activate antioxidant capacities and/or to eliminate oxidised cellular compounds can then be considered as a crucial point that allows corals to respond to the environment[64]. Associated with high biomasses, a low redox state measured in the sampled colonies could then reflect a healthy physiological status not challenged by any exogenous stressors.

The contribution of the protein ubiquitination biomarker is less resolutive at the scale of the entire transect. In corals, protein ubiquitination level has been linked to thermal stress in the field[38,39] or laboratory-controlled conditions[43,65,66] and associated to tissue thickness decrease, bleaching process and high redox state. The incongruency here observed is however not surprising since the ubiquitination profile could also be linked not only to damaged proteins degradation under stress conditions but also to other cellular processes in normal physiological conditions. Therefore, the ubiquitination profile remains more difficult to decipher. It is however interesting to note that in Gambier and Ducie, the coral colonies harbouring high protein ubiquitination presented concomitantly some of the lowest bacterial diversity[67]. This observation suggests that the presence of highly ubiquitinated proteins in corals would be an indicator of weakness of the colonies by a general bacterial dysbiosis and a signal of immune response[68,69]. Assuredly, our work points out that further efforts should be made to identify the drivers that lead to the diverse ubiquitination signature in order to gain a better insight into the biochemical coral response.

In our study, we observed phenotypes significantly linked to the island of origin for *Pocillopora* spp. and for the island of origin and the species for *Porites* spp. The analysis of *Pocillopora* samples showed that the analysed Eastern Pacific Ocean colonies (from Las Perlas and Coiba) had a strong phenotypic differentiation with high biomasses and low redox state, in contrast with the Central Pacific ones (especially Niue and Samoa), which harboured low biomasses and high redox state (Figs. 1 and 4). In the other islands, the corals harboured intermediate phenotypes defined by diverse biomarker signatures. As all Las Perlas and Coiba colonies belonged to species 4 (identified as *P. grandis* synonym of *P. eydouxi*[57]; Table 3), it is tempting to attribute a species-specific phenotype to *P. grandis* as a result of environmental selection pressure experienced in this area. On the other hand, *P. meandrina* and *P. verrucosa* (species 2 and 3, respectively, Table 3) displayed undifferentiated phenotypes wherever they have been sampled. The absence of a genetic link in *Pocillopora* spp. is also confirmed by the insignificant explanation of variance by species assignment (Fig. 5a) and the lack of phenotype–genetic correlation (Supplementary Fig. S3).

As the coral sampling has been performed during the Tara Pacific expedition within a 6-month frame, it is important to point the impact of time of sampling as a confounding factor. From July 2016 (Panama Islands) to January 2017 (Guam), the expedition spanned several seasons, making it difficult to tease apart the seasonal from the geographical effect. However, if we restrict our comparison of island phenotypes to islands sampled on a reduced time scale, we still find statistically significant differences. For example, the phenotypes of the *Pocillopora* colonies of Moorea and Aitutaki were different from those of Niue and Samoa (Fig. 4) even though sampling was carried out in less than a month within the same season (between November 6th and December 3rd, Supplementary Table S8). On the other hand, the similarity of Easter *Pocillopora* phenotypes to the ones from Aitutaki was also observed over different months (September to November) which correspond to seasonal changes (from winter

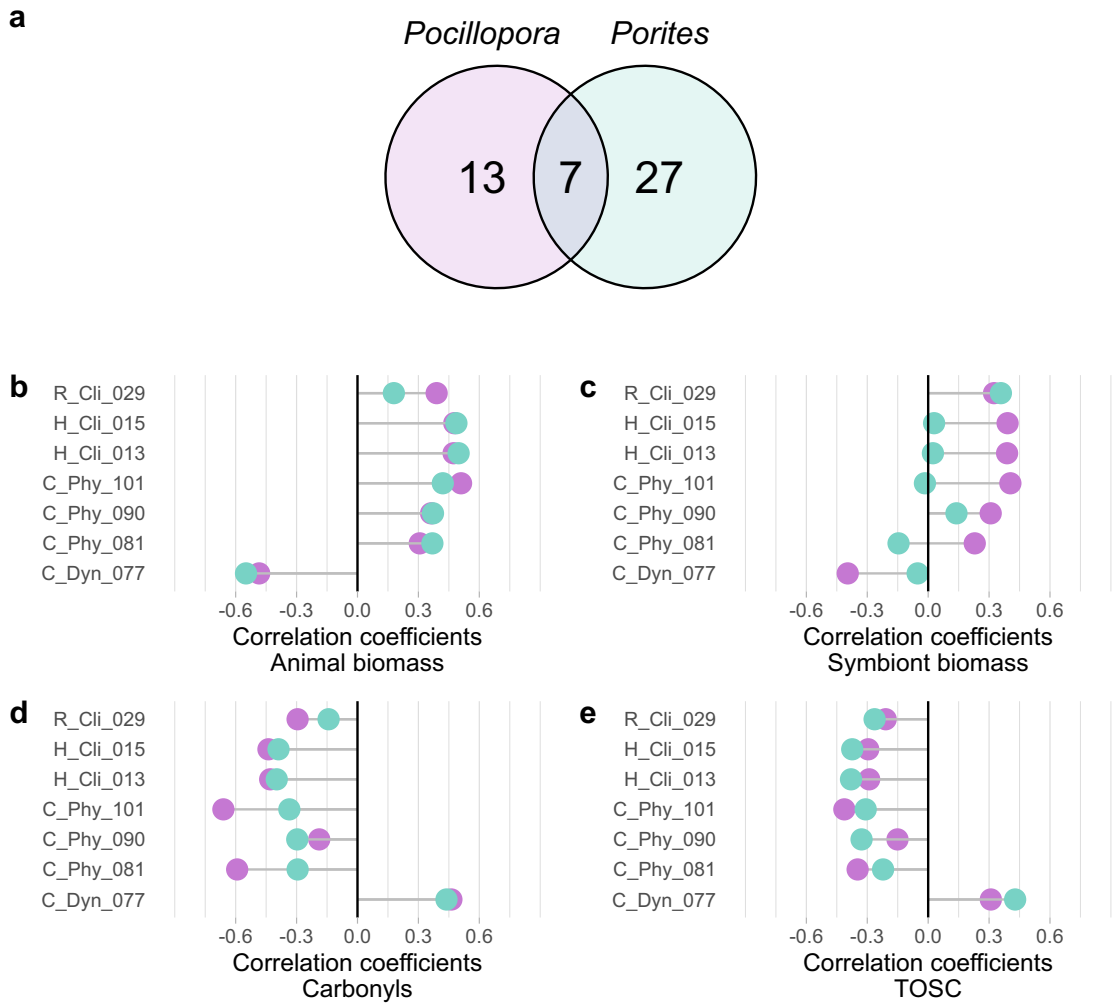

Fig. 7 Comparison of the environmental response among the two genera. Number of common and private environmental variables with a correlation coefficient higher than 0.3 for at least one biomarker in *Pocillopora* (purple-pink) or *Porites* (cyan) (**a**). Details of the correlations between *Pocillopora* and *Porites*' biomarkers with common environmental variables: animal biomass (**b**), symbiont biomass (**c**), protein carbonylation (**d**), and antioxidant capacity (**e**). The symbols on the left codes indicate the interpretation of the environmental variables also presented in Table 2 and Fig. 6. The flame points out warm anomaly (R_Cli_029: TSA_DHW_freq_snapshot_sampling_day_day), the snowflake points out temperature anomaly frequencies (H_Cli_013: SST_anomaly_freq_max_day, H_Cli_015: SST_anomaly_freq_std_day), fork & knife point out nutrition proxy variables (C_Phy_081: o2_copernicus, C_Phy_090: KD490_Sat, C_Phy_101: Sun),, and the waves point out an upwelling proxy variable (C_Dyn_077: ssh_copernicus).

to spring). Nevertheless, to definitively unravel the impact of the seasons on an expedition involving the collection of samples in time and space, it will be necessary in the future to carry out additional studies resampling the same colonies at different times (seasons and years) and also to have a larger geographical sampling with more seasonal replicates.

In conclusion, the environmental characteristics of each island seem to be the main factors structuring the *Pocillopora* physiological state with an extended phenotypic plasticity reflecting the diversity of the colonised habitats. This result is in accordance with the definition of *Pocillopora* as a weedy or competitive group of species[11,70,71] and allows the comparison to be made in terrestrial habitat with the reed lifestyle. Weedy species are indeed characterised by small morphotypes with fast growth and short lifespan. They fit in the r-selection strategy in which rapid reproduction allows to colonise rapidly a large variety of environments. As we observed in most of the *Pocillopora* species here studied, weedy corals are also characterised by a large phenotypic plasticity which can provide acclimatisation potential and represent intrinsic advantages for their survival to future environmental changes. In addition, high phenotypic plasticity can stimulate diversification and speciation by allowing adaptation to diverse conditions[72]. This interpretation is in line with the finding that species differentiation is linked to past temperature variation in *Pocillopora*[57].

Our work depicts a complex structuring of the physiological status in *Porites*, shaped not only by the environment but also by a genetic component. *Porites* spp. assuredly present less diverse phenotypes, but some phenotypic peculiarities have been found along the transect. Among them, as observed in *Pocillopora*, the Las Perlas *Porites* colonies displayed a physiological status with high animal biomass and low redox state. Again, this specific phenotype is not diagnostic of the unique genetic lineage sampled in Las Perlas (species 1 identified as *P. evermanni*, Table 3), as in Malpelo the same lineage displayed different phenotypic signatures. Finally, a strong phenotypic species specificity has been found in species 3 (SSH3_plob, Table 3), widely distributed from Easter Island to Guam, which demonstrated strong phenotypic homeostasis independent of habitat diversity. Limited range of phenotypic plasticity, slow growth and longer generation time is in accordance with the definition of *Porites* as a genus of stress-tolerant species[11].

Table 3 Metadata from Tara Pacific consortium used in this study.

Dataset	Origin	Terms and abbreviations used	References
Pocillopora species[a]	Species delimitation based on SNPs genotyping	Species 1 (*P. effusa*) Species 2 (*P. meandrina*) Species 3 (*P. verrucosa*) Species 4 (*P. grandis*) Species 5 (SSH5_pver)	Voolstra et al.[57] Deshuraud et al.[56]
Porites species[a]	Species delimitation based on SNPs genotyping	Species 1 (*P. evermanni*) Species 2 (SSH2_plob) Species 3 (SSH3_plob)	
Symbiont composition	*Symbiodiniaceae* diversity characterised by ribosomal nuclear ITS2	10 Pocillopora's ITS2 Clusters 11 *Porites*' ITS2 Clusters	Hume et al.[105]
Bacterial Microbiome composition	Bacterial microbiome defined on ribosomal 16 S marker	5 *Pocillopora*'s 16 S clusters 7 *Porites*' 16 S clusters	Galand et al.[67]
Environmental data	Biological (Bio), physico-chemical (Phy), hydrodynamical (Dyn) and climate (Cli) data collected during the Tara Pacific expedition Historical climate data recovered since 2002 to more recent past	101 historical (H), recent (R) or contextual (C) variables	Lombard et al.[98]

[a]In addition, *Pocillopora* and *Porites* species distribution on each island is shown in Supplementary Fig. S5.

While *Pocillopora* and *Porites* species show different strategies of environmental response, we observed in some islands some convergence in phenotypes. More specifically, we measured in both genera high biomasses and low redox states in Las Perlas and Coiba islands. These samplings were performed in the two largest marine protected areas of Panama (the Coiba National Park and the Archipiélago de Las Perla), both inscribed from 2004 in the UNESCO World Heritage List of Natural Sites. Among the reasons for this protection, the presence of extreme environmental disturbances, from short-term variability in sea temperature and seasonal upwelling to long-term temperature excursions was considered[73]. The convergent phenotypes could then be attributed to the success of the ecosystem protection and/or to the result of the natural selection of less susceptible corals due to repetitive perturbation episodes, suggesting that this specific physiological status (high biomasses and low redox state) is a trait of low susceptibility (or high capacity for survival) to local perturbations. It is interesting to note that the sampling in the Panama island has been performed during the wetter and warmer season (July 2016) with poorly nutrient-rich seawater[74]. In this environmental context, corals tend to have low tissue thickness (reflecting low nutrient reserves) and a seasonal decrease in symbiont density[75]. The observation of a completely opposite phenotype reinforces our conclusion about the particularly pristine state of the Panama colonies.

Pocillopora colonies, and to a lesser extent *Porites* colonies sampled in Niue and Upolu (Samoa Archipelago) islands, showed phenotypic specificities. More precisely, they accumulated low biomasses and a high redox state, suggesting a fragile physiological state. Few data are available concerning the health status of these coral reefs, but recent reports underlined low to extremely low coral coverage (down to <1% in some Upolu sites) with coral communities that remain under stress from recurrent storms and coral bleaching[76,77]. In the light of climate predictions for the coming years, our observations could then constitute a solid argument to reinforce coral conservation in suffering reefs. Indeed, stronger marine protected area policy, as set up in Las Perlas and Coiba, can reduce the direct anthropogenic pressure, mitigating the impact of the more difficult to control climate change.

In both coral genera, Symbiodiniaceae and bacterial compositions were not detected as explanatory factors of the diverse phenotypes. However, previous studies focused on some coral populations and reefs have highlighted that low bacterial diversity may be indicative of a less resilient status of the reef[68]. It is plausible that the discrepancy with our findings stem from our field approach, as the analysis of colonies under natural and non-extreme conditions reveals various stable physiological states well adapted to their environment and therefore without any signs of dysbiosis (excepted for few highly ubiquitinated colonies as discussed previously).

Furthermore, enrichment with specific thermotolerant Symbiodiniaceae (i.e., *Durusdinium* spp.)[61,78,79] in some *Pocillopora* colonies from the most warm equatorial waters (such as Panama and Guam) did not confer a unique phenotype. For example, two hypotheses on the *Pocillopora-Durusdinium* couple could then be made: (i) this couple can harbour diverse warm adapted/acclimatised phenotypes; (ii) this couple in warm water cannot be systematically an acclimatisation sign of the holobiont but reflect the opportunistic capacity of *Durusdinium* to proliferate in warm water. The latter hypothesis is supported by experiments on symbiotic cnidarian models which have shown that hosts harbouring *Durusdinium* can be unproductive and highly stressed[80].

Our results, summed up in Table 2, show that the characteristics of the environment experienced by the colonies at the time of sampling, but also the past climatic events, shape the coral phenotypes of both genera. Nevertheless, *Pocillopora* phenotypes were linked to a large diversity of contemporary environmental factors including biological, physico-chemical, dynamic and climate variables, while *Porites* was mainly only linked to the past climate. Extreme past and recent cold anomalies (in intensity, duration and frequency) seem to fragilize *Pocillopora* and *Porites* phenotypes that systematically presented low biomass and high redox state (Table 2). Even if, in the context of global ocean warming, the impact of heatwaves on coral reefs was strongly documented, several studies highlighted the impact of severe cold waves on corals, demonstrating an even stronger effect on modulation of gene expressions[81] on bleaching or mortality susceptibility[82]. The strong common correlation with sea surface height can also be linked to strong cold upwelled waves reaching the reefs that can increase coral stress susceptibility[83].

In contrast, the frequency of recent or past sea surface temperature anomalies (including heat and cold waves) was among the strongest explanatory factors that correlated equally in both genera with almost all biomarkers and leading to colonies with low redox state and high biomasses. This link was more expected

as the analysed biomarkers have been shown to be sensitive to temperature increases in the laboratory or in the field. It can however reinforce the statement that recurrent exposures to sea surface temperature anomalies play an important role in coral acclimatisation[84], reducing the cost of stress response (i.e., low redox state) and enhancing coral tissue reserves (i.e., high animal biomass). Our results were also in accordance with the conclusions of ref. [70] that stressed the importance of the past climate and especially repeated marine heat and cold waves in the sensitivity of massive corals, like Poritidae[25]. This hormesis phenomenon can also explain the overall more stable phenotypes observed in *Porites* spp.. On a different note, this behaviour could also be a resultant of their long-life strategy, as environmental selection pressures could have shaped *Porites* spp. to deal with frequent environmental fluctuations without acting on their sensitivity to extreme events.

In addition, *Porites* spp. and *Pocillopora* spp. shared similar responses to turbidity, light exposure duration and oxygen (Fig. 7 and Table 2). The positive correlation between those factors and the animal biomass low redox state revealed an important weight of the nutrient-enriched water in the trophic state of the corals. Several studies have demonstrated that naturally turbid coral reefs exhibit high coral cover with fast-growing coral species[85–87]. Indeed, an increase of suspended particulate matter and light exposure can very likely favour the nutrition state of the corals, thus enhancing their mixotrophic nutrition. This is even more notable in *Pocillopora* phenotypes that are strongly and positively linked with the seawater richness in zoo- and phytoplankton, suggesting that *Pocillopora* spp. are able to adjust the autotrophic/heterotrophic balance in response to the environment variability with the capacity to maintain or even increase their energy reserves. In addition, some studies have already linked large polyp phenotypes with increased dependence on heterotrophy and stress resistance[88–91]. We can therefore suggest that this capacity of trophic modulation could explain the extended distribution of *Pocillopora* genus in the Pacific Ocean and its stress resistance.

Finally, our work highlighted the sensitivity of *Pocillopora* colonies to phosphate and acidification. Indeed, in our data, phosphate accumulation in the environment was associated with high redox state and small polyps with low symbiont density confirming the sensitivity of *Pocillopora* physiology to an imbalance in nutrient level[92]. This is in accordance with previous studies performed in other coral species, showing that phosphate contamination (mainly due to eutrophication through the addition of fertilisers) negatively affects coral traits as skeleton production, reproduction and symbiont photosynthesis[93] but can also provoke increase in DNA damages and lipid peroxidation[94]. Finally, carbonate chemistry also exhibited a link with the *Pocillopora* phenotypes harbouring high redox state and low biomass. Branched corals, such as the Pocilloporidae, are very sensitive to acidification that provokes a decrease in growth and/or increase in skeletal porosity[95] but also oxidative stress response[96,97].

Conclusions. In this work, by comparing the phenotypic signatures of the widespread *Pocillopora* and *Porites* genera, we confirmed that those two genera present two different strategies of environmental response that we have synthesised as 'the Oak and the Reed' strategies. This terrestrial and poetic metaphor helps to illustrate the diverse phenotypic plasticities and sensitivities to environmental factors observed in the genera here studied and their implication to future environmental changes. The reduced plasticity quantified in *Porites* species is consistent with stress tolerance in a wide range of habitats through a strong investment in homeostasis regulation. However, this robustness can potentially limit, as in the case of an oak tree, their rapid response to drastic and rapid environmental changes. In contrast, under severe environmental changes, *Pocillopora* species would have, like a reed, an extended ability to rapidly modify its physiology (i.e., activating antioxidant capacities) allowing it to be resilient to stress. This shows unequivocally that natural populations of corals sharing the same habitat can have diverse responses that are influenced by different environmental parameters. It also allows for a reconsideration of the subdivision into loser and winner species, suggesting that it may not be the largest and strongest species of today that will be the most resilient tomorrow.

Methods

Unless otherwise specified, all chemicals were obtained from Merck (France).

Animal sampling. Coral colonies of *Pocillopora* spp. and *Porites* spp.[57] were sampled between July 2016 and February 2017 across the Pacific Ocean during the Tara Pacific expedition (see Supplementary Table S8 for sampling sites, GPS coordinates and sampling date). They have been sampled according to UNCLOS and CITES permits (see Supplementary Note S1) and to the sampling protocol described in ref. [98]. Briefly, 40 g of coral fragments from 155 *Pocillopora* spp. branched colonies and 166 *Porites* spp. massive colonies were sampled from 11 islands (but unfortunately *Pocillopora* samples from Malpelo island have been lost during the shipping), in at least three different sites at around 5 metres depth, and frozen onboard in liquid nitrogen. The fragments remained then stored at −20 °C until analysed. The time before freezing varied in respect to the distance between the *Tara* shooner and the sampling site, we performed a preliminary and complementary experiment to assess any artifactual results due to the freezing time lag (Supplementary Fig. S5).

Phenotypic biomarkers assays. Each coral sample was fragmented into two parts, a 10 g fragment was used for the biochemical biomarker analyses and a fragment of about 1 cm was used for the biomass analyses.

Animal and Symbiont biomasses: To assess animal and symbiont biomasses, the individual coral fragments were incubated at 37 °C in 4 M sodium hydroxide solution for 1–3 h[99]. Following the NaOH incubation, aliquots of the lysate were used for Symbiobiodiniaceae cell counting using the improved Neubauer hemocytometer and for protein concentration determined by Bradford protein assay[100]. The surface area of the remaining coral fragments was then measured using the aluminium foil technique[101]. Animal biomass was expressed in mg of protein per cm^2, and symbiont biomass was expressed in number of cells per mg of protein and per cm^2.

Proteins extraction. Each fragmented coral sample was mechanically grinded to powder with a Qiagen Tissue LyserII at 25HZ for 10 s. Soluble cytoplasmic protein were extracted by resuspending the obtained powder in a hypo-osmotic lysis buffer consisting of 25 mM 2-[4-(2-hydroxyethyl)piperazin-1-yl]ethanesulfonic acid (HEPES), 5 mM $MgCl_2$, 5 mM 4-dithiothreitol (DTT), 5 mM ethylenediaminetetraaceticacid (EDTA), 2 mM phenylmethylsulfonylfluoride (PMSF), protease inhibitor cocktail (1 µl ml^{-1}) and anti-phosphatase (10 µl ml^{-1}) at pH 7.5 (ThermoScientific). Lysates were centrifuged at 12,000×*g* for 5 min, and only the supernatant was recovered containing the cytosoluble protein extracts. All extraction steps were performed under constant cooling. A Bradford protocol was followed to determine supernatant protein concentration using bovine serum albumin (BSA) solution (2 mg ml^{-1}) as standard[100].

Protein ubiquitination. Ubiquitinated proteins were assayed by dot-blotting 3 µg of *Pocillopora* protein samples and 0.5 µg of *Porites* protein samples on nitrocellulose membranes following ref. [102]. The membranes were blocked in 5% milk in PBS-Tween (0.05%) overnight and then incubated with primary antibody (1:1000; mouse mono- and polyubiquitinylated conjugate recombinant, Enzo Life science) and Goat anti-mouse IgG HRP-conjugated antibody (1:5000; Bio-Rad) as secondary antibodies. HRP signals were visualised using chemiluminescent substrates (Immobilon classico, Merck) and acquired using a FusionSolo imaging system (Vilber). Levels of spot density were measured using the image analysis system G:Box (SynGene). To ensure the comparison of blotted membranes, a complementary normalisation has been performed with a standard curve of known protein concentration blotted in each membrane. The known proteins came from a unique extraction of protein from the sea anemone *Anemonia viridis*. The standard curve included a range of 0.5–4 µg of *A. viridis* protein extracts. The amount of ubiquitinated protein has been defined as arbitrary units (AU) per milligrams of protein.

Protein carbonylation. Carbonylated protein contents were measured using ELISA assay followed by spectrophotometric quantification according to ref. [103]. A total of 0.5 mg ml^{-1} of protein were derivatized using dinitrophenylhydrazine (DNP)

solution (10 mM in 6 M guanidine hydrochloride and 0.5 M potassium phosphate, pH 2.5). Antibody against DNP component (anti-rabbit DNP; 1:2000) was used as primary antibody and a Goat anti-rabbit IgG peroxidase conjugate (1:3000) was used for detection as secondary antibody. A standard curve of reduced and oxidised BSA was included in each microplate. Derivatized proteins were finally revealed by incubation of the microplate with a solution containing o-phenylenediamine (0.6 mg ml^{-1}) and hydrogen peroxide (1:2500) in 50 mM Na_2HPO_4 plus 24 mM citric acid. Absorbances were read at 490 nm by spectrophotometer (Safas, Monaco). Carbonyl contents were expressed as nanomoles per mg of protein.

Antioxidant capacity. The total antioxidant capacities of protein samples were tested with the total oxidant scavenging capacity (TOSC) assay according to Naguib[104], with modifications allowing measurement in black 96-well microplates (96-wells Grener Bio-One). Protein extracts were diluted in a 75 mM phosphate buffer (pH 7.0) to obtain protein concentrations in the reactive medium between 0.01 and 0.045 mg mL^{-1}. The fluorescence signal was obtained by the oxidation of the fluorescent probe (180 nM; 6-carboxylfluorescein) by the peroxyl radical generator (36 mM AAPH (2,2′-azobis (2-amidinopropane) dihydrochloride), and Trolox (6-hydroxy-2,5,7,8-tetramethyl-1-chroman-2-carboxylic acid; 20 µM) was used as antioxidant calibrator for the assay. The fluorescence decay was measured by a spectrofluorometer (Safas, Monaco) at an excitation/emission wavelength of 520/495 nm every 2 min for a total duration of 1 h. Relative antioxidant activities of protein samples were measured by comparison with Trolox standard and results are reported as µmol Trolox equivalents mg^{-1}.

Tara Pacific metadata. To explore the relationships between the measured phenotype data and the genetics and the associated microorganism diversity from the samples and the environment variables from the sampled sites, we used metadata from the Tara Pacific consortium (Table 3). The coral-species identification was performed on genome-wide markers[57] and sequencing of divergent genomic fragments[56] and resulted in five different identified species within the *Pocillopora* genus and three species within the *Porites* genus. The geographical distribution of the species analysed in the present work is shown in Supplementary Fig. S6. For the coral-associated microorganisms, on the one hand, we used the Symbiodiniaceae symbiont composition identified by the analysis of ribosomal nuclear ITS2[105]. For the colonies analysed in our study colonies, Symbiodiniaceae composition was divided into 10 and 11 clusters for *Pocillopora* and *Porites* respectively. Concerning the microbiome, we used the bacterial diversity obtained thanks to ribosomal 16 S analysis for bacterial microbiome[67]. For the colonies analysed in our study, microbiome composition was divided into five and seven clusters for *Pocillopora* and *Porites*, respectively. Finally, we also considered 101 contemporary (abbreviated to C), recent (R) and historical (H) environmental variables collected during the Tara Pacific expedition[98]. Contemporary data correspond to a rich collection of measurements of environmental variables collected onboard the day of sampling or recovered by satellite imagery and operational models. Recent and historical data correspond to past climate recordings extracted from climate satellite measurements, from respectively one year before sampling or from 2002. All the environmental variables were classified in four variables categories: Biological, Climate, Dynamism, or Physico-chemical (abbreviated to Bio, Cli, Dyn and Phy, respectively). The complete code-names of the environmental variables used in the present study are available in Supplementary Table S9.

Phenotypic analysis. The phenotypic signature from *Pocillopora* and *Porites*' colonies were analysed through the pipeline summarised in Supplementary Fig. S7.

Data visualisation and exploration. The specific distribution of variance by biomarker was displayed as boxplots by islands or coral species which were generated with the ggplot2 v3.3.5 R package[106]. The integrative phenotypic signal, combining the different biomarkers, was visualised by PCA with a comparison either between the two genera or within a given genus and displaying island or species belonging, with FactoMineR v2.4 package[107] and factoextra v1.0.7[108].

Statistical analysis. Statistical pipelines and figures were made with R v4.1.1[109].

Global variation of biomarkers through the Pacific Ocean. Biomarker by biomarker, distributions were compared by island or by species with Kruskall–Wallis' test and a Dunn's test as post hoc when necessary with the dunn.test v1.3.5 package[110], after filtering individuals with missing data. Because of the complementary and eventual redundancy of some of the biomarkers used, we tested their correlation with Kendall's tau before using all the biomarkers into the integrative phenotypic signal (Supplementary Fig. S2). We hence conserved all of them except the symbiont biomass reported by the surface of tissue.

Identification of putative drivers of coral phenotypic responses. The comparison between the coral genera, or among the islands and the coral species of a whole phenotypic signature was tested with a PERMANOVA (vegan v2.5-7[111] and pairwiseAdonis v0.4[112] packages using Bray–Curtis distance). This last analysis was run three times to ensure the repeatability of the outputs. To limit the number of false positive comparisons in the pairwise analyses, we applied a false discovery rate correction using the method described in ref. [113], implemented in the *adonis* function. The comparison at the coral genus scale was completed with a test of homogeneity of dispersion with *betadisper* function in vegan v2.5-7[111]. To estimate the influence of the origin island, coral species belonging or the symbiotic diversity of coral, the percentage of explained variance by each was measured with variancePartition v1.23.4 package[114]. We considered only coral colonies from islands containing more than one coral species per genus to limit bias (i.e., 87 *Pocillopora* colonies and 96 *Porites* colonies). An additional analysis was performed within coral species to determine a possible correlation between phenotypic and genetic distances (Mantel's tests computed with the package vegan v2.5-7[111]).

Biomarkers and environment variables correlation. The influence of the environment on the phenotypic signal was assessed using 101 environmental variables. To identify correlations among the biomarkers and environmental variables, an sPLS (sparse Partial Least Squares) analysis was performed (mixOmics v6.17.29 package[115]). The sPLS analysis, designed to treat multicollinear variables and noise, allowed us to model multiple correlated response variables, considering the biomarkers as multiple responses and the environmental variables as multiple predictors of the coral phenotypes. Briefly, the values (from biomarkers and environmental data) were first turned into absolute values and then transformed with BoxCox transformation (caret v6.0-90[116]), tending toward normal distribution. The correlation among the predictor variables (here the environmental data) and the response variables (here the biomarkers) was measured in regression mode. Only 20% of the most correlated variables for the two components of the analysis were retained, i.e., a maximum of 20 for each component. We also added a correlation coefficient cut-off of 0.3 to highlight the strongest correlations. Then the common environmental variables between *Pocillopora* spp. and *Porites* spp. were identified with ggvenn v0.1.9[117] and compared for each biomarker.

Data availability

Data generated during the study are available in the public repository (https://doi.org/10.5281/zenodo.7148413). The additional interpreted data, generated by the Tara consortium are the environmental variables[98,118], the Symbiodiniaceae (ITS2)[105] and bacterial (16 S)[119] communities, and species delimitation[56,57].

Received: 9 November 2022; Accepted: 26 July 2023;
Published online: 06 September 2023

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Acknowledgements

This work would not have been possible without the support, help and dedication of Etienne Bourgeois, the Tara Ocean Foundation's teams and crew and all the Tara Pacific Expedition Participants (https://doi.org/10.5281/zenodo.3777760). We are keen to thank the commitment of the following institutions for their financial and scientific support that made this unique Tara Pacific Expedition possible: CNRS, PSL, CSM, EPHE, Genoscope, CEA, Inserm, Université Côte d'Azur, ANR, agnès b., UNESCO-IOC, the Veolia Foundation, the Prince Albert II de Monaco Foundation, Région Bretagne, Billerudkorsnas, AmerisourceBergen Company, Lorient Agglomération, Oceans by Disney, L'Oréal, Biotherm, France Collectivités, Fonds Français pour l'Environnement Mondial (FFEM), the Ministère des Affaires Européennes et Etrangères, the Museum National d'Histoire Naturelle. For the experimental and analytic support, we thank Noemie Dechaux, Nina Luckas, Alexia Oechsel, Brigitte Poderini, Guillaume Signoret, Ludovic Toisoul and Marion Tredez. For the statistical discussions and advice, we warmly thank Diane Bailleul, Marc Bailly-Bechet, Jérôme Laurent, Mélanie Pousse and Florentine Riquet. For the sample storage and management, we also thank Alice Rouan. The work was supported by the ANR CORALGENE (ANR-17-CE02-0020), the 'Investments for the Future' programs LABEX SIGNALIFE (ANR-11-LABX-0028) and IDEX UCAJedi

(ANR-15-IDEX-01) as well as the master fellowship from the french 'Fondation pour la recherche sur la biodiversité'. This is publication number #30 of the Tara Pacific Consortium. We are keen to thank the local people and authorities who made this study possible. Specifically, we thank the people of Colombia and the following local institutions for their administrative and scientific support that made this singular expedition possible, the Prime Minister Office and their teams; the Ministry of Environment and National Natural Parks of Colombia with Guillermo Alberto Santos Ceballos, Edna Carolina Jarro Fajardo, and their teams; la Fundacion Malpelo y Otros Ecosistemas Marinos with their Executive Director and Founder Sandra Bessudo, with Felipe Orlando Ladino and their teams; el Santuario de Fauna y Flora Malpelo and their teams; la Direccion General Maritima with Ivan Fernando Castro Mercado and their teams; The Pacific Territorial Directorate and their teams; the Colombian biodiversity information system and their teams; and all other locally supports. We are keen to thank the commitment of the people of Panama and the following local institutions for their administrative and scientific support that made this singular expedition possible: The Ministry of Environment of Panama with Samuel Valdès Diaz, Lissette Trejos, Patricia Hernandez and their teams; the Smithsonian Tropical Research Institute with Rachel Page, Zurenayka Alain, Juan Mate and their teams; the Head of MPA at Coiba Park Didiel Nunez and their teams; and all other locally supports. We are keen to thank the commitment of the people of Pitcairn Islands and the following local institutions for their administrative and scientific support that made this singular expedition possible: the Government of Pitcairn Islands with Melva Evans and their teams; the Office of the Mayor and Council for Pitcairn, Henderson, Ducie and Oeno Islands with Shawn Christian and their teams; the Environmental, Conservation & Natural Resources Division with her Manager Michele Christian, and their teams; the Police & Immigration Officer with Christian Brenda, and their teams; and all other locally supports. We are keen to thank the commitment of the people of French Polynesia and the following local institutions for their administrative and scientific support that made this singular expedition possible: Le Haut-commissaire de la République en Polynésie française and their teams; The City of Papeete with its Mayor, its Port Commander, and their teams; le Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) and their teams; and all other locally supports. We are keen to thank the commitment of the people of the Cook Islands and the following local institutions for their administrative and scientific support that made this singular expedition possible: the Government of the Cook Islands and their teams; the Office of the Prime Minister with Tina Samson, Elizabeth Wright-Koteka from the Cook Islands Research Committee, and their teams; the Ministry of Marine Resources with its Director Dorothy Solomona, and their teams; the National Environment Service with its Director Joseph Brider, Elizabeth Munro, Bobby Bishop, and their teams; the City of Aitutaki, its mayor, and their teams; the Aitutaki Marine Research Station with its station manager Richard Story, and their teams; the Cawthron Institute with Lesley Rhodes, Kirsty Smith, and their teams; and all other locally supports. We are keen to thank the commitment of the people of Niue and the following local institutions for their administrative and scientific support that made this singular expedition possible: the Government of Niue with Richard Hipa, James Tatafu, Aldric Hipa, and their teams; the Office of External Affairs of the Government of Niue with its Director Emi Hipa, and their teams; the Cabinet and Parliamentary Services with its Director Christine External; the Ministry of Infrastructure and its Department of Transport, with Lynsey Talagi, and their teams; the Ministry of Natural Resources and its Director-General Josie Tamate, and their teams; the Department of Agriculture, Forestry and Fisheries at the Ministry of Natural Resources with its Director Brendon Pasisi, and their teams; the Department of Environment of the Ministry of Natural Resources and its Director Sauni Tongatule, and their teams; the Pacific Community with its Deputy Director-General Cameroun Diver, Coral Pasisi, and their teams; and all other locally supports.We are keen to thank the commitment of the people of Samoa Islands and the following local institutions for their administrative and scientific support that made this singular expedition possible: the Government of the Independent State of Samoa, and their teams; the Ministry of Foreign Affairs and Trade with its CEO Peseta Noumea Simi, its Acting CEO Leroy E. Hunkin-Mamae, Sapeti Titiii, and their teams; the Ministry of Natural Resources and Environment with its Principal Marine Conservation Officer Maria R. Satoa Peni, and their teams; the Ministry of Agriculture and Fisheries with its Assistant CEO Magele Etuati Ropeti, and their teams; and all other locally supports. We are keen to thank the commitment of the people of Guam and the following local institutions for their administrative and scientific support that made this singular expedition possible: the Department of Agriculture Division of Aquatic and Wildlife Resources (DAWR), its Director Matthew L.G. Sablan, its Assistant Chief Jay Gutierrez, and their teams; the Division of Management Authority Branch of Permits, the Senior Biologist Anna Barry, and their teams; the U.S. Fish and Wildlife Service—Office of Law Enforcement, its Wildlife Inspector Arthur T. Taimanglo, and their teams; and all other locally supports.

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Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s43247-023-00946-8.

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Peer review information *Communications Earth & Environment* thanks Raphael Ritson-Williams, Marina Tonetti Botana and Thierry Work for their contribution to the peer review of this work. Primary Handling Editors: Christopher Cornwall and Clare Davis. A peer review file is available.

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