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Author for correspondence:
Danielle M. Barnas
e-mail: dmbarnas@hawaii.edu

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Submarine groundwater discharge drives both direct and indirect effects on organismal and community metabolism on coral reefs

Danielle M. Barnas[1,2], Maya Zeff[2,3] and Nyssa J. Silbiger[2,4]

[1]University of Hawai'i at Mānoa, Hawai'i Institute of Marine Biology, Kāne'ohe, HI, USA
[2]Department of Biology, California State University Northridge, Northridge, CA, USA
[3]Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA, USA
[4]Department of Oceanography, Uehiro Center for the Advancement of Oceanography, University of Hawai'i at Mānoa, Honolulu, HI, USA

DMB, 0000-0001-7225-1413; MZ, 0000-0002-1002-9187; NJS, 0000-0003-4916-3217

Coral reefs experience numerous environmental gradients affecting organismal physiology and species biodiversity, which ultimately impact community metabolism. This study shows that submarine groundwater discharge (SGD), a common natural environmental gradient in coastal ecosystems associated with decreasing temperatures, salinity and pH with increasing nutrients, has both direct and indirect effects on coral reef community metabolism by altering individual growth rates and community composition. Our data revealed that SGD exposure hindered the growth of two algae, *Halimeda opuntia* and *Valonia fastigiata*, by 67 and 200%, respectively, and one coral, *Porites rus*, by 20%. Community metabolic rates showed altered community production, respiration and calcification between naturally high and low exposure areas mostly due to differences in community identity (i.e. species composition), rather than a direct effect of SGD on physiology. Production and calcification were 1.5 and 6.5 times lower in assemblages representing high SGD communities regardless of environment. However, the compounding effect of community identity and SGD exposure on respiration resulted in the low SGD community exhibiting the highest respiration rates under higher SGD exposure. By demonstrating SGD's role in altering community composition and metabolism, this research highlights the critical need to consider compounding environmental gradients (i.e. nutrients, salinity and temperature) in the broader context of ecosystem functions.

1. Introduction

Ecosystem metabolic processes that cycle carbon and nutrients, such as net ecosystem production (NEP) and net ecosystem calcification (NEC), maintain ecosystem functioning and stability [1–3]. At the community level, ecosystem functioning and stability are supported by the continuous uptake and release of carbon and nutrients (e.g. nitrogen and phosphorus) in a stable environment [1,4,5]. There are many pathways that can lead to changes in ecosystem metabolism including processes that alter the physiology of organisms within the community (e.g. through changing environmental conditions) [6–8] or a shift in the community composition as a result of disturbance [5,9–11]. Indeed, organisms and their environment persist in a biological feedback loop to preserve ecosystem functioning: communities drive shifts in local biogeochemistry through metabolic activity (i.e. altering oxygen, pH and total alkalinity), while changes in environmental conditions subsequently drive

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shifts in community composition [12–14]. Therefore, it can be difficult to determine the mechanisms by which disturbances alter ecosystem metabolism. Understanding how these mechanisms may affect ecosystem functioning via metabolic shifts bears great importance in demonstrating community and ecosystem responses to rapid global environmental change [7].

Within relatively stable environmental conditions, community diversity has a saturating effect on ecosystem functioning [9]. However, in a dynamic environment (e.g. via changes in pH, temperature, salinity and nutrient input), diversity shifts over time, altering ecosystem functioning [15–17]. In a benthic temperate reef community, exposure to a strong pH gradient (6.6–7.2) reduced species diversity and increased functional trait redundancy while depleting functional diversity (richness, abundance and evenness) compared to low (7.5–7.8) or ambient (8.0) pH [10]. Under spatial and temporal thermal gradients, phytoplankton communities exhibited diverse composition and functional traits through niche partitioning [5]. This self-assemblage into a diverse community structure yielded elevated ecosystem productivity and stability over modelled community composition for species exhibiting lower thermal performance in certain temperature regimes [5]. When exposed to elevated nitrates, coral reefs have experienced phase shifts towards an algae-dominated system [18,19], particularly in close proximity to anthropogenic nutrient sources [17].

Environmental variability also impacts coral reef communities at the organismal level. Environmental gradients can alter the physiology of individuals (i.e. growth, respiration or photosynthesis), which scale up to affect community ecosystem metabolism [3,20–22]. For example, corals experiencing nutrient enrichment through natural (i.e. terrestrial runoff and groundwater) or experimental (i.e. nutrient diffuser) inputs may exhibit increased or decreased growth and elevated gross photosynthesis (GP) compared to corals in ambient conditions [23–26]. Meanwhile, macroalgae have shown augmented growth rates under elevated nutrients [17,27]. Environmental variables affecting organismal physiology and community composition are not solitary actors but rather are complex multivariate gradients of many parameters (e.g. nutrients, temperature, pH and salinity) acting jointly to impact ecosystem metabolism and functioning.

One common multivariate natural gradient known to drive shifts in marine environments and community composition is submarine groundwater discharge (SGD) [3,11,28]. SGD, the flow of water from land through the seabed into the coastal ocean [29], is a widespread natural phenomenon on coral reefs worldwide known to alter environmental biogeochemistry [30–34]. SGD serves as an important natural source of land-based nutrients, while also acting as a potential conduit for anthropogenic pollution [35,36]. SGD creates a unique biogeochemical environment, where high SGD is commonly associated with decreased temperature, salinity and pH, with elevated nutrients and variable total alkalinity [31,34,35,37]. Each of these parameters has individually been shown [22,26] to alter biodiversity and/or ecosystem metabolism (primarily NEP and NEC) on coral reefs [3,8,11,28,38]. Within an SGD regime, strong SGD exposure has led to reduced coral and calcifying algae abundance [11], reduced coral growth [8] and decreased photosynthetic and calcification rates [3]. Biodiversity near an SGD seep has shown patterns of reduced algal diversity with elevated biomass of tolerant species (i.e. turf, zoanthids and invasive macroalgae) [38,39]. Due to the distinct biogeochemical properties of SGD compared to ambient reef environments, SGD gradients can act as model systems for examining the impacts of environmental variation on community composition and ecosystem functioning.

Coral reefs are highly susceptible to compounding local and global stressors [40], and there is a need to understand the positive and negative effects of land-based processes like SGD on community identity (species present within the community) and functioning (metabolic trends under variable SGD influence) [41]. In this study, we tested the direct and indirect effects of SGD on benthic community metabolism through altered organismal physiology and community composition on a coastal coral reef in Mo'orea, French Polynesia. We hypothesized that (i) the presence of SGD would impact the growth of individual community members by augmenting growth of fleshy macroalgae and hindering growth of coral and calcifying algae compared to low or ambient conditions, and (ii) that benthic assemblages with differing species identities defined by long-term SGD influence would drive changes in community ecosystem metabolism, such that increased presence of calcifying and photosynthetic species in response to SGD would elevate rates of net calcification and net community production, respectively.

2. Methods

(a) Study site and experimental design

Mo'orea, French Polynesia is a tropical volcanic island that has recently been investigated for SGD [42–45]. Similar to other tropical islands with steep topography, SGD is channelled into Mo'orea's coastal fringing reef through fissures in the reef flat [44]. We chose a site on the western side of Mo'orea with known SGD that has a previously characterized biogeochemical gradient along 140 m of reef from a primary seepage point (figure 1) [43–45]. SGD at this site is tidally driven, supplying the highest quantities of biogeochemically distinct water to the impacted community at low tide. Prior studies at this site showed that SGD has higher nutrients and total alkalinity, and lower temperature, salinity and pH than ambient seawater [45]. Our field site also exhibits consistent unidirectional alongshore flow of 0.15 m s^{-1}, based on data collected from an ADCP [45], where the SGD is expelled from a small cluster of nearshore seeps both up- and downcurrent of the primary seep and then moves northwestward across the reef (figure 1).

We created two SGD exposure treatments based on environmental data from Silbiger *et al*. [45] and two SGD assemblage treatments based on benthic community surveys from naturally high or low SGD influence to test the effect of SGD on organismal growth and community metabolism (i.e. photosynthesis, respiration and calcification). Specifically, we subjected multiple reef taxa in curated assemblages to high or low SGD exposure for 6 weeks during the rainy season, when SGD fluxes are highest. Ten replicate assemblages of the two community types were placed in each exposure treatment (two assemblage treatments × two exposure treatments) for a total of 40 assemblages.

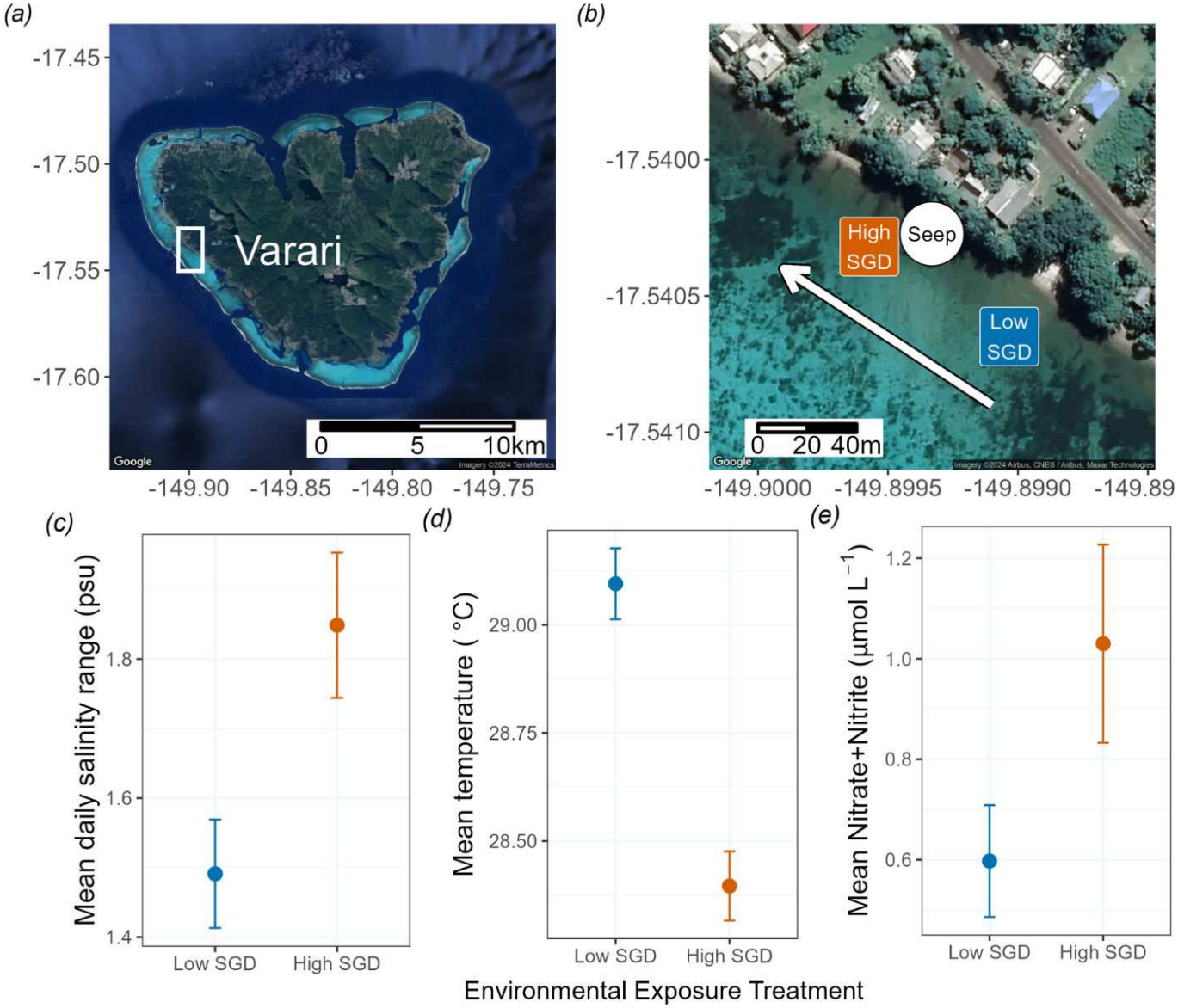

Figure 1. (*a*) Map of Mo'orea, French Polynesia, indicating the study site region. (*b*) Study site map with labels for the seepage point and two *in situ* platform locations, one in high SGD exposure and one in low exposure, with the white arrow indicating the predominant north-westward flow direction. (*c*) Mean minimum salinity (psu), (*d*) mean temperature (°C) and (*e*) mean (±s.e.) nitrate + nitrite (µmol l^{-1}) ($n = 4$ measurements per metric) at both platforms during the *in situ* soaking period.

(b) SGD exposure treatments

Due to the predictable flow regime along the fringing reef, we selected two experimental locations: one 50 m upstream (low SGD exposure) and one 27 m downstream (high SGD exposure) of the known SGD seepage point (figure 1*b*). These sites were chosen to minimize differences in flow, sedimentation, and light regime, while also keeping distance offshore constant (18 m). To monitor SGD presence at each exposure site at high and low tides, we collected continuous measurements of salinity (accuracy ± 5%, precision = 2 uS cm^{-1} conductivity) and temperature (accuracy ± 0.1°C, precision = 0.01°C) (HOBO U24 Saltwater Conductivity Logger, Onset Computer Corporation, Massachusetts) at the seepage point and each exposure location at 5 min intervals (figure 1). We also collected four discrete water samples in acid-washed triple-rinsed 125 mL Nalgene bottles during low and high tides at day and nighttime within a 24 h period from 9 to 10 March 2023. From each sample, we measured instantaneous salinity (accuracy ± 1.0% psu, precision = 0.1 psu) and temperature (accuracy ± 0.3°C, precision = 0.1°C) (YSI Pro2030, Xylem, Washington, DC), pH_T (tris-calibrated [total scale] ROSS double junction electrode, accuracy ± 0.002, precision = 0.001, Orion Star A325, Thermo Fisher Scientific, Massachusetts), nutrients (Silicate [SiO_3^{2-}], phosphate [PO_4^{3-}], and nitrate +nitrite [N + N]) and total alkalinity (A_T).

pH_T was corrected for *in situ* temperature using the seacarb package [46]. Nutrient samples were filtered through a 0.22µm Sterivex filter before being frozen at −20°C for subsequent nutrient analysis at the S-LAB at University of Hawai'i, where they were analysed on a Seal Analytical AA3 HR Nutrient Analyzer (N + N: detection limit [DL] = 0.009 and coefficient of variation [CV] = 0.3%; PO_4^{3-}: DL = 0.011 and CV = 0.2%; SiO_3^{2-}: DL = 0.03 and CV = 0.5%) at the UH SOEST Lab for Analytical Chemistry. Total alkalinity samples were fixed with 50% saturated mercuric chloride in deionized (DI) water following protocols by the Dickson lab [47]. We analysed A_T using a Mettler Toledo T5 autotitrator for open-cell potentiometric titrations [47], and accuracy and precision of titrations were tested against a certified reference material (CRM Reference Material for Oceanic CO_2

Measurements, A. Dickson, Scripps Institution of Oceanography) at the beginning of each set of titrated samples (accuracy < 0.5% off from reference material, precision = 5 µmol kg^{-1}).

(c) SGD assemblage treatments

Benthic community composition surveys were used to determine the species identities of benthic communities to deploy at high and low SGD exposure locations. We selected eight total survey sites, four exhibiting the highest and four exhibiting the lowest environmental SGD exposure based on prior data [45]. Benthic communities were surveyed via snorkeling at each site from June to July 2022 to estimate species composition of coral, macroalgae, sponges, corallimorphs, anemones and cyanobacteria. Composition was assessed within 2 m × 2 m plots using a uniform point-count method with 200 evenly distributed points at each site (4 m^2 per site, 16 m^2 total area per SGD exposure type). Organisms at each point were identified to species level when possible, or the lowest possible taxonomic unit [48,49]. We determined the top eight most abundant benthic species from each environmental exposure area for our assemblage treatments (figure 2 and table 1). While species richness was consistent across assemblage types (n = 8 species, abundance = 1 per species), the types of functional traits expressed by community members varied across each group (table 1).

(d) Organism collection and deployment

A total of 320 organisms across all treatments (n = 80 individuals per treatment) were collected for this experiment. All species were hand collected by snorkel on the fringing reef at least 100 m upcurrent of the known seepage point to avoid confounding effects of SGD on life history. To allow for direct comparison of individual response to SGD, replicate individuals of non-colonial organisms were collected in pairs to place one individual in each exposure treatment. Similarly, colonial species in each assemblage type were fragmented into two organisms, such that one organism was placed in high SGD exposure and one was placed in low SGD exposure. Both assemblage types therefore experienced each SGD exposure condition before being tested for changes in community metabolism (NEC and NEP). Replicates of species pairs or colonies were collected at least three meters away from each other to minimize genotypic duplication across assemblages in each exposure treatment.

All organisms were transported submerged to the Richard B. Gump South Pacific Research Station on Mo'orea and held in flow-through water tables. A supply of fresh seawater was continuously pumped from nearshore to provide an ambient coastal environment similar to the collection site, and the water was supplementally oxygenated using air bubblers (Tetra Whisper Air Pump, Virginia, USA). Water tables were cleaned daily to remove algae and avoid settlement. Organisms were fragmented and cleaned to remove excessive epiphytes and epifauna. We used forceps to remove epiphytes and epifauna from organisms and additionally removed epifauna from interstitial spaces of *Lithophyllum kotschyanum* by submerging fragments in freshwater for up to 15 s, following protocols from Glanz [53]. Species with hard substrate (Scleractinia: *Pocillopora acuta*, *Porites rus*, *Montipora grisea*; crustose coralline algae [CCA]: *L. kotschyanum*; Corallimorpharia: *Discosoma nummiforme*; sponge: *Porifera* unk) were attached to wide flat-headed bolts with hot super glue (Gorilla Hot Glue, The Gorilla Glue Company, Ohio). Species not attached to the bolts (macroalgae: *Dictyota bartayresiana*, *Turbinaria ornata*, *Halimeda opuntia*, *Valonia fastigiata*; sponge: *Lendenfeldia chondrodes* were wrapped loosely in clear nylon netting to allow sufficient space and light for growth (8 mm × 8 mm mesh size).

Organisms were deployed in either the high or low exposure location for 5–6 weeks from 8 February to 24 March 2023. Species were held *in situ* in a metal cage (13 mm × 13 mm mesh size) at each exposure site to reduce grazing and predation. Cages were fastened atop cinder block platforms raised above the benthos to 0.6 m depth at each site. Bolt-mounted species were fastened to the cage along the mesh base with washers and nuts, while netted organisms were attached to the base with zipties. Cages were consistently cleaned and checked for the overall health condition of species throughout deployment.

(e) Individual growth rate

Species were measured before and after deployment for weight (±0.1 g, Adam Equipment CQI-2601 balance, NY, USA) to determine growth of species across exposure treatments. Bolt-mounted organisms were buoyant-weighed (Scleractinia and CCA) following standard protocols [54] or wet-weighed (*D. nummiforme* and *Porifera* unk) by patting the organism with a dry cloth to remove excess water. All other species (macroalgae and *L. chondrodes*) were wet-weighed before being wrapped in mesh and after mesh removal by using a centrifugal spinner with a standard timed rotation. We estimated individual growth as the daily change in growth normalized to biomass (mg g^{-1} d^{-1}) [55], and we converted buoyant weight to dry weight [56] using the skeletal density of each species: aragonite (2.93 g cm^{-3}) for corals [56] and calcite (2.71 g cm^{-3}) for CCA [57]. All individual weights were normalized to biomass for consistency across species [55,57,58], but surface area-normalized growth rates were also calculated for the three coral species [59] and the CCA [60] to verify that growth was consistent with previous literature (electronic supplementary material, figure S1).

(f) Community metabolism

After deployment, we formed complete assemblages based on the species in table 1 through random selection of healthy individuals from each species group. We measured four biomass-normalized community metabolism rates for each of the 40 assemblages: dark respiration (R_d), net photosynthesis (NP), gross photosynthesis (GP) and net calcification (NC). Community dark respiration and net production were calculated from oxygen evolution, and community calcification was estimated using

Figure 2. Images of species used in the creation of two assemblage treatments: (*a*) *Discosoma nummiforme*, (*b*) *Lendenfeldia chondrodes*, (*c*) *Valonia fastigiata*, (*d*) *Pocillopora acuta*, (*e*) *Dictyota bartayresiana*, (*f*) *Lithophyllum kotschyanum*, (*g*) *Montipora grisea*, (*h*) *Porites rus*, (*i*) *Porifera* unknown, (*j*) *Halimeda opuntia* and (*k*) *Turbinaria ornata*.

Table 1. High and low SGD assemblage treatments, with corresponding species and functional traits ranked by percent cover within either high or low SGD exposure areas. Novel species from each treatment are indicated in bold. Species were categorized by phyla and one functional trait within each of three functional groups selected for their contribution to broader community ecosystem functioning. Categorization of each species was accomplished using the World Register of Marine Species [50], Coral Traits Database [51], AlgaeTraits database [52], species identification guides and primary literature.

species	phyla	morphology	calcification type	energetic resource	benthic % cover
low SGD assemblage					
Turbinaria ornata	Phaeophyta	branching	non-calcifying	autotrophic	**19.3**
Pocillopora acuta	Cnidaria	branching	hermatypic	mixotrophic	**10.0**
Porites rus	Cnidaria	massive	hermatypic	mixotrophic	**6.6**
Dictyota bartayresiana	Phaeophyta	branching	non-calcifying	autotrophic	**4.0**
Halimeda opuntia	**Chlorophyta**	**branching**	**articulated**	**autotrophic**	**3.6**
Montipora grisea	**Cnidaria**	**encrusting**	**hermatypic**	**mixotrophic**	**3.4**
Porifera unknown	Porifera	encrusting	non-calcifying	heterotrophic	**3.2**
Valonia fastigiata	**Chlorophyta**	**cushion-like**	**non-calcifying**	**autotrophic**	**2.5**
high SGD assemblage					
Porites rus	Cnidaria	massive	hermatypic	mixotrophic	**10.2**
Turbinaria ornata	Phaeophyta	branching	non-calcifying	autotrophic	**9.3**
Pocillopora acuta	Cnidaria	branching	hermatypic	mixotrophic	**8.6**
Discosoma nummiforme	**Cnidaria**	**polypoid**	**non-calcifying**	**mixotrophic**	**4.6**
Dictyota bartayresiana	Phaeophyta	branching	non-calcifying	autotrophic	**2.3**
Porifera unknown	Porifera	encrusting	non-calcifying	heterotrophic	**1.8**
Lithophyllum kotschyanum	**Rhodophyta**	**encrusting**	**non-articulated**	**autotrophic**	**1.8**
Lendenfeldia chondrodes	**Porifera**	**encrusting**	**non-calcifying**	**heterotrophic**	**1.4**

the total alkalinity anomaly technique [61] in closed-system chambers (6 l) with ambient filtered seawater (20 µm-rated sand filter). For each community metabolism trial, we placed four high SGD assemblages and four low SGD assemblages (two from high SGD exposure and two from low SGD exposure per assemblage type) each in individual 6 l water-tight transparent chambers (Rubbermaid, Georgia; n = 8 chambers) with a circulation pump (Aquaneat Submersible Pump, 80 GPH), fiber optic oxygen sensor (PSt7, accuracy ± 0.05% O_2) and temperature sensor (Pt100, accuracy ± 1.0°C) (PreSensPrecision Sensing GmbH, Germany), and overhead light source (Prime 16 HD LED Reef Light, AquaIllumination) equipped for each chamber. A ninth chamber without organisms was also included as a control to account for any background changes in oxygen or total alkalinity from the seawater.

NP and NC were measured simultaneously for 60 min under saturating light conditions (I_k = 440 µmol photons m^{-2} s^{-1}). Saturating light was determined from photosynthesis-irradiance curves from prior coral and algal studies conducted at fringing reef sites at the same depth in Mo'orea [22,62–64]. Notably, the organisms in the current study experienced *in situ* light conditions ranging from 0 to 1800 µmol photons m^{-2} s^{-1} (miniPAR, accuracy ± 5% in air traceable to NIST, Precision Measurement Engineering, California). Given the high light intensity experienced *in situ*, we do not anticipate photo-inhibition of communities at 440 µmol photons m^{-2} s^{-1}. After refilling the chambers with oxygenated filtered seawater, chambers were then run in darkness for 20 minutes to measure R_d. Oxygen concentration (µmol l^{-1}) and temperature (°C) were recorded at a frequency of 1 Hz (Oxy10 St, PreSens Measurement Studio 2, PreSens Precision Sensing GmbH, Germany).

Rates of oxygen release (NP) and uptake (R_d) were calculated by repeated local linear regressions used to obtain the best-fit linear regression through a bootstrapping technique with the package *LoLinR* [65] in R [66], corrected for chamber volume, blank rates, and normalized to the total organic biomass of each assemblage. We calculated GP of assemblages by

$$GP = NP + |R_d|,$$

where the absolute value of R_d is added to NP to account for O_2 consumption.

To measure NC, water samples were collected before and after each 60 min light trial in triple-rinsed 120 ml acid-washed Nalgene bottles. We measured A_T using the same methods detailed above. NC (µmol $CaCO_3$ g^{-1} h^{-1}) was calculated by the total alkalinity anomaly technique [61] using the following equation:

$$NC = \frac{(\Delta A_{Tsample} - \Delta A_{Tblank}) \cdot V \cdot \rho SW}{2 \cdot t \cdot AFDW}.$$

ΔA_T (µmol kg^{-1}) is the change in A_T from initial to post-trial water samples, with $\Delta A_{T\ blank}$ as the control chamber, V is total water volume in each chamber (mL), ρ_{SW} is the average density of seawater (1.023 g cm^{-3}), t relates to total incubation time of assemblages in their respective chambers (h^{-1}) and AFDW is the total ash-free dry weight of each assemblage relating to total organic biomass (g^{-1}). An individual's AFDW was calculated using standard methods [22] (electronic supplementary materials), and AFDW of each assemblage was obtained through the sum of its respective set of organisms.

(g) Statistical design

Environmental variation between high and low SGD exposure was assessed via individual linear models. We used individual linear mixed-effects models to test the effect of SGD exposure on growth for each species, where the growth rate was the dependent variable, exposure treatment was the fixed effect, and paired organism ID was a random effect. To test the interactive effect of SGD exposure and assemblage treatment on community metabolism (NP, GP, R_d and NC), we used individual two-way Type II ANOVA and Tukey post-hoc tests for each rate with assemblage type and exposure treatment as interactive effects. Analyses were performed in R [66] using the *lmer* function in *lme4* [67] for a mixed effects model, *anova* in the *stats* package [66] to produce an ANOVA table of summary statistics, and *HSD.test* in *agricolae* [68] to perform the Tukey tests. Assumptions of homogeneity of variance and normality were met and checked using *leveneTest* function in the *car* package [69] and Shapiro–Wilk's test for normality using the *shapiro.test* function in the *stats* package [66].

3. Results

(a) Environmental conditions are altered by SGD exposure

Based on data collected at the seepage point, there were substantial pulses of SGD to our field site which altered seawater physicochemical conditions during the soak period. Specifically, the sensor data revealed significant variability during the 6-week deployment in continuous salinity (min = 13.1 psu, max = 37.5 psu) and temperature (min = 25.4°C, max = 32.8°C) measurements. From the discrete 24 h sampling event, N + N, PO_4^{3-}, and SiO_3^{2-} at the seepage point ranged from 0.53 to 19.03 µmol l^{-1}, 0.11 to 1.1 µmol l^{-1}, and 2.83 to 199.23 µmol l^{-1}, respectively, while A_T varied from 2363 to 2752 µmol kg^{-1}, and pH_T ranged from 7.40 to 8.04. These SGD signatures at the seep translated to significant differences in the salinity, temperature, and nutrient conditions at the high and low SGD exposure locations. Specifically, mean daily salinity range was 0.4 psu higher ($F_{1,90}$=7.528, p = 0.007) and mean temperature was 0.5°C lower ($F_{1,90}$=37.20, p < 0.001) in high SGD than low SGD (figure 1). The standard deviations of nutrients were also higher at the high SGD exposure sites than the lower SGD sites (N + N: $F_{1,3}$=11.17, p = 0.044; PO_4^{3-}: $F_{1,3}$=10.20, p = 0.049; SiO_3^{2-}: $F_{1,3}$=222.4, p < 0.001). In particular, nutrient concentrations ranged from 0.73 to 1.61 µmol l^{-1} N + N, 0.07 to 0.23 µmol l^{-1} PO_4^{3-}, and 1.53 to 11.44 µmol l^{-1} SiO_3^{2-} in high SGD, compared to 0.38–0.84 µmol l^{-1} N + N,

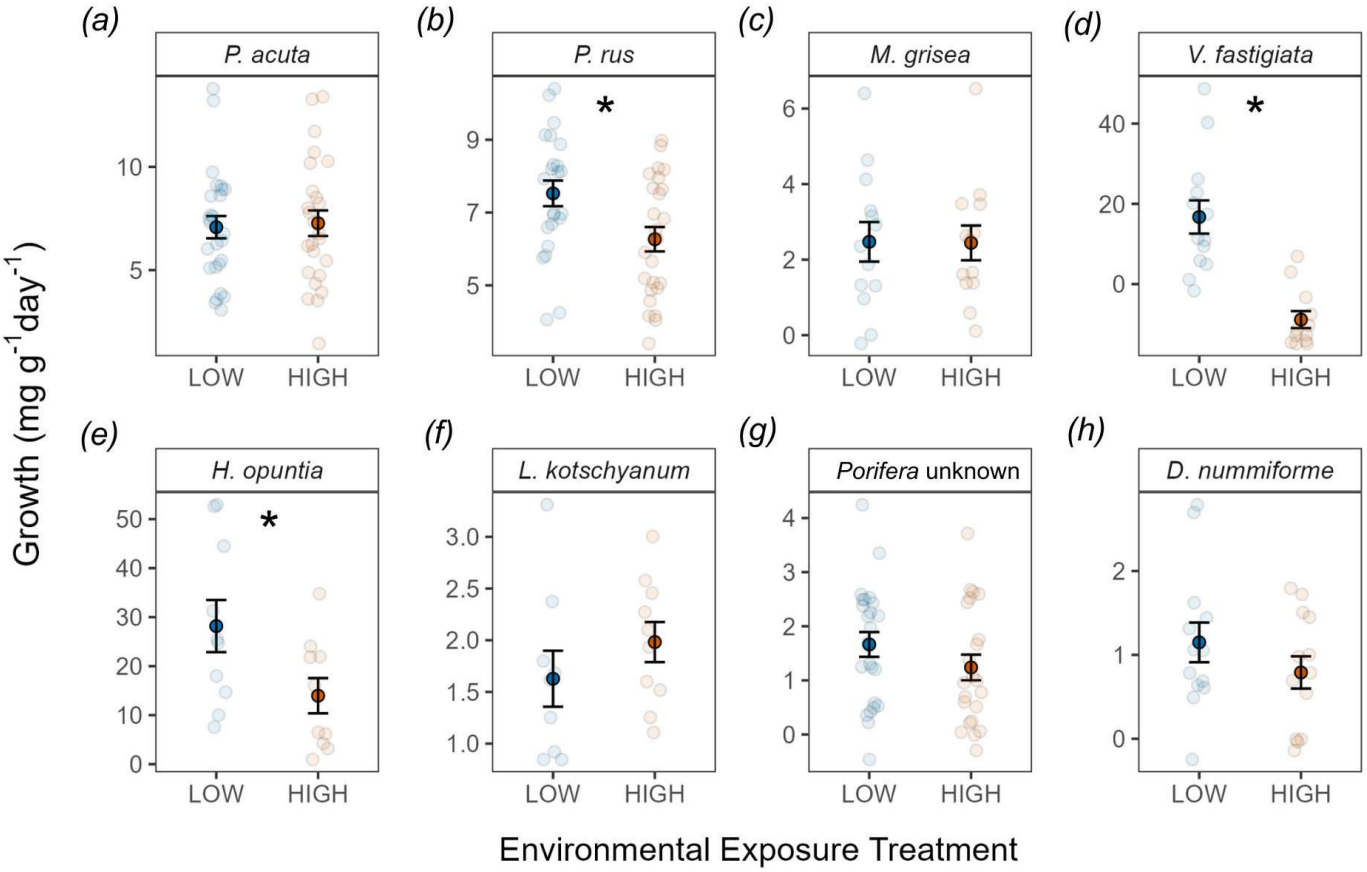

Figure 3. Biomass-normalized rates of growth (mg g^{-1} day^{-1}) of paired individuals across species groups and SGD exposure treatment. High transparency points indicate each individual's growth rate, and solid points show mean growth within treatment (±s.e.). Asterisks indicate significant effect of exposure treatment ($a < 0.05$) (electronic supplementary material, table S2).

0.07–0.10 µmol l^{-1} PO_4^{3-} and 0.97–1.76 µmol l^{-1} SiO_3^{2-} in low SGD (figure 1). SGD treatments exhibited no significant differences in pH_T, with pH_T ranging from 7.99 to 8.07 in high SGD exposure and 7.99 to 8.09 in low SGD exposure.

(b) Physiological response to SGD exposure varies by species

When comparing across exposure treatments, *P. rus*, *H. opuntia*, and *V. fastigiata* showed significantly reduced growth in the high SGD environment relative to low SGD (figure 3; electronic supplementary material, table S2). *V. fastigiata* displayed visible atrophy, yielding approximately 50% total tissue loss in high SGD exposure—a decline in growth at an average rate of 8.84 mg g^{-1} d^{-1} (±2.11). Conversely, *V. fastigiata* nearly doubled in size, with a growth rate of 16.7 mg g^{-1} d^{-1} (±4.13), while exposed to the low SGD ($F_{1,23} = 28.77$, $p < 0.001$). *H. opuntia* and *P. rus* had a positive growth rate in both treatments; however, in high SGD exposure, *H. opuntia* grew half as fast as the low SGD exposure (13.9 mg g^{-1} d^{-1} [±3.59] relative to 28.2 mg g^{-1} d^{-1} [±5.32]; $F_{1,9.2} = 7.837$, $p = 0.020$). *P. rus* grew 20% slower in the high SGD than low exposure (6.26 mg g^{-1} d^{-1} [±0.33] relative to 7.53 mg g^{-1} d^{-1} [±0.54]; $F_{1,22} = 13.31$, $p = 0.001$). All remaining measured species showed similar growth rates between treatments (*P. acuta*, *M. grisea*, *L. kotschyanum*, *Porifera* unk and *D. nummiforme*). The remaining species were only used for community metabolism because of *in situ* tissue loss (*T. ornata*) or intraspecific overgrowth causing difficulty in tracking individual growth rates (*D. bartayresiana* and *L. chondrodes*).

(c) Community metabolism changes as a function of assemblage type

There was a significant effect of assemblage type on NP, GP and NC across both environmental exposure treatments (figure 4; electronic supplementary material, table S3). Rates of NP and GP were 95.5% ($F_{1,33} = 19.57$, $p < 0.001$) and 74.0% ($F_{1,33} = 30.39$, $p < 0.001$) greater in the low SGD assemblage groups than high SGD assemblage groups, respectively. Similarly, communities within low SGD assemblage groups calcified 6.5 and 3.6 times (in low and high SGD exposure, respectively) more than high SGD assemblage communities ($F_{1,33} = 16.24$, $p < 0.001$). R_d was the only metabolic rate that showed a significant interaction between the community and exposure treatments ($F_{1,33} = 2.599$, $p = 0.016$). Specifically, the difference between assemblage types was only evident in the high SGD exposure treatment, with low assemblage communities exhibiting 66% higher respiration rates than high assemblage communities (figure 4*c*).

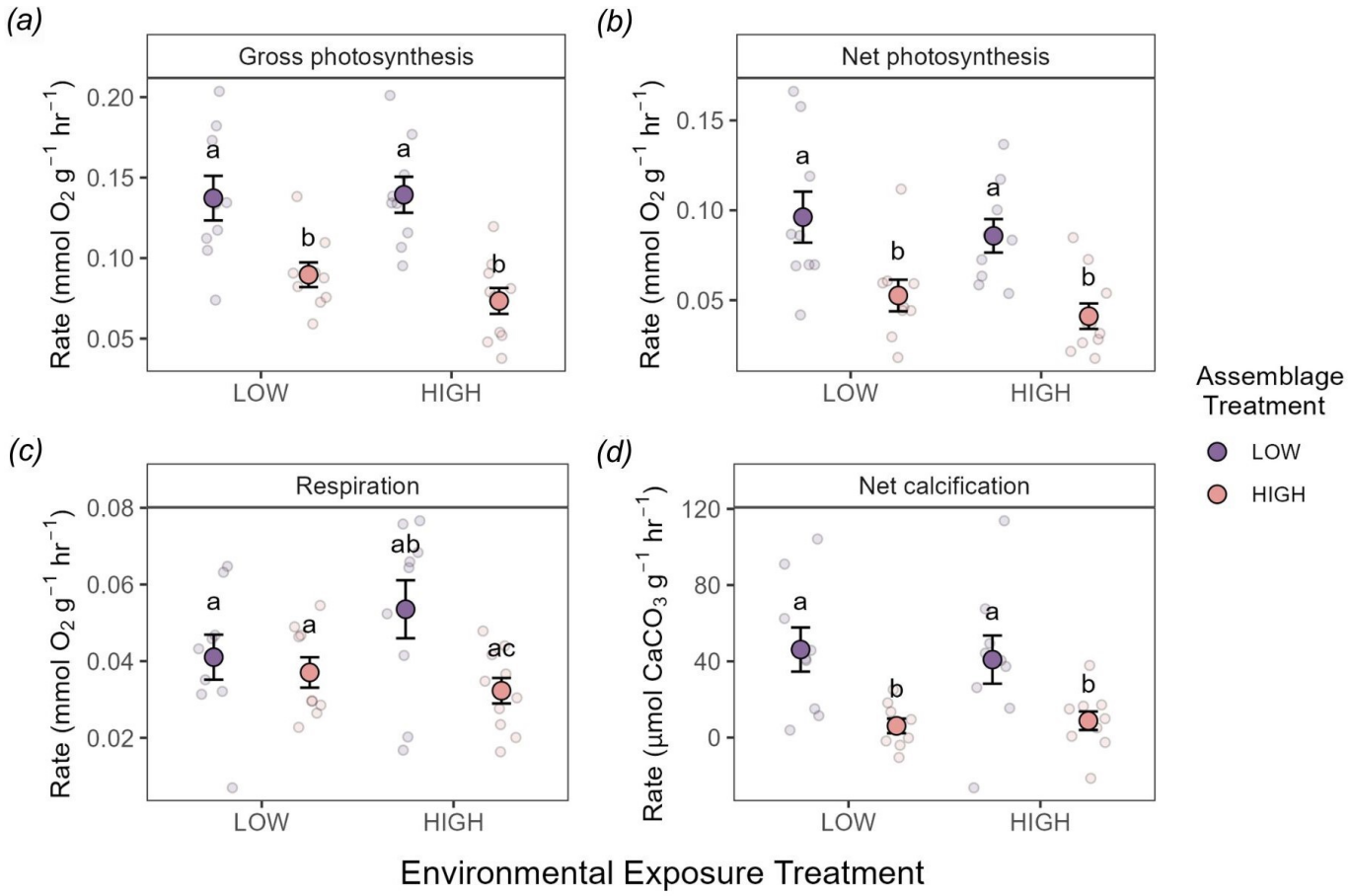

Figure 4. (*a*) Organic biomass-normalized rates of gross photosynthesis (GP), (*b*) net photosynthesis (NP), (*c*) respiration (R_d) and (*d*) net calcification (NC) of two assemblage types (low SGD and high SGD assemblage groups) in either low or high SGD exposure. High transparency points indicate each assemblage's individual rate within exposure treatment, while solid points show mean rates within assemblage and exposure treatments (±s.e.). Similar letters above error bars indicate nonsignificance, while differing letters indicate significance based on Tukey's HSD post-hoc tests.

4. Discussion

Submarine groundwater discharge directly affected the growth of several benthic coral reef species, and indirectly affected community metabolism through changes to community composition. Many of the different physicochemical parameters that vary with SGD, including elevated nutrients, lower salinity and cooler temperatures, could be responsible for the growth differences that we saw between the high and low SGD exposure treatments [20,21,26,70]. Nutrient enrichment may be one of the most notorious consequences of SGD in coastal ecosystems [33]. Although multiple processes may provide nutrients to coral reef communities (i.e. roving species waste [71] or benthic community metabolic inputs [72]), we observed a high correlation between salinity and nitrate+nitrite ($R^2 = 0.96$, $p < 0.001$). In an otherwise nutrient-depleted environment, this relationship shows that SGD is the driving force of nutrients to the communities in our experimental locations, and the effect of other nutrient sources is therefore minimal in comparison to SGD.

These new nutrients may have positive or negative impacts on growth of coral reef taxa. Previous studies have found that coral growth was dependent on the source of nutrients, where fish-derived nutrient enrichment increased growth, and human-derived enrichment decreased growth [71]. Other studies have shown that specific nutrients yield differing results, where nitrate hindered growth while elevating photosynthetic rates [71], and phosphate augmented coral growth [73]. The extent or variability of nutrient exposure may also have an impact. Adam *et al*. [17] showed that elevated nutrients from coastal development activities led to a shift from coral- to macroalgal-dominated communities. *P. rus* and two chlorophyte algal species (*H. opuntia* and *V. fastigiata*) all had significantly lower growth rates in the high SGD exposure location, which experienced 36% higher average nitrate+nitrite and 20% higher average phosphate concentrations in proximity to the groundwater seepage point at low tide. The coral species, *P. rus*, may have been especially sensitive to the elevated nutrient conditions as studies often show negative effects of nutrients on coral growth. For example, a meta-analysis from multiple coral species revealed that nitrate enrichment led to declines in coral calcification, while elevated phosphate resulted in enhanced coral calcification [71,73]. The negative effect of nitrate enrichment on calcification was further intensified for mounding coral, like *Porites*, compared to branching morphologies, like *Pocillopora*. In the present study, the presence of nitrate as a possible hindrance to calcification, without a possible growth enhancement effect from high phosphate input, may have led to the reduction in calcification of *Porites rus*. Growth of macroalgae, however, is often nutrient-limited, augmented by elevated phosphorus (i.e. phosphate) or nitrogen (i.e. nitrates, nitrites or ammonium) [27]. Despite nutrient enrichment under higher SGD exposure, growth of macroalgae was unaffected or reduced compared to low SGD, suggesting growth may have been influenced by other environmental factors attributed to SGD. We observed net positive growth in nearly all species, particularly in the low SGD

environment, indicating that organisms, in particular coral and CCA, sufficiently recovered from any handling or fragmentation stress before deployment. Furthermore, growth rates for coral and CCA within low SGD aligned with previously observed rates for *P. rus* [57,64,74], branching *Pocillopora* spp. [57], encrusting *Montipora* spp. [55] and *L. kotschyanum* [75] (figure 3; electronic supplementary material, figure S1), indicating that species had sufficient time to acclimate to their environmental treatment conditions.

Within an SGD regime, growth of algae and coral may also be inhibited by reductions in temperature and salinity [39]. The high SGD exposure site experienced cooler temperatures and more variable salinities throughout the *in situ* soak period compared to the low SGD site. Decreased temperatures (on the order of 1–5°C) are often associated with reduced metabolic rates for functions such as photosynthesis [20] across multiple taxa. This metabolic reduction may be due to the slowing of ion or nutrient diffusion [76], ultimately leading to decreased organismal growth [77]. Additionally, osmotic stress of a lower salinity environment may disrupt physiological and metabolic processes by altering ion uptake of individuals [78]. Of the three species whose growth was directly impacted by high SGD exposure in the present study, both algal species (*H. opuntia* and *V. fastigiata*) were commonly found in a low SGD reef environment, which seldom experienced the high biogeochemical variability observed in high SGD exposure. Within a high SGD environment, *V. fastigiata* was rare (<0.3% benthic cover), and *H. opuntia* was absent. The negative growth response of *V. fastigiata* in response to SGD was consistent with the anticipated response of a vesicular alga. Organisms with such morphology in high SGD exposure may have experienced either hindered ion uptake due to a small surface area:volume ratio by the combined effect of lower salinity and temperature throughout their diurnal cycle or possible loss of ions and disruption of intracellular fluid ion concentrations [78].

In addition to direct impacts on physiology, our results also show that SGD-driven community composition shifts lead to indirect effects of SGD on ecosystem metabolism. Specifically, the low SGD assemblage group always exhibited higher photosynthesis and calcification rates regardless of the SGD exposure treatment. These augmented rates for the low SGD assemblage group supported our assumptions that communities with higher densities of corals and fast-growing algae would boost ecosystem functioning, specifically primary production and calcification, despite constant species diversity across both assemblage treatments. Notably, all community respirometry measurements were collected in ambient seawater, conditions that reef communities in the study experience daily during high tide and episodically during high wave events, which reduce or halt SGD delivery [31]. Therefore, when seawater conditions are comparable across the reef, on diurnal (tidal) and episodic or seasonal (wave events) time scales, communities naturally found in low SGD influence exhibit higher metabolic rates than communities from high SGD influence. Future studies should examine if community metabolism changes as a direct result of changing seawater conditions from SGD.

Our hypothesis that greater rates of net production and GP in assemblages containing higher abundances of photosynthetic species was supported. Low SGD groups contained two additional autotrophic and one mixotrophic species, while high SGD groups included one autotroph, one mixotroph and one heterotroph. The combined effect of fewer autotrophs with the presence of an additional non-photosynthetic species likely reduced the overall photosynthetic rate of high SGD compared to low SGD groups. This finding is in line with other studies showing reduced NP and GP for communities with lower producer abundance [79]. The processes of calcification and photosynthesis in corals and calcifying algae are coupled, such that calcification byproducts (i.e. protons) support photosynthesis during daylight and byproducts of photosynthesis (i.e. CH_2O and O_2) in turn support calcification [80]. We therefore expected that rates of calcification and photosynthesis would show similar trends in both assemblage groups. To understand across-group differences, we hypothesized that assemblages containing a greater abundance of calcifying species would show increased NC compared to assemblages with fewer calcifiers. We observed elevated rates of NC for low SGD assemblages containing two additional calcifying species compared to one additional calcifier in high SGD assemblages. With four total calcifying species present in low SGD and only three calcifiers in high SGD groups, our hypothesis was supported by a more than threefold increase in calcification rates of low SGD over high SGD assemblages. The elevated performance displays the high efficiency of calcification by *M. grisea*, *H. opuntia*, or both, or possibly the synergistic effects of all calcifying species present [81,82]. The similar photosynthetic and calcification metabolic responses across the high and low exposure treatments could indicate that instantaneous changes in the environment (i.e. exposure to ambient vs SGD-influenced seawater) play an outsized role in community functioning compared to environmental history. However, when assessing community respiration, we saw the highest rates in the low assemblage with high SGD exposure. The increased respiration rate could be an environmentally driven stress response [78] as there were two unique algal species within the low SGD group (*V. fastigiata* and *H. opuntia*) that had lower or negative growth rates in response to high SGD exposure compared to low exposure.

We observed both direct and indirect impacts of SGD on coral reef community metabolism. The complex biogeochemical variability of SGD provides important ecological context for studying interactive environmental impacts. Species responses to SGD exposure were less ubiquitous than we anticipated, leading to the assumption that certain species experience counteracting growth enhancement or growth inhibition from the various physicochemical components of SGD. Coral reef communities under SGD influence experience high environmental variability on small spatiotemporal scales (within meters and over diurnal cycles) [33]. The high variability of multiple parameters associated with SGD makes these ecosystems intriguing testbeds for understanding the impacts of multivariable changes in coastal ecosystems. With the expectation of increased biogeochemical variability of coral reef environments due to natural and anthropogenic impacts [83], understanding how these communities respond to multiple sources of variability is crucial to predicting the resilience and resistance of these important ecosystems. This study shows that high SGD hinders the growth of certain reef taxa (i.e. one coral, *P. rus*, and two macroalgae, chlorophytes *H. opuntia* and *V. fastigiata*) but suggests the resilience of other taxa to high environmental variability. Additionally, this work displays the indirect effect of SGD on community ecosystem metabolism through altering species and functional composition along the gradient. In particular, communities containing species and functional identities naturally observed in low SGD

outperformed communities naturally observed in high SGD when exposed to ambient seawater. While the present study used a block design at a single site, other studies examining organismal responses along continuous SGD gradients have shown nonlinear patterns, with increases in growth and metabolism [3,8]. However, we recognize that further work is needed to address the mechanisms behind physiological and functional responses to compounding environmental variables. Concomitant studies along our same SGD gradient have addressed some of these knowledge gaps for common reef species along coastal reefs in Mo'orea [84,85], isolating drivers within the SGD gradient on organismal growth and benthic biodiversity shifts. The present work importantly observed the impacts of multiple concurrent variables on individuals and communities, and future studies should expand this work across and along multiple SGD gradients. This study highlights the importance of community composition for ecosystem functioning in a variable environment, and future studies should additionally assess the impact of species-specific and community-level functional identities on ecosystem functioning under natural and projected environmental gradients.

Ethics. Research was completed under permits issued by the French Polynesian Government (Délégation à la Recherche) and the Haut-commissariat de la République en Polynésie Française (DTRT) (Protocole d'Accueil 2005–2023).

Data accessibility. Data and code are available through Zenodo [86].

Supplementary material is available online [87].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. D.M.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, validation, visualization, writing—original draft, writing—review and editing; M.Z.: data curation, methodology, writing—review and editing; N.J.S.: conceptualization, funding acquisition, investigation, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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