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Submarine groundwater discharge alters coral reef ecosystem metabolism

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Submarine groundwater discharge (SGD) influences near-shore coral reef ecosystems worldwide. SGD biogeochemistry is distinct, typically with higher nutrients, lower pH, cooler temperature and lower salinity than receiving waters. SGD can also be a conduit for anthropogenic nutrients and other pollutants. Using Bayesian structural equation modelling, we investigate pathways and feedbacks by which SGD influences coral reef ecosystem metabolism at two Hawai'i sites with distinct aquifer chemistry. The thermal and biogeochemical environment created by SGD changed net ecosystem production (NEP) and net ecosystem calcification (NEC). NEP showed a nonlinear relationship with SGD-enhanced nutrients: high fluxes of moderately enriched SGD (Wailupe low tide) and low fluxes of highly enriched SGD (Kūpikipiki'ō high tide) increased NEP, but high fluxes of highly enriched SGD (Kūpikipiki'ō low tide) decreased NEP, indicating a shift toward microbial respiration. pH fluctuated with NEP, driving changes in the net growth of calcifiers (NEC). SGD enhances biological feedbacks: changes in SGD from land use and climate change will have consequences for calcification of coral reef communities, and thereby shoreline protection.

1. Background

Submarine groundwater discharge (SGD) is a natural and understudied feature of many near shore ecosystems that may play a key role in ecosystem functioning. SGD is the flow of water—meteoric, marine or a composite of both—from the land through the marginal seabed and into the coastal ocean [1,2]. SGD is a widespread phenomenon on near shore coral reefs as evidenced by reports from Hawai'i [3–6], Mo'orea [7,8], Florida [9], Israel [10], the Great Barrier Reef [11], Jamaica [12], Mexico [13] and Japan [14]. While there is an extensive body of literature describing high fluxes of SGD to coral reefs and other coastal ecosystems [15,16], there is a critical need to better understand the biological and ecological consequences of SGD [17].

SGD can be a source of high nutrient, low pH and cool water to coastlines [6,11,18,19], which can benefit oligotrophic systems [20] or put coral reefs at risk of eutrophication [15], depending on the watershed conditions and local environmental context. While SGD is natural, it can also act as a conduit for anthropogenic pollutants and lead to reef degradation [21]. Additionally, SGD can be fresh or saline and often has different concentrations of total alkalinity (TA), silicate and dissolved organic compounds than seawater [6,19,22]. Because each of these biogeochemical parameters can affect biological and ecological processes on coral reefs, it is important to understand how the unique environments created by SGD affect coral reef ecosystems.

The altered biogeochemistry in coastal waters from SGD can affect organismal physiology and species interactions that will ultimately lead to changes in key ecosystem functions, such as net ecosystem calcification (NEC) and net ecosystem production (NEP). For example, chronic nutrient loading of coastal waters can destabilize reefs by shifting competitive dominance away from corals and other calcifiers toward fleshy algae, and by increasing bioerosion rates through enhanced growth of bioeroding invertebrates and endoliths [18,21,23–27]. Conversely, slight increases in nutrients can be beneficial to reefs: a recent *in situ* experiment showed that *Porites lobata* grew fastest at intermediate levels of nutrient-rich SGD [18]. Nutrient loading from SGD can also lead to shifts in macroalgal composition and biomass [28] and microbial community composition to enrich copiotrophic and pathogenic taxa [29–31]. At an ecosystem scale, added nutrients can directly increase NEP rates on fringing reefs [32] or decrease NEP and/or NEC when coupled with other geochemical parameters associated with SGD [33,34]. Further, nutrient loading at concentrations associated with SGD can alter the quality and quantity of organic matter released by benthic communities [29].

SGD-associated changes in carbonate chemistry (e.g. CO_2, pH, TA, dissolved inorganic carbon [DIC]) and temperature will also affect reef dynamics and ecosystem functioning. Lower pH (or high CO_2) typically leads to decreased growth rates of corals and coralline algae [35,36], higher bioerosion rates [37–39] and lower NEC rates [40]. TA or DIC from SGD may be higher or lower than the receiving seawater, depending on the conditions of the aquifer, and altered TA will affect carbonate buffering. Where TA of SGD is elevated relative to the receiving waters, SGD may buffer reefs from ocean acidification, as calcifiers are more resistant to declining pH at higher concentrations of TA [22,41]. In locations where TA of SGD is lower than the receiving waters, SGD may make reefs more susceptible to ocean acidification. Nutrient and carbonate parameters can also interact: elevated nutrients can strengthen the negative relationship between pH and bioerosion [42] and disrupt the relationship between calcification and aragonite saturation state [43]. Increased temperature variability from the SGD could also affect community production and calcification rates [44]. Further, SGD could create biological feedbacks, where changes in production rates from the elevated nutrient concentrations will change local pH conditions, which can ultimately lead to changes in NEC [43,45]. Notably, seasonality, oceanographic conditions [46] and anthropogenic stressors (e.g. nearby cesspools or injection wells) [21] can also affect the relationships between SGD and ecosystem functions. As SGD is a common feature of near shore reef habitats, understanding the mechanisms by which SGD affects ecosystem functioning is a critical need for coral reef management.

Here, we use Bayesian structural equation models to better understand how SGD directly affects the biogeochemical and thermal environment in a shallow reef flat, and how this unique environment directly and indirectly affects key ecosystem functions. We focus on two sites in Hawai'i with differing SGD fluxes, oceanographic conditions and anthropogenic impacts. We hypothesize that SGD will drive a biological feedback loop, whereby SGD indirectly affect NEP and NEC through altered nutrient, temperature and pH values; however, the strength of the relationships will differ between the sites due to differences in local environmental conditions (e.g. aquifer biogeochemistry, residence times, exposure). Fluxes and the biogeochemistry of SGD are highly linked to changes in precipitation, land use, sea-level rise, tidal amplitude and groundwater usage [47]. As the drivers of SGD flux are rapidly changing, we must improve our understanding of the biogeochemical and ecological consequences of SGD to better predict how both natural and human-induced changes in SGD will affect reef ecosystem functioning in the future.

(a) Study area

Maunalua Bay is an 8 km embayment on the southeast side of O'ahu with known inputs of SGD [6,48,49]. There are nine watersheds that feed into Maunalua Bay, each with unique hydrology and history of human impacts [50]. Our study is based at sites adjacent to two of these watersheds: Kūpikipiki'ō (also known as Black Point) and Wailupe (electronic supplementary material, figure S1). Both sites are shallow reef flats (<1 m depth at mean lower low water): the reef flat at Wailupe is approximately 500 m wide, with fine sediment close to shore that gives way to carbonate platforms in a spur and groove pattern, and the reef flat at Kūpikipiki'ō is approximately 200 m wide and has a mix of isolated basalt boulders and carbonate shelves [18]. Both sites are dominated by macroalgae (approx. 50% at Wailupe and approximately 15% at Kūpikipiki'ō) with very low coral cover (<1% at both sites) [28,51]. The dominant algal taxa at Kūpikipiki'ō were *Pterocladiella* sp., turf and *Bryopsis pennata*; at Wailupe, the community was dominated by *Acanthophora spicifera*, *Gracilaria salicornia*, *Halimeda discoidea* and *Lyngbya* sp. The dominant corals at both sites were *Porites lobata* and *Montipora* spp., although they were in very low abundance. Kūpikipiki'ō has a freshened SGD flux of 11 700 ± 5900 m^{-3} d^{-1} (mean ± SD) over a 30-day period, with approximately 4.4% of the total recharge due to wastewater effluent from nearby cesspools; Wailupe has a freshened SGD flux of 9100 ± 2700 m^{-3} d^{-1}, with 0.7% of the total recharge is due to wastewater [33,48]. Further, the SGD from Kūpikipiki'ō has substantially higher nutrient concentrations in the groundwater than Wailupe (approx. 170 versus 70 µmol l^{-1} [6,48]), with wastewater accounting for 54 to 95% of the total N and P loads, and higher N : P ratios in the source water [48] (electronic supplementary material, figure S2). The contribution of wastewater to nutrient concentrations in Wailupe is negligible. The oceanographic conditions are also quite different between the two sites: the reef flat at Kūpikipiki'ō is narrowed and the site is more exposed and has shorter residence times than Wailupe [33], but tidal forcing is the dominant driver of diel SGD fluxes and diel current speed and direction at both sites [52]. The differences in hydrology, biogeochemistry and oceanography between Kūpikipiki'ō and Wailupe could lead to differing effects of SGD on ecosystem functioning.

2. Materials and methods

(a) Sampling design

Detailed sampling design, collection and processing of water samples can be found in [18], which we briefly summarize here. Twenty water sampling locations were established at each site ($n = 40$ total) in an approximate grid, scaled to the width of the reef flat, for biogeochemistry measurements (electronic supplementary material, figure S1). At each location, we collected discrete diel water samples across four timepoints (during daytime and nighttime high and low tides) in the spring and fall (totalling eight samples per location, 320 samples overall). Sampling dates were 18 April 2015 and 28 September 2015 at Wailupe, and 2 May 2015 and 26 October 2015 at Kūpikipiki'ō. Circulation on the shallow reef flat is primarily wind-driven [52], and northeast trade winds prevailed during all four sampling events, and wave heights ranged from 1.1 to 1.45 m. All sampling events happened during spring tide events. Water samples for pH, TA, nitrate + nitrite ($NO_3^- + NO_2^-$), phosphate (PO_4^{3-}) and silicate (SiO_3^{4-}) were hand collected directly above the benthos within 30 min of high or low tide in acid-washed HDPE bottles. pH was measured immediately using a tris calibrated Orion ROSS Ultra pH/ATC Triode following Dickson SOP 6a [53]. TA samples were immediately preserved with 50% saturated $HgCl_2$ in deionized water, stored in a cool dark place and later analysed on a Mettler Toledo T-50 autotitrator following Dickson SOP 3b [53] (precision = 2.68 µEq, accuracy = 0.48% ± 0.33% SD). Inorganic nutrient samples (SiO_3^{4-}, $NO_3^- + NO_2^-$, PO_4^{3-}) were immediately filtered through pre-combusted GF/F filters (0.7 µm) and stored in a −20°C freezer until further processing. Nutrient samples were processed at the SOEST Laboratory for Analytical Biogeochemistry at the University of Hawai'i at Mānoa using a Seal Analytical AA3 nutrient autoanalyser (reported error [coefficient of variance]: 0.5% for SiO_3^{4-}, 0.3% for $NO_3^- + NO_2^-$, and 0.2% for PO_4^{3-}). Temperature was recorded every 15 min on HOBO TidbiT v2 loggers and temperature values were extracted to match the time-discrete water samples were collected.

(b) Characterizing relative submarine groundwater discharge

Silicate is a common tracer for SGD [54] and was used to calculate the relative amount of SGD in the water column at each location during the time of collection. Notably, silicate is a non-conservative tracer and can be influenced by uptake from siliceous phytoplankton or benthic organisms, like sponges [55]. However, a strong significant relationship between silicate and radon (Rn, a common conservative tracer for SGD [56], $r^2 = 0.98$, $p < 0.0001$) from prior data at the same sites [6] indicates that biological uptake of SiO_3^{4-} is minimal at Maunalua (electronic supplementary material, figure S3). Therefore, SiO_3^{4-} can be used as a tracer for SGD at our research sites. The standardized measure of SGD, presented as %SGD, was calculated as

$$\%SGD = \frac{Si_{mix} - Si_{SW}}{Si_{GW} - Si_{SW}},$$

where Si_{mix} is the concentration at each location, Si_{SW} is the ambient concentration in seawater (1.03 µmol l^{-1}, the lowest concentration during the sampling points) and Si_{GW} is the concentration of the mean groundwater endpoint (810 µmol l^{-1} ± 52 (SD) for Wailupe ($n = 6$) and 740 ± 13 (SD) µmol l^{-1} for Kūpikipiki'ō ($n = 9$); values from Richardson *et al.* [33]). The associated salinities were 4.9 ± 0.2 (SD), 2.0 ± 0.2 (SD) and 35.2 for Kūpikipiki'ō, Wailupe and the open ocean endmembers, respectively.

(c) Calculating net ecosystem production and net ecosystem calcification

To account for changes in geochemical parameters due to mixing between groundwater and seawater, we normalized all geochemical data to a common reference concentration using the following equation:

$$C_1 = C_{mix} + (C_{mix} - C_{SGD})\left(\frac{Si_{mix} - 1.17}{Si_{SGD} - Si_{mix}}\right),$$

where C_1 is the silicate-normalized concentration at the reference value (1.17 µmol l^{-1}), C_{mix} is the measured concentration (groundwater-marine mixture), C_{SGD} is the average groundwater endmember concentration, Si_{mix} is the measured concentration (groundwater-marine mixture) and Si_{SGD} is the average concentration of the groundwater endmember [33]. The reference value was taken from the Hawaii Ocean Time-series at Station ALOHA in 2015 [57]. Groundwater endmembers for TA and DIC for Kūpikipiki'ō were 2946 ± 8 (SD) µmol kg^{-1} and 3038 ± 8 (SD) µmol kg^{-1}, respectively, and at Wailupe were 1754 ± 35 (SD) µmol kg^{-1} and 1779 ± 40 (SD) µmol kg^{-1} [33].

We estimated the NEC and NEP potential [58] for each location × timepoint by comparing the change in TA or DIC from each water sample with open ocean values from Station ALOHA [57]. NEC potential was calculated as ΔTA/2, while NEP potential was calculated as ΔDIC. ΔTA was divided by two because 1 mol of $CaCO_3$ is produced per 2 mol of TA uptake [59]. Differences in TA or DIC are commonly used in the literature as a proxy for whether reefs are net calcifying/producing (TA or DIC depletion) or net dissolving/respiring (TA or DIC repletion) [58,60]. We use the terms NEC and NEP for brevity throughout the remainder of the paper. Positive and negative ΔTA/2 represent net calcification and net dissolution, respectively. Likewise, positive and negative ΔDIC represent net photosynthesis and net respiration, respectively. DIC was calculated from pH_T and TA using seacarb [61]. The mean ± SE error propagation of DIC calculated from TA (error of 5 µmol kg^{-1}) and pH_T (error of 0.01) is 9.6 ± 0.05 µmol kg^{-1}. We did not calculate true rates (normalized to residence time) because Maunalua Bay is a shallow embayment with a complex hydrodynamic environment [52], and small uncertainties in residence time measurements can lead to highly inaccurate NEP and NEC calculations [62].

(d) Model description

We used Bayesian structural equation models (SEM) to uncover the pathways and feedback loops by which SGD affects ecosystem functioning. SEMs are useful tools for evaluating multivariate hypotheses under a flexible statistical modelling framework [63]. We specify the SEM using five equations that describe the influence of SGD on NEP and NEC as mediated by inorganic nutrients, temperature and pH, which can vary with season, day/night, or tide. The system of equations, with associated hypotheses, are as follows:

Model 1: $\log(N + N) \sim \log(SGD)$.

Model 1 represents that nitrogen concentration increases directly with %SGD and that nitrogen concentration is primarily a function of mixing [48].

Model 2: $\text{temperature} \sim \log(SGD) \times \text{season} \times \text{day or night}$.

Model 2 represents our hypothesis that temperature decreases as a function of %SGD and that the relationship can vary with time of day and season (i.e. the difference between SGD, temperature and surface water temperature varies by season and by time of day and their interaction).

Model 3: $pH \sim \log(SGD) + NEP$.

Model 3 represents our hypotheses that pH is a function of mixing between surface water and SGD (which has a distinct pH signature from surface water) and, critically, that there is a feedback between NEP and pH.

Model 4: $NEP \sim \log(N + N) \times \text{tide} \times \text{day or night} + \text{season} \times \text{temperature}$.

Model 4 represents our understanding that NEP is fuelled by nutrients (i.e. nitrate + nitrite) and that this response to higher nitrogen concentration is stronger during the day (when light is available for photosynthesis). Notably, phosphate can also drive NEP rates. However, $NO_3^- + NO_2^-$ and PO_4^{3-} were highly collinear (Pearson's R = 0.95 at Wailupe and 0.96 at site Kūpikipiki'ō; electronic supplementary material, figure S2); therefore, we only included $NO_3^- + NO_2^-$ in the model to represent inorganic nutrients. We also hypothesized that the relationship may interact with tidal mixing (higher concentrations of nutrients coupled with increased organic matter are released during low tide). In addition, we represent the hypothesis that NEP increases as a function of temperature, which is enhanced under longer daylength (season).

Model 5: $NEC \sim pH + \text{temperature}$.

Model 5 reflects our mechanistic understanding that NEC increases with pH and with temperature.

(e) Model fitting and analysis

The SEMs were run for Kūpikipiki'ō and Wailupe separately. All data were scaled and centred for the analysis; SGD and $NO_3^- + NO_2^-$ were log-transformed because they were highly left-skewed, and two extreme outliers were removed from the analysis. There were 15 samples missing from the dataset (5 from Wailupe and 10 from Kūpikipiki'ō) due to sea conditions for a total sample size of 149 and 155 at Kūpikipiki'ō and Wailupe, respectively. The Bayesian SEM models were run using the Hamiltonian Monte Carlo algorithm from STAN in the R package *brms* [64,65]. We ran three parallel chains of length 2000, with a warm-up of 1000, and a thinning parameter of 1. The posterior was modelled from a multivariate normal distribution with relatively uninformative priors for all parameters (student *t* distribution (d.f. = 3, $\mu = 0$, $\sigma = 10$)). We assessed model convergence by visually checking all trace plots, ensuring that the chains were well-mixed and calculating Gelman–Rubin statistics [66] for all parameters (which were all = 1). To assess model fit, we used posterior predictive checks where we visually inspected the relationship between the empirical distribution and 10 posterior draws using the *pp_check* function in the *tidybayes* package [67]. All results are reported as medians with two-tailed 95% Bayesian credible intervals (essentially Bayesian confidence intervals). Effect sizes with credible intervals that do not overlap zero are considered to be statistically significant.

To characterize the sensitivity of ecosystem metabolism to changes in SGD, we simulated data where we uniformly increased and decreased the relative amount of SGD at each sampling location × timepoint by 50%. We chose a ±50% change in SGD for the sensitivity analysis to capture the natural range in SGD fluxes experienced at both sites ($11\,700 \pm 5900\ \mathrm{m^{-3}\ d^{-1}}$ and $9100 \pm 2700\ \mathrm{m^{-3}\ d^{-1}}$ [48]). This simulated data was then used to generate predictions for how each state variable (i.e. NEC, NEP, pH, N + N and temperature) would change as a result of increased SGD from the posteriors. All data and R code are available at https://github.com/njsilbiger/MaunaluaSEM and at Zenodo (doi:10.5281/zenodo.4281383).

3. Results and discussion

Overall, our study showed that SGD significantly altered the local biogeochemical and thermal environment, which ultimately led to changes in NEC and NEP. We also showed evidence of SGD fuelling biological feedbacks, where changes in NEP as a function of nutrients and temperature led to changes in pH, which ultimately drove NEC. However, the strength (and sometimes direction) of the relationships between SGD, temperature, nitrogen concentration, pH, NEP and NEC differed between the two sites (figure 1; electronic supplementary material, figure S4, S5), highlighting that local oceanographic conditions and aquifer geochemistry can alter the effect of SGD on coral reefs.

(a) Direct and indirect effect of submarine groundwater discharge on nitrogen, temperature and pH

For nutrients, there was a strong positive relationship between %SGD and $NO_3^- + NO_2^-$ concentration at both sites, but the effect size was 1.5 times higher at Kūpikipiki'ō than Wailupe (figure 1*a*; electronic supplementary material, figure S4A and S5A). The difference in slopes between these two sites is likely to be due to the substantially higher nutrient concentrations in the groundwater at Kūpikipiki'ō relative to Wailupe (169 versus 69 $\mu\mathrm{mol\ l^{-1}}$; [48]). Many studies show high nitrogen fluxes as a result of SGD [19]. High nutrient fluxes from SGD could be a critical source of exogenous nutrients necessary for sustaining high coastal production rates [20], or it could lead to eutrophication risk if associated with anthropogenic pollution [15]. Notably, approximately 14% of global coral reefs are at risk of eutrophication from SGD [15]. Given the major differences in nitrogen fluxes from SGD between the two sites in our study, and the fact that the nutrients at Kūpikipiki'ō are heavily impacted by wastewater [48], the nutrient-rich SGD could lead to different biological responses at each site.

The presence of SGD also decreased water temperature at both sites, which is consistent with studies showing that fresh SGD is typically cooler than ambient seawater [16]. The effect of SGD on temperature was stronger at Wailupe than at Kūpikipiki'ō (figure 1*b*; electronic supplementary material, figure S4B and S5B), where the 2°C difference between groundwater and ambient seawater was only evident during the day. At night, the differences in temperature as a function of groundwater were undetectable at Kūpikipiki'ō. The stronger effect of SGD on temperature during both the day and night at Wailupe is probably due to differences in mixing rates between the two sites. Wailupe has longer residence times (mixing rates are lower) than Kūpikipiki'ō [33], probably enhancing the difference in temperature between groundwater and ambient seawater. Further, there was no significant interaction between season and %SGD on the temperature at either site, but there was a significant main effect of season: fall was on average 2°C warmer than spring at both sites (electronic supplementary material, table S1, figure S4B).

There was a small, but a significant direct effect of %SGD on pH at both sites (figure 1*c*; electronic supplementary material, figure S4C and S5C). However, the indirect biological effect of pH from changes in NEP was 5.5 and 8.1 times higher than the direct effects on pH from freshwater intrusion at Kūpikipiki'ō and Wailupe, respectively (figure 1*c*; electronic supplementary material, figure S4 and S5D). SGD typically has lower pH values than seawater [11,22], which was evident at Wailupe. However, the direct effect of lower pH from SGD mixing with surface water was completely masked by the biological feedbacks at Kūpikipiki'ō, where the net effect of SGD on pH was positive. The site differences in the relationship between SGD and pH are probably due to differences in NEP (the maximum and range in NEP was higher at Kūpikipiki'ō than Wailupe; electronic supplementary material, table S1). Prior studies have shown that NEP can have an overwhelming effect on pH relative to other physical drivers [45] and that nutrient addition could augment biological feedbacks in coastal ecosystems [43,68]. Additionally, vastly different TA values between the source groundwater in Kūpikipiki'ō and Wailupe could be affecting the relationship between %SGD and pH as well [6,33]. The TA at Kūpikipiki'ō is considerably higher than ambient seawater (approx. 3000 versus 2300 $\mu\mathrm{mol\ kg^{-1}}$), where at Wailupe it is lower (approx. 1750 $\mu\mathrm{mol\ kg^{-1}}$). TA affects the buffering capacity of seawater, or how much CO_2 seawater can absorb before decreasing pH, where higher TA seawater has a higher buffering capacity than lower TA [69]. The positive and negative relationships between %SGD

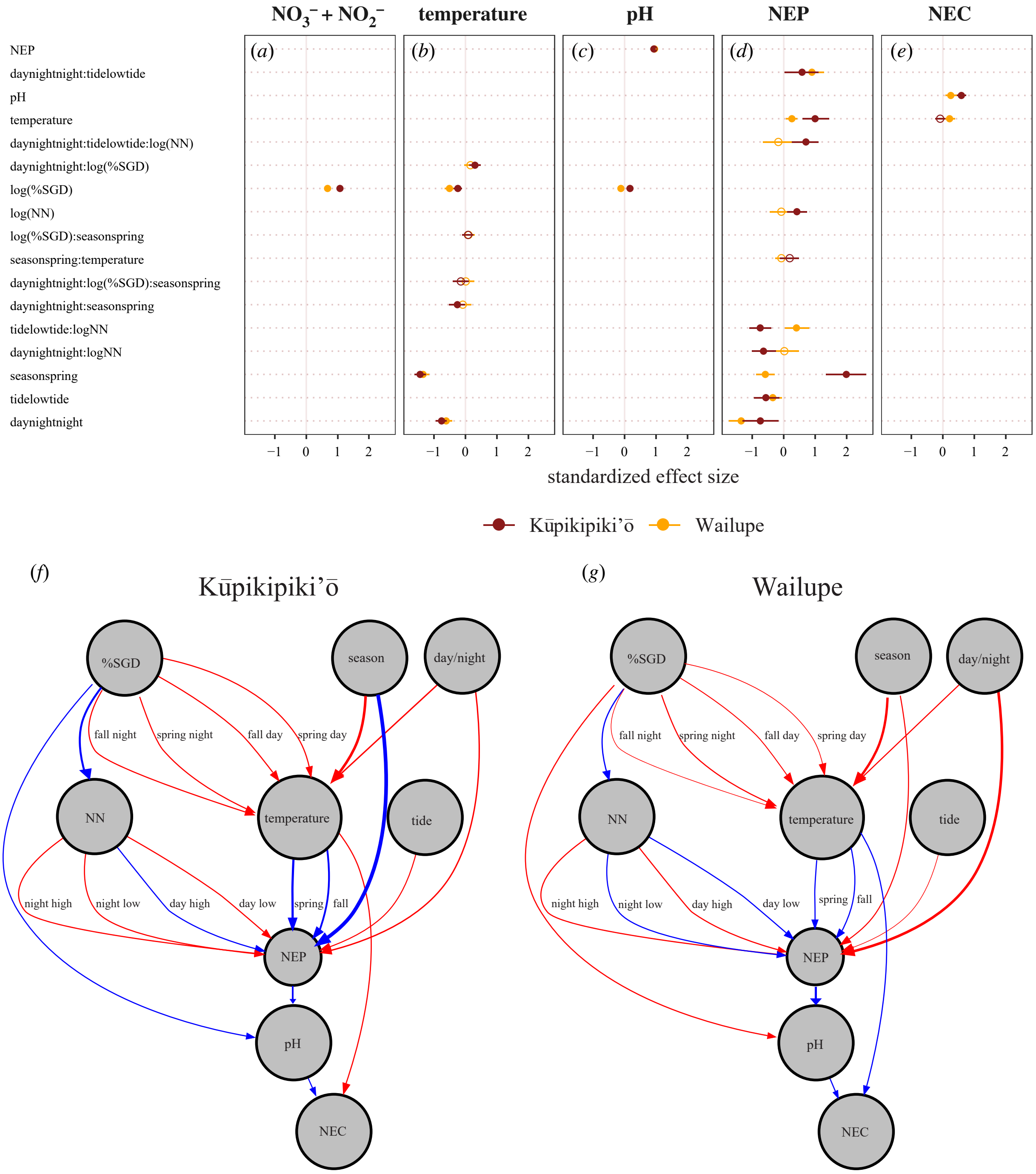

Figure 1. (*a–e*) Coefficient plot and (*f,g*) directed acyclic graphs (DAG) from structural equation models. (*a–e*) Standardized effect sizes for parameters in models 1–5 (left to right), where each point is the median value ± 95% Bayesian credible interval (BCI). Values with BCIs that do not overlap zero are statistically significant. Open symbols in the figure are not significant. Kūpikipiki'ō and Wailupe values are represented in maroon and gold, respectively. Subsets F and G are DAGs for Kūpikipiki'ō (left) and Wailupe (right). Colours of the arrows represent positive (blue) or negative (red) relationships and the thickness of the lines are correlated with the effect size.

and pH at Kūpikipiki'ō and Wailupe, respectively, could also be influenced by the higher and lower TA concentrations in the groundwater relative to seawater.

(b) Direct and indirect effect of submarine groundwater discharge on net ecosystem production and net ecosystem calcification

The unique thermal and biogeochemical environment created by SGD drove changes in NEP and NEC at both sites. For NEP, there was a strong positive relationship between NEP and temperature, though the effect was 3.8 times stronger at Kūpikipiki'ō than Wailupe (figure 1*d*; electronic supplementary material, figure S4F and S5F). There was also a significant seasonal effect (though, notably with opposite patterns between the sites), probably due to seasonal differences in circulation leading to greater differences wave energy and surface currents between the two sites, with higher wave energy and stronger offshore flow at Kūpikipiki'ō than Wailupe [52].

The relationship between $NO_3^- + NO_2^-$ and NEP was mediated by day/night and tidal cycle as indicated by the significant three-way interactions, though the relationships

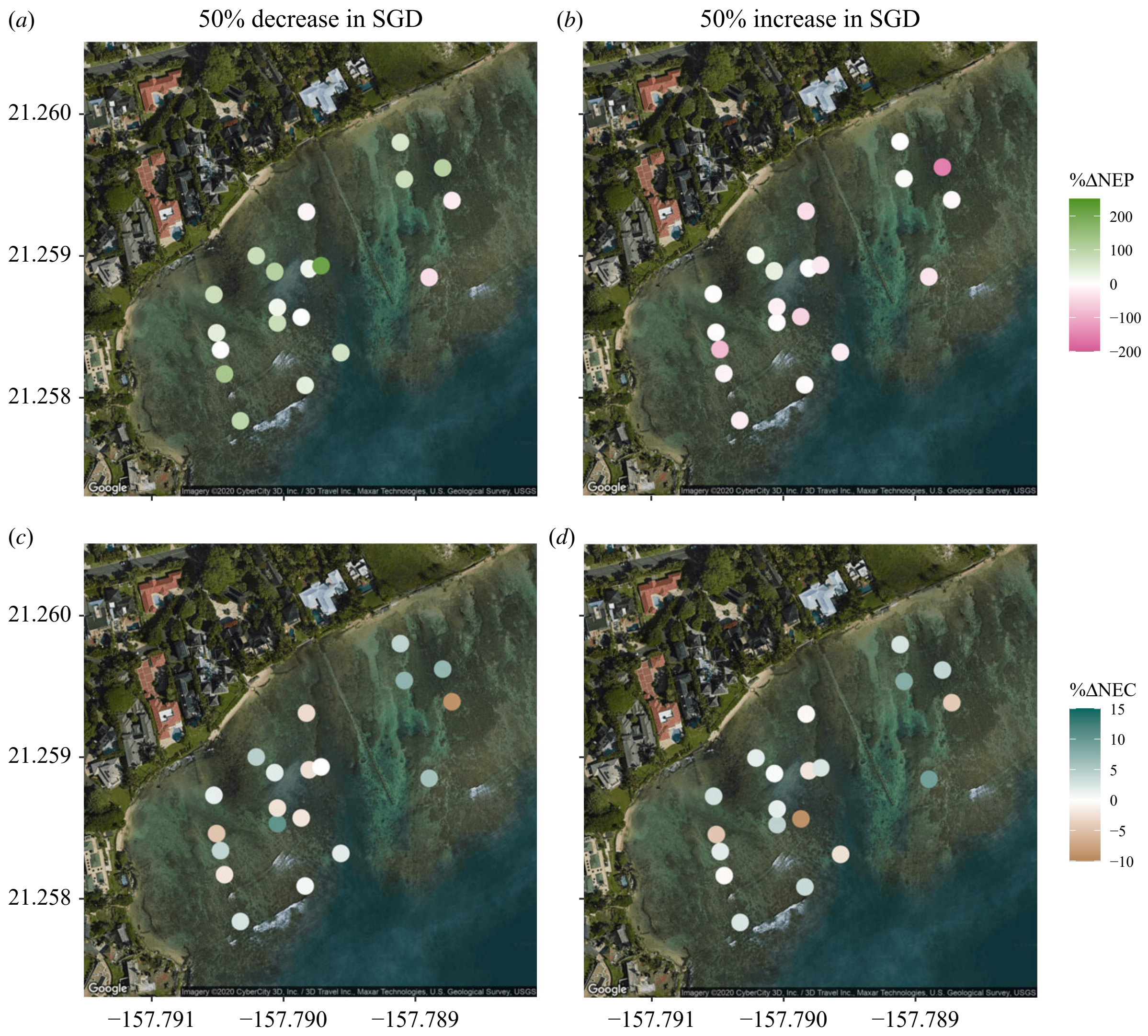

Figure 2. Maps of predicted change (%) in (*a*,*b*) NEP and (*c*,*d*) NEC at a (*a*,*c*) 50% decrease and (*b*,*d*) 50% increase in SGD in Kūpikipiki'ō. Dots are median predictions across all eight timepoints for each sampling location.

were different between the sites (figure 1*d*; electronic supplementary material, figure S4E and S5E). At Kūpikipiki'ō, there was a negative relationship between $NO_3^- + NO_2^-$ and NEP at night, regardless of the tide. This relationship is probably driven by increased microbial respiration at night. During the day, however, there was a positive effect of $NO_3^- + NO_2^-$ on NEP during high tide, but a negative effect during low tide. At high tide, the SGD was still able to increase the $NO_3^- + NO_2^-$ concentrations by 1.4 µmol l^{-1}, which probably benefited producers. During low tide, $NO_3^- + NO_2^-$ concentrations were 23 times higher than high tide (up to 32.4 µmol l^{-1}), and, notably, with a significant amount of wastewater [48] and higher DOM concentrations [6], which may have benefitted microbial respiration more than gross photosynthesis. At Wailupe, tide had the opposite effect on the relationship between NEP and $NO_3^- + NO_2^-$. There was no relationship between $NO_3^- + NO_2^-$ and NEP during high tide, and there was a positive relationship during low tide (electronic supplementary material, figure S5E). Again, this may have been due to differences in nitrogen concentrations between high and low tide at Wailupe, where the nitrogen concentrations are significantly lower than Kūpikipiki'ō (max daytime $NO_3^- + NO_2^-$ at Wailupe was 0.68 µmol l^{-1} and 7.92 µmol l^{-1} at high and low tide, respectively).

The differences in the relationship between nutrients and NEP are consistent with prior studies at these sites. La Valle *et al.* [28] showed that total producer biomass increased with $NO_3^- + NO_2^-$ concentration at Wailupe, but not Kūpikipiki'ō. Several factors could be driving the differences in these relationships between our two sites. First, the N : P ratio in the source water is two times higher at Kūpikipiki'ō than Wailupe (electronic supplementary material, figure S2) and the balance between nitrogen and phosphate affects the ability of organisms to take-up nutrients [70]. The differences in macroalgal community composition between the two sites could affect the relationship between NEP and nutrients as the different dominant species have different growth rates [28]. Additionally, differences in the prevalence of human-derived nitrogen and covarying parameters such as organic matter—both of which are higher at Kūpikipiki'ō [6,48]—could be responsible for the different relationship between SGD and NEP at Kūpikipiki'ō and Wailupe. Further, Gill [71] points out the importance of nonlinear relationships between nutrient concentrations and biological responses (with a focus on coral growth) on coral reefs. He shows that, at low nutrient concentrations, reefs are likely to benefit from increases in nutrients, whereas at high concentrations the nutrient enrichment is more likely to be detrimental; Lubarsky *et al.* [18] found evidence of this pattern in coral growth at these sites in Maunalua.

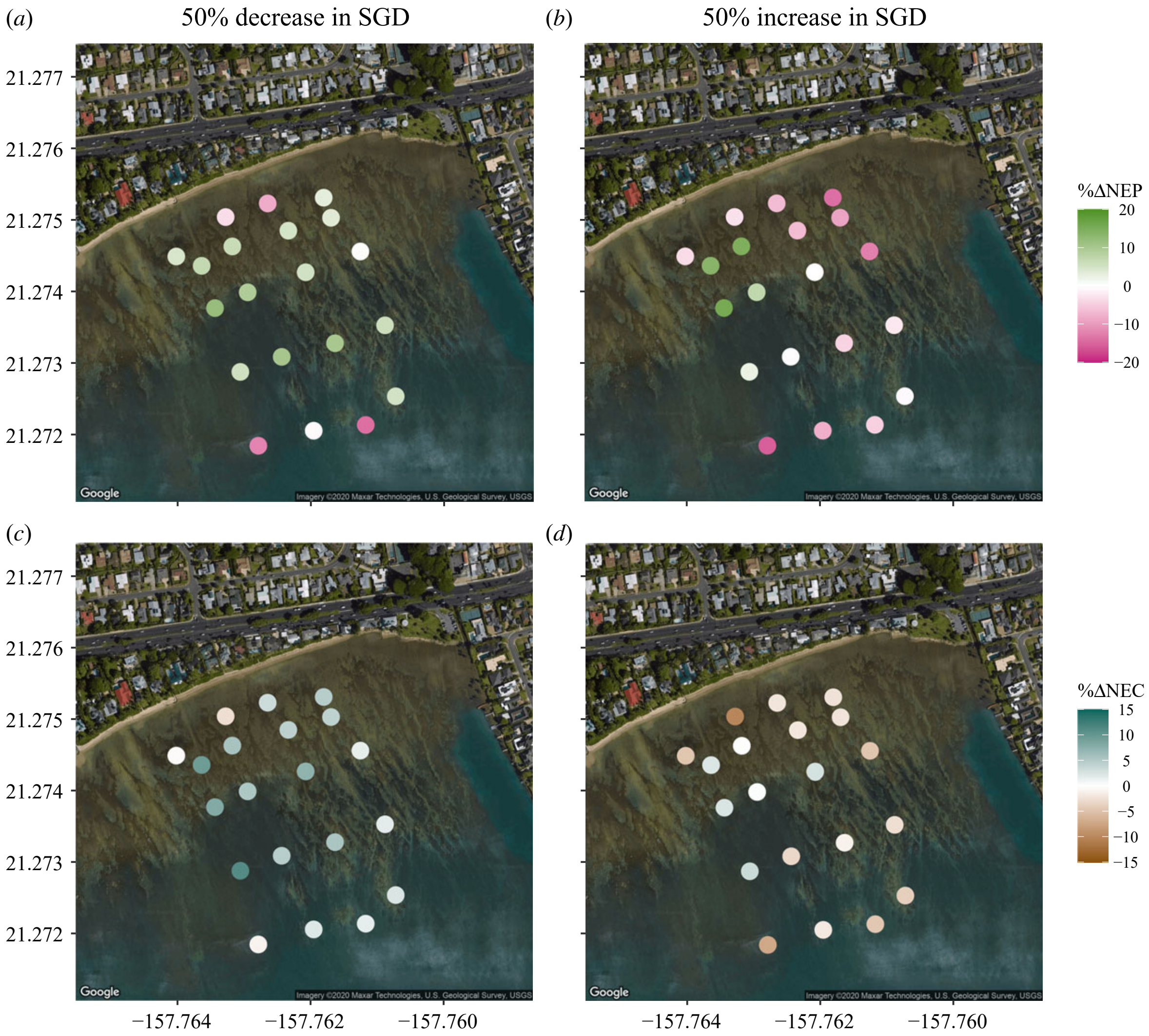

Figure 3. Maps of predicted change (%) in (*a*,*b*) NEP and (*c*,*d*) NEC at a (*a*,*c*) 50% decrease and (*b*,*d*) 50% increase in SGD in Wailupe. Dots are median predictions across all eight timepoints for each sampling location.

NEC was also affected by the biogeochemical and thermal environment created by SGD. There was a significant positive relationship between pH and NEC at both sites, although the effect size was 2.5 times higher at Kūpikipiki'ō than Wailupe (figure 1*e*; electronic supplementary material. figure S4G and S5G). There was also a significant effect of temperature on NEC at Wailupe, but not Kūpikipiki'ō (figure 1*e*; electronic supplementary material, figure S4H and S5H). These results are consistent with the expectation that natural increases pH and temperature (except during extreme heating events) increase NEC on coral reefs [39,72,73]. Notably, the stronger effect size at Kūpikipiki'ō is opposite of what we would expect based on Silbiger *et al.* [43], which showed that nutrient enrichment in a laboratory setting weakened the relationship between aragonite saturation state (which is positively correlated with pH) and NEC. However, other factors in the groundwater, such as the highly depleted total alkalinity at Wailupe, could be mediating this relationship. Regardless of the differences in effect sizes, this study provides evidence for the strong indirect effect of SGD on NEC. Specifically, SGD augments biological feedbacks: SGD increases nutrient concentrations, which fuels both production and microbial respiration, altering the local pH environment (increasing pH when NEP is positive and decreasing pH when NEP is negative) and ultimately leading to changes in NEC. NEC (i.e. the net growth of calcifiers, such as corals, on the reef) is important for creating reef structure; therefore, any declines in NEC as a result of changing SGD could lead to loss of reef-associated biodiversity and shoreline protection [74].

There are a few important limitations to consider when interpreting the results of our study. First, our sampling design prioritized high spatial resolution over high temporal resolution. Water samples were collected over two diel cycles aimed at capturing the most extreme groundwater fluxes throughout the day (high tide and low tide) and year (dry and wet season). While more frequent sampling would probably reduce the uncertainty in our models, prior studies at Maunalua Bay consistently show similar relationships between SGD and many of the parameters analysed in the current study [6,28,33,48]. Second, we calculated NEC and NEP potential because of the complex hydrodynamic environment at Maunalua Bay**.** While changes in DIC and TA are commonly used in the literature as a proxy for net calcification/net production [58,60,72], future studies at Maunalua should include high-resolution oceanographic data to better understand NEP and NEC rates, and how they are affected by SGD.

(c) Sensitivity analysis of submarine groundwater discharge on ecosystem functioning

The fluxes and biogeochemistry of SGD change with precipitation, land use, sea-level rise, tidal amplitude and groundwater usage [47], making it critical to better understand how SGD affects reef ecosystem functioning. We used our SEM models to test how a 50% change (both decrease and increase) in SGD would affect ecosystem metabolism (figures 2 and 3; electronic supplementary material, figures S6 and S7). We found that the effects of increasing SGD on NEP and NEC were highly spatially variable, probably due to differences in the distance from SGD seeps and local oceanographic conditions. Overall, the magnitude of change (both positive and negative) in both NEP and NEC was higher at Kūpikipiki'ō than Wailupe. Specifically, SGD had an order of magnitude higher effect on NEP at Kūpikipiki'ō than Wailupe, where a 50% increase in SGD led to a −154 to 34.5% change (percentage change are median values over the eight sampling timepoints for each location) in NEP at Kūpikipiki'ō and −15.4 to 15.6% change in NEP at Wailupe across all 20 sampling locations. When we decreased SGD by 50% in the model, there was a −42.4 to 208% and −14.0 to 12% change in NEP at Kūpikipiki'ō and Wailupe, respectfully, across all sampling points. The large differences in sensitivity for NEP between the two sites could be in response to the substantially higher nutrient concentrations in the SGD at Kūpikipiki'ō than Wailupe. NEC was much less sensitive to changes in SGD than NEP at both sites. A 50% increase in SGD led to a −9.16 to 9.12% and −9.96 to 3.39% change in NEC at Kūpikipiki'ō and Wailupe, respectfully, whereas a 50% decrease in SGD led to a −9.01 to 10.3% and −2.62 to 11.1% change in NEC across all sample locations. The lower sensitivity of NEC to SGD than NEP is probably due to the lower coral cover (approx. 1%) relative to macroalgal cover (approx. 15–50%) at both sites [28,51].

Importantly, the SEM models did not have a direct link between SGD and NEC or SGD and NEP; yet our model predicted that both NEP and NEC would change with an increase in %SGD. These predictions provide further evidence for (i) the cascading and indirect effect of SGD on ecosystem functioning, where the effect of SGD on ecosystem metabolism is mediated by changes in nutrients, temperature and pH, and (ii) the context dependency of SGD, as evidenced by the nonlinear relationships between SGD and ecosystem metabolism and the substantial differences in sensitivity of SGD between the two sites. As hydrologists and climate modellers advance our understanding for how SGD fluxes will change in the future, our modelling approach can be used to predict the downstream effects of altered SGD fluxes on ecosystem functioning.

Our study provides evidence that SGD leads to cascading changes in biogeochemistry and ecosystem metabolism, and that the effects of SGD on ecosystem functioning are altered by human disturbance, hydrology and oceanographic context. SGD is ubiquitous along coastlines and is directly impacted by humans through climate change and land use; yet, we have only scratched the surface on our understanding of how SGD directly and indirectly affects biological processes. These types of studies are necessary to better manage watersheds and help prepare for how coral reefs or any coastal ecosystem may change in the future. More studies should examine the relationships between SGD and ecological processes under different environmental conditions to gain a broader understanding of the mechanisms by which SGD affects ecosystem functioning.

Data accessibility. All data and R code are available at https://github.com/njsilbiger/MaunaluaSEM and at Zenodo (https://doi.org/10.5281/zenodo.4281383)

Authors' contributions. N.J.S., M.J.D. and K.L. conceived the idea. N.J.S., M.J.D. and K.L. collected the data. N.J.S. and M.J.D. statistically analysed the data. N.J.S. led the writing of the manuscript. N.J.S., M.J.D. and K.L. edited and approved of the manuscript.

Competing interests. We declare we have no competing interests.

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