



FEATURE ARTICLE

Foundation species loss alters multiple ecosystem functions within temperate tidepool communities

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ABSTRACT: Foundation species, which help maintain habitat and ecosystem functioning, are declining due to anthropogenic impacts. Within the rocky intertidal ecosystem, studies have investigated the effects of foundation species on community structure and some resource fluxes; however, how intertidal foundation species loss will affect multiple facets of ecosystem functioning in concert remains unknown. We studied the direct and indirect effects of foundation species loss of mussels *Mytilus californianus* and surfgrass *Phyllospadix* spp. on community structure, fluxes (light, temperature, dissolved oxygen [DO], dissolved inorganic nutrients, pH_T), and ecosystem metabolism (net ecosystem calcification [NEC] and net ecosystem production [NEP]) in central Oregon using *in situ* tide pool manipulations. Surfgrass loss increased microalgae cover, increased average maximum light by 142% and average maximum temperature by 3.8°C, increased DO and pH_T values, and indirectly increased NEP and NEC via increased maximum temperature and pH_T respectively. Mussel loss increased microalgae cover, increased average maximum light by 5.8% and average maximum temperature by 1.3°C, increased DO and pH_T values, and indirectly increased NEP via increased producer cover. Shifts in baseline nutrient concentrations and temperature values from coastal upwelling influenced ecosystem metabolism in pools with intact foundation species. Our results indicate that as communities respond to foundation species loss, ecosystem functioning depends on the dominant community present and biologically or physically driven shifts in biogeochemistry. This study highlights the importance of the connection between community and ecosystem ecology in understanding the magnitude of changes occurring with anthropogenically-driven intertidal foundation species loss.

KEY WORDS: Rocky intertidal · Foundation species · Ecosystem function · Tide pools · Structural equation model



Foundation species loss in surfgrass (left) and mussel (right) tidepools immediately alters multiple ecosystem functions within Oregon temperate tidepool communities.

Photos: Jenn Fields and Miranda Gilhuys

1. INTRODUCTION

Foundation species are a major focus of ecological studies due to their importance in sustaining biodiversity and ecosystem processes in the face of anthropogenic climate change (Byers et al. 2006, Angelini et al. 2011, Bulleri et al. 2018, Smale et al. 2019). As key habitat-building organisms within biological communities, foundation species ameliorate physical stressors and facilitate interactions that promote biodiversity, stabilize community structure, and maintain fluxes (e.g. nutrient cycling, carbon cycling, or production rates) of ecosystem functioning (Bruno & Bertness 2001, Angelini et al. 2011, Ellison 2019). Recent studies have emphasized the consequences of coastal foundation species loss on ecological services and functioning, such as nutrient cycling, water filtration, food security, and ecosystem production (Altieri &

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Witman 2006, zu Ermgassen et al. 2013, Smale et al. 2019, Edwards et al. 2020). However, the connection between community and ecosystem ecology with regard to foundation species loss within the marine environment is overlooked relative to other ecosystems (Ellison et al. 2005, Orwig et al. 2013, Gamfeldt et al. 2015, Narwani et al. 2019). Within the marine environment, the majority of biodiversity–ecosystem function studies have focused on consumption and production, but fewer have measured multiple biogeochemical fluxes interacting with natural systems under realistic foundation species loss scenarios (Gamfeldt et al. 2015). Because nearshore marine habitats provide over 43% of the global total ecosystem goods and services per year (Costanza et al. 1997), understanding the impact of foundation species loss on both community and ecosystem processes is essential for conservation management (Ellison 2019).

In coastal marine ecosystems worldwide, anthropogenic climate change and acute temperature anomalies have caused latitudinal shifts (Sagarin et al. 1999, Angelini et al. 2011) and losses (Alongi 2002, Orth et al. 2006, Smith et al. 2006, Dudgeon et al. 2010, Byrnes et al. 2011, Sorte et al. 2017) of foundation species, including seagrasses, mangroves, corals, kelps, and mussels. For example, kelp beds along the west coast of Australia decreased by ~2300 km² and experienced a 100 km range contraction due to decades of ocean warming and a marine heat wave event (Wernberg et al. 2016). Further, coral cover on the Great Barrier Reef declined by ~40–90% due to a single marine heat wave event in 2016 (Hughes et al. 2018). Foundation species declines have already led to significant and documented losses in ecosystem functioning, (Waycott et al. 2009, zu Ermgassen et al. 2013, Hughes et al. 2018, Edwards et al. 2020), and foundation species will continue to be removed from systems via natural and anthropogenic disturbance (Dayton 1972, Ellison et al. 2005, Castorani et al. 2018).

One ecosystem with significant and recently documented depletion of multiple foundation species is the rocky intertidal, a coastal ecosystem commonly dominated by the foundation species mussels (e.g. *Mytilus* spp.) and seagrasses (e.g. *Phyllospadix* spp.). *Mytilus californianus* cover and biomass in southern California have decreased by 40.2 and 51.3%, respectively, since the mid-1970s and 1980s (Smith et al. 2006), and localized massive die-offs have occurred during recent terrestrial heat wave events (<https://www.kqed.org/science/1944593/interview-researcher-on-bodega-bay-mussel-die-off>). Seagrasses are among

the most rapidly declining marine foundation species in the world, and have decreased within nearshore and intertidal environments by 58% worldwide due to habitat loss, eutrophication, and climate change (Orth et al. 2006, Waycott et al. 2009). Temperate seagrass habitats have already experienced substantial (>90%) localized diebacks related to marine heat wave events (Thomson et al. 2015), which are increasing with anthropogenic climate change (Laufkötter et al. 2020). In the northeastern Pacific, the dominant rocky intertidal seagrass surfgrass *Phyllospadix* spp. is particularly susceptible to desiccation and heat stress during low midday tides, coastal development, and nutrient addition (Littler & Murray 1975, Raimondi et al. 1999, Honig et al. 2017). Both mussels and surfgrasses will continue to disappear as a result of increasing anthropogenic impacts (Wootton et al. 2008, Waycott et al. 2009, Honig et al. 2017), which will cause extensive changes in ecosystem functioning and threaten the ecological services these foundation species help provide (Christensen et al. 1996, Smale et al. 2019).

Mussels and surfgrasses not only maintain ecosystem functioning by creating habitat for mobile and sessile flora and fauna (Stewart & Myers 1980, Suchanek 1992), but also by regulating the fluxes of the ecosystem. Specifically, *M. californianus* recycles nutrients and promotes primary productivity through increased nutrient availability (Bracken & Nielsen 2004, Pfister 2007, Pfister & Altabet 2019), decreases pH and dissolved oxygen (DO) through respiration (Silbiger & Sorte 2018, Ninokawa et al. 2020), decreases temperature within mussel beds (Stephens & Bertness 1991), and maintains net ecosystem calcification (NEC) as a dominant calcifier in the intertidal (Bracken & Nielsen 2004, Pfister 2007, Silbiger & Sorte 2018, Pfister & Altabet 2019). *Phyllospadix* spp., as primary producers, take up nutrients (Terrados & Williams 1997), modulate pH and DO over diel cycles (Duarte & Chiscano 1999, Silbiger & Sorte 2018), decrease temperature (Shelton 2010), and increase net ecosystem production (NEP), which increases pH, making the environment more favorable for calcification (Pfister 2007, Bracken et al. 2018, Silbiger & Sorte 2018). The loss of *Mytilus* or *Phyllospadix* species could have both direct (loss of food and habitat) and indirect (altered biogeochemistry and thermal environment) effects on ecosystem functioning (Pfister 2007, Bracken et al. 2018, Silbiger & Sorte 2018).

Several studies have investigated the effect of *Mytilus californianus* and *Phyllospadix* spp. (hereafter mussel and surfgrass) removal on individual

fluxes or community metrics over a variety of timescales: 1–2 yr timescales for surfgrass removal (Shelton 2010), and 1–3 (Pfister 2007) and 10–15 yr timescales (Wootton 2010) for mussel removal. However, the relative importance of foundation species loss for multiple fluxes of ecosystem function in concert remains unknown (Gamfeldt et al. 2015). To address this knowledge gap, we used *in situ* tide pool manipulations to test how intertidal foundation species removal affects ecosystem function via changes in community structure and resource fluxes 1 mo post-removal. Specifically, we examined the direct and indirect effects of mussel and surfgrass removal from tide pools on (1) community composition of sessile and mobile species, (2) thermal and light environments, (3) local biogeochemistry, and (4) ecosystem metabolism (NEC and NEP) 1 mo after species removal using multivariate analyses, general linear models, and a structural equation model (SEM). We hypothesized that (1) community structure will shift towards more early-succession species, (2) temperature and light will increase, (3) biogeochemistry will shift in accordance with community composition changes, and (4) foundation species loss will have indirect effects on ecosystem metabolism (NEP and NEC) via altered local biogeochemistry. By addressing both direct and indirect effects using a causal approach, we broaden the mechanistic understanding of how tide pool communities will respond immediately to mussel and surfgrass loss.

2. METHODS

We selected 32 tide pools within the Oregon Department of Fish and Wildlife's (ODFW) Otter Rock Marine Reserve (ORMR) and Marine Garden, Oregon USA (44° 45' 09.1" N, 124° 03' 58.0" W) during the months of June–August 2019 (Fig. 1). One mussel species (*M. californianus*) and 2 surfgrass species (*P. scouleri* and *P. torreyi*) were present at the site. Of the 32 tide pools, 16 were dominated by California mussel *M. californianus* and 16 were dominated by surfgrass (10 pools contained *P. scouleri* and 6 pools had both *P. scouleri* and *P. torreyi*). Percent cover of foundation species ranged from 45.3 to 98.9% in the mussel-dominated pools and 49.5 to 100% in the surfgrass-dominated tide pools. Some tide pools had both mussels and surfgrasses; however, the presence of a second foundation species did not exceed 7.2% of the remaining tide pool cover. Tide pools were located in the mid- to low-intertidal zone, ranging from 0.71 to 1.77 m above mean lower-

low water. At this tide height, tide pools were isolated for 4 to 6 h during summer low tides.

A Before-After Control-Impact (BACI) design was used to account for changes in ocean chemistry, timing of low tide, and variability within tide pools throughout the experimental period. The BACI design consisted of two 29 d time periods (before and after removal) with control and removal tide pools (Stewart-Oaten et al. 1986), where foundation species were removed from removal tide pools ($n = 8$ tide pools per foundation species) between the before and after periods (Fig. 1). The before removal period occurred June to mid-July 2019 and the after removal period occurred mid-July to August 2019. Tide pools were selected for control or removal groups using a random number generator, while accounting for the surface area to percent cover of foundation species (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m683p001_supp.pdf). Removal of foundation species from removal tide pools occurred in mid-July 2019 and tide pools had a 1 wk recovery period before any surveys were done or samples were taken. Rhizomes were also removed in surfgrass removal pools due to their ability to alter nutrient cycling (Terrados & Williams 1997). During each time period, we characterized physical parameters (pool volume and tide height), community composition, light, temperature, and biogeochemical fluxes (e.g. DO, pH_T, nutrients) in each tide pool.

2.1. Tide pool physical parameters

Tide pool physical parameters measured included tidal height (location within intertidal) and tide pool volume (size of pool). Tide heights for each pool were surveyed with a laser level and stadia rod (DeWalt). Tide pool volume (V) was determined using a dye method (Pfister 1995) and measured with a Smart-Spec3000 spectrophotometer (Bio-Rad Lab). Water volume in the tide pools changed by 0–20% between the 2 timepoints due to removal of foundation species (Table S1B). To account for the slight effect of changing biomass on volume, volume was re-measured post-removal and the average of the time periods was used in statistical analyses.

2.2. Community changes as a function of foundation species loss

We conducted 2 rounds of community composition surveys for sessile percent cover and mobile



	Community composition survey	Tide height & pool volume	Biogeochemistry sampling	Foundation species removal	Tide pool volume	Biogeochemistry sampling	Community composition survey
H							

August 2019

July 2019

June 2019

Fig. 1. Map of (A) the west coast of North America and (B) the study site at Otter Rock Marine Reserve and Marine Garden, where blue circles are mussel-dominated pools ($n = 16$) and green triangles are surfgrass-dominated pools ($n = 16$). (C) Community composition surveys were conducted in June and August 2019, (D) tide height and pool volume were measured in June 2019 and tide pool volume was repeated in July 2019 after (E,F) removal of foundation species from $n = 8$ pools each for mussel-dominated and surfgrass-dominated pools. (G) Day and night biogeochemistry sampling occurred 1 wk before and 3 wk after foundation species removal. Subset (H) shows the timeline of all events from early-June through mid-August 2019

organism counts: 3 wk before removal and 1 mo post-removal. We temporarily removed seawater from the tide pool and placed a flexible mesh quadrat (Nielsen 2001) with demarcations in 10×10 cm squares over the bottom of each pool to survey the entire community (pools ranged from 58 to 754 squares). We measured percent cover for sessile organisms by counting the number of quadrat squares covered by each sessile species and counted the number of mobile organisms, identifying down to the lowest possible taxonomic unit in the field (usually genus level; Table S2). We normalized the sum of non-foundation species sessile cover to 100% for each tide pool, including the second foundation species if present (e.g. mussel cover within surfgrass pools was normalized to 100% cover). The foundation species cover remained the raw percent cover for their respective tide pools and did not exceed 100%. Both sessile and mobile organisms were grouped into larger functional groups based on their ecological role for data visualization (Table S2; see Fig. 2). All tide pool characterization and community composition surveys were completed at least 24 h before any water sampling event to allow the pools to be flushed at least twice by the ocean before measurements.

2.3. Direct effect of foundation species loss on temperature and light environment

Temperature ($^{\circ}\text{C}$) and light intensity (lumens m^{-2}) were recorded continuously every 15 min for 29 d during each time period using HOBO[®] Pendant loggers bolted facing up on the flattest part of the tide pool on a level platform in the interstitial spaces of the foundation species (Onset[®] HOBO[®] Pendant light intensity data logger MX2202, Bourne). Light intensity (lumens m^{-2}) was converted to photon flux density (PFD; $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) following Long et al.'s (2012) field experiment values. We measured the change in maximum temperature between the before and after removal period (i.e. the average daily hottest temperature between 18 July and 16

August 2019 minus the average daily hottest temperature between 16 June and 15 July 2019) and the percent change in maximum light (i.e. the average maximum light between 18 July and 16 August 2019 minus the average maximum light between 16 June and 15 July 2019 divided by the average maximum light between 16 June and 15 July 2019 multiplied by 100). For the causal model, maximum temperature was extracted from the logger data for the specific dates and times of water collection for comparison with biogeochemistry and ecosystem metabolism measurements. Hourly ocean temperatures over the experimental period were extracted from a near-shore ODFW Marine Reserve mooring sensor at 1 m depth within ORMR to compare tide pool temperatures to the local ocean.

2.4. Effects of foundation species loss on biogeochemistry and ecosystem metabolism

To determine biogeochemistry fluxes and ecosystem metabolism (NEC and NEP) before and after removal of foundation species, we collected daytime and nighttime water samples during low tide. We used a block design for water sampling with 2 daytime and 2 nighttime sampling events due to the timing of low tide and time constraints on sampling, where $n = 16$ pools ($n = 8$ per foundation species type) were measured on separate day and night sampling events (Tables S3 & S4). Each sampling event included an equal number of pools per foundation species and treatment group (removal or control: $n = 8$ pools). *In situ* temperature, DO, salinity, pH using the total scale (pH_T), and discrete samples for dissolved inorganic nutrients (NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$, PO_4^{3-}) were collected hourly over a 4 h period in each pool and the adjacent ocean following methods in Silbiger & Sorte (2018). Temperature, DO, and salinity were measured with a calibrated multi-parameter pro meter directly in each pool (YSI Pro 2030, Lot #18B100763). For pH_T , nutrients, and total alkalinity (TA), we collected 400 ml discrete water samples from the deepest part of the pool into a sealed Erlenmeyer flask using a vacuum hand pump (Mityvac). Discrete samples ($\sim 250\text{ml}$) for TA

were taken 4 times over the low tide period. To compare tide pool conditions to the open ocean, ocean measurements were taken from the surface adjacent to the site. pH_T was measured within 1 h of water collection in the sealed Erlenmeyer flask using an Orion Star Multiparameter Meter with a ROSS Ultra glass electrode (Thermo Scientific; accuracy = ± 0.2 mV, resolution = ± 0.1 mV, drift < 0.005 pH units d^{-1}) and a traceable digital thermometer (FisherBrand™ Traceable™; Model 5-077-8, accuracy = 0.05°C , resolution = 0.001°C) following Dickson Standard Operating Procedure (SOP) 6 (Dickson et al. 2007). The glass electrode measured millivolts (mV) and was calibrated within 48 h of each sampling event using a multipoint calibration to a tris standard solution from the Dickson Lab at Scripps Institution of Oceanography following Dickson SOP 6a (Dickson et al. 2007). TA seawater samples were placed in 250 ml Nalgene bottles with 100 μl of 50 % saturated HgCl_2 to preserve the water within 5 h of collection. Seawater samples for nutrient analysis were filtered through GF/F filters (0.7 μm) with a syringe into designated 50 ml centrifuge tubes and frozen within 5 h of collection. All sampling and storage containers were soaked in 10 % HCl for 24 h, rinsed with MilliQ water, and rinsed 3 times with sample water before sampling events.

2.5. Sampling processing

In situ pH_T was calculated using the seacarb package in R (Gattuso et al. 2018) by correcting for the *in situ* temperature in each tide pool from a multi-parameter pro meter. TA seawater samples were processed using open-cell potentiometric titrations on a Mettler-Toledo T5 auto-titrator following Dickson SOP 3b (Dickson et al. 2007). A certified reference material (CRM) from the Dickson Lab at the Scripps Institution of Oceanography was used at the beginning of each sample group run. The accuracy of the CRM never exceeded $\pm 0.79\%$ (precision = 5 $\mu\text{mol kg}^{-1}$) deviation from the standard value and TA samples were corrected for deviations. Dissolved inorganic nutrients (NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$, PO_4^{3-}) were analyzed at Moss Landing Marine Laboratory using a Lachat Quickchem 8000 Flow Injection Analyzer (Hach; instrument precision: $\pm 1.21\%$ NH_4^+ , $\pm 0.26\%$ $\text{NO}_2^- + \text{NO}_3^-$, $\pm 3.57\%$ PO_4^{3-}). After processing nutrients, 1 mussel control pool (pool ID 30) was removed from all resource flux analyses due to abnormally high values of ammonium relative to other pools on 1 sampling day ($4290 \pm 188.1 \mu\text{mol g}^{-1}$), likely due to contamination, leaving $n = 7$ control pools.

2.6. Ecosystem metabolism calculations

We used the total alkalinity anomaly technique (Chisholm & Gattuso 1991) to calculate NEC ($\text{mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$) with the following equation:

$$\text{NEC} = \frac{\Delta\text{TA} \times \rho \times V}{2 \times \text{SA} \times t} \quad (1)$$

Total alkalinity values were divided by 1000 to convert from $\mu\text{mol kg}^{-1}$ to mmol kg^{-1} . $\Delta\text{TA}/2$ is the salinity-normalized and nutrient-corrected TA (mmol kg^{-1}) between each time point ($n = 2\text{--}3$ values per pool) divided by 2, where one mole of CaCO_3 is formed per 2 moles of TA; ρ is the density of seawater (1023 kg m^{-3}); V is the volume of water in the pool at each time point (m^3); SA is the bottom surface area of the tide pool (m^2); and t is the time between sampling points (h). TA was normalized to a constant salinity of 34 units to account for changes in evaporation during sample processing. Samples were corrected for the effect of nutrients on carbonate chemistry with the following equation (Wolf-Gladrow et al. 2007):

$$\begin{aligned} \text{Nutrient corrected TA} = \\ \text{TA} - [\text{NO}_2^- + \text{NO}_3^-] - (2 \times [\text{PO}_4^{3-}]) + [\text{NH}_4^+] \end{aligned} \quad (2)$$

Positive NEC values indicate net calcification while negative values indicate net dissolution.

NEP rates ($\text{mmol C m}^{-2} \text{ h}^{-1}$) were calculated from differences in dissolved inorganic carbon (DIC), calculated from pH_T and TA (error propagation = $7.09 \pm 0.06 \text{ mmol kg}^{-1}$) with the seacarb package in R (Gattuso et al. 2018), using the following equation (Gattuso et al. 1999):

$$\text{NEP} = \frac{\Delta\text{DIC} \times \rho \times V}{\text{SA} \times t} - \text{NEC} - \text{FCO}_2 \quad (3)$$

where ΔDIC is the difference in salinity-normalized DIC (mmol kg^{-1}) between each time point (around $n = 3$ values per pool). NEC is subtracted to account for changes in DIC by the precipitation or dissolution of CaCO_3 , and FCO_2 ($\text{mmol m}^{-2} \text{ h}^{-1}$) is the air–sea flux of CO_2 , which was subtracted to account for the flux in CO_2 from the air–sea exchange. FCO_2 was calculated as:

$$\text{FCO}_2 = k \times s (\text{CO}_{2\text{-water}} - \text{CO}_{2\text{-air}}) \quad (4)$$

where k is the gas transfer velocity (m h^{-1}) calculated from wind speed (Ho et al. 2006) using the closest weather station, around 10 miles south of Otter Rock (NOAA Station NWPO3: $44^\circ 36' 46.8'' \text{N}$, $124^\circ 04' 01.2'' \text{W}$); s is the solubility of CO_2 in seawater calculated from *in situ* temperature and salinity (Weiss 1974); CO_2 (μatm) in water is calculated from

pH_T and TA values; CO₂ in air was 410 μ atm based on concurrent measurements at the Mauna Loa Observatory (Tans & Keeling 2019). Positive NEP values indicate net photosynthesis and negative NEP values indicate net respiration.

2.7. Statistical analysis

We conducted separate statistical analyses for surfgrass and mussel tide pools for all response variables due to differences in effects of each foundation species on the ecosystem. Change in foundation species loss between the before and after removal periods varied continuously across treatment groups from -27.5 to 100% change in cover in the surfgrass tide pools and -10.4 to 98.5% change in cover in the mussel pools (Fig. S1), with negative values indicating there was an increase in foundation species cover between time points. Therefore, we investigated foundation species loss as a continuous gradient rather than using a categorical ANOVA-style design typical for BACI studies (Smith 2002). All data were processed and analyzed using R (v 4.0.2; R Core Team 2020).

Multivariate plots and analyses were used to assess how community composition and biogeochemistry parameters changed between time periods. We used a principal coordinate analysis (PCoA) using the 'vegdist' function in the vegan package (Oksanen et al. 2020) to visualize how the gradient of percent foundation species loss altered the change (after-before removal) in the cover of sessile organisms and count of mobile organisms grouped by functional group (Table S2). Mobile community data were square root transformed to reduce the effect of rare values. One surfgrass control tide pool (pool ID 18) was removed from the mobile community analysis because of outlier values of limpets and littorine snails (Table S5, Fig. S2). A PERMANOVA using the 'adonis' function in the vegan package (Oksanen et al. 2020) was used to test if foundation species loss altered functional community composition, with tide height and tide pool size included as covariates. For the biogeochemistry data, principal component analyses (PCA) were used to reduce the dimensionality and visualize the multivariate data. Data were centered and standardized before visualizing the PCA using the 'prcomp' function in the stats package (R Core Team 2020). Specifically, shifts in biogeochemistry (DO, nutrients, and pH_T) and temperature (mean, maximum, and variance) between the before- and

after-removal periods, measured at $n = 8$ (4 day and 4 night) time points, were visualized to observe differences in local tide pool conditions and adjacent ocean between water sampling events.

We used general linear models to test the effect of foundation species loss on change (after-before removal) in species richness, percent maximum light, and maximum temperature in tide pools, with tide height and tide pool volume as covariates, using the 'lm' function in the stats package (R Core Team 2020). The 'ggpredict' function from the ggeffects package (Lüdtke 2018) was used to compute marginal effects for each model for data visualizations. Model assumptions were verified by investigating residual plots for normality and homogeneity of variance using 'qqp' and 'plot' functions in base R (R Core Team 2020), and data that did not meet assumptions were transformed. Multicollinearity was tested using Pearson correlations between each pair of predictors using the 'ggpairs' function in the GGally package (Schloerke et al. 2018).

We conducted a piecewise structural equation model (SEM) using the R package PiecewiseSEM 2.1.0 (Lefcheck 2016) to understand how mussel and surfgrass percent loss and tide pool physical characteristics affected community changes, physical environmental conditions, biogeochemistry, and ecosystem metabolism of tide pool communities. Piecewise SEMs combine multiple linear models into a single causal framework (Shipley 2009, Lefcheck 2016). Because the model is pieced together with local estimation, it is more flexible than traditional SEMs and allows for inclusion of non-normal distributions, random effects, nested models, and smaller sample size (e.g. <10 samples per parameter) within the causal model network (Lefcheck & Duffy 2015). Specifically, we tested direct and indirect pathways of the effect of surfgrass and mussel loss on ecosystem metabolism (NEC and NEP) mediated by changes in micro/macroalgae cover, temperature, nutrients (dissolved nitrogen to phosphate ratio), pH_T, and physical parameters of the tide pool. We conducted a multigroup analysis using the 'multigroup' function in PiecewiseSEM 2.1.0 (Lefcheck 2016) to test if each path varied by day and night, as expected from previous tide pool studies (Kwiatkowski et al. 2016, Bracken et al. 2018, Silbiger & Sorte 2018, Wolfe et al. 2020). The fit of each model was determined with a Shipley's test of d -separation, which verifies there are no missing inferences from the model using a Fisher's C statistic, where $p > 0.05$ indicates the model is a good fit for the data (Shipley 2009). However, our study's ratio of total number of samples (16)

to number of variables (9) is 1.78 versus the recommended 5 (Grace et al. 2015, Lefcheck 2016), which could influence the goodness of fit of the model. Path coefficients were standardized, allowing for comparisons of the magnitude of effects among groups.

2.8. Structural equation model framework and hypotheses

For all model components, we averaged values over the low tide period ($n = 3\text{--}4$ values per tide pool for pH_T , nutrients, and temperature; $n = 2\text{--}3$ values for NEC and NEP), and then calculated the difference between the before and after removal time periods ($n = 16$ pools for the surfgrass model and $n = 15$ pools for the mussel model). Positive values indicate an increase, zero indicates no change, and negative values indicate a decrease in that parameter after removal. For the community composition components of the model, we used the sessile community metrics that changed the most between the before and after removal periods, including surfgrass, mussels, and non-surfgrass, non-calcifying producers (all fleshy micro and macroalgae). We excluded coralline algae from the analysis due their different functional roles within the tide pool (e.g. calcification and production) and to reduce the number of pathways in our analysis. Tide pool size, represented as volume, and tide pool height were used as covariates in all models because physical parameters can affect temperature and biogeochemistry (Legrand et al. 2018, Wolfe et al. 2020).

Due to the collinearity between nutrient species, the dissolved nitrogen to phosphate ratio ($[\text{NO}_2^- + \text{NO}_3^- + \text{NH}_4^+]:\text{PO}_4^{3-}$) was used as the measurement for nutrients in SEMs. Because temperature and light were highly correlated and change in light was zero in most pools at night, only maximum temperature was used within the SEM framework (Fig. S3). We used existing knowledge of intertidal systems to create hypothesized paths within each of the models (Grace 2008, Grace et al. 2012), as follows:

$$\text{Micro/macroalgal cover} \sim \text{Foundation species loss} + \text{Volume} + \text{Tide height} \quad [1]$$

Model 1 represents the hypothesis that loss of surfgrass and mussel cover will increase producer cover by increasing free space for fast colonizers, with the size of the pool and tide height as covariates (Dethier 1981, 1984).

$$\text{Maximum temperature} \sim \text{Foundation species loss} + \text{Volume} + \text{Tide height} \quad [2]$$

Model 2 tests the understanding that temperature will increase with surfgrass and mussel loss (Stephens & Bertness 1991, Shelton 2010), with size of the pool and tide height as covariates.

$$\text{N:P} \sim \text{Foundation species loss} + \text{Volume} + \text{Tide height} \quad [3]$$

Model 3 represents the hypothesis that the N:P ratio will increase with surfgrass loss because the loss of dominant producers will lead to less nitrogen uptake (Terrados & Williams 1997, Ramirez-Garcia et al. 2002). We hypothesized that the N:P ratio will decrease with mussel loss due to mussels' ability to recycle nitrogen (Nielsen 2003, Bracken & Nielsen 2004, Pfister 2007, Pfister & Altabet 2019). The N:P ratio may be affected by the size of the tide pool, due to diffusive properties of tide pools (Hurd 2000) and tide height due to emersion time.

$$\begin{aligned} \text{Surfgrass model: NEP} &\sim \text{Maximum temperature} + \\ &\text{Micro/macroalgal cover} + \text{N:P} + \\ \text{Tide height; Mussel model: NEP} &\sim \text{N:P} + \\ &\text{Micro/macroalgal cover} + \text{Tide height} \end{aligned} \quad [4]$$

Model 4 represents the different mechanisms that influence NEP. NEP is increased by producer cover, temperature, and nutrients (N:P) and affected by tide height (Pfister 2007, Kwiatkowski et al. 2016, Take-shita et al. 2016, Bracken et al. 2018, Duarte & Krause-Jensen 2018, Silbiger & Sorte 2018, Pfister & Altabet 2019, Wolfe et al. 2020). Surfgrass and mussel loss were both correlated with most of the components of the NEP model and were therefore excluded from the NEP model. Since volume was already accounted for in the calculation of NEP, it was removed from the model equation. Maximum temperature and N:P were correlated within mussel pools, so N:P ratio was used because there is more background knowledge on mussels' effect on production via altering nutrients (Pfister 2007, Pfister & Altabet 2019).

$$\text{pH} \sim \text{NEP} + \text{Foundation species loss} + \text{Volume} + \text{Tide height} \quad [5]$$

Model 5 represents our understanding that there is a positive relationship between NEP and pH (Silbiger & Sorte 2018). Production increases pH, while respiration decreases pH due to the uptake and release of CO_2 respectively. Foundation species loss, size of tide pool, and tide height may also affect pH. Foundation species loss was included within the pH model be-

cause it was determined as a necessary association for the model fit by tests of direct separation.

$$\text{NEC} \sim \text{pH} + \text{Maximum temperature} + \text{Tide height} \quad [6]$$

Model 6 represents our understanding that NEC increases with pH and temperature and may be affected by the tide height (Kwiatkowski et al. 2016, Silbiger & Sorte 2018, Wolfe et al. 2020). Since volume was already accounted for in the calculation of NEC, it was removed from the model equation. Foundation species loss was correlated with both pH and maximum temperature and therefore was excluded from the model.

3. RESULTS

3.1. Foundation species loss and physical parameters alter tide pool communities

Within surfgrass pools, surfgrass loss significantly affected sessile community composition (Fig. 2A; PERMANOVA: $F_{1,15} = 4.79$, $p = 0.003$) but not mobile communities (Fig. 2B; PERMANOVA: $F_{1,14} = 1.91$, $p = 0.15$). Shifts in sessile communities with surfgrass loss were driven mostly by change in cover of microalgae and foliose algae (Fig. 2A). There was no effect of tide pool size or tide height on surfgrass pool sessile or mobile communities (Table S5, Fig. 2). Species richness in sessile or mobile communities 1 mo after

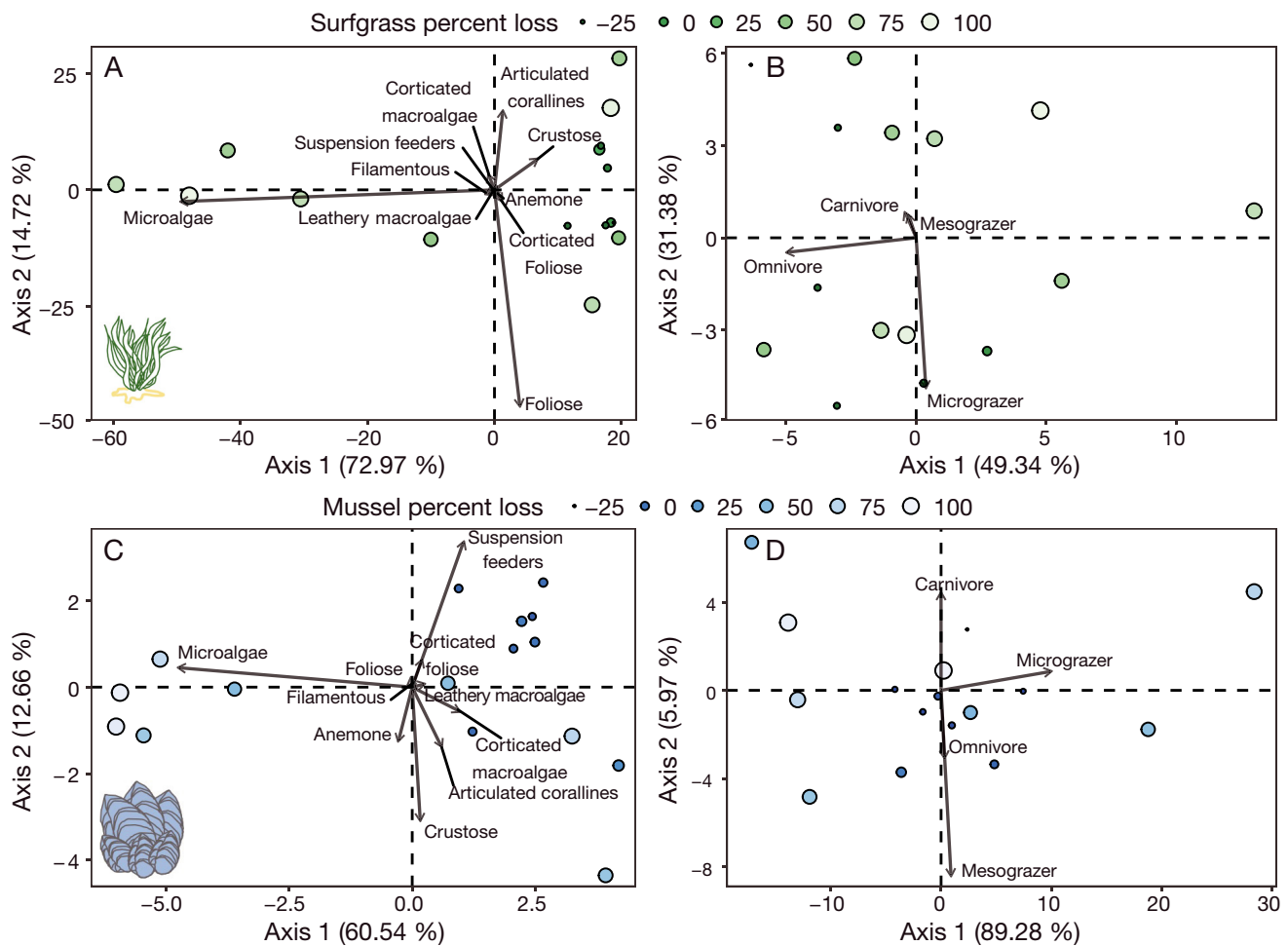


Fig. 2. Principal coordinate analysis (PCoA) plots of (A,B) surfgrass- and (C,D) mussel-dominated tidepool (A,C) sessile and (B,D) mobile communities. Mobile communities (counts) were square root transformed. Green (surfgrass) and blue (mussel) points represent the scores for each tide pool and are sized proportional to foundation species percent loss (0 before species removal, with positive values showing an increase in foundation species loss and negative values indicating a decrease in foundation species loss between the 2 periods). PCoA vectors are labeled for each functional group. The first 2 axes explained 87.69 (surfgrass sessile), 80.72 (surfgrass mobile), 73.2 (mussel sessile), and 95.2% (mussel mobile) of the variation in multivariate space. Data were analyzed with foundation species loss as a continuous variable

removal was not affected by surfgrass loss, size of tide pool, or tide height (Table S6, Fig. S4).

Mussel loss significantly affected sessile community composition (PERMANOVA: $F_{1,15} = 7.15$, $p = 0.001$), driven mostly by changes in microalgae cover (Fig. 2C). Mobile communities did not significantly change as a function of mussel loss (Fig. 2D, PERMANOVA: $F_{1,15} = 0.22$, $p = 0.75$). Tide height significantly affected mobile community composition in mussel pools (PERMANOVA: $F_{1,15} = 5.15$, $p = 0.03$), but not sessile community composition (PERMANOVA: $F_{1,15} = 1.58$, $p = 0.18$). Mussel pool sessile and mobile community composition was not significantly affected by size of the tide pool (Table S5). In addition, sessile species richness decreased by $0.98 \pm 1.01\%$ (mean $\pm$ SE) per change in mussel percent loss, which equates to approximately 2 species with 50% mussel loss (Fig. S4; linear regression: $t_{3,12} = -3.74$, $p = 0.002$), but was not affected by size of pool (linear regression: $t_{3,12} = -0.53$, $p = 0.61$) or tide height (linear regression: $t_{3,12} = -1.80$, $p = 0.10$). Mobile species richness significantly increased by approximately 2 species ($9.34 \pm 2.42\%$) per one meter in tide height (linear regression: $t_{3,12} = 3.85$, $p = 0.002$), but was not affected by mussel loss (linear regression: $t_{3,12} = -0.82$, $p = 0.43$) or size of the tide pool (linear regression: $t_{3,12} = -0.54$, $p = 0.60$).

3.2. Foundation species loss increased light and temperature in tide pool environments

Over the 2 mo study, temperature increased as a function of both surfgrass and mussel loss in the tide pools (Table S7). Surfgrass loss had a strong positive effect on maximum temperature (Fig. 3A), increasing by $1.01 \pm 1.00\%$ per percent loss of surfgrass (linear regressions: $t_{3,12} = 5.24$, $p < 0.001$). Overall, daily maximum temperature was on average $3.8 \pm 0.44^\circ\text{C}$ higher in surfgrass removal pools than controls. Mussel loss also significantly increased max temperature in tide pools by $0.02 \pm 0.009\%$ per percent loss (Fig. 3B, linear regressions: $t_{3,11} = 3.00$, $p = 0.01$), with temperatures increasing by an average $1.33 \pm 0.76^\circ\text{C}$ in removal pools. Daily average change in ocean temperature decreased by $0.55 \pm 0.43^\circ\text{C}$ between time periods due to upwelling (Fig. S5). There was no effect of tide pool physical parameters on maximum temperature over the two-month period in surfgrass (linear regressions; size of pool: $t_{3,12} = 0.81$, $p = 0.43$; tide height: $t_{3,12} = -2.07$, $p = 0.06$) or mussel (linear regressions; size of pool: $t_{3,12} = 1.53$, $p = 0.15$ and tide height: $t_{3,12} = 1.80$, $p = 0.10$) pools. For maximum temperature, the model components (foundation species

loss, tide height, and volume) accounted for 72 and 69% of the variation within the system for surfgrass and mussel pools respectively (Table S7A).

There was a similar trend for percent change in light, where surfgrass loss increased percent max light by $1.07 \pm 1.01\%$ per percent surfgrass loss (Fig. 3C; linear regression: $t_{3,12} = 5.45$, $p < 0.001$). Overall, average percent max light increased by $142.02 \pm 45.70\%$ in surfgrass removal pools between periods. Mussel loss increased percent max light by $1.04 \pm 1.01\%$ per percent mussel loss (Fig. 3D; linear regression: $t_{3,11} = 3.34$, $p = 0.01$), with percent max light increasing by $5.80 \pm 4.19\%$ in removal pools. There was no effect of tide pool physical parameters on percent max light (Table S7), reinforcing that biological removal of foundation species exceeded the effect of physical parameters of the tide pool 1 mo post removal. For percent max light, the model components (foundation species loss, tide height, and pool volume) accounted for 72% of variation in surfgrass pools and 68% of the variation in mussel pools (Table S7A).

3.3. Ocean conditions and foundation species loss shift tide pool biogeochemistry

The biogeochemistry of surfgrass and mussel control pools (i.e. pools with intact foundation species) shifted in a similar direction to changing ocean conditions, whereas removal pools deviated substantially from the ocean conditions (Fig. 4). During the after-removal sampling period, ocean samples and control pools both had higher nitrate + nitrite and phosphate concentrations as well as lower temperatures as a result of coastal upwelling. Surfgrass control pools were more similar to the ocean biogeochemistry in the after period than in the before period, whereas surfgrass removal pools shifted in a different direction than ocean and control pools (Fig. 4A). Mussel control pools also shifted in accordance with changing ocean biogeochemistry and mussel removal pools became more similar to the ocean biogeochemistry than control pools in the after period (Fig. 4C). Pools with surfgrass and mussel loss became higher in DO and pH_T in the after period and had a more variable temperature environment.

3.4. Foundation species loss and tide pool physical parameters alter ecosystem fluxes

Using a SEM model, we demonstrated the relative magnitude of the effects of tide pool physical

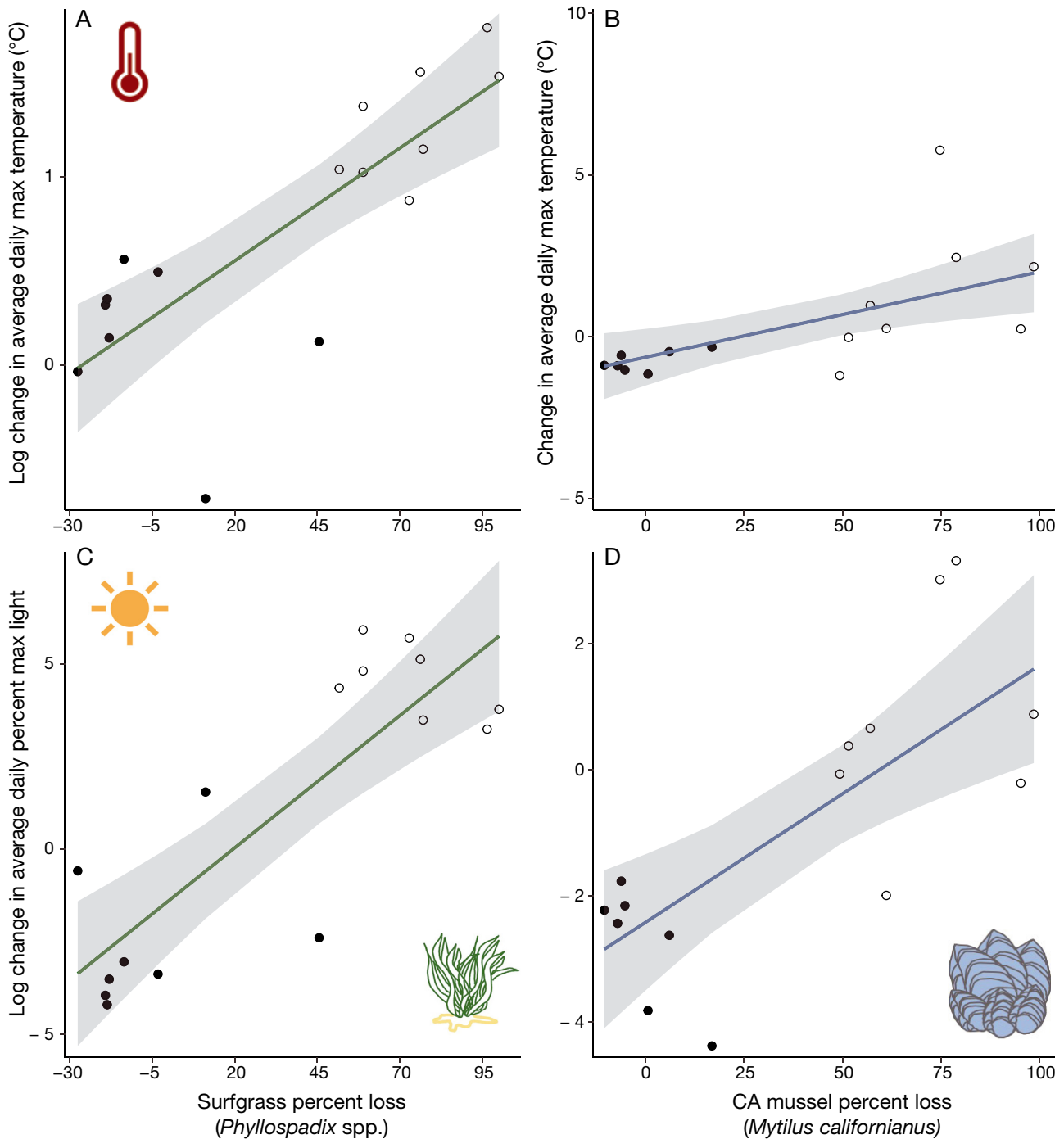


Fig. 3. Relationships between foundation species loss and change in (A,B) max temperature and (C,D) percent change in max light in (A,C) surfgrass tide pools and (B,D) mussel tide pools. Solid dots represent control pools, and open dots represent removal pools. Solid lines with gray shaded 95 % confidence intervals represent significant relationships. Light and temperature in surfgrass pools and light in mussel pools were log transformed to meet assumptions of normality

parameters (volume and tide height) and foundation species loss on ecosystem metabolism (NEP and NEC) mediated by changes in community structure (% cover producers), biogeochemistry (nutrients and pH), and physical environment (temperature)

during day and night low tides. Structure of the overall model was a good fit using Fisher's C ($p > 0.05$) for both surfgrass ($C_{26} = 33.43$, $p = 0.15$, Fig. 5A) and mussel ($C_{28} = 33.94$, $p = 0.20$, Fig. 5C) SEM models.

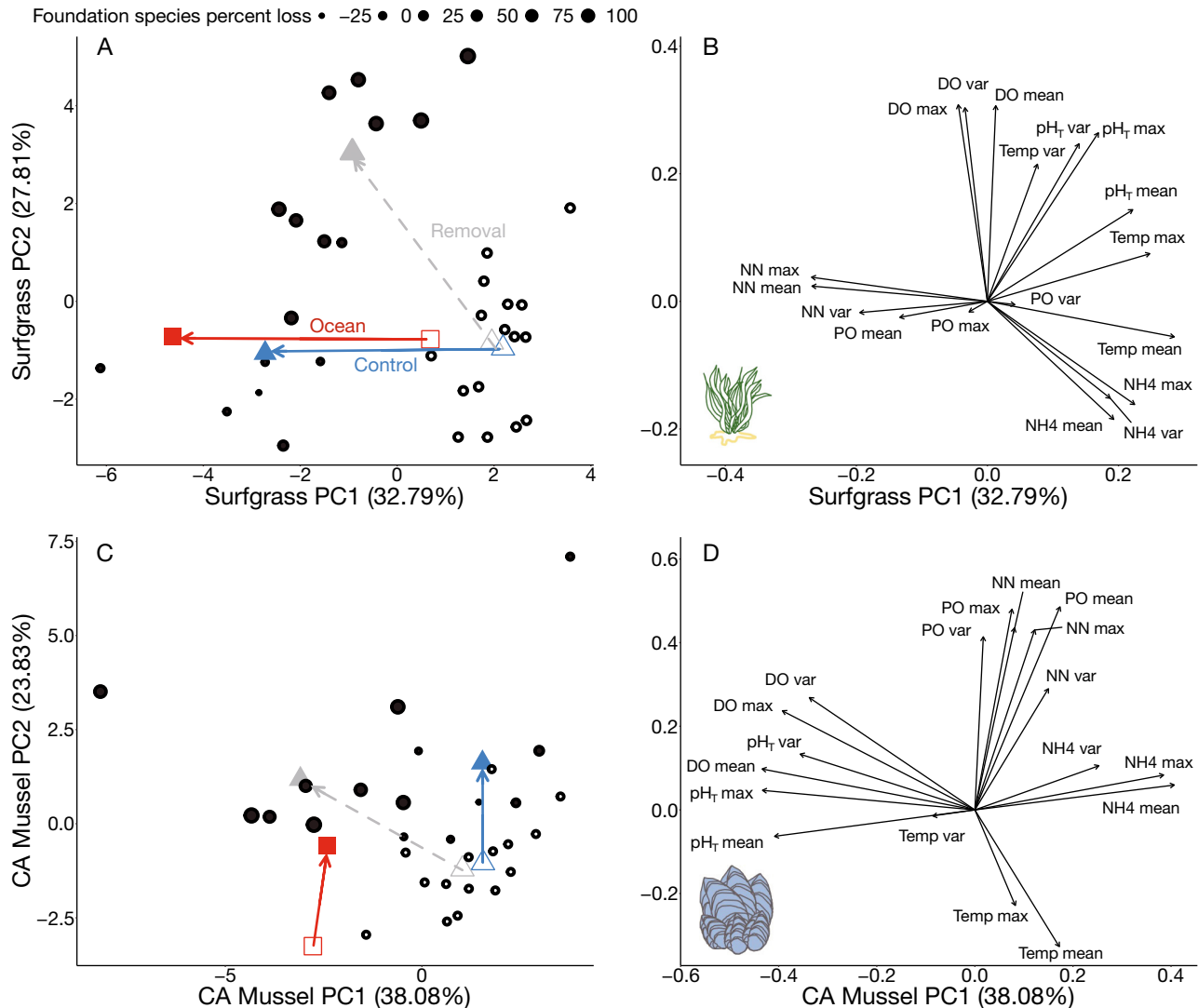


Fig. 4. Principal component analysis of the biogeochemistry (pH_T, DO [mg l⁻¹], and nutrients [μmol l⁻¹] NH₄⁺, NO₂⁻ + NO₃⁻, PO₄³⁻) and temperature mean, max, and variance of (A,B) surfgrass and (C,D) mussel pools before and 3 wk after foundation species removal. (A,C) Black points represent PC scores of each pool, where open circles represent the before period and size is proportional to foundation species percent loss in the after period. Data were analyzed with foundation species percent loss as a continuous variable. Gray triangles represent the centroids (means) of removal pools, blue triangles are centroids of control pools, and red squares are ocean samples. Arrows between before (empty shape) and after (filled shape) period show the magnitude of change. (B,D) Loadings of the PCA for each biogeochemical parameter. PC axes 1 and 2 explain (B) 60.60% and (D) 61.91% of the variation in the data

Surfgrass loss directly increased fleshy micro/macroalgae cover by $0.36 \pm 0.10\%$ per percent loss ($p = 0.002$) and increased maximum temperature during the day by $0.04 \pm 0.01^\circ\text{C}$ per percent loss (Fig. 5A, $p = 0.002$). Surfgrass loss did not significantly affect maximum temperature at night over the 24 h period (Fig. 5B, $p = 0.21$). The change in temperature significantly increased NEP by $1.03 \pm 0.30 \text{ mmol C m}^{-2} \text{ h}^{-1}$ per change in $^\circ\text{C}$ ($p = 0.002$). N:P negatively affected NEP with a $0.34 \pm 0.16 \text{ mmol C m}^{-2} \text{ h}^{-1}$ decrease along the N:P gradient ($p = 0.04$). Change in pH_T sig-

nificantly increased 0.002 ± 0.001 units per percent surfgrass loss ($p = 0.01$) and had a positive but non-significant association with NEP ($p = 0.06$). NEC significantly increased by $5.26 \pm 1.23 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ per unit change in pH_T ($p < 0.001$). NEC decreased $2.20 \pm 0.96 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ per m of tide height ($p = 0.03$).

Within mussel tide pools, mussel loss increased change in fleshy micro/macroalgae cover by $0.71 \pm 0.13\%$ per percent of mussel loss ($p < 0.001$). Algal cover had a significant day and night interaction with

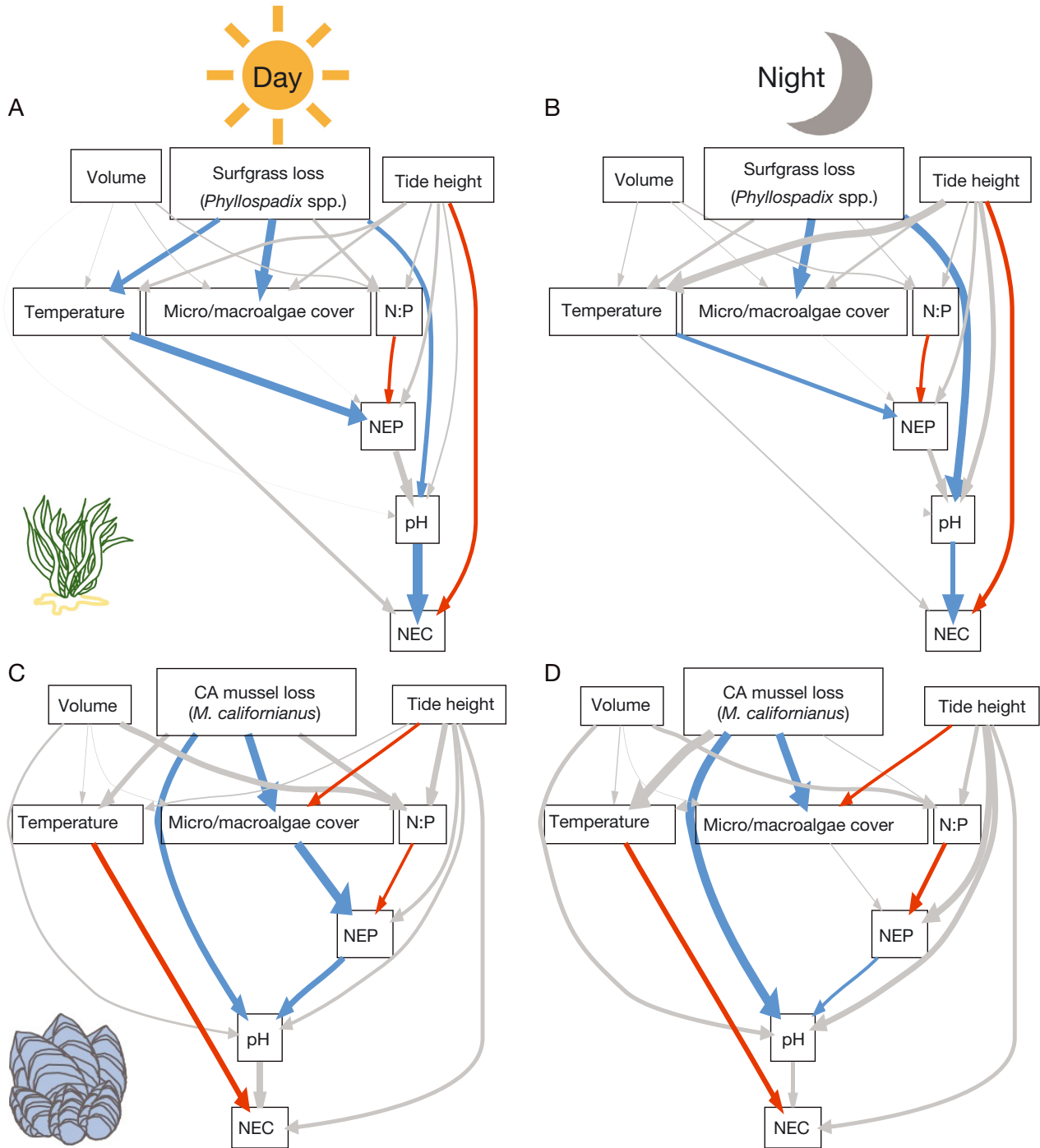


Fig. 5. (A,C) Day and (B,D) night structural equation models showing how (A,B) surfgrass and (C,D) mussel loss and physical parameters (tide pool volume and tide height) directly and indirectly affect community structure, biogeochemistry, and ecosystem metabolism. Blue lines represent positive paths, red lines represent negative paths, grey lines represent nonsignificant paths ($p \geq 0.05$). Arrow width is proportional to standardized path coefficients (Table S8). Paths that differ between models indicate significant day/night interaction

NEP, where during the day, algal cover led to a $0.11 \pm 0.02 \text{ mmol C m}^{-2} \text{ h}^{-1}$ increase in NEP rate per percent change of algal cover (Fig. 5C, $p < 0.001$) and there was no effect of algae cover at night (Fig. 5D,

$p = 0.28$). Change in N:P decreased NEP by $0.33 \pm 0.14 \text{ mmol C m}^{-2} \text{ h}^{-1}$ along the N:P gradient ($p = 0.02$). Change in pH_T increased by 0.003 ± 0.001 units per percent change in mussel loss ($p = 0.001$).

Change in NEP increased pH_T as well by 0.02 ± 0.01 units per $\text{mmol C m}^{-2} \text{ h}^{-1}$ change in NEP ($p = 0.005$). Maximum temperature negatively affected NEC by $0.69 \pm 0.28 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ per 1°C change ($p = 0.02$). Tide height had a significant effect on algal cover, where algal cover decreased $54.78 \pm 20.97\%$ per m increase in tide height ($p = 0.01$). There was no effect of volume on any parameters in surfgrass or mussel pools (Table S8).

4. DISCUSSION

While studies have linked foundation species loss to changes in community structure, the physical environment, and biodiversity (Ellison et al. 2005, Shelton 2010, Maggi et al. 2012, Castorani et al. 2018, Smale et al. 2019), few have focused on a causal approach with multiple facets of ecosystem functioning. This study fills a crucial gap in understanding the cascading impacts of foundation species loss on biogeochemical fluxes and ecosystem metabolism through experimental removal within the natural system (Gamfeldt et al. 2015). We measured the magnitude of immediate effects of intertidal foundation species loss on ecosystem functioning through changes in community structure and resource fluxes over a 2 mo experimental period. Our results show that foundation species loss from tide pool ecosystems had significant cascading and causal impacts on multiple components of ecosystem function. Surfgrass and mussel loss led to significant changes in sessile communities, light, temperature, and pH_T . Surfgrass and mussel loss also indirectly affected ecosystem metabolism (NEC and NEP) mediated by changes in temperature, producer cover, and pH_T . Our study is the first to quantify the magnitude of change of multiple ecosystem functions after intertidal foundation species loss.

Foundation species loss increased the presence of inferior space competitors after 1 mo in both mussel- and surfgrass-dominated tide pools. Specifically, both surfgrass and mussel pools saw an increase in early-succession species like diatoms, similar to foundational disturbance studies of the benthic intertidal community (Littler & Murray 1975, Emerson & Zelder 1978, Dethier 1981, 1982, 1984, Dethier & Duggins 1984, Benedetti-Cecchi & Cinelli 1996, Bertocci et al. 2005). Only mussel sessile species richness decreased along the gradient of mussel loss as seen in studies of loss of similar mussel species (*Perumytilus purpuratus*) (Valdivia & Thiel 2006). Increasing disturbance usually decreases species rich-

ness due to the facilitation of secondary sessile and mobile species by the presence of foundation species (Kimbrow & Grosholz 2006). However, recovery and community stability after disturbance of tide pool communities can take more than 3 yr (Dethier 1984, Shelton 2010). Therefore, it is likely the pools will continue to be dominated by a suite of early successional species along with seasonal increases in ephemeral diatom algae (Dethier 1982, 1984, Shelton 2010) and corticated algal species during upwelling along the Oregon coast (Nielsen & Navarrete 2004, Wieters 2005). There was no significant change in mobile communities in surfgrass or mussel pools, possibly because external environmental factors (e.g. recruitment and local scale dispersal) may have had a stronger effect on the mobile community than foundation species presence, as seen in previous studies (Shelton 2010, Valdivia et al. 2014). However, it is possible that the presence of grazers could have had a stronger impact on community structure than foundation species loss. There was an average of 11.5 ± 2.79 grazers m^{-2} in mussel pools and 4.37 ± 1.23 grazers m^{-2} in surfgrass pools across both time points, which could control ephemeral algae communities, but this effect will likely shift and dissipate over longer time scales (Aguilera & Navarrete 2012, Tejada-Martinez et al. 2016). Our results show the immediate response of tide pool communities to foundation species loss, which may continue to change with grazer presence and increased thermal and light stress.

Foundation species help maintain lower stress environments through shading and decreased temperature (Bruno & Bertness 2001). With their removal, wide-reaching organismal, community, and ecosystem level effects occur with the change in physical environment. For example, increased maximum light can bleach light sensitive algae, like coralline algae, reducing the production of the functional group, as was seen in other surfgrass studies (Shelton 2010). Increased temperature from foundation species loss can increase success of less temperature sensitive invasive species within marine systems (Sorte et al. 2010, Olabarria et al. 2013). Temperature extremes as a result of foundation species loss will alter metabolic rates of individuals and may also cause mortality if temperatures exceed thermal tolerances of tide pool species (Somero 2002, Shelton 2010). Our study found the daily maximum temperature of pools exceeded on average 3.8°C in removal surfgrass pools and 1.3°C in removal mussel pools compared to control pools. In addition, surfgrass loss significantly increased maximum tempera-

ture during daytime low tides rather than at night (Fig. 5), demonstrating the impact of foundation species loss also depends on diurnal timing of low tide periods. The changes in maximum light and temperature during our two-month-long analysis are in accordance with previous studies (Stewart & Myers 1980, Stephens & Bertness 1991, Shelton 2010). Because some removal pools in this study had maximum temperatures exceeding 30.0°C—which is a maximum threshold for many northeast Pacific temperate tide pools species, including *Tegula* spp. (Tomanek & Somero 1999, Tomanek & Helmuth 2002), tidepool sculpin (*Oligocottus* spp.) (Nakano & Iwama 2002), and >40 macrophyte species (Lüning & Freshwater 1988)—the temperatures seen in the current study could indicate that pools without foundation species act as ecological traps (Vinagre et al. 2018). Organisms may not survive >30.0°C temperatures over summer daytime low tide periods (4–6 h).

Using causal models, we determined that surfgrass and mussel loss have cascading indirect effects on ecosystem metabolism mediated by changes in algal cover, temperature, and pH_T. Further, these ecosystem metabolism changes are influenced by changing diurnal and ocean patterns. Algal cover significantly increased NEP during the day but not at night within mussel pools, as described in previous tide pool studies (Bracken et al. 2018, Duarte & Krause-Jensen 2018). Changes in N:P negatively affected NEP within both surfgrass and mussel pools. Shifts in N:P in the after-removal period were driven by coastal upwelling rather than foundation species removal (Fig. 5, Tables S3 & S4). Tide pools that were less phosphate limited (smaller N:P ratios) had higher increases in NEP, especially in pools with intact foundation species (Figs. S6 & S7). Although less likely than in terrestrial or freshwater systems, phosphate limitation can hinder production rates within the marine environment (Harrison et al. 1990, Elser et al. 2007). In addition, surfgrass and mussel loss directly increased pH_T, which demonstrates how biological processes can impact the biogeochemical environment (Silbiger & Sorte 2018). With shifts in the dominant producer after surfgrass loss, the combination of algal species with high metabolisms colonizing empty space and a higher light/temperature environment may account for the increased pH_T within surfgrass pools. The lack of a statistically significant relationship between NEP and pH_T within surfgrass pools ($p = 0.06$) may be due to the smaller sample size of our study relative to recent studies that showed a strong relationship ($n = 16$ tide pools in this study versus 57 in Silbiger & Sorte 2018).

Surfgrass pools showed a significant causal pathway from pH_T → NEC, which was expected based on prior tide pool and coral reef studies (Andersson & Gledhill 2013, Silbiger & Sorte 2018). Within mussel pools there was no effect of pH_T on NEC, but rather a negative relationship between change in maximum temperature and NEC in mussel pools. It is possible that the negative effect of maximum temperature on NEC is a result of confounding changing ocean conditions from upwelling, such as higher nutrient concentrations (e.g. phosphate) which could negatively affect NEC (Bjork et al. 1995). When looking at the raw environmental data (rather than the change between timepoints), we saw the expected significant positive relationships between pH_T and NEC, temperature and NEP, and temperature and NEC (Fig. S8). However, when analyzing difference between timepoints to account for the effects of upwelling or other seasonal changes, we did not see an effect of pH_T on NEC. This could be because (1) oceanic changes in pH_T had a stronger effect on NEC than local tide pool conditions due to upwelling (ocean pH_T decreased 0.18 ± 0.01 units whereas mussel pools' pH_T increased by 0.07 ± 0.04 units) or (2) the large change in temperature ($-3.14 \pm 0.19^\circ\text{C}$) in mussel tide pools had a stronger effect on NEC than pH_T. Additionally, the relationships between pH_T and NEC may have differed between surfgrass- and mussel-dominated pools because of biological differences in the type of dominant calcifiers. The dominant calcifier in surfgrass pools, crustose coralline algae (CCA), calcifies nearly twice as fast as mussels: studies have shown the temperate CCA species *Lithothamnion corallioides* calcifies as much as $9.7 \pm 0.5 \mu\text{mol CaCO}_3 \text{ g}^{-1} \text{ dry wt d}^{-1}$ (Martin et al. 2006), whereas mussel *M. edulis* calcification rates did not exceed $4 \mu\text{mol CaCO}_3 \text{ g}^{-1} \text{ dry wt d}^{-1}$ (Wahl et al. 2018). Therefore, changes in TA (an instantaneous measure of calcification) may have detected stronger calcification signals in surfgrass pools than mussel pools.

Our study demonstrates immediate changes in the ecosystem functioning after removal of foundation species. It is likely that as community structure and the physical environment shift, ecosystem function will shift along with it (Takeshita et al. 2016, Silbiger & Sorte 2018). Even with the short-term nature of the study, we saw strong causal relationships not previously described in concert. However, to make informed conservation management decisions, longer-term and seasonal impacts of mussel and surfgrass loss should be addressed (Ellison et al. 2005). Our relatively small sample size ($n = 15$ for mussels and $n =$

16 for surfgrass pools) may have impacted the results of our study. For example, SEM model fit may have been influenced by the sample size, since the ratio of the number of samples to the number of variables was below the recommended ratio. Although tide pools can be used as a natural laboratory to better understand the intertidal system, the relative effect of physics during high tide on biological processes in tide pools is unknown. The strong mechanistic signaling in this study could be either amplified or dulled during high tide, when larger-scale physical processes (e.g. waves and currents) are at play or change seasonally when environmental conditions are less stressful. Nevertheless, this study underscores that intertidal foundation species loss alters multiple facets of ecosystem function, and is likely to have lasting effects on ecosystem functioning in the future.

This research connects foundational studies of disturbance dynamics and ecological succession (e.g. Odum 1969) with contemporary studies focused on the influence of community structure on the physical, biogeochemical, and ecosystem metabolism landscape of tide pools. Dominant organisms (e.g. surfgrass, mussels, diatoms) within the system are driving changes in ecosystem functioning. It will be of increasing importance to measure the magnitude of the effects of foundation species loss not only on biodiversity and community structure, but also on fluxes of biogeochemical cycling and ecosystem metabolism (Ellison 2019). These flux processes in turn influence the broader ecological community (Silbiger & Sorte 2018) and the ecological services (Angelini et al. 2011) we depend on from the ecosystem.

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is CSUN contribution #367. J.B.F. and N.J.S. designed the project and contributed to fieldwork. J.B.F. collected and analyzed the data and wrote the manuscript. N.J.S. provided advice on statistical analyses and revised the manuscript. All data and code are publicly available at <https://github.com/jenniferfields/EcoFunORTidepools>.

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