Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness

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Abstract. Foundation species structure communities by creating habitat and modifying environmental conditions, and there is increasing interest in how foundation species, such as corals and mangroves, interact with one another as these interactions can have cascading effects on diversity and abundance of associated organisms. Given recent reports of corals living on or between mangrove roots under the canopy, we hypothesized that mangroves can serve as a refuge for corals from stresses such as high solar irradiance and temperatures that are associated with the adjacent shallow reef. Using field surveys and a reciprocal transplant experiment, we tested the effects of light and habitat (e.g., reef or mangrove) on coral community structure (i.e., coral species richness, abundance, and diversity) and condition (i.e., level of bleaching, tissue loss, and mortality). The surveys revealed higher coral richness in mangroves than on the adjacent reef, indicating that mangroves can serve as refugia for numerous coral species. Our experimental manipulation of light in mangrove and reef habitats indicated that light intensity is a key environmental parameter mediating coral bleaching and survival, with mangrove habitats providing a refuge from the light stress experienced on nearby shallow reefs. Moreover, our experiment revealed that reef corals bleached less than mangrove corals following transplantation, regardless of whether they were transplanted into mangrove or reef habitats. We suggest that the lower coral richness of the shallow reef is the result of the extreme environmental conditions that select for a subset of coral species able to tolerate these conditions. The facilitative interactions that allow mangroves to act as coral refugia by reducing environmental stress will likely become increasingly important with global climate change.

Key words: Bocas del Toro; Caribbean; climate change; coexisting mangrove-coral; foundation species; light stress; prop root; reciprocal transplant; refugia; Rhizophora mangle.

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INTRODUCTION

Tropical coral reefs are the most biodiverse marine ecosystems, harboring an estimated one third of all described marine species (Knowlton et al. 2010). Coral reefs are also one of the most sensitive ecosystems to climate change (Van Hooidonk et al. 2013) with global mass bleaching events becoming increasingly frequent and severe, typically followed by reduced coral growth rates, decreased fecundity and recruitment, and high coral mortality (Hoegh-Guldberg 1999, Hughes et al. 2003). Human activities can have negative local impacts on reefs through...
sedimentation, nutrient runoff, pollution, and overfishing (Hughes et al. 2003, Carpenter et al. 2008), potentially reducing the resilience of corals to global stressors such as ocean warming and acidification (Carpenter et al. 2008). A combination of these local and global factors have made Caribbean coral reefs among the most threatened reefs in the world, having suffered an estimated 80% reduction in live coral cover from 1975 to 2000 (Gardner et al. 2003, Guzmán 2003, Côté et al. 2005, Contreras-Silva et al. 2020) with current cover of live coral averaging just 10–13% (Schutte et al. 2010, Jackson et al. 2014, Tkachenko 2017). Therefore, understanding mechanisms of coral resilience, including positive species interactions that can ameliorate stressors, is of utmost importance (Bulleri 2009).

Among coral reef habitats, the shallow reef (≤3 m deep) is typically an extreme reef environment with high temperature and light conditions (Spalding et al. 2001). For this reason, shallow reefs are a sentinel system for how corals are likely to respond to anthropogenic stressors, with low coral diversity and corals adapted to extreme environmental conditions (Camp et al. 2018). However, the future success of shallow reef corals under global climate change is dependent on both coral adaptation to increasingly challenging environmental conditions and the availability of refuge habitats that can maintain coral diversity (Wild et al. 2011). Coral habitats adjacent to shallow reefs, such as intermediate (4–29 m) and mesophotic (≥30 m) reefs (Aronson et al. 2004, Bongaerts et al. 2015, Camp et al. 2018) and mangroves (Rogers and Herlan 2012, Yates et al. 2014, Camp et al. 2019) may serve as crucial refugia for corals increasingly exposed to stressful environmental conditions. We define refugia here as habitats where species may retreat to and persist in under changing and/or unfavorable environmental conditions and may serve as a potential source population to expand from (Keppel and Wardell-Johnson 2012, Cacciapaglia and van Woesik 2015). Refuge sites can ameliorate both acute environmental stress such as short-term thermal anomalies and more chronic stressors such as ocean acidification (Oliveira 2020). The use of these habitats could be a key survival mechanism for corals (Camp et al. 2018). Persistence in refugia may be enhanced by acclimatization to the unique conditions of refuge habitats initially through phenotypic plasticity, or in the long-term through adaptation to the refugia conditions over multiple generations (Torda et al. 2017).

Red mangroves (Rhizophora mangle) frequently occur in close proximity to reefs, and there are a few studies documenting the occurrence of corals growing among and near the mangrove roots such as in the saltwater ponds and channels of Belize (Macintyre et al. 2000, Rutzler et al. 2000, Bengtsson et al. 2019, Scavo Lord et al. 2020), bays of the U.S. Virgin Islands (Rogers 2009, Rogers and Herlan 2012, Yates et al. 2014), and the Florida Keys (Kellogg et al. 2020). These observational studies suggest that mangroves can serve as an alternative habitat for corals and perhaps a refugium in the face of continued reef degradation. In Bocas del Toro on the Caribbean coast of Panama, we observed the mangrove-coral association extending past the mangrove fringe (i.e., edge where mangrove forests meets open water) to several meters into the mangrove forests with corals growing both on and between the prop roots (Fig. 1). This overlapping distribution makes it an ideal system to experimentally test the nature of mangrove-coral interactions.

Most ecosystems are structured by multiple foundation species that influence the community by creating habitat and modifying environmental conditions. Coral reefs are an example of an ecosystem composed of multiple foundation species (e.g., corals) where multiple clonal organisms form complex structures that promote species diversity (Angelini et al. 2011). Coexisting foundation species occur in either (1) nested assemblages where a facilitation cascade allows the first foundation species to colonize a habitat and then facilitate another foundation species or (2) adjacent assemblages where foundation species compete for space and create discrete competitively determined zones (Angelini et al. 2011). Traditionally, corals and mangroves would be considered adjacent assemblages, but corals thriving within the mangrove canopy could serve as an example of a nested assemblage. Mangroves can have positive effects on scleractinian corals of nearby reefs at the seascape scale through long-distance positive interactions (e.g., reducing sediment flux and retaining nutrients; Gillis et al. 2014, van de Koppel et al. 2015), but it remains unclear whether corals growing on and
between the mangrove roots benefit from an association with mangrove habitats. Mangrove forests are typically thought to be unsuitable habitat for coral recruitment and growth (Yates et al. 2014), yet increasing reports of overlapping coral and mangrove habitats suggest there could be positive interactions between these foundation species. Where foundation species co-occur, their interactions can have cascading effects on diversity and abundance of associated organisms (Angelini et al. 2011, Thomsen et al. 2018) so understanding these interactions can provide insights into the entire community. We hypothesize that overlapping zonation occurs where corals benefit from a close association with mangroves due to amelioration of high light and temperature stress, creating suitable conditions for the corals to thrive. For example, large (1 m

Fig. 1. Coral species growing within the mangrove habitat of Bocas del Toro, Panamá. Photographs © Heather A. Stewart.
across) scleractinian corals within mangroves of the U.S. Virgin Islands are believed to have survived bleaching events that caused high mortality on the adjacent reef (Rogers and Herlan 2012). Experimental shading on reefs has been shown to be a local mitigation tool for coral bleaching (Coelho et al. 2017), suggesting that shading by the mangrove canopy may be a mechanism of local-scale facilitation of corals. While observational data are highly suggestive of coral facilitation by mangroves, no study has tested whether light intensity in mangroves influences coral survival relative to adjacent reefs. Further, no study has compared the ability of different coral species to survive in the mangrove habitat. Identifying local-scale positive associations between corals and mangroves, that is, interactions in the area of distributional overlap of corals on and within the mangroves, that drive their co-occurrence would change the view on what determines the relative distribution of mangroves and corals, and would have significant implications for predicting the importance of refuge habitats where corals might persist with increasing climate change stress.

In this study, we examined the effects of light and habitat (i.e., reef or mangrove) on coral bleaching, tissue loss, and survival using field surveys and a reciprocal coral transplant experiment. In the transplant experiment, we tested the effects of light conditions by increasing light levels in the mangrove habitat with canopy removals and by decreasing light levels on the reef with shade cloths. To determine whether mangroves can act as coral refugia, we used the results of our surveys and experiment to answer three questions: (1) Are some coral species better able to survive and persist in the mangroves than others? (2) Is refuge from the high light levels found on adjacent shallow reefs one of the main local-scale advantages of mangrove habitats for corals? (3) Are corals from the reef or mangroves better able to acclimate to new environments?

**METHODS**

**Reciprocal transplant experimental design**

To study the importance of light and habitat, we ran a reciprocal transplant experiment at the site Fuego off of the Island of Bastimentos in the Bocas del Toro archipelago on the Caribbean coast of Panamá from June to September 2019 (Fig. 2a). We created four experimental treatments with 10 replicate plots each: reef natural light (reef control), mangrove natural light (mangrove control), mangrove high light created by pulling back canopy, and reef low light created by installing a shade cloth (Fig. 2b, c). In June 2019, we identified six coral species to transplant into each experimental plot from an initial qualitative assessment: two that more commonly occurred in mangroves (Montastraea cavernosa and Pseudodiploria clivosa), two that more commonly occurred on the reef (Diploria labyrinthiformis and Porites astreoides), and two that were observed in similar frequency in both habitats (Colpophyllia natans and Orbicella faveolata). Colpophyllia natans and Orbicella faveolata were collected from both mangrove and reef habitats to test for evidence of intraspecific variation in coral bleaching and mortality related to source habitat.

One colony was selected per coral species as the source of experimental fragments, except for C. natans and O. faveolata where a colony was collected from both mangrove and reef habitats. We opted to select one colony per species rather than multiple colonies to minimize impact on this undescribed system of mangrove-coral habitat. Each colony was divided into 40 fragments of 2–3 cm diameter, mounted to 3 cm diameter ceramic plugs (Oceans Wonders) with reef glue (Sea Chem Cyanoacrylate Gel), and secured in a random order to weighted rigid eggcrate. Only healthy colonies without signs of bleaching or disease were used in the transplant experiment. Since abruptly transplanting coral fragments, particularly to higher light levels, can initially cause bleaching (Richier et al. 2008, Forrester et al. 2012, Cohen and Dubinsky 2015), all corals were placed in the intermediate fringe habitat between the reef and mangrove canopy and allowed to recover for a week. Since all the experimental corals experienced the same level of handling stress, we did not test the effects of transplant directly again on non-transplanted controls, rather we compared corals that were transplanted back to their source habitat to corals that were transplanted to the other habitat. For the reef low light treatment, 1 × 1 m shades were created from a double layer of 40% sunblock shade cloth (Agfabric UV stabilized High UV Stabilized Sunblock Shade Cloth) from a shade cloth (Agfabric UV stabilized High UV Stabilized Sunblock Shade Cloth) from the mangrove canopy may be a mechanism of local-scale facilitation of corals. While observational data are highly suggestive of coral facilitation by mangroves, no study has tested whether light intensity in mangroves influences coral survival relative to adjacent reefs. Further, no study has compared the ability of different coral species to survive in the mangrove habitat. Identifying local-scale positive associations between corals and mangroves, that is, interactions in the area of distributional overlap of corals on and within the mangroves, that drive their co-occurrence would change the view on what determines the relative distribution of mangroves and corals, and would have significant implications for predicting the importance of refuge habitats where corals might persist with increasing climate change stress.

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Density Polyethylene), held in place 65 cm above the plot by a PVC frame, to mimic the light levels found within the mangrove canopy. All plots where transplant corals were placed had corals currently growing within them, indicating it should be a suitable environment for corals. Mangrove high light treatments were created by pulling back canopy branches with plastic locking tree ties (Dimex EasyFlex), so that at midday no shadows were cast upon a 1 x 1 m plot area. In total, nine coral fragments were removed from analyses as a result of being dislodged or bleached during the first two days of the experiment (i.e., evidence of transplantation shock) including seven mangrove-sourced corals (4 C. natans, 1 M. cavernosa, 2 P. clivosa) and two reef-sourced corals (1 C. natans, 1 D. labyrinthiformis). No signs of disease were observed during the acclimation period or throughout the experiment.

**Light and temperature measurements**

Light, recorded as photosynthetically active radiation (PAR), was measured during the
experiment to quantify relative differences in the light level of each plot. Prior to setting up the experiment, we measured the average peak mid-day PAR levels that were over 3.5 × higher on the reef (729 ± 118 μmol·s⁻¹·m⁻², mean ± SE) than in the mangrove canopy (203 ± 80 μmol·s⁻¹·m⁻²). These data were used to determine the amount of shading needed on the reef to approximately match light levels within the mangrove canopy. During the experiment, light measurements were made between 11:00 and 13:00 on a cloud-free day in September 2019. We used a pair of spherical underwater quantum sensors (Licor LI-193s) to take our readings within mangrove canopies and reef habitats simultaneously. The light measurements used in analyses were an average of three PAR readings per plot. To quantify variation in temperature among treatments, we deployed five data loggers (HOBO Pendant 64K Data Logger) per treatment to record a week-long water temperature profile.

Coral condition and mortality
Coral condition was scored visually on an index of 5 = completely healthy corals/no visible bleaching/no tissue loss, 4 = <50% bleaching, 3 = ≥50% bleaching, 2 = visible tissue loss, or 1 = dead (Fig. 2d). We observed algal overgrowth only after the coral died, so those corals remained in category 1. None of the coral fragments showed visual signs of disease so disease was not included in our index. Coral condition was scored one week after the treatments were established and again three months later at the end of the experiment. Plots were visited weekly to clean the shades and maintain canopy restraints.

Coral community surveys
The coral community in Bocas del Toro is diverse, containing 87% of the scleractinian coral species reported in Caribbean Panamá (Guzmán 2003, Guzmán et al. 2005). To characterize the coral community in the mangrove canopy and adjacent shallow reef, and to show that the association between corals and mangroves appeared similar at multiple sites, we conducted surveys in March 2020, expanding from the initial site (Fuego) where the reciprocal transplant experiment ran to two additional sites (Fig. 2a). In these surveys, we quantified live coral species richness, abundance (percent cover), and diversity. Criteria for site selection were area (needed to be large enough to run our transects, ≥60 m long), distance from one another (>5 km apart to allow ecological independence), and proximity of mangroves and shallow reef (<2 m apart). Although many mangrove islands in the archipelago have corals growing within them, mangrove-coral areas can be patchy due to development, deforestation, and freshwater inflow, so we avoided such locations in our study. Since we were interested in contrasting corals within mangroves and reefs to examine potential factors driving use of refugia habitat, we selected sites with established coral communities both on the reef and in the mangrove canopy. At each site, we placed 16 to 24 replicate 1-m² quadrats at semi-regular intervals (>2 m apart) along a mangrove and a reef transect placed parallel to one another. Each transect was 4 m apart (2 m from the mangrove fringe in both directions). If root density prevented placement of the quadrat in the mangrove habitat, we moved to a position 1–2 m adjacent to that spot. Each quadrat was divided into a grid with 25 points, and we identified the benthic substrate or organism that was dominant under each point. Water depth was recorded in each quadrat, and the average depth relative to mean lower low water (MLLW) was 0.5–1.0 m. Mangrove-coral areas had corals growing from the fringe of the mangrove to >7 m into the canopy. Corals grew both on and between the mangrove roots. Corals growing between roots were typically found on substrates including coral rubble, shells, or peat.

Analyses
All data were analyzed with R version 3.6.3 (R Core Team 2020). Since light (PAR) was recorded in all 40 plots and there was overlap in the PAR values among treatments, we treated light as a continuous variable independent of habitat in our experimental analyses. Light and mean temperature were positively correlated ($P < 0.001$, $t$-test = 10.577, df = 145, correlation coefficient = 0.660; Appendix S1: Fig. S1), so temperature was excluded from the overall model to avoid confounding effects from multicollinearity. As coral condition was measured with an index (ordinal data), we used an ordinal logistic regression model to test for effects of habitat (i.e., plot...
location in mangrove or reef), light, source (i.e., coral collection site in mangrove or reef), coral species, depth, interaction terms (source × habitat, source × light, and species × light), and a random effect of plot. We were unable to include the interaction term of species × habitat due to limitations in sample size. Models were fit using the polr function from the MASS package. We tested the proportional odds assumption and checked for multicollinearity with the GGally package. We used the ANOVA function from the car package and summary functions to perform a Type II sum of squares to look at the main effects and compare coefficients. The lsmeans package was used to run pairwise comparisons when interaction terms were significant. We used ggpredict from the ggeffects package to obtain predicted probabilities to plot modeled data.

We analyzed complete mortality separate from the coral condition analysis to provide further resolution on the effects of predictor variables on coral survivorship by fitting a binomial generalized linear mixed-effects model (GLMM) using the glmer function with the effects of habitat, light, source, coral species, interaction term of source × light, and a random effect of plot. Light used in the binominal model was treated as high (reef control and mangrove high light treatments) or low (mangrove control and reef low light treatments) within a given habitat because the model failed to converge using PAR measurements. We used a chi-squared likelihood ratio test of our model fit and performed residual diagnostics with the DHARMA package.

For the surveys, coral species diversity (Shannon-Wiener and Simpson indices) and richness were calculated from the percent cover of live coral using the vegan package. Effects of habitat type (reef vs. mangrove) and site on diversity and richness were analyzed using linear models and two-way ANOVAs.

**RESULTS**

**Light and temperature measurements**

Although we succeeded in creating a mangrove high light treatment (571 ± 43, 333.4–952.2 μmol·s⁻¹·m⁻², mean ± SE, range) that overlapped with the reef control (1341 ± 67, 869.1–1833 μmol·s⁻¹·m⁻²) and whose range was outside of the mangrove control treatment (193 ± 16, 101.3–322.7 μmol·s⁻¹·m⁻²), we could not further increase light in the mangroves, likely because of colored dissolved organic matter (CDOM) in the water and the trees circling the experimental plot that blocked indirect sunlight. Our reef low light treatment (276 ± 15, 109.9–468.5 μmol·s⁻¹·m⁻²) aligned well with the mangrove control, but also overlapped with the mangrove high light treatment. Both reef treatments had greater average temperatures and depths than mangrove treatments, but mangroves had a larger diel temperature range (28.1–33.0°C) and less variance in depth (Appendix S1: Table S2, Fig. S2).

**Coral condition and mortality**

Corals from the reef had significantly higher condition scores than corals sourced from mangroves across treatments (P < 0.001, t = 3.643, Chi-squared test; Fig. 3a, b). This trend was evident both across species and within the two species (C. natans and O. faveolata) sourced from both habitats. Reef-sourced C. natans and O. faveolata did better on the reef than those same species when sourced from mangrove habitat (Fig. 3a, b). Even though there was no significant interaction between source and light (P = 0.815, t = 0.271) on coral condition, there was an interaction between species and light (P = 0.018), where condition was negatively correlated with light for all coral species, except D. labyrinthiformis where it was positively correlated (Fig. 3c). When light was held at a mean level of 529 μmol·s⁻¹·m⁻² in the model, coral condition significantly differed between species in 10 of the 14 pairwise comparisons, with D. labyrinthiformis consistently showing worse condition than all other coral species. Mangrove-sourced O. faveolata had the highest condition in the mangrove control, then mangrove high light, reef low light, and finally reef control (the only treatment with O. faveolata death). C. natans and O. faveolata had the least visible bleaching and 100% survival, regardless of source, in the reef shade treatment. There was no effect of habitat (P = 0.786, t = −0.845) or depth (P = 0.695, t = 0.393), and no significant habitat by source interaction (P = 0.081, t = 1.710) on coral condition.

Across all treatments and coral species, only 25 coral fragments of the original 311 died during the experiment (5% placed on the reef and 12%
Fig. 3. (a) Raw data of coral condition scores from which we used ggpredict to obtain predicted probabilities to plot modeled data. (b) Modeled coral health data with the main effects of coral source ($P < 0.001$), habitat
placed in the mangroves). There was a significant interactive effect of the source of corals and light on mortality ($P = 0.005$, $F$ value = 7.997 Chi-square test) with corals sourced from the reef having lower levels of mortality under higher experimental light levels than corals sourced from the mangroves. Complete mortality experiment-wide differed among species ($P < 0.001$, $F$ value = 2.867) with *D. labyrinthiformis* having significantly greater levels of mortality ($P < 0.001$) compared with the other coral species. Mortality did not significantly differ among the other coral species (Appendix S1: Table S3). The habitat that corals were transplanted into also significantly affected mortality ($P = 0.026$, $F$ value = 2.548).

**Coral community surveys**

We recorded a total of 23 scleractinian coral species and two milleporid coral species (colonial hydrozoans) in our surveys: 22 scleractinian species were found in the mangrove habitats and 10 on the adjacent shallow reef, although only a subset of those species were found in the respective habitat at a given site. Both milleporid coral species were found in both habitat types (Appendix S1: Table S1). Nine of the scleractinian species were observed in both habitat types, whereas 13 were found exclusively in mangroves and one exclusively on reefs (Appendix S1: Table S1). Our reef sites had an average depth of 89 ± 2 cm (mean ± SE), and our mangrove canopy sites had an average depth of 68 ± 2 cm. Live coral had the highest average percent cover of all benthic groups across habitats and sites (32–36%), followed by dead coral (10–21%; Fig. 4a) with the exception of Cayo Ramirez reef which had 30% live coral and 37% dead coral cover (Table 1). There was no significant difference in live coral cover ($P = 0.923$, Chi-squared test) or dead coral cover ($P = 0.193$) between habitats. Although it was not possible to determine the cause of coral mortality in these surveys, it could have been due to bleaching events in 2005, 2010, and 2015, hypoxia events, or subsequent disease outbreaks (Neal et al. 2017). However, based on observations in the area of phase shifts to algae and increased land clearing activities, it is likely to be linked to land-based runoff and algal overgrowth. Observed elevated sea surface temperatures, increased nutrients, and overexploitation of herbivorous reef fishes in the area could all promote algal growth (Cramer et al. 2020).

There was no interactive effect of habitat × site on coral richness ($P = 0.482$, F test) or Shannon-Wiener ($P = 0.231$) or Simpson’s Diversity indices ($P = 0.107$). Coral species richness ($P < 0.001$, $t = −2.916$), Shannon-Wiener Diversity index ($P < 0.001$, $t = −3.735$), and Simpson’s Diversity index ($P < 0.001$, $t = −4.096$) were significantly higher in mangroves than in the reef habitat. There was a site effect, with coral species richness ($P = 0.009$), Shannon-Wiener Diversity index ($P = 0.012$), and Simpson Diversity index ($P = 0.019$) significantly lower at Cayo Ramirez than at the other two sites. Of the live coral observed in the surveys, the most abundant species in the reef community were *Millepora alcicornis* (22–57%) and *Porites furcata* (18–68%). In contrast, within the mangrove canopy *Siderastrea siderea* (15–51%), *Agaricia tenuifolia* (6–31%), and *Porites astreoides* (3–17%) were the most abundant species (Fig. 4b).

**DISCUSSION**

Given the high diversity of the corals observed in the mangrove habitat, the presence of several large colonies within the mangrove canopy, and the fact that the majority of the corals survived transplantation into the mangrove, it is reasonable to speculate that mangroves could serve as long-term coral refugia. We found that corals...
generally fared better when transplanted to lower light levels and that shade from the mangrove canopy had a positive effect on coral condition and survivorship by ameliorating stressful light conditions that limited coral success on shallow reefs. Therefore, we conclude that refuge from high light levels of the adjacent shallow reef is an advantage of the mangrove habitat. If mangroves are able to provide refuge from bleaching stress, they may also reduce coral disease incidence which has been shown to increase following a bleaching event (Miller et al. 2009). By providing a refuge for coral species not able to survive on the harsh shallow reef environment, we found mangroves host coral communities with higher species richness and diversity than the adjacent shallow reef with similar live coral cover. Our surveys detected 24 coral species within the mangrove habitat, a coral refuge community only surpassed by a study in the U.S. Virgin Islands that observed >30 coral species (Yates et al. 2014), although notably that record was prior to extensive hurricane damage (Rogers 2019). Bocas del Toro lies outside the hurricane belt, primarily receiving the associated rainfall (Lovelock et al. 2005), and thus, the mangrove...
forests and coral reefs are not subjected to the same stress as many other parts of the Caribbean. Since our surveys revealed twice as many coral species in the mangrove compared with the adjacent shallow reef, it is possible that the source of the mangrove corals could be larvae from deeper corals.

Our study is the first to quantitatively measure coral richness within the mangrove habitat compared with the adjacent shallow reef, setting a baseline for future studies. In our reciprocal transplant experiment, corals sourced from the reef had less bleaching and mortality than corals sourced from the mangrove canopy whether transplanted to reef or mangrove habitats, suggesting that corals from the reef are better able to acclimate to new environments. This finding is consistent with previous tests of refugia habitats that found the subset of corals species living on the reef to be physiologically adapted to high irradiance levels and the more diverse community of corals in dimly lit areas (e.g., mesophotic reefs) to be adapted to low light (Cohen and Dubinsky 2015). Although it is known that shading can protect corals from UV radiation (Coelho et al. 2017), light availability influences coral calcification and photosynthesis rates and lower light availability can increase some coral species susceptibility to ocean acidification (Suggett et al. 2013); so it was previously unclear whether shading by mangroves was beneficial or detrimental to corals in this system. Our study was the first to test bleaching thresholds of corals growing within the mangrove habitat compared with that on the shallow reef.

Corals living in low light environments have adaptations that may be shared by corals living in mangroves. Within mangroves, the majority of corals we observed had flattened tri-dimensional morphologies as described in mesophotic coral reef ecosystems (Dustan 1979, 1982, Kühlmann 1983, Kahng et al. 2010). This morphology is typically an adaptation to low light conditions as it reduces the ratio of tissue to projected area needing to be sustained by light (Stambler and Dubinsky 2005), reduces self-shading, and maximizes light captured by increasing light-harvesting pigments (Kahng et al. 2012, 2019). This growth form may also be a response to shallow water conditions within the mangrove (~0.5 m depth on average), as the coral colony grows laterally to avoid air exposure. Corals from low light habitats such as mesophotic reefs have also been shown to host different species of Symbiodiniaceae than those in high light environments (Iglesias-Prieto et al. 2004), and to have mono-layered zooxanthellae packaging to increase photosynthetic efficiency (Dustan 1982, Kahng et al. 2010, 2012). Whether corals in mangrove habitats have such adaptations is yet to be explored.

We propose that a reason why mangrove-sourced corals in our study did not fare as well as reef-sourced corals when transplanted onto the reef is related to the differences in their levels of mycosporine-like amino acids (MAAs). Reef corals are known to have greater concentrations of MAAs in response to the increased UV radiation as these compounds protect the host and their symbionts (Corredor et al. 2000). Furthermore, it has been demonstrated that MAA concentrations in corals decrease with increasing depth and decreasing UV levels (Corredor et al. 2000, Lesser 2000). We expect MAA concentrations to be lower in corals originating from the mangrove canopy than corals

### Table 1. Average ± SE richness, abundance (percent cover that was comprised of live or dead coral), and diversity (Shannon-Wiener and Simpson indices) of live coral from surveys within the mangrove canopy and on the adjacent reef at three sites and combined by habitat type in bold.

| Site                  | Richness | Live coral % cover | Dead coral % cover | Shannon diversity | Simpson diversity |
|-----------------------|----------|--------------------|--------------------|-------------------|-------------------|
| Cayo Ramirez Mangrove | 12       | 32 ± 0.75          | 10 ± 0.02          | 0.88 ± 0.11       | 0.50 ± 0.06       |
| Cayo Ramirez Reef     | 8        | 30 ± 0.92          | 37 ± 0.03          | 0.29 ± 0.09       | 0.17 ± 0.05       |
| Fuego Mangrove        | 17       | 35 ± 0.66          | 20 ± 0.03          | 1.03 ± 0.11       | 0.55 ± 0.05       |
| Fuego Reef            | 11       | 36 ± 0.67          | 21 ± 0.03          | 0.74 ± 0.10       | 0.41 ± 0.05       |
| Sunny Mangrove        | 11       | 35 ± 0.81          | 14 ± 0.03          | 1.00 ± 0.08       | 0.57 ± 0.03       |
| Sunny Reef            | 6        | 36 ± 0.87          | 17 ± 0.03          | 0.42 ± 0.10       | 0.26 ± 0.06       |
| Combined Mangrove     | 24       | 34 ± 0.01          | 14 ± 0.03          | 0.97 ± 0.06       | 0.54 ± 0.03       |
| Combined Reef         | 12       | 34 ± 0.02          | 25 ± 0.06          | 0.52 ± 0.06       | 0.30 ± 0.04       |
that originated on the reef, as the mangrove canopy attenuates light intensity while CDOM and suspended sediments in the water absorb light and UV (Maie et al. 2008). Without this additional UV protection, the mangrove corals could be at greater risk of UV damage and physiological shock when transplanted to the reef where they are exposed to high light and UV. This may indicate that long-term exposure to mangrove habitat reduces the stress tolerance of corals to reef conditions. Alternatively, corals sourced from the mangroves may need a more gradual transplant process. Cohen and Dubinsky (2015) found that when incrementally transplanting corals between shallow and deep reefs, with 10-d intervals between transplanting to the next shallower depth, coral bleaching and mortality from light stress was minimal. Mangrove-sourced corals in our study were transplanted across a similar magnitude light gradient from mangrove to reef but only provided with one intermediate habitat, the mangrove fringe, to acclimate to prior to the start of the experiment. The relatively poor condition of mangrove corals in the high light environment of the reef indicates that either a one-week acclimation period on the mangrove fringe was not sufficient for induced protective traits, an incremental acclimation with more stages would be necessary to decrease transplant stress, and/or traits underlying stress tolerances are fixed in populations of the respective habitats. Additionally, outside of *Siderastrea siderea*, the majority of coral species (abundance and diversity) in the mangroves were brooding species. The community structure of many Caribbean reefs have been shifting from a dominance of long-lived broadcast spawning species to brooding corals with shorter life spans and resilient life history strategies (Vermeij et al. 2011). Studies comparing broadcast spawning corals to brooding corals suggest that larvae produced by deeper water colonies may be more susceptible to UV radiation than those produced by colonies from shallow water (Gleason et al. 2006). Further, coral larval behaviorally avoid damaging UV radiation during planktonic dispersal and subsequent settlement (Gleason et al. 2006); therefore, coral larvae from deeper water may be selecting for the mangrove habitat rather than the shallow reef to reduce UV exposure.

The aforementioned mechanisms (e.g., alternate morphologies, changing zooxanthellae packaging, hosting different species of Symbiodiniaceae, differences in MAA levels) that allow corals to specialize in high light or low light settings could explain the variation in condition and mortality within and among species across light, habitat, and source revealed in our experiment, but were not quantified in this study. We tested for evidence of intraspecific variation in coral condition related to source habitat with *C. natans* and *O. faveolata*. Reef *O. faveolata* had less bleaching than mangrove *O. faveolata*, which could be related to the adaptations of corals on the shallow reef to extreme environmental conditions that increase coral resilience to variation in light conditions. Further, it has been shown that corals have a smaller physiological response when moved from high light to low light than vice versa, as observed in reciprocal transplantation of coral fragments between deep and shallow reef depths (Richier et al. 2008, Cohen and Dubinsky 2015). However, the only bleaching that did occur within reef-sourced *O. faveolata* was in the reef control treatment, suggesting that prior exposure to higher levels of irradiance does not necessarily pre-empt a stress response to subsequent exposure to higher light levels in *O. faveolata*. Our finding that *C. natans* and *O. faveolata*, regardless of coral source, had the least bleaching and no mortality in the reef low light treatment indicates that shallow reef high light conditions are challenging even for coral species that routinely live on the reef. When controlling for source and habitat, and modeling only light, the patterns of how different coral species perform in relation to light is clearer. Nearly all coral species declined in health with increasing light intensity. This supports the conclusions that the shallow reef represents a stressful environment and that most species of corals, with the rare exception, can take advantage of mangroves as an alternative habitat. The only coral that had improved condition with increasing light was *D. labyrinthiformis*, which notably was also the only coral never seen in the mangrove habitat in Panamá. However, *D. labyrinthiformis* is one of the most abundant mangrove corals in other parts of the Caribbean (Yates et al. 2014). In bleaching censuses of *D. labyrinthiformis* and *C. natans* colonies in the U.S. Virgin Islands, *C.
natans only bleached 2–5% where D. labyrinthiformis bleached 17–59% (Rogers and Herlan 2012) at the same sites over the same time frame. These data in combination with our own findings suggest that C. natans is more of a generalist species, resistant to variation in environmental factors, compared with D. labyrinthiformis, which is more sensitive to fluctuations and extremes in temperature and light (Rogers and Herlan 2012). Differences in environmental conditions of these sites could explain the regional variation in D. labyrinthiformis abundance within mangroves of the Caribbean. Although both D. labyrinthiformis and C. natans are broadcast spawning corals, the timing of gamete release by D. labyrinthiformis differs among locations throughout the Caribbean with one versus multiple spawning events per year (Chamberland et al. 2017). These differences in reproductive timing are not related to latitude nor sea temperature, and the cause of spatial differences is suspected to be linked to other environmental cues (e.g., photoperiod, monthly rainfall, internal rhythms inherited from ancestral populations; Chamberland et al. 2017). It should be noted that colony identity may have contributed to differences we observed since replicates for a given species were sourced from the same colony. This study found that some coral species are better able to survive in the mangroves than others and sets the foundation for future studies to examine why, which should expand to exploring genotypic variation in the responses that we observed.

Shading has been proposed as a mechanism by which mangroves serve as refugia for corals by ameliorating stresses associated with shallow reef environments such as solar radiation, which alone or in combination with temperature, can induce bleaching in corals (Siebeck 1988, Gleason and Wellington 1993, Lesser and Farrell 2004). Reducing irradiance during periods of thermal stress can prevent bleaching (Coelho et al. 2017), and corals found growing in mangroves with >70% attenuation of incident PAR were able to thrive in higher temperatures than corals in nearby reef habitat (Yates et al. 2014). We found that reduction in solar radiation minimized the impact of stress-induced bleaching from transplantation into a new environment. Since temperature and light values were highly correlated, we could not separate the effects of each in this study. However, mean PAR readings were seven times greater in the reef control than in the mangrove control even with reef plots being twice as deep as mangrove plots, whereas temperature varied little between treatments, with a maximum temperature in the mangrove high light treatment of 33°C compared with 32°C for all other treatments, and all mean and minimum temperatures of the various treatments falling within the error range of the data loggers (±0.53°C; Appendix S1: Table S2). The temperature difference between mangrove canopy treatments (high light, low light) may be a product of minimal water circulation and shallow depths of the mangrove habitat that rapidly warms the water without the shade provided by the mangrove canopy. We acknowledge that additional abiotic factors will vary between the mangrove and reef; however, a spot check of salinity and turbidity of these habitats at our experiment site showed little difference in average values. We measured salinity in the mangrove and shallow reef habitats as 33.67 ± 0.01 ppm mean ± SE and 33.83 ± 0.01 ppm, respectively. Turbidity was 0.598 ± 0.026 FNU and 0.572 ± 0.007 FNU in the mangrove and shallow reef habitats, respectively. Further research is needed to explore additional abiotic factors and the influence they have on the corals within these habitats. This is especially important since the environmental conditions that may preclude coral settlement and growth on the reef may be different (average, minimum, maximum) within the mangrove habitat and are potentially species specific. As this study used coral fragments, it did not test whether mangroves can serve as a source population to recolonize disturbed areas. In order to address this, recruitment rates and survival of propagules would need to be quantified; however, the response of coral fragments following transplantation can be used to determine whether mangroves could be used in coral restoration efforts.

The importance of mangroves as refugia for corals is likely to increase as ocean warming makes coral bleaching events more frequent and severe. As ocean conditions (e.g., temperature, light, pH, and O2) change and the shallow reef environment degrades, alternative habitats may become relatively more beneficial to corals (Yates et al. 2014). For example, some have suggested
that deep reefs, such as mesophotic reefs, may serve as refugia for shallow reef corals as they experience less stress (Holstein et al. 2015, Semmler et al. 2017, Lesser et al. 2018), although others have questioned the generality of their effectiveness (Bongaerts et al. 2010, Smith et al. 2016, Rocha et al. 2018). Some regions, including our study area of Bocas del Toro, Panamá, do not have mesophotic reefs (Guzmán et al. 2005), making alternative refugia all the more important. Although both coral reefs and mangroves are threatened by climate change, the greatest threat to mangrove survival is local anthropogenic stressors (e.g., land conversion for aquaculture, palm oil plantations, coastal development, and pollution) and pending rates of deforestation, mangroves are predicted to survive into the foreseeable future even with global temperatures, atmospheric CO₂ concentrations, and sea levels continuing to rise (Alongi 2015, Friess et al. 2019). At a global scale, hurricanes and associated extreme weather events are predicted to increase with climate change and the high energy winds, destructive waves, and storm surges can cause severe damage to mangrove habitats (Walker et al. 2019). However, under natural conditions, mangroves are resilient and storm damage is rarely persistent. It is when anthropogenic stressors degrade the mangrove ecosystem and alter flow regimes that mangroves are unable to recover (Walker et al. 2019). If mangroves can be protected from human destruction, they may serve as refugia for corals under climate change and a global strategy for coral reef persistence. Although the field of overlapping mangrove-coral systems is in its infancy, studies are showing that when these foundation species co-occur, they alter ecological functioning. Mangroves with corals had greater fish species richness compared with mangroves without corals; however, adding artificial corals to mangroves only increased fish abundance (Wright 2019). There is still much to understand about this ecosystem and how it functions, but at least in the Caribbean it has been found to be beneficial to corals. We suggest that the shading by mangroves buffers corals and that impact is not limited to this region, so there should be a global effort to protect mangroves, especially in locations where mangroves and corals co-occur, and further explore the ecological functioning of these systems.

**Significance**

Our study revealed that mangroves provide habitat for a diverse assemblage of coral species and that transplanted corals generally fared better in lower light levels, suggesting that mangroves can serve as a refuge from the light stress associated with shallow reef environments. Additionally, increased light levels were more harmful to shade-acclimated corals; thus removal of mangroves or their canopy from mangrove-coral systems could induce coral bleaching and mortality. Positive interactions between mangroves and corals where they co-occur could play an increasingly important role as solar irradiance and thermal stress continue to negatively affect shallow reefs with climate change. This research highlights the importance of habitats with overlapping foundation species such as mangrove-coral systems, which currently do not have special protection status and should be prioritized in conservation efforts.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3413/full