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Local human impacts decouple natural biophysical relationships on Pacific coral reefs

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Abstract: Human impacts can homogenize and simplify ecosystems, favoring communities that are no longer naturally coupled with (or reflective of) the background environmental regimes in which they are found. Such a process of biophysical decoupling has been explored little in the marine environment due to a lack of replication across the intact-to-degraded ecosystem spectrum. Coral reefs lacking local human impacts provide critical baseline scenarios in which to explore natural biophysical relationships, and provide a template against which to test for their human-induced decoupling. Using 39 Pacific islands, 24 unpopulated (relatively free from local human impacts) and 15 populated (with local human impacts present), spanning 45° of latitude and 65° of longitude, we ask, what are "natural" biophysical relationships on coral reefs and do we see evidence for their human-induced decoupling? Estimates of the percent cover of benthic groups were related to multiple physical environmental drivers (sea surface temperature, irradiance, chlorophyll-*a*, and wave energy) using mixed-effects models and island mean condition as the unit of replication. Models across unpopulated islands had high explanatory power, identifying key physical environmental drivers of variations in benthic cover in the absence of local human impacts. These same models performed poorly and lost explanatory power when fitted anew to populated (human impacted) islands; biophysical decoupling was clearly evident. Furthermore, key biophysical relationships at populated islands (i.e. those relationships driving benthic variation across space in conjunction with chronic human impact) bore little resemblance to the baseline scenarios identified from unpopulated islands. Our results highlight the ability of local human impacts to decouple biophysical relationships in the marine environment and fundamentally restructure the natural rules of nature.

Key words: biophysical decoupling; coral reef benthic regimes; crustose coralline algae; hard coral; human impacts; human-environment interactions; macroalgae; mixed-effects models; natural variation; physical drivers

Introduction

Long-term environmental regimes, interspersed with anomalous disturbance events, play a crucial role in determining both the rate and path of ecological succession (Odum 1969, Connell and Slatyer 1977, Sousa 1984). When disturbances are rare, competitive exclusion results in mature climax communities and the system can approach relative stability (Pianka 1970, Margalef 1975, Stearns 1977, Hughes and Connell 1999). In contrast, when disturbance events are frequent or the system experiences continually harsh environmental conditions, the abundance of stress-tolerant species with weedy life history strategies can increase, leading to seemingly stochastic fluctuations of community structure (Stearns 1977, Sousa 1984, Hughes and Connell 1999, Reznick et al. 2002). Across gradients in environmental regimes, therefore, biological communities often change in discernable (and predictable) ways; adult survivorship and community composition are often strongly coupled with and reflective of their surrounding physical environment (Margalef 1975, Stearns 1977, Sousa 1984).

Superimposed over these naturally coupled biophysical relationships are the effects of human activities. Humans can act to homogenize and simplify ecosystems (Odum 1969, Western 2001, Riegl et al. 2012), artificially favoring stress-tolerant species (Darling et al. 2013) and forcing the system into an earlier successional state (Schulte et al. 2007, Sandin and Sala 2012). Under chronic anthropogenic stress, the community becomes a product of human-induced change (Graham et al. 1963, Odum 1969, Möllmann et al. 2009) and is no longer naturally coupled with (or reflective of) the background environmental regime in which it is found (Curran et al. 2004, Folke et al. 2011); we term this process *biophysical decoupling*. For example, in the Borneo rainforest, human activities have shifted climax forest communities to expanses of early successional plant communities fragmented by low diversity monoculture (Curran et al. 2004). Under such human-induced change, wildfires associated with El Niño events, instead of being a key natural driver of regenerative processes and ecological succession in the forests, are actually detrimental to ecological succession. The natural biophysical relationships that once existed have become decoupled and novel feedbacks have established (Curran et al. 2004, Folke et al. 2011). Separating the independent and interacting relationships between naturally coupled biophysical relationships versus those established or modified by local human impacts, however, remains hard to test in many ecological systems. Human-induced change is so ubiquitous that unaltered communities, ones that provide replication at the intact end of an intact-to-degraded spectrum, often do not exist (Steffen et al. 2011). Testing for evidence of biophysical decoupling in ecological systems, therefore, poses some practical challenges.

Coral reefs provide an interesting case study in which to examine the effects of human-induced change to biophysical relationships in ecological communities as they provide example of some of the most human-degraded (Pandolfi et al. 2003, Mora 2008, Hughes et al. 2010) but also the most pristine (Sandin et al. 2008, Vroom et al. 2010, Williams et al. 2013) ecosystems on our planet. In particular, remote islands harboring coral reefs relatively free from local human impacts provide replication at the intact end of the spectrum, enabling biophysical relationships, and their potential for human-induced decoupling, to be investigated. The foundational benthic organisms that contribute to coral reef development and persistence are those that deposit calcium carbonate, particularly hard (scleractinian) corals and crustose coralline algae (CCA). The latter are critical for reef growth, acting to consolidate reef substrate (Littler and Littler 1984) and facilitate coral recruitment (Price 2010). When conditions are such to allow community succession, CCA provide a mechanism for ecological resilience following disturbance (Nyström et al. 2008), and the system may transition to a state where hard corals hold competitive superiority against algal turfs and larger macroalgae (Grigg 1983, Littler and Littler 1985, Barott et al. 2012). Macroalgae represent another community attractor on coral reefs that directly compete with corals and CCA for space. Both calcifying and fleshy forms exist, with the former more typical of functionally intact systems (Vroom and Braun 2010, Williams et al. 2013) and the latter characteristic of more degraded, human-impacted coral reef environments (Littler and Littler 1985, Hughes et al. 2010).

Here we use 39 Pacific coral reef islands and atolls (hereafter referred to as islands) in a macroecological setting to test the hypothesis that local human impacts are capable of decoupling natural biophysical relationships in the marine environment. These islands span 45° of latitude and 65° of longitude, crossing multiple gradients in physical environmental drivers (Gove et al. 2013) and human population density (Williams et al. 2011). We quantify changes in the percent cover of three major benthic groups (hard coral, crustose coralline algae, and macroalgae) to ask two questions: 1) Given the absence of local human populations (and thus direct local human impacts), under which set of physical environmental drivers do individual benthic groups predominate (i.e. what are “natural” biophysical relationships on coral reefs?), and 2) Do we see evidence for human-induced decoupling of these natural relationships?

Methods

Study regions

Benthic surveys were conducted as part of the Coral Reef Ecosystem Division (CRED) of the NOAA Pacific Island Fisheries Science Center’s (PIFSC) Pacific Reef Assessment and Monitoring Program (RAMP). The 39 islands are located within four major geopolitical regions: the Hawaiian Archipelago, the Mariana Archipelago, the Pacific Remote Island Areas (PRIAs), and the islands of American Samoa (Fig. 1). With the exception of the unpopulated PRIAs, some islands within each region harbor dense human populations and are directly impacted by human activities (e.g. fishing and coastal development), such as Oahu in the Hawaiian Islands, Guam in the Mariana Archipelago, and Tutuila in American Samoa. Conversely, islands that are unpopulated and far from human population centers are relatively free of local human impacts (Williams et al. 2011). In this study, we describe islands as either ‘unpopulated’ (relatively free of local human impacts) or ‘populated’ (local human impacts are present). In this manner, 24 islands were classified as unpopulated and 15 as populated.

Benthic community surveys

Inter-island variation in the percent cover of benthic groups was quantified using a towed-diver survey method, a spatially expansive method that is effective at characterizing benthic communities at a coarse taxonomic resolution (hard coral, crustose coralline algae, and macroalgae) (Kenyon et al. 2006). Although the towed divers also recorded percent cover of sand, rubble, and ‘other’, these categories were not investigated in detail here (raw data presented in Supplementary material Appendix 1, Fig. A1). For each island, all tows over the forereef habitat (depth range of 8 – 20 m) crossing consolidated hard (habitable) substrate were averaged to give an island mean percent cover of each benthic group. We used surveys carried out during the shortest interval of consecutive years that had the largest number of islands surveyed (2008 and 2009) to maximize sample size while minimizing temporal variation (*sensu* Mora 2008). A more detailed description of the towed-diver survey technique is given in Supplementary material Appendix 2 and details pertaining to the location, timing, and relative effort of surveys are given in Supplementary material Appendix 3, Table A1.

Predictor variables

We quantified four major physical environmental drivers known to structure coral reef benthic communities: sea surface temperature (SST), irradiance, wave energy, and chlorophyll-*a* (as a proxy for phytoplankton biomass) (Odum and Odum 1955, Glynn 1976, Done 1983, Brown 1997, Hoegh-Guldberg 1999). SST data were generated using Pathfinder v5.0, irradiance and chlorophyll-*a* using the Moderate Resolution Imaging Spectroradiometer (MODIS) and wave energy using the global, full spectral Wave Watch III wave model (see Appendix 2 for full details on how these data were generated). Each of the satellite-derived (SST, irradiance, chlorophyll-*a*) and modeled (wave energy) time series data sets were quality controlled and proportionally scaled to the size of each island in order to control for variable island sizes across our data set (*sensu* Gove et al. 2013). The following metrics were derived from the above time series data sets: long-term climatological mean and standard deviation and positive anomalous events, represented as both the frequency of positive anomalies (the annual average percentage of time above the maximum climatological value) and the magnitude of positive anomalies (the annual average magnitude of events above the maximum climatological value) (Gove et al. 2013). Only information up to the survey date for each individual island was included. Human population density estimates were obtained from Williams et al. (2011). A summary of these data, with their units and range across our study region, are provided in Supplementary material Appendix 3, Table A2.

Statistical modeling

We constructed a series of models to test our questions: 1) a best-fit model across unpopulated islands – to quantify "natural" biophysical relationships in the absence of local human impacts, 2) the unpopulated island best-fit model structure fitted anew to populated islands – to test whether biophysical relationships remained unaltered in the presence of local human impacts, 3) the unpopulated island best-fit model structure fitted anew to populated islands with variations in human population density forcibly included as a predictor – to assess for improved model performance, 4) a best-fit model across populated islands – to test whether novel biophysical relationships can emerge on coral reefs under the influence of local human impact, and 5) a best-fit model across all 39 islands – to quantify biophysical relationships when no *a priori* groups across the islands were defined.

To build each of the models we used generalized additive mixed-effects models (GAMM) (Wood 2012). We incorporated a random factor (island groups) to account for possible spatial autocorrelation between islands. Groupings were identified using hierarchical clustering based on pairwise Euclidean distances between each of our 39 islands and an inflection point in the intra-island group variance identified (n = 12 groups total, see Supplementary material Appendix 2 for more details on these methods). GAMMs were fitted using the *gamm4* and *lme4* packages for R. Predictor variables were investigated for co-linearity (with a threshold correlation for inclusion set at 0.75) and normalized to account for the large variation in their numerical values (see Appendix 3, Supplementary Tables A2 and A3 for the list of final predictor variables included, their ranges, and their co-lineation values). Non-linear smoothness was determined using penalized cubic regression splines, with the number of knots spread evenly throughout each covariate value and limited to four to reduce overfitting. We coded a convenience wrapper R function (*all.subsets.gamm*) to fit each GAMM to all possible combinations of the predictors to avoid stepwise selection procedures (see Appendix 4 for the *all.subsets.gamm* R code). Candidate models were subsequently ranked based on AICc relative-importance weights (w_i), with the most plausible model having the highest weight (Wagenmakers and Farrell 2004). We report all models with >15 % of the model-based support from the w_i results (MacNeil et al. 2009), or the top three where this resulted in a single model to highlight the rapid drop in w_i. To assess the stability of the best-fit models, we sequentially deleted single data points from the original response variable data set (delete-one jackknife) and re-calculated the GAMM. We then calculated the percentage of times this resulted in the same model structure. Finally, we calculated a measure of predictor variable relative importance within each candidate model by calculating the sum of AICc model weights for each predictor (i.e. the sum of model weights across all models containing each predictor). A more detailed outline of our statistical modeling methods is given in Supplementary material Appendix 2.

Results

Spatial variation in benthic cover

Across our study system, mean percent cover of hard coral equaled 18.8 % (upper CI =15.7, lower CI = 22.1), crustose coralline algae 12.5 % (9.6, 15.8), and macroalgae 15.0 % (12.1, 18.1), but there was considerable variation across a variety of hierarchical scales (Fig. 2). In summary, hard coral cover was higher at unpopulated islands (22.5 %) than at populated ones (12.9 %) (see Fig. 2 for associated CIs). Across regions, hard coral cover was highest in the Pacific Remote Island Areas (PRIAs) (30.7 %) and lowest in the Hawaiian Archipelago (13.4 %). Within any single region harboring both unpopulated and populated islands, only within the Mariana Archipelago was hard coral cover higher at unpopulated islands (20.1 %) than at populated ones (10.6 %) (Fig. 2).

The overall mean percent cover of crustose coralline algae (CCA) did not differ with island status (unpopulated *versus* populated islands) (Fig. 2). Across regions, CCA cover was highest in American Samoa (31.2 %) and the PRIAs (16.2 %) and lowest in the Hawaiian (9.5 %) and Mariana Archipelago (6.5 %) (see Fig. 2 for associated CIs). Within any single region harboring both unpopulated and populated islands, CCA cover did not differ with island status. Similarly, the overall mean percent cover of macroalgae did not differ with island status or across regions (Fig. 2); however, macroalgae cover was higher at unpopulated (23.4 %) than populated (10.8 %) islands within the Hawaiian Archipelago and higher at populated (25.5 %) than unpopulated (8.6 %) islands within the Mariana Archipelago. In summary, the complex variation in benthic cover across regions and island status (unpopulated *versus* populated islands) provided motivation for an island-level model-fitting approach.

Biophysical relationships across Pacific coral reefs

Hard coral: Across unpopulated islands, mean sea surface temperature (SST), the magnitude of wave anomalies, and mean chlorophyll-*a* formed the best-fit model, explaining 72.3 % of the variation in hard coral cover (Table 1). Hard coral cover was higher at unpopulated islands experiencing a higher mean SST (> 28°C), wave anomaly events of a lower magnitude (< 30 kW m^{-1} above the maximum climatological value), and higher levels of mean chlorophyll-*a* (> 0.15 mg m^{-3}) (Fig. 3a). Within our confidence set of models, hard coral cover was also higher at unpopulated islands where mean wave energy was lower (< 25 kW m^{-1}) and where wave anomalies were rare (< 2 % of the time); however, these predictors had low relative importance scores (Table 1, Supplementary material Appendix 1, Fig. A2).

The unpopulated island best-fit model structure performed poorly when fitted anew to populated islands, explaining only 14.7 % of the variation in hard coral cover (Table 1); $p > 0.05$ for all the smooth terms (Fig. 3b). The addition of human population density as a predictor across populated islands did not improve model performance (Table 1) and no significant relationship was seen with hard coral cover (Fig. 3c). The populated islands best-fit model identified mean irradiance as the strongest predictor, explaining 25.7 % of the variation in hard coral cover (Table 1). Hard coral cover was generally higher at populated islands experiencing a lower mean irradiance (< 42 E m^{-2} d^{-1}); above this value the relationship appeared to level off but was associated with increased error (Fig. 3d). This single model had strong relative plausibility, as shown by the high Akaike weight (Table 1). The best-fit model for hard coral cover across all 39 of our study islands, with no *a priori* grouping of the data, performed more poorly than each of the unpopulated island and populated island models (Supplementary material Appendix 3, Table A4).

Crustose coralline algae (CCA): Across unpopulated islands, the frequency and magnitude of chlorophyll-*a* anomalies formed the best-fit model, explaining 80.2 % of the variation in CCA cover (Table 1). CCA cover was higher at unpopulated islands with frequent chlorophyll-*a* anomalies (> 10 % of the time) of a high magnitude (> 0.02 mg m^{-3} above the maximum climatological value) (Fig. 4a). Within our confidence set of models, CCA cover was also higher at unpopulated islands experiencing higher mean wave energy (> 40 kW m^{-1}), but where wave anomaly events were of a low magnitude (< 20 kW m^{-1} above the maximum climatological value); however, these predictors had low overall relative importance scores (Supplementary material Appendix 1, Fig. A3).

The unpopulated island best-fit model structure performed poorly when fitted anew to populated islands, explaining only 11.7 % of the variation in CCA cover (Table 1). The relationships with the frequency and magnitude of chlorophyll-*a* anomalies decoupled ($p > 0.05$ for the smooth term) and reversed in direction, respectively (Fig. 4b). CCA cover was lower at populated islands experiencing chlorophyll-*a* anomalies of a high magnitude (> 0.015 mg m^{-3} above the maximum climatological value); however, this relationship was associated with increased error in the smooth term at very high magnitudes (Fig. 4b). The addition of human population density as a predictor improved model performance across populated islands and suggested an increase in CCA cover at lower population densities; however, the relationship was weak (Fig. 4c) and increased the overall variation explained by only 6.9 % (Table 1). The populated islands best-fit model identified the magnitude of irradiance anomalies as the strongest predictor, explaining 87.0 % of the variation in CCA cover (Table 1). CCA cover was higher at populated islands where irradiance anomalies were of a high magnitude (> 3.4 E m^{-2} d^{-1} above the maximum climatological value) (Fig. 4d), and this single model heavily dominated in terms of relative plausibility as shown by the high Akaike weight (Table 1). The best-fit model for CCA cover across all 39 of our study islands, with no *a priori* grouping of the data, performed more poorly than each of the unpopulated island and populated island models (Supplementary material Appendix 3, Table A4).

Macroalgae: Across unpopulated islands, the frequency of chlorophyll-*a* anomalies formed the best-fit model, explaining 61.2 % of the variation in macroalgae cover (Table 1). Macroalgae cover was higher at unpopulated islands experiencing lower frequencies of chlorophyll-*a* anomalies (< 1 % of the time) (Fig. 5a). Within our confidence set of models, relationships with mean SST and the frequency of wave anomalies also featured (Table 1), with macroalgae cover higher at unpopulated islands experiencing a lower mean SST (< 23.5 °C) and lower frequencies of wave anomalies (< 1 % of the time) (Supplementary material Appendix 1, Fig. A4).

The unpopulated island best-fit model structure performed poorly when fitted anew to populated islands, explaining only 18.1 % of the variation in macroalgae cover (Table 1). The overall negative effect of increasing chlorophyll-*a* anomaly frequencies on macroalgae cover still held at populated islands, but was associated with increased error in the relationship (Fig. 5b). Variations in human population density across populated islands had no significant effect on model performance (Table 1) and showed no significant relationship with macroalgae cover (Fig. 5c). The populated islands best-fit model for macroalgae identified mean wave energy as the strongest predictor, explaining 87.7 % of the variation in macroalgae cover (Table 1).

Macroalgae cover was lower at populated islands experiencing a higher mean wave energy (> 20 kW m^{-1}) (Fig. 5d), and this single model dominated in terms of relative plausibility as shown by the high Akaike weight (Table 1). The best-fit model for macroalgae cover across all 39 of our study islands, with no *a priori* grouping of the data, performed more poorly than each of the unpopulated island and populated island models (Supplementary material Appendix 3, Table A4).

Discussion

Using 39 coral reef islands across the Pacific, we show that local human impacts fundamentally alter natural biophysical relationships in the marine environment. Relationships across unpopulated islands (i.e. natural biophysical relationships in the absence of local human impacts) were easily discernable and had high explanatory power. Here variations in physical drivers were linked in a predictable manner to variations in the percent cover of each of the three benthic groups (hard coral, crustose coralline algae, and macroalgae). In contrast, these same model structures performed poorly when fitted anew to populated (human impacted) islands, with many of the biophysical relationships predominating at unpopulated islands becoming decoupled or altering in the direction of their relationship; we term this process *biophysical decoupling* (Fig. 6). To our knowledge, our study is among the first to take a macroecological approach to demonstrate a clear human-induced decoupling of natural biophysical relationships in the marine environment.

In the absence of local human impacts, the principal physical drivers of variations in benthic groups were largely consistent with natural history gleaned from decades of coral reef science. For example, hard coral cover was higher at unpopulated islands experiencing a higher mean sea surface temperature; where mean temperatures were lower, corals decreased in cover and competitive macroalgae increased in cover. Such latitudinal limits to coral reef development have been previously noted (Johannes et al. 1983, Lough and Barnes 2000) and are thought to reflect variations in energy influx into the system dictating community diversity and succession (Fraser and Currie 1996). Hard coral cover also declined under conditions of high wave energy, particularly anomalous, high-magnitude events. This is a common biophysical relationship on Pacific coral reefs (Dollar 1982, Grigg 1983, Page-Albins et al. 2012, Williams et al. 2013, Gove et al. *In Press*) and often results from colony dislodgement and abrasive damage (Madin and Connolly 2006) and the inability of coral larvae to settle under high hydrodynamic disturbance (Abelson and Denny 1997). In contrast, crustose coralline algae (CCA) increased in cover at unpopulated islands experiencing higher mean wave energy (i.e. higher levels of disturbance) as predicted by the relative dominance model proposed by Littler and Littler (1985). Similarly to hard corals, however, CCA cover was lower at unpopulated islands experiencing a higher frequency of large-magnitude wave anomalies. Although physically adapted to high wave energy environments (Sheppard 1980), CCA are still vulnerable to abrasion at very high levels of wave energy and can give way to earlier successional states, such as algal turfs (Williams et al. 2013, Gove et al. *In Press*). As well as increasing in cover in warmer waters, hard coral cover also increased under conditions of higher mean chlorophyll-*a* (indicative of more nutrient-rich waters). Under oligotrophic conditions, increased nutrient supply to corals may act to promote persistence and resilience following disturbance (Grottoli et al. 2006, Connolly et al. 2012). CCA also positively responded to increased chlorophyll-*a*, increasing in cover particularly where there were frequent anomalies of a large-magnitude. These paralleled relationships between hard coral and CCA with increases in chlorophyll-*a* likely reflect the positive effects CCA can have on hard coral cover (Price 2010) and the negative effects CCA can have on competitive macroalgae (Vermeij et al. 2011). In the absence of local human impacts, it would appear background increases in chlorophyll-*a* drive macroalgae cover down, likely reflecting a loss of competitive dominance with hard corals and CCA for space.

Across populated islands, all the natural biophysical relationships identified from unpopulated islands decoupled, lost explanatory power, or became fundamentally altered in the direction of their relationship (Fig. 6). Hard coral cover no longer showed a significant relationship with either mean temperature or mean chlorophyll-*a* and the relationship between CCA cover and the frequency and magnitude of chlorophyll-*a* anomalies decoupled and reversed, respectively. On occasion, novel biophysical relationships even appeared to develop. For example, hard coral cover across populated islands decreased as mean irradiance increased, perhaps reflecting a stress-reinforcing factor reducing the persistence of corals in an already chronically stressed system (Lesser and Farrell 2004). In contrast, CCA cover increased as the frequency of irradiance anomalies increased, particularly anomalies of a large magnitude. CCA possess a tremendous ability to photoacclimate (Bulleri 2006) and thus often thrive under well-lit conditions (Sheppard 1980, Williams et al. 2013). Incoming irradiance may therefore be a key physical driver allowing CCA to persist in more chronically stressed reef systems. Finally, across populated islands, the relationship between macroalgae cover and mean chlorophyll-*a* substantially weakened; macroalgae cover was instead primarily related to wave energy, with cover higher at populated islands experiencing a lower mean wave energy. Macroalgae, like corals, are vulnerable to dislodgement (Dethier et al. 1991, Engelen et al. 2005) and it therefore follows that increased wave energy can reduce their overall cover on coral reefs (Gove et al. *In Press*). Also, it is interesting to note that our findings do not follow a common expectation that the cover of macroalgae should be positively related to factors associated with human presence on coral reefs (Littler and Littler 1985, Hughes 1994, Mora 2008). Only within the Mariana Archipelago did this expectation hold true and the opposite trend was actually observed within the Hawaiian Archipelago. Across the Hawaiian Archipelago, macroalgae cover was 2.5 times higher across the unpopulated and highly protected Northwestern Hawaiian Islands than in the populated Main Hawaiian Islands. Such disparities have been previously noted within the Hawaiian Archipelago (Vermeij et al. 2010, Vroom and Braun 2010, Jouffray et al. In Press) and likely reflect the broad functional roles different types of macroalgae have on coral reefs (Vroom 2011, Williams et al. 2013).

Future work to further our understanding of biophysical decoupling

We hypothesize that the decoupling of natural biophysical relationships across populated (human impacted) islands reflects, in part, human-induced ecological homogenization (Riegl et al. 2012). In other words, while human impacts may not always result in wholesale changes to benthic cover (as was largely the case in our study), the dominant species within each group may shift as a result of human-induced selective pressure. For example, the relative dominance of fleshy *versus* calcified macroalgae often differs across gradients of human impact (Vroom et al. 2006, Vroom 2011) and coral communities are flexible and can reorganize in response to selective pressure, each species differing in their degree of stress-tolerance (Darling et al. 2013). Local human impacts may be artificially selecting for more stress-tolerant, weedy species within each benthic group whose abundances are dictated more by stochastic recruitment processes and less by adult survivorship across gradients in natural physical drivers (Margalef 1969, Pianka 1970, Reznick et al. 2002, Darling et al. 2013). The result is an overall decoupling of natural biophysical relationships within the system. To test this working hypothesis would require data across similar spatial scales but at a finer taxonomic resolution and likely reveal more intricate ways in which human impacts disrupt and decouple natural biophysical relationships on coral reefs. Furthermore, we require information pertaining to the types of human impacts occurring across our large spatial gradient. Our binary split of ‘unpopulated’ and ‘populated’ islands as a proxy for local human impacts, while necessary for the current analysis, is likely reducing model performance. For example, in a meta-analysis by Cinner et al. (2013), distance of the island to local markets was a better predictor of total reef fish biomass than variations in local human population density. Quantifying the types of human impacts and their severity across our gradient would likely improve future interpretation of the spatial patterns in benthic cover we observed. Also, our analysis did not examine for the effects of intra-island spatial gradients in physical drivers on biophysical relationships. Wave energy, for example, often varies around an island, leading to complex intra-island patterns of benthic cover (Williams et al. 2013, Gove et al. *In Press*). Human impacts to biophysical relationships may not, therefore, be uniform around entire islands and future work should focus on determining the range of spatial scales at which human-induced biophysical decoupling is evident. Finally, changes in reef fish biomass are often more sensitive to local human impacts than changes in benthic cover on coral reefs (McClanahan et al. 2011). Future work should therefore focus on whether a similar phenomenon of biophysical decoupling occurs within the reef fish community across similar spatial scales on coral reefs.

Conclusion

Using 39 Pacific coral reef islands, we show that considerable spatial variation exists in the cover of three benthic groups (hard coral, crustose coralline algae, and macroalgae), even in the absence of local human impacts, as a result of broad spatial gradients in key physical environmental drivers. We further show that local human impacts appear capable of disrupting and fundamentally altering these natural biophysical relationships, a process we term *biophysical decoupling*. At populated islands, chronic human impacts do not simply result in wholesale changes in benthic cover, instead they likely alter communities in such a way that they are no longer reflective of (or reactive to) the background physical regimes in which they reside. These findings demonstrate the ability of local human impacts to fundamentally disrupt the natural rules of nature in the marine environment.

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Supplementary Material

Appendix 1. Supplementary partial residual plots from the generalized additive mixed-effects models (GAMM).

Appendix 2. Supplementary methods for benthic community surveys, satellite-derived and modeled predictor variable data, and statistical modeling procedures.

Appendix 3. Supplementary tables, including location and timing of all benthic surveys, predictor variable codes and units, predictor variable correlation values, and summary outputs of GAMMs across all 39 islands.

Appendix 4. R code for our *all.subsets.gamm* convenience wrapper function.

Figure legends

Figure 1. Location of the 39 U.S.-affiliated coral reef islands surveyed within four geopolitical regions in the Pacific Ocean: Hawaiian Archipelago (Northwestern Hawaiian Islands and the Main Hawaiian Islands), Mariana Archipelago, the Pacific Remote Island Areas (PRIAs), and the islands of American Samoa. Islands are classified as unpopulated (filled circles) and populated (open circles). Island codes are defined in full in Appendix 3 (Table A1).

Figure 2. Island mean (+ 95 % confidence interval) percent cover of three benthic groups: hard coral (a), crustose coralline algae (b), and macroalgae (c) across 39 U.S.-affiliated coral reef islands spanning four geopolitical regions in the Pacific Ocean (left panels). Islands are classified as unpopulated (U, grey shading) or populated (P, no shading). Bootstrapped means and 95 % confidence intervals (generated using 10,000 random iterations of the data with replacement) are shown across a series of hierarchical levels (right panels): *geopolitical region*, *island status* (unpopulated *versus* populated islands) within each region, and *island status* across all 39 islands (ALL, far right). Samoa, American Samoa; PRIAs, Pacific Remote Island Areas.

Figure 3. Generalized additive mixed-effects models (GAMM) showing the influence of predictor variables on hard coral cover variation across unpopulated and populated islands in the

U.S. Pacific. a) best-fit model across unpopulated islands (*n* = 24), b) unpopulated island best-fit model structure fitted anew to populated islands (*n* = 15), c) unpopulated island best-fit model structure fitted anew to populated islands with the forced inclusion of variations in human population density as a predictor, and d) best-fit model across populated islands. Data points represent distribution of standardized partial residuals (SPR). The y-axes are on the scale of the linear predictor of the model, i.e. the units are link (response units) with the smooth terms centered to ensure model identifiability (sum to zero over the covariate values). The number center-top within each plot represents the relative importance of each predictor variable (sum of AICc model weights across all models containing each predictor). The deciles of the distribution of the predictors are indicated by tick marks along the bottom of the plots. Black lines represent model-fitted splines of the estimated smoothing functions bounded by 95 % Bayesian credible intervals (solid grey shading).

Figure 4. Generalized additive mixed-effects models (GAMM) showing the influence of predictor variables on crustose coralline algae cover variation across unpopulated and populated islands in the U.S. Pacific. See Fig. 3 legend for details.

Figure 5. Generalized additive mixed-effects models (GAMM) showing the influence of predictor variables on macroalgae cover variation across unpopulated and populated islands in the U.S. Pacific. See Fig. 3 legend for details.

Figure 6. *Biophysical decoupling* on Pacific coral reefs – the natural biophysical relationships predominating at unpopulated islands decouple (i.e. flat-line or dramatically weaken) or alter in the direction of their relationship at populated (human impacted) islands. The percentages indicate the overall spatial variation in benthic groups explained by the physical environmental

drivers: hard coral (top), crustose coralline algae (middle), and macroalgae (bottom). SPR, standardized partial residuals. Temp, mean sea-surface temperature; WAV_mag, mean magnitude of wave anomalies; Chl-*a*, mean chlorophyll-*a*; CAV, frequency of chlorophyll-*a* anomalies; CAV_mag, mean magnitude of chlorophyll-*a* anomalies. Imagery obtained from the University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).