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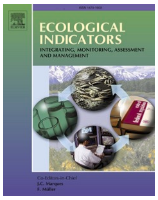

Examining variations in functional homogeneity in herbivorous coral reef fishes in Pacific Islands experiencing a range of human impacts

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ABSTRACT

Habitat loss from human impacts can lead to functional homogenization, whereby natural communities become less diverse. Herbivorous coral reef fishes display varying specialization and unique functional roles among closely related taxa, making homogenization relevant to ecosystem function. To explore whether the functional homogeneity of herbivore assemblages correlate with human impacts, we combined an index of diet specialization and a functional trait matrix with fish abundance data for > 3000 sites across the Pacific that encompass intact to degraded coral reefs. We determined the relative abundance of specialized species and the functional dissimilarity in an assemblage. Assemblage composition varied between islands, regions, and human population densities, with generalist species such as *Acanthurus nigrofuscus* dominating in highly populated locations. Spatial patterns and variability in the relationship between herbivorous reef fish assemblages and human impacts showed local and indirect effects. Despite broad variability, herbivore diversity decreased with human impacts among populated islands, consistent with the hypothesis that human impacts can lead to functional homogenization of coral reef fish communities.

1. Introduction

Humans fundamentally alter ecosystems, and these impacts are generally assessed through the analysis of habitat loss, diminished biomass, or changing community composition (Sala and Knowlton, 2006, De'ath et al., 2012, Alvarez-Filip et al., 2015). These factors can be used to evaluate community function following an acute or prolonged disturbance. Though traditional measures of ecosystem integrity (e.g., species richness, diversity, or biomass) are important, they may not capture the functional changes in an ecosystem in response to human stressors (Devictor and Robert, 2009). The multiplicity of pressures on natural systems requires new ways of examining functional changes in ecological communities. Several terrestrial studies have employed community specialization indices to examine biotic homogenization (i.e., the increasing abundance of generalists versus specialists) in the context of habitat degradation (Julliard et al., 2006, Devictor et al., 2008, Clavel et al., 2011). This has proven to be an effective way of examining homogenization on large spatial scales, but to our knowledge, a similar approach using community specialization indices has not yet been used in marine ecosystems.

Several recent studies have examined biotic homogenization in reef fishes, however, using different approaches. Trait-based analyses demonstrated a greater similarity among communities following disturbance events and a prevalence of generalist taxa; functional redundancy, as measured by functional originality, declined as a result (Richardson et al., 2018). Unique trait combinations in coral reef fishes, as well as in other systems, are often supported by rare species, making them particularly vulnerable to anthropogenic stressors (Mouillot et al., 2013). Across the western Pacific, targeted taxa, such as parrotfishes, exhibit reduced phylogenetic diversity and functional diversity in areas with high human populations; reductions that far exceeded the comparable reductions in species richness indicate impacts that might be overlooked if richness were examined independently (D'Agata et al., 2014).

In this study, we adopted the assemblage specialization approach used in terrestrial studies, in conjunction with more common approaches including species diversity and functional dissimilarity, to examine biotic homogenization in herbivorous fish assemblages throughout the U.S.-Affiliated Pacific Islands. Herbivorous reef fishes have received increased attention in recent years because of their role in

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mediating competition between corals and algae (Hixon, 2015), and several studies have highlighted the complementarity that exists among these fishes (Brandl et al., 2015, Kelly et al., 2016, Nalley et al., 2021a). Though the term 'herbivore' can encompass a varied suite of taxa depending on the definition used, their importance in mediating increasingly prevalent shifts in benthic composition has been widely recognized (Tebbett et al., 2023). As the complexity of this broad functional group is better understood, their vulnerability to habitat degradation, sedimentation, and altered resource availability is increasingly apparent (Tebbett et al., 2017a,2017b, Tebbett et al., 2018; Tebbett et al., 2022). This study offers a unique perspective to assessing ecological indicators for impacted coral reef ecosystems. Metrics that are commonly used to assess the health of these ecosystems are combined with non-traditional approaches in order to assess both direct and indirect effects in these systems.

While some metrics of community health, such as species richness, may not vary following disturbance events, more nuanced contributors to resilience such as community composition and the distribution of individuals fulfilling certain functional roles may be altered (Bellwood et al., 2012, Goatley et al., 2016). Response diversity, whereby functionally redundant species have unique reactions to disturbance events, may be a necessary component of resilience (Nash et al., 2015). While certain characteristics, such as diet or size, are often used to represent function, the working definition of an ecological function has been evolving in recent years and in many ways reflects an organism's resource use (Nash et al., 2015, Brandl et al., 2016, Bellwood et al., 2019, McLean et al., 2019, Williams and Graham, 2019). Even among fish that are closely related, the functional roles filled by each species can vary quite dramatically (Nalley et al., 2021b,2021a). This can in turn have profound effects on their response to climate stress and habitat degradation. A generalist species that has the capacity to use a variety of resources or live in a degraded, less complex habitat may be less affected by stressors, such as sedimentation or bleaching events, than a more specialized species.

In the case of herbivorous reef fishes, certain species, such as *Acanthurus nigrofuscus*, stand out as more likely to thrive in a variety of conditions which can include degraded reefs because of its very broad diet (Nalley et al., 2021b). In contrast, *Ctenochaetus striatus* feeds on detritus, but the deposition of fine sediment on the reef, as can occur with excessive terrestrial runoff, actually inhibits its specialized ability to feed on this resource (Tebbett et al., 2017b). This species transports much of its ingested sediment off the reef into deeper water, so reduced consumption can in turn have negative consequences for sediment removal on reefs (Goatley and Bellwood, 2010, Krone et al., 2011). This feeding selectivity has also been documented in other species that feed on the epilithic algal matrix, such as *Scarus rivulatus*, despite the fact that the two species have distinct feeding strategies (Gordon et al., 2016).

To test for biotic homogenization in reef fish communities, we integrated a previously published index of diet diversity in herbivores (Nalley et al., 2021a) with abundance estimates based on visual surveys, to generate a measure of the relative abundance of diet specialists at a site. To understand the effects on functional homogenization in herbivores, this measure was then included as a response variable in a model with environmental and human drivers. Simpson's Diversity, an established metric, and functional dissimilarity, a more comprehensive metric, were also used as response variables in an additional set of models, using the same drivers. Our aim was to determine (1) the relationship between the functional homogenization of herbivore assemblages and a suite of human impacts, (2) how herbivore assemblage composition reflects these changes, and (3) which drivers have the greatest effect on herbivore assemblage specialization, diversity, and functional dissimilarity.

2. Methods

2.1. *Quantifying herbivore assemblage homogenization in response to human impacts*

The following three metrics were used in this analysis to test for functional homogenization in herbivore assemblages:

2.1.1. *Relative abundance of diet specialists in herbivore assemblages*

To create a site-level diet specialization index for the assemblage (akin to the Community Specialization Index in Devictor et al., 2008), a published species-level diet diversity index was used as a base (Nalley et al., 2021a). Diet diversity estimates were added for some species based on the known values of ecologically similar species for which diet data was available, which ensured that all islands had at least 80% of their total herbivore assemblage represented in the index (Fig. S1). A total of 79 herbivorous reef fish species were included from the Hawaiian Islands (Main Hawaiian Islands and the Papahānaumokuākea Marine National Monument), the Marianas Islands (Northern and Southern), the Pacific Remote Islands Marine National Monument (also known as the Pacific Remote Island Areas, PRIAs), and Samoa (Fig. 1). Data from ~ 4000 stationary point count fish surveys from 2010 to 2016 in U.S. islands and atolls in the western central Pacific were used to represent the relative species abundance of herbivores (Coral Reef Ecosystem Program, 2016, Heenan et al., 2017, Oksanen et al., 2017, R Core Team, 2020). If a site did not have any species with diet diversity values, then it was removed from the analysis (<2% of the sites). A vector of diet specialization values for every species was multiplied by the species' relative abundance at each site and summed to get an overall index of diet diversity for that site. Higher values indicate a greater proportion of species with diverse diets, so the inverse was used to indicate higher specialization. The relative abundances of specific functional groups and species, such as the established generalist *Acanthurus nigrofuscus*, were also examined independently as response variables to investigate how certain taxa may serve as indicator species (Nalley et al., 2021b).

The relative abundance of diet specialists, determined as described above, was used to examine homogenization through the lens of diet exclusively. Diet is a foundational component of an animal's ecosystem function, so diet diversity offers great insight into the degree of specialization. This metric can then be used to test the hypothesis that sites experiencing greater human impacts will have fewer diet specialists. Nonparametric permutation tests using 10,000 permutations in the package *rcompanion* in R were used to compare the relative abundance of diet specialists between regions (Mangiafico, 2016).

2.1.2. *Species diversity of herbivore assemblages*

The species diversity of herbivores present in an assemblage was also used as a more standard metric of functional dissimilarity, and this enabled us to test the hypothesis that human impacts can lead to functional homogenization of coral reef fish communities. The diversity of herbivores present, as measured by the Simpson's Diversity Index using the *Vegan* package in R, was determined for each site, which allowed for direct comparisons to site and island level measures of human impacts, such as human population or the benthic composition (Oksanen et al., 2017).

2.1.3. *Functional dissimilarity of herbivore assemblages*

The functional dissimilarity of herbivores present in an assemblage was used as the most comprehensive metric of homogenization, where less dissimilarity (i.e., greater similarity) among herbivores indicated greater homogenization. A matrix of Community Cluster Traits (Streit and Bellwood, 2023) for each species was generated using published data and FishBase (Froese and Pauly, 2017, Nalley et al., 2021a). The traits included were the species' diet diversity (as described above), feeding type, territoriality, schooling behavior, and size class. A full

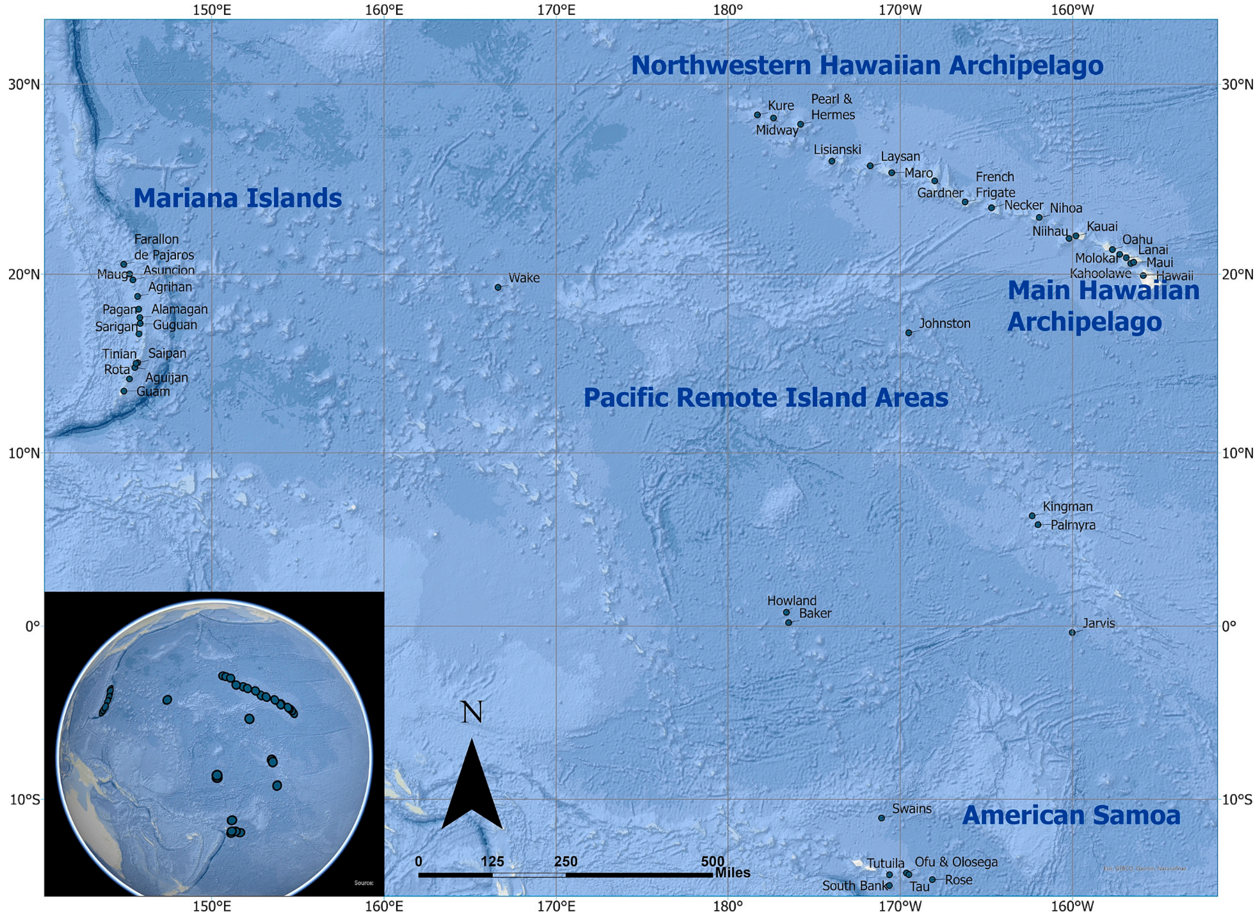

Fig. 1. Map of Pacific Islands included in this study grouped by region.

description of the traits used is provided in the Supplemental Materials (Text S1). These were combined with the species abundance data to generate a value of Rao's Quadratic Entropy at each site, which uses the Gower's Dissimilarity Index as a measure of dissimilarity combined with species' proportional abundance data to determine the assemblage functional dissimilarity, using the *SYNCSA* package in R (Rao, 1982, Ricotta and Szeidl, 2009; Debastiani, 2012). Data and code are available on GitHub (enalley/FunctionalHomogenization).

2.1.4. Species composition of herbivore assemblages

In addition to the metrics to quantify functional homogenization in herbivore assemblages (i.e., the relative abundance of diet specialists, herbivore species diversity, and functional dissimilarity), the species composition of these assemblages was also examined (Figs. S2 & S3a-S3f). Assemblage composition dissimilarity was assessed using a nonmetric multidimensional scaling (MDS) analysis with a Bray-Curtis dissimilarity index using the *Vegan* package in R (Oksanen et al., 2017). *PERMANOVA* was used to examine the distance among centroids associated with unpopulated (no humans), minimal inhabitants (less than 100 humans), populated (more than 100 and less than 10,000 humans), and densely populated (more than 10,000 humans) sites. *SIMPER* analysis was used to examine influential species, and indicator species analysis (*indicspecies* package in R) was used to further examine species that were associated with different types of sites.

Environmental and ecological variables that could be significant in determining differences in herbivore assemblage composition between regions were also examined using the *envfit* function in the *Vegan* package in R, which projects points onto vectors to show maximum correlation with dependent variables explained by ordination scores. These included depth, sea surface temperature, mean wave energy, irradiance, structural complexity, island forereef area, human population, total fish biomass, herbivore abundance, herbivore diversity, hard coral cover, macroalgae cover, EAM cover, proportion of herbivores in total fish biomass, and human impact score. A detailed explanation of these variables is provided in the (Supplemental Materials Table S1). The relative abundance of known generalist *Acanthurus nigrofuscus* was examined independently as a response variable to investigate how certain taxa may serve as indicator species for habitat degradation and functional homogenization (Nalley et al., 2021b,2021a).

2.1.5. Measures of human impacts

The National Center for Ecological Analysis and Synthesis' (NCEAS) Human Impact Score, developed using multiple anthropogenically derived stressors that affect the condition of marine ecosystems, was used as one composite measure of human impacts (Halpern et al., 2015, McDole Somera et al., 2016). Scores incorporated the following measures: fishing (artisanal, destructive demersal, non-destructive demersal, pelagic high-bycatch, and pelagic low-bycatch); pollution (inorganic, organic, and nutrients); invasive species; ocean acidification; sea surface temperature and ultraviolet insolation anomalies; commercial activity; and human population pressure (McDole Somera et al., 2016). This value was available at the island scale for 38 islands. Data on human populations within 20 km were available at a site scale for 41 islands.

2.2. Assessing drivers of homogenization

Linear mixed-effects models were used to test the hypothesis that the presence of humans (measured by the Human Impact Score and human population) would be associated with increased functional homogenization (measured by relative abundance of diet specialists, species diversity, and functional dissimilarity) (Table S2). Linear mixed-effects models were fitted using the *lmer* function in the *lme4* package in R to test the relationship between herbivore abundances and the two measures, with region and island included as random effects to account for the nested spatial structure of the data (Bates et al., 2015). Model fit was assessed using residual plots, and goodness of fit was assessed using R-squared values.

Linear mixed-effects models were also used to test the hypothesis that human influences would outweigh inherent environmental differences between sites, using environmental covariates previously shown to be important drivers in coral reef fish assemblages (Bates et al., 2015). These covariates are described in detail in the (Supplemental Materials Table S1). In all mixed effects models, region and island were included as random effects to account for the nested spatial structure of the data. All predictors were scaled and centered on a normal scale to facilitate direct comparison of their effect sizes. Variables were examined for collinearity using Pearson's correlation, and variables with $r > 0.70$, which is considered representative of a strong correlation, were not included in the model together (Fig. S4).

To assess the differences in herbivore composition at sites that vary in their human population, a Bray-Curtis dissimilarity matrix was used with non-metric multidimensional scaling plots. The human population within a 20 km radius of a site was binned into groups designated as unpopulated, minimal inhabitants, populated, and densely populated, which were used to visualize differences between groups with colors and 95% CI ellipses. The correlation of clusters with environmental drivers, influential species, and site characteristics were examined using *envfit*.

3. Results

3.1. Quantifying herbivore assemblage homogenization

Herbivore assemblages differed between islands and between regions. Differences among islands were particularly evident in the Hawaiian Islands, comparing the populated Main Hawaiian Islands with the uninhabited and protected Papahānaumokuākea Marine National Monument (Northwestern Hawaiian Islands, PMNM) (Fig. 2). Permutation tests indicated significant differences in the herbivore assemblage diet specialization index between all regional pairs (all $P < 0.05$), except between the PRIAs and the Southern Marianas, with the highest mean herbivore assemblage diet specialization in the uninhabited PMNM (Fig. S5a). There were also significant differences between regions in herbivore diversity (Fig. S5b); all regions were significantly different from each other (all $P < 0.05$), except the PRIAs (mean +/- SD = 0.73 +/- 0.12), which were not significantly different from the PMNM (mean +/- SD = 0.72 +/- 0.18) or from Samoa (mean +/- SD = 0.75 +/- 0.11). Functional dissimilarity followed this same trend and was also lower in the Main Hawaiian Islands (mean +/- SD = 0.44 +/- 0.16, all $P < 0.05$), followed by the southern Marianas which include populated and developed Guam (mean +/- SD = 0.50 +/- 0.14, all $P < 0.05$) as compared to all other regions (Fig. S5c).

Herbivore assemblage composition also differed significantly between locations (PERMANOVA: $P = 0.02$; Fig. 3; Table S2a). The Hawaiian Islands, which have the largest gradient of human population within a 20 km radius (ranging from 0 to 723,248 people), exhibited clear differences in community composition (Fig. 2; other regions in Fig. S2). On islands like Oʻahu (the most populated) that are heavily impacted by humans through urbanization, residential development,

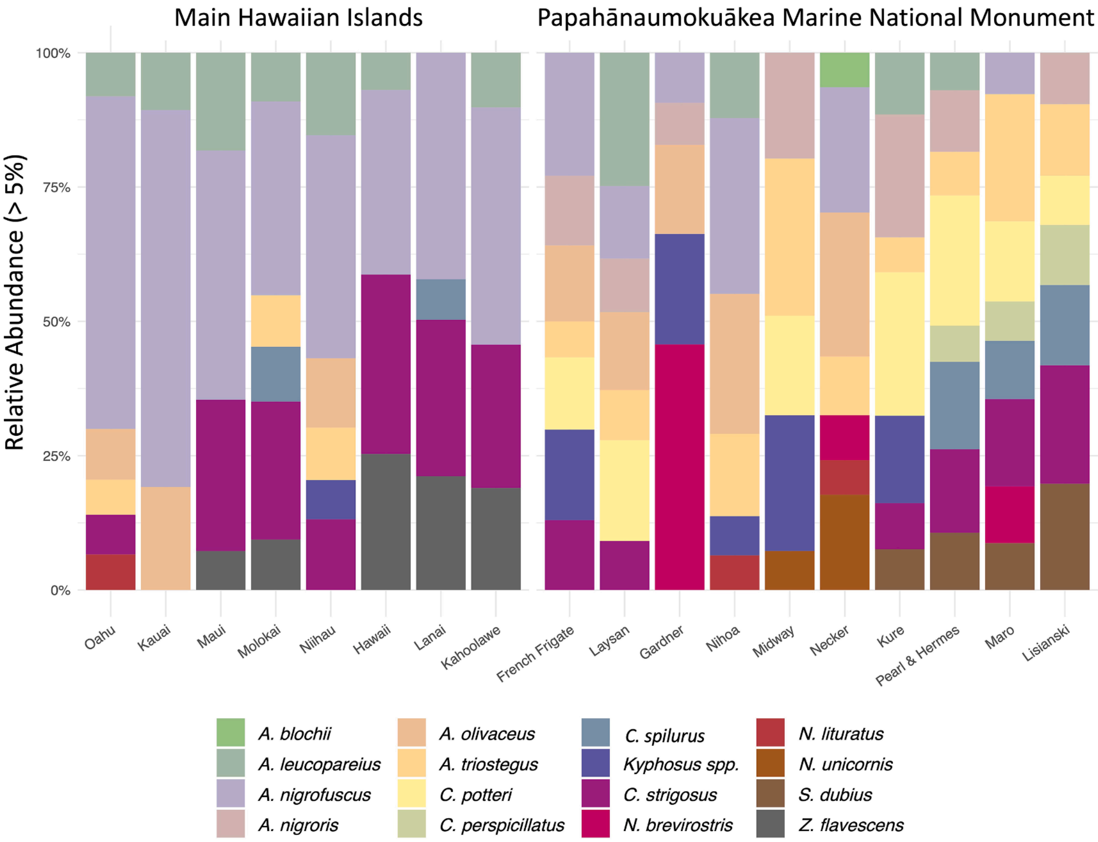

Fig. 2. Herbivore assemblage composition in the Hawaiian Islands with herbivore diversity increasing from left to right (i.e., most diverse assemblages as measured by Simpson's Diversity Index on the right). Only species that made up at least 5% of the relative abundance of herbivores present at an island were included.

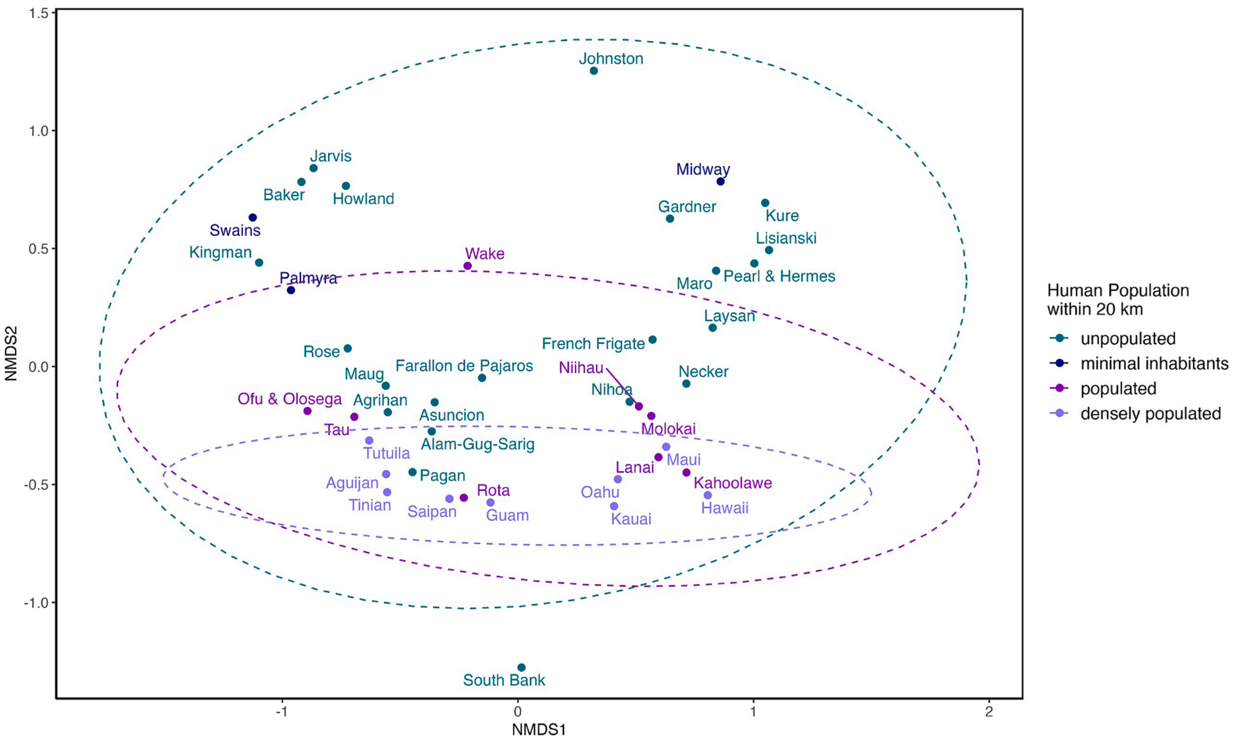

Fig. 3. Non-metric Multidimensional Scaling plot using Bray-Curtis dissimilarity between herbivore assemblages grouped by human population within 20 km. Minimally inhabited sites had less than 100 human residents within 20 km. Populated sites had more than 100 but less than 10,000 human inhabitants within 20 km, and densely populated sites had more than 10,000 human inhabitants within 20 km. Some islands, such as Aguijan, are uninhabited but are within 20 km of densely populated islands.

industrial agriculture, and militarization, generalist herbivores like *Acanthurus nigrofuscus* are more abundant than specialists. As a result, *A. nigrofuscus* was more prevalent in populated locations as compared to unpopulated ones (SIMPER: $P = 0.04$; Table S2b) and dominated assemblages in islands with greater habitat degradation like O'ahu, Kaua'i, Maui, and Guam (Figs. S3 & S6-S7). Conversely, *Naso annulatus, Ctenochaetus* spp., *Zebrasoma rostratum,* and *Scarus xanthopleura* were all associated with sites with minimal inhabitants (MULTIPATT: $P = 0.03$, 0.04, 0.03, and 0.04, respectively; Table S2c). The relative abundance of grazers decreased with the Human Impact Score (Linear Mixed-effects Model: $P < 0.0001$, Estimate = -0.13, R^2 marginal = 0.02, R^2 conditional = 0.12; Table S2d). In contrast to the overall abundance of grazers, when examined independently the abundance of the generalist *Acanthurus nigrofuscus* actually increased with human impacts (Linear Mixed-effects Model: $P < 0.0001$, Estimate = 0.29, R^2 marginal = 0.09, R^2 conditional = 0.23; Table S2e;Fig. S7).

3.2. *Assessing drivers of homogenization*

The species composition of herbivore assemblages varied by region (Fig. S3). The relative abundance of diet specialists, which increased with herbivore species diversity (Linear Mixed-Effects Model: $P < 0.001$, Estimate = 0.34, R^2 marginal = 0.11, R^2 conditional = 0.30; Table S2f), also varied by region (Fig. S5), but it did not have a significant relationship with the Human Impact Score (Linear Mixed-Effects Model: $P = 0.57$; Table S2g). When examined in isolation, it did have a positive relationship with the human population within 20 km (Linear Mixed-Effects Model: $P < 0.001$, Estimate = 0.47; R^2 marginal = 0.10, R^2 conditional = 0.38; Table S2h), but regional differences explained 21% of the variance in the model. This relationship is likely driven by low relative abundance of specialists as compared to the generalists *A. nigrofuscus* and *Centropyge shepardi* in the unpopulated Northern Marianas Islands (Fig. S5a), which is more aligned with that seen in the populated Main Hawaiian Islands than in the unpopulated Northwestern Hawaiian Islands.

When looking at human population as a measure of human impacts, it is critical to remember that human settlement on islands is not random and in many cases is determined by the site characteristics (e.g., reef area, high island, protected back reefs, abundant fish) that make them appropriate to support human needs. In fact, we see that forereef area was greater in populated and densely populated sites (envfit: $P = 0.001$; Table S2i), while wave action was greater in unpopulated or minimally populated sites (envfit: $P = 0.002$; Table S2i; Fig. S8). Further, the presence of humans can directly influence biophysical processes (Williams et al., 2015a). When comparing all islands (populated and not) across this entire spatial extent, there was no significant relationship between the Human Impact Score and herbivore diversity or functional dissimilarity (Linear Mixed-effects Models: $P = 0.11$ (Table S2j) and $P = 0.34$ (Table S2k), respectively), indicating that broad regional distinctions overwhelm individual effects within regions. Benthic complexity, hard coral cover, predator biomass, and depth all had significant positive relationships with herbivore diversity and functional dissimilarity (Linear Mixed-effects Model: all $P < 0.001$; Tables S2l-m).

When populated and unpopulated islands were separated, however, there were clear differences along the gradient of human impacts. Herbivore assemblages at unpopulated islands were distinct from those at densely populated or populated islands (Fig. 3, Figs. S8 and S9). Total fish biomass, hard coral cover, crustose coralline algae (CCA) cover, functional dissimilarity, and herbivore diversity all were higher in the unpopulated and minimally populated sites (envfit: all $P < 0.005$; Table S2h). *Scarus frenetus, S. tricolor*, and *Zebrasoma scopas*, which have been linked to high coral cover in other studies (Maire et al., 2018), all had significantly higher abundance in unpopulated and minimally populated sites (envfit: all $P \leq 0.005$; Table S2n). When only populated sites were examined, herbivore diversity decreased with human impacts (as measured by the Human Impact Score), (Linear Mixed-effects Model:

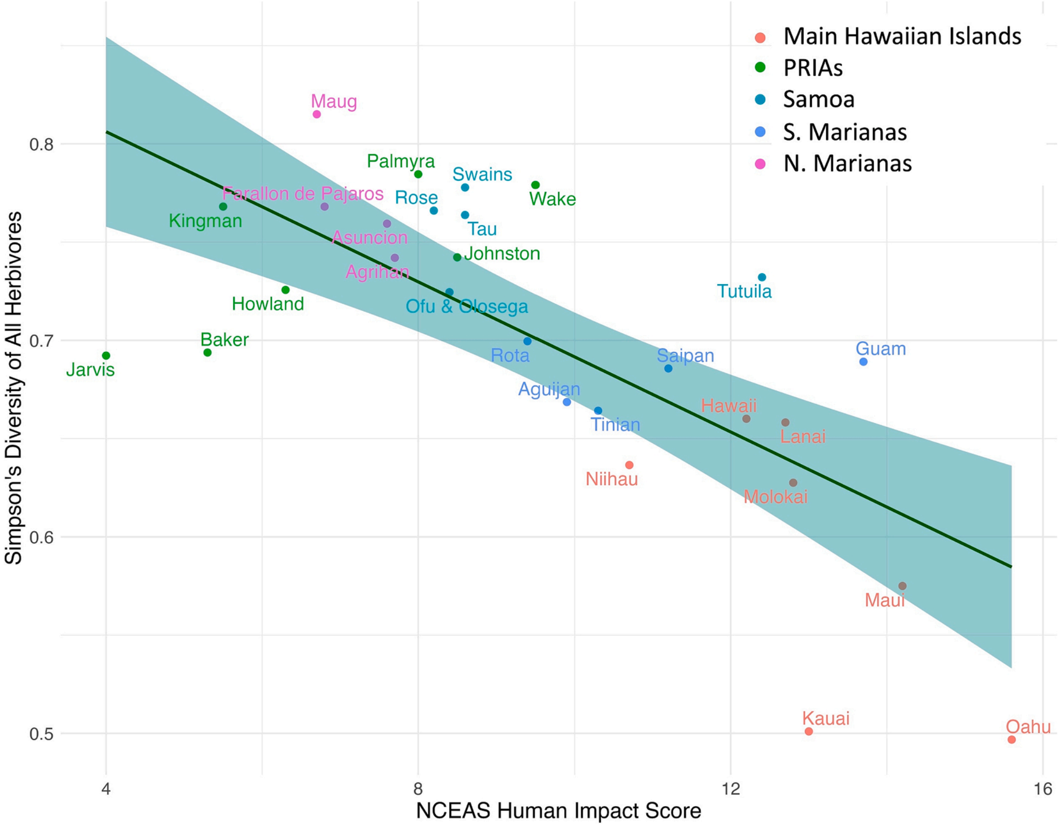

Fig. 4. Diversity of herbivores compared to NCEAS Human Impact Score. The shaded area shows a 95% confidence interval. Colors correspond to regions. NCEAS Human Impact Scores were not available for the Papahānaumokuākea Marine National Monument (Northwestern Hawaiian Islands).

$P = 0.01$, Estimate = -0.53, R^2 marginal = 0.31, R^2 conditional = 0.64; Table S2o; Fig. 4). The generalist species *Acanthurus nigrofuscus*, *A. leucopareius,* and *A. dussumieri* were all more abundant at populated and densely populated sites (envfit: all $P \leq 0.005$; Table S2n), whereas the more specialized *A. triostegus* was associated with unpopulated and minimally populated sites (envfit: $P = 0.001$; Table S2n).

4. Discussion

Coral reef ecosystems have been severely modified by human activities, threatening the long-term persistence of specialized organisms with specific habitat or diet requirements. This can result in functional homogenization and assemblages dominated by generalists that thrive in degraded habitats – a situation that has been well described in terrestrial (Devictor et al., 2008), freshwater (Rahel, 2000), and other marine assemblages (Magurran et al., 2015). This study examined the relationship between human stressors and functional homogenization in herbivorous reef fish assemblages throughout the Pacific. Our findings indicate greater diversity in sparsely populated locations within geographic locations. In light of the spatial variability and complexity of these systems, it is essential that these potential impacts on ecosystem function are considered alongside both the natural drivers of variation that exist in herbivorous fish community composition, as well as the effects of human activities, which can in some cases be mediated through the habitat. Much as there have been recent calls for researchers and managers to consider the varying adaptive capacity of corals in response to climate stressors (McClanahan et al., 2023), we must similarly use comprehensive measures to assess the resilience of reef fishes to human impacts.

Herbivore diversity decreased with increasing human impacts, which is indicative of biotic homogenization (Fig. 4) (Halpern et al., 2012, McDole et al., 2012), and less degraded reefs had a greater relative abundance of diet specialists. The significant positive relationship between the relative abundance of diet specialists and the diversity of herbivores present in an assemblage further suggests that biodiversity loss contributes to functional homogenization (Table S2). Examining the regionally similar Main Hawaiian Islands versus the Papahānaumokuākea Marine National Monument, herbivore assemblage diversity is far greater in the less impacted Monument sites (Fig. 2). The assemblages in the Main Hawaiian Islands are clearly dominated by known diet generalists, such as *A. leucopareius* and *A. nigrofuscus* (Nalley et al., 2021a). Though the breadth of biophysical and biogeographical factors present when all sites are included clouds this relationship and may overwhelm community composition trends at this scale, when these are controlled for by only including sites that are populated, functional homogeneity increases at more populated, impacted sites.

We also assessed shifting species composition in herbivore assemblages in sites that vary in human population. There were clear differences in the composition of herbivore assemblages between regions (Fig. S3) and between islands within regions (Fig. 2). For example, in the Main Hawaiian Islands, which are the most densely populated islands in this analysis, *Acanthurus nigrofuscus*, a known generalist, dominated more sites than any other species (Fig. S3a). In the virtually uninhabited Papahānaumokuākea Marine National Monument, which is the closest geographically, not a single island exhibited this trend (Fig. S3b). Guam, Saipan, and Rota in the populated Southern Marianas all had a much higher frequency of sites dominated by *A. nigrofuscus* than by any other species. Guam, which is the most developed island in this region, had a prevalence of *A. nigrofuscus* that was comparable to Oʻahu, the most heavily populated island in this analysis, but Guam also had several sites where more specialized detritivores (e.g., *Ctenochaetus striatus*) and parrotfishes were the dominant species (Fig. S3f), indicating some degree of variability even on very local scales.

Spatial differences can be further complicated by varied land use and management in each location. For example, highly populated locations may have greater diversity and specialization if there are protected areas where fishing and other direct, local stressors are restricted and regulations are enforced (Smith et al., 2014). Conversely, less densely populated islands may still be heavily influenced by land based human activities that were not explicitly accounted for in these models, such as industrial farming or intensely developed tourist areas (e.g., Kaua'i and Maui, in Fig. 4). There is also historic and current military infrastructure on many of the uninhabited or sparsely inhabited islands (e.g., Wake and Johnston) in the Pacific, but this type of use and the resultant changes to community composition can be difficult to characterize and quantify (Athens et al., 2007, Papahānaumokuākea Marine National Monument, 2011, Boyle et al., 2017). Further, some islands experience natural disturbance events that can result in habitat degradation and shifts in community composition. For example, Pagan in the Northern Marianas had high relative abundance of generalists but is also unpopulated due to recent volcanic activity in the 1980s, so while humans are a pervasive and impactful driver of habitat degradation globally, there are other naturally occurring sources of disturbance that can influence reef ecosystems and fish assemblages. The types of stress experienced by a reef ecosystem in the past influences its response to future stressors (González-Barrios et al., 2023), so the history of impacts at a site has important implications for its current state and resilience.

Spatial variation seen at an island and regional scale suggests local drivers influence functional dissimilarity, diversity, and specialization (Friedlander et al., 2018). On an ocean-wide scale human population density can be a predictor of reef fish biomass (Mora et al., 2011), but human populations are, in the absence of more specific data, only a proxy for more direct stressors such as fishing (Brewer et al., 2012). However, not all herbivores are targeted, and the effectiveness of fishing intensity as a predictor of declines in herbivore biomass varies by functional group and species (DeMartini et al., 2008, Williams et al., 2015b, Heenan et al., 2016). Herbivore biomass may also vary with the local environment (Helyer and Samhouri, 2017), so it is also important to account for spatial variation in environmental conditions in any analyses.

Degraded Pacific reefs are often covered by turf algae and sediment (Jouffray et al., 2014), and while many herbivores consume turf, degraded turf covered reefs do not necessarily offer greater resources (Letourneur et al., 2017). Similarly, reefs with high rates of terrigenous sedimentation are not preferred by species that feed on detritus and the epilithic algal matrix, such as detritivores, scrapers, and excavators (Tebbett et al., 2017a), and different types of turf algae may accumulate sediment in ways that reduce palatability to herbivores, potentially altering herbivore abundance and assemblage composition (Goatley et al., 2016).

On reefs that have become overgrown with macroalgae the likelihood of algal consumption may vary widely depending on physical and chemical defenses. Though large browsers consume macroalgae (Hoey and Bellwood, 2009, Lefévre et al., 2011, Loffler et al., 2015) and naturally occurring macroalgae meadows can provide important habitat and refuge for numerous taxa particularly in the juvenile life stage (Fulton et al., 2020), habitats that have shifted to macroalgae dominance because of human stressors do not typically host high herbivore diversity or abundance (McClanahan et al., 1999, Hoey and Bellwood, 2011, Chong-Seng et al., 2012, Bauman et al., 2017). As a summary metric, the percent cover of macroalgae can also belie the diversity of responses among macroalgae to human impacts, as different taxa have unique responses to stressors and changing conditions (Cannon et al., 2023). Different functional groups and species within functional groups respond uniquely to anthropogenic impacts (Figs. S6-S7) (Heenan et al., 2016, Nalley et al., 2021a), so response diversity may thus be an important additional metric of resilience (Elmqvist et al., 2003, Bellwood et al., 2019).

Some of the variables examined showed a different response when only populated islands were included, but decoupling between biophysical site characteristics and benthic cover in populated sites has been shown for many of these islands (Williams et al., 2015a). Likewise, the range of human stressors extends far beyond fishing pressure and is thus well represented in the composite Human Impact Score developed by NCEAS. Human impacts have negative effects on the abundance of predators and benthic cover in the regions examined (Ruppert et al., 2017), and benthic characteristics (i.e., complexity and benthic cover) showed significant relationships with homogenization metrics, suggesting that they are robust predictors of herbivore assemblage specialization on coral reefs. Though the clear direct relationships between human impacts and herbivore specialization were not as pronounced as was originally expected, given that the relationship between functional homogeneity and human impacts holds both within archipelagos, and among all populated islands across the surveyed Pacific, these data provide support for the hypothesis that human impacts lead to the functional homogenization of coral reef fish communities. Thus, it is important to note that habitat and species richness are also linked to genetic diversity at the seascape scale, suggesting that these drivers have a profound influence not only on specialization but also on diversity at the most fundamental level (Selkoe et al., 2016).

5. Conclusions

Humans are undoubtedly altering coral reef habitats in what some have called a “flattening”, or the loss of live reef building corals and the structural complexity that they provide (Alvarez-Filip et al., 2009, Darling et al., 2017). Our study demonstrates that there is regional variability in the relationship between human population and the relative abundance of herbivores with specialized diets. Functional homogenization is also more visible in some regions, such as the Hawaiian Islands, which may be attributable to a greater range of human impacts within a single archipelago. Communities that are dominated by just a few generalist herbivores exist without the functions performed by specialized species, which can in turn exacerbate degradation via feedback loops (Munday, 2004, Worm et al., 2006). Other local processes, such as land use, runoff, pollution, and management effectiveness, also affect the composition of coral reef communities and are important for consideration in future work. As coral reefs continue to deteriorate at an exceptional rate (Hughes et al., 2017), we must take stock of how these stressors may be interrelated and cascading, and this analysis underscores the importance of maintaining biomass, diversity, and intact benthic structure for the persistence of specialized organisms.

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CRediT authorship contribution statement

Eileen M. Nalley: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Adel Heenan:** Conceptualization, Data curation, Project administration, Supervision, Writing – review & editing. **Robert J. Toonen:** Conceptualization, Methodology, Project administration, Supervision, Writing – review & editing. **Megan J. Donahue:** Conceptualization, Funding acquisition, Investigation, Project administration,

Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available on Github at enalley/FunctionalHomogenization.

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Appendix A. Supplementary data

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