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NOTE

Co-variation of fish and coral traits in relation to habitat type and fishery status

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Abstract Escalating climate impacts on coral reefs are increasingly expanding management goals beyond preserving biodiversity to also maintaining ecosystem functions. Morphological and ecological species traits can help assess changes within reef communities beyond taxonomic identities alone. However, our limited understanding of trait interactions between habitat-building corals and associated reef fishes and whether they are captured by current monitoring practices hampers management. Here, we apply co-inertia analyses to test whether trait assemblages in corals and fishes co-vary across different habitats and test whether different components of the reef fish community (fisheries vs. non-target species) display distinct relationships. We find that spatial co-variation across habitat types between coral and fish traits is strengthened by the addition of non-target fishes. Additionally, even in fisheries with diverse targets, non-target species make unique contributions to the overall trait structure and highlight the importance of considering monitoring protocols when drawing conclusions about traits and ecosystems.

Keywords Corals · Reef fishes · Community structure · Co-variation · Traits · Functions

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Introduction

On coral reefs, habitat-building corals are linked to fishes and other associated species through processes that include herbivory (Richardson et al. 2020; Darling et al. 2017), predation (Hempson et al. 2018), and habitat provisioning (Table S1) (Rogers et al. 2014). Traits can in some instances inform our understanding of functions performed by groups of species across spatial, temporal, and disturbance gradients (McLean et al. 2019; Pecuchet et al. 2020) and have applications in management, conservation prioritisation, restoration, and forecasting change (Laughlin et al. 2017; Beukhof et al. 2019; Grenié et al. 2018). A detailed understanding of trait-based composition of communities at relevant scales can thus guide decision-making in fisheries management, invasive species management, and spatial conservation (Givan et al. 2017; McLean et al. 2019; Mbaru et al. 2019). Fundamental to these applications is the use of existing monitoring datasets, but it is unclear whether current programs can effectively address trait-based research questions and support decision-making.

The composition of coral traits, affected by processes such as wave energy exposure and temperature regimes, shapes fish assemblages. For example, morphological traits determine structural complexity and therefore habitat provisioning, food availability, and size-specific refugia for fish assemblages (Darling et al. 2017). This non-random coral trait filtering also mediates disturbance responses (Richardson et al. 2018). Loss of corals with vulnerable traits through disturbances like bleaching-induced mortality affects the structure of fish communities, with planktivore, corallivore, and small-bodied fishes particularly vulnerable (Brandl et al. 2016), whilst herbivore abundances typically increase (Robinson et al. 2019a). The trait composition of fish assemblages in turn can also influence coral recovery trajectories through herbivory (Mumby and Harborne 2010). However, cross-taxon associations between different trait combinations are rarely evaluated, despite the importance of shared relationships across habitat-building and associated taxa.

Here, we explore linked spatial community trait structure of corals and fishes across reef habitats. Some monitoring programs focus on fisheries target (food fish) species (Houk et al. 2015; Andrew et al. 2011; Muller-Karanassos et al. 2021), but clearly, survey methods, trait selection, and trait data availability all impact the results and interpretations of trait-based research (Hadj-Hammou et al. 2021). We highlight the role that non-target fish play in detecting associations between coral and fish trait structure and how this varies across habitats, even on reefs that are subject to frequent disturbance. The objectives of this study are to (1) examine the trait-based structure of coral and fish communities, compare the relative contributions of non-target versus food-fish species to overall trait community structure, and identify traits that characterise specific reef habitats and (2) to test whether this is reflected in a higher correlation of the entre fish community with the coral community compared to food fish alone. Given the general differences in body size, motility, and association with the reef matrix between food and non-target fishes, we expect that non-target species occupy a different trait space and will contribute to stronger co-variation between the coral and fish communities.

Methods

In 2019, we surveyed 39 sites on outer, channel, patch or back and inner reefs at Chuuk Lagoon and Kuop Atoll in Chuuk State, Federated States of Micronesia (Houk et al. 2015) (Fig. 1). Coral bleaching occurred in 2016, causing significant declines in coral cover, particularly at outer reefs. Fish diversity and abundance were recorded with 12 stationary point counts per site (SPCs) (five metre radius, three minutes), distributed evenly across five 50 m transects. Previous monitoring focused on food-fish families identified through landings data (Houk et al. 2015; Cuetos-Bueno et al. 2018), a diverse group comprising of 136 reef fish species (Anderson et al. 2021). In 2019, we also recorded all non-cryptic, non-target families (188 species) (Table S2). Corals (identified to species level) and colony diameter were recorded with ten 1m^2 quadrats per site placed along the fish transects (Houk et al. 2015).

To characterise co-occurring coral and fish assemblages, we compiled categorical and numeric trait information

Fig. 1 Chuuk Lagoon and Kuop Atoll survey sites and reef habitat types
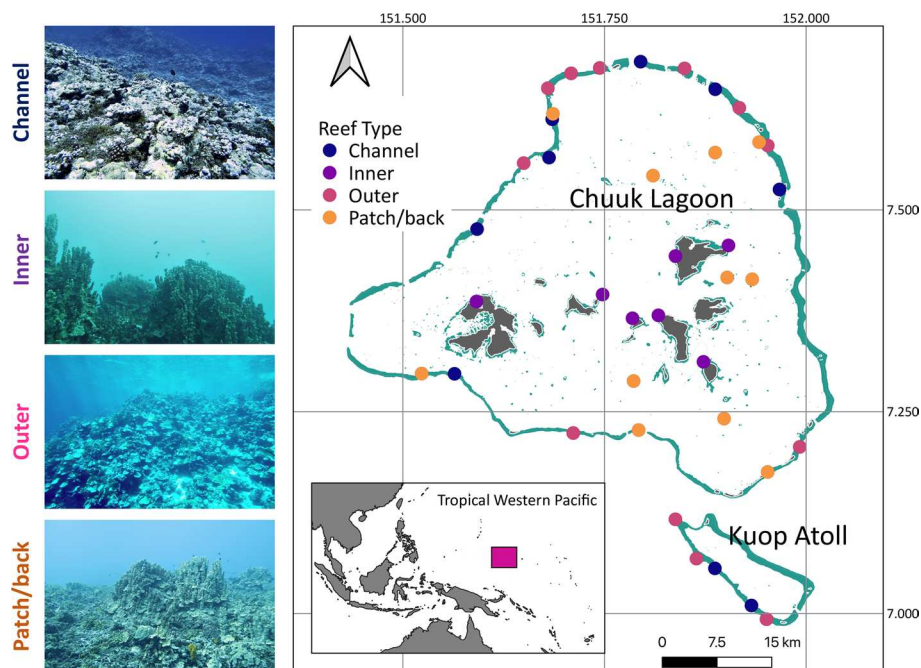
related to species' ecology, morphology, and life history. Coral traits were growth form, larval development mode, growth rate (mm/year), lower depth limit (m), and bleaching susceptibility traits derived from The Coral Trait Database and bleaching vulnerability assessments (Madin et al. 2016; Foden et al. 2013). Fish traits were maximum total length (cm), maximum water depth (m), mean pelagic larval duration (PLD) (days), trophic mode, aggregation type, and water column position, assembled from FishBase (Froese and Pauly 2019) and the literature (Table S1). Where feasible, gaps were imputed within genera using the mean of available trait values (numeric) or the dominant trait (categorical) (Taugourdeau et al. 2014).

All analyses were conducted in R (Supplement). First, we built separate fish and coral trait spaces with principal coordinate analyses (PCoA) on Gower dissimilarity matrices. Within the fish trait space, three distinct fish trait groups were examined—all species, non-target, and food fishes. We then calculated community weighted mean (CWM) values for coral and fish communities from trait tables and log-transformed abundance data (to moderate the effects of extremely abundant species). CWM measures the contribution of each trait to the overall community at each site, weighted by species abundances (Garnier et al. 2004). To pinpoint the traits that characterise coral and fish assemblages across habitats, we ran an indicator species analysis on the CWMs (hereafter indicator trait analysis) (Dufrêne and Legendre 1997). We evaluated co-variation and identified shared patterns between the coral and fish trait communities (CWMs) with two co-inertia analyses. Co-inertia analysis is a flexible multivariate method for examining the shared structure of a pair of data tables (Dray et al. 2003). The first analysis included the whole fish community (both food and non-target species), whilst the second excluded non-target fishes to explore if detecting shared structuring was dependent on these species. For each co-inertia analysis, we ran a permutation test (n = 999) that yielded a p value to test significance, and an RV value to indicate the strength of the co-inertia (0–1, values closer to one indicate stronger correlation between communities).

Results and discussion

Our findings broadly meet our initial expectations of unique trait space contributions and stronger habitat associations with the inclusion of non-target fish species. The coral trait space in Chuuk Lagoon is generally homogenously populated, except for several taxa with unique sets of traits. These are mostly brooding corals with branching or encrusting morphologies (i.e. *Isopora palifera*) (Fig. 2). There is considerable overlap between food (91.18% of the total trait space) versus non-target fish (73.53% of the trait space),

but both also make unique contributions to the trait space (Fig. 2). For the food fish, these are larger species occupying higher trophic levels (e.g. *Gracila albomarginata*) and for the non-target fish are small, reef-associated species (e.g. *Chaetodon ornatissimus*) (Fig. 2). There is a greater degree of overlap than we initially expected between food and non-target fish groups, and this reflects the diversity species targeted by Chuuk's reef fishery. It is important to acknowledge that species traits will change at different life history stages, which we do not address here. The distinct contributions of functionally unique species could indicate candidates for focused monitoring and protection under a trait-based management strategy (McLean et al. 2021). We would expect to see further expansion of the trait space if specific monitoring of cryptobenthic fishes was included (Brandl et al. 2019). The choice to include or exclude different parts of the fish community has wider implications for how we detect and respond to anthropogenic change on coral reefs (Brandl et al. 2018).

Different habitats support assemblages characterised by different traits for both corals and fishes (Table 1). For example, outer reefs host encrusting and sub-massive coral growth forms with greater depth limits that populate the steep drop-offs. The prevalence of sub-massive and encrusting growth forms at outer reefs is probably a reflection of Chuuk's disturbance history, including past bleaching events and cyclones (Houk et al. 2016). These disturbances disproportionately reduce the abundance of species with branching, fast-growing traits that might otherwise inhabit outer reef sites (Mellin et al. 2019). Contrastingly, inner and patch or back reefs are characterised by encrusting, long upright growth forms, alluding to the high coral cover of species like *Porites rus* on shallow, inner, and patch reefs in Chuuk (Fig. 1). Broadly, this portrays a post-bleaching coral community that may become increasingly representative of reefs globally as the climate changes (Alvarez-Filip et al. 2013; Hughes et al. 2018). For fishes, traits primarily held by non-target fish species (i.e. harem aggregations, sand-associated positions) are important in characterising the spatial composition of the reef (Table 1). This highlights their role in community structuring, and so the contribution of these species should clearly be incorporated into future trait-based analyses in Chuuk.

Co-inertia between fish and coral trait communities is stronger when all fishes are included in the analysis ($p < 0.001$), compared to only food fishes ($p = 0.049$) (Fig. 3). The traits most important for driving variation within the co-inertia differ slightly for each approach (Fig. S3). Fish and coral communities are organised roughly by reef types with outliers retained in the food fish community co-inertia analysis. These outliers represent exposed outer reefs subject to high wave energy. Visually, there is clearer structuring across reef types when non-target species are included and
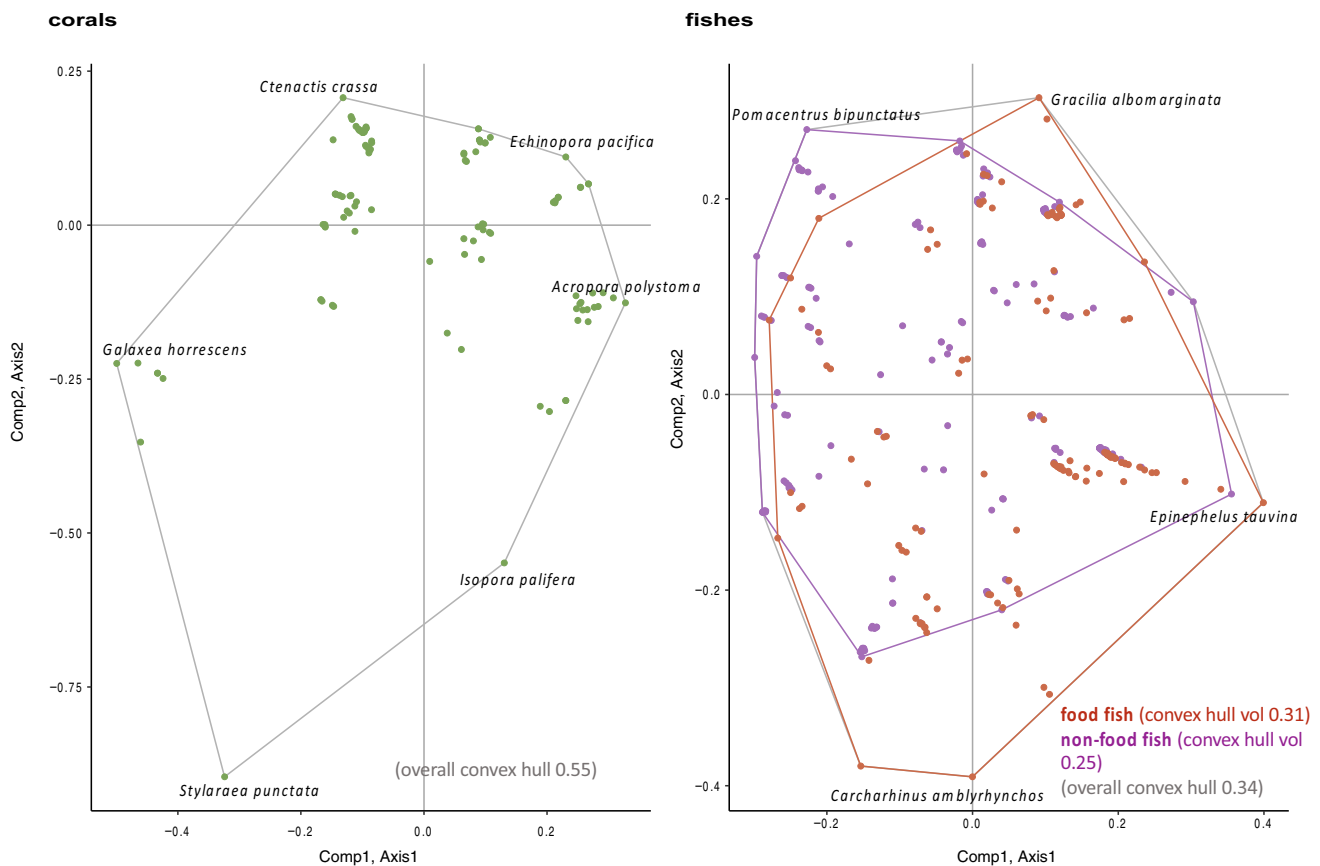
corals

fishes

Fig. 2 Principal coordinate analyses of coral and fish trait space. First two axes describe approximately 48.42% of the coral variation and 37.45% of the fish. Red convex hull (right) denotes food fish and purple for non-target fish (Table S2). Grey line denotes entire fish community trait space. See Fig. S1 for equivalent with species labels (outermost species labelled here)

Table 1 Indicator trait analysis of log-transformed CWM for corals and fish with p values < 0.05 (permutations $= 999$) (GF $=$ growth form)

	Habitat	Trait	stat	p
Corals	Outer	GF sub-massive	0.601	< 0.001
		Depth Lower	0.547	0.009
		GF encrusting	0.539	0.006
	Inner + Patch/back	GF encrusting long uprights	0.462	0.015
Fishes	Channel	Position sub-benthic	0.606	< 0.001
	Inner	Position demersal	0.764	< 0.001
		Position sand associated	0.628	< 0.001
	Outer	Trophic detritivore	0.442	0.028
	Channel + Outer	Aggregation solitary	0.629	< 0.001
	Outer + Patch/back	Aggregation harems	0.472	0.018

Reported results for maximum two combined habitat types

are supported both by the co-inertia and indicator analysis results. This pattern may relate to relative differences in size and therefore motility of food versus non-target fishes (Nash

et al. 2015), with typically smaller non-target species exhibiting the greater site specificity that creates these detectable differences in habitat types. In line with prior evidence (Darling et al. 2017), these results highlight that including a wide range of species when discerning trait-based relationships across taxa is crucial, particularly as species with unique sets of traits may support vulnerable ecological roles (Mouillot et al. 2013) that might otherwise be overlooked in monitoring and management efforts.

Monitoring in Chuuk is presently focused on food fish, reflecting local management priorities and the fact that fishing is the primary driver of decline and variability fish assemblages in this region (Harborne et al. 2018; Houk et al. 2015). However, as climate disturbances become more frequent, it may be necessary to expand monitoring to capture the wider fish community (not just food fish) in a way that is still practical and affordable. This is because climate-driven changes in coral trait composition and associated changes in dependent fish species may also have long-term implications for food fish as a resource (Robinson et al. 2019b). We illustrate that trait-based perspectives must be accompanied
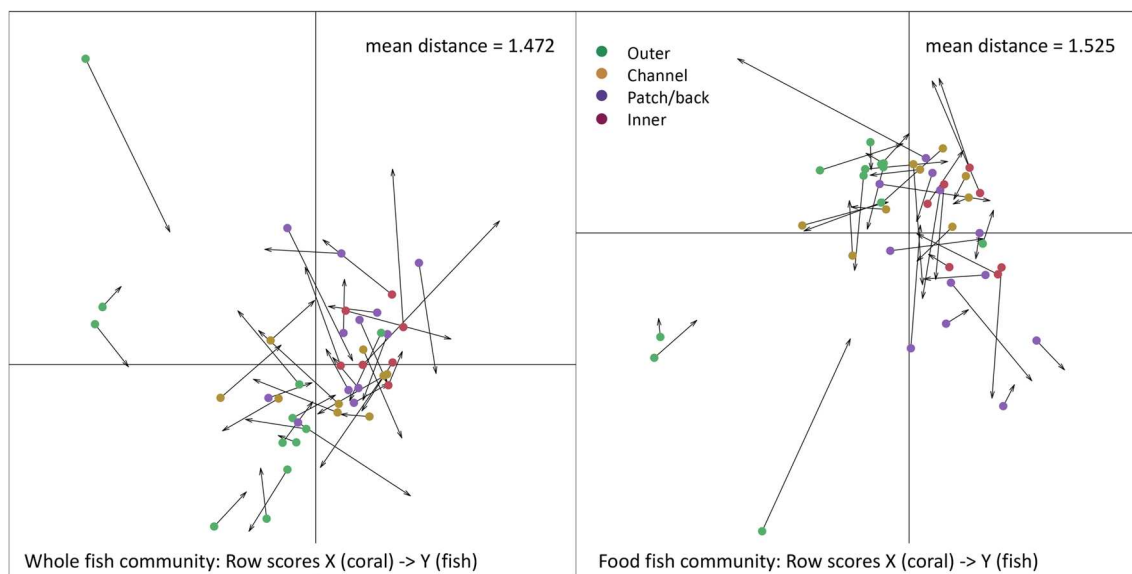
Fig. 3 Co-inertia of the whole fish and coral community (left, RV = 0.294, $p < 0.001$, reps = 999, 73.95% variation described in 1st two axes) and the coral community with food fish only (right, RV = 0.249, $p = 0.049$, reps = 999, 65.98% variation described in 1st two axes). Sites coloured by reef habitat. Beginning of each arrow is position of the site described by coral CWM, and the end the fish CWM, with arrow length corresponding to dissimilarity between the two. Mean distances given are therefore the mean Euclidean distance between coral and fish points at each site

by careful assessment of parts of the community that are excluded by sampling design.

Declarations

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