Non-trophic Interactions Along a Latitudinal Gradient

James Lock

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I confirm that the work submitted is my own and that appropriate credit has been given where reference has been made to the work of others.

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Abstract

Rising global sea surface temperatures are shifting marine species distributions, driving the tropicalisation of temperate regions. This process introduces tropical species into new environments, potentially altering existing community structures and fostering interactions among species with different thermal affinities. This study examines whether, how, and how much coral and temperate reef fishes living among coral communities interact along a tropicalisation gradient in the Ryukyu Islands and Japan's east coast. We filmed species interactions at 30 locations and performed a series of statistical tests to assess whether species with different thermal affinities interacted and how environmental factors, such as habitat type, shaped these interactions. Additionally, we investigated changes in the likelihood and frequency of cooperative and competitive interactions for tropical species in response to thermal stress using Generalized Linear Mixed-Effects Models. Our findings indicate that species with similar thermal affinities were more likely to interact in mixed communities than species with different thermal affinities, and that tropical and temperate species coexisted without significant competition. This result suggests that mixed communities were structured by species' functional niches rather than competitive exclusion. We also found that increased thermal stress was associated with a higher frequency of cooperative interactions, supporting the Stress Gradient Hypothesis where species with differing thermal affinities more commonly engaged in cooperative interactions than competitive ones. Finally, our results showed that coral habitats facilitated more diverse and frequent interactions, while turf habitats exhibited fewer less diverse interactions. These findings suggest that tropical and temperate species largely remain separate when cohabitating and that collaborative interactions are helping to support the expansion of tropical species ranges. Future research should explore longer-term trends and broader geographic areas to fully understand the effects of tropicalisation on marine community dynamics.

Table of Contents

List of figures

List of tables

1. Introduction

As ocean temperatures are increasing, more tropical species are able to expand to temperate locations (Perry *et al.*, 2005; Doak and Morris, 2010; Chen *et al.*, 2011; Fowler, Parkinson and Booth, 2018), contributing towards the redistribution of marine species from lower to higher latitudes (Perry *et al.*, 2005; Doak and Morris, 2010). In addition, increased herbivory from tropical species is leading to phase shift in temperate ecosystems from macroalgae dominated habitats to algal turf and coral communities (Vergés *et al.*, 2014; Pecl *et al.*, 2017; Fowler, Parkinson and Booth, 2018). As species' ranges expand and contract at different rates, new mixed communities of tropical and temperate species are emerging, with the potential for novel interactions to occur between species with different thermal affinities (Coni, Booth and Nagelkerken, 2021; Smith *et al.*, 2021; Miller *et al.*, 2023).

Marine species are distributed within distinct thermal guilds, with their ranges largely centred around tropical or temperate regions (Stuart-Smith *et al.*, 2015). Tropical species have narrower thermal ranges than temperate species and it is likely that species thermal ranges have evolved to be as narrow as possible, limiting the adverse physiological effects experienced outside of each species preferred range (Pörtner and Farrell, 2008). Yet tropical species have wider latitudinal ranges than temperate species (Stuart-Smith, Edgar and Bates, 2017), possibly reflecting the more stable environment found in the tropics (Stevens, 1989). Species most commonly exist closer to the warmest edge of their thermal range (Stuart-Smith *et al.*, 2015) with cooler winter temperatures primarily limiting their distribution (Tewksbury, Huey and Deutsch, 2008).

How tropical and temperate species interact has not been widely studied, but interactions between these two groups may be explained through several different ecological theories (Smith *et al.*, 2018; Coni, Booth and Nagelkerken, 2021; Miller *et al.*, 2023). Invasion theory suggests that invasive species tend to be superior competitors, allowing them to dominate or displace native (temperate) species in new environments (Sakai *et al.*, 2001). Range-expanding (tropical) species can similarly disrupt temperate systems, reshaping species dominance or replacing native species with lower competitive abilities (Nagelkerken and Simpson, 2013). However, temperate species may exhibit greater competitive ability and hinder the establishment and persistence of invasive species as predicted by biotic resistance theory (Von Holle, 2005). In their study Coni, Booth and Nagelkerken (2021) found that larger temperate species were able to inhibit the expansion of juvenile tropical species and observed several temperate species (e.g. *Atypichthys strigatus*, *Scorpis lineolatus*, and *Acanthopagrus australis*) aggressively interacting with *Abudefduf vaigiensis* (a tropical damselfish) – inhibiting their access to food. Tropical and temperate species may also be able to cohabit by occupying different niches—such as fulfilling distinct ecological roles or occupying microhabitats to which they are best adapted (Whittaker, Levin and Root, 1973) —or by exhibiting conflict-avoidance behaviours that do not negatively impact fitness (Coni, Booth and Nagelkerken, 2021). Trait analysis of species along the east coast of Australia and Japan have shown that functional niche availability, rather than resident-invader competition, is shaping species distributions in tropicalising regions (Miller *et al.*, 2023). Cooperative interactions between tropical and temperate species may also be helping tropical species to extend their range. For example, A. *vaigiensis* that formed mixed shoals with temperate species outperformed those that formed ’tropical-only’ shoals with conspecifics, having larger body sizes; mixed shoals were also more socially cohesive than ‘tropical-only’ shoals (Smith *et al.*, 2018).

Interactions within and between species play an important role in the distribution of species as well as the functioning of individual communities and ecosystems. Indeed, different types of interactions have different effects on species distributions and population dynamics (Neal, 2004; Forrester, 2015; Fontoura *et al.*, 2020; Keith *et al.*, 2023). Trophic interactions between species are widely studied, and predation (including herbivory) is probably the most obvious form of interaction between species. However, non-trophic interactions such as competition and mutualism also have a significant impact on species distributions and population dynamics (Miele *et al.*, 2019). Without considering interactions between tropical and temperate species therefore it is difficult to understand how communities may change in response in to shifts in species ranges (Coni, Booth and Nagelkerken, 2021).

Characterised as having a negative effect on one or both participants, competition is one of the most prevalent types of interaction - both within and between species (Neal, 2004; Forrester, 2015) with different forms of competition capable of altering population dynamics and distributions (Park, 1954; Bonin *et al.*, 2015). Competitive interactions may occur within a species (intraspecific) or between species (interspecific). Intraspecific competition is more common than interspecific competition (Forrester *et al.*, 2006; Bonin *et al.*, 2015; Forrester, 2015) and has a generalizing effect over time, as individuals seek to avoid competition by accessing a wider range of resources (Neal, 2004). In contrast, interspecific competition has a specializing effect, as species adapt to use less contested resources to avoid competition (Neal, 2004). Interspecific competition typically involves two or more species where their mutual existence in an area impacts the others' growth rate either at an individual level or the overall population size (Neal, 2004). For example, interspecific competition can reduce growth rates in a wide range of taxa, including several species of scleractinian corals (Tanner, 1997), species of land snails (Baur and Baur, 1990), and between two species of tadpoles (Griffiths, Edgar and Wong, 1991). In order for interspecific competition to occur, species have to possess overlapping ecological niches that result in competing needs over a limited shared resource (Sale, 1974). This does not require competition over a shared food source alone, but may include habitat or another limited resources, such as when reef fish compete over shelter (Buchheim and Hixon, 1992). A study by Fontoura *et al.*, (2020) also found evidence that competitive behaviour amongst reef fishes be driven primarily by local competition amongst closely related species with large functional overlaps.

Competitive interactions may also be categorised by the underlying mechanism through which they affect participants. Competition by exploitation occurs where one organism consumes resources, which prevents another from doing so (Hardin, 1960). In this interaction, the two individuals may never actually come in to contact with each other, the primary factor is that they depend upon a common resource (Jensen, 1987). In marine environments, a typical example of exploitation would be the competition between herbivorous parrotfish, which are active through the day, and long-spined sea urchins (*Diadema antillarum*), which are active at night. Both species feed on algae, which acts as a shared resource, but neither species directly interacts with the other due to their differing activity patterns (Hay and Taylor, 1985). Competition by interference, however, occurs when two individuals affect one another directly, preventing one or both from accessing a specific resource such as food or shelter (Neal, 2004). The type of competition between species may also change over time, oscillating between direct, interference, or indirect, exploitation, interactions (Tallian *et al.*, 2021).

Amongst reef fishes, competition for food rarely affects individual mortality, while competition for shelter is often the root cause of mortality from predation (Holbrook and Schmitt, 2002). Rather, competition for food has a limiting effect on the relative size of individuals. For example, (Kindinger, 2016) found that interference competition between fairy and blackcap basslets (*Gramma loreto* and *G. melacara*) resulted in an overall size hierarchy in the positioning of individuals, with larger individuals closer to the outer edge of ledges (where they can better access food) and smaller and juvenile individuals towards the back. Ultimately though, reduced growth may translate to reduced fecundity as well as reduced survival (Forrester *et al.*, 2006). However, reef fishes typically use the complex structural environment created by coral as shelter to avoid predator and density-dependent competition is often observed among fishes which compete with one another to access these refuges (Buchheim and Hixon, 1992; Ménard *et al.*, 2012). For example damsel fishes become more aggressive in larger aggregations with increases in interference competition for refuges (Holbrook and Schmitt, 2002).

Mutualisms have historically received less attention than competition, but may be no less important in shaping communities (Bertness and Callaway, 1994). Unlike competitive interactions, which are characterised by the negative effect they have upon participants, mutualisms are positive in nature, with both participants benefitting from the interaction (Begon, Townsend and Harper, 2006). Mutualisms have been observed across a wide range of ecosystems and between varied taxa. For example, more than 80% of all flowering plants are thought to be in a mutualistic relationship with Mycorrhizal fungi (Bronstein, Alarcón and Geber, 2006), while plant-insect mutualisms are also pervasive (Bascompte, 2019). Mutualistic interactions have also been demonstrated between the sepiolid squid *Euprymna scolopes* and luminous bacterium *Vibrio* *fischeri* (Ruby and McFall-Ngai, 1992). Simulated models have shown that mutualisms contribute to the overall stability of communities (Mougi and Kondoh, 2012) and enable the survival of participating individuals in otherwise inhospitable environments (Travis, Brooker and Dytham, 2005).

Cleaning interactions are probably the most well-known mutualism in marine environments (Begon, Townsend and Harper, 2006). They play an important role in the health of marine communities and can shape the overall population structure (Wagner *et al.*, 2015). Interactions between the bluestreaked cleaner wrasse (*Labroides dimidiatus*) and its many "clients" are a textbook example of this mutualism (Begon, Townsend and Harper, 2006) and involve frequent, daily, cleaner-client interactions where clients visit cleaners up to 144 times per day (Grutter, 1995, 1996). In these interactions, the cleaner gains food by removing parasites from the client, while the client benefits from having the parasite removed (Grutter, 1999). Fishes with access to cleaners have lower antibody responses than fishes without, suggesting that cleaners reduce the need for "active" immunity in clients (Ros *et al.*, 2011). This may allow clients to prioritise other functions, for example growth, body condition, cognitive function, and reproduction (Demairé *et al.*, 2020). The presence of cleaner fish may also enhance species diversity (Bshary, 2003; Grutter, Murphy and Choat, 2003; Sun *et al.*, 2015; Wagner *et al.*, 2015) and can promote site selection among some species (Armstrong *et al.*, 2021).

The relative importance of competitive and cooperative interactions within communities is thought to change in response to environmental stress (Bertness and Callaway, 1994). This effect is often referred to as the Stress Gradient Hypothesis and is common in plant ecology (Fowler, 1986; Bertness and Callaway, 1994; Callaway *et al.*, 2002). It has also been demonstrated within communities involving sessile marine animals (Kawai and Tokeshi, 2007), birds (García-Navas *et al.*, 2021), in plant–herbivore interactions between a species of crab and marsh plants within salt marshes (Daleo and Iribarne, 2009), within communities of aquatic detritivorous invertebrates (Fugère *et al.*, 2012), and simulated models (Travis, Brooker and Dytham, 2005). More mutualistic interactions under stress are likely to occur because cooperative interactions help to ameliorate conditions for one or both species (Bertness and Callaway, 1994).

It is therefore possible that, as tropical species ranges expand to less hospitable temperate locations, the relative importance of cooperative and competitive interactions between fish species would change as tropical species expand to temperate locations.

In this study, we investigate the impact of rising global temperatures and range shifts on interactions among coral and temperate reef fishes, focusing on sites influenced by the Kuroshio Current within the Ryukyu Islands and along Japan's east coast. We explore whether species with different thermal affinities interact when cohabiting the same sites, how environmental stress affects species interactions, and how different habitats shape the diversity of interactions. If tropicalisation is contributing to the formation of new and cohesive communities, we expect to observe interactions between species with varying thermal affinities, particularly where they compete for shared or limited resources. However, if tropicalisation was simply shifting the ranges of existing species, would wouldn't expect to observe interactions between individuals from different thermal affinities as they would be unlikely to co-exist in sufficient numbers within each location. Furthermore, we anticipate shifts in the nature of species interactions in response to environmental stress, especially at the edges of their geographic distributions. If interactions are helping to support the establishment of communities and expansion of species ranges we would expect to see an increase in the likelihood or frequency of cooperative interactions relative to competitive interactions. For tropical species, this would typically be at higher latitudes and where average sea surface temperatures are lower.

2. Methods

2.1. Study locations and environment

Survey locations were situated along the Ryukus Island chain and east coast of the Japanese mainland which is exposed to the Kuroshio Current. The Kuroshio Current brings warm tropical waters from the south to the north (Figure 1) and acts a vector for larval dispersal, while the islands and coast of mainland Japan provide suitable habitats for marine communities, facilitating high poleward connectivity and enabling species to spread along the entire gradient (Yamano, Sugihara, and Nomura 2011).

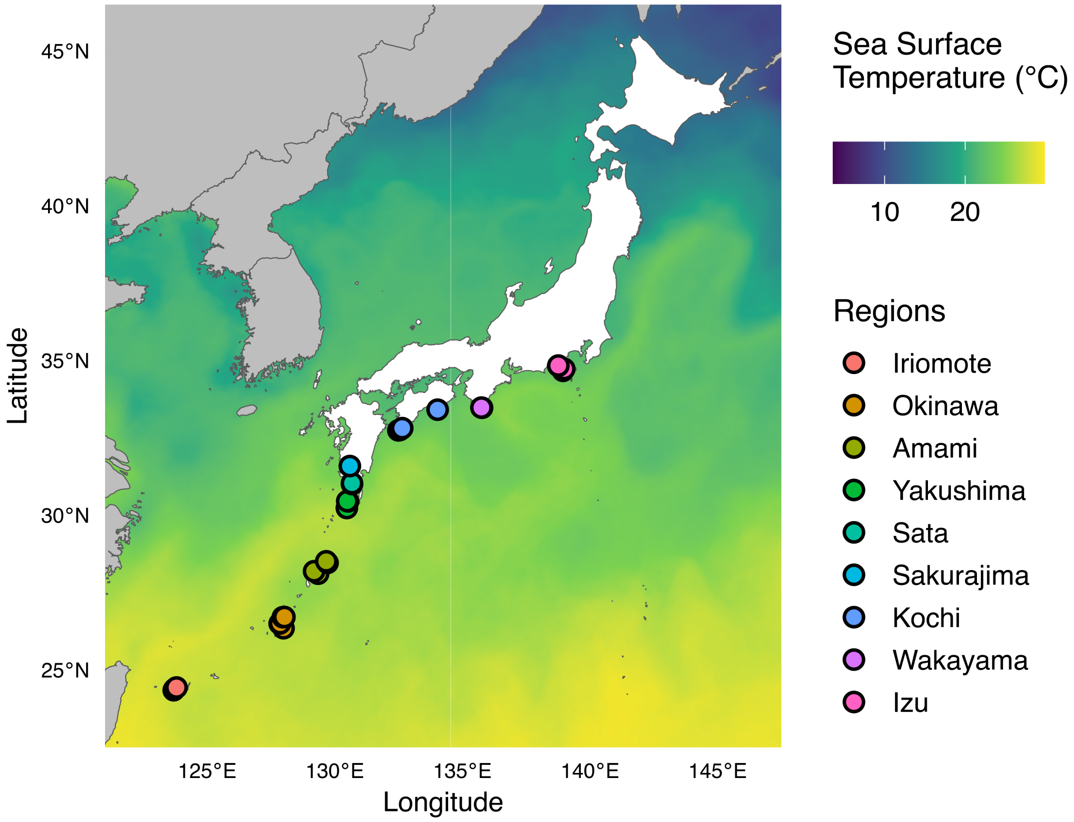

Figure 1: a map showing the average monthly sea surface temperature around Japan in June 2023 (NASA/JPL, 2015). The Kuroshio current can clearly be seen travelling north through the Ryukyus Island chain and along the Japanese coast. Points represent sites surveyed.

I conducted under water video surveys of fish interactions at 30 sites (Table 1) with coral communities in June and July 2023. The selected sites were located between 24.3457° and 34.8380°, which included subtropical (Corlett 2013) and temperate geographic areas along a strong water temperature gradient (Figure 1). The sites provided a range of habitats, including accreting coral reefs, and macro-algae & turf dominated rocky reefs, all of which hosted scleractinian coral communities.

Table 1: Table listing sites included in the study. Sites are grouped by region and arranged from lowest to highest latitude

Site	Region	Habitat	Longitude	Latitude
Amitori	Iriomote	Coral	123.6900	24.34577
Sotopanari	Iriomote	Coral	123.7196	24.38228
Nakano Beach	Iriomote	Coral	123.7924	24.43152

Nakano-Oki	Iriomote	Coral	123.7993	24.43522
Miyagi Channel	Okinawa	Coral	127.9936	26.34987
Onna 2	Okinawa	Coral	127.8409	26.50093
Onna 1	Okinawa	Coral	127.8627	26.51351
Sakiyama	Okinawa	Coral	127.9661	26.70673
Kourijima	Okinawa	Coral	128.0281	26.71213
Ankyaba	Amami	Coral	129.3473	28.11133
Saneku	Amami	Coral	129.1905	28.19227
Tomori	Amami	Mixed Coral-turf	129.7186	28.46129
Sani	Amami	Coral	129.6670	28.51297
Yudomari	Yakushima	Mixed Coral-turf	130.4736	30.23355
Shitoko	Yakushima	Mixed Coral-turf	130.5214	30.44893
Isso	Yakushima	Mixed Coral-turf	130.4883	30.45754
Tajiri	Sata	Mixed Coral-turf	130.6765	31.00671
Owase	Sata	Turf	130.6757	31.03699
Hakamagoshi	Sakurajima	Mixed Coral-turf	130.5917	31.59018
Himeshima	Kochi	Mixed Coral-turf	132.4923	32.74289
Torinonkobi	Kochi	Mixed Coral-turf	132.5493	32.75311
Amaji 2	Kochi	Mixed Coral-turf	132.6300	32.80153
Amaji 1	Kochi	Mixed Coral-turf	132.6438	32.81577
Nahari	Kochi	Macroalgae	134.0309	33.41154
Kushimoto 2	Wakayama	Mixed Coral-turf	135.7725	33.47257
Kushimoto 1	Wakayama	Mixed Coral-turf	135.7461	33.47938
Shidagaura	Izu	Macroalgae	138.9426	34.66578
Shobuzawa	Izu	Macroalgae	138.9932	34.72805
Arari 2	Izu	Turf	138.7596	34.82941
Arari 1	Izu	Macroalgae	138.7603	34.83808

2.2. Identifying species interactions

I made video recordings using GoPro 3 (n = 1), 5 (n = 2), 9 (n = 2), and 11 (n = 1) cameras placed at an average depth of 6.8m. Cameras were situated along a 30m transect and positioned with non-overlapping fields of view facing across the reef flat or along the reef slope depending on the topography at each site. Recordings were made during daylight hours between 10am and 6pm when most diurnal were expected to be active (Collette and Talbot, 1972). I left the cameras unattended to record potential interactions between and among fishes for a minimum of 20 minutes before collecting them. I repeated this process at each site with a minimum of five cameras per transect and two transects per site. A 10 minute clip from each recording was extracted for analysis. Based on the findings by (Nanninga *et al.*, 2017), the first 5 minutes of each video were discarded to allow for an initial acclimation period and account for any “observer effect” (Iredale, Nevill and Lutz, 2010) while the diver was in the immediate area. Videos were excluded where the visibility was insufficient to identify individuals or interactions, the camera was knocked over by the current (reducing the field of view), or a diver was seen entering the frame. In total we collected data from 156 recordings, with 5.3 (mean) recordings per site (min = 2, max = 7).

I identified species using visual comparison with images from ‘Reef Fish Identification – Tropical Pacific’ (Allen, 2003) and ‘Sea Fishes of Japan’ (吉野雄輔写真・解説; 瀬能宏監修., 吉野雄輔., and 瀬能宏., 2008). Observations were excluded from the analysis where the individual could not be identified to species level. Information about the assemblage at each location was recorded using the minCount/MaxN value for each species seen in the footage. The minCount/MaxN value represents the maximum number of distinct individuals observed at any one time and provides a conservative measure of the population size for each species (Baker *et al.*, 2022).

I reviewed each video and made a note of any direct interaction observed between two or more individuals and each interaction was categorised as “cooperative”, “competitive”, or “other”, depending on the perceived effect of the behaviour on participants (Table 2). I made efforts to avoid over counting of aggregative interactions (pairs, shoaling, and schooling); only recording a single observation when it was likely that the same group were moving in and out of the cameras field of view based on the direction of travel, size and composition of the group. To distinguish between shoals and loose collections of individuals holding position, shoals were only counted when individuals displayed a level of polarity (alignment in the same direction) which indicated their movement was co-ordinated as a group. Due to the difficulty in tracking specific individuals, I recorded the total frequency of each interaction type based on the combination of the participant’s species and the behaviour observed.

Table 2: Table describing the different behaviours observed grouped by interaction type and classified as positive or negative

Classification	Interaction	Behaviour	Description
Negative	Competition	Chasing	First fish, the aggressor, moves rapidly towards the second fish, the recipient. The recipient moves rapidly away from the aggressor. The interaction typically ends with a sudden change in speed or direction by either participant. Chasing may either occur over significant distance (several body lengths) or end abruptly with the initial approach from the aggressor. Participants do not appear to make physical contact.
		Nip	First fish, the aggressor, swims rapidly towards the second fish, the recipient. The aggressor then appears to make physical contact with the recipient followed by the recipient rapidly moving away from the aggressor.
Positive	Mutualism	Cleaning	Cleaner fish swims around the client making contact one or more times. Client typically poses with their head angled towards the surface and dorsal fins spread. Interaction ends

			when the either the cleaner or client move away.
	Commensalism	Follow feeding	One or more individuals followed another individual as they fed, disturbing the substrate or hunting in cracks. This type of interaction was only seen between heterospecific individuals.
	Aggregative	Paired	Two individuals moving together in a co-ordinated manner, typically travelling in the same direction or foraging at the same location before or after moving together as a pair.
		Shoal	A lose collection of three or more individuals, typically holding position or moving with the current. Individuals maintain some level of polarity and actions appear to be co-ordinated.
		School	A collection of three or more individuals moving together in a coordinated manner with a high degree of polarity. Typically seen travelling or foraging.
Other		Wrestling	Individuals approach one another butt heads and proceed to swim around each other.
		Dancing	Individuals swim around each other in concentric circles, typically considered to be

	associated with mating interactions.

2.3. Traits and Environmental Data

I assigned individuals to one of two distinct thermal guilds (Temperate or Tropical) based on the thermal midpoint of the species to which they belonged. Species with a thermal midpoint below 23.5°C were classified as members of the Temperate guild, while those with a midpoint above this threshold were assigned to the Tropical guild. The thermal midpoint represents a species' "preferred" temperature and is calculated as the mean temperature across its realized thermal niche, derived from empirical data on its global distribution. Both the thermal midpoint for each species and the 23.5°C cut-off value used to distinguish between guilds were determined following the methodology outlined by (Stuart-Smith *et al.*, 2015; Stuart-Smith, Edgar and Bates, 2017).

3. Analysis

All statistical analysis were conducted using R version 4.4.1 (2024-06-14) (R Core Team, 2023), and associated packages (Oksanen *et al.*, 2001; Lüdecke, 2018; Dray *et al.*, 2024).

3.1. Do interactions vary by habitat?

To compare interactions between habitats, I grouped recordings into one of four categories (coral, mixed coral-turf, turf, and macroalgae) based on a visual assessment of the habitat in each recording. Coral habitats were typically located on accreting reefs, while coral & turf habitats were characterized by rocky reefs where coral communities were interspersed with algal turf, turf habitats were located at rocky sites with little to no coral cover, and macro-algae habitats where macro-algae dominated the benthic cover with minimal or no coral communities present.

To compare the level of diversity between habitats I performed a series of Kruskal-Wallis tests to compare the alpha diversity of interactions at different sits, including the component elements, interaction richness, and frequency. Post-hoc pairwise comparisons were performed using the Conover-Iman test (with Holm adjustment) to confirm significant differences found in the Kruskal-Wallis tests. Kruskal-Wallis and Conover-Iman tests were used as they are suitable for comparing distributions between independent groups when data is not normally distributed - both tests compare the mean rank sum difference. A Holm adjustment was used to control for the increased chance of type I errors when making multiple comparisons. I compared the variation in interactions within habitats using a Sørensen beta diversity index which was applied to interaction types rather than species. A Sørensen index was chosen because it allowed for the measurement of overall beta diversity, the contribution of interaction richness (the number of different unique interactions), and replacement (the difference in the number of unique interactions not seen in each recording) (Legendre, 2014). I also compared the beta diversity values for interactions with the beta diversity of species within each habitat to see if differences in the magnitude of interaction diversity matched differences in species diversity. To calculate the different interaction diversity indices, I classified interactions by the combination of participants and the behaviour observed; for example, a chasing interaction between Species A and Species B was considered as one interaction type, while a shoaling interaction between the same species was classified as a different interaction type; species names were alphabetised before being combined. The vegan::diversity (Oksanen et al., 2001) and adespatial::beta.div (Dray et al., 2024) functions were used to calculate the alpha and beta diversity index values.

3.2. Do species from different thermal guilds interact?

To assess whether species from different guilds interacted systematically or randomly, I categorised interactions into two groups: a) interactions between members of the same guild, and b) interactions between members of different guilds. I compared the number of interactions in each category, their frequency per recoding, and the type of interactions observed. Tests were only conducted on data for interactions between members of different species and at sites where both tropical and temperate species were observed.

I used a Wilcoxon signed-rank test to compare the differences in the frequency of interactions between the two groups for each recording. A Wilcoxon signed-rank test was chosen as it does not assume that data are normally distributed and is suitable for comparing paired observations (Kloke and McKean, 2014). This was important to accommodate cases where a single individual may have contributed to interactions in both groups. Additionally, I performed a Chi-squared goodness-of-fit test to assess whether the observed number of interactions between members of different thermal guilds significantly deviated from the expected number of interactions; I assumed that interactions occurred randomly and were proportional to the number of individuals in each guild. Finally, I conducted a Fisher’s exact test to determine if there was a significant association between the type of interaction (cooperative or competitive) and whether the species involved were from the same thermal guild or not. A Fisher’s exact test was chosen due to its suitability for use with small sample sizes (Kloke and McKean, 2014).

3.3. Does environmental stress effect interactions?

To test the applicability of the stress-gradient hypothesis (Bertness and Callaway, 1994) and explore the relationship between species interactions and environmental stress, I predicted the frequency and likelihood of cooperative or competitive interactions based on the level of environmental stress experienced by each participant species at the location the interaction was recorded. I used thermal stress as a proxy for environmental stress, as temperature is the primary limiting factor in marine species distributions. I defined thermal stress as the difference in degrees Celsius (°C) between the observed water temperature during a recording and the species’ preferred temperature (Stuart-Smith *et al.*, 2015). Positive values indicated temperatures warmer than the species’ preferred range, while negative values indicated cooler-than-preferred conditions.

I employed a series of quadratic regressions using Generalized Linear Mixed-Effects Models (GLMM) to predict two outcomes: (a) the likelihood of observing a cooperative interaction, and (b) the frequency of both competitive and cooperative interactions. Each outcome was modelled independently using appropriate response variables and distributions. GLMMs extend Generalized Linear Models by incorporating random effects to account for variability introduced by different groupings or clusters in the dataset (Jiang and Thuan Nguyen, 2021). Site” was included as a random effect in each model to account for environmental variation across locations. Thermal stress was modelled using a quadratic regression, as a non-linear relationship between the temperature deviation from the species' thermal midpoint and overall stress levels was expected. This expectation was based on the observation that species occupy thermal niches with varying breadths (Stuart-Smith, Edgar and Bates, 2017), and the assumption that environments become increasingly inhospitable as conditions exceed the upper or lower limits of a species thermal range.

I fit each GLMM model using the lme4::glmer function (Bates *et al.*, 2015) and calculated predicted values with the ggeffects::predict_response function which generates predicted values based on the mean value of non-focal predictors (Lüdecke, 2018). The likelihood model was fit using binomial logistic regression, where the binary response variable "Mutualism" indicated whether an interaction was cooperative (1 = cooperative interaction, 0 = competitive interaction); each observation represented a single participant. The frequency model was fit using a Poisson distribution, which is suitable for count data, as in this case. Observations represented the frequency of each type of interaction a species engaged in during a recording. Interactions between individuals of the same species were counted as one interaction while interaction between different species were counted separately for each species. Both models were fit using thermal stress as the dependent variable, and site as a random effect. Due to the asymmetrical nature of the dataset, resulting from the varying distributions of tropical and temperate species; data from temperate species (frequency model) and individuals (likelihood model) were excluded. As a result, the analysis focused on tropical species, where there was sufficient data covering a broad range of conditions.

4. Results

I observed a total of 1,144 competitive or cooperative interactions across 156 recordings at 30 different sites, with an average frequency of 7.33 interactions per recording (mode = 4, max = 31). There were 13 videos where no interactions were observed.

Of the total number of interactions, 50.35% were cooperative, 49.65% were competitive. Overall, interactions were more commonly observed between individuals of the same species (73.34% of all interactions). The likelihood of cooperative or competitive interactions varied depending on whether the interactions were intraspecific or interspecific: 61.64% of interspecific interactions were competitive, whereas 54.71% of intraspecific interactions were cooperative. There was a positive correlation between both individual abundance ($\tau=0.53$, $p< 0.001$) and species richness ($\tau=0.41$, $p< 0.001$) with the frequency of interactions, indicating that interactions were more commonly observed when either a greater number of individuals or wider range of species were present. In total, we observed 5,387 individuals from 185 different species during the study and interactions were recorded between individuals from 67.03% of the species identified.

4.1. Do interactions vary by habitat?

The beta diversity of all species and interactions was highest in reef communities with mixed coral and turf habitats (Fig. 2). While the total value of beta diversity varied for species, the beta diversity of interactions was similar in assemblages within each of the four habitats. Replacement was the largest contributing factor to both interaction and species diversity, indicating that variety of species and type of interactions varied between recordings, rather than being homogeneous within habitats. In contrast, differences in richness contributed the least to species and interaction diversity, especially assemblages within turf or coral habitats (Fig. 2). This suggests there was little variation in the number of distinct species and interaction types within assemblages observed in either of these habitats.

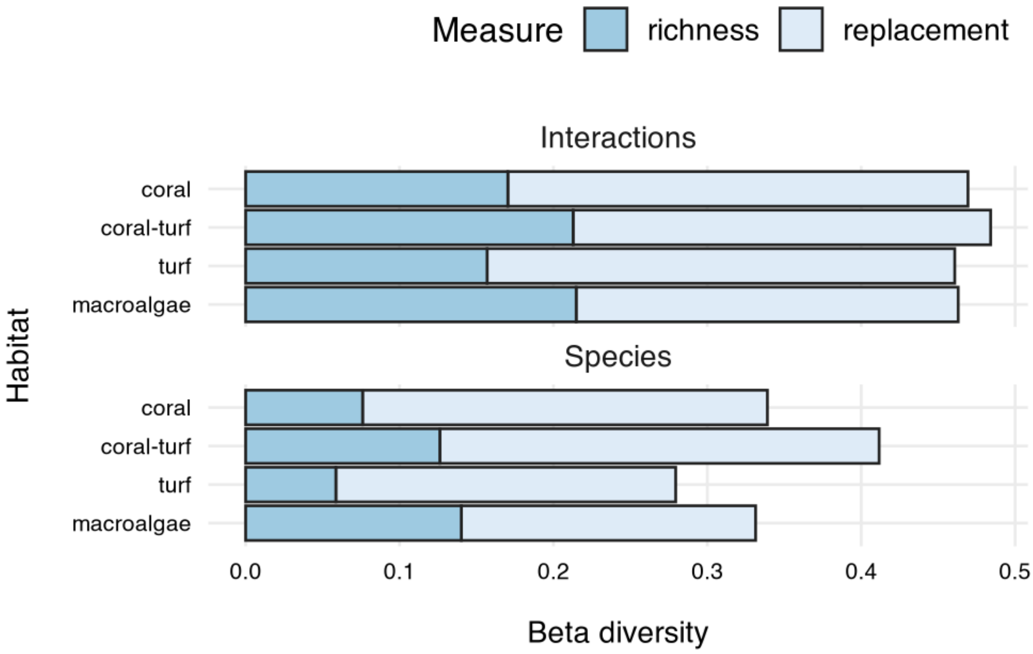

Figure 2: Bar charts displaying the beta diversity of interactions and that of all species observed within the four different habitat types. Bars are divided to show the contribution of differences in richness and replacement to the overall beta diversity values.

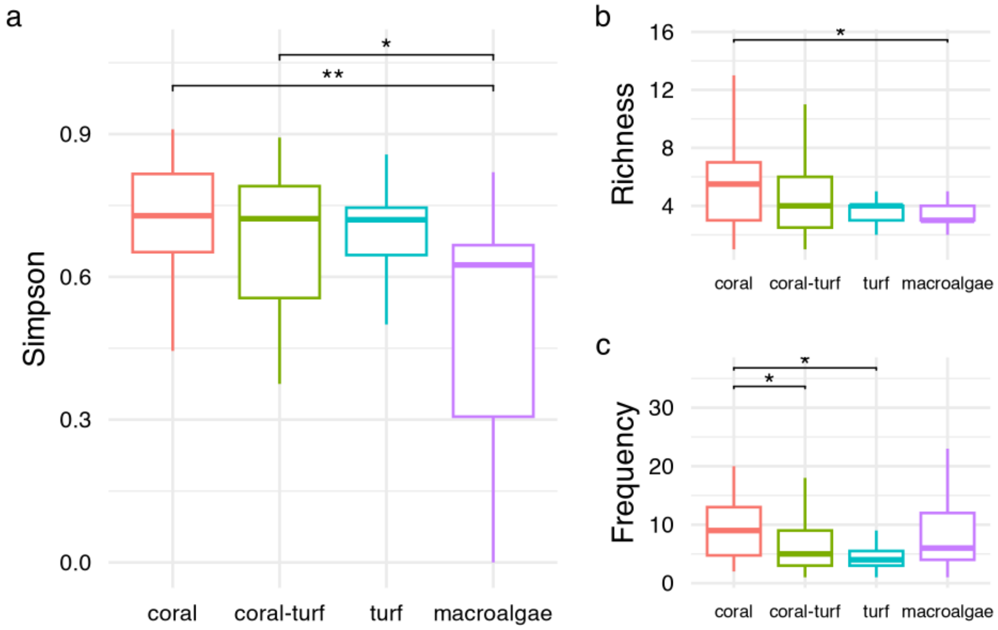

Figure 3: Box plots displaying the distribution of Simpson's alpha diversity (a), interaction richness (b), and interaction frequency (c) in communities across each habitat type. Significant pairwise Conover-Iman test results are indicated by brackets

The highest level of alpha diversity in interactions, as well as interaction frequency and richness, was observed in communities with coral habitats (Fig. 3). A Conover-Iman test revealed significant differences in the values of alpha diversity (T = -37.92, p = 0.005) and interaction richness (T = -29.62, p = 0.046) between coral and macroalgae habitats. Similarly, significant differences in alpha diversity were found between mixed coral-turf and macroalgae habitats (T = -29.54, p = 0.044), with macroalgae habitats exhibiting the lowest diversity and richness of all groups. Furthermore, interactions occurred most frequently in communities with coral habitats, with significant differences observed between coral and mixed coral-turf habitats (T = -23.08, p = 0.013) and between coral and turf habitats (T = -38.38, p = 0.019). Interaction frequency was lowest in communities with turf habitats (Fig. 3).

4.2. Do species from different thermal guilds interact?

In our survey area, tropical species were more prevalent and widely distributed than temperate species. Of the 185 species observed, 91.35% (n = 169) were classified as tropical, while 8.65% (n = 16) were temperate (Fig. 4). Tropical species were found at all sites, whereas temperate species were recorded at only 21 sites, ranging from Kourijima in Okinawa (26.71213°N) to Arari in Izu (34.838078°N). Although the richness and abundance of tropical species generally declined with increasing latitude, this pattern was not consistent. Moreover, tropical species were more abundant than temperate species at all but two sites — Shobuzawa and Shidagaura in Izu — and more diverse at all sites except Shidagaura.

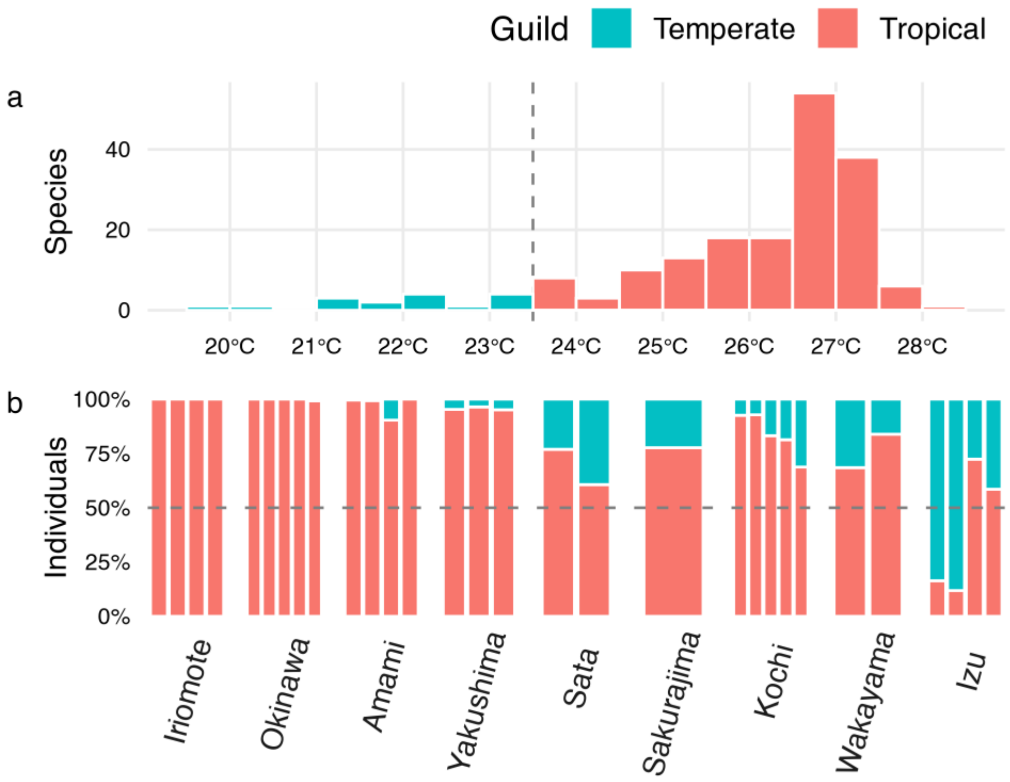

Figure 4: Plots illustrating the distribution of all species according to their thermal affiliation: a) Distribution of species based on their calculated thermal midpoint, reflecting the average temperature preference for each species. b) Proportion of individuals at each site grouped by region and arranged from lowest to highest latitude

At sites where both tropical and temperate species were present, a total of 162 interspecies interactions were observed. Of these, 85.8% (n = 139) occurred between members of the same guild, while 14.2% (n = 23) involved interactions between members of different guilds. Interactions between tropical and temperate species were observed at only seven sites: Tajiri in Sata; Himeshima, Torinonkobi, Amaji 1 in Kochi; Kamiura in Wakayama; and Arari1, and Arari2 in Izu. At three sites — Owase in Sata, Hakamagoshi in Sakurajima, and Nahari in Kochi — no interspecies interactions were observed. The majority (73.91%, n = 17) of interactions between different guild members were cooperative, while most interactions (58.99%, n = 82) between individuals from the same guild were competitive (Fig. 5). However, a Fisher's exact test found no significant association between interaction type and guild membership at any one site.

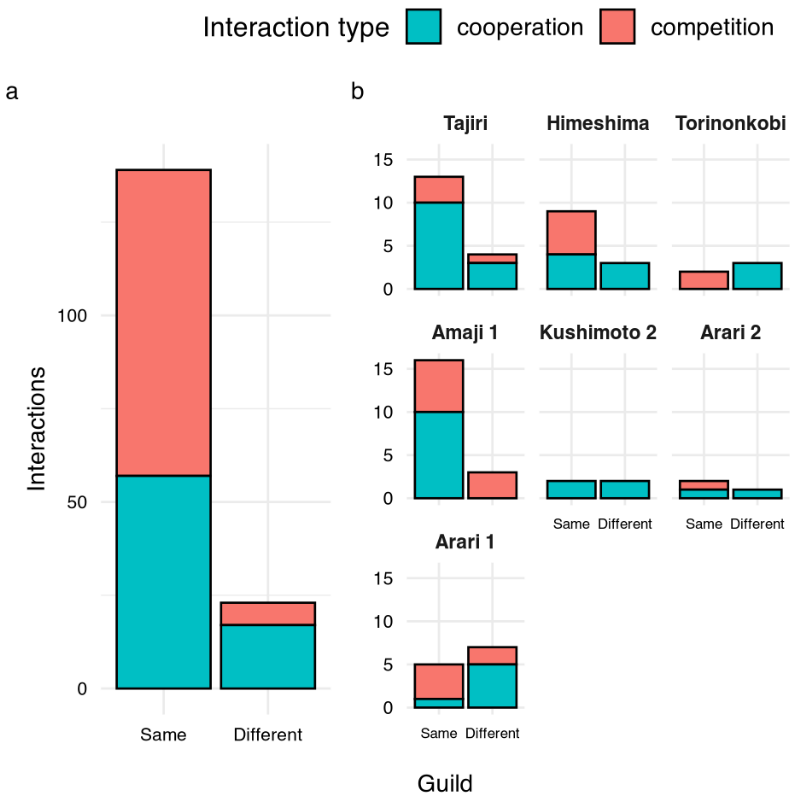

Figure 5: Bar charts displaying the total number of interspecies interactions between members of the same or different thermal guilds. The interactions are further divided into cooperative and competitive interactions for each group. a) Total number of interactions across all sites where both tropical and temperate species were present. b) Total number of interactions observed at the seven sites where both thermal guilds exhibited interactions.

Interactions between members of the same thermal guild were more frequent than those between members of different guilds. The Wilcoxon signed-rank test revealed a significant difference in the frequency of interspecies interactions between same-guild members compared to different-guild members across all sites with mixed assemblages ($W = 1392$, $p = <0.001$). However, at the individual site level, there was no significant difference in the frequency of interactions at any of the seven sites where both types of interactions occurred.

With the exception of one site, interactions between members of different guilds were randomly distributed. A Chi-squared goodness-of-fit test identified one site, Torinonkobi in Kochi, where the number of interactions was significantly higher than expected by chance ($\chi^2 = 9.35$, $df = 1$, $p = 0.002$). However, no significant deviation from random expectations was observed at any other site, nor when the test was performed across all sites with mixed assemblage. This indicated that interactions between members of different guilds did not occur more often than would be expected at random.

4.3. Does environmental stress effect interactions?

There were 652 interactions involving 1,945 individuals from tropical species across a range of sea surface temperatures (24°C to 31°C, mean = 28.4°C). These temperatures spanned from 2.6°C below to 7°C above the species' preferred temperature (mean = 2.3°C). Cooperative interactions were more common (60.12%) than competitive ones. The predicted data (Fig. 6b) indicates that the likelihood of an individual engaging in cooperative interactions increased as water temperatures drop below the species' preferred range and decreased when temperatures exceed this range. Additionally, the rate of decrease slowed when temperatures rose more than 5°C above the species' preferred temperature. The underlying model used to generate these predictions (Table 3) revealed a significant negative relationship between thermal stress, defined as the difference in degrees between the preferred and observed temperatures, and the likelihood of cooperative behaviour ($p = 0.048$). The quadratic term was not significant ($p = 0.549$), suggesting a linear relationship between these variables. The random intercept for site variability was 1.38, indicating a large amount of variation between sites.

The predicted interaction frequencies (Fig. 6a) demonstrate changes in the dominance of interaction types as a function of thermal stress. Cooperative interactions were more frequent when species were observed at temperatures more than 1.2°C below or 6.4°C above the species' preferred temperature. Within this range, however, competitive interactions were the most common. The predicted frequency of competitive interactions increased from an average of 0.88 interactions during a 10-minute period at 2.6°C below a species' preferred temperature to a peak of 2.95 interactions at 4.5°C above it, after which the frequency declined, falling to 2.49 interactions at 7°C above the species' preferred temperature. The frequency of cooperative interactions decreased from an average of 1.62 interactions during a 10-munute period at 2.6°C below the species' preferred temperature to 1.32 interactions at the preferred species' temperature, before rising again to 1.45 at 2.7°C above it and then increasing more rapidly, reaching an average 3.6 interactions at 7°C above the species' preferred temperature.

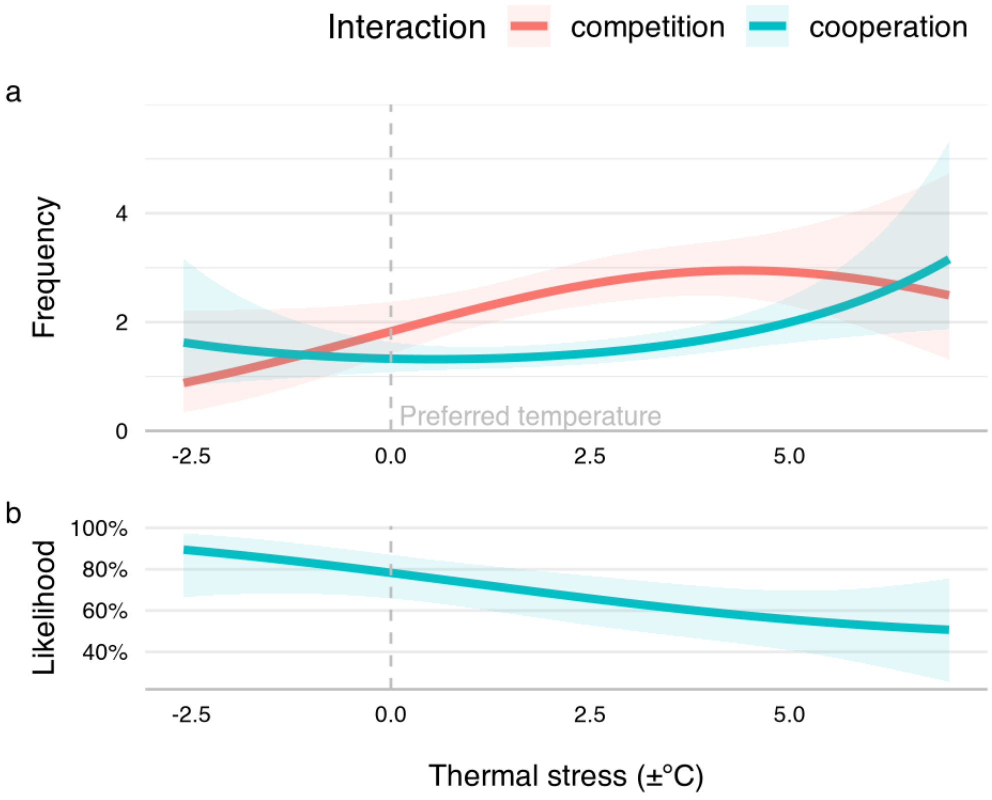

Figure 6 Line graphs showing the predicted likelihood of cooperative interactions and frequency of each interaction type; 95% confidence intervals are indicated by shaded areas

The model used to predict these interaction frequencies (Table 4) showed a significant positive relationship between thermal stress and competitive interactions ($p = 0.0217$), with a moderate but not significant association for the quadratic term ($p = 0.148$). There was also a significant difference between competitive and cooperative interactions ($p = 0.020$) and between the linear ($p = 0.025$) and quadratic ($p = 0.018$) terms for thermal stress. The random intercept for site variability was 0.260, indicating a small amount of variation between sites.

Table 3 showing the estimated value, standard error, test statistic and p-value for terms included in the poisson regression used to predict the frequency of cooperative and competitive interactions as visualised in Fig. 6a

Term	Effect	Estimate	Std Error	Statistic	P
(Intercept)	Fixed	0.605	0.135	4.474	<0.001
Linear term for thermal stress	Fixed	0.217	0.097	2.238	0.025
Quadratic term for thermal stress	Fixed	-0.025	0.017	-1.447	0.148
Interaction type (Cooperation)	Fixed	-0.322	0.139	-2.324	0.020
Linear thermal stress x interaction type (cooperation)	Fixed	-0.240	0.108	-2.227	0.026
Quadratic thermal stress x interaction type (cooperation)	Fixed	0.046	0.019	2.367	0.018
Site	Random	0.260	NA	NA	NA

Table 4 showing the estimated value, standard error, test statistic and p-value for terms included in the binomial regression used to predict the likelihood of cooperative interactions as visualised in Fig. 6b

Term	Effect	Estimate	Std Error	Statistic	P
(Intercept)	Fixed	1.280	0.323	3.960	<0.001
Linear term for thermal stress	Fixed	-0.289	0.146	-1.981	0.048
Quadratic term for thermal stress	Fixed	0.016	0.026	0.600	0.549
Site	Random	1.377	-	-	-

5. Discussion

I investigated changes in species interactions among reef fishes at 30 locations along the east coast of Japan and the Ryukyu Islands, focusing on mixed tropical and temperate assemblages. My findings revealed that species with similar thermal affinities (tropical or temperate) predominantly interacted with others sharing the same affinity at each site, cooperative interactions were more common among species exposed to greater thermal stress, and both the richness and frequency of interactions were higher at sites with coral habitats. Although not the primary focus of this study, I also observed that tropical species outnumbered temperate species along the section of Japan's east coast influenced by the warmer waters of the Kuroshio Current, which aigns ith earlier studies (Nakamura *et al.*, 2013) and reinforces the idea that these areas are suitable for studying the long-term effects of ocean warming.

At 21 sites where tropical and temperate species co-occurred, interspecies interactions were more frequent among members of the same guild, while inter-guild interactions were observed at only seven sites. Notably, most inter-guild interactions were cooperative (e.g., shoaling or schooling), whereas same-guild interactions were primarily competitive. This scarcity of competitive interactions between different guilds suggests that tropical and temperate species avoid niche overlap. This finding supports Miller et al. (2023), who argued that functional niche availability, rather than resident-invader competition, shapes the distribution of tropicalising species. If competition were the dominant force, we would expect competitive interactions to outweigh cooperative ones between guilds. Fontoura et al. (2020) showed that reef fish competitive interactions are often structured in local, nested networks driven by niche partitioning. This is consistent with our findings, which revealed continued competition within guilds, and aligns with Miller et al. (2023)'s hypothesis

However, it is possible that competition between tropical and temperate species occurs primarily in indirect forms, which were not captured by this study. Prior research (Holbrook and Schmitt, 2002) while Vergés *et al.* (2014, 2019) proposed that the influx of predominantly herbivorous tropical species leads to overgrazing, contributing to the shift from temperate, macroalgae-dominated habitats to turf-dominated ones. This behaviour could drive competitive exclusion, with invasive tropical species dominating and displacing temperate species by limiting access to their primary food sources; an effect not captured in this study. Research by Kindinger (2016) has previously shown that competition between reef fishes, particularly for shelter, primarily affects the size of individuals. Future research comparing the relative sizes of tropical and temperate species at these 21 sites, or analyzing historical shifts in species density, may help detect competitive pressures not evident here.

My findings also suggest that tropical species are more likely to engage in cooperative interactions under environmental stress, such as colder temperatures. This is consistent with the stress gradient hypothesis (Bertness and Callaway, 1994) and may represent the first demonstration of this effect in fish interactions. The stress gradient hypothesis, well documented across taxa (Brooker and Callaghan, 1998; Callaway et al., 2002; Daleo and Iribarne, 2009; Fugère et al., 2012), proposes that facilitative interactions can reduce environmental pressures and improve survival, enabling species to persist in otherwise inhospitable environments (Travis, Brooker, and Dytham, 2005). Previous studies have linked successful range expansions to behavioral adaptability in invasive species (cite), and more broadly to behavioral traits influencing invasion success (cite).

Among reef fishes, cooperative behavior between tropical and temperate species has been shown to confer benefits. For example, Smith et al. (2018) found that juvenile *Abudefduf vaigiensis* (Indo-Pacific sergeant fish) that schooled with resident temperate species at tropicalising sites along the southeast Australian coast achieved larger body sizes than those in tropical-only shoals. If temperate species similarly benefit from such interactions, it may support both tropical expansion and the persistence of temperate species at the trailing edge of their range, despite environmental and community changes.

While communities across different habitats had similar beta diversity of interactions, alpha diversity varied considerably. Vergés et al. (2019) predicted that with ongoing tropicalisation and increased herbivorous fish density, turf habitats would become dominant and less diverse than coral or macroalgal habitats. My findings support this: turf habitats exhibited the lowest frequency of interactions, second-lowest interaction richness, and the lowest beta diversity in both species and interactions. These patterns may reflect and reinforce the simplified community structures predicted by Vergés et al. (2019).

Sites with mixed coral-turf habitats—hosting both tropical and temperate species might also be expected to exhibit reduced stability and diversity, particularly under strong competition. However, my findings suggest that functional niche partitioning enables coexistence without competitive exclusion. Mougi and Kondoh (2012) showed that diverse interaction types, particularly mutualisms, are key to community stability. In this study, mixed coral-turf habitats had the highest beta diversity of both species and interactions. Nevertheless, more research is needed to assess the stability of these communities, including quantifying interaction strengths and comparing them to established tropical and temperate systems. It is possible that while interaction diversity is beneficial, community stability also depends on interaction strength reaching a certain threshold. Without achieving this threshold, communities may remain unstable or eventually favour one group over another.

While these findings provide valuable insights, several limitations should be noted. First, sites were chosen specifically for the presence of coral communities, favouring locations with higher coral cover and, consequently, more tropical species. This site selection may not fully represent interactions at locations with lower coral cover across the broader study area. Furthermore, the study area did not encompass the full leading (warming) edge of tropical species' ranges or the trailing edge of temperate species' ranges. Surveying each site only once, and only during the summer, may have further skewed the findings toward tropical species, as warmer temperatures at that time could enable seasonal expansion into areas that may be inhospitable in winter, potentially disadvantaging temperate species.

The use of a species' thermal midpoint, derived from its realized thermal niche, as a basis for assigning thermal guilds may be contentious. This approach involves a somewhat arbitrary classification system based on multi-model species distributions at a global scale and does not necessarily reflect the full range of temperatures within which a species can survive. Most marine species, particularly those within the class Actinopterygii (ray-finned fishes), typically exhibit thermal niches spanning approximately 10°C (Stuart-Smith, Edgar and

Bates, 2017). As a result, species with thermal midpoints around 23.5°C may functionally occupy both tropical and temperate environments, casting doubt on the strict delineation of thermal guilds. An alternative metric, such as the realized lower thermal limit, could arguably offer a more ecologically meaningful measure, given that species' poleward range boundaries are often constrained by cold temperatures. However, the use of the thermal midpoint in this study allowed for the modelling of how species interactions shift in response to thermal stress across both the upper and lower bounds of their realized thermal niches. This approach facilitated a more nuanced understanding of interaction patterns under warming conditions, despite the limitations inherent in guild classification.

The role of species interactions in shaping community structure under tropicalisation remains an underexplored but critical area of ecological research. To better understand how interactions are affected by warming and how these, in turn, influence species distributions, future research should aim to monitor community composition and interaction networks longitudinally, across seasons and years. Specifically, research should examine: whether the strength of cooperative interactions increases with environmental stress; how interaction networks and community stability differ across habitat types over time, particularly in mixed coral-turf systems; whether temperate species experience measurable fitness gains (e.g., increased body size, recruitment success) from cooperative interactions with tropical species; and how functional niche partitioning evolves as species compositions continue to shift under prolonged warming.

Comparative studies across latitudinal gradients and ecosystem types would also provide further insight. For example, similar facilitative dynamics have been observed in alpine and arid terrestrial systems, where environmental stress strengthens positive interactions (e.g., Callaway et al., 2002; Brooker and Callaghan, 1998). The presence of this effect in tropical reef fish suggests that the stress-gradient hypothesis may also be applied to the marine environment as a general ecological principle. It would therefore be valuable to test whether the cooperative behaviours facilitating tropical range expansion in marine systems are mirrored in other transition zones, particularly temperate–Arctic marine boundaries. Based on the multi-model distribution of marine species observed by Stuart-Smith et al. (2015), we might expect to see similar patterns of community and interaction restructuring in this zone. A broader, comparative framework would help identify global patterns and improve our understanding of how species interactions mediate ecological responses to climate change.

Despite the insights gained, several limitations must be acknowledged. First, sites were chosen specifically for coral presence, likely biasing the sample toward areas supporting more tropical species. Thus, the findings may not represent interactions at sites with lower coral cover. Additionally, the study area did not encompass the full extent of the leading (tropical) or trailing (temperate) edges of species' ranges. Each site was surveyed only once, during summer, a period when warmer waters may favor tropical species. This seasonal snapshot might miss interactions or community dynamics that occur at other times, particularly those disadvantaging temperate species.

The role of interactions in shaping tropicalising communities remains understudied, presenting several avenues for future research. Understanding how interactions influence species distributions under tropicalisation requires long-term and spatially broad monitoring. Ideally, site-specific observations should be compared with historical population data to assess deviations from past norms in the context of global warming. While this study focused on the behavior of "invasive" tropical species, it supports the presence of the stress gradient effect and highlights the role of mutualistic interactions in facilitating range expansions. However, more work is needed to confirm whether these benefits also extend to temperate species.

Given that global ocean warming is widespread, comparing behavioral patterns from tropical-temperate transition zones with those at temperate-Arctic boundaries would be valuable. Based on the multi-model distribution of marine species described by Stuart-Smith et al. (2015), similar patterns may be expected in both regions. Such comparisons would help reveal medium- to long-term ecological trends and clarify the role of environmental and habitat changes in community structure. Ultimately, a complete understanding of tropicalisation’s impact will require studies that include higher latitudes and capture the full extent of both tropical expansion and temperate retreat.

In summary, this study provides evidence that species with similar thermal affinities preferentially interact, reinforcing thermal assemblages; cooperative interactions increase under thermal stress, supporting the stress-gradient hypothesis; functional niche partitioning reduces inter-guild competition, allowing coexistence. Together, these findings advance our understanding of how tropicalisation alters community structure and species interactions.

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