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Novel species interactions and environmental conditions reduce foraging competency at the temperate range edge of a range-extending coral reef fish

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Abstract

Poleward range extensions of coral reef species can reshuffle temperate communities by generating competitive interactions that did not exist previously. However, novel environmental conditions and locally-adapted native temperate species may slow tropical invasions by reducing the ability of invaders to access local resources (e.g. food and shelter). We test this hypothesis on wild marine fish in a climate warming hotspot using a field experiment encompassing artificial prey release. We evaluated seven behaviours associated with foraging and aggressive interactions in a common range-extending coral reef fish (*Abudefduf vaigiensis*) and a co-shoaling temperate fish (*Microcanthus strigatus*) along a latitudinal temperature gradient (730 km) in SE Australia. We found that the coral reef fish had reduced foraging performance (i.e. slower prey perception, slower prey inspection, decreased prey intake, increased distance to prey) in their novel temperate range than in their subtropical range. Furthermore, higher abundance of temperate fishes was associated with increased retreat behaviour by coral reef fish (i.e. withdrawal from foraging on released prey), independent of latitude. Where their ranges overlapped, temperate fish showed higher foraging and aggression than coral reef fish. Our findings suggest that lower foraging performance of tropical fish at their leading range edge is driven by the combined effect of environmental factors (e.g. lower seawater temperature and/or unfamiliarity with novel conditions in their extended temperate ranges) and biological factors (e.g. increased abundance and larger body sizes of local temperate fishes). Whilst a future increase in ocean warming is expected to alleviate current foraging limitations in coral reef fishes at leading range edges, under current warming native temperate fishes at their trailing edges appear able to slow the range extension of coral reef fishes into temperate ecosystems by limiting their access to resources.

Keywords: range extensions, tropical vagrants, ocean warming, behavioural interference, foraging performance, aggressive interactions, temperate reefs

Introduction

Climate change is a major force driving global redistribution of species on land and in the ocean (Poloczanska et al. 2013; Pecl et al. 2017). However, the successful establishment and ecological impacts of range-extending species (i.e. species that change their distribution limits to keep pace with their shifting temperature niches, Doak and Morris 2010) on recipient communities will strongly depend on interaction strength with local species (Masciocchi et al. 2009; Gilman et al. 2010). It is common knowledge that the structure of natural communities is shaped by biological interactions (Bolker et al. 2003; Wisz et al. 2013) and such interactions are one of the pillars maintaining ecosystems in equilibrium. Thus, disruption of species interactions that have established over long evolutionary periods may lead to disruption of key ecosystem functions (Bascompte et al. 2006; Ives and Carpenter 2007; O'Gorman and Emmerson 2009). For example, the poleward influx of tropical species has already caused regime shifts in native temperate ecosystems in which recovery to the previous natural stage has become difficult (Wernberg et al. 2016). In Japan, the arrival of tropical herbivorous fishes caused the depletion of the principal habitat-forming species (kelp forests), opening up space for the colonization of corals (Nakamura et al. 2013). There is evidence that this phenomenon is rapidly occurring as well along the Australian temperate coasts, as the abundance of tropical and subtropical herbivorous fishes and corals has increased in the last few decades (Bennett et al. 2015**;** Booth and Sear 2018; Monaco et al. 2021). Yet, few studies incorporate novel ecological interactions into predictions of species range shifts and their establishment in novel ranges.

Without considering species interactions, it remains difficult to accurately forecast the impacts of range-extending species (e.g. they may be more aggressive or have higher foraging performance) on local species, and evaluate whether they are therefore likely to increase their abundances at higher latitudes to the detriment of local species under global warming (Shinen and Morgan 2009; Callaway and Ridenour 2004). Invasion theory postulates that competition is one of the main mechanisms driving successful invasion of alien species because they are usually superior competitors compared to native species (Sakai et al. 2001; Vila and Weiner 2004). Similar to alien species, the influx of range-extended species can reshuffle species dominance in temperate systems or displace native species with lower competitive performance (Nagelkerken and Simpson 2013; Milazzo et al. 2013). Although the pace of invasion by range-extending species is typically slower than that of introduced species (Sorte et al. 2010), the consequences and magnitude of their establishment might be very similar (Kola and Lodge 2001; Sorte et al. 2010). Thus, given the potential emergence of competitive interactions among range-extending and native species, there is a pressing need to understand how native species might alter the establishment and persistence of range-extending species.

Whilst many invasive species are superior competitors, this is not always the case (Kimbro et al. 2013; Levine et al. 2004; Parker et al. 2007). The biotic resistance theory postulates that native species sometimes exhibit higher competitive ability than invaders, reducing establishment and persistence of invaders (Levine et al. 2004; de Rivera et al. 2005; Von Holle 2005; Von Holle and Simberloff 2005; Fridley et al. 2007). Nevertheless, only few studies on marine and terrestrial range extensions have focussed on success or failure of local species to resist the establishment of novel species into their communities (Paini et al. 2008). Hence, competitive effects of invaders as well as natives are critical to understand potential changes to community structures under future climate (Vilá and Weiner 2004; Paini et al. 2008). Alternatively, species might change their behaviour through phenotypic plasticity and avoid or reduce direct conflicts and enable coexistence (Perri and Randall 1999; Wilson et al. 1999; Lambert 2002). For example, avoidance of dominant species and adjusted retreat and escape behaviours can facilitate the coexistence of some species by decreasing their risk of injuries and agonistic-related stress (Rychlik and Zwolak 2005). However, such adaptive behaviours might create trade-offs and incur costs to individual fitness (Chesson 2000; Liancourt et al. 2005). Therefore, it is expected that range-extending species that exhibit subordinate behavioural responses to native species may have lower likelihood to colonise non-native communities than range extending species that are stronger competitors. However, coexistence may occur if these new arrivals occupy a different niche than local species, or display conflict-avoidance behaviours that are not to the detriment of other fitness-related behaviours.

Over the last two decades, hundreds of coral reef fish species have been recruiting in temperate Australia during summer (Booth et al. 2007; Feary et al. 2013). These tropical fish species have not yet established breeding populations at temperate latitudes because the winter temperatures there are still below their minimum thermal tolerance. Each year, new pulses of tropical recruits arrive in temperate ecosystems, where they persist for several months until seawater temperatures drop too low (Eme and Bennett 2008; Figueira and Booth 2010). However, ongoing intensification of ocean warming and strengthening of poleward ocean currents is likely to relax these abiotic thresholds and facilitate the permanent establishment of tropical species in the near future (Figueira and Booth 2010; Booth et al. 2018). Under current warming, other factors such as species interactions with temperate fishes are also of importance, and these might buffer or retard the invasion of tropical range-extending species at higher latitudes (e.g. Pigot et al. 2013, Coni et al. 2021). Whilst some tropical and temperate fishes seem to positively interact (Smith et al. 2018) and co-exist in their trophic niches (Kingsbury et al. 2019), competitive exclusion might still exist, especially if tropical fishes have a reduced body condition due to environmental stress (Poulos and McCormick 2013). Additionally, the unknown environment of recipient communities (e.g. reduced water temperature and novel habitats, prey and predators) can affect some aspects of species behaviour, leading to a competitive disadvantage in range-extending species, which in turn would affect their behavioural interactions with local species (Figueira and Booth 2010; Figueira et al. 2019). Hence, understanding the competitive ability (ability to respond to the inhibitory effects of co-existing species) between tropical invader and temperate species may give insights into the competitive hierarchies that are emerging due to climate change (Lauchlan et al. 2019), and the identification of potential “winners” and “losers” (e.g. Liancourt et al. 2005; Poulos and McCormick 2013) that could compromise novel communities at high latitudes.

Native species could resist range-extending species through a variety of behaviours, including aggressive interactions and behavioural interference during feeding (see Table S1). Such behaviours are strongly mediated by body size (Robertson 1995; Munday et al. 2001). At the current early stages of warming, most tropical range-extending fishes still only occur as recruits and early-juveniles, with relatively small body sizes compared to co-shoaling temperate species, which creates a body-size disadvantage that can mediate the colonisation of these tropical range-extending species into novel environments where the native species are bigger on average. Yet, very little attention has been given to the question of how differences in body size might mediate the behavioural interactions of tropical range-extending species with native species, and if such biological effects are stronger or weaker than abiotic stressors (Louthan et al. 2015).

Here we test three hypotheses: (1) at cold-water leading edges where tropical fishes are invading novel temperate ecosystems their aggressiveness and foraging efficiency is lower than that of native temperate species, (2) tropical fishes exhibit reduced foraging ability and aggressive interactions as a function of increasing latitude, and (3) temperate species do not alter their foraging ability and aggressive interactions at their trailing warm-water edges where tropical species are invading. We test these hypotheses by comparing the foraging ability and aggressive interactions of a common tropical range-extending species (*Abudefduf vaigiensis* - Pomacentridae) and co-shoaling native temperate fish (*Microcanthus strigatus* - Microcanthidae) along a latitudinal temperature gradient (6° latitude, 730 km of coastline) under current ocean warming. These species were chosen as a model for novel species interactions because they are commonly observed using the same habitat and forming mixed-species shoals, suggesting a strong overlap in their ecological niches (Smith et al. 2016). Such a comparative approaches involving potential invaders and native species have often been useful in explaining what increases invader success in recipient communities (Daehlet 2003).

To evaluate whether foraging competency of tropical and co-shoaling temperate fishes is altered along a latitudinal temperature gradient (from subtropical to temperate waters) in a climate warming hotspot, we quantified their aggressive interactions (chasing and escaping rates) and foraging performance in terms of perceiving, inspecting, and consuming prey *in situ*. Additionally, to reveal whether altered foraging performance and aggressive interactions were related to composition of local species communities, we also quantified the abundance of all temperate and tropical range-extending fishes that shared the same habitat and belonged to the same trophic guild (omnivorous), and that could potentially interact behaviourally with invading vagrants. Understanding whether interactions with native species might act in synchrony with changing abiotic conditions is crucial to predict the likelihood of tropical fish invasions in temperate environments, and their potential effects on temperate fish communities under ongoing climate change.

Materials and Methods

Study area and species

The study was conducted at six sites ranging from low to high latitudes along the south-eastern Australian coast (Fig. 1) during the summers of 2017 and 2018 when recruitment of tropical fishes peaks (January to May). The lower latitude (two sites at South West Rocks) is considered to be the most similar environment to the tropical fish's native range, comprising subtropical reefs where the abundance of tropical fish species is highest among the three latitudes studied (Fig. S1), and the mean seawater winter temperature (Table S1) does not surpass their lower thermal tolerance (i.e. ~18-22 ºC; Djurichkovic et al. 2019). At this latitude, the benthic environment is mostly composed of bare rocks (site 1) or a mosaic of sparse oyster reefs and rocks (site 2). The middle latitude is situated around Sydney, and included three sites which reflect tropicalisation hotspots (Booth et al. 2007): Shelly Beach, Little Manly, and Narrabeen. The benthic reef community at Shelly Beach and Little Manly is composed of a mosaic of macroalgae (e.g. kelp), turf-forming algae, bare rock and sea urchin barrens, while at Narrabeen it is mainly comprised of bare rock, turf algae and sparse oyster reef. The high latitude site (Narooma) represented the coldest studied site (Table S2), and comprised the most unfamiliar and hostile environment for tropical fishes where the abundance of temperate fish species is highest among the sites (Fig. S1). At this site, tropical fishes were found on shallow bare rocks and patches of sparse oyster reefs. The sites at the low and middle latitudes were chosen based on an 18-yr study of ongoing tropical fish settlement on shallow rocky reefs along the coast of south-east Australia (Booth et al. 2007; Booth et al. 2018), while the site at the high latitude has been only recently monitored (~ 3 years). For each latitude, sites (if more than one sampled) were pooled due to the low number of replicate fishes found at some sites.

We selected one model species for each temperature affinity (tropical vs temperate): (1) the most common tropical range-extending species *Abudefduf vaigiensis*, and (2) the common co-shoaling temperate species *Microcanthus strigatus*. The tropical species is a common inhabitant of warm Indo-Pacific reefs including the Coral Sea (FishBase - Froese & Pauly 2016), but is also a vagrant that occurs every summer along the south-eastern Australian temperate coast (Booth et al. 2007). The temperate species occurs throughout subtropical (Central Queensland) and temperate (southern New South Wales) Australian reefs. These two species have coexisted for longer periods of time at our subtropical site at the low latitude (during all seasons) than at the high latitude sites where they only co-occur on a seasonal-basis, i.e. January to May (Feary et al. 2014). They often form mixed-species shoals, usually share the same habitat, and belong to the same trophic guild (omnivorous feeders).

They were also the two species most attracted to the *in situ* experimental prey releases, allowing for sufficient replication within each latitude (*Abudefduf vaigiensis*: low = 20, middle = 24, high = 22 and *Microcanthus strigatus*: low = 20, middle = 20, high = 16). Most of the tropical fishes observed from the low to high latitudes are recruits and early-juveniles. Juvenile individuals also occurs, however, in a smaller quantity.

Data collection and experimental design

For each fish species, we (1) quantified aggressive interactions with all directly surrounding species, and (2) tested their foraging performance based on various foraging behaviours, as a function of latitude (ranging from warmer to cooler sea temperatures) and abundance of all species attracted to the released prey. Abundance of species was separated into three groups: (1) abundance of conspecifics (individuals of the same species) of each studied species, (2) abundance of all native-temperate fishes, and (3) abundance of all tropical range-extending fishes. The last two groups do not include individuals of the focal species.

As tropical fish are commonly found in shallow waters (water depth ranging from 50 cm to 2 m) along the shoreline of embayments, sampling was carried out by a maximum of two divers on snorkel. Seven behaviours, five as a proxy of foraging performance and two as a proxy of aggressive interactions (see Fish Behaviour section below), were quantified *in situ* for each fish species using a maximum of 5 min. of video (GoPros) recording. A manipulative underwater experiment was performed to attract fish and instigate species interactions (foraging arena experiment) (Fig. S2). At each site, foraging arenas (low = 40, middle = 44, high = 38) were deployed over three days. On a day to day basis, data collection was carried out in different areas to avoid filming the same individuals. The experiment comprised artificial release of dead prey (brine shrimp, *Artemia*). Prey were delivered through a tube of

2.5 cm in diameter and 1 m in length attached to a dive weight that was positioned on the reef substratum at approximately 50 cm from a fixed camera (GoPro) with the camera lens directed toward the prey released point. This distance was chosen to best observe the tropical fish recruits that were usually < 5 cm in body size. A two-minute period was incorporated as acclimation time to the experimental devices before releasing prey. The observer maintained a distance of at least 2 m from the experimental prey release site during the entire video recording, only briefly approaching when release of fresh prey through the tube was needed. Recruits and early-stage individuals of tropical and temperate species are relatively site-attached, minimising the chance that the same individual was repeatedly recorded across replicate recordings. To allow for independent observations, foraging arena experiments were randomly performed with a distance of at least 2 m of each other for both tropical and temperate species. The prey were constantly released through the tube via a 60-ml syringe. Each syringe contained ~1.25 g of brine shrimp (*Artemia*) mixed with ~60 ml of salt water, but only half of the syringe content was released each time. At the start of each foraging arena experiment, half of the syringe content was released at a constant rate through the tube to attract fish and aggregate them within the field of view of the camera. Once all released prey had been consumed by the fishes or had dissipated due to water currents, an additional release of prey (i.e. another half of a syringe content) was performed. This procedure was repeated until the end of each 5-min recording (~ 10 releases of ~12.5 g of brine shrimp each per recording). Recordings were performed under the wide angle setting with a resolution of 1080p at a speed of 25 frames/sec.

The results should be interpreted within the context of experimental food provision, as patterns may differ when natural prey are considered. Nevertheless, our study provides experimental support from the wild of the inherent capacity of temperate fish to affect the performance of tropical vagrants through interference behaviours.

Fish Behaviour

The video recordings were evaluated using VLC media player 2.1.3 on a desktop computer. The following behaviours were quantified for each focal individual in each recording (Table S1): (1) prey attraction time, measured as the time (seconds) it took for the fish to swim towards the tube (i.e. prey release point) and take a bite at the prey upon their first release, (2) minimum distance to prey, measured as the shortest distance (cm) (i.e. visually estimated using a ruler) that the fish approached the prey release point during its observation time, (3) prey inspection rate, measured as the number of times an individual approached (distance of ≤ 5 body lengths) the prey release point as soon as the prey was released, (4) bite rate, continuously counted during the observation and measured as the total number of successful bites taken at the released prey, (5) retreat rate, continuously counted during the observation and measured as the number of times a fish approached the prey release point within 5 body lengths but decided to abruptly return to its previous position, (6) chasing rate, continuously counted during the observation and measured as the number of times that the focal individual swam aggressively (e.g. attacking an individual and forcing it away from the released prey) towards another individual, and (7) escaping rate, continuously counted during the observation and measured as the total number of times that the focal individual fled from an aggressor. The behaviours that were measured as continuous counts (prey inspection, bites, retreats, chasing, and escaping) were then expressed as rates per unit of time (e.g. bite rates/sec.). These were calculated by dividing the respective behavioural counts of each individual by its total observation time. When a chasing event was observed, the body size of the individuals involved in this interaction was registered to check if this behaviour could be related to differences in body size. For example, when a temperate fish chased the focal tropical individual, the size of the aggressor (if it was larger or smaller) was registered in comparison with the size of the focal fish.

To avoid pseudo-replication only one individual of each species was randomly chosen (e.g. the first individual seen in the group was selected) and analysed for each video recording, especially when they were shoaling with individuals of the same species. All behaviours of an individual were analysed from the same recording. The video recordings were a maximum of 5 min, but as fishes were mobile, the time that they were within the view of the camera ranged between 20 sec. and 5 min (average observation time ~ 2 min). Short observation times have been found to be sufficient to obtain a representative estimate of our focal behaviours (Figueira et al. 2009; Biro et al. 2010; Francini-Filho et al. 2010; Beck et al. 2016). The life stage (recruit, early-juvenile, juvenile) of the tropical fishes was recorded for each focal individual.

In each video where we recorded the behaviours of a single focal fish, we also quantified the abundance of all tropical and temperate fishes, and other individuals of *A. vaigiensis* and *M. strigatus* (i.e. their respective conspecific abundances) present within the field of view, and that were attracted to the released prey. For each individual section of the recording, the abundances of these three fish groups were quantified in intervals of 10 sec. These replicate abundance estimates were afterwards averaged for each individual recording.

Statistical Analyses

As tropical range-extending species were more abundant at lower latitudes and the opposite was true for the temperate species, first a permutational multivariate analysis of covariance (MANCOVA) was used to examine the effect of latitude (three levels of categorical and fixed factors – “low”, “middle”, “high”) on the behaviour (dependent variables: all seven behaviours) of the tropical and temperate species (species as a fixed factor

– “*A. vaigiensis*” and “*M. strigatus*”) using the total abundance of temperate fishes, total abundance of tropical fishes, and total abundance of conspecific individuals of *A. vaigiensis* and *M. strigatus* across latitudes as covariates. This analysis was performed only to evaluate if the effect of latitude on species behaviour was related to abundances of local species (covariate). Observation time was also included in this analysis as a covariate, because the observation time varied among the observed fishes (ranging from 20 sec to 5 min); not including it could provide a bias of the mean behavioural responses between latitude and species. Interactions between the categorical factors (latitude and species) and the four covariates were removed from the final model (MANCOVA) because their initial inclusion did not show a significant effect (i.e. meaning that the effect of latitude on species behaviour is independent of temperate, tropical, conspecific abundances and observation time) (Table S3), and maintaining them in the final model could lead to misinterpretation of the results (Engqvist 2005; Beck and Bliwise 2014). Univariate permutational analysis of covariance (ANCOVA) was then performed for each behaviour in order to clarify the interpretation of the MANCOVAs and evaluate the individual behaviours that were responsible for any latitudinal differences as revealed by the MANCOVAs. Fish life stage was also included as an explanatory variable with three levels of categorical and random factors: recruits (≤3 cm), early-juveniles (>3–4.5 cm), and juveniles (>4.5–7 cm). However, only the tropical species could be grouped in these three categories. Most of the temperate fish in the view of the camera were juveniles. Thus, the effect of the factor life stage is tested only for tropical fish.

Because the behaviours were measured using different units (which could bias the analyses), prior to all analyses, all behavioural data were standardised (i.e. scaling technique used for standardizing scores on the same scale by dividing a score’s deviation by the standard deviation in a data set). As a result, all behaviours are transformed to the same scale.

A posteriori pairwise comparisons of the means was used to evaluate differences among latitudes, species, and species within latitude when a significant interaction was present.

All analyses were performed on square root transformed data, and used Euclidian resemblance matrices. Where the number of permutations was low, a Monte Carlo test was used and post-hoc pooling of interaction terms was performed to enable a more powerful test of the main effect (only if their p-value was > 0.25; Winer et al. 1991). For significant effects ($p < 0.05$) pairwise tests were used to compare the respective means (Anderson 2001).

For the behaviours that showed a significant effect of the covariates in the ANCOVAs, we calculated their adjusted R^2 (also known as the coefficient of determination) to evaluate the strength of their relationships for each species separately. The R^2 can indicate to what extent (expressed in %) the variance of the covariate (abundance of temperate or tropical fishes, or individuals of the same species) explains the variance of dependent variables (behaviour) (Miles 2005).

The MANCOVAs, ANCOVAs, and *a posteriori* pairwise comparisons of the means were performed using the software Primer version 6.

Differences in density between species per body sizes, measured as small (individuals <5 cm), medium (5-10 cm) and large (> 10 cm) individuals during field surveys (see details in Booth et al. 2007) conducted at the same sites and years as for the videos recordings, were compared between the focal tropical and temperate fishes using permutational ANOVA. This analysis was performed to evaluate if differences in body size between tropical and temperate species across latitude could explain the differences detected in species behaviours.

Results

The behavioural repertoire (all seven behaviours combined) differed significantly across latitudes (Table S4, MANCOVA, F = 3.809, p = 0.033) and between tropical (*A. vaigiensis*) and temperate (*M. strigatus*) species (MANCOVA, F = 17.804, p = 0.0002). Pairwise tests revealed that the behavioural repertoire differed between low and middle latitudes, but not from high latitude, respectively, for both species. Only the abundance of temperate fishes (MANCOVA, F = 3.972, p = 0.004) had a significant effect on the species behaviours. Overall, the behaviours of the tropical fish were not affected by different life stage (recruits, early-juveniles, juveniles) (MANCOVA, F = 0.836, p = 0.559). The observation time of individuals was significantly related to the species behaviour (MANCOVA, F = 3.972, p = 0.004), but the interactions with latitude and species did not show a significant effect, meaning that the latitudinal differences of species behaviour were not influenced by the time of observation (Table S3).

Tropical fish species

Four out of seven behaviours that acted as proxies for foraging and aggressive performance differed as a function of latitude at least in one of the life stage categories (recruit, early-juvenile, juvenile). Bite rates (ANCOVA, latitude: p = 0.0002) and prey inspection rates (latitude × species interaction: p = 0.039) were lower at middle and high latitudes than at low latitude, while prey attraction time (latitude × species interaction: p = 0.009) and, minimum distance to prey for recruits of *A. vaigiensis* (latitude × life stage: p = 0.023) all increased from low to middle and high latitudes. Additionally, recruits showed a shorter distance to prey than juveniles at the low latitude (Fig. 2, Fig S3, Table S5). The behaviours that indicate direct aggressive interactions (chasing and escaping rates) did not differ as a function of latitude or among individuals of each species, heterospecific tropical and temperate fish species (Fig. S4). Only two behaviours of the tropical fish were significantly related to the abundance of temperate fishes and conspecifics: retreat rates were positively related to the total abundance of temperate fishes ($R^2 = 0.28$; ANCOVA, $p = 0.0002$, Fig. 3a and Table S5) but negatively related to the abundance of conspecific individuals ($R^2 = 0.24$, $p = 0.032$, Fig. 3b), whilst bite rates were negatively related to the abundance of temperate fishes ($R^2 = 0.08$, $p = 0.016$, Fig. 3c), but positively related to the abundance of conspecifics ($R^2 = 0.20$, $p = 0.013$, Fig. 3d).

Temperate fish species

Temperate fishes differed in three out of seven behaviours as a function of latitude. Bite rates (ANCOVA, latitude: $p = 0.0002$) and chasing rates (latitude: $p = 0.003$) were higher at low latitude than middle and high latitudes, respectively, while prey attraction time (ANCOVA, latitude: $p = 0.0002$) was higher at middle latitude than at high latitude, but the low latitude did not differ from middle and high latitudes (Fig. 2, Table S5). Unlike the tropical fish, *M. strigatus* exhibited higher chasing behaviour against individuals of the same species and tropical fishes at low latitude than at middle and high latitudes, while they escaped more from heterospecific temperate fish at the high latitude (Fig. S4). Retreat rate was positively related to abundance of other temperate fishes ($R^2 = 0.41$; ANCOVA, $p = 0.0002$, Fig. 3a and Table S4). A weak negative relationship was observed between retreat rates and abundance of conspecific individuals ($R^2 = 0.06$, $p = 0.032$, Fig. 3b), and bite rate and abundance of other temperate fishes ($R^2 = 0.11$, $p = 0.016$, Fig. 3c). Bite rate also had a weak positive relationship with the abundance of conspecifics ($R^2 = 0.09$, $p = 0.013$, Fig. 3d).

Tropical vs temperate fish species

In five out of seven behaviours, the temperate fish showed a higher foraging performance than the tropical species at least in one of the latitudes: higher bite rate (p = 0.029), higher prey inspection (p = 0.039), higher chasing rate (p = 0.006), prey attraction time (p = 0.009), and a shorter distance to prey (ANCOVA, p = 0.002), respectively (Fig. 2, Table S5).

Whilst the density of small, medium and large sizes of individuals of the focal tropical (*A. vaigiensis*) and temperate (*M. strigatus*) species were higher at the low latitude than at middle and high latitudes, the densities of large individuals of the focal temperate fish (*M. strigatus*) were higher than the densities of large individuals of *A. vaigiensis* independent of the latitude, and the tropical fish showed higher densities of small individuals than their co-shoaling temperate species, irrespective of latitude (Fig. S5, Table S6).

Discussion

The central tenet of biological invasion theory is that alien species are often competitively stronger than non-native species and therefore experience successful invasions with substantial impacts on the communities in their novel environments (Carlton et al. 1999; Branch and Steffani 2004; Davis et al. 2003; Vila and Weiner 2004). However, we here show that the foraging competency (using various foraging behaviours as a proxy) of a common tropical range-extending fish, regardless of life stage (i.e., recruit, early-juvenile, or juvenile), is lower in its novel temperate range than in its native subtropical range and lower than that of its co-shoaling temperate fish species, which may compromise its fitness in its novel invaded range. Reduced foraging performance of tropical fish at their high-latitude range edges was expressed through (1) increased prey attraction time, (2) increased distance to prey (for recruits), (3) reduced prey inspection rates, and (4) reduced bite rates, respectively, compared to their native ranges. In contrast, the aggressive interactions with local temperate fish (chasing and escaping behaviours) during foraging did not increase in their novel ranges. Although for coral reef fishes the expectation is that feeding rates reduce in cold-temperate waters (Barneche et al. 2009, Kingsbury et al. 2020), we observed that other behaviours related to foraging performance were also compromised (i.e. increased distance and attraction time to prey, reduced prey inspection rates). Thus, the reduced foraging performance as a function of latitude suggests that tropical fishes are still poorly behaviourally adapted to either lower temperatures and the novel biological conditions (e.g. surrounding habitats), which might increase their vulnerability to local competitors and predators (Figueira et al. 2019). Cooler-temperate waters are known to cause lower metabolic rates and foraging performance in *Abudefduf vaigiensis* and this is linked to a reduced energy allocation towards somatic growth (Kingsbury et al. 2020). Our observed decline from low to high latitude in foraging performance by tropical range-extending fishes may be restricting their growth, survival, and consequent permanent establishment in temperate ecosystems under current ocean warming.

Species composition at high latitudes can alter the foraging performance of tropical species in their novel temperate ranges. We show that tropical fishes were more efficient in approaching (decreased retreat rates) and consuming (increased bite rates) prey with increased abundances of conspecifics (irrespective of latitude), but contrastingly an increased abundance of temperate fishes increased their retreat rates. At sites with higher abundances of typically larger temperate fishes, these aggregated around the released prey and formed a physical barrier, preventing tropical fishes from approaching the released prey (Fig. S2). Such physical displacement has also been observed in native vs invasive terrestrial organisms (Masciocchi et al. 2009). Density-dependent competition is often observed among fishes. For example, at elevated abundance, coral-dwelling damselfishes become more aggressive and interference competition for refuge increases, leading to inferior competitors being more susceptible to predation (Holbrook and Schmitt 2002). Unexpectedly, a higher abundance of temperate fishes was not related to an increased aggression (escaping and chasing rates) between the tropical and temperate species. No signs of aggressive interactions between tropical and temperate species have been reported before. Instead, Smith et al. (2018) revealed that *A. vaigiensis* increased their growth rates at temperate reefs when schooling with temperate species. Additionally, Kingsbury et al. (2019) found that these tropical and temperate species occupied segregated trophic niches that did not overlap significantly probably due to their generalist feeding strategies. Nevertheless, in our experiment we observed *M. strigatus* and other temperate fishes (e.g. mado, *Atypichthys strigatus*; sweep, *Scorpis lineolatus*; yellow bream, *Acanthopagrus australis*) all to be aggressively interacting with *A. vaigiensis* and interfering in their performance by inhibiting their access to food resources during their feeding, indicating that native temperate fishes were capable of interfering in the performance of tropical fishes by inhibiting their access to food resources. Although *A. vaigiensis* are considered diet generalists (zooplankton, algae and invertebrates) and thus experience less competition for specific prey species (Anderson et al. 2017; Kingsbury et al. 2019), such food items differ in nutritional values. This means that temperate fishes can still limit the foraging performance and fitness of generalist tropical fishes on temperate reefs by restricting their access to more nutritious food items. With accelerating ocean warming, a higher diversity and abundance of tropical fishes is expected in temperate ecosystems (Fowler et al. 2017). Whilst under current warming, larger-sized native temperate fishes may slow the pace of tropical invasions through behavioural interference during feeding, increasing abundances and body sizes of tropical fishes under future warming can counter these species interaction effects through increased foraging performance when shoaling with their own species.

Tropical fishes appear to have a lower competency than temperate fishes in cool-water environment, as indicated by an overall lower foraging and aggressive performance (four out of seven behaviours) in their novel ranges (mid and high latitudes) than the temperate species. Inferior competitors often suffer high mortality rates by being more susceptible to predation and competition (Forrester and Steele 2000; Holbrook and Schmitt 2002; Almany 2003). In addition to low temperatures, this reduced competency compared to the temperate fish may be related to differences in body size. Most of the tropical fishes at temperate latitudes were smaller than the temperate fishes and are therefore likely to be behaviourally subordinate to larger juvenile or adult local temperate fishes in terms of feeding competency (Persson 1985; Young et al. 2003; Poulos and McCormick 2013). For instance, 91% of the escaping events registered for the tropical species were from temperate fish species, and all of the temperate fishes (100%) were larger than the tropical ones, indicating the propensity of tropical range-extending fish to be competitively excluded from native fishes in at least the initial stage of tropicalisation. However, shoaling with temperate fishes (including *M. strigatus*) can sometimes also facilitate the performance of tropical fishes in temperate ecosystems by enhancing access to resources and hence increasing growth (Smith et al. 2018) and survival rates (Paijmans et al. 2020). Under current warming, temperate fishes still seem to have a behavioural advantage at their trailing edges over range-extending tropical fishes through larger body sizes, higher foraging and aggressive performance and higher abundances.

As expected, the performance of the temperate fish species was largely similar across latitude. Only three out of seven behaviours were affected by latitude (i.e., increased bite rate and chasing rate at the warmer low-latitude and increased prey attraction time at the middle than high latitudes). Such higher foraging and aggressive performance at low latitude might be explained by the fact that the natural range of *M. strigatus* covers all sites that we studied across the latitudinal gradient (Tea et al. 2019), and that they perform best at subtropical-warmer temperatures in the centre of their distributional range (Payne et al. 2016). A similar pattern was found in other temperate marine fish species in the Tasman Sea (Neuheimer et al.

2011). As temperate species have a wider thermal niche than tropical species (Tewksbury et al. 2008; Perez et al. 2016), current ocean warming initially has positive rather than negative effects on some of the performance traits of temperate fishes at their trailing edges.

We demonstrate that at higher latitudes (in novel temperate environments) and at elevated abundance and larger body sizes of temperate fishes, the foraging performance of range-extending tropical species is currently compromised. This suggests that both physical and biological factors might be acting in synchrony to restrict the establishment of tropical species in temperate ecosystems under current warming. Behavioural interference for prey resources by larger temperate fishes can limit resource access and might force tropical species to use less desirable resources slowing the initial stages of tropicalisation of temperate ecosystems during which tropicals are overrepresented by small recruits. However, when the thermal stress of temperate environments is relaxed under future warming and the performance and survival of vagrant tropical fishes is no longer affected by low water temperatures, they will persist until adulthood and the likelihood of stronger behavioural interactions with native species may increase in temperate ecosystems.

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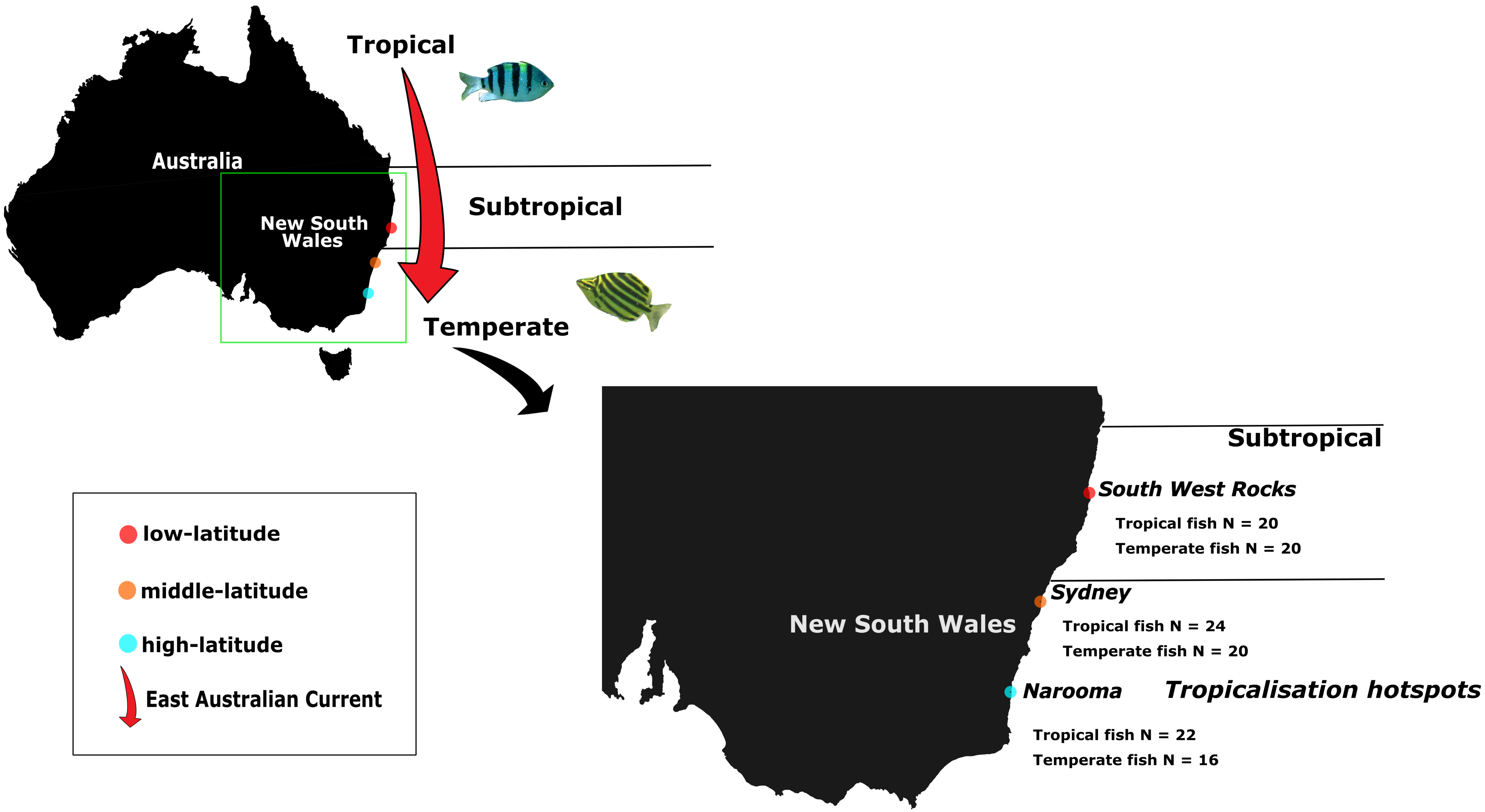
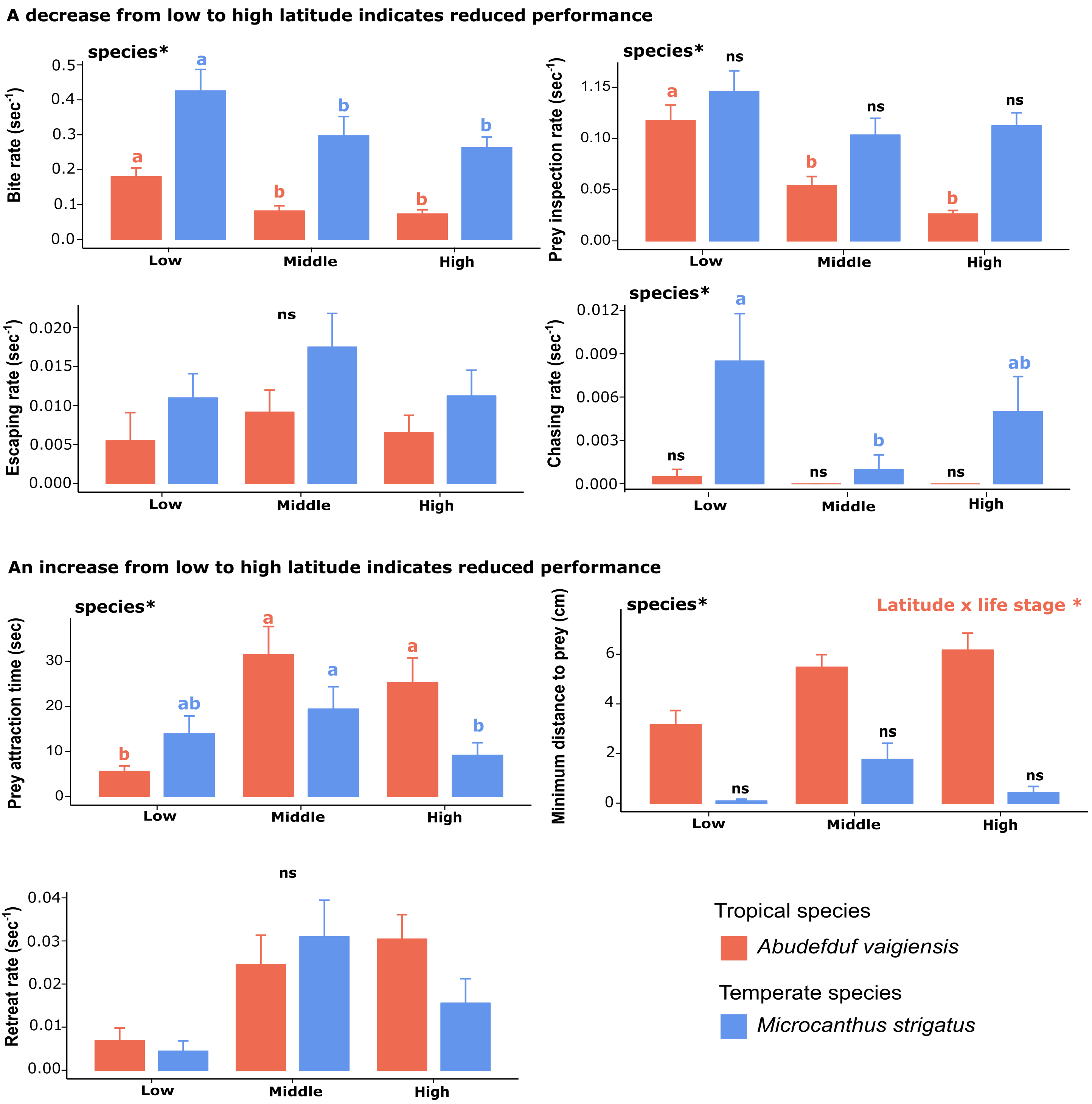
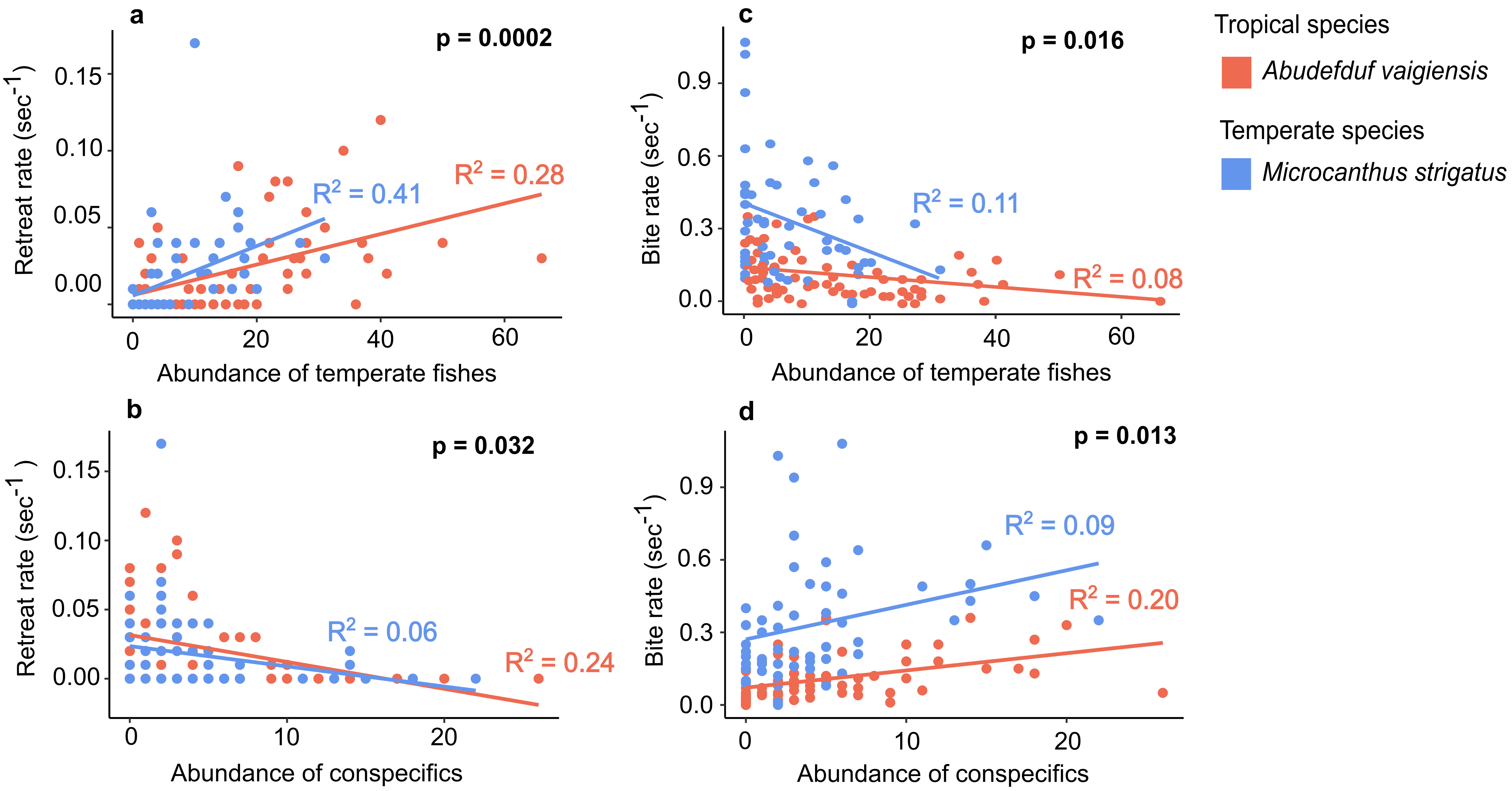
Figure 1. Map showing the sites of the *in situ* manipulative experiments and the tropical (*Abudefduf vaigiensis* - top photo) and temperate (*Microcanthus strigatus* - bottom photo) fishes studied. Red circle indicates the low latitude region: two sites at South West Rocks (30°52'34"S, 153°4'2"E and 30°53'0"S, 153°2'17"E). Orange circle indicates the middle latitude region: Shelly Beach (33°48'1.13"S, 151°17'31.23"E), Little Manly (33°48'23"S, 151°17'8"E) and Narrabeen (33°42'7"S, 151°18'21"E). Blue circle indicates the high latitude region: Narooma (36°12'54"S, 150°7'51"E). N = sample size of fishes.

Figure 2. Behavioural proxies (mean + SE) of foraging competency in tropical and temperate fishes across a latitudinal gradient (see Fig. 1) based on the food acquisition and on aggressive interactions (escaping and chasing rates). The graphs are grouped into behaviours that show reduced performance when they decrease (above 4 panels) or when they increase (lower 3 panels) from low to high latitudes, respectively. Letters indicate significant latitudinal differences within species ($p < 0.05$; see Tables S5). ns = no significant differences. Significant difference between the tropical and temperate fish species within latitudes are indicated as ‘species*’ and life stage among latitude is indicated as 'Latitude × life stage *' (only for the tropical fish as indicated by the orange colour) (see Table S5).

Figure 3. Relationship between behaviours (a, b: retreat rates; c, d: bite rates) of *Abudefduf vaigiensis* and *Microcanthus strigatus* and the abundance of temperate fishes and conspecific individuals (average of total number of temperate fishes and same individuals of each focal species per sample). Adjusted R^2 show the proportion that the respective covariate contributed to the variability of the model. Model p-values for the covariates are shown inside each panel.


Tropical
Australia
Subtropical
New South Wales
Temperate
Subtropical
South West Rocks
Tropical fish N = 20
Temperate fish N = 20
Sydney
Tropical fish N = 24
Temperate fish N = 20
New South Wales
Narooma
Tropicalisation hotspots
Tropical fish N = 22
Temperate fish N = 16
● low-latitude
● middle-latitude
● high-latitude
East Australian Current


A decrease from low to high latitude indicates reduced performance
species*
Bite rate (sec^{-1})
0.0
0.1
0.2
0.3
0.4
0.5
a
a
b
b
b
b
Low
Middle
High
species*
Prey inspection rate (sec^{-1})
0.00
0.05
0.10
1.15
a
ns
b
ns
b
ns
Low
Middle
High
Escaping rate (sec^{-1})
0.000
0.005
0.010
0.015
0.020
ns
Low
Middle
High
species*
Chasing rate (sec^{-1})
0.000
0.003
0.006
0.009
0.012
ns
a
ns
b
ns
ab
Low
Middle
High
An increase from low to high latitude indicates reduced performance
species*
Prey attraction time (sec)
0
10
20
30
b
ab
a
a
a
b
Low
Middle
High
species*
Latitude x life stage *
Minimum distance to prey (cm)
0
2
4
6
ns
ns
ns
Low
Middle
High
ns
Retreat rate (sec^{-1})
0.00
0.01
0.02
0.03
0.04
Low
Middle
High
Tropical species
🟥 Abudefduf vaigiensis
Temperate species
🟦 Microcanthus strigatus


a
p = 0.0002
Retreat rate (sec^{-1})
0.15
0.10
0.05
0.00
R^2 = 0.41
R^2 = 0.28
0
20
40
60
Abundance of temperate fishes
b
p = 0.032
Retreat rate (sec^{-1})
0.15
0.10
0.05
0.00
R^2 = 0.06
R^2 = 0.24
0
10
20
Abundance of conspecifics
c
p = 0.016
Bite rate (sec^{-1})
0.9
0.6
0.3
0.0
R^2 = 0.11
R^2 = 0.08
0
20
40
60
Abundance of temperate fishes
d
p = 0.013
Bite rate (sec^{-1})
0.9
0.6
0.3
0.0
R^2 = 0.09
R^2 = 0.20
0
10
20
Abundance of conspecifics
Tropical species
🟥 *Abudefduf vaigiensis*
Temperate species
🟦 *Microcanthus strigatus*