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RESEARCH ARTICLE

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Body size mediates trophic interaction strength of novel fish assemblages under climate change

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Abstract

1. Ecological similarity plays an important role in biotic interactions. Increased body size similarity of competing species, for example, increases the strength of their biotic interactions. Body sizes of many exothermic species are forecast to be altered under global warming, mediating shifts in existing trophic interactions among species, in particular for species with different thermal niches.
2. Temperate rocky reefs along the southeast coast of Australia are located in a climate warming hotspot and now house a mixture of temperate native fish species and poleward range-extending tropical fishes (vagrants), creating novel species assemblages. Here, we studied the relationship between body size similarity and trophic overlap between individual temperate native and tropical vagrant fishes.
3. Dietary niche overlap between vagrant and native fish species increased as their body sizes converged, based on both stomach content composition (short-term diet), stable isotope analyses (integrated long-term diet) and similarity in consumed prey sizes.
4. We conclude that the warming-induced faster growth rates of tropical range-extending fish species at their cool water ranges will continue to converge their body size towards and strengthen their degree of trophic interactions and dietary overlap with co-occurring native temperate species under increasing ocean warming. The strengthening of these novel competitive interactions is likely to drive changes to temperate food web structures and reshuffle existing species community structures.

KEYWORDS
body size, competitive interactions, ecological niche, global warming, range shifts, stable isotopes, stomach content, trait similarity

1 | INTRODUCTION

Climate change is set to alter the intensity of competitive interactions through shifts in the identity, physiological performance and fitness of competing species (e.g. Alexander et al., 2015). This is especially the case where species are extending their ranges to higher latitudes under global warming, leading to novel community structures and species interactions (e.g. Alexander et al., 2015). For example, invasions by non-native species have resulted in reduced survival and biomass (Alexander et al., 2015), increased avoidance behaviours (Raymond et al., 2015) and reduced recruitment (Arrontes, 2002; Vergés et al., 2014) of native species in recipient communities. Alternatively, segregation in dietary (Azzurro et al., 2007; Kingsbury, Gillanders, Booth, & Nagelkerken, 2019), behavioural (Coni, Booth, Ferreira, et al., 2021) or habitat niches (Altieri & Irving, 2017; Epstein et al., 2019) has facilitated coexistence between some native and range-extending species, whilst, in contrast, some tropical species show enhanced growth when schooling with temperate fishes (Smith et al., 2018). However, because our insights on novel biotic interactions are largely based on the initial stages of range extensions, there is still uncertainty about how this will unfold in the future (Donelson et al., 2019).

Niche partitioning is an important strategy for sympatric species because of the increased likelihood of trait similarity among species due to environmental conditions acting as a filter for species traits (Keddy, 1992). Theory suggests that a reduction of ecological similarity between species is mediated by evolutionary differences (e.g. competitive ability) through selection as well as differences in life history trade-offs (e.g. growth and survival rates) (Bonsall et al., 2004) (Figure S1A). Such trade-offs occur because life history is constrained such that energy investment in one component (e.g. reproduction) often comes at the expense of another component (e.g. growth) (Kingsbury, Gillanders, Booth, Coni, et al., 2019; Van Noordwijk & De Jong, 1986). Interspecific differences in life history traits allow segregation via niche shifts (e.g. ontogenetic shift in insect larvae, Woodward & Hildrew, 2002), which avoids or reduces competitive interactions (e.g. Heg et al., 2005; Kondo, 1986; Kuwamura, 1984). However, because life history traits (e.g. growth rate) are sensitive to temperature change, the level of species interactions, which is partly supported by the interspecific variation in life history traits, is also sensitive to temperature change. It has been postulated that the strength of future biotic interactions likely depends on whether existing differences in life history traits (e.g. growth rate and therefore body size) will diverge (differentiate) or converge (become similar) under warming (Lancaster et al., 2017) (Figure S1A). Divergence in life history traits between species with overlapping resources is expected to facilitate species coexistence while convergence may intensify competition between species.

Body size is a key metric that is tightly linked to various fitness-related life history traits (e.g. growth, fecundity, survival, aggression) but can show highly plastic responses to temperature change (Gardner et al., 2011; Werner & Gilliam, 1984). Organisms, particularly ectotherms, are sensitive to temperature, with the speed of biochemical reactions directly accelerated by temperature increase (Gillooly et al., 2001; Hochachka & Somero, 2002). In temperate Australia, where temperate native fish species interact with smaller range-shifting non-native species from the tropics (vagrants) (Coni, Booth, & Nagelkerken, 2021; Smith et al., 2018), cool water temperatures appear to currently restrict the growth potential of the tropical vagrants (Kingsbury, Gillanders, Booth, Coni, et al., 2019). However, future increasing ocean temperatures will boost the growth rate of tropical (Djurichkovic et al., 2019; Sasaki, Mitchell, et al., 2024) but maintain or decrease the growth rate of the temperate species (Sasaki, Mitchell, et al., 2024). Forecast shifts in species growth rates under warming mean that existing body size differences between native and vagrant species with different thermal sensitivities are subject to a convergence-divergence continuum rather than a parallel shift. Considering that the body size of consumers significantly influences the feeding ability of individuals and the size range of available prey species (Mittelbach & Persson, 1998; Werner, 1986), currently observed levels of species interactions within novel species communities will be subject to change under future warming.

Here, we investigated how body size similarity mediates interaction strength between native temperate and vagrant tropical fish species. We tested the hypothesis that increasing the body size similarity of interacting fish species will increase the level of overlap in dietary composition and consumed prey size. We study the relationship between body size difference and the level of diet overlap among nine fish species in a global hotspot of climate warming (Hobday & Pecl, 2014) along the southeast coast of Australia. We estimated the strength of interspecific trophic interactions using stomach content and stable isotope analyses. Stomach contents provide detailed information regarding the prey taxa consumed (Layman et al., 2005), however, show a high degree of variation among individuals of the same species (e.g. due to short-term temporal variation and small-scale spatial variation, Allain & Leroy, 2006). To adequately describe the dietary habits of a species, the stomach content analysis requires very large sample sizes (Allain & Leroy, 2006). This limitation can be overcome by the use of stable isotope analysis, which provides temporally integrated dietary information of an individual (weeks to months) (e.g. Busst & Britton, 2018; Weidel et al., 2011; Winter et al., 2019). Thus, the combination of stomach content and stable isotope analysis are complementary to each other, and they have been successfully used together in diet studies of aquatic species (e.g. Parkyn et al., 2001; Young et al., 2018). With these indexes, we assessed the relationship between the body size similarity and the level of dietary similarity among fishes of different thermal origins.

2 | MATERIALS AND METHODS

2.1 | Fish collection

In the current study, we only used juvenile fishes because the focal tropical vagrant species are presumably restricted mainly to the juvenile stage due to high rates of winter mortality (Booth et al., 2018). We used a small hand net and a mixture of ethanol and clove oil to capture juveniles of six native temperate species (*Ambassis jacksoniensis*, *Atypichthys strigatus*, *Microcanthus strigatus*, *Parma microlepis*, *Pempheris affinis*, *Trachinops taeniatus*) and of three tropical vagrant species (*Abudefduf sexfasciatus*, *A. vaigiensis*, *Pomacentrus wardi*) from one or two sites per latitude along the southeast coast of Australia between latitudes 30.8° S and 36.8° S, across a distance of ~900 km, during February–March 2018 (see sample size, site names and geographical locations in Table S1; Figure S2). We collected all species across a small spatial scale within a site. All species except for *P. wardi*, *P. affinis* and *T. taeniatus* were also used in the Kingsbury, Gillanders, Booth, and Nagelkerken (2019) study of the trophic overlap of tropical-vagrant and temperate-local species using stable isotopes and stomach content, with some of the species occupying the same habitat types (Coni, Booth, & Nagelkerken, 2021). The tropical species collected from the sampling sites are vagrants as many of them do not survive the cold seawater temperatures during winter (Booth et al., 2018). See Figure S3 for an occurrence map for all species mentioned above. For each collected fish, total weight (g) and standard length (cm) were measured. All fish were immediately killed using *iki jime* and kept at −30°C until further processing. Fish collections were performed under animal ethics approval numbers S-2017-002 of the University of Adelaide Animal Ethics Committee and UTS ACEC 2017-1117 of the University of Technology Sydney's Animal Ethics Committee.

2.2 | Stomach content and stable isotopes analyses

For stomach content analysis, the entire gut was removed from each frozen fish, and the abundance of each prey item (excluding vegetation) inside the stomach was visually counted, their maximum lengths measured and identified at the family level using a stereo microscope. Foraminifera were not included in the analysis as they were rare, and they are often accidentally ingested with target prey (Daniels & Lipss, 1978). Autotroph prey items including algae and seagrass were grouped together, as the partly digested vegetation could not be identified, and their contribution to the diet was estimated as a count. The number ranged from zero (no autotrophs as prey) to 114. Fish with either empty stomachs or unidentifiable content due to digestion were removed from the analysis (8.6% of fish collected).

For stable isotope analysis, white muscle tissue free from scales, skin and bone was extracted from each fish and freeze-dried for at least 36 h in individual Eppendorf tubes. Dried tissue was ground using a ball mill. Powdered muscle tissues of each fish were weighed in tin capsules individually and analysed for stable δ^{15}N and δ^{13}C isotope, using a Nu Instruments NuHorizon Continuous Flow IRMS (CF-IRMS) at the University of Adelaide. We used glycine ($\delta^{13}C = -31.26‰$, $\delta^{15}N = +1.36‰$) and glutamic acid ($\delta^{13}C = -16.35‰$, $\delta^{15}N = -6.21‰$), and TPA ($\delta^{13}C = -29.08‰$, $\delta^{15}N = -0.79‰$) as reference materials. The accuracy was 0.10% and 0.05% for δ^{15}N and δ^{13}C, respectively. Stable isotope signatures of each species were shown as ellipses using *SIBER* (Jackson & Parnell, 2023).

2.3 | Data analyses

2.3.1 | Our hypothesis

To answer how body size similarity mediates interaction strength between native temperate and vagrant tropical fish species, we hypothesised that increasing body size similarity of interacting fish species will increase their level of dietary overlap. To test this hypothesis, we analysed the relationship between changing levels of interspecific differences in fish body size and diet similarity for each species group (i.e. among natives, among vagrants and for novel assemblages). A positive slope would indicate that a convergence of fish body size increases the level of dietary similarity between species.

2.3.2 | Rules for calculating the indexes

We used indexes (i.e. similarity, not raw data) for dietary analysis, and calculated these between pairs of individuals (not groups) belonging to different species (i.e. not between conspecifics), for each species group (i.e. among natives, among vagrants and for novel assemblages). The diet of individuals was compared within a site but not across sites because biotic interactions are assumed to exist only at sites where species that are compared co-occur. Species parings and the number of unique combinations for each pairing at a given site can be found in Table S2.

2.3.3 | Calculation of similarity indexes

We estimated the level of diet similarity between pairs of species using three proxies: (1) Bray–Curtis similarity index using stomach contents, (2) Euclidean similarity index based using stable isotope signatures and (3) proportional similarity in median prey size per fish stomach. As an explanatory variable, we calculated (4) fish body size similarity.

1. For the Bray–Curtis similarity index, we first calculated the Bray–Curtis dissimilarity index based on the number of prey species found in the stomach using *vegdist* (Oksanen et al., 2022). We subtracted the Bray–Curtis dissimilarity index from 1 to obtain Bray–Curtis similarity index. This index ranges from 0 (complete separation in diet) to 1 (complete overlap in diet). The number of pairwise comparison based on Bray–Curtis similarity ranged from 188 (vagrant species group), 578 (native species group) and 1776 (novel species group).
2. For the Euclidean similarity index, we calculated the Euclidean distance index using δ^{15}N and δ^{13}C isotope values using *vegdist* (Oksanen et al., 2022). We then subtracted the Euclidean distance index from the maximum value to obtain the Euclidean similarity index. The Euclidean similarity index of 0 indicates the least similarity in isotopic signatures between two species, and as the index increases isotopic similarity also increases. The number of pairwise comparison based on the Euclidean similarity index ranged from 369 (vagrant species group), 911 (native species group) and 2511 (novel species group).
3. For proportional similarity in prey size, we estimated the median prey length of all prey taxa from a fish stomach (only heterotrophic prey) for each individual fish and calculated the proportional size difference between two prey using a

$$\textit{prop. size difference} = \frac{\left| x_1 - x_2 \right|}{\left[\frac{(x_1 + x_2)}{2} \right]},$$

where x_1 and x_2 are the median prey length of an individual fish species 1 and species 2, respectively. We then subtracted the proportional size difference from the maximum value to obtain proportional size similarity. The similarity in median prey size between two species increases as the index increases. Replication for prey size similarity was (Table S2): vagrant species group ($N=75$), native species group ($N=388$) and novel species group ($N=1120$). The proportional median prey size difference ranged from 0 to 1.76.

4. For proportional similarity in fish body size, we used the above formula under (3) replacing x_1 and x_2 with standard lengths of individual species 1 and species 2, respectively, to obtain the proportional difference, and then subtracted the difference from the maximum value to obtain the proportional similarity.

2.3.4 | The model

We used generalised linear mixed models, *glmmTMB* (Brooks et al., 2017), to test the relationship between the level of fish body size similarity and that of diet similarity (i.e. prey composition similarity, stable isotope signature similarity and prey size similarity). Prior to the analysis, we considered the variables that can potentially influence the relationships of interest and examined the importance of the random variables in each model. For this, we considered the sampling site and species pair as random intercepts and fish body size similarity as random slope to account for potential variability associated with the sampling site (not latitude) and species identity in the relationship between body size difference and dietary overlap (Figure S1B). The rationale for including sampling site as a random effect is that environmental (e.g. coral cover, Nash et al., 2012; habitat complexity, Catano et al., 2015) and biotic (e.g. predation risk, Catano et al., 2015; prey availability, Horswill et al., 2017) factors that are specific to a sampling site can generate differences in the level of diet overlap between similar-sized species across sampling sites. Species identity was included as a random effect because the degree of diet overlap between species pairs can be affected by morphological similarities (Keppeler & Winemiller, 2020; Verde Arregoitia et al., 2017) and phylogenetic relatedness (Sánchez-Hernández et al., 2021; Wiens et al., 2010). As such, in the current study, two species with close morphological features or relatedness may have had a higher inter-species diet similarity than two species with distant morphology or relatedness irrespective of body size differences. Variability in slopes was included as a random effect because of the possibility that the relationship between diet similarity and body size similarity could vary among species. The importance of our random factors (i.e. sampling site, species pair at intercepts and size difference for random slope) in the model was explored with Akaike information criterion (AIC) in R (R Core Team, 2023). To select the best-fit model, we checked the normality and the assumption of constant variance of the model with the lowest AIC value using *simulateResiduals* (Hartig, 2022). We also checked for the level of correlation of random variables and disregarded the models with correlations higher than 0.9 or lower than −0.9. Our model structure and selection can be found in Table S3. As we used lognormal distribution with a log link in all models, we added 0.001 to all data the value of zero.

3 | RESULTS

3.1 | Dietary composition

Diet composition from individual guts of the three tropical vagrant species was characterised by a total of 10 prey taxa comprising zooplankton (Calanoida and Cyclopoida copepods), benthic invertebrates (Annelida, Harpacticoida, Ostracoda, Tanaidacea), eggs (taxa unidentified), algae and terrestrial insects (Figure S4). On average, gut contents for *Abudefduf sexfasciatus* contained three prey taxa (range: 1–6), *A. vaigiensis* guts contained 3.1 prey taxa (range: 1–7), and *Pomacentrus wardi* guts contained 2.8 prey taxa (range: 2–3). Diet composition from individual guts of the six temperate native species was characterised by a total of 20 prey taxa (Figure S4). On average, gut contents for *Ambassis jacksoniensis* contained 1.6 prey taxa (range: 1–3), *Atypicthys strigatusi* guts contained 5.5 prey taxa (range: 2–9), *Microcanthus strigatus* guts contain 3.7 prey taxa (range: 1–6), *Parma microlepis* guts contained 3.5 prey taxa (range: 1–6), *Pempheris affinis* gut contained 2.8 prey taxa (range: 2–3) and *Trachinops taeniatus* guts contained 2.7 prey taxa (range: 2–4). Food items that were only found in the temperate species were Amphipoda, Cnidaria, Cumacea, fish larvae, Isopoda, Gastropoda, Porifera, Siphonostomatoida and seagrass. No prey taxa were unique to tropical species.

3.2 | Stable isotope signatures

Each species displayed spatial variation in isotopic signatures. For the tropical species, mean δ^{13}C ranged from −18.9 to −19.4 (*Abudefduf sexfasciatus*), −18.8 to −19.4 (*Abudefduf vaigiensis*) and −17.8 (*Pomacentrus wardi*) and δ^{15}N ranges from 9.8 to 10.6 (*Abudefduf sexifasciatus*), 9.3 to 11.3 (*Abudefduf vaigiensis*) and 7.9 (*Pomacentrus wardi*) (Figure S5). For the temperate species, mean δ^{13}C ranged from −17.2 to −19.5 (*Ambassis jacksoniensis*), −17.7 to −18.4 (*Atypicthys strigatus*), −16.4 to −18.9 (*Microcanthus strigatus*), −18.7 (*Pempheris affinis*), −16.5 to −17.4 (*Parma microlepis*) and −18.6 (*Trachinops taeniatus*) (Figure S5). Mean δ^{15}N ranged from 11.0 to 11.4 (*Ambassis jacksoniensis*), 11.4 to 13.2 (*Atypicthys strigatus*), 12.1 to 13.3 (*Microcanthus strigatus*), 12.2 (*Pempheris affinis*), 11.9 to 12.6 (*Parma microlepis*) and 13.0 (*Trachinops taeniatus*) (Figure S5).

Sample size-corrected standard ellipse areas (SEAc) ranged from 0.048 to 2.043 (*Abudefduf sexfasciatus*), 0.132 to 1.326 (*Abudefduf* *vaigiensis*) and 0.587 (*Pomacentrus wardi*) for the tropical species. For the temperate species, SEAc ranged from 0.822 to 1.198 (*Ambassis jacksoniensis*), 0.215 to 2.035 (*Atypicthys strigatus*), 0.454 to 1.189 (*Microcanthus strigatus*), 0.335 (*Pempheris affinis*), 0.913 to 5.230 (*Parma microlepis*) and 0.034 (*Trachinops taeniatus*).

3.3 | Effect of body size difference on diet similarity

A convergence in body size similarity between individuals was generally related to an increased diet similarity based on stomach content composition, stable isotopes and/or the similarity in the median prey size consumed (Figure 1). For stomach content, the degree of diet similarity across species pairs increased significantly as a function of increasing body size similarity for novel fish species pairs ($p = 0.016$), but not for native pairs ($p = 0.511$) or vagrant species pairs ($p = 0.671$; Figure 1; Table 1). Diet similarity based on stable isotopes also significantly increased with increasing body size similarity for novel species pairs ($p < 0.001$) but not for native species pairs ($p = 0.416$) or vagrant species pairs ($p = 0.156$). With increasing fish body size similarity, similarity in median prey size for novel species pairs ($p < 0.001$) and vagrant species pairs ($p = 0.018$) increased significantly, but this was not the case for native species pairs ($p = 0.355$; Table 1; Figure 1).

Differences among sampling sites and species pair identity were important random factors for the four models which showed a significant relationship between diet similarity and body size difference (Table S3; Table 1). Of these, random factors accounted for 47.1%, 22.7% and 8.7% of variation for the novel group based on prey composition, stable isotope signatures and prey size, respectively. For vagrant pairs based on prey size, random factors accounted for 37.9% of variance.

4 | DISCUSSION

Here, we demonstrate that in a temperate climate warming hotspot, sympatric native temperate and range-extending tropical fishes will experience increased similarity in their diets as their body sizes become more similar under continuing ocean warming. This convergence in body sizes is associated with an increase in (dietary) niche overlap based on stomach contents, stable isotope diet analysis and prey size. Because many tropical vagrants in temperate ecosystems do not yet reach maturity due to high winter mortality rates under cold stress, they remain mostly restricted to the juvenile stages at the current initial stages of their range extension (e.g. in Japan: Nishida et al., 2007; Nakamura et al., 2013; Mexico, González-Cuéllar et al., 2013; Australia: Booth et al., 2018). However, as the ocean continues to warm due to climate change, the body size of tropical

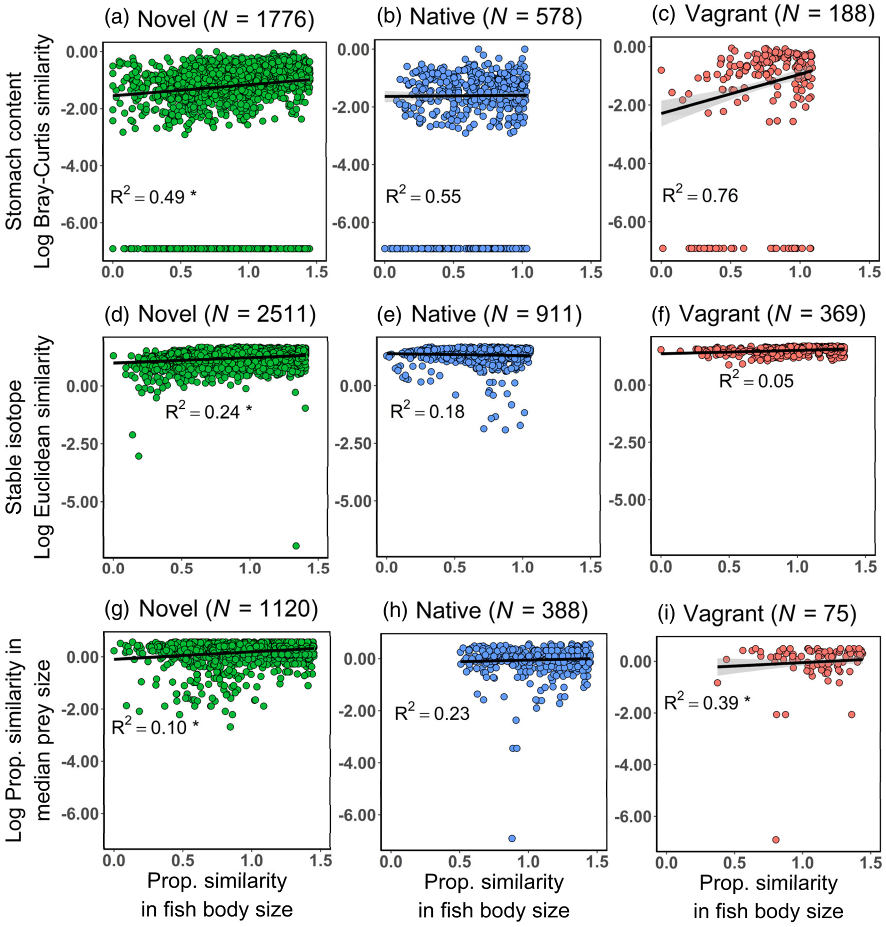

FIGURE 1 Diet similarity (log Bray–Curtis similarity, log Euclidean similarity and log proportional prey size similarity) as a function of proportional similarity in inter-individual body size for (a, d, g) novel species assemblages (temperate + tropical), (b, e, h) temperate native species (temperate + temperate) and (c, f, i) tropical vagrant species (tropical + tropical). Diet similarity was assessed on the basis of three proxies: (a–c) stomach contents, (d–f) stable isotope signatures and (g–i) median prey size difference. Each data point represents a pairwise comparison, while the fitted regression lines were obtained from generalised mixed models. Conditional R^2 statistics (including fixed and random effects) are provided with * indicating slopes that differ significantly from zero (see Table 1). The sample size for each analysis is shown between brackets with further details provided in Table S2.

TABLE 1 Generalised mixed model results testing the effect of inter-individual body size similarity (explanatory variable) on diet similarity (response variable), based on stomach contents (top), stable isotopes (middle) and median prey size (bottom), for novel species communities ('Novel'), temperate native species ('Native') and tropical vagrant species ('Vagrant').

Response	Explanatory	Competition	Estimate	95% CI	SE	*p*	R^2
Diet similarity (stomach)	Fish body size similarity	Novel	0.4907	[0.090, 0.891]	0.204	0.016*	0.487
		Native	−0.096	[−0.384, 0.191]	0.147	0.511	0.552
		Vagrant	0.319	[−1.151, 1.788]	0.750	0.671	0.757
Diet similarity (stable isotope)	Fish body size similarity	Novel	0.279	[0.255, 0.304]	0.013	<0.001*	0.235
		Native	−0.027	[−0.093, 0.038]	0.033	0.416	0.176
		Vagrant	0.137	[−0.052, 0.326]	0.097	0.156	0.05
Prey size similarity (stomach)	Fish body size similarity	Novel	0.208	[0.137, 0.279]	0.036	<0.001*	0.095
		Native	0.065	[−0.074, 0.205]	0.071	0.355	0.233
		Vagrant	0.347	[0.059, 0.635]	0.147	0.018*	0.389

Note: Estimate = slope coefficient estimated for each response for each species group, 95% CI = 95% confident interval of the estimate, SE = standard error, *p* = *p*-value, * = significant *p*-values, R^2 = proportion of total variance explained by fixed and random factors.

range-extending fishes will keep increasing in their novel cold-water ranges (e.g. Djurichkovic et al., 2019; Sasaki, Mitchell, et al., 2024), but with smaller effects on that of native temperates (e.g. Figueira et al., 2009; Sasaki, Mitchell, et al., 2024), minimising the body size differences with native temperate species. Hence, with ongoing climate change, convergence in body size between co-occurring native and vagrant species may lead to increased overlap in their dietary niches, likely resulting in increased competitive interaction strength in novel species communities.

Mixed assemblages of native temperate and tropical vagrants (our 'novel' species group) showed more consistent responses across the different dietary analyses than the other two species groups. The novel species group showed increased dietary overlap with increasing body size similarity, based on both stomach content composition as well as stable isotope analysis. Stable isotopes of muscle tissue reflect an individual's average (i.e. mixed) diet across time (i.e. weeks to months) (e.g. Ogloff et al., 2019). In contrast, stomach contents usually reveal the feeding behaviour in the short term (hours to days) and show which individual prey species are consumed (e.g. Aas et al., 2017; Fossum, 1983; Tseitlin, 1980). In our case, the existence of a relationship between body size difference and dietary overlap across both techniques suggests a temporal consistency of increased dietary overlap with reduced body size differences between species comprising novel assemblages under climate change.

In a previous study, Kingsbury, Gillanders, Booth, and Nagelkerken (2019) revealed low trophic niche overlap between native and vagrant fish species along a large latitudinal gradient along 900 km of coastline. We note that those results do not contradict the present study. If we calculate the ratio of the mean standard length of temperate species compared to that of vagrant species at each sampling site of that study (Supporting Information; Kingsbury, Gillanders, Booth, & Nagelkerken, 2019), the size ratio ranged from 0.76 to 2.60, with an average of 1.58. This indicates that their sampled population of temperate species was on average much larger than that of the vagrant species, supporting our conclusion of dietary divergence with increasing body size difference. In Kingsbury, Gillanders, Booth, and Nagelkerken (2019) 72% of the size ratio comparisons between native and vagrant species exceeded the ratio of 1.28, the latter of which is defined as the threshold above which sympatric species may coexist (Hutchinson, 1959). Hence, with decreasing body size differences between vagrant tropical and native temperate species, under future warming novel species communities are likely to become increasingly competitive.

Tropical vagrant species appear to more strongly reveal dietary overlap in response to body size differences than native temperate species in temperate warming hotspots. At their trailing edge, stomach content, stable isotope and prey size analyses of temperate fishes showed low diet similarity among species, independent of body size differences. This suggests that our co-occurring temperate species consumed taxonomically different prey species and different prey sizes throughout a range of body sizes, thereby reducing trophic nice overlap at their trailing edge of distribution. In contrast, although stomach content and stable isotope similarity among vagrants remained unchanged with changing fish body size, median prey size increased with decreasing body size differences. This suggests that in their novel ranges, tropical range-extending species occupy a smaller dietary niche than the co-occurring temperate species who have occupied these latitudes historically allowing for increased niche segregation among local temperate species.

Median prey size was a good predictor of potential dietary overlap in novel fish species communities resulting from climate change. Species without any appendages to manipulate prey like fish species usually show a positive relationship between their body size and prey size (e.g. Dunic & Baum, 2017; Mittelbach & Persson, 1998). Most of our species were omnivores/invertivores/planktivores and consumed zooplanktonic and benthic invertebrate prey types. A positive correlation between prey size similarity and decreasing fish size similarity suggests that the size range of these relatively small planktonic prey was restricted by the body size of their consumers. Hence prey size was a factor differentiating the diets of native and range-extending fish species as a function of their body size differences.

Species and sampling sites created variability for the diet correlations with body size within the novel species group. Previous studies showed that the degree of dietary overlap between species can be affected by interspecific differences in morphological features such as body shape (Russo et al., 2008), feeding apparatus (Labropoulou & Eleftheriou, 2005) and internal morphology (Ramírez et al., 2015). While many of the fish species we analysed have laterally compressed, oval-shaped, short bodies, some have slender and long body shapes (i.e. *Ambassis jacksoniensis* and *Trachinops taeniatus*). Furthermore, mouth position also differed between species (i.e. terminal and oblique). Thus, these morphological differences likely contributed to interspecific differences in feeding patterns. In addition to morphological characteristics, difference in prey availability (e.g. seasonal difference: Heng et al., 2019; Waraniak et al., 2019, spatial difference: Garcia et al., 2018; Vollrath et al., 2021) has previously been shown to affect the degree of dietary overlap between fish species. Spatial differences in biotic factors may explain why the same species pair did not show a consistent relationship across sampling sites (e.g. see *M. strigatus* × *A. vaigiensis* in Figure S5). Despite the variability observed for the diet correlations with body size across species and sampling site, the overall relationship between diet similarity and body size similarity for the novel species group supports the hypothesis that convergence in life history trait between species is associated with intensifying competition for resource (Lancaster et al., 2017).

The relationship between body size similarity and novel trophic interactions found in the current study was based on a limited number of species available at the time of sampling. Hence, it is critical to increase the empirical evidence and assess such patterns globally and for other species as well. The arrival of range-expanding tropical species is increasingly detected in Japan, Brazil and the United States (Vergés et al., 2014). In Japan, planktivores and ominivores of different thermal tolerance are already known to co-occur (Nakamura et al., 2013). Although no co-occurrence record is available, range-expanding species found in Brazil (Barneche et al., 2009; Luiz-Júnior et al., 2004) and the U.S.A. (Fodrie et al., 2010) likely share similar ecological niches with the local species, considering that both species use same environment (a.k.a., environmental filtering, Keddy, 1992). These regions will provide valuable replicates adding to the current findings and help us to assess whether the patterns that we observed are universal characteristics found between the local and range-shifting species or specific to the sites sampled from the Australian coast.

Our result has an important implication for aquatic habitats receiving vagrant species. Many of the successful range-shifting species possess the ability to utilise resources available in the habitat (Feary et al., 2013). This, in turn, increases the likelihood of interactions between vagrant and local species. Consequently, niche segregation plays a crucial role in maintaining the coexistence of vagrant and local species (e.g. Kingsbury, Gillanders, Booth, & Nagelkerken, 2019). If niche segregation is impeded by an increasing similarity in body size between vagrant and local species, resultant niche conversion may alter food web structure. For example, Vander Zanden et al. (1999) found that resident trout shifted from having a predominantly littoral fish diet to a mainly pelagic zooplankton diet, causing a drop in trophic level, following the invasion of two species of bass in Canadian lakes. They also observed that shifts in trophic position of native fish coincided with substantial declines in the abundance of littoral prey fish. The arrival of range-shifting species in the ocean is expected to be faster than on land (i.e. species redistribution speed of 72.0 km/decade vs. 6.1 km/decade for ocean and land, respectively, Poloczanska et al., 2013). Therefore, understanding how body size similarity between range-shifting vagrant and local species impacts the level of niche overlap is critical in the aquatic environment.

In conclusion, we here demonstrate that diet similarity among native temperate and tropical vagrant fish species in climate change hotspots is linked to their similarity in body sizes and not their thermal niche per se. Future warming is likely to drive convergence in body sizes between native and range-expanding species in temperate ecosystems, possibly strengthening their competitive interactions for food acquisition with ensuing results for their population sizes. Our findings emphasise the importance of demographic traits on the strength of biotic interactions between range-extending and native species in tropicalisation hotspots.

AUTHOR CONTRIBUTIONS

Minami Sasaki and Ivan Nagelkerken conceived the idea for the concept manuscript. Minami Sasaki analysed and wrote the manuscript, with SIA data supplied by Kelsey M. Kingsbury. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository, https://doi.org/10.5061/dryad.w9ghx3fx8 (Sasaki, Kingsbury, et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Conceptual diagram showing our approach to assess changes in the degree of diet overlap between two species due to body size difference (difference in life-history trait axis).

Figure S2: Map of our sampling sites as indicated by the red circles.

Figure S3: The current (i.e. including range extensions) occurrence of each of our studied species in Australia.

Figure S4: Contribution of stomach content prey composition of each species (abbreviated species name on x axis) at each sampling site.

Figure S5: Stable isotope signatures of each species at each sampling site.

Table S1: Sample sizes for stomach content analysis ('SC'—left column) and stable isotope analysis ('SA'—middle column) and average prey size ('PS'—right column) for each fish species collected at each site in New South Wales, Australia.

Table S2: The number of pairwise comparison used to calculate the index for stomach content analysis ('SC'—left column) and stable isotope analysis ('SA'—middle column) and average prey size ('PS'—right column) for each species pair occurred at each site in New South Wales, Australia.

Table S3: Table showing the combination of fixed (either body size difference or no fixed factor '1'), random intercept (sampling site 'Site' and/or species pair 'Species'), and random slope (inclusion of slope 'Y' or exclusion of slope 'N'), selected for best fitted model for the response variable for each species interaction group, based on Akaike Information Criterion (AIC) value.

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