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Trophic niche segregation allows range-extending coral reef fishes to co-exist with temperate species under climate change

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Abstract

Changing climate is forcing many terrestrial and marine species to extend their ranges poleward to stay within the bounds of their thermal tolerances. However, when such species enter higher-latitude ecosystems, they engage in novel interactions with local species, such as altered predator-prey dynamics and competition for food. Here we evaluate the trophic overlap between range-extending and local fish species along the east coast of temperate Australia, a hotspot for ocean warming and species range extensions. Stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of muscle tissue and stomach content analysis were used to quantify overlap of trophic niche space between vagrant tropical and local temperate fish communities along a 730 km (6°) latitudinal gradient. Our study shows that in recipient temperate ecosystems, sympatric tropical and temperate species do not overlap significantly in their diet – even though they forage on broadly similar prey groups – and are therefore unlikely to compete for trophic niche space. The tropical and temperate species we studied, which are commonly found in shallow-water coastal environments, exhibited moderately-broad niche breadths and local-scale dietary

34 plasticity, indicating trophic generalism. We posit that because these species are generalists,
35 they can co-exist under current climate change, facilitating the existence of novel community
36 structures.

37

38 **KEYWORDS**

39 diet, niche use, ocean warming, range shifts, stable isotopes

40

41 **Introduction**

42 To persevere in a changing environment, species must acclimate (Donelson, Munday,
43 McCormick, & Pitcher, 2011; Stillman, 2003), adapt, or relocate (Booth, Bond, & Macreadie,
44 2011; Pecl et al., 2017; Perry, Low, Ellis, & Reynolds, 2005). The balance between persistence
45 and extinction is jeopardized by climate change, causing shifts in range edges (Cheung et al.,
46 2012; Poloczanska et al., 2013; Sinervo et al., 2010), greatly impacting the structure and
47 function of ecosystems (Dawson, Jackson, House, Prentice, & Mace, 2011). Marine species
48 shift their range edges under global warming at an average rate of 19 km year⁻¹ (Sorte,
49 Williams, & Carlton, 2010), an order of magnitude faster than the average terrestrial rate of 0.6
50 km year⁻¹ (Maggini et al., 2011; Poloczanska et al., 2013; Sorte et al., 2010). Range shifts may
51 be facilitated by the strengthening of boundary currents, such as Australia's East Australian
52 Current (EAC), as well as a drought-related reduction in freshwater flow (Booth et al., 2011;
53 Johnson et al., 2011; Last et al., 2011). To date, 75% of marine range shifts occur in a poleward
54 direction (Sorte et al., 2010).

55 Whilst there are ample insights into the mechanisms and implications of species
56 invasions within terrestrial systems (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Estrada,
57 Morales-Castilla, Caplat, & Early, 2016; Peers, Wehtje, Thornton, & Murray, 2014), different
58 traits and processes (e.g. ocean currents) can regulate invasions in marine ecosystems, and

59 therefore the same principles may not be relevant to both biomes (Burrows et al., 2011; Dawson
60 et al., 2011; McKnight, García-Berthou, Srean, & Rius, 2017). Even among marine
61 ecosystems, range edge movement cannot always be generalized, in part due to the largely
62 indiscriminate nature of water movement, e.g. non-linear eddies (Bates et al., 2014; McKnight
63 et al., 2017). When range shifts occur near islands and continent edges, where habitat is limited
64 (Cahill et al., 2012; Wernberg et al., 2016), or where water movement is caused by non-linear
65 currents and eddies (García Molinos, Burrows, & Poloczanska, 2017), range shifts become
66 even more difficult to predict, and sometimes recede rather than extend.

67 Many studies have focussed on range-extensions of warm-affiliated species to higher
68 latitudes, but we still lack a detailed understanding of how recipient ecosystems and
69 communities are affected by these native invasions (Bates et al., 2014; Feary et al., 2014).
70 Several scenarios exist in which range-extending species might exert positive effects or
71 ecosystem services on recipient communities. For example, range-extending species can serve
72 as functional substitutes for extinct local species and provide food and habitat to rare local
73 species, which may be vital in achieving future conservation goals (Dudgeon & Smith, 2006;
74 Gozlan, 2008; Schlaepfer, Sax, & Olden, 2011). Research on the range extensions of boreal
75 arctic generalist fish showed an increase in connectivity between pelagic and benthic
76 communities and a subsequent reduction in modularity (Kortsch, Primicerio, Fossheim,
77 Dolgov, & Aschan, 2015). Additionally, range-extending species may be more adaptable than
78 native species, and as the climates continue to change, outlast local species and ultimately
79 evolve into new endemic species (Schlaepfer et al., 2011).

80 Negative effects of range-extensions include novel predators causing local extinction
81 of native species (Bampfylde & Lewis, 2007; Wiens, 2016), hybridization altering the integrity
82 of local species (Gozlan, 2008), threatening ecosystem functions, such as the overgrazing of
83 macrophytes (Gallardo, Clavero, Sanchez, & Vila, 2016) and the creation of urchin barrens

84 (Ling et al., 2015), and carrying infectious diseases that can harm native species (Schlaepfer et
85 al., 2011). If a non-native species has high rates of consumption and growth, they have the
86 potential to damage local communities by outcompeting, and potentially replacing, native
87 consumer populations (McKnight et al., 2017; Schlaepfer et al., 2011). This replacement could
88 intensify the local extinction rates of native species by increasing their susceptibility to
89 anthropogenic stressors, having both ecological and commercial repercussions (McKnight et
90 al., 2017). On the other hand, tropical species in temperate environments may experience
91 greater predation by local predators, as they are a novel species within the community (Almany
92 & Webster, 2004). The exact effect of range-extending species on recipient ecosystems,
93 however, depends on a variety of factors including a species' geographic range, abundance,
94 and per capita effects. Species are thought to have a high per capita effect if they are
95 functionally distinctive in their food web position, their response to environmental factors, their
96 acquisition of resources, or their effects on disturbance regimes (Chapin et al., 1997; Vitousek,
97 1990; Wardle, Bardgett, Callaway, & Van der Putten, 2011). In general, it is difficult to
98 estimate the per capita impact that a species will have until the invasion begins to happen
99 (Strayer, 2012).

100 Here we test how range-extending tropical reef fish, thought to be the most at-risk group
101 under future climate change (Comte & Olden, 2017), create novel trophic niches in temperate
102 coastal ecosystems. Novel interactions such as changes in predator-prey relationships and
103 trophic competition are likely to arise between newly sympatric groups (Alexander, Diez, Hart,
104 & Levine, 2016; Pörtner & Farrell, 2008; Wernberg et al., 2011). Using stable isotopes and
105 stomach contents, we determine how trophic niche partitioning might facilitate co-existence
106 among coastal vagrant tropical and local temperate species by exploring several scenarios of
107 niche modification: segregation, overlap, displacement, and expansion or contraction (Fig. 1).
108 Our study focuses on the temperate east coast of Australia, where coastal waters are warming

109 at a rate 3-4 times the global average (Holbrook & Bindoff, 1997; Johnson et al., 2011;
110 Ridgway, 2007).

111 **Fig. 1:** Conceptual diagram of trophic niche space of co-existing species based on existing
112 theory. Niches are displayed as convex hull polygons in isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) space. Possible
113 arrangements include niche segregation (no overlap) (a), niche overlap (b), niche displacement
114 (c), and niche expansion and/or contraction (d). The different coloured niches represent
115 different affinities (tropical vs temperate) or species. In the case of niche displacement, the
116 dashed blue line represents where the blue niche was before it was displaced.

117

118 **Materials and Methods**

119 *Study species*

120 The fish species studied were selected based on their ubiquity and ease of capture at known
121 locations, and include tropical pomacentrid damselfishes (*Abudefduf bengalensis**, *A.*
122 *sexfasciatus**, *A. vaigiensis**, *Chrysiptera brownriggii*, *Dascyllus aruanus*, *Pomacentrus*
123 *bankanensis*, *P. coelestis*, *P. moluccensis*), tropical butterflyfishes (*Chaetodon auriga**, *C.*
124 *citrinellus*, *C. flavirostris*, *C. kleinii*, *C. rainfordi*, *C. tricinctus*, and *C. vagabundus*), two
125 temperate sea chubs (*Atypichthys strigatus** and *Microcanthus strigatus**), a temperate
126 pomacentrid damselfish (*Parma microlepis**), and the temperate Port Jackson glassfish
127 (*Ambassis jacksoniensis*) (See Table S1 for fish lengths, weights, sample sizes, and *in situ*
128 densities). Some of these common tropical species, namely *A. sexfasciatus* and *A. vaigiensis*,
129 are often observed to school with the temperate *A. strigatus* and *M. strigatus* (Figueira, Curley,
130 & Booth, 2019; Smith, Fox, Booth, & Donelson, 2018). All above species were included in the
131 stable isotope analysis, but due to their small sample sizes in some regions, only species
132 indicated with ‘*’ could be used for stomach contents analysis, and consequently for
133 calculation of diet breadth and niche breadth.

134 The tropical species are commonly found in warm Indo-Pacific waters, including the
135 Great Barrier Reef (Getlekha et al., 2016; Masuda, Amaoka, Araga, Uyeno, & Yoshino, 1984).
136 The temperate species *M. strigatus* is found from Japan down into tropical and temperate
137 Australia and east towards the Hawaiian Islands, while temperate species *A. jacksoniensis*, *A.*
138 *strigatus*, and *P. microlepis* are found in south-eastern Australia only. The tropical species used
139 in this study that were observed at Sydney and further south (Fig. 2; *A. bengalensis*, *A.*
140 *sexfasciatus*, *A. vaigiensis*, *C. auriga*, *C. citrinellus*, *C. flavirostris*, *C. vagabundus*, *P.*
141 *bankanensis*, and *P. coelestis*) are considered vagrants as they only occur at these locations on
142 a seasonal-basis. Their presence drops quickly as water temperature decreases throughout the
143 seasons, and their presences are also much lower at the cold-water Merimbula site than the
144 warmer Sydney site (Table S2). The remainder of the tropical species were not observed as far
145 south as Sydney. Furthermore, the peak temperatures (below which abundances start to
146 decline) of all the selected tropical species (Booth, Beretta, Brown, & Figueira, 2018) are lower
147 than the mean winter temperatures at the two study sites (Table S2). All species studied are
148 omnivorous (Lieske & Myers, 1994; Myers, 1991; Randall, 1985). The East Australian Current
149 (EAC) transports larvae of coral reef fishes from tropical regions to southern sub-tropical and
150 temperate regions (Booth, Figueira, Gregson, Brown, & Beretta, 2007; Smith, Fox, Donelson,
151 Head, & Booth, 2016).

152

153 *Field collection*

154 Field sampling was conducted in February and March of 2017 and 2018 in four different
155 regions (Fig. 2; true coral reefs, and North, Middle, and South regions of range extensions).
156 Sample locations include South West Rocks (two sites) and Port Stephens (two sites)
157 (“North”); Sydney (two sites) (“Middle”); Bass Point (one site), Narooma (one site), and
158 Merimbula (two sites) (“South”); and One Tree Island (two sites) and Lord Howe Island (three

159 sites) (“coral reef”) (Fig. 2). One Tree Island and Lord Howe Island were sampled in 2017
160 only, and only tropical species were present and captured there. These coral reef locations were
161 chosen based on their latitude and geographical spacing, as well as *a priori* knowledge that our
162 species of interest reside there (Booth et al., 2007). Sample sizes of each species at each site
163 are shown in Table S1 and species’ seasonal ranges are shown in Table S2. Fish were caught
164 using hand nets at depths of 1-3 m using ethanol and clove oil, to anesthetize the fish. The fish
165 were immediately killed using the *iki jime* method, and placed on ice before being frozen. All
166 samples were frozen within four hours of collection and remained frozen at -30 °C before
167 processing.

168

169 **Fig. 2:** Sample locations along the southeast coast of Australia, including South West Rocks
170 (two sites; 30°52'34"S, 153°04'02"E and 30°53'00"S, 153°02'17"E) and Port Stephens (two
171 sites; 32°42'56"S, 152°10'58"E and 32°44'55"S, 152°10'19"E) (included in region “North”, red
172 marker); Sydney (two sites; 33°42'07"S, 151°18'28"E and 33°47'44"S, 151°17'25"E) (included
173 in region “Middle”, purple marker); Bass Point (34°35'54"S, 150°53'18"E), Narooma
174 (36°12'54"S, 150°07'51"E), and Merimbula (two sites; 36°44'13"S, 149°58'58"E and
175 36°53'40"S, 149°55'25"E) (included in region “South”, blue marker); and One Tree Island
176 (23°30'30"S, 152°05'30"E) and Lord Howe Island (31°33'15"S, 159°05'06"E) (“Coral reef”,
177 black marker). Tropical species were collected from study sites spanning 1,500 km (13°
178 latitude), while temperate species were collected along 730 km (6° latitude) of coastline.
179 Temperate species were not present at One Tree Island or Lord Howe Island.

180

181 *Sample preparation*

182 The scales and skin were removed from the right lateral side of each fish. After a thorough
183 cleaning of the scalpel blade, a pea-sized piece of white muscle tissue, free of bone, organs,

184 and scales, was removed and placed into a labelled tube, and immediately re-frozen. Stomachs
185 and guts were removed and frozen separately for subsequent stomach content analysis, with
186 the exception of stomachs collected in 2017, which were stored in 70% ethanol.

187 The fish tissue was freeze-dried for at least 36 hours to remove moisture. A small metal
188 ball was then placed into each individual tube, and the tissue was ground into a fine powder
189 using a ball mill. This ensured that the sample was homogeneous, and therefore representative
190 of the organism's true $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ content (Eurich, Matley, Baker, McCormick, & Jones,
191 2019). Powdered samples were then weighed into tin capsules and analysed for stable isotope
192 content using a Nu Instruments Nu Horizon Continuous Flow IRMA (CF-IRMA).

193

194 *Stable Isotope Analysis (SIA)*

195 Stable isotope analysis (SIA) can be used to estimate an individual's position in trophic space
196 (Layman, Arrington, Montana, & Post, 2007), track migration routes (Hobson, 1999), and
197 assess shifts in diet (Phillips & Eldridge, 2006). These questions can be answered by analysing
198 the type and abundance of prey and associated carbon and nitrogen stable isotopes that have
199 been incorporated into muscle tissue over the past few weeks or months (Fitzgerald,
200 Winemiller, Perez, & Sousa, 2017; Fry, 2006; Newsome, del Rio, Bearhop, & Phillips, 2007).
201 In this way, the accumulation and transformation of organic matter can be traced within a
202 community over time (Fanelli, Azzurro, Bariche, Cartes, & Maynou, 2015). SIA utilises $\delta^{15}\text{N}$,
203 the ratio of $^{15}\text{N}:^{14}\text{N}$, as an indicator of trophic position and $\delta^{13}\text{C}$, the ratio of $^{13}\text{C}:^{12}\text{C}$, as an
204 indicator of what the individual's source of prey has been over the past few weeks or months
205 (Cabana & Rasmussen, 1994; Campbell, Wandera, Thacker, Dixon, & Hecky, 2005; Newsome
206 et al., 2007). $\delta^{15}\text{N}$ increases $\sim 3.4\%$ on average (Post, 2002) at each trophic transfer due to
207 nitrogen fractionation, with different prey items resulting in different fish tissue signatures
208 (Checkley & Entzeroth, 1985; DeNiro & Epstein, 1978; McCutchan, Lewis, Kendall, &

209 McGrath, 2003). $\delta^{13}\text{C}$ varies little between trophic levels (0-1‰), as carbon fractionation is
210 primarily influenced by prey type (DeNiro & Epstein, 1978; Newsome et al., 2007; Post, 2002).

211 Here, stable isotope analysis was used to display the trophic niche of 1) temperature
212 affinity groups, and 2) individual species in isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) space. At the affinity level,
213 species were grouped into ‘tropical’ or ‘temperate’ affinities. Trophic niche areas of the two
214 affinities and of individual species were calculated for each region (North, Middle, and South)
215 using convex hulls in the rKIN package available in *R* (Albeke, 2017). Individual fish were
216 plotted in isotopic space (i.e. isospace) and a convex hull (100% of data points used) was
217 created to encapsulate the data points for each species or affinity, depending on the analysis
218 (Layman, C. A. et al., 2007; Syväranta, Lensu, Marjomäki, Oksanen, & Jones, 2013). In
219 addition to convex hulls, standard Bayesian ellipses (95% confidence interval of the bivariate
220 means) were used to calculate the niche area (SEAc) of individual species using the *R* package
221 SIBER (Jackson, Inger, Parnell, & Bearhop, 2011; Jackson & Parnell, 2019; Jackson et al.,
222 2012). Standard ellipses can correct for small sample size, such is the case for some of the
223 species used in this study, making them a more suitable tool for individual species niche area
224 analysis than convex hulls alone.

225 In addition to niche area, we also calculated the degree of overlap between niches. For
226 overlap between affinities, percentages were calculated using convex hulls in the program rKIN
227 (Albeke, 2017), with overlap expressed as the percent that each species area is being
228 overlapped. Affinity overlap percentages are from the perspective of the temperate species, as
229 it is the temperate recipient community that is being invaded and is under investigation. For
230 individual species, niche overlap was calculated using ellipses in the *R* package nicheROVER
231 (Lysy, Stasko, & Swanson, 2014). Ten random elliptical projections were created for each
232 species at each region based on posterior distribution. Overlap was then determined based on
233 the probability of one species falling into the niche of another (Swanson et al., 2015). Because

234 niches are not symmetrical, there are two possible values for each species pair, one for the
235 percent probability that hypothetical group “X” is being overlapped by group “Y”, and the
236 other for the percent probability that group “Y” is being overlapped by group “X”. For example,
237 if a large ellipse was directly on top of a smaller ellipse in isospace, one could calculate the
238 probability of overlap from the perspective of the large ellipse, e.g., 15% probability of overlap,
239 whereas the overlap probability from the perspective of the small ellipse would be 100%. Niche
240 areas which overlap by > 60% are thought to be sharing a significant amount of niche space
241 (Guzzo, Haffner, Legler, Rush, & Fisk, 2013; Schoener, 1968; Wallace, 1981). The niche
242 range, or the maximum/minimum difference of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, was also calculated
243 for each species, and then averaged across affinity for each region, to identify whether the fish
244 are occupying a similar isotopic breadth across the regions.

245

246 *Stomach Content Analysis*

247 Stomach content analysis is used to provide direct evidence of prey items consumed in the
248 hours leading up to the fish’s collection (Rybczynski, Walters, Fritz, & Johnson, 2008). Stable
249 isotope signatures provide a measure of where in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isospace fishes are situated,
250 but stomach content analysis reveals on what taxa, and in what quantities, tropical and
251 temperate fish are feeding (Svensson et al., 2017). Only stomachs collected in 2018 were used
252 for stomach content analysis, due to disintegration of the 2017 stomachs that were stored in
253 ethanol. As such, some species did not have a large enough regional sample size (e.g. *A.*
254 *bengalensis* in the Middle and *C. auriga* in the North) to be used in diet analyses (stomach
255 contents, Levins’ index of niche breadth, and Pianka’s index of diet overlap) in all regions.
256 Only species with at least 3 replicate stomachs were included for the diet analyses. However,
257 all species were still used in the isotopic niche analyses, as stable isotope data from both 2017
258 and 2018 were included.

259 The stomachs of all fish were emptied of their contents. Contents that were too digested
260 to be distinguished, as well as gastric juices, were excluded from analysis. Food items were
261 divided into broad categories, including algae, seagrass, crustaceans, worms, gastropods, eggs,
262 zooplankton, detritus, hydroids, fish larvae, parasites, nudibranchs, and terrestrial insects and
263 seeds (Layman, Quattrochi, Peyer, & Allgeier, 2007). For example, both fleshy green algae
264 and branching red algae were grouped into the broad category 'algae'. If a stomach was
265 composed of 10% zooplankton, 10% algae, 30% gastric juice, and 50% unknown matter, it
266 would be classified as containing 50% zooplankton and 50% algae to standardise diets solely
267 based on identifiable prey items consumed. The prey categories in the stomachs of each species
268 were averaged for each region to calculate diet overlap among species and across regions using
269 Pianka's index (Pianka, 1973). Pianka's diet overlap is calculated using the following equation:

270

271 (*Equation 1*)

$$272 \quad O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

273 where:

274

275 O_{jk} = Pianka's index of diet overlap between species j and species k

276 p_{ij} = proportion resource i is of the total resources used by species j

277 p_{ik} = proportion resource i is of the total resources used by species k

278 n = total number of resource states

279

280 Pianka's values range from 0-1, with 0 indicating total segregation, and 1 indicating total diet
281 overlap (Vieira & Port, 2007). Similar to isotope niche overlap, Pianka's values > 0.6 are
282 considered to represent a significant diet overlap (Wathne, Haug, & Lydersen, 2000; Zaret &

283 Rand, 1971). Statistical analyses were performed by grouping Pianka's values into either intra-
284 affinity overlap (tropical-tropical or temperate-temperate), or inter-affinity overlap (tropical-
285 temperate). ANOVA was then performed to test if there was a significant difference in overlap
286 between each of these three groups. As such, ANOVA only had region (North, Middle, South)
287 and affinity group (tropical-tropical, temperate-temperate, and tropical-temperate) as factors.

288 Niche breadth represents the range of resources that a species uses (Slatyer, Hirst, &
289 Sexton, 2013) and can be used to determine feeding strategies, and separate species into
290 specialists or generalists. Niche breadth was calculated using Levins' method (Levins, 1968)
291 and standardized using Hurlbert's method (Hurlbert, 1978). Levins' standardized niche breadth
292 equation is as follows:

293

294 (*Equation 2*)

$$295 \quad B_A = \frac{1}{\frac{\sum p_j^2}{n} - 1}$$

296 where:

297

298 B_A = Levins' standardized niche breadth

299 p_j = proportion of individuals using resource state j

300 j = resource state

301 n = number of possible resource states

302

303 Levin's standardized index produces niche breadths ranging in value from 0-1, with species
304 exhibiting a value < 0.3 considered to be specialists and values of 0.3-1 considered to be
305 generalists (Nagelkerken, Van Der Velde, Wartenbergh, Nugues, & Pratchett, 2009;
306 Novakowski, Hahn, & Fugi, 2008; Sa-Oliveira, Angelini, & Isaac-Nahum, 2014). A food

307 specialist consumes a narrow range of food sources, while a generalist consumes a wide variety
308 of food sources (Amundsen, Gabler, & Staldivik, 1996). Note that Levins' index does not take
309 into account the possibility of variation in resource abundance and availability.

310

311 *Statistical analyses*

312 Statistical analyses were performed using the program Primer-e, except the isospace niche
313 areas and overlap analyses which were calculated using the packages rKIN and nicheROVER
314 available in R (Albeke, 2017; Lysy et al., 2014). Analysis of variance (ANOVA – type III error)
315 was used to test the effects of region (“Re”; North, Middle, South; fixed factor), affinity (“Af”;
316 tropical, temperate; fixed factor), and species (“Sp”; 18 species for isotope statistics, and 7
317 species for all other analyses; random factor) on niche space. All analyses were performed on
318 fourth root transformed data, and used either Bray-Curtis or Euclidian resemblance matrices.
319 All residuals were permuted under a reduced model. Where significant differences were
320 found, pairwise tests were used to determine which treatments differed. Because the factor
321 ‘species’ is nested within factor ‘affinity’, *post-hoc* tests of any significant $Re \times Sp$ (Af)
322 interactions yielded only intra-affinity comparisons, e.g., how a particular tropical species
323 differed across regions, or how a temperate species in the North differed from other temperate
324 species in the North. As such, $Re \times Sp$ (Af) *post-hoc* results are not useful in investigating
325 dynamics between tropical and temperate affinities, only changes within each affinity.

326

327 **Results**

328 *Niche segregation*

329 Trophic niches of tropical and temperate species were largely segregated (despite their co-
330 schooling *in situ*), irrespective of latitude (Figs. 1a, 3). The niche convex hulls showed that
331 overlap between tropical and temperate niche space was minimal (28.4% in the North, 8.8% in

332 the Middle, 15.5% in the South). The negligible overlap between tropical and temperate species
333 was driven primarily by tropical *Abudefduf* species overlapping with temperate sea chubs
334 (*Microcanthus strigatus* and/or *Atypichthys strigatus*) in the North and Middle, with *Chaetodon*
335 species also overlapping temperature niche space in the South, respectively, and a combination
336 of all temperate species in the Middle (Fig. S1). In total, only four tropical-temperate species
337 pairs out of a possible 37 combinations exhibited overlap greater than 60%, above which
338 overlap is considered to be significant (Table S3). In the North, the trophic niche of tropical
339 species *A. bengalensis* was overlapped by *M. strigatus* 67.5%, yet none of the trophic niches
340 of temperate species were overlapped significantly by tropical species. In the Middle,
341 temperate species *Parma microlepis* was overlapped by tropical species *Chaetodon auriga*
342 (69.7%), but no tropical species was overlapped significantly by a temperate species. In the
343 South, temperate species *A. strigatus* overlapped tropical species *A. sexfasciatus* (76.9%) and
344 *C. flavirostris* (98.9%), but similar to the North, no temperate species was significantly
345 overlapped by a tropical species. The considerable overlap between *A. sexfasciatus* and *A.*
346 *strigatus* in the South is particularly notable because they are known to co-school.
347 Unsurprisingly, species exhibited considerable overlap with other species of the same affinity
348 (i.e. tropical species overlapping with other tropical species), regardless of region. The niche
349 segregation between affinity groups was caused by temperate species having consistently
350 higher $\delta^{15}\text{N}$ values (indicative of feeding at a higher trophic level; Fig. 3) than tropical species
351 (3-way ANOVA, $p < 0.001$), but $\delta^{13}\text{C}$ values did not differ ($p = 0.077$; Table S4a).

352 Pianka's index of diet overlap between tropical and temperate species affinities did not
353 exceed 0.6 in any region, the value above which overlap is considered significant (Fig. S3).
354 Diet overlap between species with tropical and temperate affinities was similar to the intra-
355 tropical and intra-temperate dietary overlap (Pianka's index, 2-way ANOVA, $p = 0.620$; Table
356 S4a; Fig. S3), indicating that affinity did not affect diet overlap. In contrast to isotope niche

357 area and Pianka's diet overlap, tropical and temperate species affinities had similar diet
358 compositions (3-way ANOVA, $p = 0.538$; Table S4a; Fig. 4).

359 Niche range (i.e. maximum minus minimum values) of trophic levels ($\delta^{15}\text{N}$; 3-way
360 ANOVA, $p = 0.762$) and of prey origin ($\delta^{13}\text{C}$; $p = 0.098$) did not differ between tropical and
361 temperate fishes, indicating that they feed within similar isotopic boundaries (Table S4a; Fig.
362 S4). Species with tropical and temperate affinities had similarly moderately-broad niche
363 breadths (Levins' index, 3-way ANOVA, $p = 0.455$; Table S4a; Fig. 5) with most species-
364 location combinations showing an index of > 0.3 (Fig. S5), indicative of trophic generalism.

365

366 **Fig. 3:** Trophic niche of tropical and temperate affinity groups, displayed in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$
367 space for North, Middle, and South regions (see Fig. 2) based on convex hulls. Tropical fish
368 are indicated with triangles, and temperate fish are indicated with circles. Each marker
369 represents a single fish, and polygons represent convex hulls that encapsulate 100% of data
370 points. The percentage of the temperate niche that is being overlapped by the tropical niche is
371 shown for each region. Percent overlap was calculated using the rKIN package available in R.
372 See Fig. S6 for the total niche area size of these convex hulls, and Fig. S1 for standard ellipses
373 of individual species.

374

375 **Fig. 4:** Proportional stomach contents averaged for fish species within tropical and temperate
376 affinity groups in North, Middle, and South regions from fish collected in 2018. Stomach
377 gastric juice was excluded, as was partially-digested, unidentifiable food. The remaining food
378 items were scaled up to 100%. Affinity means were calculated based on the species means in
379 each region. Algae, seagrass, crustaceans, worms, and gastropods are broad groups and may
380 contain multiple families within the taxa. See Fig. S7 for the stomach contents of individual
381 species.

382 **Fig. 5:** Mean (\pm SE) Levins' index of niche breadth (ranging from 0 to 1) for tropical and
383 temperate species across regions. A low value indicates that a species has a very small niche
384 breadth and is a specialist, and higher values (> 0.3) indicate broad niche breadth, or
385 generalism. Affinity values were calculated using species means at each region. See Fig. S5
386 for the niche breadths of individual species.

387

388 *Niche expansion/contraction*

389 When grouped into affinities, tropical species had the largest niche in the tropics (One Tree
390 Island, southern Great Barrier Reef; Figs. 1d, S2, S6a); likewise, the largest temperate species
391 niche area was found at the coldest location (i.e. highest latitude sampled). In the regions where
392 tropical and temperate species geographically overlap (North, Middle, and South), tropical
393 species had the largest niche area where temperate species had their lowest (Middle), with
394 tropical species exhibiting a niche area nearly three times the size of the temperate niche area
395 (10.5 vs 3.8, Fig. S6a). Similarly, temperate species exhibited their largest niche area where
396 tropical species exhibited their smallest (South), with the temperate niche almost double the
397 size of the tropical niche (10.9 vs 5.8). When examining species individually (using either
398 convex hulls or standard ellipses), affinity-level patterns were less discernible, although
399 temperate species continued to have a large niche area in the South and several tropical species
400 a large area in the Middle (Figs. S6b, c). The considerable dichotomy in mean tropical and
401 temperate affinity niche areas in the Middle is primarily due to the large niche areas of tropical
402 species *C. auriga* and *A. vaigiensis* (and *A. sexfasciatus* when using standard ellipses) and the
403 small niche areas of all temperate species, particularly *A. strigatus*. Both trophic level ($\delta^{15}\text{N}$;
404 3-way ANOVA, $p < 0.001$) and prey origin ($\delta^{13}\text{C}$; 3-way ANOVA, $p < 0.001$) signatures
405 differed regionally, with signatures in the tropics being lower in $\delta^{15}\text{N}$ and higher in $\delta^{13}\text{C}$ than
406 all other regions, suggesting that coral reef fishes were consuming isotopically-different prey

407 items from the far north to the South (Tables S4a, b; Fig. S2a). However, the niche range of
408 $\delta^{15}\text{N}$ (3-way ANOVA, $p = 0.624$) and $\delta^{13}\text{C}$ ($p = 0.645$) did not differ between regions for either
409 tropical or temperate species (Table S4a; Fig. S4).

410 Tropical and temperate fish consumed primarily algae, zooplankton, and crustaceans,
411 and overall decreased their consumption of algae and increased their consumption of
412 zooplankton and crustaceans as a function of increasing latitude, i.e. from North to South (Figs.
413 4, S7; Table S4a). All tropical species had different diet compositions between the latitude
414 extremes (North and South), with one species (*A. vaigiensis*) also differing between North and
415 Middle regions. Only one temperate species (*M. strigatus*) had a different diet composition
416 between the latitude extremes, yet all differed between the Middle and South regions (Fig. S7;
417 Table S4b). Additionally, temperate species decreased the number of food items consumed
418 from the highest latitude (South: 13 items) to the two lower latitudes (North/Middle: 9 and 10,
419 respectively), but tropical species ate a similar number of food items across all three latitudes
420 (9, 8, 9, respectively) (Fig. 4). Neither diet overlap (Pianka's index, 2-way ANOVA, $p = 0.702$;
421 Fig. S3) nor niche breadth (Levins' index, 3-way ANOVA, $p = 0.917$; Fig. 5) varied among
422 regions for temperate or tropical species affinity groups. On the individual species level, the
423 tropical species *A. vaigiensis* and the temperate species *M. strigatus* varied in niche breadth
424 between regions (Fig. S5; Table S4b).

425

426 **Discussion**

427 Here we show that the novel co-existence of range-extending tropical and local temperate
428 species in temperate ecosystems under climate change is facilitated by trophic niche
429 segregation (see conceptual diagram Fig. 1a). On average, temperate species had consistently
430 higher $\delta^{15}\text{N}$ values than tropical species in all regions, indicating that temperate species are
431 consuming food sources that are higher up the food chain than the tropical species they co-

432 occur with. Some individual species exhibited some degree of isotopic niche overlap, although
433 only four out of 37 tropical-temperate species combinations exhibited an overlap in niche space
434 of > 60%, above which overlap is considered to be significant. Similarly, there was a low
435 degree of overlap in stomach contents between tropical and temperate species (i.e., based on
436 Pianka's index < 0.6) in all regions. In contrast, stomach content composition revealed that
437 species of different affinities were foraging on broadly similar prey groups. This similarity in
438 prey groups is likely due to the low resolution of prey identification from stomachs (e.g. broad
439 categories like 'crustaceans' and 'algae'), which may not reflect taxonomic differences in prey
440 species within broader groups consumed. Previous studies have demonstrated that minor prey
441 items (which might not be significantly reflected within bulk stable isotope signatures) can be
442 of great importance in facilitating species co-existence (Koussoroplis et al., 2010; Nagelkerken
443 et al., 2009), and that co-existence can occur between species even when there is no apparent
444 partitioning of food resources (Pratchett, 2005). Nevertheless, niche segregation (based on
445 isotopic niche space and Pianka's dietary overlap) was observed across all latitudes studied and
446 indicates that tropical and temperate fishes are therefore less likely to compete for the same
447 prey resources at the initial phases of range-extensions in a warming ocean.

448 The fishes studied here consumed a wide range of prey groups (8-13 per region),
449 suggesting that they are generalists (Roper, 1994). Additionally, affinities exhibited
450 moderately-broad niche breadths (based on Levins' index of > 0.3) across regions, which
451 further indicates a certain degree of trophic generalism (Devictor et al., 2010; Hurlbert, 1978;
452 Sa-Oliveira et al., 2014). Generalistic feeding strategies are known to play an important role in
453 spatial partitioning and co-existence among species by minimizing competition for trophic
454 space (e.g. pomacentrid fishes) (Eurich et al., 2019). Generalists are thought to have an
455 advantage over specialists, as they are able to consume a wider array of food sources and are
456 therefore better equipped to deal with food shortages (Clavel, Julliard, & Devictor, 2011;

457 Wilson et al., 2008). Additionally, generalists are thought to be less vulnerable to climate
458 change as they have higher trophic niche plasticity and may be better able to accommodate
459 changes in resource availability and habitat (Afonso Silva et al., 2017; Slatyer et al., 2013;
460 Sunday et al., 2015; Travis, 2003). As such, trophic generalists, such as the tropical vagrants
461 and temperate locals that were examined in this study and are known to frequently co-occur or
462 school together under increasing ocean warming (Smith et al. 2018), will likely be the most
463 successful feeding strategists, or “winners”, under future climate change (Ho, Fu, Sun, Kao, &
464 Jan, 2009; Warren et al., 2001; Wilson et al., 2008). Our findings therefore provide strong
465 support that trophic generalism is mediating the co-existence of tropical fishes with various
466 local species in temperate waters under ongoing global warming.

467 Across broad spatial scales (from tropical coral reefs to temperate kelp systems),
468 tropical fishes exhibited a niche contraction with increasing latitude (as per Fig. 1d), whilst at
469 smaller spatial scales (i.e. within their novel temperate ranges) they showed niche expansion
470 where local species experienced niche contraction. In the regions where species of both
471 affinities co-occurred, tropical species exhibited their largest niche area in the region where the
472 temperate niche area was the smallest, and vice versa. This suggests that tropical and temperate
473 fish may be unable to maintain large trophic niches simultaneously, although this may simply
474 be an artefact of small and unequal sample sizes. Previous studies have suggested that an
475 expanding niche area may be a result of ecological release, or a sudden population increase due
476 to the disappearance of limiting factors (Bolnick et al., 2010; Svanbäck & Bolnick, 2007),
477 while others posit that an expansion of niche area may be due to competition (Namgail, Mishra,
478 De Jong, Van Wieren, & Prins, 2009; Schuller, Price, & Grant, 1985). In the case of
479 competition, a narrow niche may prove harmful for the local temperate fish, as a previous study
480 has shown that a small niche area and high overlap with non-native species can lead to a decline
481 in native fish populations in a freshwater lake (Córdova-Tapia, Contreras, & Zambrano, 2015).

482 A study of marine snails living along their range edge showed that thermal stress, as is possibly
483 experienced by our tropical species in the South (cool water) and temperate species in the North
484 (warm water), led to increased diet variation and therefore trophic niche expansion (Reddin,
485 O'Connor, & Harrod, 2016), highlighting the effect that range edges may have on feeding
486 plasticity. Our findings highlight that species that extend their ranges from coral reefs with high
487 prey diversity to less-diverse temperate areas may need to adjust to novel environments by
488 contracting their trophic niche. However, on smaller spatial scales local (a)biotic conditions
489 may alter trophic dynamics and lead to opposite outcomes in terms of niche expansion versus
490 niche contraction. These initially variable and plastic dynamics at the leading edges of range
491 extensions are typical of species invading new environments (irrespective of climate change)
492 (Broennimann et al., 2007; Fernández & Hamilton, 2015; Michel & Knouft, 2012), but as
493 oceans continue to warm such spatial refuges where local species can resist invasion are likely
494 to slowly disappear with more definite outcomes in terms of which species will become
495 winners versus losers under climate change (Byers, 2002; Hellmann, Byers, Bierwagen, &
496 Dukes, 2008; Moyle & Light, 1996).

497 It is important to note that stable isotope signatures may be confounded by
498 environmental stressors unrelated to changes in diet, potentially leading to inaccurate
499 depictions of trophic niche space (Karlson, Reutgard, Garbaras, & Gorokhova, 2018). A study
500 of freshwater snails showed that high temperatures, such as those experienced by temperate
501 species along their trailing range edge, may enrich $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Ek, Karlson, Hansson,
502 Garbaras, & Gorokhova, 2015). Other factors that may contribute to differential incorporation
503 of stable isotopes include body size, growth rate, and protein turnover (Martínez del Rio, Wolf,
504 Carleton, & Gannes, 2009). Because tropical species are not yet established in the southern
505 study sites, fish were caught opportunistically, making it difficult to control for body size.
506 Temperature extremes may affect metabolic rate (Clarke & Johnston, 1999; Gillooly, Brown,

507 West, Savage, & Charnov, 2001), causing altered stable isotope tissue incorporation to increase
508 for reasons unrelated to food intake (Carleton & Rio, 2005). For these reasons, other factors
509 might have also partially contributed to some of the variability in trophic niche segregation as
510 displayed by our study species.

511

512 **Conclusions**

513 How tropical and temperate species fill and share trophic niches within novel mixed
514 communities resulting from global change is a key determinant of future species persistence
515 and biodiversity. We demonstrate that range-extending tropical and local temperate fish species
516 exhibit segregated trophic niches, mediated by trophic generalism and local-scale dietary
517 plasticity. We conclude that range-expanding species adjust their trophic niches at their leading
518 edges and occupy open niche space thereby avoiding significant dietary overlap with local
519 species, despite operating under suboptimal environmental and biotic conditions that are
520 characteristic of novel ranges at the initial stages of climate change.

521

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530

531

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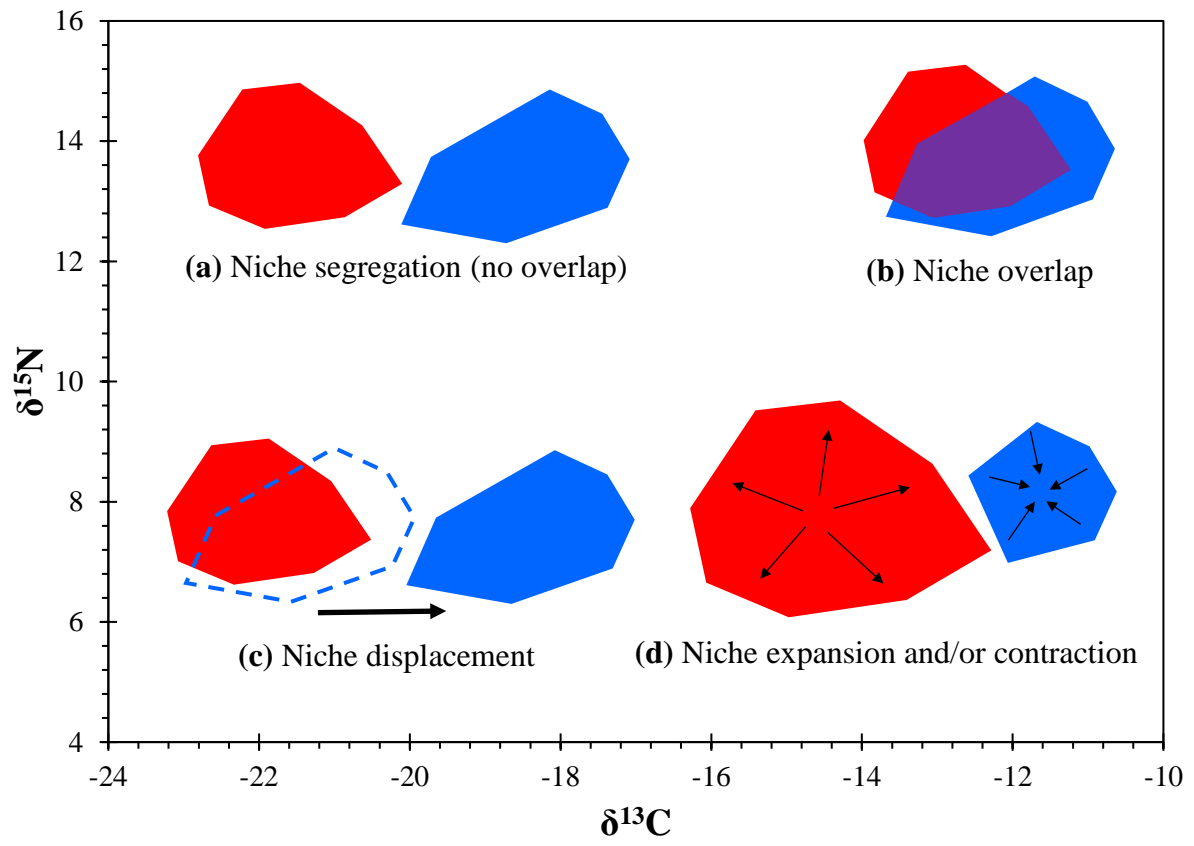


Fig. 1

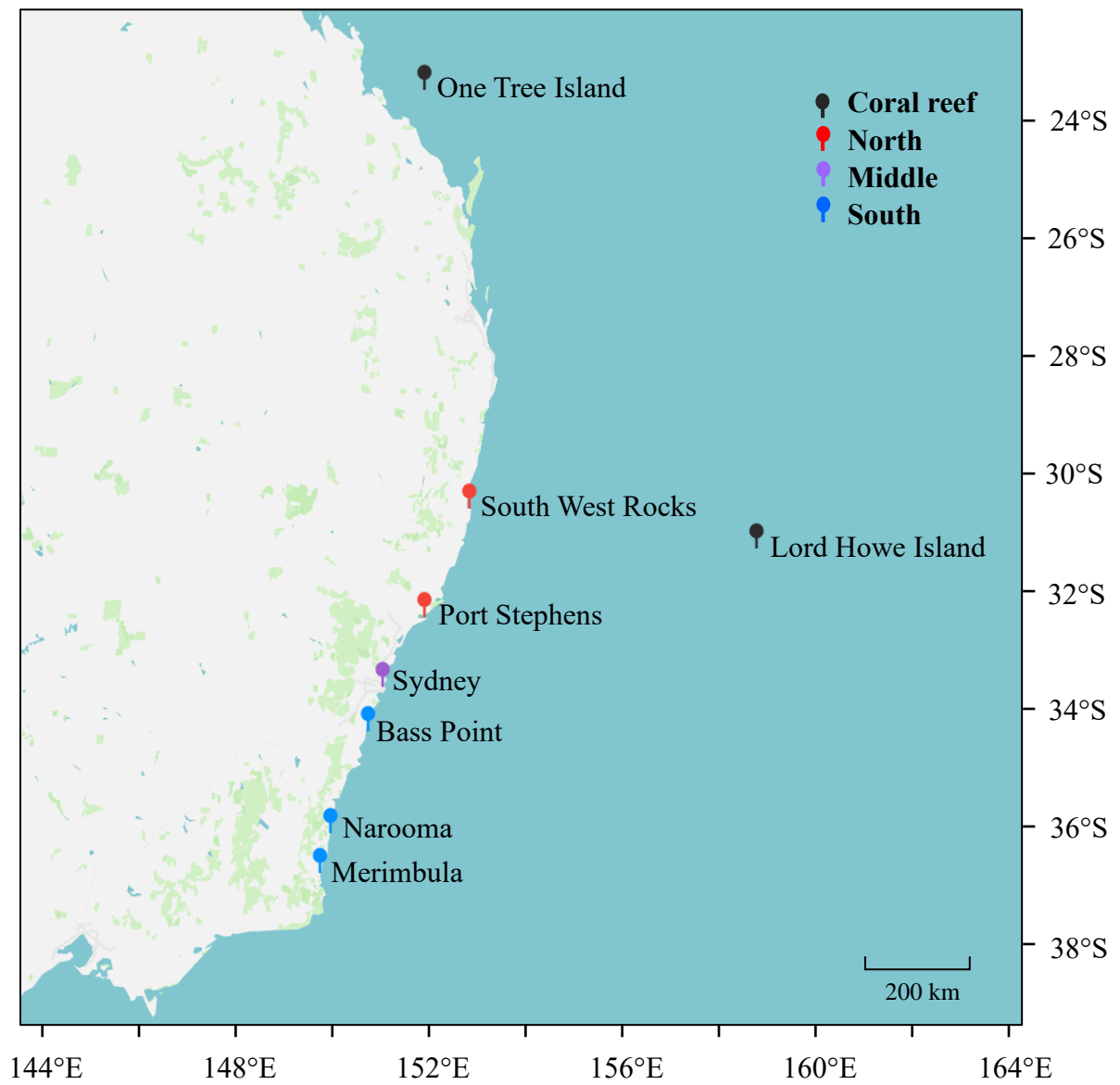


Fig. 2

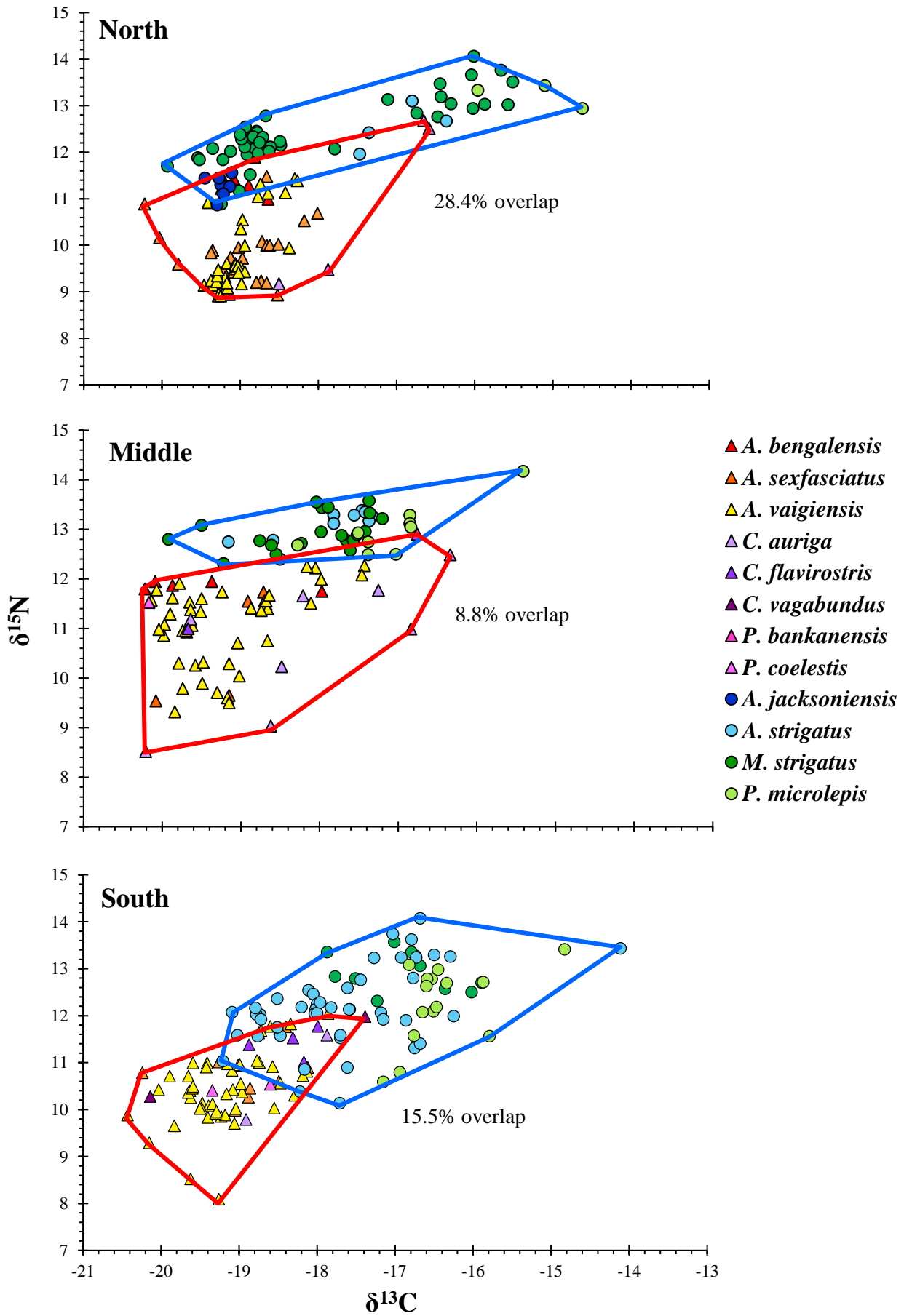


Fig. 3

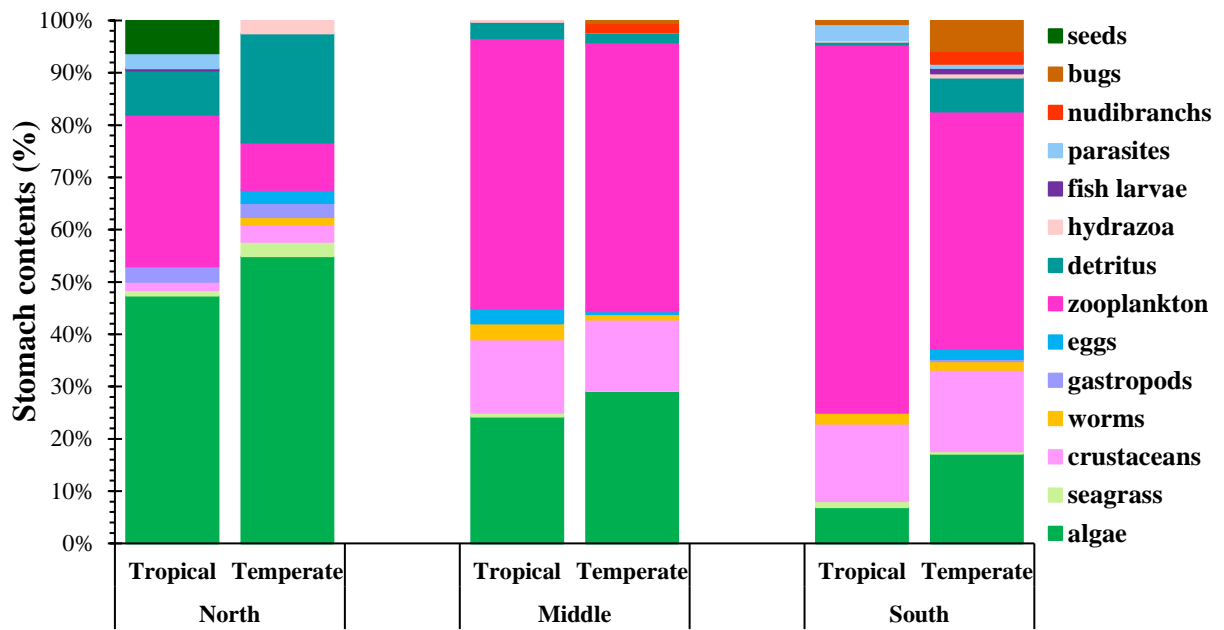


Fig. 4

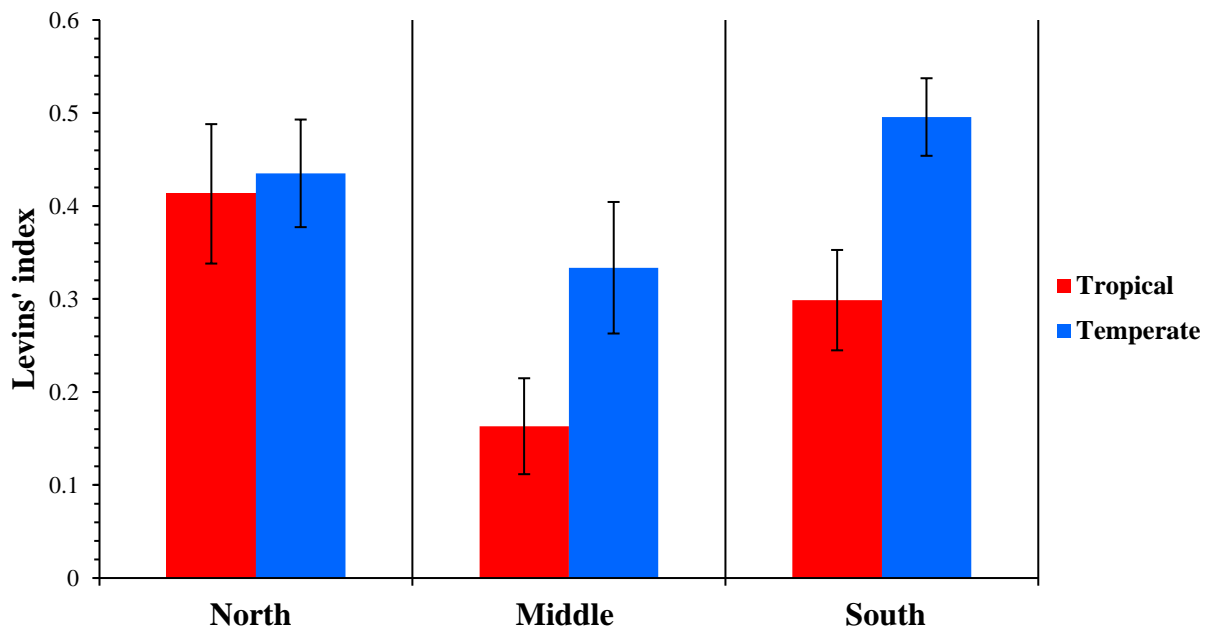


Fig. 5