

1 **Behavioural generalism could facilitate co-existence of tropical and**
2 **temperate fishes under climate change**

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14 Running head: Behaviour change facilitates range-extension

15
16 **Abstract**

17 1. Coral-reef fishes are shifting their distributions poleward in response to human-mediated
18 ocean warming, yet the consequences for recipient temperate fish communities remain poorly
19 understood. Behavioural modification is often the first response of species to environmental
20 change, but we know little about how this might shape the ongoing colonisation by tropical
21 fishes of temperate-latitude ecosystems under climate change.

22 2. In a global hotspot of ocean warming (southeast Australia), we quantified 14 behavioural
23 traits of invading tropical and local co-occurring temperate fishes at 10 sites across a 730 km
24 latitudinal gradient as a proxy of species behavioural niche space in different climate ranges
25 (subtropical, warm-temperate, cold-temperate).

26 3. We found that tropical fishes (4 species) modified their behavioural niches as well as
27 increased their overall behavioural niche breadth in their novel temperate ranges where
28 temperate species predominate, but maintained a moderate to high niche segregation with
29 native temperate species across latitudinal range position. Temperate species (3 co-occurring
30 species) also modified their niches, but in contrast to tropical species, experienced an
31 increased niche breadth towards subtropical ranges. Alterations to feeding and shoaling
32 behaviours contributed most to niche modifications in tropical and temperate species, while
33 behaviours related to alertness and escape from potential threats contributed least.

34 4. We here show that at warmer and colder range edges where community structures are being
35 reshuffled due to climate change, behavioural generalism and niche modification are potential
36 mechanisms adopted by tropical range extenders and native-temperate fishes to adjust to
37 novel species interactions under climate change.

38

39 **Keywords:** ocean warming, tropicalisation, range extensions, tropical vagrant fishes,
40 behavioural niche breadth, niche segregation, temperate ecosystems.

41

42

43 **Introduction**

44

45 Species distributions are governed by long-term dynamics of biological-physical factors
46 (MacArthur 1972; Peterson & Lieberman 2012). More recently, however, increased
47 anthropogenic disturbances have facilitated a progressive and rapid global redistribution of
48 species, intensifying species invasion rates, which is now one of the greatest impacts of
49 climate change (Pecl et al. 2017). Despite the pace of invasion being higher for introduced
50 species than range-extending species, the latter bring with them novel ecological interactions

51 resulting in impacts on the biodiversity and ecosystem functioning of recipient communities
52 at a similar magnitude as those caused by introduced species (Sorte et al. 2010, Vergés et al.
53 2014; Vergés et al. 2016). Yet, we still have little understanding of the mechanisms that allow
54 the colonization of range-extending species and their ensuing impacts on local communities
55 (Mack et al. 2000).

56 Life history traits such as propagule pressure (i.e. quantity of arriving individuals
57 depending on the number of releases and dispersing individuals; Lockwood et al. 2005) is a
58 key process determining successful species range shifts (Ben Rais Lasram et al. 2008;
59 Soeparno et al. 2012). However, traits that facilitate dispersal of larval propagules are less
60 relevant once species have arrived in their novel environments (Monaco et al. 2020). To
61 establish viable populations, animals need to cope with novel local conditions (Angert et al.
62 2011), with behavioural traits playing a crucial role in how they interact with their novel
63 environment. Broad behavioural ranges or individual-level behavioural variability should,
64 therefore, increase the ability of species to persist under altered biotic and climatic conditions,
65 especially during the early stages of invasion (Chapple et al. 2012). Still, the role of behaviour
66 of range-extending species and their interactions with local species are still poorly
67 understood.

68 One of the central tenets of species invasion success is that species that are flexible in
69 their resource use and have broad niches are more likely to prosper in novel environments
70 (Warren et al. 2001; Cassey et al. 2004; Sol et al. 2005; Slatyer et al. 2013). Individual
71 behaviours underpin the functional role and the ecological niche space of a species in its
72 environment (Bergmüller & Taborsky 2010). This means that species with a broad
73 behavioural repertoire would be favoured in novel ranges over those with a narrow repertoire,
74 as it allows them to exploit resources within a broad spectrum of ecological conditions and
75 avoid conflict with local species (Wright et al. 2010; Feary et al. 2014; Sunday et al. 2015).

76 Thus, range-extending behavioural generalist species (e.g. showing diversification in feeding
77 and shoaling strategies) have a higher likelihood to persevere in non-native communities than
78 range-extending specialist species with a more constrained behavioural repertoire (Donelson
79 et al. 2019).

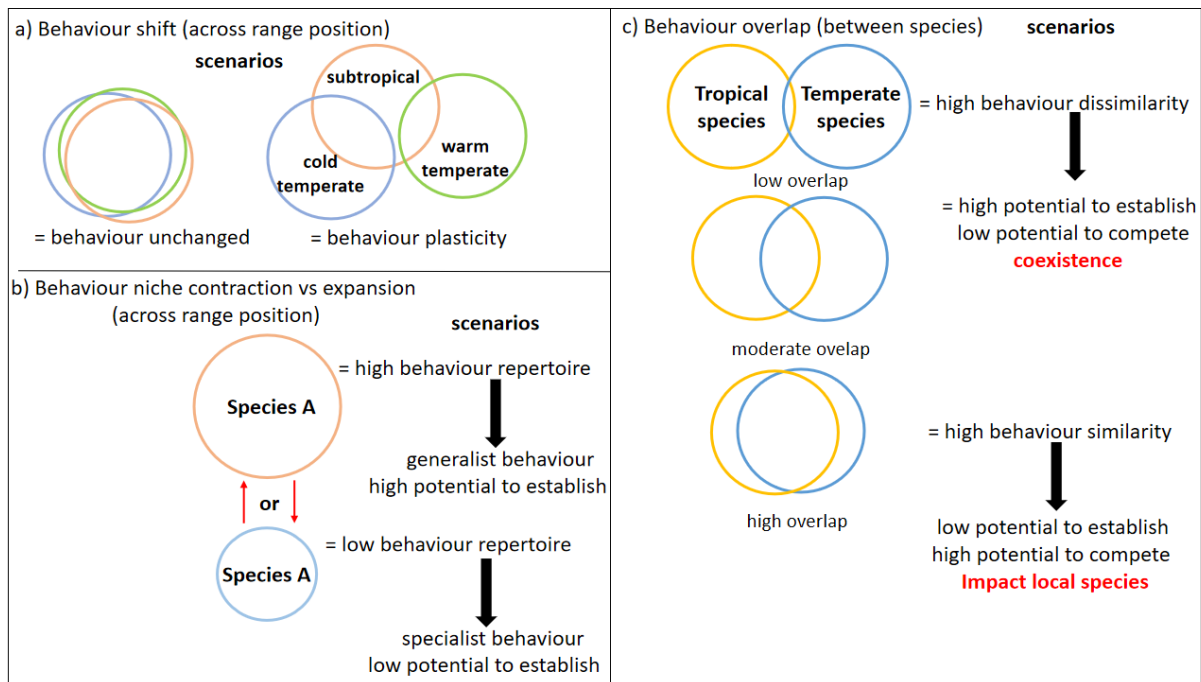
80 Non-native species often reconfigure local community structures following their
81 invasion (Mooney & Cleland 2001; Strayer et al. 2006; David et al. 2017). Such
82 modifications of native communities can be irreversible, especially when invaders become
83 well established (Harborne & Mumby 2011; Nagelkerken & Connell 2015). Despite invasive
84 species generally being stronger competitors than native species (Parker et al. 2013), they are
85 more likely to establish when they do not share the same niches as local species (Shea &
86 Chesson 2002; Thuiller et al. 2010; van Kleunen et al. 2010). For example, range-extending
87 species that are morphologically similar to native species might have lower success rates in
88 their establishment, owing to greater interspecific competition with native species (Azzuro et
89 al. 2014; Smith et al. 2016). Hence, the degree to which tropical species overlap in their
90 behavioural niches with temperate species can provide strong insights into the degree of
91 competition with local species and their likelihood to increase their population sizes in
92 temperate ecosystems under climate change.

93 The impact of range-extending species depends on the response of native species to the
94 incursion of these novel 'intruders' (Berthon 2015). In some cases, natives will fail to adjust,
95 resulting in local or global extinction (Case & Bolger 1991; Fritts & Rodda 1998).

96 Alternatively, natives may possess traits (pre-adaptation) that may diminish the impacts of
97 invaders, allowing their coexistence (Vermeij 1982; Strauss et al. 2006). Ecological insights
98 into the dynamic of invasion are typically studied by comparing traits between invaders and
99 native species (Belmaker et al. 2009; Edelist et al. 2013; Elleouet et al. 2014). Such
100 comparisons allow an understanding of how invasions might alter local communities and

101 whether the structure and fundamental niche of the recipient community influences invasion
102 success (Parker et al. 2006; Lockwood et al. 2013; Ricciardi et al. 2013). Understanding the
103 similarity in behavioural niche of invasive-tropical and native-temperate species is key to
104 understand how native species are responding to tropical invasions due to climate change.

105 Here we test the hypothesis that behavioural modification, generalism, and segregation of
106 range-extending tropical reef fish might facilitate their establishment in temperate marine
107 environments. We study two potential underlying mechanisms: 1) their behavioural niche
108 space modification (i.e. behavioural repertoire), and 2) their degree of behavioural overlap
109 with native temperate species. We assessed this for 4 tropical and 3 temperate fish species *in*
110 *situ* over a 730-km latitudinal and temperature gradient, spanning climate ranges from
111 subtropical and warmer-temperate to colder-temperate environments where tropical and
112 temperate species increasingly coexist due to ocean warming. We used a novel multivariate
113 ellipse-based metric within a Bayesian framework, to unravel behavioural modifications and
114 overlap in behavioural niche space of co-occurring tropical and temperate fishes by
115 evaluating: 1) changes in the breadth of their behavioural niches (e.g. expansion vs
116 contraction), 2) shifts in the composition of their behavioural niches (alteration in the
117 predominant behaviours expressed), and 3) differences in their degree of behavioural niche
118 overlap (Fig. 1). This approach enhances our understanding of the likelihood of tropicalisation
119 success as a function of species behavioural niche modifications, and their potential effects on
120 temperate species and ecosystems under climate change.



121

122 **Figure 1.** Conceptual diagram of possible mechanisms of behavioural niche plasticity under climate
 123 change. a) behavioural niche shift across range position (subtropical, warm-temperate, cold-
 124 temperate) based on the positioning in niche space (individual ellipses), b) behavioural niche
 125 contraction (decreased behavioural repertoire) vs expansion (increased behavioural repertoire),
 126 indicating the extent to which a species is specialised or generalised in their behavioural niche, and
 127 c) behavioural niche overlap measured as the percentage of behavioural niche space shared between
 128 two species.

129

130

131 **Methodology**

132

133 **Study area**

134 Ten sites at five locations were selected over a latitudinal gradient along the SE Australian

135 coastline (Fig. 2) and sampled during the summers of 2017 and 2018 when recruitment of

136 tropical fishes peaks. Southeast Australia is a hotspot of range-shifting tropical species

137 mediated by ocean warming (Ridgway 2007; Hobday & Pecl 2014), thus this is a natural

138 climate change laboratory for a unique investigation of the performance of sympatric novel

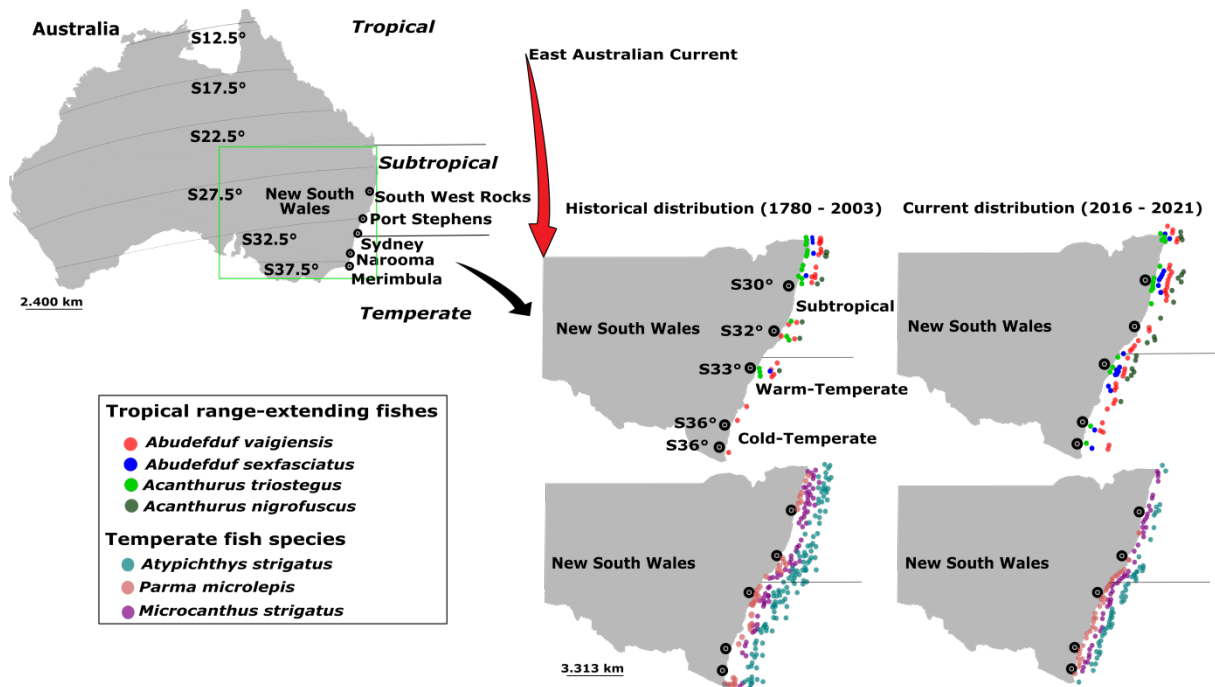
139 tropical and native temperate species under ongoing climate change in the wild. Two sites at

140 South West Rocks (30°52'34"S, 153°4'2"E and 30°53'0"S, 153°2'17"E) and two sites at Port

141 Stephens (32°42'56"S, 152°10'58"E and 32°44'55"S, 152°10'19"E) are located at subtropical

142 range position and represented reefs with abiotic-biotic features (e.g. mean summer
143 temperature ~ 25 °C and kelp-free reefs) closest to that of the native ranges of tropical fish.
144 Despite the lack of evidence of significant breeding populations, tropical reef fishes have been
145 present at these subtropical locations for a long time, and during the study their abundances
146 were higher at the subtropical than at the temperate range positions (Fig. S1), especially for
147 juveniles (Fig. S2). The studied temperate fishes naturally occur at these subtropical locations
148 (i.e. their natural trailing edges). These tropical and temperate fishes have coexisted for longer
149 periods of time at these subtropical reefs (during all seasons). However, there is no evidence
150 of how long they have been coexisting at warm-temperate and cold-temperate locations where
151 until now they only coexist during the summer.. Three sites at two locations were selected at
152 the cold-temperate range position (mean summer temperature ~ 21 °C) with unfamiliar
153 environmental features (i.e. sites with abiotic-biotic features dissimilar to those of the native
154 ranges of tropical fish) for tropical fishes: Narooma (one site, 36°12'54"S, 150°7'51"E) and
155 Merimbula (two sites, 36°53'40"S, 149°55'25"E and 36°44'13"S, 149°58'58"E). This
156 southernmost cold location is representative of a fully temperate rocky reef ecosystem, and
157 harbors much higher densities of temperate fishes and much lower densities of tropical fishes
158 than the subtropical location (Monaco et al. 2021) (Fig. S1). Finally, three sites at one location
159 were selected at Sydney, which is considered here as the warm-temperate range position:
160 Shelly Beach (33°48'1.13"S, 151°17'31.23"E), Little Manly (33°48'23"S, 151°17'8"E) and
161 Narrabeen (33°42'7"S, 151°18'21"E). The warm-temperate range position represented a
162 transition zone with intermediate temperatures (seawater ~23 °C during summer) and habitats
163 (kelp as well as increasing tropical coral presence, Booth & Sear 2018) compared to the
164 subtropical and cold-temperate locations. This location is a hotspot of tropicalisation, which
165 has seen increasing rates of tropical fish invasions over the last two decades (Fowler et al.
166 2018). The sites were chosen based on an 18-yr study of ongoing tropical fish settlement on

167 shallow rocky reefs along the coast of SE Australia (Booth et al. 2007; Booth et al. 2018).
 168 From the perspective of tropical fishes, the cold-temperate locations are considered as their
 169 extreme leading edges (coolest area of a species' range) where they are invading, while for
 170 the co-occurring temperate species the subtropical latitudinal locations are considered as their
 171 trailing warm-water edges.
 172



173
 174 Map showing the 5 sampling locations (black circles) with their respective absolute
 175 latitudes. 'Subtropical': South West Rocks and Port Stephens. 'Warm-temperate': Sydney.
 176 'Cold-temperate': Narooma and Merimbula. The coloured circles indicate the spatially-
 177 validated records (i.e. records that have highly accurate coordinates entries) of historical
 178 (limited by a date range before the tropical fish surveys started, from 1780 to 2003) and
 179 current (last five years, from 2016 to 2021) distribution of the studied fishes along the coast of
 180 SE Australia based on the number of occurrences. Species distributional ranges were adapted
 181 from the Atlas of Living Australia (<https://spatial.ala.org.au/#>).
 182
 183

184 **Study species**

185 Only the most commonly observed tropical coral reef fish species had their behaviours
186 quantified to allow for sufficient replication within each latitudinal range position, while the
187 temperate native species were chosen based on their known shoaling interactions with the
188 respective tropical fishes (see Smith et al. 2018). The tropical fishes used in this study are
189 called vagrant species because they have not established breeding populations at any of our
190 study sites yet, and co-occur with local species at temperate latitudes only on a seasonal-basis
191 (warm seasons – January to May; Feary et al. 2014). Their abundances drop quickly as water
192 temperature decreases through the season resulting in a heavy overwinter mortality (Booth et
193 al. 2011), but the expectations are that their abundances will continue to increase with the
194 intensification of ocean warming and strengthening of poleward ocean currents (Figueira &
195 Booth 2010; Booth et al. 2018). A total of 7 species (4 tropical vagrants and 3 temperate
196 native species) were investigated. The four tropical fish species selected and the number of
197 replicates (i.e. individual fishes sampled for behaviours per latitudinal range position) were:
198 two water-column omnivorous feeders (1) sergeant major, *Abudefduf vaigiensis* (subtropical =
199 22, warm-temperate = 22, cold-temperate = 20) and (2) scissor tail, *Abudefduf sexfasciatus*
200 (subtropical = 8, warm-temperate = 6, cold-temperate = 7), and two grazing benthic
201 herbivores (3) dusky surgeonfish, *Acanthurus nigrofasciatus* (subtropical = 19, warm-temperate
202 = 17) and (4) convict surgeonfish, *Acanthurus triostegus* (subtropical = 19, warm-temperate =
203 18). As the number of tropical fish recruits varies annually, the two surgeonfishes could not
204 be found in sufficient numbers ($n \geq 5$) at the high latitude sites during the sampling years
205 (2017-2018). Thus, they were not included in the analysis for this location. The three
206 temperate native species selected and their number of replicates were one pelagic omnivore
207 (1) mado, *Atypichthys strigatus* (subtropical = 6, warm-temperate = 10, cold-temperate = 8)
208 and one benthic omnivore (2) stripey, *Microcanthus strigatus* (subtropical = 21, warm-
209 temperate = 17, cold-temperate = 17), and one territorial benthic herbivore (3) white-ear

210 damselfish, *Parma microlepis* (subtropical = 9, warm-temperate = 20, cold-temperate = 20)
211 (Fig. S3).

212

213 **Data collection and study design**

214 Behaviours of each fish were quantified from underwater video recordings. First, visual
215 surveys were performed to locate recruits and juveniles of tropical fishes at the selected sites.
216 Then, underwater cameras (GoPro's) attached to dive weights were placed on the reef
217 substratum at a distance of ~ 50 cm from the temperate and tropical fishes found during the
218 surveys, regardless if the fish were solitary or in a school. This distance was based on a trade-
219 off between being able to film recruits of tropical fishes with a relatively small body size (< 5
220 cm) on temperate reefs versus maintaining some distance to avoiding disturbing them with the
221 presence of a camera. Usually recruits and early-stage individuals of these species are site-
222 attached, allowing suitable recordings of their behaviours *in situ*. At each site, cameras were
223 deployed over several consecutive days (maximum of 10 cameras deployed on a single day)
224 in different areas to avoid filming the same individuals. Some of the video recordings had to
225 be discarded due to the low image quality and when the focal fishes were out of the camera
226 view. Based on Nanniga et al. (2017), after placing the cameras, the first 3 min of recording
227 was considered as acclimation time to the recorder before behaviours were quantified for a
228 total of 10 min. per recording. We did not observe any clear disturbance of the fish by the
229 presence of the camera such as rapid swimming towards or away from the camera. To
230 evaluate whether species behaviour differed over a range of climatic and biotic conditions,
231 recordings were conducted over a latitudinal temperature gradient ranging from native to non-
232 native habitats for both tropical and temperate fish assemblages (see under Study area above).
233 The data collection was performed under animal ethics approval S-2015-222A and S-2017-
234 002 (University of Adelaide) and ETH17-1117 (University Technology of Sydney).

235

236 **Fish behaviour**

237 Fourteen behavioural variables within seven behavioural traits were quantified for each
238 individual fish from the video footage (Table S1): (1) water column position (proportion of
239 time spent on the bottom vs. midwater), (2) boldness (estimated by the proportion of time
240 away from shelter vs. near to shelter), (3) alertness (number of times that an individual
241 showed a rapid increase in their swimming speed, often when larger temperate fishes
242 approached), (4) feeding (proportion of time spent feeding, and bite rate on the substratum vs
243 water column), (5) shoaling interactions (proportion of time solitary, or shoaling with
244 conspecifics, heterospecific tropical species, heterospecific temperate species, and mixed-
245 species groups), (6) agonistic behaviour (number of times chasing or escaping from other
246 individuals), and (7) activity levels (proportion of time that the individual was moving).

247 All observations were consecutively quantified from the videos using the software VLC
248 media player (version 2.1.3) and for each focal individual all 14 behaviours were analysed. To
249 avoid pseudo-replication only one individual of each species was analysed in each video
250 recording when they were shoaling with conspecifics. Due to the variable time that
251 individuals spent in front of the camera, each individual was analysed for a max. of 2 min. so
252 as to standardise the data collection and effort. Observation times of a few minutes per
253 individual have been found to suffice for a representative estimate of an individual's
254 behaviour (McClanahan et al. 1999; Biro et al. 2010; Francini-Filho et al. 2010). Behaviours
255 were analysed using two different approaches, either through the number of times that the
256 behaviour occurred during the period of observation — point behaviour (e.g. bite rates) or in
257 each 10-sec interval ongoing observation — state behaviour (e.g. shoaling), which were then
258 transformed to proportion of time (%) spent performing the behaviours (see Table S1 for
259 more details).

260 **Statistical analyses**

261 To assess the multidimensional behavioural niche space (i.e. behavioural repertoire) of
262 species across a latitudinal gradient the SIBER R-package was used. Because of the high
263 multivariate space of our data set (14 behaviours) and because SIBER only works with two
264 axes, we first performed a Redundancy Analysis (RDA) on the 14 behaviours to reduce the
265 multidimensional data set to bidimensional coordinates (i.e. along two axes, Table S2). This
266 allowed us to establish the relative position in the behavioural space for each individual per
267 species (these values are based on the relative importance of behavioural traits in the initial
268 dataset; Villéger et al. 2008, Laliberte & Legendre 2010). As long as we do not calculate p-
269 values or confidence intervals using RDA, we do not need to satisfy the data normality
270 assumption. RDA was only performed as a dimension reduction technique and to reveal the
271 most important behavioural traits driving latitudinal range position differences in behavioural
272 niche space. As behavioural observations were measured on different scales (e.g. count and
273 percentage data), we first standardised the data using the Hellinger method (Legendre &
274 Gallagher 2001) which was also used as a transformation approach to avoid zero inflation in
275 the RDA (Paliy et al. 2016) to calculate a distance matrix that was used as the basis for the
276 RDA. RDA outputs are similar to those obtained from Principal Component Analysis
277 (Legendre & Legendre 1998). However, RDA is a constrained ordination that assesses how
278 much variation in the response variables (behaviours) can be explained by variation in the
279 explanatory variables (species and latitudes) (Paliy et al. 2016). The first two RDA axes
280 together accounted for 68% of the observed variation in behavioural data for the tropical and
281 temperate species. The order of the behaviours that showed the best representation of the two
282 principal RDA axes are listed in (Table S2).

283 The two axes that were extracted from the RDA analysis were then used to create
284 standard ellipse areas (SEA) representing relative behavioural niche breadths in a bivariate

285 space, where the standard ellipse area represents the bivariate standard deviation. We
286 generated Bayesian credible intervals of the standard ellipse area for each species at each
287 latitude position (subtropical, warm-temperate, and cold-temperate), which is analogous to a
288 bootstrapping procedure. In this analysis, the probability that two niche areas differed from
289 each other is determined using Bayesian inference based on the 10,000 posterior draws (i.e.
290 the probability that the niche area of group 1 is greater than group 2 is the proportion of group
291 1 standard ellipses that are greater than group 2 standard ellipses, based on the 10,000
292 replicates). Species with larger ellipse areas therefore exhibit a higher variability among
293 individuals in behavioural trait space, and can therefore be considered as a behaviourally
294 more generalistic species (Fig. 1). In contrast, species with smaller ellipse areas express only
295 a restricted range of behavioural traits, tending towards behavioural specialisation. Although
296 the unbalanced number of replicates among species and range positions, and the low number
297 of replicates for some species, this did not affect the interpretation of our results. These issues
298 are dealt with by application of a small sample size correction using metrics based on
299 standard ellipses (SEA) which were corrected to minimize bias caused by small sample sizes
300 (SEAc). Additionally, Bayesian estimation of standard ellipses (SEAb) allows for an unbiased
301 estimate of relative niche area even for small sample sizes, in contrast to metrics such as
302 convex hulls, which are sensitive to small sample size (see details in Jackson et al. 2011,
303 2012).

304 The SEAc was used to compute the overlap between species of tropical and temperate
305 fish populations within each latitude position and the overlap of each individual species
306 across latitudes. The overlap is expressed as a proportion of the sum of the non-overlapping
307 areas of the ellipses, which is calculated as the proportion of the overlapping area between the
308 two species divided by the sum of the ellipses areas of the species minus the proportion of the
309 overlap as shown in the formula below:

310
$$\text{Overlap proportion} = \frac{\text{Overlap}_{sp1 vs sp2}}{(\text{SEA}_{sp2} + \text{SEA}_{sp1} - \text{Overlap}_{sp1 vs sp2})}$$

311 We consider a significant species overlap to have a proportion of >60%, the same
312 criteria as used in the Schoener diet overlap index (Schoener 1968; Guzzo et al. 2013). We
313 then used a Bayesian approach (SEA_b) as described in Jackson et al. (2011) to obtain
314 confidence intervals for behavioural niche space. These confidence intervals allow for
315 statistical comparisons of the sizes of behavioural niche areas among species within
316 latitudes. All analyses were performed using the Stable Isotope Bayesian Ellipses in R
317 (SIBER) package (Jackson et al. 2011).

318 To understand whether social interactions would explain the extension or contraction of
319 the species behavioural niche space, agonistic interactions and shoaling composition were
320 compared between tropical and temperate species among the latitudinal positions using
321 permutational ANOVAs. Agonistic interactions were measured as the number of chases per
322 minute, and shoaling behaviour was measured as the proportion of time. Whether these
323 behaviours occurred between individuals of the same species (conspecifics), or with
324 heterospecific tropical species, heterospecific temperate species, or the mixture of all these
325 species (only for shoaling) was also considered as a factor in the analyses.

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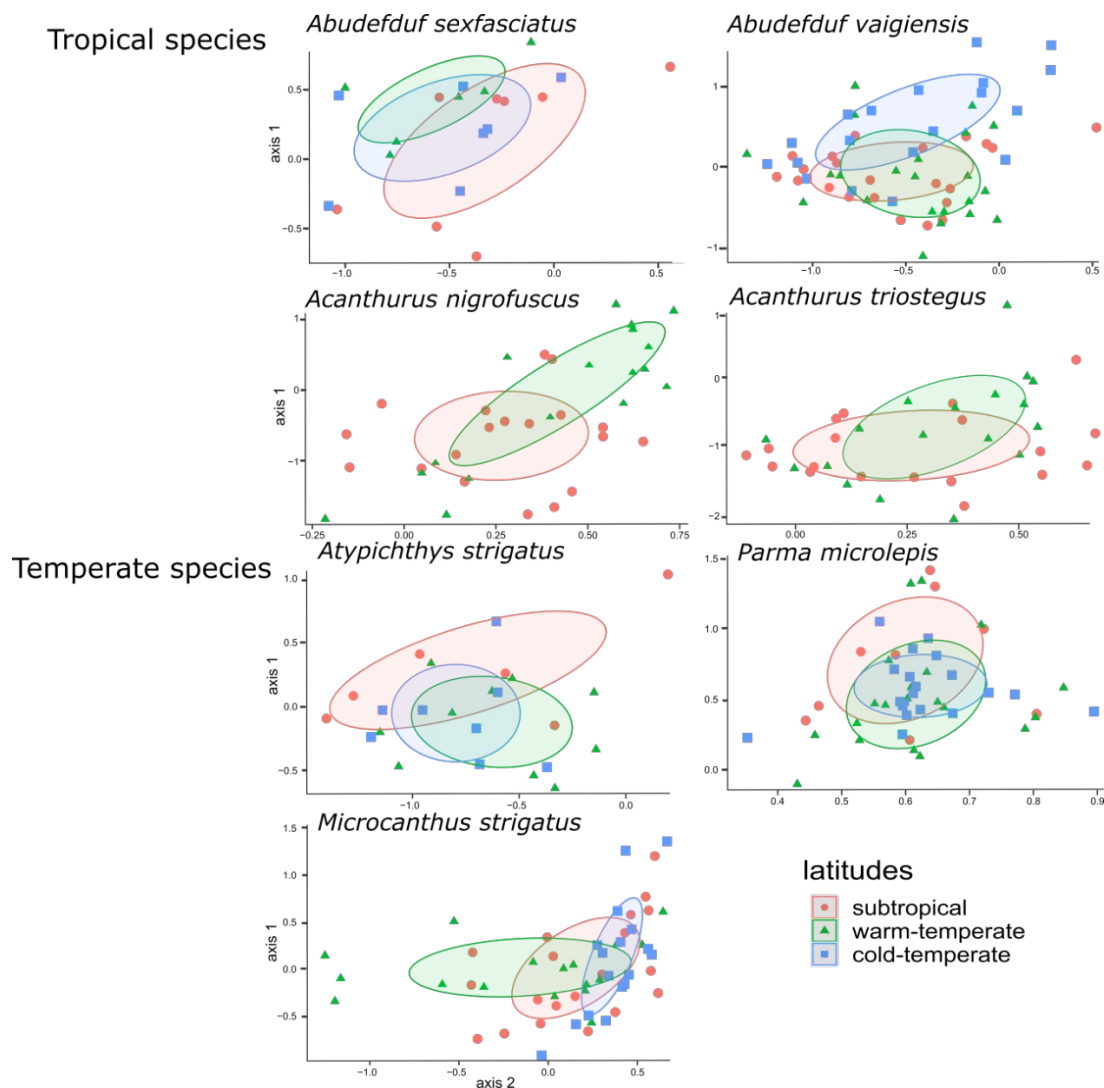
328 **Results**

329

330 **Behavioural niche shifts across latitudinal range positions**

331 Both tropical and temperate species reshuffled their behavioural niche as a function of range
332 position (Fig. 3, Fig. 1a). In general, behavioural niche space (based on standard ellipse areas)
333 of individual species showed low to moderate overlap among range positions (19–60%
334 overlap, Table 1). Only 5 out of 17 species-range position comparisons showed relatively

335 high overlap (62–70%, Table 1) in behavioural niche space. Feeding, shoaling interactions,
 336 and to a lesser extent activity levels appear to be the most important behavioural traits driving
 337 latitudinal range position differences in behavioural niche space within individual tropical and
 338 temperate species (Fig. S4).



339
 340 **Figure 3.** Behavioural niche space based on the 14 behaviours measured for each tropical
 341 vagrant and native-temperate species at three different range positions (subtropical =
 342 equatorward, warm-temperate and cold-temperate = poleward). The standard ellipses (SEAc)
 343 for each species are based on a 40% confidence interval. The data points represent each
 344 observed fish (sample) per species. See Table 1 for overlap in niche space.
 345

346 **Table 1.** Behaviour similarity among range positions based on the overlap (%) of the standard
 347 ellipses area (SEAc) of each species per latitude position. Bold numbers indicate the latitudes
 348 that showed a negligible behavioural shift (behaviour similarity between latitudes > 60%)
 349 following the criterion used by Schoener 1968 and Guzzo et al. 2013.

Affinity	Species	Latitude	Overlap (%)
Tropical	<i>Abudefduf sexfasciatus</i>	subtropical vs. warm-temperate	42
		subtropical vs. cold-temperate	68
		warm-temperate vs. cold-temperate	68
	<i>Abudefduf vaigiensis</i>	subtropical vs. warm-temperate	70
		subtropical vs. cold-temperate	45
		warm-temperate vs. cold-temperate	46
	<i>Acanthurus nigrofuscus</i>	subtropical vs. warm-temperate	50
	<i>Acanthurus triostegus</i>	subtropical vs. warm-temperate	59
Temperate	<i>Atypichthys strigatus</i>	subtropical vs. warm-temperate	30
		subtropical vs. cold-temperate	37
		warm-temperate vs. cold-temperate	61
	<i>Parma microlepis</i>	subtropical vs. warm-temperate	56
		subtropical vs. cold-temperate	39
		warm-temperate vs. cold-temperate	62
	<i>Microcanthus strigatus</i>	subtropical vs. warm-temperate	41
		subtropical vs. cold-temperate	37
warm-temperate vs. cold-temperate		19	

350

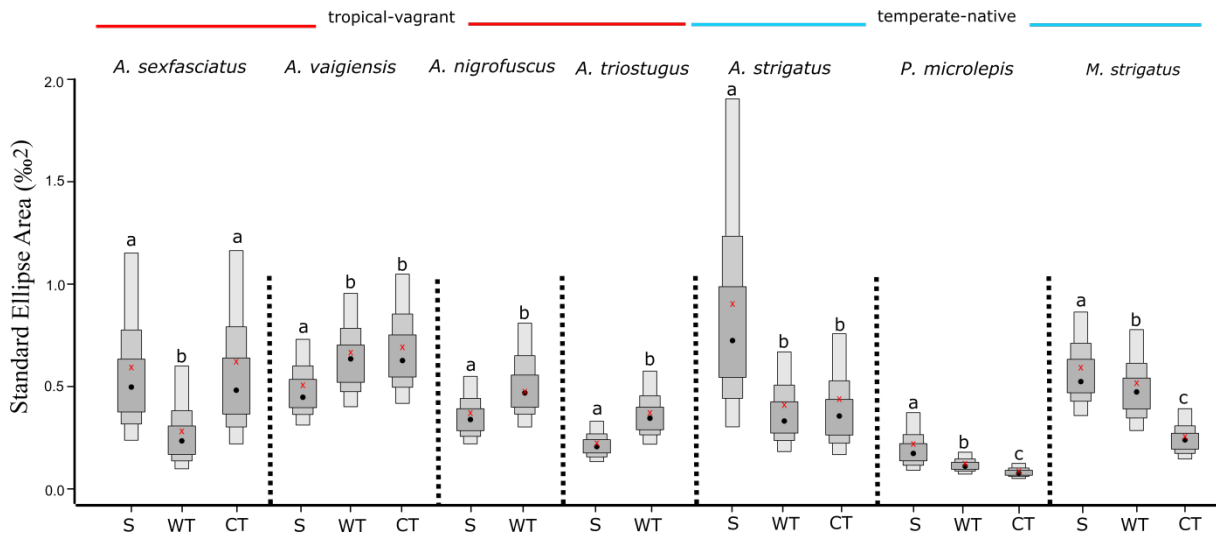
351 Behavioural niche expansion across latitudinal range positions

352 The behavioural niche breadth (behavioural repertoire) of tropical vagrant fishes showed an
 353 expansion with increasing latitudinal position (i.e. from warm to colder waters), except for a
 354 deviation of *A. sexfasciatus* at the cold-temperate latitude (Fig. 4, Fig. 1b, Table S3).

355 Temperate native fishes showed the opposite pattern, with an increase in niche space towards
 356 subtropical latitudes (i.e. from cold to warmer waters). In general, tropical species exhibited a
 357 wider behavioural niche breadth than temperate species, although *A. strigatus* had the largest
 358 niche area of all species (0.90%²) at the subtropical latitude (Table S3). The species that had
 359 the smallest behaviour niche space in all range positions was the territorial damselfish *P.*

360 *microlepis* (smallest area 0.09 %² at cold-temperate latitude), indicating their narrow
 361 behavioural repertoire.

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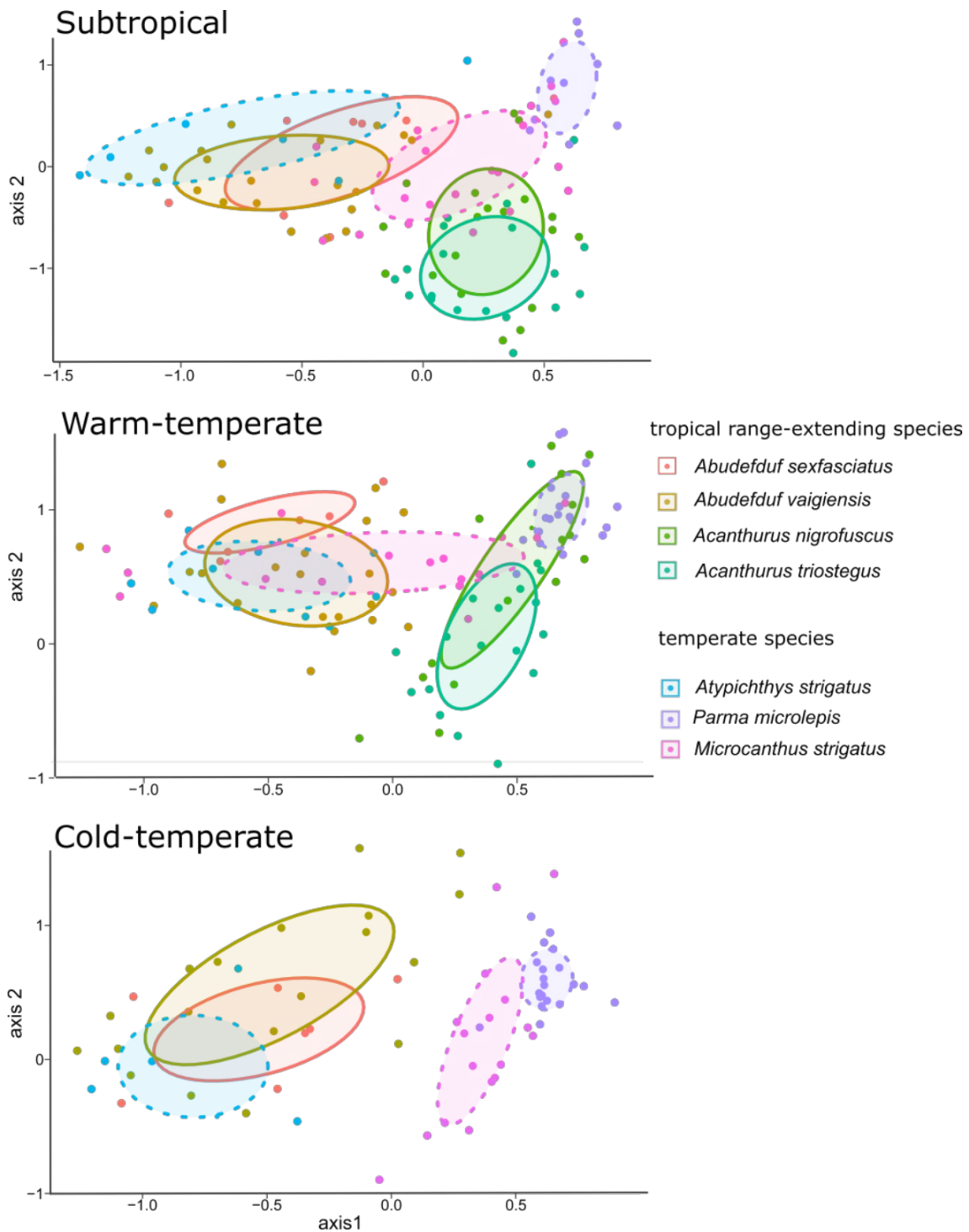
364 **Figure 4. Results of Bayesian estimation of the size of the standard ellipses areas (SEAb) based on**
 365 **14 behaviours (i.e. behavioural niche space) of tropical and temperate species at each range position**
 366 **(S = subtropical, WT = warm-temperate, CT = cold-temperate). Shown are Bayesian estimates (• =**
 367 **mode) with 50%, 75% and 95% credible intervals (shaded boxes), and maximum likelihood**
 368 **estimates of the means (x). Different letters above the bars indicate significant differences (increase**
 369 **or decrease) in behavioural niche breadth among latitudes for each species (see Table S3 for**
 370 **statistical results).**

371

372 Behavioural niche overlap between tropical and temperate species

373 Behavioural niche space of tropical and temperate species exhibited a low to moderate
 374 overlap independent of latitudinal range position, ranging from 0% to 53% at the subtropical
 375 latitude, 0% to 61% at the warm-temperate latitude, and 1% to 59% at the cold-temperate
 376 latitude (Fig. 5, Fig. 1c, Table 2). Moderate niche overlap between tropical and temperate
 377 species was driven at all three latitudinal range positions by planktonic feeders that form
 378 social groups, viz. the tropical *Abudefduf vaigiensis* and *Abudefduf sexfasciatus* with the
 379 temperate *Atypichthys strigatus*, whilst significant niche overlap (61%) between tropical and
 380 temperate species was only found for one species pair (*Abudefduf vaigiensis* vs *Atypichthys*
 381 *strigatus* at middle latitude) out of all 30 species-pair combinations across range positions.
 382 Moderate and significant overlap in behavioural niche space between these tropical and

383 temperate zooplanktivores was driven by feeding and shoaling behaviours at all three range
 384 positions, but especially in the warm-temperate range (Fig. S5).



385
 386 **Figure 5.** Standard ellipse areas (SEAc) showing the degree of overlap in behavioural niche
 387 space among and within tropical species (solid circles) and temperate species (dashed circles)
 388 across a latitudinal gradient. SEAc were calculated from the two axes extracted from a
 389 multivariate analysis (RDA) based on 14 species behaviours per latitude. The data points
 390 represent each observed fish (sample) per species. The ellipses are based on a 40% confidence
 391 interval. See Table 2 for degree of niche overlap.

392 **Table 2.** Behavioural similarity between species at different range positions (a: subtropical, b:
393 warm-temperate, c: cold-temperate) based on the overlap of the standard ellipses area (SEAc).
394 Bold numbers (*) indicate the pairs of species that showed a high overlap (overlap >60%)
395 following the criterion used by Schoener (1968) and Guzzo et al. (2013).

396
397 a)
398

Subtropical	Pairs of species		Overlap (%)
Affinity			
Tropical vs. Tropical	<i>Abudefduf sexfasciatus</i>	<i>Abudefduf vaigiensis</i>	60*
	<i>Abudefduf sexfasciatus</i>	<i>Acanthurus nigrofuscus</i>	18
	<i>Abudefduf sexfasciatus</i>	<i>Acanthurus triostegus</i>	8
	<i>Abudefduf vaigiensis</i>	<i>Acanthurus nigrofuscus</i>	14
	<i>Abudefduf vaigiensis</i>	<i>Acanthurus triostegus</i>	10
	<i>Acanthurus nigrofuscus</i>	<i>Acanthurus triostegus</i>	70*
Tropical vs. Temperate	<i>Abudefduf sexfasciatus</i>	<i>Atypichthys strigatus</i>	53
	<i>Abudefduf sexfasciatus</i>	<i>Parma microlepis</i>	15
	<i>Abudefduf sexfasciatus</i>	<i>Microcanthus strigatus</i>	42
	<i>Abudefduf vaigiensis</i>	<i>Atypichthys strigatus</i>	43
	<i>Abudefduf vaigiensis</i>	<i>Parma microlepis</i>	2
	<i>Abudefduf vaigiensis</i>	<i>Microcanthus strigatus</i>	31
	<i>Acanthurus nigrofuscus</i>	<i>Atypichthys strigatus</i>	9
	<i>Acanthurus nigrofuscus</i>	<i>Parma microlepis</i>	12
	<i>Acanthurus nigrofuscus</i>	<i>Microcanthus strigatus</i>	41
	<i>Acanthurus triostegus</i>	<i>Atypichthys strigatus</i>	0
	<i>Acanthurus triostegus</i>	<i>Parma microlepis</i>	5
	<i>Acanthurus triostegus</i>	<i>Microcanthus strigatus</i>	25
Temperate vs. Temperate	<i>Atypichthys strigatus</i>	<i>Parma microlepis</i>	6
	<i>Atypichthys strigatus</i>	<i>Microcanthus strigatus</i>	24
	<i>Parma microlepis</i>	<i>Microcanthus strigatus</i>	24

399

400 b)

Warm-temperate	Pairs of species		Overlap (%)
Affinity			
Tropical vs. Tropical	<i>Abudefduf sexfasciatus</i>	<i>Abudefduf vaigiensis</i>	37
	<i>Abudefduf sexfasciatus</i>	<i>Acanthurus nigrofuscus</i>	0
	<i>Abudefduf sexfasciatus</i>	<i>Acanthurus triostegus</i>	0
	<i>Abudefduf vaigiensis</i>	<i>Acanthurus nigrofuscus</i>	0
	<i>Abudefduf vaigiensis</i>	<i>Acanthurus triostegus</i>	12
	<i>Acanthurus nigrofuscus</i>	<i>Acanthurus triostegus</i>	56
Tropical vs. Temperate	<i>Abudefduf sexfasciatus</i>	<i>Atypichthys strigatus</i>	37
	<i>Abudefduf sexfasciatus</i>	<i>Parma microlepis</i>	0
	<i>Abudefduf sexfasciatus</i>	<i>Microcanthus strigatus</i>	30
	<i>Abudefduf vaigiensis</i>	<i>Atypichthys strigatus</i>	61*
	<i>Abudefduf vaigiensis</i>	<i>Parma microlepis</i>	0

	<i>Abudefduf vaigiensis</i>	<i>Microcanthus strigatus</i>	47
	<i>Acanthurus nigrofuscus</i>	<i>Atypichthys strigatus</i>	5
	<i>Acanthurus nigrofuscus</i>	<i>Parma microlepis</i>	26
	<i>Acanthurus nigrofuscus</i>	<i>Microcanthus strigatus</i>	18
	<i>Acanthurus triostegus</i>	<i>Atypichthys strigatus</i>	6
	<i>Acanthurus triostegus</i>	<i>Parma microlepis</i>	20
	<i>Acanthurus triostegus</i>	<i>Microcanthus strigatus</i>	20
Temperate vs. Temperate	<i>Atypichthys strigatus</i>	<i>Parma microlepis</i>	0
	<i>Atypichthys strigatus</i>	<i>Microcanthus strigatus</i>	49
	<i>Parma microlepis</i>	<i>Microcanthus strigatus</i>	12

401

402 c)

Cold-temperate Affinity	Pairs of species		Overlap (%)
Tropical vs. Tropical	<i>Abudefduf sexfasciatus</i>	<i>Abudefduf vaigiensis</i>	59
	<i>Abudefduf sexfasciatus</i>	<i>Atypichthys strigatus</i>	59
Tropical vs. Temperate	<i>Abudefduf sexfasciatus</i>	<i>Parma microlepis</i>	2
	<i>Abudefduf sexfasciatus</i>	<i>Microcanthus strigatus</i>	9
	<i>Abudefduf vaigiensis</i>	<i>Atypichthys strigatus</i>	43
	<i>Abudefduf vaigiensis</i>	<i>Parma microlepis</i>	1
	<i>Abudefduf vaigiensis</i>	<i>Microcanthus strigatus</i>	7
Temperate vs. Temperate	<i>Atypichthys strigatus</i>	<i>Parma microlepis</i>	0
	<i>Atypichthys strigatus</i>	<i>Microcanthus strigatus</i>	0
	<i>Parma microlepis</i>	<i>Microcanthus strigatus</i>	20

403

404

405 **Aggressive behaviours among species**

406 Although not statistically significant, aggressive behaviours of most tropical and temperate
 407 species towards other individuals was always highest against their own species, and very low
 408 towards heterospecific tropical or heterospecific temperate species, independent of latitudinal
 409 range position. *A. nigrofuscus* showed to be the most aggressive species with individuals of its
 410 own species and other tropical and temperate species. *Parma microlepis* was the only
 411 temperate species that showed aggression towards other species (Fig. S6, Table S4).

412

413 **Shoaling preferences across range positions**

414 Some of the tropical and temperate fishes showed changes in shoaling preference as a
415 function of range position (Fig. S7, Table S5). Two tropical fishes showed a decrease in their
416 shoaling with their own species (*A. triostegus*) and other tropical species (*A. nigrofuscus*) with
417 increasing latitudinal ranges. One tropical species (*A. vaigiensis*) increased their shoaling time
418 with temperate fishes with increasing latitudinal range, whilst one temperate species (*M.*
419 *strigatus*) showed an increase in shoaling with other tropical species with increasing
420 latitudinal range.

421

422

423 **Discussion**

424

425 We here show that behavioural niche shifts and expansions are potential mechanisms adopted
426 by sympatric tropical vagrant and native-temperate fishes to adjust to changing community
427 structures under climate change. Whilst tropical fishes showed changes in their behavioural
428 repertoire at cold-temperate latitudes, temperate species exhibited a behavioural niche shift
429 and expansion at subtropical latitudes. As such, temperate species show niche expansion at
430 their trailing warm-water edges where tropical species have higher abundances and where
431 they have been coexisting for a longer period of time, whilst tropical species show niche
432 expansion at their leading edges where they are invading novel temperate ecosystems.

433 Behavioural niche expansion reflects increased generalism, which might be beneficial under
434 environmental change (Whitney & Gabler 2008) and increased competition (Svanback &
435 Bolnick 2007; Huss et al. 2008). Generalists are more flexible in resource use than specialists,
436 facilitating species adaptation and coexistence (Clavel et al. 2011; Slatyer et al. 2013; Ducatez
437 et al. 2015). As such, tropical and temperate fishes that are behavioural generalists are more
438 likely to colonise non-native temperate areas and resist tropicalisation, respectively.

439 Behavioural niche segregation facilitates the colonisation of temperate reefs by tropical
440 fishes, and allows their coexistence with native species. Such segregation can also provide
441 advantages to temperate fishes under invasion of tropical species. Overall, tropical fishes
442 showed only a low to moderate degree of behavioural niche overlap with temperate native
443 species, independent of range position. However, where their behaviours overlap, temperate
444 fishes might negatively interfere with the foraging activities of tropical fishes (Coni et al.
445 2021). It has been postulated that species that highly overlap in any of their n-dimensional
446 niche space (e.g. climatic, diet) with other species are more susceptible to competition
447 (Hutchinson 1957). When resources are sparse, and species share niches, extinction may
448 eventually occur if they do not shift their niches (Human & Gordon 1996). Conversely, high
449 resource availability may allow coexistence regardless of significant niche overlap (Sale
450 1974; Connell 1980). This niche differentiation may have allowed the historical coexistence
451 of tropical and temperate species at subtropical latitudes, and this together with flexibility in
452 their behavioural niche repertoire might contribute their future coexistence at temperate
453 latitudes. Additionally, aggressive behaviour was almost absent among tropical and temperate
454 species, with the highest rates of aggressiveness observed towards individuals of the same
455 species. When the competitive ability between species is small, species can coexist despite
456 occupying relatively similar niches (Mayfield & Levine 2010). Our findings therefore suggest
457 that the behavioural segregation and the low incidence of inter-species aggression could
458 facilitate the increasing coexistence of tropical and temperate fishes in temperate ecosystems.

459 Feeding behaviour (foraging position) was one of the most important behaviours
460 responsible for behavioural niche alteration and segregation across range positions for both
461 tropical and temperate species. A possible explanation is the difference in prey availability
462 across these latitudes. Optimal foraging theory predicts that individuals modify their
463 behaviour to maximise their physiological integrity (fitness) as prey availability changes

464 (Stephens & Krebs 1986; Sih & Christesen 2001). A study using stable isotopes performed at
465 the same sites and on the same species showed that prey types consumed by tropical and
466 temperate species differed regionally (from warmer to cooler latitudes) (Miranda et al. 2018;
467 Kingsbury et al. 2019), which can explain the changes in their foraging behaviour as observed
468 in the present study.

469 Shoaling composition was also responsible for behavioural niche alteration and
470 segregation across range positions for both affinities. Although some tropical species may
471 exhibit maladaptive behaviours in temperate environments, with resulting fitness loss (e.g.
472 decreasing foraging efficiency due to high abundance of larger temperate fishes and
473 unfamiliarity with novel conditions) (Coni et al. 2021), the tropical vagrant and temperate
474 species also showed some favourable behavioural traits. On temperate reefs, the studied
475 tropical vagrant fishes shoal with local species, suggesting that they are flexible in employing
476 social interactions with unknown species (see Figures S7, S8). This novel mixed-species
477 shoaling can increase survivorship of tropical vagrants in temperate ecosystems (Smith et al.
478 2018; Pajimans et al. 2019). Shoaling behaviour with native fishes provides a source of
479 information about the new environment (e.g. recognition of unfamiliar prey and predators)
480 (Hoare & Krause 2003), a strategy that is advantageous to range-extending tropical social
481 species, especially during their initial stages of range-extension. Although alterations to
482 shoaling preferences along the studied climate range might also have contributed to the
483 changes in species behavioural niche space, this is only one of many factors altering the
484 behavioural niches. The overall latitudinal effect was more important than the few changes in
485 shoaling preference, because all studied species changed their behavioural niche as a function
486 of range position.

487 The importance of behavioural niche space has been largely overlooked in climate
488 change studies. Studies of ecological niche breadth and niche overlap have mainly been based

489 on diets, e.g. stomach contents or stable isotope analyses (Newsome et al. 2007; Kingsbury et
490 al. 2019). Only recently, other proxies such as morphology and foraging behaviour have been
491 used to measure ecological niche space, which can be related to habitat use, feeding and
492 locomotion (Azzuro et al. 2014; Brandl & Bellwood 2014; Smith et al. 2016). However,
493 studies using these realised niche metrics mainly focus on feeding ecology and habitat use,
494 ignoring the fact that species show complex adaptive behaviours that reflect an important
495 ecological niche as well (Gouraguine et al. 2019). Furthermore, instead of relying on a single
496 behaviour, as is common in climate change studies (Beck et al. 2016), we use an established
497 approach from stable isotope studies to calculate niche breadth in a multivariate space as a
498 proxy of behavioural modification. This novel approach shows that specific behaviours
499 contribute more to the observed differences in niche breadth across species and range
500 positions, emphasising the importance of using multiple behaviours to test species responses
501 to altered environments or climate change. Although suggestions about the underlying
502 mechanisms should be interpreted with some caution due to the lack of manipulative
503 experimental approaches, or behavioural comparison between range-extending and non-
504 range-extending species, we show that modification of behavioural repertoires can be a
505 potential mechanism that could allow coexistence with temperate species and successful
506 establishment by tropical vagrants invading temperate ecosystems under climate change.

507

508

509 **Conclusions**

510 We reveal that behavioural niche modification and behavioural generalism may be critical
511 mechanisms that allow tropical fish species that extend their ranges to cold-temperate
512 latitudes under climate change to reduce competition with local temperate species and cope
513 with novel temperate climate and biotic conditions. Additionally, maintenance of behavioural

514 niche segregation among tropical and temperate fish species combined with flexible shoaling
515 behaviour and the low incidence of inter-species aggression, may further mediate successful
516 invasion of tropical fishes into temperate environments under climate change, whilst allowing
517 generalist temperate fish species to persist.

518

519

520 **Ethics.** All experiments were performed under animal ethics approval numbers S-2015-222A
521 and S-2017-002 (University of Adelaide) and ETH17-1117 (University of Technology
522 Sydney) and followed the University's animal ethics guidelines.

523

524 **Authors' contributions.** E.O.C.C, I.N., and D.J.B. conceived and designed the study,
525 E.O.C.C. and C.M.F. collected the data, E.O.C.C. analysed the data. E.O.C.C, I.N., and D.J.B
526 wrote the article.

527

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529

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536 **Data accessibility.** All data will be made available in a Mendeley Data repository.

537

538

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