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1 **Climate change erodes competitive hierarchies among native, alien and range-**

2 **extending crabs**

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14   **Abstract**

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16   Global warming and ocean acidification alter a wide range of animal behaviours, yet the effect on

17   resource competition among species is poorly understood. We tested whether the combination of

18   moderate levels of ocean acidification and warming altered the feeding success of co-occurring

19   native, alien, and range-extending crab species, and how these changes affected their hierarchical

20   dominance. Under contemporary conditions the range-extending species spent more time feeding,

21   than the alien and the native species. Under conditions simulating future climate there was no

22   difference in the proportion of time spent feeding among the three species. These behavioural

23   changes translated to alterations in their dominance hierarchy (based on feeding success) with the

24   most dominant species under present day conditions becoming less dominant under future

25   conditions, and vice versa for the least dominant species. While empirical studies have predicted

26   either reversal or strengthening of hierarchical dominance in animal species, we suggest that even

27   moderate increases in ocean temperature and acidification can drive a homogenisation in

28   behavioural competitiveness, eroding dominance differences among species that are linked to

29   fitness-related traits in nature and hence important for their population persistence.

30

31   **Keywords:**

32   competition, species interactions, invasive species

33

34   **Summary:**

35   Exposure to moderate ocean warming and acidification resulted in the degradation of competitive

36   hierarchies of a native, a range-extending, and an alien crab species, driving a homogenisation in

37   behavioural competitiveness.

Introduction

39

40   As global temperatures increase, species can respond through shifting their native ranges,

41 typically in a poleward direction (Chen et al., 2011). This phenomenon can result in novel species

42 interactions and communities, often with negative consequences for recipient ecosystems (Vergés

43 et al., 2016). At the same time, the number of emerging alien species is increasing globally, due to

44 the concomitant increases in global transport and trade (Seebens et al., 2018). Like species range

45 shifts, alien invasions produce novel species interactions and community assemblages, and can lead

46 to biotic homogenisation.

47   Biotic homogenisation of communities occurs when genetic, taxonomic or functional

48 similarities increase, and differences decrease (Clavel et al., 2011; Olden et al., 2016). The

49 consequences of biotic homogenisation include increased vulnerability to invasion and disease, and

50 reduced community or ecosystem resilience to stressors and disturbances (Olden et al., 2004). In

51 marine environments, biotic homogenisation has been observed as temperate community

52 compositions become more tropicalised (Magurran et al., 2015), where habitat-modifying species

53 expand their ranges (Ling, 2008), and when non-native species are introduced (Villeger et al., 2014).

54 Globally, marine alien species have resulted in rapid declines in localised abundances of native

55 species, with invasive crustaceans resulting in an overall decrease in the abundance of native marine

56 taxa (Anton et al., 2019). Biotic homogenisation is facilitated by changing species interactions,

57 including competition.

58   Species interactions, much like environmental stressors, affect the persistence and fitness of

59 individuals. Novel community structures, which can result from climate change, will expose species

60 to new competitors for resources. Concerns have been raised about the effects that novel

61 competitors may have on biodiversity and local extinctions, as some studies have shown

62 competition to intensify under climate change (Milazzo et al., 2013). Furthermore, empirical studies

63 have predicted either reversal or strengthening of dominance in species under climate change

64 (Milazzo et al., 2013; Van de Waal et al., 2011). How these changes in competition will affect

65 community assemblages and community functioning is poorly understood, particularly when

66 combined with the abiotic impacts of climate change.

67   How species behaviours change in the future will be highly dependent on the rate and

68 extent of climate change. Current climate projections suggest the likely climate pathway for 2081-

69 2100 will fall within the medium emissions scenarios, being the Intergovernmental Panel for Climate

70 Change's (IPCC) RCP4.5 or RCP6.0 climate scenarios (Allen, 2018). The global mean sea surface

71 temperature changes projected for 2081-2100 in scenarios RCP4.5 and RCP6.0 are a mean increase

72 of 1.8 °C and 2.2 °C, respectively (IPCC, 2014). Concurrently are increases in the partial pressure of

73 CO_2 in sea water, commonly referred to as ocean acidification, more easily measured by a decrease

74 in ocean pH. In RCP4.5 a decrease in pH of 0.13 is projected, and in RCP6.0 the projected decrease in

75 pH is 0.2 units (IPCC, 2014). Few studies have looked at how medium emissions scenarios will affect

76 competitive behaviours in marine taxa, as the majority of studies use the RCP8.5 scenario in their

77 experimental designs (+3.7 °C and -0.31 pH units).

78   Hierarchies among competitors are important for ecosystem maintenance and functioning,

79 for example, by regulating population sizes and their distributions, and partitioning of resources

80 (Case and Gilpin, 1974; Merkle et al., 2009; Savolainen and Vepsäläinen, 1988). These hierarchies

81 can be linear, with a clear order of dominance, or homogenous, where there is no single best

82 competitor (Chase and Seitz, 2011). When an alien species enters a new community, native species

83 will respond through behavioural changes, often resulting in decreased dominance within the

84 community (Anton et al., 2019). In response to competition from alien species, native species have

85 been observed reducing their use of shelter (Grabowska et al., 2016), being displaced out of invaded

86 areas (Holway, 1999; O'Dowd et al., 2003), and being outcompeted for resources such as food

87 (Grosholz et al., 2000; Kenward and Holm, 1993). Alien species can also facilitate potential native

88 competitors through mechanisms such as competitive release, habitat modification, and predatory

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89   release (Grosholz et al., 2000). Regardless of whether the alien species impedes or facilitates the

90   native species, the presence of an alien species can alter the dominance hierarchy in a community.

91   Here, we tested the combined effects of moderate ocean warming and acidification on

92   species resource competition, using a native, range-extending, and an alien crab species with

93   different, but currently overlapping latitudinal distributions. We tested whether a range-extending

94   species can mitigate the negative competitive impacts of alien invaders on local species threatened

95   by climate change, and as such test whether species range extensions can provide benefits to

96   recipient communities.

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99   **Methods**

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101   **Study organisms and experimental seawater manipulation**

102   Our study used three consumer species, consisting of a native, range-extending, and an alien

103   crab species with different latitudinal distributions. Crabs were chosen as the model organism for

104   this experiment due to their distinct competitive behaviours, a pre-existing population of the alien

105   species in our study area, thereby easing the logistics of keeping them in captivity, and due to the

106   lack of studies that quantify direct interactions between native and non-native crabs (Howard et al.,

107   2017). The native crab species was the common sand crab (*Ovalipes australiensis*) which has a

108   southern distribution, stretching along the southern Australian coast from Perth, Western Australia

109   to Wide Bay, Queensland. The range-extending species was the blue swimmer crab (*Portunus*

110   *armatus;* previously *Portunus pelagicus*; Lai et al., 2010) which has a more northern distribution from

111   Perth, Western Australia through the tropical coastal waters of the Western Indian Ocean and the

112   Eastern Pacific, down through to southern Victoria, with well-established populations occurring

113   along the southern tip of its distribution on the South Australian coast (Noell et al., 2014). In South

114   Australia the blue swimmer crab has only been commercially harvested since the 1980's, so there is

115 very limited information about its presence in the area prior to this time. The alien species was the

116 serial invader, the European green crab (*Carcinus maenas*). Outside of its native Europe, it has

117 successfully invaded Atlantic North America, South Africa, Japan, Pacific North America, and

118 Australia (Carlton and Cohen, 2003). In Australia the European green crab is distributed along the

119 south-eastern coast from Gulf St Vincent in South Australia through to southern New South Wales,

120 and Tasmania (Thresher et al., 2003). It is believed to have been first introduced Australia in the late

121 1800's, with established populations first appearing in Port Phillip Bay, Victoria in 1900 (Carlton and

122 Cohen, 2003). In South Australia, where we collected, the first population of European green crabs

123 were identified in 1976 (Thresher et al., 2003). All three species co-occur in shallow waters <5m on

124 sand and mudflats, including mangrove and seagrass habitats, along the southern Australian

125 coastline, where they consume molluscs and small fish (Figure 1; Gowlett-Holmes, 2008).

126   Blue swimmer, common sand, and European green crabs were caught using baited traps and

127 physical raking along the eastern coast of Gulf St Vincent, South Australia in November 2016. A total

128 of 18 crabs were used in the experiment, with three replicates per species per treatment of either

129 ambient seawater temperature and pCO_2, based on local environmental conditions, or elevated

130 values. Individuals were size matched as closely as possible prior to the acclimation period; however,

131 prior to filming the trials, after four weeks in captivity, four of the crabs had moulted and grown

132 (Figure S1). Crabs were kept individually in 52 L tanks containing 18 L of natural filtered seawater

133 which was partially exchanged with pre-treated water approximately every 3 days, and 1-2 cm of

134 sand at the bottom of the tank. The crabs were acclimatised over a period of seven days during

135 which temperature was increased by 2 °C, at a rate of approximately 0.5 °C every second day, and

136 pH was decreased by 0.25 units, equivalent to a pCO_2 decrease of 320 μatm, at a rate of

137 approximately 0.05 units every second day. The crabs were maintained during three weeks in either

138 ambient (control) conditions, with a temperature of 17.43°C (± 0.05) and pCO_2 of 552 μatm (± 17), or

139 in a future climate, based on RCP 6.0 projections for 2090-2099 (IPCC, 2014), where elevated

140 temperature was 19.71°C (± 0.07) and elevated pCO_2 was 870 μatm (± 41) (Table 2). Temperature

141 was maintained by placing the tanks in water baths heated with heater-chiller units (TR15 Aquarium

142 chillers), and 1000 W titanium heaters. Pumps were connected to the chiller units which ensured an

143 even temperature distribution throughout the water baths. Elevated CO_2 concentrations in the

144 seawater were maintained using a PEGAS 4000 MF Gas Mixer (Columbus Instruments, Columbus,

145 Ohio) that mixed pure CO_2 with ambient air. The CO_2-enriched air was then bubbled into each tank

146 separately. pH_{NIST}, temperature and salinity were measured daily in each tank using a pH (Ionix pH5)

147 and salinity meter (Ohaus ST10S; Figure S2). Total alkalinity of seawater from each tank was

148 estimated weekly by Gran titration. Alkalinity standards were accurate within 1% of certified

149 reference material from Dr. A. Dickson (Scripps Institution of Oceanography). Average seawater

150 pCO_2 was calculated using CO2SYS using already established constants (Dickson and Millero, 1987;

151 Mehrbach et al., 1973)

152

153 **Behavioural observations**

154 After three weeks of exposure to ambient and future seawater climate conditions,

155 competitive behaviours were quantified. Trials were conducted in an arena (59 × 44 cm) filled with

156 27 L of water pre-treated to the respective climate treatment. Crabs were starved for a minimum of

157 36 hours prior to the first feeding trial. Each trial consisted of three crabs inside the arena, one of

158 each species, competing for a defrosted bivalve mollusc (*Plebidonax deltoids*). Crabs were given a 5-

159 minute acclimation period together where they were free to roam around the arena prior to the

160 addition of the food item. The food item was dropped from a height of approximately one metre to

161 minimise observer interference with the crabs, after which each trial was filmed for 5 min from

162 above with a GoPro camera (Hero 4 Silver). Video recorders were used to avoid potential bias in

163 behaviour due to presence of an observer. In order to minimise stress and fatigue, individual crabs

164 were not used in consecutive trials within one day, and after 2 days of trials a rest day was given. All

165 possible combinations of individual crabs were trialled (n = 48 tests), with the exception of two trials,

166   where one individual died before they could occur. Trials where feeding did not occur (n = 4) were

167   also excluded from the analysis as feeding was the response variable tested.

168   Behaviours were analysed from the video recordings using the behavioural coding program

169   Solomon Coder (Péter, 2017). The behaviours recorded were: the individual that was the first to

170   reach the food ('first to food'), the number of seconds spent feeding per individual, the number of

171   seconds spent threatening per individual, the number of times that an individual attacked another of

172   the two species, and the number of times that an individual fled from an attack by another species

173   (Table 1). None of the behaviours described were mutually exclusive.

174

175   **Statistical analysis**

176   *Mixed models*

177   We conducted all of our analyses in the R software environment version 3.4.4 (R Core Team,

178   2018). We constructed a series of general linear mixed effects models (GLMMs) within the package

179   glmmADMB (Fournier et al., 2012; Skaug, 2016) to examine the effect of increased seawater

180   temperature and pCO$_2$ on the relationship between three competitive behaviours and feeding

181   success. We set individual as a varying intercept random effect. Feeding success was recorded as a

182   ratio of time spent feeding by the focal species relative to total time feeding by all individuals in the

183   match and was analysed using a beta distribution with a logit link function. Trials where no feeding

184   occurred within the five min recording were excluded from the analysis (two trials out of 25 for

185   current climate, and two out of 23 from the future climate treatment).

186   Initially, we analysed the data to determine if there was a difference in feeding success

187   among species and between treatments. Then we analysed what was driving differences in feeding

188   success between species, with each analysis repeated with a different species (k = 3) as the focal

189   species (Table S1). The three independent explanatory variables were: (i) threatening, recorded as a

190   ratio of time spent threatening by the focal species relative to total time threatening by all

191   individuals in the match; (ii) fleeing, which was the number of times the focal species retreated

192   relative to the number of attacks against it by the competing species; and (iii) first to food, a binary

193   categorical variable (yes, no) for the focal species (Table 1). The best model was selected with the

194   dredge function in the package *MuMin* (Barton, 2016) based on the Akaike's information criterion

195   corrected for small samples (AICc). Mean Estimates were calculated for model averaged effects from

196   the 95% confidence best model set (Anderson and Burnham, 2002; Gruber, 2011).

197

198   *Hierarchy methods*

199   A competitive-outcomes matrix was constructed using the outcomes of each trial to

200   determine whether there was a linear or intransitive competition hierarchy. Linear competition, also

201   known as transitive competition, is defined as competitors having a clear order of rank, whereas

202   intransitive competition is defined as those in which there is no single best competitor, or

203   homogenisation of the hierarchy (Chase and Seitz, 2011). The matrix was adapted from Laird and

204   Schamp (2008) to incorporate a third co-occurring species (Table S2). Individuals were allocated a

205   value to represent number of feeding 'wins' in each trial. Each position in the matrix was filled with

206   either a 1, 0, or 0.5. A '1' was assigned to the individual with the highest proportion of time feeding

207   in the trial, a '0' was assigned to the individual with the least time feeding, and a '0.5' was assigned

208   for the remaining individuals (intermediate time feeding). Where only one individual fed in a trial the

209   other two individuals were allocated a '0'. Similar to the GLMMs, trials with no feeding results were

210   excluded from the analysis. The values for the wins were summed for each focal individual across all

211   trials and used to determine their individual position within the hierarchy. Similarly, values were

212   summed for all individuals of the same species in order to determine the rank of the three species

213   under the different experimental conditions.

214   The feeding success values were then used to generate an individual and species level

215   relative intransitivity index score using the method described in Laird and Schamp (2006). The

216   relative intransitivity index score is a measure of how equally distributed wins are amongst

217   individuals. Communities where wins are distributed unequally have low scores, a minimum of 0.25

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218   in our matrix, indicating that they have a linear hierarchy, while communities where wins are

219   distributed equally have high scores, a maximum of 1 in our matrix, indicating that they are

220   intransitive or homogenous. To determine whether the outcome of this matrix was the result of

221   biological drivers or more likely produced by chance we performed a bespoke randomisation test.

222   We randomly generated a distribution using 10,000 iterations, and overlaid each species mean rank.

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224

225   **Results**

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227   When all three species were compared simultaneously there was a significant effect of species, but

228   no effect of future climate (i.e., ocean warming and acidification combined) or the interaction

229   between species and climate treatment, on time spent feeding (Table 3). Under current conditions,

230   the alien and native species spent significantly less time feeding than the range-extending species

231   (Figure 2 and Table 4). Under future conditions, however, the three species no longer differed in

232   their proportion of time spent feeding. When a focal species was selected, the top-weighted models

233   for all three species included 'first to food' as an important predictor of a higher proportion of time

234   feeding (Table 3). The top-weighted model for the alien species also included threatening as a

235   predictor variable of significantly decreasing feeding time.

236   The competitive-outcomes matrix showed a hierarchical structure among the three species

237   under present day conditions, where the range-extending was the most dominant species, followed

238   by the alien species, then the native species (Figure 3). However, under future climate conditions the

239   hierarchical structure weakened and became more homogenous, with the range-extending species

240   becoming less dominant and the native species gaining dominance (Figure 3). The change in

241   hierarchy was based on a change in the number of 'wins' (i.e. the individual with the highest

242   proportion of time feeding), with the native species increasing the number of wins they had, the

243   number of wins for the range-extending species decreased, and the alien species maintained the

244   same number of wins. This shift in the number of feeding wins for each species resulted in the

245   relative intransitivity score increasing under future climate conditions. At an individual level the

246   relative intransitivity score was 0.53 for current conditions and 0.71 in future conditions, where 0.25

247   is a linear hierarchy and 1.0 is a homogeneous hierarchy.

248

249

250   **Discussion**

251

252   Competitive hierarchies among species can erode under climate change. Previous studies

253   found a strengthening or reversal in competitive hierarchies under elevated pCO$_2$ and/or

254   temperature (McCormick et al., 2013; Van de Waal et al., 2011). However, we show that a moderate

255   increase in seawater temperature and pCO$_2$ resulted in homogenisation of animal competitive

256   hierarchies, demonstrating that climate change can also weaken competitive hierarchies. Likewise,

257   species community structures are being increasingly homogenised by climate change, globalisation

258   and species invasions (Clavel et al., 2011). This results in increased similarities in genetic, taxonomic

259   and/or functional diversity among species communities, which can lead to a loss of ecosystem

260   resilience (Clavel et al., 2011). Competitive hierarchies play an important role in community

261   structuring by influencing aspects of an individual's life such as stress, growth rate, and ability to

262   raise viable offspring (Chase and Seitz, 2011). Loss of a structured hierarchy can result in significant

263   long-term impacts on community composition, particularly if they result in changes in species

264   abundances (Vergés et al., 2016).

265   The best predictor of whether a crab would spend the greatest proportion of time feeding

266   was first to food. The other competitive behaviours, threatening and fleeing, were not important

267   predictors for feeding success (except for the alien species). While these aggressive behaviours did

268   not change under the future climate conditions, the species which was first to food – applied as a

269   proxy for boldness in this study – did. The native species became bolder, increasing the number of

270   wins they had, the number of wins for the range-extending species decreased, and the alien species

271   maintained the same number of wins. While an increase in aggressiveness due to climate change has

272   been observed in many species (Nagelkerken and Munday, 2015), we found that when aggression

273   was an important predictor for feeding success, as in the case of the alien species, it was due to a

274   decrease in aggressive behaviour.

275   In the current conditions we found that the range-extending species outperformed both the

276   alien and native crab species. While we know that range-extending and alien species can

277   independently both have a profound affect on ecosystems through habitat modification, predation,

278   and competition, there is little research on the combination of the two on native species and

279   communities (Anton et al., 2019; Ling, 2008). The ability of the range-extending species to

280   outcompete the alien species suggests that species expanding their ranges as a result of climate

281   change may be able to slow down the establishment of alien populations through direct

282   competition.

283   Due to the varying rate of climate change and based on our understanding of how species

284   evolve and adapt, there is always the possibility that what we observed will not be realised in the

285   future. With longer exposure periods and a slower rate of change, any one of the species may adapt

286   or acclimate to future conditions like those tested, thereby changing the ultimate outcome.

287   Similarly, this study is constrained by the limited number of replicates, using repeated measures,

288   rather than a larger number of new individuals, across trials. Our results therefore provide an

289   insight, and prediction, into possible future scenarios.

290   The potential distribution of species under future climate conditions is largely inferred from

291   their niches in their current distribution, based predominately on abiotic stressors, but this may not

292   apply to their performance in novel environments. It has been postulated that species with higher

293   thermal tolerances or broader thermal realised niches, such as range-extending and alien species,

294   respectively, will likely perform better in a future climate than many native species that resist or are

295   unable to keep pace with our changing climate (Bates et al., 2013; Stuart-Smith et al., 2017).

296   However, we found that in a multi-species scenario, current distribution range was not a good

297   indicator of feeding success under climate change. Under present-day climate, the range-extending

298   species dominated the hierarchy; however, when faced with future levels of warming and ocean

299   acidification all three species performed equally. Climate change eroded dominance differences

300   among species that are linked to fitness-related traits in nature and hence are important for their

301   population persistence. We show that species success in a future climate depends heavily on species

302   interactions, with indirect behavioural changes in dominance structures having a significant effect on

303   their feeding success.

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305   **Ethics.** No permit was required.

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307   **Data accessibility.** The dataset supporting this article has been uploaded as electronic

308   supplementary material.

309

310   **Authors' contributions.** S.S.L. and I.N. conceived the study. S.S.L. and G.B. carried out data

311   collection, S.S.L analysed the data, and drafted the manuscript; P.C. helped with data analysis; I.N.

312   and P.C. contributed to writing the manuscript. All authors gave final approval for publication.

313   Competing interests. We have no competing interests.

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319   **References**
320
321   Allen MR, O.P. Dube, W. Solecki, F. Aragón-Durand, W. Cramer, S. Humphreys, M. Kainuma, J. Kala,
322   N. Mahowald, Y. Mulugetta, R. Perez, M. Wairiu, and K. Zickfeld, 2018. Framing and Context.
323   In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of
324   1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in

325   the context of strengthening the global response to the threat of climate change, sustainable
326   development, and efforts to eradicate poverty. In: Masson-Delmotte V, P. Zhai, H.-O.
327   Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S.
328   Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor,
329   and T. Waterfield, editor. In Press.

330 Anderson DR, Burnham KP, 2002. Avoiding Pitfalls When Using Information-Theoretic Methods. The
331   Journal of Wildlife Management 66:912-918. doi: 10.2307/3803155.

332 Anton A, Geraldi NR, Lovelock CE, Apostolaki ET, Bennett S, Cebrian J, Krause-Jensen D, Marbà N,
333   Martinetto P, Pandolfi JM, Santana-Garcon J, Duarte CM, 2019. Global ecological impacts of
334   marine exotic species. Nature Ecology & Evolution 3:787-800. doi: 10.1038/s41559-019-
335   0851-0.

336 Barton K 2016. MuMIn: Multi-Model Inference. Version R package version 1.15.6.

337 Bates AE, McKelvie CM, Sorte CJB, Morley SA, Jones NAR, Mondon JA, Bird TJ, Quinn G, 2013.
338   Geographical range, heat tolerance and invasion success in aquatic species. Proceedings of
339   the Royal Society B-Biological Sciences 280. doi: 10.1098/rspb.2013.1958.

340 Carlton JT, Cohen AN, 2003. Episodic global dispersal in shallow water marine organisms: the case
341   history of the European shore crabs Carcinus maenas and C. aestuarii. Journal of
342   Biogeography 30:1809-1820. doi: doi:10.1111/j.1365-2699.2003.00962.x.

343 Case TJ, Gilpin ME, 1974. Interference Competition and Niche Theory. Proceedings of the National
344   Academy of Sciences 71:3073-3077. doi: 10.1073/pnas.71.8.3073.

345 Chase ID, Seitz K, 2011. Chapter 4 - Self-Structuring Properties of Dominance Hierarchies: A New
346   Perspective. In: Huber R, Bannasch DL, Brennan P, editors. Advances in Genetics: Academic
347   Press. p. 51-81.

348 Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD, 2011. Rapid Range Shifts of Species Associated
349   with High Levels of Climate Warming. Science 333:1024-1026. doi:
350   10.1126/science.1206432.

351 Clavel J, Julliard R, Devictor V, 2011. Worldwide decline of specialist species: toward a global
352   functional homogenization? Frontiers in Ecology and the Environment 9:222-228. doi:
353   10.1890/080216.

354 Dickson AG, Millero FJ, 1987. A comparison of the equilibrium constants for the dissociation of
355   carbonic acid in seawater media. Deep Sea Research Part A Oceanographic Research Papers
356   34:1733-1743. doi: 10.1016/0198-0149(87)90021-5.

357 Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J, 2012. AD
358   Model Builder: using automatic differentiation for statistical inference of highly
359   parameterized complex nonlinear models. Optimization Methods and Software 27:233-249.
360   doi: 10.1080/10556788.2011.597854.

361 Gowlett-Holmes KL, 2008. A field guide to the marine invertebrates of South Australia. Sandy Bay,
362   TAS, Australia: Notomares.

363 Grabowska J, Kakareko T, Blonska D, Przybylski M, Kobak J, Jermacz L, Copp GH, 2016. Interspecific
364   competition for a shelter between non-native racer goby and native European bullhead
365   under experimental conditions - Effects of season, fish size and light conditions. Limnologica
366   56:30-38. doi: 10.1016/j.limno.2015.11.004.

367 Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG, 2000. THE IMPACTS OF A
368   NONINDIGENOUS MARINE PREDATOR IN A CALIFORNIA BAY. Ecology 81:1206-1224. doi:
369   10.1890/0012-9658(2000)081[1206:tioanm]2.0.co;2.

370 Gruber N, 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global
371   change. Philosophical Transactions of the Royal Society A: Mathematical,
372   Physical and Engineering Sciences 369:1980-1996. doi:
373   10.1098/rsta.2011.0003.

374 Holway DA, 1999. Competitive mechanisms underlying the displacement of native ants by the
375   invasive Argentine ant. Ecology 80:238-251. doi: 10.1890/0012-
376   9658(1999)080[0238:CMUTDO]2.0.CO;2.
377 Howard BR, Therriault TW, Côté IM, 2017. Contrasting ecological impacts of native and non-native
378   marine crabs: a global meta-analysis. Marine Ecology Progress Series 577:93-103. doi:
379   10.3354/meps12245
380 IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to
381   the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core
382   Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
383 Kenward RE, Holm JL, 1993. On the replacement of the red squirrel in Britain: a phytotoxic
384   explanation. Proceedings of the Royal Society of London Series B: Biological Sciences
385   251:187-194. doi: 10.1098/rspb.1993.0028.
386 Lai JC, Ng PK, Davie PJ, 2010. A revision of the Portunus pelagicus (Linnaeus, 1758) species complex
387   (Crustacea: Brachyura: Portunidae), with the recognition of four species. The Raffles Bulletin
388   of Zoology 58:199-237.
389 Laird RA, Schamp BS, 2006. Competitive Intransitivity Promotes Species Coexistence. The American
390   Naturalist 168:182-193. doi: 10.1086/506259.
391 Laird RA, Schamp BS, 2008. Does local competition increase the coexistence of species in intransitive
392   networks. Ecology 89:237-247. doi: 10.1890/07-0117.1.
393 Ling SD, 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a
394   new and impoverished reef state. Oecologia 156:883-894. doi: 10.1007/s00442-008-1043-9.
395 Magurran AE, Dornelas M, Moyes F, Gotelli NJ, McGill B, 2015. Rapid biotic homogenization of
396   marine fish assemblages. Nature Communications 6:8405. doi: 10.1038/ncomms9405
397 McCormick MI, Watson SA, Munday PL, 2013. Ocean acidification reverses competition for space as
398   habitats degrade. Scientific Reports 3. doi: 10.1038/srep03280.
399 Mehrbach C, Culberson CH, Hawley JE, Pytkowicx RM, 1973. MEASUREMENT OF THE APPARENT
400   DISSOCIATION CONSTANTS OF CARBONIC ACID IN SEAWATER AT ATMOSPHERIC PRESSURE1.
401   Limnology and Oceanography 18:897-907. doi: doi:10.4319/lo.1973.18.6.0897.
402 Merkle JA, Stahler DR, Smith DW, 2009. Interference competition between gray wolves and coyotes
403   in Yellowstone National Park. Canadian Journal of Zoology 87:56-63. doi: 10.1139/Z08-136.
404 Milazzo M, Mirto S, Domenici P, Gristina M, 2013. Climate change exacerbates interspecific
405   interactions in sympatric coastal fishes. Journal of Animal Ecology 82:468-477. doi:
406   10.1111/j.1365-2656.2012.02034.x.
407 Nagelkerken I, Munday PL, 2015. Animal behaviour shapes the ecological effects of ocean
408   acidification and warming: moving from individual to community-level responses. Glob
409   Change Biol:974-989. doi: 10.1111/gcb.13167.
410 Noell CJ, C.L. B, Hooper GE, 2014. Blue Crab (Portunus armatus) Fishery 2012/13. Fishery Assessment
411   Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development
412   Institute (Aquatic Sciences). Adelaide: SARDI Publication No. F2007/000729-10. p. 77.
413 O'Dowd DJ, Green PT, Lake PS, 2003. Invasional 'meltdown' on an oceanic island. Ecology Letters
414   6:812-817. doi: 10.1046/j.1461-0248.2003.00512.x.
415 Olden JD, Comte L, Giam X, 2016. Biotic Homogenisation. eLS Chichester: John Wiley & Sons, Ltd
416 Olden JD, LeRoy Poff N, Douglas MR, Douglas ME, Fausch KD, 2004. Ecological and evolutionary
417   consequences of biotic homogenization. Trends in Ecology & Evolution 19:18-24. doi:
418   https://doi.org/10.1016/j.tree.2003.09.010.
419 Péter A 2017. Solomon Coder. Version beta 17.02.15.
420 R Core Team 2018. R: A language and environment for statistical computing. Vienna, Austria: R
421   Foundation for Statistical Computing.
422 Savolainen R, Vepsäläinen K, 1988. A Competition Hierarchy among Boreal Ants: Impact on Resource
423   Partitioning and Community Structure. Oikos 51:135-155. doi: 10.2307/3565636.

424   Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, van Kleunen
425   M, Winter M, Ansong M, Arianoutsou M, Bacher S, Blasius B, Brockerhoff EG, Brundu G,
426   Capinha C, Causton CE, Celesti-Grapow L, Dawson W, Dullinger S, Economo EP, Fuentes N,
427   Guénard B, Jäger H, Kartesz J, Kenis M, Kühn I, Lenzner B, Liebhold AM, Mosena A, Moser D,
428   Nentwig W, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S,
429   Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, Walker K, Ward DF,
430   Yamanaka T, Essl F, 2018. Global rise in emerging alien species results from increased
431   accessibility of new source pools. Proceedings of the National Academy of Sciences of the
432   United States of America. doi: 10.1073/pnas.1719429115/.
433   Skaug H, Fournier, D., Bolker, B. Magnusson, A. Nielsen, A. 2016. Generalized Linear Mixed Models
434   using 'AD Model Builder'. Version R package version 0.8.3.3.
435   Stuart-Smith RD, Edgar GJ, Bates AE, 2017. Thermal limits to the geographic distributions of shallow-
436   water marine species. Nature Ecology & Evolution. doi: 10.1038/s41559-017-0353-x.
437   Thresher R, Proctor C, Ruiz G, Gurney R, MacKinnon C, Walton W, Rodriguez L, Bax N, 2003. Invasion
438   dynamics of the European shore crab, Carcinus maenas, in Australia. Marine Biology
439   142:867-876. doi: 10.1007/s00227-003-1011-1.
440   Van de Waal DB, Verspagen JMH, Finke JF, Vournazou V, Immers AK, Kardinaal WEA, Tonk L, Becker
441   S, Van Donk E, Visser PM, Huisman J, 2011. Reversal in competitive dominance of a toxic
442   versus non-toxic cyanobacterium in response to rising CO_2. Isme Journal 5:1438-1450. doi:
443   10.1038/ismej.2011.28.
444   Vergés A, Doropoulos C, Malcolm HA, Skye M, Garcia-Pizá M, Marzinelli EM, Campbell AH,
445   Ballesteros E, Hoey AS, Vila-Concejo A, Bozec Y-M, Steinberg PD, 2016. Long-term empirical
446   evidence of ocean warming leading to tropicalization of fish communities, increased
447   herbivory, and loss of kelp. Proceedings of the National Academy of Sciences of the United
448   States of America 113:13791-13796. doi: 10.1073/pnas.1610725113.
449   Villeger S, Grenouillet G, Brosse S, 2014. Functional homogenization exceeds taxonomic
450   homogenization among European fish assemblages. Global Ecology and Biogeography
451   23:1450-1460. doi: 10.1111/geb.12226.

452 **Table 1- Ethogram of behaviours.**

Behaviour	Definition	Recorded as	Analysed as
Feeding	Handling and/or consumption of food with one or both claws	Number of seconds	Ratio of time spent feeding by the focal species relative to total time feeding by all individuals in the match
Threatening	Raising one or both claws open ≥~90°	Number of seconds	Ratio of time spent threatening by the focal species relative to total time threatening by all individuals in the match
Retreat	Avoiding or retreating from a competitor's attack	Number of occurrences	Fleeing, which was the number of times the focal species retreated relative to the number of attacks against it by the competing species
Attack	Pushing, grasping or climbing over competitor	Number of occurrences	
First to food	First to grasp bait with claw/s	Yes or No	Yes or No

453

454 **Table 2 -Summary of the seawater chemistry parameters (mean ± SE) measured in ambient and**
455 **future climate (elevated) treatments.** *n* is the number of samples analysed, with some parameters,
456 such as temperature and pH of measured multiple times a day.

Treatment	Temperature (°C)	*n*	pH_{NIST}	*n*	TA (µmol.kg−1SW)	pCO_2 (µatm)*	*n*
Ambient	17.43 (± 0.05)	162	7.84 (± 0.02)	171	1720 (± 68)	552 (± 17)	27
Elevated	19.71 (± 0.07)	162	7.59 (± 0.01)	171	1654 (± 48)	870 (± 41)	27

457 *TA* total alkalinity
458 **pCO_2* calculated using CO2SYS

Table 3- General liner mixed-effects models (GLMMs) for the proportion of time feeding. The first model compares all three species, while the following three models consider each species separately as a focal species.

| Proportion of time feeding	Intercept	Species Alien	Species Native	Treatment Future	Species Alien x Treatment Future	Species Native x Treatment Future			ΔAICc	wAICc
Comparing all three species										
	-0.02 (-0.68, 0.64)	***-0.75 (-1.48, -0.01)***	***-1.03 (-1.76, -0.29)***	-0.03 (-0.62, 0.56)	-	-			2.17	0.529

Proportion of time feeding	Intercept	First to Food Yes	Threatening	Fleeing	Treatment Future	First to food Yes x Treatment Future	Threatening x Treatment Future	Fleeing x Treatment Future	ΔAICc	wAICc
Range-extending species blue swimmer crab										
	-0.70 (-2.15, 0.01)	***2.69 (1.80, 3.58)***	-0.74 (-2.70, 1.22)	0.13 (-1.02, 1.27)	-0.15 (-1.20, 0.90)	0.55 (-0.86, 1.95)	1.29 (-2.46, 5.04)	-	1.94	0.390
Alien species European green crab										
	-1.00 (-1.95, -0.05)	***2.11 (1.22, 3.00)***	***-2.26 (-4.52, -0.001)***	-1.03 (-4.70, 2.63)	0.20 (-0.91, 1.32)	-0.06 (-1.72, 1.61)	-0.86 (-4.86, 3.14)	-	1.80	0.363
Native species common sand crab										
	-1.72 (-2.36, -1.09)	***1.89 (0.64, 3.15)***	-1.37 (-6.09, 3.35)	-0.48 (-2.49, 1.52)	-0.002 (-0.79, 0.78)	1.42 (-0.65, 3.49)	-	-	2.13	0.355

461
462 All models include each individual (ID) as a random effect. All explanatory variables have been included (see Table 1 for definitions). Results show the mean
463 estimates with the 95% confidence intervals in parentheses. Results are **bold** if the 95% confidence interval around the mean estimate does not include
464 zero, and in *italics* if retained in the top weighted model. The ΔAICc is the difference between the first and second top weighted models, and the wAICc is
465 provided for the top weighted model. Terms without mean estimates, denoted by '-', were excluded from the top 95% confidence model set.

466 **Table 4. Mean and confidence interval (CI) estimates calculated from the General liner mixed-**
467 **effects model (GLMM) comparing all three species.**

| Treatment	Species	2.5% CI	Mean	97.5% CI
Current climate	Range-extending	0.34	0.49	0.66
	Alien	0.10	0.19	0.33
	Native	0.08	0.15	0.27
Future climate	Range-extending	0.21	0.33	0.47
	Alien	0.06	0.19	0.47
	Native	0.04	0.15	0.40

468
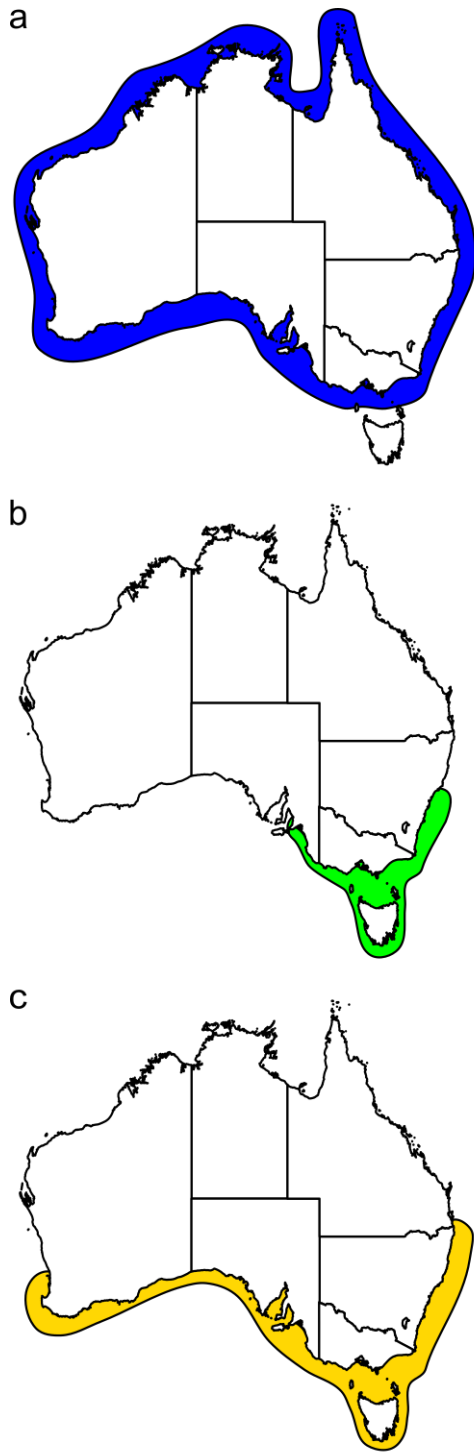
Figure 1. The distribution of (a) the range-extending species, *Portunus armatus (*previously *Portunus pelagicus*), (b) the alien species, *Carcinus maenas*, and (c) the native species *Ovalipes australiensis*, in Australia. Distributions are based on Gowlett-Holmes (2008) and Atlas of Living Australia website http://www.ala.org.au Accessed 28 March 2019

95% Confidence Interval for Mean Proportion of Time Feeding
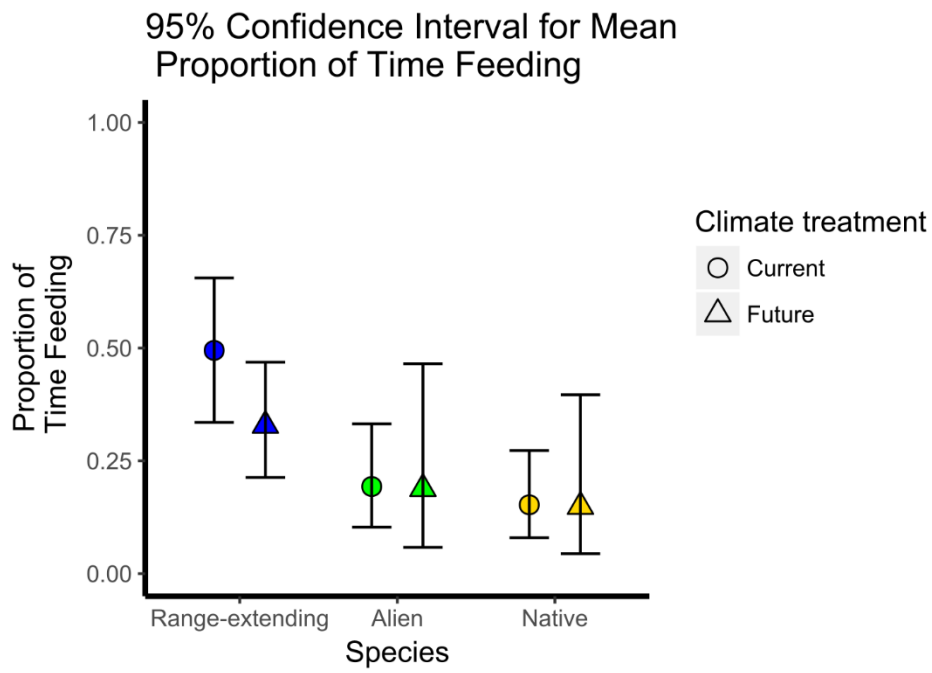
475
476 **Figure 2. The effect of climate treatment on the proportion of time feeding by crab species.**
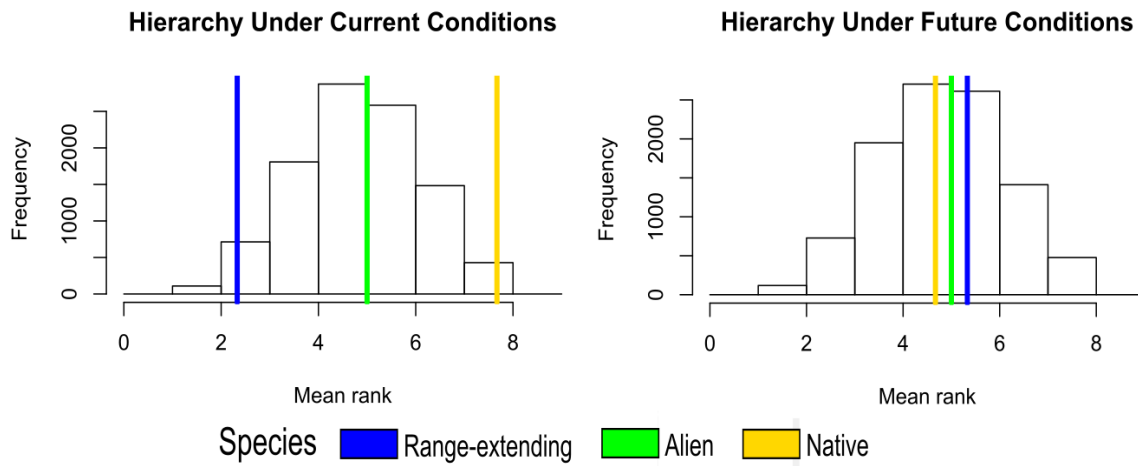
Figure 3. Difference in positioning of individuals from each crab species within the hierarchy under the different climate conditions. The bars are the bespoke randomization values, while the coloured bars are the mean rank of each species.