

## **Title**

Multi-level framework to assess social variation in response to ecological and social factors: modeled with coral gobies

## **Authors**

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## **Keywords**

Social plasticity; sociality framework; degree of sociality; ecological factors; size-based hierarchies; coral reef fishes; disturbances; climate change; coral-dwelling gobies; *Gobiodon*

## 1 **1. Abstract**

2  
3 Understanding variation in social organization that does not have a strong phylogenetic signal represents a key  
4 focus of research in behavioural and evolutionary ecology. In light of this, we established a sociality framework  
5 that identifies four categories of variation in social organisation that range from large-scale to fine-scale and can  
6 each be related to various ecological factors: (1) forms of sociality, (2) degree of sociality, (3) social plasticity,  
7 and (4) within-group plasticity. We modelled this framework by quantifying the four categories of variation  
8 over time, space and disturbance regime using multiple species of coral-dwelling gobies from the genus  
9 *Gobiodon*. Gobies are a particularly interesting model system as they vary in social structure, have within-group  
10 cooperation and form mutualistic relationships with their coral hosts which are vulnerable to climatic  
11 disturbances. We found that gobies varied in forms of sociality – from being solitary, to paired or group-living  
12 depending on location and disturbance regime. Only low or moderate degrees of sociality were observed in  
13 gobies, and this was influenced by location or disturbance regime depending on species. Gobies were more  
14 often solitary or pair-forming than group-forming (which became extremely rare) in a high disturbance regime  
15 whereas they were more often found in groups in a moderate disturbance regime. The size of coral hosts  
16 affected the social plasticity of gobies, and corals were smaller due to climatic disturbances. Gobies did not  
17 exhibit within-group social plasticity, as there were no changes to the structure of size-based hierarchies or sex  
18 allocation patterns with location or disturbance regime. Lastly, by combining the four categories of variation, we  
19 find that there is a high loss of sociality in coral-dwelling gobies due environmental disturbances, which likely  
20 affects overall goby survival as living in groups can improve survival and fitness. By using our structured  
21 framework, we identified which categories of social variation were influenced by ecological factors like location  
22 and disturbance. This framework therefore provides an excellent tool for predicting future responses of animal  
23 societies to environmental stressors.  
24

## 25 **2. Introduction**

26  
27 Social living is a common trait in many taxa, with individuals living in groups to gain some type of advantage,  
28 such as predation avoidance, improved territory defense, better survival in harsh conditions, increased mate  
29 availability, improved habitat quality, and enhanced offspring resilience (Duffy & Macdonald 2010; Firman *et al.*  
30 *et al.* 2020; Hing *et al.* 2017; Nowicki *et al.* 2018; Queller & Strassmann 1998; Rueger *et al.* 2021a). Sociality is  
31 often characterized by convergent evolution without a strong phylogenetic signal even between closely related  
32 species (Faulkes *et al.* 1997; Hing *et al.* 2019). Instead, group living and social behaviour are often more  
33 dependent on ecological pressures that alter the costs and benefits of social living (Duffy & Macdonald 2010;  
34 Emlen 1982; He *et al.* 2019; Hing *et al.* 2017).  
35

36 When considering the impact of social and ecological factors on sociality, it is important to recognize that there  
37 are multiple categories of sociality that can be measured at different scales. However, it is often the case that a  
38 clear distinction between these categories and scales is not made (Dornhaus *et al.* 2011; Jetz & Rubenstein  
39 2011). For example, a meta-analysis identified that birds in general will live in groups where rainfall patterns are  
40 fluctuating at large geographic scales (Jetz & Rubenstein 2011), yet local environmental conditions and smaller  
41 taxonomic scales have yielded alternative results (Gonzalez *et al.* 2013). Group size also tends to be the primary  
42 measure of sociality in several studies, and yet several species exhibit strong reproductive skew that requires  
43 more detailed assessment of the number of breeders and nonbreeders in a group (Avilés & Harwood 2012; Hing  
44 *et al.* 2018; Rueger *et al.* 2021a). it is important to take a comparative approach that assesses the effects of both  
45 large and small scale factors on the sociality of animal taxa.  
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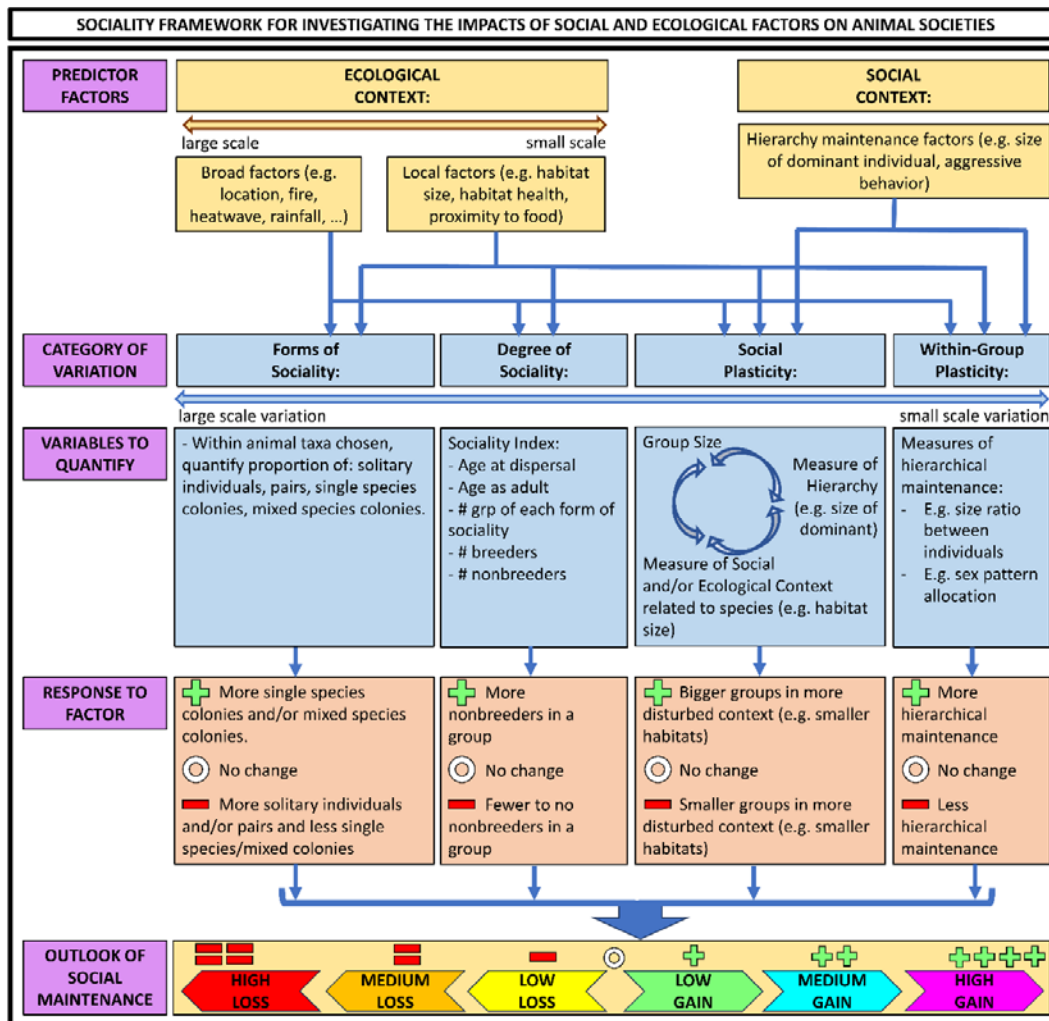
47 Here, we introduce a multi-level sociality framework that identifies four categories of social variation (from  
48 large to fine-scale variation) that highlights the extent of sociality amongst a variety of social species. These are  
49 (1) forms of sociality (i.e. proportion of individuals that live solitarily, in pairs, or groups), (2) degree of  
50 sociality (i.e. whether individuals within a species exhibit one or many forms of sociality ), (3) social plasticity  
51 (i.e. ability for group size to shift based on variation in local ecological or social factors), and (4) within-group  
52 plasticity (i.e. ability for individuals to change social behaviour and conflict resolution strategies). This  
53 framework can be applied to many social taxa and incorporates both ecological and social contexts as predictors  
54 for each category of variation (Fig 1). Ecological factors can include both large and small-scale environmental  
55 changes. How likely each category of variation will shift in response to predictor variables may affect the  
56 survival of individuals, populations or even species as a whole (Booth 1995; East & Hofer 2010; Gil *et al.* 2017;  
57 Jordan *et al.* 2009; Strauss & Holekamp 2019). Hence the vulnerability of individuals and populations can be  
58 assessed based on how each category of variation responds to predictor factors e.g. whether a taxon will be more

59 social, stay the same, or become less social following environmental challenges. This framework thus provides  
 60 an outlook of social maintenance, which determines the ability for the taxa to maintain social group living in its  
 61 entirety, i.e. the structure and the functioning of groups, despite fluctuations in external factors. Thus,  
 62 elucidating these four categories of social variation will be important for understanding the influences of  
 63 ecological and social factors on the maintenance of animal societies.

64

65 At the largest scale, the first category of variation is the form of sociality exhibited, defined as the proportion of  
 66 individuals in the population that are solitary, in pairs, in single species groups (i.e. >2 group members) or in  
 67 mixed species colonies (>1 individual of 2+ species of the same taxon) (Fig 1). Note, colony defines any  
 68 number of individuals (1+) living together, whereas group defines more than 2 individuals living together. The  
 69 form of sociality can provide an overview of the proportion of individuals living in groups depending on large  
 70 and small scale factors. The proportion of individuals living solitary, in pairs, or groups can be affected by  
 71 ecological conditions, e.g. variability of the environment (Avilés *et al.* 2007; Faulkes *et al.* 1997; Hing *et al.*  
 72 2018; Lantz & Karubian 2017) By quantifying the forms of sociality, we can assess whether ecological factors  
 73 of varying scales will impact the tendency to live solitary, in pairs or in groups.

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Fig 1. Sociality framework that tests whether ecological factors affect animal societies at four categories of variation and what outlook of social maintenance is given to the taxon based on how many variations have negative or positive responses. Colony = all individual(s) living together in a society; # = number.

80 The second category of variation is the degree of sociality, defined as the tendency for a species in a given  
 81 population to be strictly solitary, pair-forming or group-forming. The degree of sociality can be measured via  
 82 the sociality index, conceived by Avilés and Harwood (2012) using social spiders and mole rats and adapted for  
 83 fish by Hing *et al.* (2018). The sociality index provides a value on a scale from 0 (solitary living) to 1

84 (exclusively group-forming) for a species based on their dispersal, the proportion of groups in a population, and  
85 the proportion of breeding and nonbreeding individuals within colonies. Hing *et al.* (2018) proposed a threshold  
86 value of 0.5 to delineate pair-forming and group-forming fish species. The sociality index can be calculated for a  
87 species as a whole or for specific populations, depending on what is being tested. Therefore any given  
88 species/population is assigned just one value that encompasses how social that species/population is, as well as  
89 the extent of reproductive skew exhibited. For a species with the highest degree of sociality, i.e. sociality index  
90 close to 1, individuals live strictly in eusocial groups, as seen in naked mole rats, ants, and termites (Avilés &  
91 Harwood 2012; Nalepa 2015; Wilson & Hölldobler 2005). Similarly, species with the lowest degree of sociality,  
92 i.e. sociality index close to 0, are strictly solitary and hence with low skew, e.g. dune mole rats, platypuses, and  
93 solitary sandpipers (Avilés & Harwood 2012; Griffiths 1988; Oring 1973). Values closer to 0.5 are for species  
94 that exhibit a mix of social organisation within the population, such as pair-forming and group-forming, e.g.  
95 marine shrimp, social spiders, and many birds (Avilés & Harwood 2012; Duffy & Macdonald 2010; Jetz &  
96 Rubenstein 2011) with moderate degrees of skew. The degree of sociality therefore provides a value of how  
97 social a species is without too much consideration of the extent to which that species could show flexibility in its  
98 social arrangements within a set environment, i.e. equivalent to an average degree of sociality exhibited by the  
99 species, rather than a variance. The degree of sociality can then be calculated for different populations that vary  
100 in ecological conditions (e.g. habitat size, season, latitude/longitude, disturbance regime). Accordingly, the  
101 degree of sociality allows us to determine whether a particular form of sociality is consistently the form of  
102 sociality that is exhibited by a taxon, or whether ecological conditions allow for different degrees of sociality  
103 (Fig 1).

104  
105 The third and yet finer category of variation in sociality is social plasticity, defined as the extent to which the  
106 size of groups within a species or population changes in response to local conditions, such as smaller-scale  
107 ecological or social variables (adapted from Teles *et al.* 2016). For example, within a population, group sizes of  
108 some coral-reef fishes vary with the size of their habitat, and in some cases with the size of the largest, most  
109 dominant individual within a group (Buston & Cant 2006; Wong, 2011; Rueger *et al.* 2021). A larger habitat  
110 allows more individuals to live together as there is more space and resources, and larger groups in turn can  
111 promote an increase in size of the habitat via mutualistically mediated benefits (Buston & Cant 2006; Wong,  
112 2011; Rueger *et al.* 2021). In addition, the size of the largest individual can dictate the number of smaller  
113 subordinates that live within the group owing to rules of the hierarchy (Ang & Manica 2010; Buston & Cant  
114 2006; Wong 2011). Therefore, unlike the degree of sociality which essentially provides just one value to  
115 describe overall sociability of a species or population, social plasticity describes how flexible a species or  
116 population is to changes in the social and ecological environment, even up to large scale variables like  
117 disturbance regimes (Froehlich *et al.* 2021, 2023).

118  
119 Finally, the finest category of social variation relates to within-group plasticity in sociality, here defined as the  
120 extent of conflict and cooperation between individuals within groups and its higher-level consequences through  
121 its influence on group structure. In all societies, conflict over rank, resources and reproduction is unavoidable.  
122 For some societies, peaceful cooperation by subordinates is maintained through social constraint mechanisms,  
123 such as sex, size and maturity regulation, and each of these mechanisms can be influenced by ecological and  
124 social factors (Ghiselin 1969; Hing *et al.* 2019; Lassig 1977; Rubenstein 2007; Warner 1988; Wong *et al.* 2008;  
125 Wong & Buston 2013). For this category of social variation, the variables that regulate social cooperation can be  
126 quantified and related to ecological and social factors. For taxa that exhibit sex allocation patterns,  
127 environmental conditions and stressors like rainfall variability, temperature and pollutants have been shown to  
128 affect these patterns (Devlin & Nagahama 2002; Oldfield 2005; Ospina-Álvarez & Piferrer 2008; Rubenstein  
129 2007). For example, female superb starlings change their offspring sex allocations based on their own body  
130 condition in relation to rainfall variability (Rubenstein 2007). For taxa that exhibit size-based hierarchies, large  
131 scale variables like temperature and ocean acidification have been shown to impact some aspects of individual  
132 growth (Matthews & Wong 2015; McMahan *et al.* 2019). For example, temperature influences the extent to  
133 which subordinates control their own growth in relation to their immediate dominants for Eastern mosquitofish  
134 (Matthews & Wong 2015). Small scale variables like habitat size can also affect the growth of individuals  
135 depending on their ranks, as seen in hierarchical emerald coral gobies (Wong 2011). Such fine scale variation in  
136 social structure can thus be compared among many ecological factors to elucidate whether within-group  
137 plasticity exists in relation these factors.

138  
139 Here, we applied this multi-level sociality framework to understand how and why sociality varies in coral-  
140 dwelling gobies from the genus *Gobiodon*, which contains more than 13 species (Munday *et al.* 1999). Within a  
141 single colony, defined as all gobies living within a single coral host, gobies have been found living solitary, in  
142 pairs, in groups, (Hing *et al.* 2018) and even in mixed species colonies (i.e. with congeners, Froehlich *pers. obs.*)  
143 depending on the species. The composition of these mixed species colonies has yet to be quantified, but they

144 provide an additional layer of social complexity as congeners reside and breed within the same habitat and  
145 presumably compete for resources. Coral-dwelling gobies likely do not form groups with kin as they have a 3-  
146 week larval dispersal stage and then settle into coral colonies as subordinate nonbreeders with unrelated  
147 individuals (Brothers *et al.* 1983; Rueger *et al.* 2021b; Wong & Buston 2013). Within groups, individuals are  
148 suspected to exhibit peaceful cooperation within a size-based hierarchy, and only a monogamous pair breeds, as  
149 seen in the closely related Emerald coral goby *Paragobiodon xanthosoma* (Wong *et al.* 2007). Group sizes  
150 mainly depend on ecological factors, like coral size (Hing *et al.* 2019), and potentially on social factors, like  
151 body sizes of the largest individual, as seen in *P. xanthosoma* and *Amphiprion percula* (Barbasch *et al.* 2020;  
152 Buston 2003; Elliott & Mariscal 2001; Fautin 1992; Rueger *et al.* 2021a; Wong 2011; Wong *et al.* 2007).  
153 Within the *Gobiodon* genus, there is only a weak phylogenetic signal for sociality, which suggests that  
154 ecological, life history factors may play a substantial role in sociality (Hing *et al.* 2019). *Gobiodon* gobies occur  
155 across a range of areas in the Indo-Pacific Ocean, which allows us to test the influences of both large-scale  
156 ecological factors, like extreme cyclones and heatwaves, and small-scale factors, like coral size, on the structure  
157 of their societies (Froehlich *et al.* 2021; Hughes *et al.* 2018; Munday *et al.* 1999).

158  
159 Specifically, we investigated how and why sociality varies by examining each of the four categories of social  
160 variation in these coral gobies. We used data spanning multiple time points and three different geographic  
161 locations which experienced varying disturbance regimes. To use the framework, we (1) compared the forms of  
162 sociality exhibited across the *Gobiodon* genus among coral size, time, location and disturbance regimes. We  
163 then (2) assessed the impacts of these factors on the three other categories of variation - the degree of sociality,  
164 social plasticity, and within-group plasticity - for each individual species and then performed comparisons of  
165 these variables among species. Then, we took a closer look at mixed species colonies and investigated which  
166 species composed these colonies and quantified the within-group plasticity of these colonies among locations  
167 and disturbance regimes. Finally, we combined the results of each sociality metric to identify the outlook of  
168 social maintenance of coral-dwelling goby in the face of shifting environmental conditions. (Fig 1).  
169

## 170 **3. Methods**

### 171 **3.1. Site Description**

172  
173 The study was conducted at three different locations in the Indo-Pacific, the northern, central and southern  
174 locations. The northern location is made up of four inshore sites in Kimbe Bay, West New Britain, Papua New  
175 Guinea (PNG) (-5.42896°, 150.09695°). This PNG location has remained relatively undisturbed since an initial  
176 trip we conducted in Sep-Nov 2018. The central location is made up of multiple small sites around Lizard Island  
177 (LI), Queensland, Australia (-14.687264°, 145.447039°). The LI reef was relatively undisturbed in early 2014  
178 but was affected by four extreme climatic disturbances on an annual basis: category 4 cyclones Ita (2014),  
179 Nathan (2015), and two mass bleaching events (2016 and 2017). More recently, LI has sustained mild bleaching  
180 events (2020, 2021, and 2022, with only a few patches of corals bleaching) and is in a continued state of  
181 disturbances with little time for proper recovery (Froehlich pers. obs., Pratchett *et al.* 2021). The southern  
182 location is within an enclosed lagoon at One Tree Island (OTI), Queensland, Australia (-23.506565°,  
183 152.090954°). The OTI location was relatively undisturbed in 2019 but suffered from mass bleaching events in  
184 2020 with very minimal bleaching in 2022.

### 185 **3.2. Sampling Techniques and Intervals**

186  
187 All fieldwork was conducted either on SCUBA or snorkel at each location. Two types of sampling techniques  
188 were used for the study. The first technique involved conducting surveys along 30 m line transects to search all  
189 corals within 1 m on either side of the transect. The second sampling technique involved haphazardly sampling  
190 corals at each location, and only corals with a minimum of 10cm average diameter were included. When a coral  
191 was encountered, a bright torch light (Bigblue AL1200NP) was used to search for goby occupants. Within each  
192 coral, the number of gobies (i.e. group size), life stage of gobies, and goby species were noted. Goby life stages  
193 were recorded as either breeding adults (two largest adults), nonbreeding adults (all other adults smaller than the  
194 two breeders but larger than juveniles), and juveniles (a.k.a. recruits) depending on their coloration and size.  
195 Coral diameter was measured along three axes (length, width, and height), and an arithmetic average was taken  
196 to indicate coral size (i.e. average coral diameter; Kuwamura *et al.* 1994). Gobies were collected from a random  
197 selection of corals for each sampling technique to quantify body size. During collection, a clove oil anesthetic  
198 solution (clove oil, 70% ethanol, and seawater) was sprayed over the coral and fish were wafted out with hand  
199 nets (Munday & Wilson 1997). Each fish was placed in a Ziploc bag full of seawater and measured for standard  
200 length (mm, ± 0.1 mm) using handheld calipers. During later collections (as noted below), fish were also sexed  
201  
202



203 and injected with a unique visible implant elastomer identification tag (Northwest Marine Technology, Inc.,  
204 Anacortes, Washington, USA) (Munday 2001). Fish were then returned unharmed to their coral. On later trips,  
205 goby colonies containing tagged fish were revisited and re-collected to note coral size, group size, fish size and  
206 sex.

207

208 Sampling was completed at LI before climatic disturbances (Feb 2014) and three years after the four major  
209 climatic events (Jan-Mar 2020). During 2020, gobies were tagged with elastomer and sexed, and then the same  
210 colonies were revisited one and two years later (Jan-Mar 2021 and Jan-Apr 2022). Haphazard sampling was  
211 completed at PNG during one sampling event (Sep-Nov 2018) in which gobies were tagged with elastomer and  
212 were revisited six months later (May-June 2019). Haphazard sampling was completed at OTI before climatic  
213 disturbances (Jan-Feb 2019) and two years later (Mar-Apr 2022) after mass coral bleaching had occurred.

214

### 215 3.3. Data Analysis

#### 216 3.3.1. Form of Sociality – Single Species Pairs, Single Species Groups, Mixed Species

217

218 Gobies encountered during transect surveys and haphazard searches were included for analysis and were  
219 categorized into form of sociality as follows: one individual living alone (solitary), living in pairs with  
220 conspecifics only (single species pairs), living in groups with conspecifics only (single species groups), and  
221 living with congeners (mixed species). Only corals with a minimum of 10 cm average diameter were included  
222 because that was the minimum size of hosted corals measured during haphazard searches. The effect of location  
223 (fixed factor) on the form of sociality of gobies were analysed using multinomial logistic regression models for  
224 three analyses: (1) compare locations in relatively undisturbed conditions (i.e. before climatic disturbances =  
225 PNG2018, LI2014, OTI2019), (2) compare locations before and after being disturbed by climatic disturbances  
226 (i.e. pre-disturbances = LI2014 & OTI2019, post-disturbances = LI2020, LI2022 & OTI2022) and the  
227 interaction between location and pre/post-disturbances, and (3) compare LI between the two post-disturbance  
228 time points (LI2020 and LI2022) to assess recovery. For each multinomial model, the baseline reference level  
229 for the response variable was a solitary individual. Juveniles were included in the analysis if they were found  
230 with at least 1 adult, as juveniles tend to move between corals if solitary. All analyses were completed in R  
231 (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages:  
232 tidyverse (Wickham *et al.* 2019), VGAM (Yee 2010), car (Fox & Weisberg 2019), and rcompanion (Mangiafico  
2016).

#### 233 3.3.2. Degree of Sociality - Sociality Index

234

235 We calculated the sociality index for each species in which there were a minimum of 5 colonies of the species in  
236 any single location at each survey time point, including pre- and post-disturbance. The sociality index was  
adapted from Avilés and Harwood (2012) as follows:

$$S = \frac{\frac{A_d}{A_a} + \frac{N_g}{N_g + N_p + N_i} + \frac{I_n}{I_r + I_n}}{3}$$

237

238 where  $A_d$  = age of dispersal,  $A_a$  = age of adulthood,  $N_g$  = number of groups,  $N_p$  = number of pairs,  $N_i$  = number  
239 of solitary individuals,  $I_n$  = number of reproducing (dominant) adults,  $I_r$  = number of non-reproducing  
240 (subordinate) adults. The numerator is comprised of three components: the proportion of the life cycle spent in a  
241 colony, the proportion of groups encountered, and the proportion of subordinates (nonbreeding) individuals  
242 (respectively). We followed guidelines set out in Hing *et al.* (2018) to calculate biologically-relevant  
243 assumptions of the numerator. Accordingly, we set the maximum proportion of life cycle spent in a colony (i.e.  
244  $A_d/A_a$ ) to 1, which is biologically realistic even if there is some natural variation, as gobies spend only 22-41  
245 days in the larval dispersal stage (Brothers *et al.* 1983). We then calculated the sociality index for each species  
246 at each location and time point, and categorized them as either pair-forming ( $< 0.5$ ) or group-forming ( $\geq 0.5$ ), as  
247 per the threshold of 0.5 (Hing *et al.* 2018). Note, we did not calculate sociality indices for mixed species  
248 colonies as colonies were not always made up of the same species combination.

#### 249 3.3.3. Social Plasticity: Group Size – Size of the Dominant – Coral Size

250

251 To investigate the determinants of social plasticity, we only calculated the relationship for goby species that  
252 were group-forming as per sociality indices (i.e.  $> 0.5$ ; (Hing *et al.* 2018)), and for which we collected a  
253 minimum of 30 colonies. We excluded any mixed species colonies. The analysis of the synergistic relationship  
254 between group size, size of the dominant individuals and coral size was repeated for each variable by placing  
each as the focal response variable in the model. The effect of the size of the dominant individual and coral size

255 on group size were analysed using a generalized linear model using the poisson distribution. The effect of the  
256 group size and coral size on the size of the dominant individual were analysed using a linear model. The effect  
257 of the size of the dominant and group size on the coral size were analysed using a linear model. Location was  
258 included as a fixed factor in each analysis and analyses were repeated separately per species. The variables and  
259 models were assessed for normality and homoscedasticity via Q-Q plots, histograms, and residuals over fitted  
260 plots, and were transformed as required. If outliers fell outside of 2.5 standard deviation from 0, then they were  
261 subsequently removed. All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio  
262 (2022.02.2+485) (RStudio Team 2022) with the following packages: tidyverse (Wickham *et al.* 2019), lme4  
263 (Bates *et al.* 2015), lmerTest (Kuznetsova *et al.* 2017), LMERConvenienceFunctions (Tremblay & Ransijn  
264 2020), piecewiseSEM (Lefcheck 2016), and emmeans (Lenth *et al.* 2020).

#### 3.3.4. *Within-group plasticity: Size Ratios*

265  
266 To investigate within-group plasticity, we investigated the influence of several factors on the size ratios of fish,  
267 as size ratios are indicators of peaceful cooperation within size-based hierarchies. For size ratios, we only  
268 included single species colonies for which all individuals were collected, otherwise we would not have been  
269 able to confirm the correct rank placement of each individual in the hierarchy. Size ratios were calculated by  
270 dividing the standard length (SL) of the lower rank (more subordinate) individual by the standard length of the  
271 upper rank individual (its immediate bigger group member) (e.g.  $SL_{\text{rank}2} / SL_{\text{rank}1}$ ) (Wong *et al.* 2007). Size ratios  
272 were analysed separately for the breeding pair (i.e. rank 1 and rank 2) as their body sizes were predicted to  
273 converge to improve overall reproductive output (Munday *et al.* 2006). The effect of coral size (covariable),  
274 group size (covariable), species (fixed factor) and location (fixed factor) on the size ratio between rank 1 and  
275 rank 2 individuals (i.e. rankstep 1) were analysed with generalized linear models with family quasibinomial. The  
276 analyses were repeated for the size ratio between rank 2 and rank 3 individuals (i.e. rankstep 2) as the next rank  
277 after the breeding pair was expected to remain smaller in order to reduce conflict (Wong *et al.* 2007). At two  
278 locations, goby colonies were revisited in consecutive sampling events (PNG 2018 & 2019, LI 2020 & 2021);  
279 for these repeat visits, size ratios were calculated for rankstep 1 but not for further ranks as there were not  
280 enough colonies with minimum of 3 individuals per species. The effect of coral size (covariable), group size  
281 (covariable), species (fixed factor), location (fixed factor), and year (fixed factor) on the size ratio for rankstep 1  
282 was analysed with generalized linear models with family quasibinomial.

283  
284 We had enough samples to compare size ratios of rankstep 1 at LI pre- (2014) and post-disturbances (2020 and  
285 2021). Accordingly, we investigated the effects of coral size (covariable), group size (covariable), species (fixed  
286 factor) and pre- vs. post disturbance (fixed factor) on the size ratios of rankstep 1 at LI. The variables and  
287 models were assessed for normality and homoscedasticity via Q-Q plots, histograms, and residuals over fitted  
288 plots, and were transformed as required. If outliers fell outside of 2.5 standard deviation from 0, then they were  
289 subsequently removed. Models were selected based on the Akaike Information Criterion (AIC). All analyses  
290 were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with  
291 the following packages: tidyverse (Wickham *et al.* 2019), lme4 (Bates *et al.* 2015), car (Fox & Weisberg 2019),  
292 LMERConvenienceFunctions (Tremblay & Ransijn 2020), piecewiseSEM (Lefcheck 2016), emmeans (Lenth *et al.*  
293 *et al.* 2020), and ggpubr (Kassandra 2020).

#### 3.3.5. *Within-group plasticity: Sex Dominance in Breeding Partners*

294  
295 To investigate another aspect of within-group plasticity, we investigated their sex dominance in breeding  
296 partners as social coral reef fishes generally have female- or male-dominated societies (Wong & Buston 2013).  
297 For single species colonies that were revisited at LI in 2020 and 2021, the sex of the dominant individual (rank  
298 1) was identified on repeated trips. The sex ratio of rank 1 males to rank 1 females was compared to determine  
299 whether it differed from 1:1 ratio with a 1-sample proportions test with continuity correction. The effects of  
300 species (fixed factor) and year (fixed factor) on the ratio of rank 1 females to rank 1 males within breeding  
301 partners was analysed using generalized linear models with the binomial family. All analyses were completed in  
302 R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following  
303 packages: stats (R Core Team 2022), car (Fox & Weisberg 2019), and rcompanion (Mangiafico 2016).

#### 3.3.6. *Mixed Species Colonies: Social Structure and Composition*

304  
305 Across all locations, goby colonies containing mixed species were used to calculate three categorical response  
306 variables that measured whether the mixed species colony: (1) had different species intermixed within  
307 hierarchical ranks—e.g. rank 1,3,5 were species A and rank 2,4,6,7 were species B (yes, intermixed) versus rank  
308 1-4 were species A and rank 5-7 were species B (no, not intermixed); (2) had the larger-bodied species as the  
309 rank 1 individual (yes or no; larger-bodied as defined by Hing *et al.* 2019); and (3) was composed of solitary

310 individuals, pairs or groups of each species, or a combination of each. The main effect of location (fixed factor)  
311 was examined using separate multinomial logistic regression models for each response variable. As mixed  
312 species colonies were not collected post-disturbance, body sizes could not be measured and hence no pre- versus  
313 post-disturbance analyses were conducted for response variables 1 and 2. When comparing the composition of  
314 mixed species colonies (response variable 3) pre- versus post-disturbances, there were insufficient mixed  
315 species colonies post-disturbance at LI, hence this analysis is restricted to OTI. The effect of pre- vs. post-  
316 disturbance (fixed factor) on mixed species colonies at OTI (response variables 1-3) were analysed using  
317 multinomial logistic regression models. For each multinomial model, the baseline reference level for the  
318 response variable was as follows: (1) intermixed rank reference: no, (2) larger-bodied species as rank 1  
319 reference: no, and (3) mixed composition reference: solitary individuals. Juveniles were included in the analysis  
320 unless they were solitary individuals because juveniles have been seen jumping between different corals when  
321 solitary. All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485)  
322 (RStudio Team 2022) with the following packages: tidyverse (Wickham *et al.* 2019), VGAM (Yee 2010), car  
323 (Fox & Weisberg 2019), and rcompanion (Mangiafico 2016).

324  
325 In addition, we analysed variation in size ratios between adjacent ranked group members. Size ratios for each  
326 rankstep within mixed species colonies were calculated up to rankstep 8 due to large group sizes in mixed  
327 species colonies. Initially, size ratios were calculated for each species separately within mixed species colonies  
328 to test whether size ratios were equivalent to those in single species colonies. The effect of coral size  
329 (covariable), group size (covariable), rankstep (fixed factor), species (fixed factor), location (fixed factor) and  
330 single vs. mixed species group (fixed factor) on the size ratios (separated by species in mixed species colonies)  
331 was analysed with a generalized linear model with family quasibinomial.

332  
333 Then, size ratios between adjacent ranks were calculated regardless of species, as we confirmed that individuals  
334 in mixed species colonies were sometimes intermixed by size within the hierarchy (as determined in the analysis  
335 above). The effect of coral size (covariable), group size (covariable), rankstep (fixed factor) and location (fixed  
336 factor) on the size ratios (regardless of species in mixed species colonies) was analysed with a generalized linear  
337 model with family quasibinomial. Both size ratio models were assessed for normality and homoscedasticity via  
338 Q-Q plots, histograms, and residuals over fitted plots, and were transformed as required. If outliers fell outside  
339 of 2.5 standard deviation from 0, then they were subsequently removed. All analyses were completed in R  
340 (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages:  
341 tidyverse (Wickham *et al.* 2019), lme4 (Bates *et al.* 2015), car (Fox & Weisberg 2019),  
342 LMERConvenienceFunctions (Tremblay & Ransijn 2020), piecewiseSEM (Lefcheck 2016), emmeans (Lenth *et*  
343 *al.* 2020), and ggpubr (Kassandra 2020).

## 344 4. Results

345  
346 The abundance of *Gobiodon* species differed at each location and some species were found in low abundance at  
347 a given location. For example, a latitudinal gradient in opposite directions was previously reported for *Gobiodon*  
348 *histrion* and *Gobiodon erythrospilus* (Munday *et al.* 1999), which we also observed in the current study; i.e. *G.*  
349 *histrion* occurred at PNG and LI (lower latitude) but was extremely rare at OTI (higher latitude), whereas *G.*  
350 *erythrospilus* was never found at PNG but occurred at LI and OTI. Therefore, not all species could be used in  
351 each analysis.

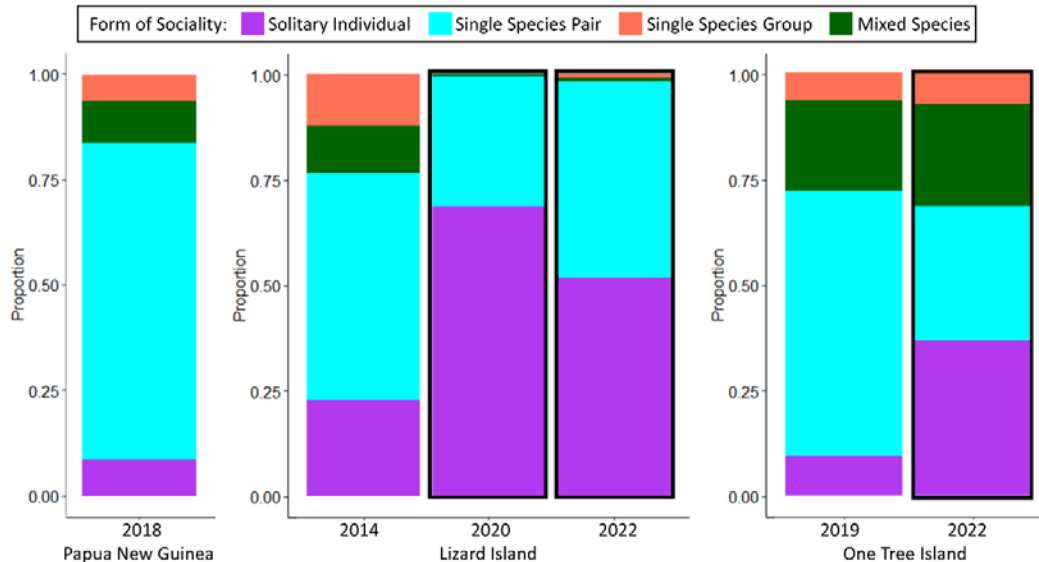
### 352 353 4.1. Form of Sociality – Single Species Pairs, Single Species Groups, Mixed Species

354  
355 We compared the form of sociality exhibited by gobies among locations by comparing the proportion of corals  
356 that had gobies living alone (i.e. solitary), living in pairs with conspecifics (i.e. single species pairs), living in  
357 groups with conspecifics (i.e. single species groups), and living with congeners (i.e. mixed species). We used all  
358 species observed for these analyses. Before any climatic disturbances, the form of sociality differed among  
359 locations (see Suppl. Tabs 6.1-4 for all statistical outputs, here Suppl. Tab 1,  $p < 0.01$ ). There were far more  
360 mixed species colonies at OTI than any other location, in contrast were more single species groups at LI than at  
361 other locations (Fig 2). Beyond these differences, single species pairs were most common at each location (Fig  
362 2). As coral size increased, there was a shift from solitary to single species pairs, to mixed species colonies then  
363 finally to single species groups ( $p < 0.01$ , Supp Fig 1).

364  
365 There was a significant interaction between location and pre/post-disturbances on the form of sociality ( $p <$   
366  $0.01$ , Fig 2). At OTI, there was a substantially higher proportion of solitary individuals and reduced proportion  
367 of pair-forming individuals post disturbance compared to pre-disturbance, but the proportion of single species  
368 groups and mixed species colonies remained similar pre- and post-disturbance (Fig 2). At LI, there were also a



369 substantially higher proportion of solitary individuals and reduced proportion of single species pairs post-  
 370 disturbance than pre-disturbance, but single species groups and mixed species colonies became extremely rare  
 371 post-disturbance even though that differed slightly among 3-yr and 5-yr mark post-disturbances ( $p < 0.001$ , 2020  
 372 v. 2022, Fig 2). In 2020, ~70% of gobies were solitary compared to just under 25% pre-disturbances, and the  
 373 remainder were pair-forming except for a single occurrence of a mixed species colony. In 2022, there was a  
 374 reduced proportion of solitary gobies (~50%), and others lived in pairs except for 5 single species groups (1%)  
 375 and 5 mixed species colonies (1%). At PNG, there was a similar proportion of solitary and paired individuals as  
 376 at OTI pre-disturbances, but there was only a slightly higher proportion of mixed species colonies than single-  
 377 species colonies (Fig 2).



378  
 379 Fig 2. Forms of sociality of all species at all three locations and pre-/post-disturbances for two locations. Data  
 380 outlined in black line is post-disturbance(s).  
 381

#### 382 4.2. Degree of Sociality - Sociality Index

383  
 384 By calculating sociality indices among locations for each species (minimum of 5 colonies) we found that pair-  
 385 forming species exhibited low degrees of sociality and remained pair-forming as per Hing *et al.* (2018), even  
 386 post-disturbances (Fig 3). For species distinctly pair-forming, their index value equaled 0.33 which is the value  
 387 when a species only ever occurs in pairs. Interestingly, *Gobiodon quinquestrigatus* was defined as pair-forming  
 388 at all locations, although it was just shy of reaching the 0.5 threshold for group-forming at PNG (Fig 3). Other  
 389 species also varied due to nonbreeding subordinates being accepted into a coral depending on location.  
 390 However, some species that were originally defined as group-forming switched to pair-forming post-  
 391 disturbances (as subordinates co-habited less often post-disturbances), suggesting that group-forming species  
 392 have moderate degrees of sociality (Fig 3). *Gobiodon citrinus* was the only species to remain group-forming  
 393 regardless of location or disturbance and to have the most subordinates in groups (highest sociality indices).  
 394 However, this species was rarely encountered and only found in sufficient numbers for sociality index  
 395 calculation post-disturbance at OTI. *Gobiodon fuscoruber* was initially group-forming at all locations albeit with  
 396 a lower sociality index than other group-forming species, except at PNG where it was defined as pair-forming.  
 397 At OTI, this species remained group-forming post-disturbance with little change to their sociality index. At LI,  
 398 this species was too rare post-disturbances for analysis to be conducted for those years. *Gobiodon rivulatus* was  
 399 another species that had the highest sociality index with many subordinates co-habiting at LI pre-disturbance,  
 400 but it became exclusively pair-forming without subordinates at LI post-disturbances. At PNG, this species was  
 401 defined as pair forming, just falling shy of a 0.5 sociality index. However, the species was exclusively pair-  
 402 forming at OTI pre-disturbances, and instead occasionally accepted subordinates at OTI post-disturbances (Fig  
 403 3).  
 404

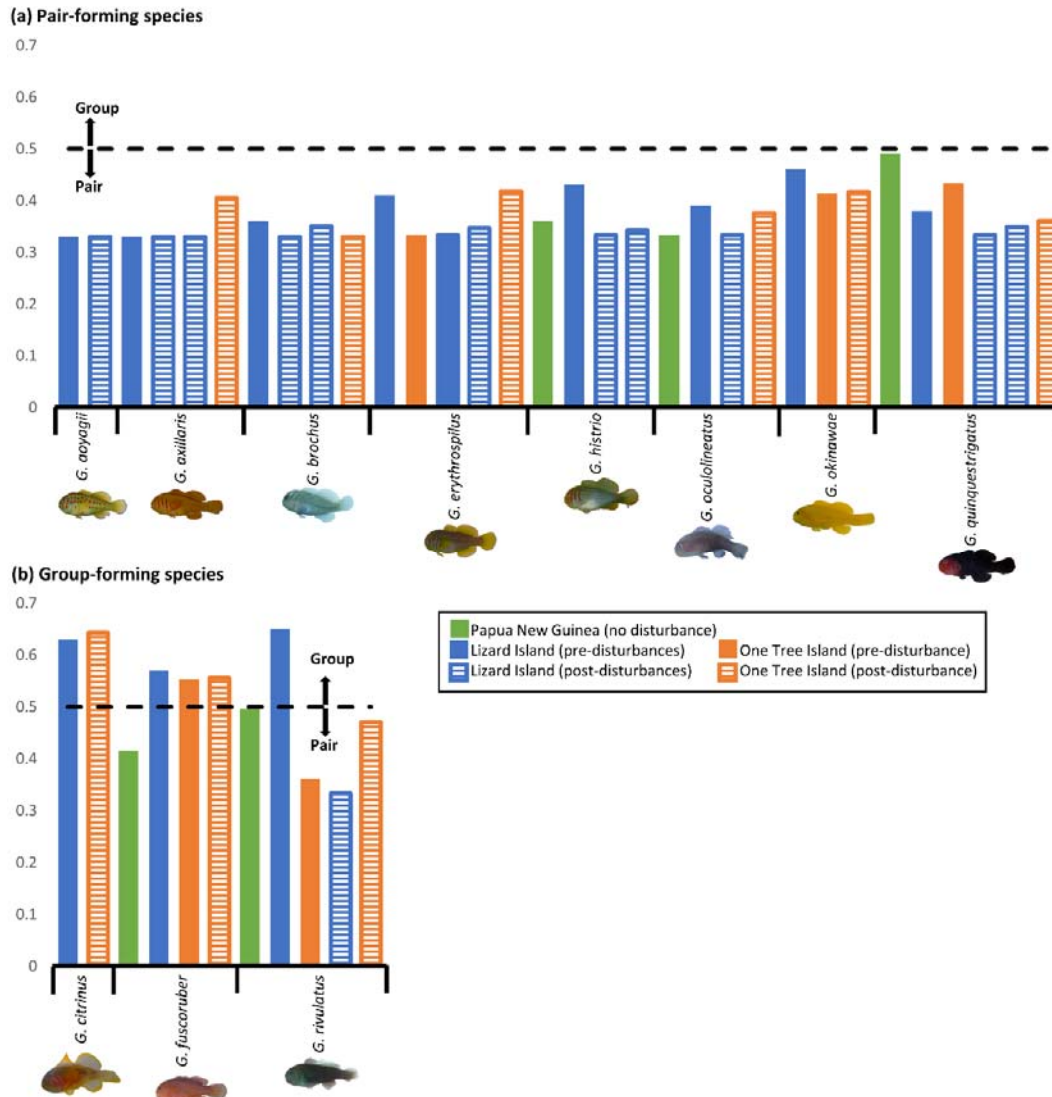
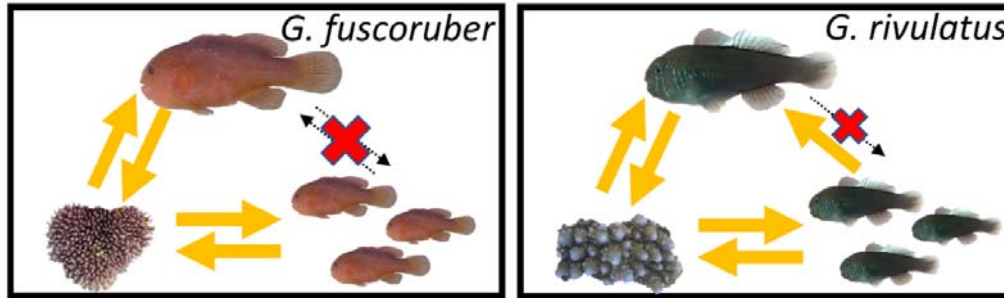


Fig 3. Sociality index of each species at different locations including repeat visits pre- and post-disturbance(s).

#### 4.3. Social Plasticity: Group Size – Size of the Dominant – Coral Size

We had sufficient sample size to compare 2 group-forming species (i.e. *G. fuscoruber* and *G. rivulatus*) at 2 locations (LI, OTI). We investigated the relationship between group size, size of the dominant individual, and coral size (Fig 4). For both species, group size was positively related to coral size (Suppl. Tab 2,  $p < 0.01$ ), but was not related to the size of the dominant individual or location ( $p > 0.40$ ). For *G. rivulatus*, the size of the dominant individual was positively related to coral size for both species ( $p < 0.05$ ), and to group size and location ( $p = 0.03$ ,  $p < 0.01$ , respectively). For *G. fuscoruber*, the size of the dominant was not related to group size or location ( $p > 0.36$ ). for both species, Coral size was positively related to group size and the size of the dominant ( $p < 0.01$ ) but was not related to location ( $p > 0.14$ ). There was no interaction between any of the variables for each analysis ( $p > 0.27$ ). Note: no analyses were completed to compare these size relationships pre-versus post-disturbance as colonies were primarily made up of pairs at LI post-disturbance and no colonies were collected at OTI post-disturbance.

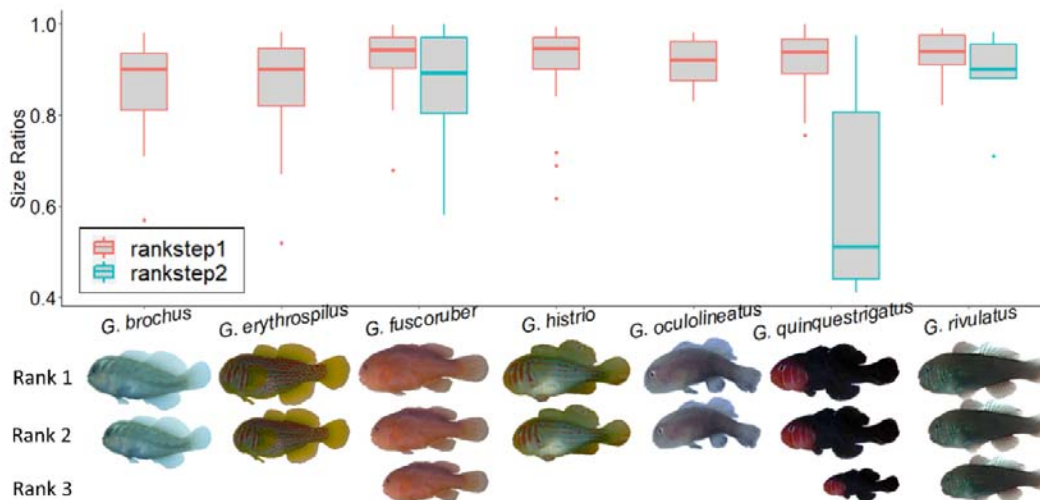


422 Fig 4. Social plasticity in group size, size of dominant, and coral size for group-forming *Gobiodon* gobies and  
 423 their *Acropora* coral hosts. Yellow arrows identify significant effect ( $p < 0.05$ ), and crossed out dashed lines  
 424 represent no significant effect ( $p \geq 0.05$ ).  
 425  
 426

#### 427 4.4. Within-group plasticity: Size Ratios

428  
 429 We compared the size ratios between rank 1 and rank 2 (i.e. rankstep 1) for six species (*G. erythrospilus*, *G.*  
 430 *fuscuber*, *G. histrio*, *G. oculolineatus*, *G. quinquestrigatus*, and *G. rivulatus*) that were found at multiple  
 431 locations with sufficient sample size. Mean size ratio for rankstep 1 ranged between 0.88 and  $0.94 \pm 0.01$ -0.02  
 432 among all species (Fig 5). Size ratios for rankstep 1 were not related to coral size (Suppl. Tab 3,  $p = 0.94$ ), group  
 433 size ( $p = 0.09$ ), species ( $p = 0.15$ ) or location ( $p = 0.52$ ), and there was no interaction between any predictors ( $p$   
 434  $= 0.24$ ). Since there was no effect of location, we then included a seventh species, *G. brochus*, that was only  
 435 found at one location (LI). Including *G. brochus* did not change the outcome of the model with size ratios for  
 436 rankstep 1 being unrelated to coral size ( $p = 0.21$ ), group size ( $p = 0.25$ ), and species ( $p = 0.12$ ).  
 437

438 For size ratios between rank 2 (second breeder) and rank 3 (first nonbreeder) (i.e. rankstep 2), there were  
 439 insufficient colonies with rank 3 individuals for four of the seven species (*G. brochus*, *G. erythrospilus*, *G.*  
 440 *histrio*, and *G. oculolineatus*), so these species were excluded. Further, we pooled the size ratios for rankstep 2  
 441 for the other 3 species among locations, because there were not enough samples per location and location did  
 442 not affect size ratios for rankstep 1. The size ratio for rankstep 2 was slightly lower than rankstep 1 for most  
 443 species (Fig 5). Size ratios for rankstep 2 were related to coral size ( $p = 0.003$ ), group size ( $p = 0.003$ ), and  
 444 species ( $p = 0.05$ ). Specifically, there was a positive relationship between size ratios, coral size and group size.  
 445 Rank 3 tended to be much smaller for *G. quinquestrigatus* (rankstep 2 mean =  $0.63 \pm 0.11$ ) than other species  
 446 (rankstep 2 mean ranging from 0.85 to  $0.90 \pm 0.03$ -0.08). for *G. quinquestrigatus*, the smaller rank 3 individuals  
 447 suggests that the species is primarily pair-forming, but that breeders will tolerate nonbreeders occasionally if  
 448 they are far smaller in size (Fig 5).  
 449



450  
 451 Fig 5. Distribution of size ratios between ranks 1 & 2 (rankstep1), and ranks 2 & 3 (rankstep2) of single species  
 452 colonies of *Gobiodon* species. Note: there is no rankstep2 data for *G. brochus*, *G. erythrospilus*, *G. histrio*, and  
 453 *G. oculolineatus* due to insufficient data; and the size differences between ranks for each species are shown with  
 454 pictures that are illustrated to scale based on rankstep means.

455

456 We revisited LI and PNG in consecutive years (LI2020 and LI2021, PNG2018 and PNG2019), and calculated  
457 the size ratio for rankstep 1 if both dominant individuals tagged in the first trip were still present in the  
458 following trip. The size ratios for rankstep 1 were related to coral size ( $p = 0.02$ ), but not to group size ( $p =$   
459  $0.76$ ), species ( $0.30$ ), location ( $p = 0.37$ ), nor year ( $p = 0.09$ ), and there were no interactions ( $p > 0.07$ ). The time  
460 between visits at LI was one year compared to only six months at PNG, and yet there was no effect of location  
461 or interaction with year on the size ratios. Although the effect of year was not significant, there is a trend for  
462 rank 1 and rank 2 individuals to converge in size overtime (Suppl Fig 2).

463

464 When comparing the size ratio of rankstep1 pre- and post-disturbances at LI, we only had sufficient sample  
465 sizes for *G. brochus*, *G. erythrospilus*, *G. histrio*, and *G. quinquestrigatus*. The size ratio of rankstep 1 was  
466 related to coral size ( $p < 0.01$ ), but not to group size ( $p = 0.06$ ), species ( $p = 0.19$ ), or pre- vs. post-disturbance ( $p$   
467  $= 0.29$ ), and there was no interaction ( $p = 0.20$ ).

468

#### 469 4.5. Within-group Plasticity: Sex Dominance Between Breeding Partners

470

471 Sex dominance was only identified during trips to LI in 2020 and 2021. We compared sex dominance in goby  
472 colonies only if both dominant individuals tagged in 2020 were still present in 2021. There were five goby  
473 species found in high enough abundance to determine whether sex dominance existed for rank 1. In 2020, 120  
474 colonies were identified for sex dominance, and 42 colonies were revisited in 2021. From both years combined,  
475 the sex ratio between rank 1 females and rank 1 males was 1:0.7 which differed significantly from unity (Suppl.  
476 Tab 3,  $p = 0.02$ ). There was also a difference among years ( $p < 0.01$ ): in 2020, the ratio of female to male rank 1  
477 was 1:1.05 among species (Suppl Fig 3), whereas in the same colonies in 2021, females often outgrew males  
478 and the sex ratio was 1:0.36 female to male rank 1 individuals for all species (Suppl Fig 3). The male never  
479 outgrew the female in any colonies (Suppl Fig 3). There was no difference in the ratio of female to male rank 1  
480 individuals among species ( $p = 0.30$ ) and no interaction between species and year ( $p = 0.29$ ).

481

#### 482 4.6. Mixed Species Colonies: Social Structure and Composition

483

484 Although we did not sex individuals to confirm they were reproductively active, we did find two nests  
485 containing eggs within the same coral on more than one occasion. Each nest was being guarded by a specific  
486 same-species pair, suggesting that sharing of nest guarding was not occurring and there was likely no  
487 hybridization. It is also important to note that no mixed species colonies were collected post-disturbance at any  
488 of the locations, therefore no pre- versus post-disturbance analyses were completed for mixed species analyses.

489

490 When quantifying the size-based hierarchy within mixed groups, we found that different species were  
491 intermixed within the ranks just under 50% of the time with no difference among locations (intermixed e.g. rank  
492 1,3,5 were species A and rank 2,4,6,7 were species B, Suppl. Tab 4,  $p = 0.91$ , Fig 6A, Suppl Fig 4). The rank 1  
493 individual within mixed groups was generally the larger-bodied species (as defined by Hing et al. 2019)  
494 approximately 75% of the time with no pattern among locations ( $p = 0.93$ , Fig 6B). Although different species  
495 were intermixed within ranks, we propose that individuals still queue for a breeding position within their own  
496 species as eggs were guarded by pairs of the same species.

497

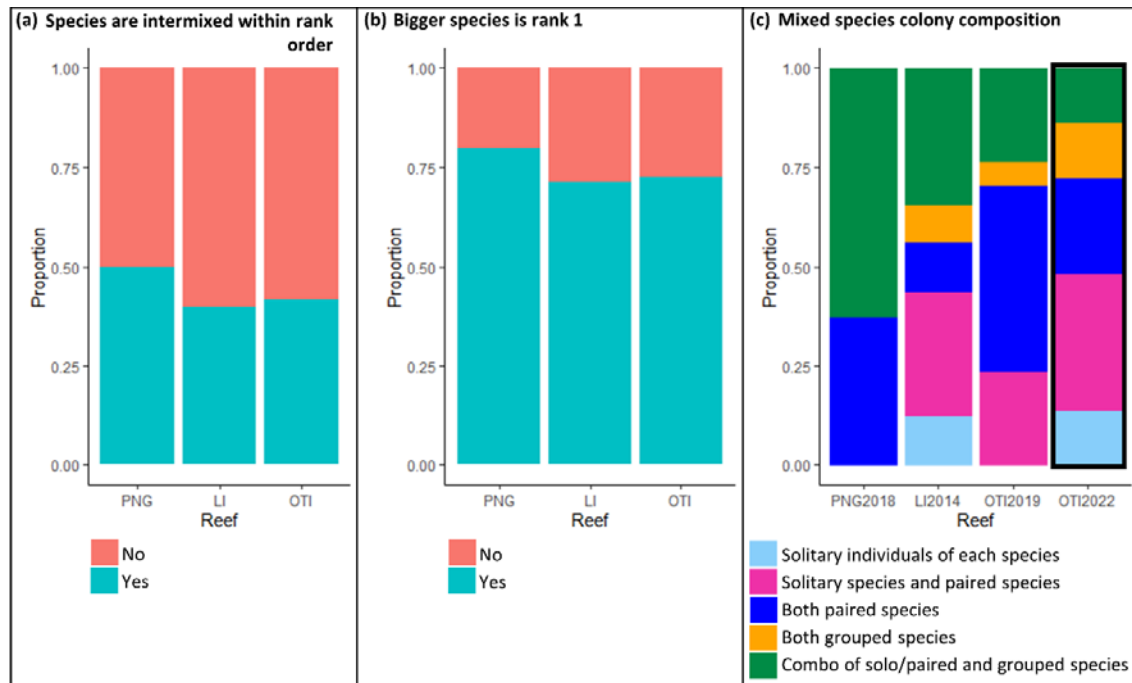


Fig 6. Proportion of intermixed ranks **a** and larger-bodied species as rank 1 **b** within size-based hierarchies of mixed species colonies of *Gobiodon* and their grouping composition **c**. PNG = Papua New Guinea; LI = Lizard Island; OTI = One Tree Island; year after the location label is the year sampled; data outlined in thick black line was taken post-disturbance while all other data was taken pre-disturbance.

When we calculated the size ratios between each rank within mixed species colonies, there were sufficient large groups to compare ranksteps 1-8 (i.e. from rank 1 down to rank 9). The size ratio of each rankstep in mixed species colonies differed by coral size (Suppl. Tab 2,  $p < 0.01$ ), group size ( $p = 0.02$ ), but not by rankstep ( $p = 0.10$ ) or location ( $p = 0.11$ ). There was no interaction between any of the variables. There was a positive relationship between size ratios and coral sizes as well as group sizes. This means that ranks were more similar in size in larger corals and in bigger groups. We found that when size ratios were separated per species, size ratios within mixed species colonies were smaller on average ( $0.88 \pm 0.01$ ) than those for that same species in single species colonies ( $0.91 \pm 0.01$ ,  $p < 0.01$ ). The smaller size ratios in mixed species colonies means that group sizes in mixed colonies may be as large as in single species groups due to rules of the size hierarchy with respect to group size (Buston & Cant 2006; Wong 2011). We then compared size ratios of mixed species colonies, regardless of species, to single species colonies and found no difference between mixed or single species colonies ( $p = 0.22$ , Fig 5& Suppl Fig 4).

Pre-disturbances, mixed species colonies were composed of solitary, pair-forming and/or group-forming species with no difference in proportion among locations (Suppl. Tab 4,  $p = 0.69$ , Fig 6C). There was also no difference in mixed species composition pre- or post-disturbance at OTI ( $p = 0.58$ , Fig 6C). Note, not enough mixed species colonies were found at LI post-disturbance, therefore LI was not compared for disturbance effect. Mixed species colonies were primarily made up of two species (89%), followed by three species (10%), and there was only a single colony of four species (1%, Suppl. Tab 5). Every *Gobiodon* species observed was found in a mixed species colony at least at one time point (Suppl. Tab 5). However, the most common mixed species colonies were made up of *G. fuscoruber*-*G. quinquestrigatus* colonies (23%), followed by *G. fuscoruber*-*G. rivulatus* colonies (10%), and then *G. oculolineatus*-*G. quinquestrigatus* colonies (9%, Suppl. Tab 5). The single most common species in mixed species colonies was *G. fuscoruber* (55%), followed by *G. rivulatus* (43%), and *G. quinquestrigatus* (41%, Suppl. Tab 4). The following species were found with similar proportions within mixed species and single species colonies: *G. citrinus*, *G. fuscoruber*, *G. oculolineatus*, and *G. diabolensis* (Hildebrandt *et al.*, in prep); all other species observed occurred more often in single species colonies than in mixed species colonies (Suppl. Tab 5).

## 5. Discussion



534 Following our sociality framework, we investigated to what extent ecological and social factors affected the four  
535 categories of social variation in coral-dwelling gobies in the *Gobiodon* genus. We chose both large-scale  
536 ecological factors, namely location and disturbance regime, and small-scale ecological factors, namely habitat  
537 characteristics like habitat size, as well as social factors, namely body size of the largest group member. Each  
538 category of variation outlined in the framework (i.e. forms of sociality, degree of sociality, social plasticity, and  
539 within-group plasticity) guided our assessment of the relevant ecological and social factors. We found that  
540 location and disturbance regimes played a substantial role in the forms of sociality exhibited within the genus  
541 and the degree of sociality exhibited by individual species, with species tending away from group-forming under  
542 high disturbance regimes. In contrast, social plasticity and within-group plasticity were not directly affected by  
543 these large-scale factors but were indirectly affected by small-scale factors like changes to coral size, which  
544 decreased following disturbances. Based on these findings, we infer that societies of coral-dwelling gobies have  
545 an extremely poor outlook in terms of persistence when facing climatic disturbances. Accordingly, this  
546 framework allowed us to identify the impacts of multiple ecological factors on animal societies over different  
547 scales.

548  
549 With respect to the form of sociality, studying multiple goby species within the *Gobiodon* genus enabled us to  
550 investigate how the form of sociality within the whole genus was affected by small and large scale ecological  
551 factors. Coral sizes affected the form of sociality, with a shift from solitary to pairs and groups as coral sizes  
552 increased. In addition, location was also a key predictor. In the northern location at Kimbe Bay, Papua New  
553 Guinea, gobies tended to form pairs; in the central reef location at Lizard Island, Australia gobies tended to form  
554 single species groups; and in the southern location at One Tree Island, Australia, gobies tended to form mixed  
555 species colonies. This gradient may indicate a latitudinal shift in social systems, as seen in ground-nesting bees  
556 (Dew *et al.* 2018) and birds (Arnold & Owens 1998). Reef type may potentially explain such differences  
557 between locations; for example, the movement of goby larvae may be limited in a lagoonal reef like at One Tree  
558 Island and prompt the formation of mixed species colonies in order for more individuals to populate an area  
559 while reducing the potential for inbreeding (Selwyn *et al.* 2016). It should be noted though that we did not  
560 sample at multiple locations at each latitude, hence limiting our ability to draw conclusions as regarding the  
561 major underlying causes of this latitudinal variation.

562  
563 Additionally, disturbance regime was a strong predictor of forms of sociality, with high disturbance regimes  
564 reducing the propensity for group-living as gobies were found either living solitary or in pairs after these  
565 disturbances. After moderate disturbance regimes, gobies were also primarily living solitary and less often in  
566 pairs, but the same proportion of groups was still found compared to pre-disturbances. Finding many solitary  
567 gobies is a cause for concern as pairs are needed for breeding. Such a loss in sociality due to disturbance is  
568 likely due to the extreme decline in populations of gobies following particularly extreme events (Froehlich *et al.*  
569 2021; Hing *et al.* 2018). The increased occurrence of solitary living could be attributed to a reduction in a) space  
570 and shelter due to corals becoming damaged and/or b) food resources which the corals provide. A similar result  
571 was reported for passerine birds when habitat size was reduced after disturbance (Lantz & Karubian 2017) and  
572 in butterflyfishes when food resources were reduced after disturbance (Thompson *et al.* 2019). Ecological  
573 factors such as environmental disturbances are therefore important predictors for the form of sociality within the  
574 genus of *Gobiodon*.

575  
576 While location and disturbance regime were observed to reduce the degree of sociality for group-forming  
577 species, they did not change the degree of sociality for pair-forming species. These latter species exhibited low  
578 degrees of sociality and tended to live in pairs (0.33-0.49) regardless of location or disturbance regime. This  
579 study further provides support that these species are generally pair-forming as was also determined by Hing *et al.*  
580 (2018, 2019). Interestingly, although these pair-forming species primarily live in pairs, some accepted  
581 nonbreeding subordinates during periods of low disturbances, but did not accept any nonbreeders during high  
582 disturbance regimes. Furthermore, some group-forming species (Hing *et al.* 2018, 2019) displayed moderate  
583 degrees of sociality (0.33-0.65) that fluctuated between group- or pair-forming depending on location and  
584 disturbance regime, and these patterns were not always similar among species. Typically, the degrees of  
585 sociality fluctuated post-disturbance depending on the species surveyed. The two group-living species, *G.*  
586 *citrinus* and *G. rivulatus* had the highest degrees of sociality at one location (i.e. LI, with most subordinates in a  
587 group), and either continued occurring in groups with many subordinates (*G. citrinus*), or became pair-forming  
588 post-disturbances (*G. rivulatus*). The third group-living species, *G. fuscuber*, remained as group-living at most  
589 locations (LI, OTI) pre-disturbances and after low disturbances, although with fewer subordinates post-  
590 disturbances. However, it is important to note that *G. citrinus* and *G. fuscuber* disappeared after extreme  
591 disturbances at Lizard Island (Froehlich *et al.* 2021). Different species appear to have different responses to  
592 disturbances in terms of their sociality index, and we need further work to understand the fitness consequences  
593 of these species-specific differences.

594

595 The life insurer hypothesis (Queller & Strassmann 1998) states that cooperative and social groups enjoy a  
596 competitive advantage in challenging habitats, hence why sociality has evolved. In support of this, several  
597 studies have demonstrated that species have a higher chance of survival in challenging environments by living  
598 socially instead of paired or solitary due to benefits of resource acquisition, brood care, and predator protection  
599 (Duffy & Macdonald 2010; Firman *et al.* 2020; Queller & Strassmann 1998; Rubenstein & Lovette 2007)  
600 (Queller & Strassmann 1998). Our results did not provide support for the life insurer hypothesis of sociality, the  
601 goby species had lower degrees of sociality in challenging environments (i.e. high disturbances). In comparison,  
602 In comparison, based on global study, many birds evolved social living as a strategy to ensure survival in  
603 environments that are constantly fluctuating and challenging (Jetz & Rubenstein 2011). Similarly, naked mole-  
604 rats have some of the highest degrees of sociality and are strictly eusocial, like *Heterocephalus glaber* (0.95)  
605 and *Fukomys damarensis* (0.80-91) (Avilés & Harwood 2012), and they live socially due to challenging  
606 environments that fluctuate substantially in rainfall (Faulkes *et al.* 1997). By comparison, gobies exhibit low to  
607 moderate degrees of sociality, and ecological conditions play a large role in their grouping tendencies. Our study  
608 suggests that gobies likely evolved social living behaviour in stable environments, as seen in hornbills  
609 (Gonzalez *et al.* 2013). In stable environments, corals can grow larger, and more gobies can reside within a coral  
610 and reap the benefits of sociality. When conditions deteriorate and corals become smaller, group-living is no  
611 longer possible hence why gobies switch to living with fewer subordinates and primarily in pairs in challenging  
612 environments.

613

614 When addressing variations in sociality at smaller scales, we found that the group sizes of group-forming gobies  
615 were plastic with respect to habitat size, but not i location. This demonstrates that coral size is a key limiting  
616 resource influencing sociality, as gobies were in smaller groups when corals became smaller after climatic  
617 disturbances (Froehlich *et al.* 2021; Hing *et al.* 2018, 2019; Madin *et al.* 2018). For the most social goby species  
618 studied at all locations, *G. fuscovuber*, the coral size influenced the size of the dominant individual and group  
619 size, but the size of the dominant was not influenced by the group size. This suggests that social constraints on  
620 group size, namely the size of the largest dominant individual, have less of an influence on group size than  
621 ecological factors like coral size. On the other hand, group sizes of *G. rivulatus* affected the size of the dominant  
622 individual, but not vice versa. Location had little impact on any of these relationships for either species. In  
623 contrast, all three variables (group size, habitat size, and size of dominant) were positively related to each other  
624 for other social fishes like *P. xanthisoma* and *A. percula*, suggesting strong social plasticity based on habitat  
625 size and social context (Buston & Cant 2006; Wong, 2011; Rueger *et al.* 2021). Social plasticity therefore  
626 appears to vary depending on the species and its ecology, and such variation highlights that integrating large-  
627 scale factors into investigations alongside small-scale factors can provide important insights into social  
628 plasticity.

629

630 In terms of within-group plasticity, we found that size ratios and sex dominance ratios of gobies were not  
631 directly affected by large scale ecological factors like location and disturbance. We found that size hierarchies of  
632 *Gobiodon* are similar to those of *Paragobiodon* (Wong *et al.* 2007, 2008); in a goby colony the two dominant  
633 individuals are slightly different in size (1:0.88 to 1:0.94) regardless of species or location. Breeding partners  
634 likely converge in size over time to maximize reproductive output (Munday *et al.* 2006), although not for all  
635 cases. Coral size influenced the size ratios between breeding partners for some but not all analyses, suggesting  
636 that size convergence may not be beneficial in all circumstances. We found that although males are often the  
637 bigger individual at first, females will outgrow males more than half of the time, owing to their growth rate  
638 advantage (Munday *et al.* 2006; Nakashima *et al.* 1996). Initially a bigger male allows for better paternal care  
639 and offspring success in the first breeding year, but then a bigger female allows for more offspring in a single  
640 egg clutch (Nakashima *et al.* 1996). Gobies also have bi-directional sex change which allows either individual to  
641 change sex if their mate dies and they find a new partner (Munday *et al.* 1998; Nakashima *et al.* 1996; Sunobe *et al.*  
642 *et al.* 2017). This suggests that while a bigger female is advantageous in the long run, groups are not strictly  
643 matriarchal like those in the anemonefish *A. percula* (Buston & Wong 2014; Rueger *et al.* 2021a; Wong &  
644 Buston 2013).

645

646 When considering variation in size ratios in colonies, specifically between rank 2 and 3, we found that their size  
647 ratio is slightly smaller (0.85 to 0.9) than that between the breeding individuals (rank 1 and rank 2) for most  
648 species i.e. there is a larger size gap between rank 2 and 3 than between rank 1 and 2. However, rank 3  
649 nonbreeders for *G. quinquestrigatus* considerably smaller than the rank 2 individuals (0.64). This is not entirely  
650 surprising as *G. quinquestrigatus* was living primarily in pairs, suggesting limited tolerance of breeders for any  
651 nonbreeder. Regardless of species, the two breeders (rank 1 and 2) were closer in size than the first nonbreeder  
652 (rank3) was to the closest breeder (rank 2). This is expected as breeders converge in size for reproductive  
653 benefits (Kuwamura *et al.* 1993; Munday *et al.* 2006), whereas nonbreeders regulate their sizes to be tolerated

654 by breeders and avoid eviction (Wong *et al.* 2007). This provides evidence that *Gobiodon* gobies cooperate  
655 within size-based hierarchies, as seen in *P. xanthosomus* (Kuwamura *et al.* 1993; Wong *et al.* 2007). Size ratios  
656 between rank 2 and 3 were affected by coral size with rank 3 being more similar in size as the rank 2 breeder in  
657 larger corals for pair-forming species. This suggests that larger corals provide nonbreeders with more  
658 opportunities to grow larger and be more tolerated by breeders. Therefore, living in groups may be costly for  
659 nonbreeders from pair-forming species as they must remain far smaller than breeders despite coral size, making  
660 group-living only potentially advantageous in large corals (Hing *et al.* 2019; Rueger *et al.* 2021a). However, for  
661 strictly group-forming species, there was little effect of coral size, suggesting that breeders are more tolerant of  
662 nonbreeders and appear to allow nonbreeders to grow larger regardless of coral size (Rueger *et al.* 2021a).

663  
664 When investigating the within-group composition of mixed colonies, we found that that different species were  
665 often interspersed in ranks within the hierarchy. Interestingly though, the size ratios between ranks remained the  
666 same regardless of which species were adjacent in ranks, and regardless of location. Instead, individuals can  
667 grow larger in larger corals as there is likely more space to avoid aggression from higher ranks. With a larger  
668 coral, dominant individuals can grow larger, thus allowing additional subordinate individuals to fit within the  
669 size-based hierarchy. Individuals were also closer in size in larger corals, suggesting that larger corals may  
670 reduce conflict among individuals. When factoring in the clear size differences between goby species, with  
671 some species growing larger on average than others (Hing *et al.* 2019), we found that the larger-bodied species  
672 tended to occupy the rank 1 position (i.e. largest individual) in mixed species colonies, regardless of location.  
673 Accordingly, this suggests that *Gobiodon* cooperate within size-based hierarchies in both single species colonies  
674 and mixed species colonies alike.

675  
676 There was no clear trend for whether mixed species colonies were composed of only pair-forming individuals,  
677 groups, or a combination of both, regardless of location or disturbance regime. However, some species were  
678 more often found in mixed species colonies than others. For example, *G. fuscuber*, *G. quinquestrigatus* and *G.*  
679 *rivulatus* were more often found in mixed species colonies than other species, suggesting they obtain some  
680 advantage to living in mixed colonies (Ellis & Good 2006). By far the most common mixed species colony was  
681 composed of *G. fuscuber* and *G. quinquestrigatus*. One potential advantage of living with congeners may be  
682 that individuals can reach breeding status quicker (as there may be fewer conspecifics queuing for breeding  
683 status) while still receiving synergistic benefits of living in a larger group (Rueger *et al.* 2021a). Indeed, we  
684 found evidence for separate breeding queues for each species within a colony. On multiple occasions mixed  
685 species colonies had two egg clutches within the coral - one guarded by a pair from one species and another  
686 guarded by a pair from another species (pers obs). Gobies in mixed species colonies can reap the various  
687 benefits of living in big groups (e.g. improved territory defence, improved coral growth, improved survival and  
688 growth rates) whilst not necessarily decreasing their likelihood of territory inheritance and securing reproduction  
689 (Goodale *et al.* 2017; Rueger *et al.* 2021a). In order to maintain cooperation, gobies in mixed species colonies  
690 regulate growth in size-based hierarchies just like in single species colonies. Future studies comparing egg  
691 clutch sizes, rates of territory defense, long term growth rates, and survivorship among single species and mixed  
692 species colonies would be important in identifying the benefits of living in mixed species colonies.

693  
694 In each of the four categories of variation, we found direct and indirect impacts of climatic disturbances,  
695 suggesting an extremely high loss of sociality (Fig 1). The form of sociality and degrees of sociality were each  
696 drastically lower after high disturbance regimes. Social plasticity and within-group plasticity were not directly  
697 affected by disturbances, but instead were indirectly affected via a decrease in coral size. Since disturbances  
698 drastically diminish the sizes of available corals (Froehlich *et al.* 2021; Hing *et al.* 2018, 2019; Madin *et al.*  
699 2018), social plasticity and within-group sociality are indirectly lost to disturbances. Accordingly, each category  
700 of variation in coral-dwelling goby societies is facing high loss to disturbances. Given that living in groups can  
701 increase individual fitness and survival (Booth 1995; East & Hofer 2010; Gil *et al.* 2017; Jordan *et al.* 2009;  
702 Komdeur & Ma 2021; Strauss & Holekamp 2019), these findings suggest that the large-scale population losses  
703 observed in coral-dwelling gobies after environmental disturbances (Froehlich *et al.* 2021, 2023) is at least in  
704 part due to a loss of sociality at multiple levels.

705  
706 By quantifying the four categories of variation, the sociality framework introduced here provides a flexible yet  
707 robust assessment of social organisation for animal societies along different scales of ecological and social  
708 factors. Depending on the factors of interest, each category of variation can be quantified at a defined spatial and  
709 temporal scale. The framework can identify limiting resources that will play important roles in the formation  
710 and maintenance of animal societies. The framework is particularly useful as it requires only monitoring of  
711 group sizes, measures of cooperation, e.g. size and sex of individuals within groups, and measures of ecological  
712 and social factors of interest, e.g. habitat size and proximity to other groups, without requiring manipulative  
713 experimentation. The categories of variation (i.e. forms of sociality, degree of sociality, social plasticity, and

714 within-group plasticity) as well as the social and ecological factors can be easily adapted to the life history,  
715 cooperation, and ecology of the social taxon (e.g. Fig 1). The framework can be adapted for any species and  
716 many different factors, including larger-scale ones like spatiotemporal and disturbance factors, thus making  
717 observational data a powerful tool for modeling the social organisation and plasticity of many taxa into the  
718 future. By assessing how each category of variation is affected by ecological factors, the metrics can then be  
719 integrated to identify the outlook of social maintenance in the taxon studied.

720

#### 721 **Data Availability Statement**

722 Data and R scripts will be available at [knb.ecoinformatics.org](http://knb.ecoinformatics.org).

723

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735

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752

#### 753 **Author contributions**

754 CF: planned study, sought funding, collected data, analysed data, wrote and edited the manuscript; SH: collected  
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756 collected data, edited manuscript; CH: collected data, edited manuscript; JS: collected data; MW: planned study,  
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