1	Long-term blooming filamentous calcareous alga provides substrate for
2	other coral-competitive macroalgae in the degraded lagoon of Dongsha
3	Atoll (Pratas), Taiwan
4 5	Short title: Filamentous calcareous alga provides substrate for other coral-competitive macroalgae
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### 16 Abstract

**Background:** Red calcareous seaweeds of the genus *Galaxaura* have been associated with coral 17 18 reef degradation. Galaxaura has low nutritional value for most herbivorous fishes and produces 19 allelopathic chemicals in competition with corals. In this study, the abundance of the filamentous Galaxaura divaricata was surveyed on 13 spatially independent patch reefs across the lagoon of 20 21 Dongsha Atoll, an isolated coral reef ecosystem in the northern South China Sea. Variations in 22 Galaxaura cover on a degraded reef were monitored over a period of 17 months. Epiphytic 23 macroalgae associated with *Galaxaura* were quantified, and species identifications aided through 24 DNA barcoding.

Results: Patch reefs in the lagoon of Dongsha Atoll were degraded, exhibiting relatively low 25 living coral cover (21 + 3%), but high cover of macroalgae (30 + 4%), and rubbles and dead 26 coral (47 + 4%). The distribution of *Galaxaura* was heterogeneous across the lagoon, with 27 highest abundance in the southeast area. In that area Galaxaura has persistently bloomed on 28 29 degraded reef for at least four years, covering up to 41% of the substrate. Galaxaura provides substrate for various macroalgae, 15 of which were identified to the species level, four to the 30 genus level, one to the order Gelidiales, and one to the phylum cyanobacteria. Some of these 31 epiphytes are allelopathic and known to frequently overgrow corals. For instance, the brown alga 32 Lobophora sp28, third most common epiphytic macroalga on Galaxaura, frequently overgrows 33 corals across the lagoon of Dongsha Atoll. 34

Conclusions: Our study demonstrated that an allelopathic and unpalatable seaweed, such as
 *Galaxaura* can bloom on degraded coral reefs for several years. The complex thallus-structure of
 *Galaxaura* provides suitable substrate for other macroalgae, some of which are noxious to corals.

38 By increasing the substrate availability for macroalgae, *Galaxaura* could facilitate the abundance

39 of macroalgae, and decrease the recovery potential of degraded coral reefs.

- 40 **Keywords:** coral reef, epiphyte; *Galaxaura*; lagoon; macroalgae; phase-shift.
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### 42 **Introduction**

Coral-macroalgae competition is a major ecological process on coral reefs [1,2]. 43 However, climate change, overfishing, and anthropogenic pollution have driven corals 44 worldwide to a decline and often facilitated macroalgae dominance on degraded reefs [3-9]. The 45 46 replenishment of corals on degraded reefs is strongly influenced by the types of dominant macroalgae [10,11]. Macroalgae that produce noxious allelochemicals in competition with corals 47 are considered most detrimental for the resilience of degraded coral reefs [10,12-14]. 48 Allelopathic macroalgae may perpetuate their dominance on degraded reefs by inhibiting the 49 process of successful recruitment of juvenile corals, the key process of coral reef recovery [15-50 51 17].

52 Species of the red, calcareous genus *Galaxaura* are common on coral reefs in the Pacific Ocean [18-22]. Galaxaura is one of the least nutritious macroalga to herbivores fish [23-26], and 53 54 highly competitive with coral because of its allelopathic effects on coral and coral larvae [15,27]. 55 Extracts of the lipid-soluble secondary metabolites of Galaxaura filamentosa were shown to cause bleaching and death of coral tissue upon direct contact [13-15,28], and deterred coral 56 57 larvae from settlement [29]. It has been suggested that high abundance of Galaxaura on degraded reefs accounts for the inhibition of coral reef recovery [12,29]. More detailed 58 59 investigations of the distribution and ecology of reef-associated seaweeds, such as *Galxaura*, and their roles in outcompeting corals will provide valuable information for coral reef managementand conservation [1,30].

Dongsha Atoll (also known as Pratas Islands) is the only large coral reef atoll (>500 km<sup>2</sup>) 62 63 in the northern South China Sea. The South China Sea is the largest tropical Pacific marginal sea in Southeast Asia [31], including numerous coral reef atolls and fringing reefs that are great 64 natural resources, supplying large numbers of people with goods and services, such as fish and 65 important ecological values [32-34]. The ring-shaped reef flat of Dongsha Atoll encircles a large 66 lagoon with seagrass beds and hundreds of coral patch reefs [35]. The Lagoon patch reefs are 67 68 structured into tops (1-5 m depth) and slopes (5-12 m depth), and provide important habitat and 69 sheltered nursery grounds for numerous marine organisms, such as green sea turtles and coral reef fish, including rays and sharks [32,35-37]. The catastrophic mass bleaching event in 1998 70 71 and reoccurring bleaching events thereafter have caused severe mass mortalities of corals in the lagoon, followed by a marked increase of macroalgae [36,38]. 72

The filamentous, calcareous macroalga *Galaxaura divaricata* is conspicuous on coral reefs in the lagoon of Dongsha Atoll [19] where it blooms in certain areas, overgrowing large parts of degraded reef substrate. Several macroalgae, e.g. *Sargassum* and *Lobophora*, are known to provide substrate and form habitats for epiphytic algae [39-41]. Increased substrate availability can lead to increased macroalgae biomass on coral reefs [1]. However, whether *Galaxaura* provides a suitable substrate for macroscopic epiphytes remains unexplored.

The aims of this study are to document the spatial patterns and persistence of *Galaxaura* blooms in the lagoon of Dongsha Atoll, show several aspects of *Galaxaura*-coral competition, and identify and quantify epiphytic macroalgae that grow on *Galaxaura*. Potential implications

of our observations, regarding the recovery potential of *Galaxaura* dominated reefs, and the role
of *Galaxaura* as substrate for the facilitation of macroalgae abundance, are discussed.

84

#### 85 Materials and methods

This study was conducted from April 2016 to September 2017 in Dongsha Atoll (Pratas 86 Island) (Latitude 20°40'43"N, Longitude 116°42'54"E), an isolated coral reef atoll in the north 87 of the South China Sea. The climate shows seasonal variability under the East Asian monsoon 88 system, with a colder northeast monsoon season (as winter) and a warm southwest monsoon 89 season (as summer) [31]. The ring-shaped atoll covers an area of approximately 500 km<sup>2</sup> and is 90 situated 450 km southwest from the coast of Taiwan and 350 km southeast from Hong Kong (Fig. 91 1). The outer reef flat is interrupted by two channels that are located north and south of a small 92 islet (1.74km<sup>2</sup>), allowing for water exchange between the lagoon and the open ocean [36,42]. 93 The semi-closed lagoon is about 20 km wide with a maximum depth of 16 m deep near the 94 95 center [36].

The abundance of the red, calcareous, filamentous seaweed Galaxaura divaricata was 96 surveyed on 13 spatially independent lagoon patch reefs with SUBA (Fig 1B and S1 Table). Two 97 45-m transect lines were laid out across the reef top (1-5 m depth) and the reef slope (5-12 m 98 depth) respectively. The percent cover of *Galaxaura*, living coral, macroalgae (MA; including 99 low growing, filamentous turf algae [23, 24]), crustose coralline algae (CCA), and other 100 101 substrate was estimated, using a 35 cm x 50 cm PVC quadrat [43]. Estimations were done at 1 m intervals and a total of 90 replicate quadrats were analyzed for each site. 'Other substrate' mainly 102 constituted dead corals, rubbles, larger rocks covered with sediments and sparse turf algae, and 103

sand. The seawater temperature was measured every 30 min from March 2016 to September
2017, using Hobo temperature loggers that were fixed at the reef top and reef slope of each site.

To assess variations over time we monitored the percent cover of *Galaxaura* and living coral across the slope of site 7 at 5 m depth in April, July, and September 2016 and in September 2017. 45 replicate photos were taken with an Olympus Stylus-TOUGH TG4 digital camera (25-109 lons, 35mm equivalent) mounted onto a PVC-quadrat at 0.64 cm above a sampling 35 cm x 50 cm quadrat [43], using the survey method described above. Percent cover estimations of *Galaxaura* were aided by superimposing a 10 x 10 reference grid onto each photograph, where 1 quadrat represented 1% of the total area.

To quantify epiphytic macroalgae associated with Galaxaura, we randomly collected 30 113 thalli of Galaxaura from site 7 at 5 m depth. The samples contained an equal proportion of small 114 115 (6 + 4 g), medium (23 + 6 g), and large (49 + 20 g) thalli. Epiphytic macroalgae were identified 116 to the closest identifiable taxonomic unit, using either the guidebook [19] or DNA barcoding. 117 The presence and absence of each taxonomic unit was recorded, and the occurrence frequency (f)118 was calculated as follows: f = c (taxonomic unit<sub>i</sub>)/n, where c (taxonomic unit<sub>i</sub>) stands for the 119 count number of thalli that have the epiphyte taxonomic unit *i*, and *n* stands for the total number 120 of thalli analyzed.

Two-paired t-tests were used to detect significant differences of live coral, macroalgae, and CCA percent cover between reef tops and reef slopes. A two-way ANOVA and a post-hoc Tukey test were applied to test for significant differences of *Galaxaura* percent cover between reef top and reef slope and among sites. Percent cover of *Galaxaura* and living coral cover at site from four surveys conducted over a 17-month period were analyzed using a two-way ANOVA, and p-values < 0.05 were considered significant.

127 Macroalgae samples were preserved in silica gel and species identified through DNA barcoding [44]. DNA was extracted with Quick-DNA<sup>TM</sup> Plant/Seed Miniprep Kit (Zymo 128 Research Co., USA). Primers for the plastid gene specific amplifications were used as follows: 129 130 rbcL F7/R753 for rhodophytes [45], rbcL F68/R708 for Phaeophyceae [46], and tufA F210/R1062 for green algae [47]. The newly generated sequences were deposited in GenBank 131 132 and searched using BLASTn against the GenBank database (S2 and S3 Tables). Sequence 133 similarities of > 98% were considered for species identification.

134

#### **Results** 135

Seawater temperatures in the lagoon were highest during the southwest monsoon season 136 (June-Sept.), averaging 30.1°C, and lowest during the northeast monsoon season (Nov.-April), 137 averaging 24.8°C. In July and August, maximum temperatures reached 34°C on reef tops and 138  $32.7^{\circ}$ C on reef slopes. Across sites the average coral cover accounted for  $21 \pm 3\%$  ( $\pm$  SE) of the 139 140 benthic substrate (range: 5-43%) (Table 1). Average coverage of the substrate was 30 + 4%141 (range: 13-58%) by macroalgae, and  $2 \pm 0.2\%$  (range: 1-3%) by crustose coralline algae (CCA). Dead corals, rubbles, larger rocks, and sand accounted for an average of 47 + 4% (range: 23-69%) 142 143 of the substrate. Living corals dominated the reef substratum on two out of 13 patch reefs (sites 1 144 and 13), whereas dead corals, rubbles, larger rocks, and sand dominated the substrate on nine out of 13 sites. Macroalgae cover exceeded live coral cover on seven out of 13 sites. No significant 145 difference in coral cover and macroalgae cover between reef tops and reef slopes was detected 146 147 (P-values = 0.394 and 0.552).

The percent cover of *Galaxaura divaricata* was significantly different between reef tops 148 149 and reef slopes (P-value < 0.01), as well as among the 13 survey sites (P-value < 0.001). The

150 post-hoc Tukey test showed that *Galaxaura* was more abundant on reef slopes than on reef tops 151 (P-value <0.05). The percent cover of *Galaxaura* was classified as very low (0-1.5%), low (1.5-152 5%), moderate (5-20%), and high (>20%) (P-value < 0.05; post-hoc Tukey). Galaxaura was 153 most abundant on patch reef sites in the southeast lagoon (Table 2). The percent cover of Galaxaura was highest at site 9 (41%) and on the slope of site 7 (16%). Patch reefs in the 154 northeast lagoon exhibited moderate, low, and very low cover of *Galaxaura* (range: 0.21-5.7%). 155 156 Survey sites in the south, center, west, and north section of the lagoon were characterized by very low cover of the alga (range: 0-1.4%). The thallus shape and size of Galaxaura varied 157 158 across sites (S1 Fig). Medium (5-15 cm diameter), ball-shaped thalli and large (15-30 cm), 159 carpet-like thalli were exclusively present in the southeast lagoon. Small (1-5 cm), ball-shaped thalli and small, slender thalli were dominant on patch reefs in the northeast lagoon. DNA 160 161 barcodes revealed that all samples of *Galaxaura* from various sites across the lagoon were 100% identical in their *rbc*L sequences, indicative of conspecificity (S3 Table). 162

163 Our observations suggest that a *Galaxaura* bloom can persist for several years. Thick 164 canopies of Galaxaura have overgrown dead Acropora rubbles for at least 4 years on a degraded patch reef in the southeast section of the lagoon, with 41 + 25% Galaxaura cover and 5 + 14%165 living coral cover (site 9, 3-5 m depth) (Fig 2A-B). Galaxaura was frequently observed in 166 contact with coral, which in some cases showed beached and dead tissue underneath or in contact 167 with Galaxaura. The holdfast of Galaxaura penetrates the calcium carbonate structure, creating 168 169 a strong attachment to the coral (Fig 2C). In some cases, fluorescent pink and bleached coral 170 tissue occurred in contact with Galaxaura, indicative of potential allelopathic effects of G. divaricata on corals (Fig 2D). 171

172	The percent cover Galaxaura did not vary significantly among surveys at site 7
173	conducted over a period of 17 months (Fig 3). The cover of Galaxaura and living corals did not
174	change significantly among surveys (P-value = 0.595). Galaxaura cover averaged $15.91 \pm 0.6\%$
175	( $\pm$ SE), and coral cover remained low, averaging 16.45 $\pm$ 1.17%. Coral cover and Galaxaura
176	cover were not significantly different (P-value = $0.770$ ), and no interaction between the two was
177	detected (P-value = $0.780$ ).

178 In our epiphyte survey we identified 21 taxonomic groups of macroalgae in association 179 with Galaxaura. Among those groups, we identified 15 to the species level, four to the genus 180 level, one to the order Gelidiales and one to the phylum cyanobacteria (Table 3 and S2 Table). 181 Among the 15 identified species, red algae were most abundant (10), followed by brown algae 182 (5), and green algae (5). The most common species associated with Galaxaura were the red 183 algae Hypnea caespitosa [48] (100% relative abundance) (Fig 4D), Coelothrix irregularis (87%), Ceramium dawsoniia (43%) and the brown algae Lobophora sp28 [49] (57%) (Fig 4D), Padina 184 185 sp5 [50] (53%), and Dictyota bartayresiana (30%). The most common green algae associated 186 with Galaxaura were Derbesia marina (37%), Caulerpa chemnitzia (27%) (Fig 4B), and Boodlea composita (20%). Epiphytic macroscopic cyanobacteria (filamentous > 1cm) had a 187 188 relative abundance of 17%. Lobophora sp28, third most common macroalga on Galaxaura, was 189 identified to frequently overgrow corals across the lagoon of Dongsha Atoll (Fig 5 and S2 Fig).

190

## 191 **Discussion**

The results of the benthic surveys indicate that coral reefs in the lagoon of Dongsha Atoll
are highly degraded, with high abundance of dead corals, rubbles, larger rocks, and sand (47%).
Our observation is consistent with previous surveys that noted signs of coral degradation in the

195 lagoon, with an extremely large proportion of coral rubbles and dead corals [36,51,52]. The 196 majority of patch reef sites exhibited a coral cover of lower than 25%, which is considered degraded [53]. Coral reefs in the South China Sea have been facing increasing chronic and acute 197 198 thermals stress over the past decades [33,38,51,54]. The summer mean sea surface temperature shows an average upward trend of  $0.2\Box$  / decade, with waters surrounding Dongsha Atoll 199 200 warming at a faster rate than other areas of the South China Sea [33]. Prior to the 2007 201 establishment of Dongsha Atoll Marine National Park, Dongsha Atoll was heavily overfished, and large coral reef areas were destroyed through dynamite and cyanide fishing [36,52,54,55]. 202 203 According to a previous survey coral cover and the number of new small corals were especially 204 low on patch reefs in the south section of the lagoon [56]. Recurrent coral bleaching events [36,38,57], coral damage by annual typhoons, and destructive fishing practices may have acted 205 206 synergistically, leading to the failure of recovery for some of the lagoon patch reefs. Coral cover and coral recruitment rate was especially low on patch reefs in the southeast lagoon [56]. 207

Species of the red calcareous alga genera *Galaxaura* occur in two morphological forms, a smooth and a filamentous form, which is characterized by fine, assimilatory filaments [21]. Our observations suggested that, under certain conditions, the filamentous *Galaxaura divaricata* can become dominant on degraded reefs and form long-standing canopies that grow frequently in contact with corals. *Galaxaura* was heterogeneously distributed across the lagoon, and bloomed on degraded patch reefs in the southeast section, where it attained largest thallus sizes. Maybe something like this:

Our observations further show the persistence of *Galaxaura* on degraded reefs both over a 17-month period and for at least four years. However, our data do not resolve potential seasonal variations of *Galaxaura* during the cooler northeast monsoon season. In the tropical waters of Florida, U.S., *Galaxaura* shows seasonal persistence with no significant change in
abundance among seasons [58].

220 The causes for *Galaxaura* blooms in the southeast area of the Dongsha lagoon are not 221 understood. The dominance of macroalgae, such as *Galaxaura*, on degraded reefs is probably the consequence rather than the cause of initial coral decline [1,30,59,60]. There are several potential 222 223 factors that could facilitate a *Galaxaura* outgrowth after a disturbance, including shallow, calm, 224 and sheltered habitats, and nutrient-rich waters with high turbidity. Other members of the 225 Galaxauraceae family, such as Tricleocarpa, are known to prefer sheltered habitats [61], and 226 bloom under high water turbidity and low irradiance [62]. The southeast section of the lagoon, 227 where *Galaxaura* is most abundant, is sheltered by the relatively wide reef flat (2 km), and characterized by shallow waters (1-5 meter) and low current [63]. Galaxaura was absent from 228 229 environments with strong water currents, i.e. west lagoon, channels, and forereef, where strong, 230 erosive currents [35,63] may create unfavorable conditions for *Galaxaura* to establish.

231 Due to limited water exchange with the open ocean, coral communities and associated 232 fauna of the shallow, semi-closed lagoons are highly vulnerable to heat stress, eutrophication, and hypoxia [64-66], especially under the backdrop of climate change [67]. Recurrent mass 233 mortality events in the Dongsha lagoon in 2014 and 2015 killed thousands of fish, cephalopods, 234 gastropods, and crustaceans, and eradicated more than 25 km<sup>2</sup> of seagrass, potentially caused by 235 hypoxia [35,68]. During our 2017 survey we recorded extremely low densities of 236 macroinvertebrates, including echinoids, sea cucumbers, lobsters, and giant clams (Table S4). 237 Galaxaura filamentosa was among the very few macroalgae that proliferated in the Hikeru the 238 239 lagoon of French Polynesia, following a hypoxia-induced mass mortality event [18]. Elevated

nutrients from seagrass die offs in the southeast lagoon and a potentially higher resistance to
hypoxia may be additional factors promoting blooms of *Galaxaura*.

A long-term bloom of *Galaxaura* is likely to have profound implications on the recovery 242 243 potential of degraded reefs. The observations of this study further suggest that Galaxaura divaricata is potentially allelopathic in competition with corals. Allelopathic competition with 244 245 corals has previously been demonstrated for *Galaxaura filamentosa* [12,14,15,27-29]. Extract of G. filamentosa were shown to inhibit the settlement of Acropora tenuis larvae [29]. The 246 247 susceptibility of coral to algal overgrowth depends on the type of coral [1,59] and the coral 248 colony form. Branching corals appear most vulnerable to algal overgrowth [69]. In the lagoon of 249 Dongsha Atoll G. divaricata frequently grew in contact with massive and branching Porites, e.g., P. lobata, P. cylindrica, and P. solida. Previous studies in the tropical Pacific reported similar 250 251 observations, where *Porites*, in particular *Porites cylindrica*, was frequently found in contact 252 with the allelopathic Galaxaura filamentosa, suggesting that Porites may be relatively tolerant to 253 Galaxaura allelopathic chemicals [15]. Acropora corals are fast growing and considered 254 competitive against macroalgae overgrowth [59]. However, the majority of the thermal-255 susceptible Acroporid species were eradicated following reoccurring bleaching events since 1998 256 [36,57]. The coral community in the lagoon of Dongsha Atoll has since been dominated by more 257 thermal tolerant genera, such as *Porites*, *Echinopora*, *Pavona*, and *Turbinaria* [51]. These coral genera are rather slow-growing, and thought to be less competitive to macroalgae overgrowth 258 259 [17,59]. Unlike crustose coralline algae (CCA), Galaxaura does not stabilize the coral reef 260 matrix, and a long-term bloom of *Galaxaura* is likely to exacerbate the flattening of the complex three-dimensional coral reef structure, which may have consequences for reef biodiversity, 261 262 ecosystem functioning and associated services [64,70].

263 Insufficient grazing after disturbance can lead to the establishment and full outgrowth of 264 macroalgae beyond their initial stages [30]. Galaxaura is known to be largely unpalatable for various herbivorous fishes due to its calcareous thallus and low nutritional content 265 266 [23,25,26,71,72]. Once established, large macroalgae are less efficiently consumed by herbivorous fishes [30,73]. Local herbivorous fish population on Galaxaura-dominated reefs in 267 the Dongsha lagoon may not be effective to prevent or reverse the space monopolization by 268 269 Galaxaura [30,74]. It is suggested that Galaxaura can alter the chemical microclimate on 270 degraded reefs with potential implications on fish behavior. Butterfly fishes and other 271 corallivores avoid corals in close association with *Galaxaura filamentosa*, making it potentially 272 difficult for these trophic guilds to find food [75,76]. Water soluble chemicals of Galaxaura rugosa negatively impact the predator risk assessment of damselfish by nullifying their 273 274 perception of predator warn odors [11]. In summary, the long-standing canopies of Galaxaura 275 are likely to hamper coral larvae recruitment through allelopathic recruitment inhibition [29], 276 ultimately preventing coral reef recovery [1,15].

277 Galaxaura divaricata provides a suitable substrate to host a variety of macroalgae. Some of the identified macroalgae on *Galaxaura* are widely important in coral overgrowth in response 278 to disturbances, and are known for their allelopathic inhibition coral larvae recruitment, e.g. 279 280 Lobophora [77,78], Dictyota bartayresiana [79,80], and cyanobacteria [81,82]. Here, we firstly report that the yet undescribed species, *Lobophora* sp28 [49], third most abundant macroepiphyte 281 on Galaxaura, was frequently observed to overgrow and kill corals, preferentially branching 282 Porites spp. (primarily P. cylindrica) through epizoism (Figs 5 and S2). Similarly, Lobophora 283 hederacea overgrows and kills corals in New Caledonia through epizoism [83]. 284

285 Galaxaura is known to be of low preference to various herbivorous fishes due to its 286 calcification [84,85] and low nutritional value [25,84,86,87]. Galaxaura was proposed to provide 287 associational refuge to more palatable macroalgae [86]. For instance, rabbitfishes prefer 288 *Caulerpa* and *Dictyota* [88,89], but avoid *Galaxaura* [23]. These epiphytic macroalgae thus could indirectly gain the benefit by growing between the branches of Galaxaura, as they are less 289 likely to be spotted by herbivorous fish. Commensalistic interactions are important for the 290 291 establishment of less common, nutrient-rich seaweeds that grow in association with common, 292 nutrient-poor seaweeds [80]. Even if the common seaweeds lowered the growth rate of the less 293 common ones (competition), evidence suggest that the benefits provided by macroalgae associations outweigh the drawbacks through competition [80,90]. Moreover, the microscopic 294 filaments of Galaxaura may facilitate the attachment of macroalgae spores, while the calcium 295 296 carbonate branches may provide structural support for other macroalgae. Considering that an increase in substrate availability can enhance the biomass of macroalgae on the reef [1], we 297 298 hypothesize that, by providing a suitable and sheltered substrate for epiphytic macroalgae, 299 Galaxaura may facilitate the diversity and abundance of macroalgae on degraded reefs. This study is merely observational and does not provide experimental evidence for the facilitation of 300 macroalgae diversity and abundance by Galaxaura. However, the abovementioned hypotheses 301 302 would be of great interest awaiting future validation.

303

#### 304 Conclusions

305 Our observations illustrated that the allelopathic and unpalatable seaweed *Galaxaura* 306 *divaricata* can become dominant on degraded reefs in shallow, sheltered environments. On 307 degraded coral reefs, the dominant macroalgae have a profound impact on coral recruitment and 308 coral recovery. Allelopathic and unpalatable macroalgae such as *Galaxaura* were proposed to 309 perpetuate their dominance on degraded reefs by chemically inhibiting the process of coral 310 recruitment. Thus, a long-term dominance by the allelopathic, nutrient-poor Galaxaura could 311 provide a negative feedback, perpetuating reef degradation. In addition, we suggest that Galaxaura provides a suitable substrate for a variety of macroalgae, potentially facilitating 312 313 macroalgae growth and abundance on degraded reefs. Several common macroepiphytes on Galaxaura have been proven to be allelopathic in competition with corals and inhibit coral larvae 314 315 settlement. Thus, degraded coral reefs dominated by Galaxaura may fail to recover, and face a 316 substantial decline in biodiversity of corals, fishes, and other associated fauna, which may have 317 far-reaching effects on coral reef ecosystem functioning and services. Macroalgal assemblages, such as the *Galaxaura*-macroepiphyte system, warrant further investigation to better understand 318 the interactions between macrophyte inhabitants and habitat forming seaweeds and their 319 ecological implications. There are 439 listed coral reef atolls on earth; among them are 335 with 320 321 open or semi-enclosed lagoons [91]. Atoll lagoons are highly productive and serve as valuable 322 and nursery habitat for marine life; however, they are most vulnerable to the effects of climate change [18,66,67]. Results from our study can be informative for the management and 323 324 conservation of lagoons and shallow, inshore coral reef ecosystems, especially for coral reefs in the South China Sea and the Pacific Ocean, where *Galaxaura* is a common seaweed. 325

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#### 336 **References**

- 1. McCook L, Jompa J, Diaz-Pulido G. Competition between corals and algae on coral reefs: a
  review of evidence and mechanisms. Coral Reefs. 2001;19: 400-417.
- 2. Tanner JE. Competition between scleractinian corals and macroalgae: an experimental
  investigation of coral growth, survival and reproduction. J Exp Mar Biol Ecol. 1995;190: 151168.
- 342 3. Done TJ. Phase shifts in coral reef communities and their ecological significance. In:
  343 Anonymous The Ecology of Mangrove and Related Ecosystems. : Springer; 1992. pp. 121-132.
- 4. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, et al. Climate change,
  human impacts, and the resilience of coral reefs. Science. 2003;301: 929-933.
- 5. Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, et al.
- Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology.
  2007;17: 360-365.
- 6. Smith JE, Brainard R, Carter A, Grillo S, Edwards C, Harris J, et al. Re-evaluating the health
- of coral reef communities: baselines and evidence for human impacts across the central Pacific.
- 351 Proc Biol Sci. 2016;283: 10.1098/rspb.2015.1985.
- 7. Hughes TP. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef.
   Science-AAAS-Weekly Paper Edition. 1994;265: 1547-1551.
- 8. McManus JW, Polsenberg JF. Coral–algal phase shifts on coral reefs: ecological and
  environmental aspects. Prog Oceanogr. 2004;60: 263-279.
- 9. Anthony K, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, et al. Operationalizing
  resilience for adaptive coral reef management under global environmental change. Global
  Change Biol. 2015;21: 48-61.
- 10. Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA. Effects of benthic algae on the
  replenishment of corals and the implications for the resilience of coral reefs. Oceanogr Mar Biol
  Annu Rev. 2008;46: 25-63.
- McCormick MI, Barry RP, Allan BJ. Algae associated with coral degradation affects risk
   assessment in coral reef fishes. Scientific reports. 2017;7: 16937.
- 12. Rasher DB, Hay ME. Seaweed allelopathy degrades the resilience and function of coral reefs.
  Communicative & integrative biology. 2010;3: 564-566.
- 13. Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME. Macroalgal terpenes function as
  allelopathic agents against reef corals. Proc Natl Acad Sci U S A. 2011;108: 17726-17731.
- 14. Bonaldo RM, Hay ME. Seaweed-coral interactions: variance in seaweed allelopathy, coral
  susceptibility, and potential effects on coral resilience. PloS one. 2014;9.

- 15. Rasher DB, Hay ME. Chemically rich seaweeds poison corals when not controlled by
   herbivores. Proc Natl Acad Sci U S A. 2010;107: 9683-9688.
- 372 16. Fong P, Paul VJ. Coral reef algae. In: Anonymous Coral reefs: an ecosystem in transition. :
  373 Springer; 2011. pp. 241-272.
- 17. Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA. Effects of benthic algae on the
  replenishment of corals and the implications for the resilience of coral reefs. Oceanogr Mar Biol
  Annu Rev. 2008;46: 25-63.
- 18. Adjeroud M, Andréfouët S, Payri C. Mass mortality of macrobenthic communities in the
  lagoon of Hikueru atoll (French Polynesia). Coral Reefs. 2001;19: 287-291.
- 19. Wei-Lung Wang, Shao-Lun Liu, Tsung-Hsuan Li. Seaweeds of Dongsha Atoll in the South
  China Sea. Kaohsiung, Taiwan: Marine National Park Headquarters; 2015.
- 20. Rasher DB, Hoey AS, Hay ME. Consumer diversity interacts with prey defenses to drive
  ecosystem function. Ecology. 2013;94: 1347-1358.
- 21. Liu S, Liao LM, Wang W. Conspecificity of two morphologically distinct calcified red algae
   from the northwest Pacific Ocean: Galaxaura pacifica and G. filamentosa (Galaxauraceae,
- Rhodophyta). Botanical Studies. 2013;54: 1.
- 22. Wang W, Liu S, Lin S. Systematics of the calcified genera of the Galaxauraceae (Nemaliales,
  Rhodophyta) with an emphasis on Taiwan species. J Phycol. 2005;41: 685-703.
- 388 23. Mantyka CS, Bellwood DR. Macroalgal grazing selectivity among herbivorous coral reef
  389 fishes. Mar Ecol Prog Ser. 2007;352: 177-185.
- 24. Mantyka C, Bellwood D. Direct evaluation of macroalgal removal by herbivorous coral reef
  fishes. Coral Reefs. 2007;26: 435-442.
- 25. Duffy JE, Hay ME. Herbivore resistance to seaweed chemical defense: the roles of mobility
  and predation risk. Ecology. 1994;75: 1304-1319.
- 26. Paul VJ, Hay ME. Seaweed susceptibility to herbivory: chemical and morphological
   correlates. 1986.
- 27. Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME. Macroalgal terpenes function as
  allelopathic agents against reef corals. Proc Natl Acad Sci U S A. 2011;108: 17726-17731.
- 28. Rasher DB, Hay ME. Competition induces allelopathy but suppresses growth and antiherbivore defence in a chemically rich seaweed. Proc Biol Sci. 2014;281: 20132615.
- 29. Dixson DL, Abrego D, Hay ME. Reef ecology. Chemically mediated behavior of recruiting
  corals and fishes: a tipping point that may limit reef recovery. Science. 2014;345: 892-897.
- 402 30. Bozec Y, Doropoulos C, Roff G, Mumby PJ. Transient Grazing and the Dynamics of an 403 Unanticipated Coral–Algal Phase Shift. Ecosystems. 2018: 1-16.

- 404 31. Fang G, Chen H, Wei Z, Wang Y, Wang X, Li C. Trends and interannual variability of the
- 405 South China Sea surface winds, surface height, and surface temperature in the recent decade.
- 406 Journal of Geophysical Research: Oceans. 2006;111.
- 407 32. Huang D, Licuanan WY, Hoeksema BW, Chen CA, Ang PO, Huang H, et al. Extraordinary
  408 diversity of reef corals in the South China Sea. Marine Biodiversity. 2015;45: 157-168.
- 33. Zuo X, Su F, Wu W, Chen Z, Shi W. Spatial and temporal variability of thermal stress to
  China's coral reefs in South China Sea. Chinese geographical science. 2015;25: 159-173.
- 411 34. Burke L, Selig E, Spalding M. Reefs at risk in Southeast Asia. 2006.
- 35. Chou Y. Dongsha Atoll Reaearch Station-A steady research platform in South China Sea. .2016.
- 414 36. Dai C. Dong-sha Atoll in the South China Sea: Past, present and future. . 2004.
- 415 37. Leis JM. Coral sea atoll lagoons: closed nurseries for the larvae of a few coral reef fishes.
- 416 Bull Mar Sci. 1994;54: 206-227.
- 38. DeCarlo TM, Cohen AL, Wong GT, Davis KA, Lohmann P, Soong K. Mass coral mortality
  under local amplification of 2° C ocean warming. Scientific Reports. 2017;7: 44586.
- 39. Fricke A, Titlyanova T, Nugues M, Bischof K. Depth-related variation in epiphytic
  communities growing on the brown alga Lobophora variegata in a Caribbean coral reef. Coral
  Reefs. 2011;30: 967-973.
- 40. Prince JS, O'Neal SW. The ecology of Sargassum pteropleuron Grunow (Phaeophyceae,
  Fucales) in the waters off South Florida: I. Growth, reproduction and population structure.
  Phycologia. 1979;18: 109-114.
- 41. Aguilar-Rosas R, Galindo AM. Ecological aspects of Sargassum muticum (Fucales,
  Phaeophyta) in Baja California, Mexico: reproductive phenology and epiphytes. 1990: 185-190.
- 427 42. Wang Y, Dai C, Chen Y. Physical and ecological processes of internal waves on an isolated
  428 reef ecosystem in the South China Sea. Geophys Res Lett. 2007;34.
- 43. Preskitt LB, Vroom PS, Smith CM. A rapid ecological assessment (REA) quantitative survey
  method for benthic algae using photoquadrats with scuba. Pac Sci. 2004;58: 201-209.
- 431 44. Liu S, Lin S, Chen P. Phylogeny, species diversity and biogeographic patterns of the genus
  432 Tricleocarpa (Galaxauraceae, Rhodophyta) from the Indo-Pacific region, including T. confertus
  433 sp. nov. from Taiwan. Eur J Phycol. 2015;50: 439-456.
- 434 45. Freshwater DW, Rueness J. Phylogenetic relationships of some European Gelidium
  435 (Gelidiales, Rhodophyta) species, based on rbcL nucleotide sequence analysis. Phycologia.
  436 1994;33: 187-194.

- 437 46. Draisma SG, Prud'Homme van Reine, Willem F, Stam WT, Olsen JL. A reassessment of 438 phylogenetic relationships within the Phaeophyceae based on rubisco large subunit and 439 ribosomal DNA sequences. J Phycol. 2001;37: 586-603.
- 47. Famà P, Wysor B, Kooistra WH, Zuccarello GC. Molecular phylogeny of the genus Caulerpa
  (Caulerpales, Chlorophyta) inferred from chloroplast tufA gene1. J Phycol. 2002;38: 1040-1050.
- 442 48. Geraldino PJL, Riosmena□Rodriguez R, Liao LM, Boo asm. Phylogenetic relationships
  443 within the genus hypnea (gigartinales, rhodophyta), with a description of h. Caespitosa sp. Nov.
  444 1. J Phycol. 2010;46: 336-345.
- 445 49. Vieira C, Camacho O, Sun Z, Fredericq S, Leliaert F, Payri C, et al. Historical biogeography
  446 of the highly diverse brown seaweed Lobophora (Dictyotales, Phaeophyceae). Mol Phylogenet
  447 Evol. 2017;110: 81-92.
- 50. Silberfeld T, Bittner L, Fernández□García C, Cruaud C, Rousseau F, de Reviers B, et al.
  Species diversity, phylogeny and large scale biogeographic patterns of the genus Padina
  (Phaeophyceae, Dictyotales). J Phycol. 2013;49: 130-142.
- 451 51. Tkachenko KS, Soong K. Dongsha Atoll: A potential thermal refuge for reef-building corals
  452 in the South China Sea. Mar Environ Res. 2017;127: 112-125.
- 453 52. Morton B. Dong-Sha Atoll, South China Sea: Ground Zero!. 2002.
- 454 53. Gomez E, Yap H. Monitoring reef condition. Coral Reef Management Handbook,
  455 UNESCO/ROSTSEA.Edt.By.Kenchington RA, Hudson BT.Jakarta. 1988: 187-195.
- 456 54. Morton B, Blackmore G. South China Sea. Mar Pollut Bull. 2001;42: 1236-1263.
- 457 55. Hughes TP, Huang H, Young MA. The wicked problem of China's disappearing coral reefs.458 Conserv Biol. 2013;27: 261-269.
- 56. Keryea Soong, Chaolun Allen Chen2. Research on the resilience of Dongsha Atoll coral reef.
  Dongsha Atoll Marine National Park. 2010;Research on the resilience of Dongsha Atoll coral
  reef: 1-205.
- 57. Li J, Lee T, Tew KS, Fang L. Changes in the coral community at Dong-Sha Atoll, South
  China Sea from 1975 to 1998. Acta Zoologica Taiwanica. 2000;11: 1-15.
- 58. Lirman D, Biber P. Seasonal dynamics of macroalgal communities of the northern Floridareef tract. Bot Mar. 2000;43: 305-314.
- 466 59. Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, et al. Doom and boom
- on a resilient reef: climate change, algal overgrowth and coral recovery. PloS one. 2009;4: e5239.
- 60. Roff G, Doropoulos C, Zupan M, Rogers A, Steneck RS, Golbuu Y, et al. Phase shift
  facilitation following cyclone disturbance on coral reefs. Oecologia. 2015;178: 1193-1203.

- 470 61. El-Manawy IM, Shafik MA. Morphological characterization of Halimeda (Lamouroux) from
   471 different biotopes on the Red Sea coral reefs of Egypt. American–Eurasian Journal of
- 472 Agriculture and Environment. 2008;3: 532-538.
- 62. Su S, Chung I, Lee T. Temporal dynamics of rocky-shore macroalgal assemblage structures
  in relation to coastal construction threats in Orchard Island (Taiwan): impacts of turbidity and
  nutrients on the blooms of Galaxaura oblongata and a red alga-sponge symbiose
  Correctediatyon/Halialona, 2000
- 476 Ceratodictyon/Haliclona. . 2009.
- 477 63. Yu-Huai Wang, Yi-Huan Li. Introduction: Marine physical environment in Dongsha Atoll.
  478 Dongsha Atoll Marine National Park. Available: http://dongsha.mr.nsysu.edu.tw/files/11-1253479 9953.php?Lang=zh-tw.
- 64. Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR. Flattening of Caribbean coral
  reefs: region-wide declines in architectural complexity. Proc Biol Sci. 2009;276: 3019-3025.
- 65. Charpy L, Dufour P, Garcia N. Particulate organic matter in sixteen Tuamotu atoll lagoons
  (French Polynesia). Mar Ecol Prog Ser. 1997: 55-65.
- 66. Andréfouët S, Dutheil C, Menkes CE, Bador M, Lengaigne M. Mass mortality events in atoll
  lagoons: environmental control and increased future vulnerability. Global Change Biol. 2015;21:
  195-205.
- 487 67. Altieri AH, Gedan KB. Climate change and dead zones. Global Change Biol. 2015;21: 1395488 1406.
- 68. Gajdzik L, DeCarlo TM. The perfect calm: Reoccurring mass die-offs on a remote coral atoll.
  Matters. 2017;3: e201707000003.
- 69. Swierts T, Vermeij MJ. Competitive interactions between corals and turf algae depend oncoral colony form. PeerJ. 2016;4: e1984.
- 493 70. Cheal A, MacNeil MA, Cripps E, Emslie M, Jonker M, Schaffelke B, et al. Coral–macroalgal
- 494 phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on495 the Great Barrier Reef. Coral Reefs. 2010;29: 1005-1015.
- 496 71. Rasher DB, Engel S, Bonito V, Fraser GJ, Montoya JP, Hay ME. Effects of herbivory,
  497 nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. Oecologia.
  498 2012;169: 187-198.
- 499 72. Wylie CR, Paul VJ. Feeding preferences of the surgeonfish Zebrasoma flavescens in relation
  500 to chemical defenses of tropical algae. Mar Ecol Prog Ser. 1988: 23-32.
- 501 73. Steneck R. Herbivory on coral reefs: a synthesis. . 1988;1: 37-49.
- 502 74. Rasher DB, Hoey AS, Hay ME. Consumer diversity interacts with prey defenses to drive 503 ecosystem function. Ecology. 2013;94: 1347-1358.

504 75. Brooker RM, Brandl SJ, Dixson DL. Cryptic effects of habitat declines: coral-associated
 505 fishes avoid coral-seaweed interactions due to visual and chemical cues. Scientific Reports.

- 506 2016;6: 18842.
- 507 76. Brooker RM, Sih TL, Dixson DL. Contact with seaweed alters prey selectivity in a coral-508 feeding reef fish. Mar Ecol Prog Ser. 2017;580: 239-244.
- 509 77. Morrow KM, Bromhall K, Motti CA, Munn CB, Bourne DG. Allelochemicals Produced by
- Brown Macroalgae of the Lobophora Genus Are Active against Coral Larvae and Associated
  Bacteria, Supporting Pathogenic Shifts to Vibrio Dominance. Appl Environ Microbiol. 2016;83:
  10.1128/AEM.02391-16.
- 78. Vieira C, Thomas OP, Culioli G, Genta-Jouve G, Houlbreque F, Gaubert J, et al. Allelopathic
  interactions between the brown algal genus Lobophora (Dictyotales, Phaeophyceae) and
  scleractinian corals. Scientific reports. 2016;6: 18637.
- 79. Barott KL, Rodriguez-Mueller B, Youle M, Marhaver KL, Vermeij MJ, Smith JE, et al.
  Microbial to reef scale interactions between the reef-building coral Montastraea annularis and
  benthic algae. Proc Biol Sci. 2012;279: 1655-1664.
- 80. Hay ME. Associational plant defenses and the maintenance of species diversity: turning
  competitors into accomplices. Am Nat. 1986;128: 617-641.
- 81. Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS. Inhibition of
  coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser. 2006;323: 107-117.
- 523 82. Jorissen H, Skinner C, Osinga R, de Beer D, Nugues MM. Evidence for water-mediated
  524 mechanisms in coral-algal interactions. Proc Biol Sci. 2016;283: 10.1098/rspb.2016.1137.
- 83. Vieira C, Payri C, De Clerck O. Overgrowth and killing of corals by the brown alga
  Lobophora hederacea (Dictyotales, Phaeophyceae) on healthy reefs in New Caledonia: a new
  case of the epizoism syndrome. Phycol Res. 2015;63: 152-153.
- 528 84. Paul VJ, Hay ME. Seaweed susceptibility to herbivory: chemical and morphological 529 correlates. 1986.
- 85. Solandt J, Campbell AC. Macroalgal feeding characteristics of the sea urchin Diadema
  antillarum Philippi at Discovery Bay, Jamaica. Caribb J Sci. 2001;37: 227-238.
- 86. Loffler Z, Bellwood D, Hoey A. Associations among coral reef macroalgae influence feeding
  by herbivorous fishes. Coral Reefs. 2015;34: 51-55.
- 87. Hay ME, Fenical W. Marine plant-herbivore interactions: the ecology of chemical defense.
  Annu Rev Ecol Syst. 1988;19: 111-145.
- 88. Paul VJ, Nelson SG, Sanger HR. Feeding preferences of adult and juvenile rabbitfish Siganus
  argenteus in relation to chemical defenses of tropical seaweeds. Mar Ecol Prog Ser. 1990: 23-34.
- 89. Wylie CR, Paul VJ. Feeding preferences of the surgeonfish Zebrasoma flavescens in relation
  to chemical defenses of tropical algae. Mar Ecol Prog Ser. 1988: 23-32.

- 540 90. Thomsen MS, Hildebrand T, South PM, Foster T, Siciliano A, Oldach E, et al. A sixth level
- habitat cascade increases biodiversity in an intertidal estuary. Ecology and evolution. 2016;6:8291-8303.
- 543 91. Goldberg W. Atolls of the world: revisiting the original checklist. Atoll Res Bull. 2016;610.

544

# 546 Tables

# 547 Table 1. Cover<sup>a</sup> (%) of live coral, macroalgae (MA), crustose coralline algae (CCA), and

	Location	Coral	MA	CCA	Other <sup>549</sup>
1	North	40 <u>+</u> 24	35 <u>+</u> 23	1.93 <u>+</u> 2.18	$23 \pm 25^{50}$
2	North	22 <u>+</u> 25	13 <u>+</u> 12	2.57 <u>+</u> 5.58	$63 \pm 3251$
3	North	24 <u>+</u> 22	29 <u>+</u> 23	1.47 <u>+</u> 2.39	$46 \pm 24_{53}$
4	Northeast	10 <u>+</u> 15	20 <u>+</u> 16	1.37 <u>+</u> 2.42	$69 \pm 2254$
5	Northeast	17 <u>+</u> 19	29 <u>+</u> 25	1.62 <u>+</u> 1.91	$53 \pm 3255$
6	Northeast	24 <u>+</u> 20	19 <u>+</u> 15	2.15 <u>+</u> 3.01	55 <u>+</u> 2 <b>5</b> 56
7	Southeast	14 <u>+</u> 17	58 <u>+</u> 24	2.79 <u>+</u> 2.59	25 <u>+</u> 2 <b>2</b> 57
8	Southeast	29 <u>+</u> 29	20 <u>+</u> 14	2.07 <u>+</u> 2.15	50 <u>+</u> 3558
9	Southeast	5 <u>+</u> 14	41 <u>+</u> 25	$0.84 \pm 0.89$	53 <u>+</u> 2559
10	Center	10 <u>+</u> 13	43 <u>+</u> 27	3.33 <u>+</u> 3.07	43 <u>+</u> 2 <b>5</b> 60
11	Center	24 <u>+</u> 27	18 <u>+</u> 19	1.07 <u>+</u> 1.27	$56 \pm 2561$
12	West	11 <u>+</u> 19	42 <u>+</u> 24	2.46 <u>+</u> 2.94	$45 \pm 26^{62}$
13	West	43 <u>+</u> 25	22 <u>+</u> 18	3.00 <u>+</u> 3.63	$32 \pm 29^{563}_{64}$
	mean <u>+</u> SE	21 <u>+</u> 3	30 <u>+</u> 4	2.05 <u>+</u> 0.21	$47 \pm 4_{565}$

566 <sup>a</sup>Data are mean (%)  $\pm$  SD of 90 replicate quadrats.

567 <sup>b</sup> "Other substrate" constituted mainly dead coral, larger rocks covered with sediments and sparse

turf algae, rubbles and sand.

# 570 Table 2. Cover (%) of *Galaxaura divaricata* on 13 patch reefs in the lagoon of Dongsha Atoll,

# 571 South China Sea.

Site	Lagation	Pate	Cover nemls	
Sile	Location	<b>Top (1-5 m)</b>	Slope (5-10 m)	- Cover ralik
1	North	0.02	0.02	very low
2	North	0	0	very low
3	North	0.27	0.31	very low
4	Northeast	1.52	1.4	very low - low
5	Northeast	5.69	3.37	low - moderate
6	Northeast	0.79	0.21	very low
7	Southeast	0.02	15.86	moderate
8	Southeast	0.17	4.31	very low - low
9	Southeast	41.87	40.87	high
10	South	0	0	very low
11	Center	0.46	0.02	very low
12	West	0	0	very low
13	West	0	0	very low

<sup>a</sup>Data are mean (%) of 45 replicate quadrats for reef top and reef slope respectively.

### 574 Table 3. Relative abundance (%) of epiphytic macroalgae on Galaxaura divaricata from a

### 575 degraded patch reef.

Epiphyte taxon	Phylum	Relative abundance
Acanthophora spicifera <sup>a</sup>	Red	3
Ceramium dawsonii (MH048927) <sup>b</sup>	Red	43
Coelothrix irregularis (MH048928)	Red	87
Dichotomaria obtusata	Red	3
Gelidiales	Red	27
Gracilaria spp.	Red	7
<i>Hypnea caespitosa</i> (мн048929, мн048930, мн048931)	Red	100
<i>Hypnea</i> sp. (MH048932)	Red	30
Laurencia dendroidea	Red	13
Laurencia spp.	Red	20
Dictyota bartayresiana	Brown	30
Dictyota spp.	Brown	13
<i>Lobophora</i> sp28 <sup>c</sup> (MH048934, MH048935, MH048936, MH048937)	Brown	57
Padina $sp5^{d}_{(MH048933)}$	Brown	53
Sargassum spp.	Brown	3
Boodlea composita	Green	20
Caulerpa chemnitzia (MH048959)	Green	27
Derbesia marina	Green	37
Phyllodictyon anastomosans	Green	10
Valonia ventricosa	Green	10
Cyanobacteria (filamentous > 1cm)	Cyanobacteria	17

576 Macroscopic epiphytes were identified from 30 thalli of *G. divaricata* from site 7 at 5 m depth.

<sup>a</sup>Identification of species and taxonomic groups according to [19].

<sup>b</sup>GenBank number in parentheses based on species identifications through DNA barcoding.

579 <sup>c</sup>Denomination according to [49].

<sup>d</sup>Denomination according to [50].

### 582 Figure legends

Fig 1. Study site. A) Geographical location of Dongsha Atoll in the northern South China Sea. B)
Lagoon patch reef sites surveyed in this study.

**Fig 2.** *Galaxaura divaricata* **overgrowth of corals.** A-B) *Galaxaura* has overgrown a degraded patch reef in the southeast lagoon of Dongsha Atoll for at last 4 years (site 9, 3-5 m depth). C) The holdfast of *G. divaricata* penetrates into a branching Porites coral (*Porites cylindrica*), creating small holes (inlet). D) Coral (*Porites solida*) tissue bleaching (arrows) following direct contact with *Galaxaura*, allelopathic chemicals produced by the alga.

590 Fig 3. Long-lasting bloom of Galaxaura divaricata on site 7 in the southeast lagoon of

Dongsha Atoll. The percent cover of *G. divaricata* did not change significantly among surveys
conducted over a period of 17 months (P-value > 0.05; Two-way ANOVA). Data are mean + SE
of 45 replicate quadrats.

Fig 4. Examples showing epiphytic macroalgae that frequently grow on *Galaxaura divaricata*. A) *Valonia ventricosa*, B) *Caulerpa chemnitzia*, C) *Dictyota* sp., D) *Lobophora* sp28
[49] (arrow head), and *Hypnea caespitosa* (arrow).

Fig 5. Coral overgrowth by *Lobophora* sp28. A) Example showing *Lobophora* sp28 growing
on *Galaxaura divaricata* (arrows), and in contact with coral (*Porites solida*) (arrowheads). B)
Coral overgrowth (*Porites cylindrica* in this case) by *Lobophora* sp28 is wide spread in the
shallow lagoon of Dongsha Atoll.

601

# 603 Supplementary information

### 604 S1 Table. GPS coordinates of patch reef survey sites in the lagoon of Dongsha Atoll, South

### 605 China Sea (Taiwan).

Site	Latitude	Longitude
1	20°44'26.28"	116°47'8.879"
2	20°43'31.62"	116°47'52.679"
3	20°42'16.14"	116°48'27.419"
4	20°44'20.52"	116°51'35.699"
5	20°42'29.88"	116°52'54.599"
6	20°42'6.72"	116°50'53.279"
7	20°38'24''	116°50'20.999"
8	20°38'3.12"	116°49'30.479"
9	20°36'52.86"	116°49'24.179"
10	20°36'53.4"	116°46'2.399"
11	20°39'52.2"	116°46'32.159"
12	20°41'49.2"	116°44'45.659"
13	20°42'12.36"	116°44'14.639"

606

# 608 S2 Table. Information and Genbank numbers of macroalgae samples used for DNA

# 609 barcoding in this study.

Species	Phylum	Voucher#	Date	Site	Area	Substrate	Marker	GenBank#
Ceramium dawsonii	Red	KO208	Oct-16	7	slope	G. divaricata	rbcL	MH048927
Coelothrix irregularis	Red	K0206	Oct-16	7	slope	G. divaricata	rbcL	MH048928
Hypnea caespitosa	Red	K0204	Oct-16	7	slope	G. divaricata	<i>rbc</i> L	MH048929
Hypnea caespitosa	Red	K0203	Oct-16	7	slope	G. divaricata	<i>rbc</i> L	MH048930
Hypnea caespitosa	Red	SD17120	Aug-17	7	slope	G. divaricata	<i>rbc</i> L	MH048931
<i>Hypnea</i> sp.	Red	K0205	Oct-16	7	slope	G. divaricata	<i>rbc</i> L	MH048932
Lobophora sp28 <sup>a</sup>	Brown	SD17023	Aug-17	7	slope	G. divaricata	<i>rbc</i> L	MH048934
Lobophora sp28	Brown	SD17021	Aug-17	7	slope	G. divaricata	<i>rbc</i> L	MH048935
Lobophora sp28	Brown	SD17019	Aug-17	7	slope	G. divaricata	<i>rbc</i> L	MH048936
Lobophora sp28	Brown	SD17017	Aug-17	7	slope	G. divaricata	<i>rbc</i> L	MH048937
Lobophora sp28	Brown	K0173	Apr-16	7	slope	Coral	<i>rbc</i> L	MH048940
Lobophora sp28	Brown	SD17058	Aug-17	9	slope	Coral	<i>rbc</i> L	MH048941
Padina sp5 <sup>b</sup>	Brown	SD17114	Aug-17	7	slope	G. divaricata	<i>rbc</i> L	MH048933
Caulerpa chemnitzia	Green	SD17117	Aug-17	7	slope	G. divaricata	tufA	MH048959

610 <sup>a</sup>Denomination according to [49].

611 <sup>b</sup>Denomination according to [50].

# 613 S3 Table. Information and Genbank numbers of Galaxaura divaricata samples from

# various locations in the lagoon of Dongsha Atoll that were used for DNA barcoding in this

#### 615 study.

Species	Voucher#	Date	Site	Area	Substrate	Thallus size	Marker	GenBank#
G. divaricata	K0210	Apr-16	7	slope	rock	medium	rbcL	MH048946
G. divaricata	R90B12	Feb-14	9	top	rock	large	<i>rbc</i> L	MH048942
G. divaricata	SD17048	Aug-17	9	slope	rubble	large	<i>rbc</i> L	MH048957
G. divaricata	SD17098	Aug-17	6	top	rock	small	<i>rbc</i> L	MH048943
G. divaricata	SD17099	Aug-17	1	top	rock	small	<i>rbc</i> L	MH048956
G. divaricata	SD17100	Aug-17	5	top	rock	small	<i>rbc</i> L	MH048955
G. divaricata	SD17101	Aug-17	5	top	rock	small	<i>rbc</i> L	MH048958
G. divaricata	SD17102	Aug-17	5	slope	rock	medium	<i>rbc</i> L	MH048954
G. divaricata	SD17103	Aug-17	1	slope	rock	small	<i>rbc</i> L	MH048953
G. divaricata	SD17104	Aug-17	6	slope	rock	medium	<i>rbc</i> L	MH048952
G. divaricata	SD17105	Aug-17	5	slope	rock	medium	<i>rbc</i> L	MH048951
G. divaricata	SD17106	Aug-17	6	slope	rock	small	<i>rbc</i> L	MH048950
G. divaricata	SD17107	Aug-17	6	slope	rock	small	<i>rbc</i> L	MH048944
G. divaricata	SD17110	Aug-17	6	top	coral	medium	<i>rbc</i> L	MH048949
G. divaricata	SD17112	Aug-17	4	slope	rock	medium	<i>rbc</i> L	MH048948
G. divaricata	SD17113	Aug-17	4	slope	rock	small	<i>rbc</i> L	MH048947

616

Macrobenthic fauna	Count	Density (individual/ 100 m <sup>2</sup> )
Diadema savignyi	3	0.03
Diadema setosum	1	0.01
Echinometra mathaei	126	1.26
Echinothrix calamaris	3	0.03
Tripneustes gratilla	4	0.04
Culcita novaeguineae	54	0.54
Echinaster luzonicus	2	0.02
Fromia spp.	8	0.08
Linckia multifora	15	0.15
Holothuria	0	0
Cypraea tigris	3	0.03
Giant clam	34	0.34
Lambis spp.	3	0.03
Lobster	0	0
Linckia multifora Holothuria Cypraea tigris Giant clam Lambis spp. Lobster	15 0 3 34 3 0	0.15 0 0.03 0.34 0.03 0

## 618 S4 Table. Paucity of macrobenthic invertebrates in the lagoon of Dongsha Atoll.

Data derived from a belt transect survey of 13 patch reefs and seven seagrass beds (10,000 m<sup>2</sup>)

total area surveyed) across the lagoon of Dongsha Atoll in September 2017.

- 622 S1 Fig. Various sizes and thallus shapes of *Galaxaura divaricata* from different locations in
- 623 **the lagoon of Dongsha Atoll**. A-B) Small, ball-shaped thalli, and C-D) small, slender thalli were
- dominant on patch reefs in the north and northeast lagoon. E) Medium, ball-shaped thalli, and F)
- large carpet-like thalli were exclusively present in the southeast section of the lagoon.
- 626 S2 Fig. Coral overgrowth by *Lobophora* sp28. A) Coral overgrowth (*Porites cylindrica* in this
- 627 case) by *Lobophora* sp28 is a wide spread in the lagoon of Dongsha Atoll. B) The same coral
- showing dead tissue (arrow) after removal of the algae.









633 Fig. 2.





635 Fig. 3.



- **Fig. 4.**



- 640
- 641 Fig. 5.



**Fig. S1**.



646

647 Fig. S2.