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1 **Canopy interactions and physical stress gradients in subtidal communities**

2

3 Scott Bennett^{1,a*}, Thomas Wernberg¹, Thibaut de Bettignies¹, Gary A. Kendrick¹, Robert J.
4 Anderson^{2,3}, John J. Bolton³, Kirsten Rodgers⁴, Nick Shears⁴, Jean-Charles Leclerc^{5,6},
5 Laurent Lévêque^{5,7}, Dominique Davoult^{5,6} and Hartvig C. Christie⁸

6

7 ¹ School of Plant Biology & UWA Oceans Institute, University of Western Australia, 39
8 Fairway, Crawley 6009, WA, Australia.

9 ² Seaweed Research Unit, Department of Agriculture, forestry and Fisheries, Pvt Bag X2,
10 Roggebaai 8012, South Africa

11 ³ Department of Biological Sciences and Marine Research Institute, University of Cape
12 Town, Rondebosch 7701, South Africa

13 ⁴ Leigh Marine Laboratory, Institute of Marine Science, University of Auckland, PO Box
14 349, Warkworth 0941, New Zealand

15 ⁵ Sorbonne Universités, UPMC Univ Paris 6, Station Biologique, Place Georges Teissier,
16 F.29680 Roscoff, France

17 ⁶ CNRS, UMR 7144, Station Biologique, Place Georges Teissier, F.29680 Roscoff, France

18 ⁷ CNRS, FR 2424, Station Biologique, Place Georges Teissier, F. 29680 Roscoff, France

19 ⁸ Section for Marine Biology, Norwegian Institute for Water Research, Oslo, Norway

20 ^a Present address: Department of Environment and Agriculture, Curtin University, Bentley,
21 WA 6102, Australia

22

23 *Email:* scott.bennett1@curtin.edu.au, thomas.wernberg@uwa.edu.au,
24 thibaut.debettignies@uwa.edu.au, gary.kendrick@uwa.edu.au, robert.anderson@uct.ac.za,
25 john.bolton@uct.ac.za, k.rodgers@auckland.ac.nz, n.shears@auckland.ac.nz, jcleclerc@sb-
26 roscoff.fr, leveque@sb-roscoff.fr, dominique.davoult@sb-roscoff.fr, hartvig.christie@niva.no

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34 *Corresponding author:* Scott Bennett, Present address: Department of Environment and
35 Agriculture, Curtin University, Bentley, WA 6102, Australia P: +614 00434898.

36 E:scott.bennett1@curtin.edu.au

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38 design. All authors help with data collection and logistics. S.B wrote the manuscript with
39 contributions from all authors.

40

41 **Abstract:**

42 Species interactions are integral drivers of community structure and can change from
43 competitive to facilitative with increasing environmental stress. In subtidal marine
44 ecosystems, however, interactions along physical stress gradients have seldom been tested.
45 We observed seaweed canopy interactions across depth and latitudinal gradients to test
46 whether light and temperature stress structured interaction patterns. We also quantified inter-
47 specific and intra-specific interactions among nine subtidal canopy seaweed species across
48 three continents to examine the general nature of interactions in subtidal systems under low
49 consumer pressure. We reveal that positive and neutral interactions are widespread
50 throughout global seaweed communities and the nature of interactions can change from
51 competitive to facilitative with increasing light stress in shallow marine systems. These
52 findings provide support for the stress gradient hypothesis within subtidal seaweed
53 communities and highlight the importance of canopy interactions for the maintenance of
54 subtidal marine habitats experiencing environmental stress.

55

56 **Introduction:**

57 Species interactions can be important drivers of community structure and function (Kikvidze
58 *et al.* 2005) from local to global scales (Cavieres *et al.* 2014) and have the capacity to buffer
59 ecosystems against stressful environmental conditions that could otherwise lead to habitat
60 loss or fragmentation (Bruno *et al.* 2003). Species interactions can change along physical and
61 biotic stress gradients from competitive in benign conditions to become increasingly
62 facilitative under stressful conditions, as the benefits of stress amelioration from neighbours
63 begins to outweigh the costs of living together (SGH: Stress Gradient Hypothesis, Bertness &
64 Callaway 1994). For terrestrial plants, the SGH has received strong empirical support within

65 a wide range of community types across physical, resource and biotic stress gradients (He *et*
66 *al.* 2013). Among subtidal marine plants (herein considered as seaweeds and seagrasses), by
67 contrast, the nature of species interactions in response to changes to the physical environment
68 are less well resolved (Bulleri 2009).

69 The physical environment has long been recognised as a strong driver of species interactions
70 in subtidal ecosystems (Kitching 1941; Reed & Foster 1984; Witman 1987; Dayton *et al.*
71 1999), however, few studies have examined whether the nature of species interactions change
72 predictably in response to physical stress gradients (Bulleri 2009). Among the few studies
73 that have examined physical gradients in subtidal systems, changes to abiotic conditions
74 appear to have strong influence on the nature of interactions (Wernberg *et al.* 2010; Bulleri *et*
75 *al.* 2011; Bennett & Wernberg 2014). Bulleri *et al.* (2011), for example demonstrated that the
76 nature of interactions between tube building gastropods and seaweed was influenced by both
77 physical (sediment deposition) and biotic (grazer density) gradients. Wernberg *et al.* (2010)
78 and Bennett and Wernberg (2014), both demonstrated that canopy-recruit interactions can
79 become increasingly positive or remain positive toward warmer latitudes along a latitudinal
80 climatic gradient, although the exact role of the canopy in modifying the physical
81 environment in these two studies remains unclear.

82 To date, positive species interactions in subtidal communities have been primarily reported in
83 response to high consumer pressure (Bulleri 2009) whereby chemical defences (Hay 1986;
84 Stachowicz & Hay 1999), mechanical defences (Anderson *et al.* 1997) and physical barriers
85 (Bennett *et al.* 2010) reduce the incidence of predation on beneficiary species. Other
86 important drivers of positive interactions in subtidal communities include demographic
87 constraints, (i.e. Allee effects), whereby population fitness displays positive density

88 dependence (Berec *et al.* 2007) and resource availability, whereby benefactors can increase
89 the nutrient availability for beneficiary species (Peterson & Heck 2001).

90

91 Physical gradients are prevalent in the subtidal, most notably from sunlight attenuation with
92 depth (Duarte 1991), water velocity which decreases with depth and increases with wave
93 exposure (Siddon & Witman 2003), and temperature which usually decreases with increasing
94 depth and latitude (Smale & Wernberg 2009). While light is often considered to be a limiting
95 resource underwater, excessive light can become stressful for organisms (Altamirano *et al.*
96 2004) and therefore any modification of these conditions could promote facilitation. Within
97 the photic zone, seaweed canopies are dominant habitat formers of benthic marine
98 ecosystems globally and dramatically alter the physical environment for organisms living
99 within them. Light levels are altered by all canopy types ranging from the surface canopies of
100 the giant kelp, *Macrocystis pyrifera* (Reed & Foster 1984) to subsurface canopies of species
101 such as *Ecklonia radiata* (Wernberg *et al.* 2005). Water velocities can also be modified by
102 seaweed canopies, reducing the amount of drag an organism experiences by over 80% in
103 dense canopies (Johnson 2001). Under low flow velocities, individuals can grow larger, than
104 in high flow areas (de Bettignies *et al.* 2013a) thereby providing a mechanism for subtidal
105 canopies to promote facilitation in high-flow environments. Temperature conditions in
106 contrast, while critical to the distribution and abundance of seaweeds (Lüning 1984) are
107 assumed to be largely unaffected by subtidal canopy conditions due to the high mixing of
108 seawater (Kordas *et al.* 2011). Nevertheless, dense shallow water canopies have been
109 observed to reduce ambient temperatures, suggesting that temperature stress amelioration
110 could occur in high density canopies (Critchley *et al.* 1990).

111 Here we test the nature of seaweed canopy interactions in subtidal marine ecosystems in
112 response to depth and latitudinal gradients in light and temperature stress respectively. We
113 also examine general patterns in the nature of canopy interactions under low consumer
114 pressure in the subtidal by observing inter-specific and intra-specific interactions among nine
115 dominant canopy formers across three continents. This study advances our understanding of
116 how subtidal canopies function under low consumer pressure and in response to increasing
117 abiotic stress. In doing so, we broaden the generality of the stress gradient hypothesis to
118 incorporate subtidal light climates and reveal widespread importance of positive canopy
119 interactions in subtidal communities.

120

121 **Methods:**

122 *Depth experiment:*

123 Intra-specific interactions within kelp, *Ecklonia radiata*, canopies were measured along a
124 depth gradient in Hamelin Bay, south-western Australia (34°S, 115°E), during Austral
125 summer, December 2013 to February 2014. Nine reefs (sites) each separated by at least 1.8
126 km, were chosen along a depth gradient (3, 5, 6, 9, 11, 12, 16, 18 and 19 m depth). Reefs in
127 the region are exposed to relatively small tidal fluctuations (<0.5 m), meaning kelps can live
128 on very shallow reefs and experience almost full sunlight conditions while remaining
129 constantly submerged. At the other end of the spectrum, kelps in south-western Australia live
130 down to 50-60 m depth where they no longer form canopies but grow as solitary individuals,
131 presumably due the limiting light availability (Marzinelli *et al.* 2015). Reefs used in our study
132 were in the upper third of kelp depth distribution where light is not a limiting resource (Staeher
133 & Wernberg 2009), but could form a ‘non-resource’ stress gradient from benign deeper reefs
134 (16-20 m) to stressful high-light shallow reefs (2-5 m). All reefs had relatively flat, ‘simple’

135 topography and were dominated by dense, closed *Ecklonia radiata* canopies (8-12
136 sporophytes m⁻², following Bennett & Wernberg 2014). Within each site, 30 adult kelps were
137 haphazardly selected and tagged around the stipe. Of those, 15 individuals were left to grow
138 inside the unaltered canopy and 15 had all surrounding neighbours removed within a 1 m
139 radius of the tagged kelp. Experimental setup was conducted by divers on SCUBA.
140 Kelp growth was measured over two months using the hole-punch method (de Bettignies *et*
141 *al.* 2013b). Two holes were punched in the centre of the primary lamina, 5 cm and 10 cm
142 above the junction between the stipe and the primary lamina. Thallus extension after the two
143 months was quantified in the laboratory by measuring the distance between the two holes and
144 the stipe-lamina-junction and subtracting the initial 10 cm distance. The kelp was then sliced
145 into segments at 5 cm intervals along the length of the primary lamina, with each segment
146 incorporating both primary lamina and lateral (secondary blades coming off the primary
147 lamina) tissue. The segment with the greatest biomass in the first 30 cm above the stipe-
148 lamina-junction was used to calculate biomass accumulation (BA, or kelp growth) as $BA =$
149 $L_{ext} \cdot W_F / 5T$ where L_{ext} is lamina extension (cm), W_F = fresh weight (g) of the heaviest
150 segment and T is the number of growth days between punching the holes and collecting the
151 kelp (de Bettignies *et al.* 2013b).

152 Differences in biomass accumulation patterns between plants with and without neighbours
153 were converted to a Relative Interaction Index (RII, Armas *et al.* 2004) to compare the nature
154 and intensity of interactions among sites of different depths. RII was calculated as $RII =$
155 $(BA_w - BA_o) / (BA_w + BA_o)$, where BA_o = biomass accumulation (g.FW.d⁻¹) without neighbours
156 and BA_w = biomass accumulation with neighbours. The RII ranges between -1 and 1 and
157 presents a continuous scale for competitive ($-1 \leq x < 0$) and facilitative ($0 \leq x < 1$) interactions
158 that is symmetrical around zero. Patterns in RII along the depth gradient were analysed by
159 comparing a set of polynomial models of degree = 1, 2, 3 using Akaike's Information

160 Criterion (AIC). Linear regression (AIC = 55.5) and second order polynomial (AIC = 54.8)
161 displayed the best relationship to the data. Linear results are presented as they provided the
162 best fit of the data and because AIC values differ by less than 2 units between the models
163 (Anderson 2008).

164 Kelp tissue 'health' was measured by quantifying the cover of epiphytic algal growth on the
165 lower and upper laterals of each kelp. Epiphyte cover was quantified by haphazardly
166 selecting four lower and four upper laterals from each replicate kelp and photographing them.
167 Each image was then analysed by randomly allocating points to the image and counting the
168 presence/absence of epiphytes under 15 random points on each lateral ($n = 120$ points per
169 kelp) using CPCe V4.1 software (Kohler & Gill 2006). Epiphyte counts on each lateral were
170 then used to calculate the mean percent epiphyte cover per kelp.

171 At the end of the experimental period the physiological acclimation of the depth and canopy
172 treatments to experimental conditions were measured by quantifying oxygen evolution of
173 kelps using photorespirometry chambers *in situ* under their respective experimental settings
174 (following Rodgers *et al.* In press). Photosynthetic rates were measured at ambient light
175 levels *in situ*, and respiration rates were measured in the dark. A detailed description of the
176 methods can be found in Appendix S1(a).

177 Temperature ($^{\circ}\text{C}$) and illuminance (Lux) was measured *in situ* at 15 min intervals in each site
178 throughout the course of the experiment using data loggers (onset HOBO[®] data
179 loggers Pendant Temp-Light, Onset Computer Corporation). Hobo pendant loggers provide
180 light intensity measurements that accurately reflect photosynthetically active radiation (PAR)
181 measurements taken in underwater marine environments, and enable cost effective
182 deployment across multiple (18) experimental treatments (Long *et al.* 2012). At each site, one
183 logger was attached to a dive weight and placed within the kelp canopy to record canopy

184 conditions. A second logger was placed in the open adjacent to the canopy-free treatments.
185 Daily minimum, maximum and mean temperatures for each site were extracted and averaged
186 among days for the duration of the experiment to compare between depth and canopy
187 treatments. For light, mean, maximum, and the standard deviation of light levels between the
188 hours of 0800 – 1600 were extracted for the first 14 days of the experiment. Fouling on the
189 logger meant that recordings taken after this time were not representative of ambient
190 conditions. Daily values were averaged among the first 14 days to compare among depth and
191 canopy treatments. Variation in water velocities among sites was measured using
192 gravitational data loggers (HOBO Pendant G, Onset Computer Corporation, Bourne, MA,
193 USA) mounted on a hemispherical float (110 mm diameter) and attached to a 750 mm length
194 of nylon rope (12 mm thickness) which was anchored to the bottom (Evans & Abdo 2010).
195 The accelerometer was laid flat on the float such that only 2 channels were used (x,y) to
196 account for horizontal acceleration (*c.f.* H2O motion V2 design; Evans & Abdo 2010). The
197 logger was set to record the acceleration (ms^{-2}) at 2 minute intervals over the duration of the
198 experiment. At each site the relative water movement (WM) was expressed as the mean of
199 the 95th percentile WM over the duration of the experiment.

200 Kelp growth, mean epiphyte cover, temperature and illuminance were compared between
201 canopy treatments along the depth gradient using an Analysis of Covariance (ANCOVA)
202 with ‘canopy-treatment’ as a categorical grouping factor (two levels: canopy and canopy-
203 free) and depth as a continuous covariate. Epiphyte cover data was arcsin-square root
204 transformed and illuminance data was log10 transformed to address the non-normality and
205 heteroscedasticity of the data, after examining the residual vs fitted value plot and the Q-Q
206 plot. Growth and temperature data met assumptions of normality and homoscedasticity and
207 no transformations took place.

208

209 *Latitudinal experiment:*

210 Latitudinal comparisons of intra-specific interactions took place along a ~2°C temperature
211 gradient in south-western Australia, on two occasions during Austral spring (August –
212 October 2012) and summer (January - March 2013), representing the periods of highest kelp
213 growth rates and temperature stress respectively (de Bettignies *et al.* 2013b). Interaction
214 experiments were conducted at nine sites (9-12m depth) across three locations, Hamelin Bay
215 (34°S), Marmion (32°S) and Jurien Bay (30°S), spanning the warmest third of *E. radiata*'s
216 latitudinal distribution in Australia (~43°S - 29°S). This north-south trending coastline is
217 characterised by the warm poleward flowing Leeuwin Current, consistent limestone habitat,
218 low nutrient conditions and a stable ocean climate gradient (Smale & Wernberg 2009).
219 Within each site, kelp growth, RII and environmental measurements in canopy and canopy-
220 free treatments were recorded as described for the depth experiment. Tissue health was
221 quantified for the summer sampling period only, by estimating the percentage cover on 4
222 replicate laterals from each of the lower, middle and upper sections of each kelp. Patterns in
223 RII between spring and summer, across the latitudinal gradient were examined with an
224 ANCOVA, using time as a fixed factor (two levels: spring and summer) and latitude as a
225 continuous covariate. ANCOVA assumptions were checked as described for the depth
226 experiment and no transformation took place. Mean epiphyte cover on kelps, temperature and
227 illuminance was compared between canopy treatments along the latitudinal gradient using an
228 ANCOVA with 'canopy-treatment' as a categorical grouping factor (two levels: canopy and
229 canopy-free) and latitude as a continuous covariate. Epiphyte cover data was arcsin-square
230 root transformed and illuminance data was square-root transformed to address the non-
231 normality and heteroscedasticity of the data.

232

233 *Interactions among different canopy types*

234 The nature of inter-specific and intra-specific interactions among different subtidal canopy
235 species experiencing low consumer pressure were tested for nine dominant canopy species (4
236 kelps and 5 fucoids) from Australia, South Africa, Norway and France (Table S1). Sites
237 varied between regions ranging from shallow (3 – 4 m) tropical *Sargassum* beds in Australia,
238 to deeper (10 – 12 m) cool temperate kelp forests in Norway (Table S1). Sites were selected
239 that had dense closed seaweed canopies (Table S2) and low apparent herbivore consumer
240 pressure. Herbivore pressure was measured during the canopy growth experiments by
241 comparing consumption rates between canopy and canopy-free treatments (kelp) and caged
242 controls (*Sargassum* only, Appendix S1b, Fig. S1). Intra-specific interaction strength was
243 tested by haphazardly selecting and tagging 30 plants, of which 15 individuals were left to
244 grow inside the canopy and 15 had the surrounding canopy removed, by clearing a circular
245 area around the tagged seaweed as described for the depth experiment. Clearing sizes varied
246 in accordance with the size of the seaweed, ensuring that no contact or shading by the canopy
247 occurred. Inter-specific interactions using *Laminaria pallida* and *Sargassum decurrens* as
248 beneficiary species were tested using the same methodology described for intra-specific
249 interactions. Inter-specific interactions using *Ecklonia radiata*, *Scytothalia dorycarpa*,
250 *Arthrophyucus* sp. and temperate *Sargassum* sp. as beneficiaries were conducted by
251 translocating individuals into the desired canopy and canopy-free treatments due to low
252 natural densities at the study sites. All translocations occurred within the same site and depth
253 contour from which they were collected, without removing the seaweed from the water
254 (Appendix S1c). For both inter-specific and intra-specific interactions kelp (*Ecklonia radiata*,
255 *E. maxima*, *Laminaria pallida* and *L. hyperborea*), growth rates were measured using the
256 hole-punch method and converted to RII as described for the depth experiment. For the five
257 fucoid species (temperate *Scytothalia dorycarpa*, *Arthrophyucus* sp and *Sargassum* sp, tropical

258 *S. illicifolium* and *S. decurrens*) net growth rates were determined by measuring the length
259 (L) and circumference (C) of tagged individuals at the beginning and end of the experiment,
260 and converting the measurement to fresh weight (W_F) using the equation $W_F = LC^2$
261 (following Aberg 1990). Each individual was also collected at the end of the experiment and
262 weighed in the laboratory to the nearest 0.1 g to calibrate the biomass conversion model for
263 each species (Fig. S2). A detailed description of the site and species specific methods can be
264 found in Appendix S1c.

265

266 **Results:**

267 *Intra-specific interactions at different depths*

268 Intra-specific interactions between *Ecklonia radiata* and the canopy changed from net
269 competitive to facilitative from deep to shallow along a 20 m depth gradient ($F_{1,7} = 7.32$, $p =$
270 0.030 , adjusted $R^2 = 0.442$; Fig. 1a). In sites deeper than 8 m, kelp growth rates were
271 generally higher in canopy-free treatments, whereas shallower than 8 m growth rates were
272 consistently higher within the canopy (Fig. S3). This transition in growth rate was coupled
273 with a dramatic increase in epiphyte loading in shallow canopy-free treatments ($73.2 \pm 9\%$ of
274 total thallus area) compared to shallow canopy treatments ($2.1 \pm 0.6\%$ of total thallus area)
275 and all deep treatments (Fig. 1b; Table 1). Interestingly, after the two month experimental
276 period, short term photosynthesis and respiration rates measured in the photorespirometry
277 chambers resulted in positive RII in five out of seven sites tested, with deep sites recording
278 the highest RII values (Fig. S4a). Large differences in interaction strength (RII) in deep sites
279 were driven by high photosynthetic rates and low respiration in canopies compared to
280 canopy-free treatments (Fig. S4b - c). In shallow sites, photosynthetic rates were higher than

281 expected for canopy-free treatments, which may be attributable to the dense epiphytic cover
282 growing on the thallus of canopy-free kelps.

283 Both light and temperature significantly increased with decreasing depth, however only light
284 was consistently modified by the canopy and represented a stress gradient per se (He &
285 Bertness 2014, Fig. 1c - d, Table 1). Shallow canopy-free treatments had ten-fold higher
286 mean light levels ($14,408 \pm 780$ Lux) than shallow canopy treatments (1352 ± 329 Lux), and
287 four-fold higher levels than deep canopy-free treatments (3673 ± 164 Lux). This pattern was
288 also consistent for maximum daily illuminance and standard deviation in daily illuminance
289 (Fig. S5). Temperature conditions by contrast changed more uniformly with depth in both
290 canopy and canopy-free treatments. Canopy treatments had significantly lower temperatures
291 than canopy-free treatments, but the difference was not uniform among sites, and small
292 (maximum difference between canopy and canopy-free treatments = 0.29°C , mean difference
293 = $0.07^{\circ}\text{C} \pm 0.04^{\circ}\text{C}$) in comparison to temperature differences along the depth gradient
294 (maximum difference between depths = 0.73°C , Fig. 1d, Table 1). Furthermore the
295 temperature gradient was relatively benign compared to the seasonal temperature range
296 experienced by kelps in the area ($16\text{-}23^{\circ}\text{C}$) and is therefore not considered to represent a
297 stress gradient per se. No clear depth pattern in relative water motion (WM) was observed
298 among the nine sites. Mean 95th percentile relative WM in both shallow and deep sites was
299 between $4 - 6 \text{ ms}^{-2}$, whereas the intermediate depths recorded between $6 - 9 \text{ ms}^{-2}$ (Fig. S6).

300

301 *Intraspecific interactions at different latitudes*

302 Intra-specific interactions along the latitudinal gradient revealed predominantly positive
303 interactions across all latitudes and did not display a significant difference in interaction
304 strength among latitudes during either spring ($p = 0.168$, adjusted $R^2 = 0.145$) or summer ($p =$

305 0.269 adjusted $R^2 = 0.052$, Fig. 2a, Fig. S6). Epiphyte cover varied among latitudes, but not
306 in accordance with the latitudinal differences in temperature (Fig. 2b - c, Table 2). Consistent
307 with long term profiles, summer temperatures were warmer at 32°S and 30°S than 34°S, but
308 did not consistently vary between canopy and canopy-free treatments (Fig. 2c, Table 2).
309 Despite differences in temperature among latitudes, nutrient levels remained relatively
310 constant (NO_3 concentrations = $0.8 - 1.5 \mu\text{mol L}^{-1}$) across all nine sites (Fig. S8). Light levels
311 did not vary among latitudes but as in the depth experiment, mean illuminance under the
312 canopy was significantly lower than in canopy-free treatments (Fig. 2d, Table 2). Patterns in
313 light and temperature were consistent among mean, maximum, minimum (temperature only)
314 and standard deviation (light only) measurements (Fig. S9 and S10).

315

316 *Generalities in intra-specific and inter-specific interactions*

317 Examining the nature of subtidal canopy interactions under low consumer pressure, across
318 dominant species from around the world, revealed that positive and neutral interactions were
319 widespread. Growth rates of seaweeds within the canopy were higher than canopy-free
320 growth rates, resulting in net positive intra-specific interactions for five of the six species
321 tested including three temperate kelp species from Australia (*E. radiata*) and South Africa (*E.*
322 *maxima* and *L. pallida*), and temperate and tropical furoids (subgen. *Sargassum* sp. and
323 *Sargassum illicifolium*, respectively; Fig. 3a). *Laminaria hyperborea*, in populations from
324 both France and Norway, was the only species to show net competitive intra-specific
325 interactions.

326 Facilitation was less pronounced among inter-specific interactions in seaweed canopies.

327 Growth rates of kelp (*L. pallida*) and temperate furoids (*Scytothalia dorycarpa*, *Arthrophyucus*
328 *sp.* and *Sargassum* sp.) species growing within kelp canopies displayed neutral interactions.

329 In contrast, kelp, *E. radiata*, displayed positive interactions within temperate *Sargassum* sp.
330 canopies while *Sargassum decurrens*, displayed net competitive interactions in tropical
331 *Sargassum illicifolium* canopies (Fig. 3b).

332

333 **Discussion**

334 Our results revealed that positive and neutral canopy interactions are common within
335 seaweed communities globally and that the nature of interactions can change in response to
336 physical stress gradients in subtidal marine ecosystems where consumer pressure is low.
337 Under benign light conditions below 8 m depth, canopy interactions were primarily
338 competitive or neutral, whereas under shallow, high-light conditions seaweed growth became
339 increasingly facilitated by the canopy. These findings provide support for the SGH and
340 represent the first example of the SGH along a light-stress depth gradient that we are aware
341 of. In contrast, interactions were neutral to positive and did not change along a latitudinal
342 temperature gradient. While these findings do not support the SGH, they do not contradict it
343 either, as canopy treatments were unable to consistently lower temperature conditions and
344 alleviate temperature stress. These results were, however, consistent with interactions among
345 nine dominant subtidal canopy species from around the world, where facilitation was the
346 most common outcome of intra-specific interactions.

347

348 Light is a fundamental resource for plants and attenuates with depth in the ocean, limiting the
349 vertical distribution of seaweeds (Staeher & Wernberg 2009). In the upper depths of the ocean
350 however, light is not a limiting resource, and high-light levels can act like a non-resource
351 stress gradient (*c.f.* resource gradient; Maestre *et al.* 2009) whereby photosynthetically active

352 radiation exceeds saturating levels (Altamirano *et al.* 2004) and ultra violet radiation can
353 penetrate the water column and potentially damage kelp tissue (Wood 1987). The reduction
354 of high-light conditions within the canopy at shallow depths appears to be fundamentally
355 important to the health and growth of seaweed canopies. As light attenuates toward deeper
356 depths, the dependence on neighbours reduces and interactions were observed to become
357 neutral to competitive. Given canopies can only reduce light levels, not increase them, it
358 would be expected that below the depths observed here, interactions would continue to
359 become increasingly competitive as light becomes limiting toward a species vertical
360 distribution limit. Indeed, this would explain the consistent thinning of canopies at deeper
361 depths. Our findings are consistent with previous studies that examined recruitment patterns
362 in response to canopy shading and observed primarily competitive interactions in depths
363 between 10-18 m where canopy shading effects were similar to those observed here (Dayton
364 *et al.* 1984; Reed & Foster 1984).

365 While light conditions appear to be the dominant driver of interaction patterns, other non-
366 stressful environmental gradients (*sensu* He & Bertness 2014) were present and may have
367 partially contributed to the nature of interactions. All depths experienced relatively high wave
368 exposure, and no clear pattern between depth and water velocities were observed, suggesting
369 that water velocity cannot explain the observed change in interactions with depth.

370 Nevertheless, the presence of a canopy can reduce drag on a thallus by over 80 %, compared
371 to a solitary individual (Johnson 2001) enabling canopy kelps to attain greater size than
372 solitary individuals in wave exposed areas (de Bettignies *et al.* 2013a), potentially promoting
373 facilitation. Water movement also influences physical scour from the canopy and is likely to
374 reduce the settlement and growth of epiphytes on kelp in the canopy. Interestingly, despite
375 high wave exposure, temperatures changed both across the depth gradient and between
376 canopy treatments, with slightly cooler temperatures recorded inside the canopy at some sites.

377 Temperature differences among canopy treatments were, however, small in comparison to
378 differences among depths and very small relative to the temperature range of *E. radiata*.
379 Temperature is therefore unable to explain the interaction patterns observed along the depth
380 gradient.

381 Temperature also did not modify interaction patterns along the latitudinal temperature stress
382 gradient, with positive interactions prevailing at five out of the six latitudinal experiments.
383 These observations are consistent with canopy-recruit interactions observed for *Scytothalia*
384 *dorycarpa* in the same region, however differ from canopy-recruit interactions for *Sargassum*
385 sp. and *Ecklonia radiata* which have been observed to change from competitive to facilitative
386 in response to latitudinal temperature gradients (Wernberg *et al.* 2010; Bennett & Wernberg
387 2014). It remains unclear why some recruits change the nature of their interaction with the
388 canopy along temperature gradients while adults do not, particularly given we observed that
389 canopies did not modify temperatures sufficiently to reduce thermal stress. These results
390 suggest that a combination of processes (i.e. light and temperature stress) can interact to
391 determine interaction patterns in subtidal canopies (Wernberg *et al.* 2010), and that there may
392 be ontogenetic changes in the nature of interactions within canopy species (He & Bertness
393 2014).

394 In subtidal systems elsewhere, combined effects of warm temperatures and low nutrients
395 have been shown to influence kelp interactions. The recovery of the competitively dominant
396 giant kelp, *Macrocystis pyrifera* following storm events depends on low-frequency cycles in
397 nutrient and temperature conditions in response to the El Niño Southern Oscillation, which in
398 turn influences the recruitment and abundance patterns of subordinate kelp species (Dayton *et*
399 *al.* 1999). *M. pyrifera* canopies have also been adversely affected by warm temperatures and
400 low nutrient conditions in south-eastern Australia (Johnson *et al.* 2011), but *E. radiata*
401 canopies have not, suggesting that *E. radiata* canopies may be more tolerant of low nutrient

402 conditions than *M. pyrifera*. High rates of canopy erosion (*c.f.* dislodgement in *M. pyrifera*)
403 could increase nutrient supply within canopies, thereby supplementing local nutrient
404 conditions within the canopy and promote facilitation (de Bettignies *et al.* 2013b). It is
405 unclear whether the small-scale clearings used in our experiment, were large enough to
406 modify local nutrient availability, nevertheless the North American example illustrates that
407 multiple stressors can influence the nature of interactions and may help explain the variable
408 responses observed along the temperature gradient.

409 The consistent pattern of neutral to positive interactions of *Ecklonia radiata* among latitudes
410 is in agreement with observed global interaction patterns, where positive and neutral
411 interactions were found to be widespread among multiple subtidal canopy types that
412 experience low consumer pressure. Among the kelp species observed, *Laminaria hyperborea*
413 in the North Atlantic was the only species to display negative interactions with the canopy,
414 whereas Australian and South African kelps displayed primarily positive interactions. Light
415 availability may have contributed to these patterns as French reefs in particular were
416 generally deeper and had lower light (due to turbidity) than canopies observed in Australia
417 and South Africa (Staehr & Wernberg 2009). Life history traits may also help to explain the
418 observed interaction patterns, particularly for *Sargassum* which displayed competitive inter-
419 specific interactions within the kelp canopy. *Sargassum* has a buoyant thallus that has
420 adapted to fragment easily as a means of propagule dispersal (Schiel & Foster 2006).
421 Fragmentation of *Sargassum* by the abrasive canopy might have contributed to the lower net
422 growth rates of *Sargassum* within the canopy, yet may assist its dispersal and reproductive
423 success.

424 In addition to contemporary environmental processes influencing interactions, the stability of
425 canopies over evolutionary time scales may contribute to the prevalence of positive
426 interactions, particularly in southern Australian. Modern canopy seaweeds (orders

427 Laminariales and Fucales) evolved during the Miocene (Silberfeld *et al.* 2010), since which
428 time the marine climate of southern Australia has been remarkably stable (McGowran *et al.*
429 1997). While the diversification of Australia's marine flora was likely to have begun prior to
430 the arrival of canopy species (Hommersand 1986), the long climatically stable history of
431 seaweed canopies in Australia and their dense cover on reefs is likely to have favoured
432 adaptations among canopy and understory seaweeds to thrive within canopy conditions.

433 Collectively, our findings highlight that canopy interactions may have an important influence
434 on the response of subtidal habitats to physical stress. Kelp forests are often thought to be
435 resilient to disturbance due to their fast growth rates and rapid colonisation of space (Dayton
436 *et al.* 1984; Steneck *et al.* 2002). Our results suggest that many seaweed communities may in
437 fact be dependent on the surrounding canopy to ameliorate stressful abiotic conditions. On
438 shallow reefs canopy loss could result in high-light conditions that inhibit kelp recovery,
439 providing a positive feedback mechanism that reinforces a canopy-free state. Such scenarios
440 may become increasingly common under climate change and may help to explain subtidal
441 community changes, as were observed following a decline in seaweed canopy cover in
442 Western Australia in response to an extreme marine heatwave (Wernberg *et al.* 2013).

443 Understanding the role of other abiotic stress gradients (i.e. wave exposure) and the additive
444 or synergistic effects of multiple stressors on interactions in the subtidal will help to improve
445 our understanding and management of subtidal communities in the face of such global
446 changes. The stress gradient hypothesis provides a useful concept to address these questions
447 and has been seldom applied in subtidal ecosystems to date (Bulleri 2009). Our results reveal
448 that neutral to positive canopy interactions are widespread throughout subtidal ecosystems
449 globally and may be critical to reduce high-light stress in shallow subtidal marine systems.

450 These findings suggest that canopy interactions are important in sustaining the function of
451 many seaweed dominated systems and could therefore provide critical information about

452 community performance across major environmental gradients and in the face of
453 contemporary changes to the physical environment in coastal marine ecosystems.

454

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469

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651

652 **Figure captions**

653 **Figure 1:** Nature of intra-specific interactions of *Ecklonia radiata* along a subtidal depth
654 gradient from 3 – 19 m. (a) Relative Interaction Index (RII) of *E. radiata* based on mean
655 growth rates in canopy and canopy-free treatments. Positive values from 0 to 1 indicate
656 increasingly facilitative net interactions and negative values from 0 to -1 indicate increasingly
657 competitive net interactions. (b) Comparison of kelp health based on mean epiphytic cover of
658 secondary laterals after the two month experimental period with (dark grey) and without
659 (open) canopy (n = 10 kelps per treatment). (c) Mean light illuminance recorded with and
660 without canopy between the hours 0800 – 1600 for 14 days among the different depths. (d)
661 Mean, maximum and minimum temperatures recorded with and without canopy over the 2
662 month experimental period among the different depths

663

664 **Figure 2:** Nature of intra-specific interactions of *Ecklonia radiata* among nine sites along a
665 subtidal latitudinal gradient from 34°S – 30°S. (a) Relative Interaction Index (RII) of *E.*
666 *radiata* based on mean growth rates in canopy and canopy-free treatments. Positive values
667 from 0 to 1 indicate increasingly facilitative net interactions and negative values from 0 to -1
668 indicate increasingly competitive net interactions. (b) Comparison of kelp health based on
669 mean epiphyte cover of secondary laterals after the two month experimental period with
670 (dark grey) and without (open) canopy (n = 10 kelps per treatment). (c) Mean temperatures
671 recorded with and without canopy over the 2 month experimental period among the different
672 latitudes (d) Mean light illuminance recorded with and without canopy between the hours
673 0800 – 1600 for 14 days among the different latitudes.

674

675 **Figure 3:** Patterns in intra-specific (a) and inter-specific (b) interactions between dominant
676 subtidal benthic habitat forming species from around the world. Positive values from 0 to 1

677 indicate increasingly facilitative net interactions and negative values from 0 to -1 indicate
678 increasingly competitive net interactions. Numbers underneath the species name indicate the
679 number of replicate reefs where each interaction type was measured. Sites range between 6-
680 12 m depth except tropical *Sargassum* sites which were recorded in 3-4 m depth (Table S1).

681

682

683

684 **Table 1:** Results of ANCOVA models comparing Growth, Epiphyte cover, Illuminance and
 685 Temperature, between canopy treatments along the depth gradient. Epiphyte cover was
 686 arcsin-square root transformed and illuminance was log10 transformed.

687

Growth	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	3.14928	0.361	8.722	0.000
Canopy treatment (CT)	-0.816	0.515	-1.583	0.115
Depth	-0.030	0.029	-1.028	0.305
CT:Depth	0.089	0.042	2.133	0.034
Epiphyte cover	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.156	0.062	2.530	0.013
Canopy treatment (CT)	0.784	0.091	8.589	0.000
Depth	-0.006	0.005	-1.170	0.244
CT:Depth	-0.051	0.008	-6.506	0.000
Illuminance (Lux)	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	2.888	0.061	47.429	0.000
Canopy treatment (CT)	1.446	0.083	17.443	0.000
Depth	-0.036	0.005	-7.024	0.000
CT:Depth	-0.005	0.007	-0.737	0.462
Temperature (°C)	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	21.394	0.074	290.516	0.000
Canopy treatment (CT)	0.222	0.100	2.219	0.027
Depth	-0.032	0.006	-5.193	0.000
CT:Depth	-0.015	0.008	-1.908	0.057

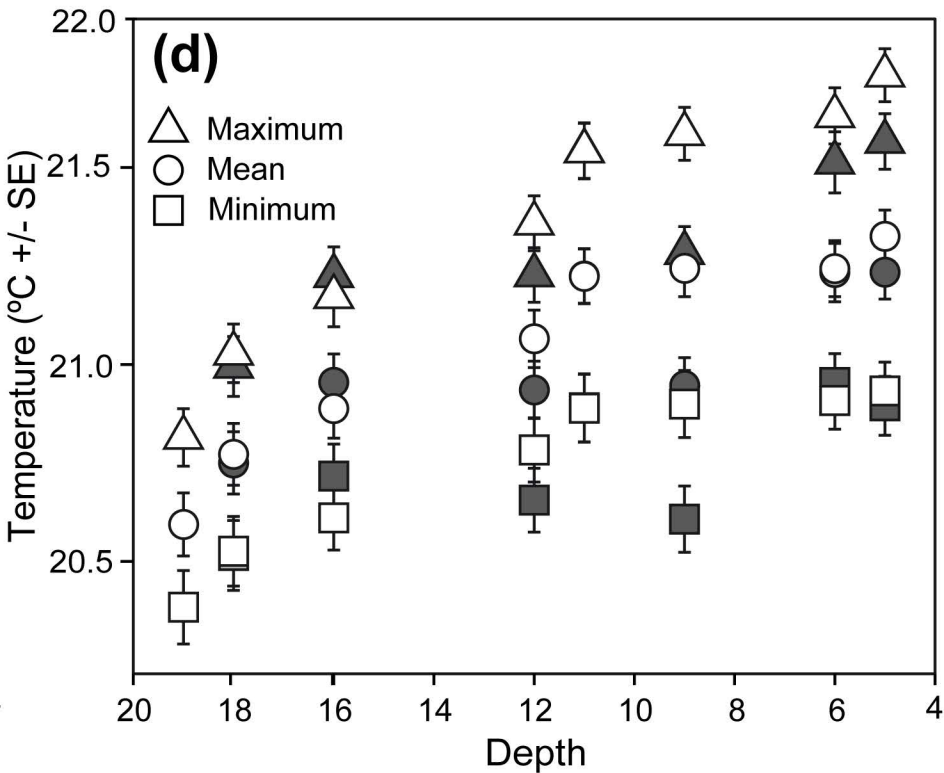
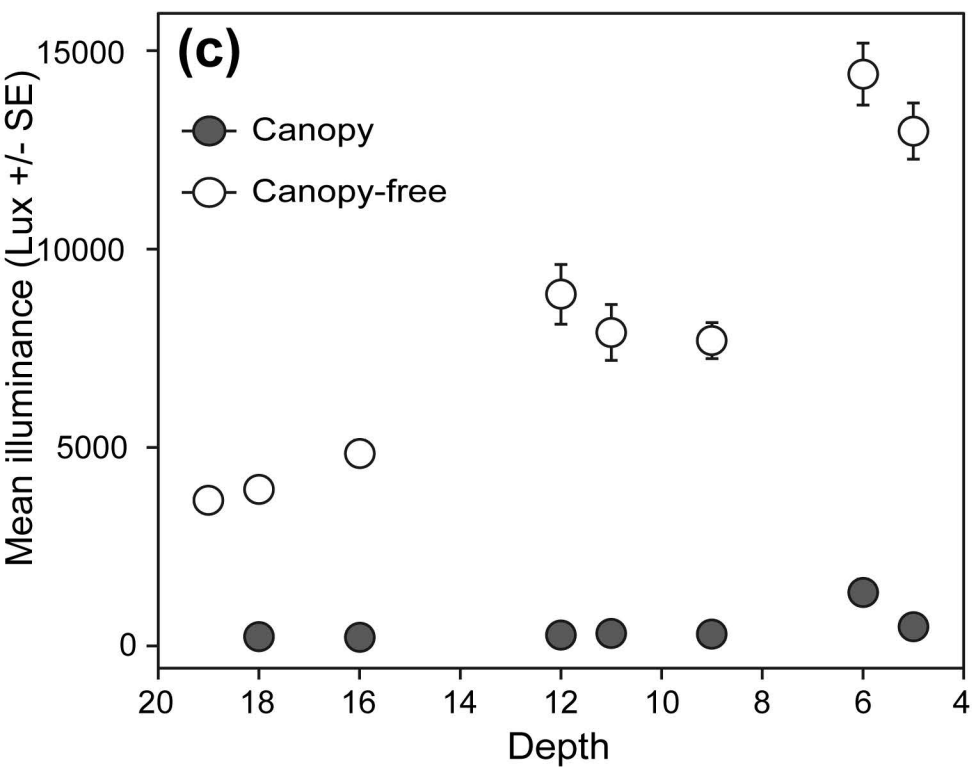
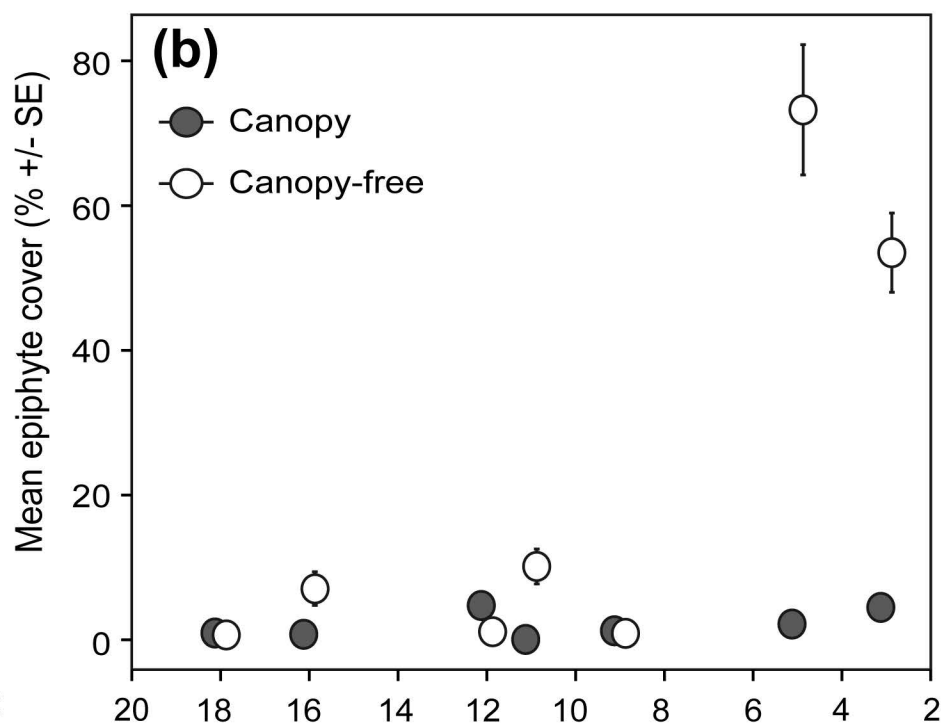
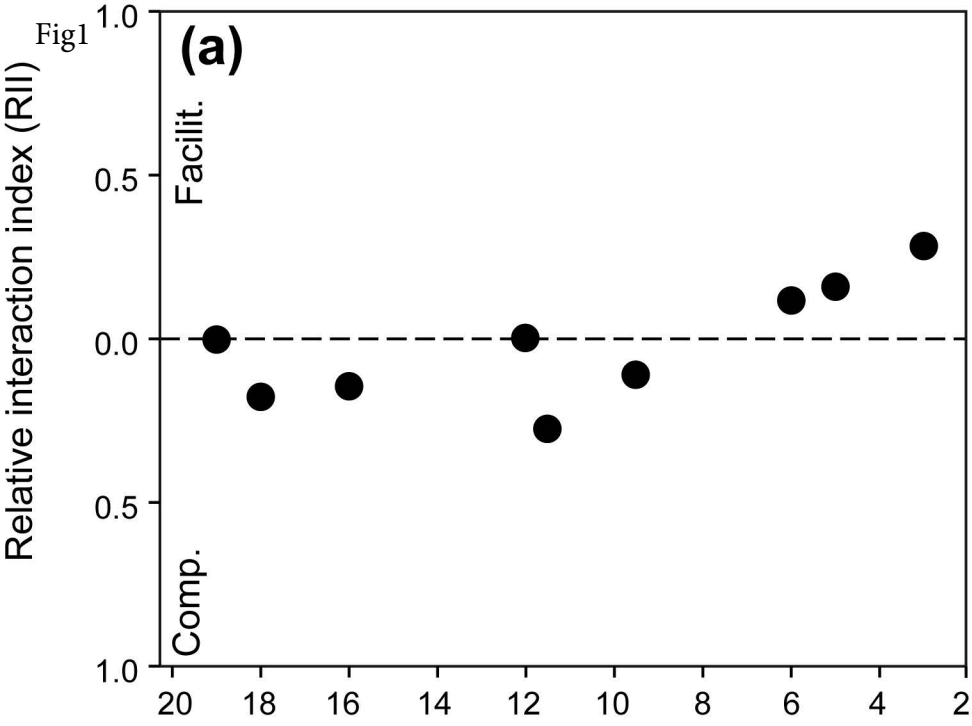
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689

690 **Table 2:** Results of ANCOVA models comparing Relative interaction index between seasons
 691 along a latitudinal gradient, Epiphyte cover, Illuminance and Temperature, between canopy
 692 treatments along a latitudinal gradient. Epiphyte cover was arcsin-square root transformed
 693 and illuminance was square root transformed.

RII	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.956	0.935	1.022	0.325
Season	-0.026	1.322	-0.020	0.985
Latitude	-0.026	0.029	-0.876	0.397
Season:Latitude	-0.003	0.041	-0.085	0.934
Epiphyte cover	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	1.018	0.262	3.892	0.000
Canopy treatment (CT)	-0.523	0.374	-1.400	0.163
Latitude	-0.024	0.008	-2.918	0.004
CT:Latitude	0.018	0.012	1.553	0.122
Illuminance (Lux)	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	52.198	25.324	2.061	0.040
Canopy treatment (CT)	103.286	35.813	2.884	0.004
Latitude	1.177	0.790	1.490	0.138
CT:Latitude	1.600	1.118	1.431	0.154
Temperature (°C)	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	37.012	0.658	56.289	0.000
Canopy treatment (CT)	-0.761	0.930	-0.819	0.413
Latitude	0.425	0.021	20.565	0.000
CT:Latitude	-0.026	0.029	-0.888	0.375

694



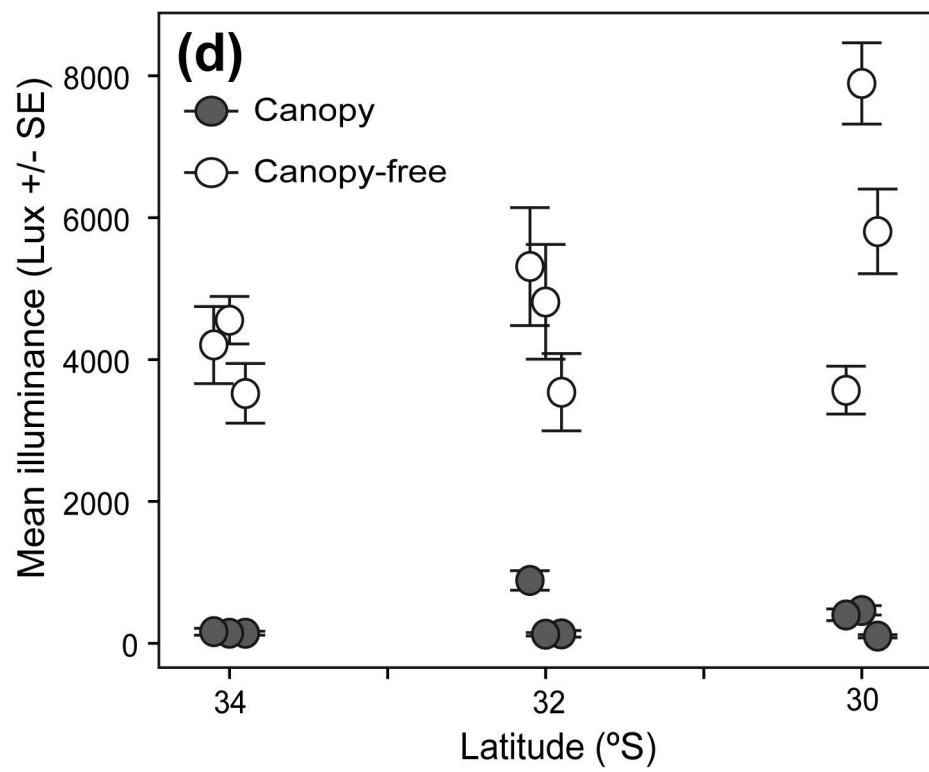
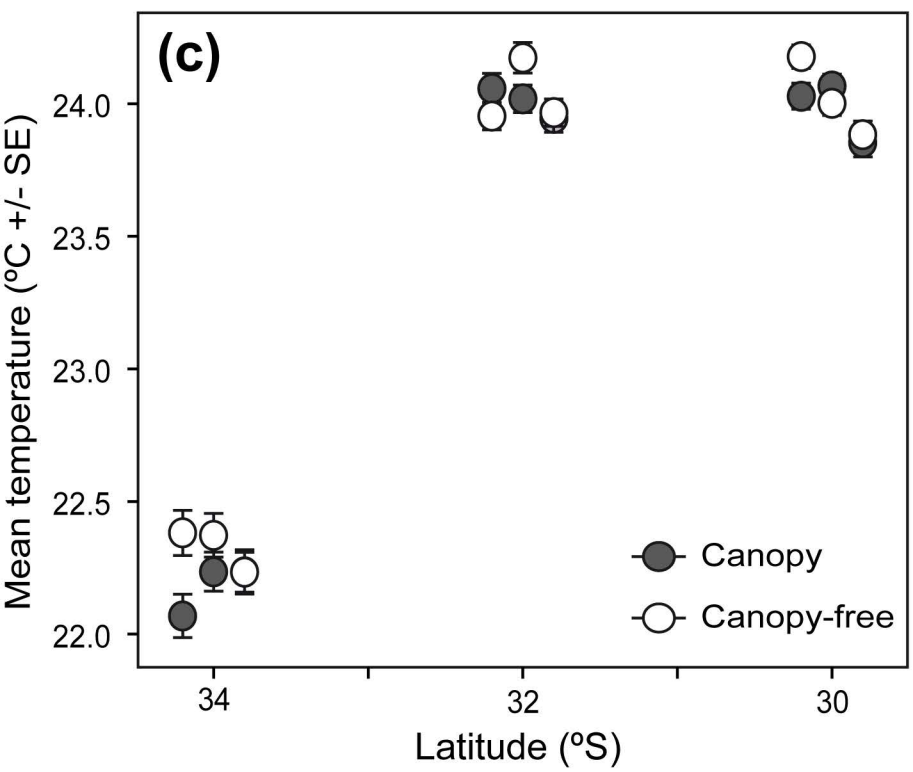
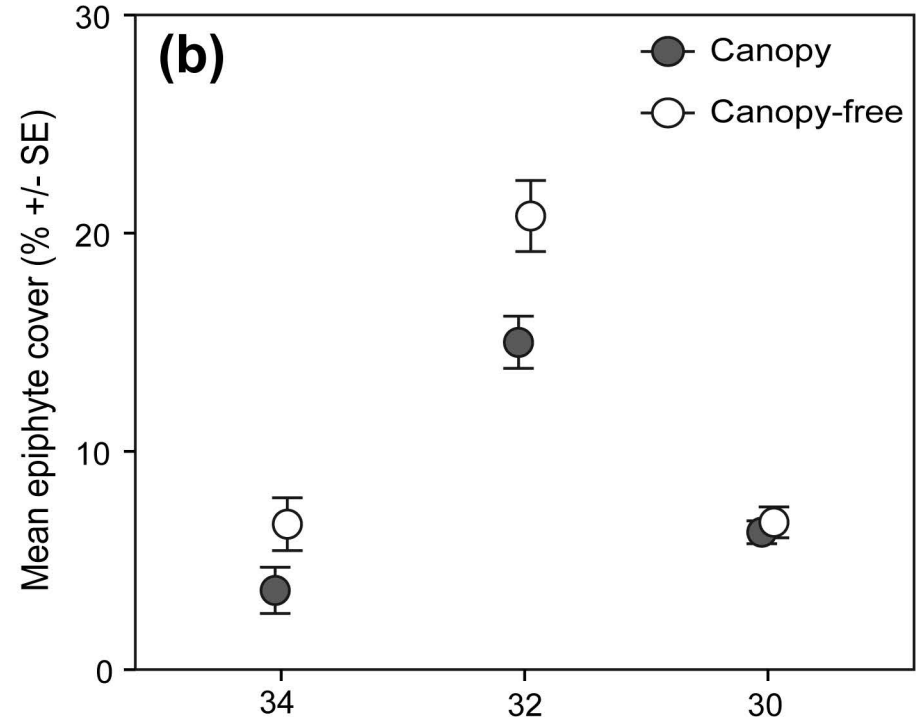
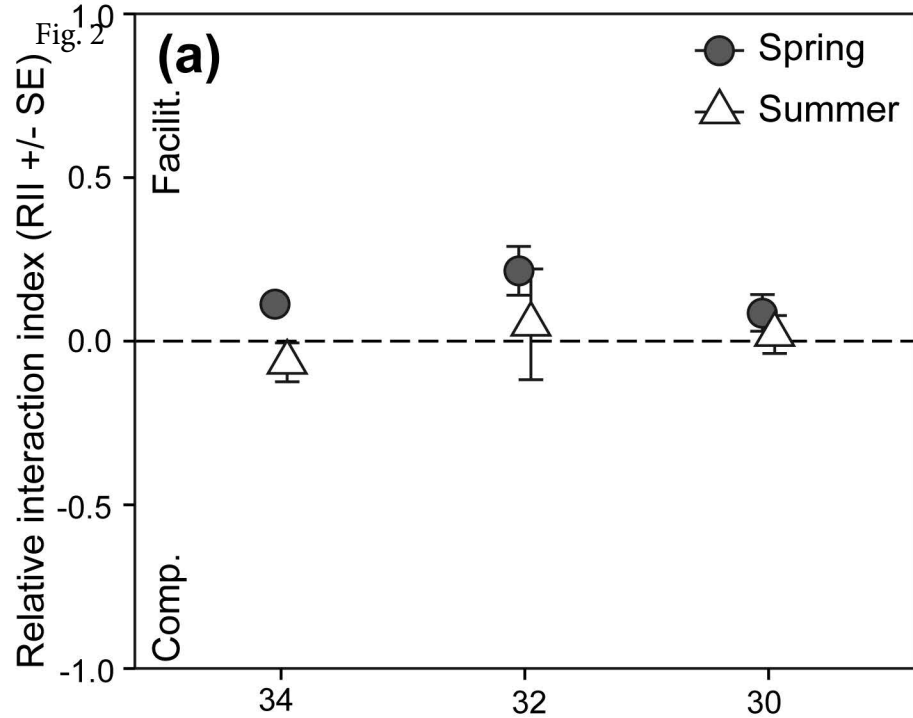


Fig. 3

