

1 **Recurrent extreme climatic events are driving gorgonian populations to**
2 **local extinction: low adaptive potential to marine heatwaves.**

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20

21 **Running title:** Low adaptability of corals to heatwaves

22

23 **Abstract**

24 Extreme climatic events (ECEs), such as marine heatwaves (MHWs), are a major threat to
25 biodiversity. Understanding the variability in ecological responses to recurrent ECEs within
26 species and underlying drivers arise as a key issue owing to their implications for conservation
27 and restoration. Yet, our knowledge on such ecological responses is limited since it has been
28 mostly gathered following “single-event approaches” focused on one particular event. These
29 approaches provide snapshots of ecological responses but fall short of capturing heterogeneity
30 patterns that may occur among recurrent ECEs, questioning current predictions regarding
31 biodiversity trends. Here, we adopt a “multi-event” perspective to characterize the effects of
32 recurrent ECEs and the ecological responses in *Paramuricea clavata*, a Mediterranean
33 temperate coral threatened by MHWs. Through a common-garden experiment repeated three
34 consecutive years with the same individuals from three populations, we assessed the respective
35 roles of environmental (year effect), genetic (population effect) and phenotypic (*population-*
36 *by-environment* interactions effect) components in the ecological response to recurrent heat
37 stress. The environmental component (year) was the main driver underlying the responses of
38 *P. clavata* colonies across experiments. To build on this result, we showed that: i) the
39 ecological responses were not related to population (genetic isolation) and individual
40 (multilocus heterozygosity) genetic make-up, ii) while all the individuals were characterized
41 by a high environmental sensitivity (*genotype-by-environment* interactions) likely driven by
42 *in-situ* summer thermal regime. We confront our experimental results to *in situ* monitoring of
43 the same individuals conducted in 2022 following two MHWs (2018, 2022). This confirms that
44 the targeted populations harbor limited adaptive and plastic capacities to on-going recurrent
45 ECEs and that *P. clavata* might face unavoidable population collapses in shallow
46 Mediterranean waters. Overall, we suggest that biodiversity forecasts based on “single event”
47 experiments may be overly optimistic and underscore the need to consider the recurrence of
48 ECEs in assessing threats to biodiversity.

49

50 **Keywords:** Mass mortality events, Mediterranean Sea, Habitat-forming octocorals,

51 Common-garden experiment, Genotype-by-environment interactions, Ecological memory.

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53

54

55 **Introduction**

56 Extreme climate events (ECE) linked to climate change such as heatwaves pose
57 significant challenges for biodiversity (Jacox et al., 2020; Maxwell et al., 2019; Parmesan et
58 al., 2000; Pinsky et al., 2019; Ummenhofer & Meehl, 2017). ECEs have been associated with
59 the increased frequency of mass mortality events (MMEs), accelerating species demographic
60 decline (Leung *et al.*, 2017; Smale et al., 2013) and questioning the future of biodiversity
61 (Smale et al. 2019). Besides demographic decline, field surveys revealed heterogeneity in the
62 patterns of ecological responses to ECEs across taxonomic (species, populations, and
63 individuals), spatial (regions) and temporal (years) scales (van Bergen et al., 2020; Hughes et
64 al., 2003; Pansch et al., 2018). Yet, to date, the potential effects of recurrent ECEs and the
65 related temporal variability in ecological responses has been poorly considered (but see Ahrens
66 et al., 2021; Brown et al., 2023; Brown & Barott, 2022; Husson et al., 2022; Logan et al., 2014;
67 Regan & Sheldon, 2023). Indeed, most of our knowledge on ecological responses to ECEs has
68 been gathered studying one particular event following a “single-event approach” (Altwegg et
69 al., 2017). This approach provides a snapshot of the ecological responses but falls short of
70 revealing the consequences of recurrent ECEs on biodiversity. Consequently, the need to
71 develop a “multi-events” perspective has been recently acknowledged to improve predictions
72 on species abilities to face ECEs (Bailey & Van De Pol, 2016).

73 Ecological responses to ECEs, considered here as phenotypes, are shaped by the
74 interplay among ‘genetic’, ‘environmental’ and ‘plastic’ components (Merilä & Hendry, 2014).
75 This interplay has been investigated using common garden experiments (Malyshev et al., 2016)
76 and long-term time series (Regan & Sheldon, 2023). The ‘genetic’ component relies on the
77 standing genetic variation (Dixon et al., 2015), shaped by the balance between evolutionary
78 forces (*e.g.* local adaptation, genetic drift; Bay & Palumbi, 2014). The ‘environmental’
79 component includes biotic (*e.g.* species interactions) and abiotic (*e.g.* temperature) factors that

80 characterize a specific habitat and influence ecological responses (Scheiner, 1993). Finally,
81 ‘plastic’ components result from the interaction of genetic and environmental components.
82 This “*population-by-environment*” and “*genotype-by-environment*” interactions underlie
83 plasticity in phenotypic response at the population and individual levels (Matesanz et al., 2019).
84 Individual phenotypic plasticity, considered as a single genotype expressing different
85 phenotypes function of the environment, can provide a short-term buffer allowing organisms
86 to immediately face ECEs before genetic adaptation occurs (Chevin et al., 2010; Reusch, 2014).

87 Marine heatwaves (MHWs), known as discrete periods of anomalously warm water
88 (Frölicher et al., 2018; Smith et al., 2023), are some of the most challenging ECEs for marine
89 diversity, threatening ecosystem’s structure and functioning (Smale et al., 2019) from kelp
90 forests (Arafeh-Dalmau et al., 2020) to coral reefs (Genin et al., 2020; Gómez-Gras et al.,
91 2021a; Hughes et al., 2021). In the last two decades, the Mediterranean Sea has been recurrently
92 impacted by MHWs driving mass mortality events (MMEs) impacting multiple phyla of
93 benthic macro-invertebrates (Cramer et al., 2018; Garrabou et al., 2022). In this particular case,
94 as in other marine ecosystems, field surveys (Garrabou et al., 2001) and long-term monitoring
95 studies (Gómez-Gras et al., 2021b; Montero-Serra et al., 2019) combined with “single event”
96 experiments in controlled conditions (Crisci et al., 2017; Gomez-Gras et al. 2022), provided
97 insights into the heterogeneity of ecological responses within species impacted by MHWs. Yet,
98 whatever the system considered, the impact of genetic, environmental, and plastic components
99 underlying the differential ecological responses remain poorly understood, particularly, in the
100 context of recurrent MHWs (but see Hughes et al., 2021).

101 We aim to advance the characterization of the impacts of recurrent ECEs on within-
102 species diversity and to infer the respective roles of the genetic, environmental, and plastic
103 components in the ecological responses. We adopt a multi-events perspective combining
104 experiments and *in-situ* survey focusing on the Mediterranean scene and on the red gorgonian

105 *Paramuricea clavata* (Risso, 1826). This habitat-forming octocoral is a well-suitable candidate
106 given the impacts of MHWs on shallow populations monitored for 20 years (Garrabou et al.,
107 2021, see below). We repeated during three consecutive years (2015, 2016, 2017) a common-
108 garden thermal stress experiment at fine spatial scale (populations separated by < 1 km), in
109 which we controlled for different aspects of genetic (same genotypes tested) and environmental
110 (same experimental set-up) components. Specifically, we; i) estimated the percentage of
111 heterogeneity in the ecological responses, respectively explained by the taxonomic (individual
112 and populations) and temporal (years) variabilities; ii) tested the significance of the genetic
113 (population effect), environmental (year effect) and plastic (population-by-years effect)
114 components on the ecological responses. We discussed the obtained results in the light of iii)
115 the populations and individuals' genetic make-up (*i.e.* genetic drift and heterosis); iv)
116 environmental sensitivity analyses looking at genotype-by-environment interactions and v) *in-*
117 *situ* summer thermal regimes. We vi) contrasted the ecological responses from the experiments
118 to the ecological responses reported from a field survey of the same individuals conducted in
119 2022 after two MHWs.

120 Compared to previously published single event approaches, our results point toward a
121 lack of adaptive potential, whether plastic or genetic, of the shallow populations of *P. clavata*
122 to the recurrent MHWs. We suggest to cautiously consider predictions of biodiversity trends
123 based on “single event” approaches.

124

125 **Materials and methods**

126 *Species of interest*

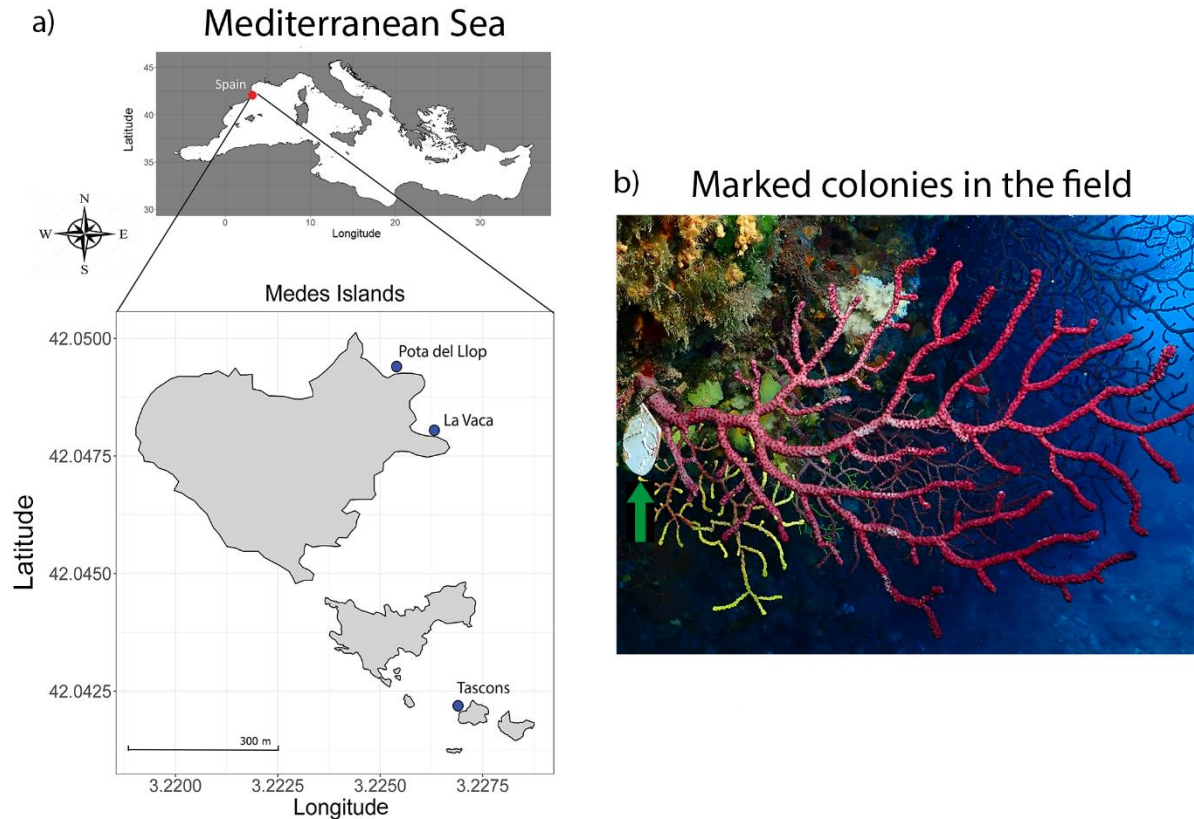
127 The red gorgonian *P. clavata* is a habitat-forming octocoral with an important role in the
128 structure and functioning of the Mediterranean coralligenous habitats (Boavida et al., 2016;
129 Gómez-Gras et al., 2021a; Ponti et al., 2014, 2018). This species displays low population

130 dynamics with slow growth, recruitment, and recovery rates (Gómez-Gras et al., 2021a;
131 Gómez-Gras et al., 2021b), as well as restricted dispersal abilities with a highly reduced
132 resilience (Coma et al., 1998; Ledoux et al., 2018; Linares et al., 2008; Mokhtar-Jamaï et al.,
133 2011). *Paramuricea clavata* has been particularly impacted by recurrent marine heat waves in
134 the past 20 years (Cebrian et al., 2012; Garrabou et al., 2021; Gómez-Gras et al., 2021b). It was
135 included in the IUCN red list of vulnerable Mediterranean Anthozoans (Otero et al., 2017).
136 “Single event” experiments using common garden set-ups identified the thermal risk zone of
137 this species for temperatures over 25° C (Crisci et al 2017). These experiments have
138 characterized ecological responses and underlying processes in populations from contrasted
139 environments (depth) and separated by distances of tens to thousands of kms (Arizmendi-Mejía
140 et al., 2015b; Crisci et al., 2017). Altogether, the ecological importance of *P. clavata* as a
141 habitat-forming species and the extensive available ecological information make this model
142 highly relevant to evaluate the roles of the genetic, environmental, and plastic components on
143 the ecological responses to recurrent ECEs.

144

145 *Identification of the colonies:*

146 Ninety adult colonies (>50 cm) were randomly chosen around 15 m depth from three different
147 sites separated by hundreds of meters at Medes Islands, Spain (42°02'60.00" N 3°12'60.00"
148 E): Pota del Llop (N=30), La Vaca (N=30) and Tascons (N=30, Figure 1a). Each colony was
149 marked during September of 2014 using plastic tags with a unique ID (Figure 1b). From every
150 marked colony, two apical fragments of 10 cm were collected between the 21st of September
151 and 22nd of October of 2015, 2016 and 2017. These fragments were retrieved in 2 L bags of
152 water and immediately transported (maximum transportation time 2h) in coolers to the
153 Aquarium Experimental Zone (ZAE) of the Institut de Ciències del Mar (ICM-CSIC,
154 Barcelona, Spain).



155

156 **Figure 1.** a) *Paramuricea clavata* sampling sites at Medes Islands, Spain, b) Tagged colony of
157 *P. clavata* in Tascon's location (green arrow).

158

159 *Common garden set-up repeated in 2015, 2016 and 2017:*

160 Upon arrival, colony fragments were mechanically fixed to experimental plates as described in
161 Crisci et al. (2017) (Figure S1). All colonies were acclimated for one week in an open water
162 system with 50 μm sand-filtered running seawater at 17-18°C. No mortality signs and tissue
163 necrosis were detected during this period in any of the colonies and/or years. Moreover, all
164 sampled colonies showed active polyps during feeding. After the acclimation period, we
165 conducted the common garden experiments as described in Crisci et al. (2017). Specifically,
166 each fragment was divided into two fragments, one for control (18°C) and one for the heat
167 stress treatment (25°C). For the heat stress treatment, temperature was increased from 18 to 25
168 °C over a period of 3 days and maintained at 25°C for the next 28 days. Colonies were fed

169 during the entire experimental course (see Supplementary information for further details about
170 the set up).

171

172 *Phenotypic response: survival analysis, individual fitness, and modeling the response to*
173 *thermal stress*

174 Several descriptors were then used to statistically compare the ecological responses
175 (differences in thermotolerance) among colonies and populations. The percentage of tissue
176 necrosis (extent of injury) by colony was monitored visually every day. Ecological impacts on
177 *P. clavata* were considered as “low” when 10-30% necrosis was observed, “moderate” when
178 necrosis was >30-60% and “severe” for >60% necrosis, following the impact classification of
179 the T-MEDNet mass mortality database (e.g. Garrabou et al., 2019). In addition, we estimated
180 for each population and year: i) the daily extent of injury per colony (% of tissue necrosis), ii)
181 the daily percentage of affected colonies (>10% of tissue necrosis), and iii) the daily percentage
182 of dead colonies (100% tissue necrosis).

183 To model the response to thermal stress across years and populations, we computed a Principal
184 Component Analysis (PCA) with individuals and years as cases and the percentage of necrosis
185 per day as variables. A first exploratory PCA explained 50.29% of the variance and was
186 strongly correlated with the percentage of necrosis from day 10th to 28th (Figure S2a). To
187 improve the fitness of the data, days 1 to 9 were removed from the data set. Thus, the second
188 PCA explained 75% of the variance for the remaining days (Figure S2b). All PCAs were
189 performed with *PCA()* function from *FactoMineR* R package (R Core Team, 2022; Lê et al.,
190 2008). Scores from the second PCA were considered as a proxy for individual fitness as they
191 were correlated to the baseline percentages of necrosis. These scores were employed as
192 response variable for two linear models: 1) including ‘population’ and ‘year’ as predictor
193 variables (*i.e.* fixed factors); 2) using ‘individual’ as a random factor, added to the previous

194 predictor variables, and affecting only the model intercepts. Available data were not sufficient
195 to fit all the extra number of parameters (*i.e.* coefficients), thus the effect of the factor
196 ‘individual’ was not tested in the slope of the model. We consider the ‘individual’ effect in the
197 intercept as a different baseline of resistance to thermal stress. Linear models were fitted using
198 *lm()* and *lmer()* functions from the *stats* and the *lme4()* R-packages (Fox & Weisberg, 2019).
199 To meet the assumptions of residual normality and homoscedasticity, we transformed the
200 response variable with the Box-Cox transformation, implemented with the *boxcox()* function
201 from *MASS* R package (Venables & Ripley, 2002). These assumptions were tested with the
202 Shapiro-Wilks and Levene tests using *Shapiro.test()* and *leveneTest()* from *car* R-package (Fox
203 & Weisberg, 2019). The best model was selected based on AIC (Akaike information criterion)
204 using the function *anova()* (R Core Team, 2022) and a *post-hoc* Tukey test with the *glht()*
205 function from *multcomp* R-package (Hothorn et al., 2008). We estimated the percentage of the
206 contribution of each factor to the total variance computing the difference in log-likelihood
207 between models with and without each factor (individual, population, and year) pondered by
208 the degrees of freedom. The random intercepts obtained for every individual in the linear model
209 2 (hereafter “*nec-int*”) were used as a proxy for individual fitness to test for heterosis (see
210 below).

211

212 *Genetic components: population structure and individual heterosis.*

213 DNA extractions, genotyping protocols, microsatellite characteristics, quality check, and
214 analyses of genetic diversity are described in Supplementary information. We characterized
215 the genetic diversity and structure of the three sampling sites by genotyping 87 individuals
216 collected in at least two of the three years with 14 microsatellites.

217 We conducted a Discriminant Analysis of Principal Components (DAPC; Jombart et al., 2010)
218 from *adegenet* R-package (Jombart et al., 2010), by implementing the function *find_clusters()*

219 and specifying a maximum number of clusters with $max.n.clust = 3$. A maximum number of
220 100 PCs was chosen and the lowest value of Bayesian Information Criterion (BIC) was applied
221 to estimate the number of clusters. GENEPOP 4.1.4 (Rousset, 2008) was used to compute the
222 overall and pairwise F_{STs} estimators from Weir & Cockerham (1984). Genotypic differentiation
223 between sites was tested using an exact test (Raymond & Rousset, 1995) with default
224 parameters. In small and isolated populations, inbreeding depression can negatively impact
225 individual fitness constraining the response to ECEs (Fitzpatrick & Reid, 2019). Accordingly,
226 we estimated the genetic differentiation proper to each site by calculating the site-specific F_{ST}
227 and 95% High Probability Density Intervals in GESTE (Foll & Gaggiotti, 2006). The site-
228 specific F_{ST} estimates the relative impact of genetic drift on the differentiation of the considered
229 site relative to the remaining ones.

230 At the individual level, a positive correlation between heterozygosity and fitness-related traits,
231 known as heterosis, has been reported in some species (David, 1997). We looked for heterosis
232 in the response to thermal stress testing the correlation between the values of *nec-int* as proxy
233 for individual fitness and the standardized individual multilocus heterozygosities (*sMLH*)
234 computed using the R package *InbreedR()* (Stoffel et al., 2016). The slope of the linear model
235 [$lm(nec-int \sim sMLH)$] was compared to its null distribution obtained with a Monte-Carlo
236 permutation test with 10,000 permutations.

237

238 *Environmental component: summer thermal environments*

239 We analyzed and compared the *in situ* thermal regime at 15m depth experienced by the colonies
240 before sampling. Temperature data for Medes islands was obtained from the T-MEDNet
241 database, which follows a continuous temperature series since 2004 (von Schuckmann et al.,
242 2019). We assessed the recent summer local thermal regime calculated over the 3-months
243 period of June, July and August, prior to collection in September. We consider the timing and

244 magnitude of the daily temperature cycles and the exposure to warm conditions; thus we
245 considered the averages of maximum temperatures during the warmest periods of the year,
246 number of days with high temperatures and the ecological threshold T23 (*i.e.* number of
247 extreme heat days at $\geq 23^{\circ}\text{C}$). In addition, we considered positive temperature anomalies as the
248 number of marine heat spikes (MHS) above the Inter-annual percentile 90th (iT90 threshold)
249 lasting less than five days, while prolonged discrete periods of anomalously warm water
250 surpassing the iT90 percentile for more than 5 days, were considered as MHWs. Presence of
251 MHWs were detected with Python module *marineHeatWaves* (Hobday et al., 2016), while
252 impact categories registered at Medes islands were assigned following the classification of the
253 T-MEDNet database (Garrabou et al., 2019; Hobday et al. 2018). MHWs categories were set
254 as significant temperature foldchanges from the Inter-annual mean temperature and the iT90
255 threshold. Thus, “Low” classifications correspond to the temperature ranges between the inter-
256 annual mean temperatures and iT90, while “Moderate” are considered as a 1-2-fold, “Strong”
257 as a 2-3-fold and “Severe” as a 3-4-fold, respectively.

258

259 *Plastic component: ‘genotype-by-environment’ interactions and environmental sensitivity*

260 We estimated the variability in the ‘*genotype-by-environment*’ interactions by characterizing
261 the environmental sensitivity of each genotype following Falconer & Mackay (1996). We
262 computed three environmental values corresponding to the yearly mean phenotypes (*i.e.* mean
263 PCA scores over individuals for each year), considering the 66 genotypes present during the
264 three years. We then plotted each individual phenotype (PCA score) against the environmental
265 value for each year and we computed the regression slope, which is considered as an estimator
266 of the environmental sensitivity of the genotype (Falconer & Mackay, 1996). We used this plot
267 to classify the sensitivity of the genotypes in three categories adapted from Bonacolta et al.
268 (2024). Resistant genotypes were expected to show low intercepts in the first year and

269 approximated null slopes (*i.e.* low and constant level of necrosis in the 3 experiments). Hyper-
270 sensitive genotypes were expected to show high intercepts in the first year and null slopes (*i.e.*
271 high and constant level of necrosis in the 3 experiments). Finally, sensitive genotypes were
272 expected to show low intercepts in the first year and positive slopes (*i.e.* increasing level of
273 necrosis through time).

274

275 *Field survey of necrosis rates following 2018-2022 MMEs:*

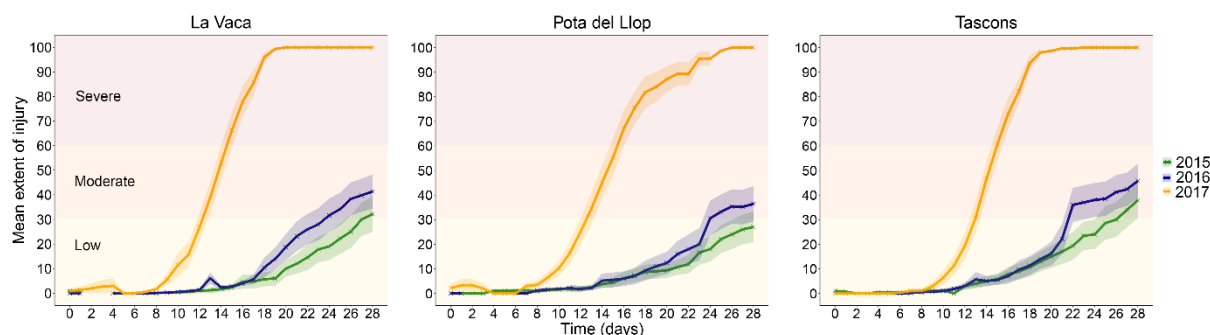
276 Medes Islands were impacted by two MHWs in 2018 and 2022 with associated mass mortality
277 events (Garrabou et al., 2022; Zentner et al., 2023). We surveyed by scuba diving the
278 percentage of tissue necrosis *in situ* for the same individuals used in the experiments. This
279 survey was done in October 2022. Differences in mean tissue necrosis of colonies between
280 populations were tested using a parametric one-way ANOVA, followed by *post hoc* Tukey's
281 HSD tests.

282

283 **Results**

284 *Phenotypic responses of P. clavata during the three common garden experiments*

285 Signs of tissue necrosis were observed for all populations in the three years. In 2015 and 2016,
286 the mean extent of injury was of moderate impact with values below the 60% at the end of the
287 experiment (day 28th; mean \pm SE): 32.14% \pm 7.25 and 38.33% \pm 6.67 for La Vaca; 27.03% \pm
288 6.20 and 35.16% \pm 7.09 for Pota del Llop and 37.89% \pm 7.26 and 41.2% \pm 6.91 for Tascons
289 (Figure 2). On the contrary, in 2017, colonies showed severe impacts with >60% of average
290 tissue necrosis earlier by day 14th in all populations, and all colonies died by day 18th (100% of
291 tissue necrosis) with the exception of Pota del Llop which reached 100% of tissue necrosis by
292 day 24th (Figure 2).



293

294 **Figure 2.** Average tissue necrosis (mean extent of injury \pm SE) of *P. clavata* colonies during
295 the 28 days of exposure in common garden experiments for La Vaca, Pota del Llop, and
296 Tascons in 2015 (green), 2016 (blue) and 2017 (yellow). Mortality severity is highlighted in
297 light yellow (low), orange (moderate), and red (severe).

298

299 *Individual fitness: modelling the response to thermal stress*

300 The linear model 2 including the random factor ‘individual’ was retained (lowest statistically
301 significant AIC = 710.88; df = 7 [Chi-square = 15.5, $p < 0.001$]). The ‘individual’ random
302 factor had a significant effect, suggesting that each individual has a different baseline of
303 resistance to necrosis. Regarding the fixed factors of the model, the deviance test showed that
304 only the ‘year’ factor was significant (Table S2a), while *post-hoc* Tuckey test showed that
305 significant differences were due to the year 2017 (Table S2b). The factor ‘year’ was
306 contributing to 95.01% of the variance of the data, followed by the random factor ‘individual’
307 with a contribution of around 11 times less (4.1%). Finally, ‘population’ and ‘population-by-
308 year interaction’ were non-significant and showed the lowest contributions: 0.5% and 0.39%,
309 respectively.

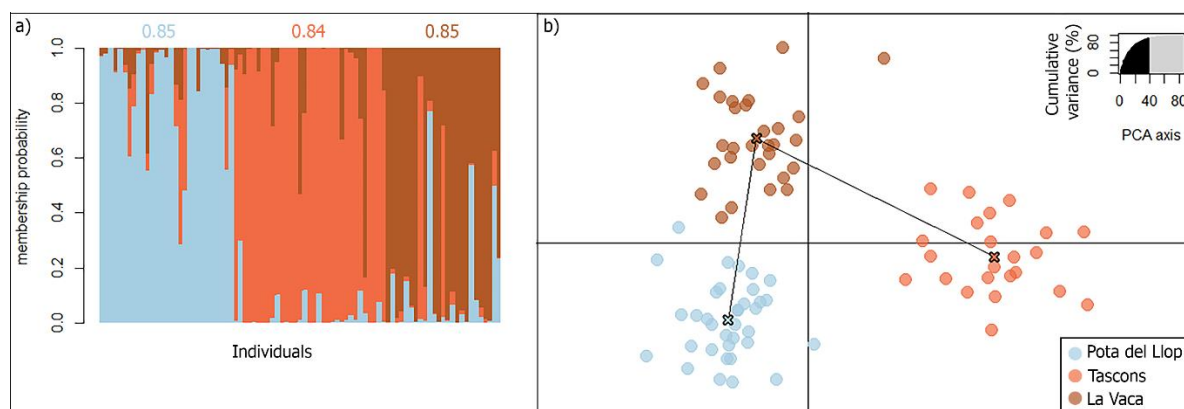
310

311 *Genetic component: Genetic structure and individual heterosis.*

312 Results on heterozygosity, Hardy-Weinberg equilibrium, allelic richness, and linkage
313 disequilibrium can be found in the Supplementary information (Tables S3 and S4, Figure S3).

314 Three distinct genetic clusters matching the three populations in Medes islands were retrieved

315 from the DAPC analysis with high mean membership probabilities over 84% for each cluster
316 (Figure 3).



317
318 **Figure 3. a)** Individual membership probabilities are represented by a vertical line, where the
319 different color segments indicate the individual proportion to each cluster ($K=3$) as estimated
320 by the discriminant analysis of principal components (DAPC): Pota del Llop (light-blue),
321 Tascons (orange) and La Vaca (brown). Mean membership probabilities are given above each
322 colored cluster **b)** Scatter plot of the DAPC: each dot corresponds to one individual ($N=87$)
323 from each of the three populations.

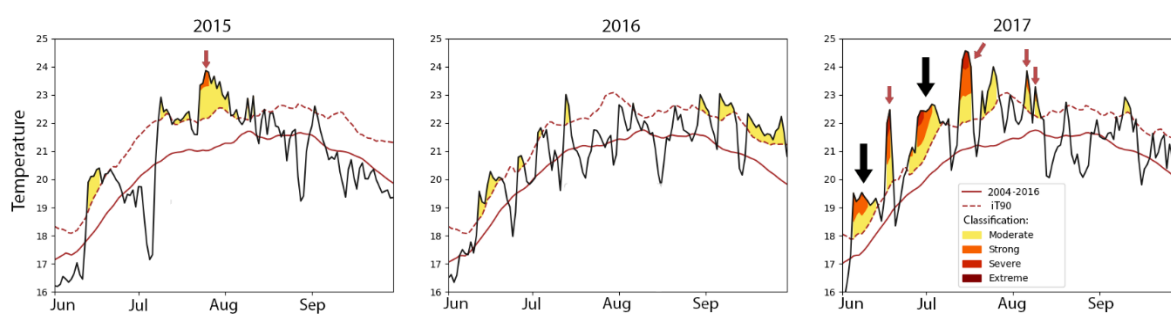
324
325 Overall, genetic differentiation was low but significant (global $F_{ST}=0.015$, $p<0.001$). All
326 pairwise F_{ST} s were significant: La Vaca vs Pota del Llop (0.013; $p<0.001$), La Vaca vs Tascons
327 (0.020; $p<0.001$), Pota del Llop vs Tascons (0.035; $p<0.001$). The analysis of site-specific F_{ST} s
328 suggested that Tascons was the most differentiated population (0.06, 95%HPDI: [0.030;
329 0.073]), followed by La Vaca (0.04, 95%HPDI: [0.022; 0.059]) and Pota del Llop (0.04,
330 95%HPDI: [0.021; 0.051]), albeit the differences were not significant (overlapping 95%HPDI;
331 Table S5).

332 The standard multilocus heterozygosity (sMLH) ranged from 0.294 to 0.882 (Figure S4). The
333 correlation between sMLH and “*nec-int*”, the proxy for individual fitness (random intercepts
334 extracted from linear model 2), was not significant ($r^2 = 0.001$, p -value = 0.66, Figure S5 and
335 Table S6).

336

337 *Environmental component: thermal environments*

338 Recent thermal history patterns, considered as June, July and August, revealed similar mean \pm
339 SD temperatures for the three years: $21.3^{\circ}\text{C} \pm 1.6$ in 2015, $21.6^{\circ}\text{C} \pm 1.0$ for 2016 and $21.8^{\circ}\text{C} \pm$
340 1.3 for 2017 (Table S7). Concomitantly, extreme heat days (T23) were detected in all years
341 during the summer season (Table S7). For 2015 and 2016, at 15m depth, maximum summer
342 temperatures reached 24.8 and 23.5°C , respectively, and a low number of total extreme heat
343 days exposure to $\geq 23^{\circ}\text{C}$ was recorded (N=12 for 2015 and N=2 for 2016; Table S7, Figure S6a-
344 b). The years 2015 and 2016 revealed several periods of anomalous high temperatures during
345 the summer season, but no MHWs (Figure 4, Table S8). Interestingly, the year 2017 reported
346 the highest maximum temperatures of 24.9°C with a total of 19 days of exposure at extreme
347 temperatures ($\geq 23^{\circ}\text{C}$), surpassing the thermal limit of *P. clavata* (Table S7, Figure S6). In
348 addition, unlike for 2015 and 2016 where no MHW occurred, two MHWs occurred in 2017
349 with strong, and severe classifications from June to July and several heat spikes (Figure 4). The
350 mean maximum temperature for these MHW was 24.1°C (Table S8).



351

352 **Figure 4.** Daily mean temperature values recorded at 15m from June to September (Summer
353 season) at Medes Islands with respect of the inter-annual climatological mean (red solid line)
354 and 90th percentile (iT90, red dotted line). Days below the red solid line were considered as
355 “cool days”, whereas days above were considered as “warm days”. Following Hobday et al.
356 2018, marine heat waves and heat spikes (MHW and MHS) severity classification is as follows:
357 “Moderate” (yellow), “Strong” (orange), “Severe” (red), and “Extreme” (dark-red). MHW are
358 highlighted with a black arrow and MHS are highlighted with red arrows. Data taken from the
359 T-MEDNet initiative (<https://t-mednet.org/>).

360

361 *Plastic component: 'genotype-by-environment' interactions and environmental sensitivity*

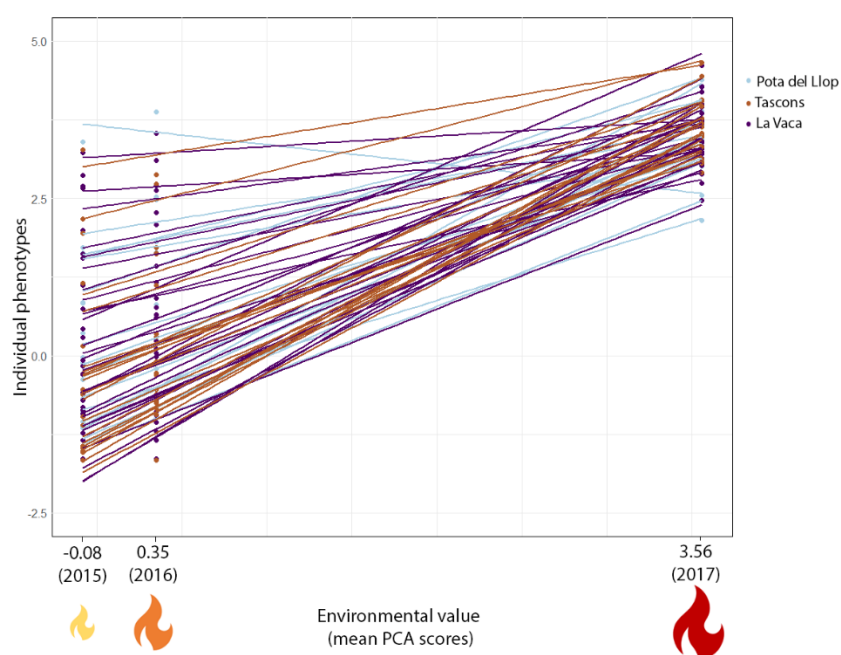
362 Regarding the sensitivity analyses, environmental values (yearly mean PCA scores) were -0.08

363 ± 1.46 for 2015, 0.34 ± 1.55 for 2016, and 3.56 ± 0.55 for 2017. All individuals but one show

364 positive slopes ranging between 0.16 and 1.65. Environmental sensitivity varied by a factor of

365 10 among individuals (Figure 5). Following our classification, genotypes were shared among

366 hyper-sensitive and sensitive categories with no resistant genotypes (Figure 5).



367

368 **Figure 5.** Sensitivity analyses and *genotype-by-environment* interactions of *P. clavata* during
369 2015, 2016 and 2017 experiments. Individual ecological response (PCA scores) was plotted
370 against each environment value (mean PCA score by year). The slope of the regression for each
371 individual is considered as an estimator of the environmental sensitivity of the individual.
372 Populations are displayed in colors: Pota del Llop (light-blue), Tascons (brown), and La Vaca
373 (purple).

374

375 *Field survey of necrosis rates following 2018 and 2022 MMEs:*

376 We encountered 17, 22, and 21 colonies out of the 30 colonies initially marked in Pota del

377 Llop, Tascons, and La Vaca, respectively. Six, three, and five colonies were not impacted (0%

378 of necrosis) in La Vaca, Pota del Llop, and Tascons (Figure S6a). All the remaining colonies

379 showed recent necrosis (>70%), albeit with different levels of impact (low, moderate, and
380 severe, Figure S6a). Statistically significant differences were found in average tissue necrosis
381 by population ($F=4.295$, $p<0.018$). Pota del Llop displayed the largest percentages of tissue
382 necrosis ($30.88\% \pm 37.22$), followed by Tascons ($28.63\% \pm 32.48$) and La Vaca ($7.38\% \pm$
383 6.25 ; Figure S6b). Finally, low impacts (<30%) were observed in all populations with seven,
384 eight, and fifteen colonies in Pota del Llop, Tascons, and La Vaca (Figure S6a). This latter
385 population did not report additional higher impacts while severe impacts (>60% tissue necrosis,
386 including dead colonies) were observed in Pota del Llop and Tascons with four (three dead)
387 and three (two dead) severely impacted colonies, respectively (Figure S6a).

388

389 **Discussion**

390 We combined replicated experiments, population genetics, and an *in-situ* field survey to reveal
391 the prominent influence of the environmental component (likely yearly variations in summer
392 thermal regime) on the heterogeneity in ecological responses to thermal stress in *P. clavata*.
393 The low influence of genetic and plastic components combined to the high environmental
394 sensitivity of the tested genotypes point toward a dramatically low adaptive potential to
395 recurrent MHWs. This “multi-event” perspective strengthens the recent call to carefully
396 consider predictions on biodiversity evolution based on single-event experiments.

397

398 **The heterogeneity in the ecological response to thermal stress is mostly driven by the**
399 **thermal regime during summer.**

400 The three populations of *Paramuricea clavata* showed high levels of tissue necrosis (moderate
401 to severe mortality) at the end of each experiment confirming the species sensitivity to thermal
402 stress (Crisci et al., 2017; Gómez-Gras et al., 2022). The ecological responses were similar
403 between populations in 2015 and 2016 (moderate mortality) compared to 2017, in which

404 colonies died before the end of the experiment (severe mortality). More than 95% of the
405 variance in the ecological response was explained by the factor year (environmental
406 component), while factors individual, population (genetic component), and the population-by-
407 year interaction (plastic component) explained only 4.1%, 0.5%, and 0.39%, respectively.
408 Factors individual and year (environmental component) were significant, which suggests
409 different baselines of resistance to thermal stress among individuals and confirms the major
410 environmental effect, mostly driven by the year 2017. This environmental effect was refined
411 by the sensitivity and thermal regime analyses. First, the environmental value (mean
412 phenotype) for 2017 was two to three times higher than the values for 2015 and 2016. Then,
413 we reported positive regression slopes for almost all genotypes supporting an increased
414 negative impact of environmental conditions (environmental sensitivity) from 2015 to 2017.
415 Summer conditions during 2017 showed the largest number of MHS and MHWs compared to
416 2015 and 2016. Consequently, we posit that colonies of *P. clavata* were driven close to their
417 physiological limits by the 2017 extreme summer conditions, which may have hampered any
418 adjustment to thermal stress, whether genetic or plastic, during the experiment.

419 The relative impact of environmental, genetic, and plastic components in differential responses
420 to ECEs has been screened in different species. For example, ubiquitous *population-by-*
421 *environment* interactions (plastic component) have been detected in 172 species of plants
422 (Matesanz & Ramírez-Valiente, 2019), but are lacking in others (Shao et al., 2022). Single
423 event experiments with tropical corals identified local adaptation (*e.g.* Thomas et al., 2022) and
424 adaptive plasticity (*e.g.* Drury et al., 2022) as drivers of differential bleaching responses. Here,
425 we found relatively similar and high levels of necrosis among populations with a prevailing
426 impact of the environmental component. These findings contrast to our previous studies based
427 on “single event” experiments at larger spatial scales where differential ecological responses
428 (distinct necrosis levels) were observed among populations in some cases (Arizmendi-Mejía,

429 et al., 2015a; Arizmendi-Mejía et al., 2015b; Bonacolta et al., 2024; Crisci et al., 2017; Gómez-
430 Gras et al., 2022). Two non-exclusive hypotheses relying on the spatial and temporal features
431 of the experiments might explain this apparent discrepancy.

432

433 **Intraspecific differences in the response to thermal stress: does the geographic scale**
434 **matter or are recent summer conditions overwhelming *P. clavata* physiological**
435 **capacities?**

436 The experiments conducted to date in *P. clavata* have considered a wide range of geographic
437 distances, from local to regional (Arizmendi-Mejía et al., 2015b; Crisci et al., 2017) and inter-
438 regional (Bonacolta et al., 2024; Gómez-Gras et al., 2022) scales. These experiments
439 demonstrated population heterogeneity in ecological responses to thermal stress triggered by
440 different drivers (*e.g.* genetic isolation, microorganisms). Considering that the impact of the
441 genetic component on ecological responses can vary over spatial distances (*e.g.* Galloway &
442 Fenster, 2000; Joshi et al., 2001), we hypothesize that the lack of significant population effect
443 observed here can be related to the fine spatial scale of the experiment, which flattened the
444 differences between populations. Contrary to previous experiments, we targeted three
445 populations from similar habitats at the same depth range in a close spatial proximity (hundreds
446 of meters). The potential for contrasted genetic make-up at such fine spatial scale is low (but
447 see Ledoux et al., 2015; Richardson et al., 2014) as supported by the comparable levels of
448 genetic isolation of the three populations (overlapping population-specific F_{ST} s). Re-analyzing
449 the different experiments in *P. Clavata* accounting for ecological or spatial distance between
450 populations should allow to go further in this hypothesis.

451 Considering a temporal perspective, the discrepancy among experiments in *P. clavata* can
452 result from an intensification of extreme climatic events from summer 2009 (Crisci et al., 2017)
453 to summer 2019 (Gómez-Gras et al., 2022) and summer 2022 (this study; Rovira et al. 2024),

454 which could have driven the colonies closer to their physiological limits in the later and warmer
455 years. That is, the summer thermal regime previous to the first experiment (summer 2009,
456 Crisci et al., 2017) was less stressful than the 2017 summer thermal regime (this study)
457 allowing some colonies to face the 2009 experimental stress while colonies were totally swept
458 by the 2017 experimental stress. Three main points support this hypothesis. First, the
459 environmental sensitivity analysis considering 2015, 2016, and 2017 experiments clearly show
460 a decrease in the variation of phenotypic responses among the individuals and an increase of
461 the yearly environmental value between 2015/2016 and 2017. Individuals that showed
462 relatively low necrosis in the first two years were as strongly impacted in 2017 (positive
463 regression slopes) as individuals showing high necrosis during the first two experiments
464 (regression slopes ~ 0). Second, necrosis was observed in a vast majority of the marked
465 colonies in the three populations (>70%) during the field survey following the 2018 and 2022
466 MHWs. Third, one of the strongest mortality events ever observed was reported in 2022
467 (Estaque et al., 2023, Rovira et al. 2024) corroborating the rise in MHWs in the Mediterranean.
468 Strengthening this hypothesis, the intensification of disastrous ECEs in the last decades is not
469 peculiar to the Mediterranean (see Stillman, 2019). The frequency of bleaching events in
470 tropical corals increased worldwide since 1980 (Hughes et al., 2018), with detrimental
471 cumulative effects of heatwaves in the last ten years (Hughes et al., 2021).

472

473 **What's next for shallow populations of *P. clavata*?**

474 Our results question the persistence of the studied shallow populations of *P. clavata*. Both the
475 experiments and field surveys conducted here supported a limited potential adaptability
476 whether based on genetic or plastic component. Yet, we revealed some variability in the
477 baseline ecological responses at the individual levels (4.1%). While this individual variability
478 may have been seen as a hopeful “raw material” for adaptation to MHWs, the sensitivity

479 analyses and the field survey showed how it was almost totally squeezed in 2017 (experiment)
480 and 2022 (in the field). Dedicated studies combining population genomics, environmental, and
481 mortality data are needed to further look for genome-environment associations, potential
482 outlier loci involved in the differential responses and to estimate of the genomic offset of *P.*
483 *clavata*. However, the lack of clear adaptive potential revealed here combined to the species
484 life history traits (*e.g.* generation time >12 years, Coma et al., 1995) are such in a contrast with
485 the current MHWs temporal dynamics that any evolutionary response seems compromised.
486 The potential for adaptation is also questioned in tropical corals in which candidate genetic loci
487 identified to date only show relatively elusive influence on heat stress tolerance (Fuller et al.,
488 2020, but see Matz et al., 2020). In the same collapsing line, the absence of *population-by-*
489 *environment* interactions suggest limited potential for evolutionary changes in adaptive
490 plasticity (Sirovy et al., 2021). Recent studies point towards ecological memory, an increase in
491 stress tolerance following previous exposure, as a key mechanism for coral acclimation to
492 MHWs (Hackerott et al., 2021; Hughes et al., 2018). Yet, results are contrasted among species
493 with a decrease in bleaching sensitivity following repeated heat stress in some species but not
494 in others (Brown et al., 2023; Hughes et al., 2021). Our study allows first insights into *P.*
495 *clavata* environmental memory. First, colony fragments used in a particular year were
496 submitted to summer thermal conditions of the previous years. Yet, the worst ecological
497 responses to thermal stress were observed during the last experiment in 2017 with high
498 environmental sensitivity (positive slopes and lack of resistant genotypes in the sensitivity
499 analyses). Then, most marked colonies showed necrosis during the field surveys following
500 2018 and 2022 MHWs events. These results question any increase in thermotolerance as
501 expected with the ecological memory hypotheses and strengthen the limited potential for
502 adaptation in *P. Clavata*.

503

504 **Conclusion**

505 As temperature and frequency of ECEs continue to rise (Hughes et al., 2021; Garrabou et al.,
506 2022), the evolution of biodiversity is more than ever a central concern for society. Adopting
507 a “multi-event” perspective that combined replicated common-garden experiments in aquaria
508 and mortality surveys in the field performed on the same colonies, our study points toward an
509 inevitable collapse of many of the shallow populations of *P. clavata*. This collapse would
510 emerge from a low to non-existent adaptive response, whether driven by genetic or plasticity,
511 combined to a high environmental sensitivity and a potential intensification of MHWs.
512 Considering the small spatial scale of our study, extrapolation at larger scale should be made
513 cautiously. Yet, population collapses of *P. clavata* linked to recurrent MHWs have been
514 observed in other Mediterranean regions (Garrabou et al., 2021; Gómez-Gras et al., 2021b).
515 Moreover, field surveys following the 2022 MHW event in this and in other regions reported
516 terrific mortality rates. Other populations from the same region showed a similar proportion of
517 total affected colonies (70%) with almost 40% of the tissue necrosis (Rovira et al. 2024).
518 Hundreds of km apart, populations until 20m depth displayed on average >80% of affected
519 colonies and an increase by 142% of the degree of impact following the 2022 MHW compared
520 to the previous MME in 2003 (Estaque et al., 2023). Worrying, this trend in *P. clavata* could
521 likely be transposable to many of the Mediterranean habitat-forming and sessile species
522 impacted by MHWs (Garrabou et al., 2022; Gómez-Gras et al., 2021a). We predict a shift in
523 these species’ upper distribution limits, which will lead to a simplification of associated benthic
524 communities hampering potentially related ecosystem functions and services (Gómez-Gras et
525 al., 2021a).

526 This study echoes two recent calls regarding the future of marine diversity in the context of
527 extreme climatic events. First, the impacts of ECEs on biodiversity should be studied from a
528 temporal perspective, which accounts for their recurrence (Hughes et al., 2021). In this line,

529 we suggest that predictions of biodiversity evolution based on “single event” approaches
530 should be considered cautiously as they can be overly optimistic. Then, while conservation and
531 restoration actions should be able to slow, and/or to some extent reverse, locally the collapsing
532 trend followed by many marine habitat-forming species, immediate action on greenhouse gas
533 emissions remains the only way to protect these species globally.
534

535 **Author's contributions**

536 **Sandra Ramirez-Calero:** Conceptualization, data curation, data analysis, writing original
537 draft. **Daniel Gomez-Gras:** experimental setup, data collection, write – review and editing.
538 **Aldo Barreiro:** data analysis and validation, write – review and editing. **Nathaniel**
539 **Bensoussan:** data collection and validation, review and editing. **Laura Figuerola-Ferrando:**
540 data collection, experimental setup, review and editing. **Marc Jou:** data visualization, review
541 and editing. **A Lopez-Sanz:** data collection, experimental setup, review and editing, **Paula**
542 **Lopez-Sendino:** data collection, experimental setup, review and editing. **Alba Medrano:** data
543 collection, experimental setup, review and editing. **Ignasi Montero-Serra:** data collection,
544 experimental setup, data analysis, review and editing. **Marta Pages-Escola:** data collection,
545 experimental setup, review and editing. **Cristina Linares:** data collection, review and editing,
546 funding acquisition. **Jean-Baptiste Ledoux:** conceptualization, data collection, experimental
547 setup, data analysis, write – review and editing, funding acquisition. **Joaquim Garrabou:**
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567

568 **Conflict of interest statement**

569 The authors declare no conflict of interest.

570

571 **Data availability statement**

572 The data that support the findings of this study are openly available in the GitHub repository:
573 “Pclavata_rec_MHW” at https://github.com/sandraracr/Pclavata_rec_MHW.git (2024)
574 including ecological data, linear models and genetic structure analysis. Temperature data and
575 associated analysis can be found in “tmednetGUI” GitHub repository at
576 <https://github.com/Damyck/tMednet.git> (2024), using the scripts: *surface_temperature.py*,
577 *data_manager.py*, *user_interaction.py* and *excel_writer.py*. Finally, microsatellite loci
578 information can be found under accession numbers GU386255–GU386265 in the Molecular
579 Ecology Resources Database and GeneBank (<https://10.1111/j.1755-0998.2010.02871.x>).

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