Characterizing the adaptive potential of north-western Pacific reef corals to empower conservation strategies: a role for seascape genomics

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Abstract (300w, last sentence focus on global change)

Coral reefs are suffering a major decline due to the environmental constraints imposed by climate change. Over the last 20 years, three major coral bleaching events occurred in concomitance of anomalous heat waves, provoking a severe loss of coral cover world-wide. Recent works, however, reported of reefs at which recurrent bleaching events resulted in reduced sensitivity to thermal stresses. Adaptation has been suggested to be responsible for this phenomenon. The conservation strategies for preserving the reefs, as they are conceived now, can not cope with global climatic shifts. In this regard, researchers advocated the set-up of a preservation framework to reinforce coral adaptive potential. The main obstacle to this approach is that studies focusing on coral adaptation usually concern a couple of contrasted reefs and their results are therefore hard to generalize at the scale of a reef system. In this work, we ran a seascape genomics analysis to study adaptation of a flagship coral species of the Ryukyu Archipelago (Japan). By associating genotype frequencies with descriptors of historical environmental conditions, we discovered six polymorphisms that might elicit resistance against thermal stress and calculated the probability of presence of these putative adaptive traits across the whole study area. Furthermore, the seascape genomics method allowed us to calculate a connectivity model based on sea surface currents and calibrated on genetic data. These results were used to compute, for every reef of the Ryukyu Archipelago, indexes describing corals adaptive and connective potential. This information can be extremely useful for preservation, since it provides an objective information on how the adaptive potential distributes and disperse across the reef system. Finally, we provide two examples of how this information can be implemented in conservation strategies commonly used such as the establishment of marine protected areas and coral nurseries. Together, the results of our work advocate the value of genetic analyses for empowering preservation efforts dedicated to the protection of coral reef from warming oceans.

Introduction

Coral reefs are suffering a severe decline due to the effects of climate change (Hughes et al., 2017). Loss of reef is already having catastrophic consequences for marine wildlife depending on these structures (Pratchett, Thompson, Hoey, Cowman, & Wilson, 2018) and disastrous

aftermaths are expected for human economies as well (Moberg & Folke, 1999). One of the major threat to the persistence of this ecosystem is coral bleaching (Bellwood, Hughes, Folke, & Nyström, 2004): a physiological response induced by environmental stress that provokes hard-skeleton coral, the cornerstone of the reef, to separate from the symbiotic microbial algae living within their cells (Mydlarz, McGinty, & Harvell, 2010). These algae, called Symbiodiniacea (LaJeunesse et al., 2018), are crucial for the host sustainment and therefore a persistent bleached state leads coral to death (Mydlarz et al., 2010). Three mass bleaching events occurred over the last 20 years in concomitance to anomalously high sea water temperatures, reason why thermal stress is now considered the main driver of this phenomenon (Hughes et al., 2017). These events struck world-wide and lead, under their most severe occurrences, to local losses of coral cover up to 50% (Hughes et al., 2018, 2017). Besides, coral bleaching was found to be associated to other stressors associated to human activity, such as ocean acidification, water eutrophication, sedimentation and overfishing (Anthony, Kline, Diaz-Pulido, Dove, & Hoegh-Guldberg, 2008; Ateweberhan et al., 2013; Maina, Venus, McClanahan, & Ateweberhan, 2008).

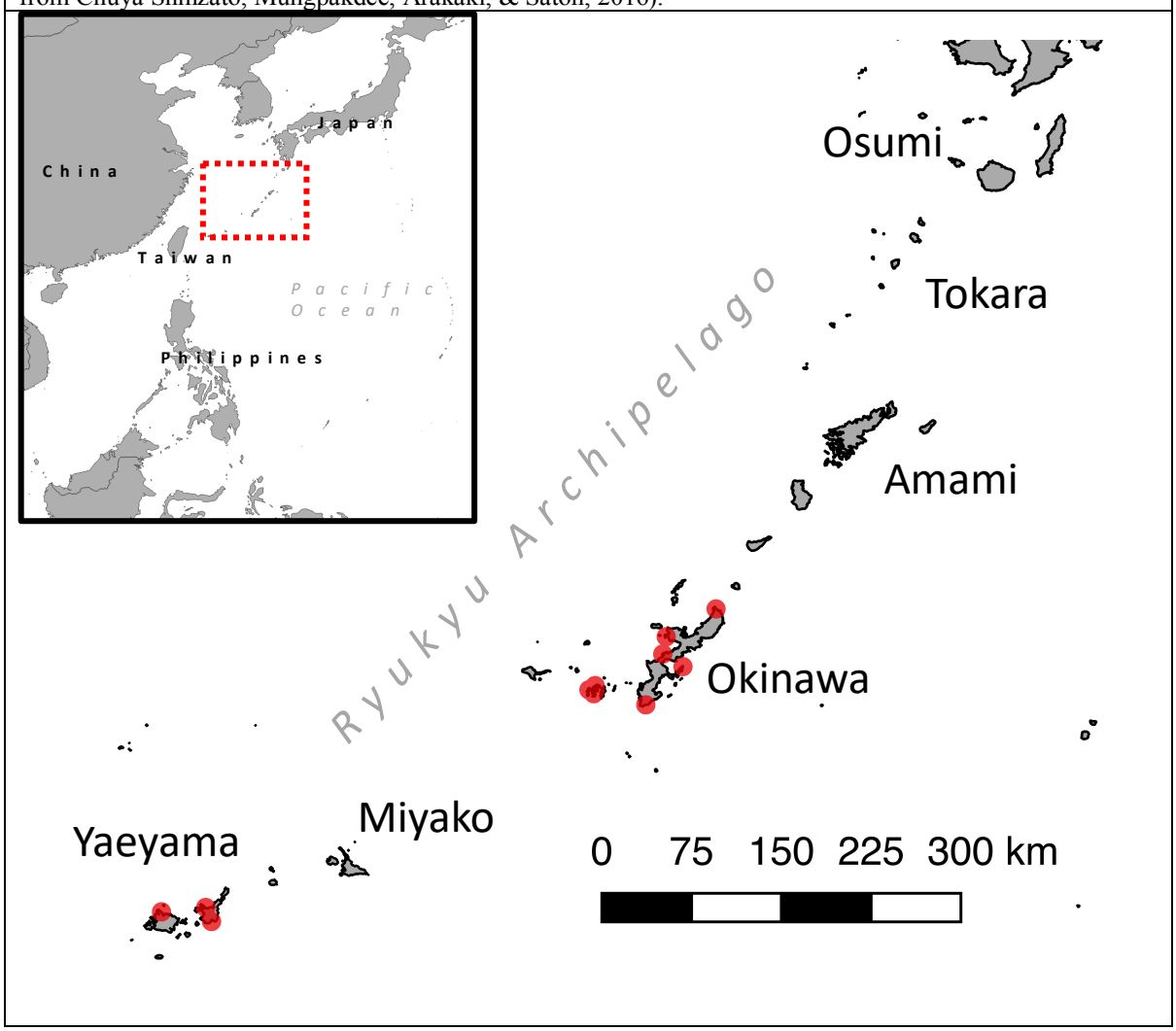
Conservation efforts facing the plague of coral bleaching aim to restore reefs that underwent severe losses and to limit the impact of future damages (Baums, 2008; Bellwood et al., 2004; Young, Schopmeyer, & Lirman, 2012). To these purposes, two tools are nowadays usually employed: the establishment of marine protected areas (MPAs) and the set-up of coral nurseries (Baums, 2008; Bellwood et al., 2004; Young et al., 2012). MPAs are designed zones in which human access and activities are severely restricted in order to alleviate the effects of local anthropogenic stressors (Lester et al., 2009). Coral nurseries are underwater gardens of transplanted colonies that can be then be employed to restore damaged reefs (Baums, 2008; Young et al., 2012). For both these strategies, researchers advocated the use of design systems accounting for demographic connectivity so that the position of a conservation measure can

75 promote resistance and resilience even on neighbouring sites (Baums, 2008; Krueck et al.,
76 2017; Lukoschek, Riginos, & van Oppen, 2016; Palumbi, 2003; Shanks, Grantham, & Carr,
77 2003). Even though beneficial effects of this kind of conservation policies have been observed
78 worldwide (Cinner et al., 2016; Rodgers et al., 2017; Selig & Bruno, 2010) these solutions, as
79 they are conceived now, can not confer resistance against the temperature oscillations
80 associated to the last mass bleaching events (Baums, 2008; Hughes et al., 2017). Coral reefs
81 that experienced past thermal stress were found to be more resistant to subsequent heat waves
82 (Hughes et al., 2019; Penin, Vidal-Dupiol, & Adjeroud, 2013; Thompson & van Woesik, 2009)
83 but to date this information is missing from conservation planning (Baums, 2008; Maina,
84 McClanahan, Venus, Ateweberhan, & Madin, 2011). There is an urgent need of understanding
85 whether these observations are due to evolutionary processes and, if so, to figure out how the
86 underlying adaptive potential could be included in predictions of climate change responses and
87 in conservation plans (Baums, 2008; Logan, Dunne, Eakin, & Donner, 2014; Maina et al.,
88 2011; van Oppen, Oliver, Putnam, & Gates, 2015).
89 Landscape genomics is a branch of population genomics that investigates adaptive potential in
90 field-based experiments (Balkenhol et al., 2017; Rellstab, Gugerli, Eckert, Hancock, &
91 Holderegger, 2015). Samples are collected across a landscape and then genotyped using next-
92 generation-sequencing techniques, resulting in the discovery of thousands of genetic
93 variants(Rellstab et al., 2015). At the same time, an environmental characterization of the study
94 area is usually derived from remote-sensing data describing specific climatic conditions
95 (Rellstab et al., 2015). Genomic and environmental information are then combined in order to
96 detect genetic polymorphisms associated to peculiar conditions (*i.e.,* potentially adaptive traits;
97 Rellstab et al., 2015). This approach has been already used on many land species and is
98 becoming more and more frequent on marine animals in what is referred to as *seascape*
99 *genomics* (exhaustively reviewed in Riginos, Crandall, Liggins, Bongaerts, & Treml, 2016).

100 To our knowledge, there are yet no reports concerning seascape genomics experiments on reef
101 corals. In fact, adaptation of these species has been mostly studied by performing
102 transplantation assays followed by conditioning in aquarium, a time and resource-demanding
103 approach that often focuses on a couple of contrasting reef (Howells, Berkelmans, van Oppen,
104 Willis, & Bay, 2013; Krueger et al., 2017; Palumbi, Barshis, Traylor-Knowles, & Bay, 2014;
105 Sampayo et al., 2016; Ziegler, Seneca, Yum, Palumbi, & Voolstra, 2017). There have also been
106 genotype-environment associations studies concerning corals but they focused on a limited
107 number of markers (Lundgren, Vera, Peplow, Manel, & van Oppen, 2013) or on a restricted
108 number of locations (Bay & Palumbi, 2014; Thomas, Kennington, Evans, Kendrick, & Stat,
109 2017). Contrarily to these works, a seascape genomics approach should cover ecologically
110 meaningful spatial scales, allowing to distinguish pressures of different climatic conditions and
111 to account for confounding effects of demographic processes (Balkenhol et al., 2017). By
112 consequence, the main (adaptive) and collateral (connectivity) information offered by this
113 method provide a valuable contribution for preservation strategies (Baums, 2008; Krueck et
114 al., 2017; Palumbi, 2003).
115 In this work we applied a seascape genomics framework to detect reefs carrying potential
116 adaptive traits and show how conservation policies could implement such findings. Our study
117 focused on *Acropora digitifera* of the Ryukyu Archipelago in Japan (Fig. 1), an emblematic
118 species of the Indo-Pacific and flagship organism for studies on corals genomics (C Shinzato
119 et al., 2011). In the first part of our work, we analysed the convergence between genomics and
120 environmental information to detect loci potentially conferring selective advantages and to
121 develop a model describing connectivity patterns. Next, we took advantage of these findings
122 to indicate which reefs were more likely to be carrying adaptive traits and to evaluate how well
123 such sites are interconnected with the rest of the reef system. Finally, we displayed how
124 conservation planning can implement these results. Together, our work provides tools at the

interface between conservation genomics and environmental sciences that can empower preservation strategies for coral reefs.

Figure 1. The Study Area. The Ryukyu Archipelago extends for more than 1,000 km in north-western Pacific. The red circles display the sites from which samples for the seascape genomics analysis were collected (adapted from Chuya Shinzato, Mungpakdee, Arakaki, & Satoh, 2016).



Materials and methods

Genomics Dataset

The genomics data we used comes from a publicly available dataset of 155 geo-referenced colonies of *A. digitifera* from 12sampling locations of the Ryukyu Archipelago in Japan (Fig. 1; Bioproject Accession PRJDB4188). Samples from this project were sequenced using a whole-genome-sequencing approach in the scope of a population genomics study. Details on

134 how samples were collected and processed for genomics analysis can be found in the
135 corresponding report (Chuya Shinzato et al., 2015).
136
137 *SNP discovery pipeline*
138 Genomics data was processed using the GATK framework following the recommended
139 pipeline with some modifications to cope with the absence of reliable databases of known
140 variants for this species (McKenna et al., 2010; Van der Auwera et al., 2013). In short, the *A.*
141 *digitifera* reference genome (v. 1.1, GenBank accession: GCA_000222465.2; C Shinzato et
142 al., 2011) was indexed using bwa (v. 0.7.5a, Li & Durbin, 2009), samtools (v. 1.9, Heng Li et
143 al., 2009) and picardtools (v. 1.95, http://broadinstitute.github.io/picard) and raw sequencing
144 reads were aligned against it using the bwa *mem* algorithm. The resulting alignments were
145 sorted, marked for duplicate reads, modified for read-group headers and indexed using picard-
146 tools. Next, each underwent an independent variant discovery using the GATK
147 HaplotypeCaller tool (using the ERC mode and setting the --minPruning flag to 10) and
148 genotypes were then jointly called by the GenotypeGVCFs tool in random batches of 18
149 samples to match our computational power (18 CPUs). The variant-calling matrices of the
150 different batches were then joined and filtered for keeping only bi-allelic Single Nucleotide
151 Polymorphisms (SNPs) using the GATK CombineVariants and SelectVariants tools,
152 respectively. This resulted in a raw genotype matrix counting ~1.2 M of SNPs. Subsequently,
153 we used the GATK VariantAnnotator tool to annotate variants for Quality-by-depth and filtered
154 for this value (<2), read coverage (>5 and <100 within a sample), minor allele frequency
155 (>0.05), major genotype frequency (<0.95) and missing rate of both individuals and SNPs
156 (<0.1) using the GATK VariantFiltrationTool and custom scripts in the R environment (v.
157 3.5.1, R Core Team, 2016). This pipeline produced the filtered genotype matrix counting 136
158 individuals and 15,516 SNPs.

Environmental Data

Eleven geoinformatics products describing atmospheric and seawater conditions were retrieved from publicly available resources (EU Copernicus Marine Service, 2017; NASA, 2016; National Oceanic and Atmospheric Administration, 2017; Tab S1). This data was remote-sensing derived and therefore provided, for each variable, temporal measurements (monthly or daily over several years) across the whole study area at a resolution usually below 10 km. We processed these products in the R environment using the *raster* package (v. 2.8, Hijmans, 2016) to compute averages and standard deviations by month and for the whole studied period. Furthermore, Sea Surface Temperature (SST) measurements were used to compute a Degree Heat Week (DHW) frequency index, representing the % of days in which the bi-weekly accumulated heat stress exceeded the 4 °C (Liu, Strong, & Skirving, 2003; Logan et al., 2014). SST and sea surface salinity records were combined to produce estimates of seawater pH (Covington & Whitfield, 1988), dissolved inorganic carbon (Loukos, Vivier, Murphy, Harrison, & Le Quéré, 2000) and alkalinity (Lee et al., 2006). Bathymetry data (Ryan et al., 2009) was used to retrieve the depth of sampling locations. Finally, population density data (CIESIN Columbia University, 2010) was averaged on a 50 km buffer to produce a surrogated variable for anthropogenic pressure (Welle, Small, Doney, & Azevedo, 2017). We used the coordinates associated to each sample of the genomics dataset to extrapolate the relative environmental conditions using the QGIS point sampling tool (v. 2.18.25, QGIS development team, 2009).

Seascape Genomics

We performed the genotype-environment association analysis using the method of logistic regressions of the software SamBada (v. 0.7; Stucki et al., 2014), customized to fasten

184 multivariate models computation in the Python environment (v. 2.7; Python Software
185 Foundation, 2018) using the *pandas* (v. 0.23.4; McKinney, 2010) and *statsmodels* (v. 0.9;
186 Seabold & Perktold, 2010) libraries. The SamBada approach allows to include proxy variables
187 for genetic structure in the analysis in order to avoid the confounding effects of neutral genetic
188 variation. In our case, we performed a discriminant analysis of principal components (daPCA)
189 on the SNPs genotype matrix using the R package *adegenet* (v. 2.1.1; Jombart, 2008). This
190 procedure highlighted that the main separation concerned two groups of samples along the first
191 discriminant function (Fig. S1) which was therefore used as co-variable in associations models.
192 In order to speed up calculations, the 315 environmental variables were grouped in 29 clusters
193 of highly correlated ($|R|>0.7$) descriptors in the R environment. For each of these groups, one
194 variable was randomly selected to build logistic models against the three genotypes of each
195 SNP. In total, the SamBada instance evaluated 1,349,892 association-models (29
196 environmental groups vs. 3 x 15,516 SNPs) that were subsequently analysed in the R
197 environment. For each association-model concerning the same environmental cluster, p-values
198 of G-scores (G) and Wald-scores (W) were corrected for multiple testing using the R *q-value*
199 package (v. 2.14, Storey, 2003). Association-models scoring $q<0.001$ for both statistics were
200 retained as significant. If a SNP was found in more than one significant association, only the
201 best model (according to G) was retained. For each significant association retained, we
202 calculated all the models of the involved genotype vs. the environmental variables in the cluster
203 of correlated descriptors and looked for the best association model (according to G). Finally,
204 we visualized the logistic regression relating to each significant association-model using the R
205 *popbio* library (v. 2.4.4; Stubben & Milligan, 2007) and manually checked the annotations
206 around significant SNPs on the NCBI genome browser (NCBI, 1988). We set our search to a
207 window of ± 250 kbs since the gene(s) potentially affected by a mutation can be up to hundreds
208 of kbs away (Brodie, Azaria, & Ofran, 2016; Visel, Rubin, & Pennacchio, 2009). We chose

209 this window size because it corresponds roughly to the scaffold N50 statistics of the reference
210 genome (*i.e.* half of the genome is contained in scaffolds of this size or longer).
211
212 *Connectivity Analysis*
213 The connectivity analysis consisted in two steps: modelling and prediction. In the first part, we
214 built a model describing the link between the measured genetic dissimilarities among reefs and
215 their distances by sea. Afterwards, we used this model to calculate the expected genetic
216 distances (GDs) between any reef of the Ryukyu Archipelago and created indexes to evaluate
217 reef-specific connectivity potential.
218 Daily records of sea surface current were retrieved from publicly available databases (zonal
219 and meridional surface velocities from the *global-reanalysis-phy-001-030* product; EU
220 Copernicus Marine Service, 2017) and used to compute currents direction and speed in the R
221 environment using the *raster* library. These day-by-day calculations were then piled-up to
222 retrieve, for each pixel of the study area (~0.083°), the cumulated speed (the conductance)
223 toward each of the eight neighbouring pixels. This information was used to calculate dispersal
224 costs (the inverse of conductance) and was summarized in a transition matrix in the format of
225 the R *gdistance* package (v. 1.2, van Etten, 2018). The transition matrix was used to calculated
226 sea-distances (*i.e.* the least-cost path) between sampling sites of the genotyped colonies.
227 Coincidentally, we performed a principal component analysis (PCA) on the filtered genotype
228 matrix. The values of the PCs were used to calculate the Euclidean distances between each
229 couple of samples that were subsequently averaged by sites in order to obtain GDs between
230 reefs. Finally, we built a linear model (hereafter referred to as the connectivity model) to
231 estimate GDs out of log-transformed sea-distances (+0.005 to allow transformation of zeros)
232 and ran a t-test to verify the statistical significance of the relationship. As a comparison, we
233 also built a connectivity model using log-transformed aerial distance as independent variable

234 and computed the coefficient of determination (R2) and the Akaike information criterion (AIC;
235 Bozdogan, 1987).
236 We then used the connectivity model to predict GDs among any reef of Ryukyu Archipelago.
237 Reefs from the neighbouring regions (Taiwan and Philippines, Fig. S5) were included in the
238 computations to avoid border-effects. By using QGIS (v. 2.18.25, QGIS development team,
239 2009), the shapes of the reefs of this region (UNEP-WCMC, WorldFish-Center, WRI, & TNC,
240 2010) were cut in a regular grid (cell size 5x5 km). Sea-distances between every couple of reef-
241 cells were computed out of remote sensing data as described above and translated in GDs by
242 fitting the connectivity model. Importantly, for every couple of reefs, two GDs were calculated
243 corresponding to sea-distances on the two opposite directions. Based on these predictions, we
244 were able to calculate, for each reef-cell, two indexes:
245 - *outbound connectivity* (OC): the % of cells reachable from the focal cell within a GD-
246 threshold (tGD).
247 - *inbound connectivity* (IC): % of cells that can reach the focal cell within a tGD.
248 Since these indexes were conceived to display contrasts in connectivity among reefs of the
249 Ryukyu Archipelago, we looked for the tGD value maximizing their variances (Fig. S3). The
250 values corresponding to the 25%-quantile and the 60%-quantile of the GD distribution were
251 those boosting the differences in both connectivity indexes. Since we wanted to portrait
252 differences at a more local scale, we set tGD at the 25%-quantile of the GD distribution (*i.e.*
253 tGD=79.861).
254
255 *Adaptive Potential Evaluation*
256 The framework proposed here empowered findings from the previous analyses in order to
257 define the adaptive potential of reefs of the Ryukyu Archipelago facing a particular
258 environmental constraint. Since most of the putative adaptive genotypes were found associated

259 to DHW frequency (Tab. 1) we designated this variable as the environmental pressure of
260 interest.
261 For each of the reef-cells constructed during the connectivity analysis, an average DHW
262 frequency value was calculated using the QGIS zonal statistics tool (v. 2.18.25, QGIS
263 development team, 2009). The significant genotype-environment association-models related to
264 DHW (association models #3, #6, #7, #9 and #15, Tab. 1) were fit with these values to
265 calculate, for each reef, the probability of carrying an adaptive genotype (Rochat, E.,
266 Leempoel, K., Vajana, E., Colli, L., Ajmone-Marsan, P., Joost, 2016). We assumed that
267 potentially adaptive traits could reach any reef of the region since several studies reported high
268 gene flow between distant islands of the Archipelago (Nakajima, Nishikawa, Iguchi, & Sakai,
269 2010; Nishikawa, 2008; Chuya Shinzato et al., 2015). Finally, these probabilities where
270 combined in an average probability of carrying adaptive traits (P_a) and we defined reef-cells
271 approaching the maximal values (P_a>0.6) as putatively adapted reefs. We then used the GDs
272 calculated during the connectivity analysis to retrieve, for each reef-cell, the GD from the
273 closest putatively adapted reef.
274 In the last part of the analysis, we wanted to verify how the adaptive potential responded to
275 alternative emplacements of two typical preservation initiatives (MPAs and coral nurseries).
276 In a first scenario, we imitated a conservation effort (such as MPAs) that allows to locally
277 alleviate coral loss (Selig & Bruno, 2010). To do so, we designed two distinct set-ups in which
278 adaptive potential was maintained only at one specific site (*i.e.* where the MPA was set). In the
279 first strategy (A), the protected area was established in Miyako-Yaeyama, while in the second
280 one (B) in Okinawa. We chose these two locations because they both enclosed reef-cells
281 previously deemed as putatively adapted reef (*i.e.* P_a>0.6, Fig. S5) but differed by connectivity
282 potential *to* and *from* neighbouring reefs (Fig. 2). At both locations, the MPAs covered an area
283 of roughly 15'000 km^2 (Fig. 4a), which is the reported median size of MPAs world-wide

284 (Hoagland, Sumaila, & Farrow, 2001). We then compared the difference in GD (ΔGD) from
285 potentially adaptive sites between the two strategies: positive ΔGD values indicated reefs
286 where the B solution reduced the GD from adaptive sites when compared to the A strategy,
287 *vice-versa* for negative values.
288 We then explored two additional artificial set-ups to assess the effects of coral nurseries on
289 adaptive potential. To do so, we changed the status of one reef-cell from "not putatively adapted
290 reef" to "adapted reef" (emulating the transplantation of adapted colonies where absent as good
291 practices for coral nurseries establishment suggest; Baums, 2008). Differently from the
292 previous case, here all the other potentially adapted reef across the seascape where maintained.
293 We tested this approach at two distinct locations: the first one in Amami (strategy C; Fig. 4b)
294 and the second one in Tokara (strategy D), differing for their connectivity potential (Fig. 2)
295 and their proximity from already existing potentially adapted reefs (Fig. S5). As in the previous
296 case, GDs from potentially adapted reef where measured for the two strategies and the ΔGD
297 was used to assess the effects on adaptive potential. A positive ΔGD designated a more
298 beneficial effect under strategy D, a negative one under strategy C.
299
300 **Results**
301 *Seascape Genomics*
302 The seascape genomics study detected 15 significant genotype-environment association-
303 models (q_G and q_W<0.001; Tab.1), referring to genetic markers from 6 distinct scaffolds of the
304 *A. digitifera* reference genome. Amid these associations, one related to SST variation in April,
305 one to changes in sea current velocity in May and thirteen to DHW frequency (or to a highly
306 correlated variable such as variation in cloud fraction in August).
307 The SNP in the significant association-model #1 was related to SST standard deviation in April
308 and fell in a genomic window (± 250 kb) counting 18 predicted genes, 7 of which were

309 annotated by similarity with known genes (Box S1). Association-models #2 to #5 concerned
310 four SNP falling on two opposite sides of a long scaffold (~1.3 Mb). Those on one side
311 (involved in association-models #2 and #3) were associated to DHW frequency and were
312 surrounded by 17 predicted genes (of which 12 have a putative encoded protein with known
313 function; Box S2) while those on the other (association-models #4 and #5) related also to Sea
314 current velocity variance in May and were enclosed by twelve putative genes (Box S3). All the
315 remaining association-models (#6 to #15) involved only DHW. Association-model #6
316 concerned a SNP surrounded by 14 putative genes, but only one was annotated and which
317 predicted protein was *JNK1/MAPK8-associated membrane protein-like* (NCBI accession:
318 LOC107334815; Box S4). In association-model #7, the SNP of interest fell in a window with
319 eleven predicted genes (only two with a known match by similarity; Box S5). Association-
320 models #8 to #14 referred to seven SNPs on the same scaffold (~195 kb long). This region
321 contained five putative genes of which two annotated by similarity (Box S6). In association-
322 model #15, finally, the SNP associated to DHW frequency was located on a ~75 kb scaffold
323 that contained only one putative gene predicted as *ATP-dependent DNA helicase RecQ-like*
324 (LOC107328703; Box S7).

Table 1. Significant genotype-environment associations. The seascape genomics analysis using the SamBada method discovered 15 significant association-models (q_G and q_W<0.001). This table shows, for each association-model, the genomic position (scaffold of the reference genome and relative situation), the genotype involved (0 and 2=homozygous, 1=heterozygous), the concerned environmental variable (in parenthesis is displayed a variable from the same group of correlated descriptors that resulted in a better model), the q-values associated to the G-score (q_G) and the Wald-score (q_W), the number of predicted genes in a ± 250 kb window around the SNP (with the number of those annotated by similarity with a known gene, in parenthesis) and the annotations from the reference genome that are in the neighborhood (± 250 kb) of the SNP and that corroborate an adaptive role against the respective environmental variable.

Association-model #	Scaffold ID	Position on Scaffold	GT	Environmental Variable	q_G	q_W	Number of Predicted Genes	Relevant Genome Annotations
1	NW_015441190.1	582812	1	SST variance in April	1.56E-08	2.68E-04	18 (7)	*Helicase RecQ at 60 kbs*
2	NW_015441080.1	208387	0	DHW frequency (Cloud Fraction variance in August)	5.83E-08	2.03E-04	17 (12)	*Cytochrome p450 at 150 kbs*
3	NW_015441080.1	208400	0	DHW frequency	2.26E-09	6.39E-05	17 (12)	*Cytochrome p450 at 150 kbs*
4	NW_015441080.1	963844	0	DHW frequency (Cloud Fraction variance in August)	4.00E-09	5.76E-04	12 (7)	
5	NW_015441080.1	963851	0	Sea current velocity variance in May	1.53E-07	9.27E-04	12 (7)	
6	NW_015441121.1	665651	0	DHW frequency	5.93E-08	1.57E-04	14 (1)	*MAPK8/JNK1 at 200 kbs*
7	NW_015441282.1	27616	0	DHW frequency	5.50E-06	5.76E-04	7 (2)	*Helicase Q at 250 kbs*
8	NW_015441785.1	16151	1	DHW frequency	6.15E-06	8.60E-04	5 (2)	*Helicase RecQ at 150kbs*
9	NW_015441785.1	68415	1	DHW frequency	5.83E-08	1.14E-04	5 (2)	*Helicase RecQ at 90kbs*
10	NW_015441785.1	68439	1	DHW frequency	3.15E-07	2.97E-04	5 (2)	*Helicase RecQ at 90kbs*
11	NW_015441785.1	68444	1	DHW frequency	5.19E-06	8.60E-04	5 (2)	*Helicase RecQ at 90kbs*

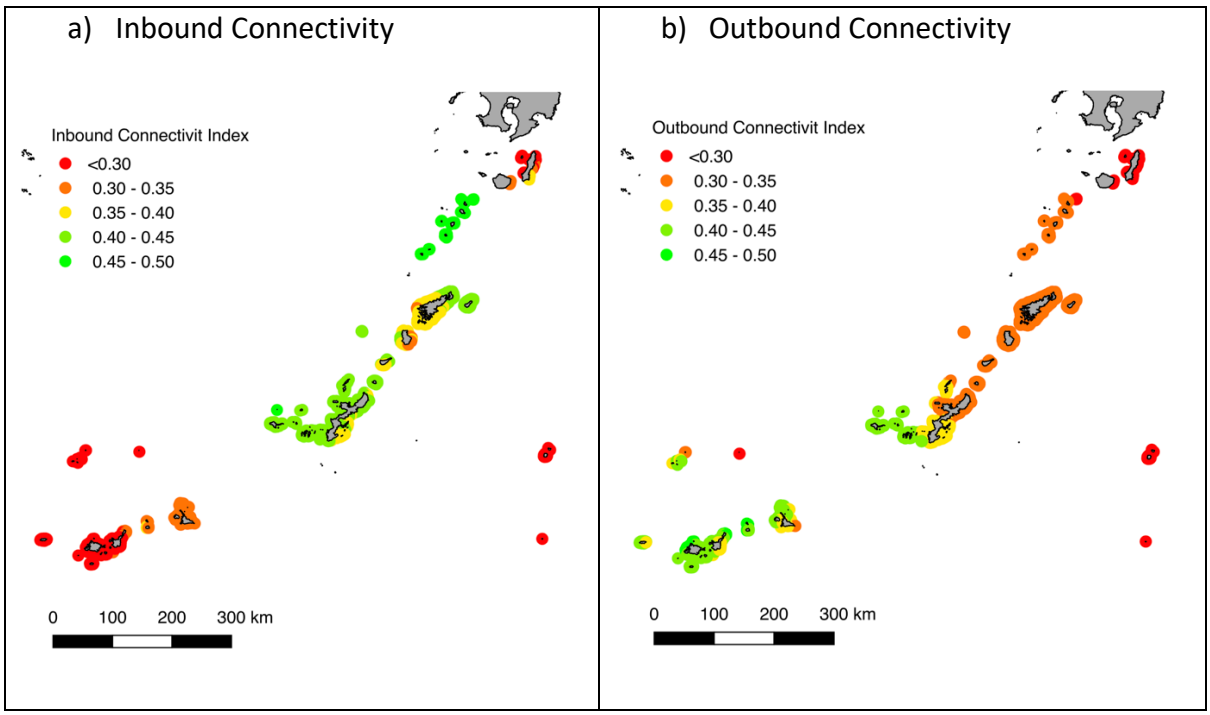
12	NW_015441785.1	68515	1	DHW frequency (Cloud Fraction variance in August)	5.93E-08	1.57E-04	5 (2)	*Helicase RecQ at 90kbs*
13	NW_015441785.1	68521	1	DHW frequency	5.83E-08	2.03E-04	5 (2)	*Helicase RecQ at 90kbs*
14	NW_015441785.1	68528	1	DHW frequency	6.89E-08	6.71E-04	5 (2)	*Helicase RecQ at 90kbs*
15	NW_015442197.1	32233	0	DHW frequency	4.45E-06	8.60E-04	1 (1)	*Helicase RecQ at 20kbs*

Connectivity Analysis

In the both the dispersal models based on sea- and aerial-distances, we found a significant association between genetic-distance (GD) and spatial separation ($p<10^{-9}$, Fig. S3). As we compared the two models, we found that the one based on sea-distances better explained the variation in GD (R2=0.57), in comparison to the one using aerial-distances (R2=0.45). The AIC comparison displayed a lower value for the model based on sea-distances (AIC=315) than in the one using aerial-distances (AIC=343).

Sea-distances linking the reefs of the region were translated in GD by fitting the connectivity model (Fig. S4a). Based on this, two indexes of connectivity (IC: *inbound* and OC: *outbound*) were computed for each reef of the archipelago (Fig. 2). The reefs around the islands of Tokara were those with the highest values of IC (0.49±0.01; Fig. 2a). The reefs in the central islands of Ryukyu Archipelago (Okinawa and Amami) showed higher values of the IC index (0.41±0.03; Fig. 2a) in comparison to those at the edges of the reef system (Yaeyama in South, Osumi in the North) had the lowest values (0.27±0.03). For which concerns the OC index, reefs in the southern part (Yaeyama and Miyako) where those predicted with the highest values (0.42±0.03; Fig. 2b) while those in the northern part (Osumi and Tokara) displayed the lowest ones (0.20±0.13).

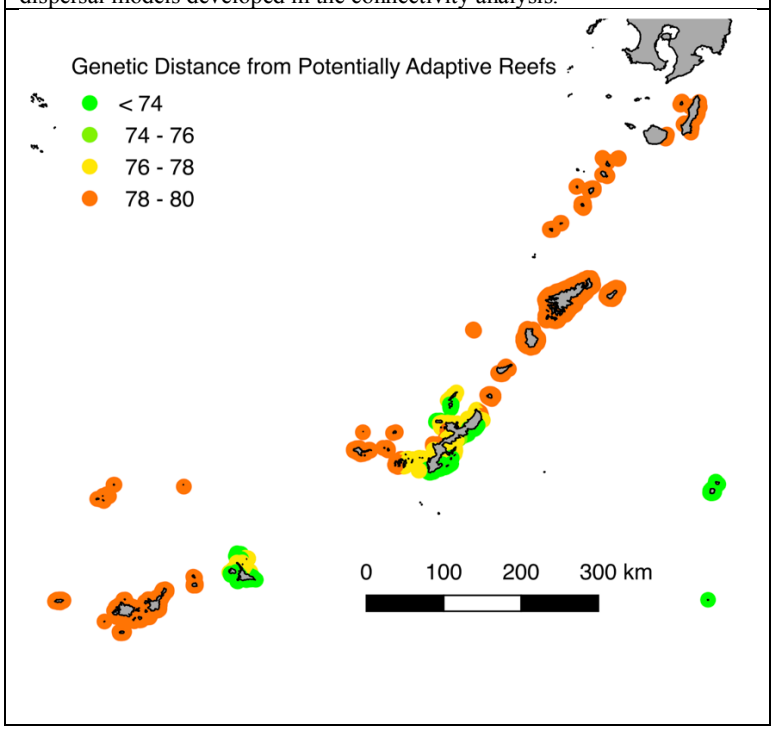
Figure 2. Connectivity Indexes. The two maps show how dispersal to and from specific reefs is expected to vary across the Ryukyu Archipelago. The dispersal model based on remote sensing data from the 1993-2010 period was used to translate sea-distance between each couple of reefs to genetic distances (GD). By setting the first quartile of the GD distribution as threshold value (tGD=80.32), inbound connectivity (IC, a) was calculated as the % of cells that can reach the focal cell within tGD. Conversely, outbound connectivity (OC, b) represented the % of cells reachable from the focal cell within tGD.



Adaptive Potential Evaluation

We then employed the findings from the seascape genomics and connectivity analyses to evaluate the adaptive potential of reefs of Ryukyu Archipelago against thermal stress. Fitting the association-models (Tab. 1) with DHW frequency values resulted in an average probability of carrying adaptive genotypes (P_a) ranging from 0.40 to 0.62 (Fig. S5). Potentially adapted reefs (*i.e.* reefs with P_a>0.6) were located in the islands of Okinawa and Miyako, in the remote Japanese islands east of the Ryukyu Archipelago and in the Northern part of Philippines (Fig. S5). We then investigated the adaptive potential the scale of the reefs system by measuring the GDs from potentially adapted reefs. Reefs in the northern Islands of the Archipelago (Osumi, Tokara and Amami; Fig. 3) were those predicted as the farthest from these kind of spots (GD=79.4±0.3) together with the southern Islands of Yaeyama (GD=79.0±0.1). Conversely, the neighbouring southern islands of Miyako and the ones around Okinawa resulted as those on average with the shortest distances from potentially adaptive reefs, despite a considerable variance (GD=73.6±3.1 and GD=76.4±2.8, respectively).

Figure 3. Distance from Potentially Adaptive Reefs. The map displays the predicted genetic-distance (GD) from the closest reef expected to carry adaptive genotypes against thermal stress. Adaptive sites are designed as those having a cumulative probability of carrying adaptive genotypes (P_a, Fig. S5) higher than 0.6. The GD are computed out of sea-distances using the dispersal models developed in the connectivity analysis.

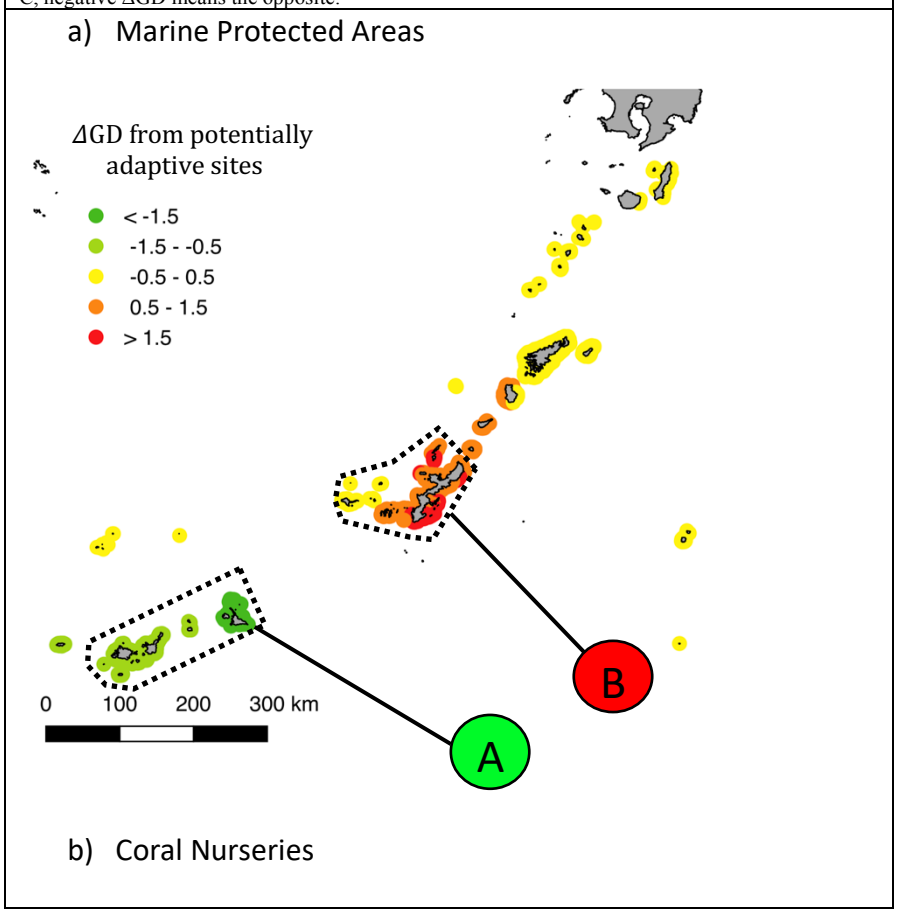


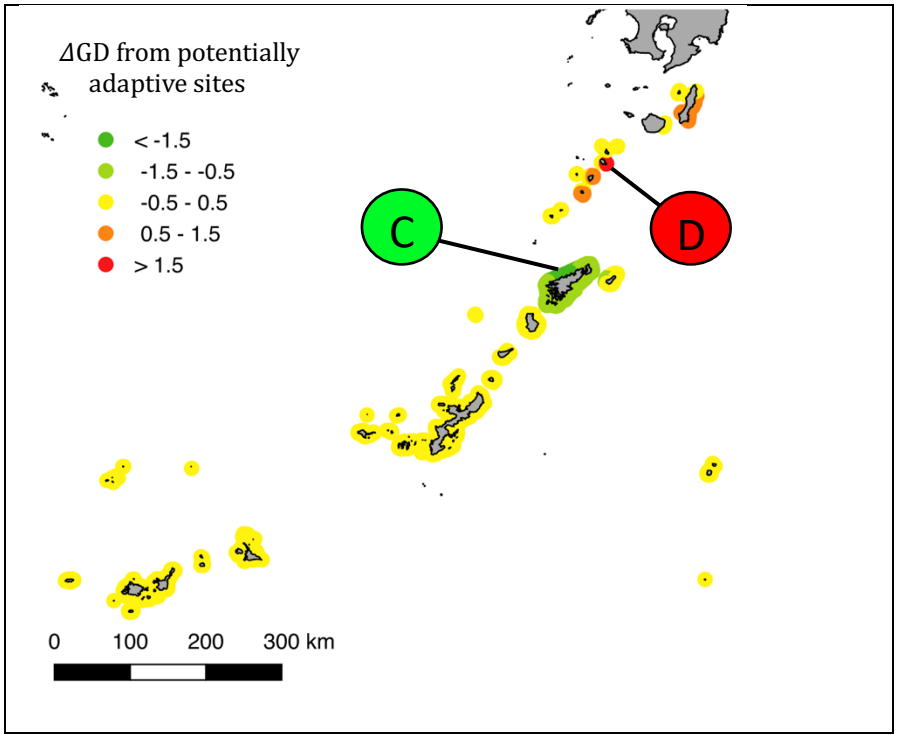
358

359 In the last part of our analysis, we imitated the effects of two types of conservation initiatives
360 and evaluated how their emplacement can influence the adaptive potential across the seascape.
361 In the first case we focused on two alternatives locations for establishing an MPA: the islands
362 of Miyako and Yaeyama (strategy A) and Okinawa (strategy B; Fig. 4a). The overall difference
363 in GD (ΔGD) across the Ryukyu Archipelago was +0.17, therefore indicating that strategy B
364 globally reduced GDs from potentially adapted reefs more than strategy A. In the reefs in the
365 south (Yaeyama and Miyako) strategy A had more beneficial effects (ΔGD=-1.30±0.72) while
366 in the central part of the archipelago (Okinawa and Amami) we found the opposite situation
367 (ΔGD=0.91±0.59). Reefs in the North (Tokara and Osumi) did not display strong differences
368 (ΔGD=0.03±0.01).
369 We then evaluated another artificial set-up to appraise the effects on adaptive potential driven
370 by the location of coral nurseries. The two emplacements we used were in Amami (strategy C)

371 and in Tokara (strategy D; Fig 4b). The southern part of the archipelago (Yaeyama, Miyako
372 and Okinawa) was unaffected by the two strategies (ΔGD=0), while in the northern part
373 (Amami, Tokara, Osumi) a ΔGD=-0.28 indicated that strategy C globally resulted as more
374 beneficial. Strategy C resulted as more efficient in Amami (ΔGD=-0.84±1.06) while plan D in
375 Tokara and Osumi (ΔGD=0.79±1.74).

Figure 4. Changes in adaptive potential under different emplacement of conservation strategies. The two maps display how differential emplacement of management strategies can modify the adaptive potential across the study area. Each map compares the same conservation measure at two different positions by displaying the relative changes in genetic-distance from potentially adaptive sites (ΔGD). In marine protected areas (MPA, a), potentially adaptive sites are maintained only on protected reefs. Positive ΔGD indicates that strategy B (MPA in Okinawa) locally increase the proximity to adaptive sites, in comparison to strategy A (MPA in Miyako). Negative ΔGD *vice-versa*. In coral nurseries (b), potentially adaptive sites are added where absent (C in Amami, D in Tokara). Positive ΔGD indicates that strategy D locally increases proximity to adaptive sites more than strategy C, negative ΔGD means the opposite.





Discussion

Signals of adaptation against thermal stress

Thermal stress is expected to be one of the major threat to coral reef survival and the quest for adaptive traits is becoming of paramount importance (Baums, 2008; Logan et al., 2014; Maina et al., 2011). In our work, the seascape genomics analysis of *A. digitifera* of the Ryukyu Archipelago revealed the presence of 6 genomic regions hosting genetic variants that might confer a selective advantage against thermal stress (Tab. 1). None of these SNPs directly fell in a coding sequence of a putative gene, but this is rarely the case for causative-mutations (Brodie et al., 2016). In fact, genetic variants in intergenic regions that play a modulatory action on the expression of neighbouring genes are more frequent and can influence loci at 1-2 Mb of distance (Brodie et al., 2016). The fragmentation of the reference genome forced us to limit our search window to ±250 Kb around each SNP and still we found several annotations corroborating a response to heat stress.

The SNP in association-model #6 had "JNK1/MAPK8-associated membrane protein" as the closest gene with a predicted function (Box S4). Mitogen-activated-protein kinases (MAPKs)

391 are proteins known to be involved in cellular responses to stress in a wide range of taxa
392 (Neupane, Nepal, Benson, Macarthur, & Piya, 2013) and the c-Jun-N-terminal kinase (JNK)
393 was experimentally proved to be activated under thermal stress in coral *Stylopohora pistillata*
394 (Courtial et al., 2017). Of the 26,060 predicted genes in the *A. digitifera* genome (C Shinzato
395 et al., 2011), 35 are annotated as "mitogen-activated protein kinase" and only one refers to the
396 "JNK1/MAPK8-associated membrane protein". Another annotation that supports these
397 findings concerns gene-models predicted as "ATP-dependent DNA helicase Q" and "RecQ".
398 These are proteins involved in the DNA repairing mechanism to UV-light damage in
399 prokaryotes (Courcelle & Hanawalt, 1999) and for which light-stress driven effects were
400 observed in eukaryotic cells as well (Sharma, Doherty, Brosh, & Jr, 2006). Annotations relating
401 to these proteins are not extremely uncommon (43 in the reference genome) but it is surprising
402 to find them around significant SNPs from four distinct genomic regions (Tab. 1). A similar
403 situation concerned genes assigned to cytochrome P450, a large family of proteins involved in
404 cellular responses to various types of stresses including heat shocks (Rosic, Pernice, Dunn,
405 Dove, & Hoegh-Guldberg, 2010; Sang, Ma, Qiu, Zhu, & Lei, 2012; Yampolsky et al., 2014)
406 and for which differential patterns of gene expression were observed in *Acropora hyacinthus*
407 under distinct thermal regimes (Palumbi et al., 2014). We detected 4 annotations relating to
408 these genes in the proximity of one region with significant SNPs (model #2-#3) but the
409 relatively high frequency of this gene-family (62 occurrences across the genome) invites to a
410 cautious interpretation.
411 Landscape genomics studies can be susceptible to high false discovery rates, especially when
412 neutral genetic structure is not accounted for (Rellstab et al., 2015). In this concern, we
413 processed data following a conservative pipeline, used models explicitly integrating
414 demographic processes and set a restrictive threshold to assess association-models significance
415 (*i.e.* $q<0.001$ in two distinct tests). Most of the significant association-models we found where

416 linked to DHW, perhaps because this represents one of the main constraint to coral survival
417 (Hughes et al., 2017). It is also possible that a sampling scheme deliberately designed for
418 seascape genomics (unlike the one of this study) would have increased sensitivity to other types
419 of adaptive signals (Riginos et al., 2016). Annotations analysis were a first step in the validation
420 of the association-models detected. Ideally, further assays as reciprocal transplantations
421 (Palumbi et al., 2014), experimental conditioning (Krueger et al., 2017) and molecular analysis
422 (Courtial et al., 2017) could ascertain and help quantifying the link between each genotype and
423 the putative selective advantage it might confer.
424
425 *Potential Connectivity Patterns*
426 Understanding the connectivity patterns across a reef system is essential in order to plan
427 effective management strategies. This is usually done by either quantifying the dispersal
428 trajectories of larvae (Storlazzi, van Ormondt, Chen, & Elias, 2017) or by studying the
429 population structure with genetic data (Lukoschek et al., 2016). The first approach has the main
430 drawback of being difficult and expensive because it requires an *a priori* knowledge on the
431 dispersal capabilities of the studied species (McCook et al., 2009). The use of genetic data, on
432 the other hand, often concerns a few sampling locations and is therefore hard to generalize to
433 a whole seascape extent (Beger et al., 2014). The framework we proposed coupled these two
434 approaches: genetic data was used to train dispersal models which were used in return to predict
435 genetic distances (GDs) at the scale of the whole reef system.
436 In model training we found that sea-distances clearly represented a better indicator of spatial
437 separation, compared to aerial distances (Fig. S4). This is probably because coral dispersal is
438 driven by the water flow (Paris-Limouzy, 2011), which in this region is strongly asymmetrical
439 (north-east oriented) because of the Kuroshio current (Nishikawa, 2008). By fitting this
440 dispersal model with sea-distances among any reef of the region we were able to evaluate the

441 patterns of connectivity. Reefs in the extreme North (Osumi) appeared to face both *inbound*
442 and *outbound* isolation (Fig. 2), a situation that might lead to inbreeding depression (Keller &
443 Waller, 2002). Reefs in the extreme south of the system (Yaeyama) also appeared as
444 endangered: despite their proximity to Miyako the strong directionality of sea-currents in the
445 region appeared to contrast south-westward dispersal.
446 This framework is potentially applicable to any coral species for which geo-referenced genetic
447 data is available and the indexes associated can be extremely valuable in management planning
448 (Beger et al., 2014). Despite that, there is still a substantial part of GD variation that remains
449 unexplained by our models and that perhaps might be better described by connectivity models
450 working at finer geographical and temporal scales (Storlazzi et al., 2017).
451
452 *Conservation and Adaptive Potential*
453 Conservation strategies to preserve coral reefs need to account for and to reinforce the adaptive
454 potential facing thermal stress (Baums, 2008; Logan et al., 2014; Maina et al., 2008; van Oppen
455 et al., 2015). In order to be integrated in prioritization frameworks, this information needs to
456 be objective and quantifiable (OECD, 2017). Previous work suggested to use climatic records,
457 but this approach neglects how organisms modulate a response to an environmental constraint
458 (Logan et al., 2014; Maina et al., 2011). The use of genetic data has also been advocated, but
459 findings from this kind of analysis are often hard to interpret in a conservation perspective
460 (Sodergren et al., 2006). In this work, we showed how a seascape genomics framework can
461 assess the adaptive potential at the scale of a reef system. The field-based fundaments of this
462 method allow a rapid and straightforward transition from analysis to predictions.
463 In the specific case of the Ryukyu Archipelago for instance, we found that reef from Miyako
464 and Okinawa islands as those more likely to carry adaptive traits against thermal stress (Fig. 3).
465 Previous work reported indeed that adapted colonies from Okinawa might have persisted to the

466 1998 and 2001 bleaching events (Van Woesik, Irikawa, & Loya, 2004). Contrastingly, reefs in
467 the northern part of the Archipelago (Amami, Tokara and Osumi) did not experience the same
468 thermal stress and therefore were not predicted to carry these adaptive traits (Fig. 3).
469 Beside pointing out weak-spots in terms of adaptive potential, our framework allowed us to
470 evaluate the expected impact of conservation strategies. Even though the conservation
471 measures we proposed were a rough imitation of real measures, they displayed how priorities
472 can be defined if adaptive and connective potential of reefs are known. For instance, the MPA
473 set-up in Okinawa provided a general adaptive benefit (strategy B; Fig. 4a), compared to the
474 one in Miyako-Yaeyama (strategy A), because it enclosed more potentially adapted reefs (Fig.
475 S5) and was better connected to the reef-dense area around Amami (Fig. 4a). Similarly, a coral
476 nursery in Amami could provide adaptive genetic material to a larger number of reefs,
477 compared to a set-up in Tokara (Fig. 4b), because of a higher outbound-connectivity potential
478 (Fig. 2b).
479
480 *Conclusions*
481 This study highlights the value of the seascape genomics approach for supporting the efforts in
482 coral conservation. We applied this approach to a flagship coral species of Ryukyu Archipelago
483 and identified genetic variants that might underpin adaptation to thermal stress. By coupling
484 this information with a genetic analysis of connectivity, we were able to define the adaptive
485 potential at the scale of the whole study area. The outputs of this analysis are quantitative
486 indexes that can strongly support objective prioritization of reefs in conservation plans. This
487 framework is transferable to any coral species on any seascape and could therefore lay the basis
488 for reinforcing the adaptive potential in the reefs worldwide.
489
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