

1 **Climate change resilience of a globally important sea turtle nesting population**

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3 **Running head: Climate change resilience of sea turtles**

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20 **Abstract**

21 Few studies have looked into climate change resilience of populations of wild animals. We
22 use a model higher vertebrate, the green sea turtle, as its life history is fundamentally affected
23 by climatic conditions, including temperature-dependent sex determination and obligate use
24 of beaches subject to sea level rise (SLR). We use empirical data from a globally important
25 population in West Africa to assess resistance to climate change within a quantitative
26 framework. We project 200 years of primary sex ratios (1900–2100), and create a digital
27 elevation model of the nesting beach to estimate impacts of projected SLR. Primary sex ratio
28 is currently almost balanced, with 52% of hatchlings produced being female. Under IPCC
29 models we predict: 1. an increase in the proportion of females by 2100 to 76–93%, but cooler
30 temperatures, both at the end of the nesting season and in shaded areas, will guarantee male
31 hatchling production; 2. IPCC SLR scenarios will lead to 33.4–43.0% loss of the current
32 nesting area; 3. Climate change will contribute to population growth through population
33 feminization, with 32–64% more nesting females expected by 2120; 4. As incubation
34 temperatures approach lethal levels, however, the population will cease growing and start to
35 decline. Taken together with other factors (degree of foraging plasticity, rookery size and
36 trajectory, and prevailing threats), this nesting population should resist climate change until
37 2100, and the availability of spatial and temporal microrefugia indicate potential for
38 resilience to predicted impacts, through the evolution of nest site selection or changes in
39 nesting phenology. This represents the most comprehensive assessment to date of climate
40 change resilience of a marine reptile using the most up-to-date IPCC models, appraising the
41 impacts of temperature and SLR, integrated with additional ecological and demographic
42 parameters. We suggest this as a framework for other populations, species and taxa.

43 INTRODUCTION

44 Anthropogenically-induced climate change is re-shaping the world's ecosystems at an
45 unprecedented rate, with major impacts on biodiversity (Hoegh-Guldberg & Bruno 2010,
46 Diffenbaugh & Field 2013, Batllori et al. 2017). Many species are already responding by
47 changing their phenology and distribution range (Root et al. 2003, Sunday et al. 2012,
48 Jenouvrier 2013), among other adaptations (Walther et al. 2002), while others seem unlikely
49 to be able to adapt sufficiently (Thomas et al. 2004, Maclean & Wilson 2011). To define
50 priority conservation targets it is thus critical to understand how organisms can resist change
51 (their capacity to withstand perturbation), and their potential for resilience (their ability to
52 return to a pre-disturbance state, Connell & Sousa 1983, O'Leary et al. 2017). Few studies
53 have attempted to make quantitative estimates of the potential resistance of a population of
54 wild animals to climate change (Williams et al. 2008).

55

56 Species with temperature-dependent sex determination (TSD) have been considered among
57 the most vulnerable to climate change, because increasing incubation temperatures may
58 favour the production of one sex at the detriment of the other (Mitchell & Janzen 2010). This
59 fundamental life history trait can have deep demographic effects in extreme conditions, as
60 highly skewed sex ratios may lower fecundity and threaten population viability (Mitchell et
61 al. 2010, Santidrián Tomillo et al. 2015) or *vice versa* (Hays et al. 2017). Excessive
62 temperatures can further lead to embryo mortality (Godley et al. 2001a). Simultaneously,
63 ocean thermal expansion and the melting of ice are leading to global mean sea level rise
64 (SLR), causing saline intrusion into the water table, flooding of coastal areas, and heightened
65 coastal erosion, further enhanced by increasing storminess, affecting mostly species which
66 rely on coastal habitats (Fish et al. 2005, Hoegh-Guldberg & Bruno 2010). Sea turtles are an
67 excellent example of a vertebrate with distinct sensitivity to climatic conditions throughout

68 incubation and development (Wibbels 2003, Girondot & Kaska 2014), and into adult life
69 stages (Hawkes et al. 2007, Anderson et al. 2013, Dudley et al. 2016). They have TSD, with
70 high incubation temperatures (above approximately 29 °C; Hulin et al. 2009) yielding more
71 females and low temperatures more males, and depend on low-lying sandy beaches for
72 reproduction. Together, these traits make sea turtles potentially highly susceptible to climate
73 change (Hawkes et al. 2007, 2009, Poloczanska et al. 2009, Hamann et al. 2010).

74

75 Relatively few studies have inferred the sex ratio of marine turtle populations, however, the
76 majority of these report female-biased primary sex ratios which are expected to skew further
77 with climate warming (Hawkes et al. 2007, Fuentes et al. 2009, Katselidis et al. 2012,
78 Reneker & Kamel 2016), and incubation temperatures above a certain threshold are expected
79 to reduce clutch survival (Santidrián Tomillo et al. 2014, Hays et al. 2017), and hatchling
80 locomotor ability (Fuentes et al. 2010a, Booth & Evans 2011). Significant losses of 8-65% of
81 nesting habitat are predicted for several sea turtle rookeries, under climate change scenarios
82 of median severity (Fish et al. 2005, 2008, Baker et al. 2006, Fuentes et al. 2010b, Katselidis
83 et al. 2014). Additionally, temporary inundation of beaches, associated with the increasing
84 prevalence and intensity of storms, is expected to lower hatching success (Van Houtan &
85 Bass 2007, Pike et al. 2015). It is yet uncertain if sea turtles will be able to adapt to the
86 current rapid changes, but they have certainly endured climate change in the past
87 (Poloczanska et al. 2009).

88

89 Both behavioural polymorphism acting on nest-site selection, and phenological changes of
90 nesting season have recently been observed in sea turtle populations (Weishampel et al. 2004,
91 Kamel & Mrosovsky 2006, Mazaris et al. 2013). Given that these processes can have an
92 impact on incubation temperatures and consequently on hatchling sex ratio and survival,

93 these observations suggest potential for adaptation to climate change. Colonization of more
94 suitable beaches may be another mechanism for adaptation, which is known to have occurred
95 in the past (Poloczanska et al. 2009). Additionally, as higher temperatures enhance female
96 hatchling production, it has been argued that climate change may boost the numbers of
97 reproductive females, and consequently nest numbers, promoting population growth (Boyle
98 et al. 2014, Hays et al. 2017). This is dependent, however, on the existence of both sufficient
99 males to fertilize clutches, and incubation temperatures within the thermal tolerance of
100 populations (Santidrián Tomillo et al. 2015, Hays et al. 2017).

101

102 Integrated assessments of climate change resilience, considering a broad range of impacts and
103 adaptive potential, will enable managers to prioritize conservation efforts, and use realistic
104 measures to mitigate threats. More often, climate change-induced threats are considered
105 independently (but see Fuentes et al. 2013, Abella Perez et al. 2016, Butt et al. 2016). Here
106 we apply and extend a vulnerability framework originally posited by Abella Perez et al.
107 (2016), to make a comprehensive assessment of climate change resistance in a globally
108 important green turtle population, to the end of this century, and make inference as to the
109 resilience capacity of this population. We make an empirically based assessment of resistance
110 to climate change in marine turtles, a key research priority (Rees et al 2016), which could
111 form an excellent blueprint for comparative studies within and among taxa.

112

113 **MATERIALS AND METHODS**

114 **Vulnerability framework**

115 For an overview of population resistance to climate change, and adapting the vulnerability
116 framework proposed in Abella-Perez et al. (2016) we scored nine criteria, on a five-point
117 scale from 0 (worst) to 100 (best), under three different climate models by the

118 Intergovernmental Panel for Climate Change (IPCC; RCP4.5, RCP6, RCP8; Collins et al.
119 2013): 1. primary sex ratio; 2. hatchling emergence success; 3. spatial microrefugia; 4.
120 temporal microrefugia; 5. sea level rise impact; 6. foraging plasticity; 7. other threats; 8.
121 rookery trend; and 9. rookery abundance. Criteria 8 and 9 are an addition to the original
122 framework. We calculated a mean score across categories, resulting in an overall score of 0 –
123 100, being 0 the most vulnerable to climate change and 100 the least vulnerable (i.e. more
124 resistant). For scoring system see Table 1.

125

126 **Climate change models**

127 We use projections from three of the four Representative Concentration Pathways (RCPs), in
128 the IPCC fifth report (Collins et al. 2013, Table 2), to provide estimates for each criterion by
129 2100. We use two intermediate (RCP4.5, RCP6) and the high emissions scenario (RCP8.5).
130 For the trajectories of annual mean incubation temperatures and primary sex ratio, however,
131 we use the Special Report on Emission Scenarios (SRES, Nakicenovic et al. 2000), as annual
132 mean temperature anomalies for the region, enabling trajectory reconstruction, are only
133 available for SRES. Additionally, as several studies indicate that the IPCC process-based
134 projections of SLR are very conservative (Horton et al. 2014, Dutton et al. 2015), and semi-
135 empirical approaches result in more extreme scenarios (Rahmstorf, 2006, Vermeer &
136 Rahmstorf 2009, Grinsted et al. 2010), for SLR impacts we consider the RCPs (Collins et al.
137 2013) plus the most recent estimate based on semi-empirical models (1.2m SLR by 2100;
138 Horton et al. 2014).

139

140 **Primary sex ratio**

141 **a. Historical and projected air temperature trajectory**

142 This research was conducted at Poilão Island (10.8° N, 15.7° W), within the João Vieira and
143 Poilão Marine National Park, in the Bijagós Archipelago, Guinea-Bissau, West Africa. The
144 green turtle population of the Bijagós is the largest in Africa, among the top six populations
145 worldwide (Catry et al. 2002, 2009, SWOT 2011), with most of the nesting concentrated at
146 Poilão (>90%, C. Barbosa *pers. comm.*). The nesting season extends from mid-June to mid-
147 December, peaking in August and September (Catry et al. 2002). This work encompassed
148 four nesting seasons, from 2013-2016. We used mean monthly historical air temperature data
149 for Bissau (*ca.* 75km distant, nearest station with historical data), for the period of 1901 to
150 2016, obtained from the Climatic Research Unit of the University of East Anglia
151 (<https://crudata.uea.ac.uk/cru/data/temperature/>), to reconstruct historical mean air
152 temperatures during the nesting season. To project the trajectory of mean air temperatures to
153 2100 we added to a historical reference (1970-1999) the mean annual temperature anomalies
154 for the region, obtained from the United Nations Development Program
155 (<http://www.geog.ox.ac.uk/research/climate/projects/undp-cp/>). We used the SRES A1B
156 scenario, which predicts a mean increase in air temperature of 3.1 °C by 2100 (most similar to
157 RCP8.5, Table 2).

158

159 **b. Sand and incubation temperatures**

160 Sand temperature was recorded at mean clutch depth (0.7m, Patrício et al. 2017a) with
161 Tinytag-TGP-4017 dataloggers (Gemini Data Loggers, Chichester, UK, ± 0.3°C accuracy,
162 0.1°C resolution), in 2013 (n=16), and 2014 (n=14). All dataloggers were calibrated before
163 and after each nesting season in a constant temperature room (24 hours at 28 °C) and used
164 only if accuracy was ≤ 0.3 °C. The sand temperature at Poilão varies in relation to the amount
165 of shading, and we defined three microhabitats: ‘open sand’, ‘forest border’, and ‘forest’, per
166 Patrício et al., (2017a). Thus, to account for spatial and temporal variability in sand

167 temperature, the dataloggers were distributed along the nesting beach, which extends for
168 1800m, throughout the nesting season, at the open sand (n=6/5 in 2013/2014), forest border
169 (n=5/4), and forest (n=5/5), with at least one datalogger every 500m at each microhabitat in
170 both years. Sand temperatures were highly correlated among habitats (open sand vs. forest
171 border $r^2 = 0.96$, and forest border vs. forest $r^2 = 0.94$), with sand temperature at the forest
172 border on average 1.0 °C below that of the open sand, and 1.5 °C above that at the forest
173 (Patricio et al. 2017a). We estimated future sand temperatures using the equation:
174 $T_{\text{sand}}=0.94T_{\text{air}}+3.04$, $r^2=0.60$, $P<0.0001$, $n=39$, T_{sand} =mean bi-weekly sand temperature at
175 Poilão in the forest border habitat, T_{air} =mean bi-weekly air temperature at Bissau, sample
176 period=1 March 2013 to 15 October 2014 (see Patricio et al. 2017a). We added to estimated
177 sand temperatures the mean metabolic heating during the thermosensitive period (TSP;
178 period during middle third of development, when sex is irreversibly defined), to estimate
179 annual mean incubation temperatures during the TSP until 2100 (Godley et al. 2002).
180 Metabolic heating during the TSP at Poilão is 0.5 ± 0.4 °C SD (Patricio et al. 2017a).

181

182 **c. Primary sex ratio and emergence success**

183 We applied a logistic function, which models the population-specific sex determination
184 response to TSP incubation temperatures (Patricio et al. 2017a), to estimate the proportion (P)
185 of female hatchlings within each microhabitat (i.e. open sand, forest border, and forest):

$$186 \quad P_{(\text{females})} = 1 / (1 + e^{(-44.856 - 1.527 * \text{TSP temperature})})$$

187 We then accounted for the microhabitat-specific hatchling survival (hatchling emergence
188 success in 2013/2014: open sand= $66.1 \pm 30.8\%$, $n=62$; forest border= $51.9 \pm 38.3\%$, $n=20$;
189 and forest= $42.2 \pm 41.6\%$, $n=16$; Patricio et al., 2017a), and the temperature-induced hatchling
190 mortality per microhabitat, using the logistic equation described in Laloë et al. (2017), which
191 models the relationship between emergence success (E) and incubation temperature (T):

192
$$E_{(T)}=A / 1+e^{-\beta(T-T_0)},$$

193 where the upper asymptote is $A=86\%$, the growth rate constant is $\beta=-1.7^\circ\text{C}$, the inflection
194 point is $T_0=32.7^\circ\text{C}$, and T =mean incubation temperature per microhabitat (Laloë et al. 2017).
195 We could not use the population-specific hatchling mortality response to incubation
196 temperature as currently natural nests in Poilão experience moderate temperatures (i.e. $27.5 -$
197 32.2°C for mean incubation temperatures during middle third of incubation, in the centre of
198 the clutch, $n= 101$, Patrício et al. 2017a), not sufficiently high to negatively affect embryo
199 survival.

200

201 **Spatial and temporal microrefugia**

202 We refer here to microrefugia as the existence of conditions that would be more suitable for
203 population persistence under global warming scenarios, both in space (i.e. more suitable
204 microhabitat), and in time (i.e. periods of the year with lower incubation temperatures).
205 We conducted daily surveys during the nesting season, from August to December, across four
206 years (2013-2016), and counted green turtle tracks to assess the temporal distribution of
207 nesting, following methodology detailed in Patrício et al. (2017a), to reconstruct mean
208 nesting frequency distribution at the start and end of the season. Data available from the
209 National Climatic Data Centre (<http://cdo.ncdc.noaa.gov/CDO/cdo>, Bolama, 50km distant),
210 were used to compare half-month mean air temperatures and total precipitation with mean
211 half-month nesting distribution, across the four years. Note that mean monthly air
212 temperatures at Bissau (used for the historical reconstruction of annual air temperatures) are
213 compatible with those at Bolama, with a mean difference of $0.4 \pm 0.3^\circ\text{C}$ during the study
214 period. To explore the availability of temporal microrefugia, we classified each half-month as
215 ‘cool’ if mean incubation temperature fell below the estimated field-pivotal temperature for
216 this population (29.4°C , Patrício et al. 2017a), and ‘warm’ if it was the same or above, and

217 estimated the percentage of nesting occurring in hot months. To assess the presence of spatial
218 microrefugia we examined the current nesting distribution across ‘thermal’ habitats according
219 to Patrício et al. (2017a; warm: open sand in beaches 3 and 4 =31% of all nests laid; medium:
220 open sand in beaches 1 and 2 and forest border =47%; and cool: forest =22%), and calculated
221 the proportion laid in the warmest habitat.

222

223 **Vulnerability to sea level rise (SLR)**

224 We assessed the proportion of nests that would be flooded under SLR scenarios if no changes
225 occur in beach morphology (as no robust method to estimate shoreline retreat in small low-
226 lying islands is yet available, Cooper et al. 2004), and used this as a proxy for nest area loss,
227 as it considers nest site preferences (Katselidis et al. 2014), as oppose to accounting for all the
228 beach area. The distribution of 1,559 nests, surveyed during the peak of the 2013 (n=407) and
229 2014 (n=1,152) nesting seasons were used to represent the overall nesting distribution (see
230 Patrício et al. 2017a), assuming no change in the spatial distribution of nesting over time. We
231 created a digital elevation model (DEM) of the beach in Agisoft Photoscan Professional
232 v1.3.1 (© Agisoft), using aerial photos (80% overlap, 35 m altitude) taken from a drone
233 (Varela et al. *in press*). During the study period, high tide at Poilão ranged from 3.2 m (neap
234 tide) to 4.8 m (spring tide), with mean high tide (MHT)=4.0 m ± 0.3 SD (Bubaque Island tide
235 tables, 40 km distant, source: Hydrographic Institute of Lisbon). In the DEM we set the MHT
236 to 0m, to measure nest elevation above it, following previous studies (Fish et al. 2005,
237 Fuentes et al. 2010b). We then exported the DEM to ArcGIS 10.3 (ESRI), together with the
238 GPS locations of the 1,559 nests surveyed, and used 3D Analyst Tools to attribute surface
239 elevation to each nest, with the DEM as the input surface. Because mean clutch depth is 0.7
240 m (Patrício et al. 2017a), a nest with a surface elevation >MHT may still be subjected to
241 varying degrees of flooding. Based on a previous study (Patrício et al. 2018) however, nests

242 with a surface elevation below the MHT have a hatching success (H%) \approx 0%, thereon
243 increasing with elevation, indicating that this is a good reference for complete loss due to
244 inundation.

245

246 **Foraging plasticity**

247 Population-level foraging plasticity would be advantageous under climate change, if future
248 climatic conditions affect trophic chains and prey availability (Abella Perez et al. 2016).

249 Limited information is available on the foraging behaviour of green turtles from Poilão. We

250 sampled 187 nesting green turtles in 2013 (n=79), 2014 (n=70), and 2016 (n=38), and

251 inferred the dietary range of this nesting population using Nitrogen stable isotope ratios

252 ($\delta^{15}\text{N} = ^{15}\text{N} : ^{14}\text{N}$), and the foraging geographical range using Carbon stable isotope ratios

253 ($\delta^{13}\text{C} = ^{13}\text{C} : ^{12}\text{C}$, see supplementary methods S1; Godley et al. 1998, Bearhop et al. 2004,

254 Lemons et al. 2011). Nesting females were sampled throughout the season in 2013 and 2014,

255 and in November 2016. Sampling followed recommended protocols (Stokes et al. 2008), and

256 guidelines approved by the research ethics committee of the University of Exeter (ref:

257 2014/710) and the Institute of Biodiversity and Protected Areas of the Government of the

258 Republic of Guinea-Bissau.

259

260 **Other threats**

261 Following Abella-Perez et al. (2016), we considered the presence of any known threats to the

262 study population, such as directed harvest, intentional and incidental captures in fisheries,

263 ship strikes, ocean and beach pollution, coastal development, invasive species, and ocean

264 acidification, using the Cumulative Impact Score (CIS; a non-linear metric from Halpern et

265 al. 2015), which quantifies 19 anthropogenic threats across the global oceans into one 'score'.

266

267 **Rookery abundance and trend**

268 **a. Female recruitment**

269 Higher temperatures are expected to increase the number of females in populations of sea
270 turtles (Hays et al. 2017). To model a ‘recruitment index’ trajectory for the study nesting
271 population, under SRES A1B, we divided annual estimates of female hatchling production
272 from 2017 to 2100 (i.e. proportion of females emerged from nests) by the current estimates of
273 female hatchling production over the four study years (2013-2016). This gives us a relative
274 index of the number of female hatchlings being produced in relation to the present (Laloë et
275 al. 2014). We then considered 20 years as the minimum age at sexual maturity for Atlantic
276 green turtles in tropical regions (Bell et al. 2005, Patrício et al. 2014), for a ‘recruitment
277 index’ of females to the effective population, assuming that other demographic patterns
278 remain unchanged (Laloë et al. 2014).

279

280 **b. Nest numbers**

281 Nesting density at Poilão is sufficiently large to preclude complete counting of nests laid
282 (Catry et al. 2009, Patrício et al. 2017a). We therefore estimated the number of nests laid per
283 season from 2013-2016, by multiplying the number of nesting female emergences (each
284 corresponding to an ascending and a descending track) by 1.05, to account for the period of
285 the nesting season not monitored these years (corresponding to ca. 5% of all emergences),
286 and by 0.813, to adjust for nesting success in Poilão estimated by Catry et al. 2009. Then, for
287 a prediction of the number of nests in the future, under the different RCPs (Table 2), we
288 multiplied the mean nest number across the four seasons by the nesting female ‘recruitment
289 index’ (above), assuming no changes in other demographic patterns.

290

291 **RESULTS**

292 **Primary sex ratio and emergence success**

293 Historical mean annual air temperatures have increased since the mid-1970s to the present,
294 with a consequent average increase of *ca.* 1.0°C in modelled incubation temperatures (Fig.
295 1a), and an estimated average increase in the proportion of female hatchlings by 20% (Fig.
296 1b). Future increase in female production will be particularly marked in the open sand (*ca.*
297 40%, Fig. 1b), whereas incubation temperatures in the forest will promote high to moderate
298 male hatchling production throughout the 21st century. Considering both the effects of
299 microhabitat and increased temperatures on hatching success, mean emergence success could
300 drop as low as 32% by 2100 (RCP 8.5, Table 2), with 93% of the hatchlings expected to be
301 female (RCP 8.5, Table 2). The relatively wide range of mean incubation temperatures at
302 which both sexes are produced in this population (27.6 – 31.4 °C, Patricio et al. 2017a),
303 however, would allow for male production even under the most extreme RCP.

304

305 **Spatial and temporal microrefugia**

306 Currently the nesting season largely coincides with both the rainy season and relatively low
307 air temperatures (Fig. 2a,b,c). We estimated that 46% of the clutches laid at present have the
308 TSP during cool periods (Table 2). Most male hatchlings are produced from clutches laid in
309 late November to early December, and in forest areas (Fig. 3). Estimated future primary sex
310 ratio here remained male-biased under RCP4.5 (42% female hatchlings by 2100), and almost
311 balanced under RCP6 (53%), only becoming female-biased under the most extreme
312 projection, RCP8.5 (82%), but still producing males, particularly towards the end of the
313 season (Fig. 3). The percentage of female hatchlings being produced in the open sand by
314 2100 is expected to increase from current 61% to 99%, with RCP8.5 (Table 2). Under the
315 same climate scenario, at the forest border, primary sex ratio will increase from 39% to 97%
316 female (Table 2).

317

318 **Vulnerability to SLR**

319 At present, most clutches are laid 0.8 to 1.0m above MHT (range: -0.6 m to 2.3 m). Because
320 the expected mean SLR according to RCP4.5 and RCP6 are very similar (0.47 vs. 0.48m;
321 Collins et al., 2013), and our DEM has a vertical accuracy ~ 10 cm, we considered these
322 climate models together for projections of SLR impacts. We estimated that by 2100, 33.4%
323 of the current nesting area will be lost under RCP4.5 and RCP6, while 43.0% will be lost
324 under RCP8.5 (Fig. 4, Table 2). Considering semi-empirical models of SLR, however, as
325 much as 86.2% of current nesting habitat could become completely flooded by 2100 (Fig. 4).

326

327 **Foraging plasticity**

328 Nitrogen isotope ratios ($\delta^{15}\text{N}$) varied from 6‰ to 16‰ (mean = $11.6\text{‰} \pm 2.4$ SD, mode =
329 12.5‰ , Fig. 5a), while Carbon isotope ratios ($\delta^{13}\text{C}$) ranged from -16‰ to -6‰ (mean =
330 $11.7\text{‰} \pm 2.7$ SD, mode = 12.2‰ , Fig. 5b), suggesting that individual green turtles from
331 Poilão are foraging at multiple trophic levels (herbivory and/or carnivory), and at different
332 geographical locations. There were significant differences in both $\delta^{15}\text{N}$ (ANOVA, $F_{2,184} =$
333 6.45 , $P = 0.002$) and $\delta^{13}\text{C}$ (ANOVA, $F_{2,184} = 7.63$, $P < 0.001$) between years. Mean $\delta^{15}\text{N}$ in
334 2016 was significantly higher than that of 2013 ($P = 0.02$), and in 2014 ($P = 0.001$), with no
335 difference between the years 2013 and 2014 ($P = 0.56$; Tukey HSD test), whereas mean $\delta^{13}\text{C}$
336 was significantly higher in 2014, compared to 2013 ($P < 0.001$), and 2016 ($P=0.04$), with no
337 difference between the years 2013 and 2016 ($P = 0.81$; Tukey HSD test). Thus, foraging
338 plasticity seems to be present at least at the nesting population level, with turtles foraging at
339 different trophic levels, and different feeding grounds (Godley et al. 2010).

340

341 **Other threats**

342 In Guinea-Bissau, although marine turtles are fully protected by the national fisheries law,
343 illegal take for local consumption continues to occur (Catry et al. 2009). Poilão and the
344 surrounding waters, however, are virtually free from illegal harvesting, as they benefit from
345 the Bijagós traditional law and modern park regulations, restricting access to the island to
346 very rare ceremonies (Catry et al. 2009). Considering other anthropogenic threats, the CIS for
347 Guinea-Bissau was 3.94, (119th of 238 Exclusive Economic Zones evaluated; Halpern et al.
348 2015) but we removed the impact score for SLR (0.38), which was already considered
349 separately above, and assumed the nesting beach threats equal to zero. Thus, the score for
350 ‘other threats’ is 3.57 (Table 2).

351

352 **Rookery abundance and trend**

353 We predicted an increase in nesting female recruitment by 2100 of 58%, 64%, or 32%
354 relative to present, under RCP4.5, RCP6, and RCP8.5, respectively (Table 2). Due to
355 temperature-linked hatchling mortality, however, female recruitment reaches a plateau
356 around 2085, and starts to decrease after 2110 (Fig. 6). Neglecting this important factor
357 would leave scenarios forecasting indefinite increase in female recruitment (Fig. 6). The
358 mean number of clutches per year from 2013-2016 was 25,436 (95% CI: 22,088-27,970;
359 2013: 20,785 (95% CI: 18,049-22,855); 2014: 35,556 (95% CI: 30,877-39,099); 2015:
360 16,054 (95% CI: 13,941-16,653); 2016: 29,348 (95% CI: 25,486-32,272). Using this value as
361 reference, and accounting for nesting female recruitment, we predicted that an average of
362 40,170 clutches could be laid by 2120 under RCP4.5, 41,602 with RCP6, and 33,588 with
363 RCP8.5.

364

365 **Vulnerability framework**

366 The corresponding estimate for each criterion of the quantitative vulnerability framework,
367 under each of the three RCPs considered in this study, can be seen in Table 2, together with
368 the scoring for each criterion, and the overall score in climate change resistance for each
369 RCP. The population of green turtles from the Bijagós, Guinea-Bissau, scored 72 (in a scale
370 of 0-100, with 100 being most resistant) under RCP 4.5, 67 with RCP 6, and 61 with RCP8.5
371 (Table 2), showing overall high to medium resistance to climate change until the end of the
372 21st century.

373

374 **DISCUSSION**

375 Ongoing climate change is simultaneously driving the adaptation and the extinction of
376 populations, species and entire ecosystems (Maclean & Wilson 2011, Xu et al. 2016). Using
377 empirical data and a quantitative framework we conducted a holistic assessment of climate
378 change resistance of a globally significant green turtle nesting population, until the end of the
379 century. We estimate that this population appears to have medium to high resistance under
380 future expected climate change. We highlight the importance of integrated assessments of
381 climate change impacts, instead of considering threats individually, the use of population-
382 specific parameters, and the applicability of this approach to make comparisons with other
383 populations.

384

385 **Sex ratio**

386 The primary sex ratio at Poilão is among the most balanced reported for green turtle
387 populations, comparable to estimates found in Suriname (54% females; Mrosovsky 1994),
388 Turkey (55.7% females; Candan & Kolankaya 2016), and in one beach of Ascension Island
389 (53.4% females; Broderick et al. 2001), with, to our knowledge, only one study reporting
390 male-biased primary sex ratios (63% males; Esteban et al. 2016). These estimates should be

391 taken with caution however, as different proxies can lead to disparate sex ratios (Fuentes et
392 al. 2017). Although the proportion of male hatchlings produced at Poilão may decrease in the
393 future, our results suggest that the complete feminisation of the hatchlings is unlikely (Jensen
394 et al. 2017). However, the threshold proportion of male hatchlings at which population
395 viability can be jeopardized is yet unknown for marine turtles (Bell et al. 2009, Hawkes et al.
396 2009). Interestingly, recent studies have found that several populations with female-skewed
397 primary sex ratios have approximate numbers of females and males breeding annually (i.e.
398 ‘operational sex ratio’; Wright et al. 2012a, Rees et al. 2013, Stewart & Dutton 2014). These
399 discrepancies between primary and operational sex ratios can result from one or a
400 combination of mechanisms, such as differential survival between female and male post-
401 hatchlings (Wright et al. 2012b), different breeding periodicities (Hays et al. 2014), and
402 males mating with several females from different populations (Roberts et al. 2004, Wright et
403 al. 2012a). Given that the population at Poilão is the largest in Africa, and the sixth largest in
404 the world (Catry et al. 2009, SWOT 2011), more males are likely produced there than in all
405 green turtle rookeries in Africa combined, given that a significant number of nests are laid in
406 the forest and forest border habitats. It is therefore possible that these males contribute
407 significantly to the wider Eastern Atlantic metapopulation, supported by evidence of male-
408 mediated gene flow across populations and tracking data in other regions (Roberts et al. 2004,
409 Wright et al. 2012a), and may become more important in the future, when sex ratios
410 elsewhere become increasingly female biased, providing that the native forest at Poilão is
411 maintained.

412

413 **Spatial and temporal microrefugia**

414 In this study, we assessed climate change impacts under the assumption that the spatial and
415 temporal distribution of nests remained unchanged. However, this may not be the case. Poilão

416 is covered by undisturbed tropical forest (Catry et al. 2002), which provides cool incubation
417 conditions, yet currently, under a quarter of the clutches are laid here. There is thus potential
418 for nesting females to use the forest as refuge, mitigating the temperature-linked impacts on
419 the sex ratio and the hatching success, while simultaneously preventing clutch flooding due to
420 SLR and storm events, as the forest sets at slightly higher elevations.

421 Adjusting the timing of the nesting season could further reduce feminisation of the
422 population. Beginning to nest two months later, would synchronize the peak of the TSP with
423 the colder period of the year. Such displacement could potentially have other associated
424 impacts, as it would move nesting to the dry season, and moisture provided by rainfall may
425 be important for nest construction (Mortimer & Carr 1987), and male hatchling production
426 (Godfrey et al. 1996; Wyneken & Lolavar 2015). Yet, there is already nesting occurring
427 during this period at Poilão (>100 clutches/year, C. Barbosa *pers. obs.*), and successful
428 populations nest under dry conditions elsewhere (Godley et al. 2001b, Marco et al. 2012). If
429 females started to nest slightly earlier instead, it would also decrease TSP incubation
430 temperatures, compared to the present. Predictions on phenological responses to climate
431 change among sea turtles remain elusive, as it is not clear if the onset of nesting is triggered
432 by sea surface temperatures at breeding (Weishampel et al. 2004) or foraging areas (Mazaris
433 et al. 2009), and whether the response to higher temperatures is anticipation (Weishampel et
434 al. 2004, Mazaris et al. 2009), or delaying of nesting (Neeman et al. 2015), in any case, there
435 is scope for adaptation.

436

437 **Vulnerability to SLR and storminess**

438 Under the most extreme IPCC projection of future SLR, over half of the current nesting
439 habitat will remain suitable by 2100. Recent studies, however, indicate that IPCC projections
440 are underestimated, and predict higher SLR (Grinsted et al. 2010, Horton et al. 2014, Dutton

441 et al. 2015), under which the proportion of nesting habitat loss at Poilão would increase
442 significantly. In addition to SLR, future increases in the prevalence and intensity of storms,
443 with heavier precipitation and higher swells, may lead to more frequent temporary inundation
444 of the nesting area (Pike et al. 2015). Large uncertainty of current models precluded us from
445 quantifying these impacts, however, as there is no physical barrier (e.g. cliff, human
446 construction) restricting the nesting beach at Poilão, a likely response to SLR and increased
447 storminess will be some coastal realignment. Thus the beach at Poilão may itself be resilient
448 to some degree of climate change. There will be, nonetheless, a limitation to coastal retreat,
449 because Poilão has a very small area (43ha; Catry et al. 2002) and is relatively low-lying in
450 its interior. Thus, SLR will likely reduce the available nesting area, potentially leading to
451 density-dependent processes reducing nesting numbers (caused by failure nest due to increase
452 disturbance by other turtles), or increasing clutch mortality (females digging out each other's
453 nests). Alternatively, turtles can adapt by starting to nest more often at the nearby islands of
454 Cavalos, Meio or João Vieira, also within the National Park, as green turtles tagged at Poilão
455 have been recaptured there (n=3, unpublished data, IBAP-Guinea-Bissau).

456

457 **Foraging plasticity and external threats**

458 Although we do not have samples of prey items to fully understand the diet of the green
459 turtles nesting at Poilão, the values reported here fall well within an omnivorous diet,
460 typically observed among the more generalists loggerhead turtles (Wallace et al., 2009,
461 McClellan et al. 2010), but also seen among green turtles (Lemons et al. 2011). Additionally,
462 individual turtles seem to be foraging in a wide range of locations, likely further contributing
463 to variation in their trophic niche. Having a wide variety of both food items and foraging
464 grounds is preferable for population persistence, thus, the foraging plasticity evident in this
465 population should be advantageous in the future. A proportion of the nesting females from

466 Poilão migrate northward after the breeding season, to forage at the Banc d'Arguin, in
467 Mauritania (>1000km; Godley et al. 2010), potentially encountering a range of threats along
468 the way. The juvenile turtles originating at Poilão recruit mainly to foraging grounds along
469 the west coast of Africa, in Cape Verde, Liberia, Benin, Equatorial Guinea, and Sao Tome
470 and Principe, with a smaller proportion recruiting to Southwest Atlantic aggregations, in
471 Brazil, and Argentina (Patrício et al. 2017b). Aside from the Equatorial Guinea and
472 Argentina, all other countries have a higher (i.e. worse) CIS, than Guinea-Bissau, with Cape
473 Verde and Mauritania scoring the worst, being 60th and 44th, respectively, in a list of 238
474 Exclusive Economic Zones, mostly due to the presence of extensive artisanal and industrial
475 fisheries, with high rates of bycatch (Zeeberg et al. 2006, Wallace et al. 2010, Halpern et al.
476 2015). This highlights that population resistance may be compromised by external threats,
477 justifying the ongoing collaborations for the conservation of these species across-boarders.
478 Future work should include satellite tracking of more individuals, in tandem with stable
479 isotope analysis of both turtles and potential food sources, to further unveil their foraging
480 behaviour.

481

482 **Population growth**

483 Female production appears to have been rising since the mid-1970s, potentially contributing
484 to current population expansion, as the number of nests in Poilão has increased by 258% in
485 the past ten years (unpublished data, IBAP-Guinea-Bissau). We predicted that this tendency
486 will continue throughout the century, thus climate change will contribute to population
487 growth, assuming that there will be sufficient food supply at the feeding grounds of this
488 population . As incubation temperatures approach lethal levels, towards the end of the
489 century, growth is expected to reach a plateau, and eventually start to decline. This is in
490 agreement with previous studies, indicating that resilience of TSD species to climate change

491 will eventually be overcome, due to unviable high temperatures (Santidrián Tomillo et al.
492 2015, Laloë et al. 2017). However, the existence of thermal microrefugia can potentially
493 allow for continued population growth.

494

495 **Climate change resilience and conservation implications**

496 Overall, we estimate that this population has medium to high resistance to climate change
497 impacts, until the end of this century. In a previous study we found that the green turtles at
498 Poilão currently nest at a preferred elevation, above the high spring tide, enhancing hatching
499 success (Patrício et al. 2018), suggesting that nest site choice is an adaptive behaviour that
500 has been under selection. Additionally, nesting turtles displayed high fidelity to nesting
501 microhabitat characteristics (i.e. habitat type, distance to the vegetation, location along the
502 beach and elevation; Patrício et al. 2018), a phenomenon also seen in hawksbill turtles
503 (Kamel & Mrosovsky, 2006, 2005), suggesting a possible genetic basis for nest site selection.
504 This provides opportunity for natural selection to act, as females deciding to lay their clutches
505 at higher elevations (safer from flooding) and under cooler conditions (in the forest, but also
506 later in the season) may have enhanced fitness under climate change scenarios. Thus, the
507 availability of spatial and temporal microrefugia, together with fidelity to nesting site, suggest
508 potential for mitigation of climate change impacts, through the evolution of nest site selection
509 behaviour. This could lead to the maintenance, or return to pre-disturbance conditions, of the
510 primary sex ratio and of unflooded nests, hence resilience to climate change. Additionally,
511 TSD species could, theoretically, mitigate the expected temperature-linked impacts on the
512 primary sex ratio, by experiencing microevolutionary shifts in threshold temperatures, i.e.
513 transitional range of temperatures (TRT: incubation temperatures at which both male and
514 female hatchlings are produced), and pivotal temperature (the incubation temperature

515 resulting in a 1:1 primary sex ratio). This is more likely in populations with more mixed
516 clutches (and wider TRTs, Hulin et al. 2009), as is the case in Poilão (Patrício et al. 2017a).
517 This is the single most comprehensive assessment to date of climate change resistance of a
518 marine reptile, using the most updated IPCC models, including the impacts of temperature
519 and SLR, and the population size and trajectory. The approach used here is highly
520 transferable to other marine turtle rookeries, enabling comparisons among populations and
521 species, potentially contributing to regional assessments.

522

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871 **Table 1.** Climate change resistance scoring for sea turtles, adapted from Abella-Perez et al. (2016). SL: sea level. Cumulative impact score from
872 Halpern et al. (2015). An option per row is selected and corresponding scores (0, 25, 50, 75, 100) for each column added and averaged, for a
873 final resistance score between 0 and 100.

Criterion	Unit	Worst	Average				Best
		0	25	50	75	100	
1. Primary sex ratio	% female hatchlings	≥ 99	91 - 98	81 - 90	61 - 80	≤ 60	
2. Emergence success	% emerged hatchlings	≤ 10	11 - 30	31 - 50	51 - 75	> 75	
3. Spatial microrefugia	% nests in warmest habitat	≤ 20	20 - 39	40 - 59	60 - 79	> 80	
4. Temporal microrefugia	% nests warmest periods	≤ 20	20 - 39	40 - 59	60 - 79	> 80	
5. Sea level rise	% nesting area below SL	> 80	60 - 79	40 - 59	20 - 39	≤ 20	
6. Foraging plasticity	putative no. prey species	1-2	2 - 5	5 - 10	10 - 20	> 20	
7. Other threats:	direct take	% take nesting population	≥ 70	> 50	> 30	> 10	0
	others	cumulative impact score	6.32 - 8.23	4.16 - 6.31	3.76 - 4.16	2.58 - 3.75	0 - 2.57
8. Rookery trend	% female recruitment	< 0	0 - 5	5 - 10	10	> 10	
9. Rookery size	no. nests	≤ 100	101 - 500	501 - 1000	1001 - 5000	> 5000	

874

875 **Table 2.** Representative concentration pathways (RCPs) from the IPCC fifth assessment
876 report (Collins et al., 2013), and estimated values for each of nine criterion used to assess the
877 resistance to climate change of the major green turtle population nesting at the Bijagós
878 Archipelago, Guinea Bissau, and respective score in parenthesis, following the framework
879 proposed in Abella-Perez et al. (2016). CIS: cumulative impact score (Halpern et al. 2015).
880 SL: sea level.

Criterion	Unit	Climate change scenario					
		RCP 4.5		RCP 6		RCP 8.5	
Peak greenhouse gas emissions	Year	2040		2080		continue to rise	
Mean AT anomaly	2081-2100 (ΔT °C)*	1.6 ± 0.4		2.0 ± 0.4		3.3 ± 0.6	
Mean SLR	2081-2100 (m)	0.47		0.48		0.63	
1. Primary sex ratio	% female hatchlings	76.3%	(75)	82.0%	(50)	93.3%	(25)
2. Emergence success	% emerged hatchlings	51.6%	(75)	49.4%	(50)	32.4%	(50)
3. Spatial microrefugia	% nests warmest habitat	50.0%	(50)	50.0%	(50)	50.0%	(50)
4. Temporal microrefugia	% nests warmest period	54.0%	(50)	54.0%	(50)	54.0%	(50)
5. Sea level rise	% nesting area below SL	33.4%	(75)	33.4%	(75)	43.0%	(50)
6. Foraging plasticity	putative no. prey species	5-10	(50)	5-10	(50)	5-10	(50)
7. Other threats	CIS and take nesting females	3.57	(75)	3.57	(75)	3.57	(75)
8. Rookery trend	% female recruitment	58.0%	(100)	64.0%	(100)	32.0%	(100)
9. Rookery size	no. nests**	40,170	(100)	41,602	(100)	33,588	(100)
Resistance score (Σ criteria/ n criteria)		72		67		61	

*Tropical regions

** Nests in 2120, considering 20 years as minimum age at maturity (Bell et al., 2005; Patricio et al., 2014)

881 **Figure captions**

882

883 **Figure 1.** Historical and projected **a.** incubation temperatures, and **b.** proportion of green
884 turtle hatchlings expected to be female, in three nesting microhabitats, at Poilão Island,
885 Guinea-Bissau. OS – ‘open sand’, FB – ‘forest border’, F – ‘forest’. Orange curve (overall)
886 shows projection of primary sex ratio accounting for the current nesting distribution across
887 microhabitats, and for the emergence success at each microhabitat. Solid horizontal line
888 indicates a. field-derived ‘pivotal’ temperature for this population (29.4 °C, Patrício et al.
889 2014), and b. 1:1 sex ratio.

890

891 **Figure 2. a.** Mean bi-weekly air temperature, **b.** precipitation and **c.** green turtle nesting
892 distribution with density curve of thermosensitive period distribution (dashed line), at Poilão
893 Island, Guinea-Bissau, averaged across four years: 2013-2016. Climate data obtained from
894 the National Climatic Data Centre (<http://cdo.ncdc.noaa.gov/CDO/cdo>, closest
895 meteorological station Bolama Island, 50km distant).

896

897 **Figure 3.** Proportions of male (black) and female (grey) green turtle hatchlings (x-axes), in
898 three nesting microhabitats, across the nesting season, at Poilão Island, Guinea-Bissau:
899 current estimates and projections for 2100, under three climate models, RCP4.5, RCP6 and
900 RCP8.5 (Collins et al., 2013). See Table 1 for climate model details, see methods for habitat
901 definitions.

902

903 **Figure 4.** Proportion of green turtle nesting area at Poilão Island, Guinea-Bissau, expected to
904 become flooded due to sea level rise (SLR). Dashed lines indicate future scenarios of SLR: a.

905 RCP4.5-0.47m, and RCP6-0.48m; b. RCP8.5-0.63m (from IPCC AR5; Collins et al. 2013),
906 and c. projection derived from semi-empirical models: 1.2m (Horton et al. 2014).

907

908 **Figure 5.** Frequency distributions of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotopic
909 signatures for nesting green turtles from Poilão Island, Guinea-Bissau, in 2013 (n=79, black),
910 2014 (n=70, grey), and 2016 (n=38, white).

911

912 **Figure 6.** Nesting female recruitment to the green turtle rookery in Poilão Island, Guinea-
913 Bissau, in relation to the present (i.e. 2013-2016), considering a minimum age at maturity of
914 20 years (Bell et al. 2005, Patricio et al. 2014). In the y-axis, a 0 (dashed line) indicates no
915 change in the number of nesting females, and a recruitment of 100% indicates a doubling.
916 The black curve accounts for the temperature-linked hatchling mortality effect, absent in the
917 grey curve.