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1  
2 **FORECASTING THE VIABILITY OF SEA TURTLE EGGS IN A WARMING**  
3 **WORLD**

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**Abstract**

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Animals living in tropical regions may be at increased risk from climate change because current temperatures at these locations already approach critical physiological thresholds. Relatively small temperature increases could cause animals to exceed these thresholds more often, resulting in substantial fitness costs or even death. Oviparous species could be especially vulnerable because the maximum thermal tolerances of incubating embryos is often lower than adult counterparts, and in many species mothers abandon the eggs after oviposition, rendering them immobile and thus unable to avoid extreme temperatures. As a consequence, the effects of climate change might become evident earlier and be more devastating for hatchling production in the tropics. Loggerhead sea turtles (*Caretta caretta*) have the widest nesting range of any living reptile, spanning temperate to tropical latitudes in both hemispheres. Currently, loggerhead sea turtle populations in the tropics produce nearly 30% fewer hatchlings per nest than temperate populations. Strong correlations between empirical hatching success and habitat quality allowed global predictions of the spatiotemporal impacts of climate change on this fitness trait. Under climate change, many sea turtle populations nesting in tropical environments are predicted to experience severe reductions in hatchling production, whereas hatching success in many temperate populations could remain unchanged or even increase with rising temperatures. Some populations could show very complex responses to climate change, with higher relative hatchling production as temperatures begin to increase, followed by declines as critical physiological thresholds are exceeded more frequently. Predicting when, where, and how climate change could impact the reproductive output of local populations is crucial for anticipating how a warming world will influence population size, growth, and stability.

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**Introduction**

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Ambient temperatures are warmer in many tropical regions than elsewhere, which allows a wide range of ectotherms to use the external environment to maintain body temperatures near their physiological optimum (Deutsch *et al.* 2008; Huey *et al.* 2009; Kearney *et al.* 2009; Sinervo *et al.* 2010; Sunday *et al.* 2011; Tewksbury *et al.* 2008). As a consequence, the maximum temperature that individual species can withstand has coevolved with preferred body temperature; generally, tropical species live closer to their physiological optimum than closely-related temperate species (Deutsch *et al.* 2008; Grigg & Buckley 2013; Sunday *et al.* 2011). Exceeding this optimum, however, can be costly and dangerous. The safety margin between the optimal temperature range and lethal maximum is often quite narrow (Huey *et al.* 2009; Tewksbury *et al.* 2008; Vickers *et al.* 2011), and climate change could make it more difficult for some tropical species to avoid overheating (Deutsch *et al.* 2008; Kearney *et al.* 2009; Logan *et al.* 2013; Sinervo *et al.* 2010; Tewksbury *et al.* 2008). In temperate environments, many species are living below their optimal temperatures much of the time, and increases in temperature are predicted to benefit a wide range of physiological processes (Deutsch *et al.* 2008; Hays *et al.* 2010; Katselidis *et al.* 2012; Kearney *et al.* 2009; Sinervo *et al.* 2010). This may also be the case for some tropical species, depending on interactions among habitat use, preferred body temperature, and critical thermal maximum (Logan *et al.* 2013; Storch *et al.* 2005). Through the same mechanism, species distributed across a wide range of different climatic conditions (e.g., latitude, altitude, canopy cover, water depth) may be able to adaptively respond to climate change, depending on how temperature increases interact with important physiological thresholds at local spatial scales (Fossette *et al.* 2012; Witt *et al.* 2010). These patterns make understanding when, where, and how local populations will experience the effects of climate change a difficult task, especially for widespread species.

66 Mobile organisms may be able to ameliorate some of the impacts of warming by  
67 changing activity patterns (Fossette *et al.* 2012; Huey *et al.* 2009; Kearney *et al.* 2009;  
68 Schofield *et al.* 2009; Sinervo *et al.* 2010), habitat use (Kearney *et al.* 2009; Logan *et al.*  
69 2013), or dispersing to limit thermal stress (Pike 2013b; Witt *et al.* 2010). For example, many  
70 large marine species select for temperature at spatial scales spanning microhabitats to regions,  
71 which can influence seasonal and daily movements and activity patterns (Rasmussen *et al.*  
72 2007; Schofield *et al.* 2009). The opportunity to avoid stressful thermal conditions may be  
73 much more restricted during life stages when mobility is limited (Godley *et al.* 2001; Hawkes  
74 *et al.* 2007; Hays *et al.* 2003; Mitchell *et al.* 2008; Telemeco *et al.* 2013; Telemeco *et al.*  
75 2009). If the thermal environment becomes unfavourable, organisms with limited mobility  
76 may be unable to avoid stressful temperatures (e.g., by shade seeking, altering activity times,  
77 etc.) and thus may be at increased risk of physiological stress and possibly death. In fact, the  
78 physical locations of immobile life stages may depend upon external factors, such as nest-site  
79 placement by the mother (Hays *et al.* 1995; Wood & Bjorndal 2000) and local environmental  
80 conditions (Godley *et al.* 2001; Hawkes *et al.* 2007; Hays *et al.* 2003; Pike 2013a). Females of  
81 many species select nest sites based on temperature, because of its direct effects on embryonic  
82 development, incubation duration, hatchling body size, and offspring survival (Ackerman  
83 1997; Davenport 1997; Telemeco *et al.* 2013; Telemeco *et al.* 2009). In some cases, however,  
84 climate change could alter the landscape such that the microhabitat characteristics formerly  
85 selected by females become rare or unavailable (Katselidis *et al.* 2012; Mitchell *et al.* 2008;  
86 Telemeco *et al.* 2013; Telemeco *et al.* 2009; Witt *et al.* 2010). This could lead to widespread  
87 changes in nest temperatures, which could directly alter hatchling phenotypes (including sex  
88 for species with temperature-dependent sex determination; Fuentes & Porter 2013; Godley *et al.*  
89 2001; Hawkes *et al.* 2007; Hays *et al.* 2003; Telemeco *et al.* 2009, 2013) or increase  
90 embryonic mortality (Tapilatu & Tiwari 2007).

91           Research into the direct effects of climate change on the vulnerable egg stage of  
92 terrestrial animals has focused on the sex ratios of the offspring in species with temperature-  
93 dependent sex determination. Primary sex ratios can directly influence population growth  
94 rates, and chronically-biased sex ratios could lead to population bottlenecks or even  
95 population collapse (Hays *et al.* 2003; Katselidis *et al.* 2012; Witt *et al.* 2010). To date,  
96 however, a much more important aspect has been overlooked: survival of the embryos. If  
97 temperatures inside the nest exceed the point at which embryonic survival decreases  
98 substantially, this could be magnify any potential demographic consequences associated with  
99 skewed sex ratios or other sublethal temperature effects. Large-scale egg mortality due to  
100 overheating already has been observed on some tropical sea turtle nesting beaches (Tapilatu &  
101 Tiwari 2007), and widespread changes in hatchling phenotypes have been predicted for a  
102 range of reptiles (Fuentes & Porter 2013; Godley *et al.* 2001; Hawkes *et al.* 2007; Hays *et al.*  
103 2003; Katselidis *et al.* 2012; Mitchell *et al.* 2008; Telemeco *et al.* 2009, 2013; Witt *et al.*,  
104 2010). To date, however, we have almost no understanding of how climate change could  
105 influence offspring production, mediated through hatching success of the eggs, across the  
106 entire distribution of widespread species. Thus, our understanding of how climate change  
107 could influence life history and population demography of ectotherms is limited.

108           Loggerhead sea turtles (*Caretta caretta*) have the widest nesting range of any living  
109 reptile, spanning temperate to tropical latitudes in both hemispheres (Pike 2013a).  
110 Loggerhead sea turtles generally nest sympatrically with the other six species of sea turtle, but  
111 are distributed further north and south. Sea turtle nesting beaches are at risk from sea level  
112 rise, which could reduce the amount of nesting habitat available and increase the water table,  
113 both of which could reduce habitat quality and reproduction (Fish *et al.* 2005, 2008; Fuentes  
114 *et al.* 2011). The embryos of all sea turtle species show similar functional responses to  
115 temperature (i.e., fixed upper lethal temperatures of 35°C; Ackerman 1997; Davenport 1997;

116 Witt *et al.* 2010), which led me to predict that the local effects of climate change on hatching  
117 success would be most pronounced in tropical regions. To understand how climate change  
118 could impact loggerhead sea turtle reproduction, I predicted spatial and temporal patterns of  
119 egg hatching success across the geographic range of this widespread species.

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121 **Materials and Methods**

122 *Modeling approach.*— I used MaxEnt version 3.3.3k (Phillips *et al.* 2006; Phillips & Dudík  
123 2008) to model loggerhead sea turtle nesting distributions under current and predicted future  
124 climate scenarios. This approach combines environmental variables with known nesting  
125 locations and randomly-selected background locations to predict the potential distribution of  
126 nesting using the principle of maximum entropy (Phillips *et al.* 2006; Phillips & Dudík 2008).  
127 Model input consisted of 933 georeferenced nesting beach locations for loggerhead turtles  
128 (compiled from State of the World’s Sea Turtles and the Wider Caribbean Sea Turtle  
129 Conservation Network; Dow Piniak & Eckert 2011; Pike 2013a) and nine climate variables  
130 (mean daily range in temperature, isothermality, maximum temperature of the warmest  
131 month, annual temperature range, precipitation seasonality, and precipitation of the wettest,  
132 driest, warmest, and coldest quarters; Hijmans *et al.* 2005). These climate variables  
133 encompass broad annual and seasonal patterns of temperature and rainfall globally (Pike  
134 2013a), and thus are relevant to loggerhead sea turtle nesting, which shows strong  
135 geographical variation in seasonality (reviewed by Dewald & Pike 2013). Climate variables  
136 covered land areas at a resolution of 4km x 4km, which was restricted to within ~8km (two  
137 grid cells) of the ocean to improve model performance (Pike 2013a, 2013b).

138 MaxEnt uses these climatic predictor variables to quantify the probability of sea turtle  
139 nesting occurring in each grid cell, ranging from 0 to 1, with values near 0.5 representative of  
140 average habitat quality (Phillips & Dudík 2008). The climatic predictor variables were used to  
141 discriminate nesting and non-nesting locations using threshold relationships. I used 10-fold  
142 crossvalidation to randomly partition the full set of nesting locations into 10 approximately  
143 equal datasets. During each of 10 model runs, nine of the data partitions are used to train the  
144 model and these results are tested against the tenth partition (for full details on the process of  
145 model building, testing, and selection see Pike 2013a, 2013b). For all analyses I used the



146 median habitat suitability value across all 10 runs of the model.

147 I calibrated distribution models using current climatic conditions (averaged over  
148 ~1950-2000; for full details on climate data, see Hijmans *et al.* 2005), and projected the final  
149 model onto future predicted climate surfaces. I used four climate change models (Canadian  
150 Centre for Climate Modelling and Analysis, Commonwealth Scientific and Industrial  
151 Research Organisation, Hadley Centre for Climate Prediction and Research (UK), and  
152 National Institute for Environmental Studies) under three emission families (A1, A2A, B2A)  
153 that encompass the central 80% of climate change predictions for 2020, 2050, and 2080 (total  
154 of 36 future scenarios; Intergovernmental Panel on Climate Change 2007; Special Report on  
155 Emission Scenarios, 2000). These estimates encompass current rates of temperature increase  
156 (i.e., a 2-7°C increase by 2100; Special Report on Emission Scenarios, 2000), and thus are a  
157 good approximation of the range of conditions likely to be experienced in the coming  
158 decades. The A2A family predicts a temperature increase within the range of 2.0-5.4°C,  
159 relative to 1980-1999 (best estimate = 3.4°C; Special Report on Emission Scenarios, 2000).  
160 The B2A family predicts a temperature increase within the range of 1.4-3.8°C (best estimate =  
161 2.4°C; Special Report on Emission Scenarios, 2000). The A1 family is intermediate to these  
162 high and low predictions.

163 I explored how climate change could influence the maximum temperature of the  
164 warmest quarter (i.e., summer, during which many loggerhead sea turtle populations are  
165 nesting; Dewald & Pike 2013) at two spatial scales: (1) regional (temperate vs tropical  
166 latitudes) and (2) among spatially and biologically distinct populations that differ in  
167 conservation status and threats (Regional Management Units, defined and delimited by  
168 Wallace *et al.*, 2010). Loggerhead turtles encompass eight Regional Management Units, two  
169 of which span both temperate and tropical latitudes. For each loggerhead nesting beach I  
170 extracted temperature data from the spatial climate datasets. These temperatures and predicted

171 hatching success (see below) were compared among regions and Regional Management Units  
172 under different climate scenarios.

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174 *Empirical hatching success.*— I used published loggerhead hatching success data from  
175 undeveloped nesting beaches (n = 21), expressed as the mean proportion of eggs hatching  
176 from each clutch (Pike 2008, 2009). These beaches were categorized as temperate or tropical  
177 based on latitude (tropical locations range between 23°26'16"N and 23°26'16"S), and habitat  
178 quality was estimated using the MaxEnt habitat suitability score for current climatic  
179 conditions. These hatching success data were obtained from different studies conducted in  
180 different years and averaged over varying time intervals, but are the best currently available  
181 (Pike 2008, 2009). To test for differences in egg viability between temperate and tropical  
182 beaches, I used ANOVA with nesting beach location (temperate or tropical) as the factor and  
183 hatching success as the dependent variable. I used logarithmic regression to test for an  
184 empirical relationship between habitat suitability and hatching success.

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186 *Forecasting hatching success.*— Species distribution modeling is a powerful way to derive a  
187 single measure of local habitat quality (i.e., suitability, probability of occurrence) across the  
188 geographic range of a species from complex environmental datasets (Phillips & Dudík 2008).  
189 These measures of habitat quality can be linked to population-level ecological traits, such as  
190 genetic diversity (Dubey *et al.* 2013), abundance (Kulhanek *et al.* 2011), maximum  
191 population size (VanDerWal *et al.* 2009), or offspring production (Brambilla & Ficetola  
192 2012), and predicted across the landscape under current and future climate scenarios (Dubey  
193 *et al.* 2013). I created spatial and temporal predictions of hatching success using the  
194 regression equation relating habitat suitability to hatching success. I extracted hatching  
195 success estimates for loggerhead nesting beaches, and graphed predicted hatching success at

196 known tropical and temperate nesting beaches under current climatic conditions and climate  
197 change scenarios (n = 433 nesting beaches; global climate datasets often are missing data for  
198 small islands, on which some sea turtle populations nest; Pike 2013a). To visualize these  
199 predictions in geographic space, I created maps showing the change in future hatching success  
200 relative to current predicted hatching success.  
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**Results**

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Only 26.6% of loggerhead sea turtle nesting beaches worldwide are located in tropical latitudes ( $n = 248$  of 933); the remaining 73.4% of nesting beaches are in temperate climates. Currently, ambient temperatures on loggerhead sea turtle nesting beaches located in tropical climates are significantly warmer than those located in temperate climates ( $F_{1,475} = 98.64$ ,  $P < 0.0001$ ; Fig. 1a). Tropical nesting beaches also produce significantly fewer hatchlings per nest than do temperate nesting beaches ( $F_{1,19} = 7.19$ ,  $P = 0.01$ ; Fig. 1b), providing strong support for a broad link between ambient temperatures and hatching success. These findings imply that climate change impacts on hatching success could be dependent upon how close current temperatures are to lethal, and the magnitude of local temperature increase. The effects of climate change on loggerhead sea turtles could thus differ regionally (temperate vs tropics), vary among spatially and biologically-distinct populations, and even among individual nesting beaches.

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The quality of loggerhead sea turtle nesting habitat (as estimated by MaxEnt species distribution modeling) is significantly and positively related to empirical egg hatching success (logarithmic regression;  $n = 21$  undeveloped nesting beaches,  $R^2 = 0.525$ ,  $F_{1,19} = 21.02$ ,  $P = 0.0002$ ; Supporting Information Fig. S1). Habitat quality explains over 50% of the variation in hatching success among populations, and thus provides a strong measure of reproductive output. Hatching success was only weakly correlated with latitude, revealing that geographic location is a poor predictor of habitat quality ( $R^2 = 0.12$ ,  $F_{1,16} = 2.19$ ,  $P = 0.160$ ).

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Under current climatic conditions, loggerhead sea turtle nesting beaches do not frequently exceed temperatures that are lethal for incubating eggs (Godley *et al.* 2001; Katselidis *et al.* 2012); however, by 2080 the maximum temperature during the nesting season could exceed lethal levels at over half of tropical nesting beaches (Fig. 2). Under future climate change scenarios, a much lower proportion of temperate nesting beaches are expected

227 to regularly exceed lethal temperatures as compared to tropical nesting beaches, despite both  
228 regions experiencing a similar magnitude of temperature increase (Fig. 2). This effect is  
229 because temperate nesting sites initially were cooler, and thus require a larger temperature  
230 increase to exceed lethal for developing embryos (Fig. 2). Under climate change, loggerhead  
231 turtles nesting in temperate environments are predicted to maintain high levels of hatching  
232 success overall, which could increase in those sites that have relatively low hatching success  
233 under the A1 and A2A future climate families for 2020-2080 (Fig. 3). By contrast, predictions  
234 from tropical nesting sites suggest that hatching success will decline overall during the same  
235 period (Fig. 3). The average predictions for all climate change scenarios produced remarkably  
236 similar hatching success estimates for both tropical and temperate locations within future time  
237 intervals (Fig. 2).

238 Nesting beach temperatures and hatching success show similar patterns between  
239 temperate and tropical nesting sites at even more local scales; individual spatially- and  
240 biologically-distinct populations in temperate locations generally have lower maximum  
241 temperatures and higher predicted hatching success than those in tropical locations (Fig. 1c).  
242 This pattern is also evident in the two individual populations that span both temperate and  
243 tropical latitudes (Fig. 1d). Overall, this strongly suggests that the impacts of climate change  
244 could differ substantially within and between populations, whether or not those populations  
245 are classified at local or regional scales.

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**Discussion**

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Understanding when, where, and how climate change will manifest, and to what degree, is crucial for ensuring the adequate conservation of imperiled species. One important, and understudied, aspect of climate change is how it will influence long-term population dynamics in terms of reproductive success, offspring production, and population demography. A necessary first step is an understanding of whether macro-scale environmental features contribute to successful reproduction, and how. The hatching success of loggerhead sea turtle eggs is strongly related to habitat quality, estimated using measures of seasonal variability in temperature and precipitation. Tropical nesting beaches experience significantly warmer ambient temperatures than do temperate beaches, and thus produce relatively fewer hatchling turtles per nest (Fig. 1). In some populations, climate change may not substantially alter hatching success of the eggs, whereas other populations could show either dramatic reductions or more complex responses, whereby hatching success initially increases with moderate warming but declines over the longer-term as warming continues (Fig. 3). These possible outcomes are likely a result of the wide geographic distribution across which loggerhead sea turtles nest, which is limited by physiological constraints of temperature and moisture on embryonic development (Pike 2013a). Overall, a regional conservation and management focus may be necessary to protect widespread and endangered species from climate change, which is difficult when populations span geopolitical boundaries across both terrestrial and marine environments (Wallace *et al.* 2010; Witt *et al.* 2010).

Visualizing hatching success in geographic space reaffirms broad differences in the hatching success of eggs from temperate and tropical loggerhead sea turtle populations; hatching success was generally predicted to be highest in temperate locations (e.g., southeastern United States, Mediterranean) and lowest in tropical locations (e.g., Central/South America, Australasia; Fig. 3). Hatching success in the Caribbean and

272 Australasian regions is not expected to show a marked change by 2020, whereas hatching  
273 success could increase in the Mediterranean Sea (Fig. 3). By 2050, however, hatching success  
274 is predicted to decline overall at many sites worldwide, which could continue through 2080  
275 (Fig. 3). The Mediterranean Sea is predicted to have the largest geographic area showing an  
276 increase in hatching success, whereas the Caribbean and Australasian regions could show  
277 declines by more than 15% in some cases (Figs. 1-3). These patterns highlight some of the  
278 complex spatial, temporal, and population-specific impacts of climate change on reproduction  
279 in widespread species.

280         Although some of the predicted reductions in hatching success may not seem large  
281 (e.g., changes of a few percentage), other more subtle temperature effects on embryonic  
282 development could have strong and direct impacts on population characteristics. The sex of  
283 sea turtle embryos is determined by incubation temperature during development, and even  
284 slight increases in sand temperatures could alter population-specific sex ratios or other  
285 morphological characteristics (Fuentes & Porter 2013; Godley *et al.* 2001; Hawkes *et al.*  
286 2007; Hays *et al.* 2003; Witt *et al.* 2010). This has led to speculation that some sea turtle  
287 nesting beaches will produce biased hatchling sex ratios, such that some geographic regions  
288 mainly produce males, and others mainly produce females (Fuentes & Porter 2013; Hawkes *et al.*  
289 *et al.* 2007). The longer-term patterns of inter-annual variability in hatchling phenotype, and  
290 how these integrate over the extended generation time of sea turtles, are an important research  
291 area (Katselidis *et al.* 2012). Recent evidence from male turtles, however, suggests that their  
292 ability to breed annually with multiple females could help buffer any negative demographic  
293 consequences of skewed adult sex ratios (Hays *et al.* 2010; Wright *et al.* 2012).

294         Habitat quality, generated using maximum entropy relationships among temperature  
295 and precipitation, explained more than half of the variation in hatching success among  
296 loggerhead sea turtle populations globally. This is exceptional explanatory power when

297 considering that local factors intrinsic to characteristics of the mother and nesting habitat  
298 influence nest temperature, including patterns of nest-site selection (e.g., by females selecting  
299 for sand albedo, aspect, slope, or other factors among and within beaches; Hays *et al.* 1995,  
300 2001; Wood & Bjorndal 2000). Nest depth also plays important roles in incubation  
301 temperature, which in turn directly influences hatching success and hatchling sex and  
302 phenotype (Ackerman 1997). Although current research has yet to tackle how these aspects  
303 influence microclimatic conditions within nests worldwide, recent advances in mechanistic  
304 modeling approaches may offer one potential solution (Fuentes & Porter 2013). Mechanistic  
305 modeling also can be used to predict much more subtle seasonal effects of nest temperature  
306 on hatchling fitness, to better integrate predictions of these variables over timescales relevant  
307 to sea turtle ecology (e.g., decades). At present, however, our understanding of how climate  
308 variability will impact the temporal pace of hatchling production and phenotype is limited to  
309 broad predictions averaged over discrete time intervals. More subtle seasonal and inter-annual  
310 patterns have, to date, received little research attention, but this natural variation has the  
311 potential to buffer the impacts of climate change (Katselidis *et al.* 2012). Likewise, testing  
312 climate change predictions is essential to refining models to increase explanatory power. The  
313 hatching success predictions that I have generated can now be tested against field data and  
314 refined as empirical datasets become available and climate change predictions are updated.  
315 Although published data on hatching success are lacking for other sea turtle species (Pike  
316 2008, 2009), these results provide a baseline prediction for other species because current  
317 evidence suggests that sea turtles have fixed thermal reaction norms (Ackerman 1997).

318 Females of most oviparous species are selective in where they place their eggs,  
319 favouring microhabitats that will reduce hatching time and maximize hatching success and  
320 offspring fitness (e.g., warmer nest temperatures; Huang & Pike 2011). This has led to  
321 speculation that nesting females could compensate for the effects of climate change by



322 continuing to locate microhabitats that maximize fitness (Mitchell *et al.* 2008; Telemeco *et al.*  
323 2009, 2013). The sandy, sun-exposed beaches upon which sea turtles nest can experience high  
324 temperatures (Katselidis *et al.* 2012; Tapilatu & Tiwari 2007), but we do not yet understand  
325 whether maternal nest-site selection could compensate for temperature increases under  
326 climate change. Data from other, smaller reptile species that dig shallower nests suggest that  
327 morphological constraints on the ability to dig deeper nests could limit potential adaptive  
328 responses to climate change, and lead to skewed sex ratios and increased embryonic mortality  
329 (Katselidis *et al.* 2012; Mitchell *et al.* 2008; Telemeco *et al.* 2013). This is also a concern in  
330 sea turtles (Katselidis *et al.* 2012), although their ability to dig extremely deep nests (>1m  
331 below the surface) could provide a mechanism by which females can buffer their developing  
332 offspring from climate change (Mitchell *et al.* 2008; Telemeco *et al.* 2013).

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### Conclusions

335 The most direct impacts of climate change will come from the interactive effects of  
336 multiple stressors, which for many ectotherms will be the diverse impacts of temperature on  
337 all aspects of life history and ecology. Integrating the varied effects of temperature on  
338 embryonic survival, hatchling phenotype, and habitat use of marine life stages with other  
339 stressors is the only way to effectively prepare for the ecological effects of climate change.  
340 Doing this collectively within a single modeling framework is extremely difficult due to the  
341 complexity of responses at different spatial and temporal scales for the different life stages.  
342 An alternative approach may be to integrate the body of accumulating information on  
343 different threats using a vulnerability assessment framework or resilience indices (e.g.,  
344 Fuentes *et al.* 2011, 2013). Novel integration of disparate predictions of climate change and  
345 anthropogenic stressors are crucial towards a fuller understanding of how we are changing the  
346 face of biodiversity.

347

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**References**

- 357 Ackerman RA (1997) The nest environment and the embryonic development of sea turtles. In:  
358 *The Biology of Sea Turtles*. (eds Lutz PL, Musick JA) pp Page. Boca Raton, CRC  
359 Press.
- 360 Brambilla M, Ficetola GF (2012) Species distribution models as a tool to estimate  
361 reproductive parameters: a case study with a passerine bird species. *Journal of Animal*  
362 *Ecology*, **81**, 781-787.
- 363 Intergovernmental Panel on Climate Change (2007) Climate Change 2007: Synthesis Report.  
364 In: *Contribution of Working Groups I, II and III to the Fourth Assessment Report of*  
365 *the Intergovernmental Panel on Climate Change* (ed Core Writing Team, Pachauri  
366 RK, Reisinger A). Geneva.
- 367 Davenport J (1997) Temperature and the life-history strategies of sea turtles. *Journal of*  
368 *Thermal Biology*, **22**, 479-488.
- 369 Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR  
370 (2008) Impacts of climate warming on terrestrial ectotherms across latitude.  
371 *Proceedings of the National Academy of Sciences*, **105**, 6668-6672.
- 372 Dewald JR, Pike DA (2013) Geographical variation in hurricane impacts among sea turtle  
373 populations. *Journal of Biogeography*, **in press**.
- 374 Dow Piniak WE, Eckert KL (2011) Sea turtle nesting habitat in the Wider Caribbean Region.  
375 *Endangered Species Research*, **15**, 129-141.
- 376 Dubey S, Pike DA, Shine R (2013) Predicting the impacts of climate change on genetic  
377 diversity in an endangered lizard species. *Climatic Change*, **117**, 319-327.
- 378 Fish MR, Cote IM, Gill JA, Jones AP, Renshoff S, Watkinson AR (2005) Predicting the  
379 impact of sea-level rise on Caribbean sea turtle nesting habitat. *Conservation Biology*,  
380 **19**, 482-491.

- 381 Fish MR, Cote IM, Horrocks JA, Mulligan B, Watkinson AR, Jones AP (2008) Construction  
382 setback regulations and sea-level rise: Mitigating sea turtle nesting beach loss. *Ocean*  
383 *and Coastal Management*, **51**, 330–341.
- 384 Fossette S, Schofield G, Lilley MKS, Gleiss A, Hays GC (2012) Acceleration data reveals the  
385 energy management strategy of a marine ectotherm during reproduction. *Functional*  
386 *Ecology*, **26**, 324-333.
- 387 Fuentes MMBP, Pike DA, Dimatteo A, Wallace BP (2013) Resilience of marine turtle  
388 regional management units to climate change. *Global Change Biology*, **19**, 1399-1406.
- 389 Fuentes MMPB, Limpus CJ, Hamann M (2011) Vulnerability of sea turtle nesting grounds to  
390 climate change. *Global Change Biology*, **17**, 140-153.
- 391 Fuentes MMPB, Porter WP (2013) Using a microclimate model to evaluate impacts of  
392 climate change on sea turtles. *Ecological Modelling*, **251**, 150-157.
- 393 Godley BJ, Broderick AC, Downie JR *et al.* (2001) Thermal conditions in nests of loggerhead  
394 turtles: further evidence suggesting female skewed sex ratios of hatchling production  
395 in the Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **263**, 45-  
396 63.
- 397 Grigg JW, Buckley LB (2013) Conservatism of lizard thermal tolerances and body  
398 temperatures across evolutionary history and geography. *Biology Letters*, **9**.
- 399 Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007) Investigating the potential  
400 impacts of climate change on a marine turtle population. *Global Change Biology*, **13**,  
401 923-932.
- 402 Hays GC, Adams CR, Mortimer JA, Speakman JR (1995) Inter-beach and Intra-beach  
403 thermal variation for green turtle nests on Ascension Island, South-Atlantic. *Journal of*  
404 *the Marine Biological Association of the United Kingdom*, **75**, 405-411.
- 405 Hays GC, Ashworth JS, Barnsley MJ *et al.* (2001) The importance of sand albedo for the

- 406 thermal conditions on sea turtle nesting beaches. *OIKOS*, **93**, 87-94.
- 407 Hays GC, Broderick AC, Glen F, Godley BJ (2003) Climate change and sea turtles: a 150-  
408 year reconstruction of incubation temperatures at a major marine turtle rookery.  
409 *Global Change Biology*, **9**, 642-646.
- 410 Hays GC, Fossette S, Katselidis KA, Schofield G, Gravenor MB (2010) Breeding periodicity  
411 for male sea turtles, operational sex ratios, and implications in the face of climate  
412 change. *Conservation Biology*, **24**, 1636-1643.
- 413 Hijmans RJ, Cameron SE, Parra JL, Jones P, Jarvis A (2005) Very high resolution  
414 interpolated climate surfaces for global land areas. *International Journal of*  
415 *Climatology*, **25**, 1965-1978.
- 416 Huang W-S, Pike DA (2011) Climate change impacts on fitness depend on nesting habitat in  
417 lizards. *Functional Ecology*, **25**, 1125-1136.
- 418 Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Álvarez Pérez HJ, Garland T (2009)  
419 Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the*  
420 *Royal Society B: Biological Sciences*, **276**, 1939-1948.
- 421 Katselidis KA, Schofield G, Dimopoulos P, Stamou GN, Pantis JD (2012) Females First?  
422 Past, present and future variability in offspring sex-ratio at a temperate sea turtle  
423 breeding area. *Animal Conservation*, **15**, 508-518.
- 424 Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to  
425 buffer “cold-blooded” animals against climate warming. *Proceedings of the National*  
426 *Academy of Sciences*, **106**, 3835-3840.
- 427 Kulhanek SA, Leung B, Ricciardi A (2011) Using ecological niche models to predict the  
428 abundance and impact of invasive species: application to the common carp. *Ecological*  
429 *Applications*, **21**, 203-213.
- 430 Logan ML, Huynh RK, Precious RA, Calsbeek RG (2013) The impact of climate change

- 431 measured at relevant spatial scales: new hope for tropical lizards. *Global Change*  
432 *Biology*, n/a-n/a.
- 433 Mitchell NJ, Kearney MR, Nelson NJ, Porter WP (2008) Predicting the fate of a living fossil:  
434 how will global warming affect sex determination and hatching phenology in tuatara?  
435 *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2185-2193.
- 436 Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species  
437 geographic distributions. *Ecological Modelling*, **190**, 231-259.
- 438 Phillips SJ, Dudik M (2008) Modeling of species distributions with MaxEnt: new extensions  
439 and a comprehensive evaluation. *Ecography*, **31**, 161-175.
- 440 Pike DA (2008) Natural beaches confer fitness benefits to nesting marine turtles. *Biology*  
441 *Letters*, **4**, 704-706.
- 442 Pike DA (2009) Natural beaches produce more hatchling marine turtles than developed  
443 beaches, despite regional differences in hatching success. *Biology Letters*, **5**, 268-269.
- 444 Pike DA (2013a) Climate influences the global distribution of sea turtle nesting. *Global*  
445 *Ecology and Biogeography*, **22**, 555-566.
- 446 Pike DA (2013b) Forecasting eange expansion into ecological traps: climate-mediated shifts  
447 in sea turtle nesting beaches and human development. *Global Change Biology*, in  
448 press.
- 449 Rasmussen K, Palacios DM, Calambokidis J *et al.* (2007) Southern Hemisphere humpback  
450 whales wintering off Central America: insights from water temperature into the  
451 longest mammalian migration. *Biology Letters*, **3**, 302-305.
- 452 Special Report on Emission Scenarios (2000) Special Report on Emissions Scenarios: A  
453 special report of Working Group III of the Intergovernmental Panel on Climate  
454 Change (eds Nakićenović N, Swart R). Cambridge.
- 455 Schofield G, Bishop CM, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC (2009)

- 456           Microhabitat selection by sea turtles in a dynamic thermal environment. *Journal of*  
457           *Animal Ecology*, **78**, 14-22.
- 458   Sinervo B, Méndez-De-La-Cruz F, Miles DB *et al.* (2010) Erosion of lizard diversity by  
459           climate change and altered thermal niches. *Science*, **328**, 894-899.
- 460   Storch S, Wilson RP, Hillis-Starr Z-M, Adelson D (2005) Cold-blooded divers: temperature  
461           dependent dive performance in wild hawksbill turtles *Eretmochelys imbricata*. *Marine*  
462           *Ecology Progress Series*, **293**, 263-271.
- 463   Sunday JM, Bates AE, Dulvy NK (2011) Global analysis of thermal tolerance and latitude in  
464           ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1823-1830.
- 465   Tapilatu RF, Tiwari M (2007) Leatherback turtle, *Dermochelys coriacea*, hatching success at  
466           Jamursba-Medi and Wermon Beaches in Papua, Indonesia. *Chelonian Conservation*  
467           *and Biology*, **6**, 154-158.
- 468   Telemeco RS, Abbott KC, Janzen FJ (2013) Modeling the effects of climate change-induced  
469           shifts in reproductive phenology on temperature-dependent traits. *The American*  
470           *Naturalist*, **181**, 637-648.
- 471   Telemeco RS, Elphick MJ, Shine R (2009) Nesting lizards (*Bassiana duperreyi*) compensate  
472           partly, but not completely, for climate change. *Ecology*, **90**, 17-22.
- 473   Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the heat on tropical animals. *Science*,  
474           **320**, 1296-1297.
- 475   Vanderwal J, Shoo LP, Johnson CN, Williams SE (2009) Abundance and the environmental  
476           niche: environmental suitability estimated from niche models predicts the upper limit  
477           of local abundance. *American Naturalist*, **174**, 282-291.
- 478   Vickers M, Manicom C, Schwarzkopf L (2011) Extending the cost-benefit model of  
479           thermoregulation: high-temperature environments. *American Naturalist*, **177**, 452-461.
- 480   Wallace BP, Dimatteo AD, Hurley BJ *et al.* (2010) Regional management units for marine

- 481 turtles: a novel framework for prioritizing conservation and research across multiple  
482 scales. *PloS One*, **5**, e15465.
- 483 Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts  
484 of climate change on a globally distributed species: the case of the loggerhead turtle.  
485 *The Journal of Experimental Biology*, **213**, 901-911.
- 486 Wood DW, Bjorndal KA (2000) Relation of temperature, moisture, salinity, and slope to nest  
487 site selection in loggerhead sea turtles. *Copeia*, **2000**, 119-128.
- 488 Wright LI, Stokes KL, Fuller WJ *et al.* (2012) Turtle mating patterns buffer against disruptive  
489 effects of climate change. *Proceedings of the Royal Society B: Biological Sciences*,  
490 **279**, 2122-2127.
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492

**Figure Legends**

493 **Figure 1:** Maximum temperatures during the warmest quarter of the year (summer, when  
494 many sea turtle populations are nesting) are higher on tropical beaches than on temperate  
495 beaches (a) and are higher on tropical Regional Management Unit (Wallace *et al.* 2010)  
496 beaches than on temperate Regional Management Unit beaches (c). Data from the literature  
497 reveal that loggerhead nests from temperate regions have higher hatching success than those  
498 laid on tropical nesting beaches (b). Median hatching success of temperate beaches is 28.7%  
499 higher than tropical beaches. Predictions of hatching success generated from Maxent  
500 modeling were higher for temperate Regional Management Unit beaches than for tropical  
501 Regional Management Unit beaches (c). The lower bound of each box represents the first  
502 quartile, the middle is the median, the upper bound is the third quartile and the error bars  
503 represent minimum and maximum values.

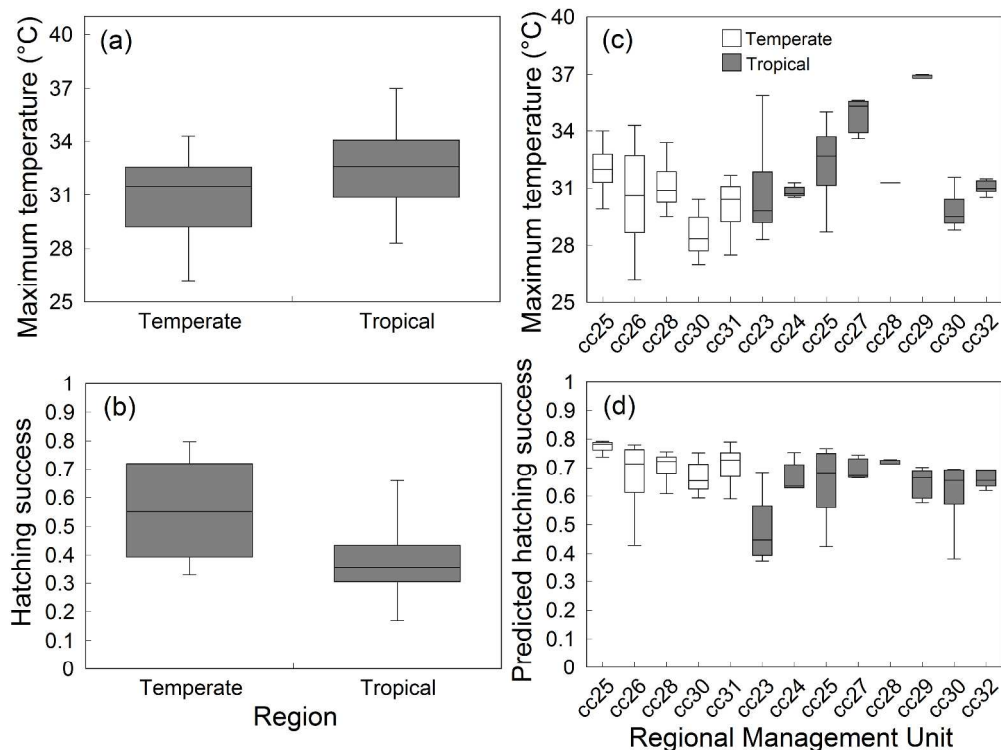
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505 **Figure 2:** Change in predicted (a) maximum temperature during the warmest quarter of the  
506 year (summer, when many sea turtle populations are nesting) and (b) hatching success,  
507 averaged under climate change emission families and shown for tropical and temperate  
508 nesting beaches. The lower bound of each box represents the first quartile, the middle is the  
509 median, the upper bound is the third quartile and the error bars represent minimum and  
510 maximum values.

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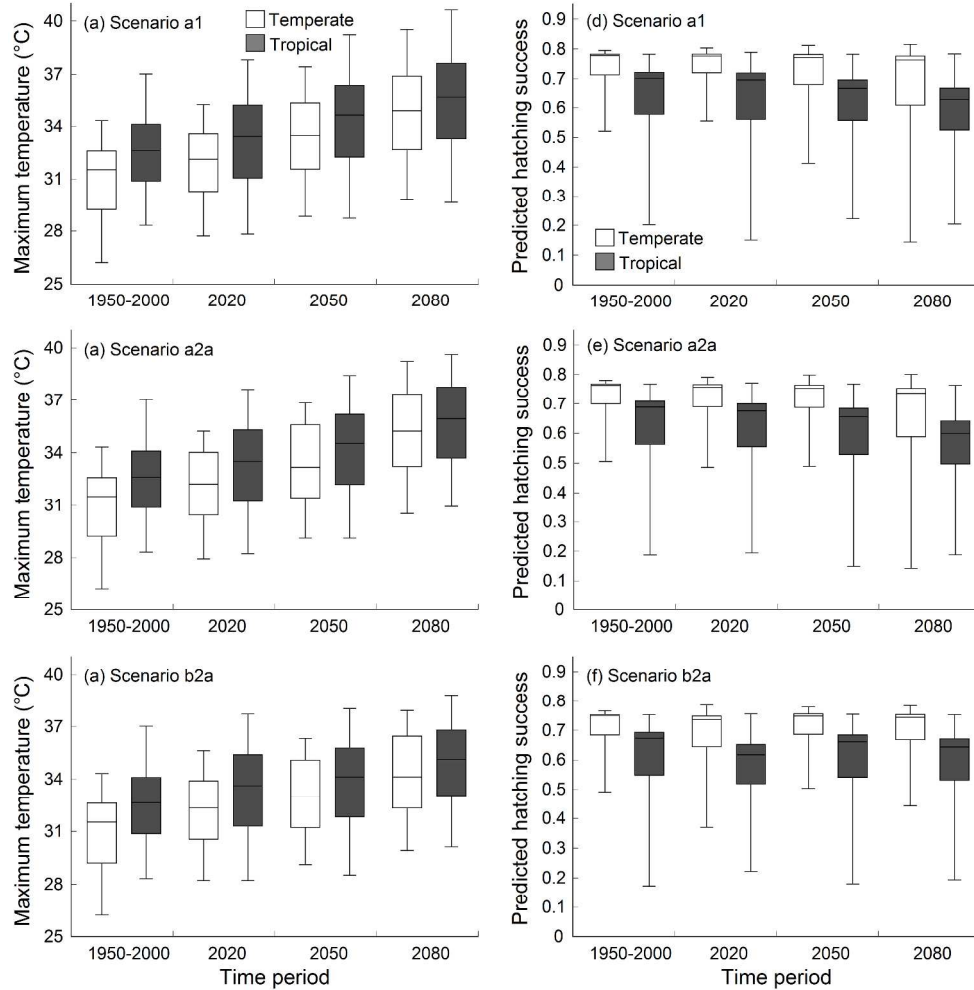
512 **Figure 3:** Maps forecasting loggerhead turtle hatching success and the change in hatching  
513 success under climate change, both spatially (Caribbean Sea, Mediterranean Sea, and  
514 Australasia) and temporally (under current and future predicted climates). Shown across the  
515 top row are predictions of hatching success under current climatic conditions (divided into six  
516 quantiles) and the remaining panels show changes in hatching success relative to current

517 conditions (divided into 5% intervals). Negative values indicate a decline in hatching success  
518 and positive values indicate an increase hatching success under future conditions. Future  
519 conditions were averaged among the different emission scenarios, resulting in one prediction  
520 for each of 2020, 2050, and 2080. Hatching success was predicted using the regression  
521 equation from the relationship between habitat suitability (estimated through MaxEnt  
522 modeling) and empirical hatching success.



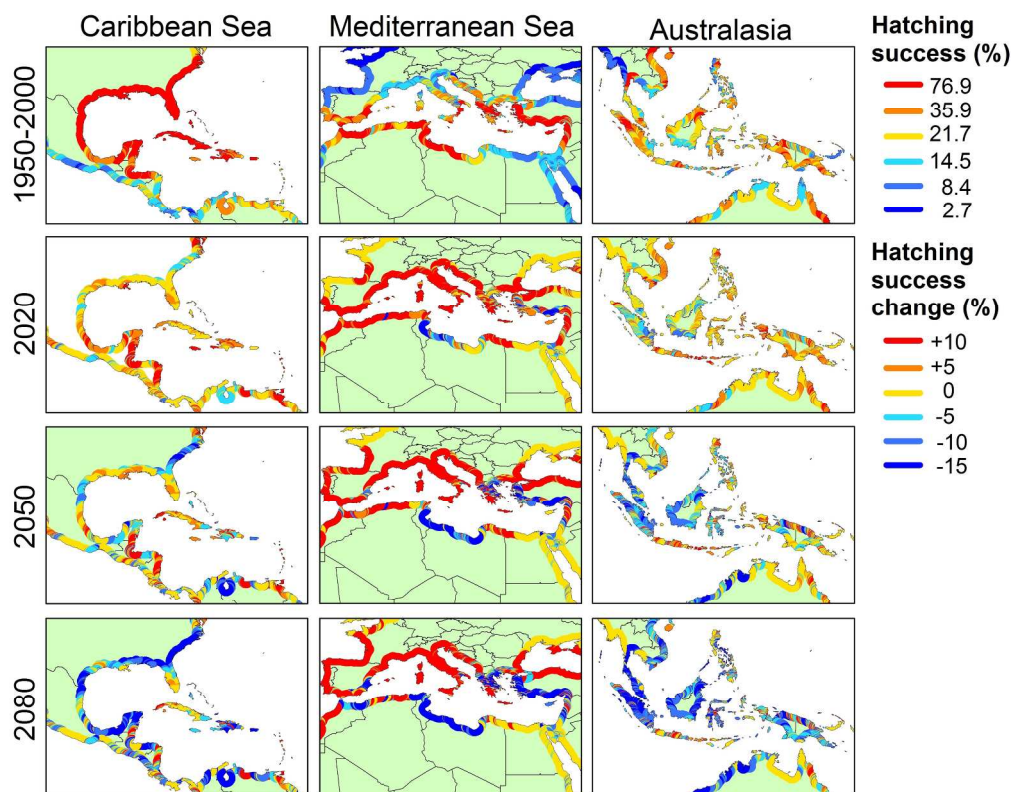
Maximum temperatures during the warmest quarter of the year (summer, when many sea turtle populations are nesting) are higher on tropical beaches than on temperate beaches (a) and are higher on tropical Regional Management Unit (Wallace et al., 2010) beaches than on temperate Regional Management Unit beaches (c). Data from the literature reveal that loggerhead nests from temperate regions have higher hatching success than those laid on tropical nesting beaches (b). Median hatching success of temperate beaches is 28.7% higher than tropical beaches. Predictions of hatching success generated from Maxent modelling were higher for temperate Regional Management Unit beaches than for tropical Regional Management Unit beaches (c). The lower bound of each box represents the first quartile, the middle is the median, the upper bound is the third quartile and the error bars represent minimum and maximum values.

398x299mm (300 x 300 DPI)



Change in predicted (a) maximum temperature during the warmest quarter of the year (summer, when many sea turtle populations are nesting) and (b) hatching success, averaged under climate change emission families and shown for tropical and temperate nesting beaches. The lower bound of each box represents the first quartile, the middle is the median, the upper bound is the third quartile and the error bars represent minimum and maximum values.

406x403mm (300 x 300 DPI)



Maps forecasting loggerhead turtle hatching success and the change in hatching success under climate change, both spatially (Caribbean Sea, Mediterranean Sea, and Australasia) and temporally (under current and future predicted climates). Shown across the top row are predictions of hatching success under current climatic conditions (divided into six quantiles) and the remaining panels show changes in hatching success relative to current conditions (divided into 5% intervals). Negative values indicate a decline in hatching success and positive values indicate an increase hatching success under future conditions. Future conditions were averaged among the different emission scenarios, resulting in one prediction for each of 2020, 2050, and 2080. Hatching success was predicted using the regression equation from the relationship between habitat suitability (estimated through MaxEnt modeling) and empirical hatching success.

229x180mm (300 x 300 DPI)