



Potential adaptability of marine turtles to climate change may be hindered by coastal development in the USA

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Abstract

Marine turtles may respond to projected climatic changes by shifting their nesting range to climatically suitable areas, which may result in either increased exposure to threats or fewer threats. Therefore, there is the need to identify whether habitat predicted to be climatically suitable for marine turtle nesting in the future will be affected by future threats and hinder marine turtles' ability to adapt. We modelled the geographic distribution of climatically suitable nesting habitat for marine turtles in the USA under future climate scenarios, identified potential range shifts by 2050, determined impacts from sea-level rise, and explored changes in exposure to coastal development as a result of range shifts. Overall nesting ranges of marine turtle species were not predicted to change between the current and future time periods, except for the northern nesting boundaries for loggerhead turtles. However, declines in climatically suitable nesting grounds were predicted; loggerhead turtles will experience the highest decreases (10%) in climatically suitable habitat followed by green (7%) and leatherback (1%) turtles. However, sea-level rise is projected to inundate 78–81% of current habitat predicted to be climatically suitable in the future, depending on species and scenario. Nevertheless, new beaches will also form, and suitable nesting habitat could be gained, with leatherback turtles potentially experiencing the biggest percentage gain in suitable habitat.

Keywords Sea turtles · Sea-level rise · Coastal development · Nesting habitat · Range shift · Climate change

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Introduction

Several marine turtle conservation success stories exist around the world with upwards trends in nesting abundance (Mazaris et al. 2017; Valdivia et al. 2019). However, upwards in nesting abundance do not necessarily translate into an increase in adult female abundance (Ceriani et al. 2019) and nesting female abundance is likely greatly overestimated (Casale and Ceriani 2020; Esteban et al. 2017). Moreover, many threats to marine turtles persist and marine turtles remain threatened on a global scale (Wallace et al. 2010a). Historically, declines have been caused by threats from fisheries bycatch, take, habitat loss, predation, and pollution (Koch et al. 2006; Schuyler et al. 2016; Wallace et al. 2011, 2010b). Further impacts to marine turtles are expected from projected changes to their nesting environment (e.g. coastal development and climatic changes) (Fuentes et al. 2011a, b, 2016a, b, 2019). The reproductive success of marine turtles is dependent on the nest incubation environment (Miller 1985), with extreme temperatures and dry/saturated substrates being unfavourable for egg development and hatching (Booth 2017; Montero et al. 2018; Wyneken and Lolavar 2015). Thus, projected changes in climate will likely impact hatching success, emergence rate, and hatching viability (Fuentes et al. 2010a).

Marine turtles may respond to projected climatic changes by shifting their range to climatically suitable areas (Abella Perez et al. 2016; Mainwaring et al. 2017). However, once turtles reach new areas with suitable conditions, it is crucial that these areas provide the environment necessary for colonization and are conducive to egg incubation (Katselidis et al. 2012; Pike 2013a, b). Yet, range shifts may result in either increased exposure to threats, such as coastal development or, more optimistically, fewer threats (Pike 2013a, b). Unfortunately, most coastal areas are now developed, with projected increases for further coastal development (Neumann et al. 2015; Sella and Fuentes 2019), affecting habitat availability and potentially hindering responses from marine turtles (Fuentes et al. 2010b; Mazaris et al. 2009). Coastal development can exacerbate potential impacts from sea-level rise by preventing natural movement of beaches and landward recession of shorelines (Fish et al. 2008; Fuentes et al. 2010b; Mazaris et al. 2009). Furthermore, coastal development, human presence, and associated pressures can modify marine turtle nesting environment and affect females 'reproductive output' (Brock et al. 2009; Grain et al. 1995; Kamrowski et al. 2012). The direct and indirect impacts of coastal development on marine turtles can potentially reduce their ability to use and colonize new areas (Fuentes et al. 2016b).

To better inform future management of marine turtles, there is the need to understand future threats, as well as to couple predictions of marine turtle distribution with an assessment of exposure to these threats (Pikesley et al. 2015). Such analyses can indicate whether habitat predicted to be climatically

suitable in the future will provide the necessary buffer for populations as an adaptive response to deal with climatic changes. This information could allow managers to anticipate and keep pace with future management needs and aid in climate change adaptation measures (Fuentes et al. 2016a, b; Jourdan and Fuentes 2015; Patino-Martinez et al. 2012). Despite the need for such information, studies that explore potential range shifts by species focus mainly on identifying areas that will be climatically suitable for species under a range of climatic scenarios, without exploring the anthropogenic disturbances found at these areas. To address this knowledge gap, we explored potential changes in nesting area suitability for three species of marine turtles in the United States of America (USA) under future climate scenarios as well as their exposure to coastal development and sea-level rise. Furthermore, to determine areas that are good candidates for conservation, we identified areas that will have high climatic suitability in the future, have reduced risk from sea-level rise, and where coastal development is projected to not substantially increase.

Methods

Modelling approach

We modelled current and future locations where climate is suitable for marine turtles with maximum entropy models (Maxent) (Phillips et al. 2006) to project the distributions of loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and leatherback (*Dermochelys coriacea*) turtle nesting grounds in mainland USA for both current (2010–2014) and future (2050) time periods. We applied Maxent because it outperforms other species distribution modelling algorithms (Elith and Graham 2009; Hijmans 2006) and has been previously applied for marine turtles (Pike 2013b). We used nesting locations for each species as occurrence data. For each Maxent model, we included 10 variables: 9 climate variables and the Relative Exposure Index (REI, see below). We parameterized Maxent with a regularization multiplier of 1 (Phillips and Dudík 2008) and we included all feature classes except threshold and hinge to produce more ecologically realistic response curves (Bateman et al. 2012). To assess the environmental suitability of coastal areas (i.e. where marine turtle nesting takes places), we restricted the turtle distribution data layers and 10,000 background points to 1-km grid cells along the majority of the coastline and to 2–3 grid cells for areas with complex coastal features (e.g. bays and/or inlets). This follows the *M*-hypothesis (where *M* is the area accessible to the species (as per Barve et al. 2011; Soberon and Peterson 2005)) approach limiting the extent of our study area to include only regions where marine turtle nesting beaches currently occur, plus some additional area that these species could realistically

move into for potential future expansion. Limiting the study area to within a limited distance of where a species is known to occur (VanDerWal et al. 2009) and where it is likely to be able to disperse to (Anderson and Raza 2010) provides more realistic study regions for sampling environmental data.

We ran a sensitivity analysis, where for each species, we applied a regularization multiplier of 0.5, 1, 2, and 4 as per Wilsey et al. (2019). We also included a sensitivity analysis for background point selection. For each species, we have sampled 500, 1000, 5000, and 10,000 points from our study area. We also mapped outputs of differences between closely performing models and compared them using the SigDiff function in the R package SDMTTools (<https://cran.rproject.org/web/packages/SDMTTools/index.html>). SigDiff computes the pairwise differences of two species distribution models for each grid cell.

For each marine turtle species, we evaluated model predictive performance based on AUC scores using a 10-fold cross-validation (Bateman et al. 2012; Elith et al. 2011). We selected the final model based on the training and testing AUC scores from the sensitivity analysis, as well as from exploring mapped outputs of differences between closely performing models. See Online Resource 1 for results of sensitivity analysis. We projected the model for each species onto the five general circulation model (GCMs) climate scenarios for 2050 (see below for information on climate scenarios). Finally, we generated an ensemble model across our five projected distributions using the average for each grid cell. We defined habitat suitability throughout our study site using thresholds. For the minimum value for which below is considered unsuitable, we used the Balance threshold calculated in Maxent. The Balance threshold balances training omission (fraction of presences omitted), predicted area (fraction of the total study area predicted present), and threshold value. It is a somewhat relaxed threshold, providing a more inclusive output (i.e. it does not only include the highest suitability locations but also those of low and moderate suitability that are marginal but could become important under other circumstances such as climate change). For our analysis, we binned all other values above this minimum threshold through the maximum of 1 into the following categories: unsuitable (0 to the threshold value specific for each species, loggerhead turtle 0.1683, green turtle 0.0952, and leatherback turtle 0.0369), low suitability (species threshold - 0.25), medium suitability (0.25–0.50), high suitability (0.50–0.75), and very high suitability (0.75–1).

To identify potential range shifts, which we defined as areas where environmental suitability differed significantly between current and future time periods, we applied the SigDiff function in the R package SDMTTools as per Bateman et al. (2012). We used SigDiff to identify where the future distribution predicted significantly higher climatic suitability ($SD \geq 0.975$) or significantly lower climatic suitability ($SD \leq 0.025$) in comparison with the current

distribution. Hereafter, we refer to these outputs as ‘significant difference models.’ We calculated the total area (km^2) and proportion (%) of habitat within each suitability category for the current, future, and significant difference models according to the number of cells in each category.

To quantify changes in exposure to residential coastal development due to range shifts, we calculated the average absolute housing and growth change using the Zonal Statistics as Table tool in ArcGIS 10.5.1 for areas with high and very high suitability in the current and future models, as well as areas significantly more suitable. To quantify exposure to sea-level rise, we identified present-day beaches projected to be inundated under three future sea-level rise scenarios. We then overlaid these inundation areas with future marine turtle distributions and habitat suitability, summarizing area (km^2) and proportion affected for each species, habitat suitability class, and sea-level rise scenario (see sea-level rise section below). Furthermore, we identified areas that will have high habitat suitability, reduced risk from sea-level rise, and no substantial increases in coastal development.

Datasets

Nesting locations

We obtained georeferenced marine turtle nesting areas (loggerhead turtles $n = 309$ nesting areas; green turtles $n = 164$ nesting areas; leatherback turtles $n = 107$ nesting areas; Online Resource 2), as well as their relative importance (in terms of nesting numbers per season) from the Virginia Department of Game and Inland Fisheries, the North Carolina Wildlife Resources Commission, the South Carolina Department of Natural Resources, the Fish and Wildlife Research Institute of the Florida Fish and Wildlife Conservation Commission, the US Fish and Wildlife Service Alabama Ecological Services Field Office, and the National Park Service Padre Island National Seashore in Texas. We only included sites where nesting activity was observed between 2010 and 2014, hereafter referred to as the study period.

Climate data and scenarios

We obtained current (1950–2000) climate data from the WorldClim global climate database (www.worldclim.org; Hijmans et al. 2005) at ~1-km resolution (30 arc-second). We sampled climate data at each of the 10,000 background points (restricted to 1–4 cells inland, dependent on coastal configuration), to minimize the influence of terrestrial and offshore environments on model performance. We selected Bioclim variables that provided the maximum climate information, whilst avoiding strongly correlated variables, and that were ecologically meaningful for marine turtles as per Pike (2013a, b). The final climate variables included in the model

were as follows: (1) mean diurnal range in temperature (°C), (2) isothermality, (3) maximum temperature of the warmest month (°C), (4) temperature annual range (°C), (5) precipitation seasonality (coefficient of variation), (6) precipitation of the wettest quarter (mm), (7) precipitation of the driest quarter (mm), (8) precipitation of the warmest quarter (mm), and (9) precipitation of the coldest quarter (mm).

For the future climate data, we obtained data for the 9 climate variables for five different GCMs (BCC-CSM1-1, CCSM4, CNRM-CM5, GISS-E2-R, and HadGEM2-AO) within the Representative Concentration Pathways (RCP) 4.5 scenario for the 2050 time period (average for 2041–2060) from CMIP5 multi-model ensemble simulations from the WorldClim – Global Climate Data portal (http://www.worldclim.org/cmip5_30s). The data were also at ~1-km resolution (30 arc-second). We selected the RCP 4.5 scenario because it represents a conservative low greenhouse emissions and medium-low mitigation scenario (van Vuuren et al. 2011). RCP 4.5 provides a realistic (i.e. captures a likely amount of climate change, range 0.9–2.0 °C for the 2050s; yet conservative (i.e. not the most extreme) baseline for this time period, and under current policies, will likely represent a best case scenario (Collins et al. 2013).

All outputs were clipped post hoc to include only areas within 2 km of sandy beaches as determined by the US Geological Survey's Coastal Change Hazards Portal (<https://go.usa.gov/xRGA9>). Given our coarse grid cell size (1 km²) relative to the width of beaches along the east USA coast, we assumed that the location and extent of the gridded sandy beaches would remain unchanged between the current and the future models.

Relative Exposure Index

Relative Exposure Index (REI) captures the exposure of coastal areas to wind and wind-generated waves (Garçon et al. 2010) and is a function of mean wind velocity (V), the directional wind percentage (P), and effective fetch (EF). Fetch is defined as the distance between a site and the nearest wave-blocking obstacle (i.e. shoreline or reef) in a given compass direction whilst EF is the average of the fetch in a given direction. Fetch was measured in ArcView 3.3 using the Radiating Lines extension. EF was then calculated by averaging the two lines radiating out from either side of the i th compass heading at 11.25° increments and the i th compass heading (total headings, $n = 5$) (Grech 2009). Fetch was assumed to be unlimited in the i th direction when greater than 50 km (Puotinen 2005).

We calculated REI for both current and future climatic scenarios for 4-km grid cells from the shoreline to 12-km offshore, which is the distance traversed by hatchlings during their first 24 h in the water (Salmon and Wyneken 1987). We calculated REIs in ArcGIS 10.0 following the equation by

Garçon et al. (2010), which is modified from Keddy (1982) and Murphey and Fonseca (1995):

$$REI = \sum_{i=1}^{16} (V_i \times P_i \times EF_i)$$

where $i = i$ th compass heading (1 to 16 [N, NNE, NE, etc.], in 22.5° increments), V = mean wind speed (m/s), P = percent frequency wind occurs in the i th direction, and EF = effective fetch (m). We then translated current and future REI values from over water to terrestrial beach zones, which we then averaged for the 12-km offshore distance using the ArcGIS Focal Statistics tool to allow incorporation into the species distribution models.

Wind conditions vary locally, so calculation of REI required high-resolution climate projections. Unfortunately these were not available from the WorldClim data source used for the other climate variables, so we obtained wind projections from the North American Regional Climate Change Assessment Program (NARCCAP, <https://www.narccap.ucar.edu/>). This program uses Regional Climate Models, driven by the familiar, coarse resolution CMIP3 GCMs, to produce climate projections at a finer scale at 50-km² resolution under the SRES-A2 emissions scenario. We selected the Hadley Centre's HRM3 Regional Climate Model because it covered the largest extent of the available models, including a large portion of the Caribbean and the Mexican coast. Because there can be considerable variability in wind among models (Pryor et al. 2005; Rasmussen et al. 2011), we examined HRM3 output driven by two GCMs: the Geophysical Fluid Dynamics Laboratory (GFDL CM2.1, (Team GGMD 2004)) and Hadley Centre Coupled Model, version 3 (HadCM3, Pope et al. 2000). We downloaded the 3-h wind northing and easting vectors from the NARCCAP data portal and converted these vectors into wind speed and direction as required for the REI. NARCCAP data is available for two 30-year time slices, the historical (1971–2000) and future (2041–2070) time periods. Therefore, the length of both the historical and future time periods was slightly different than the time periods for other climate variables, which were 1950–2000 and 2041–2060, respectively.

Housing data

We analysed housing data to capture coastal development and related disturbance to marine turtles as per Fuentes et al. (2016b). For this, we used current (2000 and 2010) US Decennial Census data at the partial block group (PBG) scale, which provides information on when housing units were built, thereby allowing analysis of past housing growth (Radeloff et al. 2010). To project future housing density, we combined housing growth at the PBG-level from 2000 to 2010 with

county household projections for 2020 to 2050 generated by Woods&Poole (<https://www.woodsandpoole.com/>), which provides the most reliable population forecasts available (Radeloff et al. 2010). Specifically, we (1) calculated absolute PBG-level housing growth in the 2000s using Census data, (2) added the same amount of housing growth to obtain 2020 housing numbers for each PBG, (3) summed all PBGs in each county, (4) calculated the adjustment factor by comparing PBG-projection-based county totals with those from Woods&Pools, (5) adjusted PBG-level housing totals based on the adjustment factor, and (6) repeated steps 1–5 for each subsequent decade through 2050. Lastly, we calculated both absolute growth (projected minus current housing units per km²) and percent growth change (projected minus current housing units per km², divided by the current housing units per km², multiplied by 100) from the current (2000–2010) to the future period (2050), and averaged this for each 1-km grid cell using the Raster Calculator in ArcGIS 10.5.1. It is important to note, however, that potential impacts from sea-level rise, particularly loss of land, could affect coastal development rates. Incorporating the negative impacts of sea-level rise on coastal development was beyond the scope of our analysis and should be considered when interpreting our results. Given the nature of percent change calculations, any new houses added to an area with zero houses at the beginning will result in an undefined percent growth rate. Thus, the percent housing growth rates only included cells in which there was at least one housing unit in the current period, but all areas were included in the absolute change results.

Sea-level rise

We mapped areas of sea-level rise-induced flooding and ensuing habitat transitions based on spatial projections from NOAA's Office for Coastal Management (available from <https://coast.noaa.gov/slr/>). Projections are based on a modified bathtub approach that incorporates LIDAR-derived elevation data and attempts to account for local and regional tidal variability (Marcy et al. 2011). Outputs are available for the conterminous USA at a 10-m spatial resolution with scenarios of up to 10 ft (~ 3 m) provided in half-foot increments. We assessed impacts under an intermediate-low scenario (0.5 m of global sea-level rise) for 2050 to match future climate projections (Sweet et al. 2017). We used a dataset from the National Climate Assessment to downscale global scenarios to local sea-level rise projections (Sweet et al. 2017). We identified transitions from areas classified as unconsolidated shore (i.e. beaches, bars, and flats) in the present to open water (i.e. completely inundated) in the future, and then overlaid these transition areas with modelled future marine turtle habitat suitability to identify habitat that is climatically suitable and at risk of inundation. We report the amount of beach

habitat inundated in terms of total area and as a proportion of current beach habitat.

Exposure of suitable nesting habitat to coastal development and sea-level rise

To quantify the exposure of suitable nesting habitat to coastal development, we calculated the average, standard deviation and range of absolute growth, and percent growth in housing for the high, very high, and significantly-more-suitable habitat categories for each marine turtle species using the Zonal Statistics tool in ArcGIS 10.5.1. In addition, we identified the location of the exposed nesting habitats by reclassifying absolute growth into two categories: increase (positive values) or decrease (negative values) in housing units, and extracting the cells that overlapped with the high, very high, and significantly-more-suitable habitat categories. Furthermore, we identified areas projected to remain or become beach habitat under future sea-level rise scenario and summarized the absolute and percent change in housing growth within areas. We then overlaid these future beach areas with areas of medium suitability (0.25–0.50) and high suitability (0.50–0.75) as well as with areas with no substantial increase in coastal development (less than + 100% change in housing growth).

Results

Model performance

All models performed better than random according to both training (> 0.77) and test AUC scores (> 0.76) (Online Resource 3) indicating that the models for all species were appropriate for defining current marine turtle nesting areas and were suitable to project the areas where climate is suitable for future marine turtle nesting areas (Online Resource 3).

Marine turtle distribution under current climatic conditions

For all three species, precipitation seasonality and isothermality were the most important variables. The highest permutation importance is a measure of how important a given variable is in the building of the Maxent model, and for loggerhead turtles, it was precipitation of the warmest quarter, for green turtles, isothermality, and for leatherback turtles, precipitation seasonality. The second most important variable for green turtles and loggerheads was precipitation seasonality, and for leatherbacks, it was isothermality (Online Resource 3).

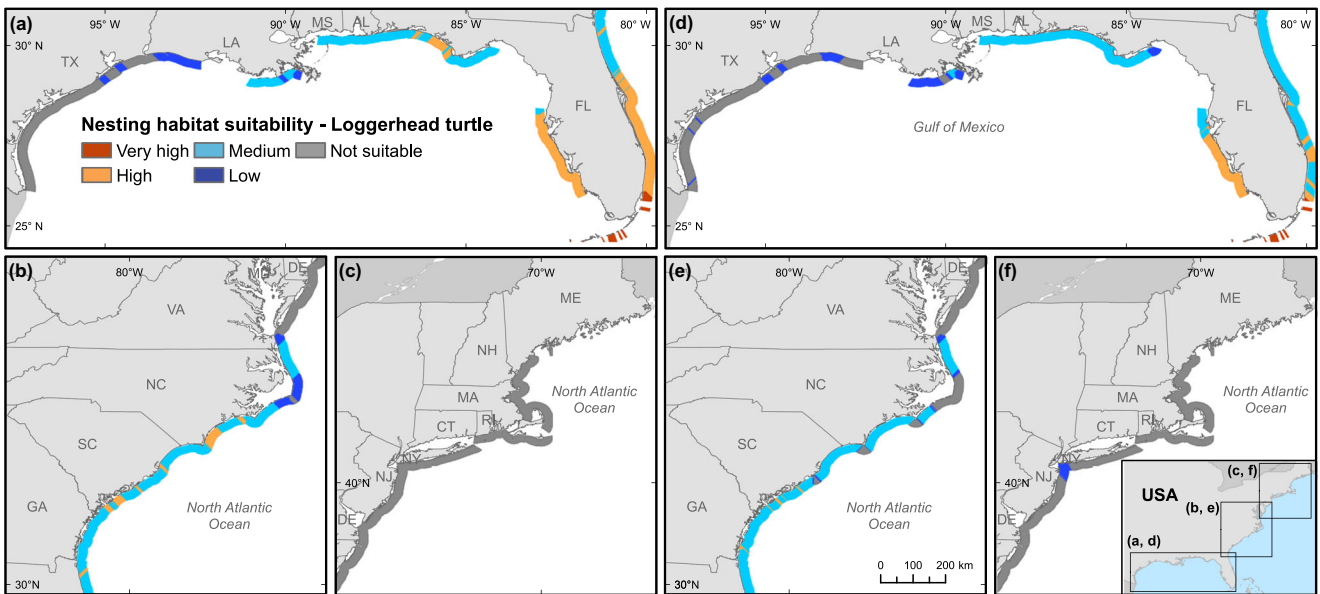


Fig. 1 Loggerhead turtle nesting habitat suitability along the USA coast based on (a–c) current (2010–2014) and (d–f) future (2050) climatic conditions

Future distribution and climatically suitable nesting areas for marine turtles

Except for the northern nesting boundaries for loggerhead turtles, the overall nesting ranges of marine turtle species were not predicted to change substantially between the current and future time periods (2050) in the USA. Our models predicted loggerhead turtle suitable areas to expand north along the coast of northern New Jersey and New York (Fig. 1). In contrast, future nesting areas for green turtle (Fig. 2) and leatherback turtles (Fig. 3) were projected to remain like the current distribution, from Texas to North Carolina. Areas of high

climatic suitability for marine turtles will likely occur along the southern coasts of Florida (east coast for all species, and west coast for loggerhead and green turtles) and the coasts of Georgia and South Carolina (only for loggerhead turtles). Very high climatically suitable areas for loggerhead turtles are likely along the Florida Keys and for green turtles, along the southeast Florida coast and Florida Keys (although those areas are predicted to be inundated by sea-level rise) (Figs. 1 and 2).

Overall, climatically suitable nesting habitat for loggerhead turtles is predicted to decrease by 4% and climatically unsuitable nesting habitat is predicted to increase by 6% (Table 1),

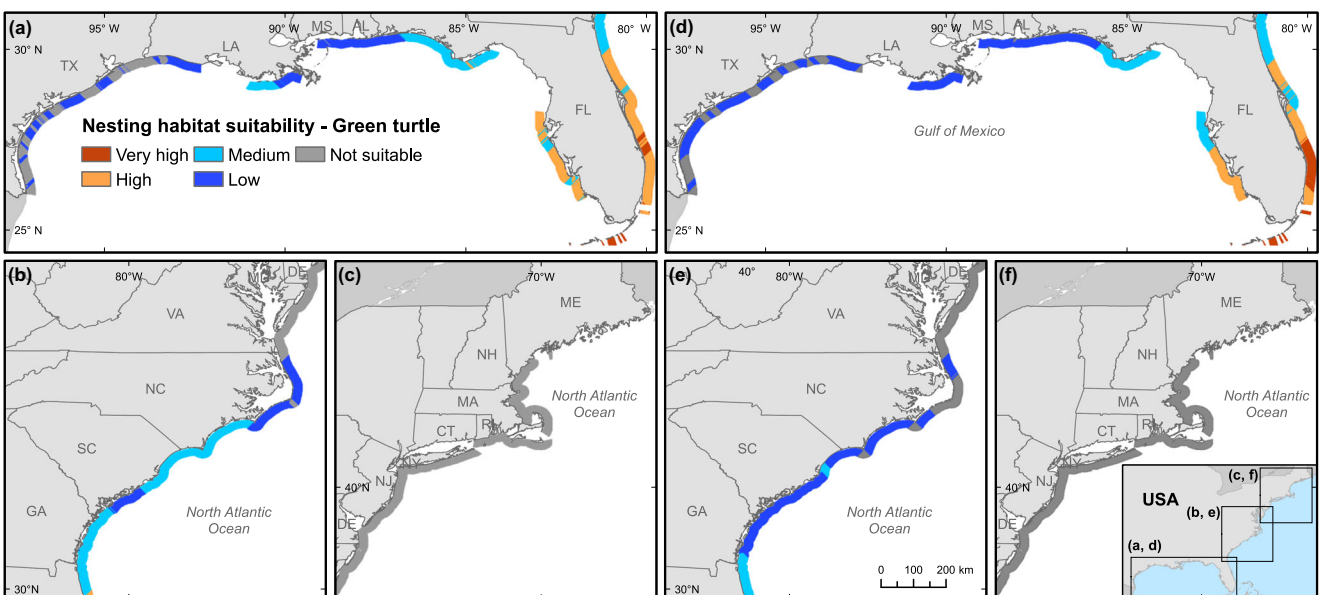


Fig. 2 Green turtle nesting habitat suitability along the US coast based on (a–c) current (2010–2014) and (d–f) future (2050) climatic conditions

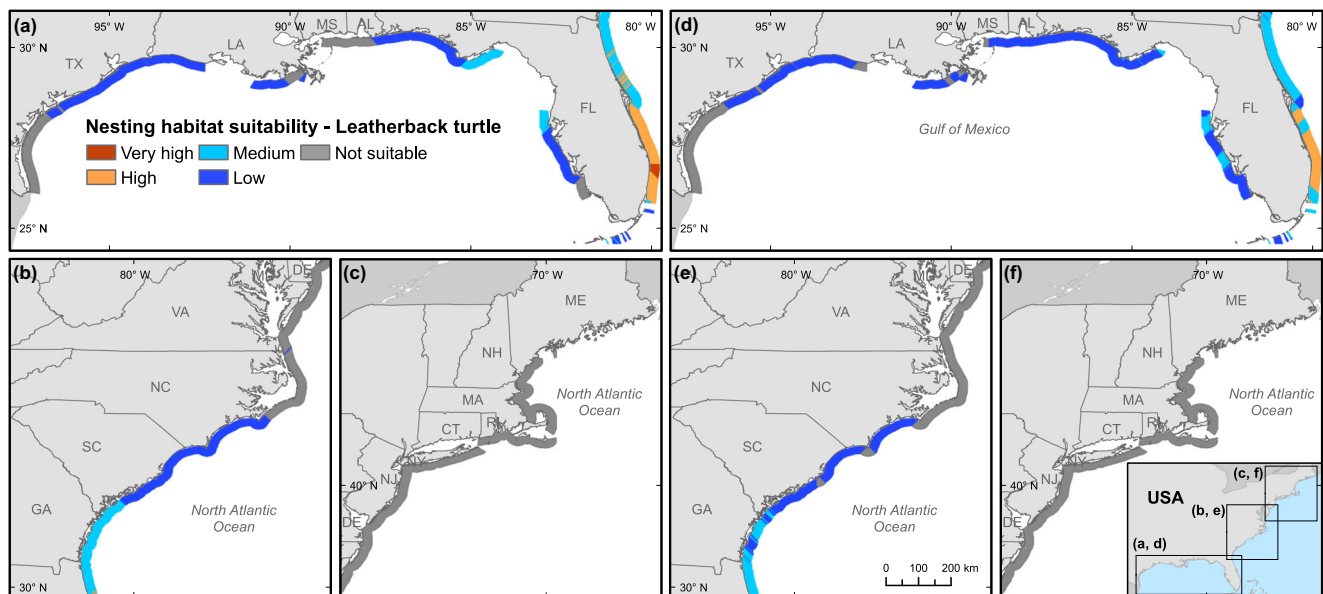


Fig. 3 Leatherback turtle nesting habitat suitability along the US coast based on (a–c) current (2010–2014) and (d–f) future (2050) climatic conditions

with 10% of nesting habitat for loggerhead turtles predicted to be significantly less climatically suitable by 2050 (Fig. 4a–c) particularly in Florida (the Panhandle and east coast; Fig. 4a) and North Carolina (Fig. 4b). Decrease in area of climatically suitable habitat is predicted to occur at regions of high and very high climatic suitability, whereas areas of medium climatic suitability are predicted to increase in area (Fig. 3). For green turtles, a 4% increase in climatically suitable nesting areas is predicted as well as a 6% decrease in climatically unsuitable areas (Table 1). In particular, very high suitability nesting areas will increase along the southeast coast of Florida and low suitability areas will increase across the species' range (Fig. 4, Table 1). Medium and high suitability nesting areas are predicted to decrease. Some areas (1%) along the southwest coast of Florida (between Fort Myers and Marco Island) will become significantly more suitable for green turtle nesting, whereas other areas (7%) along Florida (the Panhandle) and North Carolina will become significantly less suitable (Fig. 4d–f, Table 1).

No significant change is predicted in the distribution of climatically suitable nesting area for leatherback turtles by 2050, with an overall increase of 1% of suitable habitat and 1% decrease in unsuitable habitat (Table 1). Areas with very high and high climatic suitability are predicted to decrease along the east coast of Florida (Fig. 3a, d, Table 1). Areas of medium suitability are predicted to increase, particularly along the southwest coast of Florida (Fig. 3a, d, Table 1).

Marine turtle exposure to sea-level rise

Depending on species, sea-level rise could inundate 78–81% of current beach nesting habitat that is predicted to be climatically suitable in the future. Loss is high across suitability

classes, ranging from 53 to 90% (Table 2). New beaches will also form and high suitability nesting habitat could be gained by loggerhead turtles (1255 km²), green turtles (1423 km²), and leatherback turtles (1335 km²), with leatherback turtles potentially experiencing the biggest percentage gain in suitable habitat (Table 2).

Changes in marine turtle exposure to coastal development

Housing density (Online Resource 4) was predicted to increase on average by 89% in high climatically suitable areas for loggerhead turtle nesting habitats particularly in south Florida and Edisto Island in South Carolina, but decrease in Jekyll Island in Georgia and Sullivan's Island in South Carolina (Fig. 1, Table 1, Online Resource 4). In addition, the average housing growth at very high climatically suitable nesting areas for loggerhead turtles was predicted to decrease on average by 19%, especially along the Florida Keys (Figs. 1 and 5, Table 1).

Within the areas that will be significantly more climatically suitable for green turtle nesting in the future (located in west Florida), we found a predicted average growth of 163% in housing density (Fig. 4d–f, Table 1, Online Resource 4). Similarly, areas across the range (excepting the Cape Canaveral region in Florida where most of nesting habitat is found on federal land and is protected, and some areas of the Florida Keys) of high and very high suitability in the future were also expected to experience an average increase in housing density of 169% and 46%, respectively (Fig. 2, Table 1, Online Resource 4). For leatherback turtles, within areas of high climatic suitability, we found a projected future housing growth of 59% across their range, except in the Cape

Table 1 Predicted changes in area and housing density within each category of sea turtle habitat suitability. Percentage change, growth change, and absolute growth indicate changes between the future predictions (2050) and current values (2010–2014)

	Nesting habitat suitability		Percentage change	Housing density	
	Area in km ² (%)			Growth rate (%) and its SD and (range)	Absolute growth in housing units km ² ± SD (range)
	2010–2014	2050			
Loggerhead turtle					
Not suitable	4257 (41)	4500 (43)	6	45 ± 170 (– 100–6286)	26 ± 338 (– 3955–18058)
Suitable	6097 (59)	5854 (57)	– 4	-	-
Low	879 (08)	822 (08)	– 6	25 ± 318 (– 100–3983)	113 ± 1194 (– 4202–28313)
Medium	3040 (29)	4054 (39)	33	263 ± 789 (– 100–15655)	123 ± 502 (– 4434–13209)
High	2029 (20)	870 (08)	– 57	89 ± 544 (– 100–8553)	247 ± 1169 (– 9975–12547)
Very high	149 (01)	108 (01)	– 28	– 19 ± 75 (– 100–226)	72 ± 486 (– 2879–3119)
Significantly less suitable	-	1063 (10)	-	192 ± 446 (– 100–3649)	216 ± 957 (– 2666–13209)
Not significantly different	-	9291 (90)	-	118 ± 540 (– 100–15655)	75 ± 566 (– 9975–28313)
Significantly more suitable	-	0 (0)	-	-	-
Green turtle					
Not suitable	4075 (39)	3844 (37)	– 6	57 ± 175 (– 100–6286)	50 ± 657 (– 4202–28313)
Suitable	6279 (61)	6510 (63)	4	-	-
Low	2050 (20)	3897 (38)	90	160 ± 649 (– 100–15655)	97 ± 391 (– 2666–8011)
Medium	2517 (24)	1079 (10)	– 57	272 ± 740 (– 100–5328)	50 ± 244 (– 4434–1719)
High	1545 (15)	1123 (11)	– 27	169 ± 817 (– 100–8553)	175 ± 1050 (– 9975–13209)
Very high	167 (02)	411 (04)	146	46 ± 108 (– 100–559)	262 ± 964 (– 2236–9339)
Significantly less suitable	-	703 (7)	-	221 ± 534 (– 100–3649)	89 ± 298 (– 2666–2736)
Not significantly different	-	9520 (92)	-	118 ± 522 (– 100–15655)	87 ± 624 (– 9975–28313)
Significantly more suitable	-	131 (1)	-	163 ± 947 (– 62–8553)	283 ± 1203 (– 802–12547)
Leatherback turtle					
Not suitable	4503 (43)	4468 (43)	– 1	69 ± 213 (– 100–6286)	48 ± 552 (– 4202–28313)
Suitable	5851 (57)	5886 (57)	1	-	-
Low	3582 (35)	3806 (37)	6	145 ± 664 (– 100–15655)	102 ± 519 (– 2666–18058)
Medium	1399 (14)	1584 (15)	13	281 ± 849 (– 100–5328)	128 ± 845 (– 9975–13209)
High	810 (08)	496 (05)	– 39	59 ± 112 (– 100–645)	247 ± 930 (– 2879–9339)
Very high	60 (01)	0 (00)	– 100	-	-
Significantly less suitable	-	1 (0)	-	-	-
Not significantly different	-	10351 (100)	-	125 ± 533 (– 100–15655)	90 ± 619 (– 9975–28313)
Significantly more suitable	-	2 (0)	-	-	-

Canaveral region of Florida, where housing growth is predicted to stay the same (Fig. 3, Table 1, Online Resource 4). Within areas projected to remain or form beach habitat under future sea-level rise, housing density was predicted to increase on average 134% in high climatically suitable nesting areas for loggerhead turtles, 83% in very high climatically suitable nesting areas for green turtles, and 59% in high climatically suitable nesting areas for leatherback turtles (Online Resource 4). Importantly, we identified areas that will have high habitat suitability, reduced risk from sea-level rise, and reduced increases in coastal development (< 100%, Online Resource 5).

Discussion

The future availability of climatically suitable nesting area will vary across species and their range, with species predicted to experience a loss of 78–81% of climatically suitable nesting area due to sea-level rise. These projections align with current predictions of loss of sandy beaches from sea-level rises (Vousdoukas et al. 2020) and are a reflection of marine turtles requiring a specific environment to successfully incubate their eggs (Ackerman 1997; Howard et al. 2014; Mortimer 1990). It is important to note, however, that our climate suitability models are based on input nesting location points, so our

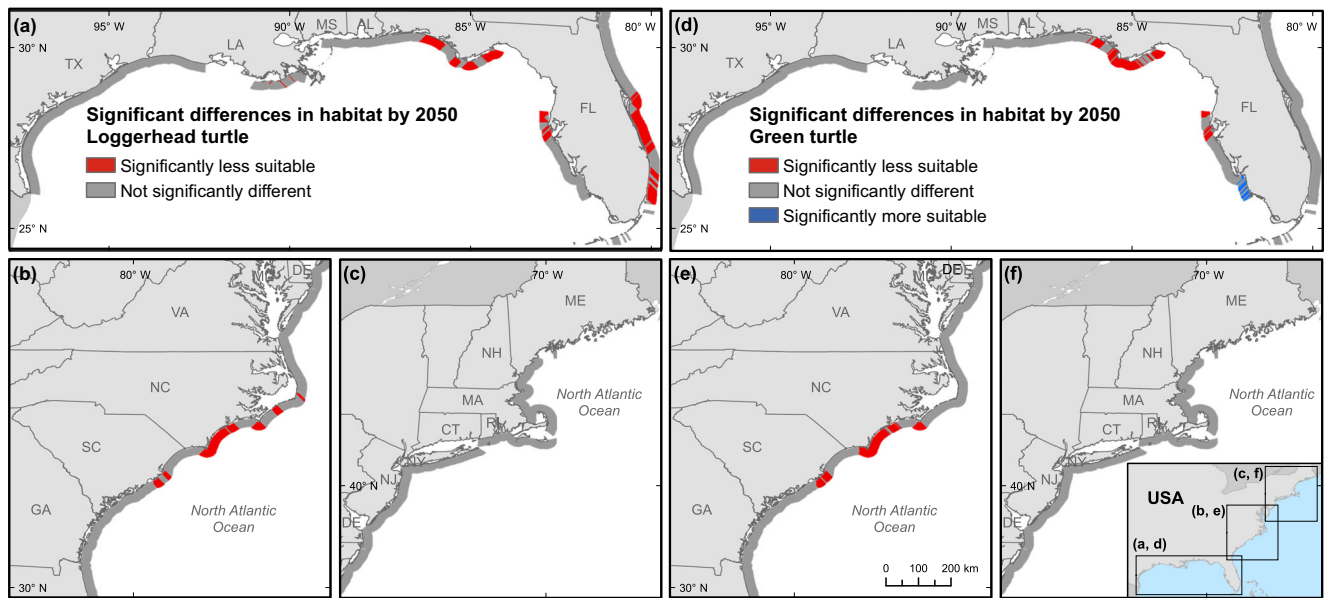


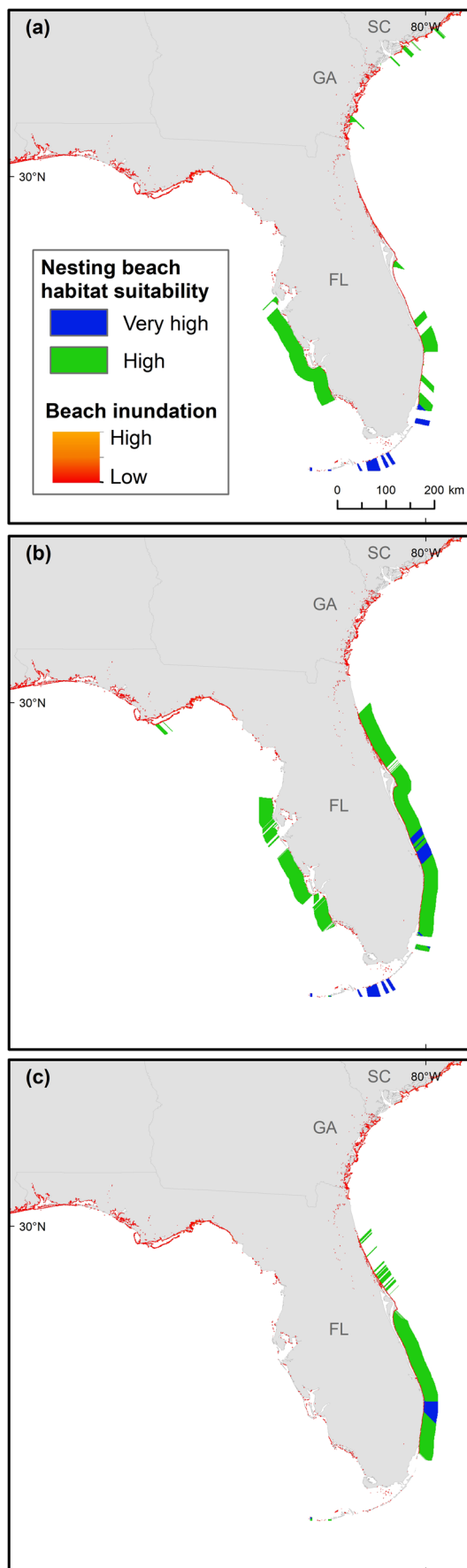
Fig. 4 Loggerhead turtle (a–c) and green turtle (d–f) nesting areas with significant changes in habitat suitability between the future predictions and current distribution. There was no significant difference in suitability for leatherback turtle nesting areas

results are more representative of areas with the most nesting points/locations. Therefore, results for areas with less nesting points, such as in Texas, are underrepresented in terms of their climatic suitability and should be interpreted with care. Precipitation seasonality was the most important climatic

variable driving the distribution of marine turtle species in the USA and the climatic suitability of their nesting areas. Precipitation and humidity can influence egg survival and hatchling physiology reducing hatchling output when the incubating environment is too moist or too dry (Montero et al.

Table 2 Predicted habitat loss and formed under different sea-level rise scenarios within each category of sea turtle habitat suitability. Percentage loss indicates changes between the future predictions (2050) and current values (2010–2014)

	Current beach (km ²)	Beaches loss 0.5 m km ² (percentage loss)	Beaches formed 0.5 m km ² (percentage gained)	Net future beach (km ²)
Loggerhead turtle (<i>Caretta caretta</i>)				
Low	178.35	158.01 (89)	127.1 (71)	147.44
Medium	284.43	220.13 (77)	867.94 (305)	932.24
High	18.42	10.62 (58)	260.27 (1413)	268.07
Very high	0.08	0.07 (88)	-	0.01
Future totals	481.28	388.83 (81)	1255.31 (261)	1347.76
Significantly more suitable	-	12.18 (66)	0.68 (4)	-
Green turtle (<i>Chelonia mydas</i>)				
Low	397.65	324.98 (82)	702.46 (177)	775.13
Medium	205.01	153.29 (75)	715.41 (349)	767.13
High	17.37	14.35 (83)	5.62 (32)	8.64
Very high	0.66	0.41 (62)	-	0.25
Future totals	620.69	493.03 (79)	1423.49 (229)	1551.15
Significantly more suitable	-	18.29 (77)	13.41 (57)	-
Leatherback turtle (<i>Dermochelys coriacea</i>)				
Low	305.40	253.99 (83)	958.38 (314)	1009.79
Medium	60.52	32.11 (53)	376.51 (622)	404.92
High	3.07	2.03 (66)	0.01	1.03
Future totals	368.98	288.13 (78)	1334.88 (362)	1415.74
Significantly more suitable	-	0.43 (61)	1.18 (166)	-



◀ **Fig. 5** Loggerhead turtle (a), green turtle (b), and leatherback turtle (c) nesting areas projected to be inundated under a conservative (0.5-m sea-level rise) sea-level rise scenario

2018; Montero et al. 2019; Rivas et al. 2018; Tomillo et al. 2012; Wyneken and Lolavar 2015). Thus, changes in precipitation and other climatic variables can affect the climatic suitability of marine turtle nesting areas, causing marine turtles to shift their ranges to align with optimal environmental conditions (Butt et al. 2016; Pike 2013a, b).

Although no major distributional range shifts were projected for green turtles and leatherback turtles nesting in the USA by 2050, it is likely that the range of suitable nesting areas for these species may expand north as climate change progresses, and temperature, humidity, and moisture levels reach/surpass incubating thresholds. A northward range shift was projected for loggerhead turtles in this study, perhaps because they nest in more temperate areas, which is in agreement with the predictions for Kemp's ridley turtles (Pike 2013b). Indeed, range shifts are predicted for several species of marine turtles globally beyond 2050 as climate change progresses (see Butt et al. 2016; McMahon and Hays 2006; Pike 2013b). However, it is crucial that newly colonized areas provide the necessary conditions for egg incubation (Katselidis et al. 2012). Unfortunately, most of the coast of the USA is now developed (Fuentes et al. 2016b; Radeloff et al. 2010; Sella and Fuentes 2019), and we found a substantial increase of at least double of the residential coastal development in areas that will be climatically suitable for marine turtle nesting in the future and not at risk from sea-level rise. Although no study to date has determined thresholds of development and associated impacts to marine turtles, increase in coastal development will likely increase associated pressures which will in turn affect reproductive output of turtles (Antworth et al. 2006; Brock et al. 2009; Kamrowski et al. 2012). Persistence of suitable nesting habitat is crucial for the reproduction of marine turtles and is one of the key factors influencing the resilience of marine turtles to climatic changes (Fuentes et al. 2013). Thus, it is important to maintain and protect nesting areas that will have climatically suitable conditions for nesting over the long-term and will have reduced impact by sea-level rise, with a focus on areas that are predicted to have reduced pressures.

Our study identified a few regions in North and South Carolina (e.g. north-western and northern coast of Hilton Head Island, and beaches along Jarret Bay) which will have high or very high climatic suitability, reduced risk from sea-level rise, and no substantial housing growth, which will provide optimal nesting environment for marine turtles as climate change progresses. Thus, intervention and continued protection of these areas may maximize conservation outcomes. Although sea-level rise was predicted to inundate a high proportion of areas with high suitability, it is important to note

that new areas will become available providing potential refuges for nesting marine turtles. However, coastal development will be a pressing issue in most of these areas, and addressing the impacts from pressures (e.g. artificial lighting, human disturbance, and noise) associated with coastal development is advised. Depending on the pressure and impacts at each location, several strategies can be undertaken, including implementation and enforcement of light-mitigation strategies (e.g. turtle-friendly lighting or vegetative barriers), reduction of human disturbance (e.g. remove unattended material/properties on the beach such as beach umbrellas), and alteration to nesting areas (e.g. limit/prohibit shoreline hardening structures and/or use turtle friendly template during full-scale beach placement projects). On-ground assessments will be necessary to identify the major threats at each location. This information should be coupled with the reproductive output of marine turtles at each location to identify the threshold of exposure at which coastal development affects populations (Fuentes et al. 2016b).

Nesting areas may also be affected by other interacting threats (e.g. hurricanes, beach armouring, beach sand placement, and predation) (Butt et al. 2016; Fuentes et al. 2011a; Fuentes et al. 2010a, 2015, 2019; Patrício et al. 2019) that were not considered here. Thus, some of the nesting areas predicted to have high nesting suitability and reduced risk from sea-level rise, such as some in North and South Carolina (Online Resource 5), may have reduced and/or limited nesting habitat as a consequence of other threats (e.g. coastal armouring) (Zhang et al. 2011). Therefore, reducing non-climate threats will build the resilience of marine turtles since a large, healthy, and stable population will ensure (1) a higher ability to recover from disturbances, (2) a wide geographic distribution, which can minimize the overall impacts of area-specific threats and increase the resistance to disturbance, and (3) genetic diversity, which will enhance resistance by increasing the range of responses to the environment and the likelihood that species can functionally compensate for one another following disturbance (Isaac et al. 2009; Purvis et al. 2000; Sgrò et al. 2011). By ensuring that populations are large and diverse, managers are enhancing species resistance to disturbance and capacity for recovery. However, resilience is also affected by the ability of the system to adapt to new conditions (Bernhardt and Leslie 2013). Hence, strategies that improve the capacity of species to adapt to climate change are also necessary (Fuentes et al. 2013).

Typically, the capacity of species to adapt to environmental changes depends on a combination of organism-level plasticity, species range shifts, and rapid evolution of traits better suited to new conditions (Bernhardt and Leslie 2013). Marine turtles have been around for millions of years and have persisted through dramatic changes in past climates, demonstrating the ability to adapt to changing conditions (Hamann et al. 2013; Hawkes et al. 2009). Marine turtles may adapt by

(1) changing the distribution of their nesting grounds, nest-site choice and nest depth, (2) adapting in situ by adjusting their pivotal temperature, and (3) nesting in cooler months (Almpanidou et al. 2018; Davenport 1989; Hawkes et al. 2014; Hays et al. 2003; Mitchell and Janzen 2010; Weishampel et al. 2004). Range shifts may offer one of the most promising avenues for adaptation in marine turtles (Schofield et al. 2009); however, it might be hindered by the ever-expanding development along coasts and consequent reduction of available nesting sites. The adaptive capacity of marine turtles may also be compromised by the unprecedented rate of current climatic changes coupled with the array of threats affecting each of their life stages (Fuentes et al. 2013). Thus, management efforts should focus on enhancing marine turtle's resilience to changing environmental conditions by mitigating other non-climatic threats that they currently experience, such as those associated with coastal development (Abella Perez et al. 2016; Fuentes et al. 2013).

It is important to note that the results presented here are derived from models and thus rely on assumptions and subjective choices. As such, we recognize the inherent limitations and the outputs should be interpreted with some caution. As a result, there may be errors associated with our models and input data. For example, our REI calculation did not consider the potential storm-surge enhancement effect from sea-level rise; thus, future studies should consider this. These results are not empirical in nature, and changes, or lack thereof, in species range shifts may not necessarily reflect ecological processes at local sites. Site-specific analysis could improve future assessments, particularly those related to impacts from sea-level rise, as it would allow considerations of site-specific geomorphic features and sediment budgets (Ranasinghe 2016). However, given our goal to proactively assess climate change and human pressures on sea turtles, the outputs provide useful information otherwise not available.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Disclaimer The conclusions in this article are those of the author(s) and do not necessarily represent the views of the US Fish and Wildlife Service or National Park Service.

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