Climate influences the global distribution of sea turtle nesting

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ABSTRACT

Aim To understand whether climate limits current sea turtle nesting distributions and shapes the ecological niche of the terrestrial life-history stage of these wide-ranging marine vertebrates.

Location Coastlines world-wide.

Methods I predicted the spatial distributions of nesting habitat under current climatic conditions for seven sea turtle species using information criteria and maximum entropy modelling. I also compared niche similarity among species using three niche metrics: *I*, Schoener's *D* and relative rank.

Results Sea turtles currently nest across their entire bioclimatic envelopes, with up to six species predicted to nest on a single beach. The Caribbean Sea, Gulf of Mexico and Australasia support high nesting diversity, with most regional areas supporting three to five species. Despite large overlap in nesting distributions among species, loggerhead and green turtles have the broadest environmental niches, while Kemp's ridley and flatback turtles have very narrow niches.

Main conclusions The terrestrial nesting habitat of sea turtles is characterized by distinct climatic conditions, which are linked to the physical conditions necessary for eggs to hatch successfully and allow hatchlings to disperse from natal areas. Despite broad geographic patterns of overlap and similar embryonic tolerances to temperature and moisture among species, sea turtles partition habitat by nesting in different niche spaces. The tight link between current geographic patterns of nesting and climate, along with the dependence of developing embryos on nest microclimate, imply that regional or global changes in environmental conditions could differentially influence the distribution of sea turtle species under climate change. This could influence the adaptive potential of different populations, and predicting these responses before they occur will be important in mitigating the effects of climate change.

Keywords
***Caretta caretta*, *Cheloniamydas*, climate, *Dermochelys coriacea*, ecological niche modelling, *Eretmochelys imbricata*, *Lepidochelys kempii*, *Lepidochelys olivacea*, marine turtle, *Natator depressus*.**

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INTRODUCTION

Marine turtles are some of the most widely distributed vertebrates on the planet; as adults, individuals of some species can range throughout tropical, temperate and subarctic waters, and can regularly migrate hundreds or thousands of kilometres between foraging areas and nesting grounds (e.g. Luschi *et al.*, 1998; Nichols *et al.*, 2000). Despite ranging widely in the oceanic environment, sea turtles are inherently tied to the terrestrial environment for reproduction. Female sea turtles return to land only to bury their eggs beneath sandy beaches. Incubating eggs are extremely sensitive to hydric and thermal conditions inside the nest, and can tolerate only narrow fluctuations in these variables (Ackerman, 1997; Davenport, 1997). Consequently, nesting beaches are much more restricted in distribution than are free-ranging turtles living in the ocean (Schroeder *et al.*,

2003). The majority of sea turtle nesting occurs in tropical and subtropical regions, with only limited nesting in temperate regions (e.g. the south-eastern United States, the Mediterranean). Despite the relatively narrow geographic range in which nesting occurs, these areas facilitate a critical component of the life cycle. Without access to sandy beaches conducive to egg incubation, successful reproduction cannot occur. The importance of these areas is underscored by the tendency for females to return regularly to the same geographic region from which they hatched (Meylan *et al.*, 1990). The long-term ability of these habitats to provide suitable incubation environments is crucial to population persistence. However, we know very little about which environmental factors influence the global distribution of nesting sites.

Sea turtle eggshells are flexible, and thus eggs are extremely sensitive to environmental conditions, especially moisture and temperature (Ackerman, 1997; Davenport, 1997). Very moist conditions will deprive the developing embryo of oxygen (Ackerman, 1997; Packard, 1999) and temperatures outside the range of 25–35 °C will halt embryonic development (Ackerman, 1997). Individual sea turtles lay multiple clutches of eggs within reproductive seasons that can last for several months (Pike & Stiner, 2007), and thus incubation conditions conducive to embryonic development must be available for an extended period. The terrestrial environment therefore plays a critical role in whether eggs will produce viable offspring, and may ultimately determine the geographic extent over which successful production of offspring can occur. Because developing embryos are extremely sensitive to environmental conditions, we can assume that marine turtles currently nest in areas with environmental conditions that are conducive to egg development (that is, they do not nest regularly in areas where the eggs will not hatch). But are there other areas, in which sea turtles are not yet known to nest that also could support hatchling production?

Despite sea turtles being recognized globally as a threatened taxon, there has been no coordinated effort to define the distribution of suitable sea turtle nesting habitat at the global scale. Instead, most efforts focus on mapping individual nesting locations (e.g. Dow *et al.*, 2007; Mingozzi *et al.*, 2007; Tomás *et al.*, 2008; Khan *et al.*, 2010; but see work on olive ridley turtles in Bernardo & Plotkin, 2007), which is more likely to reflect research or survey effort, and represents only a subset of the overall suitable nesting habitat. In fact, new and important sea turtle nesting areas are still being found, even in well-populated regions (e.g. Mingozzi *et al.*, 2007; Patino-Martinez *et al.*, 2008; Tomás *et al.*, 2008; Witt *et al.*, 2009; Khan *et al.*, 2010). Orphan haplotypes from foraging areas also suggest important genetically distinct, but as yet unknown, nesting areas that are awaiting discovery (Laurent *et al.*, 1998; Blumenthal *et al.*, 2009). This emphasizes the need to understand the distributions of sea turtles at regional and global scales, which will help reveal interspecific differences in nesting distributions. In this paper I have used ecological niche models to: (1) generate predictive maps of nesting habitat for all seven sea turtle species globally, (2) generate a predictive map of global nesting richness 'hotspots', and (3) quantitatively compare ecological niches among species to

help understand the causes of geographic differences in the distributions of species.

MATERIALS AND METHODS

Nesting localities

I obtained georeferenced nesting beach locations for all seven extant marine turtle species by compiling existing datasets (e.g. State of the World's Sea Turtles, United Nations Environment Programme – World Conservation Monitoring Centre, Wider Caribbean Sea Turtle Conservation Network; Dow *et al.*, 2007). I removed duplicate records and excluded aberrant or single observations of nesting and unconfirmed records (i.e. instances where nesting was 'suspected' or 'likely' to occur, as classified in the original dataset) to meet the fundamental assumption that occurrence records are drawn from source populations (Phillips *et al.*, 2006).

Climate data

I removed intercorrelations from an initial set of 19 climatic variables describing annual and seasonal variation in temperature and precipitation in terrestrial environments (Hijmans *et al.*, 2005). This resulted in nine independent predictor variables (all pairwise correlation coefficients < 0.85): mean diurnal range in temperature, isothermality (the mean diurnal temperature range/the annual temperature range), maximum temperature of the warmest month, annual range in temperature, precipitation seasonality (coefficient of variation), precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter. These variables are biologically meaningful to successful sea turtle reproduction because variation in temperature and moisture strongly influences the viability of incubating eggs (Ackerman, 1997; Packard, 1999; Houghton *et al.*, 2007) and phenotypes of the offspring (Booth & Astill, 2001a; Glen *et al.*, 2003), and ambient (air) temperatures correlate strongly with nest temperatures (Godley *et al.*, 2001; Hays *et al.*, 2003; Hawkes *et al.*, 2007). Note that my goal was not to predict nest temperatures, but to determine whether the beaches where sea turtles nest have distinctive climatic conditions not found elsewhere in the world. Current climatic conditions were averaged over the period *c.* 1950–2000 (Hijmans *et al.*, 2005) and consisted of grid cells at a 4 km × 4 km spatial resolution at the equator (2.5 arcmin). Sea turtles only nest along the coastline, so I restricted climate data to within *c.* 8 km (two grid cells) of the ocean to minimize the influence of terrestrial environments on model performance.

Modelling approach

I modelled nesting beach distributions using MaxEnt version 3.3.3k, which combines the climate variables with sea turtle nesting locations and randomly selected background points (from coastlines globally) to predict the potential nesting distri-

Table 1 Model summary data for all seven sea turtle species. Shown are sample sizes (number of unique nesting beaches), the area under the receiver operating characteristic (AUC; average of crossvalidation runs ± SD among runs), and a binomial probability testing whether the presence points for each species are better at predicting a distribution than randomly chosen background locations (in all cases models performed significantly better than random). Also shown are the minimum presence thresholds used to predict each species' presence, and the number (and percentage) of nesting locations excluded using these thresholds (see Materials and Methods and Fig. 2 for further details).

Species	Unique nesting beaches (n)	AUC	Model parameters (n)	P-value	Minimum presence threshold	Nesting beaches excluded (%)	Niche breadth Inverse concentration
Flatback	223	0.984 ± 0.003	44	< 0.00001	0.232	10 (4.5)	0.03
Green	1781	0.871 ± 0.008	97	< 0.00001	0.203	39 (2.2)	0.26
Hawksbill	1594	0.893 ± 0.007	112	< 0.00001	0.202	36 (2.3)	0.20
Kemp's ridley	42	0.991 ± 0.004	53	< 0.00001	0.366	1 (2.4)	0.05
Leatherback	513	0.930 ± 0.009	94	< 0.00001	0.159	4 (0.8)	0.18
Loggerhead	933	0.923 ± 0.009	109	< 0.00001	0.077	9 (1.0)	0.18
Olive ridley	198	0.953 ± 0.012	81	< 0.00001	0.154	5 (2.5)	0.13

bution of sea turtles (Phillips *et al.*, 2006). Prior to running final models, I evaluated the relative effect of different feature types (i.e. the relationship between the environmental variable and probability of presence), regularization multipliers (1,3,5,7,9,11) and combinations of environmental variables (the nine listed above; only the five highest weighted variables; and the single highest weighted variable only) on model performance. Models created using hinge features (i.e. piecewise linear splines) with a regularization multiplier of one and nine independent predictor variables consistently outperformed the other model combinations based on information criteria scores and by having biologically meaningful response curves (see Appendix S1 in Supporting Information). I thus used the default modelling parameters to reduce overfitting and hinge features to obtain smoother response curves (Phillips *et al.*, 2006, 2009; Phillips & Dudík, 2008; Elith *et al.*, 2011). For each species, I retained only one sea turtle nesting record per grid cell to help alleviate spatial bias. To investigate the robustness of predicted distributions, I used 10-fold crossvalidation to randomly partition each species' full set of nesting locations into 10 approximately equal datasets. Final models for each species were run using these 10 datasets, each time using nine of the data partitions to train the model and the tenth partition to test the model.

These models generated species-specific maps showing the likelihood of nesting occurring within each grid cell, scaled from 0 (no nesting) to 1.0 (a very high probability of nesting), with values near 0.5 representing the typical probability of nesting at locations where the species is known to occur (Phillips & Dudík, 2008). Drawing a threshold along this suitability scale to predict where nesting may or may not occur is sensitive to outliers (resulting in overestimates of a species' range). Therefore I created species-specific histograms of the MaxEnt scores of each nesting location for each species and determined the minimum presence threshold after excluding outliers (i.e. the few nesting beach locations that had scores well below the vast majority of other nesting beaches for that species; Appendix S2).

For all maps and analyses I present the median values for the 10 crossvalidation runs for each species, and used the standard deviation of those runs to evaluate model consistency (i.e. a measure of how much different subsets of nesting site data influence the model results). To better visualize the model output in geographic space, I categorized the grid cell values that were above the presence threshold into four quantiles, with habitat quality defined as (in ascending order): marginal, moderate, good or excellent (see Table 1 for thresholds used for each species). To make a global map of species richness, I converted the habitat suitability scores generated by MaxEnt into a presence/absence map for each species using the minimum presence thresholds described above (Table 1). I then combined these into a final map predicting the number of species nesting within each grid cell. For all maps, I extended the distribution of these measures inland to make the nesting distributions easier to see at regional scales.

I evaluated model performance using the area under the receiver operating characteristic curve (AUC). AUC is the probability that randomly selected occurrence points and randomly selected background points are classified correctly, with better discrimination between occurrence and background points as AUC approaches 1. MaxEnt uses a one-tailed binomial distribution to test the null hypothesis that the presence points are no better at predicting a distribution than the random sample of background points (Phillips *et al.*, 2006).

Niche similarity and overlap

Aspects of sea turtle embryology are highly conserved among species, including the temperature at which equal sex ratios are produced (Wibbels, 2003; Weber *et al.*, 2011) and the thermal tolerances within which eggs successfully hatch (Ackerman, 1997). Despite having similar constraints on successful reproduction, the distributions of individual species vary widely, as could the environmental niche space in which each species nests. I used ENMTools (Warren *et al.*, 2010) to test for ecological niche similarity between species pairs. Briefly, predictions of habitat suitability (from MaxEnt distribution models) are compared between all combinations of species pairs to determine whether the environmental niche models produced by the

species pairs are equivalent, and whether any differences are more or less similar than expected based on the differences in the environmental background in which each species occurs (Warren *et al.*, 2008, 2010). Three metrics are produced: (1) *I*, which treats the two environmental niche models as probability distributions, (2) Schoener's *D*, which assumes that the MaxEnt score is proportional to abundance (see Vanderwal *et al.*, 2009, for empirical tests of this assumption), and (3) relative rank, which estimates the probability that the relative ranking of any two nesting beaches is the same for the two species being compared, irrespective of the quantitative difference in suitability estimates (Warren *et al.*, 2008; Warren & Seifert, 2011). These metrics range from 0, which indicates discordant environmental niche models with no overlap, to 1, which indicates that the two species share identical environmental niche space. I tested whether these metrics differed significantly between species pairs using randomization tests (the 'identity test' in ENMTools). This approach pools nesting location data for both species being compared, randomizes their identity with respect to species and splits the data into the original sample size for each species. The randomized nesting site data were input into niche models in MaxEnt to derive new habitat suitability scores. When the empirically derived niche similarity metrics were outside of the 95% confidence limits of the distribution overlap scores generated from 100 randomization tests, the hypothesis that the species pair inhabits the same ecological niche was rejected. This result would indicate that the two species being compared are not drawn from identical distributions of environmental variables, and thus inhabit different niche spaces. I used non-metric multidimensional scaling on the *I* and *D* metrics to better visualize the multidimensional niche relationships among species.

One explanation for niche differences between species pairs is that underlying differences in the environmental conditions within each species' nesting distribution are driving these patterns. I tested for these 'background effects' to determine whether species pairs are more similar than expected by chance based on the geographic areas in which nesting occurs. This allowed me to evaluate whether the environmental niche models obtained from two allopatric species are more different than expected, given underlying differences in environmental variables between the regions in which each species nests. This was done by comparing known nesting locations for one species with randomly selected points from the background environmental habitat available within the nesting distribution predicted for a second species, and vice versa for all combinations of species pairs (using 100 replicates for each comparison). I used the area above the minimum presence threshold (described above) as the background for each species, which represents the geographic region in which each species has a high likelihood of nesting. Significant differences between species pairs indicate that the two species differ in their environmental niche, and that this is not because of different combinations of environmental variables available within each species' geographic range.

Finally, I estimated the niche breadth of each species using Levin's inverse concentration metric (Levins, 1968; Nakazato *et al.*, 2010), implemented in ENMTools. The niche breadth metric ranges from 0 (i.e. only one grid cell in the geographic space contains suitable habitat) to 1 (i.e. all grid cells are equally suitable), and uses the continuous habitat suitability scores generated by MaxEnt, rather than relying on a minimum presence threshold.

RESULTS

Global distribution of sea turtle nesting

The number of spatially independent nesting beaches (i.e. including only one beach per 4 km × 4 km grid cell) included in the models ranged from 42–1781, and was lowest for Kemp's ridley and flatback turtles and highest for hawksbill and green turtles (Table 1). The geographic distributions generated from nesting data predicted sea turtle nesting locations significantly better than random models (binomial probability, for all species $P < 0.00001$; Table 1). Models created using the different cross-validation datasets were very consistent, both in terms of their AUC values (as shown by low SDs among crossvalidation runs; Table 1), and in terms of the predicted probability of presence at known nesting beaches (the SD in MaxEnt scores among model runs was generally < 4% for any known nesting beach for all species; Appendix S3). Histograms of the MaxEnt values at known nesting beaches (Appendix S2) revealed distinct thresholds that are useful in predicting nesting distributions; in all cases these thresholds included >95% of the known nesting locations for each species (Table 1).

All nine climatic variables contributed to the model predictions for each species, some more so than others (Appendix S4). For five of the seven species, isothermality contributed the most to these models (ranging in contribution from 32.6–70.4%; Appendix S4). The two exceptions were Kemp's ridley and loggerhead turtles, for which maximum temperature of the warmest month contributed the most (47.1 and 65.6%, respectively; Appendix S4). For six of the seven species, maximum temperature of the warmest month contained the most useful information out of the individual variables, but for flatback turtles, isothermality captured the most useful information (Appendix S4). Overall, the different sea turtle species showed marked differences in nesting beach climates, as shown by substantial variation in the mean and range of these nine environmental variables (Appendix S5). The responses of the highest-weighted environmental predictors reflect the variation in climate space among species, and show biologically meaningful responses in their predictive power (Fig. 1).

Maximum entropy models accurately predicted the geographic range limits for most species (Figs 2 & 3, Appendix S6). For example, in the south-eastern United States loggerhead turtles nest as far north as Virginia annually, whereas green and leatherback turtles only nest regularly as far north as Georgia (Fig. 2). Although hawksbill and Kemp's ridley turtles only occasionally nest in Florida (Meylan *et al.*, 1995; Johnson *et al.*, 1999), the models predicted small areas of suitable nesting habitat in most of the state (Fig. 2). Of the six species nesting in
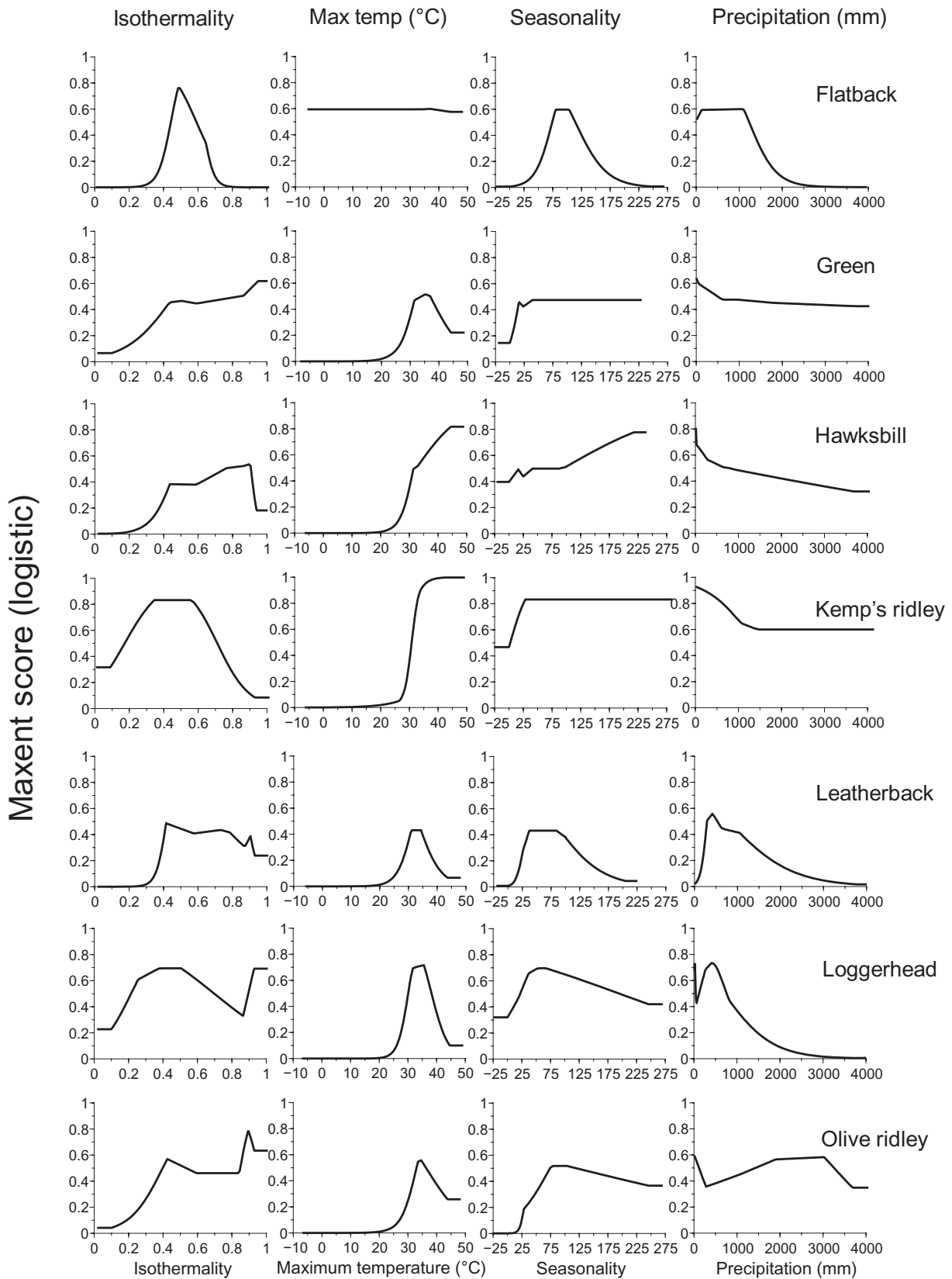
Figure 1 Example hinge (piecewise linear spline) response curves, showing the relationship between representative environmental variables [isothermality (mean of diurnal temperature range divided by annual temperature range), maximum temperature of the warmest month, precipitation seasonality, and precipitation of the wettest quarter] and MaxEnt scores for each sea turtle species. See Appendix S4 for the contribution of each variable to the species-specific models.
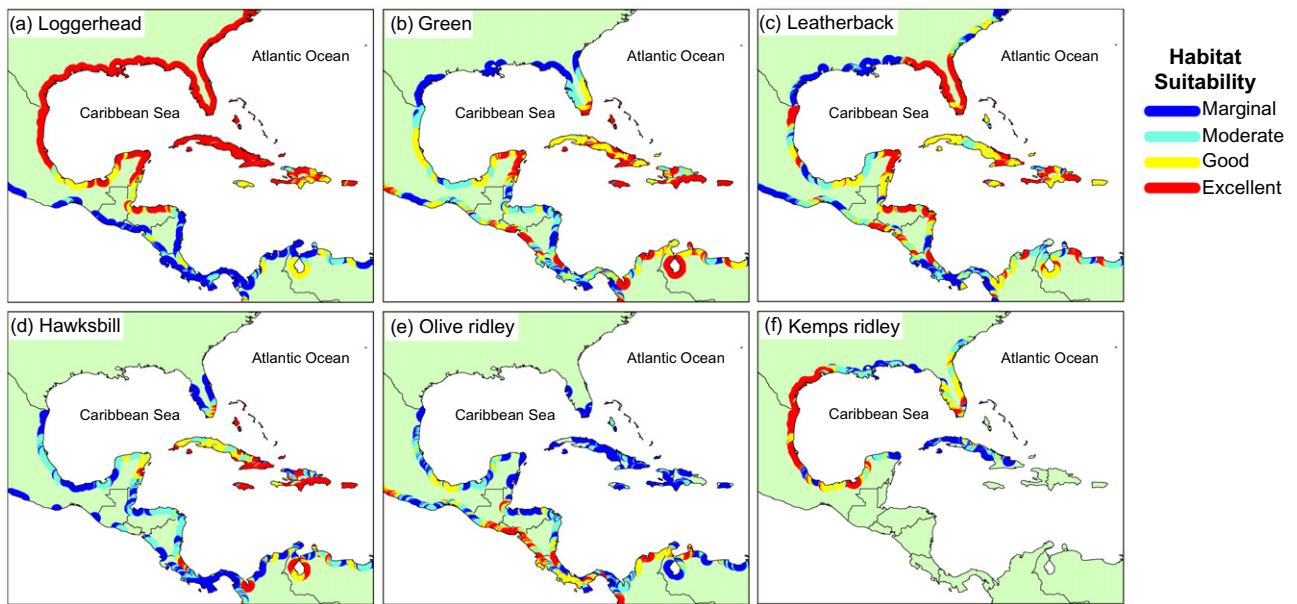
Figure 2 Predicted distribution of sea turtles in the Caribbean region, as estimated from MaxEnt models. Habitat suitability was divided into four quantiles (in increasing order of suitability): marginal–moderate–good–excellent. Shown are the six species nesting in this region.
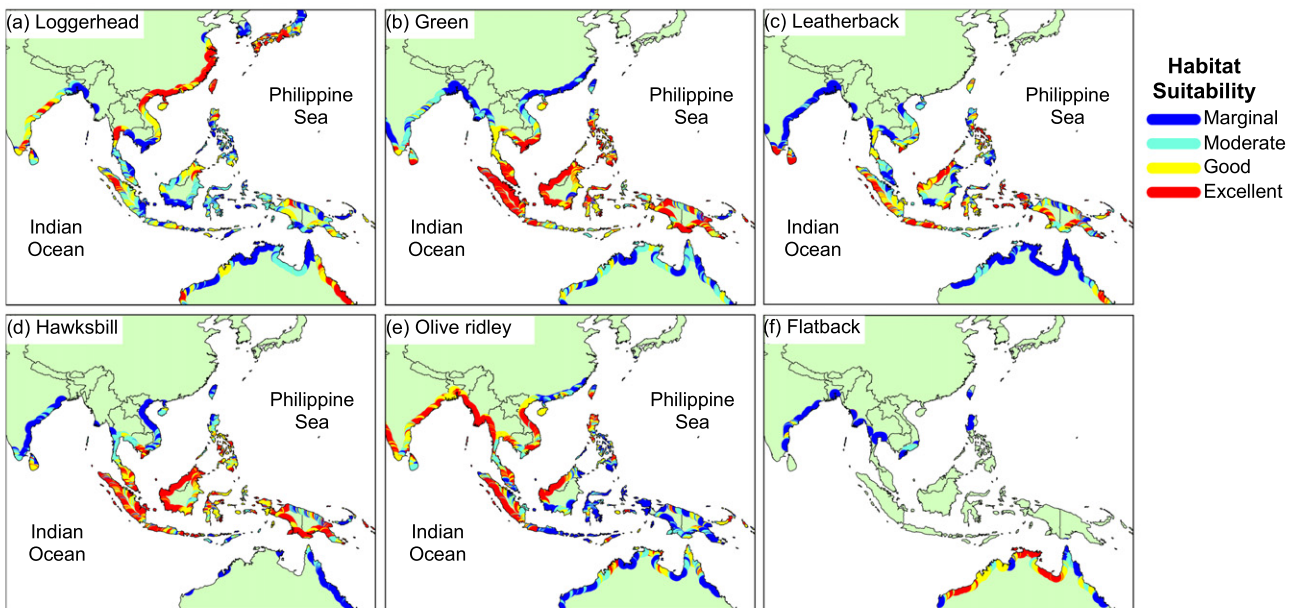
Figure 3 Predicted distribution of sea turtles in the Indopacific region, as estimated from MaxEnt models. Habitat suitability was divided into four quantiles (in increasing order of suitability): marginal–moderate–good–excellent. Shown are the six species nesting in this region.

the Caribbean region, Kemp's ridley turtles have the narrowest geographic distribution (Fig. 2f), whereas loggerhead, green, leatherback, hawksbill and olive ridley turtles have much wider distributions (Fig. 2a–e). Of the six species nesting in the Australasian region, flatback turtles have the narrowest distribution (Fig. 3f), whereas loggerhead, green, leatherback, hawksbill and olive ridley turtles have much wider distributions (Fig. 3a–e). In the Mediterranean region, only loggerhead and green turtles

were predicted to nest, and these predictions closely match the known nesting sites used by these species (Fig. 4). Taken together, these results imply that geographic distribution of sea turtle nesting is largely limited by climate, namely temperature and precipitation (Appendix S5). Some overprediction did occur in these models, with suitable nesting habitat predicted to occur in geographic areas well outside of the known nesting range of individual species (e.g. Appendices S7 & S8).
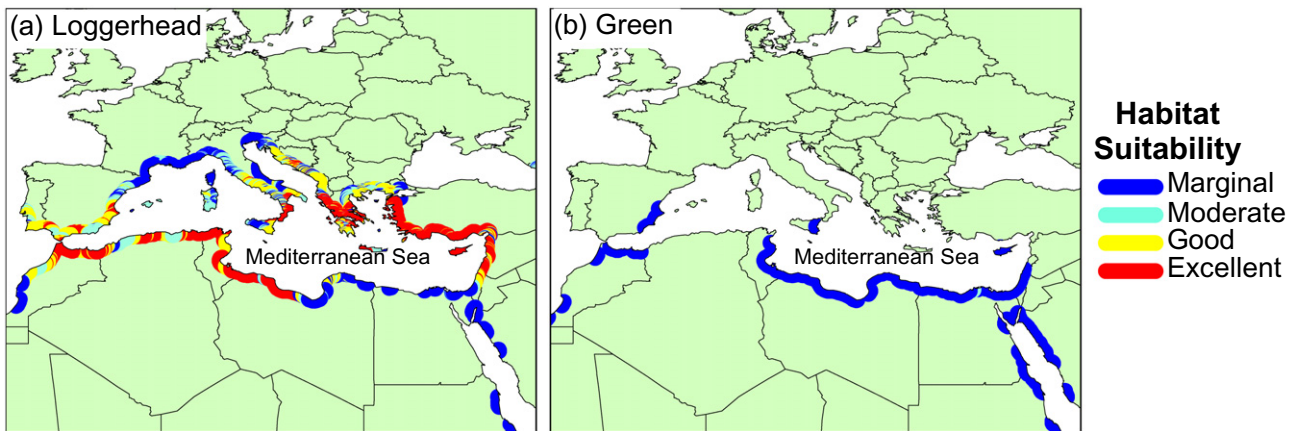
Figure 4 Predicted distribution of sea turtles in the Mediterranean region, as estimated from MaxEnt models. Habitat suitability was divided into four quantiles (in increasing order of suitability): marginal–moderate–good–excellent. Shown are the two species nesting in this region.
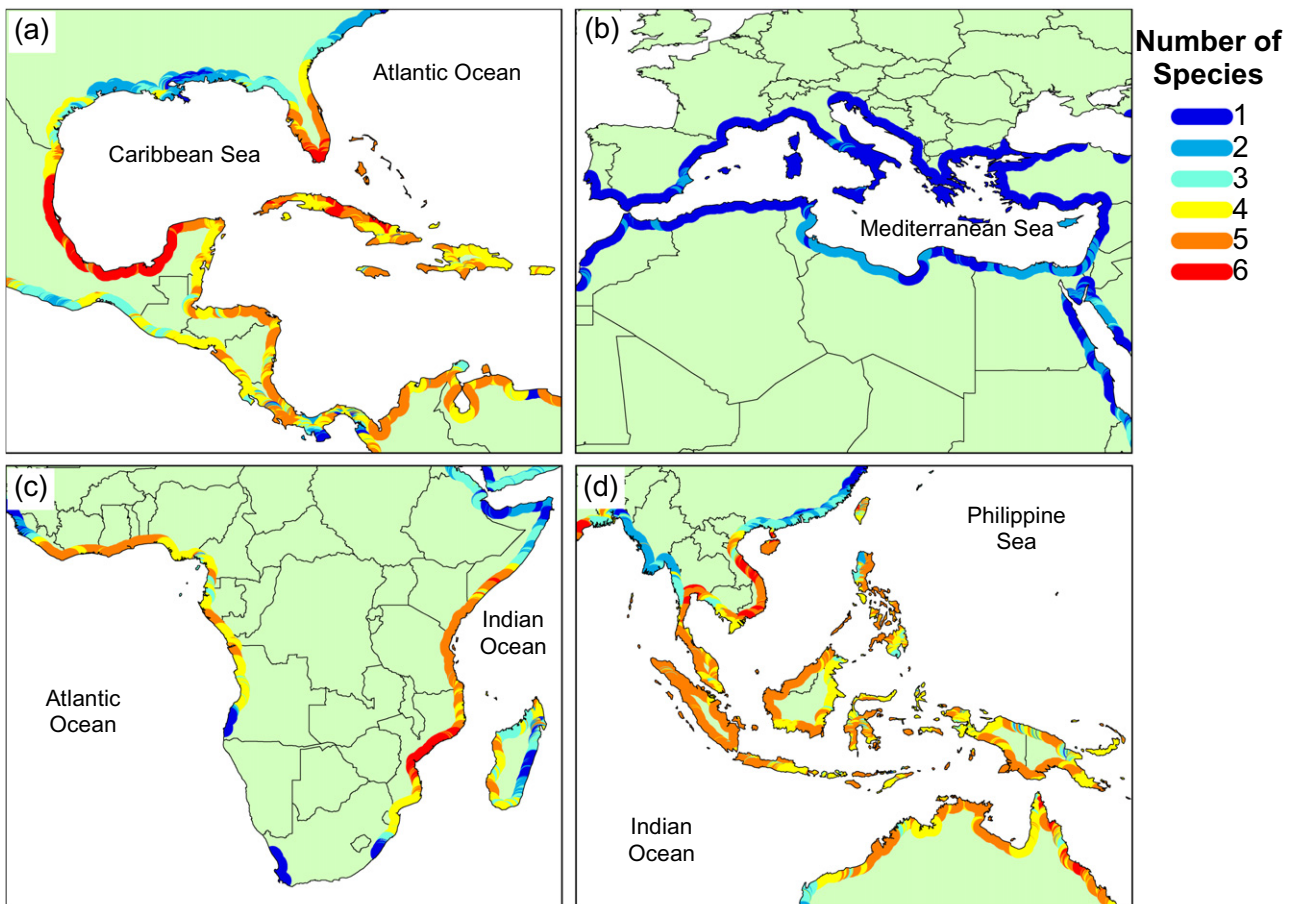

Figure 5 Global nesting hotspots for marine turtles in four representative regions. Colours represent of the number of species predicted to nest in each grid cell, as determined by MaxEnt modelling of all extant sea turtle species.

Global nesting hotspots

Sea turtle nesting occurs regularly between the latitudes of 25° N and −24.8° S. Globally, between zero and six species were predicted to nest on any particular stretch of coastline (Fig. 5). Six species were predicted to nest only in very limited geographic areas, including small and patchy areas of Caribbean Mexico, northern Cuba, southern Florida, the Bahamas, east Africa and east India (Fig. 5). Much larger geographic areas were predicted to support nesting by five species, including the entire Carib-
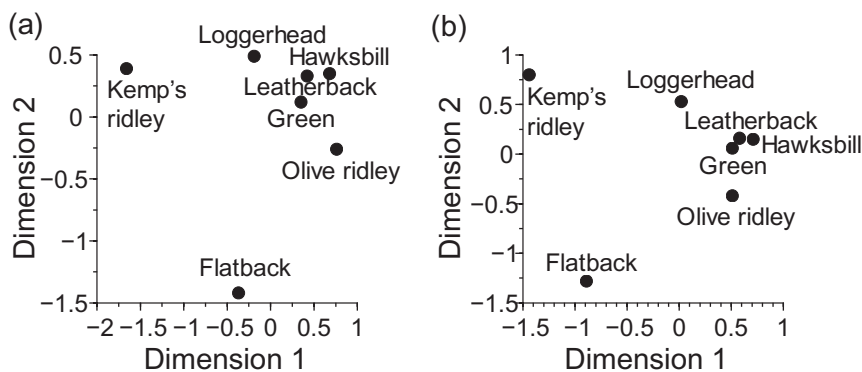
Figure 6 Non-metric multidimensional scaling plots comparing two niche metrics, (a) *I* and (b) Schoener's *D*, among sea turtle species.

bean region, pan-tropical Africa, east India and Australasia (Fig. 5). Overall, the regions with the highest number of nesting species were the Caribbean/Gulf of Mexico, Indopacific and the north-east coast of Australia (Fig. 5). Temperate regions support fewer nesting species than did tropical regions; for example, temperate areas of the south-eastern United States, the Mediterranean Sea and southern Africa only have one or two species nesting there (Fig. 5).

Niche similarity and overlap

Despite the wide geographic overlap in nesting distributions among sea turtle species (Figs 1–3), the null hypothesis of niche similarity was rejected for all species pairs using all three quantitative measures of niche similarity (*I*, *D*, relative rank; Fig. 6, Appendix S9). This implies that the nesting locations of each species are drawn from different distributions of climate variables, and thus that the core habitat (in terms of climatic conditions) differs geographically among species. The non-metric multidimensional scaling distances matched the data well; for both *I* and *D*, stress was very low (0.02 and 0.015, respectively) and the proportion of variance explained was extremely high (0.998 and 0.999, respectively). Flatback and Kemp's ridley turtles have the narrowest niche breadths (perhaps owing to their narrow geographic distributions; Fig. 1) and thus formed distinct clusters in the non-metric multidimensional scaling plots (Fig. 6). Olive ridley turtles have intermediate niche breadths, and loggerheads appear to have the widest niche breadth (Fig. 6). Leatherbacks, hawksbill and green turtles formed a distinct neighbourhood cluster, and thus have niches more similar to one another than they do to the other species (Fig. 6, Appendix S9).

The background tests for most species pairs were significantly different for all three niche metrics (all *P* < 0.0001), indicating that the locality points of one species are different from the background in which the other species nests. The only exceptions to these were the *I* metric for flatback–olive ridley, hawksbill–green and loggerhead–hawksbill comparisons, the relative rank metric for Kemp's ridley–olive ridley turtles and the *D* metric for olive ridley–Kemp's ridley turtles (all *P* = 0.99). This implies that even though these species are geographically distributed in different areas, they share similar environmental characteristics in the habitat available to them (at least according to one of the three metrics evaluated).

DISCUSSION

Sea turtles can be highly vagile and undertake extended migrations from foraging areas to nesting habitat characterized by distinct climatic conditions, including temperature and precipitation (Figs 1–4, Appendix S5). The breadth of this niche space is larger for some species (e.g. loggerhead and green turtles) than for other species (e.g. flatback and Kemp's ridley turtles). Suitable nesting habitat is restricted to areas in which sea turtles are currently known to nest (Figs 2–4), providing strong evidence that all species currently nest throughout their entire climate envelopes. These results are unlikely to be influenced by the inclusion of new nesting locality data because there was little variation in model output among the subsets of nesting locations used in the different crossvalidation runs (Table 1, Appendix S3). Overall, sea turtle nesting is largely pan-tropical, with some spillover into temperate areas by loggerhead and green turtles (Figs 2–4). Important areas supporting nesting habitat for a diverse range of species are located near the equator, in the Caribbean, Africa and Australasia (Fig. 5). Because the overall distribution of individual species can vary widely within these regions (Figs 2 & 3), protecting nesting habitat at the regional scale is crucial for sea turtle conservation.

How can sea turtle species differ in their environmental niches and vary so much in geographic distribution, yet be constrained in the same fundamental way by how their embryos respond to incubation conditions? The likely answer lies in how individual species reproduce seasonally, and in the microhabitat in which females place their nests. For example, species nesting in the same geographic areas often have species-specific nesting seasons that may or may not overlap with other species (e.g. Pike & Stiner, 2007). These seasonal differences could translate into different incubation temperatures for different species. Because the microenvironment of the nest site can have profound impacts on developing eggs (Ackerman, 1997; Packard, 1999; Booth & Astill, 2001a), females often lay their eggs in areas that provide distinctive temperature and moisture regimes (e.g. Mortimer, 1990; Wood & Bjorndal, 2000). For example, nests laid beneath trees are shadier (and thus experience lower temperatures) than nests laid in open areas (Kamel & Mrosovsky, 2006). Nesting females can also alter nest temperatures by manipulating the depth of the nest (Booth & Astill, 2001b); larger species may be able to bury their eggs at a wider range of depths than

smaller species, thereby exerting more direct control over the incubation environment than relatively smaller species. These mechanisms offer plausible ways in which sea turtles can partition different geographic spaces, each with its own distinctive environmental niche, and still produce hatchling turtles. Understanding the links between broad climatic habitat suitability scores (such as those generated here) and large-scale patterns of nest temperatures and hatchling production will be an important future step towards our understanding of how climate constrains the distribution of sea turtle nesting grounds.

Three recent studies have linked regional and local sea turtle distributions to environmental factors other than those used in my models (Putman *et al.*, 2010; Santana Garcon *et al.*, 2010; Fuentes *et al.*, 2011). For example, in north-eastern Australia, sea turtles tend to nest on beaches that are more exposed to wind and wind-generated waves, but less exposed to cyclones, than are stretches of beach not used by sea turtles (Santana Garcon *et al.*, 2010; Fuentes *et al.*, 2011). In the south-eastern United States, higher numbers of sea turtles nest at beaches that are closer to the Gulf Stream, water currents that are conducive to dispersal of hatchlings to foraging areas (Putman *et al.*, 2010). Thus, the distribution of sea turtles is related to many different biotic and abiotic factors, depending on the spatial scale and life-history stage investigated. Wind and current attributes such as those described above are likely to be limited by broader climatic conditions, such as those used here. Sea turtles also select a wide range of physical or environmental factors at local spatial scales (e.g. Mortimer, 1990; Wood & Bjorndal, 2000). Ultimately, any potential or actual nesting site is limited by being able to provide the physical and environmental conditions that are conducive to embryos developing successfully into hatchling turtles that can disperse to foraging grounds. This makes sea turtle conservation efforts extremely complex, underscoring the need for a deeper understanding of how climate influences these species.

Modelling the global distribution of any species is a difficult task with some major challenges, and sea turtles are no exception. The global climate layers I used are based on the location of individual weather stations and interpretation of the climate between individual stations to create global climate layers (Hijmans *et al.*, 2005). These layers are biologically meaningful because air temperatures place enormous constraints on nest temperatures (Godley *et al.*, 2001; Hays *et al.*, 2003; Hawkes *et al.*, 2007). Unfortunately, many of the small islands on which sea turtles nest lack any local weather stations, meaning that these areas were omitted from all models due to the lack of underlying climate data (both temperature and precipitation). This was particularly problematic for the Caribbean and Indonesian regions, which both contain vast numbers of small islands. Thus, although these models clearly defined broad-scale nesting distributions for mainland areas and moderate-sized islands, these models cannot predict into areas without underlying climate data. Devising novel ways to infer the climatic conditions in such locations will greatly benefit sea turtle conservation. Finally, some of the areas predicated as climatically suitable for nesting may not contain suitable microhabitats for egg incubation (Penman *et al.*, 2010). Sea turtles require sandy soils for nesting, but there are no global datasets on coastal soil type that could be incorporated into these models. The development of such datasets will help refine the models presented here by discriminating between substrates that are suitable for incubating embryos and those that are not.

Ultimately, the terrestrial environment is a critical, limiting factor for successful sea turtle reproduction due to the limited area in which suitable environmental conditions occur for nesting. These areas are crucial for conservation efforts because hatchling production largely determines population viability (Mazaris *et al.*, 2005). The range edges, geographic predictions of species overlap and quantitative metrics of niche overlap that I generated provide a solid baseline for understanding how the current climate has influenced sea turtle nesting distributions. Reconstructed climate data are available for past climates (for example, during the last interglacial 120,000 years ago or the Last Glacial Maximum 21,000 years ago) and have been predicted into the future (under different general circulation models assuming different carbon emissions scenarios) up to 2100. Predicting how nesting and foraging ranges have changed over time will be crucial for understanding how climate change may influence the global distribution of nesting sites. The tight link between current geographic patterns of nesting and climate, along with the dependence of developing embryos on nest microclimate, imply that regional or global changes in environmental conditions could differentially influence the distribution of sea turtle species, especially if different regional management units (Wallace *et al.*, 2010) experience different climatic conditions. Understanding whether genetically distinct nesting populations or regional management units inhabit different niches is a logical avenue for future research that may help clarify the causes and consequences of genetic differentiation. Such divergence could potentially result in differences in embryonic traits, such as thermal reaction norms (Weber *et al.*, 2012). This could influence the adaptive potential of different populations, and predicting these responses before they occur will be important in mitigating the effects of climate change. The amazing dispersal capabilities of most sea turtle species may allow them to track future changes in climate by nesting in new geographic areas as the climate becomes suitable there (Araújo & Pearson, 2005). The underlying assumption, however, is that sea turtles can predict whether a nesting beach is suitable for hatchling production, and that there is sufficient plasticity in individual sea turtle homing behaviour to allow these range shifts to occur. Given the global protected status of all sea turtle species, understanding how climate change will influence the location and extent of climatically suitable nesting habitat is an important research priority.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Example candidate MaxEnt model comparison for loggerheads.
Appendix S2 Distribution of MaxEnt suitability scores for each sea turtle species.
Appendix S3 Box plots of standard deviations among crossvalidation runs.

BIOSKETCH

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