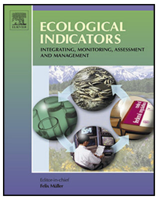
Ecological Indicators 71 (2016) 551–556

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Using climatic suitability thresholds to identify past, present and future population viability

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ARTICLE INFO

Article history:
Received 21 April 2016
Received in revised form 15 July 2016
Accepted 21 July 2016
Available online 2 August 2016

Keywords:
Adaptation to climate change
Bioclimate envelope
Climatic-based indicator
Evolutionary stable strategy
Resilience
Species persistence

ABSTRACT

Often climatic niche models predict that any change in climatic conditions will impact species abundance or distribution. However, the accuracy of models that just incorporate climatic information to predict future species habitat use is widely debated. Alternatively, environmental conditions may simply need to be above some minimum threshold of climatic suitability, at which point, other factors drive population size. Using the example of nesting sites of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean ($n = 105$), we developed climatic niche models to examine whether a climatic suitability threshold could be identified as a climatic indicator in order for large populations of a widespread species to exist. We then assessed the climatic suitability of sites above and below this threshold in the past (~1900) and future (~2100). Most large sites that are currently above the climatic threshold were above the threshold in the past and future, particularly when future nesting seasonality shifted to start 1–2 months earlier. Our analyses highlight the importance of future phenological shifts for maintaining suitability. Our results provide a positive outlook for sea turtle conservation, suggesting that climatic conditions may remain suitable in the future at sites that currently support large nesting populations. Our study also provides an alternative way of interpreting the outputs of climatic niche models, by generating a threshold as an index of a minimum climatic suitability required to sustain large populations. This type of approach offers the possibility to benefit from information provided by climate-driven models, while reducing their inherent uncertainties.

1. Introduction

Ecological niche models have become popular tools for providing quantitative estimates of how species distributions change in response to environmental variables (Araújo and New, 2007; Elith et al., 2010; Guisan and Thuiller, 2005). Widely available, free datasets on current and future climate are used to infer the current environmental niche of species and the impact of climate change (Ehrlén and Morris, 2015). These models are important because they allow the current climatic niche of the species to be described, raising conservation questions on whether the climatic conditions of currently used habitats will remain favourable in the future (Araújo et al., 2011). However, the power of models that are just built on climatic information to predict the future dynamics, range shifts, behaviour and habitat use of species is widely debated (Elith et al., 2010; Synes and Osborne, 2011). While species fitness is strongly linked to climatic conditions (Guisan and Thuiller, 2005), climate alone does not influence the size or distribution of populations (Soberon, 2007). Yet, it is difficult to incorporate the broad suite of biotic and abiotic drivers, because critical parameters vary greatly, and such data are often not available.

For example, climatic niche modelling of sea turtle distribution indicates that population ranges will shift in response to climate change to remain within a favourable climatic niche (Pike, 2013a; Reece et al., 2013). However, climate is not the only factor determining where nest sites are located. Marine conditions (e.g. sea currents and wave exposure; Garcon et al., 2010; Putman et al., 2010), beach features and threats (e.g. beach topography, vegetation, beach front development, animal predation; Katselidis et al., 2013; Schofield et al., 2009) also contribute to nest site selection (Casale, 2010). Thus, the fact that sea turtle population size may be larger at some climatically suboptimal sites when compared to

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http://dx.doi.org/10.1016/j.ecolind.2016.07.038
1470-160X/

climatically optimal sites might be attributed to a combination of these factors, highlighting the importance of incorporating these factors into such analyses (Schofield et al., 2009). Consequently, coastal sites identified to capture the climatic niche of sea turtles may not necessarily represent the whole required suite of environmental conditions (Mazaris et al., 2015; Pike, 2013a). Thus, an alternative paradigm is that environmental conditions may simply need to be above some minimum threshold of suitability, at which point other factors drive population size. Therefore, a change in environmental conditions, e.g. climate change, may only be important if conditions shift across the threshold.

Here, we applied a novel approach towards predicting the future distribution of the nesting habitat of loggerhead sea turtles in the Mediterranean. We aimed to utilise information provided by climatic niche models, but generated a threshold of climatic suitability for nesting sites, to acknowledge that future distributions may be driven by other factors. This is an excellent model species with a broad breeding distribution, whose biology is strongly related to climate. Specifically, we identified as an indicator, the baseline climatic conditions required for stable nesting, independent of population size. Our results are expected to provide an objective interpretation about the likely future suitability of existing nesting sites in the Mediterranean, with the climatic threshold defining critical limits. Thus, this approach could help reduce the uncertainties that accompany climate-driven models.

2. Material and methods

2.1. Nesting sites

We used 105 georeferenced locations of loggerhead sea turtle, *Caretta caretta*, nesting sites in the Mediterranean region obtained from the State of the World's Sea Turtles (SWOT) database (Halpin et al., 2009; Kot et al., 2013; SWOT, 2006a,b, 2008, 2009, 2010, 2011, 2012). We delineated two categories of nesting sites, large (>25 nests) and small (≤25 nests) (Table A.1, A.2; Appendix A), based on the upper bound of the lowest class in the classification scheme of nesting abundance provided by the online SWOT database for describing colony size (http://seamap.env.duke.edu/swot).

2.2. Climatic data

Previous studies have found that variables that represent mean or extreme air temperature and precipitation values or variation (i.e. mean temperature, precipitation seasonality) are strongly associated with sea turtle nesting phenology, behaviour and reproductive output (Hays et al., 2003; Pike, 2013a), and have, thus, been used to model sea turtle nesting site distribution patterns (Pike, 2013a,b) and spatiotemporal trends in reproduction (Laloë et al., 2014). We obtained climatic data for the Mediterranean region from the Climatic Research Unit Time-series Version 3.21 (CRU TS3.21) of High Resolution Gridded Data of Month-by-month Variation in Climate through University of East Anglia (http://catalogue.ceda.ac.uk/). The CRU TS series of datasets contain monthly time series for precipitation, in addition to daily maximum and minimum temperatures, covering the land area of the earth for 1901–2012, at 0.5° spatial resolution. The CRU TS datasets was selected because both recent past climatic data and future projections are provided at a temporal window that allows us to compare trends of climatic nesting suitability for periods larger than the current generation of loggerhead sea turtles, which reach sexual maturity at about 45 years of age (Scott et al., 2012). The spatial resolution of the data was adequate to capture the climatic characteristics of each nesting site. For our analyses, we restricted our study area to within 10 km of the coastline, to minimize the influence of the terrestrial environment on model performance (Pike, 2013a).

In the Mediterranean, continuous nesting begins in early June and ends in early August, with sporadic nesting occurring at some sites during 20–31 May and 10–20 August, while isolated nesting may occur as early as 5 May and as late as 20 September (Schofield et al., 2013). Therefore, to capture a core 3 month period that was most representative of current nesting, we used monthly variables for June, July and August (i.e. 30 days continuous nesting in June, 30 days of continuous nesting in July and 10 days continuous and 10 days sporadic nesting in August). To define current, past and future climatic conditions, we calculated mean values for climatic variables (i.e. temperature, precipitation) over a 30 year temporal window (i.e. 1901–1930, 1981–2010 and 2071–2100). This is because a 30 year period has been proposed as being adequate to filter out interannual variation or anomalies of climatic variables (IPCC, 2012).

Based on the monthly temperature and precipitation variables for June, July and August, we developed an initial set of 19 bioclimatic variables (Table A.3; Appendix A) of current climatic conditions that are representative of the period 1981–2010 and express seasonal trends, extreme or limiting temperature and precipitation values (Hijmans et al., 2005). The same climatic variables were generated for the recent past, covering the period 1901–1930. To project the future distribution of nesting sites in 2071–2100, we used sources in line with the Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC). To decrease uncertainty related to different global climate models (GCMs) (Nenzén and Araújo 2011), we averaged three models based on emission scenario A1B, which represents an intermediate emission scenario: (1) the Australian GCM from the Commonwealth Scientific and Industrial Research Organisation (CSIRO); (2) the fifth-generation atmospheric general circulation model of the atmosphere from the Max Plank Institute (Hamburg, Germany), which was derived from the spectral weather prediction model of the European Centre for Medium Range Weather Forecasts (ECHAM GCM5); and (3) the Hadley Centre Coupled Model, version 3 (HadCM3), which is a coupled atmosphere–ocean general circulation model (AOGCM) from the Hadley Centre.

Out of 19 developed bioclimatic variables, we excluded those that were highly correlated (Spearman correlation coefficient, $r > 0.85$), resulting in a set of four predictors: mean diurnal range (defined as the mean difference between the maximum and minimum air temperature calculated for each month of interest), mean temperature of warmest two-month period, minimum temperature of coldest month, and precipitation of warmest two-month period (see Appendix A for details on the bioclimatic variables and the procedures used for their calculation).

Acknowledging that selecting variables is a challenging task (Muttil and Chau, 2007) that has a strong influence to the final model outputs (Bucklin et al., 2015), we also used for our subsequent analysis an alternative set of predictors: mean diurnal range, maximum air temperature of warmest month, minimum temperature of coldest month, and precipitation of driest month (Table A.3; Appendix A).

2.3. Climatic suitability models

We used an ensemble ecological niche modelling (EENM) approach (Araújo and New, 2007) to generate a climatic suitability threshold of nesting sites using biomod2 package for R (Thuiller et al., 2014, 2009). Many studies have shown that the application of alternative single ecological niche modelling algorithms has a major impact on predictions, leading to the production of different outputs (i.e. Elith et al., 2010). However, to reduce intermodel variation and to develop more robust forecasts, an EENM