MODELLING LOGGERHEAD SEA TURTLE (*CARETTA CARETTA*) NESTING HABITAT

EVALUATION OF THE SPECIES DISTRIBUTION MODEL BY SPECIES-ENVIRONMENT AND ABUNDANCE-OCCUPANCY RELATIONSHIPS

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February, 2014

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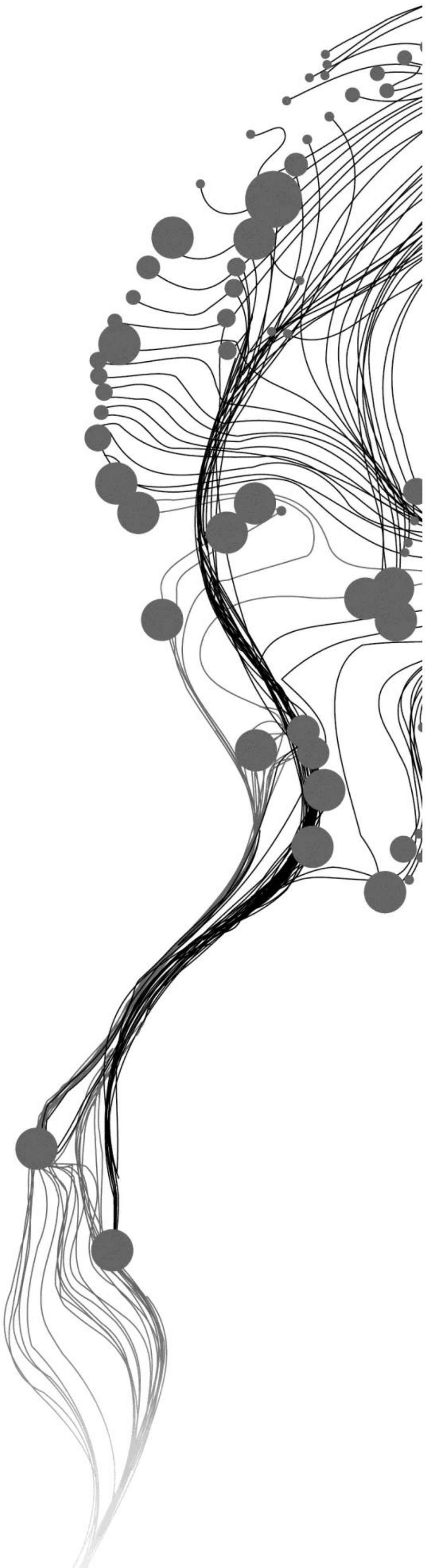

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ABSTRACT

Loggerhead sea turtle is a globally spread species, and its nesting habitat is determined by a wide range of environmental characteristics. Modelling its nesting habitat under the full range of environment condition (global) where it occupy, can make the prediction more convincing than only modelling under a limited range of environment conditions, e.g. only in the Mediterranean. A qualitative verification of species-environment relationships, and a quantitative test of the species abundance-occupancy relationship are introduced to assess models performance. The qualitative one checks if the environmental variables response curves derived from Machine learning (MaxEnt) fit expert knowledge of how loggerhead responds to its living environment; whereas the quantitative one tests the Pearson correlation coefficient between nest density and habitat suitability predicted from MaxEnt.

The species-environment relationships modelled under the full range of environment conditions are commensurate with expert knowledge, while that modelled under only limited range of environment conditions are not. Similarly, the habitat suitability modelled under full range of environment conditions has a significantly ($\alpha = 0.025$) stronger correlation with nest density than that only modelled under limited range. Moreover, the nesting habitat suitability map from full environment range model successfully estimated some suitable habitat where it has been reported that loggerhead nests occurred, but without occurrence in this study.

Therefore, modelling the loggerhead sea turtle nesting habitat under its adapted full range of environment condition is necessary, and the model performance evaluation methods could be applied on modelling the distribution of other species.

Key words: loggerhead sea turtle, Species distribution models, MaxEnt, Species-environment relationship, Abundance-occupancy relationship

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1. INTRODUCTION

1.1. Research Background

1.1.1. Loggerhead sea turtle (*Caretta caretta*)

The loggerhead sea turtle, *Caretta caretta* (*C. caretta*) is one of the most ancient reptiles, appearing approximately 40 million years ago (Spotila, 2004). It is one of only seven sea turtle species in existence, and due to the high anthropogenic and climate impacts on their marine ecosystem (Jackson et al., 2001) it is facing a high risk of extinction. It is classified as an endangered species on the (IUCN, 2013) Red List, and also listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES, 2013), which means *C. caretta* and its habitat is in need of protection.

1.1.2. Distribution and habitat of Loggerheads

C. caretta has a global distribution range which encompasses three main habitats, notably the Atlantic, Pacific, and Indian ocean (Dodd, 1988), and the Mediterranean Sea. They spend most of their life in the ocean, travelling hundreds or even thousands of kilometres between nesting and foraging areas (Plotkin & Spotila, 2002). Nesting areas occur terrestrially, with turtles returning to their spawning beaches to oviposit eggs. The eggs then undergo embryonic development for a period of around two months before hatching and returning to the open ocean (Lutz et al., 2002). Foraging occurs in habitats located in neritic zone (coastal waters) or ocean zone (open ocean) (Lutz et al., 2002). Thus *C. caretta* alternates between the beach, neritic, and ocean zone through the course of its life.

1.1.3. Environment influence loggerheads' habitat

Due to global warming, sea level rise, and increased contamination of oceans and beaches, sea turtles' habitats have been severely degraded. In oceans, sea turtles' food sources and nutritional pathways are affected by increased temperature. A suite of species interactions and food webs are changed by overfishing and pollution (Lutz et al., 2002). For example, one research (Osborne et al., 2001) concluded that outbreaks of toxic cyanobacteria *Lyngbya majuscula* potentially affect sea grass, the main food source for juvenile turtles, quality and quantity. On sandy beaches, breeding habitats are also degraded. (Defeo et al., 2009) reviewed that alternations in natural processes, such as climate change, and human activities (e.g. recreation, pollution and exploitation) brought intensive pressures on the sandy beach area.

Habitat loss, undoubtedly, has a major negative impact on sea turtle population (Lutz et al., 2002). The coastal environment is vital for loggerheads maintaining their population, because all the turtles need suitable incubation conditions to be successfully born on beaches. For scientists, since very little is known about the sea turtles population in the open ocean zone, their population was normally estimated by counting their nests. The number of nests multiplied by the average number of eggs is thought to give a good representation of all the new-born turtles. Therefore, in order to protect their habitat, in turn, to maintain and increase the population, it is necessary to understand the environmental factors that act as cues and affect nests distribution.

1.1.4. Species distribution models

Tools for understanding the distribution of species, and the environmental factors limiting this, are so-called Species Distribution Models (SDMs) (Pearson, 2007). These models commonly associate environmental variables and species' occurrence records to identify environmental conditions within which populations can thrive. The spatial distribution of environments that are suitable for the species can then be estimated across a study region. Currently, they are widely applied in biogeography, conservation biology, ecology, invasive species studies, and wildlife management etc.

One of the most popular SDMs is Maximum Entropy (MaxEnt), which origins from statistical mechanics, maximum entropy (Jaynes, 1957). MaxEnt is a general-purpose machine learning method designed for predicting species distribution from incomplete (e.g. unavailable of absence) information (Phillips et al., 2006). It estimates the most uniform distribution of presence points compared to the corresponding environmental data (Phillips et al., 2006). The output of MaxEnt consists of estimates of the habitat suitability (probability of occurrence) as predicted by the species-environment relationships that are stored in so-called response curves. These describe in what manner each variable influences the distribution of a species. Using these beyond the temporal or spatial scale of the training dataset used to discover these relationships, allows us to predict habitat suitability in to the future or into other geographic areas. The reasons for this are further detailed in section 2.4.1.

1.1.5. Species-environment relationship

A species is able to exist and reproduce successfully only within a specific and often limited range of environmental conditions. Species-environment relationships describe how species interact along this range of conditions. For instance, sea turtle eggs are coupled to incubation environment (Carthy, 2003), e.g. water content of sand. Eggs need enough water to successfully hatch. If the incubation environment is too dry, eggs will not develop (Ackerman, 1997). However, if the water contend is too high, it will influence the gas and heat exchange, which will decreases the hatching success (Carthy, 2003). This range is, however, often not well defined or known.

A way that can help us to discover the species-environment relationship is the response curves built by machine learning techniques (e.g. MaxEnt), by which the effect of environmental variables on predicted habitat suitability can be explained. Obviously, the performance of prediction relates to that whether the response curves can discover the 'true' species-environment relationships (see section 2.5.1). Therefore, in order to better understand biological processes of how environmental conditions influence loggerheads' nest distribution, in turn, to accurately predict their suitable nesting habitat, it is necessary to examine the species-environment relationships discovered from response curves.

1.1.6. Abundance-occupancy relationship

Currently, SDMs are mainly developed utilizing categorical presence/absence or presence-only data. As a consequence, predictions of the habitat conditions are also only given in terms of occupancy (absence/presence). However it is not only species occurrence, but more importantly the population density which indicates species persistence in changing environments (Oliver et al., 2012). The species density data can provide insight, additional to that which can be derived from occupancy data only, when trying to understand the factors affecting the distribution of a species, e.g. (Anna et al., 2012; Brian et al., 2012).

The abundance-occupancy relationship relates to the species density and the extent of the occupancy (Alison et al., 2002). Positive relationships between abundance and occupancy have been documented by a number of studies. These include investigations of plants (Bertrand & Moshc, 1998), butterflies (Pollard et al., 1995; Van Swaay, 1995), fish (Rose & Leggett, 1991; Swain & Sinclair, 1994) and birds (Kevin et al., 1998; Telleria & Santos, 1999). Recently, after evaluating the strength of correlation between the population density and habitat suitability for ten birds and ten butterfly species, using four different modelling methods, Oliver et al. (2012) concluded that landscapes estimated as more suitable by SDMs, on average, also host denser populations,. Based on these findings, hence, the density of turtle nests was introduced in this study to assess the goodness-of-fit of the predicted habitat suitability (see section 2.6).

1.2. Problem statement

1.2.1. Species-environment relationship

Much research has been done over the last 15-20 years in understanding the ecological requirements of sea turtles for selecting nesting sites (Fish et al., 2005; Louhenapessy, 2010; Mazaris et al., 2009; Moin, 2007; N. Mrosovsky, 1983; Pike, 2008; Wood & Bjorndal, 2000), and most of them focus on local scale. Such understanding would facilitate the identification of suitable beach locations for conservation planning on a local scale. However, as the loggerhead sea turtle is globally distributed, the local scale research may not discover 'true' species-environment relationship. The main reason is that the variation of environmental parameters at small (local or regional) scale is generally far smaller than that at large (global) scale, in turn, small scale modelling may not cover the full range of environment conditions which loggerhead occupies. This may result in the suitable habitat being underestimated, as suitable habitat is limited by strict definitions for suitable environmental condition. By contrast, modelling nesting habitat distribution at large scale is more likely to discover 'true' species-environment relationships, because the whole range of environmental conditions which loggerheads occupy are taken into consideration, and further the predicted potential suitable nesting habitat might be more accurate. Moreover, data mining species-environment relationships have lagged behind, particularly those for near-shore ocean conditions, and their evaluation against existing ecological understanding of the species.

1.2.2. SDMs evaluation

The commonly used evaluation tool for assessing MaxEnt performance is the area under the curve (AUC) of the receiver-operating characteristic (ROC). It is widely used and currently considered as best practice for assessing the predictive accuracy of distributional models (Pearce & Ferrier, 2000). The ROC plot is obtained by plotting sensitivity as a function of the falsely predicted positive fraction, or commission error (1-specificity), for all possible thresholds of a probabilistic prediction of occurrence. The resulting area under the ROC curve provides a single measure of model performance, which is independent of a particular threshold. AUC values range from 0 to 1, with a value of 0.5 indicating model accuracy not better than random, and a value of 1.0 indicating a perfect model fit (Fielding & Bell, 1997).

However, when only presence data are available for modelling species distribution, the sensitivity of AUC for measuring SDMs accuracy is low. This is mainly because the pseudo-absence is used instead of true absence data, which makes the maximum achievable AUC less than 1 (Phillips et al., 2006). If the species' distribution covers a fraction α of the study area, then the maximum achievable AUC can be shown to be exactly $1 - \alpha/2$ (Phillips et al., 2006). As α typically is not known, it is impossible to know whether a given AUC is close to the optimal value.

Moreover, considering only AUC scores as an evaluation method for model performance, may not always be the appropriate approach, as AUC depends on the relationship between the observed and predicted value (predictive success) and not on the relationship between the observed and explanatory value (Mike Austin, 2007). The AUC is not indicative of the geographical and environmental consistency of a model (Aguirre-Gutierrez et al., 2013). Some research has been done, in which it has been proven that models with the same or very similar AUC values may predict very different patterns of distribution (Elith et al., 2006). Because a high AUC does not necessarily give an accurate distribution, it should be used in conjunction with other evaluation methods. In this study, the introduced method is assessing the strength of species abundance-occupancy relationship (see section 2.5).

1.3. Research objective

1.3.1. General objective

The overall objective of this study is to model loggerhead nesting habitat at the full range of environmental conditions (e.g. global), and verifying that the global scale SDM can 'better' predict loggerhead nesting habitat than a SDM at limited range of environmental conditions (e.g. the Mediterranean).

In this dissertation, the term 'global scale' and 'regional scale' were introduced to represent the full and limited range of environmental conditions, which loggerhead occupies, respectively. This does not necessarily mean that a regional scale study area cannot cover the full range of environmental conditions.

Two indicators were used to justify the 'better' performance. One is a qualitative examination of species-environment relationships, and the 'better' one should commensurate with expert knowledge of loggerhead survival and reproduction. The other is a quantitative test of abundance-occupancy, and the 'better' one should have a stronger relationship between nest densities and predicted nesting habitat suitability. This drives two specific objectives.

1.3.2. Specific objectives

The proposed specific objectives are:

1. Verifying if the environmental variable response curves reflect published species-environment relationships.

2. Testing the difference of the strength of the abundance (loggerhead nest density)-occupancy (the predicted loggerhead nesting habitat suitability) relationship for both global and regional SDMs.

1.4. Research questions

1. Are the species-environment relationships yielded from machine learning techniques commensurate with expert knowledge, e.g. one that follows critical thresholds in well-known turtle embryology, only if run on a global scale?

2. Does the nesting habitat suitability predicted by the global scale SDM have a stronger relationship with nest density than that predicted from the regional scale SDM?

1.5. Research hypothesis

The proposed hypothesis is related to the second research question that can be quantitatively tested.

H_0: The strength of relationship (SR) between the nest density and predicted suitability from global SDM is significantly (with 95% confidence) equal to or weaker than the relation between density and suitability from regional SDM;

$$SR_{(global)} \leq SR_{(regional)}$$

H_a: The strength of relationship (SR) between the nest density and predicted suitability from global SDM is significantly (with 95% confidence) stronger than the relation between density and suitability from regional SDM.

$$SR_{(global)} > SR_{(regional)}$$

2. METHOD

2.1. Method overview

This project can be summarised into 3 stages, data preparation, modelling and assessment.

Data preparation consisted of construction of global and regional environmental parameters along coast area and loggerhead nest density. The environmental variables were calculated by averaging the monthly value over 10 years (2001-2010), which were mainly derived from satellite imagery. After then masking the coastal zone to get the final input parameters for SDMs. The nest density were collected from a variety of sources and calculated by dividing the beach length by nest number.

The modelling phase included training and validating SDMs on both global and regional scale, and analysing the nest habitat suitability against each environmental variable response curve. Maximum Entropy model (MaxEnt) was chosen as the modelling tool in this study. The AUC was used to assess the predictive accuracy from SDMs, while the Jackknife approach was employed to evaluate variable importance.

The final stage was to assess SDMs performance. Two assessments were conducted in correspondence with specific objectives. First, the species-environment relationship built from SDMs was examined, through comparison with published critical values. Critical values are thresholds that determine loggerhead survival or reproduction efficiency and are derived from expert knowledge. Second, the strength of the relationship between nesting density and the predicted suitability for each SDM was assessed. A logarithm and angular transformation were employed to nest density and habitat suitability data respectively, to improve their normality. Pearson's Correlation coefficient (R) was used to measure the strength of relationship, and the Fisher r-to-z transformation was used to statistically test the significance of difference of R between global and regional SDMs.

Figure 1 shows an overview of the method as described above.

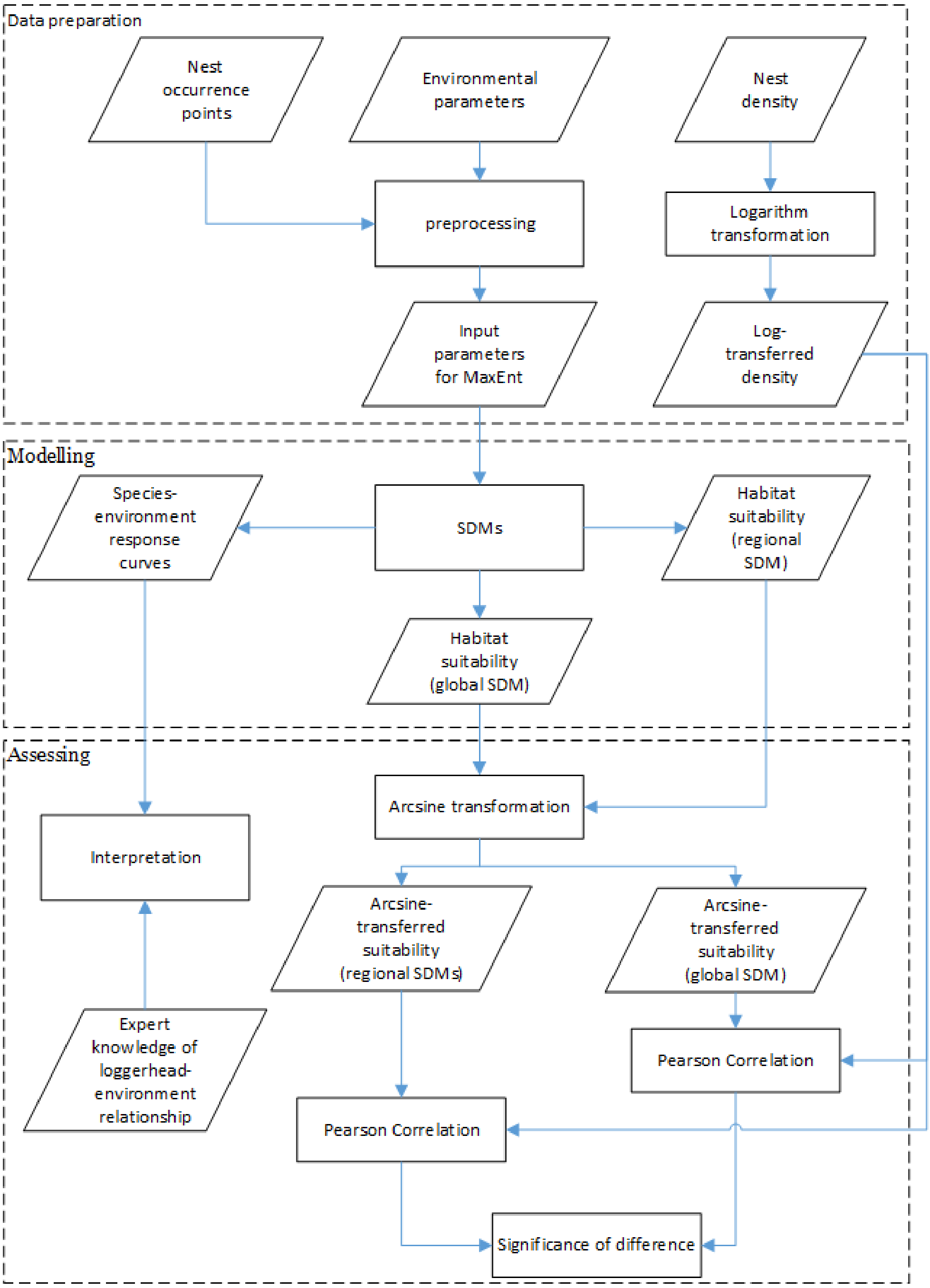

Figure 1 Summary of study approach

2.2. Study area

This study was carried out considering both a global and regional scale. Global scale was restricted by latitude (from -50 to 50 degree) both because this is the zone that loggerhead normally occupies, and some environmental data are only available in this range (e.g. precipitation). The Mediterranean Sea was selected as regional study area as it is one of the major loggerhead nesting habitats, with 3300 to 7000 nests made per season (Miller et al., 2003). Furthermore, the Mediterranean has reasonable data availability on nest density, including number of nests and beach length. Figure 2 displays the study area.

Figure 2. Study area.

Global scale and regional scale (the region highlighted by the rectangle). The dark area represents the zone that loggerhead normally occupies.

2.3. Data preparation

Data preparation was done on both loggerhead nest records and environmental data. Figure 3 shows the overview for data preparation. The nest records consisted of globally distributed nest occurrence points, and number of nests related to the occurrence points in the Mediterranean. For nest occurrence points, the point locations were checked and some of them where nesting happened by accident were eliminated. The nests number and the beach length were used to calculate the nest density of each point in the Mediterranean.

Seven steps were implemented to prepare the environmental data, which were variable determination, resolution determination, file format conversion and re-projection, monthly value calculation, extrapolation, coast area masking, and differentiating different nesting season on north and south hemisphere, and recombining environmental data.

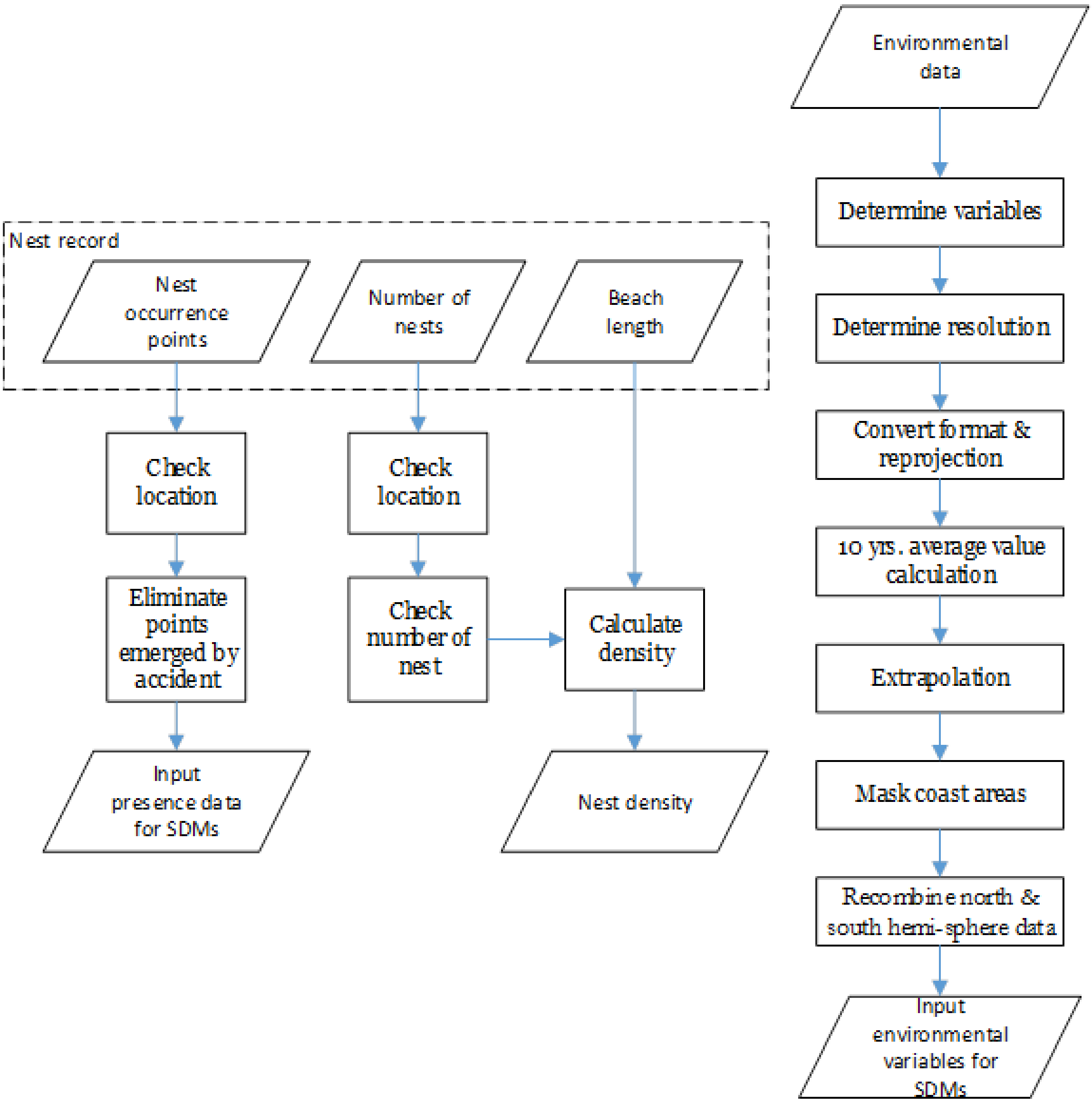

Figure 3. Flowchart of data preparation.

2.3.1. Nest records

2.3.1.1. Data sources and description

The nest records consist of the globally distributed nest occurrence points and the number of nests in the Mediterranean. The occurrence points were collected and provided by The State of the World's Sea Turtles (SWOT) which is a partnership among Oceanic Society, the IUCN Marine Turtle Specialist Group (MTSG), Duke University's OBIS-SEAMAP, and an ever-growing international team of local organizations, scientists and conservationists. There were more than 100 organisations all over the world, which cooperated with SWOT, which contributed to the data (Appendix 1).

The occurrence point records contain beach names where the nests are located, country in which said beaches occur, and the geographical coordinates (WGS 84). There were 740 loggerhead nest occurrence points, of where 174 records where duplicate from different data providers. After duplicates were eliminated, there were 566 occurrence records in total.

There were, in total, 50 records of nests number corresponding to 50 occurrence points in the Mediterranean. These were collected from SWOT, the International Union for conservation of Nature (IUCN) (Casale & Margaritoulis, 2010) and 'Seaturtle.org' etc. These numbers were counted in three different ways, nests, nesting females and crawl. Nests is a count of number of nests laid by loggerhead during the monitoring period; nesting females is a count of observed nesting female loggerheads during monitoring period at a given site; and crawl is a count of female loggerheads' emergence onto the beach to nest (SWOT, 2007). The number of nests of different beaches was collected on either same or different years, which cover a long period from 1973 to 2012, but most of them were collected between 2001 and 2010. This information can be found in Appendix 2.

The beach length in the Mediterranean collected from the 'state of the world's sea turtles report, volume 2' (SWOT, 2007), IUCN (Casale & Margaritoulis, 2010), some local website or measured on Google Earth.

2.3.1.2. Pre-processing

The location of nest occurrence points were checked to make sure that they were on a reasonable location. For instance, two nest points in Mozambique were located around 18km from coastline (Figure 4 a). Another example was in the island, Zakynthos, Greece, an island well known for its densely nested beaches. According to the literature the occurrence point should located in the Laganas Bay, south part of the island (close to Vasilikos), not along its northeast coast (Figure 4 b).

Figure 4 Incorrect nest occurrence location.
a. In Mozambique. b. In Greece

Some points were also adjusted, 18 occurrence points in total, to correspond to their location mainly based on literature. If there were no previous studies indicating where the locations should be, they were just moved to the coastline perpendicularly.

The next step was to eliminate the occurrence point that emerged on occasion or by accident. There were 59 out of the 566 beaches that reported only one nest, that were mostly found by chance or no nest was found officially but only reported from tourists or local people (e.g. Palombaggia beach, Corsica, France; Riace Marina beach, Calabria, Italy; and Palomares beach, Vera, Almeria, Spain etc.). In this study, therefore, beaches of which the number of nests that are equal or less than one were considered to be only marginally suitable. In order to reduce the uncertainty, thus, these beaches were excluded, and only 507 occurrence points remained for fitting the SDM.

The nest number data was integrated from different sources so that the average density spanning the years from 2001 to 2010 could be calculated when possible. This was done to improve consistency between nest density data and environmental data (introduced in section 2.3.2). Lastly, the nest density was calculated using nest number divided by beach length.

2.3.1.3. Statistical analysis

The distribution of nest density of 50 points was positively skewed as the population has a long right tail (Figure 5 a). This positive skewed distribution is very common in biological data because the variables often have a lognormal (measurement variables) or Poisson (count) distribution (Quinn & Keough, 2002).

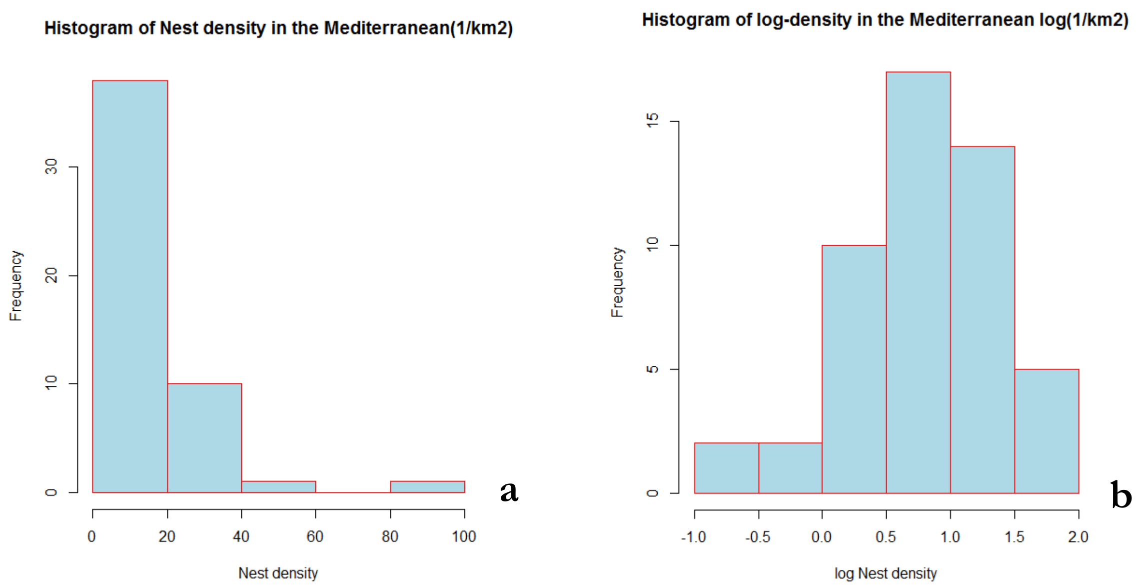

Figure 5 Histogram of nest density in the Mediterranean.
a. original distribution. b. log-transferred distribution

In order to apply a parametric correlation test (Pearson correlation coefficient) to test SDMs performance, the logarithmic transformation was used to improve the normality of data (Figure 5 b). The Shapiro-Wilk test was conducted to statistically test the normality of log-transferred nest density, from which I got the p-value equal to 0.1259 (>0.05). For a given alpha level of 0.05, the log-transferred nest density was normally distributed.

2.3.2. Environment data

2.3.2.1. Data sources and description

The environment data were mainly collected from the National Aeronautics and Space Administration (NASA). The details can be found in Table 1.

Variable	Instrument	Sensor	Spatial resolution	Temporal resolution	Coordinate system	File format	Unit	Source
LST	MODIS	Terra	0.05 degree	Monthly	GCS WGS 84	HDF	Kelvin (K)	NASA The Earth Observing System Data and Information System (EOSDIS)
PCP	TRMM Precipitation Radar, TRMM Microwave Imager, TRMM Visible Infrared Scanner	NA	0.25 degree	Monthly	GCS WGS 84	HDF	mm	The Tropical Rainfall Measuring Mission (TRMM)
SST	MODIS	Terra	4 km	Monthly	Equidistant Cylindrical	HDF	degrees Celsius (°C)	NASA OceanColor
CHL	MODIS	Terra	4 km	Monthly	Equidistant Cylindrical	HDF	$mg\ m^{-3}$	NASA OceanColor
PAR	MODIS	Terra	4 km	Monthly	Equidistant Cylindrical	HDF	Einsteins $m^{-2}\ day^{-1}$	NASA OceanColor
Bathymetry	sonar devices	NA	0.1 degree	NA	GCS WGS 84	TIFF	m	NASA Earth Observations (NEO)

Table 1 Environment data source

2.3.2.2. Pre-processing

1. Variable selection

The parameters that will be used in this study were selected based on the fact that they were biologically meaningful to Loggerheads' existence. Generally, each species has a unique ecological niche. The organism uses adaptive behaviours and traits in order to increase their overall reproductive and survival success. Since the species population can be predicted from reproduction and survival (Péter et al., 2010), I chose the environmental parameters which are biologically meaningful to successful loggerheads' reproduction and survival.

For reproduction Land Surface Temperature (LST) and Precipitation (PCP) were chosen. Variation in temperature and moisture in terrestrial environments strongly affect the viability of incubating eggs (Lutz et al., 1997; Miller et al., 2003). Sand temperature is a significant cue of sea turtle reproduction and survival. It has been shown by many studies that temperature affects hatching success (Saba et al., 2012), hatchling condition (Booth et al., 2004), hatchling sex ratio (N. Mrosovsky et al., 2002), incubation duration(Mrosovsky, 1980), hatchling emergence success (Pilar Santidrián et al., 2009), and oxygen consumption (Reid et al., 2009). Specifically, for instance, N. Mrosovsky et al. (2002) found that female loggerhead turtles in the Mediterranean were produced when incubation temperatures are greater than 29.3°C; and Drake & Spotila (2002) discovered that for leatherback turtle (Dermochelys coriacea) and Olive ridley turtle (Lepidochelys olivacea), the upper thermal limits of hatchling emergence are 36 and 37.5°C, respectively. Hatching success, and hatchling size are also significantly affected by moisture conditions in the nest incubation period (McGehee, 1990). In buried eggs, the embryo can obtain water through exchange with the environment (Ackerman, 1997). McGehee (1990) concluded that proper moisture conditions are necessary for maximum hatching success and, therefore, are important in the maintenance of a turtle egg hatchery. In his study the optimal level of moisture is 25% for maximum percent hatch and hatchling size.

As hatchlings will crawl into the sea immediately after incubation and adult female turtles occupy this area during the inter-nesting interval, suitable water temperature and sufficient food in near shore waters likely boost reproductive success. Therefore, the oceanic parameters that indicate the thermal property and the living organisms in oceans could be important for young turtles' survival. I thus chose Sea Surface Temperature (SST), Chlorophyll α concentration (CHLα) and Photosynthetically Available Radiation (PAR) as input oceanic parameters for the SDM.

Several field studies (Hays et al., 2002; Mrosovsky et al., 1980; Sato et al., 1998) have examined the effect of seawater temperature upon nesting intervals. Loggerheads usually stay in waters with SST of 13.3-28°C during the non-nesting season, but females seek out water of 27-28°C during the inter-nesting period (Hays et al., 2002). In addition, the loggerhead becomes lethargic when SST is about 13-15°C and adopts a floating posture, apparently cold stunned, in water of about 10°C (N. Mrosovsky & Yntema, 1980).

Apart from SST, undoubtedly, for feeding purpose adequate nourishment is essential for hatchlings. Juveniles normally occupy the mats of Sargrassum (one genus of phytoplankton) as foraging habitat, in which they feed on more than 100 different species of animals, such as barnacles, small crab larvae, fish eggs, and hydrozoan colonies (Spotila, 2004). As these organisms are highly reliant on the phytoplankton, measuring the phytoplankton abundance can be used to estimate the abundance of available nourishment for the Loggerhead young.

Therefore, CHLα was chosen as an input parameter, which is common to all photosynthetic organisms and is an indicator of algal abundance. Its concentration is used extensively for estimating phytoplankton biomass (Felip, 2000). In addition, PAR, the solar energy available for photosynthesis, was also chosen because it controls the growth of phytoplankton and, therefore, the development of crustaceans, fish, and other consumers. Hence it is another indicator of phytoplankton abundance.

Furthermore, offshore bathymetry was involved as it has been hypothesized as potential factors used by females to locate good beach emergence sites (Hays et al., 2001; Wood & Bjorndal, 2000), though it may not be an appropriate indicator of a successful nest location (Cuskelly, 2012).

All parameters, except for the bathymetry, are at a monthly temporal resolution in order to differentiate the start-, peak- and end-time of nesting season. For instance, in the Mediterranean Sea, the nesting season of loggerheads starts in May, peaks in July and ends in September. The LST and SST were separated into parts, day and night. This is because female adult turtles always emerge on beaches at night. Separating day and night LST and SST might contribute to a better result.

2. Determining resolution

Different grain size (spatial resolution) might influence the prediction. Seo et al. (2009) found species' SDM-derived spatial distributions were not equivalent across grid sizes. However, this was not always the case. A study from Antoine et al. (2007) concluded that change in grain size did not have a substantial effect on species distribution models and also did not equally affect model performance across regions, techniques, and species.

In this study, since the strength of relationship between habitat suitability and nest density would be applied to assess the SDMs' performance, it was assumed that higher spatial resolution data would give a better relationship of these two variables. The environment data normally consisted of discrete pixel values, while in reality, the environmental factors, such as temperature and rainfall, commonly has continuous values. Low-resolution imagery always averages the value of environment data within a pixel, which may lead to a result where the habitat suitability does not fit the nest density. For instance, in Figure 6, one pixel (with red border) of the coarse spatial resolution imagery had a very high nest density (350/km^2), which did not fit the low suitability (0.7). Nonetheless, if fine spatial resolution was implied, this pixel could split into four parts, of which each one had a sensible relationship between habitat suitability and nest density. Therefore, the high-resolution environmental data was employed to reduce this effect. In this study I used the 4×4km resolution of SST, CHL and PAR; 0.05×0.05 degree resolution of LST; 0.1×0.1 degree resolution of bathymetry; and 0.25×0.25 degree of PCP. All the chosen resolution were the highest resolution of correspondent variables' monthly data.

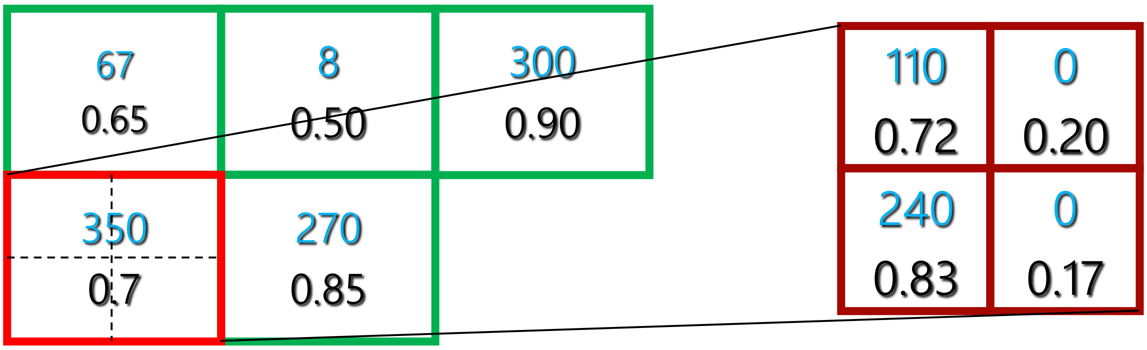

Figure 6. Nest density against habitat suitability with different spatial resolution

The red rectangle shows a high density (350) correlates with a medium suitability (0.7) in a coarse resolution data. The brown grid shows the possibility that if using high resolution data the density may fit suitability better

The temporal resolution of this study was monthly. Monthly data can be used to distinguish the different phases of nesting season (nesting start, peak and end month). It is much more biologically meaningful than just using the annually averaged data, because the averaged data cannot reveal the difference of environment between the nesting and non-nesting season. Although higher temporal resolution data such as weekly or daily, can split the nesting season into much more detailed phases, it is not likely to provide more insight in the general biological process.

The time span of environment data covered from 2001 to 2010, which was the time period where most nest occurrence points and nest number data were collected.

3. Convert file format and re-projection

Most of the environmental data were stored in a Hierarchical Data Format (HDF), which could not be directly read by most of SDMs and is difficult to process in most GIS and RS software. Thus they need to be converted in to a much common file format. In this study, I used ASCII file as it can be recognized by MaxEnt (the SDM which is used in this study, reviewed in section 2.4.1).

There were two different coordinate systems (see Table 1), GCS WGS 84 and Equidistant Cylindrical. To convert all the parameters to the same coordinate system, the Equidistant Cylindrical coordinate was re-projected into GCS WGS 84. This was done by executing codes in MatLab.

4. Average data over ten years

The purpose for averaging monthly value over ten years was to make the environmental variables for the SDMs relatively consistent to the nest number data. The nest numbers were mainly collected throughout 2001 to 2010, and the nest number of each beach was calculated by averaging the value from different years. Therefore, averaging environmental data over ten years was sensible.

All the environmental variables were averaged, except for bathymetry, as it was a constant variable. However, only averaged data on February, May, July, September, October and December were kept. This was because in the Northern hemisphere the loggerhead nesting season normally starts in May, peaks in July and ends in September, while it starts in October, peaks in December and ends in February on the Southern hemisphere. This step also done by coding in MatLab, as most of software cannot compute the missing values in raw data when averaging, which might generate abnormal values.

5. Extrapolation

The fifth step was to extrapolate the value of variables to non-value area. Due to nesting points occurring along coastal lines where usually the edge of the environmental data is, sometimes, thus, it resulted in some occurrence points not being overlaid by the environmental variables. For instance, in Figure 7, two nest points were located on the Southwest Florida coast. One point was only covered by terrestrial variables (coloured), whereas the other was only covered by the oceanic variables (grey). Therefore, the data extrapolation was applied to make sure that all the occurrence points could be overlaid by all the environmental variables. This was done using the ITC Integrated Data Viewer.

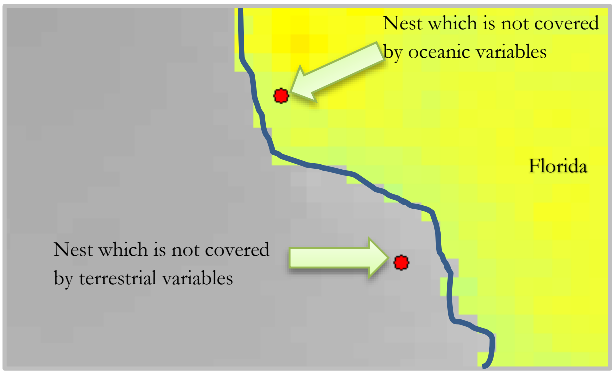

Figure 7. Nests that were not covered by all the environment data

6. Resampling and mask coast area

After extrapolation, all the environmental variables were resampled into 4×4km resolution in order to fulfil the need of SDMs. In SDMs all the input variables should have the same spatial resolution.

Masking coastal area was done to eliminate the irrelevant terrestrial area out of the model in order to minimize the influence of terrestrial environments on model performance. Considering sea turtles only nest along the coastline, the modelling area was restricted in an 8 km buffer zone along the coastline (4km each directed to the ocean and land). The global and the Mediterranean coast area were masked respectively. This step was done using ArcGIS.

7. Recombine northern and southern hemisphere data

As mentioned in this section, the loggerhead nesting season is different in the north and south hemisphere. To make sure that the variables correctly represented the environmental conditions of different phases of the nesting season, the environmental data were clipped at the equator and re-combined based one the nesting phases. The data of nesting start month on the northern hemisphere, May, was combined with the data of October on southern hemisphere; and for nesting peak and end month, data from July was combined with that from December and data of September was combined with that of February.

2.3.2.3. Statistical analysis

The mean LST at day time of nesting site on start, peak and end months of nesting season were 27.72°C, 28.69°C and 28.09°C, while they were 21.55°C, 23.72°C and 23.63°C at night. The minimum LST during the nesting season was 13.74°C at night on the start month, whereas the maximum was 44.53 at day time on the peak month (Figure 8 a).

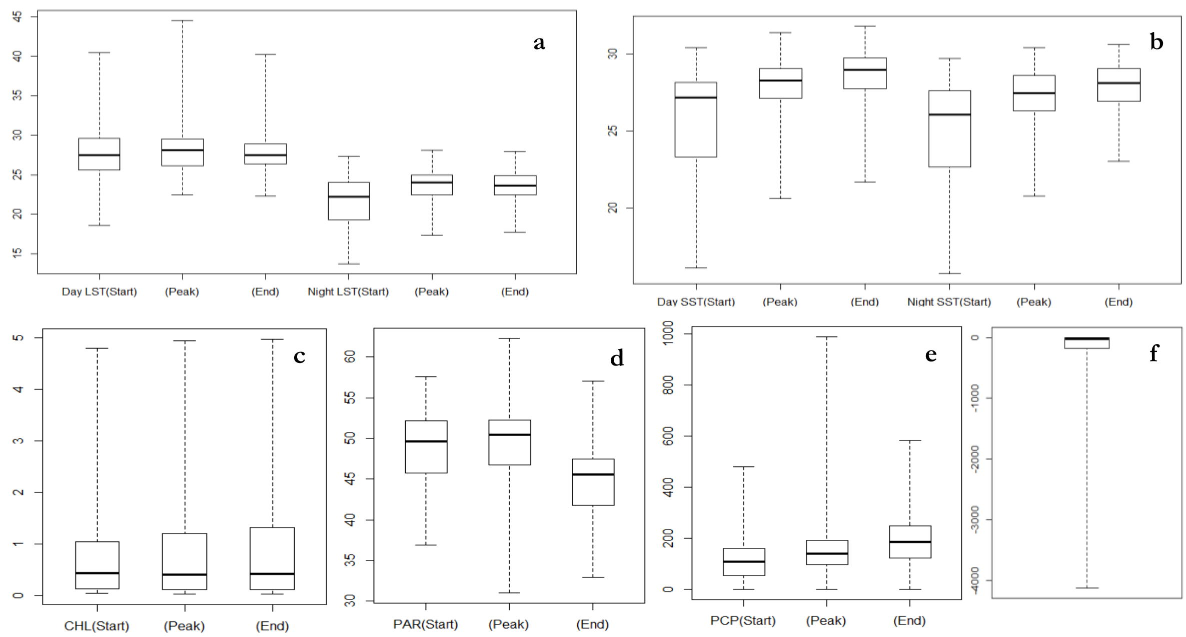

Figure 8. Boxplot of environment factors

The mean SST showed an increasing trend over the nesting season which were 25.66°C, 28.07°C and 28.65°C at day and 24.83°C, 27.30°C and 27.89°C at night. The minimum and maximum SST were 15.76°C on start month and 31.80°C on end month respectively (Figure 8 b). After removing the noise of the data (wrong value from extrapolation step), CHL like SST, which also showed an increase trend through the nesting season, and the mean value were 0.827mg/m^3, 0.849 mg/m^3 and 0.950 mg/m^3 (Figure 8 c). Average PAR were 48.90Einsteins/m^2/day, 50.15Einsteins/m^2/day and 44.64Einsteins/m^2/day (Figure 8 d). The mean PCP showed an apparent rising trend from 115.2mm at start month to 182.6mm at end month (Figure 8 e).

The collinearity analysis between each environmental variable was also done. As expected, both LST and SST in different phases of nesting season are correlated with each other ($|r| > 0.5$). However, in this study, one goal is to exam the environment-species relationship of all the selected biologically meaningful environmental variables in different phases over nesting season, and also because collinearity does not affect MaxEnt performance (Tobias et al., 2010), and there is less need to remove correlated variables (Jane et al., 2011), I kept all the variables for modelling.

2.4. Modelling Loggerheads' nests distrubution

2.4.1. SDM tool selection

Many ecological models that predict the spatial distribution of species have been developed. Generalised linear models (GLMs) and generalised additive models (GAMs) are used extensively in species' distribution modelling because of their strong statistical foundation and ability to realistically model ecological relationships (M. Austin, 2002), but both of them use presence and absence data. Since only presence data is available for loggerhead nesting site, a model that does not need real absence data would be more appropriate.

There are several modelling methods that are dealing with presence-only data, such as BIOCLIM, DOMAIN and LIVES. However, a study, did by Elith et al. (2006), which compared 16 modelling methods for 226 species from 6 regions of the world concluded that these three methods which use only presence data with no inferred absences performed relatively poorly. Therefore, in this study, maximum entropy models (MaxEnt), which uses presence and some form of absence data (e.g. a background sample), is selected as it performed relatively well according to each of the evaluation measures (AUC, COR and KAPPA) (Elith et al., 2006).

2.4.2. Modelling loggerhead sea turtle nesting habitat

There were, in total, 507 loggerheads occurrence points used as input species presence data for running MaxEnt in global scale. 55 out of 507 points within the Mediterranean zone were used for the regional model. 10 times replication runs were implemented, and for each run, MaxEnt randomly selected 30% of presence points to use for cross validation. In addition, 22 environmental variables were used during this run of MaxEnt.

The AUC was used to evaluate MaxEnt training and testing accuracy. Although AUC cannot be simply used to assess SDMs performance (see section 1.2.2), it is usually taken to be an important index because it provides a single measure of overall accuracy that is not dependent upon a particular threshold (DeLeo, 1993). Specifically, an ROC plot is obtained by plotting all sensitivity values (true positive fraction) on the y-axis against their equivalent (1 specificity) values (false positive fraction) for all available thresholds on the x-axis. Sensitivity in combination with specificity takes into account all four elements of the confusion matrix (true and false presences and absences). The ROC curve thus describes the relationship between the proportion of observed presences correctly predicted (sensitivity) and the proportion of observed absences incorrectly predicted (1 – specificity). The AUC is an indicator for summarizing predictive accuracy across the full range of thresholds. In this project, as true-absence data were not available, the AUC tests whether the model classifies presence more accurately than a random prediction.

The Jackknife test was employed to estimate variable importance. It shows you which variables have the most useful information independent of the others. The Jackknife estimation of a parameter is an iterative process. First withhold one predictor (environmental parameter) and refit model, and then withhold all predictors but one and refit the model.

2.5. Assessing SDMs performace

2.5.1. Examining species-environment relationship

In this study, the species-environment relationship derived from MaxEnt is described by 'response curves'. These curves show how each environmental variable affects the MaxEnt prediction of species habitat suitability (or occurrence probability). There are two types of curve. One is the marginal curve which shows how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. However, in this study, some of environmental variables were correlated, which means the marginal response curves can be misleading as we cannot easily hold one variable fixed while varying its correlated variable. Therefore, I chose the other type of response curve that is made by generating a model using only the corresponding variable, disregarding all other variables. This curve reflects the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.

These response curves were examined in two ways. First, the theoretical shape of response curves. Ecological niche theory suggests and most theoretical models assume that response curves are either sigmoid or Gaussian (M. P. Austin, 1999). Thus, the probability of observed species should approximate a sigmoid or Gaussian distribution over different environmental gradients. Second, check the expert knowledge about critical value of environment variables. The critical value is expected to fit the response curve. For instance, the peak of the curve is expected falling in the most suitable critical value interval.

SST and LST, but not all the environmental variables, were examined because the critical value data of loggerhead sea turtle survival and reproduction from expert knowledge can only be found about these two factors. In addition, climatic variables, and especially temperature, are among the most important factors that drive species' distribution (Antoine & Niklaus, 2000; Grinnell, 1917), especially in large extents, as they have a direct influence on the behaviour and physiology of organisms.

2.5.2. Testing the strength of abundance-occupancy relationship

The correlation between the observation (nest density) and the prediction (habitat suitability), is known as the point biserial correlation, and can be calculated as a Pearson correlation coefficient (Zheng & Agresti, 2000). It takes into account how far the prediction varies from the observation. Based on this finding, the method for quantitatively test the strength of relationship between nest density and the habitat suitability was introduced, where density refers to loggerhead nest abundance and suitability refers to occupancy.

Before doing the correlation analysis, the arcsine transformation was conducted on the habitat suitability values (independent variable) for both the global and regional SDMs in order to improve data normality. Arcsine transformations have been used for many years (reference) to transform proportions (e.g. the suitability) to make them have a better normality for statistical analysis. However, a problem with such transformations is that the arcsines do not bear any obvious relationship to the original proportions. Therefore, in order to apply arcsine transformation, the transformed values have to be numerically close to the original percentage values over most of the percentage range while retaining all of the desirable statistical properties of the arcsine transform. Here I assumed that if the difference between original and transferred value is less than 10% (0.1), the transferred value can be considered close to the original value.

Descriptive statistics and the pairwise t-test was used to exam the difference of mean between original and transferred samples. The 3rd quartiles of original samples should be less than or equal to 0.755, which means 75% of them will have a less than 10% difference after transformation (arcsine $(0.755) - 0.755 \leq 0.1$). In addition, the original and transferred values should have no significant difference or the absolute value of the mean of the differences should be less than 0.1 within a 95% confidence interval. If these two conditions are met, the arcsine transformation can be appropriate.

The appropriate method for examining the strength of relationship depends on whether both variables are normally distributed. In this study, as both transformed density and suitability data were normally distributed (see section 2.3.1.3, 3.1.5 and 3.2.5), the Pearson's correlation coefficient was used to exam this relation. After that the Fisher r-to-z transformation was employed to calculate the value of z that can be applied to assess the significance of the difference between two correlation coefficients (R. A. Fisher, 1921). The Fisher r-to-z transformation has three steps:

First, transform each of the two correlation coefficients in this fashion:

$$\mathrm{r}' = (0.5)\ln\left[\frac{1+r}{1-r}\right]$$

Second, compute the test statistic this way:

$$\mathrm{z} = \frac{\mathrm{r1}' - \mathrm{r2}'}{\sqrt{\frac{1}{n1-3}+\frac{1}{n2-3}}}$$

Third, obtain p for the computed z.

By convention, the p values less than 0.025 are considered that one the occupancy-abundance relationship represented by correlation coefficient is significant stronger than the other if a 1-tailed test is performed.

In addition, as the evaluation method was based on the assumption that abundance (density) can be explained by occupancy (habitat suitability) with a linear model, it is necessary to test the linearity of these two variables in this case. Only if the abundance-occupancy relationships can be explained by a linear model, the introduced model performance assessment method can be valid.

To apply a linear model, the residuals from the model are assumed to be normally distributed, and the response variable (here is density) and the residuals are assumed to be independent. Therefore, the Shapiro-Wilk test was conducted to test the normality of residual, followed with testing Pearson's correlation coefficient to see whether the response variable and the residuals are independent.

3. RESULT AND DISCUSSION

3.1. SDMs accuracy and Predictor Variables Importance

3.1.1. Global scale

The average training and test AUC for the 10 replicate runs was 0.942 and 0.908 (Table 2). For any given threshold, the predicted geographic distribution of loggerhead nesting location was significantly better than the random models (1-sided p-values were all less than 0.025) (Table 2).

Duplicatin run	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Average**
Training AUC	0.940	0.944	0.942	0.941	0.942	0.941	0.941	0.942	0.942	0.943	0.942
Test AUC	0.927	0.880	0.896	0.934	0.896	0.908	0.911	0.914	0.917	0.897	0.908
Threshold	**p value**										
Fixed cumulative value 1	3.092E-13	1.571E-12	1.807E-12	1.723E-12	9.19E-13	9.643E-13	8.615E-11	3.566E-13	2.881E-13	2.351E-12	0
Fixed cumulative value 5	2.988E-24	1.078E-21	6.802E-23	4.933E-23	1.731E-20	6.634E-21	7.978E-22	1.547E-21	5.996E-24	9.921E-23	0
Fixed cumulative value 10	1.422E-28	1.341E-28	2.413E-26	2.949E-30	6.037E-27	1.421E-24	6.153E-32	3.076E-28	2.218E-26	7.07E-30	0
Minimum training presence	3.696E-10	5.696E-09	1.693E-09	8.643E-09	1.069E-12	9.872E-07	1.099E-08	9.033E-10	2.63E-08	1.049E-08	0
10 percentile training presence	6.3E-46	5.792E-28	6.161E-38	1.781E-44	1.109E-38	5.282E-35	7.981E-39	2.076E-39	2.195E-35	6.017E-40	0
Equal training sensitivity and specificity	9.8E-48	2.141E-27	8.317E-34	7.094E-56	5.597E-41	1.947E-33	8.505E-45	6.155E-41	3.785E-41	9.792E-28	0
Maximum training sensitivity plus specificity	2.909E-48	9.048E-30	4.549E-36	7.175E-50	2.966E-35	1.37E-33	3.826E-40	1.752E-40	3.228E-32	2.585E-42	0
Equal test sensitivity and specificity	1.241E-46	2.809E-29	1.394E-30	6.027E-56	7.487E-37	9.472E-31	5.896E-43	8.447E-38	6.159E-28	1.403E-35	0
Maximum test sensitivity plus specificity	7.209E-49	9.146E-32	2.509E-32	7.098E-59	4.778E-39	1.134E-32	2.235E-36	4.826E-40	4.369E-25	2.326E-33	0
Balance training omission, predicted area and threshold value	5.047E-18	1.726E-16	1.145E-15	2.394E-19	8.015E-20	5.214E-18	1.019E-17	2.411E-16	5.7E-20	1.93E-17	0
Equate entropy of thresholded and original distributions	6.08E-29	1.291E-27	7.74E-27	1.716E-29	5.783E-26	1.37E-25	4.491E-30	2.946E-27	1.92E-25	2.797E-29	0

Table 2 Training and test AUC and p-value of different threshold (global)

Three models were created with the Jackknife approach, a model using each variable in isolation (Figure 9 blue bar), a model with each variable excluded (Figure 9 light blue bar), and a model using all variables (Figure 9 red bar).

From Figure 9 we can see that when MaxEnt uses only dsst_start (day SST of start month of nesting season) it achieves the most gain, therefore it allows a reasonably good fit to the training data. By contrast, bathymetry contributed almost no gain, so it is not (by itself) useful for estimating the distribution of loggerheads' nest. Turning to the lighter blue bars, omitting each variable did not considerably decrease the training gain, which means that no variable contains a substantial amount of useful information that is not already contained in the other variables.

Both training and test Jackknife plots, showed that the day SST of start month of nesting season (dsst_start) is the most effective single variable, followed by the day SST of peak month of nesting season (dsst_peak). In addition, in the training gain and test gain plots, the PAR of and the PCP of the start month of nesting season (par_start and pcp_start) are markedly shorter than the red bar, showing that predictive performance becomes worse when the corresponding variables were not used.

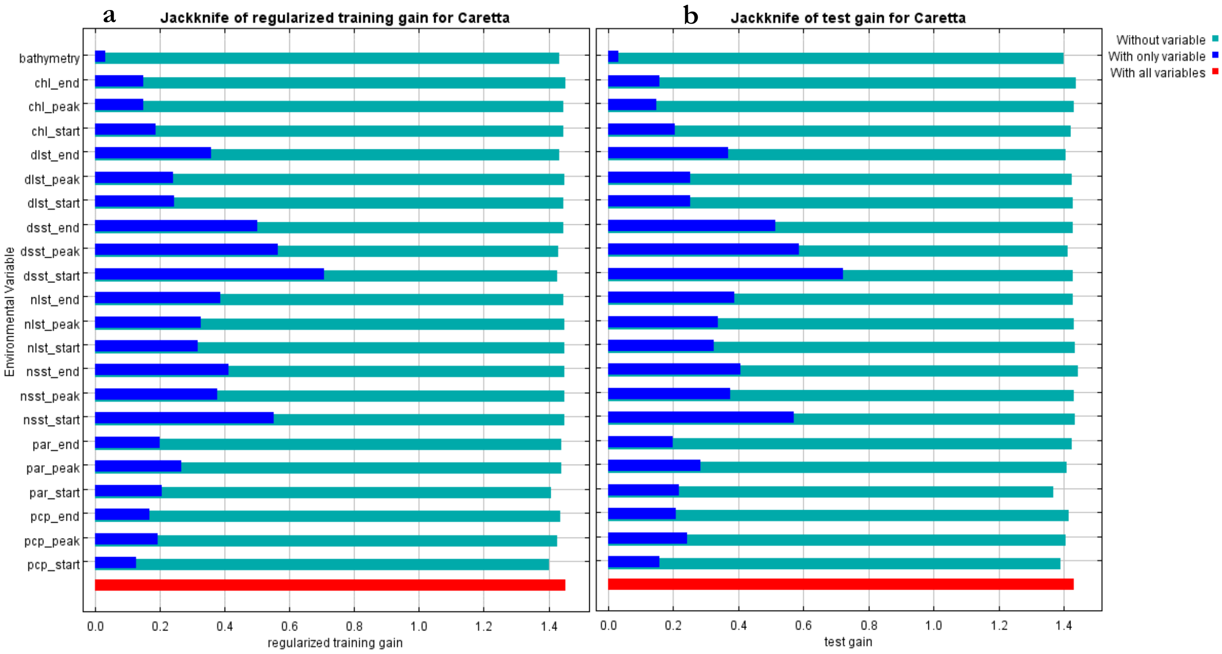

Figure 9. Jackknife of regularized gain (global)

a. training gain, b. test gain

3.1.2. Regional scale

The average mean training and test AUC were 0.938 and 0.864 (Table 3). However, only two p-values of averaged 10 duplication runs were less than 0.025 (Table 3). For all other thresholds, the test points were

Duplicatin run	1	2	3	4	5	6	7	8	9	10	Average
Training AUC	0.938	0.932	0.929	0.941	0.943	0.937	0.945	0.932	0.941	0.938	0.938
Test AUC	0.875	0.948	0.910	0.827	0.845	0.858	0.833	0.906	0.846	0.791	0.864
Threshold	**p value**										
Fixed cumulative value 1	0.058	0.062	0.068	0.048	0.057	0.102	0.095	0.107	0.103	0.084	0.078
Fixed cumulative value 5	0.007	0.008	0.009	0.005	0.006	0.020	0.131	0.021	0.148	0.126	0.048
Fixed cumulative value 10	0.020	0.002	0.002	0.017	0.001	0.006	0.055	0.006	0.063	0.055	0.023
Minimum training presence	0.003	0.003	0.003	0.004	0.002	0.012	0.093	0.007	0.105	0.113	0.035
10 percentile training presence	0.028	0.000	0.041	0.034	0.506	0.015	0.113	0.002	0.016	0.106	0.086
Equal training sensitivity and specificity	0.017	0.000	0.035	0.121	0.487	0.013	0.098	0.011	0.009	0.092	0.088
Maximum training sensitivity plus specificity	0.031	0.000	0.006	0.035	0.506	0.015	0.124	0.007	0.031	0.106	0.086
Equal test sensitivity and specificity	0.007	0.001	0.007	0.012	0.007	0.051	0.051	0.024	0.051	0.051	0.026
Maximum test sensitivity plus specificity	0.002	0.000	0.000	0.002	0.001	0.005	0.019	0.001	0.001	0.038	0.007
Balance training omission, predicted area and threshold	0.005	0.006	0.007	0.005	0.004	0.017	0.112	0.015	0.126	0.119	0.042
Equate entropy of thresholded and original distributions	0.019	0.002	0.002	0.014	0.001	0.060	0.053	0.005	0.058	0.054	0.027

Table 3 Training and test AUC and p-value of different threshold (regional)

predicted no better than by a random prediction with the same fractional predicted area (with 95% confidence).
Using only dsst_end (day SST of end month of nesting season) or par_start (PAR of the start month of nesting season) MaxEnt achieves the most gain (see Figure 10 a). By contrast, bathymetry and chlorophyll α concentration contributed almost no gain, so they are not, by themselves, useful for estimating the distribution of loggerheads' nest. Similar to the global model, no variable contains a substantial amount of useful information that is not already contained in the other variables because omitting each variable did not decrease the training gain considerably.

The day SST of end month of nesting season (dsst_end), the PAR of the start month of nesting season and the night SST of end month of nesting season (nsst_end) are the most effective single variable. Moreover, in the training gain and test gain plots (Figure 10 b), when omitting the PCP of the end month of nesting season (pcp_end), the light blue bar is apparently shorter than the red bar, which indicates that predictive performance becomes worse when the corresponding variables are not used. However, some of the light blue bars (especially for the CHL at the end month of the nesting season variable) are longer than the red bar, showing that predictive performance improves when the corresponding variables are not used.

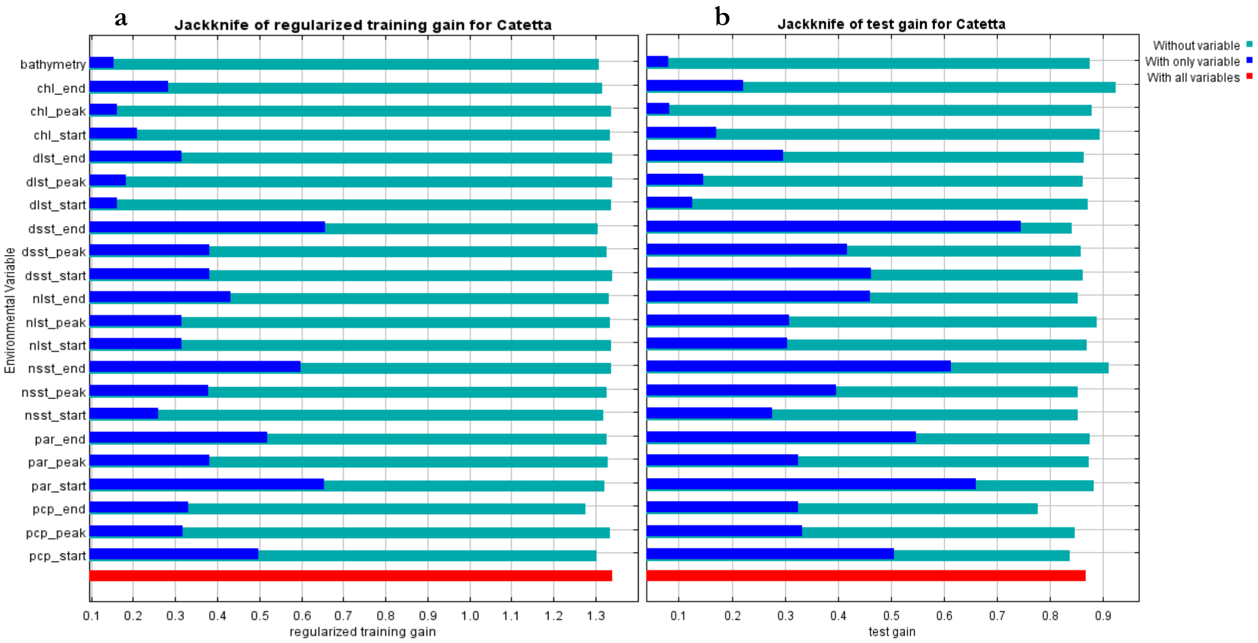

Figure 10. Jackknife of regularized gain (regional)

a. training gain; b. test gain

The degree of contribution of environmental variables from global and regional SDMs was dissimilar. Sea surface temperature, however, in general, plays an important role in both models. For example, the most contributed variable from two SDMs was day SST at start phase of nesting season and day SST at the end phase respectively.

3.2. SDMs performace

3.2.1. Species-environment relationship

3.2.1.1. Comparing with expert knowledge

Known from literature, the loggerheads occupy waters with surface temperatures ranging from 13.3-28.0°C (A) during non-nesting season (Polovina et al., 2004), whereas the range for having them survive is much larger, around 4.9-32.2°C (B) (Coles & Musick, 2000). Temperatures from 27-28°C (C) are most suitable for nesting females (Hays et al., 2002). At temperatures between 13 and 15°C (D) lethargy is induced on the loggerhead, and if temperature drop to around 10°C (E) the loggerhead takes on a floating, cold-stunned posture (Mrosovsky, 1980). For incubation, the land temperatures generally range from 26-32°C (Yntema & Mrosovsky, 1982), and eggs incubated at constant temperatures lower than 24°C or greater than 33°C seldom hatch (N. Mrosovsky & Yntema, 1980).

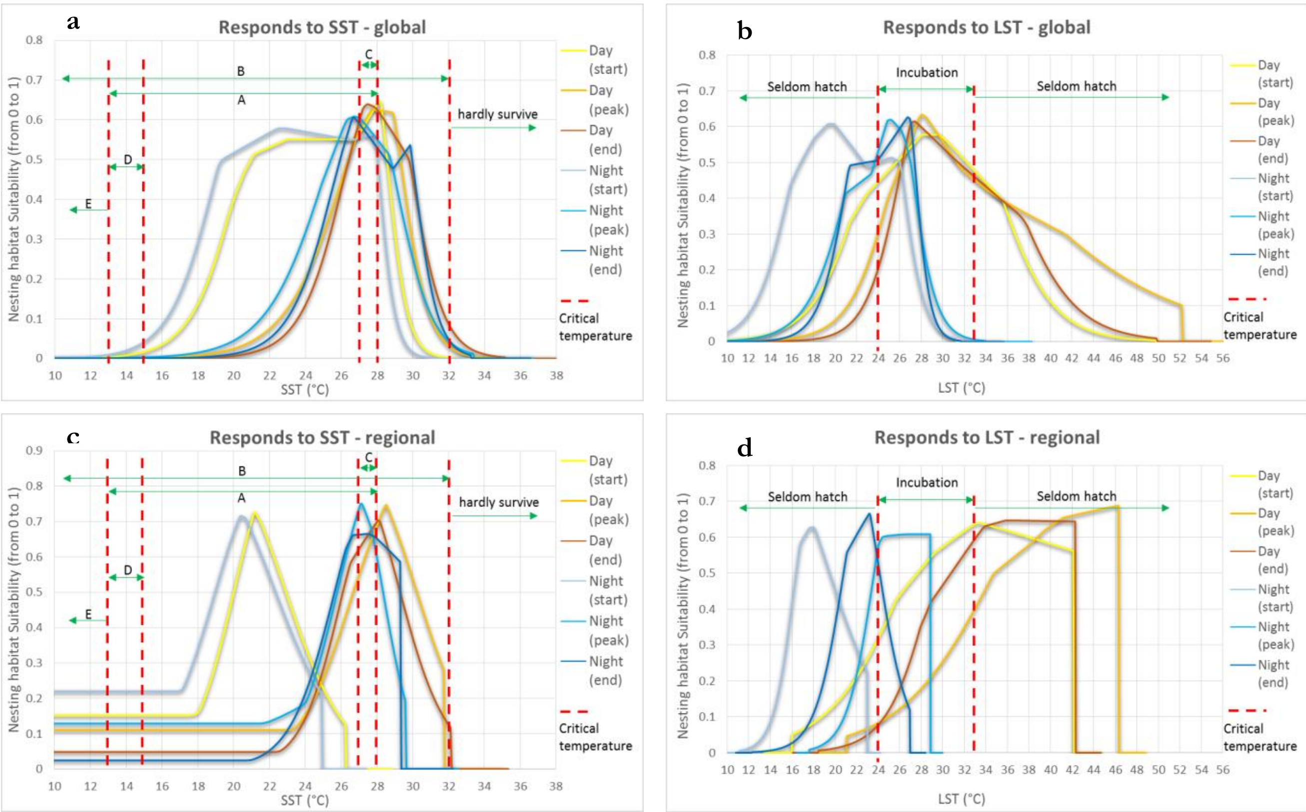

Figure 11. Response curves against expert knowledge

Six curves in each graph represent SST or LST in three nesting stage (start, peak and end), and at day and night.

a. SST response curves (global); b. LST response curves (global);

c. SST response curves (regional); d. LST response curves (regional).

The response curves of environmental parameters from global and regional SDMs were expected to be different. The curves of both SST and LST from the global model (Figure 11 a, b), show approximate Gaussian shape which are also biologically meaningful showing how the loggerheads reacts to the ambient temperature, as they cannot survive at very low nor a very high temperature. These response curves not only show the pattern of the species-environment relationship, but also are consistent with the critical temperature information for loggerhead survival and incubation. By plotting critical temperature on the SST and LST response curves, it can be clearly seen that in different critical temperature intervals the response curves show different trends, and that the habitat suitability always peaks when the temperature reaches the most suitable region.

Qualitative examination of SST and LST response curves was done by visually interpreting the response curves with expert knowledge. In Figure 11 a, in the loggerheads normally occupied water temperature range (13-28°C), the response curves gradually raised and peaked at the interval between 27-28°C. Then the suitability decreased accompanied with the SST continually increasing. By contrast, the curves from the regional SDM (Figure 11 c) did not fit this trend. They linearly increased and linearly dropped after peaking. Furthermore, the curve of the start month of nesting season unexpectedly peaks at 21°C SST.

The difference of LST curves between global and regional SDMs is also transparent. Curves from global SDMs (Figure 11 b) show nearly Gaussian shape, and the suitability peaked in the middle of the suitable incubation LST range (24-33°C); whereas the curves from regional SDM (Figure 11 d) either show continually raising trend until the LST reached the maximum value (day LST), or dramatically raised followed by a dramatic decrease in a very narrow range without reaching the full incubation temperature range. Both of these tendencies do not fit either the theoretical shape of curves or the critical temperature from expert knowledge. For example, when day LST exceeds 33°C, eggs hardly hatch, but the habitat suitability still shows increasing or stable tendency.

Due to the specific heat capacity of sand (around 1000 J/kg °C) being small, only 1/4 of specific heat capacity of water (around 4000 J/kg °C), the night LST has a large difference from day LST. This explains why, unlike the SST curves, the night LST curves shift to the lower temperature zone. However, the curves from global SDMs still show an expected shape, as habitat suitability against night LST also peaked in the published incubation temperature interval.

Consequently, in accordance with the theoretical shape of response curves and the consistency between habitat suitability and critical temperature, the global SDM discovered better species-environment relationship of loggerheads than regional SDM did.

3.2.1.2. Why curves do not exactly match the theoretical shape

How loggerhead sea turtle responds to the environment is an aim of this study. Clues to this were revealed from the response curves derived from SDMs. Whether these curves fit the theoretical shape and critical value from expert knowledge is part of evaluation of SDMs performance. Although it has been shown, in this study, that the curves of both SST and LST from the global SDM fitted expert knowledge better than the curves from the regional SDM, they did not perfectly show a Gaussian shape, and the shape from different nesting stages also did not match each other. For instance, the curve of SST in the start-nesting month (Figure 11 a) showed larger range of suitable sea surface temperature when loggerhead is looking for the spawning grounds. Thus, to more deeply investigate how loggerhead sea turtle reacts to the environment, the reason why the response curves from the global SDM performed better, and the potential factors that might cause the mismatched curves from different nesting stage were analysed. The SST was used as an example for this discussion as it made the most substantial contribution to the global SDM.

As we can see from Figure 12 a, b and c, the globally distributed loggerheads occurrence points occupied a larger range of SST during nesting season than the regional points did. This causes the regional response curves to not reflect the real species-environment relationship. The geographical location of the Mediterranean Sea is located in relatively high latitude, which results in a relatively low sea surface temperature. This difference is especially seen at the start month of nesting season (for the Mediterranean, it normally starts in May). From the Figure 12 d, we can see that the maximum SST of presence nest was less than 24°C, and the maximum SST of the entail Mediterranean coast area was around 26°C. The low SST cause the response curve peaked at around 21°C as most of presence points were aggregate in this range, and reached bottom at 26°C as no higher SST exists. This could explain why the response curve did not fit the critical SST (27 to 28°C) for nesting female loggerheads. These unrealistic curves might severely influence the predicted landscape suitability, as the place with high SST (above 26°C) would be considered unsuitable or less suitable by SDMs. This explains why the habitat suitability from the regional model might be underestimated.

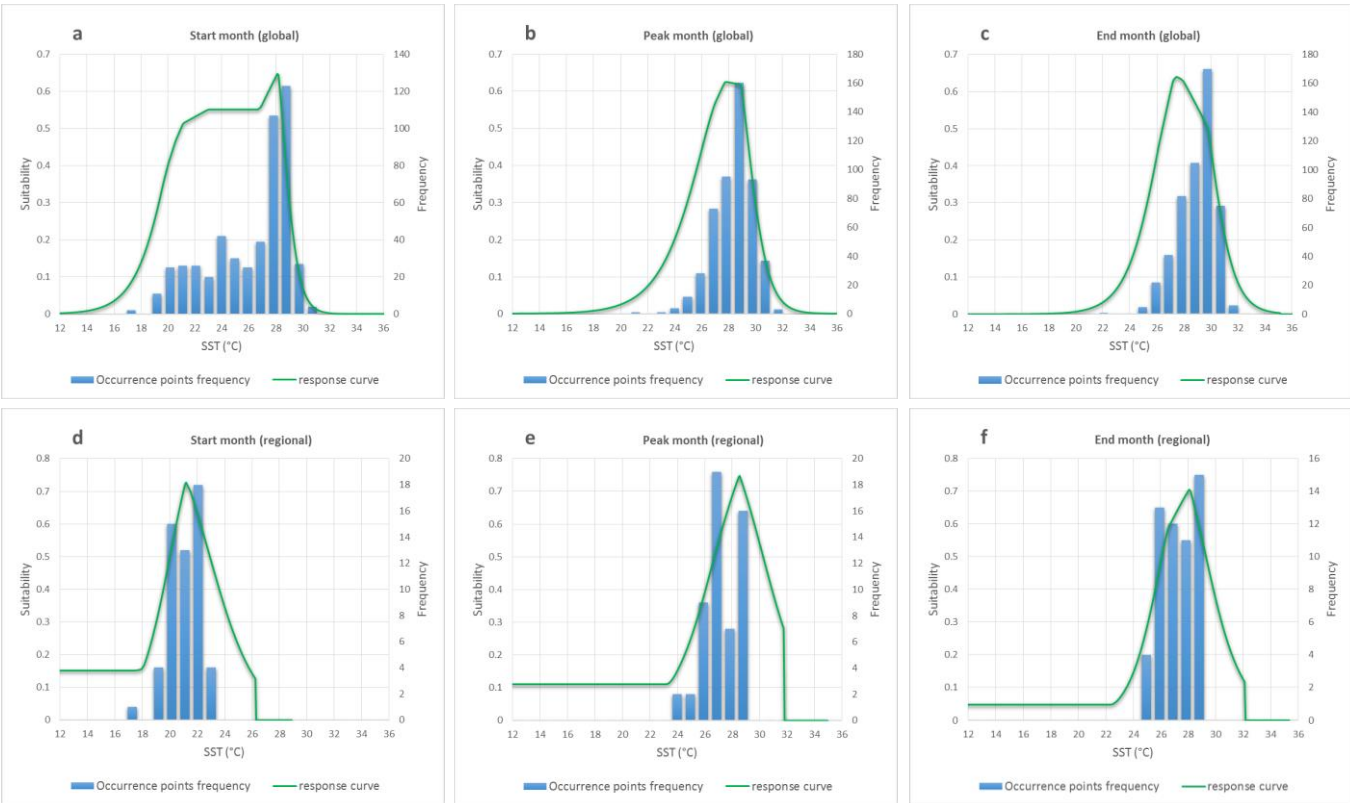

Figure 12 Day SST response curves and corresponding histogram

a, b and c were derived from global SDM; d, e and f derived from regional SDM. Histograms show the frequency of the observed variable values at

The curve for global SDMs at the start stage of nesting season also showed different tendency to that of other stages. This could result from the occurrence points not differentiating from each nesting stage in combination with the significantly lower SST in the start stage. Figure 12a shows approximately 250 occurrence points located where the SST ranges from 16 to 26°C. These points were used to formulate the response curves at the start month of nesting season, however they might not occur at that stage. It is obvious that not all the occurrence points occurred at the start stage, hence these none existing points in combination with the low SST result in the high suitability (e.g. >0.5) which started to happen at very low SST (21°C). This might make the landscape suitability overestimated.

3.2.1.3. Curves of other factors from the global SDM

Although it has been verified in this study that the global SDM built better response curves by examining the SST and LST, some other environmental factors, which also contribute to the global SDM and biologically meaningful to loggerheads survival and reproduction (e.g. PCP), were not examined in this study. This is mainly because there are no critical values of these factors to be found from previous studies. Nevertheless, whether these curves behave close to a common understanding can add additional information for judging the global SDM performance. Hence, we discuss the response curves behaviour of one of unexamined factors, PCP.

The PCP was included in loggerhead sea turtle nesting habitat distribution modelling because it is one of the factors that influence the incubation environment (Carthy, 2003). It is one of indicators of nest moisture. As we know that the eggs will not develop when incubation environments are either too dry or too wet (Ackerman, 1997), and the water content of sand at loggerhead nesting sites typically ranges from 2 to 10% (Ackerman, 1997; Bolten & Witherington, 2003; McGehee, 1990). The too dry environment will cause water loss in the eggs, whereas environments that are too wet will decrease the ability of gas and heat to move through sand (Carthy, 2003). Hence a Gaussian shaped PCP response curve is expected.

As one can see from Figure 133, the machine learning derived response curves of PCP show nearly Gaussian shape, but they are positively skewed. The unimodal shape fits the common understanding that the suitable nesting habitat, where eggs can successfully incubate, require the accumulated precipitation neither too low nor too high. The positive skew can be explained as the eggs initially contain plenty of water to complete incubation and can tolerate some loss of water (Ackerman, 1997). Therefore, even there is no precipitation at certain time, the baby turtles can still successfully hatch. However, it is impossible to validate whether the PCP range from 100 to 300mm (Figure 13, MaxEnt predicted most suitable range) is the most suitable for incubation, not only because the relevant data is unavailable, but also because there are many other factors that influence water content. For example, water tends to move more easily through sand when the sand particle size is large, which results in a potentially decreasing sand water content (Carthy, 2003). Consequently, although no critical value from previous studies exist, the overall trend of PCP response curves from global SDM fit the common understanding.

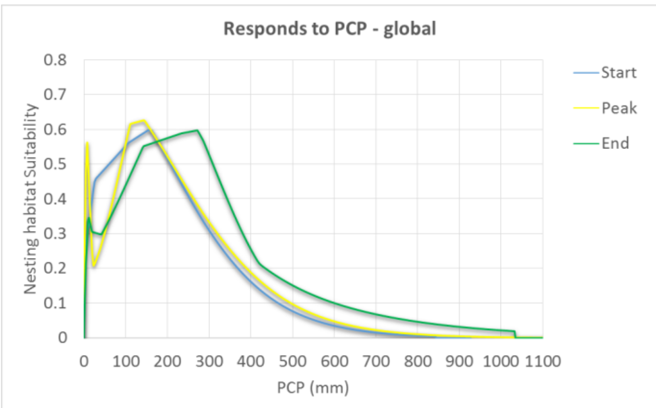

Figure 13 Response curves of PCP from the global SDM

It is not necessary to discuss the bathymetry, as it almost had no contribution to the SDM. The response curves of CHL and PAR are very difficult to interpret, as how these two factors work in biology of sea turtle, and in turn, how they biologically influence sea turtle survival and reproduction, have not been studied yet. In addition, as they both were considered as indicators of potential food availability, it is also difficult to biologically discover a general shape of these two factors. This is because unlike temperature and precipitation, which are not affected by species, the supply of food has very complicated interaction with species, such as competition and predation among species. Therefore how loggerheads respond to CHL and PAR is not known yet, and needs to be investigated in the future.

3.2.1.4. Summary

In summary, the result of examining species-environment relationship indicates that the global scale SDM discovered better species-environment relationship than the regional model did. Although it may not completely shaped as expected (e.g. perfect Gaussian shape) and may have bias due to the data quality and availability, it still fits the critical value from the known studies, and gives us an overall tendency of how loggerheads nesting suitability responds to the environment.

3.2.2. Abundance-occupancy relationship

3.2.2.1. Global scale

The distribution of habitat suitability of 50 validation points was not normal (Figure 14 a), with the p-value from Shapiro-Wilk test being 0.014 (< 0.05). The arc-sine transformation was expected to improve its normality.

The value of 3rd quartiles of habitat suitability of global model corresponding to the 50 samples was 0.663, which is less than 0.755. It indicated that at least 75% of transferred values had a less than 10% difference from the original values. Although the p-value (<0.05) from pairwise t-test showed that the mean of original and transferred samples had a significant difference, the absolute value of the mean of difference was 0.037, which is less than 0.1, within a 95% confidence interval (0.029-0.046). The arc-sine transformation, hence, was appropriate for the habitat suitability samples extracted from global SDM.

After implementing arc-sine transformation the normality improved with a p-value equal to 0.08 (>0.05), which means the distribution can be considered as normal (Figure 14 b).

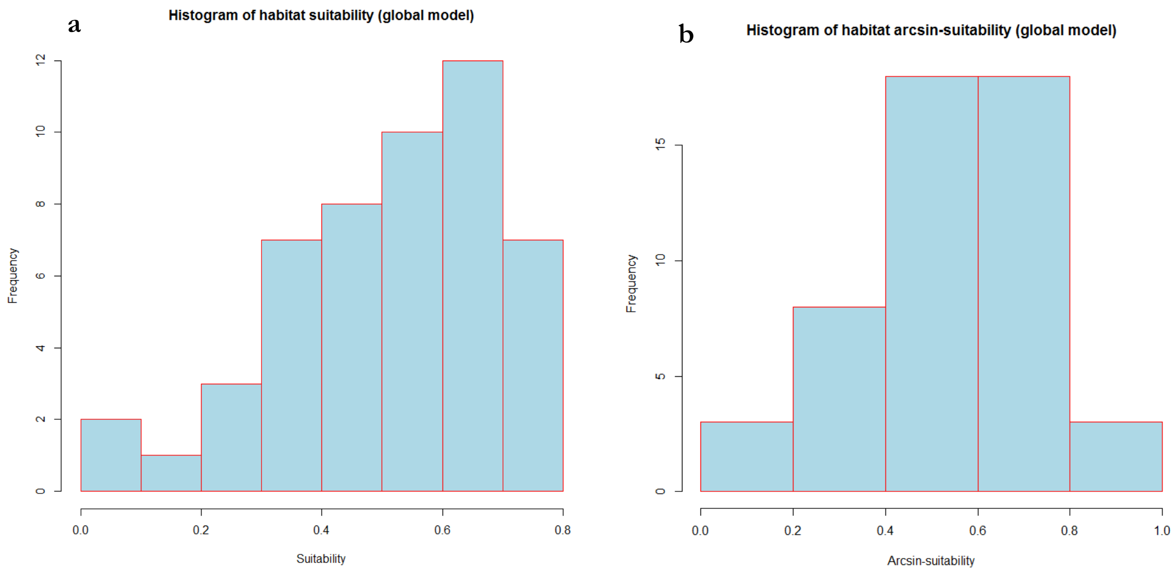

Figure 14. Histogram of predicted suitability from global SDM correspond to the 50 density points in the Mediterranean. .a. Original distribution. b. arc-sine transferred distribution.

The Pearson's correlation coefficient between the logarithm transferred nest density and the arcsine transferred suitability from the global model was 0.660 (Figure 15), which was significant as p-value equals to $1.848e^{-07}$ (< 0.05).

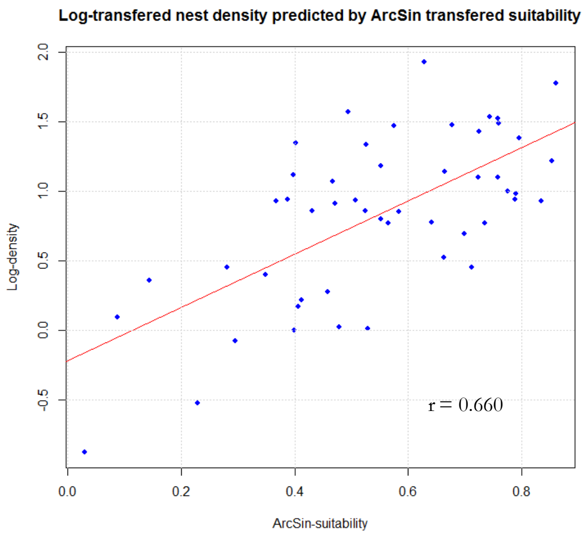

Figure 15. Correlation plot and the linear model (global)

A linear model (Figure 15) was fitted to assess the distribution of random error (residuals). The residuals from log-transferred nest density versus arcsine-transferred suitability linear model can be considered as normally distributed, as the p-value of Shapiro-Wilk normality test is 0.3558 (>0.05) (Figure 16 a). The residuals from the linear model and the predicted arcsine density were significantly independent as the p-value of Pearson correlation was 1 (Figure 16 b).

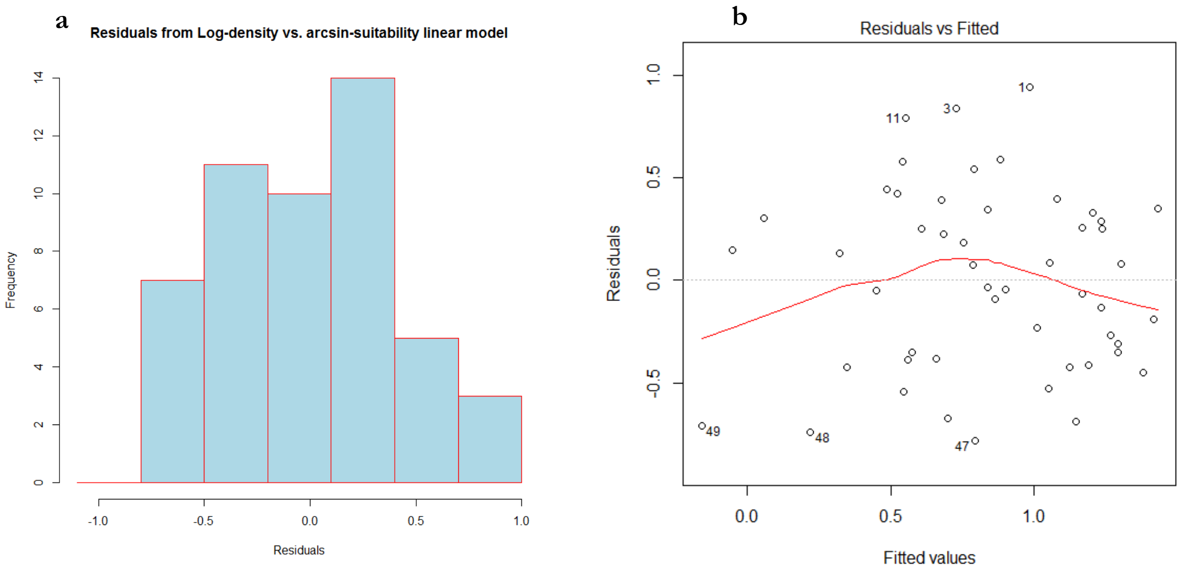

Figure 16. Histogram of residual (a) and residual against fitted value (b) (global)

Consequently, the logarithmic transferred nest density could be explained by the arcsine transferred suitability with a linear model, and their correlation was significant in correspondence with R=0.660.

3.2.2.2. Regional scale

The distribution of habitat suitability of 50 validation points was also not normal (Figure 17 a), as the p-value from Shapiro-Wilk test was 0.001 (< 0.05). The arc-sine transformation was employed to improve the normality.

The value of 3rd quartiles of habitat suitability of regional model corresponding to the 50 samples was 0.754, which is slightly less than 0.755. It indicated that 75% of transferred values had a less than 10% difference from the original values. The pairwise t-test showed the absolute value of the mean of difference was 0.061 within a 95% confidence interval (0.047 - 0.075). The arc-sine transformation, hence, was appropriate for the habitat suitability samples extracted from regional SDMs.

The transferred data was considered to be normally distributed (Figure 17 b), as the p-value from Shapiro-Wilk test was 0.043 that is very close to 0.05.

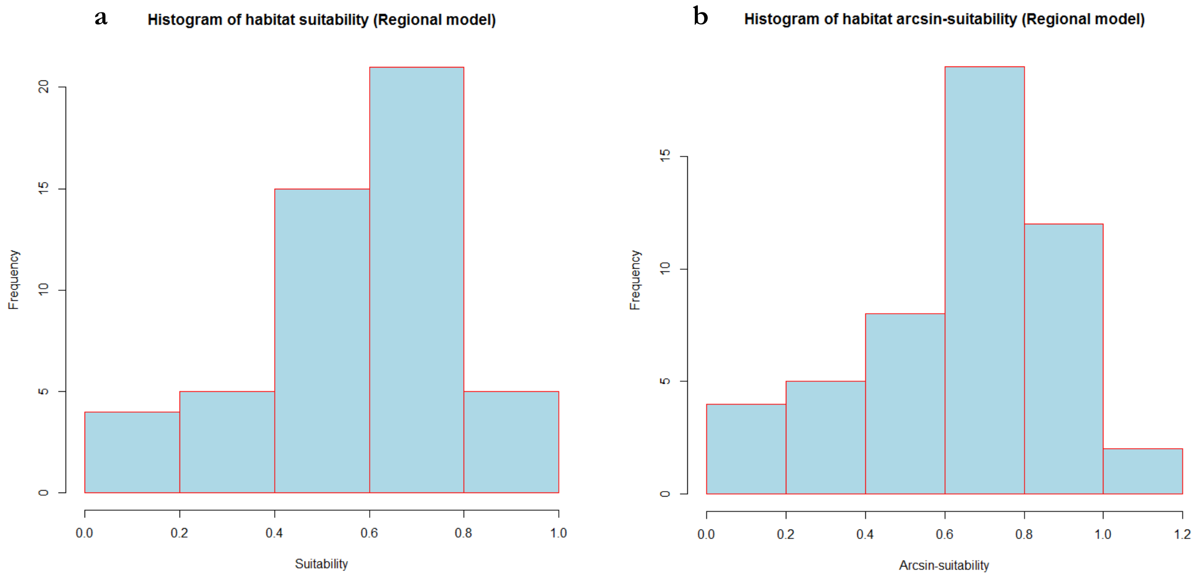

Figure 17 Histogram of predicted suitability from regional SDM correspond to the 50 density points in the Mediterranean. a. Original distribution. b. arcsine transferred distribution.

The Pearson's correlation coefficient between the logarithmic transferred nest density and the arcsine transferred suitability from the regional model was 0. 356. It is significant, as the p-value equals to 0.011 (< 0.05).

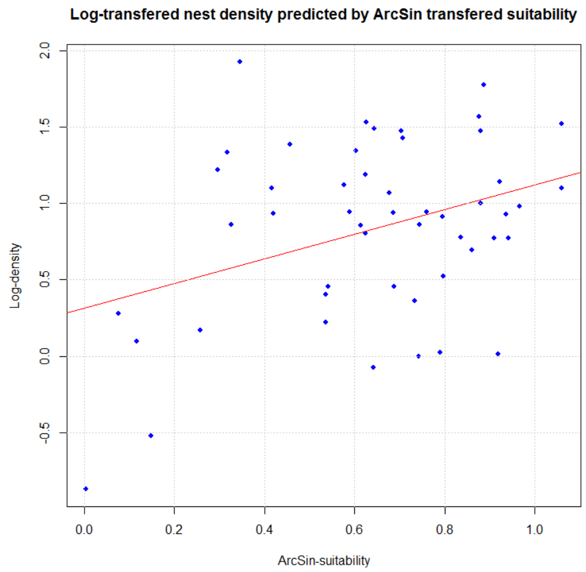

Figure 18 Correlation plot and the linear model (regional)

A linear model (Figure 18) was fitted to assess the distribution of random error (residuals). The residuals from log-transferred nest density vs arcsine-transferred suitability linear model can be considered to be normally distributed (Figure 19 a) as the p-value of Shapiro-Wilk normality test is 0.483 (>0.05). The residuals from the linear model and the predicted arcsine density were significantly independent (Figure 19 b) as the p-value of Pearson correlation was 1.

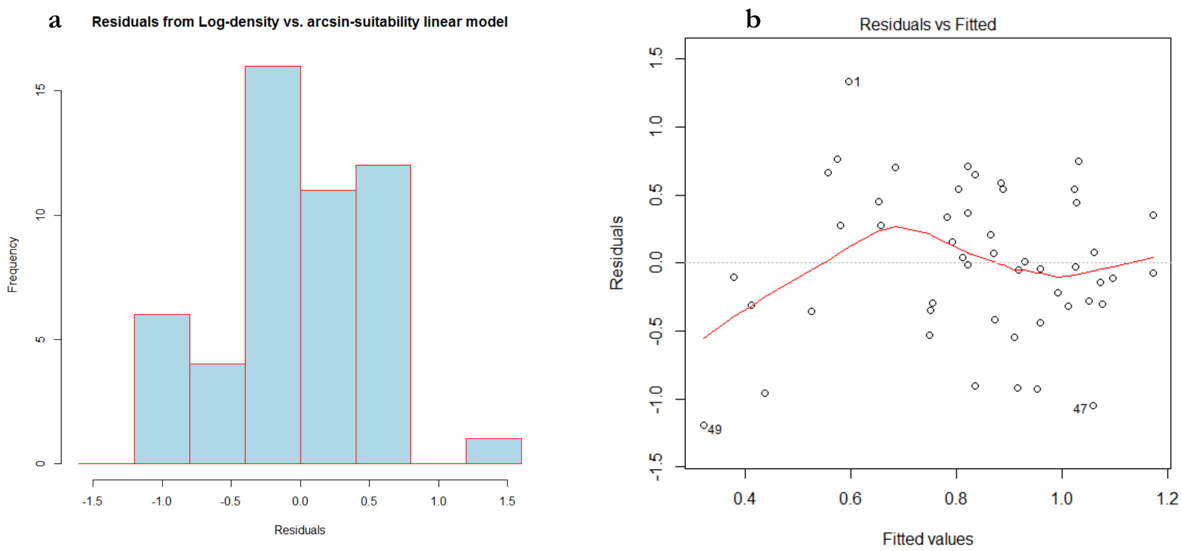

Figure 19. Histogram of residual (a) and residual against fitted value (b) (regional)

Consequently, the logarithmic transferred nest density could be weakly explained by the arcsine transferred suitability from a regional SDM with a linear model, and the correlation coefficient was 0. 356.

3.2.2.3. Hypothesis test

SDMs' performance was assessed by comparing the correlation coefficient (R). The R from global model was 0.660, while it from regional model was 0.356; and both were calculated with the sample size of fifty. The transferred correlation coefficient was 0.793 (r_1') and 0.372 (r_2') respectively. The z value gotten from Fisher r-to-z transformation was 2.04 with a corresponding one-tailed p-value 0.0207. As a result of the z value was positive and the p-value was less than 0.025, the correlation coefficient from global model was significantly greater than that from the regional model with 95% confidence interval.

Therefore, the null hypothesis was rejected, in turn, the alternative one was accepted, which was the strength of relationship between the nesting density and the predicted habitat suitability value from global model was significantly stronger than that from the regional model. This result indicated that the global scale model performed better than the regional scale model in predicting suitable loggerhead sea turtle nesting habitat.

3.2.2.4. Why is the correlation coefficient from global SDM not high?

The relationship between species population density and the predicted habitat suitability was the other core of this study. Although it has been shown in this study that the habitat suitability from the global scale SDM had significant better linear relationship with loggerhead suitability in the Mediterranean than that from regional scale SDM, the coefficient of determination (R^2) modelled with the global SDM derived suitability was not high, only 0.44. This indicates that only 44% variability of observations can be explained by the linear regression model. A number of factors might lead to the low R^2. To interpret what these factors are, and how they affected the model, will make the results of this study more convincing.

Statistical test

As we can see from Figure 15, even the better-fitted regression model (suitability derived from global SDM) could only explain 44% of sample variability (as $R^2 = 0.44$). This could result from many reasons. For instance, the intensity and sampling methods often vary widely across the study area, which results in the inaccurate observed nest density; the full species environmental requirements might not be captured or inaccuracies in the climatic models used to generate climatic variables, which may cause the predicted suitable habitat not to match the real suitable location; and also the observed density may not totally be explained by the predicted suitability with a linear model.

Figure 20 shows that the six (nest 1, 3, 11, 47, 48 and 49) out of fifty observations had their absolute difference between the actual and modelled log-density greater than 0.70 (95 percentile of residual; for population density, it is 5 nests/km).

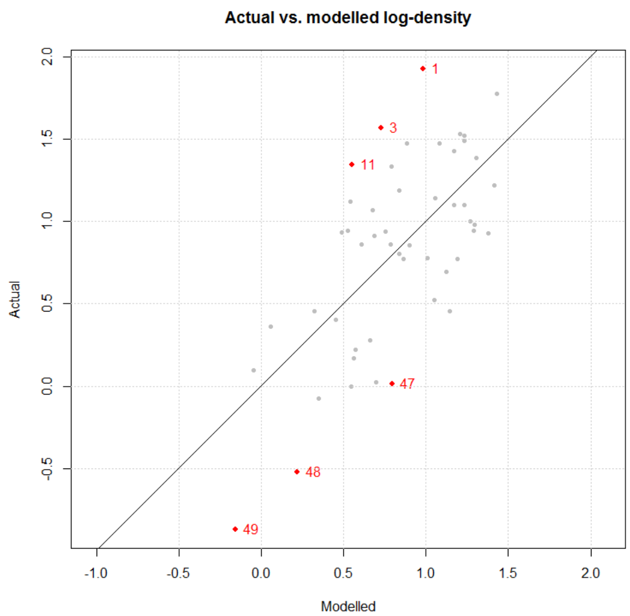

Figure 20. Actual log-density against modelled log-density
Red dots are which the margin between actual and modelled value were greater than 0.7

As expected all these six observations, especially 48 and 49 showed high Cook's distance (Figure 21 b), which means they had large influence on the fitted model. In addition, Figure 21 a showed that observation 48 and 49 also had high-leverage, but their residual were somehow higher than the average, which push the regression towards worse fits.

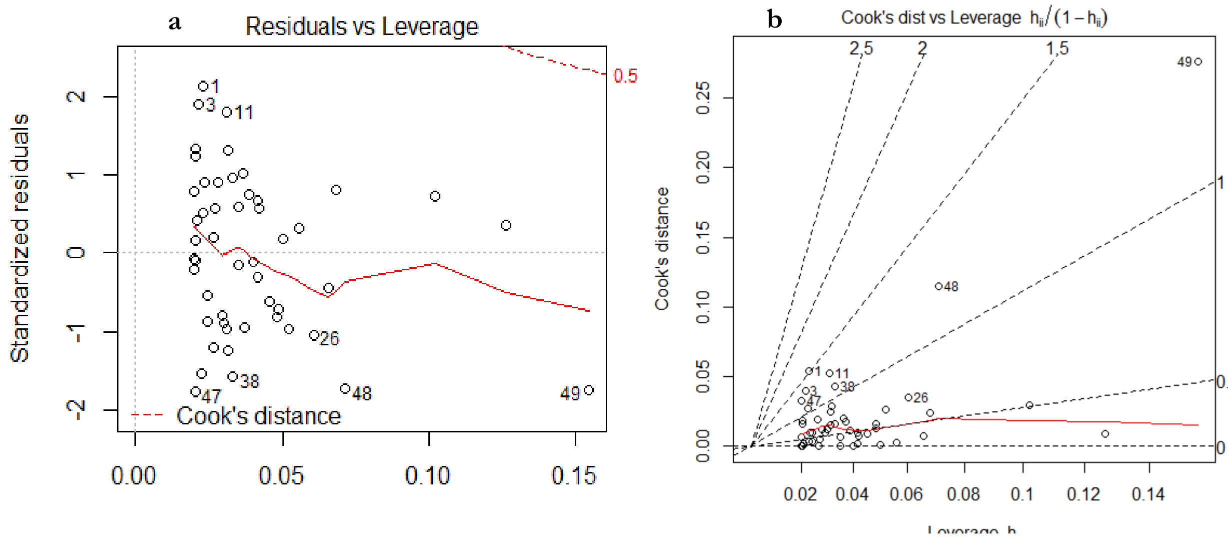

Figure 21. Model diagnostics. a. leverage. b. Cook's distance

Interpretation

The reasons that result in these unexpected plots can be many and various. Firstly, the observed beach length might greatly exceed the spatial resolution of environmental variables, which results in the nest density calculated from beach length, being not representative of the actual density within one pixel of environmental data. For instance, the beach length of observation 48 and 49 were 190.0 and 200.7km that were much longer than the 4km resolution of environment data. Therefore the densities of these two observations represent the nest abundance of two about 200km beaches, which occupied approximate 50 pixels. Nonetheless, the corresponding habitat suitability was only represent the area within one pixel. This might make the predicted density not fitting the 'real' density, as it actually was not the real density of the corresponding pixel.

Secondly, density data were collected from different organization with different observation and counting strategies. The survey frequency plays an essential role in the observation strategies, which were quite different from country to country, even from beach to beach. Some surveys were conducted with nightly and daily patrols covering the entire beach during nesting season (e.g. observation 2, 3, 5 and 23 etc.), whereas some were only with daily patrols (e.g. observation 1, 8 and 14 etc.). Others were surveyed at a lower frequency, such as two or three days once (e.g. observation 10, 20, 32 and 47 etc.), or only once a week (e.g. observation 11, 19 and 30 etc.). These inconsistent strategies might make it impossible to reveal the actual density, especially for the beaches with a low frequency survey. For example, the observation 47 was measured 2 or 3 times a week, thus some nests might be missed during the surveying interval. This might be an explanation of why the actual density was much lower than the predicted density (see Figure 20).

Another reason could be the different counting period of observations, which might explain why the density does not fit the habitat suitability. Although the nest counts were almost all collected between 2001 and 2010 in order to match the environmental data, they were not surveyed every year. The nesting density was calculated by averaging densities of data available years (e.g. density of observation 11 was derived from the survey data of 2006 and 2007, while density of observation 30 was derived from data of 2005). As the nest numbers varied every year, the density calculated from incomplete surveys could not accurately represent the average density over the 10 years. However, the modelled density was derived from SDMs which used exactly 10 years environmental parameters as predictors. This, hence, might also explain that why the surveyed density did not well match the modelled density.

Fourthly, the habitat suitability from the SMDs might not be accurate, which could result in a poor relation with population density. There are a number of potential pitfalls could affect the outputs of SMDs, such as the biased occurrence localities, inaccuracies in the climatic models used to generate environmental variables, or extrapolation of no-value areas etc. These uncertainties might affect the SMDs performance, and in turn, result in inaccurate suitability score.

Fifthly, other factors, such as life history, socio-competitive and site history probably, important for modelling observed abundance (Scott et al., 2005), were not included in the SDMs. This indicates that the habitat suitability that derived from SDMs with only environmental factors cannot perfectly predict the population density. This makes sense for loggerheads nest, as the quantity of these nests could be affected by the philopatry (nesting site fidelity) of adult female loggerheads and the human disturbance (Bolten & Witherington, 2003).

Lastly, a linear model may not be a best model to describe the species abundance-occupancy relationship. Although a general pattern of positive relationship between species abundance and occupancy has been discovered by many studies (see section 2.5.2), this relationship may not be explained by only linear models. Up to date, there are a number of different models have been proposed to describe abundance-occupancy relationships (Fangliang & Kevin, 2000; Hanski & Gyllenberg, 1997; Rosewell et al., 1990; Wright, 1991), which describe abundance-occupancy relationships reasonably well (Alison et al., 2002). Therefore, to explain the relationship between loggerhead population density and nesting habitat suitability, it is possible to find another model that might be more appropriate than the linear model.

3.2.2.5. Summary

Consequently, it was expected that for any given habitat suitability, the loggerhead nest density could not be perfectly predicted, because many factors, mentioned above, may affect population density and a linear model might not be appropriate. However, this does not change the fact that landscapes that are predicted to be highly suitable by SDMs should, on average, host larger populations (Oliver et al., 2012), and density is a key factor for population persistence (Pimm et al., 1988). The result of this study also show a significant correlation between loggerhead nest density and global scale SDM derived habitat suitability, and it was significant stronger than the correlation between density and suitability from regional SDM. The new method introduced in this study for assessing the SDMs performance could be applied to other study area or other species.

3.3. Visual interpretation of loggerheads nesting habitat

3.3.1. Predicted global nesting habitat

The geographic range of suitable nesting habitat of loggerhead predicted by MaxEnt at global scale closely match the known nesting sites. The most suitable area were aggregated in the western rims of the Atlantic (mainly in Gulf of Mexico and Caribbean Sea) (Figure 22 a), western part of South Pacific Ocean (Figure 22 b) and the Mediterranean Sea (Figure 22 c). These area are where have been reported the majority of loggerhead nests occurred.

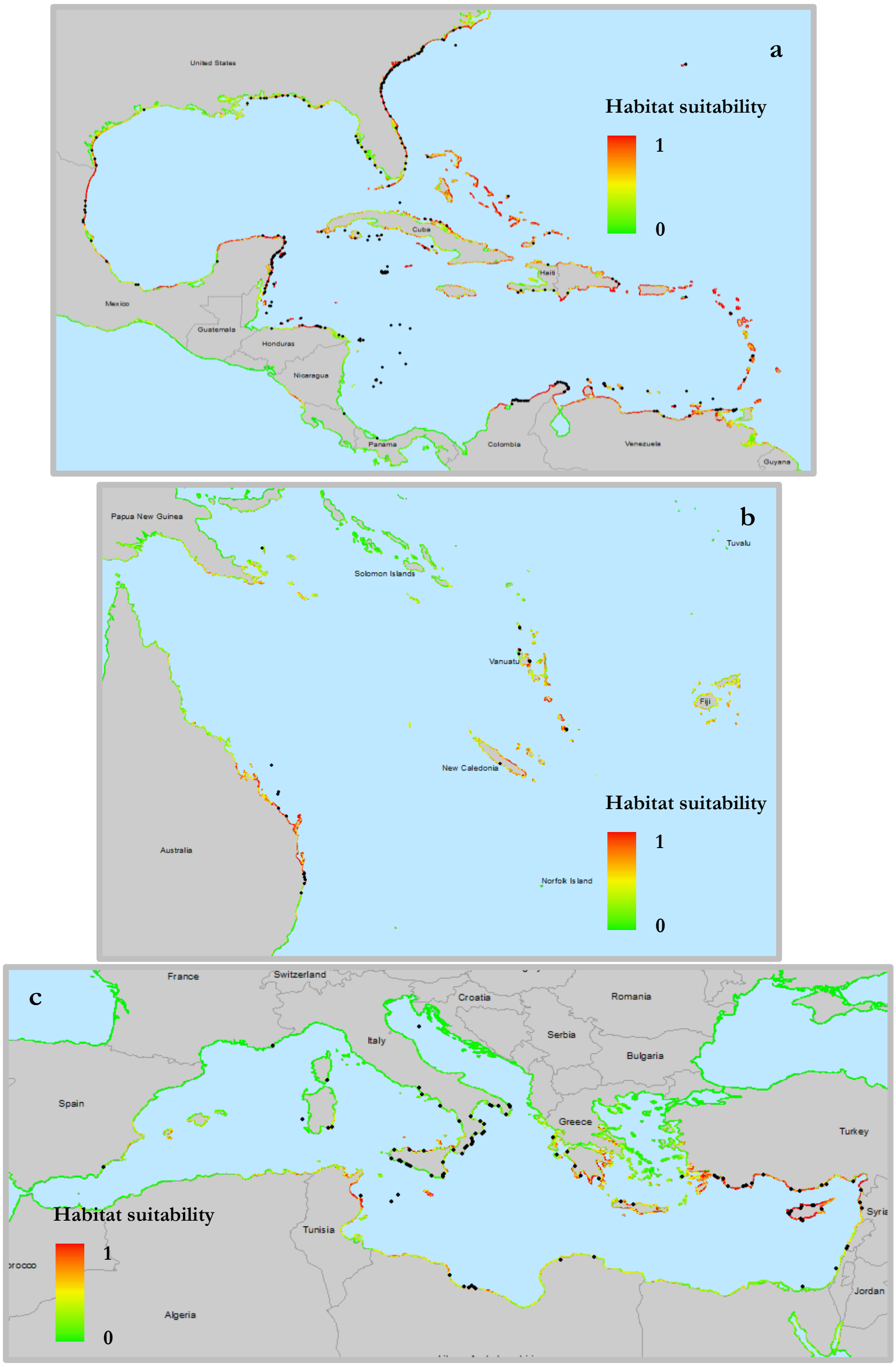

Figure 22. Predicted loggerhead nesting habitat (known nesting sites)

a. Gulf of Mexico and Caribbean Sea; b. western part of South Pacific Ocean; c. the Mediterranean Sea

Furthermore, some place without occurrence observations were also predicted to be suitable. For instance, the east coast of Brazil, from southern Bahia to northern Rio de Janiero state, south India and Tanzania coast etc. These predicted suitable areas have been proved that loggerhead nests occurred there. Scattered nesting from the states of Maranhao on the north to Santa Catarina in the south were documented (Bacon, 1981; Marquez, 1990; Soto et al., 1997) (Figure 23 a). South India (Figure 23 b) was confirmed be a loggerhead nesting area by (Dodd, 1988). Although loggerheads are relatively rare in Tanzania (Figure 23 c), other sea turtles, e.g. *Chelonia mydas* and *Hawksbill*, are reported nesting in Tanzania frequently (Muir, 2005). This means that the environmental condition may also suitable for loggerhead sea turtle, but due to the nesting site fidelity they hardly nest there. Nonetheless, few locations, which have been reported to be loggerheads nesting sites, were predicted with relative low suitability, e.g. in Oman. This may result from missing environmental factors for the SDM or just unusual distribution (Pritchard (1979) found unusual distribution for loggerhead nesting in Oman), which may not be estimated by environment condition.

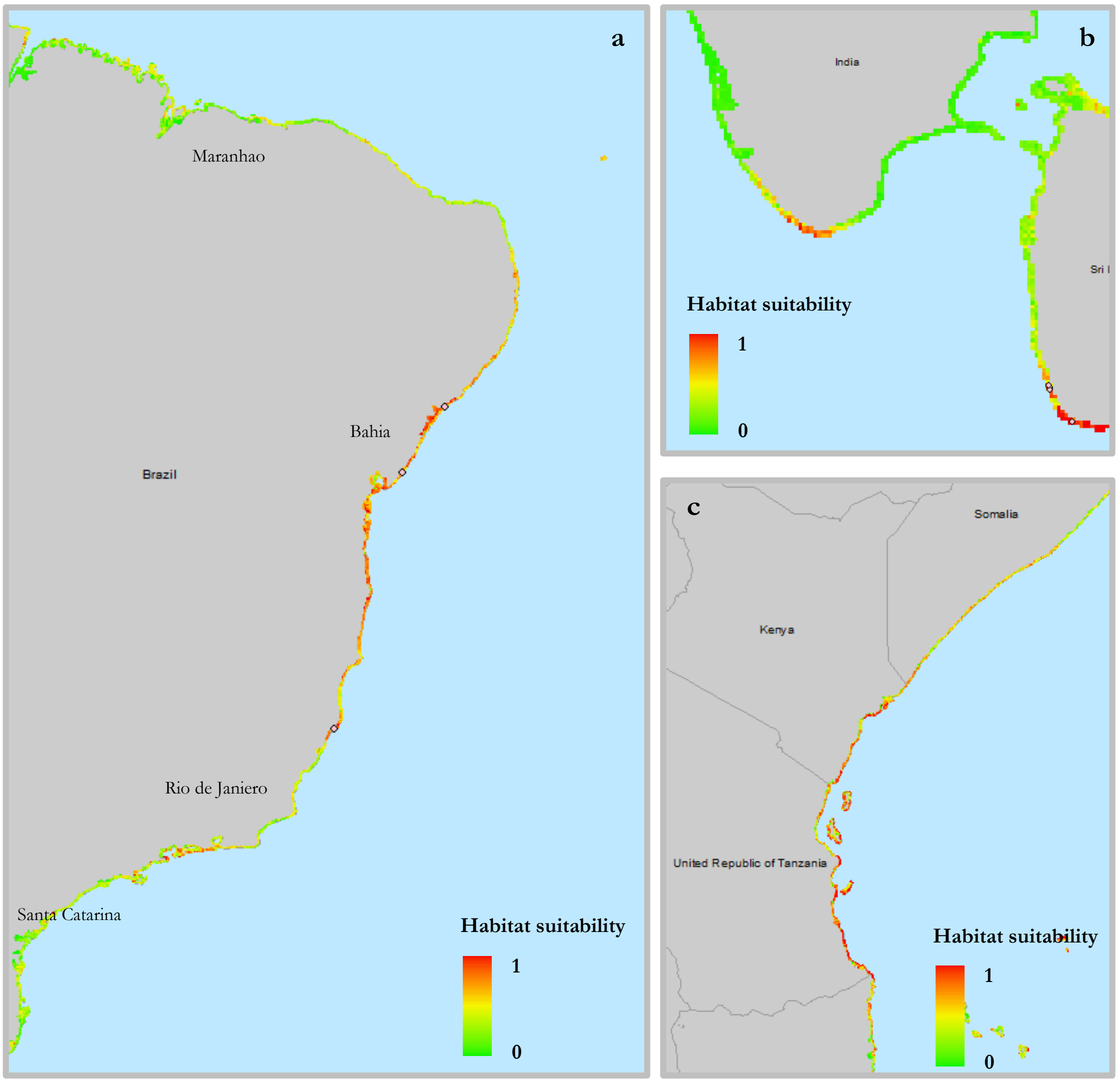

Figure 23. Predicted loggerhead nesting habitat (without occurrence points)

a. Brazil; b. South India; c. Tanzania

3.3.2. Predicted nesting habitat in the Mediterranean

Both global and regional scale SDMs predictions of loggerheads suitable nesting habitat mainly aggregated from Greece and Turkey to Cyprus and Syria, where are the places that actually the most nests occurred. However, for most of predicted habitat, their suitability derived from the global SDM is relatively higher than the corresponding suitability from the regional SDM. Comparing with the stretched (the same suitability values were represented by the same color) habitat suitability maps (Figure 24 a, b), this difference can be apparently seen in Greece and Turkey. These can be explained that either global SDM overestimated the suitable nesting habitat or the regional SDM underestimated it. Nevertheless, based on the result of species-environment relationship, which is the regional SDM did not cover the entire range of the environmental factors, where loggerhead sea turtle occupy, and also due to that global SDM had a stronger correlation between nest density and habitat suitability, the Mediterranean loggerhead nesting habitat suitability map from regional SDM tend to be underestimated.

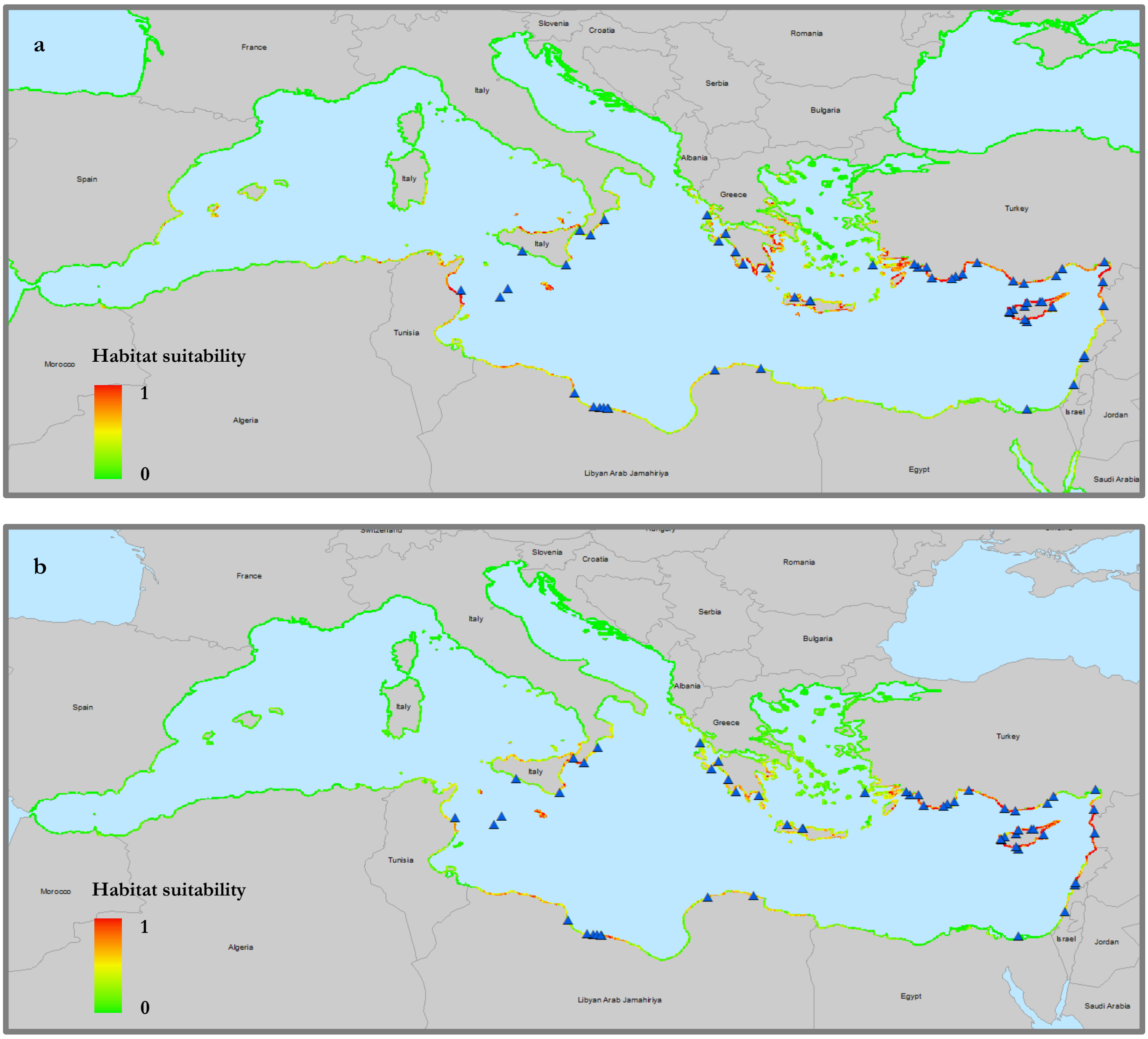

Figure 24. Predicted loggerhead nesting habitat suitability maps in the Mediterranean

a. Made by global SDM; b. made by regional SDM.

4. CONCLUSION AND RECOMMENDATION

1. Modelling loggerhead nesting habitat distribution at covering the full range of environment condition where it occupies can discover the species-environment relationship, which better fit the expert knowledge. This relationship reflects how female loggerhead responds the surrounding environment (e.g. ambient temperature), when selecting suitable sites for spawning. By contrast, modelling with limited environment condition, in this case, restricted in the Mediterranean, result in the discovered species-environment relationship do not fit the knowledge of loggerhead biology from literatures.

   However, these relationships that reveal how loggerhead responds to the environment, yet have not been well studied. The 'perfect' response curves of these relations are still unknown. Although, the result can be drawn by other works, it is just a start of investigating how loggerhead react on their living environment.

   For future work, other environmental factors can be introduced in loggerhead nesting habitat distribution modelling, such as sea current and wind stress etc., which may have biologically meaningful for nesting site selection. Furthermore, some indicators did not show expected species-environment relationship need to be deeply examined or can be replaced by much sensitive ones. For instance, the chlorophyll a concentration was assumed to be an indicator of food abundance, which was expected to have a positive or Gaussian relation with the habitat suitability. However, it showed an unexpected negative relation. Lastly, the quantity and quality of nest occurrence data are expected to be improved if possible, to make occurrence points better represent the nest presence within corresponding units of spatial resolution of environmental data, in turn, to discover better species-environment relationships.

2. The SDM, which covered the full range of environment conditions where loggerhead occupies, had a significant stronger abundance-occupancy relationship than the SDM that only covered limited range of environment conditions. This is consistent with the result of examining SDM derived species-environment relationship.

   Nonetheless, thus far, the abundance-occupancy can only be used to assess the relative performance of predicted loggerhead nesting habitat from different SDMs. It is because the perfect predictor, a model can perfectly explain how loggerhead density against its habitat suitability, is still unknown. It is necessary to try to find this predictor, in turn, to make assessment of absolute performance possible.

   However, models that are designed for population density against habitat suitability should be always treated with caution. As discussed in section 3.2.2.4, many uncertainties might affect the model. Moreover, a low goodness-of-fit does not necessarily mean that the model is inappropriate.

   Future studies can focus on repeating this work in different study areas with limited range of loggerhead adapted environment conditions. If positive results come out, the conclusion that made in this study will be more convincing.

In conclusion, this study successfully showed that for loggerhead this world wide spread species, better to model its nesting habitat under a full range of environment conditions where it occupies. Modelling under limited range of envrionment conditions might result in an underestimation of their habitat. It is possible to apply the evaluation method for model performance, qualitatively examining species-environment relationships in combination with quantitatively test the strength of correlation between population density and habitat suitability, on other corresponding studies.

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APPENDIX

Appendix 1 Loggerhead nest data contributors

Country	Organization
Aruba	Turtugaruba Foundation
Australia	Australian Seabird Rescue
	Department of Environment and Conservation, Exmouth, Western Australia
	Department of Environment and Conservation, Western Australia
	Department of Environment and Resource Management
	Gnaraloo Turtle Conservation Program
	NOAA NMFS Pacific Islands Regional Office
Bahamas	Archie Carr Center for Sea Turtle Research, University of Florida
	Department of Fisheries
	The Conservancy of Southwest Florida
Bangladesh	Marinelife Alliance
Belize	Bacalar Chico Marine Reserve
	Belize Audubon Society
	Glovers Reef Marine Reserve
	Wildlife Conservation Society (WCS)
Bermuda	Bermuda National Trust, Bermuda Sea Turtle Project
Bonaire, Sint Eustatius and Saba	Sea Turtle Conservation Bonaire
Brazil	Fundação Oswaldo Cruz
	Projeto Tartarugas Marinhas (TAMAR)
	Projeto Tartarugas Marinhas Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renovaveis (TAMAR IBAMA)
Cape Verde	Estación Biológica de Doñana, Consejo Superior de Investigaciónes Científicas
	Estacion Biologica Donana
	Universidad de Las Palmas
	University of Algarve
Cayman Islands	Cayman Islands Department of Environment
	Cayman Islands Government
Colombia	Centro de Investigación para el Manejo Ambiental y el Desarrollo (CIMAD)
	Columbia Marina Foundation
	Columbia Marina Foundation
	Corporación para el Desarrollo Sostenible del Archipiélago de San Andrés, Providencia y Santa Catalina (CORALINA)
	Fundacion Colombia Marina
	Universidad de Antioquia
	Universidad Jorge Tadeo Lozano
Costa Rica	Caribbean Conservation Corporation
	Conservation International
Cuba	Empresa Nacional para la conservación de la Flora y Fauna
	Fisheries Research Center
	Havana University
Curaçao	Caribbean Research and Management of Biodiversity (CARMABI)
	Department of Environment and Nature, Directorate of Public Health
Cyprus	Cyprus Wildlife Society
	Department of Fisheries and Marine Research
	Exeter University
	Marine Turtle Research Group
	University of Exeter
Dominican Republic	Instituto Tecnologico de Santo Domingo (INTEC)
France	Stazione Zoologica Anton Dohrn
Greece	ARCHELON
Haiti	Fondation pour la Protection de la Biodiversite Marine (FoProBim)
Honduras	Fundación Calentura y Guaimoreto (FUCAGUA)
	Moskitia Pawisa Apiska (MOPAWI)
	Nature Protection Trust of Seychelles
	Unidad Municipal Ambiental De Utila
	West End Marine Park
Israel	The Israeli Sea Turtle Rescue Centre
Italy	Dipartimento di Ecologia Univesrita della Calabria
	Stazione Zoologica Anton Dohrn
Japan	Sea Turtle Association of Japan
Lebanon	Mediterranean Association to Save the Sea Turtles (MEDASSET)
	Naucrates

Libya	Environment General Authority Libya
	Mediterranean Association to Save the Sea Turtles (MEDASSET)
Madagascar	Imperial College, London
Mexico	Banco de Información sobre Tortugas Marinas
	Centro Ecológico Akumal
	Comisión Nacional de Áreas Naturales Protegidas (CONANP)
	Comisión Nacional de Áreas Naturales Protegidas (CONANP)/La Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT)
	El Colegio de la Frontera Sur
	El Colegio de La Frontera Sur (EcoSur)
	Flora, Fauna y Cultura de México. A. C.
	Gladys Porter Zoo
	La Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT)
	Parque Xcaret
	Ría Lagartos Reserva de la Biosfera
Montserrat	Ministry of Agriculture, Trade and Environment, Montserrat
Mozambique	Associação para Investigação Costeira e Marinha (AICM)
	Oceanographic Research Institute
	World Wildlife Fund (WWF) - Mozambique Coordination Office
Oman	Marine Research Foundation
	Ministry of Regional Municipalities, Environment and Water Resources
Panama	Caribbean Conservation Corporation
Saint Lucia	Government of St. Lucia
Saint Vincent and the Grenadines	Fisheries Division - Ministry of Agriculture, Rural Transformation, Forestry and Fisheries
Sierra Leone	Conservation Society of Sierra Leon
South Africa	Nelson Mandela Metropolitan University (NMMU)
Syrian Arab Republic	Ibn Hani Marine Protected Area
Taiwan, Province of China	Institute of Marine Biology
Tunisia	Institut National des Sciences et Technologies de la Mer (INSTM) - Tunisia
	Mediterranean Association to Save the Sea Turtles (MEDASSET)
	Sfax Faculty of Sciences
Turkey	Adnan Menderes University
	Hacettepe University
	Mersin University, Faculty of Science and Letters, Department of Biology
	Mustafa Kemal University
	Pamukkale University
	Ulupinar Co-operative
Turks and Caicos Islands	Department of Environment and Coastal Resources
United States	Florida Fish and Wildlife Conservation Commission
	Georgia Department of Natural Resources
	National Park Service
	North Carolina Wildlife Resources Commission
	Share the Beach
	South Carolina Department of Natural Resources
	The Conservancy of Southwest Florida
	US Fish and Wildlife Service
Vanuatu	Wan Smolbag Theatre (WSB)
Venezuela, Bolivarian Republic of	Centro de Investigación y Conservación de Tortugas Marinas (CICTMAR)
	Comando de Guardacostas
	EDIMAR (Estación de Investigaciones Marinas de Margarita)
	Fundación Científica Los Roques
	Fundación La Salle
	Fundación para la Defensa de la Naturaleza (FUDENA)
	Ministry of the Environment
	Oficina Nacional de Diversidad Biológica
	ProCosta PROVITA
	Universidad Central de Venezuela
Virgin Islands, U.S.	National Park Service - Buck Island Reef National Monument
Yemen	Environmental Protection Agency

Appendix 2 Nest abundance data In the Mediterranean

Country	Beach	Latitude (degree)	Longitude (degree)	nest number	beach length (km)	Monitoring period (year)	Monitoring effort	source
Cyprus	Chrysochou Bay	35.036700	32.426400	376	11.00	2005-2011	DNP	SWOT
	West Coast - includes Lara/Toxeftra Turtle Reserve	34.954225	32.303533	167	5.00	2005-2011	DNP	SWOT
	Alagadi	35.334500	33.492600	123	4.60	1993-2007		STM
	North coast beaches surrounding Esentepe	35.341667	33.579167	112	4.60	2005	Every 2 or 3 days	SWOT & STM
	Morphou Bay	35.169000	32.892000	100	7.20	2010		SWOT & GE
	Toxeftra	34.920300	32.327100	63	5.00	2010		SWOT & GE
	West coast beaches surrounding Akdeniz	35.299444	32.962222	73	7.30	2005	Every 2 or 3 days	SWOT & GE
	East coast beaches surrounding Famagusta	35.125000	33.950000	49	8.20	2005	Every 2 or 3 days	SWOT & GE
	Episkopi beaches	34.658744	32.886653	5	1.50	2005	DP	SWOT & GE
	Akrotiri beaches	34.571381	32.983797	10	3.50	2005	DP	SWOT & GE
Egypt	Beaches between Rhafa and Port Said	31.177491	32.983562	27	200.70	1999		SWOT
Greece	Zakynthos	37.691828	21.009006	467	5.50	2005 & 2010	DP	SWOT
	Beaches adjacent to Kyparissa Town	37.267000	21.678000	282	9.50	2005 & 2010	DP	SWOT
	Koroni	36.795000	21.966000	50	3.00	1995-2007		STM
	Rethymnon	35.381944	24.572222	166	10.80	2005	DP	SWOT
	Lakonikos	36.660000	22.877000	197	23.00	1992-2007		STM & GE
	Bay of Chania	35.513000	23.958000	94	13.00	1992-2007		STM
	Bay of Messara	35.382000	24.577000	51	8.00	1993-2007		STM & GE
Israel	Beaches of the Mediterranean Coast	32.138879	34.777994	57	190.00	2005	DP	SWOT
Italy	Conigli Beach	35.513056	12.557222	4	0.13	2006 & 2009		SWOT & GE
	Pozzolana di Ponente Beach	35.863311	12.854789	3	0.10	2005 & 2008	NP	SWOT
	Strait of Messina Beach	38.110214	15.641625	3	1.30	2007		SWOT & GE
	Giallonardo Beach	37.319222	13.416783	2	1.60	2005	By chance	SWOT
	Marzamemi Beach	36.761456	15.101083	2	1.20	2010		SWOT & GE
	Costa dei Gelsomini Beach	37.922033	16.043969	17	16.50	2000-2004	2 or 3 times per week	STM
Lebanon	Tyre Coast Nature Reserve (TCNR)	33.273400	35.216800	10	3.97	2005	DP	SWOT
Libya	Al Mteafla	31.212000	16.724000	100	4.50	2006 & 2007	WP	STM
	Al Thalateen	31.242082	16.560077	47	3.56	2005	WP	SWOT
	Al-Arbaeen	31.216000	16.702000	100	8.50	2006 & 2007	WP	STM
	Al Ghbeba	31.243889	16.417500	50	5.67	2005	WP	SWOT
	Forteith	31.259367	16.178449	41	5.72	2005	WP	SWOT
	Boulfraies	32.759398	22.649437	4	1.40	2007	WP	SWOT & STM
	Between Misratah and Bowerat Lahsoun	31.816824	15.431786	178	120.00	2006 & 2007		SWOT & GE
Syrian	Banias Beach	35.183333	35.950000	2	2.00	2005		SWOT
	Lattakia	35.472800	35.856100	11	13.00	2004-2009		SWOT & STM
Tunisia	Kuria Kbira and Kuria Sgira	35.801389	11.034722	19	1.50	2005-2007	DNP	SWOT
Turkey	Dalyan Beach	36.788333	28.614167	282	4.70	2005 & 2008-2011	DNP	SWOT
	Belek	36.852000	31.049000	267	7.20	2005 & 2010	DNP	SWOT
	Cirali	36.400556	30.482500	54	2.50	2005	DP	SWOT
	Demirtas	36.137000	32.450000	75	7.80	2010		STM
	Fethiye Beach	36.668889	29.066667	70	8.00	2005 & 2011	DNP	SWOT
	Alata	36.621271	34.350382	26	3.00	2005	DNP	SWOT
	Kale	36.250914	30.066000	75	8.80	2010		SWOT
	Anamur	36.053000	32.849000	100	12.20	2010		SWOT
	Dalaman Beach	36.688472	28.745000	73	10.00	2005-2011	DNP	SWOT
	Patara Beach	36.271667	29.283333	83	14.00	2005	DP	SWOT
	Goksu Delta	36.368018	34.093499	151	25.60	2005	DP	SWOT
	Finike-Kumluca	36.315000	30.215000	100	20.20	2010		SWOT
	Yumurtalik-Sugozu beaches	36.897174	35.982517	7	3.70	2005	D and 10N P	SWOT
	Samandag	36.112900	35.926700	15	14.20	2006	Some part daily *	SWOT

SWOT: The State of the World's Sea Turtles; STM: Sea turtles in the Mediterranean 2010;
GE: Google Earth; DP: Daily patrols; DNP: Daily and nightly patrols; NP: Nightly patrols; WP: Weekly patrols.

* The majority of the beach was patrolled daily while the area around Meydan (approx. 4.5km) was surveyed only twice.