

# Habitat suitability models for the imperiled wood turtle (*Glyptemys insculpta*) raise concerns for the species' persistence under future climate change

Caitlin C. Mothes<sup>a,\*</sup>, Hunter J. Howell<sup>a,b</sup>, Christopher A. Searcy<sup>a</sup>

<sup>a</sup> Department of Biology, University of Miami, 1301 Memorial Drive, Coral Gables, FL, 33146, USA

<sup>b</sup> Susquehannock Wildlife Society, 1725 Trappe Church Road, Darlington, MD, 21034, USA



## ARTICLE INFO

### Article history:

Received 31 March 2020

Received in revised form 21 August 2020

Accepted 21 August 2020

### Keywords:

Chelonian

Ecological niche model

Endangered species

Global warming

Maxent

Protected areas

## ABSTRACT

The use of ecological niche models to predict how future climate change may impact habitat suitability is a critical component of imperiled species management. These models allow for the identification of areas with high future suitability that will support the persistence of the species. We developed an ecological niche model and performed protected areas analysis to assess the current and future distribution of suitable habitat for the globally endangered wood turtle (*Glyptemys insculpta*) across the northeastern U.S. portion of its range. Our model predicts that by 2070 the suitable habitat for this species will decrease by 29–52%, and the total area of optimal habitat will decrease by 62–86%, depending on emissions scenario. Furthermore, currently only 5% of suitable habitat and 8% of optimal habitat is protected, with the total area of protected suitable and optimal habitat expected to decrease by 16–28% and 31–64%, respectively, by 2070. Our results suggest that long-term wood turtle conservation efforts should be directed towards protecting habitat in higher latitudes of their range, mainly in the states of Maine, Vermont, New Hampshire, and New York where the majority of climate refugia exist. Additionally, management action will be required to facilitate the northward transition of southern populations that are threatened with extinction due to rising temperatures. Along with having important conservation implications for the imperiled wood turtle, our study also serves as an example of how climate change assessments should be used to direct long-term conservation efforts of other imperiled species across the globe.

© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

Global biodiversity is currently undergoing unprecedented declines due to a myriad of anthropogenic stressors (Pimm et al., 1995; Hoffman et al., 2010). While direct habitat destruction and subsequent fragmentation is known to be a main driver of species declines (Nori et al., 2013; Haddad et al., 2015), climate change exacerbates these impacts and further accelerates extinction risks by creating unsuitable climatic environments (Urban, 2015; Segan et al., 2016). Under the impacts of climate change, an increasing amount of habitat will become unsuitable for species across the globe as ecosystems are altered or destroyed by rising temperatures and higher frequency of extreme climatic events (Keith et al., 2014; IPCC, 2019). To reduce

\* Corresponding author.

E-mail address: [cmothes@miami.edu](mailto:cmothes@miami.edu) (C.C. Mothes).

current and future rates of biodiversity loss, it is critical that conservationists, land managers, and policymakers know what constitutes suitable habitat across species' current ranges and understand how suitable habitat will shift in the future.

Knowledge of a species' suitable habitat coupled with active management is vital to ensuring the future viability of populations. One of the major tools used to predict habitat suitability and guide such management practices are ecological niche models (ENMs), also referred to as species distribution models (SDMs). The use of SDMs has grown exponentially over the past couple of decades, with over 6000 peer-reviewed papers published in the past 20 years either using or discussing SDMs (Araújo et al., 2019). Although there are various SDM methods and algorithms, in general these approaches use occurrence data and associated environmental variables to estimate a species' niche in geographic and environmental space which can then be projected into any space or time (Peterson, 2011). A popular use of SDMs is predicting global change impacts on habitat suitability, and since the early 2000s the number of SDM studies in this major focus area has been growing exponentially (Araújo et al., 2019).

While anthropogenic impacts negatively affect all taxa across the globe, reptiles constitute one of the world's most endangered vertebrate clades, with an estimated 35% of species threatened with extinction (IUCN, 2019). Although habitat loss has been the leading cause of past reptile declines, climate change is becoming one of the major threats to these species due to a suite of life-history traits such as ectothermy, generally low dispersal ability, and temperature-dependent sex determination (TSD) that make them more susceptible to changes in their environment when compared to other taxonomic groups (Araújo et al., 2006; Irlow et al., 2012; Jensen, 2018). Within the reptile clade, turtles are the most threatened taxonomic group, with 20% of all species listed as critically endangered and ~60% of all species classified with a risk of extinction (Rhodin et al., 2018; Lovich et al., 2018). While habitat loss and climate change have been two of the main drivers of global turtle declines, turtle populations are also threatened by a host of other anthropogenic factors (e.g., poaching, introduced diseases, increased mesopredator abundance, road mortality; Lovich et al., 2018; Howell and Seigel, 2019). Due to their suite of slow life history traits (e.g., delayed sexual maturity, long life spans, iteroparity), even slight increases in adult mortality rates caused by these factors can lead to slow but steady declines of turtle populations (Lovich et al., 2018; Howell et al., 2019).

North America is home to 56 species of turtles and tortoises, and like turtle species around the globe, North American turtles are rapidly declining in the face of constant habitat loss and degradation, climate change, and other anthropogenic stressors (Mittermeier et al., 2015; Rhodin et al., 2018). Among the most imperiled North American turtles is the wood turtle (*Glyptemys insculpta*; Fig. 1), a medium-bodied turtle that generally utilizes clear, fast-flowing streams and the associated upland riparian habitat (Ernst and Lovich, 2009). *Glyptemys insculpta* is globally endangered according to the IUCN Red List (van Dijk and Harding, 2011), listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), listed as threatened at the national level in Canada (COSEWIC, 2007), and currently under review for federal listing under the U.S. Endangered Species Act (Center for Biological Diversity, 2012). This species' range extends from as far north as Nova Scotia and New Brunswick, south to Virginia and west into Minnesota, with the majority and largest contiguous portion of its range found in the northeastern U.S. (Ernst and Lovich, 2009). Wood turtles have been negatively affected by stream channelization, dam construction, agricultural expansion, collection for the pet trade, and urban sprawl (Harding and Bloomer, 1979; Ernst and McBreen, 1991; Garber and Burger, 1995; Willoughby et al., 2013), such that studies assessing *G. insculpta* populations in the northeastern portion of their range have largely concluded that their populations are dwindling (Garber and Burger, 1995; Saumurea and Bider, 1998; Ernst, 2001; Daigle and Jutrus, 2005; Saumurea et al., 2007; Willoughby et al., 2013). While habitat loss due to urbanization and other forms of land-use change has already led to the decline of many populations, it is likely that climate change will render additional large sections of *G. insculpta*'s current range unsuitable due to their reliance on cool, fast-flowing streams and their sensitivity to high temperatures (Ernst and Lovich, 2009). However, the extent of these projected losses has yet to be studied.

Understanding how future climate regimes will impact habitat suitability for this species will be critical to providing management recommendations that support the long-term persistence of *G. insculpta*. However, to this point, few studies



Fig. 1. Wood turtle (*Glyptemys insculpta*) in a small stream in central Maryland (Photo Credit: Andy Adams).

have attempted to predict the impact of future climate change on turtle species (but see [Ihlow et al., 2012](#); [Agha et al., 2018](#); [Martin and Root, 2020](#)). Here, we used ENMs to analyze current and future habitat suitability for *G. insculpta* in the north-eastern U.S. Given that chelonians are known to be especially susceptible to climate change and *G. insculpta* is dependent on cool, fast-flowing streams, a habitat type vulnerable to ecosystem degradation by increasing temperatures ([Lynch et al., 1984](#); [Daufresne et al., 2003](#); [Durance and Ormerod, 2007](#)), we hypothesized that climate change would dramatically reduce the future availability of suitable habitat for *G. insculpta*, especially in the southern extent of their range.

## 2. Methods

### 2.1. Model development

We developed a habitat suitability model for the northeastern U.S. portion of *G. insculpta*'s range, as the Northeast is the largest contiguous portion of their range and their Midwest populations are geographically distinct. The Northeast and Midwest populations are also often split into two distinct regions for other studies ([Ernst and Lovich, 2009](#); [Jones et al., 2015](#); [Lapin et al., 2019](#)), and climate change is projected to impact the Northeast differently from the Midwest ([Dupigny-Giroux et al., 2018](#)). In addition, we only modeled the U.S. portion of the range, even though populations persist in southeastern Canada, due to the limited availability of consistent environmental data between the U.S. and Canada. However, it is unlikely this would influence model calibration. Only a small portion of their northeastern range resides in Canada and the northernmost record of *G. insculpta* in Canada is less than 40 km north from the highest latitude of their U.S. range ([GBIF.org, 2018](#)). Therefore, the Canadian portion of their range that would have been added to the model likely does not include any novel environmental space compared to that found in the U.S. portion of their range.

*Glyptemys insculpta* occurrences were retrieved from the Global Biodiversity Information Facility ([GBIF.org, 2018](#)). We subsetted the occurrences to only include those in the northeastern U.S. portion of their range and then cleaned the remaining coordinates by removing duplicates and using the 'CoordinateCleaner' package ([Zizka et al., 2019](#)) in R version 3.6.0 ([R Core Team, 2019](#)), which flags temporal and spatial errors commonly found in the GBIF database. We additionally subsetted remaining occurrences to remove any from before 1980, so that the model would be built based on records from current environmental conditions. The final dataset used to train the model consisted of 177 occurrences.

To create the geographic extent that the model would be calibrated on, we calculated the Euclidean distance between the two most spatially segregated clusters of *G. insculpta* localities and then used half that distance as a buffer around all points (as in [Mothes et al., 2019](#)). This results in a geographic extent that includes the area the species would have historically occurred continuously across, or dispersed across over evolutionary time, and assumes the species would currently be present there if habitat was suitable.

The predictor variables used in this study were modeled after those identified as important to *G. insculpta* occurrence in the northeastern part of their range ([Jones et al., 2015](#); [McCoard et al., 2016](#)). Predictor variables included distance to the nearest stream ([U.S. Geological Survey, 2014](#)), percent canopy cover ([USDA Forest Service, 2019](#)), percent impervious surface ([U.S. Geological Service, 2019](#)), elevation (SRTM; [Jarvis et al., 2008](#)), slope (calculated from elevation layer), and PRISM climate variables ([Daly et al., 2008](#)) including January minimum temperature, July mean temperature, and mean annual precipitation. Distance to the nearest stream was calculated using the "Euclidean Distance" tool in ArcMap 10.5 (Esri, Redlands, CA, USA) at a resolution of 30 m to match the resolution of the canopy cover and impervious surface land cover layers. Thirty-year normal climate variables were downloaded from the PRISM database, and those along with elevation and slope were disaggregated from an original resolution of 800 m and 90 m, respectively, to 30 m to match the finer resolution of the land cover variables.

Since Maxent is a presence-only algorithm, by default it chooses random background points from within the geographic extent to act as pseudo-absences. However, this approach does not account for sampling bias, such that background points could randomly be chosen from areas of suitable habitat that are inaccessible, and where the presence of the species has thus not been determined. To account for this sampling bias, we used target-group background points ([Phillips et al., 2009](#)), which uses localities of similar species to better reflect true absences, assuming if researchers in the field identified similar species at that locality they likely would have identified our study species if it were present. We used reptiles as our target group and downloaded all localities from GBIF ([GBIF.org, 2018](#)) and cleaned them using the same methods as for the occurrence dataset. After cleaning, the total number of unique target-group background points was 16,855.

To prevent potential overfitting of the model, we performed model selection to choose the best beta multiplier for Maxent's built-in regularization procedure, which balances model fit and model complexity. To identify the optimal regularization multiplier, we followed [Warren and Seifert \(2011\)](#), running 24 models with regularization multipliers ranging from 0.2 to 1 in increments of 0.2, and integers 1–20. We chose the best model based on AIC<sub>c</sub> and ran the final model using the selected regularization multiplier, 10-fold cross validation, and the default feature settings. All models were implemented using the 'dismo' package ([Hijmans et al., 2017](#)) in R.

We used various metrics to evaluate model performance, which were all averaged across the 10 cross-validation models. To evaluate model fit, we used the average area under the Receiver Operating Characteristic curve (AUC), which represents the ability of the model to differentiate between suitable and unsuitable habitat. In addition, we evaluated model overfit using threshold-dependent and threshold-independent metrics. Our threshold-dependent metric was the omission error rate, which was calculated using the 10th percentile presence threshold, which is the value that omits 10% of calibration records with the lowest predicted suitability values. This threshold value is commonly used in ENM studies (e.g. [Radosavljevic and](#)

Anderson, 2014; Bohl et al., 2019), as it excludes outliers in the calibration dataset that have extremely low predicted suitability values, and whose inclusion would thus make the predicted range of suitable habitat overly inclusive. For the threshold-independent measure of overfit we calculated  $AUC_{DIFF}$ , which is the difference between the AUC value from the training data and the AUC value from the test data (Warren and Seifert, 2011).

## 2.2. Habitat suitability assessments

Given that this species resides in the Northeast, the most densely populated region in the U.S. (US Census Bureau, 2017), we wanted to assess how much of the species' current suitable habitat is protected. To do this, we used data from the World Database on Protected Areas, which is the most comprehensive global database on protected areas and includes all forms of land ownership (i.e., federal, state, private, etc.). We downloaded spatial protected area data using the 'wdpar' package (Hanson, 2019) in R and filtered the dataset to terrestrial areas within the species' range. We then calculated the total area of suitable habitat within these protected areas, converting the suitability map from a continuous map (logistic output ranging from 0 to 1, with 1 being the most suitable habitat) to a binary map. We did this using the same suitability threshold value used to calculate the omission error rate (10th percentile presence threshold), such that pixels greater than the threshold are categorized as suitable habitat and those less than the threshold value are deemed unsuitable habitat. In addition, we calculated the total area of highly suitable habitat that resides within protected areas, using a suitability threshold of 0.8, which we define as 'optimal' habitat because that means there is a >80% chance of the species being present there.

Due to *G. insculpta*'s sensitivity to high temperatures, which is likely what restricts the southern limit of their range (Ernst and Lovich, 2009; Greaves and Litzgus, 2008; van Dijk and Harding, 2011; McCoard et al., 2018), we also wanted to know how climate change would affect future suitable habitat for this species. We used future climate layers from the WorldClim database (Hijmans et al., 2005), using the same variables that were used to build the model (minimum January temperature, mean July temperature, and mean annual precipitation). Mean July temperature was calculated by averaging the minimum and maximum July temperatures, as this is the same way the PRISM dataset calculates mean July temperature. Given discrepancies among different climate models, we averaged across seven different global climate models, namely BCC-CSM 1-1, CCSM4, GISS-E2-R, HadGEM2-AO, IPSL-CM5A-LR, MRI-CGCM3, and NorESM1-M. We projected the model into two greenhouse gas emissions scenarios predicted for 2070, RCP 4.5 (low emissions scenario) and RCP 8.5 (high emissions scenario). We projected the current model into these future climate variables while keeping all other variables constant to identify the direct impacts of climate change if the landscape were to remain unchanged. We then calculated the multivariate environmental similarity surface (MESS) values to pinpoint the climate variables that were the strongest drivers of change in suitability at each occurrence. To calculate changes in suitable habitat under future climate conditions throughout *G. insculpta*'s northeastern range, we used the same threshold values as with the current suitability map and conducted the same protected areas analyses.

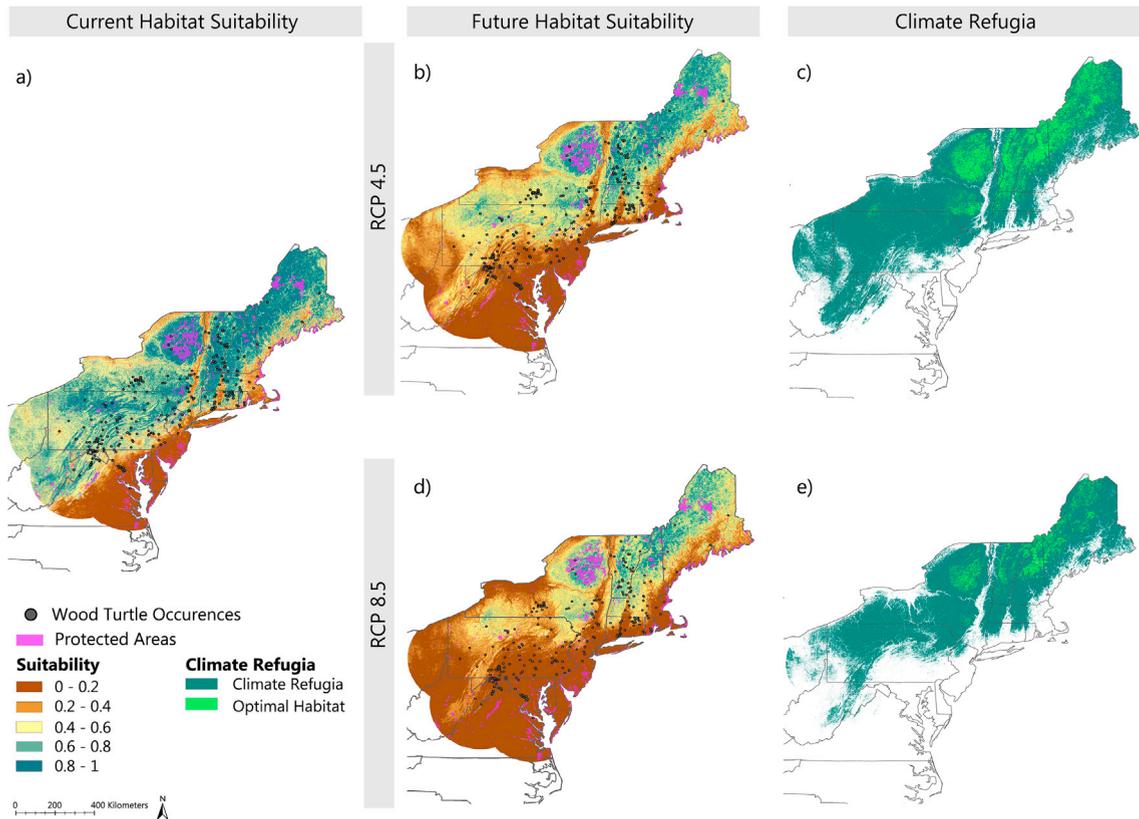
## 3. Results

Our model performed well across all evaluation metrics. The AUC value was 0.85, which is classified as reasonable to high performance in terms of differentiation between presence and absence points (Peterson, 2011). In terms of overfit, our omission error rate was 13%, which is close to the expected omission rate of 10%, thus indicative of low model overfit (Radosavljevic and Anderson, 2014). Our threshold-independent evaluation metric to test for model overfit ( $AUC_{DIFF}$ ) was 0.016 (values close to zero indicate little difference between the calibration and evaluation datasets), which again indicates low levels of model overfit (Warren and Seifert, 2011).

We found a drastic decrease in habitat suitability under future climate predictions within the northeastern U.S. portion of *G. insculpta*'s range (Fig. 2), particularly in the southern part of their range. The total area of suitable habitat decreased by 29% for RCP 4.5 and 52% for RCP 8.5. The total area of optimal habitat (habitat suitability > 0.8) decreased by 62% and 86% for low and high emissions scenarios, respectively. Under current conditions, only 5% of all suitable habitat resides in protected areas, and the total area of protected suitable habitat is predicted to decrease by 16–28% under future climate change (Fig. 3). The proportion of optimal habitat that resides in protected areas is currently 8% and total area of protected optimal habitat is predicted to decrease by 31–64%.

The most important variables for *G. insculpta* presence identified by the model in terms of percent contribution were elevation, July mean temperature, and canopy cover, while the most important variables in terms of permutation importance were January minimum temperature, canopy cover, and elevation (Table 1). For elevation, the highest presence probability occurs between 200 and 300 m, which matches other reports based on *G. insculpta* known occurrences (Jones et al., 2015; Fig. A1a). The highest presence probability for canopy cover is found in the most forested regions (>80% canopy cover; Fig. A1b), which is expected based on previous knowledge of *G. insculpta*'s preference for streams in forested landscapes (Ernst and Lovitch, 2009). However, there was also a spike in presence probability at low levels of canopy cover (Fig. S1B). This could be because, at finer scales, *G. insculpta* are known to occur in open canopy habitats (Jones et al., 2015), and due to the high resolution of our model (30 m) we were able to detect this effect.

From the MESS analysis, we found that January minimum temperature was the primary variable driving the change in suitability under both future climate scenarios for the majority of occurrence sites. As both January minimum and July mean temperature were identified as important variables to *G. insculpta* presence, we inspected the response curves of both



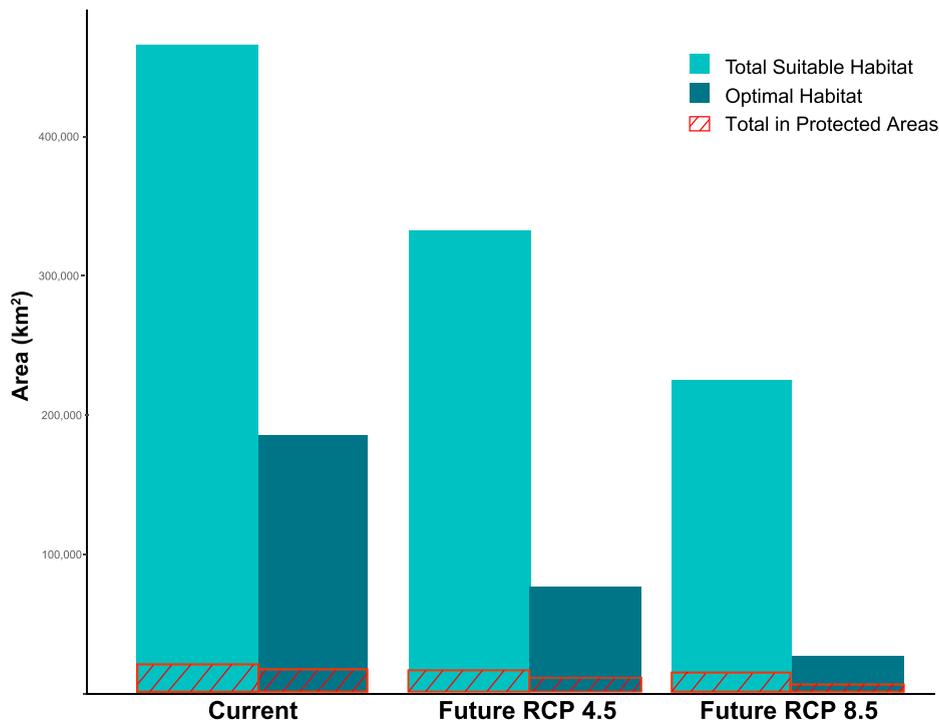
**Fig. 2.** Predicted habitat suitability for *Glyptemys insculpta* in the Northeast portion of its U.S. range under current (a) and future (b,d) climate conditions. Climate refugia (c,e) are defined as areas of habitat that will remain suitable under future climate conditions, with optimal habitat (habitat suitability >0.8) highlighted in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

variables to analyze how projected temperature changes relate to this species' suitability thresholds. Under current and projected 2070 conditions, we calculated the mean temperature for both variables across the species' range and plotted those in relation to the species' suitability threshold, using the 10th percentile training presence threshold as before. Under future climate conditions, average January minimum temperature remains within *G. insculpta*'s suitable thermal limit under RCP 4.5, but under RCP 8.5 the average temperature is above the species' limit by  $\sim 1.0$  °C. For future July mean temperature, both emissions scenarios result in an increase such that the average throughout the range is hotter than *G. insculpta*'s suitable thermal limit by  $\sim 1.0$ – $2.5$  °C (Fig. 4).

#### 4. Discussion

Many studies have shown *G. insculpta* populations rapidly declining across the Northeast portion of their range (Garber and Burger, 1995; Saumurea and Bider, 1998; Ernst, 2001; Daigle and Jutrus, 2005; Saumurea et al., 2007; Willoughby et al., 2013). While these studies demonstrated how anthropogenic disturbances such as habitat loss, fragmentation, poaching, disease, and road mortality have led to declining population sizes and extirpations, here we present one of the first studies showing the potential detrimental consequences climate change may have to *G. insculpta* persistence under both low and high greenhouse gas emissions scenarios. The results of our model predict losses up to >50% of currently suitable climatic habitat in the northeastern U.S., and up to 86% of what we define as optimal habitat by the year 2070.

Our model shows that increasing temperatures are the main drivers of this dramatic loss of suitable habitat, as both minimum winter temperature and average summer temperature were identified as important variables (Table 1). Temperatures are predicted to warm such that averages for both variables in the northeastern U.S. will likely be outside of *G. insculpta*'s suitable thermal limits (Fig. 4). Due to this species' ectothermic nature, there are obvious direct consequences when faced with extreme heat outside of its thermal tolerances. While it is unlikely that *G. insculpta* will face direct mortality from sustained temperatures above its critical thermal maximum (41.3 °C [39.6–42.5]; Hutchinson et al., 1966), increasing temperatures outside of its optimal thermal range may lead to adaptive behavioral responses that would have negative consequences on survival. Individuals may be forced to spend more time in estivation, remaining underwater or burrowing to escape extreme heat conditions (McCoard et al., 2018), thus decreasing the amount of time available on both a daily and



**Fig. 3.** Area of total suitable habitat and optimal habitat (i.e., suitability > 0.8) for current and future conditions, and the total area that resides in protected areas for each.

**Table 1**

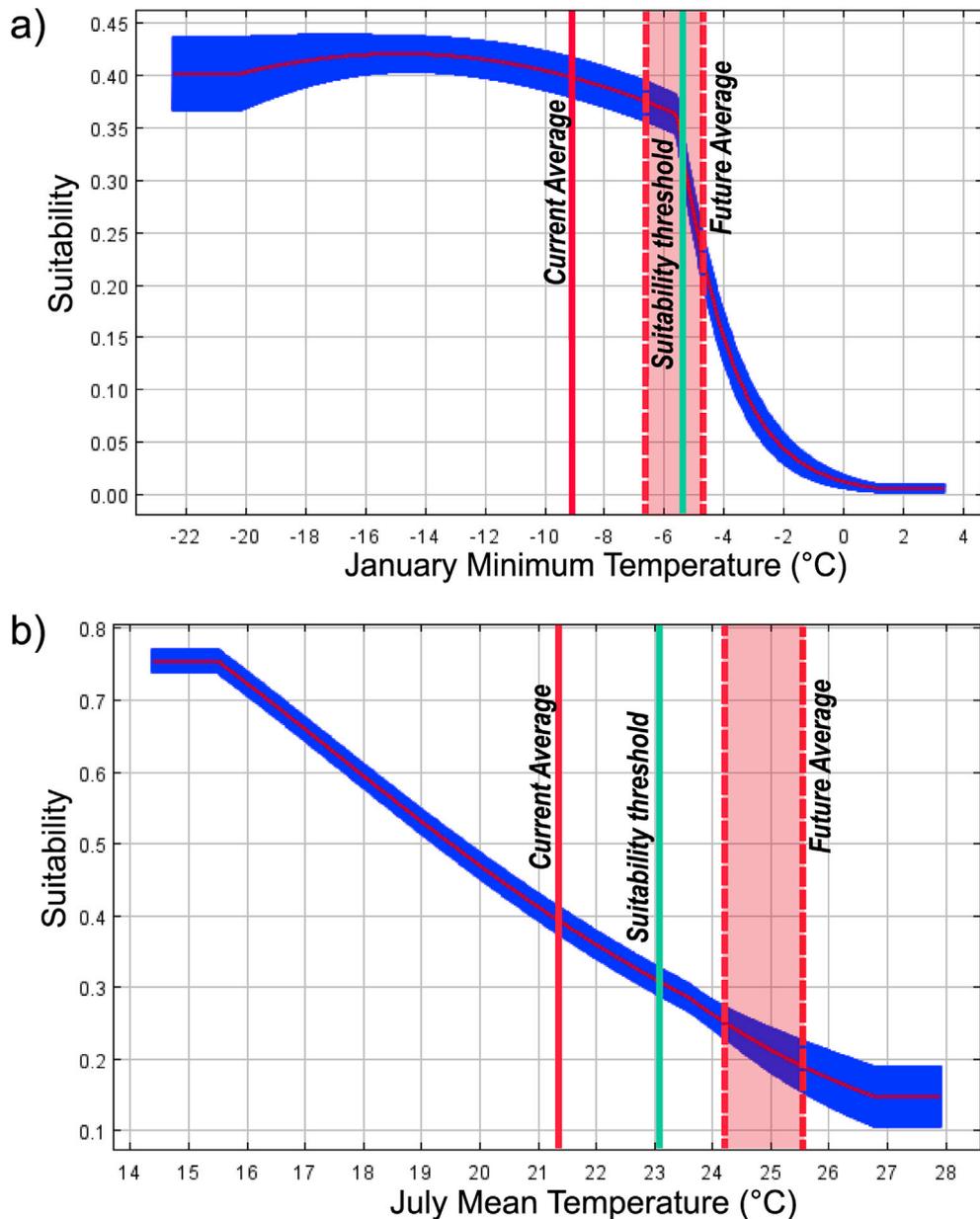
Rankings of environmental variable contributions to the model in terms of percent contribution and permutation importance. Top three variables for each ranking are in bold.

Variable	Percent contribution	Permutation importance
Elevation	<b>36.2</b>	<b>23</b>
July mean temperature	<b>26.9</b>	6.9
Canopy cover	<b>21.1</b>	<b>29.1</b>
January minimum temperature	9.2	<b>32.6</b>
Distance to stream	2.4	2.5
Impervious surface	2.1	4.6
Slope	1.3	0.6
Precipitation	0.7	0.7

season basis for foraging and dispersal. This could cause a decrease body condition, reduce reproductive output, and delay sexual maturity, all leading to reduced fitness and declining population growth rates (Ernst and Lovich, 2009).

In addition to direct consequences of warming temperatures, there are many indirect consequences as well. Given that wood turtles are highly dependent on cool, fast-flowing stream ecosystems, which provide thermal refugia and serve as an important foraging ground (Ernst and Lovich, 2009), increases in stream temperature will likely lead to widespread habitat degradation. Increasing temperatures negatively impact the productivity and stability of stream ecosystems, change flow patterns and fish community composition, decrease the abundance and survivorship of aquatic macroinvertebrates, and increase the frequency of algal blooms (Lynch et al., 1984; Daufresne et al., 2003; Durance and Ormerod, 2007). Additionally, increases in winter temperatures may decrease the number of suitable hibernacula available for overwintering due to decreases in dissolved oxygen, which may also have detrimental impacts on survivorship as this species is believed to be anoxia-intolerant (Ultsch, 2006; Greaves and Litzgus, 2008). Therefore, thermal degradation caused by climate change could lead to a widespread decline of the riparian ecosystems *G. insculpta* is dependent on, which in turn would have a large impact on the persistence of this species.

Since climatically suitable habitat is imperative to *G. insculpta* persistence given their ectothermic nature and dependence on thermally sensitive stream ecosystems, our results provide new information on the current and future spatial distribution of suitable habitat that will be critical for management of long-term persistence. The management implications of our study



**Fig. 4.** Response curves for January minimum (a) and July mean temperature (b), showing *G. insculpta*'s suitability threshold (in green) and the current and future (range between RCP 4.5 and RCP 8.5) averages for each variable across the northeastern U.S. portion of the species' range. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

include: 1) identifying where climatic refugia exist across the species range (i.e., areas of suitable habitat that will persist under future climate change) and 2) guiding the design of new protected areas and corridors that will support long-term persistence of the species and facilitate their transition from unsuitable to suitable habitats. Currently, our results show that only 5% of all suitable *G. insculpta* habitat and 8% of optimal habitat is protected, and under future conditions these protected habitat areas are predicted to decrease by 16–28% and 31–64%, respectively. Previous research has shown that *G. insculpta* requires protected habitat with little to no human interference for breeding populations to persist (Ernst, 2001), and that opening protected areas to public recreation has caused previously stable *G. insculpta* populations to decline (Garber and Burger, 1995). Therefore, the current proportion of protected *G. insculpta* habitat in the U.S. is highly concerning, and even more so considering that much of the habitat that is protected will not continue to be suitable in the future. This highlights the necessity of incorporating climate change models into management decisions to predict where highly suitable areas will persist in the future to appropriately guide the placement of protected areas (Pyke, 2004).

Based on the spatial distribution of future suitable habitat, our model suggests that conservation planning should revolve around the protection and management of suitable habitat at higher latitudes (Fig. 2). It is also important to note, as we only modeled the U.S. portion of *G. insculpta*'s range, that since we find the area of climate refugia generally increases with latitude, it is appropriate to assume that climate refugia exist in the Canadian portion of this species' range as well. Given that the majority of potential climate refugia occurs in the northern part of the species range, our model predicts southern populations will need to shift northwards to avoid extirpation. If we look at the distribution of current suitable habitat, multiple populations of *G. insculpta* in the southern portion of their range currently exist in areas of extremely low suitability (Fig. 2a). While these populations have likely declined based on anecdotal evidence, *G. insculpta* can still be seen at these sites, likely representing ghost populations. With lifespans of over 40 years in the wild (Ernst, 2001), it is likely that many southern populations will continue to persist for decades without representing viable populations (Heppell, 1998; Wheeler et al., 2003; Howell et al., 2019), demonstrating a common issue in the management and conservation of long-lived species. Therefore, in order to avoid future extirpation, these southern populations will need to shift northwards to regions of climate refugia. Even though *G. insculpta* will likely disperse through the landscape using stream corridors, facilitation of natural dispersal through the highly urbanized matrix of the northeastern U.S. will be a logistically difficult management strategy. Habitat permeability throughout this region will likely continue to decrease both as a function of increasing temperatures (Hamilton et al., 2018), and due to increasing encroachment from anthropogenic disturbances, as the human population of the Northeast is expected to grow by roughly 3 million new residents in the next 20 years (University of Virginia Weldon Cooper Center, 2018). *Glyptemys insculpta*'s low dispersal capability is further complicated by increased rates of mortality from roads and agricultural machinery (Saumurea and Bider, 1998; Saumurea et al., 2007; Castellano et al., 2008). These factors highlight the need to enact management strategies that facilitate the northward shift of southern *G. insculpta* populations to avoid extirpation, such as the implementation and protection of habitat corridors and active management strategies such as assisted migration.

Our findings show that the majority of climate refugia for *G. insculpta* occur in the states of Maine, New Hampshire, Vermont, and New York (~56–70%; Fig. 2c and e), none of which list *G. insculpta* under their state imperiled species acts. Maine is home to one of the largest portions of current and future optimal habitat for *G. insculpta* (Fig. 2) but is the only state that has no legal restrictions on the collection of wild individuals (Jones et al., 2015). Moreover, there is no legislation from any state to protect critical habitat for this species. Our findings thus provide additional support for listing this species under the ESA, which has been under review for nearly eight years (Center for Biological Diversity, 2012), to ensure the protection of critical habitat to support long-term viability. The current lack of regulatory framework for protecting *G. insculpta* in the U.S., particularly in the region with the largest climate refugia, is an obvious cause for concern as this species is faced with an increasingly inhospitable climate and disturbance-dominated landscape.

## 5. Conclusions

While it has previously been hypothesized that the southern range of this species may become climatically unsuitable in the future (van Dijk and Harding, 2011), here we provide the first body of evidence to support that claim using predictive suitability models. Our study predicts drastic range wide declines in habitat suitability for wood turtles in the northeastern U.S., especially in the southern portion of their range, due to rising temperatures. While we only modeled the predicted impacts of climate, the additional increases in land-use change and urbanization due to a growing human population will likely exacerbate this predicted loss of suitable habitat. Our study adds to the growing body of literature demonstrating the ability of global climate change to cause broad-scale declines in habitat suitability across a species' range (Carroll, 2010; Jueterbock et al., 2016; Hamilton et al., 2018; Mammola et al., 2018). Unfortunately, chelonian species are both one of the most imperiled vertebrate clades and one of the most likely to be negatively impacted by future climate change (Ihlow et al., 2012; Rhodin et al., 2018). Our study mirrors the findings of those on Blanding's turtles (*Emydoidea blandingii*; Hamilton et al., 2018), Desert tortoises (*Gopherus agassizii*; Lovich et al., 2014), and Bog turtles (*Glyptemys muhlenbergii*; Stratman et al., 2016), all reporting widespread declines in habitat suitability, dispersal capacity, or both for these imperiled chelonian species. Utilizing ENMs to predict changes in future habitat suitability can allow policymakers, non-governmental organizations, and land managers to develop management and restoration plans that account for projected climate change and development. Protecting areas that will act as refugia under future climate and land-use change will be an important component of long-term conservation strategies for this and other species, and studies such as ours are an important component to inform management actions to efficiently combat biodiversity declines across the globe.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could appear to influence the work reported in this paper.

## Acknowledgements

We thank the Susquehannock Wildlife Society for their assistance and feedback during the development of this manuscript, along with S. Clements, A. Messerman, L. Stemle, and D. Revillini for their helpful comments on the final draft of this manuscript. Funding to carry out this project was provided by the University of Miami.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01247>.

## References

- Agha, M., Ennen, J.R., Bower, D.S., Nowakowski, A.J., Sweat, S.C., Todd, B.D., 2018. Salinity tolerances and use of saline environments by freshwater turtles: implications of sea level rise. *Biol. Rev.* 93, 1634–1648.
- Araújo, M.B., Thuiller, W., Pearson, R.G., 2006. Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* 33, 1712–1728.
- Araújo, Miguel, B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., et al., 2019. Standards for distribution models in biodiversity assessments. *Science Advances* 5, eaat4858.
- Bohl, C.L., Kass, J.M., Anderson, R.P., 2019. A new null model approach to quantify performance and significance for ecological niche models of species distributions. *J. Biogeogr.* 46, 1101–1111.
- Carroll, C., 2010. Role of climatic niche models in focal-species-based conservation planning: assessing potential effects of climate change on Northern Spotted Owl in the Pacific Northwest, USA. *Biol. Conserv.* 143, 1432–1437.
- Castellano, C.M., Behler, J.L., Ultsch, G.R., 2008. Terrestrial movements of hatchling wood turtles (*Glyptemys insculpta*) in agricultural fields in New Jersey. *Chelonian Conserv. Biol.* 7, 113–118.
- Center for Biological Diversity, 2012. Petition to list 53 Amphibians and reptiles in the United States as threatened or endangered species under the endangered species act. Petition submitted to the U.S. Secretary of interior. July 11, 2012. At website. [http://www.biologicaldiversity.org/campaigns/amphibian\\_conservation/pdfs/Mega\\_herp\\_petition\\_7-9-2012.pdf](http://www.biologicaldiversity.org/campaigns/amphibian_conservation/pdfs/Mega_herp_petition_7-9-2012.pdf). (Accessed 21 August 2012).
- COSEWIC, 2007. COSEWIC Assessment and Update Status Report on the Wood Turtle *Glyptemys Insculpta* in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ont.
- Daigle, C., Jutras, J., 2005. Quantitative evidence of decline in a southern Quebec Wood Turtle (*Glyptemys insculpta*) population. *J. Herpetol.* 39, 130–132.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* 28, 2031–2064.
- Daufrense, M., Roger, M.C., Capra, H., Lamouroux, N., 2003. Long-term changes within the invertebrate and fish communities of the Upper Rhone River: effects of climatic factors. *Global Change Biol.* 10, 124–140.
- Dupigny-Giroux, L.A., Mecray, E.L., Lemcke-Stampone, M.D., Hodgkins, G.A., Lentz, E.E., Mills, K.E., Lane, E.D., Miller, R., Hollinger, D.Y., Solecki, W.D., Wellenius, G.A., Sheffield, P.E., MacDonald, A.B., Caldwell, C., 2018. Northeast. In: Reidmiller, D.R., Avery, C.W., Easterling, D.R., Kunkel, K.E., Lewis, K.L.M., Maycock, T.K., Stewart, B.C. (Eds.), *Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, II*. U.S. Global Change Research Program, Washington, DC, USA, pp. 669–742.
- Durance, I., Ormerod, S.J., 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biol.* 13, 942–957.
- Ernst, C.H., 2001. Some ecological parameters of the wood turtles, *Clemmys insculpta*, in southeastern Pennsylvania. *Chelonian Conserv. Biol.* 4, 94–99.
- Ernst, C.H., Lovich, J.E., 2009. *Turtles of the United States and Canada*, second ed. Johns Hopkins University Press, Baltimore, Maryland.
- Ernst, C.H., McBreen, J.F., 1991. Wood turtle: *Clemmys insculpta* (LeConte). In: Terwilliger, K. (Ed.), *Virginia's Endangered Species*. McDonald and Woodward, Blacksburg, Virginia, pp. 455–457.
- Garber, S.D., Burger, J., 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecol. Appl.* 5, 1151–1162.
- GBIF.org(b), 2018. GBIF Occurrence Download <https://doi.org/10.15468/dl.ooagr2>.
- GBIF.org(a), 2018. GBIF Occurrence Download <https://doi.org/10.15468/dl.543hcd>.
- Greaves, W.F., Litzgus, J.D., 2008. Chemical, thermal, and physical properties of sites selected for overwintering by northern wood turtles (*Glyptemys insculpta*). *Can. J. Zool.* 86, 659–667.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., et al., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1, e1500052.
- Hamilton, C.M., Bateman, B.L., Gorzo, J.M., Reid, B., Thogmartin, W.E., Peery, M.Z., Heglund, P.J., Radeloff, V.C., Pidgeon, A.M., 2018. Slow and steady wins the race? Future climate and land use change leaves the imperiled Blanding's turtle (*Emydoidea blandingii*) behind. *Biol. Conserv.* 222, 75–85.
- Hanson, J.O., 2019. Wdpar: Interface to the World Database on Protected Areas. R Package Version 1.0.0. <https://CRAN.R-project.org/package=wdpar>.
- Harding, J.H., Bloomer, T.J., 1979. The Wood turtle, *Clemmys insculpta* . . . a natural history. *Bulletin of the New York Herpetological Society* 15, 9–26.
- Heppell, S.S., 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998, 367–375.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2017. Dismo: Species Distribution Modeling. R Package Version 1.1-4. <https://CRAN.R-project.org/package=dismo>.
- Hoffman, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., et al., 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330, 1503–1509.
- Howell, H.J., Seigel, R.A., 2019. The effects of road mortality on small, isolated turtle populations. *J. Herpetol.* 53, 39–46.
- Howell, H.J., Legere, R., Holland, D., Seigel, R.A., 2019. Long-term turtle declines: protected is a Verb, not an Outcome. *Copeia* 107, 493–501.
- Hutchinson, V.H., Vinegar, A., Kosh, R.J., 1966. Critical thermal maxima in turtles. *Herpetologica* 22, 32–41.
- Ihlow, F., Dambach, J., Engler, J.O., Flecks, M., Hartmann, T., Nekum, S., Rajaei, H., Rödder, D., 2012. On the brink of extinction? How climate change may affect global chelonian species richness and distribution. *Global Change Biol.* 18, 1520–1530.
- IPCC, 2019. Summary for policymakers. In: Abe-Ouchi, A., Gupta, K., Pereira, J. (Eds.), *IPCC Sea Level Rise and Implications for Low-Lying Islands, Coasts and Communities*.
- IUCN, 2019. The IUCN Red List of Threatened Species. Version 2019-3. <http://www.iucnredlist.org>. (Accessed 29 January 2020).
- Jarvis, A., Reuter, H.I., Nelson, A., Guevara, E., 2008. Hole-filled SRTM for the Globe Version 4, Available from the CGIAR-CSI SRTM 90m Database. <http://srtm.csi.cgiar.org>.
- Jensen, M.P., Allen, C.D., Eguchi, T., Bell, I.P., LaCasella, E.L., Hilton, W.A., Hof, C.A.M., Dutton, P.H., 2018. Environmental warming and feminization of one of the largest sea turtle populations in the world. *Curr. Biol.* 28, 154–159.
- Jones, M.T., Willey, L.L., Akre, T.S.B., Sievert, P.R., 2015. Status and Conservation of the Wood Turtle in the Northeastern United States. Report Submitted to the Northeast Association of Fish and Wildlife Agencies for Regional Conservation Needs Grant 2011-02.
- Jueterbock, A., Smolina, I., Coyer, J.A., Hoarau, G., 2016. The fate of the Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling approach. *Ecology and Evolution* 6, 1712–1724.
- Keith, D.A., Elith, J., Simpson, C.C., 2014. Predicting distribution changes of a mire ecosystem under future climates. *Divers. Distrib.* 2, 440–454.

- Lapin, C.N., Tamplin, J.W., Cochrane, M.M., Woodford, J.E., Brown, D.J., Moen, R.A., 2019. A regional analysis of *Glyptemys insculpta* (wood turtle) survival in the Upper Midwest of the USA. *Herpetol. Conserv. Biol.* 14, 668–679.
- Lovich, J.E., Yackulic, C.B., Freilich, J., Agha, M., Austin, M., Meyer, K.P., Arundel, T.R., Hansen, J., Vamstad, M.S., Root, S.A., 2014. Climatic variation and tortoise survival: has a desert species met its match? *Biol. Conserv.* 169, 214–224.
- Lovich, J.E., Ennen, J.R., Agha, M., Gibbons, J.W., 2018. Where have all the turtles gone, and why does it matter? *Bioscience* 68, 771–781.
- Lynch, J.A., Rishel, G.B., Corbett, E.S., 1984. Thermal alteration of streams draining clearcut watersheds: quantification and biological implications. *Hydrobiologia* 111, 161–169.
- Mammola, S., Goodacre, S.L., Isaia, M., 2018. Climate change may drive cave spiders to extinction. *Ecography* 41, 233–243.
- Martin, A.K., Root, K.V., 2020. Challenges and opportunities for *Terrapene carolina carolina* under different climate change scenarios. *Rem. Sens.* 12 (5), 836.
- McCoard, K.R.P., McCoard, N.S., Turk, P.J., Anderson, J.T., 2016. Habitat characteristics that influence the occurrence of wood turtles at the southern limits of their range in the central Appalachians. *J. Herpetol.* 50, 381–387.
- McCoard, K.R.P., McCoard, N.S., Anderson, J.T., 2018. Observations of wood turtle activity, diet, movements, and morphometrics in the Central Appalachians. *Northeast. Nat.* 25, 513–531.
- Mittermeier, R.A., van Dijk, P.P., Rhodin, A.G.J., Nash, S.D., 2015. Turtle hotspots: an analysis of the occurrence of tortoises and freshwater turtles in biodiversity hotspots, high-biodiversity wilderness areas, and turtle priority areas. *Chelonian Conserv. Biol.* 14, 2–10.
- Mothes, C.C., Stroud, J.T., Clements, S.L., Searcy, C.A., 2019. Evaluating ecological niche model accuracy in predicting invasions using South Florida's exotic lizard community. *J. Biogeogr.* 46, 432–441.
- Nori, J., Lescano, J.N., Illoldi-Rangel, P., Frutos, N., Cabrera, M.R., Leynaud, G.C., 2013. The conflict between agricultural expansion and priority conservation areas: making the right decisions before it is too late. *Biol. Conserv.* 159, 507–513.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton, New Jersey, USA.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. *Science* 269, 347–350.
- Pyke, C.R., 2004. Habitat loss confounds climate change impacts. *Front. Ecol. Environ.* 2, 178–182.
- R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Radosavljevic, A., Anderson, R.P., 2014. Making better Maxent models of species distributions: complexity, overfitting, and evaluation. *J. Biogeogr.* 41, 629–643.
- Rhodin, A.G.J., Stanford, C.B., Van Dijk, P.P., Eiseberg, C., Luiselli, L., Mittermeier, R.A., Hudson, R., Horne, B.D., Goode, E.V., Kuchling, G., Walde, A., Baard, E., H.W., Berry, K.H., Bertolero, A., et al., 2018. Global conservation status of turtles and tortoises (order Testudines). *Chelonian Conserv. Biol.* 17, 135–161.
- Saumurea, R.A., Bider, J.R., 1998. Impact of agricultural development on a population of Wood turtles (*Clemmys insculpta*) in Southern Quebec, Canada. *Chelonian Conserv. Biol.* 3, 37–45.
- Saumurea, R.A., Herman, T.B., Titman, R.D., 2007. Effects of haying and agricultural practices on a declining species: the North American wood turtle, *Glyptemys insculpta*. *Biol. Conserv.* 135, 565–575.
- Segan, D.B., Murray, K.A., Watson, J.E.M., 2016. A global assessment of current and future biodiversity vulnerability to habitat loss-climate change interactions. *Global Ecology and Conservation* 5, 12–21.
- Stratmann, T.S.M., Barrett, K., Floyd, T.M., 2016. Locating suitable habitat for a rare species: evaluation of species distribution model for bog turtles (*Glyptemys muhlenbergii*) in the Southeastern United States. *Herpetol. Conserv. Biol.* 11, 199–213.
- U. S. Census Bureau, 2017. Annual Estimates of the Resident Population: April 1, 2010 to July 1, 2016.
- Ultsch, G.R., 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biol. Rev.* 81, 339–367.
- University of Virginia Weldon Cooper Center, Demographics Research Group, 2018. National Population Projections. <https://demographics.coopercenter.org/national-population-projections>.
- Urban, M.C., 2015. Accelerating extinction risk from climate change. *Science* 348, 571–573.
- U.S. Geological Survey, 2014. 1:1,000,000-Scale Streams of the United States, 2014. USGS. <http://purl.stanford.edu/fc050zj3595>.
- U.S. Geological Survey, 2019. NLCD 2016 Impervious Surface Conterminous United States. Sioux Falls, SD.
- USDA Forest Service, 2019. NLCD 2016 Tree Canopy Cover (CONUS). Salt Lake City, UT.
- van Dijk, P.P., Harding, J., 2011. *Glyptemys insculpta* (errata version published in 2016). The IUCN Red List of Threatened Species 2011: e.T4965A97416259. <https://dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T4965A11102820.en>. (Accessed 21 January 2020).
- Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21, 335–342.
- Wheeler, B.A., Prosen, E., Mathis, A., Wilkinson, R.F., 2003. Population declines of a long-lived salamander: a 20+ year study of hellbenders, *Cryptobranchus alleganiensis*. *Biol. Conserv.* 109, 151–156.
- Willoughby, J.R., Sundaram, M., Lewis, T.K., Swanson, B.J., 2013. Population decline in a long-lived species: the wood turtle in Michigan. *Herpetologica* 69 (2), 186–198.
- Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svanteson, S., Wengstrom, N., Zizka, V., Antonelli, A., 2019. CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* 10, 744–751.