THE DISTRIBUTION OF THE ELONGATED TORTOISE (Indotestudo elongata) on the Indian Subcontinent: Implications for Conservation and Management

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Abstract.—The Elongated Tortoise (*Indotestudo elongata*) is generally threatened by habitat loss, over-exploitation, and fire; however, little is known about its distribution and the specific threats it faces across its range. We used a presence-only species distribution model to determine the potential climatically suitable distribution for this species within the Indian subcontinent and then evaluated this area for fire-prone zones and protected areas. Annual precipitation, isothermality, and elevation are key predictors for the distribution of this species. Our results show that only a small percentage (5.2%) of the predicted area has a high occurrence probability for the species. On the other hand, 29% of the total predicted distribution falls within high-occurrence fire zones. Moreover, slash and burn cultivation may have a large impact on the species in the northeastern parts of India. Only 8% of the predicted distribution range falls within the network of protected areas within the Indian subcontinent. Further, a detailed finer-scale study of the habitat use would be useful to prioritize key areas for management and conservation of this endangered species on the Indian subcontinent.

Key Words.-biogeographic province; forest fire; India; niche modeling; protected area; testudines

INTRODUCTION

The tortoise genus Indotestudo currently includes three distinct species, I. elongata (Fig. 1), I. travancorica, and I. forsteni (Turtle Taxonomy Working Group 2017). Of these three species, I. travancorica and I. forsteni have limited distributions in the Western Ghats of India and on the island of Sulawesi (Platt et al. 2001a; Das and Das 2017), respectively. In contrast, I. elongata is broadly distributed across northern and northeastern India, Bangladesh, Nepal, Bhutan, Thailand, Vietnam, Cambodia, Laos, and Malaysia (Ihlow et al. 2016). In India, the species is reported from the foothills of the Himalaya, the northeastern hill forest and the Chotta-Nagpur Plateau (Smith 1931; Jayaram 1949; Frazier 1992; Das 1995, 1998). The species normally occurs in open deciduous forest patches, including Sal (Shorea robusta), as well as evergreen forest habitats, dry thorn forests and savannah grasslands (Das 2010; Ihlow et al. 2016).

Across its range, the species is threatened with habitat loss, forest fires, and over-exploitation (Choudhury 2001; Platt et al. 2007; Platt et al. 2012; Ihlow et al. 2016; Som and Cottet 2016). In recent years, several studies have pointed out the direct mortality effect of catastrophic forest fires and grass and leaf litter clearing fires set by locals during the dry season (Thirakhupt and van Dijk 1995; Hailey 2000; Platt et al. 2010; Ihlow et al. 2016; Som and Cottet 2016). The species is considered Endangered on the Red List of the International Union for Conservation of Nature (IUCN 2013; Ihlow et al. 2016) and is also listed in Appendix II (as *Testudinidae* spp.) of Convention on International Trade in Endangered Species of Flora and Fauna (CITES). It is also protected under Schedule IV of the Indian Wildlife (Protection) Act of 1972 and schedule III of the Bangladesh Wildlife (Preservation) Act.

Delineating distributions and suitable habitat of a species is an essential component for developing conservation strategies for species management at the habitat or landscape level (Ortega-Huerta and Peterson 2004). In general, species distribution models (SDM) provide a measure of the probability of presence of a species in a geographic area and aid in identifying habitat that is crucial for the management of target species (Araújo and Williams 2000; Graham et al. 2004; McFarland et al. 2013). Further, one of the fundamental requirements for large-scale habitat management is the delineation of ecologically meaningful units to provide a framework for comparison of the threats and status of ecologically similar regions (Rice et al. 2010). As a result of this requirement, biogeography has moved from a solely scholarly pursuit to an important tool for systematic conservation planning (SCP; Lourie and Vincent 2004; Whittaker et al. 2005) to protect the diverse array of species present in a planning region (Margules and Pressey 2000). Furthermore, the use of biogeographic units for conservation planning has contributed to

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FIGURE 1. Adult Elongated Tortoise (*Indotestudo elongata*) from Corbett Tiger Reserve, India. (Photographed by Abhijit Das).

policy making in multiple ways, including greater protection of biodiversity and more sustainable uses of resources beyond national jurisdictions (Rice et al. 2010; Richardson and Whittaker 2010). For example, countries such as Nepal, Bhutan, and India have emphasized transboundary conservation to safeguard Bengal Tiger (Panthera tigris) and Asian Elephant (Elephus maximus) populations in the Terai landscape which is a swampy belt of maximum width 13 km at the south of Himalaya (Borah et al. 2013). Selection of priority zones within the biogeographic units are also supported by modeling studies (e.g., Moritz et al. 2001: Sala et al. 2002: Airamé et al. 2003: Higgins et al. 2005; Richardson and Whittaker 2010), and over the past two decades, a number of international, regional and national policy developments have given increasing prominence to spatial aspects of management of wide-ranging species (Rice et al. 2010; Borah et al. 2013).

India has divided the nation into biogeographic units to ensure representation of different floral and faunal groups, ecological communities, and processes in its conservation planning (Rodgers et al. 2002). This has been done to ensure that different biogeographic zones are represented in area-based conservation approaches at the national level (Rodgers et al. 2002). In addition, international policy and management bodies have also emphasized the need for the improvement of the scientific and methodological basis for managing natural and anthropogenic activities beyond the limits of the national jurisdiction (Richardson and Whittaker 2010). Therefore, our study aimed to improve the understanding of the distribution of I. elongata to strenthen the conservation measures within the different biogeographic provinces in the Indian subcontinent by (1) identifying the environmental factors that limit the distribution and those that incorporate potentially suitable habitat, (2) identifying fire-prone zones within the modeled distribution of the species, and

(3) evaluating the current degree of habitat protection potentially afforded through the protected area (PA) network.

MATERIALS AND METHODS

Study area.—Our study area covers the known range of the species in India (Assam, Bihar, Jharkhand, Meghalaya, Mizoram, Odisha, Sikkim, Tripura, Uttarakhand, Uttar Pradesh, West Bengal), Nepal, Bhutan and Bangladesh (Das 1998; Schleich and Kastle 2002; Rahman et al. 2014; Ihlow et al. 2016). For our study, we used the biogeographic provinces delineated by Rodgers and Panwar (1988) that encompass the range of I. elongata. Rodgers and Panwar (1988) classifications are limited to within the political boundary of India, therefore we made modifications to include the remaining countries (Fig. 2). The merging of provinces that share the political boundary of Nepal, Bhutan, and Bangladesh is based on geographical features, including similar environmental conditions such as similarity in vegetation types. We encompassed the Bangladesh floodplain (including Rangpur, Rajshahi, and Dhaka Divisions) in the Lower Gangetic Plain. Nepal is considered part of the central Himalaya along with Sikkim. Bhutan is included in the Eastern Himalayas with Arunachal Pradesh. The Sylhet and Chittagong Divisions of Bangladesh are included in the North-East Hills. The Sundarban deltas of Bangladesh are included in the East Coast and Delta. The resulting study area covers about 1,731,135 km².

Niche modeling.---We used environmental niche models (ENM) to analyze the spatial distribution of I. elongata and identify key environmental variables that constrain the distribution of the species. MaxEnt is widely used in species distributional modeling, as it seems to perform better than other established methods (Phillips et al. 2004, 2006; Elith et al. 2006, 2011); however, Royle et al. (2012) suggested the use of the MaxLike occurrence model for presence only data to remedy issues that they found with MaxEnt. Subsequently, Merow and Silander (2014) found that the limitations of presence-only data constrain modelers to emphasis on relative occurrence probability and that Maxlike and MaxEnt are similarly valuable for predicting relative occurrence probability once modeling decisions have been cautiously made. Therefore, for our study, we used the Maximum entropy (MaxEnt v 3.3) species distribution algorithm (Phillips et al. 2006) to model the potential distribution of the species. We used the default parameter settings for prevalence, the regularization multiplier (Phillips and Dudík 2008, Radosavljevic et al. 2014) and background sampling density (10,000 points).

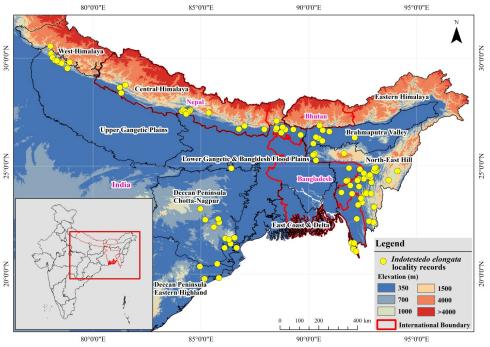


FIGURE 2. Locality records of Elongated Tortoises (Indotestudo longate) in the Indian subcontinent.

Species occurrence data.--MaxEnt is a program for modeling species distributions from presence-only species records (Phillips et al. 2006). We compiled the presence records of *I. elongata* from (1) the published literature, (2) subject experts and researchers working in the study zone, and (3) an extensive visual encounter survey in Lansdowne Forest Division (N 29.84026° E78.32388°: 433 km²) from May-September 2017 using a three person team following a random forest trail covering 450 km (75 d of field sampling, about 6 km per day) along the forest floor and stream beds. We also included a few opportunistic field records (Abhijit Das, unpublished records) of this species from the adjoining Rajaji and Corbett Tiger Reserves (Table 1). We binned the presence localities of the species into 1-km² grid cells to remove multiple presence points and retained only one presence point per grid cell (Brown et al. 2007), resulting in 103 localities for modelling the distribution of the species (see Fig. 2).

Environmental variables.—We used 19 bioclimatic variables obtained from WorldClim (Hijmans et al. 2005; Appendix 1), land cover data acquired from the Global Land Cover SHARE (https://doi.org/10.1594/PANGAEA.787668; Appendix 2), and elevation data obtained from the Global Multiresolution Terrain Elevation Data 2010 (Danielson and Gesch 2011). The bioclimatic variables are temperature and precipitation layers created by interpolation using a thin-plate smoothing spline set to a resolution of approximately 1 km, over the 30-y period from 1960 to 1990 (Hijmans et

al. 2005). We followed the methods adopted by Rissler and Apodaca (2007) for further selection of elevation and bioclimatic variables. We generated a correlation matrix of 19 bioclimatic variables along with elevation and used a Pearson correlation coefficient of 0.75 to identify highly correlated variables (Rissler et al. 2006; Appendix 3). For pairs that were highly correlated, we chose the variable that was more meaningful and easier to interpret for the niche of our study species. Ultimately, we chose the following variables for niche modelling: Isothermality, Annual Temperature Range, Annual Precipitation, Precipitation of Driest Month, Precipitation of Driest Quarter, Precipitation of Coldest Quarter, Elevation, and Land Cover.

Model selection.—We ran models with 10 crossvalidated replicates by randomly assigning the presence records as training and test datasets (90% and 10%, respectively). Additionally, we adopted a Jackknife analysis to estimate which variables were most important for model building. During this process, we excluded the environmental variable Precipitation of Driest Quarter because it gave very low information. To evaluate correspondence between model outputs and known true configurations, we calculated sensitivity and specificity and true skill statistics (TSS) in the form

TSS = 1 - sensitivity + specificity

where sensitivity is the probability that the model will correctly classify a presence and specificity is the

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Province	Place	No. of localities	Source
Western Himalaya	Phandowala	1	Frazier 1992
	Lansdowne Forest Division	1	Bhupathy et al. 1994
	Lansdowne Forest Division	4	Field Survey-Present work
	Corbett NP	4	Field Survey-Present work
	Rajaji NP	12	Field Survey-Present work
Central Himalaya	Narayani District	3	Das 1998
	Bardia NP, Beltar, Devghat, Gaighat, Kasarah, Maidhar, Mai Khola, Makwanpur, Parsa, Surkhet	10	Schleich and Kastle 2002
Eastern Himalaya	Gelephu	1	Wangyal et al. 2012
Lower Gangetic and Bangladesh	Baradighi Tea Estate	1	Das 1998
Flood Plain	Jalpaiguri District	1	Das 1998
	Jaldapara WLS, Gorumara NP	2	Choudhury et al. 2000
	Buxa TR	1	Frazier 1992
Northeast - Brahmaputra Valley	Chakrashila WLS	1	Frazier 1992
	Goalpara	1	Rhodin et al. 2017
Northeast Hill	Tulashikar District	1	Deuti and Das 2011
	Tura, West Bhanugach RF, Chittagong Hill Forest	5	Das 1998
	Ngengpui WLS, Dampa TR	2	Pawar and Choudhury 2000
	Khasi Hills and Garo Hills	1	Frazier 1992
	Mizoram Zoo	1	Santanu Kundu (pers. comm
	Barak Valley	14	Das and Gupta 2015
	Churachandpur	1	Linthoi and Sharma 2010
	Moae and Thingshul,	4	Santanu Kundu (pers. comm
	Marishbunia, Inani, Shiler Chahara, Cox's Bazar	7	Kabir et al. 2014
	Sylet and Lawachara NP	1	Rahman et al. 2014
	Teknaf WLS	1	Feeroz 2013
Coast-East Coast and Delta	Puri	1	Das 1998
Deccan Peninsula - Chotta- Nagpur	Simlipal TR	1	Das 1998
	Chaibassa	1	Das 1998
	Saranda RF	1	Das 1998
	Chhotonagpur	1	Dutta 1997
	Balasore, Keonjhar, Dhenkanal	3	Mahapatra et al. 2009
	Banapur	1	Das 1998
Indian sub-continent (within the study area)	Geo-referenced from Turtles of the World	35	Rhodin et al. 2017

TABLE 1. Locality records of Elongated Tortoises (*Indotestudo elongata*) from different biogeographic provinces of the Indian subcontinent. Abbreviations are NP = national park, WLS = wildlife sanctuary, TR = tiger reserve, and RF = reserve forest.

probability that the model will correctly classify an absence. The TSS normalize the overall accuracy by the accuracy that might have occurred by chance alone (Allouche et al. 2006). Subsequently, we used the model with highest the TSS value to prepare the distribution

map (Latinne et al. 2015; Allouche et al. 2006; Merow et al. 2013). In addition, model performance was further assessed using the receiver operating characteristic method, in which an area under curve (AUC) value of 0.7–0.8 represents acceptable models, values of 0.8–0.9

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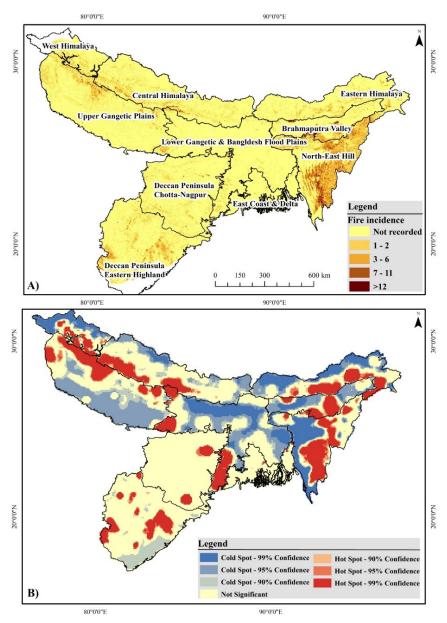


FIGURE 3. (A) Fire incidence recorded during 2000–2016 in the study area of India. (B) Fire hotspots mapped using Getis-Ord Gi statistic.

represent excellent models, and values > 0.9 represent outstanding models (Hosmer and Lemeshow 2000; Quinn et al. 2013). We calculated the significance of each environmental variables by its ability to explain the distribution of *I. elongata* by the percentage contribution assessed in the MaxEnt model. We then chose the logistic model output, which displays suitability values from 0 (unsuitable) to 1 (optimal) and we used the 10-percentile training presence logistic threshold (0.19) to create a relative occurrence probability distribution map for *I. elongata*. Subsequently, we classified the rest of the predicted area of logistic output into low (0.2– 0.5), moderate (0.5–0.75) and high (> 0.75) relative occurrence probability zones. We note, however, that relative occurrence probability can only indicate where the species is most likely to occur; it cannot determine whether the best habitat contains the species in 90% of samples, or only 10% (Merow et al. 2013).

Fire-prone zone and PA network.—To identify the fire-prone zones within the distribution of *I. elongata*, we collected historical data on the incidence of fire in the study area from 2000 to 2016 from the Fire Information for Resource Management System (FIRMS; Davies_et al. 2009; https://earthdata.nasa.gov/earth-observation-data/near-real-time/firms). Each fire location represents the center of an approximately 1-km² pixel burning area (Fig. 3a). We performed a weighted hotspot analysis

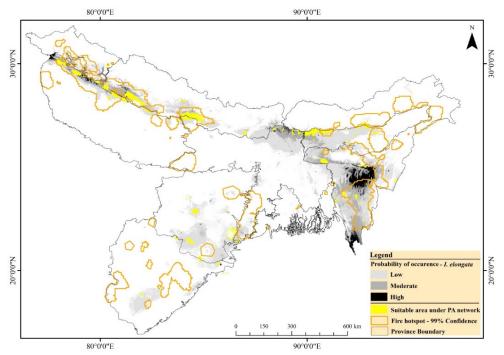


FIGURE 4. Predicted distribution map of Elongated Tortoises (*Indotestudo elongata*) showing the Protected Area (PA) network and fire prone zones in the Indian subcontinent.

individually for each province using the optimized hotspot analysis in ArcGIS 10.3, and then created a map with statistically significant hot and cold spots using the Getis-Ord Gi* statistic. Features with a Gi Bin value of -3 or +3 are statistically significant at the 99% confidence level, ± 2 bins reflects the 95% confidence level, ± 1 bin reflects the 90% confidence level, and clustering for features with a 0 Gi Bin value is not statistically significant (Getis and Ord 1992; Ord and Getis 1995; Fig. 3). We calculated area of high fire-prone zones using a 99% Gi Bin Hot spot value. Furthermore, to assess the current extent of protection received by the species as *in-situ* conservation, we overlaid the predicted range distribution with the boundaries of the PA network within the study area. We used the feature dataset of World Database on Protected Areas (WDPA) as a boundary layer for PAs of India, Nepal, Bhutan and Bangladesh (http://www.protectedplanet.net).

RESULTS

Predicted distribution range.—Our predicted map of the potential distribution for *I. elongata* has three distinctive clusters: (1) the West and Central Himalayas along with the Upper Gangetic Plains, (2) Northeast India encompassing Bhutan and Bangladesh, and (3) the Deccan Peninsular region of Chotta-Nagpur and the Eastern Highlands (Fig. 4). The area under the curve (AUC) values for the cross-validated model range from 0.910–0.926 (0.919 \pm 0.004 standard deviation); however, the models varied greatly in their classification performance (TSS = 0.35-0.50). Therefore, we prepared the final predicted distribution map using the model based on the highest TSS value (i.e., 0.50). The selected model showed that annual precipitation has the most important contribution (41.1%) in delineating the distribution of the species, followed by isothermality (20.8%), elevation (13.9%), temperature annual range (9.1%, see Fig.5), land cover (6.7%), precipitation of driest month (5.6%), and precipitation in the coldest quarter (2.8%). From the model, we inferred the potential distribution area (> 0.19 threshold value) for *I. elongata* in the study area to be 383,748 km²; however, only a small fraction of the predicted area for the species constitutes a high (5.2%; 19,977 km²) or moderate (21.9%; 84,333 km²) relative occurrence probability zone. Among the biogeographic provinces, the Northeast Hill forest comprised 31% (low: 63,349 km²; moderate: 42,739 km²; high: 15,714 km²) of the predicted distribution, followed by Central Himalaya (14%; low: 40,135 km²; moderate: 12,030 km²; high: 804 km²) and the Upper Gangetic Plains (13%; low: 17,862 km²; moderate: 10,007 km²; high: 2,113 km²; Table 2).

Fire-prone areas.—In our study area, the greatest fire incidence from 2000 to 2016 took place in the Northeast Hill province (Fig. 3a; Table 2). Accordingly, our calculation of fire-hotspots at the province level also showed that almost 29% of the total predicted area falls

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TABLE 2. Extent of different occurrence probability classes (10th percentile threshold value), area under fire, and Protected Area network of Elongated Tortoises (*Indotestudo elongata*) in different biogeographic provinces (Rodgers et al. 2002) of the Indian subcontinent. All areas are km².

		Predicte	ed area				
		ce probability		Total	Predicted area	99% hot spot fire area within	No. of fire incidence
Biogeographic Province	low	moderate	high	area	inside PA	predicted area	(2000–2016)
West Himalaya	11,737	1,260	37	13,034	172	6,645	12,200
Central Himalaya	40,135	12,030	804	52,969	9,203	24,644	44,049
Eastern Himalaya	4,841	410	14	5,265	715	1,372	32,152
Upper Gangetic Plains	17,862	10,007	2,113	29,982	5,343	19,164	56,498
Lower Gangetic and Bangladesh Flood Plains	40,983	10,097	1,087	52,167	2,267	7,227	17,424
North/ East/ Brahmaputra Valley	34,327	5,267	92	39,686	5,243	6,878	36,211
North/ East/ North-East Hill	63,349	42,793	15,714	121,856	3,331	40,718	258,779
Coast-East Coast and Delta	1,857	40	-	1,897	-	36	1,558
Deccan Peninsula/ Chotta-Nagpur	43,892	1,841	25	45,758	3,416	2,039	47,136
Deccan Peninsula/ Eastern Highland	20,455	588	91	21,134	889	915	66,036

within a regional high occurrence (99% Confidence hot spot) fire zone (Fig. 4). The majority of the fires took place from February to May (winter season) with the peak occurrence in March (Fig. 6).

Protected areas (PAs).—The overlay between the existing Protected Area Network in India, Bangladesh, Nepal, and Bhutan, and our prediction map shows that approximately 92% of the potential distribution for *I. elongata* is unprotected (Fig. 4), and fewer than 1% of protected areas overlap with the high occurrence probability zone. In relation to the predicted distribution

for *I. elongata*, Central Himalaya has the highest PA coverage, followed by the Upper Gangetic Plains and the Northeast–Brahmaputra Valley. The Northeast Hill province has the highest predicted area with the least PA coverage (2.73% of the predicted area; Table 2).

Central Himalaya and the Upper Gangetic Plains have the best representation of PAs under high occurrence probability of the species (e.g., Dudhwa Tiger Reserve, TR, Chitwan National Park, NP, Rajaji TR, Corbett TR, and Valmiki TR). In the Lower Gangetic and Bangladesh Floodplains, this species is reported from Jaldapara NP, Gorumara Wildlife Sanctuary (WLS) and

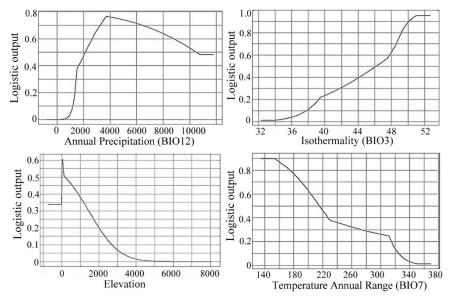


FIGURE 5. Response curves showing how key environmental variables (x-axes) affect the model predictions (i.e., suitability for the Elongated Tortoise, *Indotestudo elongata*, in the y-axis, the occurrence probability of the species).

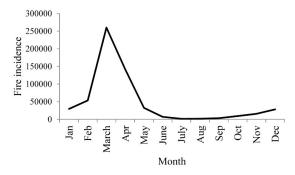


FIGURE 6. Fire occurrence trend in the study area of Elongated Tortoises (*Indotestudo elongata*) on the Indian subcontinent. (Data from: Fire Information for Resource Management System, 2000–2016; https://earthdata.nasa.gov/earth-observation-data/near-real-time/firms).

Buxa TR (Table 1). In Eastern Himalaya, our model predicted the lowland hills bordering Manas TR in the Brahmaputra Valley as suitable areas for this tortoise (Fig. 4). In Bhutan, the species is known from Gelephu region (Wangyal et al. 2012), and we have predicted the possible occurrence of the species in Phiphsoo WLS, Royal Manas NP, and Khaling WLS of Bhutan in the low elevation areas bordering Assam. In the Brahmaputra Valley, the species has been reported from Chakrashila WLS and Sal dominated Ripu-Chirang Reserve Forest in the Manas TR. Similarly, in the parts of Bangladesh under Northeast-Hill province, the species reported from both inside (Lawachara NP, Teknaf WLS, and Pablakhali WLS) and outside PAs (Chittagong Hill Tracts and Sylhet and Moulvibazar districts).

DISCUSSION

Understanding distributional patterns of threatened species is a fundamental question in conservation science. Conservation planning and implementation require determination of the habitat areas where land protection and management may improve the viability of a single or group of threatened species (McFarland et al. 2013). We provide the first predictive map of *I. elongata* distribution for the Indian subcontinent. We used a set of environmental variables to develop a species distribution model that identifies three distinct distribution clusters across a topographically diverse area. Our TSS of 0.5 indicates relatively high model accuracy, as values > 0.4are considered good (Landis and Koch 1977; Zhang et al. 2015). In addition, this model also has an AUC value of 0.92, suggesting it is reliable (Elith 2002), as models with predictive values > 0.9 are considered outstanding (Hosmer and Lemeshow 2000). We note, however, that several authors have critically discussed the drawbacks of AUC in the evaluation of predictive distribution modeling (Lobo et al. 2007, Merow et al. 2013). The present model provides a better understanding of the potential

distribution of *I. elongata* and is satisfactorily validated with TSS. We are aware, however, that some limitations may arise from the absence of important microhabitat parameters (e.g., leaf litter, ground rock cover), and biotic interactions.

Annual precipitation, isothermality, and elevation emerged as important variables in determining the distribution of I. elongata. Precipitation has been considered one of the important factors controlling life-history traits of turtles, which may include egg development, hatchling success (Tomillo et al. 2015), and availability of food resources (Mondal et al. 2016). It is also described as one of the most important variables for turtle distribution (Owen 1989). Annual precipitation approximates the total water inputs (sum of all total monthly precipitation value) and therefore may indicate the significance of water availability to the distribution of a species (O'Donnell and Ignizio 2012). In the predictive distribution zone, I. elongata occurrence probability peaks in areas of annual precipitation values between 4,000 and 6,000 mm, although a few observations of the species have been also recorded in low precipitation areas (e.g., Sivaliks) where tortoises may be using moist ravines with thick leaf litter (pers. obs.).

In addition to precipitation, temperature-associated variables like isothermality and elevation range have considerable influence on the distribution of *I. elongata*. We found that the probability of occurrence of the species is very high at places where isothermality reaches a maximum of 50%. The occurrence probability of the species is very high within the 40–50% isothermality range. We can infer from this that the species may favor areas with fluctuations in temperature. Further, we observed that the annual temperature range varies between $15-30^{\circ}$ C within the predicted range of our model. Previous studies also reported that the species withstand temperatures ranging from 2.2–48° C (Swindells and Brown 1964; Som and Cottet 2016).

This species inhabits lowlands and foothills up to approximately 1,000 m elevation within the range of the distribution of the species (Ihlow et al. 2016). In our study area, we predicted that the species ranges from 4–705 m elevation within the medium to high occurrence probability zones. Because annual mean temperature is highly correlated with elevation (Pearson correlation r = 0.99; see Appendix 3), the species may avoid colder, high elevation areas (Ihlow et al. 2016). Earlier studies have shown that the thermal physiology of tortoises is directly associated with temperature, and temperature is expected to place fundamental boundaries on distribution, as lethal temperatures go beyond those suitable for reproduction (Brattstrom 1965).

Land cover has very minimal influence on the distribution of this species; however, the predicted

model showed a positive response towards the land cover classes represented by Sal and bamboo-mixed deciduous forest in our study zone. Prior research has reported that the species occurs across diverse habitats (e.g., mountainous and hilly evergreen, mixed semievergreen, open deciduous dipterocarp, secondary forests, bamboo, pine, as well as savannah grasslands and dry thorn scrub; Ihlow et al. 2016). In the northwestern part of India and Nepal, the distribution of this species is associated with Sal-dominated forest patches (e.g., Rajaji NP, Corbett NP), whereas in northeastern parts of India it is associated with bamboo-mixed deciduous forest on lowland and hilly terrain (Barak valley-Assam, Mizoram, Manipur; Kumar et al. 2015; Pawar and Choudhury 2000; Das and Gupta 2015).

Fire is known to be harmful to this species and therefore, presumably, there is some level at which fire may limit survival and recruitment (Ihlow et al. 2016). For example, in some studies, living tortoises were found to bear fire scars covering up to two-thirds of their carapace surface (van Dijk 1998; Platt et al. 2001b). Furthermore, a few authors have reported that the frequency and intensity of the fire in the study area have increased in recent decades (Thirakhupt and van Dijk 1995; Toky and Ramakrishnan 1981), possibly surpassing a level that populations can tolerate. We believe that the Rajaji TR, Lansdown Forest Division, Corbett TR, Nandhaur Wildlife Sanctuary, Pilibhit TR, Chitwan NP, Valmiki TR, Manas TR, Nameri TR, Pakke TR, and most of the places of North-East Hill Province are areas where site managers need to take measures to prevent fire for the viability of tortoise populations. Joshi and Singh (2009) have reported that the wildfire has devastating yearly impacts in Rajaji and Corbett TR, which is at the westernmost limit of the distribution of the species (Kumar et al. 2015). In northeast India, the extensive Jhum cultivation practice that uses fire has already cleared more than 44,000 km² of forest (Lele and Joshi 2008). In recent years, the frequency of the Jhum cycle has decreased from 20-30 y to about 5-8 y, which leads to more frequent clear burning of the forest floor (Toky and Ramakrishnan 1981). Most of these fires have been reported between February to May. We recommended that special efforts such as fire line establishment, controlled burning, maintenance of forest roads, engagement of efficient fire watchers, strict vigilance and communication of fire events, vegetation and landscape management that decreases burning potential, controlling soil erosion, increasing awareness among the public, especially forest dwellers (Parsons et al. 1986, Rawat 2003, Dogra et al. 2018) should be taken by the PA managers during these months to minimize the impact of fire that could affect the sustainability of the species. Furthermore, studies that are more empirical and include monitoring are required to understand the

level of impact of fire on populations of this species. Moreover, identification of fire hot spots is useful from a policy standpoint within the context of any given region. For example, the Northeast Hill province is more fireprone than other regions and most of the suitable area for the species in this province falls outside protected area network. Therefore, additional considerations should be made both in terms of capacity building of forest frontline staff on fire management and awareness of local communities associated with Jhum cultivation for the long-term survival of the species.

PAs are considered key to safeguarding habitat for this *I. elongata* (Ihlow et al. 2016). We showed that >90% of the predicted distribution area falls outside of the PA network for the Indian subcontinent. Moreover, the PA network subset that does cover the distribution of the species is highly diffuse, with distant, fragmented PAs with little to no connectivity. Henceforth, there is an urgent requirement to conserve or restore critical habitats outside of protected areas to sustain the functional connectivity of habitat linkages for the species. We highly recommend the enforcement of community-based conservation and awareness program and formulation of sustainable resource use policy to safeguard the habitat of the species outside PAs. We also recommend raising the protection status of the Reserve Forests where the species is reported and where our distribution model has predicted moderate to high occurrence probability (e.g., Lower Jiri, Upper Jiri, Barak, Innerline, Sonai, Katakhal, Longai, Singla and Patheria hills in southern Assam. India: Das and Gupta 2015) under the Indian Wildlife (Protection) Act of 1972.

Finally, an isolated population cluster with few locality records for this species from the Deccan Peninsula, Chotta-Nagpur and Eastern Highlands of India requires systematic studies to safeguard the species in its southernmost range. Our study specifically focused on the potential distribution of *I. elongata*, its vulnerability to fire, and the identification of gaps in Protected Area coverage. It is essential to further determine small-scale response variables that influence *I. elongata* distribution and density at the landscape level. We believe that future conservation of the species will depend on increasing protected areas boundaries into regions identified as potentially suitable zones for the species.

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APPENDIX TABLE 1. Bioclimatic data (Hijmans et al. 2005) used as predictor variables to model the distribution of the Elongated Tortoise (*Indotestudo elongata*) in the Indian subcontinent. A dagger (†) indicates only these bioclimatic variables were used for final MaxEnt model run.

- BIO1 = Annual Mean Temperature
- BIO2 = Mean Diurnal Range (Mean of monthly [max temp min temp])
- BIO3 = Isothermality (BIO2 /BIO7) (* 100)†
- BIO4 = Temperature Seasonality (standard deviation *100)
- BIO5 = Max Temperature of Warmest Month
- BIO6 = Min Temperature of Coldest Month
- BIO7 = Temperature Annual Range (BIO5-BIO6)[†]
- BIO8 = Mean Temperature of Wettest Quarter
- BIO9 = Mean Temperature of Driest Quarter
- BIO10 = Mean Temperature of Warmest Quarter
- BIO11 = Mean Temperature of Coldest Quarter
- BIO12 = Annual Precipitation⁺
- BIO13 = Precipitation of Wettest Month
- BIO14 = Precipitation of Driest Month⁺
- BIO15 = Precipitation Seasonality (Coefficient of Variation)
- BIO16 = Precipitation of Wettest Quarter
- BIO17 = Precipitation of Driest Quarter⁺
- BIO18 = Precipitation of Warmest Quarter
- BIO19 = Precipitation of Coldest Quarter*

APPENDIX TABLE 2. Land cover class (https://doi.org/10.1594/PANGAEA.787668) used as predictor variable to model the distribution of the Elongated Tortoise (*Indotestudo elongata*) in the Indian subcontinent.

Post-flooding or irrigated croplands (or aquatic)

Rainfed croplands

Mosaic cropland (50–70%) / vegetation (grassland /shrubland /forest) (20–50%)

Mosaic vegetation (grassland /shrubland /forest) (50–70%) / cropland (20–50%)

Closed to open (> 15%) broadleaved evergreen or semi-deciduous forest (> 5m)

Closed (> 40%) broadleaved deciduous forest (> 5m)

Open (15–40%) broadleaved deciduous forest/woodland (> 5m)

Closed (> 40%) needleleaved evergreen forest (> 5m)

Open (15–40%) needleleaved deciduous or evergreen forest (> 5m)

Closed to open (> 15%) mixed broadleaved and needleleaved forest (> 5m)

Mosaic forest or shrubland (50-70%) / grassland (20-50%)

Mosaic grassland (50-70%) / forest or shrubland (20-50%)

Closed to open (> 15%) (broadleaved or needle-leaved, evergreen or deciduous) shrubland (< 5m)

Closed to open (> 15%) herbaceous vegetation (grassland, savannas or lichens/mosses)

Sparse (< 15%) vegetation

Closed to open (> 15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water

Closed (> 40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water

Closed to open (> 15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water

Artificial surfaces and associated areas (Urban areas > 50%)

Bare areas

Water bodies

	BI01	BI02	BI03	BI04	BI05	BIO6	BI07	BI08	BI09	BI010	BI011	BI012	BI013	BI014	BI015	BI016	BI017	BIO18	BI019
Elevation	96.0	0.08	0.24	0.18	0.88	0.95	0.06	66.0	0.91	0.95	96.0	0.25	0.32	0.21	0.37	0.32	0.25	0.01	0.35
BIO1		0.03	0.30	0.18	0.92	0.97	0.12	0.98	0.92	0.98	0.98	0.17	0.26	0.27	0.43	0.26	0.32	0.12	0.40
BI02			0.42	0.84	0.30	0.25	0.93	0.02	0.13	0.15	0.16	0.68	0.48	0.49	0.69	0.54	0.46	0.57	0.26
BI03				0.59	0.56	0.18	0.72	0.29	0.43	0.44	0.20	0.46	0.27	0.25	0.65	0.31	0.16	0.60	0.04
BI04					0.14	0.39	0.87	0.08	0.06	0.01	0.35	09.0	0.42	0.26	0.58	0.49	0.15	0.43	0.08
BIO5						0.83	0.47	06.0	0.92	0.98	0.86	0.13	0.05	0.41	0.69	0.02	0.43	0.40	0.40
BIO6							0.10	0.92	0.85	0.91	66.0	0.30	0.35	0.16	0.27	0.36	0.22	0.02	0.33
BIO7								0.15	0.30	0.31	0.03	0.69	0.46	0.47	0.80	0.52	0.41	0.67	0.19
BIO8									0.92	0.96	0.94	0.17	0.26	0.25	0.42	0.25	0.29	0.06	0.37
BIO9										0.94	0.87	0.03	0.16	0.28	0.56	0.14	0.31	0.22	0.30
BIO10											0.94	0.03	0.17	0.33	0.57	0.15	0.38	0.25	0.40
BI011												0.25	0.31	0.22	0.32	0.32	0.30	0.06	0.40
BIO12													0.93	0.43	0.38	96.0	0.32	0.89	0.10
BI013														0.26	0.05	66.0	0.18	0.79	0.02
BIO14															0.59	0.28	0.81	0.46	0.70
BIO15																0.13	0.58	0.49	0.42
BIO16																	0.19	0.81	0.01
BIO17																		0.38	0.92
BI018																			L1 0

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