Diversity and Distributions, (Diversity Distrib.) (2016) **22**, 1199–1211

A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY RESEARCH

Predicted Pleistocene–Holocene range shifts of the tiger (*Panthera tigris*)

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ABSTRACT

Aim In this article, we modelled the potential range shifts of tiger (*Panthera tigris*) populations over the Late Pleistocene and Holocene, to provide new insights into the evolutionary history and interconnectivity between populations of this endangered species.

Location Asia.

Methods We used an ecological niche approach and applied a maximum entropy (Maxent) framework to model potential distributions of tigers. Bioclimatic conditions for the present day and mid-Holocene, and for the Last Glacial Maximum (LGM), were used to represent interglacial and glacial conditions of the Late Pleistocene, respectively.

Results Our results show that the maximum potential tiger range during modern climates (without human impacts) would be continuous from the Indian subcontinent to north-east Siberia. During the LGM, distributions are predicted to have contracted to southern China, India and Southeast Asia and remained largely contiguous. A potential distribution gap between Peninsular Malaya and Sumatra could have effectively separated tigers on the Sunda Islands from those in continental Asia during interglacials.

Main conclusions The continuous modelled distribution of tigers in mainland Asia supports the idea of mainly unimpeded gene flow between all populations throughout the Late Pleistocene and Holocene. Thus, our data support a pragmatic approach to tiger conservation management, especially of mainland populations, as it is likely that only recent anthropogenic changes caused separation of these populations. In contrast, Sunda tigers are likely to have separated and differentiated following the Last Glacial Maximum and thus warrant separate management.

Keywords

ecological niche model, evolutionary history, maximum entropy, *Panthera tigris*, Pleistocene distribution, Toba.

INTRODUCTION

Tigers are endangered and occupy only a small fraction of their historical range (Walston *et al.*, 2010). The changing isolation or interconnectivity of tiger populations has wide-ranging implications for both *in situ* and *ex situ* conservation efforts, as conservationists currently aim to preserve what are assumed to be genetically distinct populations whilst attempting to strengthen the numbers of captive and wild tiger populations. This article presents a new, geographically based assessment of changes in tiger distribution during the Late Pleistocene and Holocene, to understand the degree of natural connectivity between separate tiger populations and thus inform current conservation efforts.

With a large subcontinental-scale geographical range, it is not surprising that tigers display morphological variation in response to regional differences in climate and habitat. This differentiation is reflected in the recognition of up to nine subspecies of tiger (Goodrich *et al.*, 2015; but see Wilting *et al.*, 2015; Fig. 1a), and these are the focus of current

DOI: 10.1111/ddi.12484
http://wileyonlinelibrary.com/journal/ddi

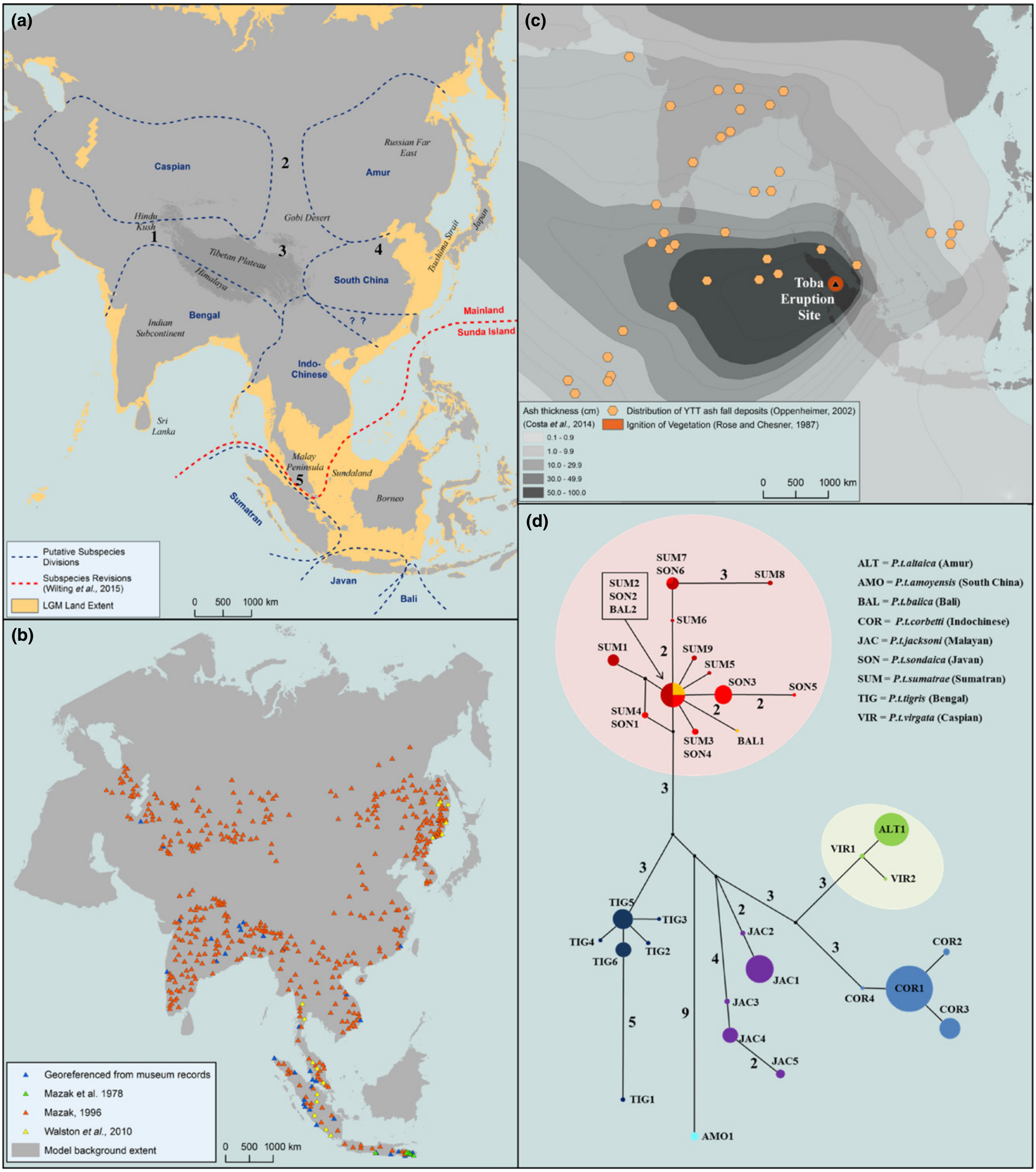

Figure 1 (a) Established subspecies divisions (Mazák, 1996) and revised divisions (Wilting *et al.*, 2015). Potential corridors for tiger dispersal between populations are (1) Southern/Himalayan Corridor, (2) Northern Corridor and (3) Gansu/Silk Road Corridor (Driscoll *et al.*, 2009). (4) Huanghe river catchment and site of human agricultural civilization ca. 8 ka, (5) Additional recognition of a Malayan tiger (*P.t. jacksoni*) (Luo *et al.*, 2004). (b) Tiger locality data, coloured by data source, with the background extent used for modelling. (c) Effects of the 73 ka Toba super-eruption. The initial eruption effects, cooler temperatures and drought induced by the ejecta, followed by rapidly decreasing tree cover in the decades following the Toba eruption, might have been responsible for genetic bottlenecks in Southeast Asia (Robock *et al.*, 2009; Williams *et al.*, 2009; Wilting *et al.*, 2011, 2012). (d) Haplotype network of nine putative subspecies (Wilting *et al.*, 2015) – circle size is proportional to haplotype frequency; lines represent a single mutational step, or multiple steps as indicated by numbers.

conservation efforts. However, the scientific integrity of so many subspecies has been questioned (e.g. Herrington, 1987; Kitchener, 1999; Kitchener & Yamaguchi, 2010; Wilting *et al.*, 2015). It is possible these apparent patterns of variation are the result of genetic drift due to increasing recent fragmentation of tiger populations (Luo *et al.*, 2004; Mondol *et al.*, 2013), but lack conservation and evolutionary significance (Wilting *et al.*, 2015). Although the fossil record of the tiger stretches back more than 2.5 million years (Mazák *et al.*, 2011), studies of mitochondrial DNA have estimated that the most recent common ancestor for today's tiger populations existed 72–108 ka (Luo *et al.*, 2004; Wilting *et al.*, 2015). As a result, environmental changes in the Late Pleistocene and Early Holocene are most relevant when trying to understand differentiation of today's local tiger populations. For example, Sunquist (1981) suggested that the initial adaptive radiation of modern tigers may have occurred during the Pleistocene glaciations when Southeast Asian climates were drier (Whitmore, 1984), sea levels were lower, the Sunda Islands were linked by land to the Asian mainland, and insular and mainland populations could mix. Subsequent sea-level rises isolated tigers of the Sunda Islands from mainland tigers and each other, possibly leading to local differentiation. In addition to range changes driven by glacial cycles, the super-eruption of Toba ca. 73 ka in northern Sumatra (Fig. 1c) may have played a key role in the evolutionary history of tigers through extensive habitat loss. This eruption produced around 2500–3000 km^3 of dense rock-equivalent pyroclastic ejecta (Rose & Chesner, 1987) with associated Younger Toba tuff (YTT) deposits found in cm–scale thicknesses across the Indian subcontinent (Acharyya & Basu, 1993; Shane *et al.*, 1995), and at a thickness of more than four metres close to the Toba caldera (Oppenheimer, 2002). The outflow of m-scale deposits of YTT could have resulted in the ignition of vegetation across 30,000 km^2 around the caldera (Oppenheimer, 2002).

The evolutionary history of modern tiger populations has been assessed phylogenetically based on geographically referenced specimens (or at least specimens from known putative subspecies) and the analysis of mitochondrial DNA (Cracraft *et al.*, 1998; Luo *et al.*, 2004; Driscoll *et al.*, 2009; Wilting *et al.*, 2015; Xue *et al.*, 2015), and/or nuclear microsatellite genotypes (Luo *et al.*, 2004). A haplotype network was constructed by Wilting *et al.* (2015) (Fig. 1d). Phylogenetic approaches to understanding tiger populations are constrained because they are based on limited sampling of already fragmented populations (Luo *et al.*, 2004). Additionally, current phylogeographical studies, for example Luo *et al.* (2004), Driscoll *et al.* (2009) have only a limited spatial component (Waltari *et al.*, 2007; Kozak *et al.*, 2008). To help understand phylogeographical patterns seen today, there is a need for a geographically explicit understanding of the expansion and contraction of tiger ranges during glacial/interglacial cycles.

The understanding of the evolutionary history of tigers is of great importance for the successful conservation of this highly threatened species. Recognizing too few differentiated populations could see the loss of important evolutionary diversity, but recognizing too many would lead to a waste of resources and may compromise conservation efforts because some remaining populations are too small to survive (Bay *et al.*, 2014). In contrast to some molecular studies which support high differentiation among mainland tiger populations (Luo *et al.*, 2014; but see Wilting *et al.*, 2015), Kitchener & Dugmore (2000) used a biogeographical approach and their results showed a considerable contiguity between mainland tiger populations. However, 16 years have elapsed since that research was undertaken, and there is scope for radical improvement using new and improved modelling techniques and data. Here, we examine the global distribution of the tiger using a maximum entropy (Maxent) niche modelling approach to reconstruct the current range of the tiger based on bioclimatic variables, assuming no human impacts. We further modelled the global ranges at the LGM and mid-Holocene to represent the maximum range of bioclimatic variation to impact tiger distribution and to assess potential differentiation by isolation since modern populations originated ca. 100 ka.

METHODS

Tigers need access to water, and they require dense vegetation cover of sufficient area to support large ungulates and to hunt their prey successfully (Nowell & Jackson, 1996). Therefore, the modelling approach used here assumes that tigers are generalists, operating within certain kinds of vegetation cover, and prey size and abundances that are dictated by climate. Climate is a key factor in defining ecological niches and the geographical distribution of species at continental scales (Geffen *et al.*, 2004; Varela *et al.*, 2010) and has been used to model megafaunal ranges (Varela *et al.*, 2010; Lorenzen *et al.*, 2011). Niche models, comparing recent and fossil locality records, have shown that mammal species have tracked consistent climate profiles since the LGM (Martínez-Meyer *et al.*, 2004) and therefore climate change may be used to infer differences in mammal range as it is unlikely that a generalist, adaptable carnivore such as the tiger has shifted climatic niche through the Late Pleistocene.

Tiger locality records were taken from Mazák (1996) (448 locations), Walston *et al.* (2010) (16 locations), Mazák *et al.* (1978) (7 locations) and 40 localities georeferenced from European museum specimens (Fig. 1b). The records cover the geographical extent of the known distribution of tigers in modern times and likely represent the potential climatic niche of the tiger, but it cannot be discounted that human extirpation of the tiger has reduced the potential niche space represented by our records. Nine contemporary WorldClim bioclimatic variables (Hijmans *et al.*, 2005), in combination with the tiger localities, were used to produce a global habitat suitability model for the tiger using Maxent.

Of *presence only* modelling techniques, Maxent models have been shown to perform as well or better than other existing approaches (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Phillips *et al.*, 2006). Hernandez *et al.* (2006) found that MAXENT performed well regardless of the number of species records or the geographical extent of records, compared to Mahalanobis Typicalities and Random Forests methods. MAXENT software (Phillips *et al.*, 2006) was used for modelling. In addition to MAXENT, a boosted regression tree (BRT) model was created for comparison (see Appendix S1 in Supporting Information). Models were created using WorldClim variables at a 2.5-arc-minute resolution (<5 km), which is between one and two orders of magnitude less than the scale of individual tiger ranges. This resolution was chosen to show potential habitat suitability through narrow geographical corridors such as through valleys or mainland connections to peninsulas which may affect gene flow between tiger populations. Elevation was not included as a separate independent variable because it is accounted for in the bioclimatic datasets. In contrast to Kitchener & Dugmore (2000), vegetation data, such as Biome 4 (Kaplan *et al.*, 2003), have not been included in the model, because they can decrease performance in predicting presences compared to models based only on climatic variables (Martínez-Meyer *et al.*, 2004). A comparison with Biome 4 data was used as a post-modelling measure of validity, by checking that modelled high habitat suitability does not occur in highly unfavourable habitats (Desert and Tundra), as they are unequivocally not recognized as tiger habitat (Nowell & Jackson, 1996).

Highly correlated variables were removed from the modelling process to reduce over-parameterization and loss of predictive power (Buermann *et al.*, 2008; Garcia-Porta *et al.*, 2012). The removal of highly correlated variables ($r \geq 0.8$), calculated using ArcGIS Band Collection Statistics (ARCMAP v10.1), from the 2.5-arc-minute WorldClim bioclimatic dataset reduced the number of variables from 19 to nine (annual mean temperature, mean diurnal range, isothermality, mean temperature of the wettest quarter, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, precipitation of the coldest quarter). Where one or more variables were highly correlated, the one deemed most important was selected using indicators, such as performance in a jackknife test (Pearson *et al.*, 2006).

MAXENT models were run under settings so as to fit a Poisson point-process model –'noremoveduplicatepresencerecords' and 'noaddsamplestobackground', with final projections displaying MAXENT raw output (Renner *et al.*, 2015). MAXENT models were evaluated under a range of settings to assess their effects on model performance – see Appendix S1 for a full analysis of parameter selection. Final MAXENT models were run using a regularization multiplier (RM) of 2, and 100,000 background points. Ideally, models would be evaluated with independent observation data; however, these data are not available. Instead, cross-validation was performed using replicates in MAXENT to assess each model. Ten runs of each model were performed, and the mean area under the receiver operating characteristic curve (AUC) was used as a measure of overall performance (Phillips & Dudík, 2008). Additionally, spatially independent cross-validation was performed using the checkerboard2 method implemented via the ENMeval package (Muscarella *et al.*, 2014) in R (R Core Team, 2015) to reduce the potential effects of spatially autocorrelated localities, which may inflate the AUC (Veloz, 2009). Checkerboard2 was implemented with coarse grids 200 and 400 times the resolution of the bioclimatic variables (~450 km^2 and ~900 km^2 at the equator, respectively) to ensure considerable geographical separation of training and testing localities. Models were run over a geographical extent covering the known and potential distribution of the tiger (82° N to 10° S, 20° W to 144° E). Africa and islands not connected to continental Asia during glacial conditions, such as those east of the Wallace's Line, were removed from the extent before modelling.

Following assessment, the model was fitted using all localities and projected to the LGM at 21 ka and mid-Holocene at 6ka, using WorldClim data derived from the MIROC-ESM, CCSM-4 and MPI-ESM-P coupled general circulation models (GCMs) (Hijmans *et al.*, 2005) based on CMIP5 (Taylor *et al.*, 2012) data. Model clamping was implemented to restrict variables to the range of values encountered during training. An ensemble projection was created for the mid-Holocene and LGM based upon the mean raw value of the projected models from the three coupled GCM datasets for each time period. The individual projections and range of the projection values can be viewed in Appendix S1. The present/mid-Holocene and LGM climates provide bounding values of the climatic fluctuations of the Pleistocene and thus likely represent environmental changes that influenced tiger distribution and potential range shifts. Whilst the present and mid-Holocene both represent interglacial climatic conditions, with both periods exhibiting similar global annual mean temperature and precipitation, the mid-Holocene is associated with an enhanced seasonal cycle in the Northern Hemisphere and wetter conditions within eastern Asia (Braconnot *et al.*, 2007; Tao *et al.*, 2010), which may have affected tiger distributions.

Georeferenced fossil records of the tiger from the Late Pleistocene (Kitchener & Yamaguchi, 2010) are presented on the relevant glacial/interglacial habitat suitability map based on their estimated age (Fig. 2a,b). The Late Pleistocene distribution of the ancestors of the modern lion (*Panthera leo*) and of the Eurasian cave lion (*Panthera leo spelaea*) (Barnett *et al.*, 2009) have been superimposed onto modelled tiger distributions [Fig. 3(6)], because where open habitat is dominant, it is expected that the group-living modern lion, and likely group-living Eurasian cave lion (Yamaguchi *et al.*, 2004) would out-compete tigers and prevent their dispersal. Estimates of ashfall from the very large scale volcanic eruption of Toba ca. 73 ka (Costa *et al.*, 2014) have also been added post-modelling [Fig. 3(1)] to assess their potential impacts on tiger distributions. The minimum values of the raw output between present day, mid-Holocene and LGM projections are presented in Fig. 3[~73ka(+1k)], to represent a rapid shift from interglacial to glacial conditions during the 1000 years following the Toba eruption (Rampino & Self, 1992; Harris, 2008).

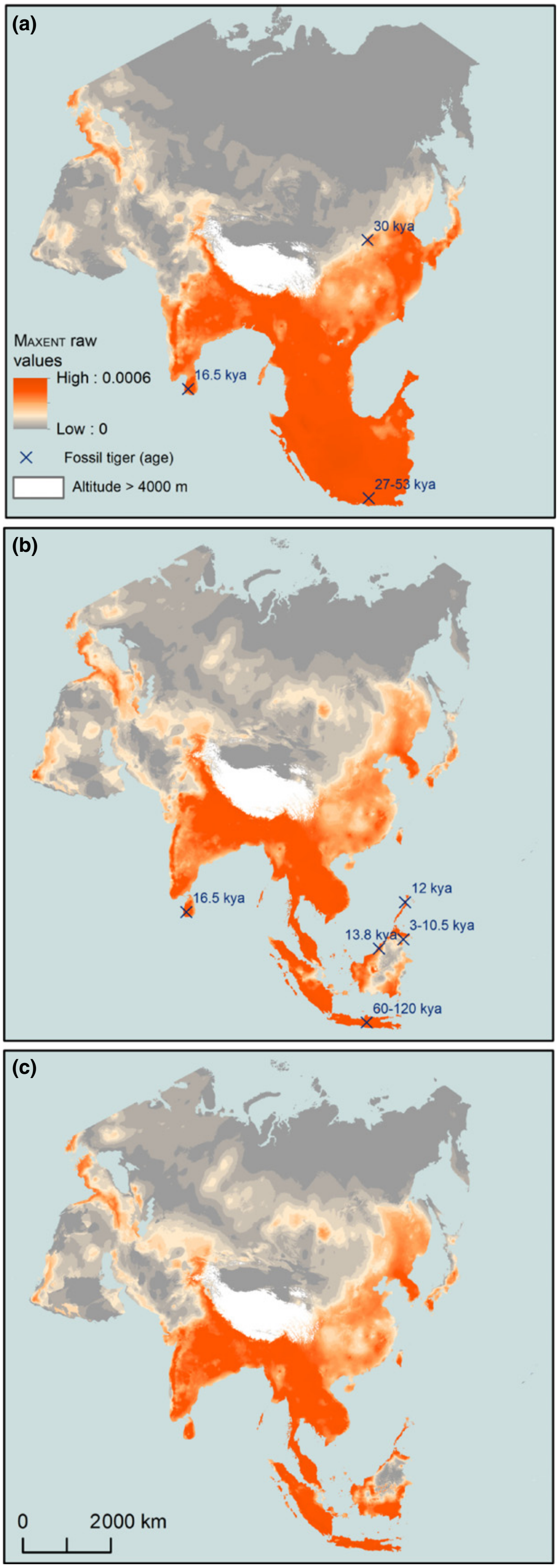

Figure 2 Raw Maxent output displaying modelled tiger habitat suitability based on nine bioclimatic variables, projected using an Asia Lambert Conformal Conic Projection, for the LGM (a), mid-Holocene (b) and present day (c). Elevations > 4000 m (highlighted in white) have been included as a possible barrier to dispersal. Fossil tiger localities are laid over glacial (a) and interglacial (b) projections in accordance with the fossil age (note 16.5 kya from Sri Lanka is included in both scenarios due to the transitionary time period following the LGM).

RESULTS

The tiger distribution model run under final parameters with cross-validation produced a mean AUC of 0.843, representing the probability of a randomly chosen presence locality being ranked above a random background point (Phillips *et al.*, 2006). The same parameters, but run with spatially independent cross-validation, gave a mean AUC of 0.780. Under a point-process framework, the Maxent raw projection is viewed as the intensity of potential locality reportings within a given area (Renner *et al.*, 2015), which for our projected models can be interpreted in terms of habitat suitability. Model sensitivity is further discussed in Appendix S1 – conclusions regarding tiger distributional changes from our chosen Maxent model are consistent with Maxent models created under a range of parameters, and with a simply implemented BRT model.

The fossil record of tigers corresponds well with predicted habitat suitability maps for glacial/interglacial conditions (Fig. 1a,b), although this evaluation method is limited by the scarcity of dated archaeological finds. A comparison of model projections with unfavourable vegetation provides support for past outputs, as strong modelled habitat suitability has not occurred in biomes deemed unfavourable (Appendix S1). Modelling the likely ranges for present-day climate (Fig. 2a) indicates a potentially contiguous tiger distribution from southern India to the Amur region, and presence throughout the Malay Peninsula, Sumatra, Java and Bali. The present model suggests that tigers in the Caspian region existed within suboptimal habitat, and likely connected through corridors of favourable habitat to tiger populations in northern India, and the Amur region. The core areas of tiger habitat, defined as those suitable at present, mid-Holocene and during the LGM (Fig. 1a–c), exist within the Indian subcontinent and Southeast Asia.

DISCUSSION

The present-day model corresponds well with the Habitat Topography Precipitation model of present tiger distribution (Kitchener & Dugmore, 2000) and historic tiger distributions during the Holocene (Dinerstein *et al.*, 2006). However, the present model predicts low habitat suitability for central and northern Borneo, whereas past studies have modelled this as suitable habitat (Kitchener & Dugmore, 2000). One implication is that simple associations with forest cover, annual

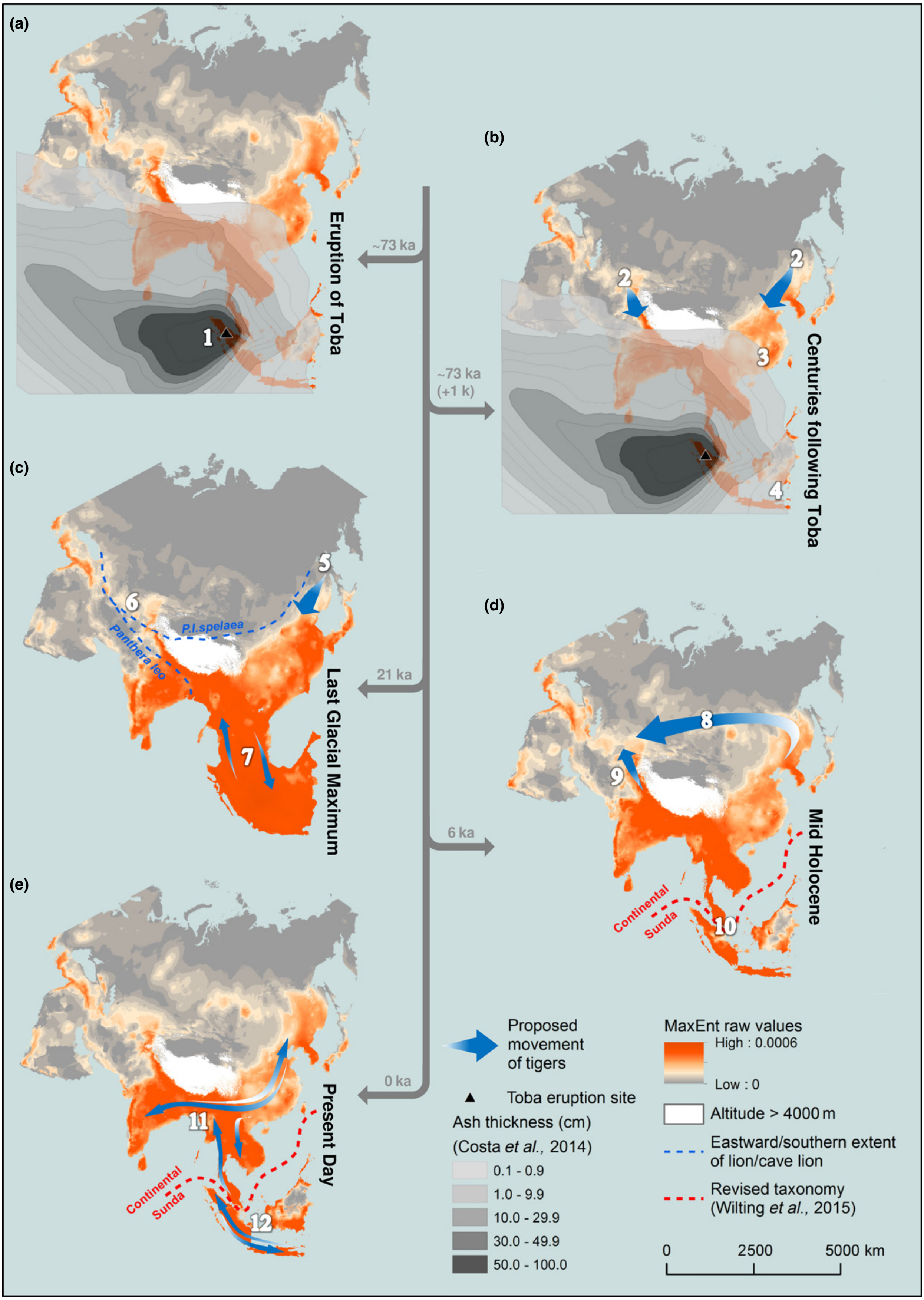
(a)
Eruption of Toba
1
~73 ka
(b)
Centuries following Toba
2
2
3
4
~73 ka
(+1 k)
(c)
Last Glacial Maximum
5
6
7
P.l.spelaea
Panthera leo
21 ka
(d)
Mid Holocene
8
9
10
Continental
Sunda
6 ka
(e)
Present Day
11
12
Continental
Sunda
0 ka
Proposed movement of tigers
▲ Toba eruption site
Ash thickness (cm)
(Costa et al., 2014)
0.1 - 0.9
1.0 - 9.9
10.0 - 29.9
30.0 - 49.9
50.0 - 100.0
MaxEnt raw values
High : 0.0006
Low : 0
Altitude > 4000 m
Eastward/southern extent of lion/cave lion
Revised taxonomy (Wilting et al., 2015)
0
2500
5000 km

Figure 3 Proposed range shifts of the tiger since the ~73 ka eruption of Toba (a) (1). Immediate impacts (1), and millennial scale cooling (b), likely reduced the northern range (2), leading to a probable refugium (3), associated with the genetic bottleneck of the tiger. Suitable (but fragmented) habitats (4) were unlikely to have harboured the tiger during this time due to a single source of molecular variation. The northern range of the tiger would have been suppressed by unfavourable conditions at the LGM (c) (5), and Caspian/western Indian marginal habitat may have been impacted by the distribution of the lion (6). LGM conditions likely allowed the free movement of the tiger between the Sunda Islands and the continent (7). Post-LGM conditions (d) saw the retreat of the lion range, which, along with more favourable habitat suitability, would have allowed the colonization of the Caspian region via a northern corridor (8), southern corridor (9) or concurrent corridors (8 + 9). Tigers would have been separated by rising sea levels following the LGM through the Strait of Malacca (10), leaving a contiguous population of Continental tigers (11), and Sunda tigers which were likely able to disperse between islands until modern times (e) (12).

rainfall and altitude (Kitchener & Dugmore, 2000) do not reflect the true variability in habitat suitability. Our modelled low habitat suitability on Borneo, compared to Sumatra, Java and Bali, shows that, whilst still forested, the environmental conditions of Borneo are different from those of the other Sunda Islands. Using the 'explain' tool in Maxent (see Appendix S1), it is apparent that precipitation seasonality is the driving factor behind modelled habitat suitability with lower precipitation seasonality causing lower suitability. Borneo exhibits lower prey densities than the other Sunda Islands, associated with seasonal precipitation events that affect flowering and fruiting (Wong *et al.*, 2005), which have been linked to the absence of large carnivores in Borneo (Meijaard, 2004; Wong *et al.*, 2005). Whilst tigers may have been present in Borneo up until recent times (Hooijer, 1963), decreasing habitat suitability from glacial to interglacial conditions, as suggested by Harrison (1996) and supported by our modelling, may have contributed to an extirpation driven by human impacts. It is likely that the inclusion of more complex environmental variables, which incorporate seasonal environmental variability, has highlighted important bioclimatic differences between the Sunda Islands that mirror significant ecological variation.

A key difference between our LGM model and those of previous biogeographical studies is the favourable habitat suitability modelled within the Indian subcontinent, which was predicted as poor habitat by Kitchener & Dugmore (2000). Whilst habitat suitability is reduced in the northern range of the tiger, such as Siberia, it is expanded within the Sunda Shelf and may have led to an increase in overall available tiger habitat during glacial conditions compared to interglacial conditions. Reduced habitat suitability found around the Caspian during the LGM (Fig. 2a) diminishes the likelihood of a viable population during glacial conditions in this region.

The modelling reported here does not support the dispersal of tigers through the Silk Road/Gansu Corridor [Fig. 1(a) – route 3] from China to central Asia and the Caspian (Driscoll *et al.*, 2009). Even considering marginal environments suitable only for dispersal (Fig. 2), this route is deemed improbable. More likely is a colonization of the Amur region from northern China, followed by a post-LGM westward dispersal of tigers through a northern corridor [Figs 1(a) – route 2, 3(8) & 4(d–f)]. Considering the potential rapidity of tiger dispersal – individuals have been known to travel up to 1000 km (Kitchener, 1999), then it is probable that use of the northern corridor and gene flow through optimal interglacial and seasonal conditions would have resulted in low genetic variation between the Amur and Caspian tigers, and this is supported by molecular studies (Driscoll *et al.*, 2009; Wilting *et al.*, 2015).

Significant areas of suitable habitat are modelled along the southern route between the Indian subcontinent and the Caspian during interglacial conditions [Figs 1(a) – route 1, 3(9) & 4(a–c)]. However, a lack of genetic affinity between Caspian and Bengal tigers (Driscoll *et al.*, 2009) argues against this route. Whilst the elevation of the southern route falls within the limits of known tiger dispersal [tigers have been found at altitudes of 4000 m in Bhutan (Sangay & Wangchuk, 2005)], the Hindu Kush mountain range extends directly through the modelled corridor (Fig. 4a–c), and may have acted as a significant barrier to tiger dispersal. A higher tree line in northern Bhutan [4750 m (Miehe *et al.*, 2007)] compared with the central Hindu Kush [3200 m (Schickhoff, 2005)] could account for the presence of tigers at higher altitudes in Bhutan. Alternatively, given the strength of habitat suitability through the southern corridor, colonization of the Caspian may have occurred through simultaneous dispersal via Siberia and the northern corridor and through the southern corridor [Fig. 3(8, 9)].

The Maxent models indicate suitable tiger habitat through the Indian Subcontinent during the LGM, and this is supported by evidence of tigers in Sri Lanka 16.5 ka (Fig. 2a), a time when lower, glacial, sea levels would have allowed colonization from India (Manamendra-Arachchi *et al.*, 2005). Whilst our models appear to show a connection between Korea and Southern Japan during the LGM, which could have allowed the movement of tigers, a 20 km wide Korean/Tsushima Strait existed between the two land masses throughout the LGM (Park *et al.*, 2000) which is 33% further than tigers have been known to swim across seas, even under more benign conditions, and was likely too inhospitable a barrier to allow dispersal. Therefore, it is probable that the extinct Japanese tiger colonized the islands during a previous glacial period, when eustatic sea levels were lower than at the LGM (Rohling *et al.*, 1998), and thus represents a distinctly different population from mainland tigers, as proposed by Kitchener & Dugmore (2000).

The extent of the Toba super-eruption ashfall, in relation to likely suitable tiger habitat at the time, can be seen in Fig. 3(1). Whilst it is probable that many mammal species were able to survive the Toba eruption in geographically

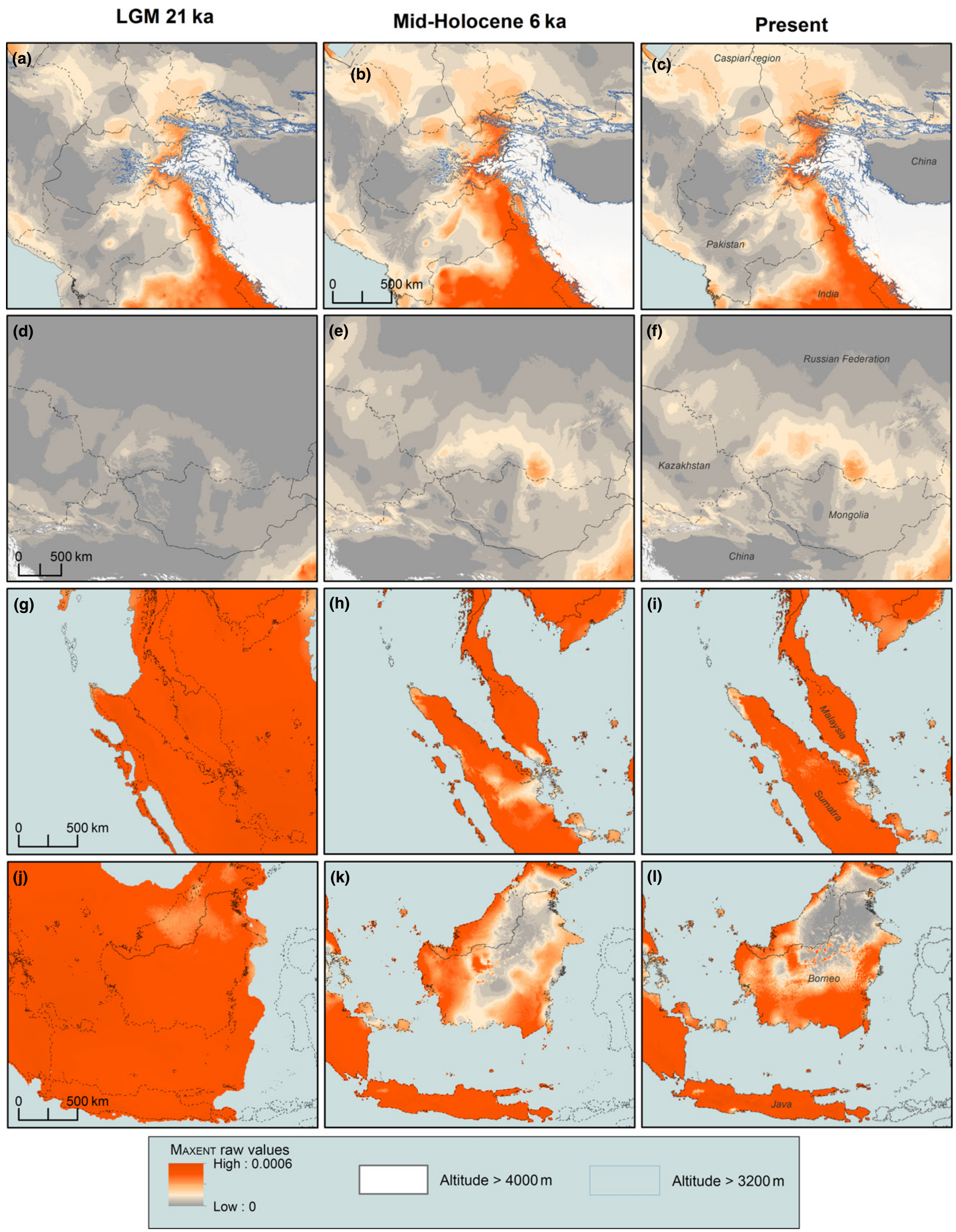

Figure 4 Detailed view of final model projections for the LGM, mid-Holocene and present conditions. In addition to elevations > 4000 m (white areas), included as a possible barrier to tiger dispersal, elevations > 3200 m are shown between India and the Caspian region (a–c) to delineate the regional tree line. Further image tiles show the proposed northern corridor between Amur and Caspian populations [(d–f)], the continental/Sundaland divide (g–i) and range shifts within the Sunda Islands (j–l).

isolated refugia (Prothero, 2004; Louys, 2007), large carnivorans, such as the tiger, are likely to have been particularly susceptible to extinction if confined to limited areas, owing to their requirement for large home range sizes (O'Regan *et al.*, 2002), a notion supported by a demographic reconstruction of the tiger during the Late Pleistocene (Wilting *et al.*, 2015). It is conceivable that direct damage caused by the YTT, and rapid cooling and drought in the following decades, was responsible for the eradication of tigers from most, if not all of, Sumatra and the Malay Peninsula, and might have significantly impacted populations farther afield.

In addition to the direct and indirect environmental effects of the Toba eruption, tigers could have been affected by cooler, stadial conditions lasting around 1000 years after the eruption (Rampino & Self, 1992; Harris, 2008). A subsequent shift from interglacial to glacial conditions (or from present day to LGM tiger distributions by proxy) and its impact on woodlands would have limited the recovery of tigers in the areas affected by Toba [Fig. 3 – ~73ka(+1k)]. An exception could have occurred within the Sunda Islands, where a glacially driven decrease in global sea level during this time (Chappell & Shackleton, 1986) may have allowed the recolonization of Sumatra from Java through temporary land bridges. Even if this opportunity was missed, tigers swim well and have been known to cross rivers 29 km wide and expanses of sea 15 km wide (Kitchener, 1999), so it is conceivable that tigers could have swum between the Sunda Islands even after land bridges were inundated. Indeed, it is likely that tigers swam between Java and Bali into recent times (Kitchener, 1999) a notion supported by the genetic similarity between Javan and Bali tigers, and high morphological affinity between all Sunda Island tigers (Wilting *et al.*, 2015; Fig. 1d).

Southern China/Southeast Asia and the eastern Sunda Islands of Java and Bali represent the 'core' areas of the modelled tiger range that have endured through both glacial and interglacial periods, and they lie outside the major ash fallout zones of the Toba eruption. However, a Sunda Island refugium is unlikely because of the phylogenetic position of the putative South China tiger (*P.t. amoyensis*), which suggests it is ancestral to other tiger lineages (Luo *et al.*, 2004; Driscoll *et al.*, 2009; Wilting *et al.*, 2015), and indicates a population collapse and re-dispersal out of southern China/south-eastern Asia during the Late Pleistocene, including into the Sunda Islands.

At the LGM, and into post-glacial times until the 19th century, suitable habitats existed in India for both the ancestors of modern lions and tigers [Fig. 3(6)], enabling them to be sympatric, but in separate habitats. Indeed, the latest phylogeographical study of lions suggest that they entered the Indian subcontinent around the LGM (Barnett *et al.*, 2014), because of more arid conditions at that time. The disappearance of Eurasian cave lions from northern Asia around 11 ka (Barnett *et al.*, 2009) coincided with climatic and vegetation shifts that favoured the western dispersal of tigers throughout this region, so it is difficult to assess the extent to which competition may have limited one species or the other. The presence of both modern lions and Eurasian cave lions in the Near East may have reinforced the separation between tiger populations of the Indian Subcontinent and the Caspian region.

Our models indicate a recent northern dispersal of tigers, beginning after the LGM, and before the mid-Holocene Climatic Optimum. It is likely that the early rise of civilizations in China, especially along the rivers of the Huanghe catchment over 8 ka (Kong, 1992) resulted in local extirpations of tigers and thus reduced contact, and division between northern continental tigers (Caspian and Amur populations) and southern continental tigers (remaining mainland populations). Major early impacts on Chinese tiger populations are likely because of the danger posed to both humans and livestock, their prized fur and use in traditional medicine. This is supported by studies which show that Amur/Caspian populations are genetically close to Indochinese tigers (Driscoll *et al.*, 2009; Wilting *et al.*, 2015; Fig. 1d), suggesting that there has been insufficient time for any local genetic differentiation despite current isolation of northern populations. However, given their dispersal outside of the core Late Pleistocene habitat of southern Asia, their adaptation to a temperate ecosystem, and their longer term separation compared to more recently fragmented populations of mainland tiger, our results complement the recognition of separate conservation management of northern continental tigers from that of southern continental tigers, as proposed by Wilting *et al.* (2015).

The modelling we present indicates there has been significant separation between continental and Sunda Island populations of tigers since the Last Glacial Maximum, which led to significant population differentiation. This has been proposed by previous genetic, morphological and biogeographical studies (Cracraft *et al.*, 1998; Kitchener, 1999; Kitchener & Dugmore, 2000; Kitchener & Yamaguchi, 2010; Mazák, 2010). There is a clear disparity between current classifications that recognize up to nine tiger subspecies and the contiguity between continental tiger populations during the period of the adaptive radiation of modern populations over the last ca. 100 ka. In comparison with the contiguity of continental tigers, and their proposed post-LGM northward radiation, it is suggested that Asiatic lions constitute the same Evolutionary Significant Unit as North African lions, despite radiating to their currently fragmented position ~21 ka (Barnett *et al.*, 2014). Whilst biogeographical models are not taxonomic tools for deciding the validity of species and subspecies, they provide a deeper time framework against which to judge the significance of genetic and morphological differences between the fragmented populations of today. Thus, they can inform current conservation strategies for endangered widespread species, such as the tiger, and be used to question traditional taxonomies that are based on poor levels of evidence. The scale-dependent nature of taxonomy (Crandall *et al.*, 2000) benefits from an understanding of the changing relationships between populations through space and time. This broader biogeographical approach adds important perspectives to current debates about what we are trying to conserve both in the wild and captivity, and adds additional scientific weight to arguments for more pragmatic and realistic approaches to conservation.

CONCLUSIONS

Using a niche modelling approach, we have been able to reconstruct the probable dynamic range shifts of the tiger during the Late Pleistocene and Holocene, a period when genetic data suggest that modern populations colonized southern and eastern Asia. We project that throughout this period the tiger's core distribution was in south-eastern Asia, southern China and eastern Sundaland and that tigers colonized north-eastern and central Asia from south-eastern Asia. Owing to continuing geographical contiguity during glacial–interglacial cycles, which allowed for continuing potential gene flow, corroborated by recent molecular studies (Wilting *et al.*, 2015), there is a clear disparity with classifications that recognize six subspecies among mainland populations. The separation of the Sunda Islands from the mainland through sea-level rise since the LGM is consistent with the recognition of potential island population differentiation.

The notion that mainland tiger populations remained contiguous with each other through the Late Pleistocene until Holocene anthropogenic impacts fragmented populations has significant implications for management and conservation. The recognition of only two tiger subspecies (Sunda – *Panthera tigris sondaica,* and Continental tigers – *Panthera tigris tigris*), with the later split into northern and southern populations, which are proposed as separate continental management units (Wilting *et al.*, 2015), would benefit current tiger conservation efforts by allowing more genetic interchange between currently isolated and limited populations. The biogeographical modelling presented here supports only a significant differentiation between Continental and Sundaland tiger populations and thereby offers important insights relevant to both future research and discussions on current tiger conservation.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge support from NERC PhD studentship NE/L002558/1 to D.M.C. and National Science Foundation award 1249313 to A.J.D.

We thank Jane Elith and the anonymous referees for their invaluable comments and suggestions throughout the review process.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Ecological niche model evaluation, parameter selection and projection process to past conditions.

BIOSKETCH

David M. Cooper is a PhD student and biogeographer whose research focuses on the evolutionary history of big cats over the Late Pleistocene and Holocene. Thus, far ecological niche modelling onto past climatic conditions has been a key theme.

D.M.C., A.J.D., A.C.K. and B.M.G. are members of the Vertebrate Biogeography Research Group at the National Museums of Scotland and University of Edinburgh. This group brings together research in taxonomy, morphometrics and phylogeography in the Department of Natural Sciences at the National Museums of Scotland, with physical geography, ecology, GIS and modelling in the School of GeoScience at the University of Edinburgh.

Author contributions: A.C.K., A.J.D. and D.M.C. designed the research; A.W., A.K.S. and D.M.C. collated the data; D.M.C, A.C.K., A.J.D. and B.M.G. performed the research; all co-authors contributed to writing that was led by D.M.C.

Editor: Jane Elith