



Going back for the future: Incorporating Pleistocene fossil records of saiga antelope into habitat suitability models

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Abstract

Aim: Many species have suffered anthropogenic range contraction and no longer occupy all available suitable environmental conditions. This is particularly problematic for the construction of habitat suitability models (HSMs), which assume that a species' contemporary range reflects its full species–environment relationship. HSMs therefore risk underestimating suitable environment areas, and misinforming conservation decisions. Incorporating historic (centuries-old) records partly reduces this bias, but even these records are also subject to human disturbance. We incorporated fossil records of the critically endangered saiga antelope (*Saiga tatarica*, L., 1776), alongside historic and current records, into current and future habitat suitability models. Saiga has experienced drastic range contraction and may have a truncated species–environment relationship. The results allowed us to test whether its current habitat provides optimal environmental conditions, or whether saiga should be considered a refugee species.

Location: Northern Hemisphere.

Taxon: *Saiga tatarica* (Bovidae, Artiodactyla).

Methods: We collated historic and fossil saiga occurrence records from published literature, museum archives and global databases. Modern occurrence records were obtained from the International Union for Conservation of Nature Red List assessment. Four bioclimatic variables were downloaded from Worldclim.org. HSMs were generated through Maxent, using the *maxnet* package in R. Three HSMs were developed: present only, present historic and present fossil. Each of these models was projected onto current and two future (2070) climate change scenarios.

Results: Saiga fossil records increased the predicted suitable environment area by 783% and 1416% for current and future climate projections respectively. Our results suggest the saiga is not a refugee species but occupies only a portion of its potential environmental niche. The saiga's contemporary range is predicted environmentally suitable throughout all models and projections, and therefore in situ conservation management is recommended.

Main Conclusions: This study highlights the importance of incorporating fossil records into HSMs to better understand species–environment relationships and develop more robust conservation strategies for appropriate endangered species.

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KEYWORDS

conservation palaeobiology, habitat suitability, niche truncation, Pleistocene fossils, *Saiga tatarica*, species distribution model

1 | INTRODUCTION

Amid the ongoing biodiversity crisis, there has been increased scientific recognition of the need to recover species populations and designate specific protected areas for conservation, whilst also considering future climate change forecasts (Dinerstein et al., 2017). Effective conservation strategies over short and long-term time scales require reliable information on species' environmental requirements (Asaad et al., 2017). However, many species have experienced extensive geographic range contractions driven by both natural and anthropogenic factors, the latter beginning during the Late Pleistocene (Faurby & Svenning, 2015; Martínez-Freiria et al., 2016). In the past 50 years, 50% of non-volant mammal species have experienced range contractions, with 20% losing over half of their range through anthropogenic pressures (Pacifi et al., 2020). Species currently absent from large portions of their former range may experience a truncated species–environment relationship, whereby their current range does not reflect the full range of environmental conditions in which they could occur (Faurby & Araújo, 2018; Monsarrat, Novellie, et al., 2019). For some species, referred to as refugees, species–environment truncation is so pronounced that they now only occur within suboptimal habitats of their former range (Cromsigt et al., 2012). For instance, research suggests the European Bison (*Bison bonasus*, L., 1758) now inhabits sub-optimal forest environments, whereas its evolutionary background is more characteristic of an open grassland species (Cromsigt et al., 2012; Kerley et al., 2012). Not accounting for truncated species–environment relationships risks misinforming our understanding of suitable environmental conditions and limiting the scope of current and future conservation strategies (Bush et al., 2018; Faurby & Araújo, 2018; Monsarrat, Novellie, et al., 2019).

Addressing species–environment truncation is particularly important within the field of habitat suitability modelling. Habitat suitability models (HSMs) are a widely used conservation tool that relate species occurrence records to environmental variables (Elith & Leathwick, 2009; Monsarrat, Novellie, et al., 2019). Their application within conservation includes predicting suitable sites for reintroductions (Ardenstani et al., 2015; Jarvie & Svenning, 2018), quantifying a species' environmental niche (Vetaas, 2002) and assessing species invasions (Dullinger et al., 2009; Lozier & Mills, 2011; Ward, 2007). A problematic assumption of HSMs is that the contemporary occurrence records of a species reflect its full species–environment relationship. Failure to recognise species–environment truncation can subsequently cause HSMs to underestimate where suitable environments could occur (Barbet-Massin et al., 2010; Bleyhl et al., 2015). Analysis of such outputs for climate change forecasts may shift baselines and misinform conservation strategies by underestimating future species richness and overestimating local extinction

rates (Barbet-Massin et al., 2010; Cromsigt et al., 2012; Faurby & Araújo, 2018; Papworth et al., 2009). One way to overcome species–environment truncation when generating HSMs is via the use of historic occurrence records in combination with contemporary range data to generate the models (e.g. Chatterjee et al., 2012; Lentini et al., 2018; Monsarrat, Novellie, et al., 2019; Owen et al., 2000). However, whilst historic records can provide a more extended temporal insight into species–environment relationships than contemporary ranges alone, these records still fail to account for historic anthropogenic range contractions and subsequent truncation (Faurby & Svenning, 2015; Veloz et al., 2012).

Incorporating deeper-time fossil occurrence records, and temporally associated palaeoenvironment data, into HSMs may better capture the species–environment relationship prior to the onset of extensive anthropogenic pressures and range contractions (Chiarenza et al., 2023). The fossil record contains long-term distribution and ecological data on species responses to past climatic change (Myers et al., 2015; Waterson et al., 2016). In particular, fossil records can capture the occupied niche of a species during multiple climate episodes, which may vary due to changes in environmental parameters through time (Maguire et al., 2015). This gives an insight into the species' fundamental niche, the multidimensional abiotic space occupied indefinitely, as well as any changes to the realised niche overtime (e.g. range shifts, contractions and evolutions), which together can improve the overall predictive ability of HSMs (Jones et al., 2019; Myers et al., 2015).

One such species that may benefit from incorporating fossil occurrence records into HSMs is the saiga antelope (*Saiga tatarica*, Linnaeus 1776). The saiga antelope is a non-territorial, long distance migratory species that today occupies the dry steppes and semi-arid environments of central Asia (Singh, Gracher, et al., 2010; Vremir, 2004). Five populations exist, one in south-west Russia, three in Kazakhstan and one in Mongolia (Jürgensen et al., 2017). The climate governing saiga range is strongly continental, with warm summers, up to 28°C, and severe winters, down to –45°C (Harrington & Cinq-Mars, 1995). The species' is perceived to be restricted to areas with snow depths <20 cm, as deeper snow impedes foraging leading to potential malnutrition and starvation (Sher, 1968). Saiga is also believed to require flat topography, having been observed walking round the slightest obstruction (Heptner et al., 1961). Their diet is variable, including grasses, summer cypress (*Bassia scoparia*) and lichens, with individuals covering long distances to find suitable forage (Bannikov et al., 1961).

Until recently, saiga was considered critically endangered (IUCN, 2018) having experienced over 90% population decline since the early 20th century, predominantly from poaching of male horns for traditional Chinese medicine (Milner-Gulland et al., 2003; Singh, Grachev, et al., 2010). Saiga is also threatened by extreme climate

events, particularly severe winters and mass disease outbreaks (Kock et al., 2018). Saiga is now classified as near threatened due to population recovery (IUCN, 2023). Owing to their fluctuating conservation status, modelling globally suitable environmental conditions under current and future climate scenarios is important for the conservation of the species, especially if the population continues to grow and additional habitat areas are required. However, as saiga has experienced extensive range contraction, they may be occupying a reduced set of environmental conditions with a truncated species–environment relationship and realised niche. Potentially a refugee species, using their contemporary range data alone risks biasing or limiting suitability projections and misinforming subsequent conservation management decisions (Milner-Gulland et al., 2001).

However, saiga has a vast Late Pleistocene (125–11.7kya BP) fossil record, with palaeontological evidence indicating the greatest geographical distribution during the Last Glacial Period, where they occurred from England, across Eurasia, to the Northwest Territories of Canada (Campos et al., 2010; Sher, 1974). Multiple saiga dispersal events are recorded from the Last Interglacial Period (125kya BP) onwards, analysis of which has revealed that contemporary saiga occupy just a portion of their potential environmental niche (Jürgensen et al., 2017; Nadachowski et al., 2016). Incorporating the species' fossil records into HSMs may broaden understanding of the species–environment relationship, prior to extensive range contraction.

Here, we modelled suitable environmental, predominately climate, conditions for saiga antelope under current and future (2070) climate projections using Late Pleistocene fossil records in combination with historic and contemporary range data. Multitemporal HSMs have been used by the palaeontological community for various applications, including understanding extinction events (Varela et al., 2010), locating glacial refugia areas (Schmickl et al., 2010), documenting Neogene horse diversification (Maguire & Stigall, 2008) and tracing climatic range shifts in Cenozoic birds (Saupe et al., 2019). More recently, palaeo HSMs have predicted the vulnerability of specific groups to future climate change forecasts, including reptiles (Chiarenza et al., 2023; Waterson et al., 2016), corals (Jones et al., 2019) and birds (Crees et al., 2023; Lentini et al., 2018). Although some studies have used historic and early Holocene records to model contemporary environmental suitability for extant terrestrial mammals (e.g. Chatterjee et al., 2012; Gavin et al., 2014; Laliberte & Ripple, 2004; Lima-Ribeiro et al., 2017; Monsarrat, Jarvie, & Svenning, 2019; Monsarrat, Novellie, et al., 2019), this study is one of few, if any, to incorporate deeper time, Late Pleistocene (ca. 125kya BP), mammalian fossil records into HSMs for current and future projections. We predict that including saiga fossil records into HSMs will increase the amount of suitable environmental conditions predicted globally for saiga compared with contemporary and historic occurrences alone, under both current and future climate change scenarios. We further predict that the inclusion of saiga fossil records into HSMs will broaden the saiga's species–environment relationship and reveal that species–environment truncation is invisible when using contemporary and historic occurrence records alone.

2 | MATERIALS AND METHODS

2.1 | Saiga occurrence data

Two datasets of saiga occurrence records were constructed for this study: present and past. The present contains modern saiga records from 1950 onwards and was obtained from the International Union for Conservation of Nature (IUCN) red list assessment of saiga antelope (IUCN, 2018). Presence points were randomly sampled with the IUCN range polygons for saiga. The past contains fossil and historic records from the Last Interglacial (140–120kya), Last Glacial Period (30–22kya), Heinrich Stadial 1 (17–14.7kya), Bølling-Allerød (14.7–12.9kya), Younger Dryas Stadial (12.9–11.7kya), Holocene (11.7kya–275AD) and historic (275AD – 1950) periods. These records were obtained from published academic research, museum collections and global databases, including GBIF (Global Biodiversity Information Facility) and PBDB (Paleobiology Database) (see Appendix S1 in Supporting Information).

Fossil records are prone to spatial, temporal and environmental bias (Jones et al., 2019; Maguire et al., 2015; Varela et al., 2011), therefore extensive efforts were made to reduce this (following Crees et al., 2019; Monsarrat et al., 2019; Monsarrat & Kerley, 2018). Spatial and environmental bias can occur from opportunistic fossil collection without using modern protocols (Monsarrat et al., 2018). To account for this, records within 20km of one other were spatially thinned using the *spThin* package in R, v. 4.2.0 (Alello-Lammens et al., 2019). Temporal bias also exists, with younger fossils more common than older specimens (Valentine, 1974). To reduce this bias, eight different time periods from ca. 125kya – 1950 were sampled. Only saiga specimens georeferenced and dated at specific excavation sites were used. For any records with potentially dubious identifications, additional verification was sought from academics and museum curators to eliminate any incorrectly identified specimens (Newbold, 2010).

2.2 | Environmental variables

Two types of environmental (predictor) variables were used: climate and topography (Table 1). These variables are ecologically meaningful to saiga and represent some important environmental requirements or limiting factors in their distribution (Costamagno, 2001; Cui et al., 2017). All environmental variables were standardised to 5km grid cells (2.5 arcminutes) resolution using the *raster* package in R v. 4.2.0 (Hijmans et al., 2020). The variables were assessed for collinearity using the variance inflation factor (VIF) (Dormann et al., 2013). Environmental variables with VIF values >3, indicating high multicollinearity and potential statistical bias, were excluded (Craney & Surlis, 2002; Zuur et al., 2010).

Four bioclimatic variables were downloaded for the following time periods: present (1970–2000), Mid-Holocene (6kya BP), Younger Dryas Stadial (12.9–11.7kya BP), Bølling-Allerød (14.7–12.9kya BP), Heinrich Stadial 1 (17–14.7kya BP), Last Glacial Maximum (30–22kya

TABLE 1 Environmental predictor variables used in the habitat suitability models for saiga antelope.

Type	Variable	Indicator	Source
Climate (past, current, future)	BIO 11—mean temperature of the coldest quarter	Snow depth	WorldClim.org; PaleoClim.org
Climate (past, current, future)	BIO 14—precipitation of the driest month	Water availability	WorldClim.org; PaleoClim.org
Climate (past, current, future)	BIO 18—precipitation of the wettest quarter	Water availability	WorldClim.org; PaleoClim.org
Climate (past, current, future)	BIO 19—precipitation of the coldest quarter	Snow depth	WorldClim.org; PaleoClim.org
Topography	Slope	Topographic steepness	Global-Multi resolution Terrain Elevation Data 2010 (GMTED, 2010)

BP) and Last Interglacial period (140–120 kya BP) (see Appendix S2) from WorldClim and Palaeoclim websites (Hijmans et al., 2005). For future 2070 climate, the same four bioclimatic variables were downloaded for two different emission scenarios, RCP 2.6 (warming $\leq 2^\circ\text{C}$) and RCP 8.5 ('business as usual') averaged over 2061–2080 (see Eyring et al., 2016; Hausfather, 2020). Current climate variables were downloaded from WorldClim v. 2.1, based on the latest CMIP6 climate projections (Fick & Hijmans, 2017). The past and future climate variables were sourced from WorldClim v. 1.4, based on CMIP5, as newer climate data were not available at the time of writing. Topographic steepness was considered using slope elevation data from the Global Multi-resolution Terrain Elevation Dataset 2010 (GMTED, 2010) available at EarthEnv.org.

2.3 | Habitat suitability models

2.3.1 | Maxent

Habitat suitability models were generated through Maxent, using the *maxnet* and *glmnet* packages in R v. 4.2.2 (Phillips, 2017). Maxent is a statistical method for characterising a species probable distribution using occurrence and environmental data (Pearson et al., 2007; Phillips et al., 2006). Maxent was chosen over other modelling approaches as it requires presence only data and has been found to perform well, if not better, than other methods across a range of ecological data types (Ardenstani et al., 2015; Elith, 2010; Poor et al., 2012). To reduce the inherent sampling bias in the saiga occurrence records Maxent's 'presence-background' approach was employed. This approach compares the environment from the presence records with the environment from generated background points (Lentini et al., 2018). Buffers of 500km were created around the presence records for each time period, from which 10,000 background points, as per Maxent's default settings, were generated (Lui et al., 2005).

2.3.2 | Model types

Three habitat suitability models for saiga were developed: present only, present historic and present fossil. Each of these models was

then projected onto current and future (2070) RCP 2.6 and 8.5 climate scenarios (see Appendix S3 and S4). Once these projections were established, gridded raster layers of global forest cover, icesheets and glaciers, downloaded from the Global Land Analysis and Discovery, National Oceanic and Atmospheric Administration and the Randolph Glacier Inventory, respectively, were overlain onto the projections. Each projection's cell values were then reclassified, using the *reclassify* function in R v. 4.2.2, to N/A for cells with dense forest cover, ice sheets or glaciers and 1 for cells without these features (Hijmans et al., 2020). The *mask* function was then applied to the projections to exclude the N/A values, as these values represent areas with dense forest or ice cover, which are known to be unsuitable habitat for the saiga (Currant, 1987).

2.3.3 | Model performance

Spatial blocking was applied to each model to allow an assessment of the model's predictive performance. Spatial blocking partitions the model into training data, to create the model and testing data, to assess model performance (Guevara et al., 2018). This process is required as ecological data frequently exhibits spatial and temporal structure, and without spatial blocking this can remain unaccounted for leading to predictive error (Roberts et al., 2017). The R package *blockCV* v. 4.2.0 and the functions *spatialAutoRange* and *spatialBlock* were used (Valavi et al., 2018).

Predictive model performance was assessed through the area under the curve (AUC). The AUC represents a threshold measure of predictive performance, with values indicating the probability that random locations will be accurately predicted (Hoffman et al., 2008). The values categorise model outputs as excellent (>0.9), good ($0.8 < \text{AUC} \leq 0.9$), acceptable ($0.7 < \text{AUC} \leq 0.8$), bad ($0.6 < \text{AUC} \leq 0.7$) and invalid ($0.5 < \text{AUC} \leq 0.6$) (Ardenstani et al., 2015; Pearce & Ferrier, 2000). The Continuous Boyce Index (CBI) was used as a second predictive performance test (Manzoor et al., 2018). Values range from -1 for counter predictions, 0 for random predictions and $+1$ for predictions consistent with actual occurrence data (Hirzel et al., 2006). Models were assessed for overfitting through two omission rates: minimum training presence (ORMTP) and 10% omission rate (OR10). Overfitting occurs when models are too complex and begin to describe random errors rather than the relationship between occurrence data and environmental

variables (Boria et al., 2014). Omission values that are close to or equal to zero are indicative of high-quality models without overfitting (Radosavljevic & Anderson, 2014). In addition, the 10% omission rate sets a threshold value that excludes 10% of localities with the lowest prediction (Gonzalez & Anderson, 2011).

Finally, the response curves for each model were calculated. Response curves are used to determine how each predictor variable influences model predictions (Mercow et al., 2013). Response curves were calculated by changing one predictor variable whilst the others were held constant (Hortal et al., 2008).

3 | RESULTS

From our review of published literature, global databases and museum collections, a total of 177 past and 200 modern saiga occurrence records were obtained. The past occurrence records are dated to the following time periods: 29 from the Last Interglacial, 129 from the Last Glacial Period (7 from the Younger Dryas Stadial, 30 from Bølling-Allerød, 31 from Heinrich Stadial 1, 61 from the Last Glacial Maximum), nine from Holocene and 10 the historical period. The occurrence records are located exclusively in the Northern Hemisphere, across sites within North America and Canada, Europe, Russia and Central Asia (Figure 1).

Model performance metrics revealed AUC values of 0.88 (good) for the present only, 0.9 (excellent) for the present historic and 0.82

(good) for the present fossil, indicating good predictive accuracy across all models (Table 2). The CBI values of 0.942 (present only), 0.929 (present historic) and 0.981 (present fossil) also demonstrate good model performance with predictions consistent to the actual occurrence data. None of the models are considered overfit as the omission rate values are close to or equal to zero. Overall, the test results suggest very good predictive performance for all three models, with the present fossil model having the highest CBI value, and the two past models (present historic and present fossil) having the lowest omission rates.

Under current climate conditions, the addition of historic saiga occurrence records into the model increased the predicted area of suitable environmental conditions (>0.8 AUC) predicted by 113% (336,475.6 km²), compared with modern occurrence records alone (Figure 2). The inclusion of fossil records into the present fossil model, increased the area of predicted suitable environmental conditions by 783% (2,327,572.2 km²) (Figure 3). Additional areas predicted suitable outside the saiga's present range include Turkmenistan, Iran, Turkey and northern China, as well selected regions of Greenland, Iceland and Northern Canada (Figure 2c). Unsuitable saiga habitat (<0.2 AUC) increased by 0.67% with the addition of historic records and decreased by 26.13% with fossil records (see Appendix S5).

In the future 2070 climate projections, the addition of historic saiga records increased the predicted area of suitable environments by 288% (449,531.7 km²) and 472% (519,720.5 km²) in RCP 2.6 and 8.5, respectively, compared to the present only models

FIGURE 1 World map with the locations of the saiga antelope occurrence records used in the habitat suitability models. Yellow circles are the saiga's modern IUCN range, blue circles are historic records, green triangles are Holocene, purple diamonds are Younger Dryas Stadial 1, pink diamonds are Bølling-Allerød, brown diamonds are Heinrich 1 Stadial, red diamonds are the Last Glacial Maximum and orange squares are the Last Interglacial Period.

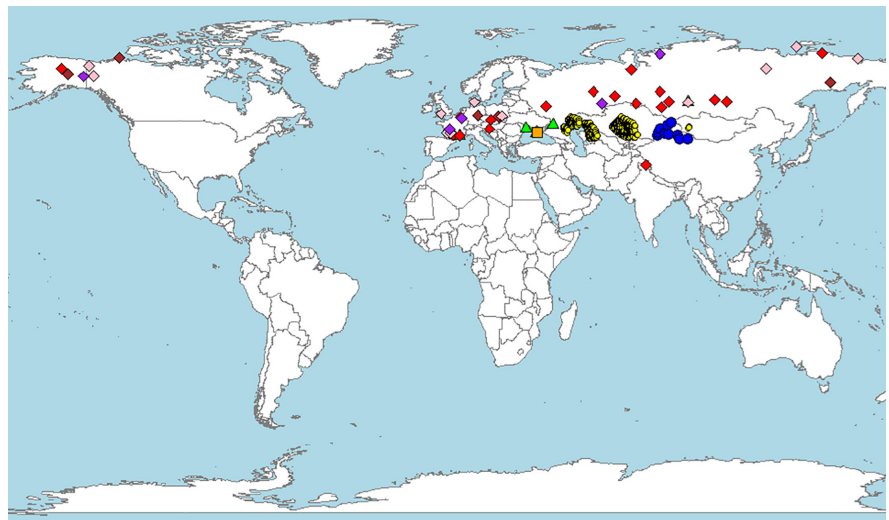


TABLE 2 Model performance metrics and standard deviations for the three habitat suitability models produced for saiga antelope: present only, present historic and present fossil.

Model	AUC	SD	CBI	SD	ORMTP	SD	OR10	SD
Present only	0.877	0.028	0.942	0.033	0.021	0.024	0.374	0.069
Present historic	0.9	0.037	0.929	0.022	0	0	0.321	0.251
Present fossil	0.821	0.043	0.981	0.011	0.001	0	0.257	0.041

Abbreviations: AUC, Area under the curve, CBI, Continuous Boyce Index, ORMTP, minimum training presence; OR10, 10% omission rate.

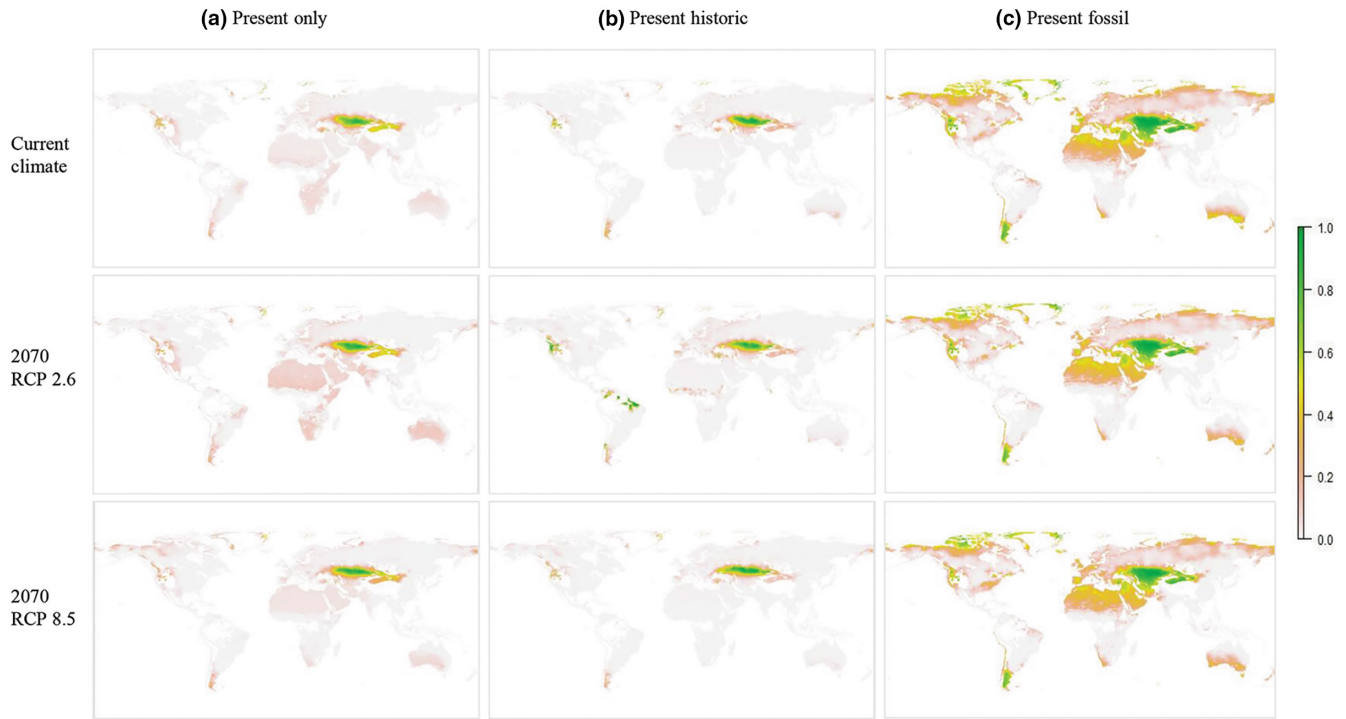


FIGURE 2 Global habitat suitability models for saiga antelope for current climate conditions, and future 2070 RCP 2.6 and RCP 8.5 climate projections, with (a) present only records, (b) present and historic records and (c) present, historic and fossil records. The scale represents predicted environmental suitability of saiga, with 1 representing highly suitable environments and 0 representing unsuitable environments.

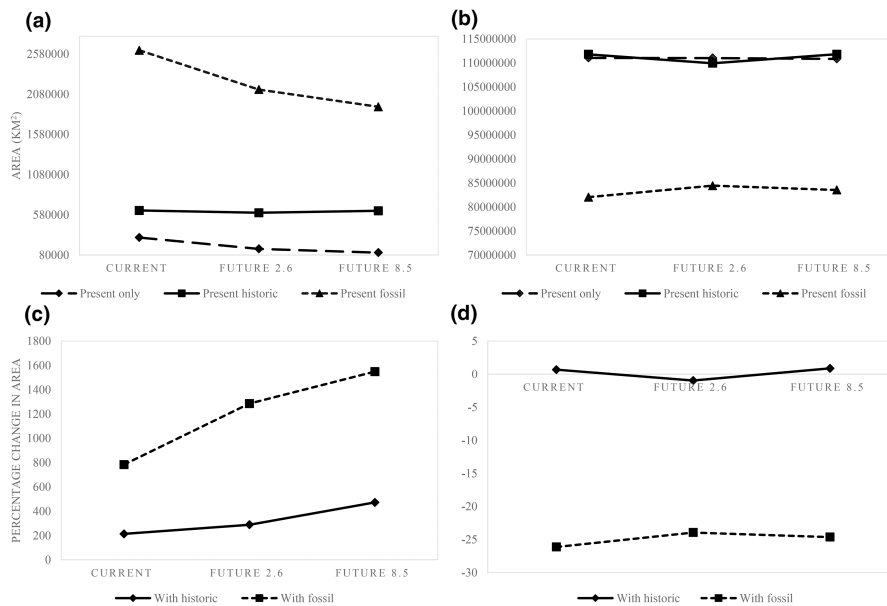


FIGURE 3 The area of predicted suitable (>0.8) and unsuitable (<0.2) environmental conditions for saiga antelope for the present only, present historic and present fossil models as follows: (a) area (km²) of suitable environment predicted, (b) area (km²) of unsuitable environment predicted, (c) percentage change in area of suitable environments predicted with the inclusion of historic and fossil records and (d) percentage change in unsuitable environments predicted with the inclusion of historic and fossil records.

(Figure 3). In contrast, the inclusion of fossil records into the present fossil model increased predicted suitable area by 1285% (2,162,292.4) and 1548% (1,813,074.6) in RCP 2.6 and 8.5 respectively. These predicted suitable environment areas include countries within and south and east of the species' current range, as well as fragmented areas of northern Greenland, northern Canada and northwest United States. In contrast to the current present fossil model, Arctic regions including Svalbard and eastern and

western Greenland are predicted lower quality habitat (Figure 2c). Predicted unsuitable environment areas decreased by 0.98% (1,084,689 km²) and increased by 0.87% (963,321 km²) with the addition of historic records and decreased by 23.93% (26,576,646 km²) and 24.64% (27,318,849 km²) with fossil records under RCP 2.6 and 8.5 respectively (see Appendix S5). Overall, the present fossil model predicted the most suitable and least unsuitable saiga habitat across all three climate projections (Figure 3).

The response curves demonstrate different thresholds of suitable environmental conditions (>0.6 AUC) for saiga in the present only, present historic and present fossil models (Figure 4). Including historic records, and associated environmental conditions, into the present historic model narrowed the threshold for suitable environmental conditions for BIO 14 (precipitation of the driest month) from 0–120 to 4–40 mm, BIO 18 (precipitation of the warmest quarter) from 0–70 to 0–60 mm and BIO 19 (precipitation of the coldest quarter) from 20–500 to 25–300 mm (see Appendix S6). The thresholds for topographic steepness and BIO 11 (mean temperature of the coldest quarter) changed by 1 km and 2°C respectively. By comparison, including fossil records into the models widened the parameters for suitable environmental conditions for BIO 11 from –2 to –17°C to –2 to 28°C, BIO 14 from 0–120 to 10–200 mm, BIO 18 from 0–70 to 0–100 mm, BIO 19 from 20–500 to 0–1500 mm and topographic steepness from 0–5 to 0–8 km.

4 | DISCUSSION

Incorporating the saiga's fossil record into the HSMs broadened the parameters used to predict suitable environmental conditions, causing a significant increase in area of predicted suitable environment globally. This has implications for our understanding of the environmental tolerances and occupied niche breadth of past and present saiga populations, and may in the future, with more complex models, contribute to the species' conservation management. The present fossil models generated in this study provide a framework for incorporating fossil records and temporally associated palaeoenvironmental data, into HSMs for other mammalian species of conservation interest. Here, we focus on the significance of our results for contemporary saiga populations.

4.1 | Global suitability predictions

On average, the inclusion of fossil records increased the predicted suitable environment area for saiga globally by 1205% and decreased predicted unsuitable areas by 24.9% (Figure 3). This is attributed to the saiga's fossil records occurring over a greater range of environmental conditions, including the Mendip Hills of Southwest England, compared to modern saiga populations. These broader environmental conditions widened some of the bioclimatic and topographic parameters governing suitable environmental areas, which were then used to calibrate the models. In particular, the threshold for BIO 11, mean temperature of the coldest quarter, decreased from –17 to –28°C, BIO 14, precipitation of the driest month, increased from 120 to 200 mm and topographic steepness increased from 0–5 to 0–8 km from the present only to present fossil model respectively (Figure 4). This means that in addition to the saiga's current range, colder regions with greater snowfall and steeper terrain were predicted to be environmentally suitable in the present fossil model. These include large areas of Kazakhstan, Uzbekistan and

southern Russia, as well as countries south of the species present range such as Turkmenistan, Tajikistan, Kyrgyzstan, northwest China and northern regions of Iran, Afghanistan and Pakistan. Small, fragmented areas outside the saiga's known range, including Greenland, Svalbard, Iceland and northern Canada, are also predicted to be climatically and topographically suitable (Figure 2c).

By contrast, the models generated using modern saiga data alone predicted significantly less environmentally suitable areas for saiga, under both current and future climate change scenarios (Figure 2a). This is attributed to the narrower bioclimatic and topographic parameters used by the present only model to identify suitable environmental conditions for saiga, compared to the present fossil model (Figure 4). These parameters, defining suitable environment areas, are derived from the saiga's modern range, which is restricted to fragmented regions of Central Asia. These semi-arid steppe environments are characterised by flat topography and snowfall <20 cm and are considered necessary environmental conditions for saiga (Cui et al., 2017; Heptner et al., 1961; Sher, 1968). As a result, only the species' current and recent historic range are predicted suitable, including eastern and western regions of Kazakhstan, northwestern Uzbekistan and northern Kyrgyzstan. Very small areas of northwest China, Mongolia and Svalbard are also predicted suitable. However, under the future 2070 scenarios, Svalbard is predicted to be less environmentally suitable which is in line with forecasts of increased ice crusting (Descamps et al., 2017). The saiga's modern range is geographically and environmentally restricted compared to Pleistocene populations and this has led to a significant decrease in the amount of suitable environment areas predicted in the present only compared to present fossil model. Using environmentally restricted modern data to generate HSMs is known to produce incomplete response curves and severely limit suitable area predictions (Thuiller et al., 2004).

Incorporating the saiga's historic occurrence records and associated environmental conditions into the present historic model, resulted in a slight increase in the area of predicted suitable environmental conditions compared with the present only model (Figure 3). This is attributed to the historic records broadening the parameter for BIO 11, mean temperature of the coldest quarter, from –18 to –20°C from the present only to present historic model. Consequently, slightly colder regions with deeper snowfall are predicted to have suitable environmental conditions, including areas of Turkmenistan and Tajikistan, alongside the species' current range countries, Kazakhstan, Uzbekistan and southern Russia (Figure 2). As saiga has experienced recent anthropogenic range contraction, their historic records introduced environmental conditions into the model that the species no longer occupies but which may still be environmentally suitable, thereby increasing the predicted area of suitable environmental conditions. This agrees with existing research (e.g. Chatterjee et al., 2012; Faurby & Araújo, 2018; Lentini et al., 2018; Monsarrat, Novellie, et al., 2019), that for environmentally truncated species, including their historic occurrence and environmental data into HSMs may better represent their species–environment relationship prior to extensive range decline and increase suitable area

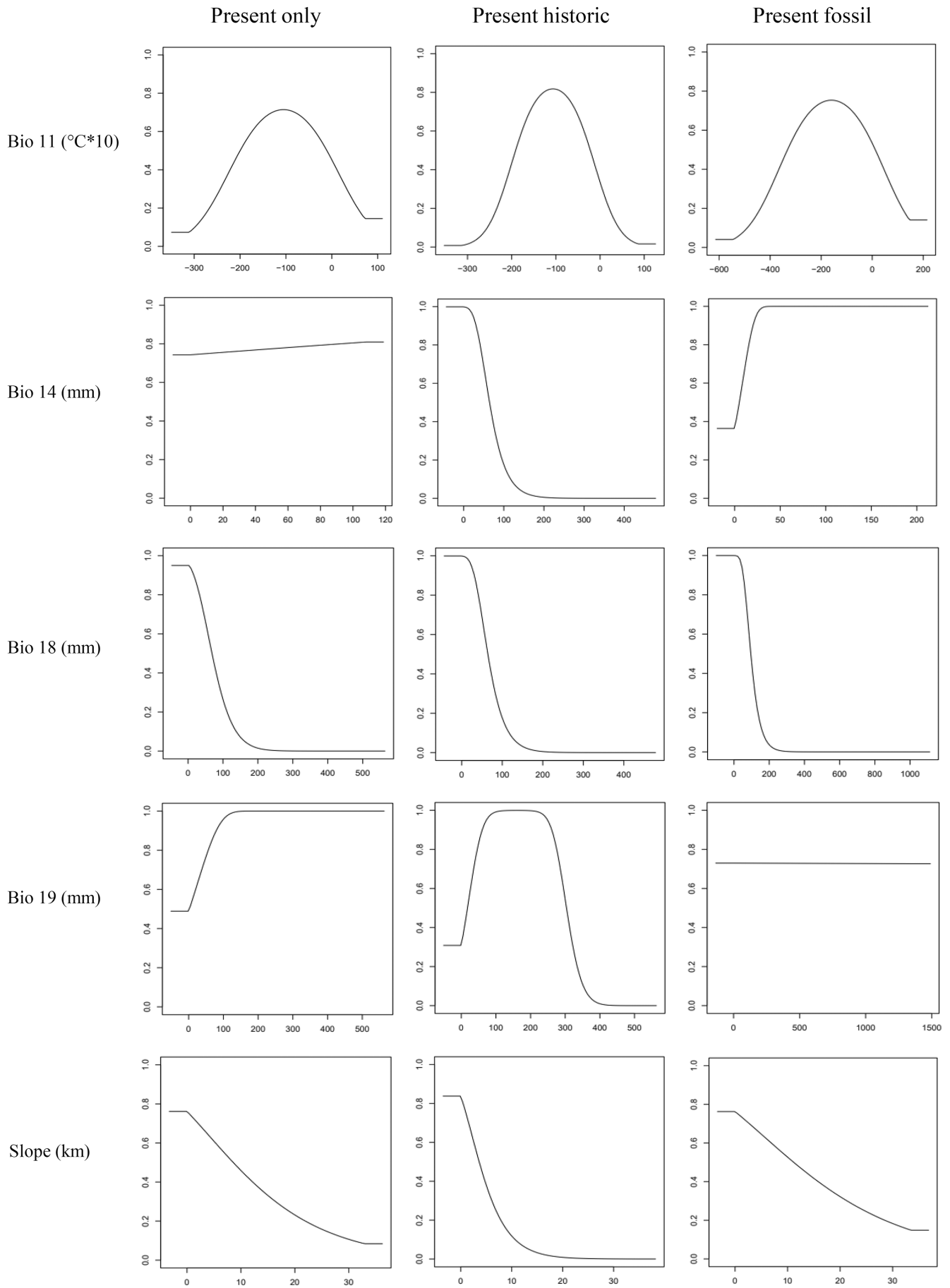


FIGURE 4 Response curves for the present only, present historic and present fossil habitat suitability models for saiga antelope. Individual graphs show the response of predicted environmental suitability for saiga when the value of one predictor variable is changed, whilst the others are held constant. Y axis values denote predicted environmental suitability for saiga antelope, with 1 indicating highly suitable environmental conditions and 0 indicating unsuitable environmental conditions. X axis values correspond to the units of each environmental predictor variable, given on the left side of the figure. Bio 11 units are in °C multiplied by 10.

projections. However, these records can still be prone to historic range contraction and local extirpations and may therefore fail to capture a species' full environment relationship (Hortal et al., 2008). Records of saiga hunting for traditional Chinese medicine and subsequent range contractions can be traced back 2000 years (Bekenov et al., 1998; Cui et al., 2017). The saiga's historic record, similar to its modern range, may therefore capture only a portion of its potential environmental range. This may be the reason why the present historic model predicted significantly less suitable environment areas compared to the present fossil model.

4.2 | Ecological significance

Our results have potential implications for contemporary understanding of the saiga's species–environment relationship. Modern saiga is perceived to be restricted geographically to flat topography and snow depths <20 cm (Heptner et al., 1961; Sher, 1968). However, the broader environmental thresholds from the present-fossil models suggest that Pleistocene saiga populations were more environmentally flexible than modern populations, with a greater realised niche breadth (Figure 4). The widening of predicted environmental tolerances suggests that Pleistocene saiga were able to survive in colder regions with slightly steeper terrain and deeper snow depths. This inference supports existing research detailing Pleistocene saiga's broader environmental tolerance and realised niche. Harrington and Cinq-Mars (1995) recognised that Pleistocene saiga would have experienced severe winters and rough terrain in the Northwest territories of Canada and concluded that saiga must be more adaptable than previously thought. Jürgensen et al. (2017) concluded that Pleistocene saiga endured harsher and drier environmental conditions, but that these environments were likely not providing optimal conditions. Our results, combined with the existing literature, suggest that modern saiga has experienced species–environment and niche truncation from extensive range contraction and now occupies only a portion of the Pleistocene saiga's environmental range. These inferences suggest that modern saiga could be more environmentally flexible than currently perceived and may be able to persist within a wider variety of environmental conditions, including colder areas with steeper terrain. However, these potentially suitable environmental conditions that are no longer occupied by modern saiga may be inaccessible due to anthropogenic factors such as human occupation, poaching, border fences or other environmental reasons we have not explored.

In addition, as the saiga has experienced environmental truncation, the species may be susceptible to the niche reduction hypothesis (NRH). The NRH details a situation whereby a species contracts

from its previous range (fundamental niche) to a narrower subset of environmental conditions (contemporary niche) and as a result experiences a reduced realised niche breadth, lower adaptability and reduced capacity to deal with threats (Scheele et al., 2017). Such species can also experience lower genetic diversity, as Campos et al. (2010) found with modern saiga antelope. This combination of lower adaptability and genetic diversity could limit the capacity of saiga to successfully inhabit regions outside its contemporary niche breadth and environmental range (Macdonald et al., 2011). Holt (2009) notes that for a species with a reduced realised niche breadth and loss of genetic diversity, the environmental parameters of its former range may not reflect the species' current environmental requirements. The saiga's ability to thrive in the environmental conditions outside of its contemporary environmental range and occupied niche may therefore be reduced.

Our results also suggest that saiga is not a refugee species. Refugee species are those that have been trapped by threats, including anthropogenic pressures, into suboptimal conditions and are then mistakenly conserved within this environment by conservationists perceiving it to be optimal (Kerley et al., 2012; Kummerle et al., 2012). However, the saiga's current range is considered environmentally suitable even with the addition of historic and fossil records (Figure 2). If the saiga was currently confined to suboptimal environmental conditions, the inclusion of fossil records, prior to extensive anthropogenic pressures on saiga, would have lowered the environmental suitability of their current range. Instead, the results confirm that contemporary saiga inhabit optimal environmental conditions but have suffered species–environment truncation with their contemporary range and occupied niche restricted compared to the full range of environmental conditions the species could occur within (Veloz et al., 2012). Truncation is present in both contemporary and historic saiga occurrence records, as demonstrated by the little variation in suitable area predicted between the present only and present historic models, thereby confirming that the saiga are an historically truncated species (Figure 2). This confirmation further emphasises the importance of incorporating fossil records, and consequently past occupied niches, into HSMs to improve understanding of the species' potential niche breadth and environment relationship. HSMs trained with data from a single period can fail to capture potential temporal changes in species–environment relationships and occupied niches and may therefore not represent the full range of environmental conditions a species could occupy (Maguire et al., 2015; Waterson et al., 2016). This may lead to an underestimation of predicted suitable habitat area under future climate forecasts and inaccurate biodiversity risk assessments. Including the saiga's past niche breadth, through their Late Pleistocene fossil record, is particularly important for improving the predictive power

of HSMs under future environmental forecasts, as portions of the saiga's fundamental niche may become available that are currently inaccessible to modern populations (Veloz et al., 2012; Williams & Jackson, 2007).

4.3 | Conservation implications

As the saiga's current range remains highly suitable throughout all three climate projections, and with the inclusion of fossil records, conservation priority should be given to in situ management within their current range. The saiga is not a refugee species and its current range provides optimal environmental conditions, therefore in situ conservation, combined with the species' rapid reproductive capacity, should stabilise and encourage population growth (Milner-Gulland et al., 2001). In situ conservation strategies should focus on reducing current threats, such as illegal poaching and mass disease outbreaks. Studies have demonstrated that saiga poaching is driven by poverty, unemployment and lack of law enforcement (Kühl, 2008). Since the Soviet Union breakup in the early 1990s unemployment has been high in regions over which saiga range and hunting has provided a viable income (Kühl et al., 2009). The socio-economic factors driving saiga exploitation must therefore be addressed if illegal poaching is to be eliminated. Better research into mass disease outbreaks is also imperative to prevent future drastic saiga die offs. In 2015 over 88% of a single saiga population in Kazakhstan died from haemorrhagic septicaemia, and in 2017, 57% of the endemic Mongolian population was affected (Kock et al., 2018). Consequently, even though saiga numbers have recently improved enough for their conservation threat status to be reduced from critically endangered to near threatened, drastic population crashes remain a threat. Prioritising these in situ conservation strategies should help to secure saiga populations within regions that remain climatically suitable through future climate scenarios.

The areas south and east of the saiga's contemporary range are also predicted environmentally suitable under current and future climate scenarios (Figure 2c). These regions, encompassing Turkmenistan in the south and northern China in the east, are part of the saiga's recent historic range. Recolonisation into these areas may in the future be possible for the saiga and could facilitate the establishment of new populations to improve genetic security for the existing populations. Within Turkmenistan, saiga sightings were reported until recent decades, however, their extirpation was thought to be a result of border fences preventing long-distance migration through Uzbekistan (Milner-Gulland, 2012). Therefore, although environmentally plausible, border fences between Turkmenistan and Uzbekistan would need to be removed to facilitate natural saiga dispersal and recolonisation. This has been successfully achieved between Kazakhstan and Uzbekistan to allow the Ustyurt saiga population to migrate across national boundaries (Linnell et al., 2016). Regarding China, the saiga historically migrated from Kazakhstan into the northern regions of the Junggar Basin. However, a combination of over-hunting, human encroachment and border fences led to

their extirpation by the 1960s (Jiang et al., 1996). Our results found certain areas of northern China to be environmentally suitable under current and future climate scenarios. However, Cui et al. (2017) found this only to be seasonal and concluded that any reintroductions into China would require transboundary migration into Kazakhstan to avoid the harsh winter conditions. Like Turkmenistan, saiga migration barriers as well as illegal poaching would need to be reduced to facilitate any potential recolonisation of saiga into China.

Finally, the present-fossil models have identified potentially suitable environmental conditions for saiga outside their known historic range, including fragmented regions of Greenland and northern Canada. However, potential introductions of saiga into these areas should only be considered as a very last resort, in the unlikely situation that their contemporary and historic range becomes unviable for the species' recovery (Seddon, 2010). This is due to the extreme risk, complexity and expense associated with species introduction strategies (Earnhardt, 2010). Future introductions into these areas may be beneficial for saiga if the anthropogenic pressures within their current and historic range cannot be reduced and their population continues to decline (Archer et al., 2019; Macdonald et al., 2011; Scheele et al., 2017). Such introductions could allow the establishment of additional saiga populations within new areas, which may strengthen overall population numbers and improve genetic diversity (Pritchard et al., 2011).

It is important to acknowledge the limitations of the models used in this study, which may impact the environmentally suitable areas predicted. Our models do not include biotic variables, such as anthropogenic pressures, competitors, or predators, all of which could affect the saiga's distribution and abundance (Azevedo et al., 2017). For instance, the models may be optimistic in predicting suitable habitat within areas of high human occupation, such as urban and agricultural environments, which may prevent the saiga from migrating and recolonising. This was also a concern for suitability projections of turtle and coral species migrating to human occupied northern latitudes under future climate change forecasts (Chiarenza et al., 2023; Jones et al., 2019). However, it must be noted that the saiga's current range, and predicted suitable historic range, are arid steppe and mountainous environments with minimal human occupation, so the potential risk of human-saiga conflict is currently low. In addition, both Greenland and northern Canada have established populations of potential saiga predators, such as polar bears (*Ursus maritimus*, Phipps 1774) and wolves, as well as reindeer (*Rangifer tarandus*, L., 1758) that were identified as competitors for Pleistocene saiga populations (Jürgensen et al., 2017), all of which could negatively impact suitability projections. These factors are not accounted for in this investigation.

Saiga are also highly migratory animals that move seasonally in response to precipitation and productivity (Singh, Gracher, et al., 2010). Seasonal models of environmental suitability are therefore necessary to ensure regions remain environmentally suitable for the saiga all year round. This was overlooked for the reintroduction of saiga into China in the 1980s, and the population was unable to withstand or migrate away from the harsh Chinese winters

(Cui et al., 2017). This study therefore offers a starting point for the exploration of potential areas for recolonisation within the saiga's historic range. This study recommends the immediate focus of the limited saiga conservation resources to be directed towards in situ threat management. These areas currently support viable saiga populations and represent the most cost and time-effective conservation strategies presently available to aid the species' recovery.

5 | CONCLUSION

Our study demonstrates how incorporating fossil occurrence records into HSMs can improve environmental suitability predictions by including past occupied niches into the models that may become available under future climate change scenarios. These portions of the fundamental niche may currently be unavailable to contemporary populations and would therefore remain unaccounted for in HSMs with modern only data. Such models could inaccurately predict or underestimate future environmental suitability and misinform biodiversity risk assessments. For saiga antelope, including fossil records into the models broadened the environmental predictor variables, causing a significant increase in predicted suitable area. These broader environmental conditions support previous suggestions that Pleistocene saiga populations occurred in more environmentally diverse regions than current populations, with a broader realised niche breadth. Through extensive range contraction and species-environment truncation, modern saiga now occupy a truncated portion of their potential environmental range and fundamental niche. However, whether modern saiga can inhabit the rest of their environmental range is undetermined and requires further research. Our results demonstrate that the saiga is not a refugee, with its current range remaining highly suitable across all models and climate projections. Therefore, conservation priority should remain with in situ strategies, namely reducing poaching and mass disease outbreaks, to strengthen current populations. Areas within the saigas historic range have been identified for potential recolonisation, however more complex HSMs, inclusive of seasonality, human occupation and other biotic factors, are required to demonstrate future viability. In summary, we demonstrate the importance of incorporating fossil records into HSMs for endangered species that have suffered extensive range contraction, in order to better capture a more complete potential environmental range and increase the scope of their conservation strategies.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Scripts of the habitat suitability models used in this research in the programming language R are available in the Supporting information. The database of saiga presence records from the Last Interglacial to historic period are provided in the Supporting Information. Modern saiga occurrence records were obtained from the IUCN Red List assessment for saiga antelope (<https://www.iucnredlist.org/>), which can be freely downloaded. The bioclimate variables used for each time period are detailed in the Supporting information. The bioclimate data were obtained from the WorldClim database (<https://worldclim.org/>), which can be freely downloaded. The topographic variable was obtained from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED 2010) and can be freely downloaded (<https://www.usgs.gov/>).

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BIOSKETCHES

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Author contributions: Mollie Mills conceived the initial research idea. All authors contributed to the final study design. Mollie Mills collected the data, analysed and interpreted the results and led the writing with assistance from all other authors. Mollie Mills and Owen Middleton designed the methodology and developed the species distribution models. All authors contributed critically to the drafts and approved the final manuscript for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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