

# Human-driven habitat conversion is a more immediate threat to Amboseli elephants than climate change

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## Abstract

Global ecosystem change presents a major challenge to biodiversity conservation, which must identify and prioritize the most critical threats to species persistence given limited available funding. Mechanistic models enable robust predictions under future conditions and can consider multiple stressors in combination. Here we use an individual-based model (IBM) to predict elephant population size in Amboseli, southern Kenya, under environmental scenarios incorporating climate change and anthropogenic habitat loss. The IBM uses projected food availability as a key driver of elephant population dynamics and relates variation in food availability to changes in vital demographic rates through an energy budget. Habitat loss, rather than climate change, represents the most significant threat to the persistence of the Amboseli elephant population in the 21st century and highlights the importance of collaborations and agreements that preserve space for Amboseli elephants to ensure the population remains resilient to environmental stochasticity.

## KEYWORDS

climate change, conservation planning, elephants, habitat loss, individual-based model

## 1 | INTRODUCTION

African elephants (*Loxodonta africana*) face an array of threats, from ivory poaching to negative human–elephant interactions (HEI), habitat loss, and climate change. Poaching has been responsible for the drastic reduction of elephant populations across Africa, from an estimated one million in 1970 (Douglas-Hamilton, 1987) to around 400,000 in 2016 (Chase et al., 2016). Although poaching continues to pose a threat, the sharing of space between people and elephants in the face of environmental change is of growing concern.

Limited financial resources available for biodiversity conservation must identify and prioritize responses to future threats.

In 2009 Africa's human population hit one billion, having doubled since 1982, and it is expected to double again by 2050 (UNDESA, 2017). The associated conversion of natural habitats into human-dominated landscapes squeezes wildlife into smaller and increasingly isolated pockets of land, where resource availability is reduced and dispersal is constrained. Habitat fragmentation due to human encroachment also increases interactions between humans and wildlife (Hoare, 1999), where undesirable elephant behaviors

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reduce tolerance by people (Browne-Nunez, Jacobson, & Vaske, 2013; Dickman, 2010). As the absolute space available to wildlife declines, climate change may alter the quality of remaining habitats: rising global temperatures and CO<sub>2</sub> along with shifts in the amount, distribution, and timing of rainfall are expected to alter vegetative communities, with implications cascading up the trophic web (Walther, 2010). Given large body size and range requirements as well as slow rates of reproduction, elephants are expected to be amongst the hardest hit by these changes (Martínez-Freiría, Tarroso, Rebelo, & Brito, 2016).

Food availability is a key driver of elephant population dynamics (Boult, Quaife, et al., 2018; Rasmussen, Wittemyer, & Douglas-Hamilton, 2006; Wittemyer, Rasmussen, & Douglas-Hamilton, 2007) and movement behavior (Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Boult et al., 2018; Loarie, Van Aarde, & Pimm, 2009), but availability and distribution are expected to change as environmental conditions shift. Here we estimate the food available to elephants inhabiting the Amboseli ecosystem in southern Kenya under projected climate change and anthropogenic habitat loss scenarios. Projected food availability is used to drive an individual-based model (IBM) which predicts vital elephant demographic rates through an energy budget. IBMs present a powerful tool for future scenario modelling as their process-based approach maintains their predictive ability under novel environmental conditions (Stillman, Railsback, Giske, Berger, & Grimm, 2015) and can capture the cumulative impacts of multiple environmental changes (Nabe-Nielsen et al., 2018). Projected elephant population size emerges from IBM simulations, providing vital information on the potential outcomes of environmental change scenarios. Results are used to identify scenarios which pose the greatest threat to the Amboseli elephants and will aid in prioritizing land management policy and conservation efforts.

## 2 | METHODS

### 2.1 | The individual-based model

We previously developed an IBM relating variation in food availability to elephant life histories through individuals' energy budgets (Boult, Quaife, et al., 2018).

The model environment represents the landscape available to elephants in the Amboseli ecosystem and is characterized by vegetation biomass, which represents the food available to elephants. Biomass was estimated using remotely-sensed measures of vegetation. Specifically, we used the normalized difference vegetation index (NDVI) retrieved by the Terra MODIS (Moderate Resolution Imaging Spectroradiometer) mission as a proxy for vegetation biomass. NDVI was validated using ground-based measures of vegetation biomass collected by the Amboseli Elephant Research Project from

1979 to 2018 to provide estimates of food availability across the landscape over time (see Appendix S1).

The model incorporates females of all ages and males prior to dispersal from their natal family at approximately 12 years old. Elephants are represented as individuals and each experiences life processes through its own energy budget. Energy is taken from food available in the environment and allocated to the energy-expending processes of life by order of priority (Sibly et al., 2013). Maintenance fuels the basic processes of life and so takes first priority. If sufficient energy is available following maintenance, individuals will commit energy to growth and reproduction, the order of which depends on age and sex. Sexually immature individuals allocate energy to growth and store any remaining energy as fat. Sexually mature individuals first cover the costs of reproduction but continue to grow throughout life if energy is available. Again, any remaining energy is stored to be drawn on in times of food limitation. Therefore, when food is abundant, energy is allocated maximally to maintenance, growth and reproduction, and storage tissues are accumulated. When food is limited, maintenance takes priority and growth and reproductive rates reduce. If the costs of maintenance cannot be met, individuals die. In this way birth and death rates, and ultimately population size, emerge from variation in food availability. Further details, including the equations describing processes in the IBM are included in the Appendix S1. During initial model development, uncertain parameters were calibrated using approximate Bayesian computation (ABC) to maximize the fit of the model to the observed population dynamics of four elephant family groups from 2000 to 2016. Here, the model was recalibrated by fitting to historic (2000–2016) data of Amboseli elephant demographic rates for the whole population (> 50 families), again using ABC (van der Vaart, Beaumont, Johnston, & Sibly, 2015) to describe the uncertainty in parameter values (Figure S1). The uncertainty arising from unknown parameters in the IBM was propagated to population projections in the climate and habitat scenarios below by running the model for each of the 30 parameter sets that best fitted historic data. We chose to use the 30 best fitting simulations as a compromise between including only well-fitting runs and the need to produce posterior distribution to represent uncertainty in parameter values. Full details of the IBM development, parameterization and validation are presented in Boult, Quaife, et al. (2018).

### 2.2 | Habitat loss scenarios

The risk of loss of a habitat is not equal across ecosystems and some areas, such as those with irrigation potential, are more susceptible to anthropogenic conversion than others. At present, there is little consensus on how best to predict

the location and extent of habitat loss. We therefore developed six possible scenarios of habitat loss for Amboseli based on empirical data and stakeholder opinion (Figure 1). We divided the ecosystem into administrative units and ranked each unit based on change in human population density (from 1989 and 2009 Kenyan censuses; CBS, 1994; KNBS, 2013; Figure 1b), incidences of negative HEI (2014–2018; Big Life Foundation data; Figure 1c), stakeholder opinion ranking areas based on the likelihood that elephants would have continued access (Figure 1d; stakeholders listed in Table S1) and conservation area (CA) status (KWCA, 2017; Figure 1e and f). We believe these metrics give a good indication of possible habitat loss: change in human population density is closely related to habitat conversion and infrastructural development; in CAs people are committed to protecting wildlife, supported by economic benefits; frequency of non-crop-foraging HEIs affect human tolerance for wildlife and may align with areas that, although not physically lost to elephants, are avoided by elephants due to the perceived risks in the area (Roever, van Aarde, & Chase, 2013; Wittemyer, Keating, Vollrath, & Douglas-Hamilton, 2017). We excluded crop-foraging because occurrence coincides with crop areas near areas of high human population growth, which is covered in Figure 1b and is geographically limited to relatively small areas of the ecosystem where irrigation is possible.

### 2.3 | Climate change scenarios

We used climate change simulations supplied by the ISI-MIP 2b project, developed to provide information about the impacts of different greenhouse gas (GHG) emissions scenarios (Warszawski et al., 2014). The ISI-MIP 2b simulations incorporate four general circulation models (GCMs; GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, and MIROC-ESM-CHEM) and two representative GHG concentration pathways (RCP2.6 and RCP6.0). The RCP2.6 pathway is broadly consistent with the United Nations Paris Agreement targets to limit global temperature rise, and RCP6.0 produces a roughly 3°C rise in global temperatures above pre-industrial levels by the year 2100. The ISI-MIP dataset covers 2006–2099 at a 0.5° × 0.5° resolution and is bias-corrected to provide long-term agreement with observed historic data (Hempel, Frieler, Warszawski, Schewe, & Piontek, 2013).

### 2.4 | Combined stressor scenarios

Since aspects of environmental change interact and may have additive or antagonistic effects on elephant demographics, we also considered the impacts of climate change and habitat loss in combination. We simulated the IBM

under both HadGEM2-ES emissions scenarios (RCP2.6 and RCP6.0) for each habitat loss scenario. We chose to only use HadGEM2-ES as all GCMs showed good agreement in elephant population projections, but HadGEM2-ES projected the largest difference between RCPs and thus represented the greatest uncertainty.

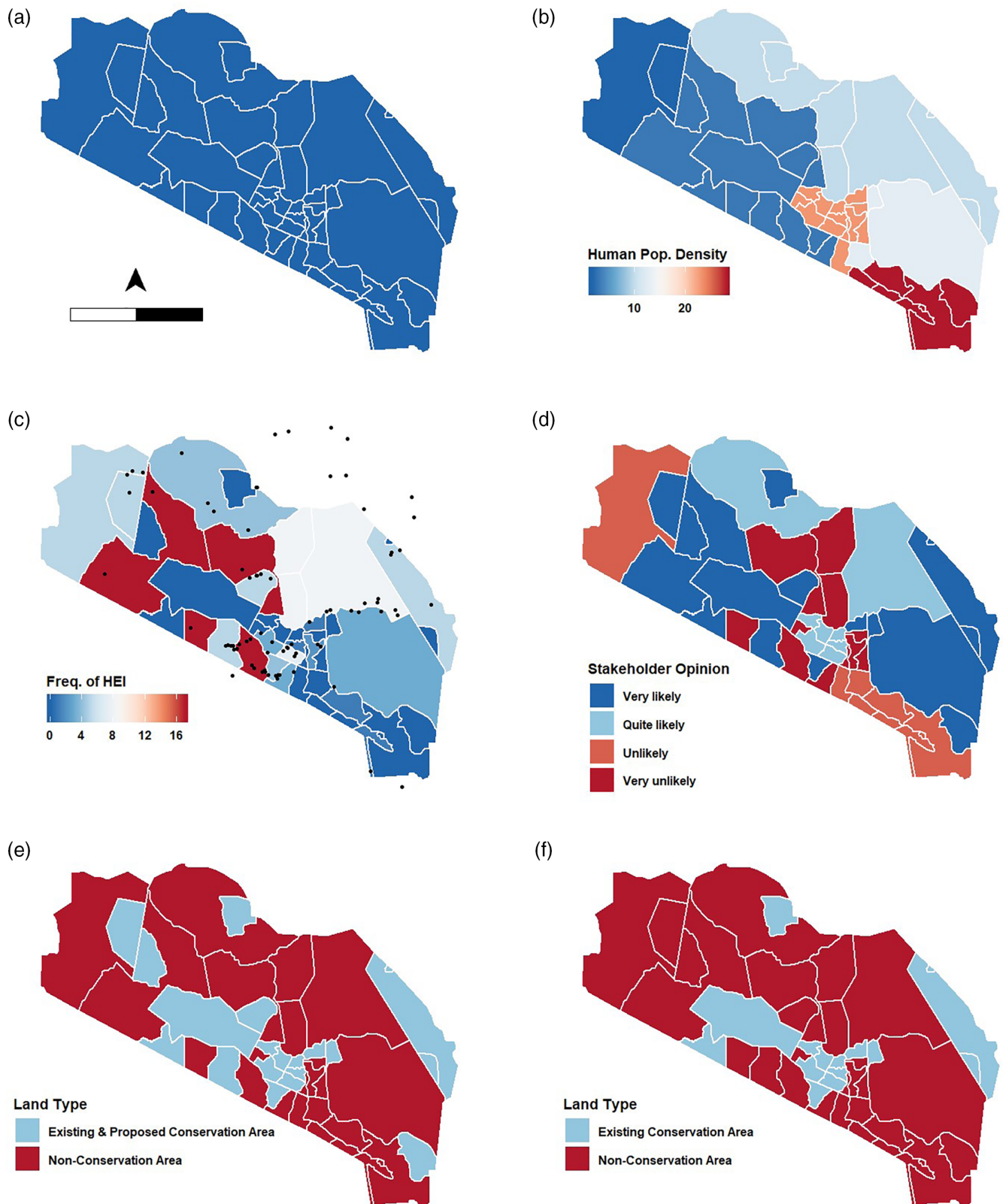
### 2.5 | Projecting food availability

Food availability is used to drive elephant population dynamics in the IBM. To determine future food available to elephants, we projected vegetation biomass under our climate and habitat scenarios. Biomass is not a standard output of climate models and as such, we had to develop a means of projecting it throughout the 21st century. To do so, we established the historic relationship between biomass and rainfall in Amboseli (see Appendix S1), then used ISI-MIP rainfall estimates to project future biomass. We classified historic Amboseli years 1968–2016 by rainfall collected at the Amboseli Elephant Research Camp gauge (coordinates: 2.68S, 37.27E) using the standard precipitation index (SPI; McKee, Doesken, & Kleist, 1993). Amboseli years run from October to September to align with the annual rainfall cycle (i.e., Amboseli year 2000 runs October 1999 to September 2000; Croze & Lindsay, 2011). Each Amboseli year was classified by its SPI as follows:  $\geq 2$  = very wet, (1, 2) = wet, (-1, 1) = normal, (-2, -1) = dry, and  $< -2$  = drought.

The SPI is the World Meteorological Organisation's recommended index for monitoring rainfall extremes globally (Hayes, Svoboda, Wall, & Widhalm, 2011) and describes the deviation of observed rainfall from the climatological average. Due to its relative simplicity, requiring rainfall data alone, and its ability to be applied at any timescale, SPI is widely used by meteorological agencies around the world to monitor rainfall anomalies (Ntale & Gan, 2003). In addition, SPI has been shown to relate strongly to vegetation dynamics (Measho, Chen, Trisurat, Pellikka, & Guo, 2019).

Historic biomass values (2000–2016) were obtained for the area available to elephants under each habitat loss scenario. Biomass was estimated using NDVI from the Terra-MODIS (Didan, 2015) mission (see Appendix S1). Specifically we used the MOD13Q1 product accessed via the Oak Ridge National Laboratory web service (Vannan, Cook, Pan, & Wilson, 2011). For each SPI class (very wet, wet, normal, dry, and drought), we calculated a median biomass value per month for each area available to elephants. These values were used to construct monthly biomass time series for the projected period (2007–2099) under scenarios of habitat loss only, climate change only and their combined effects.

For habitat loss scenarios, we assumed a stable average climate throughout and used monthly biomass values from “normal” SPI years only. For climate scenarios, we first



**FIGURE 1** Predicted Amboseli habitat loss scenarios. Scenarios were based on empirical data and stakeholder opinion. In each scenario, the red and orange areas are lost. (a) The full-area scenario: Elephants have access to the full extent of the ecosystem. (b) Areas which have experienced the greatest increase in human population density could be converted to non-habitat and become inaccessible to elephants. (c) Areas with the highest frequency of non-crop-raiding human-elephant interactions (black points) may be avoided by elephants due to perceived risks. (d) Habitats thought by stakeholders to be unlikely or very unlikely to remain suitable elephant habitats are lost. (e) Only existing and proposed conservation areas remain suitable, accessible habitats for elephants. (f) Only existing conservation areas remain suitable, accessible habitats for elephants. We assumed that elephants could move through lost habitats, but that these areas no longer represented forging opportunities. Arrow = north. Scale bar represents 20 km (divisions of 10 km)



calculated the SPI of Amboseli years for the projected period using monthly precipitation totals from the eight ISI-MIP climate scenarios (four GCMs and two RCPs; Figure S2). Using monthly biomass values from habitat scenario A assuming no habitat loss, we arranged monthly biomass values by projected SPI. In combined scenarios, monthly biomass was projected according to HadGEM2-ES RCPs and all habitat loss scenarios.

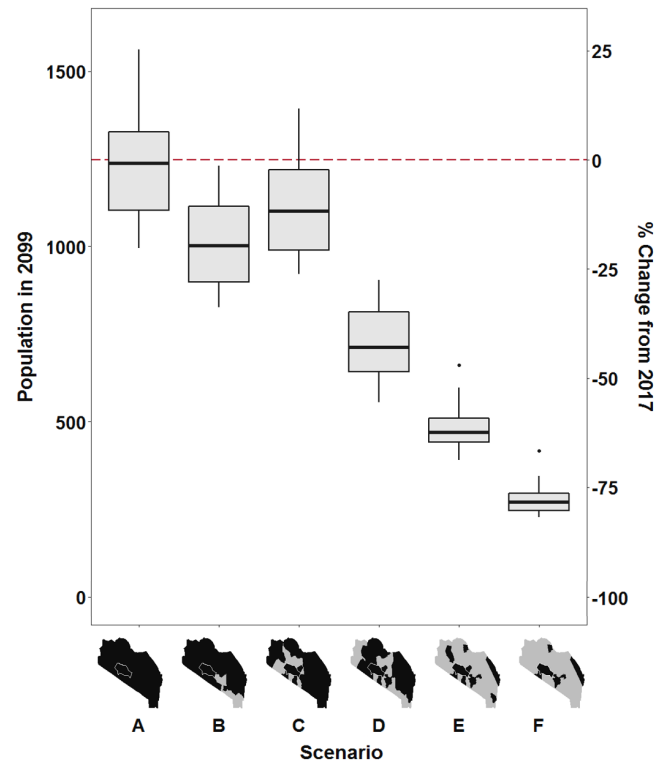
## 2.6 | Model simulations

We assumed the elephant population used the available dispersal areas evenly. Under habitat loss scenarios, we assumed that elephants could move through lost habitats, but that these areas no longer represented foraging opportunities. Therefore, where scenarios include habitats only accessible via converted habitats, our projections may be conservative. We did not model changes in water availability under climate change (a known limiting factor for elephants: Chamaillé-Jammes, Fritz, & Madzikanda, 2009) as artificial water sources and abundant swamps within the ecosystem currently determine the population distribution. For all scenarios, the IBM was simulated from 2007 until 2099 for each of the 30 best calibrated parameter sets to indicate uncertainty arising from parameter uncertainty in the IBM. The IBM was initiated with the known elephant population on the 1<sup>st</sup> January 2007. Under habitat loss and combined scenarios, the *area* parameter in the IBM was adjusted at model initiation to indicate the habitat remaining (Table S2) and population size was recorded at the end of 2099. In climate simulations, elephant population size was recorded at the end of each Amboseli year (30<sup>th</sup> September).

## 3 | RESULTS

### 3.1 | Habitat loss projections

Scenario A, in which current ecosystem limits remain unchanged, shows the elephant population remains stable around its current size. Habitat loss inevitably reduces the number of elephants supported by the ecosystem (Figure 2), though elephant numbers are not directly proportional to the amount of area lost (Table S2). Scenario B, where habitat is lost to human population growth, supports fewer elephants than scenario C, where areas become avoided due to risks associated with HEI, despite the amount of area lost being similar. In scenario F, where only existing CAs remain accessible, the model predicts an approximately 80% reduction in elephant numbers.

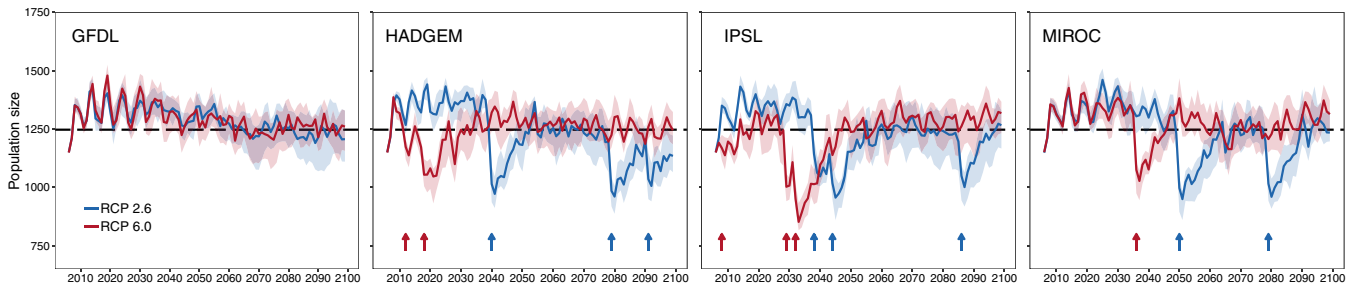


**FIGURE 2** Projected elephant population size in 2099 and percent change from the 2017 population for habitat loss scenarios (a–f) assuming “normal” climates (see methods). Boxplots (median and interquartile ranges) indicate uncertainty arising from parameters used in the IBM. Points show outliers. Dashed line = elephant population size in 2017 ( $n = 1,247$ ). Maps: Black polygons = remaining elephant habitats; grey polygons = lost habitats

### 3.2 | Climate change projections

The projected precipitation changes in the four GCMs show relatively small long-term trends compared to the variability from year-to-year, and the simulated timing and frequency of droughts varies across the simulations (Figure S2). Ideally a larger set of precipitation projections would be used to account for uncertainty due to precipitation variability and uncertainty in long-term trends, but only one simulation per GCM is available in ISI-MIP 2b. There is little agreement amongst a broader set of GCMs about whether precipitation will increase or decline over the coming century for the Amboseli region (Figure S3).

In all climate scenarios, the IBM projected an increase in the initial elephant population of 1,099 individuals, with early growth (2007–2015) slowing and stabilizing around 1,250 elephants (Figure 3). The elephant population is thus not expected to deviate much from the current size under any climate scenario. Droughts intersperse the time-series and generate population crashes, as vegetation availability limits survival and reproduction (Figure 3: arrows), and subsequent population recovery. These dynamics suggest that



**FIGURE 3** Elephant population projections given expected scenarios of climate change. Four GCMs (GFDL, HadGEM, IPSL, and MIROC) and two GHG emissions scenarios (RCP2.6 and RCP6.0; blue and red lines, respectively) are included to account for uncertainty in climate projections. Lines = median, shading = interquartile range indicating uncertainty arising from parameters in the IBM, arrows = drought years. The dashed line shows elephant population size in 2017 ( $n = 1,247$ )

drought frequency is an important determinant in population stability, as regularly recurring droughts may not allow enough time for population recovery. Frequent droughts may therefore result in overall population decline and warrants future investigation (see Wato et al., 2016). Interquartile ranges for projections indicate that some uncertainty arises due to parameter values used in the IBM.

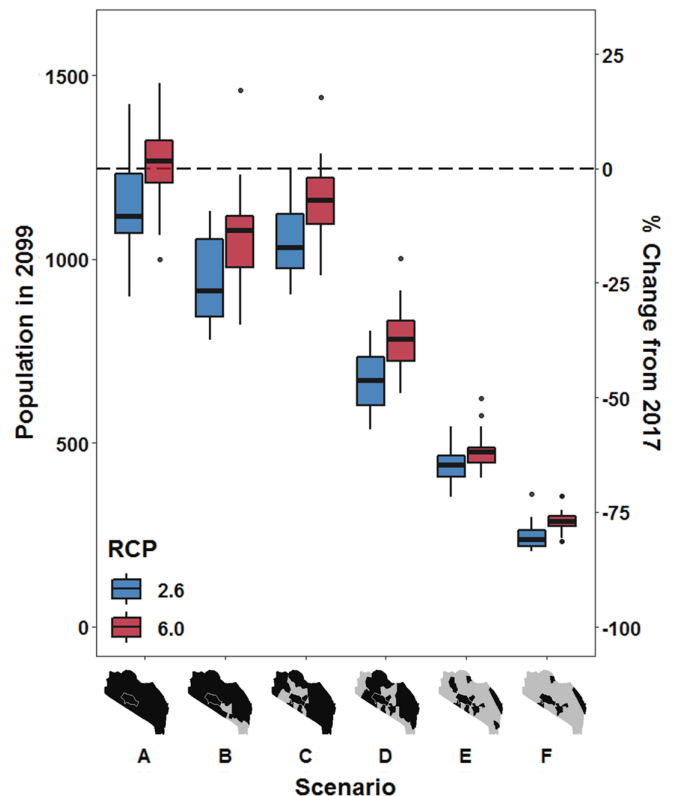
### 3.3 | Combined stressor projections

The combined effects of habitat loss and climate change are shown in Figure 4. In all habitat scenarios, the higher emission climate scenario (RCP6.0) projected a larger elephant population than the low emission scenario, but these differences were smaller than the differences between habitat scenarios.

## 4 | DISCUSSION

Models suggest that habitat loss, rather than climate change, is the most significant immediate threat to the Amboseli elephants. The elephant population declines under all scenarios of habitat loss, though declines are not directly proportional to the amount of area lost since affected areas vary in vegetation quantity and quality. Despite the areas lost due to human population growth and HEI (scenarios B and C) representing roughly the same total space, our IBM predicted bigger losses of elephants resulting from human population growth rather than HEI. This is likely because HEI currently occurs where people and livestock share space with elephants. Livestock grazing tends to occur on drier land where crop production is difficult; in contrast, human population growth is usually concentrated around highly productive and well-watered areas for farming. This underscores the problems posed by agricultural encroachment into key foraging areas for the Amboseli elephants and highlights the need for landscape-scale planning of human development.

Like many areas, Amboseli faces increasing pressure on the space and resources available to people and wildlife. With growing competition, the government has encouraged people to settle and farm, resulting in widespread subdivision of land, an expansion of agriculture, and the emergence



**FIGURE 4** Elephant population size in 2099 and percent change from 2017 under combined climate change and habitat loss scenarios. For each habitat scenario (a–f), the IBM was simulated with RCPs 2.6 (blue) and 6.0 (red). Boxplots (median and interquartile ranges) indicate uncertainty arising from parameter uncertainty in the IBM. Points show outliers. The dashed line shows elephant population size in 2017 ( $n = 1,247$ ). Maps: Black polygons = remaining elephant habitats; grey polygons = lost habitats

of many unplanned developments (Croze, Moss, & Lindsay, 2011; Schübler, Lee, & Stadtmann, 2018). Community choices and human tolerance will shape Amboseli's conservation success, and our model has begun to identify how these choices would impact elephants. Scenario E, representing the accessibility of only existing and proposed CAs, suggests that dialogue to promote human-elephant coexistence beyond the boundaries of CAs may be worth approximately 800 elephants, or approximately 60% of the current population. Models predict an approximately 80% decline, to around 300 elephants supported by the ecosystem if elephants were confined to existing CAs alone (scenario F). Such small elephant populations are vulnerable to stochastic perturbations including demographic and environmental stochasticity, and natural disasters (Shaffer, 1981). Fewer elephants may also decrease tourism revenues (Naidoo, Fisher, Manica, & Balmford, 2016) which represent a key component of successful balance between biodiversity conservation and socio-economic development in many African landscapes.

It is impossible to overstate the importance of local community decisions for the future of Amboseli's elephants, limiting habitat conversion and mitigating HEI to ensure continued accessibility of the ecosystem for all wildlife. Amboseli stakeholders are well aware of these needs. Land management planning is a new part of the Kenyan constitution, and Amboseli's ecosystem management plan was the first to be formally gazetted. Amboseli has several projects in place to ease HEI, including Amboseli Elephant Research Project's (AERP) livestock loss consolation scheme (Sayialel & Moss, 2011) and Big Life Foundation's elephant-proof fence to prevent crop foraging by elephants and the further expansion of agriculture (Big Life Foundation, 2017). More broadly, Amboseli is developing community-led multi-stakeholder initiatives under the Amboseli Ecosystem Trust, to promote evidence-based and transparent landscape planning to balance human and wildlife needs.

The modelling approach taken here will provide a useful tool for conservation agencies and NGOs. Our model enables the identification of priority areas and sets out the challenges for targeted efforts and funding. More specifically, as Amboseli stakeholders engage in the next round of ecosystem management planning, our model could be run in real time in workshop scenarios or community meetings to simulate the impact of the landscape management strategies being discussed. The powerful community-led conservation movement in Kenya is increasingly keen to use real-world data to evaluate decisions for stakeholders and Amboseli's data-driven partnership approach is of great interest. Many African landscapes have enough data to populate their own versions of the model, which could be adapted for other species of conservation concern.

Whilst climate change does not appear to present a significant direct threat to the Amboseli elephants, we advise caution based on potential interactions between climate change and human behavior which may indirectly impact elephants. For example, more rainfall in the area may draw more people seeking to expand and intensify agriculture to the region. In addition, we have only considered the four GCMs which participated in the ISI-MIP 2b experiments, and these may not be fully representative of the broader set of more than 40 different GCMs which participated in the underlying Coupled Model Intercomparison Project, phase 5 (CMIP5; Figure S3). We note that if these simulations under-represent the frequency of droughts then the assessed effect of climate change on Amboseli elephants would be too small. Another issue not addressed here is the impact of rising atmospheric CO<sub>2</sub>. It is well established that increased CO<sub>2</sub> makes vegetation more tolerant to droughts (Morison, 1985), and hence the impact of low rainfall on available food may be less than suggested here. Additionally, increasing CO<sub>2</sub> levels are likely to drive increased bush growth (Devine, McDonald, Quaipe, & Maclean, 2017) and thus not necessarily produce food limitation for elephants. It is also important to note that the impacts of climate change on elephant populations will vary by location given disparities in projected rainfall across African elephant range states. In southern Africa in particular, climate projections suggest rainfall will decline (Serdeczny et al., 2016), potentially resulting in reduced vegetation productivity and food limitations for elephants. Alternatively, given the possible alleviating effects of increased CO<sub>2</sub> on vegetation, the more pertinent issue in areas where rainfall declines may be limitations on the availability of drinking water.

It should also be noted that our biomass projections are based on only a short 17-year timeseries of historical data, potentially introducing biases when projecting food availability. For example, there was only a single SPI-classified drought year in the 2000–2016 period and biomass in projected drought years was necessarily based on this year alone, potentially introducing bias if the drought year was unusual.

Our results suggest that while most of the uncertainty about the future stems from different potential scenarios of habitat loss, there is significant uncertainty stemming from unknown parameters in the IBM. The latter will hopefully reduce as improved methods are developed in data assimilation (see, e.g., van der Vaart, Prangle, & Sibly, 2018).

Further improvements to the model and in turn our population projections may be made by addressing the assumption that elephants use the space available to them evenly. Rather, elephants utilize established home ranges and move seasonally to maximize resource availability. Movement decisions are guided not only by food availability, but also

by perceived risks (Graham, Douglas-Hamilton, Adams, & Lee, 2009), water availability (Chamaillé-Jammes et al., 2009), and social companions (Goldenberg, Douglas-Hamilton, & Wittemyer, 2016), among other factors. We acknowledge that incorporating spatially explicit elephant ranging may alter our results. For example, areas which are deemed important in terms of food availability may not represent functional elephant habitats for females and calves due to an absence of drinking water or cover for resting. Considering the impacts of climate change and habitat loss on these factors and thus on elephant space use, will improve the realism of our modelling and may allow our model to more accurately pinpoint regions of significance for elephants and identify specific elephant families most at risk from change.

Future efforts must also consider adult males, who occupy different ecological niches that vary their needs and interactions with humans (Shannon, Page, Duffy, & Slotow, 2006), and the impacts of other change scenarios, such as variation in livestock density or demand for ivory, which may act to exacerbate or alleviate the scenarios presented here. In addition, while the energy budget included in the IBM mechanistically relates food availability to demographic rates, the relationship between rainfall and food availability is not mechanistically modelled. If we are to maximize the predictive ability of our model under future global change, we should seek more realistic representation of vegetation responses to rainfall. Land surface models may present the opportunity to simulate vegetation dynamics based on rainfall projections (Yu et al., 2014).

The approach used here relies on modelling the relationship between food availability and demographic rates. How food availability is influenced by environmental change is estimated and underlies IBM predictions of elephant population size. We believe IBMs present a strong option for improving our ability to predict the responses of animal populations to combined stressors and novel environmental conditions (Nabe-Nielsen et al., 2018; Stillman et al., 2015). The IBM employed here uses a general energy budget framework, calibrated to the Amboseli elephants, and could be readily adapted for other elephant, or mammalian herbivore, populations. We therefore see that this approach provides the basis for the development of a broader toolkit for use by stakeholders to assess the consequences of policy decisions for animal populations.

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## CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

## AUTHORS' CONTRIBUTIONS

V.L.B. performed modelling and analysis and wrote the first draft of the manuscript and supplementary materials; R.M.S., T.Q., V.F., and P.C.L. contributed to the design of the model; all authors contributed to the writing of the manuscript; T.Q. provided scripts for MODIS data retrieval and technical guidance regarding remote sensing; E.H. provided guidance on ISI-MIP climate projections; P.C.L. contributed to long term study design; C.M. is the founder of the long-term study and is holder of intellectual property.

## ETHICS STATEMENT

All AERP long-term research is carried out with permission from the Kenya Government National Commission for Science, Technology and Innovation (NACOSTI/P/15/9605/5732), in affiliation with the Kenya Wildlife Service (who is responsible for collaring permits and all collaring operations), and conducted with approval from the Animal Welfare and Ethics Review Board, University of Stirling (AWERB/1,718/018/New Non ASPA).

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## SUPPORTING INFORMATION

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

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