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RESEARCH ARTICLE

Dynamic modeling of African elephant populations under changing climate and habitat loss across the Greater Virunga Landscape

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Abstract

Elephants in Africa are declining rapidly due to habitat loss and human-wildlife conflicts, with these problems worsening with climate change. Understanding how age classes respond to such events is crucial to designing and implementing mitigation strategies and developing the adaptive capacity of wildlife managers to respond to these challenges adequately. This study builds a dynamic simulation model of the age classes of elephants and their interaction with habitat, water, and climate. The dynamic response of elephant populations to habitat change, water resources, and climate change is assessed. It is observed that climate change affects older elephants more than young ones in terms of survivability and migration. It is also likely that the undetected direct climate change impact on the elephant population is due to changes in habitats, particularly forests and wetlands used for thermal regulation. An improvement in the habitat type and availability of water resources improved the age classes of populations. The results suggest that if the environmental and anthropogenic stressors are not mitigated, Greater Virunga Landscape (GVL) will face a change in population demography for younger elephants and impact overall populations. Such age-class-specific stress could substantially affect African elephants' long-term population viability and sustainability. Conservation of elephants requires a transboundary management approach to climate change mitigation, cooperation among conservation agencies, and effective partnerships with all relevant stakeholders for conservation.

Author summary

Transboundary wildlife like elephants requires a regional approach to assessment and conservation. This requires a better understanding of the elephant age-specific responses to landscape-level changes in habitat, water availability, and climate change to enable conservationists to develop landscape-wide conservation strategies. More importantly, water availability and its distribution within the landscape will be critical to the survival of elephants amidst the effects of climate change. Long-term simulations of age-class-specific

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elephant populations are used in a high biodiversity landscape in Africa. The dynamic impacts of climate and habitat changes on the African elephant population demography are significant. Loss of habitat and water resources can be critical to the long-term survival of elephant populations. With elephants dependent on large landscapes, transboundary cooperation becomes vital for long-term survival and regional sustainability.

Introduction

Elephants are of global conservation concern due to a dramatic reduction in numbers over the last 100 years and now occur in specific locations with highly discontinuous populations [1]. The 2016 IUCN African Elephant Status Report estimates about 415,428±20,111 elephants in surveyed areas over ten years ending in 2015, using a variety of databases in elephant range states. The Great Elephant Census led by the Wildlife Conservation Society and conducted in 18 African range states in 2016 reported 352,271 elephants, representing a decline of 30%, with Tanzania recording the highest loss on the African continent and the majority occurring in southern Africa. The African elephant is listed as Vulnerable [1] on the IUCN Red List, with multiple environmental stressors contributing to its population decline. Consequently, there is a need to assess the impacts of climate and hydrologic changes on habitats supporting elephant populations on a landscape. The elephants play a critical role in modifying the landscape through seed dispersal of some plant species, felling down trees, and soil fertility enrichment from the dung, creating suitable habitats for insects to thrive. In many African cultures, the elephant symbolizes strength, resilience, and the ability to overcome challenges. It is a source of pride for some ethnic groups.

On the other hand, elephants cause extensive damage to crops and sometimes threaten human life, resulting in Human Elephant Conflicts (HEC). Elephant decline is mainly attributed to poaching. HEC has resulted in ecosystem change from savanna grassland to woodlands, contributing to disruptions in predator-prey dynamics, the spread of native species, and recolonization by other species. Consequently, it affects the tourism benefits to African economies. This study aimed to determine the effects of habitat, water resources, and climate change on age-class-specific elephant population dynamics. These results inform conservation interventions and policy changes to enhance elephant population recovery.

The Greater Virunga Landscape (GVL), a part of the Albertine Rift (Africa), is a biodiverse landscape with three world heritage sites and a Ramsar site. By 1979, the African elephant range declined from three million square miles to just one million in 2007, distributed across Africa, namely the southern, eastern, western, and central parts of Africa in 37 countries occupying mainly savanna woodlands and forests. Elephants are an essential component of this vast ecosystem and play a significant role in vegetation distribution and change [2–9]. Several elephant studies have been conducted specifically regarding ivory poaching [10–18]. However, despite the effort to understand the ecology of elephants, fewer studies have focused on the dynamics of the environment, climate change, habitat change influences on the elephant population, and demography over long periods. For example, the effect of human population, land use change, civil wars, and overexploitation of resources in historically suitable areas, including the loss of elephants' preferred plant species, must be better understood. To manage large wild herbivores like elephants effectively, wildlife managers need information on how habitat quality and climate influence the wildlife population. It also requires long-term planning based on a deep understanding of how population processes such as birth and death rates and age structure are affected by habitat size and quality changes, climate, and how they influence management decisions. The differences in governance and management regimes in the Transfrontier Conservation Areas (TFCA) make combatting wildlife crime challenging. For example, poaching conducted by nationals from one country on a foreign territory can only be prosecuted if legal extradition mechanisms exist.

Furthermore, the differences in human resource capacity (numbers, training, equipment, and financial resources) make it very difficult to achieve effective conservation. Yet, the elephants move back and forth from one country to another. In GVL, insecurity in DR Congo and poor infrastructure make it very difficult to achieve transboundary collaboration and management of elephants between Uganda and DR Congo. Ethnic heterogeneity, differences in cultural value attachments, and varied legal regimes complicate the management of TFCA as well. The general objective of this study was to assess the effects of changes in habitat, water resources, and climate on the elephant population in GVL. Specific objectives were to: 1) develop a comprehensive system dynamic model of age class-specific elephant population; 2) assess the impact of habitat change on elephant populations in GVL; and 3) assess the effect of climate change on the elephant population. The hypotheses (alternate) tested were: (i) conversion of habitat from forest to savanna grassland substantially influences age-class specific elephant population structure and dynamics; (ii) significant correlations exist between elephant population size, water resources, and climate change.

Materials and methods

Study area

The Greater Virunga Landscape (GVL) (Fig 1) straddles Uganda, Rwanda, and the Democratic Republic of Congo (DRC). The GVL covers an area of 15,700 km^2, of which 13,200 km^2 (88%) is protected [19]. The protected area includes seven national parks, three large tropic high forest reserves, and three wildlife reserves, including Bwindi Impenetrable National Park, which became isolated about 50 years ago. It is one of the six critical landscapes in the Albertine Rift and is among the most species-rich of any landscape in the world [20–21]. This landscape includes the Virunga Volcanoes, famous for their population of mountain gorillas (*Gorilla beringei beringei*), the savanna parks of Virunga and Queen Elizabeth, the Kibale National Park, having high diversity and biomass of primates, and the Rwenzori massif, also known as the 'Mountains of the Moon.' Altitude ranges from 5,109m at the top of the Rwenzori massif to 600m in Semliki Park.

Consequently, the landscape supports a wide variety of habitats [22]. These habitats include alpine moorland, giant heather, bamboo, montane, and submontane forest, savanna woodland and grassland [20], high and low-altitude wetlands, lakes, and vegetation types in specific lava colonization and thermal pools around the active volcanoes of Nyamluagira and Nyiragongo in Virunga Park. In addition, Papyrus and Carex wetlands are found around the lakes and some streams, and the lakes have habitat types varying from rocky and sandy edges to the pelagic zones in their depths. Virunga, Rwenzori Mountains, and Bwindi Impenetrable national parks are World Heritage Sites, Queen Elizabeth Park is a Biosphere Reserve, and Lake George is a Ramsar Site.

Virunga National Park is in the Albertine Rift, a part of the Great Rift Valley, designated as a National Park in 1925, covering an original area of 8,090 km^2. The Queen Elisabeth National Park (QENP), which covers 2,080 km^2, is a crucial component of GVL [22]. It is connected to Kigezi Wildlife Reserve (265 km^2), Kyambura Wildlife Reserve (154 km^2), Kibale National Park (795 km^2) in Uganda, and linked to Virunga National Park in the Democratic Republic of Congo. It also is contiguous with Uganda's central forest reserves of Kasyoha-Kitomi Forest Reserve (399 km^2), Kalinzu and Maramagambo Forest Reserves (428 km^2) in the east and

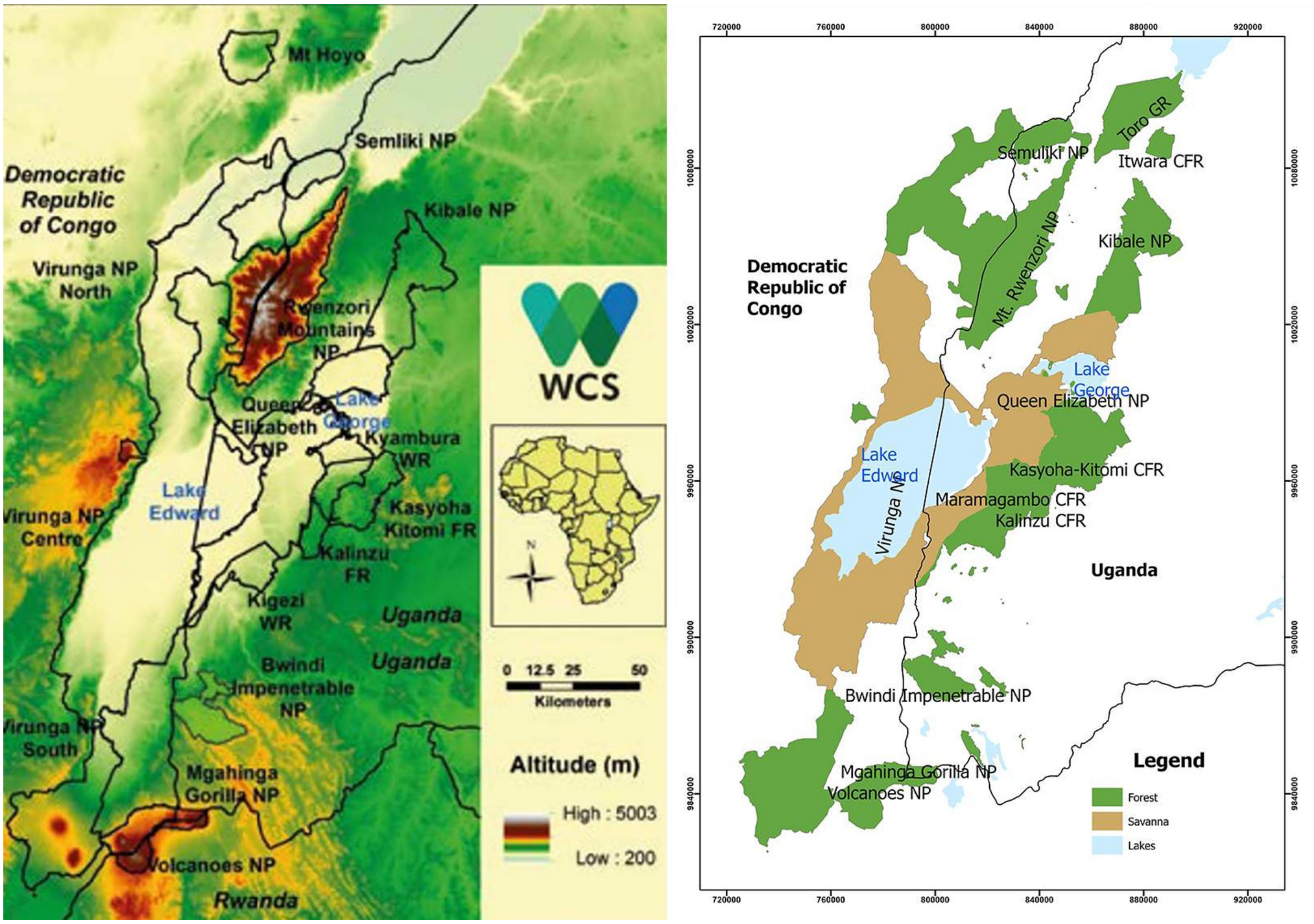

Fig 1. Greater Virunga Landscape with vegetation map [20]. Developed by authors in collaboration with the WCS Uganda program.

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borders Lake George and Edward, which are both connected by the Kazinga channel and a range of crater lakes and a significant wetland included on the Ramsar Convention's list of wetlands of international importance. The Rwenzori Mountains National Park is shared between Uganda and the Democratic Republic of Congo and is less than a kilometer from the equator. It is the third-highest mountain in Africa at 5,109 m (after Kilimanjaro and Mount Kenya). The park is contiguous with the Virunga National Park in the Democratic Republic of Congo (DRC). It forms part of the Queen Elizabeth Conservation Area in Uganda, covering an area of 996 km^{2,} of which the most substantial portion (70%) lies over an altitude of 2,500 m. Bwindi Impenetrable National Park (BINP), a world heritage site, is located on the eastern side of the Albertine Rift Valley, covering 32,092 ha (331 km^2), the most extensive Afromontane lowland forests in East Africa. Volcanoes National Park (Parc National des Volcans) lies in northwestern Rwanda and borders Virunga National Park in the Democratic Republic of Congo and Mgahinga Gorilla National Park in Uganda.

Conceptual model

The model presents elephant population–habitat dynamics with water resources and climate change effects (Fig 2). By modeling vegetation cover change and type, elephant–habitat

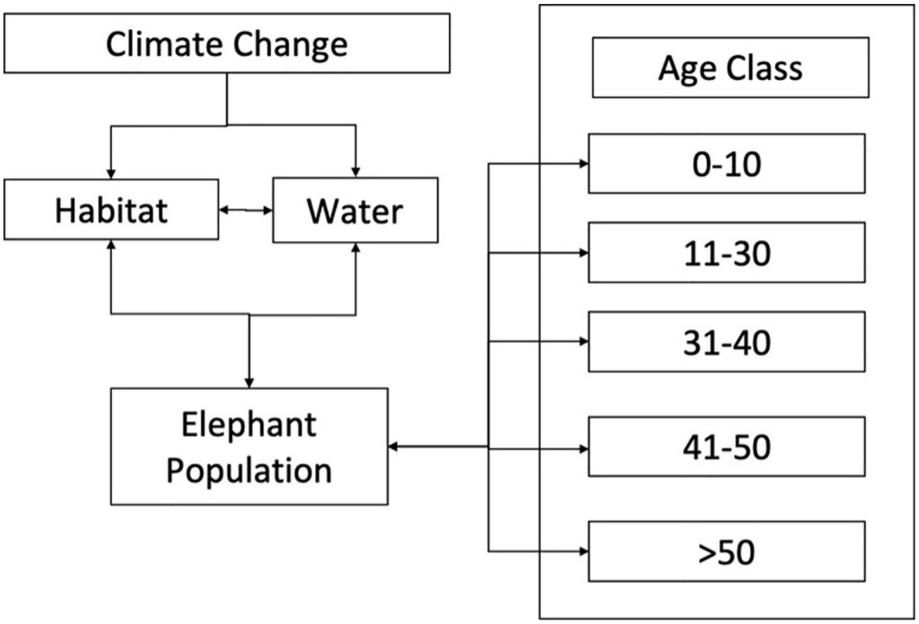

Fig 2. Conceptual model for population dynamics of elephants in GVL.

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interactions, stochastic environmental variables such as precipitation and temperature, and spatial variability of water supplies, including glacier melt contribution on top of Mt. Rwenzori and runoff, the model is used to analyze changes in elephant population acting via natality and mortality over the last 55 years. In the conceptual model, the elephant population is influenced by several factors or stressors. First, the density-dependent factors, mainly food, space, and water resources, limit population growth beyond the area's carrying capacity [23–26]. Second, climate change affects the elephant population both directly and indirectly. In high temperatures, the direct consequence is physiological stress, resulting in a diminished reproduction rate and increased mortality risk among calves and juvenile elephants. Climate change also affects the elephant population by reducing water resources and biomass production due to increased evapotranspiration and loss of suitable habitat. Habitat change is also driven by human activities, particularly the expansion of agricultural land, settlement in wildlife corridor areas, and burning suitable habitats.

Similarly, climate change negatively impacts the habitat, including accelerating the loss of native vegetation or increasing the colonization and spread of native invasive species, mainly where temperatures are high and rainfall is declining. In such scenarios, habitat loss and fragmentation are disproportionately severe, although impacts vary across vegetation types. For example, elephants depend mainly on savanna and forest vegetation, occasionally relying on wetlands/swamps for water, salt, body temperature regulation through wallowing, and migration to other landscape patches.

The habitat component of the model simulates long-term vegetation conversions associated with emergent declines in precipitation and Mount Rwenzori glacial stock. The water supply and climatic changes modules within the elephant age-specific population-land cover change model aim to model the expected effect of increasing water availability and food abundance, which are essential for elephant reproduction success. However, with a vegetation cover change of nearly one percent and an elephant population density of 1.0 elephant/km^2, savanna woodlands have become the most suitable habitat for elephant survival. The baseline model consists of both climate and habitat as interacting drivers. The scenarios of climate and habitat models additional individual effects of these stressors as future scenarios.

Empirical model

In the dynamic model, $A_{i,t}$ represents the population in i^{th} age class at time t. The number of elephants in each particular age class for the entire landscape at a given time (t) was calculated as

$$A_{it} = A_{i(t-1)} + (N + I_{it} - S_{it} - M_{it})$$

where, N is the natality rate (elephants/km2/year), I_{it} is immigrating population into age class i at time t, S_{it} is the number of surviving individuals in age class i at time t, and M_{it} is the mortality in age class i at time t (elephants/km^2/year). Natality and mortality are density-dependent, while natality is influenced by precipitation, water, and habitat quality. The natality rate N for the entire population is adjusted based on the maximum reproduction rate ($MaxN$) in the population as $N = MaxN \,/ \sum_{i=a}^{b} N_{it}$, Where N_{it} is the adjusted natality in age class i in time t, a is the starting age class of reproduction, and b is the last reproducing age class in the population.

The survival rate of elephants in each age class is specified as $S_{it} = (A_{it} – M_{it}) * \gamma_{it}$. Mortality rates for each age class were represented as

$$M_{it} = (MN_{it} * A_{it} * MI_t * Z_{it}) * (1 + P * PI) * (1 + WP * WI)$$

where MN_{it} *is* the minimum mortality rate for the respective age classes, MI is the mortality rate index, Z is the calf risk (suppressed for age classes 2 and higher), WP is the war pulse function, and WI is the war influence coefficient.

The habitat at time t (H_t) is represented $H_t = H_{t-1} + (HI_t – HD_t) * dt$, where HI_t is habitat increase in km^2, HD_t is habitat decrease in km2, but $HI_t = H_t * FP_t$, and $HD_t = H_t * SP_t$ where FP_t and SP_t are proportions of the forest, and savanna grassland and woodlands in the entire landscape, respectively.

The elephant population dynamics model was specified using Structural Thinking, Experimental Learning Laboratory with Animation (STELLA) software (High Performance Systems, Inc.). The STELLA is a dynamic systems software for visual simulation that uses differential equations of stocks and flows. This software has been used for understanding population dynamics and economic fluxes [27–30]. The converters represent input parameters, and the arrows represent mathematical relationships between the elements. A Fourth Order Runge-Kutta method was used to perform the integration because it estimates stock changes by making more flow forecasts, unlike the other two techniques. Runge-Kutta-4 is also known to provide the best results with relatively large tolerances when simple, functional evaluations are conducted [31–33].

Data compilation

The initial values of the elephant population under A_i are presented in Table 1. The total annual reproduction rate ($TOPR$) for the entire population was 40 percent, and the natality rate index was modeled as a graphic function of the whole observed population. Its values ranged from 1 to 2.5 for the period 1960–2010. Where γ_{it} is assigned 10 percent for i = 1,4,5, and 0.05 for i = 2,3. The survival rate of age classes A2 and A3 was slightly lower because the elephants in this age group are more susceptible to poaching and killed by humans in retaliation for lost human lives or physical injury and crop loss. This age class is when sub-adult males abandon their social groups in search of mates [28]. It was reported that the survival probabilities for females were slightly higher (89%) than for males (82%) [28]. The annual population

Table 1. Population change by age group.

Age structure	Elephant population 1960	Elephant population 2006	Change (Proportion)
0–10	660	1,240	0.375
11–30	531	998	0.302
31–40	319	599	0.181
41–50	212	398	0.120
>50	38	72	0.022
Total population	1,760	3,307	1.000

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growth, including immigration and emigration, averaged 0.17% and 2.8% when migration is excluded over 14 years for the Samburu National Park (Kenya) population [29], the most accurately studied population in East Africa. The mean annual mortality was 4.71% and a maximum of 14.1 percent, while the mean yearly natality was 7.21% (maximum 14.4% and minimum 2.1%).

Reproduction starts at ages 11–30 and lasts 50 years and above. The observed (census) population of 2006 published by UWA, ICCN, WCS, & WWF) was used to assign the number of elephants in each age class for the year 1960 based on the protected area management agencies (UWA, ICCN, and ORTPN) reports and peer-reviewed publication [34–35]. The proportions of each age class are based on research on savanna elephants by specialized scientists, as shown in (Table 2) [32–34]. Of the total population in 2006, 37% of the elephants observed were in the age class 0–10, and the rest of the distribution was as follows: 11–30 (30%), 31–40 (18%), 41–50 (12%) and ≥50 years (2%). Therefore, 2006 was treated as the base year, and the observed population was used in 1960 for model calibration.

The information collected includes observed elephant numbers, habitat change, hydroclimatology, and water resources. Elephant population data were obtained from the large mammal census databases and associated government reports of protected area authorities of Uganda (Uganda Wildlife Authority), DRC (ICCN), and Rwanda (RDB), and conservation organizations such as WCS and WWF that have worked in the region and supported conservation programs in the area for a long time [35]. Reviews of published survey reports in peer-reviewed articles were also conducted to validate the database information [36–39]. From the early 1950s till the late 1970s, most of the census of large mammals was performed by a ground survey by walking along transects systematically designed for this purpose and identifying all scats such as dung, footmarks, and physical count of live animals. After the 1970s, most large mammal counts were done by aerial means, specifically using a four-person carrier light aircraft, and animal counts were done following the standard method.

Survival data for ten-year intervals is based on elephant counts by wildlife authorities in the region, including the Uganda Wildlife Authority (UWA) and *Institut Congolais pour la Conservation de la Nature* (ICCN) of the Democratic Republic of Congo. The first-age class values are modified for males and females with a value of 0.388, based on an estimate of natality and

Table 2. Scenarios and parameters selected for model simulation over a period of 51 years.

Scenarios	Description	Parameter values		
		Low	Medium	High
Climate change according to IPCC AR5 RCP2.6, RCP6.0, & RCP8.5 scenarios	Temperature Precipitation	1.6˚C 2% increase	2.8˚C 10%	4.3˚C 18%
Habitat change	Increase in forest & savannas	50%		
Water resources	Increase	Determined RCP scenarios		

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extrapolation from adult mortality rates but excluded from the age classes contributing to natality [40]. However, this consideration is essential for tracking when the sudden influx in births associated with the second age class is accounted for. This value suggests that 37.5% of the population would be comprised of 0-10-year age class graduates.

During the twenty-year interval, individual birth and death were simulated using the Leslie method [41]. A random built-in function is used to generate uniform random numbers. The reproductive probabilities are evaluated using the counter and delay built-in functions based on the total population size from the last time step. Individual females give birth to zero or two offspring with density-dependent probabilities. A random number then determines the state of the environmental parameters and the corresponding survival values generated from the dynamic population submodel. Individuals survive to the next age class or die based on the mortality rate index driven by habitat quality (habitat quality index). This yields the state of the population at the end of a ten-year step. A higher number of simulations were conducted to attain acceptable statistical confidence levels.

Habitat change

As part of the long-term vegetation change mapping for Virunga National Park and Queen Elizabeth National Park, the Wildlife Conservation Society [42] calculated the woody cover change and estimated increases and decreases in woody cover in different parts of the GVL between the 1950s and 2006. Woody cover changes generally ranged from a rise of 1,579 km^2 in some parts to a decrease of 334 km^2 in others [42]. They attributed the net gain in woody vegetation cover (1,245 km^2) to a reduction of large mammals in the landscape from the 1970s (as demonstrated by the observed elephant population trend), the continued recovery of the vegetation from the human resettlement away from the landscape in 1880s [43]. Increasing rainfall, climatic variability, and changes in fire frequency. In Virunga National Park alone, 98.2 km^2 was encroached upon by humans, and the new settlement within 2 km of QENP was recorded to have 179,200 people.

The land cover map produced by WCS in 2006 [42] was reclassified into four significant land uses: forest, savanna woodland and grasslands, wetlands and water, and human settlement and agriculture. This broad classification was made because elephants depend greatly on savanna woodland, grasslands, and forest habitats for food but need water for drinking and body temperature regulation. Elephants, however, use less dense human settlements and agricultural areas during migration and occasionally feed on the crops during their movement to other patches within the landscape.

Hydroclimatology

According to the study conducted by the WCS [42], rainfall in and around the GVL has mostly stayed the same since the early 1900s. Climate variability and change are simulated with the prior knowledge that there are two drought seasons in a year: December to February and June to August. Analysis of climatologic data from nine different sites with at least 20 years of continuous data showed an increasing trend in annual rainfall [42]. The study results revealed significant ($P<0.05$) increases in total annual rainfall in Beni (1974–2007), Mweya (1958–2007), Kabale (1918–1996), Kiamara (1982–2007), and Ruhengeri airstrip in Rwanda (1928–1986) over time but the rest of the stations did not show any significant trends. At the local scale, rainfall varies greatly across the landscape. The driest parts of the landscape are in the savanna areas north and south of Lake Edward, recording an average monthly rainfall of 30–40 mm. The Albertine Rift climatological assessment studies show that precipitation and temperature in the region will increase over the next 100 years. According to this study, the mean annual temperature in the base year (1990) was recorded as 22.7˚C (max 26˚C and min 15˚C), and the modeled temperature for 2030, 2060, and 2090 were 23.6, 24.7, and 26.3˚C, respectively. Similarly, the mean annual precipitation in 1990 was noted to be 1199 mm, 1233 mm (2030), 1287 mm (2060), and 1406 mm in 2090 [44]. Across the modeling period, precipitation variation ranges from 821 mm– 2098 mm.

For this study, weather data from the Lwiro weather station provided by the *Observatoire Volcanoligue de* Goma was selected for use in the computation of ET. Data from other weather stations, such as Beni, Butembo, and Mweya, were available but had several missing data for some years. Other sources of hydroclimatological data are the Climate Research Unit (CRU) at the University of East Anglia, the UK, and NOAA CIRES Twentieth Century Global Reanalysis Version 2, Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory [45]. However, the CRU data was summarized to historical monthly averages for the years, and the variability at an annual scale needed to be improved to ensure data quality.

This study used 51 years of historical climate observations of daily temperature and precipitation from two of the eight weather stations–Lwiro and Butembo in DRC located within the study region. The climate data from these two weather stations were selected for use because they had the highest consistent record of observations from 1960 to 2010 compared to the rest of the stations in the region. Following the description of the IPCC AR5 climate change results based on the four RCP scenarios earlier discussed, East Africa was one of the five regions identified by the IPCC for analyzing regional climate change [42]. Of the four scenarios, future climate change values based on RCP2.6, RCP6.0, and RCP8.5 were selected to implement the climate change effect on elephant population dynamics. Before integrating future climate change prediction, the annual historical precipitation data were detrended to incorporate climate change induced by temperature increase. This procedure was achieved by performing a regression analysis to estimate the temporal trend in the time series. For example, if P is precipitation and t is the time in years, the fitted regression $\acute{P} = \alpha+\beta t$. The time scale, in this case, was from 1960 to 2010. The fitted regression equation $\acute{\mathrm{P}} = 1.4024x - 1493.9$ was used to estimate the average historical precipitation (β) of 1254.80 mm for annual precipitation and an average historical annual precipitation increase of 25.86 mm. The detrended equation is given as $P - \beta(t) + RCP_{\acute{p}}/100)$, where P is the historical precipitation, t is the year, and $\mathrm{RCP}_{\acute{p}}$ is the future annual precipitation change percentage. The recorded precipitation trends calculated from the regression analysis were removed from the observed temperature data to isolate climate change trends from natural variability. This was done by subtracting the trend component derived from the regression model from actual observation. In so doing, it allowed various climate change scenarios to be incorporated into the model. The baseline assessment (BL scenario) is a 51-year scenario without the influence of historical warming and helps evaluate the exclusive effects of climate change scenarios. The detrended baseline data from 1960 to 2010 was then recalculated to reflect the three precipitation change scenarios identified as RCP2.6, the lowest, RCP6.0 (medium with a 10% precipitation increase), RCP8.5, the highest with an 18% precipitation increase.

The warming trends predicted by IPCC represent long-term increases over the current temperature data over the next 100 years. The IPCC warming predictions were added to the baseline data as a linear trend for mean annual precipitation. Over the next 100 years, the future temperature change was modeled as an absolute value for each RCP [42]. The future temperature change values for East Africa selected were RCP2.6 = 1.6˚C, RCP6.0 = 2.8˚C, and RCP8.5 = 4.3˚C [46]. As such, incorporating temperature change did not require detrending, which would be necessary if observation time series data were used. Instead, a straightforward calculation of the annual increment to the historical values was done as per the equation below:

$$T = T_h + \left(\frac{T_f}{100}\right) \times t$$

where T is the new calculated temperature for the elephant modeling scenario, T_h is the historical temperature, $T_f/100$ is the RCP scenario temperature per year, and t is the year.

To account for the available water resources in the landscape, surface runoff, glacier melt contribution to river discharge, and water in reservoirs, mainly lakes and rivers, were considered. Surface runoff refers to water flow over the land surface. Runoff flow comprises two main elements: base flow, which originates in groundwater, and surface runoff, which accumulates rainfall that drains into the stream. Several models for computing runoff and soil loss do exist such as the Rational model commonly used to compute the peak runoff rate from small watersheds and assumes the uniformity of rainfall intensity for the duration at least equal to the time of concentration of and throughout the watershed, Cook's Method, which requires an evaluation of four watershed characteristics, i.e., relief, infiltration rate, vegetal cover and surface storage to determine the runoff rate, Soil and Water Assessment Tool (SWAT), and Curve Number method. The SWAT developed by the USDA Agriculture Research Service (USDA-ARS) is a small watershed to river basin-scale model used to simulate the quality and quantity of surface and groundwater and predict the environmental impact of land use, land management practices, and climate change. SWAT is widely used in assessing soil erosion prevention and control, non-point source pollution control, and regional management in watersheds. The SWAT model operates on a daily time step and is designed to predict the impact of land use and management on water, sediment, and agricultural chemical yields in ungauged watersheds. However, several of these hydrological models, including the Environmental Policy Integrated Climate (EPIC) model [47] and SWAT [48], use the SCS curve number method for estimating storm runoff. Ponce and Hawkins [49] provided a detailed account of the conceptual and empirical foundations of the curve number method, emphasizing its wide use in the United States and worldwide. For this study, the Soil Conservation Service (SCS) Curve Number Method was used to compute the runoff in ESRI's ArcGIS with the help of the arc hydrology tools. The Soil Conservation Service (SCS) Curve Number Method is a versatile and widely used procedure for runoff estimation because it gives consistently usable results [50–53].

The Curve Number (CN) measures the relationship between initial abstraction and potential maximum retention of an area after a storm. The *CN* method is based on the relationships between rainfall depth, P (inches), runoff depth, stormflow, Q in inches, and storage factor [50–51]. The Q is represented as:

$$Q = \frac{(\mathrm{P} - 0.2\mathrm{St})^2}{(\mathrm{P} + 0.8\mathrm{St})} \text{ and } S_\mathrm{t} = \frac{1000}{\mathrm{CN}} - 10.$$

The maximum potential retention (*S*) is related to the watershed's soil and land cover conditions through the curve number equation above, and *S* is a dimensionless watershed parameter ranging from 0 to 100. The USDA SCS developed tables of runoff curve numbers corresponding to various land use and land cover types available in the SCS-SA User Manual [54]. A *CN* of 100 represents a limiting condition of an entirely impermeable watershed with zero retention; thus, all the rainfall becomes runoff [55]. Conceptually, a CN of zero represents the other extreme, with the watershed abstracting all rain with no runoff regardless of the rainfall amount. The water balance is computed using the Thornthwaite- Mather approach [56–57]. Thornthwaite's method underestimates potential evapotranspiration during the summer when the solar radiation received at the surface is at its annual maximum [58]. This method also does not capture local soil moisture patterns that vary with slope and aspect and are essential state variables in capturing the ecological differences in high-altitude and forest-dominated areas. Penman-Monteith equation or Hargreaves method are best alternative methods widely used, but are data-intensive.

The Penman-Monteith equation is a combined equation considering the energy supply and mass transfer of water vapor from the evaporating surface derived from the leaf energy balance equation [59–60]. The Penman-Monteith method is very rigorous. However, it was noted to have limitations when applied to highly forested areas because the canopy resistance term cannot be easily parameterized [59–61]. It was also developed to predict evaporation from open water, bare soil, and grass. Furthermore, since it is derived from the energy balance of a leaf, the Penman-Monteith equation ignores the fluxes of water vapor to and from the soil [61]. Despite its shortcomings, the Thornthwaite method was selected for the compilation of evapotranspiration (ET) because of several reasons, namely: 1) scarcity of climatic and adequate land-atmospheric data required for the compilation of ET; 2) the Thornthwaite method has been used extensively in North America and is proved to produce consistent results regardless of its shortcomings. In Africa, this method was used to evaluate the effects of soil water holding capacity assumptions on estimates of African evapotranspiration rates, moisture deficit, and moisture surplus conditions. Thornthwaite's method is as follows:

$$E'_p = \begin{cases} 0, & T < 0^\circ C \\ 16\left(\frac{10T}{I}\right)^a, & 0 \le T < 26.5^\circ C \\ -415.85 + 32.24T - 0.43T^2, & T \ge 26.5^\circ C \end{cases}$$

Where *E'p* is monthly unadjusted potential evapotranspiration in mm, ***T*** is mean monthly surface air temperature (^{o}C), and ***I,*** the annual heat index, is given by the equation

$$I = \sum_{i=1}^{12} \left(\frac{T_i}{5.0}\right)^{1.514}$$

$$\text{Where a} = 6.75{*}10^{-7}\, I^3 \; - \; 7.7 \,{*}10^{-5}\, I^2 + 1.79{*}10^{-2}\, I + 0.49.$$

If the air temperature is measured on a monthly scale, then potential evapotranspiration is adjusted for the variable day (h) and month (θ) lengths as follows:

$$E_p = E'_p \frac{\theta}{30} \frac{h}{12}.$$

In this study, the temperature data used was already compiled on an annual basis, and no adjustment of ET was needed. After processing the data in Microsoft Excel, the calculated ET was used in the STELLA model to implement the water balance computation.

This region's primary water source is precipitation, which ends up as runoff, groundwater, and reservoirs through river discharge. The other water source is glacier melt, which contributes less than 1% toward river discharge. In STELLA, water stock was computed as the difference between sources of water (i.e., runoff, glacier contribution) minus the loss through evapotranspiration (ET) and expressed in the form of an equation: $Y = Y(t - dt) + (Y_i – Y_o) * dt$

where Y_o is water loss in the form of ET, Y_i is water available in the landscape given as: $Y_i = R + (Y * gm)$ where R is the runoff in mm, *gm* is the contribution from glacial melt from mountain Rwenzori ice fields. Runoff was compiled following the Curve Number (CN) methodology already described in the methodology section implemented in both ArcGIS, specifically to assign the curve numbers to the land cover matched with the corresponding soil hydrologic group, and in STELLA where a composite curve number (COMPCN) was calculated as:

$$\begin{gathered}
COMPCN = (CNFO_A * wFO_A) + (CNFO_B * wFO_B) + (CNFO_C * wFO_C) + CNFO_D * \\
wFO_D + (CNS_B * wS_B) + (CNS_C * wS_C) + (CNS_D * wS_D) + (CNWET_A * wWET_A) + \\
(CNWET_B * wWET_B) + +(CNWET_C * wWET_C) + +(CNWET_D * wWET_D) + +(CNH_A * wH_A) + \\
(CNH_B * wH_B) + (CNH_C * wH_C) + (CNH_D * wH_D)
\end{gathered}$$

CNFO, CNS, CNWET, and CNH are curve numbers of the forest, savanna, wetland, human settlement, and agriculture land cover classes associated with the soil hydrologic group represented by the subscripts A to D.

Policy scenarios

Scenarios for the anthropogenic factors were assessed for the impact of climate change, specifically precipitation and temperature, under three different RCP scenarios, changing water volume and habitat impacts. To determine the effect of habitat quality on age-specific elephant population dynamics, three scenarios of habitat loss (low, medium, and high), particularly savanna grassland and forests/woodlands, were conducted over 20 years using a monthly simulation scale for each year. Similar simulation experiments were conducted for water resources to assess the changes in age-specific dynamics associated with each experiment (Table 2). Quantitative models presented here provide a valuable tool for exploring the consequences of management decisions involving manipulating habitats and watershed ecosystems to achieve viable elephant population densities. Dynamic modeling allows the evaluation of feedback loops and stock changes related to climate and habitat conditions that will enable the identification of interventions that protect and enhance elephant populations and the development of management strategies under changing climate and habitat conditions. Quantitative tools allow the assessment of critical needs and evaluation of strategies for the effective conservation of transboundary populations like elephants.

Results

Calibration and validation of baseline results

The simulated population was plotted and compared with the observed population (Fig 3). Furthermore, a scatter plot fitted with a linear regression of simulated vs. observed values and the coefficient of determination (R^2) was used to assess the fitted model. A high $R^2 = 0.78$ showed that the model explained the observed data very well, providing a high degree of confidence in the model. The model's performance validation was done using observed data from QENP (Uganda), a savanna park within the GVL. Forty-nine years of census data for this park were accessed from Uganda Wildlife Authority, thoroughly cross-checked with the reports from Uganda National Parks currently housed by the Ministry of Tourism and Antiquities, and corroborated with census figures published in peer-reviewed journals, mainly the African Journal of Ecology. The observed and simulated populations are well explained by the model ($R^2 = 0.68$), and the trend was well represented. The computed PBIAS for the simulation model was PBIAS = -2.86, and the Root Mean Square Error-observations standard deviation ratio (RSR) = 0.48, and for the validation model was PBIAS = 17.21(0.02); RSR = 0.74, further confirming the validity of simulation results.

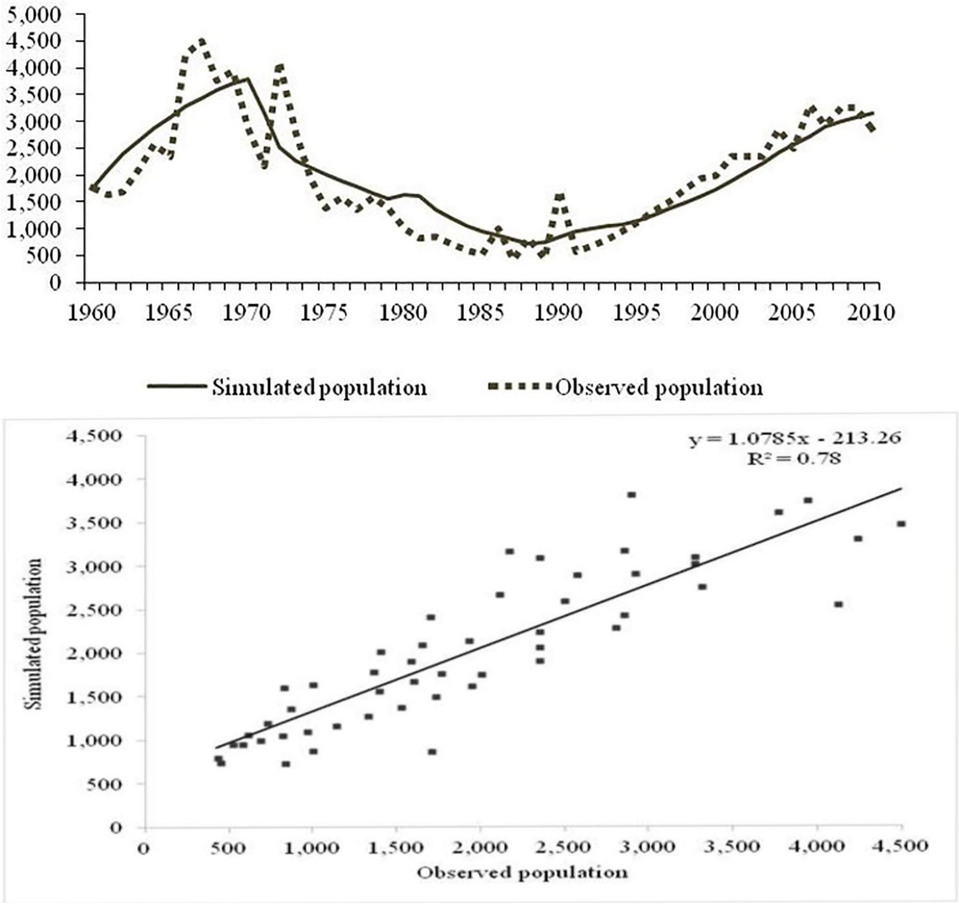

Fig 3. Calibration of the elephant population model for GV.

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Baseline results

The baseline results from the calibrated model (Fig 4) show that the elephant population peaked in the early 1960s, declined tremendously from 1970 to the 1990s, and steadily rose in the 2000s. The decline in elephant population from 1970 until 1990 is attributed to the collapse of Uganda National Park management and the large-scale slaughter of large mammals during the regime of Idi Amin [42]. The recovery after 1990 can be attributed to improved security in Uganda [42]. In terms of individual age-specific classes, baseline results indicate that age classes 0–10, 11–30, and 31–40 years are recovering from the dramatic decline that occurred in the mid-1990s, while the age classes 41–50 and >50 years completed phased out during the same catastrophic period. Baseline results also show that the number of elephants in age classes 0–10 and 11–30 is the highest or greatest across the modeling period (1960–2010). It is reasonable to suggest that the declining trend would not be expected to behave the same way, given that a large proportion of the elephants at the baseline level is high among these classes compared to other classes. However, this argument is weak because adult elephants are expected to have a lower risk of death compared to juveniles and calves.

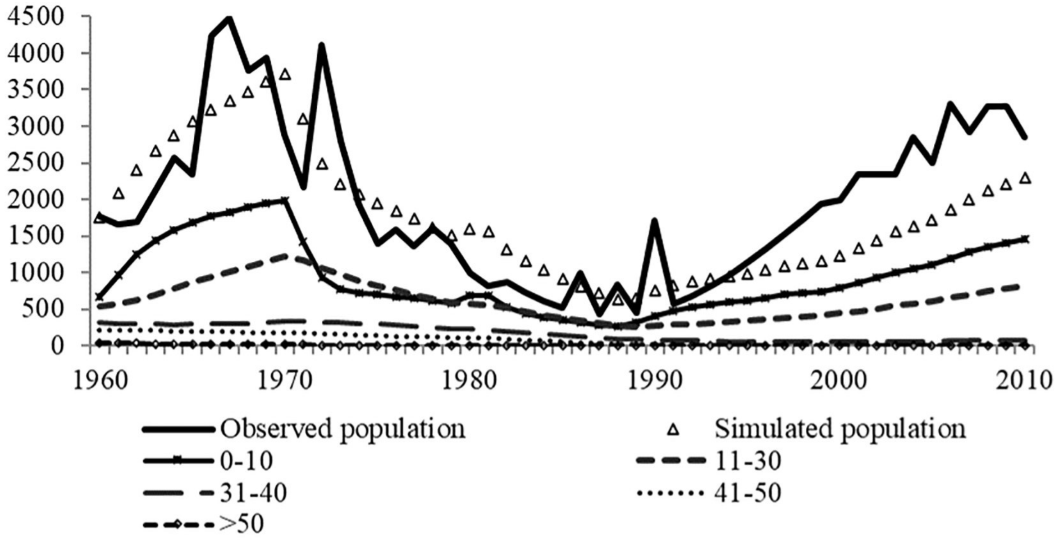

Fig 4. Baseline results for the elephant population dynamics.

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Climate change impacts

The results of the climate change analyses based on the IPCC RCP2.6, RCP6.0, and RCP8.5 scenarios showed that climate change has the potential to eliminate elephants in the age classes 41–50 and >50 years (Fig 5) attributed to direct and indirect effects. Large mammals are at risk of succumbing to the effects of climate change from both direct and indirect causes. Indirect causes include resource depletion, habitat change, competition and disease [62], low adaptability. Old elephants are expected to be highly vulnerable to diseases, and drought induced deaths such as fire and risk of predation. The remediation interventions include provision of watering points for thermal regulation, habitat management, and prevention of hazards and risks such as fire. However, a small number of elephants in the age groups 31–40 and 41–50 have the potential to survive under these climatic conditions. The numbers of elephants in the age group 0–10 and 11–30 showed an initial increase followed by a sharp decline from the late 1970s to the 1990s, and in the late 1980s, the numbers in these classes began to rise again. Increase in the numbers could be attributed to migrating elephants with a reasonable number of calves. The total population of elephants simulated under different RCP scenarios was similar. Climate change is a slow-acting environmental process whose effects take years to influence the species or system [63]. Once the impacts of climate change become eminent, they cause long-term effects such as fire occurrence risk, the emergence of zoonotic diseases, invasive species, and suitable habitat degradation and loss, which conservationists must plan for early by implementing fire management practices, disease monitoring to enable early detection and control spread, and habitat manipulation to avoid disastrous events. However, it demands that the spatial and temporal scales of conservation be aligned with the scales of climate-change projections to develop management strategies that enhance the resilience of the ecosystems. The GVL is characterized by spatially varied climatic conditions attributed to the diversity in ecosystem types, vegetation, and topography. These conditions enhance the elephants' ability to deal with local-level climatic changes by switching habitats from savannas to forests and wetlands during extreme drought conditions and returning to savannas during the wet seasons. Local-scale variations mentioned above often override the projections of broad-scale climate models, resulting in high uncertainty.

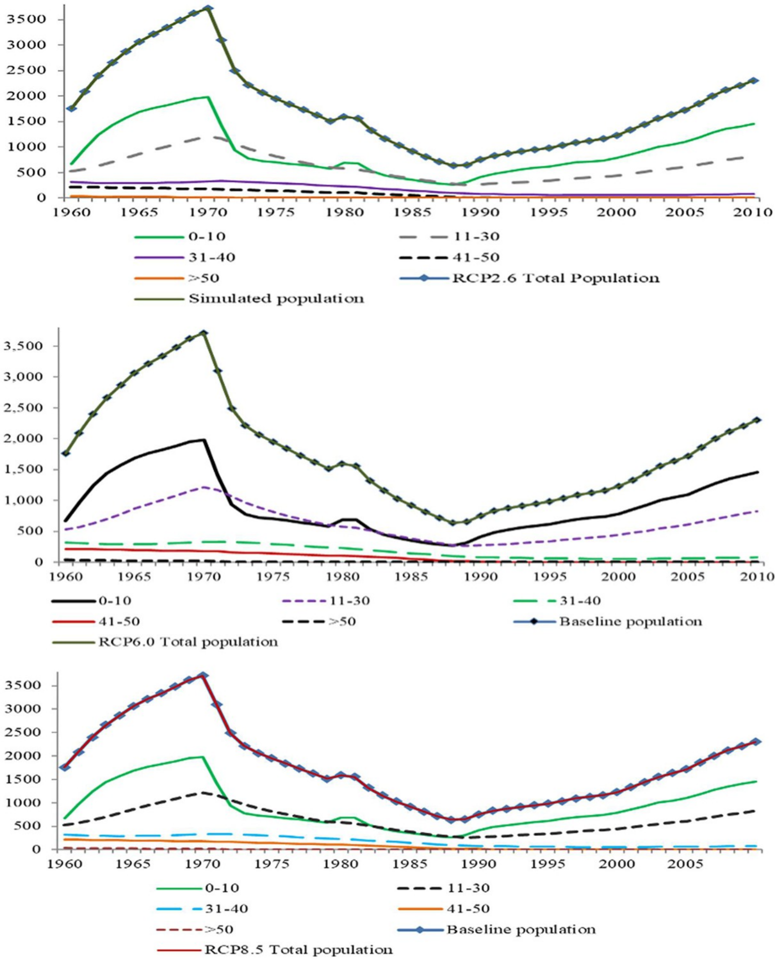

Fig 5. Age class-specific impacts under climate change scenarios.

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Mann–Whitney U test is a nonparametric test of the null hypothesis that two populations are the same against an alternative hypothesis [10–13]. The same test was applied to test the impact of climate change under the extreme representative concentration pathway scenario 8.50 on the elephant population, and the results did not show a significant influence of climate change on elephant population dynamics (RCP8.5>B0, $p<0.5$; W = 1300.5, P = 0.5), making it consistent with the baseline simulated population response representing a conservative climate change scenario. This confirms the results observed by examining the graphic population trend presented under the RCP8.5 scenario. Thus, with the baseline, climate change impact did not show such dramatic change In elephant population dynamics.

Habitat change

Habitat change in this landscape is mainly driven by frequent fires inside the savanna parks, and agricultural expansion, especially commercial plantation crops such as tea, sugarcane, tobacco, palm oil, and cocoa, and potentially climate change as evidenced by the displacement of native vegetation with native invasive plant species such *Dichrostachys cinerea*, *Lantana camara*, and *Imperata cylindrica* [64–65]. The protected area authorities have developed fire management plans, including the maintenance of fire lines, early or pre-emptive burning and removal of biomass. To mitigate agricultural expansion, the management has opened and erected permanent pillars and planted trees along the park boundary and some locations constructed an electric fence or elephant barrier. Elephants spend nearly 80% of their time in savanna woodlands and grasslands, only moving to forest areas during the dry season to feed on tree leaves and search for water and salt leaks [4,8]. They also frequently move to the wetlands in search of water. Therefore, a fifty percent increase in the proportion of woody vegetation (forest and savannas) was implemented to investigate the impact of an immediate increase in the suitable habitat for elephants. Results suggest that an increase in woody vegetation may increase populations of all age classes (Fig 6) through habitat management to favor palatable plant species, enrichment planting, and suppression of fires, allowing the transition to happen. However, the rise in population for age classes 41–50 and >50 years was slightly low, declining to zero in 1990.

Discussion

This study aimed to assess the effect of poaching, habitat management, and climate change on the elephant population dynamics in GVL. This was unique because it involved testing three policy changes: biodiversity conservation, water resources management, and carbon sequestration about the elephant population response amidst climate change considered at low to high-temperature change scenario. Furthermore, this study tested three options: strengthening law enforcement, implementing community-focused livelihood interventions, and iii) a market-based solution to stop the supply and demand for elephant ivory using a multicriteria decision support model. These study results are interesting and very helpful to the protected area managers in ensuring that the elephant population in GVL is stable and well-protected.

Aerial surveys conducted in Queen Elizabeth Protected Area (QEPA) showed that elephant numbers fluctuated between 1,300 and 4,000 during the 1960s and early 1970s [4,63]. During that period, elephants migrated not only between QEPA and Virunga National Park, but also northward to Kibale National Park, Rwenzori Mountains National Park, and the grasslands surrounding these areas [59]. Similarly, surveys of elephants in Virunga in the 1960s estimated about 3,500 elephants [64], only to drop drastically in the 1990s and 2000s because of the insecurity and presence of rebel groups in the park. In the 1970s, heavy poaching in Queen Elizabeth National Park is reported to have led to elephants fleeing into Virunga [63]. Conversely, the instability and rise in poaching in Virunga since 1996 resulted in elephants fleeing into Queen Elizabeth [64]. There is undisputed evidence that the population in Queen Elizabeth National Park rose from 150 individuals to 2,950 in 2006 over 25 years, an increase that could not have been achieved solely by births alone [64].

The increase in human population, coupled with a decline in large mammal populations due to poaching [38,65–67], partly contributed to the increase in woody vegetation cover and a reduction in savannah habitats suitable for elephants and other mammals. For example, Plumptre et al. [68] assessed the land cover land use change in GVL and showed that the grassland cover registered the highest net loss by 33% followed by wooded grassland at 29%. These changes were further emphasized when overall woody cover was assessed where QENP registered a 25% increase between 1954 and 2006. In terms of the entire landscape, there was a 14% increase in woody cover between 2006 and 2017, which is a slightly higher rate of loss over 11 years compared to the period of 52 years [68]. Similarly, the increase in human population has also contributed to the loss of connectivity between protected areas. Yet, these wildlife corridors are crucial to elephant movements seeking food and promoting genetic diversity [21,62]. These changes are predicted to increase with climate change, resulting in increased elephant movements in GVL and exacerbating human-wildlife conflicts because of the increased

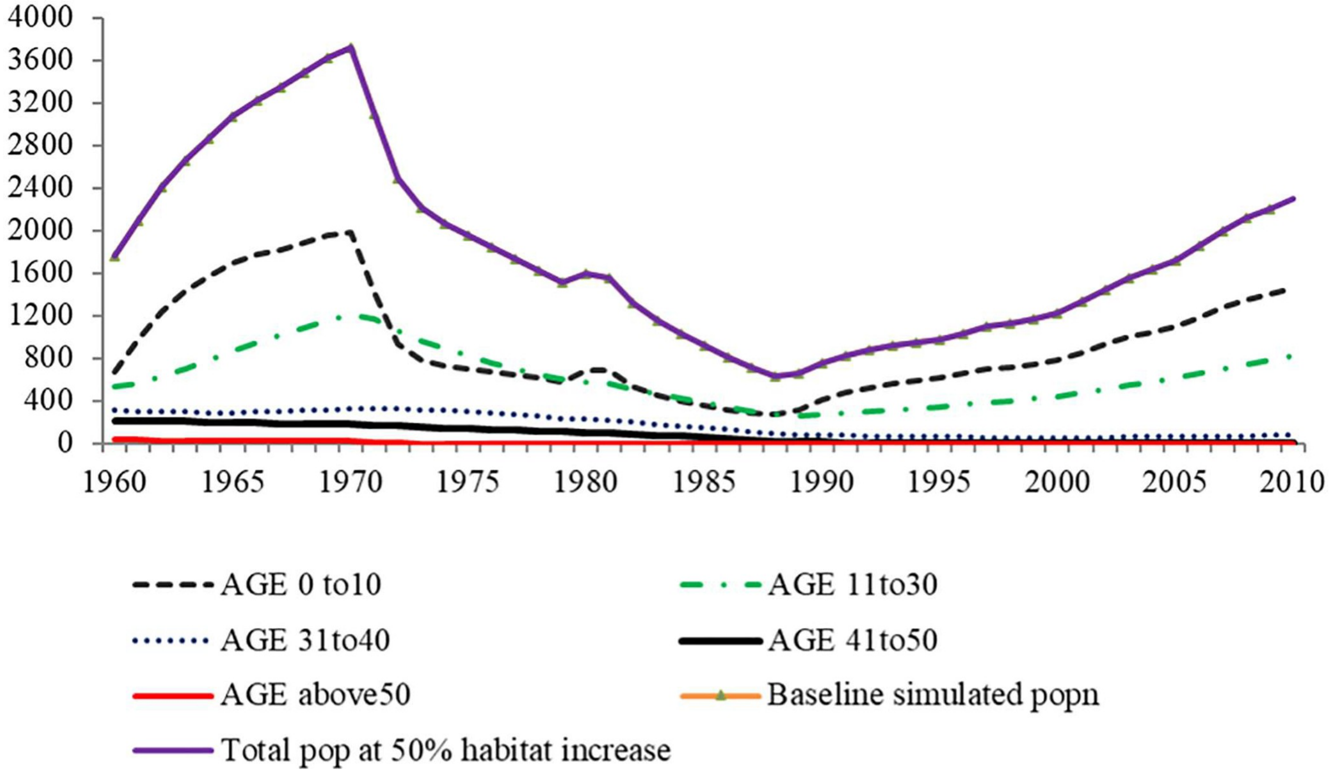

Fig 6. Impact of doubling habitat on elephant population by age class.

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human population and agricultural increase around protected areas. The study results showed that the protected area managers need to create an appropriate balance between achieving conservation and meeting the needs of the people, reconciling economic development with wildlife conservation. Fundamentally, conservation delivers economic benefits to the citizens in GVL through tourism revenue, construction of supportive infrastructure such as roads, creation of incentives and compensation models to mitigate human-wildlife conflicts, and initiation of nature-based solutions such as carbon credit projects or schemes to secure financing for the management and protection of wildlife. Private landowners living adjacent to the parks must be given fiscal and monetary incentives to maintain some of their land under conservation to create or maintain wildlife corridors to allow elephants to move from one protected area to another. It is a known fact that frontline communities are economically disenfranchised poor, and yet they depend on the park resources for their livelihoods. In such circumstances, the park managers are unlikely to receive conservation support from conflicted communities. As such, economic empowerment and the development of community capacity to engage in income-generating activities is vital, an aspect noted from this study's results.

The climate of the GVL varies because of its changing altitude and habitats. Ranging from glaciers and afro-alpine vegetation around 5,100 meters above sea level (a.s.l.) to humid lowland rainforest at 600 meters a.s.l., there are extremes in temperature and rainfall within the same landscape, which is what creates the diversity of niches for the many species that occur here [62]. Climate change modeling results for the region predict that the GVL will become wetter and warmer over time [69]. Our study results reinforce the necessity to secure and maintain wildlife corridors and restore degraded forests and savannah woodlands to guarantee elephant adaptability to climate change. Habitat quality and condition are critical to the survival of elephants by providing a reliable and sustainable source of food, water, and shelter for thermal regulation.

On the other hand, if the suitable habitat is degraded or heavily fragmented, it predisposes the ecosystem to invasive colonization, fire risk, and flooding triggered by the climate change scenario. For example, under the RCP8.5, temperature is expected to be high, resulting in increased biomass accumulation, low elephant adaptability, and death, as witnessed in Tanzania in 2022, displacement of species, and competition for resources between people and wildlife. Conversely, suppose precipitation is very high in the case of RCP2.5. In that case, the elephant conservation area may suffer from flooding, vegetation cover modification, and reduced elephant mobility, making the population vulnerable to diseases and other risks. In partnership with conservation organizations, national governments have established policies and legal frameworks, the development of National Elephant Action plans, wildlife corridor protection plans, and climate change mitigation and adaptation plans. These measures have created considerable attention to climate change impacts through conservation planning programs, policy adjustments, increased awareness, and education to mitigate potential climate change impacts and developing new management and financing strategies.

This study considered these challenges as nested, multiscaled, and multidisciplinary, demanding a holistic approach. It was also recognized that hierarchical conservation planning helps prioritize the places with the greatest conservation need and focuses on species population management. The conventional management system, with wildlife managers and researchers examining these inextricably linked problems in total isolation, needs new approaches. As such, an integrated approach was necessary to explore these challenges collectively. Under this approach, policy options and conservation efforts can be evaluated, strategic decisions made to allocate scarce resources effectively, and critical players persuaded to intervene on a broader scale. In GVL, the presence of landscape species such as elephants, lions, and Mountain Gorillas created the impulse for transboundary resource management and collaboration. It also catalyzed the creation of the Greater Virunga Transboundary Collaboration (GVTC) Secretariat established under a tripartite agreement among Rwanda, DR Congo, and Uganda to coordinate investments, secure cooperation and collaboration among the three states together with the protected area institutions (UWA, ICCN, and Rwanda Development Board). In addition, an independent entity, the International Gorilla Conservation Program (IGCP), was established to handle tourism development and monitoring of the species in the region. The transboundary nature of the GVL landscape has resulted in strong partnerships between and among stakeholders such as governments, Civil Society Organizations, Conservation NGOs, development partners, donors, academia, and researchers, as well as helped to unlock funding for implementing the GVL strategic plan. In turn, it has helped to protect and conserve biodiversity, including elephants, created the need for regional peace-building and economic integration, and helped to support the sustainable socio-economic development of rural communities. Cross-border collaboration and eco-tourism became a vehicle for building institutional capacity and reducing poverty at the regional scale.

Another strategy is establishing community-led programs like community wildlife scouts, eco-guards, or lion guardians focusing on protecting and conserving species at the local level. There are three broad advantages of establishing community wildlife scouts, eco-guards, or lion guardians as an incentive for communities to participate in conservation and develop community-led ecotourism namely a) it entrenches local communities' active participation in protected area conservation and facilitates information sharing between conservation managers and stakeholders, and b) it results in greater appreciation of the need for protected areas by communities and promotes the integration of indigenous ecological knowledge as well build community-led conflict management, and c) is less costly. The community wildlife scouts, or the eco-guardians have been tested and rolled out in Kenya and Tanzania, mainly in the conservancies. The Human Gorilla (HUGO) Conflict Resolution around Bwindi Impenetrable National Park, and Community Wildlife Scouts established around Queen Elizabeth National Park, and Murchison Falls National Park have proved to be a big success in catalyzing community participation in conservation in Uganda.

Several policy experiments were conducted in this study to sustain or improve the elephant populations of GVL, these include suitable habitat increase through the mitigation of forest and savanna vegetation loss to human settlement and agriculture. Results of the policy experiment suggest that increasing the current suitable habitat by 50% would significantly improve elephant population numbers. This could be achieved mainly by reducing forest and savanna vegetation loss and conversion to human settlement and agriculture, as well as properly managing fires and invasive species. In addition, it supports private landowners to protect wildlife on their land to secure wildlife corridors and mitigate human-wildlife conflicts. The dynamic model can be used to simulate the adaptation potential of elephants to stressors, which is often difficult to research over long periods.

Conclusions and recommendations

Elephants in Africa are disappearing at an alarming rate, mainly due to habitat degradation and loss and human-wildlife conflicts. The situation is expected to worsen with the advent of climate change impacts, resulting in a high occurrence of prolonged droughts in both arid and semiarid regions. Understanding how animal populations will respond to such dramatic events is crucial to designing and implementing mitigation strategies and developing the adaptive capacity of wildlife managers to respond to these challenges adequately. Therefore, this study explores how GVL age-class-specific elephant populations will likely respond to habitat change, water resources, and climate change. Also, climate change affected the old elephants more than the young ones regarding survival abilities, but this could be due to immigration from other areas. It is also likely that the undetected direct climate change impact on the elephant population is due to a desirable features of suitable habitat, particularly forests and wetlands used for thermal regulation. However, this does not rule out the idea that indirect impacts, such as thermal and latent flux impacts, are occurring already.

On the other hand, an improvement in the habitat type and availability of water resources resulted in a slight increase in all age class populations. In all the analyses, the results suggest that if the environmental and anthropogenic stressors are not mitigated, GVL will have only a very young population of elephants. Studies elsewhere have shown that elephants are susceptible to drought, and calf mortality was higher among young mothers than the more experienced mothers.

Elephants in GVL are transboundary resources requiring a transboundary management approach, cooperation between conservation agencies, and effective partnerships with relevant stakeholders. The stakeholders include local and regional governments, wildlife protected area authorities of DRC, Rwanda, and Uganda, and law enforcement agencies such as the military, police, judiciary, customs, and border control authorities. Countries in the Albertine Rift region have established collaborative management frameworks that allow all interested parties to develop management plans [70] and implement them jointly for the common good [14]. Collaboration is fundamental to effective conservation [15,20], and regional governments must be willing to develop institutional frameworks to allow it to happen. The major limitation of this study was securing quality data collected at the regional scale, format, and historical vegetation cover data for some countries that overlap GVL. There are few functioning weather stations, hydrometeorological stations, and cloud-free satellite imagery. The elephant population survey data was also inconsistent and lacked some attributes such as age and sex, which forced us to rely on data from other countries where it has been collected over time using the same methodology.

The methodology developed for this study and the analyses conducted can be replicated in other sites such as the Kidepo complex (Kidepo Valley National Park (Uganda) and Kidepo Reserve (South Sudan)), and Mt Elgon shared between Kenya and Uganda, both landscapes that in habit elephants. Similarly, the study approach can be applied to other species, such as lions and Mountain Gorillas. The future applications of the study can include stochasticity in the model, spatial dynamics and optimization, societal valuation of conservation and governance arrangements.

Supporting information

S1 Text. Model info.
(DOCX)

S1 Data. Elephant population baseline data.
(XLSX)

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Methodology: Simon Nampindo, Timothy O. Randhir.

Supervision: Timothy O. Randhir.

Validation: Simon Nampindo.

Writing – original draft: Simon Nampindo.

Writing – review & editing: Simon Nampindo, Timothy O. Randhir.

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