

RESEARCH ARTICLE

Extinction risks and mitigation for a megaherbivore, the giraffe, in a human-influenced landscape under climate change

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Abstract

Megaherbivores play “outsized” roles in ecosystem functioning but are vulnerable to human impacts such as overhunting, land-use changes, and climate extremes. However, such impacts—and combinations of these impacts—on population dynamics are rarely examined using empirical data. To guide effective conservation actions under increasing global-change pressures, we developed a socially structured individual-based model (IBM) using long-term demographic data from female giraffes (*Giraffa camelopardalis*) in a human-influenced landscape in northern Tanzania, the Tarangire Ecosystem. This unfenced system includes savanna habitats with a wide gradient of anthropogenic pressures, from national parks, a wildlife ranch and community conservation areas, to unprotected village lands. We then simulated and projected over 50 years how realistic environmental and land-use management changes might affect this metapopulation of female giraffes. Scenarios included: (1) anthropogenic land-use changes including roads and agricultural/urban expansion; (2) reduction or improvement in wildlife law enforcement measures; (3) changes in populations of natural predators and migratory alternative prey; and (4) increases in rainfall as predicted for East Africa. The factor causing the greatest risk of rapid declines in female giraffe abundance in our simulations was a reduction in law enforcement leading to more poaching. Other threats decreased abundances of giraffes, but improving law enforcement in both of the study area's protected areas mitigated these impacts: a 0.01 increase in giraffe survival probability from improved law enforcement mitigated a 25% rise in heavy rainfall events by increasing abundance 19%, and mitigated the expansion of towns and blockage of dispersal movements by increasing abundance 22%. Our IBM enabled us to further quantify fine-scale abundance changes among female giraffe social communities, revealing potential source–sink interactions within the metapopulation. This flexible methodology can be adapted to test additional ecological questions in this landscape, or to model populations of giraffes or other species in different ecosystems.

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KEYWORDS

demography, *Giraffa camelopardalis*, global change, individual-based modeling, population dynamics, population viability analysis

1 | INTRODUCTION

Since the Late Pleistocene and early Holocene eras, human population growth and overhunting have led to widespread extinctions, particularly of megafaunal species (Alroy, 2001; Ripple et al., 2015). Local extirpations of remaining populations of megafauna will likely facilitate co-extinctions and drastically alter ecological systems because of the diversity of interactions and important functional roles played by large animals (Galetti et al., 2018). Megaherbivores—plant-feeding animals that can attain an adult body mass of at least 1000 kg (Owen-Smith, 1988)—comprise a trophic group that dominates the mammal biomass in African savannas, particularly in ecosystems with high rainfall and nutrient-poor soils (Fritz et al., 2002). They have “outsized” impacts on their ecosystems, shaping vegetation characteristics such as woody plant spinescence and species composition (Augustine & McNaughton, 2004; Strauss et al., 2015), spreading nutrients and seeds over vast areas (Bunney et al., 2017; Doughty et al., 2016), and maintaining mutualisms that improve tree growth and survival (Palmer et al., 2008). Anthropogenic pressures like overhunting and habitat destruction as well as recent human-caused climate changes comprise serious threats to African megaherbivores (Bond et al., 2023; Boulton et al., 2019; Foley et al., 2008; Muller et al., 2018; Ripple et al., 2015). However, it is not well understood which among those pressures are most important in mediating demographic rates and driving population declines because such pressures, in particular combinations of pressures that may further exacerbate extinction risks, are rarely analyzed together (but see Boulton et al., 2019). Understanding the drivers of megaherbivore population dynamics and extinction risks in a rapidly changing world will expedite evidence-based management and conservation of these ecologically critical animals and their ecosystem services in the 21st century.

Wildlife managers are in urgent need of quantitative assessments of the vulnerability of megaherbivore species to global change; for instance, only 10% of IUCN mammal assessments used quantitative population biology (Paniw, James, et al., 2021). There is also a need to improve predictive models with empirically derived data on key mechanisms like demography (births, deaths, and movements) and biotic and abiotic interactions to aid in conservation management decision-making, but a primary obstacle is that much of these data are unavailable (Lasky et al., 2020; Urban et al., 2016). Long-term demographic studies of individually recognized organisms are rare—especially for long-lived animals with slow life histories—but invaluable for providing the data to parameterize predictive models and realistically project extinction risk (Beissinger & McCullough, 2002; Clutton-Brock & Sheldon, 2010; Morris & Doak, 2002).

Structured population models, which are parameterized from age- or stage-specific demographic rates and then project population dynamics in discrete time steps (Legendre, 2020), have been used for quantitative conservation assessments of populations (e.g., polar bears *Ursus maritimus*: Hunter et al., 2010). At the same time, such models cannot incorporate individual interactions, especially for populations with complex social structure (Paniw et al., 2022), including movements among social groups (Bauduin et al., 2020; Conner et al., 2008). Individual-based models (IBMs) are able to capture spatial and temporal changes in multiple individual traits and interactions and scale such changes to changes in social-group living and population persistence (Grimm & Railsback, 2005). IBMs can also more easily incorporate demographic stochasticity and its effects on population persistence, which can be of particular importance in declining populations of conservation concern (Paniw, Cozzi, et al., 2021). Here, we developed a stochastic, socially structured IBM to simulate population dynamics and explore extinction risks for a megaherbivore, the giraffe (*Giraffa camelopardalis*), inhabiting a coupled human–natural African savanna landscape. We parameterized the IBM with data on social structure and individual survival, reproduction, and movement probabilities gleaned from a long-term demographic study of a metapopulation of thousands of Masai giraffes (*G. c. tippelskirchi* [subsp.] or *G. tippelskirchi* [spp.]) in the human-influenced Tarangire Ecosystem of northern Tanzania (Lee & Bond, 2022; Lee et al., 2022).

Earlier research offered insights about some of the environmental mechanisms mediating variation in demographic rates of giraffes in this landscape. These mechanisms included natural factors like season of birth (Lee et al., 2017), natural predation pressure (Lee, Kissui, et al., 2016), and rainfall anomalies (Bond et al., 2023). Anthropogenic factors such as land use (Lee, Bond, et al., 2016) or proximity to human settlements (Bond, König, Ozgul, et al., 2021; Bond, Lee, Farine, et al., 2021; Bond, Lee, Ozgul, et al., 2021; Knüsel et al., 2019) also influence demographic rates. These studies provided robust estimates of components of the demographic processes, some ecological and anthropogenic factors driving those processes, and potential selective forces. However, as yet no study has examined how changes in these factors—and combinations of these factors—might affect long-term population persistence of this endangered megaherbivore (Bolger et al., 2019).

Studies of giraffe demography in other regions of Africa have occurred within protected national parks (Brown et al., 2019; Strauss et al., 2015) or had very small populations (<200 individuals: Suraud et al., 2012; Muller, 2018), but the unfenced Tarangire study area supports thousands of giraffes and encompasses savanna habitats with a wide gradient of anthropogenic pressures, from areas deep inside national parks to unprotected village lands. Thus, the Tarangire

Ecosystem is representative of the current mix of anthropogenic threats and conservation opportunities across the range of giraffes in Africa. Our first objective was to integrate environmental data with knowledge of female giraffe metapopulation social structure and their demographic responses to the main anthropogenic pressures, in order to project population abundances under various realistic future land-use and climatic scenarios. We focused on females because they contribute the most to population dynamics in polygynous, long-lived mammals (Caswell, 2006). The scenarios included increased human presence in giraffe habitats, loss of connectivity among habitats, reduced or increased anti-poaching law enforcement measures, and changes in natural predation pressures and local rainfall. Our second objective was to explore whether targeted management actions could mitigate the negative effects of some of the more severe anthropogenic threats. A deeper understanding of the mechanisms that exert the strongest influences on abundance, as well as potential mitigations, will help managers develop targeted conservation actions to effectively sustain giraffes in this system under global change. Furthermore, this flexible methodology can be adapted to test additional scenarios in this landscape, or to model populations of giraffes or other species in different ecosystems.

2 | MATERIALS AND METHODS

2.1 | Study system

We developed an IBM parameterized with demographic data from the Masai Giraffe Project (Lee & Bond, 2022; Lee et al., 2022; Table 1), one of the biggest individual-based demographic studies of a large mammal, with more than 3100 giraffes of all sexes and age classes reliably identified over 8 years in an unfenced 4500 km² area of the Tarangire Ecosystem in Tanzania (latitude 3.27°–4.08°S and longitude 35.73°–36.23°E). Like other East African savannas, Tarangire has three distinct precipitation seasons but unpredictable amounts of seasonal rainfall (Foley & Faust, 2010; Prins & Loth, 1988). Our simulated population represents the socially structured female giraffe metapopulation within and surrounding Tarangire National Park and Manyara Ranch, which together constitute the core giraffe habitat in the system (Lee & Bond, 2022). Tarangire National Park allows tourism but no livestock or land conversions and has high levels of law enforcement efforts. Manyara Ranch and two community wildlife management areas adjacent to Tarangire National Park permit tourism and livestock but no land conversions and have intermediate levels of law enforcement. The remaining areas are unprotected village lands with livestock, land conversions, human settlements, and low levels of law enforcement (Lee & Bond, 2022; Figure 1a). Giraffe habitat outside the protected areas has been conserved by traditional pastoralists, or increasingly degraded by agriculture, charcoal making, busy tarmac roads, and other human activities (Msoffe et al., 2011). The entire area is unfenced so giraffes can roam freely throughout the landscape (Lee & Bolger, 2017).

2.2 | Individual-based model for giraffes

IBMs simulate the fate of individuals interacting with each other or their environment, and population-level results emerge from individual-level simulations (Railsback & Grimm, 2012; Revilla, 2020). These models are built as a series of submodels that represent a component of the life cycle of the species, such as a survival submodel, or an external factor that influences the population structure (Bauduin et al., 2020). Our model describes giraffe population dynamics using a stochastic, socially structured IBM and projects how populations respond to a set of external changes. The IBM allowed us to easily (without parameterizing large, age-specific matrix meta-population models) account for individual age and association with a social community in demographic rates. We could also easily account for demographic stochasticity. It is possible to incorporate demographic stochasticity into MPMs and IPMs, but this can jeopardize the analytical tractability of these models (Ovaskainen & Meerson, 2010). Lastly, the flexible parameterization of IBMs allows us to use this model as a foundation upon which to expand with more complex parameterizations as data become more readily available, including tracking how individual social group status affects dispersal success or how individual parent–offspring interactions affect reproductive success.

Our methodological steps involved designing, parameterizing, and validating a core model that reasonably reflected the observed short-term dynamics of the Tarangire giraffe metapopulation, and then testing the effects of environmental changes on extinction risk by altering demographic parameters in the core model based on known responses to external influences and examining abundances over a time frame of 50 years. These steps are summarized below, but we provide additional details in Supporting Information, including fuller background on the life history of giraffes (Supporting Information 2), the socio-ecological drivers of giraffe demographic rates in the Tarangire Ecosystem (Supporting Information 3), and a comprehensive Overview, Design concepts, and Details (ODD) protocol (Grimm et al., 2006, 2010) of our individual-based modeling process (Supporting Information 4).

2.3 | Core model design and parameterization

For the design phase (Revilla, 2020), we first constructed a life-cycle graph to describe female giraffes in equatorial Africa with a discrete time interval of 4 months to match the three precipitation seasons (Figure 2a; Figure S1). Giraffes in the life-cycle graph exist in 4-month age classes where survival and reproductive rates vary according to age class.

Female giraffes in the Tarangire Ecosystem exhibit social structure, with preferred and avoided relationships that scale up to nine spatially overlapping yet modular social communities of ca. 60–90 individuals in our study area (Figure 1b) in which membership is stable over time (Bond, König, Lee, et al., 2021; Bond, Lee, Ozgul, et al., 2021) and that exhibit different demographic

TABLE 1 Parameters used in the giraffe IBM survival and dispersal submodels, showing linear coefficients (underlined) or change to coefficient (**bold**) used to predict survival and dispersal rates and adjustments to predicted survival rates estimated in 4-month times steps, and literature references.

Parameter	Submodel	Variable	Linear coefficient (or change to coefficient) used in submodels applied to all social communities (SE)
Calf (seasons 1–3) and subadults (seasons 4–12)			
Age	Survival	Survival by each 4-month time step	<u>0.3</u> (0.072)
Age ²	Survival	Survival increases with age	<u>–0.005</u> (0.004)
Season of birth			
Dry	Survival	Survival highest for calves born in dry season, lowest in long rains	<u>0.26</u> (0.04)
Short rains			<u>0.13</u> (0.04)
Long rains			<u>0</u>
Predation pressure (calves only)	Survival	Predation higher in TNP in long and short rains Predation lower in TNP in dry season	
Social community effect	Survival	Survival of calves varies by Adult Female Community	
Population density	Survival	Lower survival when community density reaches 150 to prevent indiscriminate population growth	When density >150 then add –1.0 to intercept (calves) and –0.7 (subadult)
Rainfall	Survival	Higher rainfall anomalies reduce survival	<u>–0.061</u> (0.03)
Dispersal (subadult, 13 seasons)	Movement	Probability of socially dispersing	<u>0.13</u>
Adult (seasons 13–87)			
Social community effect	Survival	Survival of adults varies by Adult Female Community	
Population density	Survival	Lower survival when community density reaches 150 to prevent indiscriminate population growth	When density >150 then add –0.5 to intercept
Rainfall	Survival	Higher rainfall anomalies reduce survival	<u>–0.466</u> (0.107)

Note: SE (italics) is standard error used for analysis of parameter uncertainty. Values were either applied to all communities or differed among social communities. Blank cells indicated no change to linear coefficients or adjustments to predicted survival rates.

Abbreviations: Social communities; Central TNP, central Tarangire National Park; N MR, northern Manyara Ranch; NNE TNP-LGCA, north-northeastern Tarangire National Park and Lolkisale Game Controlled Area; NNW TNP, north-northwestern Tarangire National Park; SE MR, southeastern Manyara Ranch; SSE TNP-LGCA, south-southeastern Tarangire National Park and Lolkisale Game Controlled Area; SW MR, southwestern Manyara Ranch; SW TNP, southwestern Tarangire National Park; W TNP, western Tarangire National Park. Super-communities: MR, Manyara Ranch; N TNP, northern Tarangire National Park; S TNP, southern Tarangire National Park.

rates (Bond, König, Ozgul, et al., 2021). Adult males moving among groups connect female communities into three mixed-sex super-communities, each incorporating three female social communities (Lavis Ferres et al., 2021 and Figure 1b). Thus, our IBM was socially structured, with survival varying among the social communities. Females sometimes disperse from their natal community when they reach 4 years of age (Bond, Lee, Ozgul, et al., 2021), which we incorporated into our core model. We chose not to make our model spatially explicit because individual movements of giraffes within each of the communities across seasons is not well

known, while the location of the communities which determines the demographic rates is relatively stable. However, spatial variation is implicitly represented by dispersal and social community membership, as some communities are located relatively closer to the edge of the protected area boundary, human settlements, busy tarmac roads, or proposed railway and pipeline routes, affecting demographic rates of female giraffes in our model (Figure 1a,b). Temporal variation in demographic rates is incorporated as seasonal rainfall anomalies affecting all social communities equally, and spatiotemporal variation is included in the influence of natural

Adjustments to predicted survival rates used in submodels (SE) for each social community and super-community									References
W TNP	SW MR	N MR	SE MR	NNW TNP	SW TNP	Central TNP	SSE TNP-LGCA	NNE TNP-LGCA	
1 <i>red</i>	2 <i>light green</i>	3 <i>blue</i>	4 <i>orange</i>	5 <i>mint green</i>	6 <i>dark blue</i>	7 <i>yellow</i>	8 <i>blue-green</i>	9 <i>black</i>	
N TNP	MR	MR	MR	N TNP	S TNP	S TNP	S TNP	N TNP	
SC2	SC3	SC3	SC3	SC2	SC1	SC1	SC1	SC2	
									Lee et al., (2017)
									Lee et al. (2017)
									Lee et al. (2017)
-0.1 (0.06)	0 (0.06)	0 (0.06)	0 (0.06)	-0.1 (0.06)	-0.1 (0.06)	-0.1 (0.06)	-0.1 (0.06)	-0.1 (0.06)	Lee, Kissui, et al. (2016)
0.03 (0.007)	0 (0.007)	0 (0.007)	0 (0.007)	0.03 (0.007)	0.03 (0.007)	0.03 (0.007)	0.03 (0.007)	0.03 (0.007)	
0.046 (0.002)	0.036 (0.002)	0.046 (0.002)	0.036 (0.002)	0.006 (0.002)	-0.074 (0.002)	-0.034 (0.002)	-0.044 (0.002)	-0.015 (0.002)	Bond, König, Ozgul, et al. (2021)
									Bonenfant et al. (2009)
									Bond et al. (2023)
									Bond, Lee, Ozgul, et al. (2021)
0.005 (0.0002)	0 (0.0002)	0 (0.0002)	0.0075 (0.0002)	0.005 (0.0002)	0.0075 (0.0002)	0.01 (0.0002)	0.005 (0.0002)	0.01 (0.0002)	Bond, König, Ozgul, et al. (2021)
									Bonenfant et al. (2009)
									Bond et al. (2023)

predation pressure on giraffe calves, which differs by dry versus wet seasons and in Manyara Ranch versus Tarangire National Park (see Table 1).

Our core IBM submodels include survival, reproduction, and dispersal (Figure 2b and Supporting Information 4 D7 Submodels). State variables include age (in seasons) and social community membership. Individuals transition through the life cycle, with lower level determinants of the demographic rates (e.g., age, rainfall, land use, predation) governing their transitions. After each time step in the IBM, abundance by age class and community is the emergent property.

Demographic rates we use in the core IBM are summarized here and presented in Table 1, but for further details, please see Supporting Information 3. Giraffes are long-lived (up to approximately 30 years; Lee et al., 2020) and slow breeding, with females producing their first offspring at about 6 years of age with a mean interbirth interval of 20 months (Lee & Strauss, 2016). They are typically categorized into three age classes including calf (first year of life), subadult (2nd through 5th years of life), and adult (6 years and older). For the calf and subadult survival submodels, we included effects of covariates including age and age² because survival increases

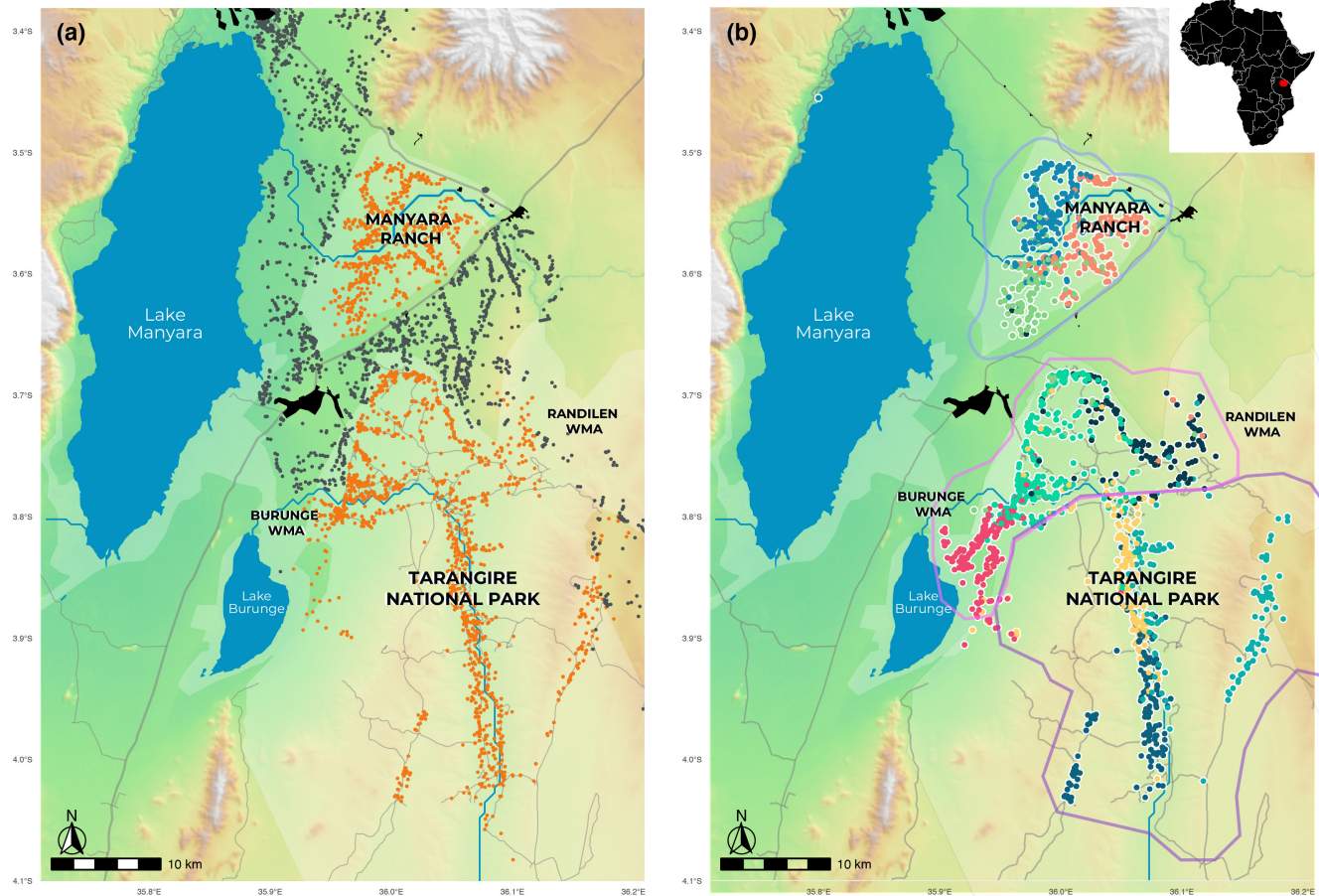


FIGURE 1 Tarangire Ecosystem, Tanzania. Inset (red point) is location within Africa. (a) Light green polygons are protected areas Manyara Ranch, Tarangire National Park, and Randilen and Burunge wildlife management areas. Black polygons are towns and developed areas with hardened concrete buildings, gray points are bomas (traditional livestock herder compounds made of natural materials like wood, mud, and cow dung), and gray lines are major tarmac roads. Orange points are locations of Masai giraffes recorded from 2012 to 2020. (b) Colored points are locations of members of nine adult female social communities that overlap in space but are socially discrete: each community—depicted in a different color—consists of ca. 60–90 adult female giraffes. Blue, pink, and purple open polygons are three mixed-sex super-communities. Each super-community encompasses three adult female social communities. Community and super-community colors correspond with locations and numbers in Table 1. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

with age (Lee et al., 2017); *season of birth*, with highest survival for calves born in the dry season and lowest for those born in the long rains (Lee et al., 2017); *natal social community* (Bond, König, Ozgul, et al., 2021); *predation pressure* affecting survival of calves, which is constant for communities in Manyara Ranch but higher during the wet seasons and lower during the dry seasons in communities in Tarangire National Park due to the presence or absence of migratory ungulates (Lee, Kissui, et al., 2016); and *rainfall*, with lower survival during higher rainfall anomalies (data from Bond et al., 2023). For the adult survival submodel, we included effects of the covariates *social community membership* (Bond, König, Ozgul, et al., 2021; Lee & Bond, 2022) and *rainfall anomalies* (data from Bond et al., 2023). To calculate rainfall anomalies (variation around a mean of zero from 2001 to 2022), we used Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) data produced by the USGS Earth Resources Observation and Science (EROS) Center ([\[ng.usgs.gov/fews\]\(https://earlywarni.usgs.gov/fews\)\). We then sampled from the dataset of observed seasonal rainfall anomalies from 2001 to 2022 for the effect on survival rates for the core model. The survival rates were linked to the current season's rainfall anomaly, as Bond et al. \(2023\) found no evidence for cumulative or lag effects of anomalies from the previous two and three seasons.](https://earlywarni</p>
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We incorporated negative density dependence in the survival submodels such that if the total community population size exceeds 150, survival of all age classes is reduced to reflect habitat carrying capacity, with calves, subadults, and adult females experiencing, respectively, lower reductions in density-dependent survival (calves = -1.0 , subadults = -0.7 , adults = -0.5 ; Table 1) because younger age classes are more sensitive (Bonenfant et al., 2009). Maximum age for our giraffes is 87 seasons (equates to 30 years), after which the individual is removed from the population (Lee et al., 2020).

Little is known about factors influencing individual reproductive rates and success in wild giraffes, so in our model individual calves are not linked to individual mothers. Instead, an adult female produces a calf and the calf, if female, is added to the population and survives probabilistically, but we include no individual effects on the mother such as a cost of reproduction or the onset of estrous immediately after a calf dies. For simplicity, each adult female in our simulated population reproduces at the same rate. Females begin giving birth at age 19 seasons (= age 6 years) and produce a single calf then and subsequently every five seasons. Calf sex is randomly allocated at a 50:50 ratio, and male calves are immediately removed from the population. Some subadults aged 13 seasons (= age 4 years) are randomly selected with a probability of 0.13 to switch social community in an instance of natal dispersal (Bond, Lee, Ozgul, et al., 2021).

2.4 | Core model implementation

We started with an initial population of 1000 female giraffes distributed in the nine social communities and ran 1000 simulations of the population for 50 years (150 seasons), which is approximately five giraffe generations (Suraud et al., 2012; Muller et al., 2018). At initialization, the age distribution in all communities reflected the observed age distribution and abundances of the actual Tarangire metapopulation (Bond, König, Ozgul, et al., 2021; Lee & Bond, 2022). See [Supporting Information 4 Table S2](#) for initial age class distribution in each community/super-community and [Supporting Information 4 D5](#) for initialization details. We randomly selected females that were ≥ 19 seasons old in the initial population to have a female calf between the ages of 1:5 seasons, based on the age structure in each community that we observed from our field data. In each time step of the simulation, individuals survived and aged. Conditional on survival, a mother was assigned a “reproductive countdown” (repCount) according to the age of her calf. After she produces a calf at repCount=0, the mother is subsequently assigned repCount=6 at the next time step and she cannot birth again until her repCount returns to 0. This is to ensure mothers with young calves are not available to give birth again, but every adult female gives birth after five seasons have passed (Lee & Strauss, 2016).

In sum, each giraffe is imbued with individual traits including: (1) *unique ID*; (2) *age* in seasons (=4-month steps); (3) *reproductive countdown* (repCount) for mothers to ensure those with calves cannot produce for another five seasons (=20-month interbirth interval); and (4) *adult female social community* (=9) with different survival rates, as well as natal dispersal movements among the communities for a subset of subadults aged 13 seasons.

As model outputs, we recorded age class- and community-specific abundances for each season; as well as extinction, defined as when population declined to <1 individual. We incorporated stochasticity by sampling from a binomial distribution for survival and dispersal rates (see [Supporting Information 4 O2](#)).

2.5 | Core model validation and sensitivity analysis

We evaluated whether our simulated population generally reflected the “real-world” giraffe population trends in the Tarangire Ecosystem by performing both in- and out-sample comparisons with core model output (Grimm & Railsback, 2005). Our in-sample validation compared community-specific abundances and lambdas (λ =population growth rate) derived from mark-resight analysis of empirical data of giraffes from 2012 to 2016 in our study area, with community-specific abundances and λ from the core IBM simulations. Our out-sample validation compared the simulated population trend with the metapopulation trend based on an independent dataset from the Tarangire Ecosystem from 1980 to 2011 (Lee & Bond, 2016). After validating that the simulation from our core model adequately represented observed patterns of giraffe abundances over time, but before the final step of exploring external drivers of giraffe population dynamics, we assessed the sensitivity of giraffe abundance to age class-specific survival, reproduction, and dispersal (Grimm & Railsback, 2005; Revilla, 2020). We ran 100 simulations of the IBM where we decreased and increased predicted demographic rates by a small fixed amount in each iteration. Details can be found in [Supporting Information 5 Validation](#) and [Supporting Information 6 Sensitivity Analysis](#).

2.6 | Scenarios of impacts of environmental change on the giraffe metapopulation

Giraffe demographic rates in the Tarangire Ecosystem exhibit significant spatial and temporal variation resulting from dynamic environmental conditions (summarized in Lee et al., 2022). Our core IBM incorporates the influence of climate and anthropogenic activities on giraffe demographic rates that we learned from previous research, enabling us to then explore how varying these factors might affect abundances and extinction risk and how targeted management actions might mitigate some of the potentially severe effects. Thus, our final step was to use the IBM to simulate population dynamics after modifying demographic rates under different scenarios, and examine abundances over time.

We based our scenarios on realistic threats to giraffes in the Tarangire Ecosystem. The possibilities of a pipeline and/or railroad track bisecting the landscape have been proposed, and the tarmac road between Tarangire National Park and Manyara Ranch, which leads to Tanzania's capital city of Dodoma, has been growing in size as government headquarters were recently moved there (starting in 2016) from the coastal city of Dar es Salaam. These infrastructures would pose serious barriers to movements for giraffes and other wildlife in the heart of the system, which we modeled here by blocking dispersal but might also impact giraffes by reducing survival of dispersers. The human population in the Tarangire Ecosystem has increased at a $>3\%$ annual growth rate from 1978 to 2002 (Msoffe et al., 2011), and consumption of illegally obtained bushmeat is widespread among the local population (Kiffner et al., 2015). Finally, high rainfall anomalies from 2012 to 2020

were correlated with lower giraffe survival, possibly due to increased parasites and diseases (Bond et al., 2023). We tested the effects of the following scenarios on giraffe abundances and extinction risk (Table 2): (1) An expansion of human presence in towns in the study area, which increases giraffe mortality in communities closest to these human settlements (Bond, Lee, Farine, et al., 2021). (2) Loss of connectivity because of physical barriers such as a pipeline, a railway, or increased motor traffic that block natal dispersal between social communities in Tarangire National Park and Manyara Ranch. (3) Reduced or improved wildlife law enforcement measures in Tarangire National Park and/or Manyara Ranch that lower or increase giraffe survival in the respective communities in those management areas. (4) Community-specific changes in predation pressure on giraffe calves due to loss of migratory white-bearded wildebeests (*Connochaetes taurinus*) and plains zebras (*Equus quagga*) from bushmeat poaching and land conversion which would decrease giraffe calf survival, or to loss of lions (*Panthera leo*) from escalating human–lion conflicts which would increase giraffe calf survival. (5) Increased rainfall as projected for East African savannas (Cook et al., 2020; IPCC, 2022; McSweeney et al., 2010) which would reduce adult and calf survival. We included two levels of increased rainfall, a 10% and 25% increase, which is the lower and upper range projected by the IPCC for the region (2022). These corresponded to increasing the frequency of above-average (>0) rainfall anomalies by 10% and 25%, respectively. This way, the magnitude of the anomalies was not extrapolated beyond the observed values from the recent time period. Bond et al. (2023) found stronger adverse effects of higher rainfall anomalies for giraffes living closer to the edges of protected areas during the short rains, but we did not track individual movements in our IBM, so for rainfall anomalies, we used an age-class-specific beta effect (the coefficient in the survival model) on survival that reduced adult and juvenile survival in all communities and all seasons equally.

The effects resulted in realistic differences in survival between low and high rainfall anomalies that matched our empirical observations from Bond et al. (2023). Some of the scenarios involved increasing or decreasing a demographic rate by a percent change in the predicted rate, whereas others were modifiers of the beta coefficient corresponding to lower level covariate effects in the model functions (Table 1).

The demographic rate changes for wildlife law enforcement measures were derived from a study comparing adult female survival rates in protected Tarangire National Park and Manyara Ranch with survival rates in unprotected village lands north and east of the current study area, in which survival probability was >0.10 lower in the village lands (see Figure 2 in Lee, Bond, et al., 2016). However, because most of our study area, consisting of a national park, a ranch conservancy, and Wildlife Management Areas, already experiences ample law enforcement measures—the effects of which are reflected in the relatively high survival rates of adult females—for the scenarios in which law enforcement measures are improved further we added 0.01 to predicted juvenile and adult survival probabilities as a reasonable increase.

We ran models where only one of each scenario was applied, as well as combinations of scenarios, with scenario descriptions and demographic rate changes presented in Table 2. A set of the models (scenarios 19–32) was designed to test whether certain management actions, such as conserving predators and migratory alternative prey and improving wildlife law enforcement, could mitigate the effects of greater rainfall anomalies or expansion of human settlements and dispersal barriers (Table 2). We did not test mitigation scenarios where migratory species but not predators were protected, as this was not a desirable management option, given the important role played by predators in maintaining general ecosystem function (Ripple et al., 2014). Systematic computer simulations quantified the relative importance of different factors, the effects of combinations

(a)

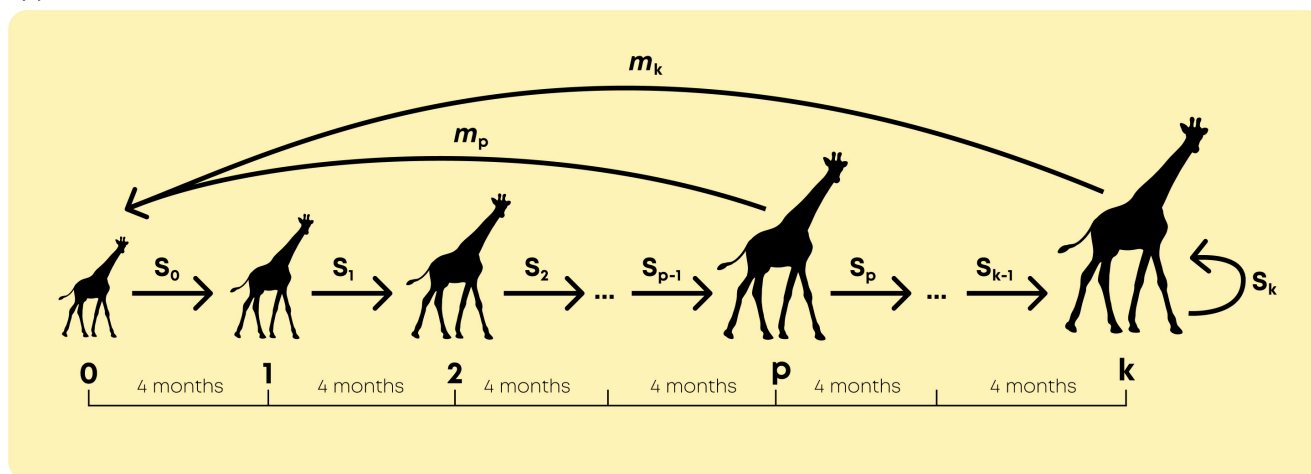


FIGURE 2 (a) The age-classified life cycle for female giraffes is 4-months time steps: S_i = survival rate, m_i = reproduction, p = age at first breeding, k = adult, where i = seasonal time step. (b) Diagram of initialization and submodels of survival, reproduction, and dispersal for core socially structured and spatially implicit individual-based model of giraffe population dynamics. After initialization, the temporal loop begins with the short rains. Individuals survive at rates affected by current season, season of birth, rainfall, predation risk, population density of the community, and proximity to human settlements. Surviving adult females reproduce with a sex ratio of 1:1 and female calves are added to the population. Subadults aged 13 seasons (SA4) remain in their natal community or disperse, and the temporal loop begins again.

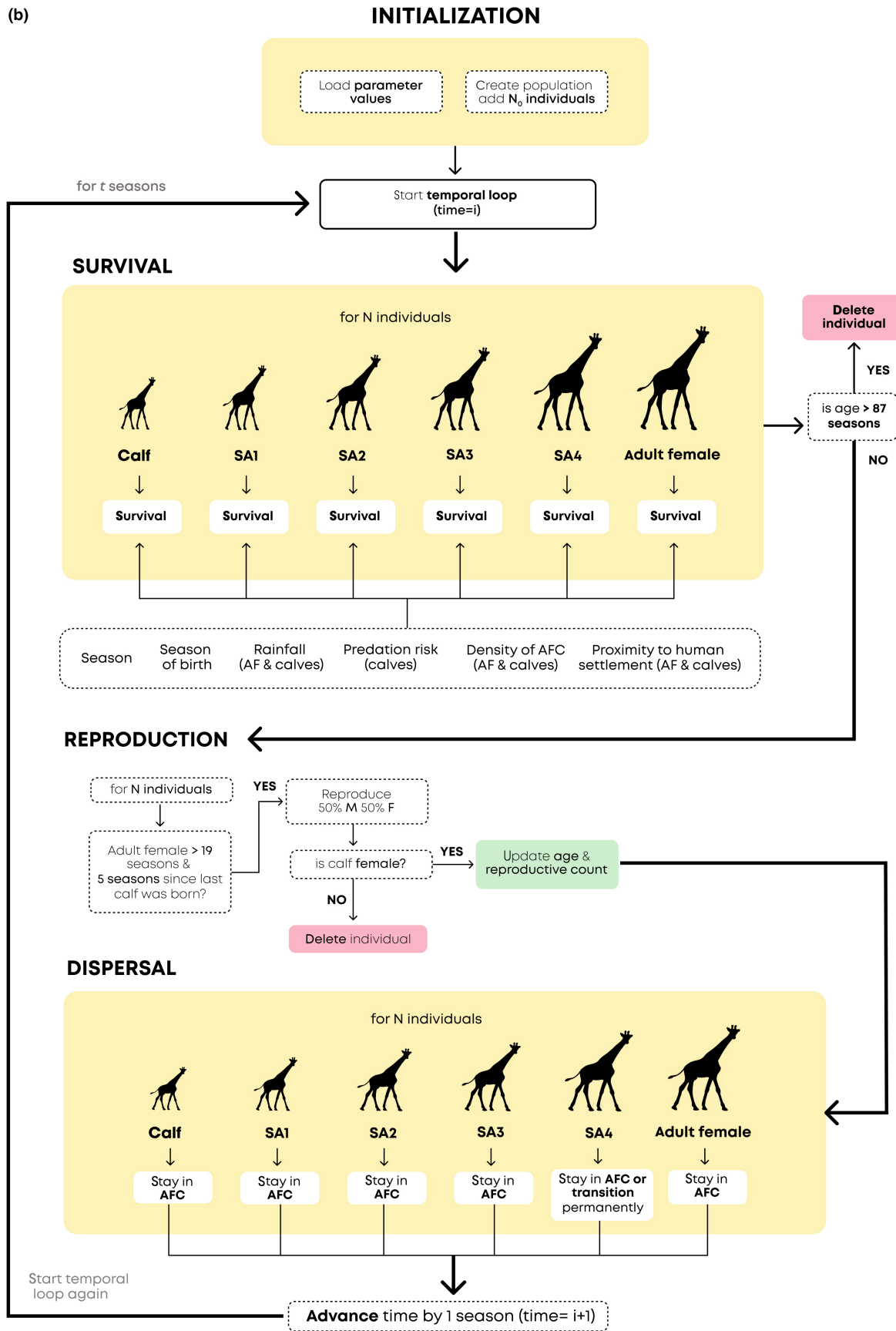


FIGURE 2 (Continued)

TABLE 2 Scenario numbers, model description, changes to demographic rates applied in the scenarios, and total giraffe metapopulation abundance after 50 years (+SD) and CV.

Scenario number	Scenarios applied in model	Model description	Demographic rate changes	Mean total abundance (+SD) after 50 years	CV total abundance
1	1	Control		975 (42)	0.04
Single scenarios					
Human settlements and infrastructure					
2	2	Expansion of towns decreases survival rates in AFCs and SCs closer to existing towns (poaching, loss of habitat) ^a	Reduce S in AFCs 1,2,3,4,5,9 (not SC1)	963 (46)*	0.05
3	3	Blocked movement between MRC and TNP SCs reduces the probability of dispersal and transitions between the two areas to zero ^b	Dispersal only allowed between groups 2,3,4 & between groups 1,5,6,7,8,9	937 (46)*	0.05
Law enforcement measures					
4	4	Reduced law enforcement measures by TANAPA decreases survival rates in TNP ^c	Reduce S by in AFCs 1,5,6,7,8,9	583 (21)*	0.04
5	5	Reduced law enforcement measures in MRC decreases survival rates ^c	Reduce S in AFCs 2,3,4	457 (40)*	0.09
6	6	Reduced law enforcement measures in both MRC and TNP ^c	Reduce S in all AFCs	2 (1)*	0.61
7	7	Improved law enforcement measures by TANAPA increases survival rates ^c	Increase S in AFCs 1,5,6,7,8,9	1174 (43)*	0.04
8	8	Improved law enforcement measures in MRC increases survival rates ^c	Increase S in AFCs 2,3,4	1016 (48)*	0.05
9	9	Improved law enforcement measures by both TANAPA and in MRC increases survival rates ^c	Increase S in all AFCs	1201 (41)*	0.03
Alternative prey and predation					
10	10	Losing migratory species increases predation pressure in MRC in every season and in TNP during dry season ^d	Decrease calf S by 0.03 in AFCs 2,3,4 in all seasons (= no season difference in TNP)	1030 (46)*	0.05
11	11	Losing lions makes predation pressure in MRC equal to TNP in dry season ^d	Increase calf S by 0.1 in all AFCs in all seasons (= no season difference in TNP)	1250 (42)*	0.03
Climate					
12	12	Heavier rainfall decreases survival rates in all AFCs ^e	Rainfall increase at lower end of projection = 10%, includes more drought	971 (44)	0.03
13	13	Much heavier rainfall decreases survival rates in all AFCs ^e	Rainfall increase at higher end of projection = 25%, includes more severe drought	943 (53)*	0.06
Additive scenarios					
Worst-case scenarios: more infrastructure and less law enforcement					
14	2+3	Expand towns and block movements, reducing survival, and preventing dispersal		920 (48)*	0.05
15	2+4	Expand towns and reduce law enforcement measures in TNP		577 (22)*	0.04
16	2+5	Expand towns and reduce law enforcement measures in MRC only		447 (40)*	0.09
17	2+6	Expand towns and reduce law enforcement measures in both MRC and TNP		2 (1)*	0.50
18	2+3+6	Expand towns, block movements, and reduce law enforcement measures in both MRC and TNP		3 (2)*	0.68

TABLE 2 Continued

	Can improving law enforcement mitigate human expansion?		
19	2+7 Expand towns but improve law enforcement measures in TNP only	1176 (43)*	0.04
20	2+8 Expand towns but improve law enforcement measures in MRC only	973 (49)*	0.05
21	2+9 Expand towns but improve law enforcement measures in both TNP and MRC	1200 (39)*	0.03
	Can conserving predators and alternative prey mitigate climate effects?		
22	12+reverse10 Heavier rainfall but protect migratory species and protect lions	969 (46)	0.05
23	13+reverse10 Much heavier rainfall but protect migratory species and protect lions	948 (53)*	0.06
	Can improving law enforcement mitigate climate effects?		
24	12+7 Heavier rainfall but improve law enforcement measures in TNP only	1163 (47)*	0.04
25	12+8 Heavier rainfall but improve law enforcement measures in MRC only	1012 (50)*	0.05
26	12+9 Heavier rainfall but improve law enforcement measures in both TNP and MRC	1190 (41)*	0.03
27	13+7 Much heavier rainfall but improve law enforcement measures in TNP only	1135 (54)*	0.05
28	13+8 Much heavier rainfall but improve law enforcement measures in MRC only	981 (55)*	0.06
29	13+9 Much heavier rainfall but improve law enforcement measures in both TNP and MRC	1162 (49)*	0.04
	Can improving law enforcement AND protecting predators and prey mitigate the strongest climate effects?		
30	13+7+reverse10 Much heavier rainfall but increase migratory species and protect lions and improve law enforcement measures in TNP only	943 (52)	0.06
31	13+8+reverse10 Much heavier rainfall but increase migratory species and protect lions and improve law enforcement measures in MRC only	946 (52)	0.05
32	13+9+reverse10 Much heavier rainfall but increase migratory species and protect lions and improve law enforcement measures in TNP and MRC	947 (51)	0.05

*Scenarios where the 95% confidence intervals of mean abundance after 50 years did not overlap with the control scenario abundance, indicating significant differences.

^aBond, Lee, Farine, et al., 2021.

^bBond, Lee, Ozgul, et al., 2021.

^cLee, Bond, et al., 2016.

^dLee, Kissui, et al., 2016.

^eBond et al., 2023; IPCC, 2022.

of factors, and the magnitude of external forces required to push the giraffe metapopulation off an extinction cliff. We ran 500 simulations of each of the 32 models, including a control model.

2.7 | Parameter uncertainty

We tested for the effect of parameter uncertainty on outputs from the core model and scenarios using parametric bootstrapping, in which we resampled parameters using a normal distribution with mean and standard error (SE) as indicated in Table 1. Details can be found in Supporting Information 7 Parameter Uncertainty. Parameter uncertainty contributed little to the overall variation in output metrics (0.1%–8% depending on the metric; Table S4), and we present the result as average parameter values.

We developed the IBM using the R statistical software (R Core Team, 2017). All code and datasets can be found in https://github.com/MariaPaniw/Masai_giraffe_ibm.

3 | RESULTS

3.1 | Core model implementation, validation, and sensitivity analysis

Implementation of our core model over 150 seasons ($N=1000$ simulations) showed that female giraffe social communities in the northernmost part of the Tarangire Ecosystem study area (Figure 1b), in Manyara Ranch (communities 2–4) and western Tarangire National Park (community 1), started with the highest giraffe abundances (range 133–144 individuals) and maintained their total abundances (i.e., all ages) over time at a mean of 147–150 individuals (combined 95% CI=135–160; Supporting Information 8 Figure S5). The northern Tarangire National Park community (community 5), which started at 119 individuals, stabilized over time at a mean of 130–132 individuals (95% CI=83–178; Supporting Information 8 Figure S5). Community 9, in the northeastern part of Tarangire National Park and Randilen Wildlife Management Area (Figure 1b), started with the lowest abundance of 75 individuals but ended with a mean abundance of 102–103 individuals (95% CI=55–163; Supporting Information 8 Figure S5). Communities 6–8 started at 88–93 individuals. Community 7, in central Tarangire National Park, decreased slowly over the entire time period and ended with a mean of 74 individuals (95% CI=38–122; Supporting Information 8 Figure S5), and communities 6 and 8, both in southern Tarangire National Park, decreased throughout the entire time period and at the end numbered a mean of just 35 (95% CI=20–61) and 44 individuals (95% CI=22–76), respectively (Supporting Information 8 Figure S5). Abundances by age classes followed similar trends, but with the greatest declines of adult females for the southern and central Tarangire National Park communities (Supporting Information 8 Figure S6).

In-sample validation, comparing derived abundances from capture–resight data over 15 seasons with simulated abundances from the core IBM over the same time frame, suggested that our

IBM was a good representation of “real world” short-term giraffe dynamics in Tarangire. Nearly all (96%) of the seasonal 95% confidence intervals of the derived abundances fell within the 95% CIs of the 1000 simulated abundances (Figure 3). Our additional in-sample validation of our core IBM using λ indicated the simulated λ by community was highly correlated ($R^2=0.802$) with the observed λ (Supporting Information 5 Figure S2). Finally, out-sample validation showed that λ from aerial survey population estimates for giraffes in Tarangire ($\lambda=0.9962$) was very similar to λ from our simulation output ($\lambda=0.9988$). The core IBM was able to reproduce observed population trends, and therefore, we were confident that our model captured giraffe population dynamics in the Tarangire Ecosystem (Grimm & Railsback, 2005).

The sensitivity analysis from 100 population simulations indicated giraffe abundances in our IBM were not sensitive to a decrease or increase in dispersal rates or calf survival and moderately sensitive to reproduction and subadult survival parameters, but highly sensitive to changes in adult female survival (Supporting Information 6 Table S3 and Figures S3 and S4).

3.2 | Environmental change scenarios

Our analysis from 500 simulations of 12 single environmental scenarios (i.e., testing only a single scenario that mediates demographic rates) indicated that by far the strongest influence on long-term abundances of the metapopulation of giraffes in the Tarangire Ecosystem was a reduction in wildlife law enforcement (scenarios 4–6; Table 2 and Figures 4 and 5). These were the only scenarios we tested that resulted in extinction probabilities >10%, with the reduction of law enforcement in both Tarangire National Park and Manyara Ranch (scenario 6) causing a nearly 100% probability of metapopulation extinction (Supporting Information 8 Figure S7) before 20 years (Figure 5). A reduction in law enforcement in just Manyara Ranch (scenario 5) produced a worse outcome for the metapopulation than reducing law enforcement in just Tarangire National Park (scenario 4), but an increase in law enforcement (and thus giraffe survival) in just Tarangire National Park (scenario 7) resulted in a mean of 158 (95% CI=150–166) more animals in the metapopulation compared with an increase in law enforcement in just Manyara Ranch (scenario 8; Table 2 and Figures 4 and 5). Improving law enforcement in both Tarangire National Park and Manyara Ranch (scenario 9) resulted in only slightly increased abundances (+ mean of 27 animals, 95% CI=20–35) above increasing law enforcement in Tarangire National Park alone (Figures 4 and 5).

Human settlements and infrastructure, including expansion of towns that reduces survival in town-adjacent giraffe communities (scenario 2) as well as blocking dispersal movements between Tarangire National Park and Manyara Ranch (scenario 3), also reduced the metapopulation abundance after 50 years compared to the control scenario (Figure 4). Climate effects (scenarios 12 and 13) additionally suppressed population abundances compared with the control population (Figure 4). However, the influences of human infrastructure

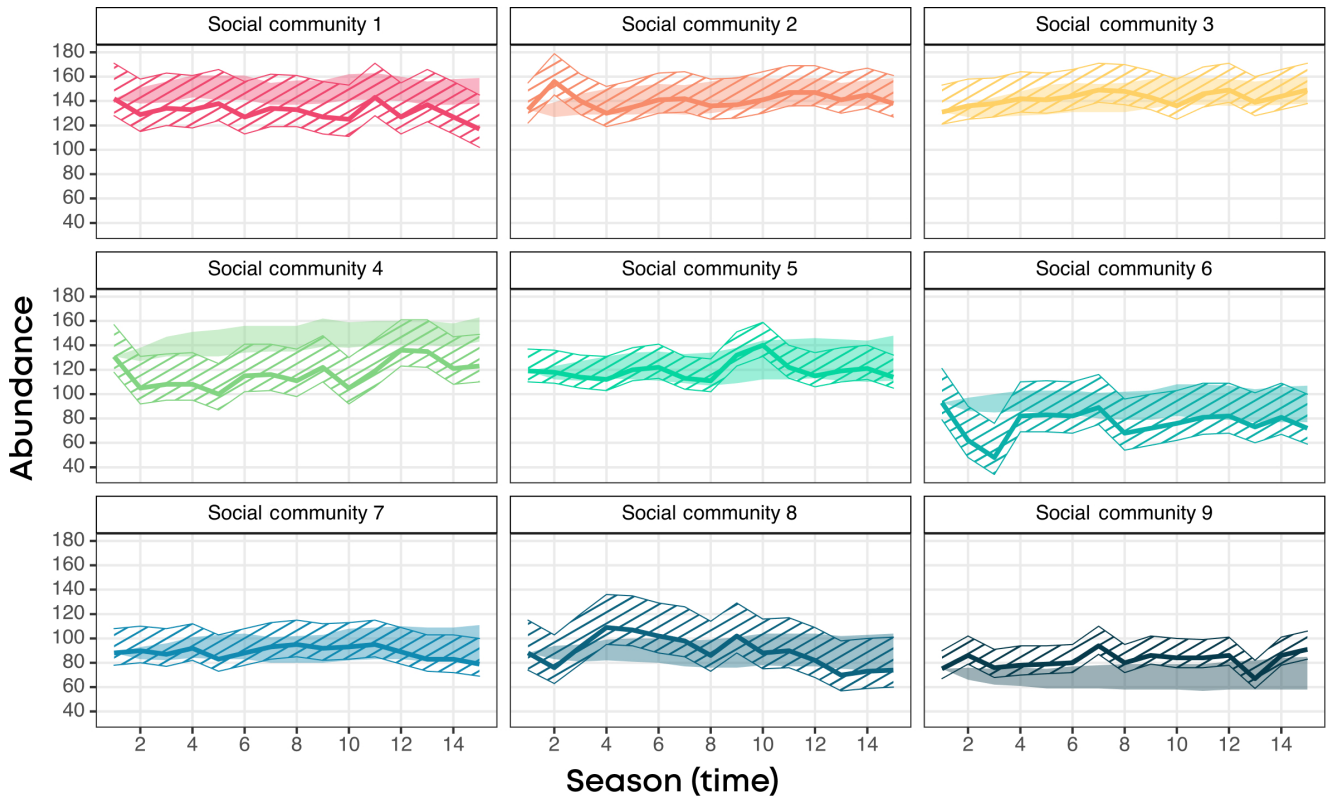


FIGURE 3 Validation of core model. Comparison of total abundance of female giraffes per adult female social community over 15 seasons based on derived abundances from capture–resight statistics (2012–2016), with mean shown as a line and 95% confidence interval as diagonal lines, and simulated abundances from 1000 simulations of the core IBM, expressed as the solid color. Social community numbers and colors correspond with Figure 1b and Table 1.

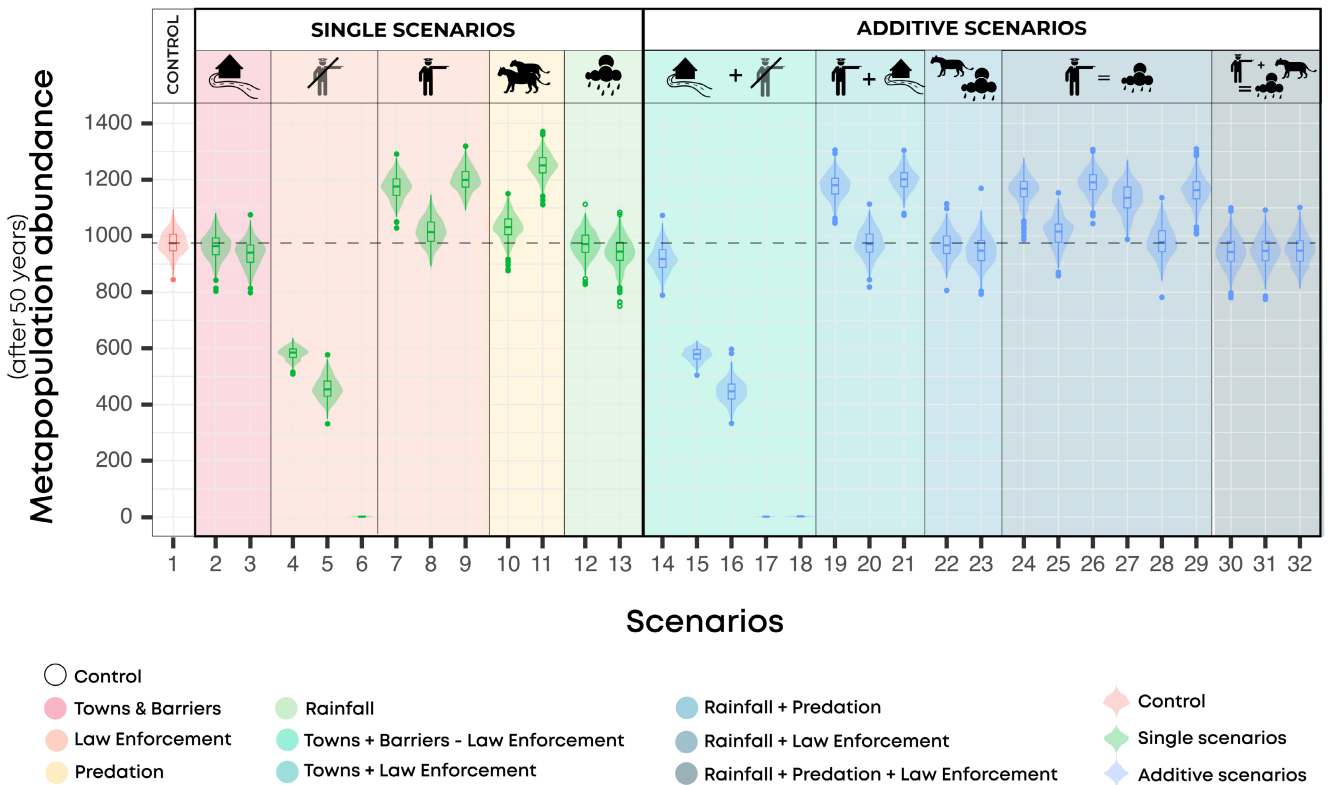


FIGURE 4 Mean abundance (± 25 th and 75th quantiles) of female giraffes in the Tarangire Ecosystem metapopulation after 50 years, by IBM scenario and with 500 simulations. Scenario numbers on the x-axis correspond to Table 2. Dotted line indicates ending abundance from control scenario.

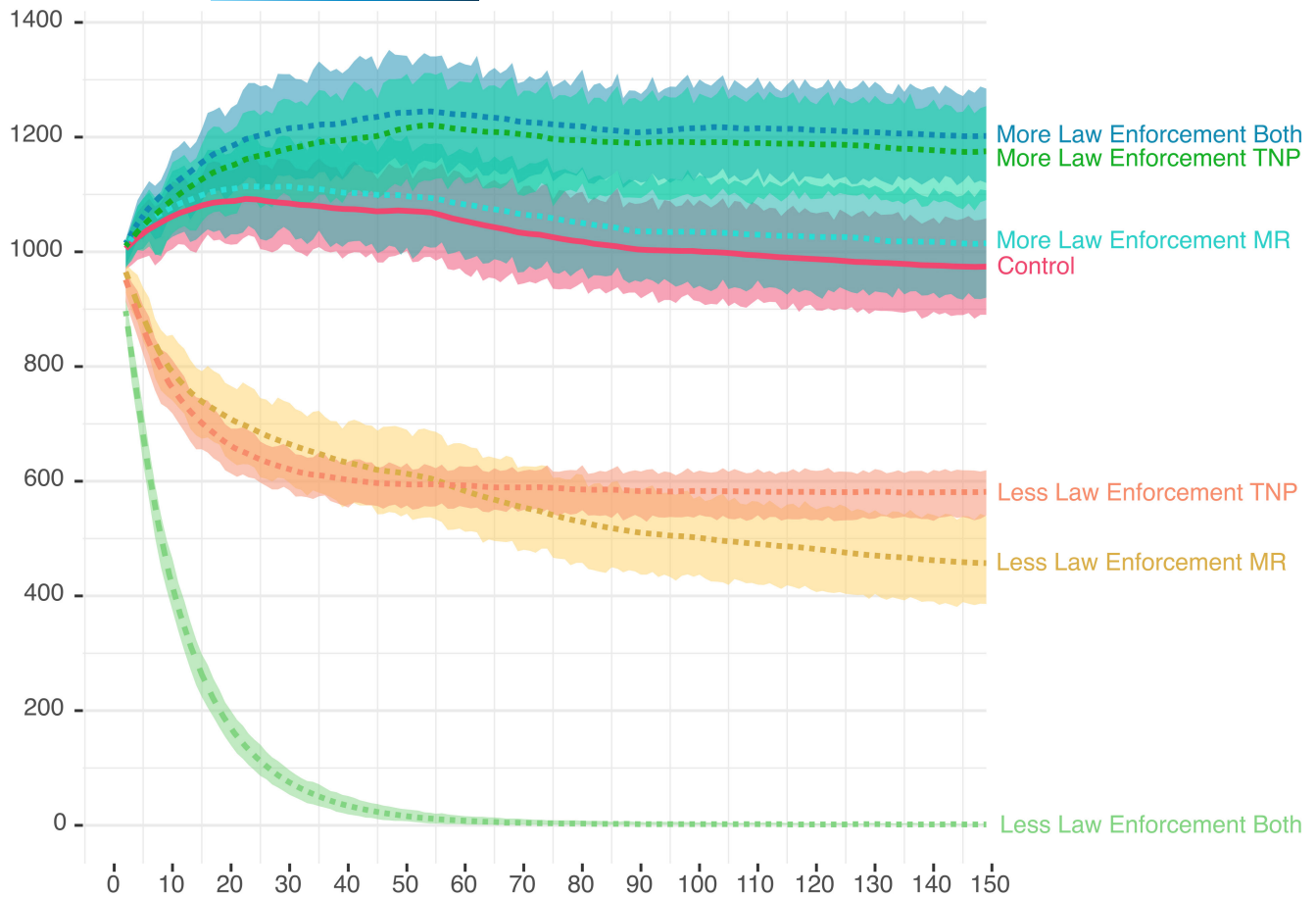


FIGURE 5 Mean abundance (+95% CI) of female giraffes in the Tarangire Ecosystem over 150 seasons (50 years) if conditions remain the same (control), compared to more or less wildlife law enforcement in Tarangire National Park, Manyara Ranch, or both protected areas. Results from 500 simulations of IBM scenarios.

and climate on long-term giraffe population abundances were substantially less severe compared to the influence of law enforcement measures, as the confidence intervals for abundances over time overlapped in all scenarios other than reduced law enforcement scenarios. The CVs of total abundance varied substantially by social community, depending on the scenario (Supporting Information 8 Figure S8).

The scenario whereby the loss of lions and other natural predators boosts survival of giraffe calves in Tarangire National Park in the wet seasons (scenario 11) increased the final abundance of the giraffe metapopulation in this ecosystem more than any other single or combined scenario that we tested (Figure 4).

Any combination of scenarios that involved a reduction in wildlife law enforcement in both Tarangire National Park and Manyara Ranch (6, 17, 18) had the greatest extinction probabilities (Supporting Information 8 Figure S7) and resulted in the near extinction of the metapopulation within 20 years (Table 2 and Figures 4 and 5). The expansion of towns and blocking dispersal did not decrease the time to extinction, as the trajectories were the same for all three scenarios that included less law enforcement in both the park and ranch.

Alternatively, mitigation scenarios that involved improved law enforcement in both Tarangire National Park and Manyara Ranch (Table 2, scenarios 21, 26, 29) had strong effects of preventing extinction risk (Figure 4), with the exception of scenario 32 which involved protecting lions in addition to improving law enforcement. Improving law enforcement in only Manyara Ranch did not ameliorate the effects of expanding human settlements, as this scenario increased abundance by a mean of only 10 animals compared to the town expansion scenario (95% CI=2–18; Table 2). Both scenarios that improved law enforcement in Tarangire National Park as towns expanded (19 and 21) increased abundances over the town expansion only scenario (mean of 213 more animals in scenario 19 vs. 2; 95% CI=205–221, and 237 more animals in scenario 21 vs. 2; 95% CI=230–245, respectively) by just slightly more than improved law enforcement without the combined pressure of human expansion: scenario 7 [improved law enforcement in Tarangire National Park] resulted in a mean of 199 more animals than the control scenario; 95% CI=203–207, and scenario 9 [improved law enforcement in both Tarangire and Manyara Ranch] resulted in a mean of 226 more animals than the control; 95% CI=219–234; Table 2.

In the mitigation scenarios that involved protecting migratory species and lions as mitigation for climate (scenarios 22, 23, 30–32), abundances were a mean of 30 animals lower than both the scenario with 10% more heavy rainfall events and the control scenario, and very similar to final abundances with 25% more rainfall (Table 2).

4 | DISCUSSION

One objective of an individual-based model (IBM) is to create the simplest population model that can still closely resemble “real world” populations and thus provide robust emergent properties and effectively guide wildlife management decisions (Pitt et al., 2003; Ramsey & Efford, 2010). IBMs that incorporate social structure for social species vastly improve the simulation of real-world population dynamics (e.g., coyotes *Canis latrans*, Conner et al., 2008; Pitt et al., 2003; Red-cockaded Woodpeckers *Picoides borealis*, Ziegler & Walters, 2014; meerkats *Suricata suricatta*, Ozgul et al., 2014; Paniw et al., 2022; wolves *Canis lupus*, Bauduin et al., 2020). Our long-term demographic study of giraffes in the Tarangire Ecosystem of northern Tanzania revealed female social structure (Bond, König, Lee, et al., 2021) that plays a role in demographic (Bond, König, Ozgul, et al., 2021) and natal dispersal dynamics (Bond, Lee, Ozgul, et al., 2021). We therefore developed a socially structured IBM of population dynamics of nine female giraffe social communities, using parameter estimates derived from empirical data, to investigate the single and combined impacts of local anthropogenic and climatic pressures on metapopulation abundances and extinction risk over 50 years in this human-influenced savanna landscape. Our results consistently showed that the factor posing the greatest risk of extinction of giraffes in the Tarangire Ecosystem is a reduction in wildlife law enforcement in both of the system's protected areas of Tarangire National Park and Manyara Ranch (Figure 5). Our IBM law enforcement scenarios were parameterized with observed estimates of significantly lower giraffe survival in places outside of protected areas that were subjected to higher levels of poaching, compared to protected areas with active law enforcement operations (Lee, Bond, et al., 2016). These current law enforcement activities in protected areas are clearly the key anthropogenic measure that is sustaining the giraffe metapopulation in the heart of the Tarangire Ecosystem. Should the efficacy of law enforcement in Tarangire National Park, Manyara Ranch, and Randilen and Burunge wildlife management areas be reduced to levels observed in the outlying, less-protected parts of the Masai Giraffe Project boundaries, the extinction—or at least the drastic decline—of giraffes in this landscape is virtually guaranteed. Other anthropogenic threats such as the expansion of towns (Bond, Lee, Farine, et al., 2021), and barriers that block natal dispersal (Bond, Lee, Ozgul, et al., 2021), also lowered the total final abundance of all giraffe social communities compared with the control scenario, as did a 25% increase in the frequency of heavy rainfall events (Bond et al., 2023), but these

factors were less severe and immediate—and less certain—than the strong positive or negative impacts of law enforcement.

4.1 | Giraffe metapopulation dynamics and environmental change scenarios

Our simulations from the core IBM revealed community-level population risks to giraffes in the Tarangire Ecosystem in the near future even without any changes in present conditions. Two social communities in the southern part of Tarangire National Park have higher adult female survival rates than two of the Manyara Ranch communities (Bond, König, Ozgul, et al., 2021), but this difference was evidently not enough to offset the southern communities' substantially lower calf survival rates and subsequently lower recruitment into the breeding pool. These demographic dynamics in our core IBM resulted in fewer adult females over time in these southern communities (Supporting Information 8 Figure S6), producing a negative feedback loop of steadily decreasing abundances during the 50-year simulation (Supporting Information 8 Figure S5). Conversely, the western and northern giraffe communities have the highest calf survival rates (Bond, König, Ozgul, et al., 2021), and these communities stabilized over time at relatively high abundances in our simulations despite the social community effect on adult female survival in two of these communities being among the lowest (Table 1). This result was likely because variation in adult female survival among communities is very low compared to variation in calf survival (i.e., social community effect on adult female survival was substantially lower than on survival of younger age classes, Table 1), as is expected in wild populations of large herbivores with natural rates of predation on juveniles (Eberhardt, 2002; Gaillard et al., 1998; Lee, Bond, et al., 2016). Additional supporting evidence for these dynamics is the environmental change scenario that removed predation effects on giraffe calves in Tarangire National Park (Lee, Kissui, et al., 2016), which was the greatest contributor to increasing the overall metapopulation abundances over time (Figure 4). Thus, our simulations agree with previous research showing that in long-lived species with relatively high and stable adult female survival, juvenile mortality is a major contributor to population growth rates (Gaillard et al., 1998, 2000; Gaillard & Yoccoz, 2003). As seen in other mammals with slow life histories and confirmed in our IBM, adult female survival exerts the most powerful influence on population stability (evidenced by our sensitivity analysis), but most variation in short-term population dynamics is often due to variation in survival of the youngest age classes (Eberhardt, 2002; Gaillard et al., 1998, 2000; Rotella, 2022).

The complexity of these demographic dynamics, however, is illustrated by the long-term decline of the two southern Tarangire communities in the core IBM, despite high and constant adult female survival. We suspect that the southern Tarangire communities in the “real world” are maintained by immigration of subadult females from adjacent communities, which offsets their higher rates

of calf mortality from predation. Pulliam (1988) asserted that active dispersal from source areas can maintain sink populations, and such dispersal could be evolutionarily stable. We infer that without constant immigration of subadult female giraffes, the lower recruitment of resident calves into the breeding pool, combined with mortality of aging adults, results in fewer reproductive females over time which eventually causes community abundances to crash. A similar phenomenon was observed when eggs of common murre (*Uria aalge californica*), a long-lived seabird, were harvested so intensively from the Farallon Islands during the California Gold Rush that the murre population plummeted from an estimated 400,000–600,000 to just 20,000 over five decades, despite few adults being killed (Stark, 2023).

When we modeled the effects of higher giraffe mortality from poaching in scenarios where law enforcement is reduced, we saw the greatest probabilities of metapopulation extinction, which we attribute to the loss of breeding females. Our results are in agreement with several studies of ungulates that found variance in population growth rates were driven primarily by low and variable adult survival in declining populations where hunting effects were present (Coulson et al., 2005; Johnson et al., 2010; Lee, Bond, et al., 2016; Nilsen et al., 2009; Wisdom et al., 2000). In the Tarangire Ecosystem, as in other regions of Africa (Suraud et al., 2012; Strauss et al., 2015) adult giraffes are far less vulnerable to natural predators than juveniles, but they experience mortality from illegal poaching by people (Kiffner et al., 2015). Our sensitivity analysis established that reducing adult female survival by the same amount as the other demographic rates had by far the strongest adverse effect in abundances over time, confirming that the best way to conserve giraffes in Tarangire and other regions of Africa is through effective law enforcement that maintains high and stable adult female survival. Developing and promoting legal livelihoods for local people living adjacent to Tarangire's protected areas also might reduce reliance on income from poaching and contribute to improving giraffe survival (Wilson-Holt & Roe, 2021).

But where to concentrate such efforts? Adult giraffes have slightly higher survival in Tarangire National Park than in Manyara Ranch (Lee & Bolger, 2017; Lee & Bond, 2022), and this demographic phenomenon is clearly important to overall dynamics of our metapopulation. Tarangire supports the largest subpopulation of giraffes in the Masai Giraffe Project study area (Lee & Bond, 2022), hosting six of the nine female social communities (Figure 1b and Bond, König, Ozgul, et al., 2021) and with the greatest net export of females to Manyara Ranch and game controlled areas outside the study area boundaries (Lee & Bolger, 2017). Lee and Bolger (2017) demonstrated with source–sink statistics that Manyara Ranch had the highest per capita contribution of any subpopulation to the overall giraffe metapopulation, but the subpopulation of giraffes in Tarangire had the highest average relative contribution to metapopulation growth, in line with our simulations. Thus, improving law enforcement in Tarangire National Park resulted in >150 more animals in the metapopulation after 50 years compared to improving law enforcement in Manyara

Ranch (Table 2 and Figure 5), because Tarangire has a larger pool of animals to contribute to overall numbers.

4.2 | Mitigating factors

Not surprisingly, the best mitigation for expansion of human settlements and barriers to dispersal for giraffes was to improve law enforcement, which always resulted in higher abundances no matter which combination of threats was tested. A 0.01 increase in giraffe survival probability from improved law enforcement mitigated a 25% rise in heavy rainfall events by increasing abundance 19%, and mitigated the expansion of towns and blockage of dispersal movements by increasing abundance 22%. Our results illustrating the importance of law enforcement echo the findings of both a study of West African giraffes (*G. c. peralta*) in Niger, which showed remarkably high population growth rates after strong law enforcement efforts drastically reduced poaching (Suraud et al., 2012), as well as a population viability analysis conducted for a small population of Kordofan giraffes (*G. c. antiquorum*) in Cameroon (Colston et al., 2023). If effective wildlife law enforcement were to be expanded to village lands outside of our IBM study area, legal livelihoods were promoted, and wildlife movement pathways were permanently protected to enable giraffes as well as migratory ungulates to access high-quality habitats (Bond et al., 2017; Lee & Bolger, 2017; Lohay et al., 2022), these measures would very likely increase the metapopulation of Masai giraffes in the greater Tarangire Ecosystem and contribute toward the recovery of this endangered (sub)species (Bolger et al., 2019).

4.3 | Climate change and giraffes

The relatively minor effect of higher rainfall anomalies on giraffe population trajectories—at least over our time period of 50 years—is likely linked to their long lifespan and high adult survival rates, and supports previous research showing such animals with slower life histories appear to be relatively buffered against climate perturbations (Jackson et al., 2022; Le Coeur et al., 2022; Paniw, James, et al., 2021). An IBM of African elephant (*Loxodonta africana*) population dynamics in southern Kenya demonstrated that this megaherbivore, like the giraffe, was also significantly more vulnerable to an increase in the human population and habitat loss than to climate effects (Boult et al., 2019), suggesting that the most effective conservation efforts are those focused on securing habitat and protecting individuals from illegal killing. Our climate scenarios were based on one study, Bond et al. (2023), which identified immediate adverse effects of high rainfall and vegetation greenness anomalies on giraffes, with lower survival occurring during the same precipitation season as the heavy rainfall or increased greenness. The study found no lag or cumulative survival effects of these climate metrics, either negative or positive, of up to a year. However, vegetation composition in the

African savanna, specifically the balance of grass, shrub, and tree species, responds to environmental conditions at larger temporal scales (Bond, 2008). While we parameterized our IBM with immediate, within-season adverse effects of higher rainfall anomalies on survival, it is likely that prolonged periods of above-average rainfall would increase vegetation biomass and expand woody vegetation into grassy areas of the savanna, and thus increase the overall quantity and distribution of forage available to giraffes in the future.

4.4 | Future applications of the IBM

The insights from our IBM raise new questions and possible applications of this tool. For example, questions about community-level source–sink dynamics such as how giraffe numbers in southern Tarangire are sustained could be answered by quantifying natal dispersal rates among social communities using empirical data, and applying those rates to this IBM to estimate the impacts of among-community immigration—and any perturbation of immigration rates—on long-term abundances. We could also test the effects of lower survival of dispersing individuals from increasing traffic along the tarmac road between Tarangire National Park and Manyara Ranch on metapopulation abundance. The IBM could be modified to link individual calves with individual mothers and explore the costs of skipping one or more reproductive cycles on lifetime reproductive success, or potential effects of changes in demographic parameters like age at first reproduction or interbirth intervals when adult female population densities are very low or very high. Spatially explicit effects of increases in rainfall anomalies could be modeled by including distance to the edge of the protected area boundaries as an individual covariate, as giraffes closer to the edges experienced greater adverse effects of high rainfall anomalies on survival (Bond et al., 2023). Another application of our IBM could involve the incorporation of giraffe pedigrees determined from genetic sampling to examine gene flow among the social communities, and the consequences of blocking such flow in terms of potential inbreeding effects on population viability (e.g., Bauduin et al., 2020 accounting for genetic relatedness for wolves).

4.5 | Conservation implications

A primary task of ecologists is to understand mechanisms that mediate increases or decreases in populations, and provide the scientific basis for management and conservation (Fredricksen et al., 2014). Population viability analyses are growing ever more important as anthropogenic activities drive local population declines and extirpations in addition to global extinctions (Ceballos et al., 2017), but such analyses rely on sufficient empirical data which are often lacking in mammals (Paniw, James, et al., 2021). Fredricksen et al. 2014, (p. 72) noted that “long-term or large-scale studies are...particularly valuable for investigating links between demography and the

environment, both because of increased statistical power and because they are more likely to include periods with contrasting environmental conditions.” Such studies are especially important for understanding population dynamics of large-bodied, long-lived megafauna like giraffes that roam over vast areas of a heterogeneous landscape (Knüsel et al., 2019) and that exert important ecosystem effects (Palmer et al., 2008; Strauss et al., 2015). Given the precipitous decline of giraffe populations across Africa (Bolger et al., 2019; Muller et al., 2018) and rapidly changing environments due to an explosion of the human population (Kiffner et al., 2022) and climate change (Bond et al., 2023), state-of-the-art population modeling approaches such as IBMs that are parameterized with empirical data can facilitate a better understanding of the effects of landscape and environmental changes to guide effective management and conservation of this megaherbivore.

Our “future” scenarios in this IBM are based on realistic threats to giraffes and other wildlife in the Tarangire Ecosystem. For example, law enforcement activities over the past decades have fluctuated based on available funding, resulting in varying levels and efficacy (Kideghesho et al., 2021). Previous global economic recessions and unforeseen events such as the recent COVID-19 pandemic reduced revenue-generating tourism and thus the capacity of Tanzania to enforce laws against poaching (Kideghesho et al., 2021). The dense human population along the edges of Tarangire National Park was identified by park staff, regional natural resource officers, and regional district game officers as the most severe pressure on the park; other pressures they identified included poaching and encroachment of settlements (Abukari et al., 2018). Therefore, our scenarios determined how these realistic threats would help or hurt giraffe populations within a long term but reasonable time frame to provide critical data to land and wildlife managers for evidence-based decision-making in this changing world.

IBMs allow maximum flexibility in scaling from individual traits to population dynamics to make robust inferences about causality (Paniw, Cozzi, et al., 2021; Revilla, 2020), and as such are an important but underutilized tool in the conservation toolbox. Our study system represents the range of threats to giraffes and conservation opportunities throughout Africa; this methodology of determining the population consequences of a set of realistic future scenarios can be adapted to conserve giraffes in other regions—or even for other species—with relatively straightforward modifications of the code, so long as sufficient estimates of demographic rates are available.

AUTHOR CONTRIBUTIONS

Monica L. Bond: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; validation; writing – original draft; writing – review and editing. **Derek E. Lee:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; validation; writing – original draft; writing – review and editing. **Maria Paniw:** Conceptualization; data curation; formal analysis; investigation; methodology; supervision; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data and code to run the spatially implicit IBM for a giraffe metapopulation in the Tarangire Ecosystem are available at <https://doi.org/10.5281/zenodo.8371784>.

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SUPPORTING INFORMATION

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

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