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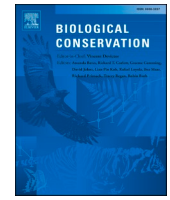

Identifying sustainable coexistence potential by integrating willingness-to-coexist with habitat suitability assessments

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ABSTRACT

Persistence of species in the Anthropocene depends on human willingness-to-coexist with them, but this is rarely incorporated into habitat suitability or conservation priority assessments. We propose a framework of sustainable coexistence potential that integrates human willingness-to-coexist with habitat suitability assessments. We demonstrate its applicability for elephants and rhinos in the socio-ecological system of Maasai Mara, Kenya, by integrating spatial distributions of peoples' willingness-to-coexist based on Bayesian hierarchical models using 556 household interviews, with socio-ecological habitat suitability mapping validated with long-term elephant observations from aerial surveys. Willingness-to-coexist was higher if people had little personal experience with a species, and strongly reduced by experiencing a species as a threat to humans. The sustainable coexistence potential framework highlights areas of low socio-ecological suitability, and areas that require more effort to increase positive stakeholder engagement to achieve long-term persistence of large herbivores in human-dominated landscapes.

1. Introduction

Human coexistence with other species is increasingly recognised as one of the keys to successful conservation and restoration in areas where humans and other species share space and resources (Frank & Glikman, 2019; König et al., 2020). But if people are unwilling to coexist—share

Abbreviations: MMWCA, Maasai Mara Wildlife Conservancies Association; MMNR, Maasai Mara National Reserve; WAC, Wildlife Acceptance Capacity; SDM, Species Distribution Model; INLA, Integrated Nested Laplace Approximation; ZANB, Zero-Altered Negative Binomial hurdle model; BYM, Besag-York-Mollié; CAR, Conditional Autoregressive; NDVI, Normalized Difference Vegetation Index; CrI, Credible Intervals; SI, Supplementary Information.

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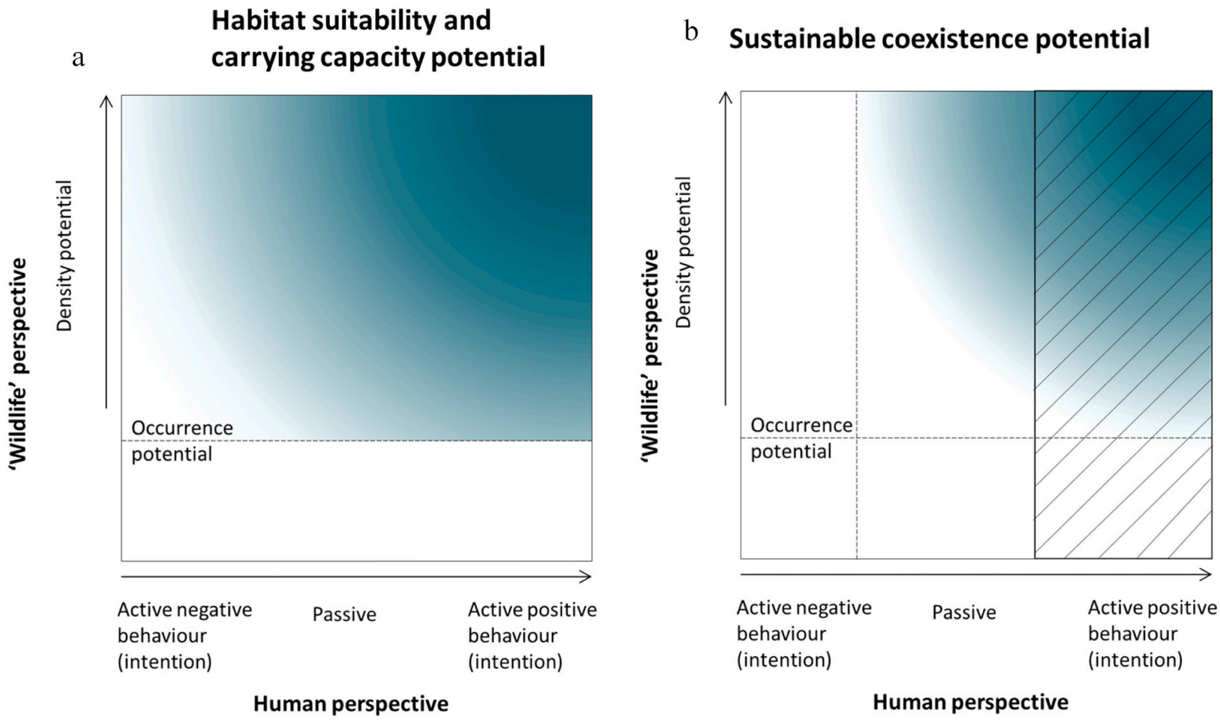

Fig. 1. Conceptual diagram representing **a)** socio-ecological habitat suitability for wildlife (occurrence potential) and carrying capacity (density potential), this could also represent the perspective from a plant species, and **b)** sustainable human wildlife coexistence potential. The x-axes represent a negative-positive scale for attitude, behavioural intent and behaviour of people, and the y-axes represent wildlife density potential. In **a)**, we assume that human perspective only plays a role as active negative behaviour, e.g. killing of wildlife, and that a socio-ecological threshold exists below which wildlife cannot occur. In **b)** we assume a threshold exists for both axes below which sustainable coexistence is not possible. The darker the colour, the higher is the suitability and carrying capacity potential **(a)** or potential for sustainable coexistence **(b)**. The hatched area in b) represents the space where people can be expected to express a willingness-to-coexist, an attitudinal measure for positive active stewardship.

space and resources—with animals (or plants), the prospect of these species' long-term persistence or population growth will be low in the shared spaces, even in socio-ecologically suitable habitats (Franco and Eivin, 2021; Pebsworth and Radhakrishna, 2021; Manfredo et al., 2021). This can for example be linked to intensive human–wildlife and human–human conflicts, to the detriment of wildlife, local communities and conservation programs (Dickman, 2010). Ignoring willingness to coexist when assessing coexistence potential thus limits the practicability of potential conservation interventions (Cretois et al., 2021; IUCN Species Survival Commission (SSC) Human-Wildlife Conflict Task Force, 2020). In addition to the assessments of species' needs and constraints, it is therefore necessary to incorporate the perspectives of the people coexisting with the species into conservation research and policies (Ardiantiono et al., 2021; Bruskotter and Wilson, 2014; Frank & Glikman, 2019; St John et al., 2010; Pooley, 2021).

Through evaluation of socio-ecological spatial variables expected to be relevant for the wildlife or plant species, and the habitat use of those species, habitat suitability assessments can be considered as 'letting' animals or plants voice their requirements (Buller, 2015), or more specifically, a human perspective on their needs and preferences (Lötter et al., 2008; Wemmer & Christen, 2008). Joining this with a measure of coexistence potential from a human perspective (König et al., 2020) by integrating it with willingness-to-coexist, leads to a sustainable –and realistic– measure of the potential for human–wildlife (or human-plant) coexistence. This results into the *sustainable coexistence potential*: the sustainable sharing of space and resources between humans and other species such as wildlife. This represents a non-anthropocentric perspective that values both human and non-human lives (van den Born et al., 2001), aiming for a common ground between people-centred conservation and science-led ecocentrism (Sandbrook et al., 2019).

There are however challenges in integrating habitat suitability assessments with reliable measures of peoples' perspective. Attitudes are linked to behavioural intent and behaviour, and can be considered to follow a scale from active negative resistance, to passive tolerance, and finally active positive stewardship (Bruskotter and Fulton, 2012; Treves, 2012). There is however a bias towards research on negative experiences and attitude towards unwanted species instead of their acceptance, which may tend to oversimplify our understanding of the plurality of people's perspectives and experiences with wildlife (Bruskotter and Wilson, 2014; Buijs and Jacobs, 2021). Since attitudinal research relies on self-reporting, there is also a risk of false positive and false negative reporting errors, as people can overstate or understate their opinions (sub-) consciously (Vasudev et al., 2020; Vasudev and Goswami, 2020).

Evidence for a clear link between attitude and actual behaviour of people is currently limited (Ajzen and Fishbein, 2021; Liu et al., 2011; St John et al., 2010). For example, there is limited quantitative evidence for a link between stakeholder attitudes and the socio-ecological suitability of an area for large herbivores such as elephants (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis;* Vogel et al., 2021). Nevertheless, a positive attitude can be linked to behaviour supporting conservation at a local scale, and can thus be expected to increase suitability of an area as a habitat or movement conduit for a species (Behr et al., 2017; Broekhuis et al., 2018; Liu et al., 2011; Vasudev et al., 2020). To successfully integrate anthropogenic and ecological perspectives into sustainable coexistence potential, we need to recognize and overcome these challenges of negative research bias, self-reporting errors and limited established links between attitude and conservation success.

To incorporate attitudes in habitat suitability assessments, we therefore calculated a 'willingness-to-coexist' score which represents *the probability that people have a positive attitude towards sharing space and resources with other species on a local scale.* We do so using hierarchical

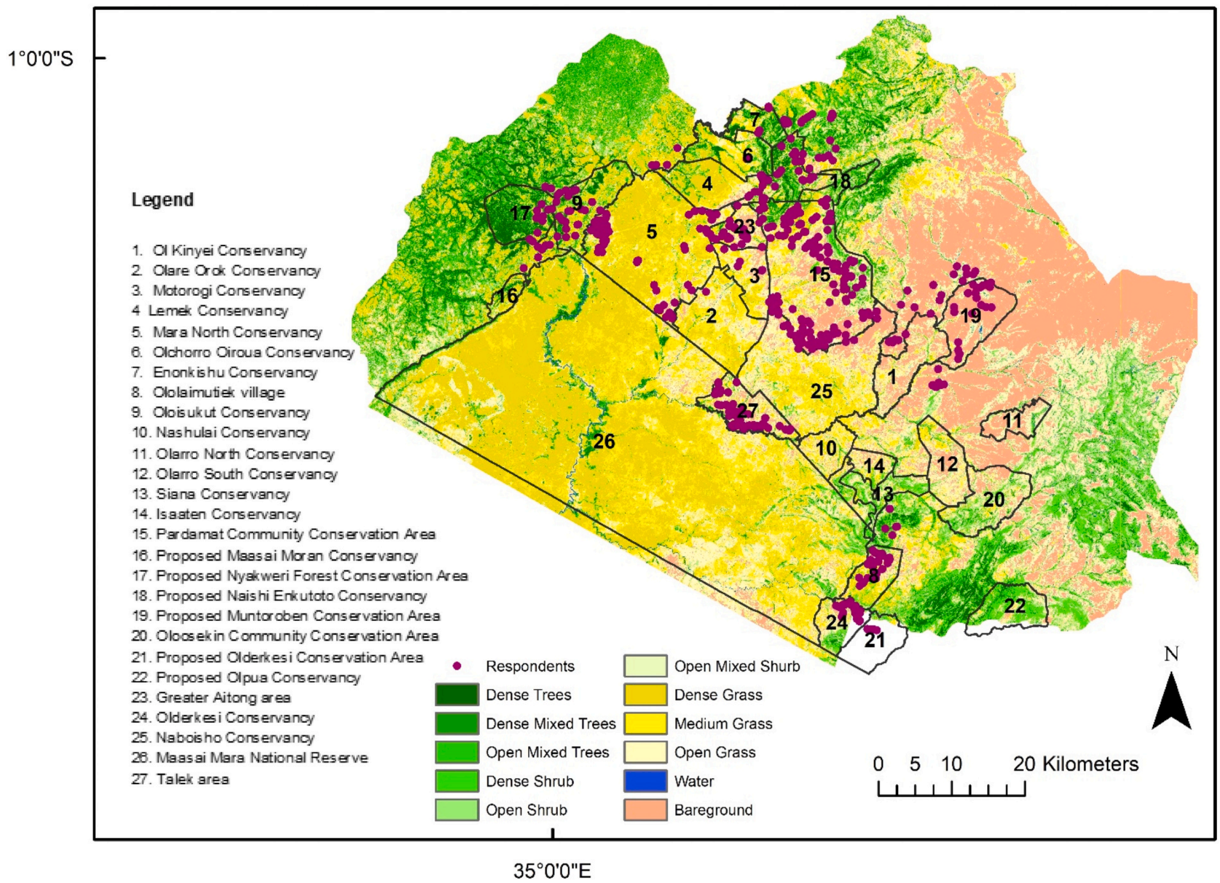

Fig. 2. Location of respondents interviewed during the study, the names and demarcations of Maasai Mara National Reserve, (proposed) conservation areas, villages, towns and community lands and most dominant vegetation types across the study site (Li et al., 2020). Most of the study site is covered by dense to medium-dense grasslands and open shrubland, interspersed with clusters of trees and grasses typically fringing drainage lines and on ridges, and bareground around areas such as in Talek and Aitong towns, and in the north-east of the study site.

Bayesian models that account for misreporting errors, developed by Vasudev and Goswami (2020) based on the occupancy modelling framework used in ecology. While anyone can have a notional, or generic attitude towards wildlife (or plants), willingness-to-coexist (or its lack thereof) follows from, and pertains to, living in close contact on a local scale (Vasudev et al., 2020; Vasudev and Goswami, 2020). We consider willingness-to-coexist to be a higher-order or active positive attitude, meaning that it is closer to active support and stewardship than normative attitudes, basic beliefs and values (Bruskotter and Fulton, 2012; Fulton et al., 1996). Willingness-to-coexist thus goes beyond mere inaction (Treves, 2012) or passive tolerance (Bruskotter and Wilson, 2014).

From a wildlife (or plant) persistence perspective, there is a socio-ecological threshold below which the potential for occurrence is too low for the landscape to fulfil the species' needs (Fig. 1a; Svenning and Faurby, 2017). Yet, to achieve sustainable coexistence, both animal and human occurrence potential thresholds must be met (Jochum et al., 2014; Fig. 1b), with sufficiently suitable environmental conditions and the satisfaction of human interests *'without depriving species, native ecosystems or native populations of their health'* (Vucetich and Nelson, 2010). Without the later, continued human support for wildlife is unlikely (Franco and Eivin, 2021; Pebsworth and Radhakrishna, 2021). Besides sufficient resources, this requires socially just conservation through effective institutions that aim to satisfy the needs and desires of both people and other species like wildlife, while minimizing interactions that jeopardise each other's safety, and result in a sustainable dynamic state in which people and wildlife co-adapt, and thus coexist (Büscher and Fletcher, 2019; Carter and Linnell, 2016; Frank and Glikman, 2019; Vucetich et al., 2018; Clark et al., 2021). While passiveness may be sufficient to achieve conservation, less active negative behaviour (e.g. political acts such as voting or signing petitions) could still negatively affect wildlife's ability to survive or thrive in the long-term (Bruskotter and Fulton, 2012). Therefore, willingness-to-coexist corresponds to active positive behavioural intention (Fig. 1b, hatched area). Sustainable coexistence potential should be the highest when there is potential for high densities of wildlife based on socio-ecological suitability of the landscape, and high levels of peoples' expressed willingness-to-coexist (Fig. 1b, upper right corner).

This sustainable coexistence framework therefore encourages us to explicitly value both wildlife and human perspectives equally. Instead of only including people's active negative perspective into habitat suitability assessments, it is therefore necessary to also fully integrate people's willingness-to-coexist –which we consider to be relevant for future species density potentials- through conservation priority zoning (Whitehead et al., 2014). The result is a tool that can aid spatial planning for coexistence in a human-dominated world by highlighting areas of low willingness-to-coexist or low habitat suitability, and identify conservation priorities (Broekhuis et al., 2017; Marchini et al., 2019). This integrated coexistence framework is therefore relevant across regions and species, wherever people's willingness-to-coexist is acting as a major and concrete factor in a species' future persistence.

We apply the framework of sustainable coexistence potential to African savannah elephants and black rhinos in the Maasai Mara Ecosystem, Kenya. In this ecosystem there are concerns that consequences of human activities and livestock numbers are compromising wildlife persistence and movement connectivity (Ogutu et al., 2011, 2016; Stabach et al., 2022). There is also a long history of land appropriation for conservation, disempowering the pastoralist Maasai communities, weakening their traditional coping strategies, and deepening their livelihood vulnerability, thereby creating disincentives for conservation (Fernández-Llamazares et al., 2020; Goldman, 2011; Western et al., 2019). Coexistence between people and African savannah elephants is of high conservation interest and concern given the elephant's currently endangered status (Knox et al., 2021), and has significant implications for the wellbeing of people living in conservancies and pastoral lands around the Maasai Mara National Reserve (Nyumba et al., 2020).

2. Methods

2.1. Study site

Our study site included the Naboisho, Ol Kinyei, Mara North, Lemek, Ol Chorro Oiroua, Olare-Motorogi, Proposed Muntoroben Conservancy, Olarro, Siana Mara and Olderkesi conservancies, Nyakweri Forest Conservation Area and the proposed Pardamat Conservation Area which we divided into the northern, middle and southern sections (Fig. 2). We also included Aitong, Talek and Mara Rianta, three of the largest towns in the ecosystem (MMWCA, 2019).

Land around the Maasai Mara National Reserve in Kenya is either communally or individually owned. Some landowners have organised themselves into conservancies aimed at community-based conservation, as part of the Maasai Mara Wildlife Conservancies Association (MMWCA), through partnerships with investors in eco-tourism enterprises and receive direct financial benefits, e.g., from land leases (MMWCA, 2019; Thompson et al., 2009). Elephants (3404 ± 1156 animals or 0.54 animals /km^2 in 2022) are common throughout the ecosystem but black rhinos are rare (< 40 animals or < 0.006 animals/km^2) and restricted to the Maasai Mara National Reserve (MMNR), and are actively pushed back by rangers into the MMNR whenever they wander into the adjoining areas to reduce the likelihood of negative human-rhino interactions. Therefore, we focused on both elephants and rhinos in the attitude assessments, but only on elephants in the potential habitat suitability and sustainable coexistence assessments. This research has been reviewed and approved in accordance with Aarhus University's guidelines for the university's Research Ethics Committee (IRB), and was completed under NACOSTI permit License No: NACOSTI/P/19/3156. Please find more details and our authors' reflexivity statement in **SI 1.**

2.2. Willingness-to-coexist model

2.2.1. Interviews

We collected interview data during January–April 2020 in Maa. Interviewers were 10 men and one woman, all Maasai. Respondents were selected through stratified random sampling of 60 households from each trading centre and (proposed) conservancy, using the most complete spatial dataset on household distribution available for this region (Broekhuis et al., 2017). A total of 556 households were interviewed with each interviewer covering 40–60 households, with a non-response rate of <1 %. Each interview took around 30 min to complete on average (**SI 1**).

During the interviews we collected socio-demographic information, asked about preferred elephant and rhino densities, experiences with both species, and collected responses to both notional and localized attitudinal statements on a five point Likert-scale (Bernard, 2006; Vasudev and Goswami, 2020; **SI 1 & 2**). Notional attitudinal statements were abstract, while localized statements related directly to the respondent's lives and livelihoods. We used the free Cybertracker software to develop an English and a Maa (most commonly spoken language among Maasai) data collection application for each of the sites and to upload these on to the interviewers' smartphones. We also developed a measurement of acceptable wildlife density levels in areas of low literacy rates to interpret our results (**SI 1**).

2.2.2. Model construction and evaluation

To measure the probability of a positive attitude towards living with elephants and rhinos —i.e. willingness-to-coexist—we grouped the negative and passive responses to attitudinal questions into non-positive attitudes and compared these to positive responses. We applied a Bayesian hierarchical model related to ecological multiple-detection models (Miller et al., 2011; Vasudev & Goswami, 2020), which allowed us to determine false positive and false negative errors (misreporting errors) in reported attitudes, and therefore provides a more reliable measure of acceptance than methods based on self-reporting only (Vasudev and Goswami, 2020). To do so, our survey included uncertain questions, where we accounted for potential false positive and false negative response from respondents, and certain questions to which we reasonably expected only either a false positive or a false negative response (**SI** 1 Table S2). The model enables quantifying both a notional or generic attitude (ψ) and a localized attitude (φ) towards elephants and rhinos, while accounting for reporting biases (Vasudev et al., 2020; Vasudev and Goswami, 2020).

We ran three models (Model I–III), each with different sets of variables. As socio-demographic information from respondents we included age, gender, the highest level of formal education, owning livestock and having an alternative livelihood strategy as covariates in all our models (**SI 3.3**, Table S5). Model I also included a binary variable indicating whether respondents lived inside a conservancy, as we expected this to play an important role in explaining willingness-to-coexist. We also included spatially explicit variables on reported crop loss, property loss, threat to humans, threat to livestock, and benefit from tourism. It was not possible however to include these in the other two models due to high spatial correlation between the variables (**SI 3**). Model II included, instead of the binary conservancy/non-conservancy variable, the more spatially explicit covariate indicating the identity of each of the (proposed) conservancies and trading centres (towns). However, some conservancies contained few respondents, making results from this model less reliable. Therefore, we also fitted Model III in which we divided respondents into 11 spatial clusters with similar numbers of respondents based on spatial proximity and (potential) conservancy or trading centre.

In this manuscript we focus on the results from Model I and III (**SI 3** for details and model evaluation). As we constructed the Likert scale by averaging at least eight Likert items on a five-point scale each, we consider it meaningful to compare means between the spatial clusters (Norman, 2010; Wu and Leung, 2017), to illustrate the importance of correcting for reporting errors.

2.3. Habitat suitability models

2.3.1. Species occurrence and density data

We used decadal averages of elephant numbers obtained from aerial survey monitoring data by the Directorate of Resource Surveys and Remote Sensing of Kenya (DRSRS, Ogutu et al., 2016). The decadal averages were computed for 284 sampling units, each of size 5 × 5 km and located in the MMNR as well as most of the conservancies. Surveys were separately conducted for the wet season of 2015, 2016 (two surveys), 2018 and 2022, and dry season of 2010, 2011, 2012, 2013 and 2014, and adjusted for the sampling fraction used in each survey, with sampling fraction varying from 5 to 11 %. Observers counted groups of >10 twice, during the aerial survey, and from photographs displayed on a large digital screen. Calibration experiments done in the 1980s indicate that counting efficiency of this method in the field site averaged 70–80 % for large wild herbivores (15 kg and above) and 80–90 % for livestock (Stelfox et al., 1986).

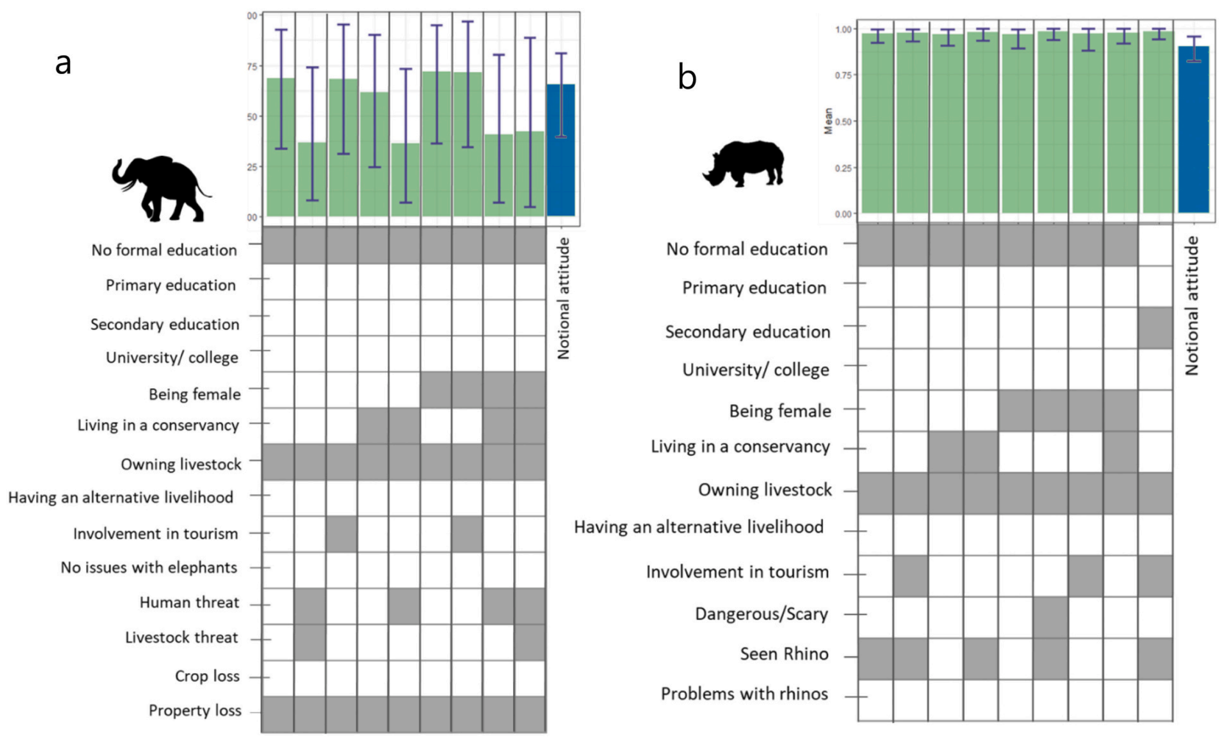

Fig. 3. The notional attitude (ψ), and willingness-to-coexist (φ) for the most common combinations of social demographic characteristics among the respondents ($n = 556$), expressed in the bar plot as the probability of having a positive attitude to live with elephants **(a)** and rhinos **(b)**, with 95 % Credible Intervals. The x-axes of the bar plots are visualized by the matrix columns with greyed cells indicating the combinations of social demographic characteristics corresponding to the bar displayed above each matrix column (except for notional attitude or probability to have a positive attitude in general). For example, the first bar in Fig. 2a represents the willingness-to-coexist for a man with no formal education, who owns livestock and has experienced property loss due to damage by elephants.

2.3.2. Excess sampling zeros

The aerial surveys only captured a snapshot of the elephant distribution, while elephants are highly mobile animals that typically occur in herds, resulting in generated excess sampling zeros (zero-inflation) in cells that contain suitable habitat, but were unoccupied during the survey periods (Martin et al., 2005). False zeros can also arise from not observing present elephants. We can address excess zeros by limiting observer bias in data collection (Section 2.3.1), and distinguishing between structural (true) zeros and false zeros due to temporary absence and imperfect detection (Dénes et al., 2015). Imperfect detection can be accounted for by using n-mixture models (Meehan et al., 2020; Royle and Kéry, 2007), while zero-inflation distribution models –despite not explicitly separating detection from abundance patterns- account for both types of false zeros (Lahoz-Monfort et al., 2014; Nolan et al., 2022). Hence, both tools have the potential to address detection bias problems (Banks-Leite et al., 2014; Goldstein and de Valpine, 2022; Wenger and Freeman, 2008).

We therefore applied three types of habitat suitability models: I. Zero-inflated species distribution models (Poisson and negative binomial models), II. Zero-inflation Integrated Nested Laplace Approximation models with explicit modelling of spatial dependence between observations, and III. N-mixture Integrated Nested Laplace Approximation models. We did not use hierarchical occupancy models as we were interested in potential elephant density, not potential occupancy across the study site (Fig. 1).

2.3.3. Spatial data and covariate selection

We identified relevant ecological and anthropogenic predictors of elephant presence and density in an extensive literature review of factors known to influence elephant and rhino habitat suitability (Vogel et al., 2021) and based our final set of covariates included in the species distribution model on (multi-) collinearity between identified relevant covariates (**SI 4**). Based on these assessments, the final covariates we included in our habitat suitability models were the proportion of the 5 × 5 km grid cells with permanent water, average terrain elevation, average terrain slope, average NDVI (Normalized Difference Vegetation Index), livestock biomass (kg) and total number of houses in each 5 × 5 km grid cell (i.e. settlement density). As the Species Distribution Model also contained data from both the wet and dry seasons, we included, as an additional covariate, the average precipitation for each season.

2.3.4. Species distribution model construction and evaluation

The previously mentioned false absences may cause an artificial inflation of predicted absences (Martin et al., 2005), and our zero-inflation test using the performance R-package (Lüdecke et al., 2021), suggested a zero-inflated or hurdle (zero-altered or two-part) model was more suitable than one ignoring excess zeros (Zuur et al., 2009). Visualisations of the presence-absence data overlaid on the spatial covariate data layers (**SI 4.2**) suggested the potential presence of both sampling and structural zeros in our dataset. Therefore, we used a zero-altered negative binomial hurdle model (ZANB) to account for excess zeros taking both zero structures that emerge from unsuitable areas, and potential overdispersal (emerging from clumped distribution of elephants) into account (Blasco-Moreno et al., 2019; Martin et al., 2005; Zuur et al., 2009) using the pscl R-package (Hadfield, 2021), see **SI 4.3** for model evaluations.

2.3.5. INLA models construction and evaluation

Our models using the Integrated Nested Laplace Approximation (INLA) framework allowed us to predict elephant density through approximate Bayesian inference assuming latent Gaussian processes (Moraga, 2020). We constructed two types of INLA habitat suitability models by using the R-INLA package (Martins et al., 2013; Rue et al., 2009; www.r-inla.org). First, we used a spatial INLA model with the zero-inflated Poisson Type 1 function because our data contains both structured and unstructured zeros (Blangiardo and Cameletti, 2015) and constructed them as a Besag-York-Mollié (BYM) model (Besag et al., 1991). This BYM model includes two types of random effects, an unstructured random effect that accounts for uncorrelated noise, and a Conditional Autoregressive (CAR) distribution that accounts for the spatial structure in the mapped data, by feeding into the model a neighbourhood matrix that identifies areas as neighbours if they share a boundary, and uses this information to smooth the data (Blangiardo and Cameletti, 2015; Moraga, 2020).

Second, we used N-mixture models, which account for imperfect detection associated with wildlife surveys and can thus produce potentially less biased abundance estimates (Goldstein and de Valpine, 2022; Meehan et al., 2020). In order for the n-mixture model to converge it was necessary to scale all covariates. We applied the negative binomial-binomial mixture likelihood family to account for over dispersion (Zuur et al., 2009), and followed Meehan et al. (2020) in model building. We constructed the spatial model separately for the wet and dry season data, and combined both into the n-mixture model with averaged covariate values. We modelled the hyper parameters of both models using a Gaussian prior distribution $N\sim$ (0,1) and evaluated model fit using leave-one-out cross-validation (Blangiardo and Cameletti, 2015), see **SI 4.3** for model evaluations.

2.4. Sustainable coexistence potential map

To obtain a map of *sustainable coexistence potential*, we changed the projection and resolution of the willingness-to-coexist map (coexistence potential from the human perspective) to match the habitat suitability maps (coexistence potential from the 'wildlife' perspective, Fig. 1). Based on frequency plots of the predicted elephant densities and willingness-to-coexist scores, we reclassified both habitat suitability maps and the willingness-to-coexist map to convert them into a binary map (**SI 5**). We then created a combined mosaic raster plot overlapping the binary maps and summing the values of both maps, and clipped this to the area for which we had elephant density estimates. We also overlaid a difference map to highlight the areas which were socio-ecologically suitable, but not so from a human perspective, and vice versa. Most of the attitudinal survey data was collected during a prolonged dry season, a period during which coexistence challenges are most pronounced in the study site (Bedelian and Ogutu, 2017; Miller et al., 2014). Thus, we focus on the dry season survey data (which comprised most of our elephant survey) for mapping (**SI 4.3**).

3. Results

3.1. Notional attitude towards elephants and rhinos

In general, people in the Maasai Mara had a more positive notional (or generic) attitude towards rhinos (ψ_{rhino} = 0.91 [95 % CrI = 0.82–0.96]), than towards elephants (ψ_{elephant} = 0.66 [95 % CrI = 0.40–0.81]; **SI** Fig. S16 a-b). The false negative reporting error was just over 30 % for elephants (p^{10}_{uc} = 0.35, **SI** Table S8 for the non-zero Credible Intervals and certain question reporting errors for each species) and rhinos (p^{10}_{uc} = 0.32), while the false positive reporting error was higher for elephants than rhinos ($p^{01}_{\mu c\,\text{elephant}}$ = 0.57, $p^{01}_{\mu c\,\text{rhino}}$ = 0.30). This shows that a larger proportion of the respondents who were not positive towards elephants tended to report positive attitudes towards rhinos. The influences of covariates on these attitudes were consistent for both elephants and rhinos. Men had a higher likelihood of being positive towards elephants and rhinos notionally, while there was some tendency for older educated persons to be positive towards elephants and rhinos (Fig. 3, **SI** Fig. S16 a-b).

3.2. Willingness-to-coexist with elephants and rhinos

Respondents were generally more positive towards rhinos than elephants (Fig. 3, **SI** Fig. S16 a-b, S5). There was a broad consensus among the respondents that both animal species are intelligent, important, have a right to live in the Mara, and that people are happy the animals are in Maasai Mara, occur in and use their conservancies and should continue living in the area. After correcting for reporting errors, willingness-to-coexist —relating to a localized positive attitude conditional on a notional positive attitude— was generally higher for rhinos with less variation between combinations of social demographic characteristics ($\varphi_{\text{rhino weighted average}}$ = 0.98 [95 % CrI $_{\text{weighted average}}$ = 0.93–1.00]) than for elephants ($\varphi_{\text{elephant weighted average}}$ = 0.59 [95 % CrI $_{\text{weighted average}}$ = 0.24–0.89], Fig. 3, **SI** Fig. S16 a-b). Willingness-to-coexist with elephants also varied strongly across the Maasai Mara, as with the probability of having a positive attitude towards living with elephants; from 0.13 for Talek town (s.d. = 0.01) to 0.62 for the south of Paradamat (s.d. = 0.00), close to Naboisho Conservancy (**SI** Table S7 for all weighted willingness-to-coexist scores).

Table 1
Comparative results based on the quantiles in which each of the spatial clusters performed for three measures: our willingness-to-coexist score corrected for reporting error represented by a probability score from 0 to 1, the uncorrected Likert score represented by the average response on a scale of 1–5, and the Wildlife Acceptance Capacity score, which represents the proportion of change people desired in the density of elephants. Cluster codes correspond to Fig. S13.

Cluster	Willingness-to-coexist [0−1]		Uncorrected Likert [1–5]		WAC [proportion]	
J. Southern part of Pardamat	0.618	Q1	2.479	Q3	1.363	Q1
F. Proposed Muntoroben, Ol Kinyei,Olarro	0.473	Q1	2.735	Q1	1.307	Q2
D. Northern part of Mara North	0.355	Q1	2.566	Q2	0.968	Q4
B. Lemek, Olchoro Oiroua, Enonkishu	0.350	Q2	2.540	Q3	0.922	Q4
A. Greater Aitong area	0.288	Q2	2.370	Q3	1.325	Q2
I. Northern part of Pardamat	0.248	Q2	2.152	Q4	1.412	Q1
L. Nyakweri Forest Conservation Area, Oloisukut, Masaai Moran (Trans Mara)	0.200	Q3	2.944	Q1	1.096	Q4
H. Central part of Pardamat	0.195	Q3	2.352	Q4	1.048	Q3
G. Olderkesi, Siana, Ololaimutiek	0.187	Q3	2.315	Q4	1.217	Q3
M. Talek town	0.175	Q4	2.604	Q1	1.164	Q3
E. Mara Rianta village	0.146	Q4	2.602	Q2	1.413	Q1
C. Mara North, Motorogi, Olare Orok	0.132	Q4	2.580	Q2	1.315	Q2

3.2.1. Importance of correcting for reporting error

The false negative reporting error was similar for elephants (q^{10}_{uc} = 0.42, **SI** Table S8 for the non-zero Credible Intervals and for certain questions, the reporting errors for each species) and rhinos (q^{10}_{uc} = 0.41), whereas the false positive reporting error was higher for elephants than for rhinos ($q^{01}_{\mu c\,\text{elephant}}$ = 0.55, $q^{01}_{\mu c\,\text{rhino}}$ = 0.42). Without quantifying and correcting for reporting error, and thus only using the raw Likert scores, we would have only correctly estimated support for living with elephants in the cluster combining the proposed Muntoroben conservancy, and the Ol Kinyei and Olarro conservancies (Table 1, Fig. S14). We would have overestimated support for coexistence in four, and underestimated it in seven of the spatial clusters. Also, if reporting error were not corrected for and we used the Wildlife Acceptance Capacity (WAC) as an indicator for support for coexistence with elephants, this would have been overestimated for three and underestimated for five of the spatial clusters (Table 1, Fig. S13).

3.2.2. Threat to humans

There was a stronger effect of covariates in determining peoples' willingness-to-coexist with elephants than with rhinos, and less variance in answers among respondents (Fig. 3). In particular, the threat it poses strongly reduces peoples' willingness-to-coexist with elephants. Where willingness-to-coexist with them was low, elephants were perceived as posing greater threats to human life than other threats (Fig. 3a; **SI**

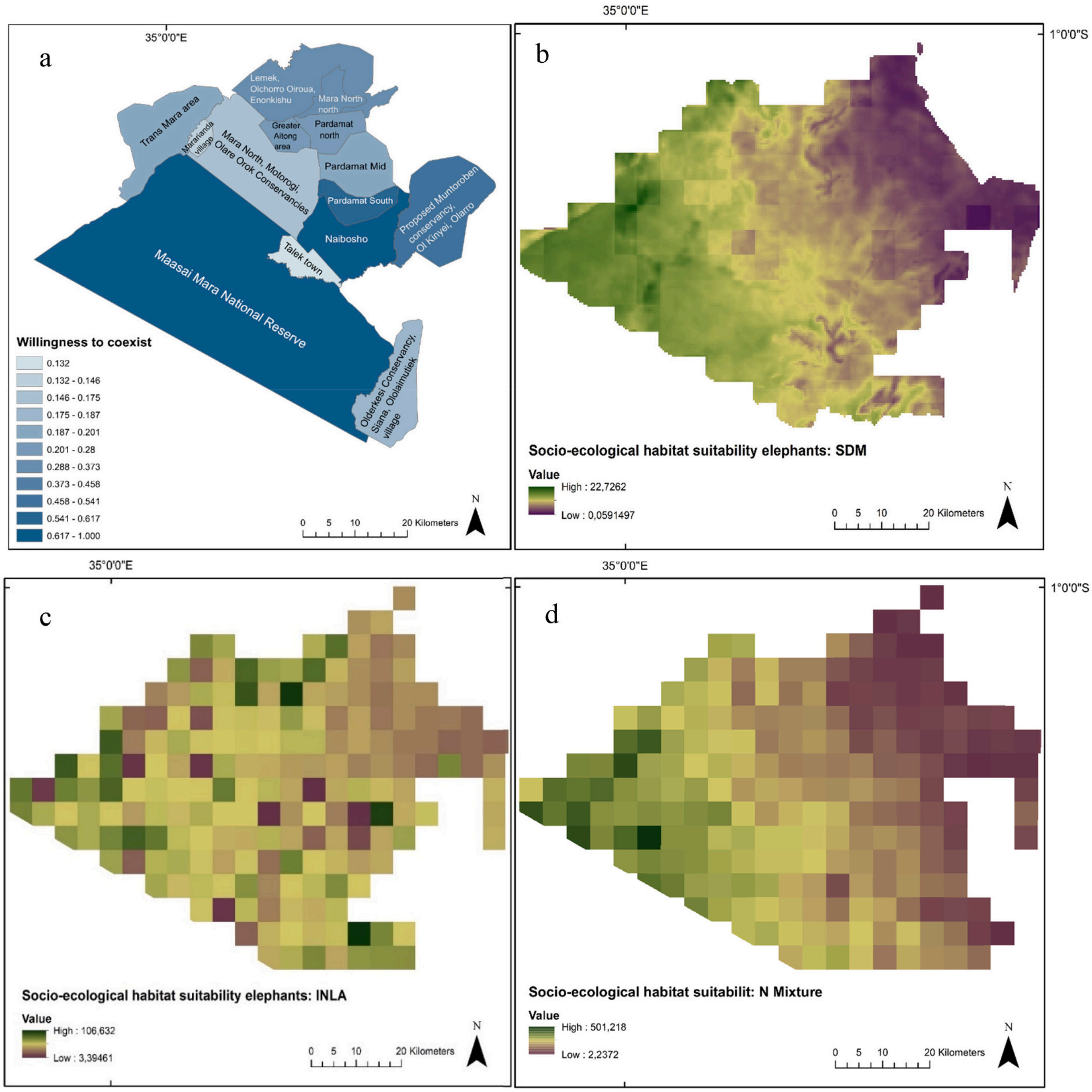

Fig. 4. a) Probability of a positive attitude towards living with elephants (willingness-to-coexist) as measured across the (proposed) conservancies and other regions in the Maasai Mara, based on the average willingness-to-coexist weighted by the prevalence of a combination of social demographic characteristics (n = 556); b) Habitat suitability map and the predicted elephant density across the Maasai Mara based on model I: SDM; c) Habitat suitability map and the predicted elephant density across the Maasai Mara based on model II: spatial INLA model, d) Habitat suitability map and the predicted elephant density across the Maasai Mara based on model III:N-mixture INLA model.

Fig. S14, S15). Elephants obstructed people's daily activities, and were described as "*causing fear and frustration in human[s] if they come around*", "*They have jammed every space around here. We fear them a lot.*" Some of the open answers people gave also indicated the complexities of the issues involved, for example, "*They disturb our school going children, [but] on the other hand there are no means of transport, and the school is very far*". At the same time, people expressed that "*these animals are bringing a lot of income into this country, therefore maximum protection is needed [for] this species*" and that "*elephants and rhinos [should] be secured for the future generations*".

3.2.3. Personal experience

Willingness-to-coexist with elephants tended to be lower among younger respondents, and higher among people with primary education than those with no formal education. Those who had seen rhinos and owned livestock were more willing-to-coexist with rhinos (Fig. 3). Many respondents emphasised their limited experience with rhinos, "*I've never seen a live rhino. Only on phone pictures*", and "*I saw one 15 years ago. It was an amazing experience*". This also resulted in inconsistencies in the description of the animals, both on its appearance "*it's like [a] hippo but the difference is [that] the rhinos have the horn*", "*it's like [a] warthog*" or people referring to it as a "*brownish elephant-like monster*"; on the animal's character, descriptions varied from "*very rude*", "*very stubborn*", "*very hateful to people*", to "*very polite, it's a shy animal*" and a "*very friendly animal*".

3.3. Habitat suitability model I: species distribution model (SDM)

In the final selected model used to construct the potential elephant density map (Fig. 4b, **SI 4**), several ecological variables were significant

Table 2
Parameter estimates and the associated standard errors for the truncated negative binomial with a log link function constituting the count part of the hurdle model used to predict the potential elephant density, and the binary model with a logit link function constituting the zero part of the hurdle model used to predict the potential presence of elephants across the Maasai Mara. The *Z*-test tests if a parameter estimate is different from zero. Significant variables are highlighted in bold face font.

	Variable	Estimate	Std. error	Z-value	*P*-value
Truncated negative binomial with a log link function	**Intercept**	**2.982**	**0.148**	**20.089**	**<0.000**
	Water	0.072	0.081	0.0886	0.376
	NDVI	0.153	0.178	0.856	0.392
	Elevation	0.165	0.150	1.097	0.273
	Total number of houses	−0.087	0.197	−0.444	0.657
	Precipitation	**0.312**	**0.122**	**2.614**	**<0.001**
Binary model with a logit link function	**Intercept**	**−0.699**	**0.133**	**−5.254**	**<0.000**
	Water	−0.077	0.123	−0.600	0.550
	NDVI	**0.623**	**0.163**	**3.860**	**<0.000**
	Elevation	**−0.990**	**0.159**	**−6.218**	**<0.000**
	Total number of houses	−0.089	0.213	−0.413	0.201
	Precipitation	0.173	0.136	1.279	0.595

in predicting both the density and occurrence probability of elephants (Table 2). Precipitation (seasonality) was an important predictor of elephant absences, but not their density. NDVI and Elevation were important as predictors of elephant density but not their absence (Table 2).

3.4. *Habitat suitability model II and III: integrated nested laplace approximation (INLA)*

In the zero-inflation INLA model NDVI is positively correlated with and is the most important predictor of the potential number of elephants in the study site, based on the posterior marginal of the fixed effect parameters, calculated by smoothing the marginal distribution of the coefficients (Moraga, 2020; Table 3; **SI 4** Fig. S26). Terrain slope and the amount of water present also appear to positively influence the elephant density potentials, with very small effects of elevation and the total number of houses, and no effect of livestock biomass (Table 3; Fig. 4c). While detection probability in the n-mixture model results had a relatively strong negative correlation with potential elephant densities, the dense vegetation covariate did not have a strong influence on this. Similarly as in the other models, NDVI had a positive and elevation a negative effect on elephant density predictions.

3.5. *Sustainable coexistence potential*

The spatial distribution of sustainable coexistence potential in the Maasai Mara conservancies is the highest around Naboisho, Pardamat South and the Proposed Muntoroben Conservancy, Ol Kinyei and Olarro conservancies as both willingness-to-coexist and potential elephant densities are high in these areas (Fig. 5). These areas therefore appear to fall within the top right corner of our conceptual Fig. 1b. While parts of the proposed Muntoroben Conservancy, Ol Kinyei and Olarro cluster do appear to lie in the hatched area of Fig. 1b with its relatively high willingness-to-coexist, lack of measured habitat suitability places this location in the bottom-right corner, above the occurrence potential line of the conceptual diagram. Talek Town, an area in between these areas and the MMNR, however has low sustainable coexistence potential due to low values of both willingness-to-coexist and habitat suitability, placing it outside the dark blue area of our willingness-to-coexist diagram (Fig. 1b).

4. Discussion

We proposed and demonstrated how to integrate coexistence potential from both human (willingness-to-coexist) and wildlife (socio-ecological habitat suitability) perspectives into *sustainable coexistence potential*, by accounting for issues that have previously prevented the inclusion of willingness-to-coexist into habitat assessment models.

Results of our hierarchical attitudinal model highlight the impact of (negative) experiences with wildlife on peoples' willingness-to-coexist. Compared to elephants, willingness-to-coexist with rhinos was higher and closer to the notional attitudes towards rhinos, and varied less between –and thus depended less on- socio-demographic characteristics. As few people had experienced rhinos themselves, this highlights that willingness-to-coexist originates from people's actual lived experiences with a species. The threat to their lives people perceived from living with elephants was the main factor reducing willingness-to-coexist, which is consistent with results reported for Asian elephants (Ardiantiono et al., 2021). This suggests that perceived threats to human life (Dickman, 2010; Zimmermann et al., 2020), can potentially serve as a proxy for willingness-to-coexist in spatial planning, and that targeted conservation interventions addressing this perception of risk can enhance overall potential for sustainable coexistence. However, in other socio-ecological landscapes economic losses due to crop or livestock depredation and property damage could be more important, as except for Trans Mara, planting of crops was limited in our study site.

The results from the habitat suitability models highlight the importance of using a holistic perspective, and considering as direct proxies as possible for both the ecological and anthropogenic factors in species

Table 3
The estimated posterior mean and its standard deviation and quartiles for parameters of the fixed effects in the spatial INLA model (II) and N-mixture INLA model (III) used to predict the potential elephant density across the Maasai Mara. Please note that in model III standardization of covariates was required to achieve model convergence. Variables for which the estimated [0.025-0.975] credible intervals for the effect sizes exclude zero are highlighted in bold face font.

	Variable	Mean	s.d.	0.025 quantile	0.500 quantile	0.975 quantile
Model II	Intercept	7.038	4.688	−2.913	7.306	15.498
	Water	1.692	15.218	−28.175	1.702	31.497
	NDVI	**8.682**	**3.651**	**1.545**	**8.674**	**15.863**
	Elevation	**−0.006**	**0.002**	**−0.010**	**−0.006**	**−0.001**
	Slope	0.129	0.074	−0.017	0.129	0.275
	Total number of houses	0.013	0.006	0.000	0.013	0.024
	Biomass of livestock	0.000	0.000	0.000	0.000	0.000
Model III: density	Intercept	3.515	0.148	3.229	3.513	3.812
	Water	0.055	0.148	−0.232	0.054	0.350
	NDVI	**0.710**	**0.235**	**0.249**	**0.710**	**1.173**
	Elevation	**−0.841**	**0.235**	**−1.302**	**−0.841**	**−0.380**
	Total number of houses	−0.110	0.164	−0.427	−0.112	0.217
	Biomass of livestock	0.068	0.194	−0.311	0.067	0.450
Model III: detection probability	Intercept	−1.611	0.039	−1.688	−1.611	−1.533
	Dense vegetation	0.023	0.089	−0.154	0.024	0.195

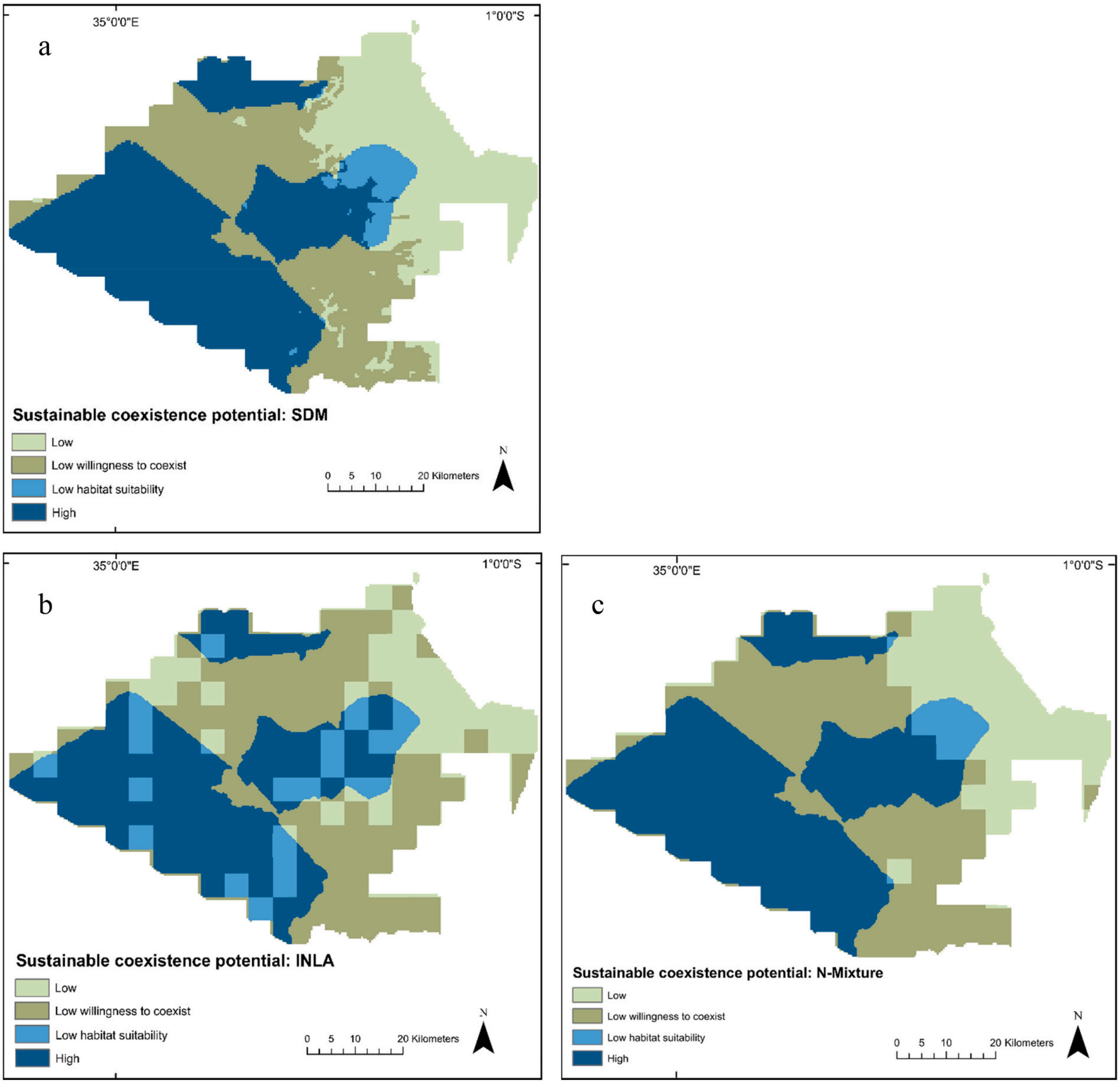

Fig. 5. Overlaid map indicating the sustainable coexistence potential of elephants and people across the Maasai Mara, based on binary suitability as predicted by the probability of a positive attitude towards living with elephants (willingness-to-coexist) as measured across the (proposed) conservancies and other regions in the Maasai Mara. The estimated potentials are based on the average willingness-to-coexist weighted by the prevalence of a combination of social demographic characteristics ($n = 556$) and a) Habitat suitability map and the predicted elephant density across the Maasai Mara based on model I: SDM; b) Habitat suitability map and the predicted elephant density across the Maasai Mara based on model II:INLA model; and c) Habitat suitability map and the predicted elephant density across the Maasai Mara based on model III:N-mixture INLA model.

distribution models (Vogel et al., 2021). It also highlights the complexity and spatial variability inherent in the factors driving both elephant presence and density. While the absence and density of elephants was mainly determined by ecological variables, models performed better if anthropogenic variables were included, in particular the number of houses. The presence and density of human settlements has been previously demonstrated to have a strong negative influence on elephant space use and movement in Asia (Goswami et al., 2014, 2021). The importance of precipitation, and the NDVI, a measure of vegetation greenness, in driving elephant density predictions, suggest that wildlife in this socio-ecological system is strongly depended on rainfall, similar to people and their livestock (Miller et al., 2014). This also highlights the danger of climate change, and in particular droughts, to further reduce human–wildlife coexistence potential and increase the risks of land use change and physical conflicts between people and wildlife. Formal direct comparison of the habitat suitability models fitted within the frequentist two-part zero-inflated SDM framework, with either the models fitted within the Bayesian INLA zero-inflated spatial, or the n-mixture framework is not straightforward. Nevertheless, we demonstrate our theoretical framework by integrating the proposed willingness-to-coexist concept with all the three habitat suitability modelling approaches, to illustrate its flexibility and robustness to influences of potential biases in animal counts. The multiple modelling approaches are not only complementary but also serve to illustrate that the integration of willingness-to-coexist with habitat suitability assessments to identify sustainable coexistence potential is largely insensitive to the choice of method for handling excess zeros in count data.

The distribution of sustainable coexistence potential for elephants and people across the Maasai Mara suggests that sustainable coexistence is contingent upon increasing habitat suitability for wildlife (Ogutu et al., 2019) without (further) stigmatizing the pastoralist community and with incorporating their experiences and willingness to share space and resources with wildlife (Cavanagh et al., 2020; Weldemichel, 2020; Weldemichel et al., 2019). We identified areas that had low habitat suitability for elephants during the dry season, but high willingness-to-coexist, highlighting an underutilized potential of such areas for promoting wildlife-human co-existence. On the other hand, we also found socio-ecologically suitable areas, but where people showed low willingness-to-coexist with elephants. This demonstrates opportunity for increasing sustainable coexistence potential by targeted conservation action in areas covering a significant proportion of our landscape. Exact interventions to invest in could differ between regions and periods, yet factors influencing willingness-to-coexist can inform us about these. Our case-study highlights the need to reduce concerns about human safety, for example through investments in safety strategies and training.

5. Conclusion

We believe there is an urgent need to move beyond habitat suitability assessments for species based on their socio-ecological requirements alone, and embrace the concept of sustainable coexistence potential. For such an endeavour, we argue and demonstrate that it is necessary to include spatially explicit willingness-to-coexist proxies and equally integrate a wildlife perspective and human perspective. If local attitude towards wildlife and willingness-to-coexist cannot be quantified, perceived wildlife-induced threat reported by people could potentially serve as a valuable indicator of willingness-to-coexist.

When we asked respondents what they considered necessary to achieving sustainable coexistence, they repeatedly mentioned compensation, benefits and protection for both wildlife and people, as "*authorities concerned should also feel the loss I get*", "*the solution is for [the] government to share the benefit with local people and employment to local people [is] required so the benefits can be seen by locals*" and "*there should be adequate protection for both people and wildlife*". This latter point was also mentioned in concerns about the prioritisation of those organisations advocating on behalf of wildlife in the areas, a suggestion was made to be "*treating people as more important than elephants to reduce conflict*".

The areas we highlight that are low in sustainable coexistence potential because people are not willing-to-coexist with elephants, suggest that if conservationists address reasons underlying the lack of willingness-to-coexist, persistence of wildlife species such as elephants could be better achieved. Only then can sustainable coexistence be realized. At the same time, strategic land use planning, taking into consideration those areas with high willingness-to-coexist but low habitat suitability, could increase the currently underused coexistence potential of these areas. Where feasible and realistic, this may necessitate active restoration of wildlife habitat in areas that are currently less suitable for them.

Finally, the looming threat posed by climatic change to humans, vegetation and wildlife (Bedelian and Ogutu, 2017; Hunninck et al., 2020), increases the urgency and importance of quantifying potentials of sustainable human-wildlife co-existence in ecosystems such as the Mara. Incorporating livelihood vulnerability and changes to habitat suitability linked to climatic and demographic changes is therefore an important next step in advancing our ability to reliably assess sustainable coexistence potential.

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Declaration of competing interest

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Data availability

The data that has been used is confidential due to the sensitivity of the data, however could potentially be made available upon request. SI contains detailed information on model construction.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.109935.

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