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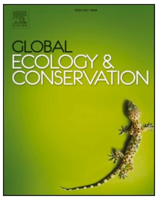

Nationwide abundance and distribution of African forest elephants across Gabon using non-invasive SNP genotyping

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ABSTRACT

Robust monitoring programs are essential for understanding changes in wildlife population dynamics and distribution over time, especially for species of conservation concern. In this study, we applied a rapid non-invasive sampling approach to the Critically Endangered African forest elephant (*Loxodonta cyclotis*), at nationwide scale in its principal remaining population strongholds in Gabon. We used a species-specific customized genetic panel and spatial capture-recapture (SCR) approach, which gave a snapshot of current abundance and density distribution of forest elephants across the country. We estimated mean forest elephant density at 0.38 (95% Confidence Interval 0.24–0.52) per km^2 from 18 surveyed sites. We confirm that Gabon is the main forest elephant stronghold, both in terms of estimated population size: 95,110 (95% CI 58,872–131,349) and spatial distribution (250,782 km^2). Predicted elephant densities were highest in relatively flat areas with a high proportion of suitable habitat not in proximity to the national border. Protected areas and human pressure were not strong predictors of elephant densities in this study. Our nationwide systematic survey of forest elephants of Gabon serves as a proof-of-concept of application of noninvasive genetic sampling for rigorous population monitoring at large spatial scales. To our knowledge, it is the first nationwide DNA-based assessment of a free-ranging large mammal in Africa. Our findings offer a useful national baseline and status update for forest elephants in Gabon. It will inform adaptive management and stewardship of elephants and forests in the most important national forest elephant stronghold in Africa.

1. Introduction

African savanna elephants (*Loxodonta africana*) and forest elephants (*Loxodonta cyclotis*) are listed as Endangered and Critically Endangered, respectively, by the International Union for Nature Conservation (Gobush et al., 2021a, 2021b). Across the African continent, elephant populations have been declining – principally due to poaching to support the international illegal ivory trade

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(Schlossberg et al., 2020; Wittemyer et al., 2014). African elephants are also declining due to habitat loss and fragmentation, and due to the associated increasing human-elephant conflict as agriculture encroaches on their range (IUCN Human Elephant Conflict Group, 2020). However, there remain some areas where there is both high quality habitat and stable elephant populations, above all in Gabon and in the northern Republic of Congo for forest elephants, and in northern Botswana, northern Tanzania and northern Kenya for savanna elephants (Chase et al., 2016; Morrison et al., 2018; Thouless et al., 2016). Gabon is the last stronghold offering a large quasi-continuous habitat to forest elephants ($>$ 250,000 km^2; de Flamingh et al., 2015). Safeguarding this key elephant stronghold is of critical importance to ensure that ecological functions and processes, and ecosystem benefits remain intact (Berzaghi et al., 2019, 2018; Campos-Arceiz and Blake, 2011; Doughty et al., 2016). Evaluating the effectiveness of management necessitates monitoring the elephant populations in these strongholds. This study therefore focuses on estimating the density and distribution of forest elephants across Gabon.

Gabon's forest and forest-savanna mosaic elephant habitats cover more than 200,000 km^2 (Thouless et al., 2016; Verhegghen et al., 2012). Elephant surveys within Gabon since 2004 have covered just under a quarter of the nation's elephant habitat, but since 2011 (the last ten years) only 14% of habitat was surveyed. Although these surveys were reasonably standardized (Blake, 2005), methods have been confined to dung counts. These were either distance sampling along line transects to obtain estimates of dung density, converted to elephant density using dung deposition and decay rates that are not always applicable to the site or season, or using reconnaissance (recce) survey methods, which give only an encounter rate of dung, with no indication of dung or animal density. Compared to the eastern and southern African elephant range states, where aerial surveys are generally used to directly estimate elephant population numbers (Thouless et al., 2016), Gabon's elephant estimates have thus been less robust. Although published over a decade ago in the 2008 IUCN Red List assessment, Gabon was one of two countries omitted from the species' population reduction analysis, because past national figures were deemed underestimates (Blanc et al., 2007). The latest status report by the IUCN African Elephant Specialist Group (Thouless et al., 2016) considers about 90% of data available to inform a Gabonese elephant abundance estimate of low reliability because they fall into one of three categories: outdated estimates (classified as over ten years old); where dung decay studies were not site and time-specific; or not based on systematic survey data (i.e. modeled extrapolations). That report provided an estimate of 7058 (95% Confidence Interval 4755–9361) forest elephants, plus an additional 59,057–67,094 forest elephants where the estimates fell into one of the three categories outlined above. Prior to 2005, a national estimate of just under 62,000 elephants in Gabon had been published, based on nationwide, stratified distance sampling along line transects, carried out in the mid-1980 s (Barnes et al., 1995). Using the same dataset, and using a model based on the distances from roads, which was known to be correlated with elephant density, a similar estimate of 55,000 animals was published (Michelmore et al., 1994). Others had earlier also produced estimates within Barnes et al., 1995's reported confidence interval of about 41,600–82,000 elephants (Burrill and Douglas-Hamilton, 1987; Douglas-Hamilton and Burrill, 1991; Martin, 1986).

In 2002, Gabon established 13 national parks covering 11% of the country (approximately 30,000 km^2; Government of Gabon, 2002). Additional areas are under consideration for increasing the protected area coverage of Gabon to 30% by 2030 (L. White 2020, pers. comm.). Monitoring these parks individually began in earnest in 2002 using standardized methods. An assessment of forest elephants across their central African range inferred a 62% population decline in less than a decade (Maisels et al., 2013), corresponding to a taxon-wide steep population decline of around 9% annually. This was seemingly reflected, for example, in the dramatic poaching losses reported in the former Gabonese stronghold in the northeast of the country (ANPN et al., 2013; Poulsen et al., 2017). Nearly two decades since the creation of Gabon's national parks network, a status update of Gabon's forest elephants was sorely needed to help inform management actions and drive additional conservation investment in this country. Recent developments in field techniques, and in both laboratory and data analysis methods now greatly facilitate a synchronized, nationwide approach, as opposed to the site-based estimates that preceded them.

Robust monitoring programs are essential for understanding changes in wildlife population dynamics and distribution over time. Reliable monitoring is central to an adaptive management approach for implementing government agency mandates related to endangered species protection, sustainable habitat use, and pertinent law enforcement (Lindenmayer and Likens, 2009). While monitoring elusive and cryptic forest wildlife is known to be challenging, methods, such as spatial capture-recapture (SCR) modeling, using non-invasive sampling techniques, are increasingly applied to provide estimates of density and abundance plus insights related to distribution, sex ratio, and movement (DeAngelis and Yurek, 2017; Strindberg and O'Brien, 2012). The performance and feasibility of this method for monitoring forest elephants in Gabon has recently been established through a number of studies within a range of forest habitats across the country (Brand et al., 2020; Head et al., 2013; Laguardia et al., 2021). Based on optimized non-invasive molecular sampling and laboratory protocols (Bourgeois et al., 2019), a novel single nucleotide polymorphism (SNP) panel for genetic individual identification (Bourgeois et al., 2018) and a multi-method comparison repeated at three large sites, Laguardia et al. (2021) demonstrated that applying a DNA-based SCR approach to monitor Gabon's forest elephants has several advantages over other methods. These include the ability to sidestep the difficulties and costs associated with quantifying dung decay and defecation rates in conventional dung-density line transect methods (Hedges, 2012; Hedges et al., 2012; Strindberg, 2012). The three-site study suggested that DNA-based SCR could be used at the national scale, with possible refinements to improve sample size and reliability of genetic individual identification.

In this paper, we apply a non-invasive sampling approach using a species-specific customized genetic panel and SCR methods to provide (i) design-based estimates of forest elephant density and abundance for Gabon, and (ii) a model-based nationwide predicted density surface using the drivers of forest elephant distribution identified in previous studies. Our study serves as a proof of concept of application of these methods for rigorous population monitoring of this species at large spatial scales. It also provides a current snapshot of the abundance and density distribution of forest elephant in Gabon. Before this study, wildlife survey work in Gabon (2004–2015) had covered about 62,000 km^2, of which about 46% was protected areas and almost all the rest was logging concessions.

However, a systematic, representative survey design aimed at covering the whole country as a single unit had never been done. Indeed, national, wall-to-wall systematic wildlife surveys using any method are rare in forested Africa: only Equatorial Guinea has been so covered within Central Africa (Murai et al., 2013), and farther afield in West Africa, Sierra Leone (Brncic et al., 2015).

2. Materials and methods

2.1. Study area and site selection

We conducted our study in Gabon in Central Africa, which is part of the extensive Guineo-Congolian Forested region (White, 1983) and is estimated to cover about a third of the African forest elephant's current range (Maisels et al., 2013; Thouless et al., 2016). The country straddles the equator, with the Gulf of Guinea to the west, Equatorial Guinea and Cameroon to the north, and the Republic of Congo to the east. Forest elephant habitat throughout the country is varied and includes the beaches and coastal forests of the Atlantic coast, interior old growth humid forests, papyrus-dominated areas and swamp forests along the main rivers, extensive forest-savanna mosaic patches, and supports a high diversity of mammals (i.e., 80 species excluding micro-mammals; Vande weghe, 2007). The climate is a transitional equatorial type with a dry season from June/July to early September. National mean annual rainfall for 2018–2020 was 1823 mm and mean annual temperature was 25.7 °C during our study. Elevation of survey sites ranged from sea-level to 850 m.

To ensure that the sampling design was representative of elephant density across Gabon and captured the variation in the predicted drivers of elephant density, a systematic sampling design with a random start was used (Fig. 1). It was based on a hexagonal grid across the entire area of Gabon, consisting of 168 potential survey sites, each ~2000 km^2 in area (partial hexagons along the borders or coast were smaller). Each hexagon corresponded to a potential survey site with the general exception of those that fell in areas included in a related pilot study completed just prior to this one (Laguardia et al., 2021). In the pilot study, which used the same methods as the current study, we sampled three protected areas known to hold large forest elephant populations (two National Parks: Loango and Ivindo, and the Wonga Wongué Presidential Reserve). We sampled hexagons systematically spaced 144 km apart across Gabon with a

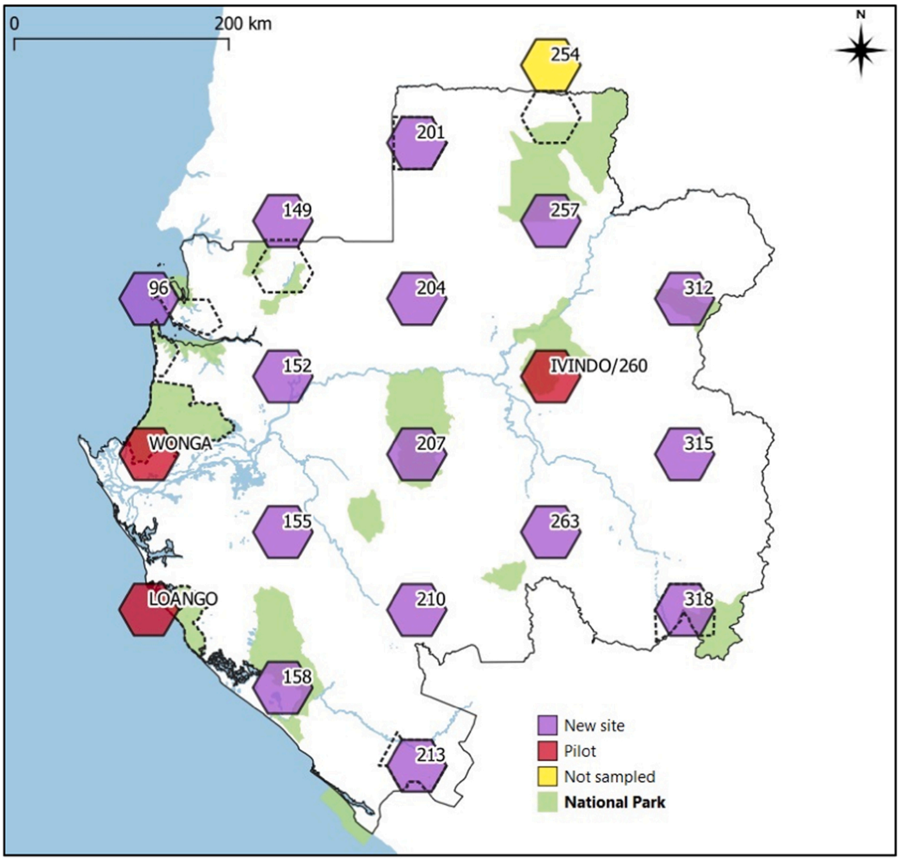

Fig. 1. Nineteen sites (2000 km^2 each) in Gabon included in analyses of African forest elephant density and abundance; 15 sites ("New site") were sampled between August 2019 and Match 2020, 1 site ("Not sampled") was planned but not sampled due to security concerns and 3 sites ("Pilot") were sampled as a part of a related pilot study in 2018 and 2019. Relocations and exceptions to the sampling design (dotted lines) are detailed in Annex 1.

random start point, which combined with the three areas of the pilot study gave a total sample size of 18 sites. Security concerns during project execution meant that we could not sample one of the sites (Fig. 1 and Annex 1 for detailed description and exceptions). Our sampling design provided spatial representation of approximately 336,000 km^2 across the categories or range of values of known drivers of forest elephant density distribution: protection status, human pressure, distance from the national borders of Cameroon and the Republic of Congo, slope, and habitat type.

2.2. Sample collection and laboratory analyses

The DNA-based SCR approach used an unstructured non-invasive sampling design at the site level and individual identification via genotyping with a species-specific SNP (single nucleotide polymorphism) panel. Our first aim was to collect a target number of elephant fecal samples as rapidly as possible throughout each site, in order to meet the population closure assumptions of SCR (Dupont et al., 2019; Royle et al., 2013). We timed our surveys to avoid seasons when local concentrations and/or long-distance movements of forest elephants were likely and a population closure assumption potentially violated. For planning purposes and to assure consistent effort across sites, we set a collection target of ~210 samples and 420 km across 21 field days per site (Table 2). This was based on our previous experience of an encounter rate of 0.5 dung samples per km and walking 10 km per day with two teams of four field staff.

Initial genotyping to determine individual identity was performed with a panel of 15 SNPs using Kompetitive Allele-Specific PCR (KASP, LGC Genomics) assays and sex was determined by amplifying small fragments of the orthologous sexual chromosome zinc finger protein genes ZFX/ZFY (Bourgeois et al., 2021, 2018; Laguardia et al., 2021). In order to guard against the possible presence of false identifications caused by allelic dropout, we applied a number of quality filtering steps and a targeted multi-tube approach in order to correct potential allelic dropout in the dataset (Fig. 2). First, elephant fecal DNA samples were screened before genotyping using an elephant-specific quantitative PCR targeting a short nuclear DNA fragment (~100 bp). After the first genotyping run, we calculated the allelic error rate for each group of samples with 0 to more than 10 missing loci. This error rate was estimated through the repetition of three samples from the previous plate in each 48- or 96-wells plate. Based on this assessment, we replicated all samples with a risk of allelic error rate $>$ 0.031% (i.e., between two to five missing loci after the first run, Fig. S1) once, to ensure that the final allelic error rate was reduced below this threshold of one allelic dropout per sample before applying the targeted multi-tube approach. In addition, we discarded all samples with $>$ 30% missing data ($>$ 5 missing loci) because these samples were more prone to genotyping errors. We checked that missingness per locus was $<$ 30% at all loci, in order to ensure that there was no bias introduced in our reduced dataset. All missing loci were also rerun once. We obtained the consensus genotypes between replicates and discarded all loci with less than two reliable genotypes for samples with two to five missing loci after the first run. Then, we retained all consensus genotypes with zero or one missing locus. Using the targeted multi-tube approach defined above, we identified all pairs of consensus genotypes with one or two locus difference and reran the homozygotes to confirm or correct the genotype. Finally, all genotypes matching at all loci, or all but 1 missing locus per sample, were considered as belonging to the same individual.

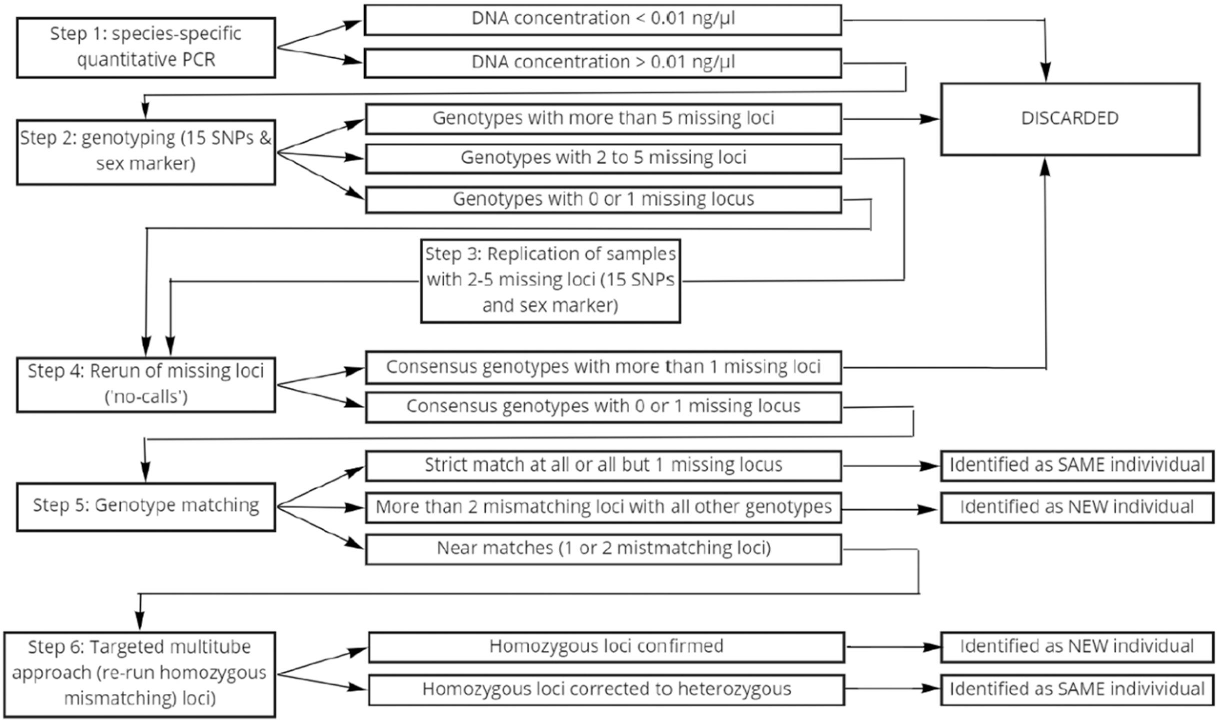

Fig. 2. Diagram describing the DNA analysis workflow in the laboratory.

2.3. Density estimation per site

To estimate forest elephant density at each site, we fit a set of up to seven full likelihood-based models (Table 1) using the *secr* library version 4.3.3 (Efford et al., 2009) in the R programming environment (R Development Core Team, 2020, R version 4.0.3) as described in Laguardia et al. (2021) with the following improvements. We implemented a sampling grid cell size of 250 m x 250 m instead of 1 km x 1 km. This was to balance the need to avoid possible autocorrelation issues while maximizing sample size and number of recaptures. We included effort per grid cell measured in meters (Efford, 2019) and removed from analysis grid cells with $<$10 m effort to reduce the effect of potentially influential observations. We note that Laguardia et al. (2021) used the natural logarithm of effort, which makes the detectability parameters difficult to interpret. We fit full likelihood models with a "group" argument based on the sex covariate, since our DNA-based approach ensured that nearly all fecal samples could be assigned to a sex category, in order to derive sex-specific estimates of density, D, detectability, g_0, and spatial scale of detectability, σ, which is related to movement. Accordingly, we omitted any samples for which we were unable to determine genotypic sex in these analyses ($n = 7$).

The models detailed in Table 1 were run for each site data permitting. For sites with several candidate models the AIC weighted model averaged parameter estimates for Density (D), detectability (g0), and spatial scale (σ) were obtained to reduce model selection bias and provide more robust estimates (Burnham and Anderson, 2002). To avoid overfitting or spurious results for sites with data sparsity, the permitted complexity of the models fit to the data from each site was dictated by the value of the recapture index (total number of detections divided by number of unique individuals that ranged in value from 1 to 1.61 for our sites; Table 2). The recapture index range of 1–1.65 was divided into six equal intervals with each interval assigned a level of model complexity. For instance, the most complex model with six parameters was used only for sites with a recapture index between 1.52 and 1.65, five parameters with 1.39–1.51, four parameters with 1.26–1.39, and three parameters with 1.13–1.26. For a recapture index below 1.13 the value of g_0 was fixed to the average value from the models using 3 or more parameters. Finally, for data deficient sites with less than 3 recaptures, we calculated a density by rescaling the density of site 152 with a high recapture index (1.59) using relative encounter rates (number of samples per km walked).

2.4. Nationwide density estimation and model-based distribution

We derived the nationwide estimate of forest elephant density by computing the mean of all the site-specific density estimates. The sampled area within the sites ranged from 44 km^2 to 325 km^2 (as estimated using the integrated approach in secr; Table S2) and an unweighted mean of densities was taken to avoid ad hoc decisions regarding potential weighting factors. We note that these estimates of sampled area may differ, and be possibly lower, than those derived using the buffer-based approach (Royle et al., 2013). The variance around these estimates were derived using the variance-decomposition approach of Link and Nichols (1994), and eliminating the covariance terms in their formula. In addition, since each site occupied a non-negligible proportion of the landscape ($\sim$1/125 of elephant habitat in Gabon), and we had 18 such sites (excluding unsampled site 254), we utilized the sampling without replacement formula to compute the standard error of the sample mean. Accordingly, the estimate of forest elephant abundance was computed by appropriately scaling the mean density and its associated coefficient of variation across the total estimated elephant range within Gabon (Sutherland and Royle, 2016).

Generalized Linear Models (GLMs; Venables and Ripley, 2002) were fit to the SCR density estimates for the sampled sites to quantify known or suspected drivers of elephant density and distribution across Gabon (Blake et al., 2007; Maisels et al., 2013). Independent explanatory variables included the amount of elephant habitat (HABITAT), the Human Pressure Index (PRESSURE), the distance to the Cameroonian or Congolese border (BORDER), slope (SLOPE), and degree of protection (PROTECTION). The source of these variables, their hypothesized relationship to elephant density distribution, and the process for extracting and standardizing them are described in the supplementary materials (Annex 2 and Table S1). The complete data set used in the model-based analysis is described and shown in Table S2. Elephant density was predicted at a 1 km^2 resolution across Gabon using the same explanatory variables (see Annex 2 for a detailed description).

Due to suspected over-dispersion in the data, a negative binomial distribution with a log link was used in fitting the GLMs, whilst permitting the estimation of a scale parameter (theta). The original density estimates were multiplied by a thousand and rounded to a whole number in order to obtain a count response variable with the natural logarithm of the associated area included as an offset term

Table 1
Model set considered during spatial capture-recapture analyses for 18 sites. Density (D), detectability (g_0), and spatial scale (σ) are either modeled as constant (.) or grouped by sex (g). In cases of data sparsity detectability (g_0) was fixed (fix) at the average estimated value for detectability obtained from the sites without data sparsity.

Model	Number of Parameters	Density (D)	Detectability (g_0)	Spatial scale (σ)	Description
$D(.)\ g_0(_{fix})\ \sigma(.)$	2	*Constant*	*Fixed*	*Constant*	D and σ constant, g_0 fixed
$D(.)\ g_0(.)\ \sigma(.)$	3	*Constant*	*Constant*	*Constant*	All parameters constant
$D(.)\ g_0(g)\ \sigma(.)$	4	*Constant*	*Sex*	*Constant*	D and σ constant, g_0 grouped by sex
$D(.)\ g_0(.)\ \sigma(g)$	4	*Constant*	*Constant*	*Sex*	D and g_0 constant, σ grouped by sex
$D(.)\ g_0(g)\ \sigma(g)$	5	*Constant*	*Sex*	*Sex*	D constant, g_0 and σ grouped by sex
$D(g)\ g_0(g)\ \sigma(.)$	5	*Sex*	*Sex*	*Constant*	σ constant, D and g_0 grouped by sex
$D(g)\ g_0(.)\ \sigma(g)$	5	*Sex*	*Constant*	*Sex*	g_0 constant, D and σ grouped by sex
$D(g)\ g_0(g)\ \sigma(g)$	6	*Sex*	*Sex*	*Sex*	All grouped by sex

Table 2
Gabon survey results and SCR density estimates with associated percent coefficient of variation (%CV) for each survey site. Shown is the distance walked (Effort) and time spent (Sampling) collecting the data, the total DNA samples obtained together with the number of samples that were successfully genotyped and the number of unique individuals identified, as well as the observed female to male sex ratio and the aggregate of all the unique detections within each 250 m by 250 m grid cell comprising the sampling grid used in the SCR analysis along with the recapture index obtained by dividing the number of detections by the unique individuals.

Site	Effort (km)	Sampling (days)	DNA samples	Genotyped	Individuals	Observed sex ratio	Detections	Recapture index	Density	%CV
LOANGO	509	58	394	309	270	3.03	295	1.09	0.637	7.79
IVINDO&260	1568	104	887	442	364	2.09	402	1.10	0.199	9.8
WONGA	1012	17	653	472	337	2.44	402	1.19	0.927	13.14
96	375	32	162	132	71	1.15	109	1.54	0.347	25.4
149	354	32	61	21	18	0.80	19	1.06	0.131	21.19
152	303	26	107	66	34	1.43	52	1.53	0.269	21.19
155	391	36	230	162	117	2.08	146	1.25	0.228	19.29
158	484	39	212	121	84	2.11	113	1.35	0.387	11.45
201	329	28	0	0	0	/	0	0	0	0
204	340	30	389	180	132	2.56	160	1.21	1.257	22.62
207	309	35	113	49	36	1.00	42	1.17	0.184	48.87
210	308	28	7	4	4	0.00	4	1.00	0.017	21.19
213	273	35	117	51	32	1.00	40	1.25	0.577	43.26
254	Not sampled due to security concerns									
257	479	38	171	46	41	5.83	42	1.02	0.272	21.19
263	202	18	80	36	27	1.89	29	1.07	0.302	21.19
312	333	35	200	103	83	2.46	87	1.05	0.124	13.51
315	395	36	16	0	0	/	0	0.00	0.031	21.19
318	320	34	259	176	107	0.84	138	1.29	0.936	17.31

in each model. Thus, elephant density was in effect being modelled. A total of 32 models each with an intercept and offset term were fit to all possible combinations of the five explanatory variables (HABITAT, PRESSURE, BORDER, SLOPE, PROTECTION) and ranked by AIC weight (Burnham and Anderson, 2002). Model averaging by AIC weight across this model set was used to predict forest elephant density across Gabon to account for model selection uncertainty and avoid undue influence from overparamaterized models given the small number of sampling sites. The models were fit in R x64 4.05 (R Development Core Team, 2020) using the *MASS* package (Venables and Ripley, 2013). The *car* package (Fox and Weisberg, 2019) was used in variable standardization and the *vif* function was used to investigate the degree of multicollinearity in the variables. The *MuMIn* package (Barton, 2020) was used to generate the 32 models in the model set and to conduct model averaging.

3. Results

3.1. Data collection

Fecal DNA sampling covered 6548 grid cells (1 km^2 each) totaling 8285 km walked (average 460 km per site and 12 km/day/team). All 15 hexagons were sampled between August 2019 and March 2020. The three pilot sites had been sampled in 2018 (Loango and Ivindo) and 2019 (Wonga Wongué; Laguardia et al., 2021). We collected a total of 4058 dung samples (average 214 dung samples per site) with an encounter rate of 0.5 dung piles per km (minimum of 0 to maximum of 1.1), over a combined 713 sampling days in the field (Table 2 for site specific data). After discarding low quality samples (1108 inadequate DNA quantity, 405 with more than 30% missing data, and 175 consensus genotypes with $>$ 1 missing loci), we generated 2370 consensus genotypes. Furthermore, using our $>$ 30% rejection rule, no locus was deleted from our panel. Before applying corrections, the mean allelic error rate for all sites combined was 2.7% (based on 10,546 replicated alleles). After initial PCR, 19.4% of the data was considered missing (no-calls) and re-run once. In addition, 1055 genotypes (35.8%) with 2–5 missing loci were replicated once at all loci. Homozygous genotypes from near-matching pairs of samples (3.9%) were also re-run once to confirm or correct their scores according to our targeted multi-tubes approach (8.4% corrected as heterozygous). The probability of identity ranged from 4.3×10^{-7} to 1.2×1^{-6} for unrelated individuals and from 4.8×10^{-4} to 8.2×10^{-4} for siblings across the sites.

We identified 1757 unique individuals with 1175 females, 575 males and 7 not assigned. We could formally estimate sex ratios in only 3 sites. These were: 0.42:1 (site 96), 0.98:1 (site 152) and 0.99:1 (site 318) females to males. Observed sex ratios were on average 1.7:1 females to males, with a maximum skewedness of 5.83:1 (site 257 in Fig. 1). Inferences from the observed sex ratios are not necessarily unbiased, since they do not result from modelled sex differences in parameters, and can be affected by uneven detectability (e.g., more female dung sampled because elephants in groups are easier to track).

3.2. Site densities and national estimate

After collapsing data for binary proximity detectors, we retained a total of 2080 captures; recapture rates were on average 17.3% and recapture index 1.1. Two sites (96 and 152) had recapture indices above 1.52 allowing the use of all SCR models, including the most complex model with 6 parameters, two sites (158 and 318) used models with up to 4 parameters, five sites (Wonga Wongué, 155, 204, 207, 213) used up to 3, and three sites (Loango, Ivindo, 312) had a fixed g_0. Number of recaptures were too low (< 3) for 5 sites (149, 210, 257, 263 and 315). Only one site (201) had zero samples collected, with no elephant signs of any age (e.g., dung, tracks, paths etc.) recorded, even with considerable sampling effort (329 km and 28 days).

We estimated an average density of 0.38 (95% CI 0.24–0.52) forest elephants per km^2 for the 18 sites. Densities ranged from a minimum of zero to an estimated maximum of 1.26 (site 201 and site 204, respectively) forest elephants per km^2 (Table 2). Average g_0 was 0.0002 and average sigma was 1305 m. Density estimates for the three pilot sites differ to our previously reported estimates (1.59, 0.49 and 0.80 for Loango, Ivindo and Wonga Wongué, respectively, Laguardia et al., 2021), but remain within or close to the confidence interval for two of the sites. However, for Loango the previous density estimate was more than double, due to changes in the methodology described above and correction of false identifications of individuals in the previous dataset.

The area of elephant distribution was represented by the country's extent, excluding habitat unsuitable for elephants (i.e., water, agricultural land, buildings, roads, and the Bateke savanna north of the Lewou River), covering a total of 250,782 km^2. Nationwide forest elephant estimates therefore equate to 95,110 (95% CI 58,872–131,349, %CV 19.44) forest elephants.

3.3. Drivers of elephant distribution

Model-averaged predicted elephant density across Gabon is shown in Fig. 3, and the density predicted at each of the survey sites is

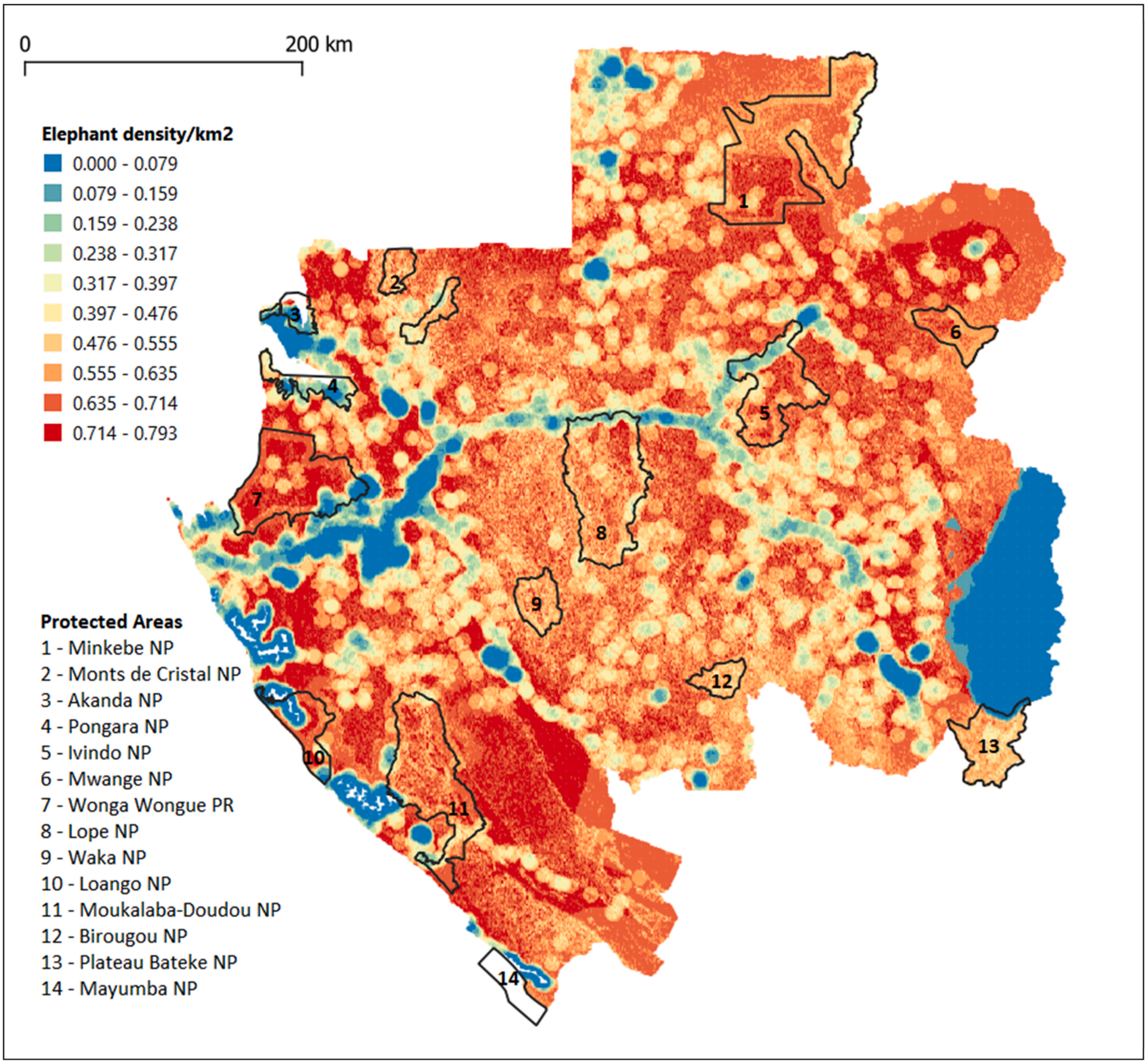

Fig. 3. Model-averaged predicted elephant density (elephants/km^2) across Gabon.

included in Table S2 with the full model set detailed in Table S4. Across the 32 models, the model-averaged coefficient values were 0.60 (HABITAT), 0.10 (BORDER), −0.05 (SLOPE), −0.01 (PRESSURE), and −0.02 (PROTECTION). With each of the explanatory variables included in half of the entire set of models, the importance of each of the variables based on the sum of model weights over all models including that variable was highest for HABITAT (0.55) followed by similar weight for PROTECTION (0.21), SLOPE (0.20), BORDER (0.20), and PRESSURE (0.18). There was no indication of severe multicolinearity for the explanatory variables used in the model set (for example, the generalized variance-inflation factor values for the general model were 2.95 (PRESSURE), 2.60 (HABITAT), 1.96 (PROTECTION), 1.63 (BORDER), and 1.35 (SLOPE). Average theta, the over-dispersion parameter, was low (0.642) (Table S2). Visual inspection of these relationships appear to suggest strongly that it is over-dispersion, which may be the larger reason as to why the null model is gaining a disproportionate amount of support.

The lowest elephant densities were located in areas with low proportions of suitable habitat (e.g. along roads, in proximity to major cities, in water bodies and across the Bateke savanna). Highest predicted densities were in areas with suitable habitat exclusively, low human pressure with absence of slope, such as the northeast, and the Gamba complex (including Loango NP) in the southwest. Protected areas and human pressure did not predict either lower or higher elephant densities in our study.

4. Discussion

4.1. Forest elephant density and abundance in Gabon

To our knowledge, our nationwide systematic survey of forest elephants of Gabon is the first national DNA-based assessment of a free-ranging large mammal in Africa (excluding instances of species reintroduction to a former range state). Our survey cannot directly be compared to previous work in the country (Barnes et al., 1995; Maisels et al., 2013; Thouless et al., 2016), because of the difference in survey methods and uncertainties regarding auxiliary parameters used in dung-based line transect distance sampling surveys, acknowledged by the authors themselves in their manuscripts (and more recently in Meier et al., 2021). With due caution, we note that the upper bounds of the most recent IUCN African Elephant Status Report (Thouless et al., 2016) values yields a maximum combined abundance of 76,455 forest elephants across the reported 213,373 km^2 of habitat and a rough nationwide density of 0.36 individuals/km^2. Thus, our study suggests that the mean density of forest elephants in Gabon is just above the maximum value derived from the most recent available national estimate (Thouless et al., 2016) (bearing in mind that the latter is the sum of twenty separate site-level surveys carried out over a period of 13 years, and not a snapshot in time, plus an area that was not surveyed, but within which a model prediction was made). Our estimate falls between the upper confidence intervals of 82,012 and 97,417 elephants, reported in the other two national estimates (Barnes et al., 1995; Maisels et al., 2013). We suspect our overall elephant population estimate to be larger than previous mean estimates for two principal reasons. Overestimating decay rate of a proxy for animal density (such as animal dung or ape nests) will underestimate animal density (Bessone et al., 2021). The estimated mean of 52,000 elephants for Gabon (Maisels et al., 2013) used dung counts, and a mean regionwide dung decay rate of 81.8 days, roughly double that of rates directly estimated within Gabon in 2018 (Laguardia et al., 2021): if a decay rate of, say, 41 days had been used in 2013, the Gabon elephant population would have been estimated at 103,000 animals. Of much less significance, but still of note, our survey area includes areas previously considered unsuitable (e.g. the south western savannas) and did not a priori exclude buffered areas around cities and roads. The snapshot of forest elephant density distribution and abundance we report is good news for the species in Gabon, though it does not discount significant local declines between 2004 and 2014 reported for Minkebe National Park (NP) on the north-east border (Fig. 3). These declines were due to heavy poaching that is consistent with a female skewed sex ratio found in our study in that area.

This is the first study to document sex ratios in forest elephants across Gabon. At birth, the forest elephant sex ratio is 1:1 (Turkalo et al., 2018). This can remain roughly stable in the absence of poaching (Turkalo et al., 2013) but can also change rapidly - in the well-studied Dzanga population, females outnumbered males 3:1 after just 15 years of increasing poaching pressure (Turkalo et al., 2013). Ivory poachers typically first target adult male forest elephants (as elsewhere), due to males' high ivory volume (Turkalo et al., 2018). However, sex ratios could only be formally estimated for sites where results from the most complex models were available (3 out of 18 sites). Approaches using likelihoods based on abundance (e.g. oSCR/Bayesian types), rather than density, could be more successful for this purpose along with survey protocols to ensure larger recapture indices.

Gabon constitutes the principal remaining stronghold of a species that once numbered in the millions (Milner-Gulland and Beddington, 1993). Gabon's forest elephants were, in 2013, estimated to constitute 52% of the central African population (Maisels et al., 2013) and the results from this study are likely to increase that proportion further. Securing this stronghold is vitally important to the species' future. Given the slow rate of forest elephant reproduction and recruitment (Turkalo et al., 2018) species recovery in more depleted areas will be slow.

4.2. Drivers of forest elephant density and distribution in Gabon

We note that high overdispersion in the covariate-density relationships justified our use of negative binomial GLMs and we recognize the relatively low strength in inference whilst assessing drivers of forest elephant density. Yet, the dominant positive effect of habitat in driving forest elephant density was expected and confirmed in this study, with higher elephant densities found where more suitable habitat is available. Previous studies have highlighted the tendency of elephants to avoid mountainous terrain (Wall et al., 2006); they have smaller range sizes where the land is steep (Wall et al., 2021). We also saw that elephant density is lower on the steep slopes of the Monts de Cristal-Monts du Chaillu mountains that run from the northwest to the southwest across the country. Other important covariates, such as the presence of protected areas, did not show a strong signal. This may be due to the fact that there remain large extents of Gabon's forests, both inside and outside of protected areas, with low human pressure and suitable elephant habitat. This includes around 140,000 km^2 (nearly two thirds of the country's forested extent) within logging concessions. Our findings do not judge the efficacy of protected areas, or of FSC-certified logging concessions in Gabon – this was not the intention of the study. However, our findings do highlight that elephants occur at high density both inside and outside protected areas. To protect elephants nationwide requires holistic conservation management strategies across a range of land-use types. Human pressure also did not produce the expected (inverse) relationship with elephant density. Although this index seemed to accurately represent human population and accessibility, minimum values in Gabon were rather high (all lay between 0 and 0.3, where zero represents the highest human pressure and 1 the lowest). Thus, the higher values of human pressure did not occur in our study area. Human population density in Gabon in general is low. A previous study identified a threshold for a different indicator of human pressure, namely the human footprint index (Hoare and DuToit, 1999; Lohay et al., 2020; Wall et al., 2021), above which coexistence (of savanna elephants with humans) is not possible. However, these values are known to change locally according to elephant perception of risk, and perhaps species, and could not be applied directly here.

Given the scale of this investigation, we only considered variables with recent data available across the entire country. Therefore, this analysis of drivers can be considered coarse.

4.3. Application of the methodological approach to other forest elephant populations

The scenario of a large forest elephant population distributed over a very large spatial scale, spanning almost the entire country, required a systematic survey approach that made no a priori assumptions about density distribution. This approach to wildlife surveys has only been used in two other African countries where forest fauna was of interest (Brncic et al., 2015; Murai et al., 2013). Most wildlife landscapes in the real world are characterized by a high degree of patchiness or heterogeneity in abundances, largely due to anthropogenic pressures. Hence, species conservation monitoring programs have been tailored accordingly using, predominantly, model-based thinking, especially for low density charismatic megafauna. For example, tiger recovery programs have used source-sink theory (Pulliam, 1988) as a means of framing conservation policy measures (Walston et al., 2010) and for designing an appropriate monitoring program (Karanth and Nichols, 2017). We applied a hybrid approach by combining design-based (systematic design at large scales) and model-based thinking (DNA-based SCR at a site level) into a single survey to infer elephant density at the country-wide scale. Additionally, we applied a model (GLM) using covariates, where ground-based information was lacking, to produce a density surface. The situation for forest elephants in Gabon is also quite rare, in that the population is still distributed across the vast majority of the country at densities high enough to justify the application of such a hybrid approach. With the exception of some sites within the northern Republic of Congo (Bohm, 2020; Brncic et al., 2018) many other forest elephant populations have experienced steep declines and/or range fragmentation from increased anthropogenic pressures and habitat modification (ANPN et al., 2013; Beyers et al., 2011; N'Goran et al., 2020; Nzooh Dongmo et al., 2016b, 2016a).

Together, the strong political will, scientific and laboratory capability in-country and collaborative, science-led decision-making in Gabon were key enabling factors in large-scale survey implementation and impact. We developed our novel sampling design in concert with national wildlife agency information goals and in collaboration with an established national genetics and wildlife forensics laboratory. Our largescale design and modeling approach was informed by a prior pilot study involving three distinct forested landscapes in Gabon to test applicability (Laguardia et al., 2021).

In terms of improvements for field data collection, our recommendations are to increase the number of sites surveyed (replicates). The next iterations of this approach in Gabon or elsewhere should sample around 30 replicates, to increase model explanatory power and parameter estimate precision. We found that the number of DNA samples collected in some sites was low, presumably due to low elephant density. In addition, recapture rates were low (this occurred both in situations of low and relatively high fresh dung encounter rates). Thus, we recommend that either field teams be prepared to sample for longer durations, or additional field teams be deployed to add sufficient effort to obtain an adequate capture rate and capture–recapture ratio for analysis. The latter suggestion (which keeps the survey timespan quite short for each hexagon or similar sample area) would be most consistent with the SCR assumption of population closure. This would also ensure that any increases in survey effort will increase the recapture rates. Our dung DNA amplification varied across sites; a rapid and random sample test to detect low amplification success in near-real time mid-way through a site's field effort would provide valuable information for managing appropriate sampling targets (e.g., if low amplification success becomes apparent, sampling targets should be increased). This is akin to examining photo-detection rates in camera trap studies mid-study to determine total camera setting period.

Molecular genetics approaches to individual identification are in continuous development. This was the case even in the relatively short duration of our study: we improved our methods between the pilot sites of 2018 and the subsequent surveys within the hexagons in 2020. While this is certainly an opportunity to refine estimates, it may also be a challenge when comparing studies between sites or across time. For our study to serve as a baseline estimate used for population trend analysis in the future it will be important to standardize laboratory analysis or develop ways to calibrate error rates in the algorithms developed for matching individuals. Improvements in parameter estimation in SCR modeling include streamlining protocols and procedures related to modelling decisions. Our team included two highly experienced modelers and until the analyses are constructed to be more routine, such expertise is expected to be necessary. Detection and recapture success were quite variable across the survey sites and the site-specific particularities needed deep consideration in this first test of our largescale approach. For example, despite near-equivalent field effort, one site had low detections and no recaptures, another site had adequate detections and low recaptures, and yet another had low detections and high recaptures. Such results cannot be known a priori when sampling new sites for the first time, or as forest elephant population parameters change between sampling years. Thus, we recognize such variability in sample success to be inherent to our approach. We recommend that guidelines be developed that describe protocols for each instance in order to derive site-specific results as planned while ensuring standardization and consistency across repeated surveys.

4.4. Importance of findings for conservation and management of forest elephants and their habitats

The abundance of forest elephants in Gabon now presents a complex management challenge. Reports of human-elephant conflict are frequent in some locales (ANPN/MINEF, 2018; Lahm, 1996; Mihindou Mbina et al., 2016; Walker, 2012). Indeed, human-elephant conflict has become a highly charged political issue, which undermines conservation efforts. The country's human population density is one of the lowest in Africa and thus the resulting ratio of humans to forest elephants may approximate 1 elephant for 20 people. Moreover, because 89% of Gabon is considered forested, and 22% of it protected, then the pattern of forest elephant distribution that we report translates to a large number of these animals occurring outside of protected areas. This study estimated 61,822 forest elephants and 65% of the country's total to occur in logging concessions. How to best manage forest elephants outside of protected areas while also promoting the national economy and rural development remains uncertain, yet of critical importance to the species persistence from national and global perspectives. For Gabon, this highlights the importance of defining nationwide and holistic conservation management strategies for forests and elephants across a range of land-use types. To this end, Gabon has made several high-level commitments under international conventions to further enhance its existing protected area network. Furthermore, the Gabonese government has recently taken a number of policy steps to improve forest management in its forest concession estate – with a declaration in 2018 from the Gabonese Head of State to commit to 100% certification of its production forests.

Forest elephants have been found to provide unique ecological services related to seed dispersal, trampling, and herbivory (Berzaghi et al., 2019; Terborgh et al., 2016); and have indeed been termed "ecosystem engineers" (Lacher et al., 2019) and "Mega-gardeners" (Campos-Arceiz and Blake, 2011). More recent work has shown the link between elephants and carbon sequestration. The tree species that are dispersed by elephants tend to be much larger, with higher wood density (Bastin et al., 2015) and higher carbon content than the forest trees dispersed by other methods (Stephenson et al., 2014). Finally, we know that where climate change has reduced the fruiting frequency of elephant-dispersed trees, it is resulting in declining body condition, and thus presumably reproductive and other health metrics of forest elephants (Bush et al., 2020). In this sense, we suggest that forest elephant functional density and population stability may be considered an integrative indicator of 'good forest governance' and our study provides a useful baseline with which to regularly monitor Gabon's ambitious environmental and development policy goals.

5. Conclusions

We confirmed that Gabon remains the principal stronghold for forest elephants, both in terms of estimated numbers (95,110 forest elephants: 95% CI 58,872–131,349) and spatial distribution (250,782 km^2). However, pockets of low elephant density from recent poaching events remain and have yet to recover. Our findings offer a useful nationwide baseline and status update for forest elephants that will inform adaptive management and stewardship of one of the last remaining forest elephant strongholds. These results are of interest to local, national, and international decision-makers concerned with the conservation of this species and its habitat, with the important ecological role of forest elephants on climate regulation potential of forests, and with forest elephants as a useful indicator for healthy, intact and well-governed forests.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01894.

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