Kent Academic Repository

Nguimdo, Vianny R. V., Tobler, Mathias W., Abwe, Ekwoge E., Ketchen, Marcel E., Betobe, Nelson E., Morgan, Bethan J., Kamp, Johannes, Soofi, Mahmood and Waltert, Matthias (2026) ***No safe refuge? Contrasting effects of hunting on rainforest mammal persistence and (re)colonisation.*** **Journal of Applied Ecology, 63 (6). ISSN 0021-8901.**

Received: 13 October 2025 | Accepted: 6 April 2026
DOI: 10.1111/1365-2664.70434

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology

RESEARCH ARTICLE

No safe refuge? Contrasting effects of hunting on rainforest mammal persistence and (re)colonisation

Vianny R. V. Nguimdo[1,2] | **Mathias W. Tobler**[3] | **Ekwoge E. Abwe**[2,3] | **Marcel E. Ketchen**[2] | **Nelson E. Betobe**[2] | **Bethan J. Morgan**[2,3,4] | **Johannes Kamp**[1] | **Mahmood Soofi**[5,6,7] | **Matthias Waltert**[1]

[1]Department of Conservation Biology, University of Göttingen, Göttingen, Germany; [2]Cameroon Biodiversity Association, Douala, Cameroon; [3]Population Sustainability, San Diego Zoo Wildlife Alliance, Escondido, California, USA; [4]Biological and Environmental Sciences, University of Stirling, Stirling, UK; [5]Durrell Institute of Conservation and Ecology (DICE), University of Kent, Canterbury, UK; [6]Department of Environmental Sciences, Faculty of Fisheries and Environmental Sciences, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Iran and [7]Geography Department, Humboldt-University Berlin, Berlin, Germany

Correspondence
Vianny R. V. Nguimdo.
Email: vnguimd@uni-goettingen.de;rodel@cambiodiversity.org

Funding information
San Diego Zoo Wildlife Alliance; U.S. Fish and Wildlife Service; Arcus Foundation; Tusk Trust; Research England

Handling Editor: Rachakonda Sreekar

Abstract

1. Defaunation in tropical forests represents one of the most urgent biodiversity crises of our time, driven largely by unsustainable hunting. Understanding how species persist or disappear under intense hunting pressure is critical for designing effective conservation strategies, especially in unprotected areas.
2. We quantified how hunting influences species dynamics in an unprotected Afrotropical rainforest by analysing monitoring data collected from 2016 to 2023 for eleven terrestrial and arboreal mammal species in the Ebo forest, Cameroon. Using Bayesian dynamic occupancy models with correlated detections, we assessed how species occupancy changes along environmental and anthropogenic gradients, explicitly including hunting intensity and hunters' travel cost as predictors for persistence and colonisation.
3. Elevation emerged as the strongest predictor positively influencing the occupancy of all eleven species, with some species exhibiting non-linear trends along the elevation gradient. Most species generally occupied areas with high travel cost, especially elephant, chimpanzee, crowned monkey and red river hog. Meanwhile, terrain ruggedness had variable effects, with a strong positive effect on chimpanzee and a negative effect on mona monkey.
4. Surprisingly, hunting showed a positive though weak association with the persistence probability of some species, suggesting that the areas used as refuges by wildlife were not exempt from hunting. Species persistence was generally unaffected by travel cost, except for chimpanzees. In parallel, colonisation probability was lower in areas with past hunting history, indicating that previously hunted areas were less likely to be recolonised by wildlife. Similarly, colonisation

tended to be higher in areas with high travel cost, suggesting that more accessible areas were less likely for recolonisation.

5. *Synthesis and applications*. These results imply that hunting not only targets areas used as refuges by wildlife, but also reduces recolonisation potential and may therefore alter source–sink dynamics. We recommend spatially targeted community-led actions to limit hunting where wildlife still persists through the creation of no-hunting areas to ensure the long-term persistence of wildlife within the forest.

KEYWORDS
African rainforest, bushmeat hunting, defaunation, dynamic occupancy modelling, multi-use landscape, source–sink dynamics, unprotected areas, wildlife persistence

1 | INTRODUCTION

Hunting-driven wildlife decline in tropical forests is an important facet of the current biodiversity crisis (Abernethy et al., 2013; Benitez-Lopez et al., 2019). Across Afrotropical landscapes, escalating demand for bushmeat is intensifying hunting pressure, pushing hunters into increasingly remote and previously undisturbed forest areas (Abernethy et al., 2013; Froese et al., 2023). As primary targets of bushmeat extraction, mammals are especially vulnerable (Dobbins et al., 2020), with some West African species having already experienced 70% to 100% hunting-induced population declines (Benitez-Lopez et al., 2019). To mitigate this crisis, conservation must also encompass unprotected multi-use landscapes (Fonteyn et al., 2024; Plumptre et al., 2024), which often face more intense hunting and resource extraction, driven by competing economic interests and weak governance (Abernethy et al., 2013; Fa & Brown, 2009). Robust conservation planning in these landscapes is hindered by a lack of fine-scale data on species occurrence patterns and their responses to hunting and habitat features (Coad et al., 2019; IUCN, 2023).

Many ecological and conservation studies focus on a small number of charismatic or globally threatened species (Cavada et al., 2019; McGowan et al., 2020), which often fail to capture broader community dynamics (Ardiantiono et al., 2024; Breckheimer et al., 2014). Species exhibit different responses to habitat and human disturbance, with some persisting in hunted landscapes while others rapidly disappear (Benitez-Lopez et al., 2019; Linder & Oates, 2011). Consequently, what constitutes a refuge from hunting is not uniform across species (McCollum et al., 2017; Rist et al., 2009), yet our understanding of these differential responses remains limited (Beirne et al., 2019; Chazdon et al., 2009). A multispecies approach is therefore critical to capturing community-level dynamics and informing more comprehensive conservation strategies (Cavada et al., 2019; Wang et al., 2018).

Occupancy models have become a common toolbox for wildlife monitoring (MacKenzie et al., 2017), especially in tropical forests where direct abundance estimates are challenging (Burton et al., 2015; Rovero et al., 2014). Within human-dominated landscapes, wildlife often tend to change their spatial distribution in response to human activities (Fournier et al., 2022; Parsons et al., 2022). At sites affected by hunting, species may not only disappear, resulting in local extinctions, but they may also fail to recolonise areas with high human activities (Beirne et al., 2019; Coad et al., 2019; Nguyen et al., 2024). Dynamic occupancy models explicitly estimate extinction and colonisation probabilities in relation to covariates, while accounting for imperfect detection (Peach et al., 2017; Semper-Pascual et al., 2023). Despite their potential, these models remain underused due to technical complexity and the scarcity of long-term and replicated data (Zurell et al., 2022). However, recent advances in single-visit dynamic models offer a promising solution to this challenge (Lauret et al., 2021; Peach et al., 2017).

Importantly, few dynamic models explicitly incorporate direct hunting data as a covariate. Instead, they often rely on proxies such as distance to villages or forest edges (Moore et al., 2021; Semper-Pascual et al., 2023). But these proxies may poorly reflect hunter's movements which often show complex and non-linear patterns along roads, rivers and elevation gradients (Deith & Brodie, 2020; Nguimdo, Abwe, Morgan, et al., 2025). Moreover, treating hunting as a simple predictor of occupancy (Dobbins et al., 2020; Oberosler et al., 2020) may overlook its more relevant ecological effects which include driving local extinction and impeding (re)colonisation (Moore et al., 2021; Zurell et al., 2022).

Here, we investigated how hunting and landscape heterogeneity influence the dynamics of rainforest mammals in the unprotected Ebo forest, Cameroon, a representative multi-use landscape within the Gulf of Guinea biodiversity hotspot. Between 2016 and 2023, we monitored eleven medium- to large-bodied terrestrial and arboreal species along 23 systematically placed recce lines while documenting hunting activity. Using a Bayesian multispecies dynamic occupancy model with correlated detections (Dorazio & Royle, 2005; Hines et al., 2014), we quantified how environmental and anthropogenic factors, including elevation, terrain ruggedness and proximity to rivers and hunters' travel cost, affect species occupancy dynamics. We tested the hypothesis that hunting undermines both species persistence and colonisation. We also examined the hypothesis that higher travel cost would promote higher species

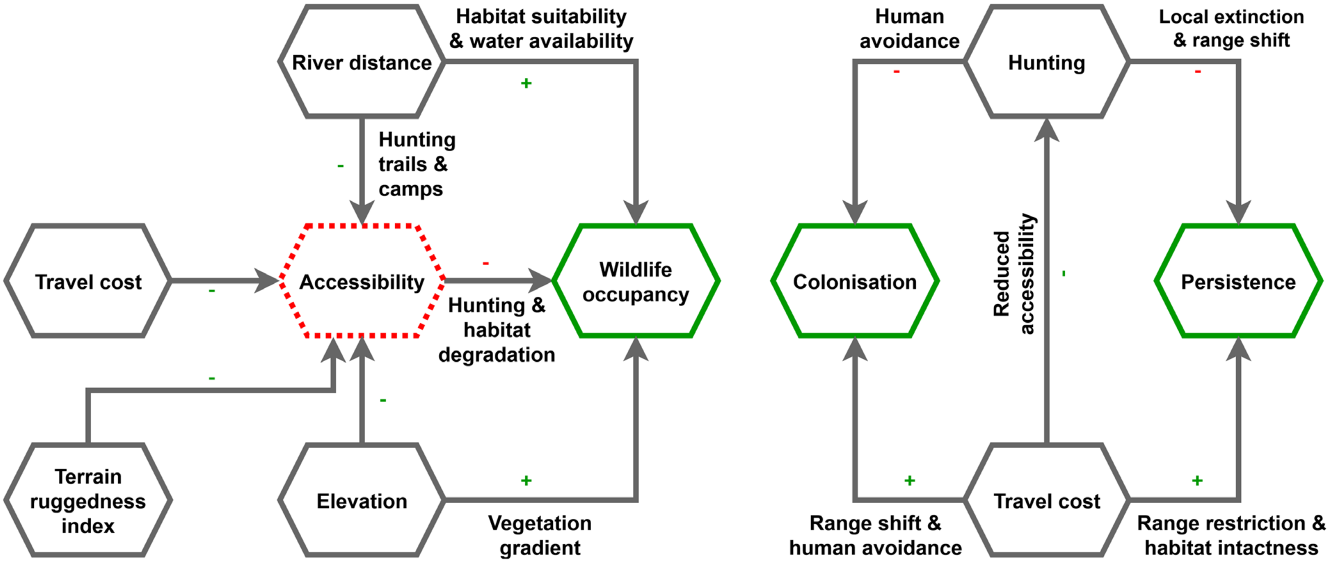

FIGURE 1 Potential influence of various landscape-level anthropogenic and environmental gradients on wildlife occupancy, colonisation and persistence. Extinction (opposite of persistence) denotes the probability that a species present at a site during one time period is absent in the next, reflecting local disappearance or temporary absence. Colonisation represents the probability that a species absent from a site becomes present in the subsequent period, indicating re-occupancy or establishment in previously unoccupied sites.

occupancy, persistence and colonisation (Figure 1). We further hypothesised that other accessibility proxies such as elevation and terrain ruggedness would be associated with higher occupancy. By explicitly modelling colonisation and extinction processes in relation to hunting and landscape features, our study provides a scalable framework for understanding how Afrotropical mammal communities persist, or fail to recover, under sustained hunting pressure.

2 | MATERIALS AND METHODS

2.1 | Study area

The Ebo forest, Cameroon (Figure 2), is part of the Gulf of Guinea biodiversity hotspot and is one of the most important tracts of intact forest in the Cross-Sanaga ecoregion (Potapov et al., 2017). It covers about 1400 km^2, representing approximately half of the Yabassi Key Biodiversity Area which is characterised by a rich assemblage of wildlife and plant species (Abwe, 2018; Cheek et al., 2018). However, it is located in a region reported to have a high hunting-induced defaunation index (Benitez-Lopez et al., 2019; Fonteyn et al., 2023), which mainly results from its proximity to major cities considered regional markets for bushmeat (Fa et al., 2014; Morgan et al., 2013). Consequently, some of its iconic mammals are now extirpated, including the black-and-white colobus (*Colobus guereza*), the African leopard (*Panthera pardus*), the forest buffalo (*Syncerus caffer nanus*) and the giant pangolin (*Smutsia gigantea*) (Whytock et al., 2021). The Critically Endangered and range-restricted Preuss's red colobus (*Piliocolobus preussi*) is now also nearing local extinction (Linder et al., 2021; Nguimdo, Abwe, Betobe, et al., 2025). Acknowledging its biological richness, the Ebo forest was planned to become a national park since 2006, but disagreement among stakeholders with conflicting interests regarding its status and future endured for almost two decades. In 2020, the Government of Cameroon changed its plans and decided to turn it into two logging concessions, a project that encountered global opposition (Nanda et al., 2023; Whytock et al., 2021). Nevertheless, two decrees signed in April 2023 acted the creation of the logging concessions (Nguimdo, Abwe, Morgan, et al., 2025). As logging activities will likely exacerbate the already high hunting pressure (Abernethy et al., 2013), it becomes urgent to understand the spatiotemporal patterns of various wildlife species to ensure that spatial planning of human activities takes their long-term persistence into consideration (IUCN, 2023; Walters et al., 2021).

2.2 | Survey design and data collection

Long-term monitoring of wildlife and human activities in the Ebo forest was conducted along 23 parallel recce lines placed at 4-km intervals across the entire forest (Figure 2), totalling 345 km, with a mean length of 15 km and a standard deviation of 5.17 km (Nguimdo, Abwe, Morgan, et al., 2025; Whytock et al., 2021). These recce lines were oriented perpendicularly to the main drainage system to reduce potential habitat-related biases (Buckland et al., 2015; Rist et al., 2009). We surveyed all recce lines once per year during the dry season (October–April) between 2016–2018 and 2021–2023, for a total of six survey years. No surveys were conducted in 2019 and 2020 due to the COVID-19 pandemic (Nguimdo, Abwe, Morgan, et al., 2025). Two to three trained observers moved at approximately 1 km per hour, using a handheld Garmin GPS device and a manual compass to navigate (White & Edwards, 2000; Whytock et al., 2021).

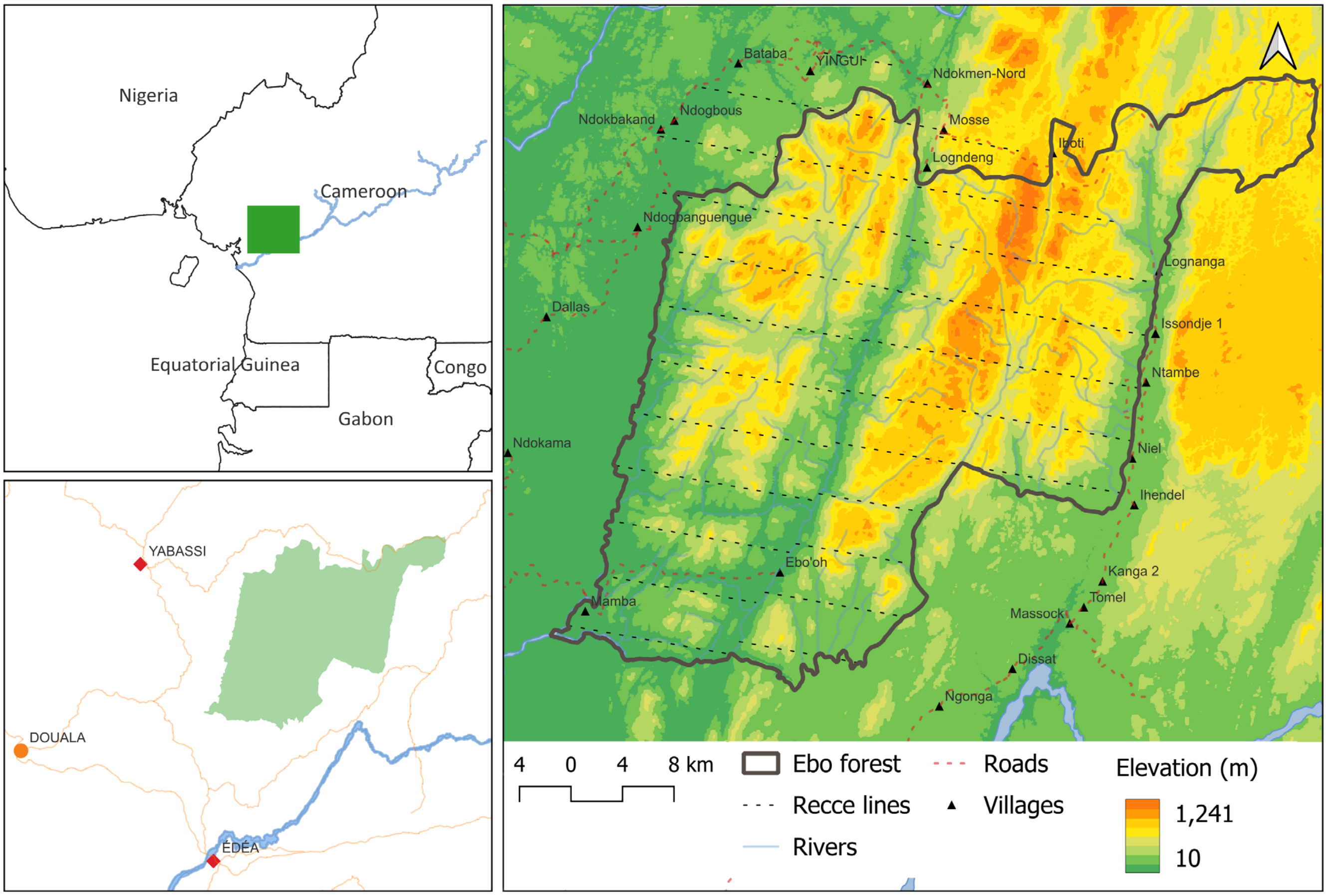

FIGURE 2 Map of the Ebo forest located in the Littoral Region of Cameroon, Central Africa.

The survey generally started at 07:00 AM and ended latest at 05:00 PM. At the end of the day, the survey team recorded the point where they stopped with the GPS and marked it with a flagging tape so that they could start at the exact same position the following day. We used a pair of secateurs to ease movement in dense vegetation while maintaining minimal damage, therefore reducing the risk of hunters using the recce lines, and ensuring a clear distinction between our cuts and those made by hunters. These surveys followed the Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations (Kühl et al., 2008).

Along the recce lines, we recorded direct and indirect signs of large and medium-sized mammals, as well as their geographic coordinates as described by Whytock et al. (2021). Indirect signs were only recorded when the survey team could confidently assign them to a given species. For the purpose of this study, we selected ten species and one species group (Table 1), based on their conservation status in the landscape and the abundance of the recorded signs (Table S1; Whytock et al., 2021). Since it is often difficult to distinguish several duiker species (Table 1), we grouped them as 'red duikers' (Whytock et al., 2021). With the exception of chimpanzees and elephants, all other taxa included in the analyses are known to be targeted by local hunters (Mfossa et al., 2025; Whytock et al., 2014).

We also recorded evidence of human activities, especially hunting signs such as wire snares, shotgun cartridges, trails, signs of passage (machete cuts and shrub breakings), audible gunshots and direct encounters with hunters (Table S2), as described by Nguimdo et al. (2024) and Nguimdo, Abwe, Morgan, et al. (2025). To ensure that the same hunting signs were not repeatedly recorded during consecutive surveys, we visually inspected them and only documented those that were estimated to be less than 1 year old (Nguimdo, Abwe, Morgan, et al., 2025). Similarly, we did only record hunting trails if they showed signs of use since the last annual survey, and we collected and destroyed all shotgun cartridges (Nguimdo, Abwe, Morgan, et al., 2025). This study was conducted with authorisation from the Cameroon Ministry of Scientific Research, permit number N°000169/MINRESI/B00/C00/C10/C13.

2.3 | Data preparation

We placed 1 × 1 km grid cells across the whole study area and selected a total of 341 grid cells which intersected with the recce lines (Nguimdo, Abwe, Morgan, et al., 2025). We considered these grid cells as primary sampling units, each covering approximately 1 linear km of surveyed recce line. Within each of these primary sampling units, we divided the recce line into 200-m segments, representing our spatial replicates that replace temporal replicates for the occupancy modelling (Hines et al., 2010). On each 200-m

TABLE 1 List of species considered within this research with their common and scientific names and conservation status in the IUCN Red List.

Order	Common name	Scientific name	Status	Signs recorded
Proboscidea	Forest elephant	*Loxodonta cyclotis*	CR	Sightings, dung, tracks
Primates	Chimpanzee	*Pan troglodytes ellioti*	EN	Sightings, calls, nests
	Red-capped mangabey	*Cercocebus torquatus*	EN	Sightings, calls
	Preuss's guenon	*Allochrocebus preussi*	EN	Sightings, calls
	Crowned monkey	*Cercopithecus pogonias*	VU	Sightings, calls
	Putty-nosed monkey	*Cercopithecus nictitans*	VU	Sightings, calls
	Red-eared monkey	*Cercopithecus erythrotis*	VU	Sightings, calls
	Mona monkey	*Cercopithecus mona*	NT	Sightings, calls
Ungulates	Red river hog	*Potamochoerus porcus*	LC	Sightings, rooting
	Blue duiker	*Philantomba monticola*	LC	Sightings, dung
	Red duikers:			
	• Bay duiker	*Cephalophus dorsalis*	NT	Sightings, dung
	• Ogilby's duiker	*Cephalophus ogilbyi*	LC	Sightings, dung
	• Yellow-backed duiker	*Cephalophus silvicultor*	NT	Sightings, dung

segment and for each surveyed year, we recorded detection (1) or non-detection (0) for each species to form the detection history needed for occupancy analyses. We used GPS tracklog data to determine the duration (in minutes) the field team spent on each 200-m survey segment, and this duration was used as a proxy for survey effort.

To quantify the influence of hunting pressure on wildlife distribution patterns, we recorded the presence/absence of evidence of each hunting indicator (direct encounters, hunting trails, hunting camps, shotgun cartridges, snare traps and signs of hunter's passage) along each 200-m segment nested within each 1 × 1 km grid cell following Nguimdo, Abwe, Morgan, et al. (2025). For each grid cell, we then summed the presence records of all hunting indicators across surveyed segments and divided the total by the length of recce line (km) to obtain a relative abundance index of hunting signs, which we used as a proxy for hunting intensity.

We derived topographic variables from a Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) with a spatial resolution of 30 m, sourced from NASA's Earthdata repository (https://search.earthdata.nasa.gov; Rabus et al., 2003). From this DEM, we extracted the mean elevation of each grid cell to capture potential environmental and anthropogenic gradients associated with altitudinal variation (Brodie et al., 2015; Whytock et al., 2021). We also used this DEM to quantify travel costs across the Ebo forest using the *r.cost* function in GRASS GIS (QGIS Development Team, 2024; Romo et al., 2022). The *r.cost* algorithm calculates the accumulated least-cost distances from source locations (surrounding villages) by propagating movement costs across a raster cost surface which represents topographic resistance to movement, with steeper or more rugged terrain imposing higher costs (Gietl et al., 2007). The resulting cost-distance surface represents the minimum cumulative cost required to reach each grid cell, accounting for spatial heterogeneity in movement resistance (Gietl et al., 2007). By incorporating terrain-driven constraints, this approach provides a spatially explicit measure of travel difficulty that better captures landscape accessibility than simple Euclidean distance from villages (Nguimdo, Abwe, Morgan, et al., 2025). Additionally, we computed the mean terrain ruggedness index for each cell as a quantitative proxy for topographic heterogeneity (Elsen et al., 2020; Riley et al., 1999). This index has been shown to influence hunting patterns and habitat intactness, with areas exhibiting greater ruggedness often experiencing lower hunting pressure and higher vegetation intactness due to physical constraints on resource extraction (Nguimdo, Abwe, Morgan, et al., 2025; Tagg et al., 2013). We calculated the Euclidean distance from the centroid of each grid cell to the nearest river. The full description and rationale for including different covariates are provided below (Table 2). We performed all spatial analyses using QGIS 3.34 (QGIS Development Team, 2024).

2.4 | Data analysis: Dynamic occupancy model with correlated detections

We used a Bayesian multispecies dynamic occupancy model with correlated detections to jointly model detections and non-detection data for the eleven mammal species. This model combines the multi-season occupancy model with correlated detections (Hines et al., 2014) with a hierarchical multispecies formulation (Dorazio et al., 2010; Dorazio & Royle, 2005). The dynamic multispecies occupancy model estimates initial occupancy, colonisation and persistence (or survival) probabilities for each species *i*, with parameters allowed to vary as a function of environmental and anthropogenic covariates. Persistence and colonisation are modelled as a first-order Markovian process where the probability that a site *j* is occupied at time $t+1$ (denoted $\Psi_{i,j,t+1}$) is

TABLE 2 Covariates included in the multispecies dynamic occupancy models, with their mean, standard deviation (SD) and minimum and maximum values.

Parameter	Predictor	Description	Mean ± SD (min – max)	Rationale for inclusion
Detection	Survey effort (min)	Time spent on each 200 m segment (replicate unit)	11.96 ± 8.84 (1.00–71.00)	The time spent surveying a site influences the detection of wildlife species
Occupancy	Travel cost	Cumulative cost of travelling from villages to each grid cell	8243.2 ± 4398.52 (496.5–19220.9)	Some tropical mammals avoid anthropogenic pressures such as hunting and habitat degradation that are usually higher in easily accessible areas (Beirne et al., 2019)
	River distance (km)	Euclidean distance from the centroid of grid cells to the nearest river	0.73 ± 0.54 (0.00–2.41)	Rivers provide water and suitable habitat that may attract some species (Cavada et al., 2019). However, riverine areas might experience increased hunting, since hunting camps are usually established near rivers (Nguimdo, Abwe, Morgan, et al., 2025; Pardo et al., 2022)
	Elevation (m)	Mean elevation of grid cells	468.85 ± 262.25 (61.21–1120.28)	Vegetation may be better preserved at higher elevation, with positive effects on some mammals (Fotang et al., 2021)
	Elevation^2	Quadratic term of the mean elevation		Some mammals often show peaks in species occurrence at intermediary elevations (Alexiou et al., 2024)
	Terrain ruggedness index	Mean elevation difference between adjacent pixels of the DEM layer in grid cells	25.39 ± 8.61 (7.03–58.59)	Since they are difficult to access, rugged areas preserve vegetation and intact habitats for wildlife, and experience lower hunting (Nguimdo, Abwe, Morgan, et al., 2025)
Persistence and Colonisation	Travel cost	Cumulative cost of travelling from villages to each grid cell	8243.2 ± 4398.52 (496.5–19220.9)	Due to higher human pressures, the chances of species persistence may be lower in accessible areas and wildlife may refrain from colonising such areas (Semper-Pascual et al., 2023)
	Hunting intensity	Relative abundance index of hunting signs in grid cells	1.93 ± 1.81 (0.00–28.00)	Since hunters primarily target mammals, wildlife persistence may be lower in areas that previously experienced hunting (Moore et al., 2021). Similarly, such areas may be avoided by wildlife (Nguyen et al., 2024)

dependent on its occupancy probability at time t, the persistence probability Φ and colonisation probability γ:

$$\Psi_{i,j,t+1} = \Psi_{i,j,t}\Phi_{i,j,t} + \left(1 - \Psi_{i,j,t}\right)\gamma_{i,j,t} \tag{1}$$

Given our single-survey study design along recce lines, we substituted temporally replicated samples that are commonly used in occupancy models (MacKenzie et al., 2002) with spatial replicates along segments of the recce lines (Hines et al., 2010). Since segments taken along a continuous recce line are not independent, we modelled this dependency as a Markovian process where the probability of a species (or its sign) being present on a segment is dependent on whether they were present on the previous segment. For this, we introduced two parameters:

$$\theta_{i,j,k} = \Pr(\text{species } i \text{ present on segment } k \mid \text{site } j \text{ is occupied and the species is not present on segment } k-1)$$

$$\theta'_{i,j,k} = \Pr(\text{species } i \text{ present on segment } k \mid \text{site } j \text{ is occupied and the species is present on segment } k-1)$$

An additional parameter p_{ij} represents the probability that a species (or its sign) is detected given that it is present on a segment:

$$p_{i,j} = \Pr(\text{species } i \text{ detected} \mid \text{species present on segment } k)$$

The detection probability was modelled as a function of survey duration (time spent) $d_{j,t,k}$ on each 200 m segment k *and* $p_{i,j}$ therefore is the detection probability per unit effort:

$$\hat{p}_{i,j,k,t} = 1 - \left(1 - p_{i,j}\right)^{d_{j,t,k}} \tag{2}$$

The full hierarchical model is:

$$z_{i,j,t} \sim \text{Bernoulli}\left(\Psi_{i,j,t}\right)$$

$$y_{i,j,k,t} \sim \text{Bernoulli}\left(\theta_{i,j,k} z_{i,j,t}\right)$$

$$h_{i,j,k,t} \sim \text{Bernoulli}\left(\hat{p}_{i,j,k,t} y_{i,j,k,t}\right) \tag{3}$$

where z and y are latent variables and h is the observed detection history.

Regression parameters for all model parameters (occupancy, persistence, colonisation, presence and detection) were modelled with a hierarchical random-effect structure where species-specific parameters are sampled from a community-level distribution (Dorazio et al., 2006, 2010). Occupancy probability Ψ was modelled as a linear function of covariates including travel cost, distance to river, elevation and its quadratic term and terrain ruggedness index. Colonisation probability γ and persistence probability Φ were modelled as functions of hunting intensity and travel cost. We modelled hunting solely as a driver of colonisation and persistence, as it represents a proximate and temporally variable pressure influencing short-term local extinction and recolonisation, with effects on overall occupancy mediated through these dynamic processes.

To allow for comparison of the effect size across different covariates, we standardised all continuous predictors to a mean of zero and a standard deviation of one (Schielzeth, 2010). We checked the correlation between all covariates using the Spearman correlation test and considered a cut-off point of $|r| \geq 0.7$ above which predictors were not included together in a model, as recommended by Dormann et al. (2012). We also checked the Variance Inflation Factor (VIF) to assess collinearity among variables, considering collinearity among variables with VIF <3 to be acceptable (Zuur et al., 2010).

We implemented the model in a Bayesian framework in JAGS (Plummer, 2003) using rjags version 4.17 (Plummer, 2025) in R version 4.5.1 (R Core Team, 2025). Models were fitted with three MCMC chains, each run for 100,000 iterations, with a burn-in period of 50,000 and thinning interval of 25. For all covariates, we specified weakly informative hierarchical priors, with community-level means following a normal distribution centred at zero and standard deviations drawn from uniform distributions. Convergence was assessed using visual inspection of trace plots and the Gelman–Rubin diagnostic (Gelman & Rubin, 1992), and all model parameters had R-hat <1.1. Posterior distributions were used to derive species-specific and community-level estimates of initial occupancy, colonisation, persistence and detection probabilities, as well as temporal changes in occupancy dynamics. The full model code is provided in Text S1. We considered the effect of a covariate to be strong when its 95% Bayesian credible interval (BCI) did not overlap zero, moderate when its 75% BCI did not overlap zero, but its 95% BCI overlapped with zero, and weak when both its 95% and 75% BCI overlapped with zero (Nguimdo, Abwe, Betobe, et al., 2025; Nguyen et al., 2024).

3 | RESULTS

The elephant and the red-capped mangabey had the lowest occupancy probabilities, which remained relatively stable over the years with mean occupancies of $\Psi = 0.16 \pm 0.04$ and $\Psi = 0.30 \pm 0.12$, respectively (Figure 3). The mean occupancy probability of the chimpanzee was $\Psi = 0.42 \pm 0.03$ and also remained relatively stable from 2016 to 2023. The occupancy of all other species tended to increase with the highest increase observed for the red river hog, the Preuss's guenon, the putty-nosed monkey and red duikers (Figure 3). However, the occupancy of the red river hog and red duikers drastically decreased after a peak in 2021, and the red-eared monkey also showed a mild decrease around the same period (Figure 3, Table S3).

3.1 | Predictors of species occupancy

Elevation had a strong positive effect on the occupancy of all eleven species (Figure 4). Its quadratic term also had a positive and strong effect on the occupancy probability of elephants ($\beta = 0.78$; 95% BCI = 0.32 to 1.28), a positive and moderate effect on the blue and red duikers, and a negative and moderate effect on chimpanzees ($\beta = -0.28$; 75% BCI = −0.52 to −0.04). Meanwhile, the effect of the travel cost on the occupancy probability was very variable among species. It had a strong positive effect on the occupancy probability of the elephant ($\beta = 1.01$; 95% BCI = 0.50 to 1.53), crowned monkey and red river hog, and a moderate positive effect on the chimpanzee ($\beta = 0.40$; 95% BCI = −0.00 to 0.83). Interestingly, it tended to have a negative but weak effect on the occupancy of the mona monkey ($\beta = -0.37$; 95% BCI = −1.40 to 0.52). We found no evidence of an effect of the covariate on the occupancy of other species (Figure 4, Table S4).

The effect of terrain ruggedness index was also highly variable among species, with a strong positive effect on the occupancy of chimpanzee ($\beta = 0.92$; 95% BCI = 0.37 to 1.57) and a moderately positive effect on red-capped mangabey ($\beta = 1.05$; 75% BCI = 0.27 to 1.91). Conversely, this covariate had a strong negative effect on the occupancy probability of mona monkey ($\beta = -1.13$; 95% BCI = −2.52 to −0.48), and a negative and moderate effect on red river hog ($\beta = -0.34$; 75% BCI = −0.56 to −0.11) and red-eared monkey ($\beta = -1.00$; 75% BCI = −1.87 to −0.21).

Greater distances to the nearest river were moderately associated with lower occupancy probabilities for the putty-nosed monkey ($\beta = -0.23$; 75% BCI = −0.47 to −0.03) and tended to also have a negative, though weak effect on the chimpanzee, crowned monkey, mona monkey and red river hog (Figure 4).

3.2 | Predictors of species persistence and colonisation

We found very little evidence for an influence of the travel cost on the persistence probability for almost all species (Figure 5a). Only the chimpanzee showed a moderately positive association between persistence and travel cost ($\beta = 0.74$; 75% BCI = 0.05 to 1.43), while the mona monkey tended to have low persistence probabilities in areas with high travel cost (Figure 5a). In contrast and surprisingly, hunting seemed to have a positive relationship with the persistence probability of eight of the eleven species (Figure 5a, Table S5). However, this relationship was weak for most species, and only moderate for the elephant ($\beta = 0.41$; 75% BCI = 0.05 to 0.83) and blue duiker ($\beta = 0.72$; 75% BCI = 0.12 to 1.37).

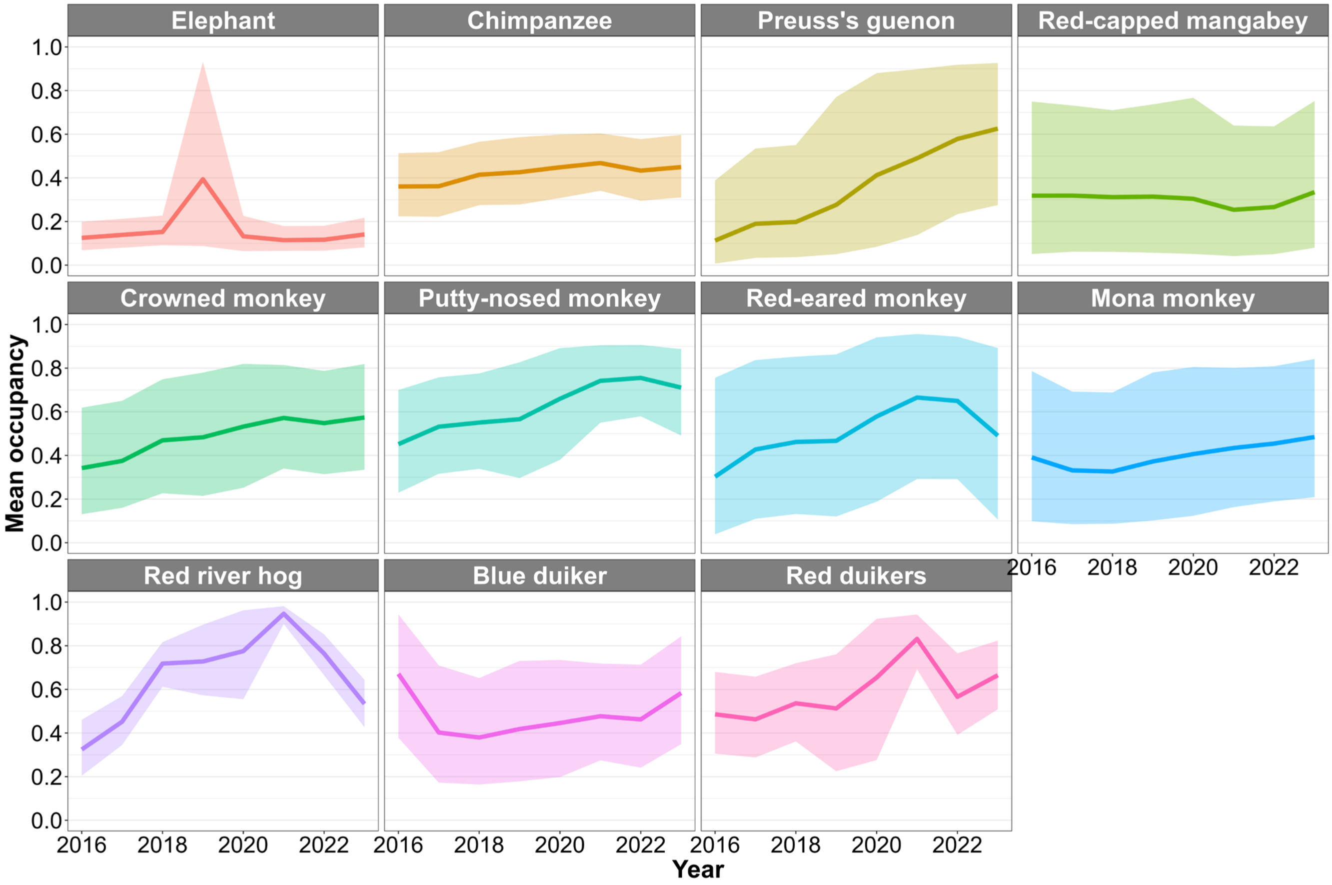

FIGURE 3 Annual occupancy estimates for the selected eleven Afrotropical rainforest mammals in the period 2016–2023 in the Ebo forest, Cameroon, predicted with Bayesian dynamic occupancy models.

Species colonisation probability tended to be higher in areas with high travel cost, except for the red river hog (Figure 5b). This relationship was strong for the elephant (β=0.50; 95% BCI=0.18 to 0.82), chimpanzee (β=0.44; 95% BCI=0.01 to 0.88) and red duikers (β=0.85; 95% BCI=0.28 to 1.58), and only moderate for the putty-nosed monkey, blue duiker, crowned monkey, Preuss's guenon and red-capped mangabey (Figure 5b). Similarly, hunting negatively affected species colonisation probability, except for elephants. It had a strong effect on the chimpanzee (β=−2.08; 95% BCI=−4.71 to −0.39), putty-nosed monkey (β=−1.38; 95% BCI=−3.10 to −0.14) and red duikers (β=−1.66; 95% BCI=−3.27 to −0.57). Its effect was moderate on crowned monkey (β=−1.11; 75% BCI=−1.99 to −0.32), red-eared monkey (β=−1.42; 75% BCI=−2.81 to −0.25) and red river hog (β=−0.21; 75% BCI=−0.40 to −0.03), and weak on Preuss's monkey, red-capped mangabey, blue duiker and mona monkey (Figure 5b, Table S6).

4 | DISCUSSION

We used dynamic multispecies occupancy modelling, fitted to monitoring data from 2016 to 2023, to assess how landscape features shape the occupancy of arboreal and terrestrial medium- and large-bodied mammal species, while explicitly modelling the effect of hunting intensity on their persistence and (re)colonisation. To our knowledge, this is the first study that applies this methodological approach in unprotected Afrotropical rainforests. Against our expectations and despite the high hunting pressure in this landscape, the occupancy probability of most species was found to be either stable or increasing. This is surprising given the high hunting pressure in the region (Fa & Brown, 2009; Nguimdo, Abwe, Morgan, et al., 2025), and the fact that both snares and shotguns are used by hunters in the Ebo forest (Nguimdo, Abwe, Morgan, et al., 2025), targeting both ungulates and arboreal primates. In addition, in Ebo as well as the broader Afrotropical region, gun hunting is increasing (Ingram et al., 2025; Nguimdo, Abwe, Morgan, et al., 2025), contrasting with the increase in primate occupancy found in this study. Nevertheless, our results align with findings from Whytock et al. (2021) who reported increasing abundance of hunted species in the Ebo forest, and related it, at least partially, to long-term community-based conservation efforts in the landscape (Mfossa et al., 2025). This increase seems to have slowed after 2021, possibly due to the change of the status of the forest from a proposed national park to logging concessions which may have diminished its previously perceived protection status, thereby making it more attractive to hunters. Future surveys would be useful to monitor wildlife occupancy and abundance in order to confirm the observed trends.

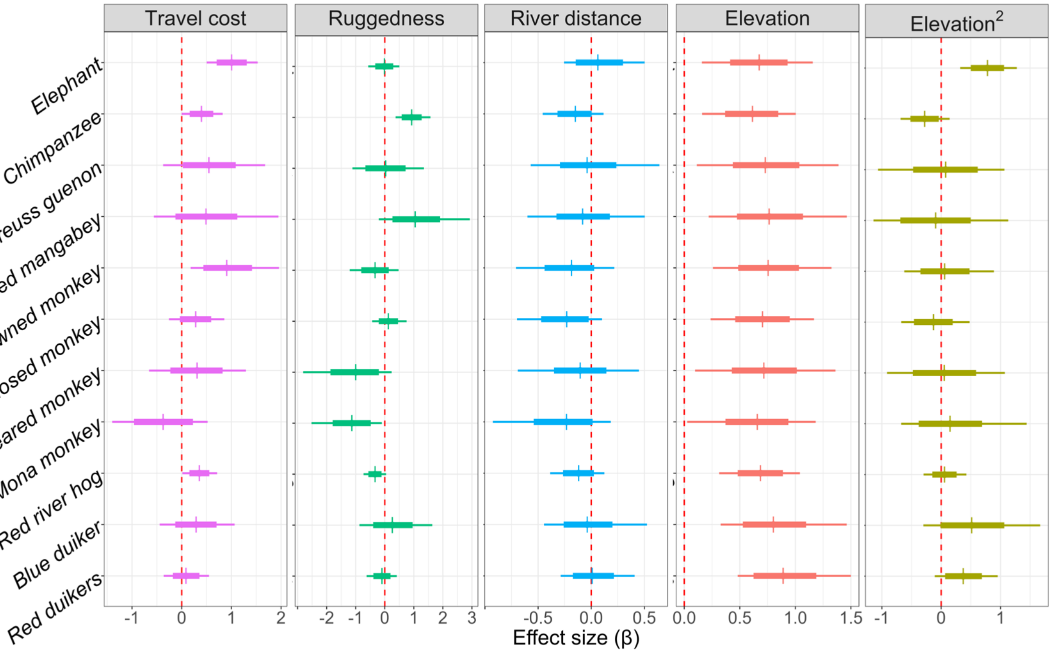

FIGURE 4 Effect size (β) of covariates from the dynamic occupancy model showing the influence of landscape predictors on the occupancy probability of eleven mammal taxa. The short vertical segments represent the mean, and the thin and thick error bars show the 95% and 75% Bayesian credibility intervals, respectively.

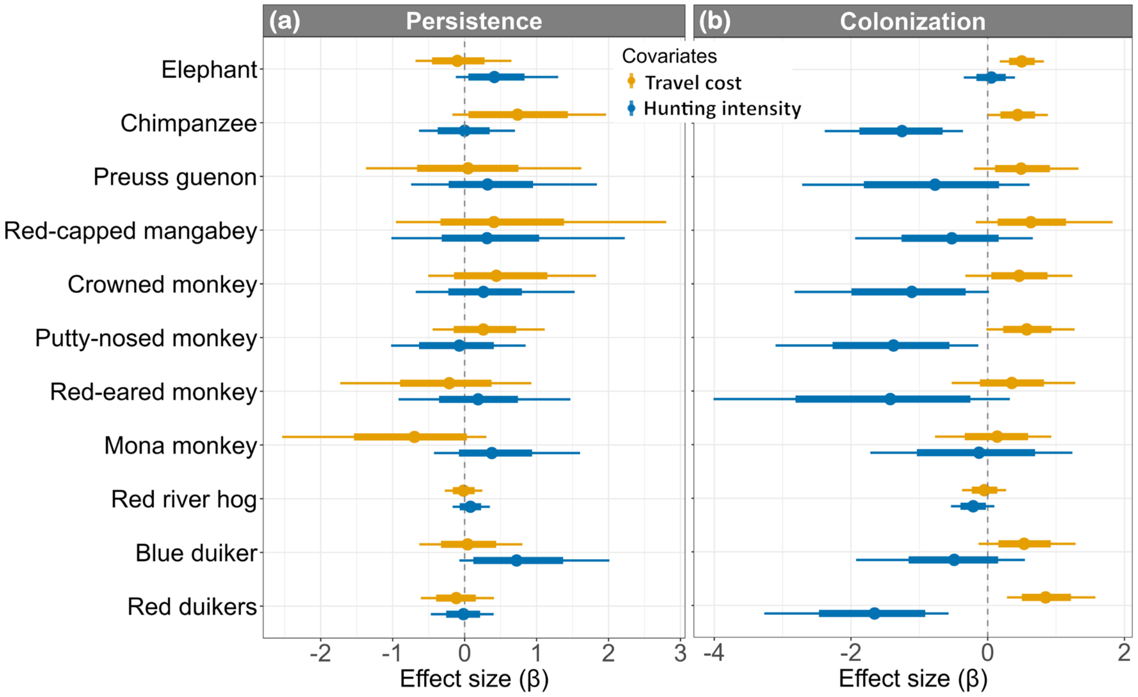

FIGURE 5 Effect size (β) of covariates from the dynamic occupancy model showing the influence of distance to the nearest village and hunting on the probability of persistence (a) and colonisation (b) for the eleven mammal taxa. The dots represent the mean and the thin and thick error bars show the 95% and 75% Bayesian credibility intervals, respectively.

4.1 | Predictors of species occupancy

Travel cost generally had a positive effect on the occupancy probability of ten of the eleven studied species. Elephant occupancy increased strongly as accessibility decreased, consistent with findings from Maisels et al. (2013) who reported that elephants across Central Africa preferred areas away from roads, likely reflecting the landscape of fear as explained by Blake and Maisels (2023). The occupancy of other species such as chimpanzees, crowned monkeys, and red river hogs also increased strongly with the travel cost. This may be related to village-centred defaunation which has been well documented in tropical regions (Beirne et al., 2019), since areas near villages are likely to have lower travel costs and are easily accessible to hunters. For instance, in the Udzungwa Mountains in Tanzania, Cavada et al. (2019) reported increased mammal community occupancy away from human settlements. These results may illustrate the generally higher hunting pressure and habitat degradation in highly accessible areas near villages and roads (Branch et al., 2022; Espinosa et al., 2014).

Travel cost had a moderate to strong positive effect on the occupancy of five species, and a positive but weak effect on five other species. Nguimdo, Abwe, Morgan, et al. (2025) showed that, due to Ebo's high topographic heterogeneity, the cost of travelling was a better predictor of hunting activities than the simple Euclidean distance to roads and villages. However, for some mammal species, habitat preferences may be more important than anthropogenic pressures such as hunting (Rist et al., 2009; Rovero et al., 2014). For instance, the occupancy probability of the mona monkey tended to be higher in more accessible areas. The species has been described as a generalist adapted to most habitats including human-dominated landscapes (Olaleru et al., 2023), forest edges and degraded habitats (Bowers-Sword, 2020), with a high tolerance for hunting (Linder & Oates, 2011; Waltert et al., 2002).

As predicted, the occupancy of all eleven species, both terrestrial and arboreal, was positively and strongly influenced by increasing elevation. However, the effect of elevation on wildlife distribution is very context-specific and can vary between species and regions (Nguyen et al., 2024; Rovero et al., 2014; Snider et al., 2024). In the Ebo forest where the maximum elevation is around 1250 m, research has shown that forest cover increases with elevation (Whytock et al., 2021). Likewise, in the Kom-Wum Forest Reserve located in the same ecoregion, Fotang et al. (2021) reported that forest intactness increased with elevation, translating into more chimpanzee presence at high elevations where forest cover is better preserved. The southern part of the Ebo forest has lower elevations (Figure 2), was logged in the past, and likely witnesses higher hunting pressure from immigrant hunters (Nguimdo, Abwe, et al., 2026). Meanwhile, the northern part has higher elevations and is recognised as one of the last Intact Forest Landscapes in the Gulf of Guinea (Potapov et al., 2017). Previous studies have shown that elephants mainly occur in the northeastern part of the Ebo forest where elevations are highest (Whytock et al., 2021), which also corresponds to the distribution range of the relic gorilla population of the Ebo forest (Mfossa et al., 2022).

Elevation also plays a role in the spatial distribution of hunting pressure, with higher elevations correlated with lower accessibility to hunters. For instance, Nguimdo, Abwe, Morgan, et al. (2025) found a negative relationship between the presence of snares and elevation and a positive effect of elevation on gun hunting in the Ebo forest, suggesting that hunters mostly set snares at lower elevations to reduce the physical effort needed to revisit the snares, while hunting with guns at higher elevations. Interestingly, in central Vietnam where only snares and traps are used, Tilker et al. (2024) found a positive relationship between snaring and elevation, suggesting that hunters have moved away from low-elevation areas which have witnessed higher defaunation. The strong positive effect of elevation on wildlife occupancy observed here indicates that low-elevation areas, especially to the south of the Ebo forest, have also lost most of their wildlife as a result of higher accessibility to hunters and other land uses such as logging.

We found that the terrain ruggedness index had a very variable influence on the occupancy of both terrestrial and arboreal mammal species, with a strong positive effect on the occupancy of chimpanzees, red-capped mangabeys and putty-nosed monkeys, mirroring previous research in the same landscape (Bowers-Sword, 2020; Nguimdo, Abwe, Betobe, et al., 2025). In the Western Ghats biodiversity hotspot in India, Pillay et al. (2022) also found a consistent positive effect of terrain ruggedness on the occupancy of mammal species across different functional groups. Rugged areas are generally less accessible to humans and may therefore preserve more intact habitats (Tagg et al., 2013; Whytock et al., 2021), while experiencing lower hunting pressure (Nguimdo, Abwe, Morgan, et al., 2025). In contrast, terrain ruggedness had a negative effect on the occupancy of mona monkeys and red river hogs. Rugged areas have been reported to serve as dispersal barriers for some mammal species such as the black-and-white ruffed lemur (*Varecia variegata*) in Madagascar (Mancini et al., 2023). By preserving primary forests, rugged areas may be unsuitable for secondary forest species such as the mona monkey (Bowers-Sword, 2020). In addition, these areas may also be unsuitable to species such as the red river hog which is known to prefer swampy habitat that is usually found in areas with flat terrain (McCollum et al., 2017). There was weak evidence of any effect of terrain ruggedness on the occupancy of other species including elephants, Preuss's guenons, crowned monkeys, red-eared monkeys and duikers. These mixed results have also been reported by other studies (Nguyen et al., 2024; Wong et al., 2022). We argue that the varying species-specific responses to terrain ruggedness observed in our study area are certainly related to a trade-off between avoidance and adaptations to hunting pressures and habitat preferences.

4.2 | Predictors of species persistence and colonisation

Hunting pressure is often assumed to be highest in the most accessible areas, particularly near villages where defaunation is expected to be more pronounced. However, our results challenge this assumption. Surprisingly, the persistence probability of ten of the eleven mammal species studied was only weakly influenced by the travel cost. This suggests that persistence rates are relatively consistent across the accessibility gradient, possibly related to the highly heterogenous topography of the Ebo forest, with pockets of highly rugged forest near villages. But our result could also mean that species most sensitive to hunting have already been extirpated from areas close to villages. Only the persistence probability of chimpanzee was moderately positively influenced by accessibility, corroborating previous research (Kamgang et al., 2018).

More surprisingly, we found that hunting intensity tended to have a positive relationship with most wildlife persistence probability, although the effect was generally weak, except for elephant and blue duiker for which it was moderate. This contradicts previous studies, such as Brodie et al. (2015) who reported strong negative impacts of hunting on mammal populations in northern Borneo. However, our results align with findings from Southeast Asia, where Tilker et al. (2024) found that snaring was highest in remote areas where wildlife occurrence was also high. Similarly, while our study revealed a positive association between elevation and wildlife occupancy, Nguimdo, Abwe, Morgan, et al. (2025) found that shotgun hunting also increased with elevation. These observations suggest a shift in hunting patterns: more accessible areas may have already been depleted of wildlife, prompting hunters to venture deeper into remote and rugged habitats which are now acting as the last refuges for many species. This is highly concerning, as it indicates that very few, if any, forest areas are exempt from hunting pressure, and that hunting may now be targeting wildlife populations in their last refuges, which play a crucial role in maintaining species persistence through dispersal into edge areas (van Vliet et al., 2010). This might lead to local extinctions in the near future, especially for large-bodied or behaviourally inflexible mammals that cannot adapt to increased hunting pressure.

In contrast, the patterns of wildlife colonisation generally aligned with expectations. Sites located with high travel cost tended to have higher colonisation probabilities for nearly all species, with the exception of the red river hog. However, for the red-eared monkey and the mona monkey, there was weak evidence for the effect of travel cost. Similarly, hunting also negatively influenced colonisation, with most species, except the elephant, showing reduced colonisation probabilities in areas which exhibited hunting intensity during the previous survey year. For elephants which are not targeted by hunters in this landscape, inaccessible sites had more chances to be (re)colonised, and hunting only had no effect on site colonisation. This result aligns with previous findings in this landscape that showed that elephants are insensitive to hunting pressure, as most trails are used by both hunters and elephants, but preferred areas that are away from roads and villages (Whytock et al., 2021). Chimpanzees in particular exhibited a strong negative relationship between hunting intensity and site colonisation and a strong positive relationship with travel cost, consistent with previous studies that investigated the distribution of the species in human-dominated landscapes (Fotang et al., 2021; Strindberg et al., 2018). Overall, these patterns suggest that despite the increasing occupancy and longing persistence of some species, hunting impedes the recolonisation of habitats, thereby limiting the potential for population recovery of most species, at least in areas with recent hunting history.

4.3 | Conservation implications for unprotected Afrotropical forests

Defaunation in easily accessible areas of African rainforests is pushing hunting pressure deeper into more remote and topographically challenging parts of forests (Batumike et al., 2020; Coad et al., 2019). This shift in hunting patterns undermines traditional assumptions that remote areas can serve as natural refuges for wildlife. Our findings, which reveal a weak positive relationship between hunting and species persistence, suggest that some wildlife populations may already be confined to their last refuges, reflecting both long-term adaptations to hunting, and their inability to further respond spatially to current and future hunting pressure. The higher species occupancy in highlands and in inaccessible and rugged areas may already reflect their response to previous hunting pressure in the landscape. Despite the stable and even increasing occupancy observed for some species, the local extinction of some iconic species in the Ebo forest such as the leopard, the black-and-white colobus and the giant pangolin reported by Whytock et al. (2021) underscores the severity of past hunting and is a reminder of its consequences: Not all species have the ecological flexibility to persist in increasingly restricted habitats. With increasing hunting in the most remote parts of unprotected landscapes as is the case in the Ebo forest (Nguimdo, Abwe, Morgan, et al., 2025), topographical heterogeneity alone may no longer be sufficient to safeguard viable wildlife populations. The recent conversion of the Ebo forest into logging concessions is likely to worsen the situation by increasing forest access, further exacerbating hunting pressure in formerly remote areas. The long-term persistence of mammals in such landscapes will depend on the integration of sustainable logging practices with robust hunting regulations (Tobler et al., 2018).

In Central Africa, village-based hunting typically occurs within 10 km of settlements, but the use of hunting camps enables exploitation of areas over 40 km away (Abernethy et al., 2013). Similar patterns have been observed in Ebo, where hunters penetrate deep into the forest (Whytock et al., 2014), further diminishing the effectiveness of spatial refuges. Effective conservation planning must acknowledge the spatial extent and complexity of hunting practices, recognising hunting as a multifaceted phenomenon that impacts various species differently (Rist et al., 2009). Conservation strategies must be species-specific and context-sensitive, and understand species sensitivity to different hunting methods, to determine pragmatically which species may be suitable for regulated subsistence hunting and which hunting tools should be restricted to reduce ecological harm. Moving forward, conservation in unprotected rainforest landscapes must also focus on securing a network of no-hunting zones that can function as source populations to sustain species across the broader matrix of hunted areas (Gilroy & Edwards, 2017; Novaro et al., 2005).

In many unprotected rainforest landscapes across Africa, community-based conservation initiatives already safeguard biodiversity (Mfossa et al., 2025) by reducing hunting pressure and enhancing species persistence (Coad et al., 2019). These initiatives should be expanded and strengthened to ensure the long-term viability of wildlife within unprotected landscapes through the creation and maintenance of no-hunting zones that would serve as wildlife refuges.

AUTHOR CONTRIBUTIONS

Vianny R. V. Nguimdo, Mathias W. Tobler, Matthias Waltert, Mahmood Soofi, Johannes Kamp, Ekwoge E. Abwe and Bethan J. Morgan conceived the ideas and designed methodology; Vianny R. V. Nguimdo, Marcel E. Ketchen and Nelson E. Betobe collected the data; Mathias W. Tobler and Vianny R. V. Nguimdo analysed the data; Vianny R. V. Nguimdo led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Data collection was funded by San Diego Zoo Wildlife Alliance, the Arcus Foundation, and the US Fish and Wildlife Service. We thank Fiona Maisels and Robin Whytock for their contributions to the survey design. We are grateful to local communities who facilitated field activities and participated in data collection. We sincerely thank the two anonymous reviewers for their constructive comments on this manuscript. Vianny Nguimdo is supported by the San Diego Zoo Wildlife Alliance and the Tusk Trust. Mahmood Soofi is supported by Research England's Expanding Excellence in England (E3) Fund, UK Research and Innovation. Open Access funding enabled and organised by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest that could have influenced this work.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.rr4xgxdp3 (Nguimdo, Tobler, et al., 2026).

ORCID

Vianny R. V. Nguimdo https://orcid.org/0000-0003-1081-3630
Johannes Kamp https://orcid.org/0000-0002-8313-6979
Mahmood Soofi https://orcid.org/0000-0002-6167-2527

REFERENCES

Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E., & Maisels, F. (2013). Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*(1625), 20120303. https://doi.org/10.1098/rstb.2012.0303

Abwe, E. E. (2018). *Linking behavioral diversity with genetic and ecological variation in the Nigeria-Cameroon chimpanzee (Pan troglodytes ellioti)* [PhD thesis]. Drexel University.

Alexiou, I., Coudrat, C. N. Z., Niedballa, J., Wilting, A., & Tilker, A. (2024). Multi-species occupancy modeling of ground-dwelling mammals in central Laos: A case study for monitoring in tropical forests. *Wildlife Biology*, *2025*(2), e01261. https://doi.org/10.1002/wlb3.01261

Ardiantiono, Deere, N. J., Ramadiyanta, E., Sibarani, M. C., Hadi, A. N., Andayani, N., Ginting, Y., Bull, J. W., & Struebig, M. J. (2024). Selecting umbrella species as mammal biodiversity indicators in tropical forest. *Biological Conservation*, *292*, 110511. https://doi.org/10.1016/j.biocon.2024.110511

Batumike, R., Imani, G., Urom, C., & Cuni-Sanchez, A. (2020). Bushmeat hunting around Lomami National Park, Democratic Republic of the Congo. *Oryx*, *55*(3), 421–431. https://doi.org/10.1017/s0030605319001017

Beirne, C., Meier, A. C., Mbele, A. E., Menie Menie, G., Froese, G., Okouyi, J., & Poulsen, J. R. (2019). Participatory monitoring reveals village-centered gradients of mammalian defaunation in central Africa. *Biological Conservation*, *233*, 228–238. https://doi.org/10.1016/j.biocon.2019.02.035

Benitez-Lopez, A., Santini, L., Schipper, A. M., Busana, M., & Huijbregts, M. A. J. (2019). Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biology*, *17*(5), e3000247. https://doi.org/10.1371/journal.pbio.3000247

Blake, S., & Maisels, F. (2023). Forest elephant movements in central Africa: Megafauna need megaspaces. In R. Reyna-Hurtado, C. A. Chapman, & M. Melletti (Eds.), *Movement ecology of Afrotropical forest mammals*. Springer. https://doi.org/10.1007/978-3-031-27030-7_3

Bowers-Sword, R. (2020). *Population status, threats, and conservation of Preuss's red colobus (Piliocolobus preussi) and other diurnal primates in the Ndokbou forest, Littoral Region, Cameroon* [MS thesis]. James Madison University. https://commons.lib.jmu.edu/masters202029/12

Branch, D., Moka Sharpe, S., Maho, L. M., Silochi Pons, M. Á., Mitogo Michá, F., Motove Etingüe, A., Nze Avomo, J. C. O., Owono Nchama, P. O., Esara Echube, J. M., Fero Meñe, M., Featherstone, B., Montgomery, D., Gonder, M. K., & Fernández, D. (2022). Accessibility to protected areas increases primate hunting intensity in Bioko Island, Equatorial Guinea. *Frontiers in Conservation Science*, *3*, 780162. https://doi.org/10.3389/fcosc.2022.780162

Breckheimer, I. A. N., Haddad, N. M., Morris, W. F., Trainor, A. M., Fields, W. R., Jobe, R. T., Hudgens, B. R., Moody, A., & Walters, J. R. (2014). Defining and evaluating the umbrella species concept for conserving and restoring landscape connectivity. *Conservation Biology*, *28*(6), 1584–1593. https://doi.org/10.1111/cobi.12362

Brodie, J. F., Giordano, A. J., Zipkin, E. F., Bernard, H., Mohd-Azlan, J., & Ambu, L. (2015). Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conservation Biology*, *29*(1), 110–121. https://doi.org/10.1111/cobi.12389

Buckland, S. T., Rexstad, E. A., Marques, T. A., & Oedekoven, C. S. (2015). Designing distance sampling experiments. In S. T. Buckland, E. A. Rexstad, T. A. Marques, & C. S. Oedekoven (Eds.), *Distance sampling: Methods and applications* (pp. 29–34). Springer International Publishing. https://doi.org/10.1007/978-3-319-19219-2_3

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., Boutin, S., & Stephens, P. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675–685. https://doi.org/10.1111/1365-2664.12432

Cavada, N., Worsoe Havmoller, R., Scharff, N., & Rovero, F. (2019). A landscape-scale assessment of tropical mammals reveals the effects of habitat and anthropogenic disturbance on community occupancy. *PLoS One*, *14*(4), e0215682. https://doi.org/10.1371/journal.pone.0215682

Chazdon, R. L., Harvey, C. A., Komar, O., Griffith, D. M., Ferguson, B. G., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Van Breugel, M., & Philpott, S. M. (2009). Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica*, *41*(2), 142–153. https://doi.org/10.1111/j.1744-7429.2008.00471.x

Cheek, M., Prenner, G., Tchiengué, B., & Faden, R. B. (2018). Notes on the endemic plant species of the Ebo Forest, Cameroon, and the new, Critically Endangered, *Palisota ebo* (Commelinaceae). *Plant Ecology and Evolution*, *151*(3), 434–441. https://doi.org/10.5091/plecevo.2018.1503

Coad, L., Fa, J., Abernethy, K., Vliet, N., Santamaria, C., Wilkie, D., El Bizri, H., Ingram, D., Cawthorn, D.-M., & Nasi, R. (2019). *Toward a sustainable, participatory and inclusive wild meat sector*. https://doi.org/10.17528/cifor/007046

Deith, M. C. M., & Brodie, J. F. (2020). Predicting defaunation: Accurately mapping bushmeat hunting pressure over large areas. *Proceedings of the Biological Sciences*, *287*(1922), 20192677. https://doi.org/10.1098/rspb.2019.2677

Dobbins, M., Sollmann, R., Menke, S., Almeyda Zambrano, A., Broadbent, E., & Mukul, S. (2020). An integrated approach to measure hunting intensity and assess its impacts on mammal populations. *Journal of Applied Ecology*, *57*(11), 2100–2111. https://doi.org/10.1111/1365-2664.13750

Dorazio, R., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, *100*, 389–398. https://doi.org/10.1198/016214505000000015

Dorazio, R., Royle, J. A., Söderström, B., & Glimskär, A. (2006). Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, *87*, 842–854. https://doi.org/10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2

Dorazio, R. M., Kéry, M., Royle, J. A., & Plattner, M. (2010). Models for inference in dynamic metacommunity systems. *Ecology*, *91*(8), 2466–2475. https://doi.org/10.1890/09-1033.1

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2012). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Elsen, P. R., Monahan, W. B., & Merenlender, A. M. (2020). Topography and human pressure in mountain ranges alter expected species responses to climate change. *Nature Communications*, *11*(1), 1974. https://doi.org/10.1038/s41467-020-15881-x

Espinosa, S., Branch, L. C., & Cueva, R. (2014). Road development and the geography of hunting by an Amazonian indigenous group: Consequences for wildlife conservation. *PLoS One*, *9*(12), e114916. https://doi.org/10.1371/journal.pone.0114916

Fa, J. E., & Brown, D. (2009). Impacts of hunting on mammals in African tropical moist forests: A review and synthesis. *Mammal Review*, *39*(4), 231–264. https://doi.org/10.1111/j.1365-2907.2009.00149.x

Fa, J. E., Farfan, M. A., Marquez, A. L., Duarte, J., Nackoney, J., Hall, A., Dupain, J., Seymour, S., Johnson, P. J., MacDonald, D. W., & Vargas, J. M. (2014). Mapping hotspots of threatened species traded in bushmeat markets in the Cross-Sanaga rivers region. *Conservation Biology*, *28*(1), 224–233. https://doi.org/10.1111/cobi.12151

Fonteyn, D., Fayolle, A., Fa, J. E., Vanthomme, H., Vigneron, P., Vermeulen, C., Malignat, R., Konradowski, B., Yia Okanabene, M. N., Dibotty-di Moutsing, S. A., Pereira Dias, S., Deniau, C., Cornu, G., Groschene, M., & Cornelis, D. (2024). Hunting indicators for community-led wildlife management in tropical Africa. *npj Biodiversity*, *3*(1), 15. https://doi.org/10.1038/s44185-024-00048-4

Fonteyn, D., Vermeulen, C., Gorel, A. P., Silva de Miranda, P. L., Lhoest, S., & Fayolle, A. (2023). Biogeography of central African forests: Determinants, ongoing threats and conservation priorities of mammal assemblages. *Diversity and Distributions*, *29*, 698–712. https://doi.org/10.1111/ddi.13677

Fotang, C., Bröring, U., Roos, C., Enoguanbhor, E. C., Abwe, E. E., Dutton, P., Schierack, P., Angwafo, T. E., & Birkhofer, K. (2021). Human activity and forest degradation threaten populations of the Nigeria–Cameroon chimpanzee (*Pan troglodytes ellioti*) in Western Cameroon. *International Journal of Primatology*, *42*(1), 105–129. https://doi.org/10.1007/s10764-020-00191-2

Fournier, C. S., Graefen, M., McPhee, S., Amboko, J., Noonburg, E. G., Ingram, V., Hart, T. B., Hart, J. A., & Detwiler, K. M. (2022). Impact of hunting on the Lesula Monkey (*Cercopithecus lomamiensis*) in the Lomami River Basin, Democratic Republic of the Congo. *International Journal of Primatology*, *44*(2), 282–306. https://doi.org/10.1007/s10764-022-00337-4

Froese, G. Z. L., Ebang Mbélé, A., Beirne, C., Bazza, B., Dzime N'noh, S., Ebeba, J., Edzidzie, J., Ekazama Koto, S., Metandou, J. L., Mossindji, C., Ngoboutseboue, I., Nzemfoule, E., Ingram, D. J., Krapu, C., Baral, A., Saha, S., & Poulsen, J. R. (2023). Fluid hunter motivation in Central Africa: Effects on behaviour, bushmeat and income. *People and Nature*, *5*, 1480–1496. https://doi.org/10.1002/pan3.10502

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*, 457–472. https://doi.org/10.1214/ss/1177011136

Gietl, R., Doneus, M., & Fera, M. (2007). Cost Distance Analysis in an Alpine Environment: Comparison of Different Cost Surface Modules. *Layers of Perception* 35th International Conference on Computer Applications and Quantitative Methods in Archaeology (CAA), Berlin, Germany.

Gilroy, J. J., & Edwards, D. P. (2017). Source-sink dynamics: A neglected problem for landscape-scale biodiversity conservation in the tropics. *Current Landscape Ecology Reports*, *2*(1), 51–60. https://doi.org/10.1007/s40823-017-0023-3

Hines, J. E., Nichols, J. D., & Collazo, J. A. (2014). Multiseason occupancy models for correlated replicate surveys. *Methods in Ecology and Evolution*, *5*(6), 583–591. https://doi.org/10.1111/2041-210X.12186

Hines, J. E., Nichols, J. D., Royle, J. A., MacKenzie, D. I., Gopalaswamy, A. M., Kumar, N. S., & Karanth, K. U. (2010). Tigers on trails: Occupancy modeling for cluster sampling. *Ecological Applications*, *20*(5), 1456–1466. https://doi.org/10.1890/09-0321.1

Ingram, D. J., Froese, G. Z. L., Carroll, D., Bürkner, P. C., Maisels, F., Abugiche, A. S., Allebone-Webb, S., Balmford, A., Cornelis, D., Dethier, M., Dounias, E., Ekodeck, H. G., Emogor, C. A., Fa, J. E., Fonteyn, D., Ghiurghi, A., Greengrass, E., Kümpel, N. F., Lupo, K., … Coad, L. (2025). Regional patterns of wild animal hunting in African tropical forests. *Nature Sustainability*, *8*, 202–214. https://doi.org/10.1038/s41893-024-01494-5

IUCN. (2023). *IUCN SSC guidelines on human-wildlife conflict and coexistence* (1st ed.). IUCN. https://doi.org/10.2305/YGIK2927

Kamgang, S. A., Bobo, K. S., Maisels, F., Ambahe, R. D. D., Ambassa Ongono, D. E., Gonder, M. K., Johnson, P., Marino, J., & Sinsin, B. (2018). The relationship between the abundance of the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*) and its habitat: A conservation concern in Mbam-Djerem National Park, Cameroon. *BMC Ecology*, *18*(1), 40. https://doi.org/10.1186/s12898-018-0199-3

Kühl, H., Maisels, F., Ancrenaz, M., & Williamson, L. (2008). *Best practice guidelines for surveys and monitoring of great ape populations*. IUCN SSC Primate Specialist Group (PSG). https://doi.org/10.2305/IUCN.CH.2008.SSC-OP.36.en

Lauret, V., Labach, H., Authier, M., & Gimenez, O. (2021). Using single visits into integrated occupancy models to make the most of existing monitoring programs. *Ecology*, *102*(12), e03535. https://doi.org/10.1002/ecy.3535

Linder, J. M., Astaras, C., Oates, J. F., Abanyam, P. A., Abwe, E. E., Betobe, E. N., Diotoh, R. O., Dunn, A., Eniang, E. A., Fonkwo, S. N., Hofner, A. N., Imong, I. S., Jost Robinson, C. A., Bobo, K. S., Morgan, B. J., Okon, D. T., & Ormsby, L. J. (2021). Population status of the critically endangered Preuss's red colobus monkey (*Piliocolobus preussi* Matschie 1900) and recommendations for its conservation. *International Journal of Primatology*, *42*(2), 262–282. https://doi.org/10.1007/s10764-021-00202-w

Linder, J. M., & Oates, J. F. (2011). Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biological Conservation*, *144*(2), 738–745. https://doi.org/10.1016/j.biocon.2010.10.023

MacKenzie, D., Nichols, J., Lachman, G., Droege, S., Royle, J. a., & Langtimm, C. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*, 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

MacKenzie, D., Nichols, J. D., Royle, J. a., Pollock, K., Bailey, L. L., & Hines, J. (2017). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence: Second edition*. https://doi.org/10.1016/C2012-0-01164-7

Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E. A., Aba'a, R., Abitsi, G., Ambahe, R. D., Amsini, F., Bakabana, P. C., Hicks, T. C., Bayogo, R. E., Bechem, M., Beyers, R. L., Bezangoye, A. N., Boundja, P., Bout, N., Akou, M. E., … Warren, Y. (2013). Devastating decline of forest elephants in central Africa. *PLoS One*, *8*(3), e59469. https://doi.org/10.1371/journal.pone.0059469

Mancini, A. N., Chandrashekar, A., Lahitsara, J. P., Ogbeta, D. G., Rajaonarivelo, J. A., Ranaivorazo, N. R., Rasoazanakolona, J., Safwat, M., Solo, J., Razafindraibe, J. G., Razafindrakoto, G., & Baden, A. L. (2023). Terrain ruggedness and canopy height predict short-range dispersal in the critically endangered black-and-white ruffed lemur. *Genes (Basel)*, *14*(3), 746. https://doi.org/10.3390/genes14030746

McCollum, K. R., Conway, A. L., Lee, M.-B., & Carroll, J. P. (2017). Occupancy and demographics of red river hog *Potamochoerus porcuson* Tiwai Island, Sierra Leone. *African Journal of Ecology*, *55*(1), 47–55. https://doi.org/10.1111/aje.12314

McGowan, J., Beaumont, L. J., Smith, R. J., Chauvenet, A. L. M., Harcourt, R., Atkinson, S. C., Mittermeier, J. C., Esperon-Rodriguez, M., Baumgartner, J. B., Beattie, A., Dudaniec, R. Y., Grenyer, R., Nipperess, D. A., Stow, A., & Possingham, H. P. (2020). Conservation prioritization can resolve the flagship species conundrum. *Nature Communications*, *11*(1), 994. https://doi.org/10.1038/s41467-020-14554-z

Mfossa, D. M., Abwe, E. E., Whytock, R. C., Morgan, B. J., Huynen, M. C., Beudels-Jamar, R. C., Brotcorne, F., & Tchouamo, R. I. (2022). Distribution, habitat use and human disturbance of gorillas (*Gorilla gorilla*) in the Ebo forest, Littoral Region, Cameroon. *African Journal of Ecology*, *60*(4), 895–907. https://doi.org/10.1111/aje.13052

Mfossa, D. M., Gazagne, E., Abwe, E. E., Vermeulen, C., Michel, B., Mate, J.-P. M., Beudels-Jamar, R. C., Tchouamo, R. I., & Brotcorne, F. (2025). Assessing the impact of community-led conservation approach in the preservation of the cryptic gorilla (*Gorilla gorilla*) population in the Ebo forest, Littoral Region-Cameroon. *Biodiversity and Conservation*, *34*, 1881–1902. https://doi.org/10.1007/s10531-025-03052-7

Moore, J., Uzabaho, E., Musana, A., Uwingeli, P., Hines, J., & Nichols, J. (2021). What is the effect of poaching activity on wildlife species? *Ecological Applications*, *31*, e02397. https://doi.org/10.1002/eap.2397

Morgan, B. J., Abwe, E. E., Dixson, A. F., & Astaras, C. (2013). The distribution, status, and conservation outlook of the drill (*Mandrillus leucophaeus*) in Cameroon. *International Journal of Primatology*, *34*(2), 281–302. https://doi.org/10.1007/s10764-013-9661-4

Nanda, S. S., Nguimdo, V. R. V., Jatmika, S., Sahide, A., Temgoua, L. F., & Tchamba, M. (2023). Communication as a tool for biodiversity conservation: Case of Ebo Forest, Cameroon. *Applied Environmental Education & Communication*, *23*, 71–84. https://doi.org/10.1080/1533015x.2023.2285460

Nguimdo, V. R. V., Abwe, E. E., Betobe, N. E., Morgan, B. J., & Waltert, M. (2025). Rethinking spatial prioritisation for primate conservation in an unprotected intact forest landscape in the gulf of guinea. *Animal Conservation*, 1–15. https://doi.org/10.1111/acv.70045

Nguimdo, V. R. V., Abwe, E. E., Ketchen, M. E., Mfossa, D. M., Abwe, A. E., Betobe, N. E., Tobler, M. W., Maisels, F., Morgan, B. J., Kamp, J., Soofi, M., & Waltert, M. (2026). Immigrant-driven hunting and wildlife decline in an Afrotropical rainforest landscape. *Research Square*. https://doi.org/10.21203/rs.3.rs-6700922/v1

Nguimdo, V. R. V., Abwe, E. E., Morgan, B., Ketchen, M. E., Mfossa, D., Abwe, A. E., Ekole, N. B., Whytock, R., Tobler, M., Kamp, J., Balkenhol, N., Waltert, M., & Soofi, M. (2024). Hunting data collected in the Ebo forest, Cameroon from 2008 to 2023. *Dryad*. https://doi.org/10.5061/dryad.8931zcrzk

Nguimdo, V. R. V., Abwe, E. E., Morgan, B. J., Ketchen, M. E., Mfossa, D. M., Abwe, A. E., Betobe, N. E., Whytock, R. C., Tobler, M. W., Kamp, J., Balkenhol, N., Waltert, M., & Soofi, M. (2025). Long-term monitoring of hunting signs reveals complex spatiotemporal patterns of hunting activities in an unprotected African rainforest. *Diversity and Distributions*, *31*(1), 1–17. https://doi.org/10.1111/ddi.13951

Nguimdo, V. R. V., Tobler, M. W., Abwe, E. E., Ketchen, M. E., Betobe, N. E., Morgan, B. J., Kamp, J., Soofi, M., & Waltert, M. (2026). *Data from: No safe refuge? Contrasting effects of hunting on rainforest mammal persistence and (re)colonisation*. Dryad Digital Repository. https://doi.org/10.5061/dryad.rr4xgxdp3

Nguyen, A., Tilker, A., Le, D., Niedballa, J., Pflumm, L., Pham, X. H., Le, V. S., Luu, H. T., Tran, V. B., Kramer-Schadt, S., Sollmann, R., & Wilting, A. (2024). Ground-dwelling mammal and bird diversity in the southern Annamites: Exploring complex habitat associations and the ghost of past hunting pressure. *Conservation Science and Practice*, *6*(4), e13093. https://doi.org/10.1111/csp2.13093

Novaro, A. J., Funes, M. C., & Walker, R. S. (2005). An empirical test of source-sink dynamics induced by hunting. *Journal of Applied Ecology*, *42*(5), 910–920. https://doi.org/10.1111/j.1365-2664.2005.01067.x

Oberosler, V., Tenan, S., Zipkin, E. F., & Rovero, F. (2020). When parks work: Effect of anthropogenic disturbance on occupancy of tropical forest mammals. *Ecology and Evolution*, *10*(9), 3881–3894. https://doi.org/10.1002/ece3.6048

Olaleru, F., Agbaosi, J., Tijani, O., Emmanuel, M., Agidi, H., & Otusanya, O. (2023). Assessment of Mona monkey (*Cercopithecus mona*) population dynamics, human-monkey interactions, and land use changes in selected areas of Lagos Megacity, Nigeria. *African Primates*, *17*, 63–76.

Pardo, J. M., Cruz, P., Moya, S., Pizzio, E., Foletto, F., Robino, F., Aquino, J., Costa, S., Barros, Y., Cleo, F., Di Bitetti, M. S., Iezzi, M. E., Paviolo, A., & De Angelo, C. (2022). Predicting poaching hotspots in the largest remnant of the Atlantic Forest by combining passive acoustic monitoring and occupancy models. *Biological Conservation*, *272*, 109600. https://doi.org/10.1016/j.biocon.2022.109600

Parsons, A. W., Wikelski, M., Keeves von Wolff, B., Dodel, J., & Kays, R. (2022). Intensive hunting changes human-wildlife relationships. *PeerJ*, *10*, e14159. https://doi.org/10.7717/peerj.14159

Peach, M. A., Cohen, J. B., Frair, J. L., & Tulloch, A. (2017). Single-visit dynamic occupancy models: An approach to account for imperfect detection with atlas data. *Journal of Applied Ecology*, *54*(6), 2033–2042. https://doi.org/10.1111/1365-2664.12925

Pillay, R., Miller, D. A. W., Raghunath, R., Joshi, A. A., Mishra, C., Johnsingh, A. J. T., & Madhusudan, M. D. (2022). Using interview surveys and multispecies occupancy models to inform vertebrate conservation. *Conservation Biology*, *36*(2), e13832. https://doi.org/10.1111/cobi.13832

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. 3rd International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, 20-22 March 2003.

Plummer, M. (2025). rjags: Bayesian Graphical Models using MCMC. https://CRAN.R-project.org/package=rjags

Plumptre, A. J., Baisero, D., Brooks, T. M., Buchanan, G., Butchart, S. H. M., Bowser, A., Boyd, C., Carneiro, A. P. B., Davies, T., Elliot, W., Foster, M., Langhammer, P. F., Marnewick, D., Matiku, P., McCreless, E., Raudsepp-Hearne, C., Tordoff, A. W., Azpiroz, A. B., Trisurat, Y., & Upgren, A. (2024). Targeting site conservation to increase the effectiveness of new global biodiversity targets. *One Earth*, *7*(1), 11–17. https://doi.org/10.1016/j.oneear.2023.12.007

Potapov, P., Hansen, M. C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., & Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances*, *3*(1), e1600821. https://doi.org/10.1126/sciadv.1600821

QGIS Development Team. (2024). *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. (Version 3.34.6). http://qgis.osgeo.org

R Core Team. (2025). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rabus, B., Eineder, M., Roth, A., & Bamler, R. (2003). The shuttle radar topography Mission—A new class of digital elevation models acquired by Spaceborne Radar. *ISPRS Journal of Photogrammetry and Remote Sensing*, *57*, 241–262. https://doi.org/10.1016/S0924-2716(02)00124-7

Riley, S., Degloria, S., & Elliot, S. D. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Internation Journal of Science*, *5*, 23–27.

Rist, J., Milner-Gulland, E. J., Cowlishaw, G., & Rowcliffe, J. M. (2009). The importance of hunting and habitat in determining the abundance of tropical forest species in Equatorial Guinea. *Biotropica*, *41*(6), 700–710. https://doi.org/10.1111/j.1744-7429.2009.00527.x

Romo, C., Torres, J., Arroyo, G., & León Salas, A. (2022). A new approach for computing anisotropic cost surfaces and least-cost paths. *Global and Planetary Change*, *10*, 2334–2455. https://doi.org/10.15640/jges.v10n1a1

Rovero, F., Martin, E., Rosa, M., Ahumada, J. A., & Spitale, D. (2014). Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. *PLoS One*, *9*(7), e103300. https://doi.org/10.1371/journal.pone.0103300

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Semper-Pascual, A., Sheil, D., Beaudrot, L., Dupont, P., Dey, S., Ahumada, J., Akampurira, E., Bitariho, R., Espinosa, S., Jansen, P. A., Lima, M. G. M., Martin, E. H., Mugerwa, B., Rovero, F., Santos, F., Uzabaho, E., & Bischof, R. (2023). Occurrence dynamics of mammals in protected tropical forests respond to human presence and activities. *Nature Ecology & Evolution*, *7*(7), 1092–1103. https://doi.org/10.1038/s41559-023-02060-6

Snider, M. H., Helgen, K. M., Young, H. S., Agwanda, B., Schuttler, S., Titcomb, G. C., Branch, D., Dommain, R., & Kays, R. (2024). Shifting mammal communities and declining species richness along an elevational gradient on Mount Kenya. *Ecology and Evolution*, *14*(4), e11151. https://doi.org/10.1002/ece3.11151

Strindberg, S., Maisels, F., Williamson, E. A., Blake, S., Stokes, E. J., Aba'a, R., Abitsi, G., Agbor, A., Ambahe, R. D., Bakabana, P. C., Bechem, M., Berlemont, A., Bokoto de Semboli, B., Boundja, P. R., Bout, N., Breuer, T., Campbell, G., De Wachter, P., Ella Akou, M., … Wilkie, D. S. (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western equatorial Africa. *Science Advances*, *4*(4), eaar2964. https://doi.org/10.1126/sciadv.aar2964

Tagg, N., Willie, J., Petre, C. A., & Haggis, O. (2013). Ground night nesting in chimpanzees: New insights from central chimpanzees (*Pan troglodytes troglodytes*) in south-East Cameroon. *Folia Primatol (Basel)*, *84*(6), 362–383. https://doi.org/10.1159/000353172

Tilker, A., Niedballa, J., Viet, H. L., Abrams, J. F., Marescot, L., Wilkinson, N., Rawson, B. M., Sollmann, R., & Wilting, A. (2024). Addressing the southeast Asian snaring crisis: Impact of 11 years of snare removal in a biodiversity hotspot. *Conservation Letters*, *17*(4), e13021. https://doi.org/10.1111/conl.13021

Tobler, M. W., Garcia Anleu, R., Carrillo-Percastegui, S. E., Ponce Santizo, G., Polisar, J., Zuñiga Hartley, A., & Goldstein, I. (2018). Do responsibly managed logging concessions adequately protect jaguars and other large and medium-sized mammals? Two case studies from Guatemala and Peru. *Biological Conservation*, *220*, 245–253. https://doi.org/10.1016/j.biocon.2018.02.015

van Vliet, N., Milner-Gulland, E., Bousquet, F., Saqalli, M., & Nasi, R. (2010). Effect of small-scale heterogeneity of prey and hunter distributions on the sustainability of bushmeat hunting. *Conservation Biology*, *24*, 1327–1337. https://doi.org/10.1111/j.1523-1739.2010.01484.x

Walters, G., Sayer, J., Boedhihartono, A. K., Endamana, D., & Angu Angu, K. (2021). Integrating landscape ecology into landscape practice in Central African Rainforests. *Landscape Ecology*, *36*(8), 2427–2441. https://doi.org/10.1007/s10980-021-01237-3

Waltert, M., Lien, Faber, K., & Mühlenberg, M. (2002). Further declines of threatened primates in the Korup project area, south-west Cameroon. *Oryx*, *36*(3), 257–265. https://doi.org/10.1017/s0030605302000479

Wang, F., McShea, W. J., Li, S., Wang, D., & Lahoz-Monfort, J. (2018). Does one size fit all? A multispecies approach to regional landscape corridor planning. *Diversity and Distributions*, *24*(3), 415–425. https://doi.org/10.1111/ddi.12692

White, L., & Edwards, A. (2000). *Conservation research in the African rain Forest: A technical handbook*. Wildlife Conservation Society.

Whytock, R. C., Abwe, E. E., Mfossa, D. M., Ketchen, M. E., Abwe, A. E., Nguimdo, V. R. V., Maisels, F., Strindberg, S., & Morgan, B. J. (2021). Mammal distribution and trends in the threatened Ebo 'intact forest landscape', Cameroon. *Global Ecology and Conservation*, *31*, e01833. https://doi.org/10.1016/j.gecco.2021.e01833

Whytock, R. C., Buij, R., Virani, M. Z., & Morgan, B. J. (2014). Do large birds experience previously undetected levels of hunting pressure in the forests of Central and West Africa? *Oryx*, *50*(1), 76–83. https://doi.org/10.1017/s0030605314000064

Wong, S. T., Guharajan, R., Petrus, A., Jubili, J., Lietz, R., Abrams, J. F., Hon, J., Alen, L. H., Ting, N. T. K., Wong, G. T. N., Tchin, L. T., Bijack, N. J. C., Kramer-Schadt, S., Wilting, A., & Sollmann, R. (2022). How do terrestrial wildlife communities respond to small-scale Acacia plantations embedded in harvested tropical forest? *Ecology and Evolution*, *12*(9), e9337. https://doi.org/10.1002/ece3.9337

Zurell, D., König, C., Malchow, A.-K., Kapitza, S., Bocedi, G., Travis, J., & Fandos, G. (2022). Spatially Explicit Models for decision-Making in animal Conservation and restoration. *Ecography*, *2022*(4), e05787. https://doi.org/10.1111/ecog.05787

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

SUPPORTING INFORMATION

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

Text S1. Code for a dynamic multi-species occupancy model with correlated detections.

Table S1. Number of detections of each species on 200 m segments along recce lines.

Table S2. Number of detections of each Hunting signs on 200 m segments along recce lines.

Table S3. Species-specific occupancy probability (Mean) per year (2016–2023) with the standard deviation (SD) and the lower and upper limits of the 95% credible interval.

Table S4. Beta coefficients (Estimate), standard deviation (SD) and 95% and 75% credible intervals of the effect of covariates on the occupancy of different wildlife species.

Table S5. Beta coefficients (Estimate), standard deviation (SD) and 95% and 75% credible intervals of the effect of covariates on the persistence probability of different wildlife species.

Table S6. Beta coefficients (Estimate), standard deviation (SD) and 95% and 75% credible intervals of the effect of covariates on the colonisation probability of different wildlife species.

How to cite this article: Nguimdo, V. R. V., Tobler, M. W., Abwe, E. E., Ketchen, M. E., Betobe, N. E., Morgan, B. J., Kamp, J., Soofi, M., & Waltert, M. (2026). No safe refuge? Contrasting effects of hunting on rainforest mammal persistence and (re)colonisation. *Journal of Applied Ecology*, *63*, e70434. https://doi.org/10.1111/1365-2664.70434