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Spatiotemporal patterns of elephant and chimpanzee occurrence amid hunting in an unprotected African rainforest

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Abstract

Anthropogenic pressures are driving major declines in mammals, especially in unprotected areas. However, our understanding of how mammals coexist with humans and adapt to hunting in human-dominated landscapes remains limited. Here, we used long-term data (2008–2023) from an unprotected biodiversity hotspot facing hunting pressure and impending logging to model how Nigeria-Cameroon chimpanzees and African forest elephants respond to hunting. We found that elephant occurrence was mostly associated with higher elevations and greater village distance, declined with increasing terrain ruggedness, and was not sensitive to hunting. In contrast, chimpanzee occurrence increased strongly with terrain ruggedness, moderately with elevation, and non-linearly with village distance. It decreased with increasing hunting intensity. During 2008–2023, elephant occurrence remained generally stable but increased in high elevations and near rivers. Concurrently, chimpanzee occurrence declined, especially in areas with high hunting intensity and the species occurred increasingly away from villages. Overall, our findings suggest that hunting may predominately impact chimpanzees. Meanwhile, elephants may be more vulnerable to industrial logging that began after this study, likely outcompeting them in flatter areas. Our results highlight the urgent need to identify and secure key areas for both species to ensure their long-term persistence alongside other land uses in this biodiversity hotspot.

KEYWORDS

African forest elephant, human-wildlife coexistence, Nigeria-Cameroon chimpanzee, response to hunting, spatiotemporal patterns, unprotected rainforest

1 | INTRODUCTION

Large flagship mammal species such as great apes and elephants play a crucial role in biodiversity conservation; they are often used as flagships for conservation awareness campaigns both at local and global scales (Chapman et al., 2022; Verissimo et al., 2011). Their role as ecological engineers and seed dispersers is critical for the integrity, the regeneration and the long-term persistence of their habitat (Abernethy et al., 2013; Bennett & Robinson, 2023; Strindberg et al., 2018). Additionally, public support for the conservation of these species also benefits other wildlife species that share the same habitat (McGowan et al., 2020; Morgan et al., 2023). Furthermore, the economic value of the flagship species is non-negligeable as they contribute to both local and national revenues through scientific research and recreational tourism in some countries (Ardiantiono et al., 2021; Eppley et al., 2024; Gobush et al., 2021; Mitani et al., 2024). However, despite their socioeconomic and ecological values, as well as the high protection status they benefit from globally and in the countries where they occur, those species remain highly threatened by habitat loss, habitat degradation and hunting (Fa et al., 2014; Junker et al., 2012; Maisels et al., 2013; Strindberg et al., 2018). For instance, the African forest elephant (*Loxodonta cyclotis*) was reported to have declined by more than 60% and to have lost 30% of its geographic range between 2002 and 2011 as a result of human population growth and related infrastructure development, as well as poaching and insufficient law enforcement (Maisels et al., 2013); a more recent study revealed a 90% decline in the density of the species between 1964 and 2016 (Edwards et al., 2024).

The suitable habitats of African forest elephants and great apes are expected to witness a considerable degradation in the near future (Gobush et al., 2021; Junker et al., 2012; Strindberg et al., 2018). In Central Africa, while protected areas may provide a certain level of protection to wildlife (Benitez-Lopez et al., 2019; Correa et al., 2024), the major proportion of the distribution range occupied by chimpanzees and elephants lies outside areas with formal protection (Doumenge et al., 2021; Strindberg et al., 2018; Zwerts et al., 2024). Consequently, unprotected areas are increasingly recognized as crucial in achieving national and global biodiversity conservation goals (Cook, 2024; Donald et al., 2019; Estrada, 2013), not only due to their biodiversity importance, but also because protected areas alone cannot maintain viable wildlife populations, especially for wide-ranging species such as elephants (Blake et al., 2008; Blanco et al., 2020). Therefore, future conservation interventions should also aim to preserve wildlife species in these human-dominated landscapes, which are often subject to a wide range of unsustainable activities leading to habitat loss and fragmentation (Mitani et al., 2024; Potapov et al., 2017; Shapiro et al., 2023). Even in areas with relatively intact forest cover across Central Africa, bushmeat hunting is often rampant, and its highly cryptic nature allows it to go undetected, leading to catastrophic consequences for many wildlife species (Abernethy et al., 2013; Benitez-Lopez et al., 2019). In such areas, effective conservation planning depends on a clear understanding of how wildlife responds and adapts to human pressures (Hockings et al., 2015; Muthiuru et al., 2024; Wall et al., 2021).

While numerous studies have investigated the factors influencing the spatial distribution of forest elephants and chimpanzees (Fotang et al., 2021; Junker et al., 2012; Maisels et al., 2013; Strindberg et al., 2018; Wall et al., 2021), research has been considerably biased toward protected areas—often the only areas where long-term monitoring programs exist (Brand et al., 2020). Some taxa have also been highly neglected in the literature. For instance, African forest elephants have suffered from considerable underrepresentation in scientific research compared to their savanna counterparts. This is partly due to political instability in the countries across their range (Blake et al., 2007; Gross & Heinsohn, 2023; Nneji et al., 2023), as well as their cryptic nature and the challenges posed by their often inaccessible forest habitats (Blake & Maisels, 2023; Brand et al., 2020). Research on chimpanzees has similarly been skewed, with most long-term studies focusing on populations habituated to humans which are easier to follow, while wild and cryptic populations remain largely neglected (Hockings et al., 2015; Mayoukou et al., 2024; Wessling et al., 2020). Of particular concern is the Nigeria-Cameroon chimpanzee subspecies (*Pan troglodytes ellioti*) which occurs in highly fragmented habitats from western Cameroon to the southwest of Nigeria (Oates et al., 2016). This subspecies is reported as the most threatened and the least studied of all four subspecies of chimpanzees, with probably less than 6000 individuals remaining (Abwe, 2018; Kamgang et al., 2018;Morgan et al., 2011; Oates et al., 2016). Important populations of the subspecies also inhabit unprotected areas where they face intense human pressures including habitat conversion and hunting (Morgan et al., 2011; Oates et al., 2016). Consequently, our understanding of the spatial and temporal patterns of the Nigeria-Cameroon chimpanzee and African forest elephant remains limited, particularly in human-dominated landscapes.

The Ebo forest is a globally recognized but unprotected biodiversity hotspot in Central African rainforests (Whytock et al., 2021) and represents one of the main tracts of remaining intact forest within the Gulf of Guinea. However, it is located in an area recognized as having a high defaunation index caused by bushmeat hunting to satisfy the demand in neighboring major cities (Fa et al., 2014). Industrial logging activities are also imminent in the Ebo forest as it was classified into logging concessions by the Government of Cameroon in April 2023 (Nguimdo et al., 2025). Previous research has reported the likely hunting-induced local extinction of several mammal species in the Ebo forest, while also confirming the persistence of the Endangered Nigeria-Cameroon chimpanzee and the Critically Endangered African forest elephant (Abwe et al., 2019; Whytock et al., 2021). Whytock et al. (2021) investigated the spatial patterns of both species across the forest but only modeled their occupancy as a function of road distance and elevation, assuming a linear relationship between wildlife occupancy and anthropogenic variables. The study also omitted other potentially important factors such as terrain ruggedness and hunting intensity. A recent study revealed increasing hunting pressure in the most remote parts of the Ebo forest (Nguimdo et al., 2025), which could have substantial impacts on the spatial and temporal dynamics of wildlife across the area. As flagship species in the landscape, Nigeria-Cameroon chimpanzees and African forest elephants deserve increased research and conservation attention to ensure their persistence in the area, particularly given the industrial logging activities that started after the data collection phase of this study. The availability of long-term monitoring data offers a unique opportunity to understand how these species have managed to persist and coexist with humans despite increasing bushmeat hunting in the area.

Here, using data collected systematically across the Ebo forest from 2008 to 2023, we tested the effect of different environmental (distance to rivers, elevation, terrain ruggedness) and anthropogenic (distance to the nearest village, hunting intensity) factors on the occurrence of elephants and chimpanzees. We also examined whether the two species have shifted or extended their occurrence along the gradients defined by those environmental and anthropogenic factors over time. Finally, we discussed the implications of our findings for conservation and their significance in the context of industrial logging in the Ebo forest, which was about to start when we were collecting the data for this study. By studying both species simultaneously, we provide comprehensive information necessary to account simultaneously for the spatial and temporal patterns of both species in landscape-level conservation planning.

2 | METHODS

2.1 | Study area

The Ebo forest is located in the Littoral Region of Cameroon, Central Africa, spanning approximately 1500 km^2 (Abwe, 2018), and covering half of the Yabassi Key Biodiversity Area (Whytock et al., 2021). It is globally recognized for its rich biodiversity, but is not legally protected and is therefore exposed to high hunting pressure, partly related to its location, only 50 km from Douala, a major city in Central Africa and an important bushmeat market (Benitez-Lopez et al., 2019; Fa et al., 2014; Morgan et al., 2011). The Ebo forest is also surrounded by more than 40 human communities, who rely heavily on forest resources for their livelihoods (Mfossa et al., 2025; Whytock et al., 2021). Conservation efforts in the landscape have largely focused on engaging local communities to help preserve wildlife, focusing on iconic mammals such as gorillas, chimpanzees, and forest elephants which serve as flagship species to raise awareness (Abwe et al., 2015; Mfossa et al., 2018, 2025). In 2020, the Government of Cameroon decided to open the Ebo forest to industrial timber exploitation (Nanda et al., 2023; Whytock et al., 2021), which began after the data presented in this research were collected. The logging activities are expected to exacerbate the already high hunting pressures, while disturbing the spatial patterns of wildlife, including flagship species such as chimpanzees and elephants. Nevertheless, the decrees establishing the logging concessions recognize the need to balance the economic, social, and conservation interests in the landscape (Decree No 2023/01630/PM and 2023/01631/PM of 27 April 2023). Therefore, spatially explicit information is critical to help guide conservation planning in the area, to ensure the long-term survival of these species (IUCN, 2023; Walters et al., 2021).

2.2 | Data collection

We collected wildlife data along parallel recce lines placed 4 km apart, across the entire Ebo forest totalling 345 km (Figure 1) (Nguimdo et al., 2025; Whytock et al., 2021). All recce lines were surveyed eight times between 2008 and 2023 (2008, 2012, 2016, 2017, 2018, 2021, 2022, and 2023). Each recce line was surveyed once every year, generally during the dry season (from October to April, with the initial year considered as the year of the survey). The team consisted of 2–3 trained observers moving at approximately 1 km per hour (White & Edwards, 2000; Whytock et al., 2021; Zausa et al., 2023). During the surveys, we recorded all direct sightings and vocalizations of chimpanzees and elephants. Both sides of the recce lines were searched within 1 m for indirect signs (e.g., footprints, dung, feeding signs and nesting sites). We also recorded evidence of human activities, including hunting signs such as snares, shotgun cartridges, machetes cuts, shrub breaks, footprints, hunting

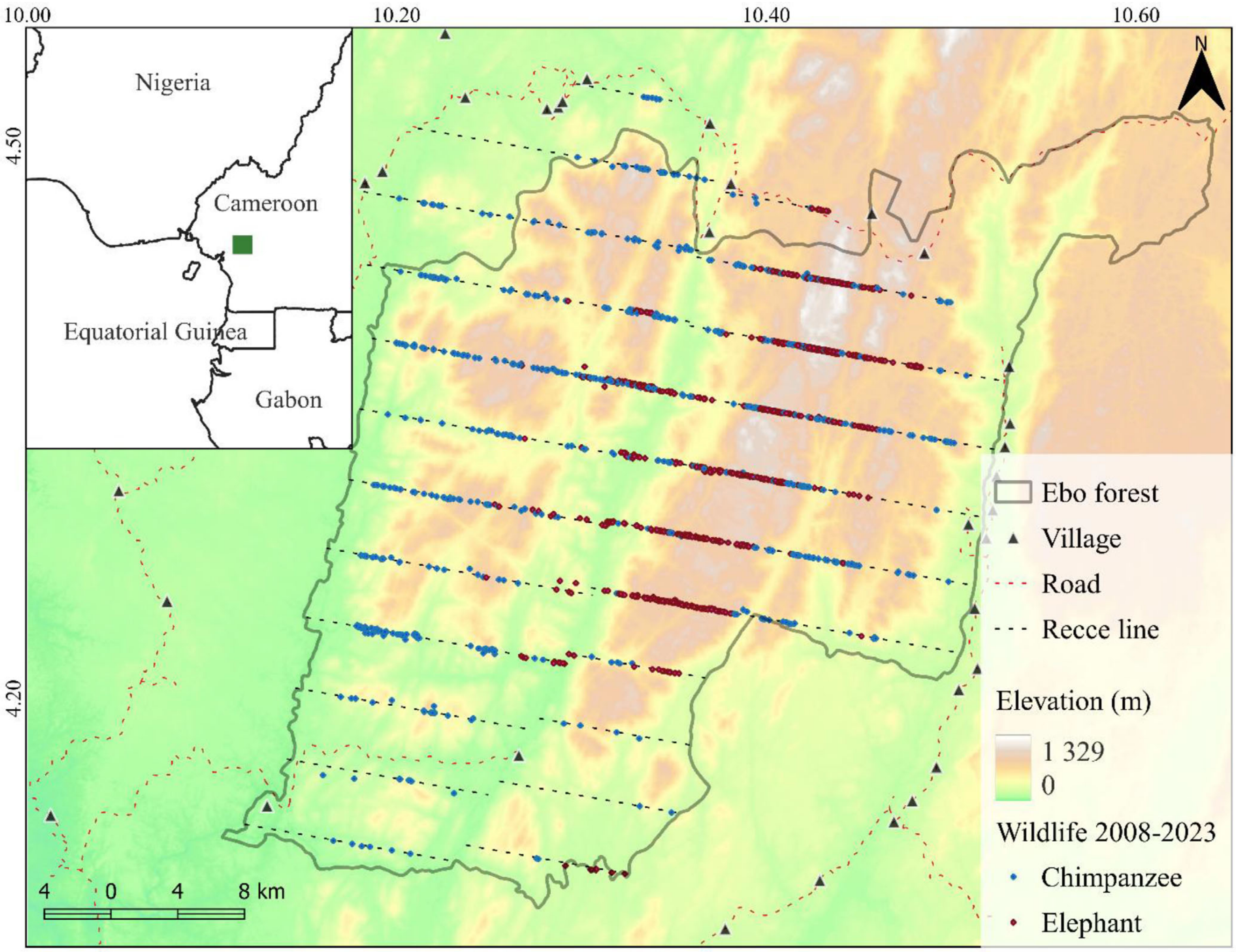

FIGURE 1 Map of the Ebo forest showing its location in Cameroon, the villages around the forest, and the surveyed recce lines.

trails and direct encounters with hunters. Geographic coordinates for all signs were recorded. Nguimdo et al. (2025) provide more details on the collection of hunting signs.

2.3 | Data preparation

We assigned all the annually collected occurrence data on chimpanzees and elephants to 1×1 km grid cells overlaid across the entire Ebo forest. Additionally, we calculated the relative abundance of hunting signs in each cell, used as a proxy of hunting intensity. To do this, we divided the number of hunting signs (shotgun cartridge, snare, sign of passage, hunting trail and direct encounter with hunters) by the survey effort (i.e., the distance in kilometer walked within each grid cell) (Maisels et al., 2013). Furthermore, we obtained spatial covariates related to environmental and anthropogenic factors for each grid cell. Using the shapefiles from the GIS database of Cameroon (MINFOF, 2013), we calculated the Euclidean distance from the center of each grid cell to the nearest village, road and river (in kilometer). We measured the mean elevation of each grid cell (in meter) from the Shuttle Radar Topographic Mission layer of 30 m resolution (Rabus et al., 2003). We also measured the mean terrain ruggedness index in each cell to account for the topographic heterogeneity (Riley et al., 1999). We performed all these spatial data computations using QGIS Version 3.34.6 (QGIS Development Team, 2024).

2.4 | Data analysis

Prior to the analyses, we standardized (mean 0 and standard deviation of 1) all the covariates using the *scale* function in R (Schielzeth, 2010). We also checked all covariates for multi-collinearity using Pearson's correlation coefficient test and refrained to include a pair of covariates in the same model if their correlation coefficient was larger than the cut-off point of $|r| > 0.7$ (Dormann et al., 2012).

We fitted Bayesian generalized linear mixed models with Bernoulli distribution to assess the determinants of space use by elephants and chimpanzees across the Ebo forest. We modeled each species separately. Specifically, we fitted the linear effects of hypothesized covariates including distance to the nearest village, distance to the nearest river, elevation, terrain ruggedness index and hunting intensity (i.e., the relative abundance index of hunting signs). Given the known complex distribution of hunting activities across the Ebo forest (Nguimdo et al., 2025), we included the quadratic term of the distance to the village to account for potential nonlinear patterns in species occurrence along the village-distance gradient. As we wanted to assess changes in the occurrence of chimpanzees and elephants along various gradients over time in response to increasing hunting activities, we included the interaction terms between year and the distance to the village, year and terrain ruggedness index, year and the distance to the river, and year and hunting intensity (Nguimdo et al., 2025). Overall, we fitted six competing models for each species. In all models, we included the grid cell ID as a random effect to account for potential pseudo-replication. We also included the survey effort within each grid cell as an offset to account for variations in sampling effort across grid cells. Furthermore, we checked potential spatial autocorrelation in the residuals of the models using the Moran's I through the "DHARMa" (Hartig, 2022) and 'DHARMa. helpers' packages (Rodríguez-Sánchez, 2024).

All models were fitted using "brms" package (Bürkner, 2017) in R version 4.4.0 (R Core Team, 2024). We used 4000 iterations with 4 parallel Markov chain Monte Carlo chains with 2000 warm-ups each (Bürkner, 2017). We used weakly informative priors for our models, assuming normal distribution with a mean of 0 and a standard deviation of 1 (Gatiso et al., 2022; Kalan et al., 2020). We checked the convergence of the four chains using the Gelman-Rubin's convergence "Rhat" value (Brooks & Gelman, 1998). We selected the best fitting model using the Leave-One-Out Cross-Validation technique and only used the top model of each response variable for inferences (Vehtari et al., 2016). The effects of covariates were considered substantial if their 95% Bayesian credible interval did not overlap with 0, and moderate if only their 75% Bayesian credible interval did not include 0 (Figure 2) (Nguyen et al., 2024; Simo et al., 2023).

3 | RESULTS

Due to the high correlation coefficient between the distance to the nearest road and the distance to the nearest village ($r = 0.96$), we excluded the distance to the nearest road from the analyses. All the model converged with no divergent transition after warmup and all "Rhat" were below 1.01 (Table S1). The results of Moran's I indicated an absence of spatial autocorrelation in the residuals of the models (p-value = .3224).

3.1 | Spatiotemporal patterns of elephant occurrence

Elevation was the most important predictor in the elephant occurrence model across the Ebo forest, with a strong positive and substantial effect ($\beta = 1.66$, 95% Bayesian Credible Interval, BCI = 1.29–2.05; Figures 2, 3a). The distance to the nearest village also had a positive and substantial effect on elephant occurrence ($\beta = 1.23$, 95% BCI = 0.78–1.73). The quadratic term of distance to the nearest village had a negative but non-substantial effect, suggesting a non-linear increase in elephant occurrence along the village-distance gradient (Figure 3c). Conversely, the probability of elephant occurrence decreased substantially with increasing terrain ruggedness index ($\beta = -0.60$, 95% BCI = −0.99 to −0.22), and moderately with increasing distance to the nearest river ($\beta = -0.30$, 95% BCI = −0.65 to −0.02; Figure 3e). The occurrence probability of elephants tended to increase over the years, but this trend was not substantial ($\beta = 0.15$, 95% BCI = −0.13, 0.43; Table S1). We found no evidence of the effect of hunting intensity on the occurrence of elephants across the Ebo forest. Our results further indicated that over the 16 years covered by this study (2008–2023), the occurrence probability of elephants increased substantially in areas with high elevation ($\beta = 0.58$, 95% BCI = 0.38–0.78; Figure 3b) and decreased at greater distances from villages, with a substantial tendency for a mid-village distance peak in elephant occurrence (Table S1, Figure 3d). Elephant occurrence also increased substantially along the rivers during the same period (Figure 3f).

3.2 | Spatiotemporal patterns of chimpanzee occurrence

The terrain ruggedness index was the strongest predictor of chimpanzee occurrence, with a positive and substantial effect on its occurrence probability ($\beta = 0.94$, 95% BCI = 0.70–1.18; Figures 2, 4a). Similarly, elevation had a positive and substantial effect on chimpanzee occurrence ($\beta = 0.42$, 95% BCI = 0.19–0.64; Figure 4b). The effect of distance to the nearest village was also positive and substantial ($\beta = 0.67$, 95% BCI = 0.44–0.92).

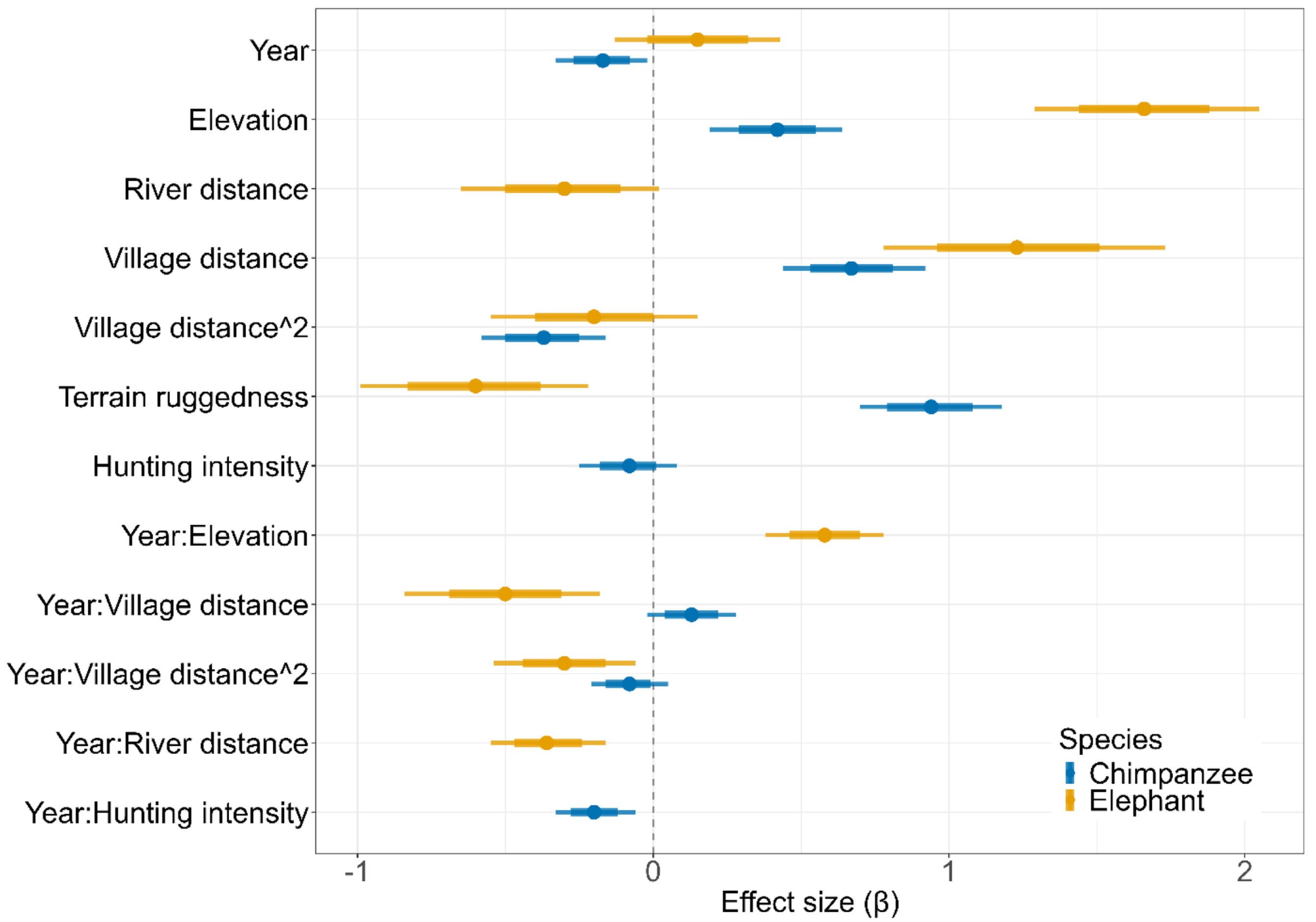

FIGURE 2 Standardized beta coefficients (posterior means, solid dots), 95% credible intervals (thin lines) and 75% credible intervals (thick lines) of the effect of the covariates from the best-fitting Bayesian generalized linear mixed models for elephants (orange color) and chimpanzees (blue color) in the Ebo forest, Cameroon, based on data collected between 2008 and 2023. The circumflex "^" denotes the quadratic function and the colon ":" specifies the interaction between two covariates.

However, the relationship was non-linear, with a negative and substantial effect of the quadratic term ($\beta = -0.37$, 95% BCI $= -0.58$ to -0.16), and a mid-distance peak in the occurrence of chimpanzees at approximately 10 km from the village (Figure 4c). Moreover, we found a negative, but non-substantial effect of hunting intensity on chimpanzee occurrence probability ($\beta = -0.08$, 95% BCI $= -0.25$ to 0.08; Table S1, Figure 4e). The occurrence probability of chimpanzees decreased substantially over the years from 2008 to 2023 ($\beta = -0.17$, 95% BCI $= -0.33$ to -0.02; Figure 2). During the same period, chimpanzees tended to move away from villages, as evidenced by the positive coefficient of the interaction between the year trend and village distance ($\beta = 0.13$, 95% BCI $= -0.02$ to 0.28). The interaction between the year trend and hunting intensity was negative and substantial ($\beta = -0.20$, 95% BCI $= -0.33$ to -0.06), suggesting that chimpanzee occurrence declined over time in areas with high hunting intensity (Figures 2 and 4f).

4 | DISCUSSION

4.1 | Spatiotemporal patterns of forest elephants

Our results revealed a strong and positive relationship between the occurrence of forest elephants and elevation in the Ebo forest, which is consistent with findings from Whytock et al. (2021). Conversely, Brittain et al. (2018) found a negative effect of elevation on the occupancy of forest elephants in the south east of Cameroon, while Maisels et al. (2013) did not include topography among the covariates expected to influence the distribution of forest elephants across Central Africa. Elephant distribution in the Ebo forest seems to be mostly restricted to the north-eastern part of the forest (Whytock et al., 2021), an area with generally higher elevations (see Figure 1). From 2008 to 2023, the occurrence probability of elephants tended to increase, confirming findings from

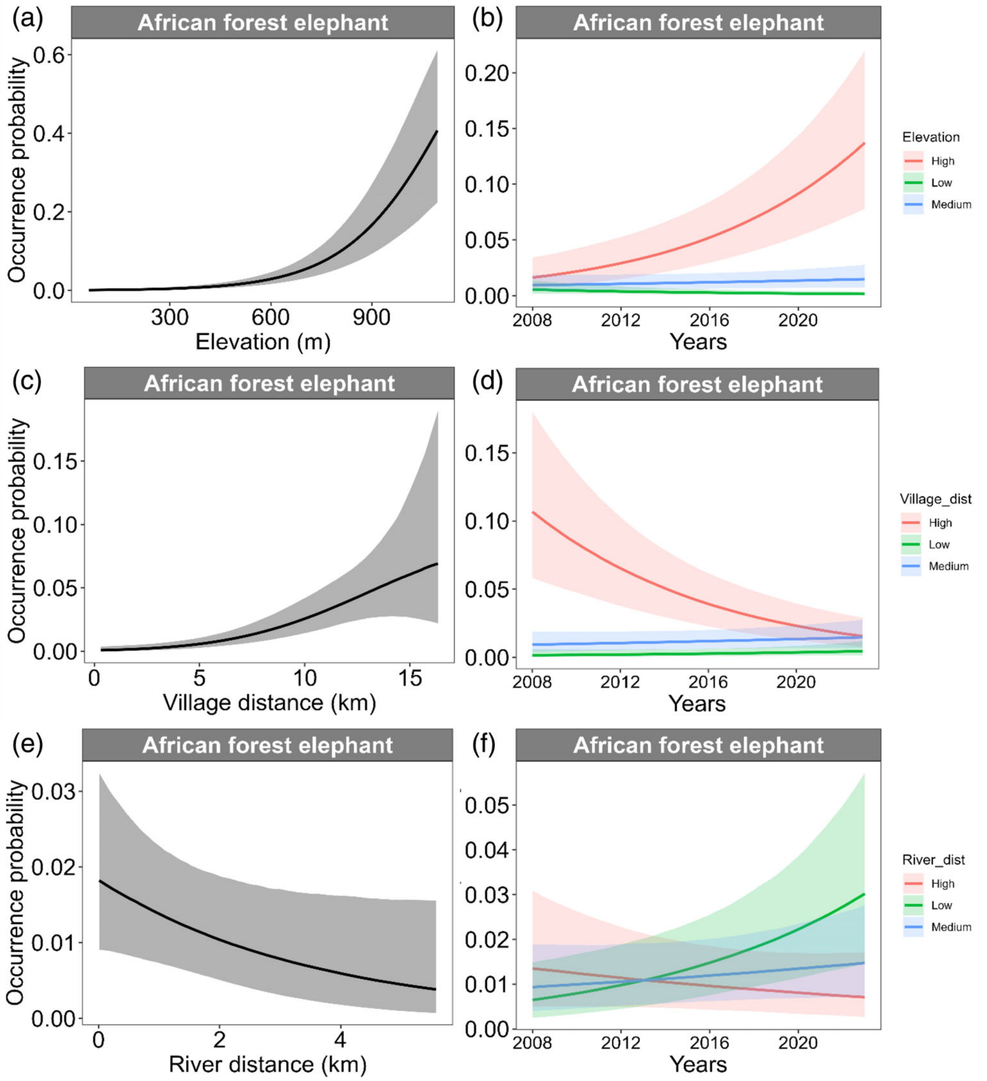

FIGURE 3 Effects of elevation, village distance, village distance (with quadratic term), and river distance on the occurrence probability of elephants in the Ebo forest, Cameroon, based on data collected between 2008 and 2023. Estimates were derived from the best fitting Bayesian generalized linear mixed model. The solid lines denote the posterior mean estimate, and the shaded areas indicate the 95% Bayesian credible interval.

(Whytock et al., 2021), but this increase was mainly limited to areas of high elevation. The north-eastern part of the Ebo forest corresponds to the site where community-based conservation interventions are ongoing since 2012 (Abwe et al., 2015; Mfossa et al., 2018, 2025). This area is also the most remote part of the Ebo forest, with poorly maintained roads that are almost inaccessible from the nearest urban centers during the rainy season. Therefore, it is possible that the topographic and geographic inaccessibility as well as the community-based conservation interventions in the area have preserved its population of elephants.

Interestingly, our results showed that elephant occurrence decreased substantially with increasing terrain ruggedness. This suggests that within the areas of high elevation inhabited by elephants in the Ebo forest, they still prefer relatively flat terrain. Terrain ruggedness has not been considered in most studies investigating the determinants of elephant distribution (e.g., Whytock et al. (2021), Maisels et al. (2013), Brittain et al. (2018), Yackulic et al. (2011)). As large-bodied animals, it is likely that elephants would have difficulties moving in rugged areas, which necessitate climbing and descending steep slopes (Ngama et al., 2019). Consequently, they may not be able to evade hunting pressure. Our results also showed that elephants preferred areas along the rivers, consistent with findings from Brittain et al. (2018). These riverine areas are usually relatively flatter, potentially easing elephant movements. In addition, elephant preference for riverine habitats may also be related to higher water and food resource availability (Cavada et al., 2019; Wall et al., 2021).

Our results also revealed a positive and substantial effect of the distance to the nearest village on the occurrence probability of elephants. Noting that the distance to the nearest village was very strongly correlated with the distance to the nearest road ($r = 0.96$), our results are therefore consistent with previous studies on forest elephants in Cameroon and Central Africa (Blake et al., 2007; Brittain et al., 2018; Whytock et al., 2021;

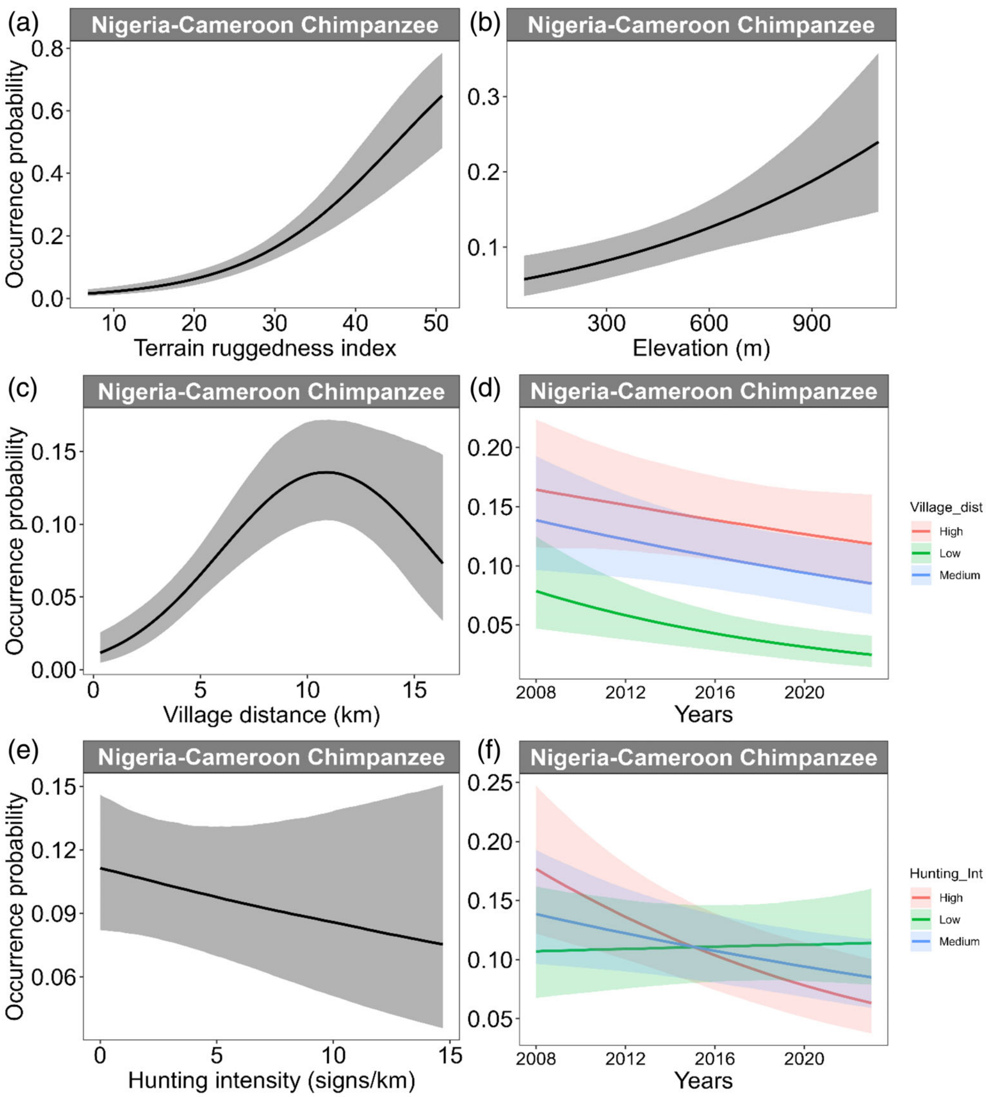

FIGURE 4 Effects of terrain ruggedness index, village distance (with quadratic term), elevation and hunting intensity on the occurrence probability of chimpanzees in the Ebo forest, Cameroon, based on data collected between 2008 and 2023. Estimates were derived from the best fitting Bayesian generalized linear mixed model. The solid lines represent the posterior mean and the shaded areas indicate the 95% Bayesian credible intervals.

Yackulic et al., 2011). However, our analyses also showed that this relationship was non-linear and changed over our study period (2008–2023), with elephant occurrence decreasing in the center of the forest and slightly increasing mid-distance to the nearest village with time. A recent study reported increasing hunting activities in the center of the Ebo forest and attributed it to non-native hunters settling in the landscape and hunting in the most remote parts of the forest (Nguimdo et al., 2025). We believe that this increase in hunting intensity, which is often accompanied by the creation of semi-permanent hunting camps regularly occupied by hunters, may be leading to the observed decrease in elephant occurrence in the center of the Ebo forest. However, unlike Maisels et al. (2013) and Kely et al. (2021), we found no effect of the relative abundance of hunting signs on the occurrence probability of elephants. In our study area where hunting is spread across the entire forest, elephants are not believed to be targeted by hunters who are more interested in species that can be killed easily using shotguns and snares for bushmeat trade in local markets. During the surveys, we observed many hunting signs on trails created by elephants, indicating that hunters frequently use elephant trails to ease their movements when navigating through the forest (Remis & Jost Robinson, 2020).

4.2 | Spatiotemporal patterns of chimpanzees

Unlike elephants, chimpanzees showed a strong preference for highly rugged areas, mirroring results from Sesink Clee et al. (2015). While Carvalho et al. (2022) suggested that chimpanzee preference for steep slopes may be an anti-predation strategy, we believe that in the Ebo forest, chimpanzees mostly occur in rugged areas to avoid encounters with hunters. This aligns with results from Fotang et al. (2021) in the Kom-Wum Forest Reserve, another site in the same ecoregion, although chimpanzees are not known to be directly targeted by hunters in the Ebo forest (Nguimdo et al., 2025). Large carnivores are now extinct in the Ebo forest (Whytock et al., 2021), and it is unlikely that chimpanzees are avoiding elephants as suggested by Tagg et al. (2013) in the Dja Biosphere Reserve in the south of Cameroon. However, bushmeat hunting is currently the main human disturbance widespread across the entire Ebo forest (Whytock et al., 2014; Whytock et al., 2018), but rugged areas are less likely to be explored by hunters (Nguimdo et al., 2025; Strindberg et al., 2018). In addition to terrain ruggedness, we also found that elevation had a positive effect on chimpanzee occurrence, which is consistent with previous studies in the same ecoregion (Fotang et al., 2021; Whytock et al., 2021). Whytock et al. (2021) found a strong positive correlation between elevation and forest cover in the Ebo forest, indicating that chimpanzees may favor higher elevations due to their association with primary forest habitats. Beyond the presence of primary forest, Fotang et al. (2021) suggested that chimpanzee preference for elevated areas could also stem from reduced human presence at higher altitudes, as well as the abundance of fruiting trees that serve as a key food source for the species. However, Abwe (2018) reported no significant relationship between chimpanzee nesting sites and the presence of fruiting trees in the Ebo forest. Considering that most chimpanzee signs observed during our surveys were nesting sites, we surmise that their preference for higher elevations in the Ebo forest may also be driven by potentially lower hunting pressure in these areas.

Our results showed that the distance to the nearest village had a positive effect on chimpanzee occurrence, as reported by previous studies (Fotang et al., 2023; Whytock et al., 2021). But interestingly, we found that the effect of the distance to the nearest village was substantially non-linear; chimpanzee occurrence probability peaked at mid-distance from villages (i.e., at about 10 km) and decreased as we moved further into the forest. This, as mentioned above, may be related to increasing hunting activities in the central part of the forest (Nguimdo et al., 2025). From 2008 to 2023, chimpanzee occurrence decreased across the entire forest, and they tended to be increasingly distant from villages. Similarly, while the relative abundance of hunting signs had a negative but non-substantial effect on chimpanzees, over the years, chimpanzee occurrence decreased in areas with greater hunting intensity. While this suggests that chimpanzees may modify their spatial patterns to adapt to hunting, it also shows how deeply they may be affected by increasing hunting activities, especially if hunters were now to expand their activities into the rugged areas that serve as a refuge for the species (Fotang et al., 2023; Nguimdo et al., 2025).

5 | CONSERVATION IMPLICATIONS

The Ebo forest is one of the most important habitats for the Nigeria-Cameroon chimpanzee across it range (Morgan et al., 2011), and very likely the last suitable habitat for the African forest elephant in the Littoral Region of Cameroon (Gobush et al., 2021; Wall et al., 2021). The strong preference of chimpanzees for highly rugged areas may explain the long-term persistence of the species in this landscape, which is located near one of the largest cities and bushmeat markets in Central Africa (Fa et al., 2014; Sesink Clee et al., 2015). However, increasing hunting activities in the most remote parts of the forest, as reported by Nguimdo et al. (2025), is worrying and needs to be urgently tackled, as it suggests that chimpanzees may have to face hunters even in those rugged areas. Chimpanzee preference for rugged areas may also confer some protection against industrial logging, as logging activities would primarily take place in relatively flat areas, which are easily accessible for logging engines (Putz et al., 2019). Nevertheless, it is important to note that logging activities may still lead to the loss of vital fruiting trees and herbaceous plants that serve as essential food resources for the species (Abwe, 2018; Fotang et al., 2021). Conversely, elephant preference for areas with low terrain ruggedness index, suggests a passive form of coexistence with hunters. However, those flat areas will likely be the most targeted by logging actors as they are the most accessible to their heavy logging machines (Putz et al., 2019). As logging expands, elephants may be forced to move to other areas in the future, leading to potential conflicts with the human communities living around the forest. Our study, consistently with the results from Whytock et al. (2021), identified the north-eastern part of the Ebo forest as the main area occupied by elephants. Future conservation interventions and logging activities should therefore take into consideration the importance of this area for forest elephants. Notably, this area also correspond to the range of the small population of gorillas inhabiting the Ebo forest (Mfossa et al., 2022).

Until its classification as a logging concession in 2023, the Ebo forest had no legal status and consequently no entry regulations (Whytock et al., 2021). Despite this unprotected status, conservation actors succeeded in engaging local communities to preserve its rich biodiversity, with a focus on species such as chimpanzees, gorillas, and elephants (Abwe et al., 2015; Abwe &

Morgan, 2008; Mfossa et al., 2018, 2025). There is no recent evidence of the killing of those species in the landscape, and local communities seem to be well aware of the necessity to preserve them (Mfossa et al., 2018, 2025). Nevertheless, the commencement of logging activities poses a significant threat to these species, especially if the best management practices are not implemented (Scalbert et al., 2022; Zwerts et al., 2024). In addition, logging activities will open new roads across the forest, therefore facilitating access to hunters (Estrada, 2013; Morgan et al., 2019). Furthermore, logging companies are likely to attract workers from other regions, with less concern for the sustainability of wildlife in the Ebo landscape, leading to increased demand for wildlife protein (Coad et al., 2019; Linder et al., 2021; Oates, 1995). Given these potential risks, we recommend that conservation actors work closely with the logging companies, the Cameroon wildlife authority, and local communities to ensure that wildlife conservation is taken into consideration within the management plans of the logging concessions, in a way that reflects the unique biodiversity value of the area. Key actions may include (i) identifying key areas for wildlife and preserving them from logging activities, (ii) dismantling all semi-permanent hunting camps inside the forest and enforcing wildlife control across the landscape, and (iii) enhancing conservation education and strengthening community-based wildlife conservation in villages surrounding the Ebo forest.

AUTHOR CONTRIBUTIONS

V.R.V.N., M.S. and M.W. conceived this research based on data collected over the years by V.R.V.N., E.E.A., B.J. M., R.C.W., A.E.A., D.M.M., M.E.K. and N.E.B. V.R.V.N. curated and analyzed the data, and drafted the manuscript with advice from M.S., M.W., J.K. and M.W.T. All authors critically reviewed the manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dataset used in the publication is subject to restrictions as it involves two threatened mammal species. The data can be obtained from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

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