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Long-Term Monitoring of Hunting Signs Reveals Complex Spatiotemporal Patterns of Hunting Activities in an Unprotected African Rainforest

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ABSTRACT

Aim: The long-term survival of many mammal populations relies on how effectively we mitigate the threat from unsustainable hunting. Yet, hunting activities are often cryptic, especially in unprotected forests. Here, we investigate whether hunting signs can help understand the spatiotemporal dynamics of hunting activities in an unprotected African rainforest and examine how landscape characteristics predict various indicators of hunting.

Location: Ebo forest, Cameroon, Central Africa.

Methods: We recorded hunting signs (e.g., shotgun cartridges, wire snares, direct sightings) systematically on 23 parallel recce lines across the Ebo forest from 2008 to 2023. We assigned hunting data and spatial covariates (e.g., elevation, distance to village) to 1 × 1 km grid cells and applied generalised linear mixed models to predict the effects of these covariates on hunting.

Results: We found that hunting was commonplace across the entire Ebo forest. The best-fitting models for each hunting sign differed considerably. Shotgun cartridges and all hunting signs combined increased significantly from 2016 to 2023 and varied non-linearly along the village-distance gradient. We found a progressive inversion of hunting trends along the anthropogenic gradient; between 2016 and 2018, wire snares declined with the distance to road but from 2021, they increased along the road-distance gradient. Wire snares showed a similar pattern along the river-distance gradient. Our results also revealed differences between shotgun hunting and snaring along the altitudinal gradient; the effect of elevation was positive on shotgun cartridges and negative on wire snares. Hunting signs and trails decreased significantly with increasing terrain ruggedness.

Main Conclusions: Using long-term monitoring data, we show how hunting patterns change dynamically with respect to human and landscape-related features. We also demonstrate complex hunting patterns along the gradient of human influence, therefore questioning the use of proxies such as the distance to human settlements and even topography to account for hunting pressure. Overall, we show that hunting sign data can reveal the spatiotemporal patterns of hunting, crucial in evaluating the effectiveness of conservation interventions and guiding the prioritisation of limited conservation resources.

1 | Introduction

Hunting is reported as the main cause of defaunation in African rainforests, driven in part by the increasing demand for bushmeat in urban areas (Abernethy, Maisels, and White 2016; Abernethy et al. 2013; Benitez-Lopez et al. 2019; Bolam et al. 2021; Dounias 2016). Even in remote areas where wildlife is still common, harvest rates are often unsustainable (Abernethy et al. 2013; Bennett et al. 2007; Fa and Brown 2009; Mikolo Yobo et al. 2022). Consequently, the long-term survival of large and medium-sized mammal populations relies on how effectively this key threat can be mitigated (Bolam et al. 2021; Coad et al. 2019). Understanding and mapping hunting activities within a particular landscape is of critical importance for effective spatial conservation planning (Critchlow et al. 2015; Grantham et al. 2020; Tulloch et al. 2015). But, unlike other major threats (e.g., habitat destruction), hunting is a cryptic phenomenon and thus notoriously difficult to detect (Deith and Brodie 2020).

One of the challenges in studying hunting arises when it comes to deciding which indicator to measure so as to best understand hunting patterns, as there are considerable differences in the predictive accuracy of each indicator (Rist et al. 2008). Choosing the right indicator is critical for obtaining results that are suitable to inform conservation planning and/or properly understand the studied system. Some studies consider the amount of time spent hunting in a particular area using all or specific hunting methods (Riddell et al. 2022; Rist et al. 2009), but this approach can overestimate hunting effort as it often ignores the time spent travelling to hunting locations (Rist et al. 2008). Other studies have analysed hunting activities based on wildlife biomass harvested (Coad et al. 2019), but may fail to accurately capture hunting as it often ignores losses related to animals that were only injured and succeeded to escape or those that were killed and left to rot in snares; it also ignores the success of different hunting methods in catching animals (Coad et al. 2019; Rist et al. 2008). Furthermore, the encounter rates of hunting signs may also be used to understand the patterns of hunting activities, but this may be biased if hunters hide their traces to escape anti-poaching patrols (Astaras et al. 2017). In addition, different hunting signs may indicate different aspects of hunting. For instance, shotgun cartridges and snares may indicate where active hunting is taking place and what hunting methods are being used (Coad et al. 2019); hunting trails and hunters' traces and encounters may show how hunters travel across the landscape and which areas they explore (Branch et al. 2022), whereas hunting camps may depict secondary central points from where hunting takes place (Abernethy et al. 2013; Rist et al. 2009).

Another constraint is often related to the logistical and financial resources needed for data collection. Some studies have relied on information obtained directly from hunters through interviews or by following them in the forest (Fa et al. 2021; Fournier et al. 2022; Griffiths et al. 2022; Teutloff et al. 2021; Whytock et al. 2014). However, the information provided by hunters may be biased or incomplete as a consequence of the illegal nature of hunting in most areas (Abernethy et al. 2013; Brodie et al. 2015; Dobbins et al. 2020; Solomon et al. 2007; Wright and Priston 2010). Hunters may also inflate their hunting success to show how good they are (Rist et al. 2009). Passive acoustic monitoring has also been suggested as a reliable method for investigating hunting patterns at the landscape scale (Astaras et al. 2017; Dobbins et al. 2020), though it is only effective for shotgun hunting, and requires significant financial and technical capacities for data collection and analysis (Dobbins et al. 2020; Zwerts et al. 2021). In protected areas, indirect evidence of hunting from signs collected during patrols or monitoring programmes is usually available although often collected in a non-systematic manner (Critchlow et al. 2016; Ghoddousi et al. 2022; Moore et al. 2018). Earlier studies have successfully used such data to depict hunting patterns and support conservation planning (Critchlow et al. 2015; Dobson et al. 2020; Ghoddousi et al. 2022; Plumptre et al. 2014). But in unprotected areas across Central African rainforests, very few long-term monitoring programmes exist, and this is reflected in the scarcity of robust data (Dounias 2016; Duporge et al. 2020). Consequently, most studies rely on data collected over relatively short periods and are therefore unlikely to provide insights into long-term hunting patterns (Dobbins et al. 2020).

Due to the scarcity of hunting data, proxies such as distance to villages and roads are widely used to account for the spatial distribution of hunting activities (Cavada et al. 2019; N'Goran et al. 2012; Rao et al. 2005; Van Kuijk et al. 2022). However, our knowledge of how landscape features affect hunting activities is still limited (Bachmann et al. 2020; Datta-Roy 2022; Froese et al. 2023). In fact, some studies have underlined the complexity and dynamism of hunting activities in tropical regions, revealing that such proxies may not always capture the spatial patterns of hunting activities (Abernethy et al. 2013; Deith and Brodie 2020; Vanthomme et al. 2017). For instance, the accessibility of an area defined by its topography and vegetation density tends to influence its use by hunters (Brodie and Fragoso 2021; Deith and Brodie 2020). In addition, hunters' movements in an area may also be influenced by the local prevailing sociocultural and economic context (Bachmann et al. 2019; Froese et al. 2023), therefore limiting the possibility of generalising observations from specific sites (Rist et al. 2008). Moreover, based on their motivation and local territorial restrictions, hunters travel to areas where target species are known to be abundant (Coad et al. 2019; Ghoddousi et al. 2022). These factors jointly hinder our capacity to understand the patterns of hunting activities without locally collected data.

Here, we used an exceptional long-term database on hunting signs systematically collected from 2008 to 2023 across the ecologically important but unprotected Ebo forest in Cameroon in order to assess the spatial and temporal dynamics of hunting activities across the landscape. We sought to test the effect of habitat characteristics (elevation, terrain ruggedness and distance to the nearest river) and anthropogenic pressure (distance to the nearest road, distance to the nearest village, human footprint index) on different indicators of hunting activities. We also investigated how these hunting signs changed over the years along anthropogenic gradients (see Table 1 for the full list of hypotheses and rationale).

2 | Methods

2.1 | Study Area

The Ebo forest landscape is located in the Littoral Region of Cameroon. It is an evergreen and deciduous submontane

TABLE 1 | Covariates hypothesised to influence the spatial distribution of hunting signs in the Ebo forest, Central Africa.

Variable	Description	Hypothesis	References
Year	The year during which the data were collected	Hunting signs would increase over the years as a result of increasing demand for bushmeat across tropical areas	Abernethy et al. (2013), Riddell et al. (2022)
Distance to village	The Euclidean distance from the centre of sites to the nearest village	Hunting activities would reduce as the distance to the village increases	Fa et al. (2021)
Distance to village^2	The quadratic term of the distance to the nearest village	The hunting trend would be non-linear along the village-distance gradients as a consequence of the highly heterogeneous terrain	Rist et al. (2009)
Distance to village:year	The interaction between the distance to the nearest village and the year	Over the years, hunting activities would increasingly take place farther away from villages due to decline of wildlife populations near villages and increasing hunting efforts	Abernethy et al. (2013)
Distance to road	The Euclidean distance from the centre of sites to the nearest road	Hunting activities would reduce as the distance to the road increases	Benitez-Lopez et al. (2019)
Distance to road^2	The quadratic term of the distance to the nearest road	Hunting trend along the road-distance gradient would be non-linear as a consequence of the highly heterogeneous terrain	Rist et al. (2009)
Distance to road:year	The interaction between the distance to the nearest road and the year	Over the years, hunting activities would increasingly occur farther away from roads as a consequence of wildlife population decline near roads and increasing hunting efforts	Abernethy et al. (2013)
Distance to river	The Euclidean distance from the centre of sites to the nearest road	Since trails and camps are mostly located along river borders in the Ebo forest, so we assumed that hunting would decrease with the distance to rivers	Griffiths et al. (2022)
Distance to river:year	The interaction between the distance to the nearest river and the year	Since trails and camps are mostly located along rivers in the Ebo forest, over the years, so we assumed hunting would increasingly expand away from the rivers	Abernethy et al. (2013)
Elevation	Mean elevation of each site	Hunting signs would reduce as elevation increases as a result of decreased accessibility	Brodie et al. (2015)
Terrain ruggedness index	The quantitative measurement of terrain heterogeneity	Hunting signs would reduce as terrain ruggedness increases	Branch et al. (2022), Brodie et al. (2023)
Movement cost	The mean anisotropic cumulative cost of moving from villages to different sites	Sites with high movement costs would display lower hunting activities as a result of decreased accessibility	Deith and Brodie (2020)
Movement cost:Year	Interaction between the movement cost and the year	Over the years, hunting signs would increase in less accessible areas	Abernethy et al. (2013)
Human footprint index	Mean human footprint index depicting human influence in each site	Hunting signs would be higher in areas with high human footprint index as those areas are more exposed to human influence	Venter et al. (2016)

forest covering an area of *ca*. 2000 km^2 with annual precipitation exceeding 2500 mm (Abwe 2018; Cheek et al. 2018). It is recognised as a biodiversity hotspot and forms a considerable part of the most important tract of intact forest landscape in the Cross-Sanaga ecoregion (Potapov et al. 2017; Whytock et al. 2021). The forest is home to a variety of diurnal primate species such as western gorilla (*Gorilla gorilla* Savage, 1847), Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti* Matschie, 1914), drill (*Mandrillus leucophaeus* F. Cuvier, 1807) and Preuss's guenon (*Allochrocebus preussi* Matschie, 1898) as well forest elephants (*Loxodonta cyclotis*), red river hog (*Potamochoerus porcus*) and several species of duikers and pangolins (Abwe et al. 2020; Mfossa et al. 2022; Morgan et al. 2013; Whytock et al. 2021). The Ebo forest is customary land for > 40 human communities, depending on small-scale agriculture, hunting, as well as employment with oil palm plantations and logging operators for their subsistence (Abwe and Morgan 2020; Mahmoud et al. 2019; Mfossa et al. 2022).

Despite its rich biodiversity, the Ebo forest is not protected and no law enforcement measures exist (Mfossa et al. 2022). Thus, it is vulnerable to habitat degradation and hunting (Mahmoud et al. 2019; Morgan et al. 2011). Following the discovery of gorillas in the area in 2002 (Morgan, Wild, and Ekobo 2003), the Cameroon Biodiversity Association (formerly Ebo Forest Research Project) initiated research and conservation outreach in the landscape with activities focused on biological research from three research stations in the forest, as well as awareness campaigns and community empowerment in surrounding villages (Abwe, Mfossa, and Morgan 2015; Abwe and Morgan 2008; Mfossa, Abwe, and Morgan 2018). In 2006, part of the Ebo forest (ca 1400 km^2) was proposed as a national park (Figure 1) to preserve its rich biodiversity (Cheek et al. 2018) but while the process of creating the park was thought to be ongoing, in February 2020, the Government of Cameroon announced plans to convert the entire forest into two logging concessions (Abwe and Morgan 2020; Mfossa et al. 2022; Whytock et al. 2021). Due to objections from grassroots groups and conservation actors, these plans were suspended in July 2020 (Whytock et al. 2021). However, in April 2023, despite ongoing negotiations to carry out an inclusive and participatory local land use planning to reconcile the economic, sociocultural and ecological interests of the parties, two decrees were enacted to establish logging concessions in the forest (Decree N^o 2023/01630/PM and 2023/01631/PM of 27 April 2023). Nevertheless, these decrees recognise biodiversity conservation as one of the land-use types that need to coexist in the landscape.

2.2 | Hunting in the Ebo Landscape

The Ebo forest is located in a region with a high hunting-induced defaunation index, affecting animals of all sizes (Benitez-Lopez et al. 2019; Fonteyn et al. 2023). In addition, it is only 50 km away from the city of Douala, one of the main bushmeat markets for threatened species in the Cross-Sanaga region (Fa et al. 2014; Morgan et al. 2011, 2013). Consequently, a considerable proportion of community members in the Ebo landscape rely on hunting as source of income. Additionally, given the ideal position of the Ebo forest near major markets, many hunters have travelled from other regions of Cameroon to resettle in the landscape specifically for bushmeat hunting (Whytock and Morgan 2010). Although the spatial extent of hunting activities and the territoriality of hunters across the forest has never been investigated, a study on bird hunting by Whytock et al. (2014) revealed widespread use of hunting camps to access remote areas within the forest. These hunting camps are often the centre of a rich

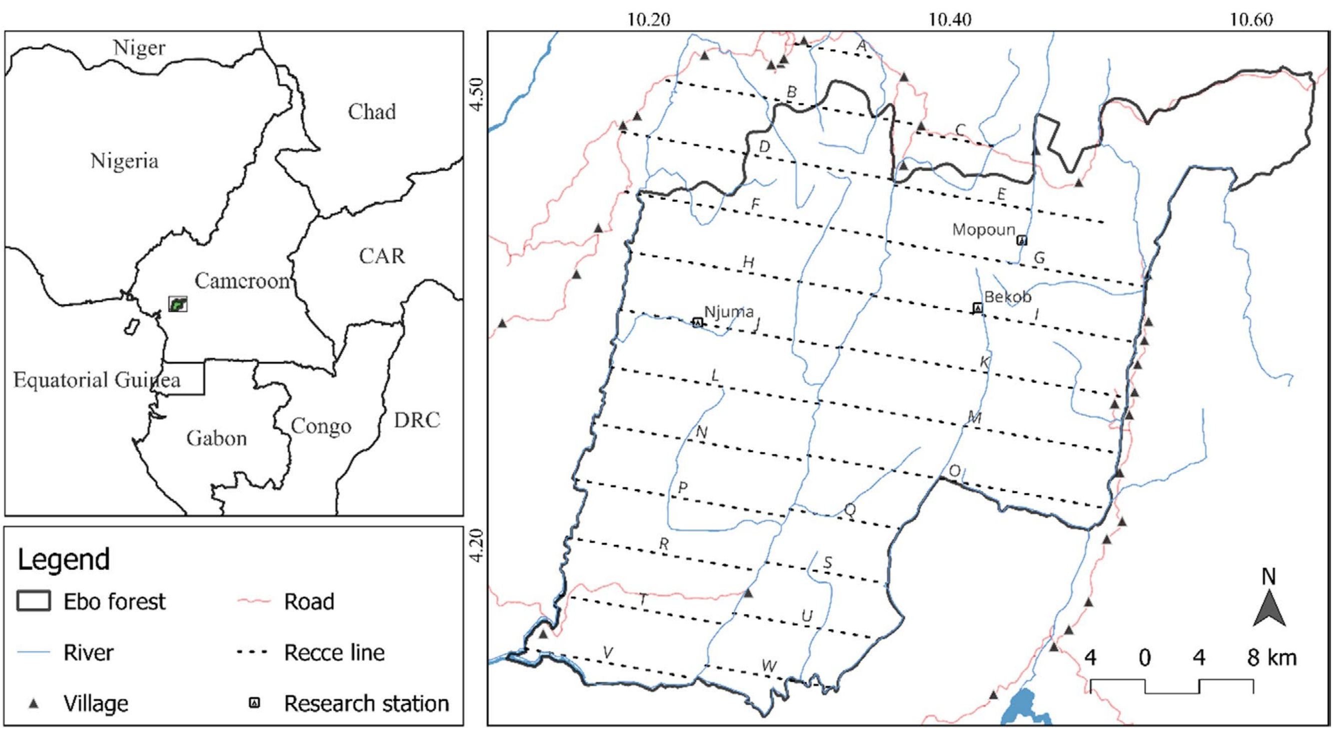

FIGURE 1 | Map of the Ebo forest located in the Littoral Region of Cameroon, Central Africa. The letters A–W represent the 23 recce lines.

network of trails, with the main ones leading to the village or to other hunting camps. Discussions with some community members showed that non-native hunters mentioned above often get permission from traditional authorities before settling in their village and hunting in their forest. Based on our knowledge of the forest, we also believe that non-native hunters may be dominant far inside the forest as compared to the vicinities of the village.

Similar to other tropical forests, hunting takes place in the Ebo forest not only during the day, but also at night using LED flashlights (Abwe 2018; Bowler et al. 2020). Across the landscape, hunters use both wire snares and shotguns (Bowers-Sword 2020; Mfossa et al. 2022). Wire snares are often set in groups and target a wide range of terrestrial wildlife such as duikers, red river hogs, rodents, pangolins and porcupines. Shotguns are mainly used to target arboreal and semi-arboreal primates such as the putty-nosed monkey, crowned monkey, mona monkey, red-capped mangabey, Preuss's guenon and the drill (Whytock et al. 2014), but may also be used to kill medium- to large-sized terrestrial mammals such as red river hogs and duikers. Birds are also hunted, although mainly for consumption while camping in the forest (Whytock et al. 2014, 2018). Whytock et al. (2021) showed that the populations of most hunted mammal species were relatively stable between 2008 and 2019. It is also believed that iconic species such as the gorilla, chimpanzee and elephant which are not reported as the most hunted species across Central Africa (Coad et al. 2019), are not targeted by bushmeat hunters in the Ebo landscape. This may be related to their conservation value and their central position in most conservation programmes, as well as their cultural value for local communities (Mfossa, Abwe, and Morgan 2018).

2.3 | Data Collection

2.3.1 | Survey Design

We established twenty-three parallel recce lines placed 4 km apart (also referred to as guided recces, e.g., Whytock et al. (2021)) and totalling 345 km across the entire Ebo forest in 2008 (Figure 1). These recce lines were oriented perpendicular to the main rivers (approximately east–west) to reduce potential topographical and ecological biases (Buckland et al. 2015; Rist et al. 2009). The recce lines were surveyed once per year in 2008, 2012 and every year from 2016 to 2023, except for 2019 and 2020 when surveys were paused due to the COVID-19 pandemic. The surveys generally took place from October to April in the subsequent year, with the initial year regarded as the year in which the survey occurred. The survey team consisted of 2–3 trained observers followed by three porters, all moving at about 1 km per hour, using a handheld GPS (Garmin) and a manual compass to navigate along the predefined recce lines (White and Edwards 2000; Whytock et al. 2021; Zausa et al. 2023). The survey team used only pruning shears to ease movement, minimise damage to the vegetation, minimise the risk of hunters using the recces and distinguish their cuts from hunters' machete cuts. Over the years, as discussions for the protection of the Ebo forest were moving forward, its boundaries (Figure 1) evolved to take into consideration the interests of some local stakeholders. Therefore, only the area covered by the recce lines which was the initial extent of the forest was surveyed from 2008 to 2023.

2.3.2 | Hunting Signs

We recorded different types of signs indicating human activities, including locations of wire snares (both active and inactive), hunting camps, trails regularly used by humans, machete cuts and shrub breakings made by hunters while moving across the forest, human footprints, gunshots and shotgun cartridges on both sides of the recce lines (Cameron et al. 2016; Fournier et al. 2022; Mfossa et al. 2022; Vanthomme et al. 2017). The team members consensually guesstimated the approximate age of the signs (based on the rusting state and smell of shotgun cartridges (Soofi et al. 2018), and the state of wooden sticks and wires used in snares) and recorded their geographic coordinates using a GPS device. Perennial signs such as hunting camps and trails were recorded when it was evident that they were used after the previous survey. All the detected shotgun cartridges were collected and later destroyed to avoid double counting during subsequent surveys (Mfossa et al. 2022). We also recorded all direct encounters with humans in the forest. These humans were classified as hunters if they self-identified as hunters or if there was clear evidence that they were in the forest for hunting activities.

2.3.3 | Data Preparation

We placed 1 × 1 km grid cells (hereafter referred to as site) across the entire study area using QGIS version 3.28.5 (QGIS Development Team 2022; Whytock et al. 2021), and extracted a total of 346 sites which intersected with recce lines. We considered each site as a sampling unit (Wessling et al. 2020; Whytock et al. 2021) and assigned the data collected on recce lines across the years to their respective sites using their coordinates. We also calculated the survey effort (i.e., the kilometres walked) in each site. We considered all machete cuts, shrub breakings and footprints as hunters' signs of passage. We only used hunting signs (shotgun cartridge, wire snare, hunters' sign of passage) that were assumed to be less than 1 year old. The age of hunting signs was not documented in 2008 and 2012; we therefore excluded them from in-depth analyses, but used them to map the encounter rates of hunting signs (shotgun cartridges and wire snares which are the indicators of the main hunting techniques in the area) across the years within 4 × 4 km grid cells (Figures 3 and 4). Since there were no law enforcement activities undertaken in the area during the period of surveys, we assumed that the number of shotgun cartridges displaced from the original location where they were produced was negligible, as hunters would not attempt to hide their traces, unlike reported by Astaras et al. (2017) in the Korup National Park.

For each site, following Soofi et al. (2018), we created secondary sampling units by dividing the recce line into segments of approximately 200 m each. On these segments, for each survey year, we recorded each hunting sign only once per segment to obtain presence and absence data (Karanth et al. 2011; Laurance et al. 2008; Soofi et al. 2018). Then, we summed the results from the segments within each site and obtained the number of events for each hunting sign which could vary from 0 to 5 given that each site had a maximum of five 200 m segments. This allowed us to reduce potential pseudoreplication and increase independence of the signs (Soofi et al. 2018) which may arise from multiple signs created by the same hunter at the same place (e.g., group of snares deployed by the same hunter, multiple shotgun cartridges produced by a hunter when attempting to kill one animal). As we were also interested in modelling the events of all hunting signs together, we pooled the events of shotgun cartridges, wire snares, direct sightings of hunters and hunters' signs of passage within each site to obtain the overall hunting events (which could therefore vary from 0 to 20).

2.3.4 | Spatial Covariates

We selected several spatial covariates potentially influencing the spatiotemporal patterns of hunting signs in the Ebo forest (Table 1). We obtained the shapefiles of roads, rivers and villages from the spatial database of the Interactive Forest Atlas of Cameroon (MINFOF 2013). We calculated the distance from the centroid of each site to the nearest village, river and road using the Euclidean distance algorithm in QGIS (Plumptre et al. 2014; QGIS Development Team 2022). To further account for anthropogenic pressures in each site, we obtained the 2020 raster layer of the human footprint index (https://search.earthdata.nasa.gov, downloaded in June 2024) (Venter et al. 2016). To estimate the mean elevation and terrain ruggedness index for each site, we obtained a Shuttle Radar Topography Mission (SRTM) layer of 30 m resolution (https://search.earthdata.nasa.gov, downloaded in May 2023; Figure S3) (Rabus et al. 2003). We derived the terrain ruggedness index using the raster terrain analysis tool in QGIS (QGIS Development Team 2022). We also calculated the cost of moving across the landscape from different villages using the *r.walk.points* function in QGIS (Gietl et al. 2008). This function generates a raster map that displays the cumulative cost of travels from villages to different regions of the forest, measured in seconds (hereafter referred to as movement cost, Figure S4), taking into account the direction of the movement and topography (QGIS Development Team 2022). We then used the zonal statistics tool in QGIS to measure the mean human footprint index, elevation, terrain ruggedness and movement cost for each site (Nayeri et al. 2022; Riley, Degloria, and Elliot 1999).

2.4 | Statistical Analyses

We performed all the statistical analyses in R version 4.3.0 (R Core Team 2024). We modelled the events of each hunting sign (i.e., shotgun cartridges, wire snares, direct encounters with hunters and hunters' sign of passage) separately. We fitted a set of models for 'all hunting', considered as the sum of the events of those four hunting signs in each site. Because the same trails were repeatedly used by hunters over the years, we modelled trails using only spatial covariates (i.e., we did not include the year as a covariate in models using trails as response variable). We excluded gunshots from the modelling because we assumed that they are already captured by shotgun cartridges. To examine how hunting events vary in relation to the covariates described above (Table 1), we fitted generalised linear mixed models (GLMMs) for each of the six response variables described above (i.e., shotgun cartridges, wire snares, direct encounters with hunters, and hunters' sign of passage, all hunting, and trails). Before analyses, we scaled (mean centered to 0 with standard deviation of 1) all covariates (Schielzeth 2010), and checked them for multicollinearity using Pearson's correlation coefficients (Figure S2). Covariates were not included together in models if their pairwise relationship was higher than the cut-off point of $|r| \geq 0.7$ (Dormann et al. 2012). We included the year as a continuous variable. For each of these response variables, we started by fitting the null model (i.e., with no covariate), then we subsequently added the covariates described above (Table 1), excluding models that failed to converge. This resulted in a total of 118 models (16–30 models per response variable). To ensure a suitable distribution link, we fitted all the models using three distributions including Poisson, zero-inflated and negative binomial models (see Appendix S1). We fitted Poisson and negative binomial GLMMs with 'lme4' R package (Bates et al. 2015) and zero inflated models using 'glmmTMB' package of R (Brooks et al. 2017). We used the 'MuMIn' package of R (Barton 2023) to select the best-fitting candidate models based on the Akaike Information Criterion corrected for a small sample size ($\Delta AIC_C < 2$, Table 2) (Burnham and Anderson 2002). Finally, we tested model assumptions and assessed the goodness of fit of our models using the R package 'DHARMa' (Hartig 2022). In these assessments, we ran simulations with 250 iterations based on our best-fitting models, and examined our models using QQ plots and residual diagnostic tests (Figure S1; Hartig 2022).

We found a significant spatial autocorrelation between sites with DHARMa and included the site as a random effect in all the models (Whytock et al. 2021). To account for the underestimation of hunting events in sites with lower sampling effort, we accommodated effort (defined as the number of kilometres walked) as a log-transformed offset in each site (Critchlow et al. 2015; Soofi et al. 2018). Covariates were considered statistically significant if the confidence intervals of their effect did not overlap with zero (Benjamin et al. 2018).

3 | Results

3.1 | Description of Hunting Activities

Overall, our surveys led to the detection of 9011 hunting signs during nine surveys, with an average of 2.82 ± 2.25 signs per km (Table S1). Trails (33%) and signs of passage (31%) were the most common hunting signs recorded, followed by wire snares (26%) and shotgun cartridges (8%) (Figure 2, Table S1). Additionally, hunting camps, direct sightings and gunshots were recorded during the study period; each represented less than 1% of all hunting signs (Figure 2). During the initial survey in 2008, we recorded old 'pitfall traps' ($n = 26$), a traditional hunting technique practised in the past, but no new pitfall traps were recorded during any subsequent survey.

Our results showed that the mean encounter rate of combined hunting signs dropped sharply from 4.61 (SD ± 2.46) signs per km in 2012 to 1.60 (SD ± 1.14) signs per km in 2016 (Table S1). Specifically, between 2012 and 2016, the encounter rate of wire snares declined from 1.78 (SD ± 1.52) to 0.27 (SD ± 0.45) wire snares per km. However, the encounter rate of shotgun

TABLE 2 | Parameters of the top-ranked generalised linear mixed models explaining the effects of landscape and anthropogenic factors on different indicators of hunting activities across the Ebo forest. In all models, the site was included as a random parameter, and the survey efforts (kilometre walked) as an offset. Covariates: VillDist denotes the distance to the nearest village, RoadDist is the distance to the nearest road, MovCost is the movement cost, Rugg is the terrain ruggedness index, RivDist is the distance to the nearest river, Elev denotes the elevation and HFI is the human footprint index. Parameters: Degree of freedom (df) and Akaike Information Criterion corrected for a small sample size (AICc). The superscript "2" denotes the quadratic terms.

Signs	Model specifications	df	AICc	delta	weight
Shotgun cartridge	Year + Elev + VillDist + VillDist^2 + HFI	7	1624.9	0.00	0.22
	Year + Elev + VillDist + VillDist^2	6	1625.1	0.22	0.19
	Year + Elev + VillDist + VillDist^2 + Rugg	7	1625.4	0.53	0.17
	Year + Elev	4	1626.7	1.75	0.09
Wire snare	Elev + Year*(RoadDist + RivDist)	6	2710.3	0.00	0.76
Direct encounter with hunters	Year * MovCost	5	297.2	0.00	0.34
	Year + MovCost	4	299.0	1.80	0.14
	Year + MovCost + HFI	5	299.0	1.83	0.14
	Year * MovCost + RivDist	6	299.1	1.89	0.13
Signs of passage	Year + MovCost + Rugg + HFI	6	4214.1	0.00	0.37
	Year * MovCost + Rugg	6	4214.5	0.37	0.31
	Year + VillDist + Rugg	5	4215.6	1.45	0.18
Trail	Rugg+Elev	5	4715.9	0	1
All hunting	Rugg + Year * (VillDist + VillDist^2)	9	5588.1	0.00	0.38
	Rugg + Year * (VillDist + VillDist^2) + RivDist	10	5588.6	0.44	0.30
	Rugg + Year * (VillDist + VillDist^2) + Elev	10	5589.9	1.79	0.15

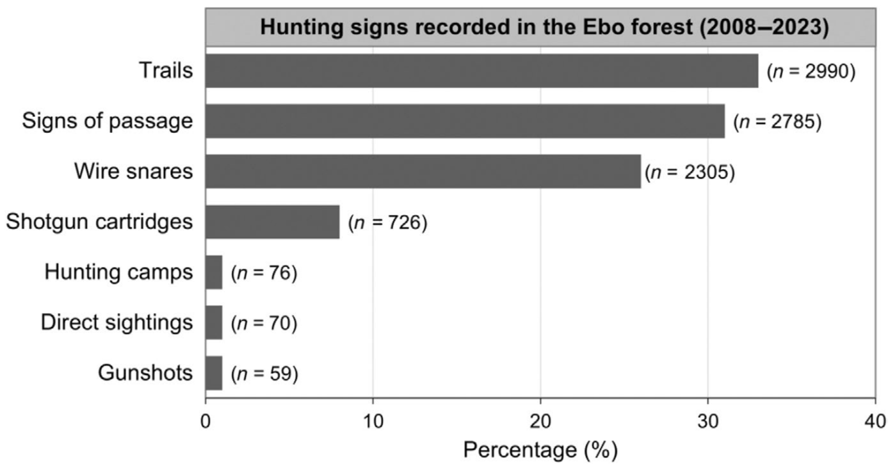

FIGURE 2 | Relative representation of different hunting signs detected along the recce lines from 2008 to 2023 throughout the Ebo forest in Cameroon, Central Africa.

cartridges did not show a concomitant decline over the same period (Table S1, Figures 3 and 4).

3.2 | Spatiotemporal Predictors of Hunting Signs

There was a high correlation between the distance to the nearest village and the distance to the nearest road ($r = 0.96$); consequently, we fitted both covariates in different models. We also did the same with the distance to the nearest village and the movement cost ($r = 0.95$) and with the distance to the nearest road and movement cost ($r = 0.93$). For shotgun cartridges, wire snares, direct encounters with hunters and signs of passage, models with Poisson distribution performed better (lower AICc) than zero-inflated and negative binomial distributions and did not present significant overdispersion (Figure S1). However, for trails, the zero-inflated distribution outperformed the Poisson distributions while for the overall

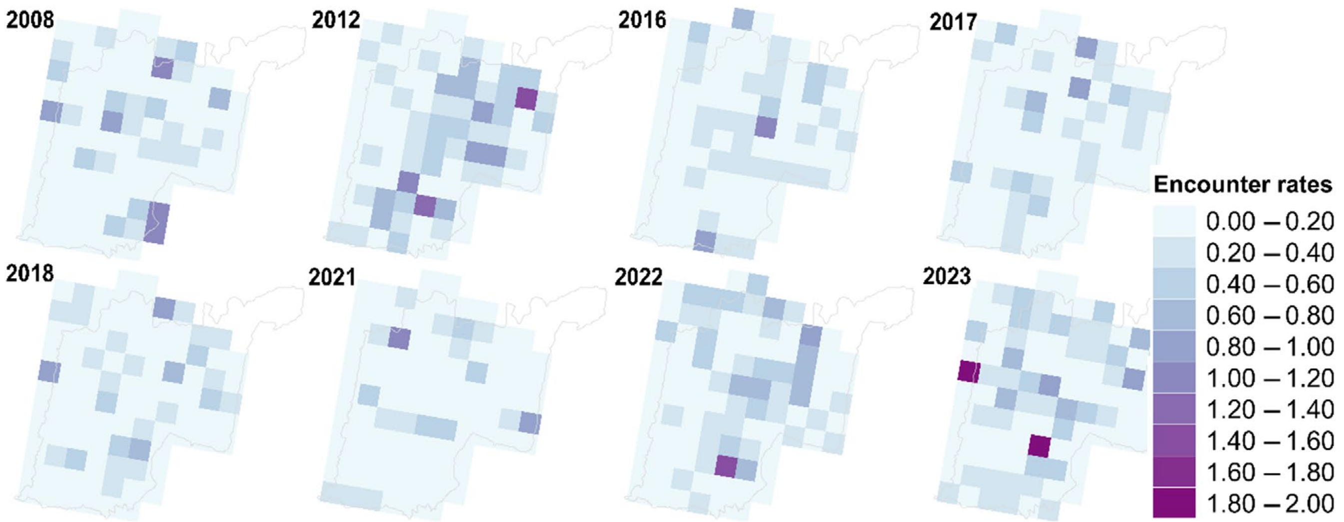

FIGURE 3 | Spatial and temporal variations in the encounter rates of shotgun cartridges from 2008 to 2023 in the Ebo forest, Cameroon.

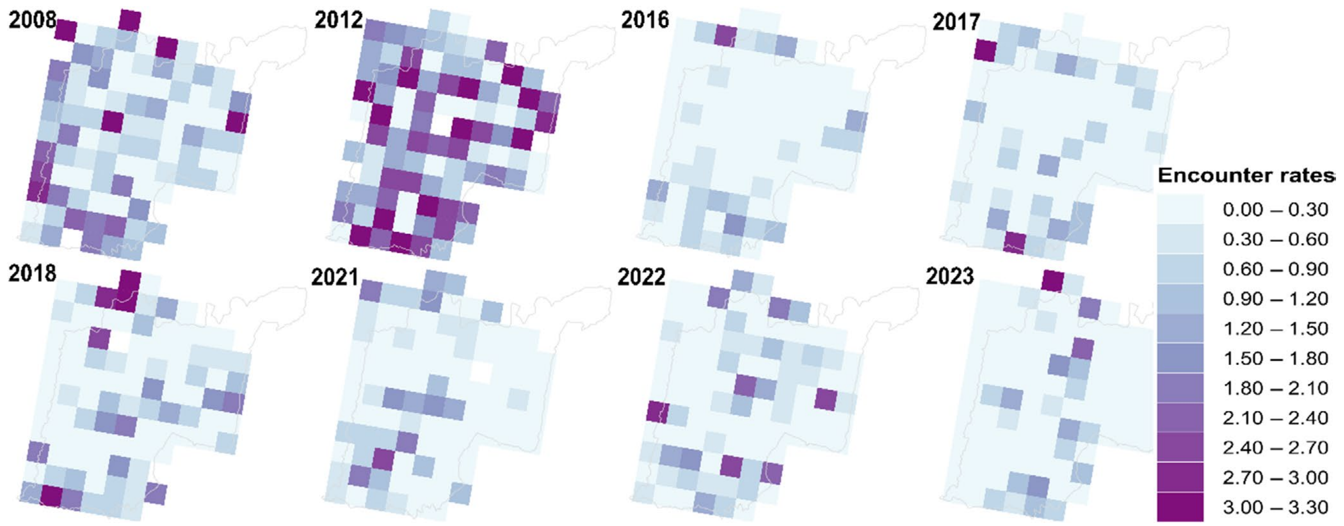

FIGURE 4 | Spatial and temporal variations in the encounter rates of wire snares from 2008 to 2023 in the Ebo forest, Cameroon.

hunting events, the models with a negative binomial distribution which account for overdispersion were best. For wire snares, direct encounters with hunters and trails, there was a clear top model based on the AICc and the Akaike weight (Table 2). For other response variables (shotgun cartridges, hunters' signs of passage and all hunting), there were multiple models with similar support based on their AICc values and model weight (Table 2). However, these models only differ with one covariate with no significant effect and no considerable impact on the effect of other covariates (Table S2). We therefore decided to only use the top model (ΔAICc = 0) for inferences on all the response variables (Burnham and Anderson 2002).

3.3 | Shotgun Cartridges

Shotgun cartridge events increased significantly from 2016 to 2023 ($\beta = 0.26$, 95% CI = 0.14, 0.38; Table 3, Figure 5). There was also a positive and significant relationship between the events of shotgun cartridges and elevation ($\beta = 0.17$, 95% CI = 0.03, 0.31). The distance to the nearest village was a better predictor than movement cost and distance to the nearest road. Its effect was negative, but not statistically significant ($\beta = -0.19$, 95% CI = −0.40, 0.01). However, its quadratic term was positive and significant ($\beta = 0.21$, 95% CI = 0.06, 0.36), suggesting that the events of shotgun hunting do not vary linearly with the distance to the nearest village (Figure 6). Shotgun cartridges also decreased with the human footprint index, but this relationship was not significant (Table 3).

3.4 | Wire Snares

We found a negative and significant effect of elevation on wire snares ($\beta = -0.30$, 95% CI = −0.43, −0.18, Figure 7, Table 3), which suggests that hunters tend to set more snares at lower elevations. The effect of interaction between the year and the distance to the nearest road on the events of wire snares was positive and significant ($\beta = 0.13$, 95% CI = 0.04, 0.21, Figure 8a, Table 3), suggesting that over the past 6 years, hunters travelled longer distances from the roads to set snares.

TABLE 3 | Standardised coefficients and confidence intervals of the parameters from the best-fitting generalised linear mixed model for each of the six indicators of hunting activities in the Ebo forest. Covariates: VillDist denotes the distance to the nearest village, RoadDist is the distance to the nearest road, MovCost is the movement cost, Rugg is the terrain ruggedness index, RivDist is the distance to the nearest river, Elev denotes the elevation and HFI is the human footprint index. Parameters: Mean (Est.) and standard error (SE) of the posterior distributions of standardised coefficient estimates of covariates. The superscript "2" denotes the quadratic terms.

Hunting sign	Parameter	Estimate	SE	95% lower	95% upper
Shotgun cartridge	Intercept	−2.52	0.13	−2.79	−2.28
	Year	0.26	0.06	0.14	0.38
	Elev	0.17	0.07	0.03	0.31
	VillDist	−0.19	0.10	−0.40	0.01
	$VillDist^2$	0.21	0.07	0.06	0.36
	HFI	−0.18	0.12	−0.43	0.05
Wire snare	Intercept	−1.56	0.07	−1.70	−1.42
	Year	−0.01	0.04	−0.09	0.07
	Elev	−0.29	0.07	−0.42	−0.16
	RoadDist	−0.03	0.06	−0.15	0.10
	RivDist	0.10	0.06	−0.02	0.21
	Year:RoadDist	0.13	0.04	0.04	0.21
	Year:RivDist	0.10	0.04	0.02	0.18
Direct encounter with hunters	Intercept	−6.15	0.70	−7.52	−4.78
	Year	−0.28	0.26	−0.79	0.23
	MovCost	−0.85	0.31	−1.46	−0.24
	Year:MovCost	0.47	0.24	0.00	0.93
Signs of passage	Intercept	−0.60	0.04	−0.67	−0.53
	Year	0.09	0.03	0.03	0.15
	MovCost	0.21	0.04	0.13	0.29
	Rugg	−0.18	0.04	−0.25	−0.11
	HFI	0.03	0.05	−0.07	0.13
Hunting trail	Intercept	−0.37	0.04	−0.45	−0.28
	Rugg	−0.35	0.05	−0.45	−0.25
	Elev	0.23	0.05	0.14	0.32
All hunting	Intercept	−0.16	0.05	−0.25	−0.07
	Rugg	−0.13	0.03	−0.19	−0.06
	Year	0.11	0.03	0.05	0.18
	VillDist	0.05	0.03	−0.02	0.11
	$VillDist^2$	0.09	0.03	0.03	0.15
	Year:VillDist	0.08	0.02	0.03	0.12
	$Year{:}VillDist^2$	−0.04	0.02	−0.08	0.01

A similar result was obtained from the interaction between the year and the distance to the nearest river ($\beta = 0.10$, 95% CI = 0.02, 0.18, Figure 8b). The effect of the distance to the nearest river itself was positive, but not significant ($\beta = 0.09$, 95% CI = −0.02, 0.21; Table 3).

3.5 | Direct Sightings

Movement cost had a strong and negative effect ($\beta = -0.85$, 95% CI = −1.46, −0.24; Figure 6, Table 3) on direct encounter events with hunters in the forest, suggesting that hunters are likely to be less frequently encountered in less accessible areas. However, the interaction between the movement cost and the year had a positive and significant effect ($\beta = 0.47$, 95% CI = 0.00, 0.93, Table 3) on direct encounters with hunters. This suggests that over the past 8 years (2016–2023), hunters were increasingly being sighted in less accessible areas (Figure 8). Direct encounter events with hunters decreased over the years, but this relationship was not significant ($\beta = -0.28$, 95% CI = −0.79, 0.23; Table 3).

3.6 | Signs of Passage

We found significantly more hunters' signs of passage in areas with high movement cost ($\beta = 0.21$, 95% CI = 0.13, 0.29, Table 3), suggesting that hunters produce more signs when they are in less accessible areas. However, these signs reduced with increasing terrain ruggedness index ($\beta = -0.18$, 95% CI = −0.25, −0.11; Table 3). Over the past eight years (2016–2023), hunters' signs of passage increased significantly ($\beta = 0.09$, 95% CI = 0.03, 0.15; Table 3).

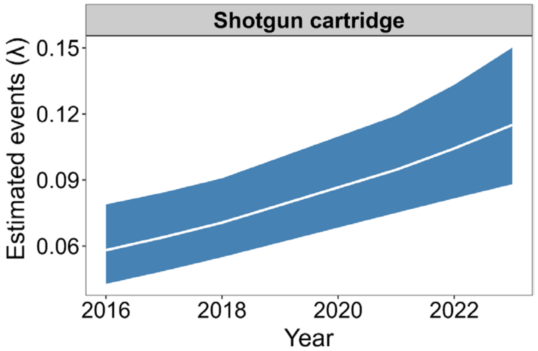

FIGURE 5 | Temporal patterns of the events of shotgun cartridges (λ) in the Ebo forest from 2016 to 2023 obtained from the best-fitting generalised linear mixed model. The white line represents the expected mean and the blue area represents the 95% confidence interval.

3.7 | Trails

Terrain ruggedness and elevation were the only important predictors of trails. We found a significant decrease in the events of trails with increasing terrain ruggedness index ($\beta = -0.35$, 95% CI = −0.45, −0.25, Table 3, Figure 7e). Meanwhile, elevation had a positive and significant relationship with trails ($\beta = 0.23$, 95% CI = 0.14, 0.32, Table 3), suggesting more trails at higher elevations (Figure 7c).

3.8 | All Hunting

In our global model (all hunting signs), we found a negative and significant effect of the terrain ruggedness index ($\beta = -0.12$, 95% CI = −0.19, −0.06; Table 3). The overall hunting events also increased significantly over the years ($\beta = 0.11$, 95% CI = 0.05, 0.18; Table 3). While the linear effect of the distance to the nearest village was very weak, its quadratic effect was positive and statistically significant ($\beta = 0.09$, 95% CI = 0.03, 0.15; Table 3), suggesting that hunting events followed a non-linear trend from villages to the more central part of the forest. The interaction between distance to the nearest village and the year was positive and significant (Table 3), translating into an increase of hunting events along the village-distance gradient over the years (Figure 8d).

4 | Discussion

4.1 | Hunting Activities

Our results revealed widespread hunting across the entire Ebo forest (Figures 3 and 4). This is similar to other areas in Central African rainforests where hunting has been reported to occur even in the most remote areas (Abernethy, Maisels, and White 2016; Abernethy et al. 2013; Vanthomme et al. 2017).

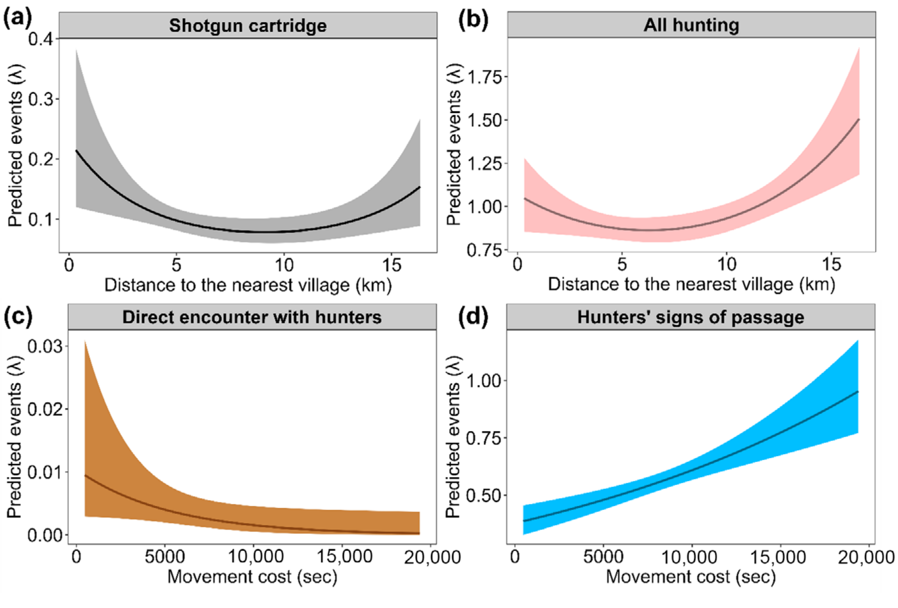

FIGURE 6 | Estimated events (λ) of different hunting signs along the village distance (a and b) and the movement cost (c and d) gradients, obtained from the best-fitting model for each hunting sign. The dark lines represent the expected mean and the light areas represent the 95% confidence intervals.

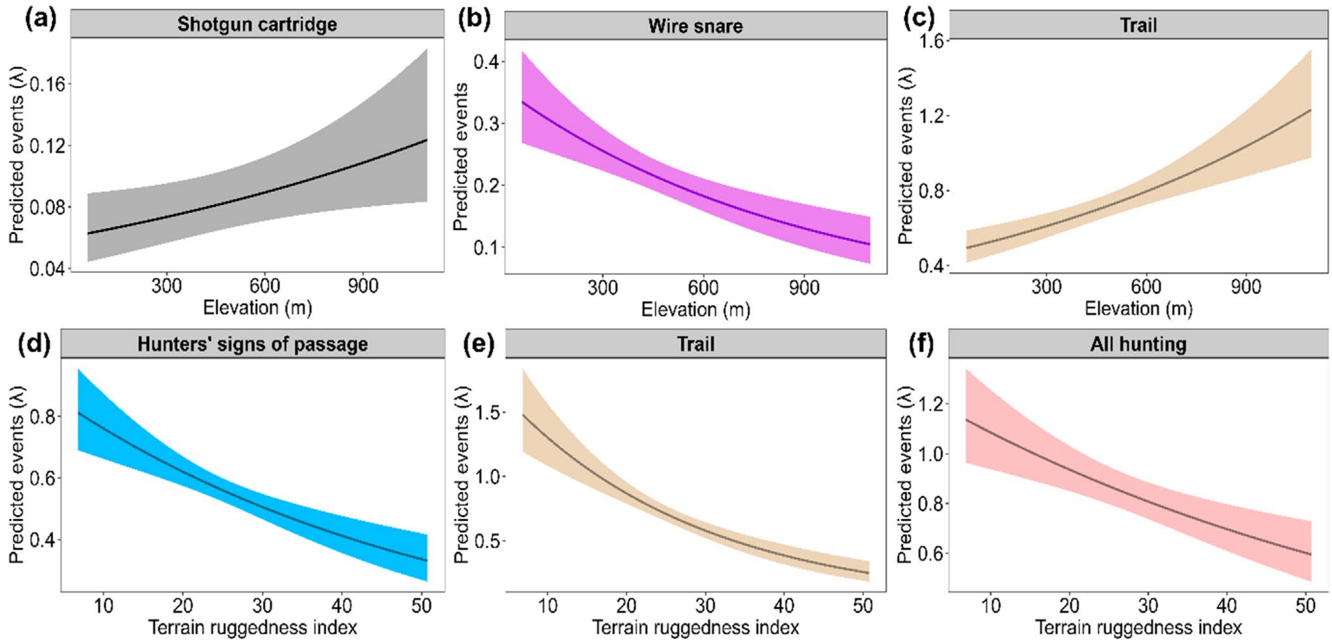

FIGURE 7 | Predicted events (λ) of different indicators of hunting along the elevational (a, b and c) and the terrain ruggedness (d, e and f) gradients, obtained from the best-fitting generalised linear mixed model for each hunting sign. The dark lines represent the expected mean of the predicted mean and the coloured areas represent the 95% confidence intervals.

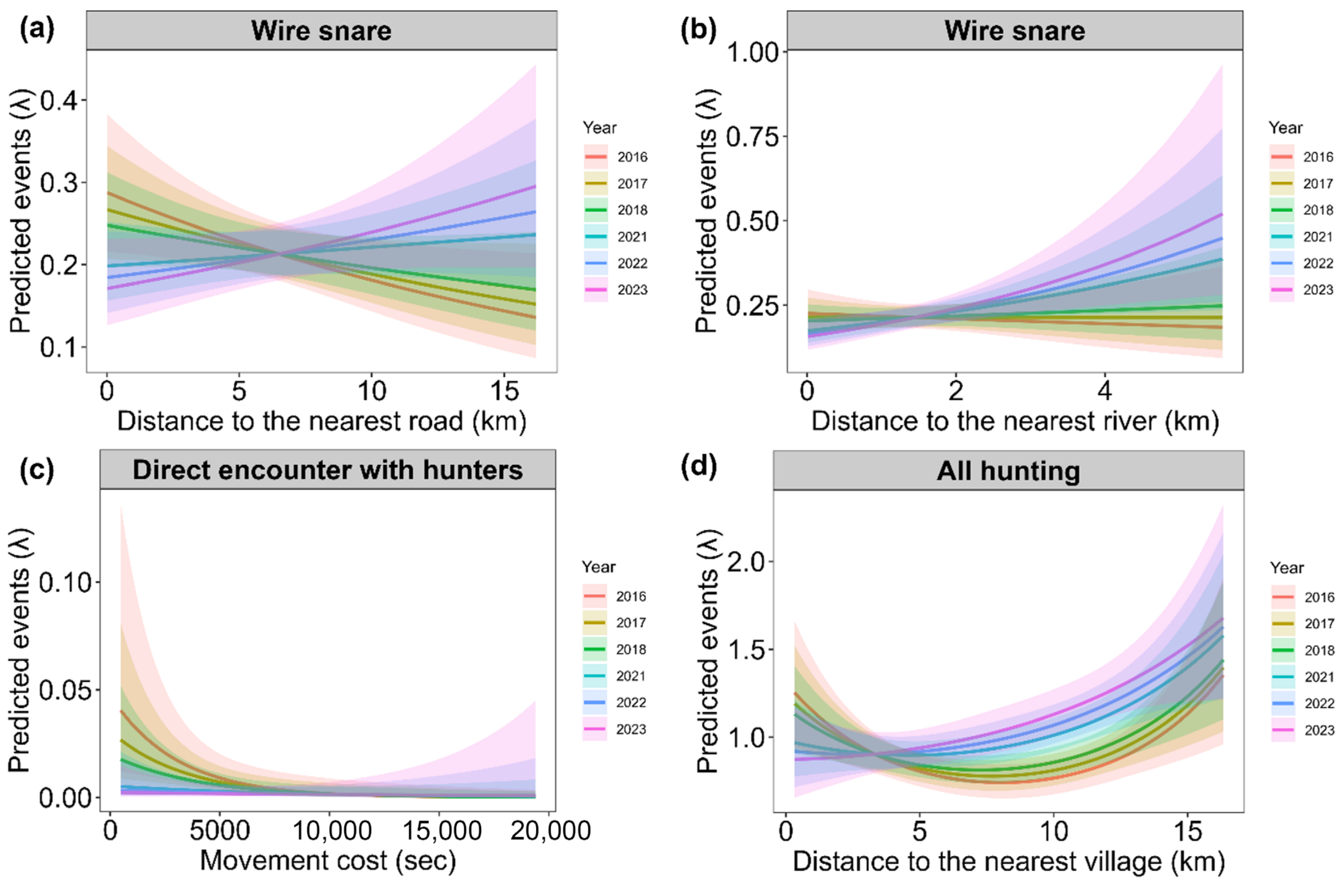

FIGURE 8 | Effect of the interaction between the year and (a) distance to the nearest road, (b) distance to the nearest river, (c) movement cost, and (d) distance to the nearest village on the events (λ) of wire snares, direct encounters with hunters, and all hunting signs combined (global model). The dark lines represent the expected mean and the light areas represent the 95% confidence intervals.

In fact, with the rise of commercial hunting, hunters across many landscapes in Central Africa are travelling longer distances in the forest, using hunting camps as satellite central places, and therefore covering more extensive areas (Abernethy et al. 2013). For instance, in the southeastern part of Cameroon, Fa et al. (2021) revealed that hunters from only ten villages covered as much as 2000 km^2, approximately the size of the Ebo forest. This situation can have catastrophic consequences for the long-term persistence of mammal populations in the landscape as it leaves no unhunted pockets of forest which can act as reservoirs to ensure the long-term persistence of species across the forest through source-sink dynamics (Coad et al. 2019; Novaro, Redford, and Bodmer 2000). Some species are reported to have become locally extinct or extremely rare in the Ebo forest in recent years, including the black and white colobus (*Colobus guereza*) and the Preuss's red colobus (*Piliocolobus preussi*) (Whytock et al. 2021).

We found that both snares and shotguns were used across the Ebo forest by hunters, as also reported by Mfossa et al. (2022) in the northeastern part of the forest. These two hunting methods are also used in other areas across the tropics (Froese et al. 2023; Kandza et al. 2023; Laurance et al. 2006; Lewis and Phiri 1998; Rist et al. 2009). We found that wire snares were the most frequently recorded hunting tool, likely related to the low cost of making and replacing snares and the high detectability of snares in the forest (Fournier et al. 2022; Froese et al. 2023; Gray et al. 2017; Teutloff et al. 2021; Wright and Priston 2010). These snares are very damaging to wildlife, not only because of their large number but also because they target wildlife species indiscriminately (Gray et al. 2017). Additionally, many animals killed by wire snares are often left uncollected in the forest (Rao et al. 2005; Rist et al. 2008) as we observed on several occasions during the surveys. Although shotgun cartridges represented only 8% of hunting signs, this does not necessarily reflect the damage to wildlife, because shotgun hunting is reported as being a more effective hunting method and the low encounter rate of shotgun cartridges could be related to their low detectability (Dounias 2016; Yasuoka et al. 2015). Unlike snares, shotgun cartridges are likely to be covered by the leaves falling from surrounding trees. Since the surveys only took place once a year, with approximately 12 months between two visits in the same site, it is plausible that a considerable proportion of cartridges were not detected. The combination of these two hunting techniques (i.e., shotgun hunting and snaring) in the area is therefore likely to imperil wildlife as it allows hunters to target both terrestrial and arboreal species (Jones et al. 2020).

4.2 | Spatial Predictors of Hunting

Our results revealed that in the Ebo forest, hunting signs were most influenced by the topography (elevation and terrain ruggedness index) and the anthropogenic gradient (distance to the nearest road and village). For instance, all combined hunting events tended to increase non-linearly with the distance to the nearest village, with considerably more hunting events occurring near the villages and far away (at distances greater than 10 km away from villages), while the area in between experienced less hunting. Additionally, hunting events decreased significantly with increasing terrain ruggedness index. However, hunting patterns along these gradients were also highly dependent on the hunting sign considered. Specifically, similar to Dobbins et al. (2020), we found a negative relationship between shotgun cartridges and the distance to the nearest village, but this relationship was not statistically significant. However, as expected, the quadratic effect of the distance to the nearest village on shotgun cartridges was significant, suggesting that high shotgun hunting is likely to occur near villages and in the central zone of the forest (Figure 6). These results are consistent with those of Roopsind et al. (2017) who reported no significant relationship between hunting intensity and the distance to the nearest village and road in central Guyana. This may result from the highly heterogeneous terrain, combined with increasing economic-driven motivation, which can increase the complexity of hunters' movements and activities in the forest (Froese et al. 2023). For instance, the establishment and use of hunting camps facilitate shotgun hunting in the core zone of the forest (Abernethy et al. 2013; Froese et al. 2023; Rist et al. 2009; Whytock et al. 2014). Other variables such as the existence of trails and the topography likely facilitate hunters' access to the most remote parts of the forest (Deith and Brodie 2020). These results suggest that Euclidean distance alone does not explain how people access hunting areas (Deith and Brodie 2020). In this context, Rist et al. (2009) suggested that in some areas, hunting activities may not continuously decline with increasing distance from villages, but may be heterogeneously distributed in hotspots across the landscape. In the Ebo forest, our findings showed that shotgun hunting events were abundant near villages and then decreased and remained relatively low between 5 and 11 km from villages, but increased again very sharply more than 12 km from villages. Such strong fluctuations suggest the complexities of hunting activities along the village-distance gradient which might be associated with several factors including terrain heterogeneity, prey abundance and local hunting habits (with some hunters leaving the village and coming back daily with activities limited around the village, and others staying in hunting camps inside the forest to hunt in that locality for several days) (Abernethy et al. 2013; Rist et al. 2009).

As expected, we found that direct encounters with hunters mainly occurred in the most accessible areas. However, hunters' signs of passage increased significantly with movement cost. A similar pattern was found by Branch et al. (2022) on Bioko Island, where they reported frequent direct encounters with hunters near roads while most hunting happened farther away from roads. The most accessible parts of the forest are usually those near villages and main roads, from where hunters spread across the forest. Most hunters are skilled, with a good knowledge of those areas near their villages, and therefore do not need any physical reference markers to find their way out of the forest. However, when hunting far away from villages, they certainly need to leave more signs behind them so that they can find their way back to the camp or village.

Elsewhere, hunting intensity has been shown to decrease with elevation, as a consequence of decreased accessibility (Griffiths et al. 2022). However, our results revealed interesting differences along the elevation gradient related to hunting methods. While shotgun hunting increased significantly with elevation, wire snares instead decreased. These results may be related to the fundamental differences in hunting methods. After setting their snares in the forest, hunters need to revisit them regularly to remove any catch while it is still fresh. Hunters may therefore choose to set their snares in areas of lower elevation to reduce the time and physical effort necessary to revisit them. Conversely, shotgun hunting does not necessitate any revisit, and is consequently more appropriate for areas with challenging terrain as hunters will kill and carry the animals directly while hunting. The significantly positive relationship between trails and elevation revealed by this study may also be related to hunting strategies as hunters may navigate the lower areas more freely, but mostly use trails to access the areas located at the top of the mountains.

We also found that hunters' signs of passage decreased significantly with increasing terrain ruggedness index. This suggests that even though hunting activities are spread across the entire forest, hunters were more inclined to avoid areas with highly rugged terrain where movement is more difficult (Branch et al. 2022; Brodie et al. 2023; Deith and Brodie 2020). In line with this, we found significantly lower encounter events of trails with increasing terrain ruggedness index.

4.3 | Temporal Patterns of Hunting Activities

Although we did not find sufficient evidence of change in snaring activity over the past 8 years (2016–2023) in the Ebo forest, our results revealed increasing shotgun hunting since 2016. As a more effective hunting method, people may be investing in shotguns to increase their revenue from hunting (Abernethy et al. 2013). In addition, the observed immigration of specialised hunters in some villages around the forest (Morgan et al. 2013) may be leading to this increase (Coad et al. 2019). Likewise, we also observed a significant increase in hunters' signs of passage, as well as all hunting events during the same period. Conversely, direct encounters with hunters tended to decrease, although not significantly. These results may be related to our observations showing that non-native hunters are generally less comfortable and more nervous when they meet researchers in the forest as compared to local hunters, which can be related to the differences in the sense of belonging and ownership between both groups (Coad et al. 2019; Oates 2009). We believe that many non-native hunters hide or move away when they feel the presence of other people, especially researchers as they may not always understand the purpose of research activities in the areas, as well as the use of the data collected.

In accordance with our expectations, our results also showed interesting hunting dynamics along the anthropogenic gradient during the study period. For instance, we showed that between 2016 and 2018, wire snare events declined along the road-distance gradient. Conversely, from 2021, wire snare events increased with the distance to the nearest road (Figure 8). Our results showed that this inversion of the trend along the road-distance gradient occurred incrementally, with every subsequent year having more events of wire snares farther away from the nearest road than the previous year (Figure 8). We observed a similar change in the events of all hunting signs in our global model. We also found that direct encounters with hunters also increased in less accessible areas (Figure 8). Dounias (2016) found similar results in the south of Cameroon and attributed them to the depletion of wildlife around villages. This may suggest that hunters are increasingly moving to the core area of the forest where wildlife is still relatively common. However, this could also be related to increasing hunting activities in the inner part of the forest, resulting from the increasing influx of non-native hunters (Morgan et al. 2013), who are more susceptible to hunt in the most remote areas. We also found that snaring increased away from rivers over the years (Figure 8). In the Ebo forest, hunting camps are usually established along river borders for easy access to water while hunters are resident at the camp. Additionally, the main trails follow the river system, along which the terrain is usually less rugged which therefore facilitates less costly pathways for hunters. Overall, our results suggest increasingly higher hunting activities in the central area of the Ebo forest where Whytock et al. (2021) found that most wildlife, including flagship species such as the chimpanzee, mainly occur.

4.4 | Study Caveats

Earlier studies have demonstrated the relevance of using other covariates such as vegetation density to predict hunters' movement (e.g., Deith and Brodie (2020)). Vegetation density may also have an influence on the detectability of hunting signs as it does for wildlife signs (Whytock et al. 2021). However, in this study, we were unable to include vegetation as a predictor due to the cloud coverage on the sentinel layers of the Ebo forest (Mahmoud et al. 2019). In addition, because their geographical location was not known, we were unable to include hunting camps in our movement cost raster calculation. Doing this would have certainly improved our results as these camps are used by hunter as semi-permanent settlements to hunt across the forest (Abernethy et al. 2013; Whytock et al. 2014). Human population densities would have been an important covariate for this study (Ziegler et al. 2016), but reliable estimates of the population size of the villages across the landscape were not available. Nevertheless, we included the Human Footprint Index which includes population density, among other parameters (Venter et al. 2016). Conservation interventions have been implemented in some villages across the landscape. Although we believe that they may have had an impact on hunting activities, we did not have clear covariates such as the level interventions in each village, as well as the limits of the hunting territories of these villages to include in the models so as to assess the effect of conservation interventions on hunting patterns.

4.5 | Future Analyses

Future research should seek to produce a comprehensive map of hunting camps and major trails throughout the forest. These hunting camps could then be treated as settlements in statistical analyses to enhance the accuracy of the landscape accessibility layer. Accounting for the distance to the nearest hunting camp, similar to how the distance to the nearest village is considered here, may improve the results. In addition, applying a more rigorous and robust statistical framework that addresses the observation error and temporal changes such as dynamic occupancy models could improve both the quality and the interpretability of the results. In such occupancy models, variables such as vegetation density and the survey duration (time spent) in each sampling unit may be included as detection covariates.

With the recent decision to convert the Ebo forest into logging concessions additional years of data would help to understand what impact this change will have on hunting activities. Finally, future analyses might also start by understanding and mapping hunting territories across the forest, so as to measure the changes in hunting activities in the territory of different villages, and thereby investigate if there is any relationship between conservation interventions in these villages and hunting activities within their territory.

5 | Conclusions

Negative impacts of hunting activities can be moderated if we understand the processes underpinning their distribution patterns at the landscape scale. In this study, we have demonstrated that in unprotected areas where hunter behaviour is not influenced by law enforcement-induced sanctions, systematic long-term monitoring data on hunting signs can be instrumental in understanding the spatial and temporal patterns of hunting pressure. To our knowledge, this is the first study to use a long-term dataset on hunting signs to analyse the spatial and temporal patterns of hunting activities in an unprotected Central African rainforest. We argue that even though we cannot directly quantify the relationship between the observed hunting signs and wildlife offtake (Astaras et al. 2017), these hunting signs reflect the efforts and means deployed by hunters and provide information about their spatial and temporal use of the forest (Critchlow et al. 2015; Dobson et al. 2020). Our results suggest that in areas where the demand for bushmeat is high, as is the case in the Ebo landscape and other places across the region (Fa et al. 2006), the patterns of hunting activities along the anthropogenic gradient (e.g., distance to villages, distance to roads) may depend on factors such as local hunting techniques, and may change over time. Hence, using these features alone as proxies of hunting intensity may not be sufficient to capture the spatial patterns of hunting activities. These results highlight the importance of refraining from generalising observations from one site to other areas, therefore emphasising the necessity of collecting local hunting data when integrating hunting into ecological studies and conservation planning.

Despite the challenges in measuring the spatiotemporal patterns of hunting, using long-term monitoring data on hunting signs collected between 2008 and 2023 we have shown how hunting patterns change dynamically with respect to both human and landscape-related features. We have also shown that in the Ebo forest, hunters combine shotgun hunting and wire snaring to explore the entire landscape, as demonstrated along the elevational gradient, thus increasing the susceptibility of all terrestrial and arboreal species across the area. Moreover, we have revealed increasing hunting activities in the core area of the forest, which calls for urgent actions to regulate wildlife hunting and ensure the long-term persistence of wildlife populations in the landscape. Overall, our results are particularly important for conservation planning in large, ecologically important but unprotected landscapes where non-governmental actors are working with local stakeholders to ensure the sustainable use of natural resources through community-based approaches. It is likely that many conservation organisations possess databases of hunting signs collected during wildlife surveys, but believe that they are of poor quality. Our results show that by using such data, we can, at least partially, understand the spatial and temporal patterns of hunting activities, which is crucial in evaluating the effectiveness of conservation interventions and guiding the prioritisation of limited conservation resources.

Author Contributions

V.R.V.N., M.S. and M.W. conceived this research. B.J.M., E.E.A. and M.W.T. led funding acquisition for data collection. 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. collected the data over the years based on the survey design initially conceived by B.J.M., E.E.A. and R.C.W. V.R.V.N. curated and analysed the data, and drafted the manuscript with the help of M.S., M.W., N.B., J.K. and M.W.T. All authors critically reviewed the manuscript and approved the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset supporting the results presented within this manuscript will be accessible in Dryad through the following link: https://doi.org/10.5061/dryad.8931zcrzk.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13951.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.