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Research Article

Humans acting as 'super predators' in Central African forests: trophic downgrading and disruption of predator–prey dynamics

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Predator–prey interactions are key ecological processes structuring wildlife communities by shaping species abundances and distributions, thereby influencing ecosystem functioning. They result from the interplay of bottom–up (e.g. prey availability) and top–down (e.g. predator control) forces. By altering species diversity and behaviors, humans can reshape trophic structures and predator–prey relationships. In Central African forests, where leopards *Panthera pardus* and African golden cats *Caracal aurata* are the largest carnivores, we examined trophic structure, spatiotemporal predator–prey dynamics, and responses to human presence and hunting pressure, a largely understudied issue. We hypothesized that increasing human pressure alters community structure and trophic organization, consistent with trophic downgrading and the view of humans as 'super predators'. Using camera trap data from three sites along a human pressure gradient in the Republic of Congo and Cameroon, we tested two predictions: (P1) in low-pressure forests, functional diversity is higher and predator–prey dynamics are shaped by ecologically-driven bottom–up and top–down processes; (P2) in high-pressure forests, humans exert top–down control across multiple trophic levels, reducing functional diversity and disrupting spatiotemporal predator–prey relationships. Combining community diversity analyses, structural equation modeling, and diel activity analyses, we found patterns consistent with both predictions. In low-pressure areas, prey availability and predator presence jointly structured spatiotemporal patterns, supporting functionally rich communities. Conversely, in the most disturbed area with higher human density and intense hunting, both focal predators were absent, ungulate detections declined by 41–89%, and small generalists became up to 23 times more common than in undisturbed areas. Prey spatiotemporal patterns also shifted, reflecting human avoidance. These findings suggest that humans can act as 'super predators' in Central African forests, overriding natural predator–prey spatiotemporal

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organization and disproportionately altering mammal communities. Together, our results indicate that limiting hunting pressure across large, connected landscapes appears critical for maintaining trophic network integrity and ecosystem functioning.

Keywords :carnivore, community ecology, defaunation, felid, landscape of fear, trophic cascade

Introduction

Predator–prey dynamics emerge from a combination of resource-driven (bottom–up) and predation-driven (top–down) mechanisms that collectively structure communities and ecosystems (Hairston et al. 1960, Hunter and Price 1992). Bottom–up processes reflect the influence of food and habitat availability on higher trophic levels, while top–down processes involve control from predators on prey populations through consumptive (i.e. density-mediated) and non-consumptive (i.e. behaviorally mediated) effects (Laundré et al. 2014, Tossens et al. 2024). Across spatial and temporal scales, these forces drive evolutionary adaptations in behaviors, such as predation avoidance and hunting strategies (Preisser et al. 2005, Murphy et al. 2021). This intricate 'hide-and-seek' interplay extends beyond pairwise predator–prey relationships, with cascading effects through food webs. These influence both biotic (e.g. vegetation regeneration) and abiotic processes (e.g. nutrient cycling) (Estes et al. 2011), ultimately shaping broader ecosystem properties, such as habitat heterogeneity and biodiversity (Paine 1980, Ford et al. 2014).

The relative strength of bottom–up and top–down forces varies across ecological contexts, depending on local environmental conditions, species traits and disturbance regimes (Kuijper et al. 2016, Haswell et al. 2017). Perturbations to these forces can alter food web structure and drive ecosystems to divergent configurations or 'alternative states' (Terborgh and Estes 2010). In an era of rapid environmental change, understanding how predator–prey interactions respond to shifting conditions, such as intensified human activities, has become increasingly important to predict and mitigate ecosystem change (Kuijper et al. 2016, Prugh et al. 2023). This is especially relevant in systems with multiple predators and prey, where complex interdependencies further complicate our understanding, and modeling, of community dynamics (Montgomery et al. 2019, Curveira-Santos et al. 2024).

In human-dominated landscapes, anthropogenic influences can reshape predator–prey relationships by altering species abundances, distributions, and trophic organization (Dorresteijn et al. 2015, Kuijper et al. 2016). While some species benefit from land use modifications, such as increased food availability or novel habitats, most are adversely affected by anthropogenic disturbance such as hunting, poaching, resource depletion and habitat loss (Crawford et al. 2022, Bassing et al. 2024a). Globally, and especially in tropical regions, large- and medium-sized mammals are disproportionately affected (Dirzo et al. 2014, Benítez-López et al. 2019), whereas smaller species often thrive in disturbed areas, notably benefiting from the extirpation of both predators and competing species (e.g. larger frugivores) (Galetti et al. 2015, Gutiérrez-Granados and Dirzo 2021). Through this process of 'trophic downgrading' (Estes et al. 2011), humans disrupt body-mass distributions among trophic guilds, with cascading consequences for ecological processes including prey limitation, competition, herbivory and seed dispersal (Terborgh and Estes 2010, Dirzo et al. 2014). Beyond direct effects on population densities, human pressure can also indirectly alter the spatial and temporal behaviors of both predators and prey (Gaynor et al. 2022, Van Scoyoc et al. 2023). By exerting fear-mediated top–down effects on large- to medium-sized mammals, human presence and activities can override natural interspecific interactions, disrupting the balance of bottom–up and top–down forces that structure food webs under relatively undisturbed conditions (Suraci et al. 2019, Gilbert et al. 2022).

Collectively, such disruptions erode wildlife functional diversity by reducing the range of trophic roles, body-size classes and behavioral niches represented within communities (Ahumada et al. 2011, Resende et al. 2024). As a result, ecosystem functioning becomes increasingly constrained, promoting homogenized and simplified community structures characteristic of disturbed environments (Dirzo et al. 2014, Pires and Galetti 2023). In this context, humans have been described as 'super predators', reflecting their disproportionate influence on mammal populations and trophic interactions compared to other predators (Darimont et al. 2015, Clinchy et al. 2016).

Central African tropical forests are biodiversity-rich ecosystems, supporting highly diverse animal assemblages and intricate trophic networks (Fonteyn et al. 2023). In these forests, leopards *Panthera pardus* and African golden cats *Caracal aurata* are the largest predators, preying on a wide range of taxa (Henschel et al. 2011, Tossens et al. 2026). Yet, empirical studies of mammal communities, and of carnivore guilds in particular, remain scarce in Central African forests (Bahaa-el-din et al. 2016, Bruce et al. 2018a). Existing research has largely focused on the effects of hunting on species richness or abundances (Laméris et al. 2019, Lhoest et al. 2020), rather than on community-level trophic structure and predator–prey interactions, despite increasing ecosystem vulnerability (Say-Sallaz et al. 2019). These forests face growing threats from expanding human populations and extractive activities (Gallego-Zamorano et al. 2020, Fonteyn et al. 2023). In particular, the concurrent activities of bushmeat hunting and large-scale poaching (hereafter, 'hunting activities') have severely reduced mammal populations across much of the Congo Basin (Benítez-López et al. 2019), driven by rising demand for meat, improved access to remote forests and more efficient hunting techniques (Abernethy et al. 2013, Ziegler et al. 2016). To mitigate the community-wide effects

of defaunation, protected areas (PA) and sustainable forest management (SFM)-certified concessions may play complementary roles as refuges and buffer zones through wildlife conservation measures (Zwerts et al. 2024). However, landscape-level anthropogenic pressures, such as human density and forest fragmentation, often exert stronger influences on mammalian communities in tropical forests than management status alone (e.g. PA, SFM-certified forests, managed forests) (Greco et al. 2025).

In this context, we aimed to provide the first comprehensive insights into trophic structures and spatiotemporal organization between the two largest carnivores and their prey in Central Africa's semideciduous forests. Specifically, we examined mammalian functional diversity and evaluated the relative roles of bottom–up (prey availability) and top–down (predator control) processes in structuring predator–prey interactions along a human pressure gradient, using co-occurrence and activity pattern analyses. We hypothesized that increasing human presence and hunting pressure alter community structure and trophic relationships, consistent with trophic downgrading and the view of humans as 'super predators'. We tested two predictions: (P1) in low human pressure forests, functional diversity is higher and predator–prey dynamics are shaped by ecologically-driven bottom–up and top–down processes; (P2) in high human pressure forests, humans exert strong top–down control across multiple trophic levels, reducing functional diversity and disrupting natural spatiotemporal predator–prey dynamics.

Material and methods

Study areas

The study was conducted within the region designated as 'Moist Central Africa' (Fayolle et al. 2014), characterized by semideciduous forests (Réjou-Méchain et al. 2021). The mammal assemblage in this area belongs to the 'inland' zoogeographical district (Fonteyn et al. 2023). This region experiences annual rainfall ranging around 1684 mm, with two distinct rainy seasons from August to November and April to June (Morgan et al. 2019). The mean annual temperature varies slightly between 23 and 25°C. The landscape is largely a mosaic of protected areas, logging concessions and community forests (Lhoest et al. 2020). The forest is thus variably fragmented and exposed to a gradient of anthropogenic impacts, including hunting activities, associated with local human density and proximity.

Three distinct areas along a gradient of human pressure (HP) were selected based on local human density and landscape-scale anthropogenic threat indices, from least to most impacted: 1) Nouabale-Ndoki National Park (hereafter 'NP') in northern Republic of Congo, 2) a large SFM-certified logging concession south of NP with low human population density (hereafter 'LowHP'), and 3) a smaller SFM-certified concession in southeastern Cameroon with higher population density (hereafter 'HighHP') (Table 1, Fig. 1). Site selection was guided by our aim to assess how varying levels of human pressure affect mammal communities, with a particular focus on leopards and golden cats, whose status across the three landscapes was unknown prior to our surveys. To assess landscape-scale anthropogenic threats, we extracted mean values of the Defaunation index (DI; Benítez-López et al. 2019) and the Forest landscape integrity index (FLII; Grantham et al. 2020) (Table 1). The size of the monitored forest entities reflects local socio-political realities, with southeastern Cameroon being characterized by a more fragmented landscape of smaller administrative units compared to the larger, more continuous forest management blocks in northern Congo (Table 1).

Established in 1993 and part of a UNESCO Natural World Heritage Site since 2012, the NP comprises unlogged forests that are strictly protected from hunting activities (Morgan et al. 2019). In contrast, the two logging concessions, LowHP and HighHP, have implemented selective and reduced-impact timber harvesting practices since acquiring concessionary rights in 1997 and 2004, respectively, and achieving Forest Stewardship Council (FSC) certification in 2006 and 2008, respectively (Morgan et al. 2019, Lhoest et al. 2020).

Table 1. Description of the three study areas. Human population density estimates were derived from census data from management plans (NP: 2022; LowHP: 2010; HighHP: 2008). 'SFM' means sustainable forest management (Forest Stewardship Council certification). DI – represents the mean defaunation index, where 0 indicates a nearly completely defaunated mammal community, and 1 an intact community (Benítez-López et al. 2019). FLII – indicates the mean forest landscape integrity index, ranging from 0 (no forest integrity) to 1 (complete forest integrity) (Grantham et al. 2020).

Study area	Country	Location	Forest management status	Area (km^2)	Human population density (inhabitants km^{-2})	$\overline{DI}$	$\overline{FLII}$	No. of stations	Survey duration (trap days)	
									Mean ± SD per station	Total
NP	Republic of Congo	02°14′N, 16°25′E	National Park	4300	~0	0.87	0.96	63	131±8	8246
LowHP	Republic of Congo	01°55′N, 16°25′E	Logging concession (SFM-certified)	7482	2.2	0.80	0.91	62	185±42	11478
HighHP	Cameroon	03°13′N, 14°18′E	Logging concession (SFM-certified)	1180	6.4	0.58	0.93	57	119±42	6802

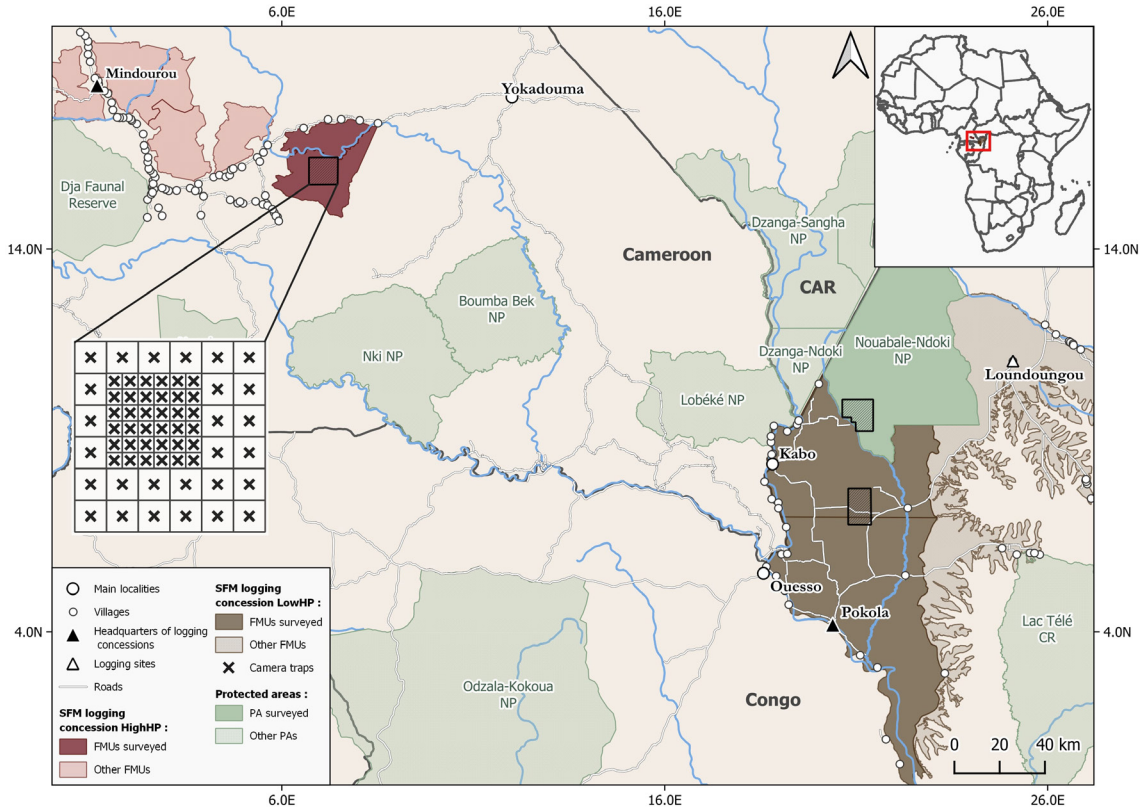

Figure 1. Camera trap surveys conducted across a human pressure gradient in three study areas, from least to most impacted: (i) Nouabale-Ndoki National Park (NP), (ii) a SFM-certified logging concession in northern Congo (LowHP), and (iii) another SFM-certified concession in southeastern Cameroon (HighHP). The monitoring network consisted of a nested grid, with an internal grid of 1 × 1 km and a larger grid of 2 × 2 km. Only villages surrounding the surveyed concessions are indicated. 'FMUs' means forest management units.

In compliance with FSC certification requirements, both concessions adhere to wildlife management plans to conserve protected species and sustainably manage other wildlife resources. However, LowHP has benefited from sustained conservation efforts and investments since 1999 through an effective public-private partnership (Poulsen et al. 2009), whereas HighHP received limited external support for wildlife monitoring and anti-poaching efforts between 2008 and 2015.

Camera trap surveys

We conducted a camera trap survey to inventory (semi-)terrestrial vertebrate communities larger than 0.5 kg, a threshold chosen to account for the reduced detectability of smaller species with this method. Surveys were conducted in the three areas over a period of at least 4 months (Table 1), covering both rainy and dry seasons: from August 2022 to February 2023 in NP and LowHP, and from August 2023 to February 2024 in HighHP.

In each study area, we deployed a grid of 63 paired camera trap stations (Bolyguard SG2060-D), each consisting of two cameras placed on opposite sides of the same trail, following standard spatially-explicit capture–recapture (SCR) protocols for leopard (Henschel 2008) and golden cat (Bahaa-el-din et al. 2015) monitoring. The survey design featured a 1 × 1 km inner grid (36 km^2) nested within a 2 × 2 km outer grid, covering a combined area of approximately 144 km^2 (Fig. 1). This layout was originally developed for density estimation of leopards and golden cats, ensuring an appropriate spatial scale for detecting individuals of both species and both sexes. In this study, we focused on community-level analyses: each paired station was treated as a single sampling unit, and only one camera per pair (the one that recorded the highest species richness) was retained to avoid pseudo-replication. In NP, the grid was installed in the southern part of the park. In both logging concessions, grid locations were selected in collaboration with logging managers, targeting areas that 1) had not yet been logged by the current concessionaire to avoid short-term logging impacts, 2) exhibited a relatively high concentration of wildlife signs within the concession to maximize capture probability of focal predators, given their presumed avoidance of disturbance, and 3) remained logistically and physically accessible.

Camera trap stations were installed as close to the grid cell centroids as possible (Fig. 1). Around each centroid, existing wildlife trails were searched within a 150 m radius to identify the most suitable locations for camera trap placement, on trails as felids preferentially use pathways in tropical forests (Jenny 1996, Carter et al. 2015). When present, trails showing signs of leopards or golden cats (e.g. spoor, scratch

mark, scat) and major trail intersections were prioritized. Roads were avoided to reduce the risk of camera trap theft. Camera traps were mounted 40 cm above ground level and set to capture a single picture per trigger (Horion et al. 2024). During this same search effort, human signs (e.g. gun cartridges, camps, wire snares) encountered along wildlife trails were recorded using a GPS, as well as opportunistically while moving between camera trap stations during camera trap deployment.

After camera retrieval, images from 63, 62 and 57 stations in NP, LowHP and HighHP, respectively, were used in the analyses, as some cameras were stolen or damaged at seven stations (Table 1). Mammal and ground bird species were identified using the Trap Tagger online platform (https://wildeyeconservation.org/traptagger/). Detection events of the same species at the same station separated by at least 30 minutes were considered independent (O'Brien et al. 2010, Meek et al. 2014).

Diversity analysis and focal species selection

To explore community structure and diversity in each area, we estimated 1) species richness, 2) non-parametric indices (i.e. Shannon's diversity index, Evenness index, Berger–Parker index, and Jaccard similarity index, equations provided in the Supporting information, Drouilly and O'Riain 2019), and 3) detection rates (i.e. the number of independent capture events per 100 camera trap days) for each species (Rovero et al. 2014). Although these metrics do not account for imperfect detection (Sollmann et al. 2013), they provide a rapid assessment and comparison of species site use patterns across areas with comparable habitats and survey designs (Royle and Nichols 2003, Palmer et al. 2018).

Species rarefaction curves were constructed for each study area to compare species richness while accounting for differences in sampling effort. These curves were derived from cumulative camera trap days, with 95% confidence intervals derived from 1000 randomizations with replacement using the 'vegan' package (Oksanen et al. 2024).

We identified prey species of both leopards and golden cats by reviewing dietary studies (Henschel et al. 2011, Bahaa-el-din 2015, Tossens et al. 2026) conducted at sites in the Republic of Congo and Gabon with comparable mammal communities and anthropogenic disturbance (Fonteyn et al. 2023).

Structural equation modeling

We used a piecewise structural equation modeling (SEM) approach to investigate predator–prey spatial dynamics across a gradient of human pressure. This framework was chosen because it enables the disentangling of both direct and potential indirect effects (i.e. cascading impacts of one variable mediated through other variables) of human pressure, environmental variables, and predator–prey interactions on species' site use intensity, a level of complexity that would be difficult to capture with traditional regression approaches. Unlike standard linear models, which typically assess only direct relationships between variables, SEMs allow for the simultaneous modeling of multiple interdependent relationships within a hypothesized causal framework (Sirén et al. 2021, Curveira-Santos et al. 2024). This is achieved by translating a conceptual path diagram into a series of statistical models (e.g. linear regressions). While this approach enables a more holistic understanding of complex ecological interactions, it does not establish causation. Instead, it evaluates whether the data align with hypothesized causal relationships (Grace 2008, Lefcheck 2016, Sirén et al. 2021).

We used the number of independent capture events at each sampling point as our measure of species' site use intensity. This metric reflects both local abundance and habitat use dynamics within landscapes (Curveira-Santos et al. 2024). As we attempted to minimize variation in detection rates between study areas through standardized study design (i.e. camera placement and settings), variation in detection rates can serve as a reliable proxy for capturing fine-scale spatial patterns of interest.

We incorporated human pressure and environmental factors as exogenous predictors (i.e. independent variables not influenced by other covariates in the model) and the site use intensity of focal predators and prey as endogenous variables (i.e. response variables influenced by other covariates in the model) (Table 2) (Dyck et al. 2025). To measure the impact of human pressure, we used proxies specific to each site, derived from either our camera trap (detection rate of hunters) or remote sensing data (distances to park boundary, human signs, roads and villages) (Table 2). Environmental covariates that could have a potential effect on species-specific spatial patterns, including distances to rivers/swamps (i.e. linear water bodies identified through vegetation differences indicative of hydromorphic soils) and bais (i.e. islands of open-canopy habitat within a forest matrix), were extracted from Google Satellite imagery (Hockridge et al. 2024) and added to the models (Table 2).

As there are no prior studies on spatial predator–prey interactions in Central African forests, we adopted a two-step exploratory approach to identify ecologically relevant patterns of association among species' site use intensities. First, plausible pathways (i.e. bottom–up and/or top–down) were defined a priori for each predator–prey pair based on ecological theory (e.g. prey availability influencing predator space use versus predator effects on prey space use) and species' traits. Second, initial generalized linear models (GLMs) were used to explore the emergence and directionality of these relationships, which then informed the final SEM construction (details in the Supporting information) (Dyck et al. 2025).

We implemented a single SEM structured as a series of generalized linear models (GLMs) for each study area, with a negative binomial distribution (log-link function). The logarithm of active trap days was included as an offset term to account for variations in sampling effort across camera trap stations. Although spatial autocorrelation is an inherent limitation of grid-based camera trap designs, we did not model it explicitly, as our primary focus was to compare structural relationships between landscapes rather than capturing fine-scale spatial dependencies within study areas. Importantly,

Table 2. Variables used to investigate predator–prey spatial dynamics within central African tropical forests using a structural equation model (SEM) framework, incorporating camera trap detection patterns of focal predators and prey as endogenous predictors and responses, and human pressure and environmental factors as exogenous predictors. [a]Endogenous variable (response and predictor), [b]Exogenous variable (predictor), [c]Source: camera trap data from this study, [d]Source: extracted GIS data from this study, [e]No predator detected, [f]No hunter or hunting sign detected.

Covariate	Description	Considered study areas	Mean (range)	Hypothesis	Predicted effect
Site use intensity[a,c]	Species-by-camera count data of independent detections (<30 min) for each focal predator and prey species	NP, LowHP, HighH[e]	22.5 (0–551)	Interspecific interactions, local anthropogenic disturbance, and environmental characteristics influence predator and prey site use intensities (Haswell et al. 2017, Bassing et al. 2024a, 2024b).	(+/−)
Distance to park boundary[b,d]	Distance to the boundary of the National Park (km)	NP	5.30 (0.90–10.9)	Park boundaries, more accessible than cores, face higher illegal hunting pressure, reducing site use by hunting-sensitive species (i.e. edge effect, Woodroffe and Ginsberg 1998, Kiffner et al. 2013).	(+)
Detection rate of hunters[b,c]	Standardized number of independent detections (<30 min) of hunters and dogs	NP[f], LowHP[f], HighHP	0.55 (0–14.6)	Higher hunter and dog detection rates or signs of hunting activities indicate higher local hunting pressure and influence species distribution (Laurance et al. 2006, Laméris et al. 2019).	(−)
Distance to human signs[b,d]	Distance to the nearest human sign (comprising cartridges, camps, cables, traps) identified in the field (km)	NP[f], LowHP[f], HighHP	1.96 (0.20–4.20)		(+)
Distance to road[b,d]	Distance to the nearest permanent road within the concession (km)	LowHP, HighHP	3.15 (0.10–9.70)	Roads are open areas that influence certain species' habitat use for movement or resources (Clark et al. 2009).	(+/−)
Distance to village[b,d]	Distance to the nearest village (km)	LowHP, HighHP	19.7 (13.1–25.4)	Increased human activities are associated with proximity to roads and villages, exposing formerly remote areas to higher hunting pressure and affecting species site use intensity (Vanthomme et al. 2013, Lhoest et al. 2020).	(+)
Distance to river/swamp[b,d]	Distance to the nearest river and swamp (km)	NP, LowHP, HighHP	1.06 (0–3.80)	Proximity to rivers and swamps influences species distribution, as they can serve as resources or barriers (Fonteyn et al. 2023).	(+/−)
Distance to bai[b,d]	Distance to the nearest bai (km)	NP, LowHP, HighHP	2.26 (0.10–9.90)	Bais attract certain prey species due to mineral resources and vegetation or serve as hunting grounds for predators (Clark et al. 2009, Hockridge et al. 2024)	(−)

the standardized sampling design applied across all study areas ensures that any potential bias introduced by spatial clustering is consistent and therefore unlikely to affect inter-site comparisons.

Model fit was assessed using Fisher's C test (Lefcheck 2016) and marginal R^2 values were reported for each species-specific model to quantify explained variance. Direct and indirect effects were derived from univariate path coefficients. Indirect pathways were considered significant ($p < 0.05$) only if both intermediary paths were significant, with the indirect effect size calculated as the product of the two direct path coefficients (Sirén et al. 2021, Dyck et al. 2025). Following Curveira-Santos et al. (2024), we did not use standardized coefficients, as the variation in species-specific traits and site-specific conditions could distort the comparability of pathway strength effects and lead to misleading conclusions. Before modeling, covariates were tested for multicollinearity using variance inflation factors (VIFs), with only those scoring VIF < 2 included in the final models. Full SEM construction details, including preliminary GLMs, are provided in the Supporting Information.

Temporal analysis

To model the activity patterns of predators, prey species, and hunters at each study area, we applied kernel density functions to timestamp data from independent capture events, using the 'overlap' package (Meredith and Ridout 2024). Temporal overlap between predators and their prey was assessed by calculating

the non-parametric overlap coefficient (Δ) for each predator–prey pair in NP and LowHP (as leopards and golden cats were not detected in HighHP), and between prey species and hunters in HighHP (since no hunters were detected in NP or LowHP). For animal species, we used the estimator Δ_4, recommended for sample sizes of at least 50 observations, while Δ_1 was applied for comparisons with hunters' activity in HighHP (n = 33 observations) (Ridout and Linkie 2009). Both coefficients range from 0 (no overlap) to 1 (complete overlap). To obtain 95% confidence intervals (CI), we generated 1000 bootstrap samples for each pairwise comparison. To test whether the activity patterns of each species varied significantly between the three study areas, we used Watson's two-sample test of homogeneity (U^2). All analyses were implemented in R ver. 4.4.1 (www.r-project.org), using the packages 'piecewiseSEM' (Lefcheck 2016), 'lme4' (Bates et al. 2015), 'car' (Fox and Weisberg 2019), and 'circular' (Agostinelli and Lund 2023).

Results

Community structure and diversity

For each of the three study areas, we conducted animal community surveys over a minimum of 6802 camera days (Table 1), recording 30 (semi-)terrestrial mammal species and three ground bird species (>0.5 kg) in NP, 31 mammals and three birds in LowHP, and 26 mammals and three birds in HighHP (Fig. 2, see the Supporting information for the complete species list and their record details). Non-parametric indices revealed no significant differences in diversity, evenness, or dominance between study areas (Fig. 2). However, the Jaccard Similarity index highlighted that HighHP had the highest dissimilarity in species composition when compared to the other two landscapes (0.72–0.73), which shared greater compositional similarity (0.89) (Fig. 2).

Detection rates varied substantially by study area and species (Supporting information). Large- and medium-sized animals, including the two focal predators and ungulate prey, were recorded more frequently in NP and LowHP than HighHP (Table 3, Supporting information). In contrast, smaller species, such as rodents, were detected up to 23 times more in HighHP than in NP, whereas detection rates of large- to medium-sized prey declined, on average, by a factor of 9 (Table 3). No leopards or golden cats were detected in HighHP (Table 3).

Human–predator–prey spatial dynamics

Our three SEMs provided an adequate fit to the data: NP (Fisher's C = 102.4, df = 112, p = 0.73), LowHP (Fisher's C = 123.5, df = 120, p = 0.40), and HighHP (Fisher's C = 93.9, df = 74, p = 0.06) (Supporting information). For predators, the NP and LowHP models explained on average 41% of the variation in leopard (NP: 43%; LowHP: 39%) and 18% in golden cat site use intensity (NP: 23%; LowHP: 12%). Across the three study areas, prey species' site use intensities were explained between 3 and 45, with an average of 25 for mammal prey and 16% for ground bird species (Fig. 3). There was a greater number of significant ($p < 0.05$) biotic associations and fewer negative pathways between anthropogenic variables and species' site use intensities in NP and LowHP relative to HighHP (Fig. 3).

Predator–prey relationships

The SEM analysis revealed both positive and negative significant associations between the leopard occurrence and its prey in the two study areas with predators. In contrast, no statistically

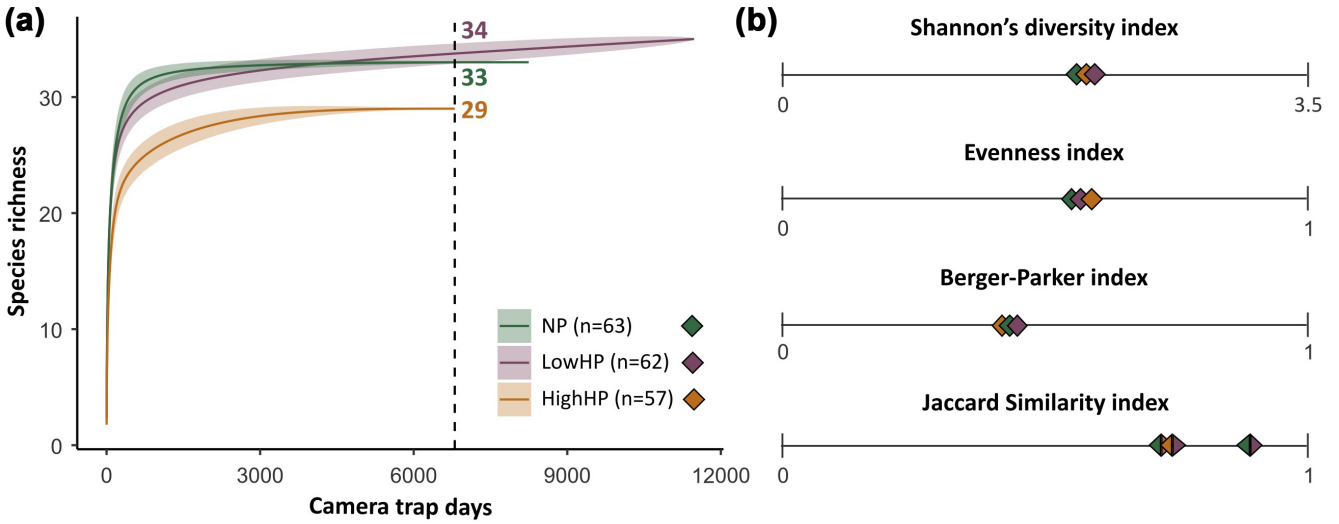

Figure 2. (a) Species rarefaction curves for (semi-)terrestrial mammals and ground birds (>0.5 kg) detected by camera traps in each study area, with 'n' representing the number of camera trap stations at each study area. Shaded polygons represent 95% confidence intervals drawn from 1000 randomizations performed with replacement, and the dashed line is the specific richness at each study area extracted from the rarefaction curves for 6802 camera days. (b) Non-parametric indices of community structure and diversity (Supporting information) calculated for each study area.

Table 3. Detection rates (/100 camera trap days) of predator and prey species across three study areas: Nouabale-Ndoki National Park (NP), a logging concession with low human pressure (LowHP), and a logging concession with higher human pressure (HighHP). Average body mass (ABM, across both males and females) is provided for each species, based on Kingdon (2015) for mammals and BirdLife International (2024) for birds. Prey species confirmed by the literature in the diets of leopards and golden cats are marked with an 'x,' while potential prey is denoted by an '*'. Species having less than 20 observations in each study area were not included (e.g. *Cephalophus nigrifrons*). ♀ denotes ABM for which only female body mass was reported.

Common name	Scientific name	ABM (kg)	Leopard's prey	Golden cat's prey	NP	LowHP	HighHP
Predator species							
Leopard	*Panthera pardus*	42.7	–	–	2.0	1.4	0.0
Golden cat	*Caracal aurata*	9.1	–	–	1.6	1.4	0.0
Prey species[1]				–			
Yellow-backed duiker	*Cephalophus silvicultor*	69.2	x	–	20.9	12.2	2.2
Gorilla	*Gorilla gorilla*	63.0♀	x	–	6.0	4.8	0.7
Red river hog	*Potamochoerus porcus*	53.3	x	–	9.2	6.2	1.2
Peters' duiker	*Cephalophus callipygus*	20.8	x	x	82.7	54.1	9.6
Bay duiker	*Cephalophus dorsalis*	20.6	x	x	6.8	4.5	2.2
White-bellied duiker	*Cephalophus leucogaster*	16.2	x	x	3.9	0.2	0.0
Blue duiker	*Philantomba monticola*	5.1	x	x	145.8	118.1	85.5
African brush-tailed porcupine	*Atherurus africanus*	3.0	x	x	1.8	3.9	16.0
Giant rat	*Cricetomys emini*	0.9	x	x	1.5	2.5	34.2
Plumed guineafowl	*Guttera plumifera*	0.9	*	*	1.7	3.4	1.0
Black guineafowl	*Agelastes niger*	0.7	*	*	1.4	0.9	1.1
Nkulengu rail	*Himantornis haematopus*	0.5	*	*	0.7	0.9	1.4

significant relationship was detected between golden cat site use and prey occurrence in any study area (Fig. 3). Leopard site use intensity was strongly associated with the detection rates of red river hogs in both NP and LowHP, white-bellied duikers in NP and gorillas in LowHP. Conversely, site use intensities of blue duikers (NP) and African brush-tailed porcupines (hereafter, 'porcupines') (NP and LowHP) were negatively associated with leopard site use. No significant relationships were identified between the detection rates of focal predators and those of yellow-backed duikers, bay and black-fronted duikers, giant rats or ground bird species (Supporting information).

Direct and indirect effects of human pressure on predator–prey relationships

Anthropogenic variables were found to have mixed, context-dependent effects on species detection rates, but tended to have more negative impacts on prey species site use in HighHP than in other study areas (Fig. 3, Table 4). In NP, Peters', bay and blue duikers exhibited increased site use with greater distance from the park boundary. In LowHP, both positive and negative associations were observed between anthropogenic factors and species site use. Gorillas and porcupines were less frequently detected near villages, while road proximity increased site use by yellow-backed and Peters' duikers, red river hogs, and gorillas. Indirectly, leopards appeared to be positively influenced by roads and negatively by villages' proximity through their association with red river hogs and gorillas. In HighHP, anthropogenic factors had a predominantly negative effect on species site use patterns, except for a positive relationship between Peters' duikers and road proximity. Human signs had the most pronounced influence, correlated with reduced detections of Peters' duiker, gorilla and red river hog (Table 4).

Temporal interactions mediated by humans and predators

Predator–prey temporal overlap

Leopards and golden cats wjere cathemeral in NP and LowHP. Leopard daily activity followed a slight bimodal distribution, with peaks in the morning (around 06:00–09:00) and at dusk (18:00). Golden cat activity peaked in the morning, especially in LowHP (Fig. 4). Their activity patterns were similar between NP and LowHP (leopard: $U^2 = 0.14$; golden cat: $U^2 = 0.07$; $p > 0.05$; Supporting information).

Except for yellow-backed and bay duikers, leopard prey species were primarily diurnal, and golden cat prey species had more diverse activity patterns (Fig. 4). In NP and LowHP, leopards exhibited the highest temporal overlap with red river hogs ($\Delta > 75\%$), followed by yellow-backed duikers ($\Delta_{NP} = 0.75$, $\Delta_{LowHP} = 0.71$), while Peters' duikers showed notable overlap with both predators (with leopard: $\Delta_{NP} = 0.58$, $\Delta_{LowHP} = 0.66$; with golden cat: $\Delta = 0.68$; Fig. 4). Golden cat activity overlapped moderately with its diurnal prey (blue duiker and ground birds) but was low with its nocturnal prey (Fig. 4).

Human influence on prey activity patterns

In HighHP, where no predator species was detected, hunter activity was strongly diurnal, peaking around 13:00 (Fig. 4). While most prey species had relatively similar activity rhythms between NP and LowHP, the activity patterns of ten

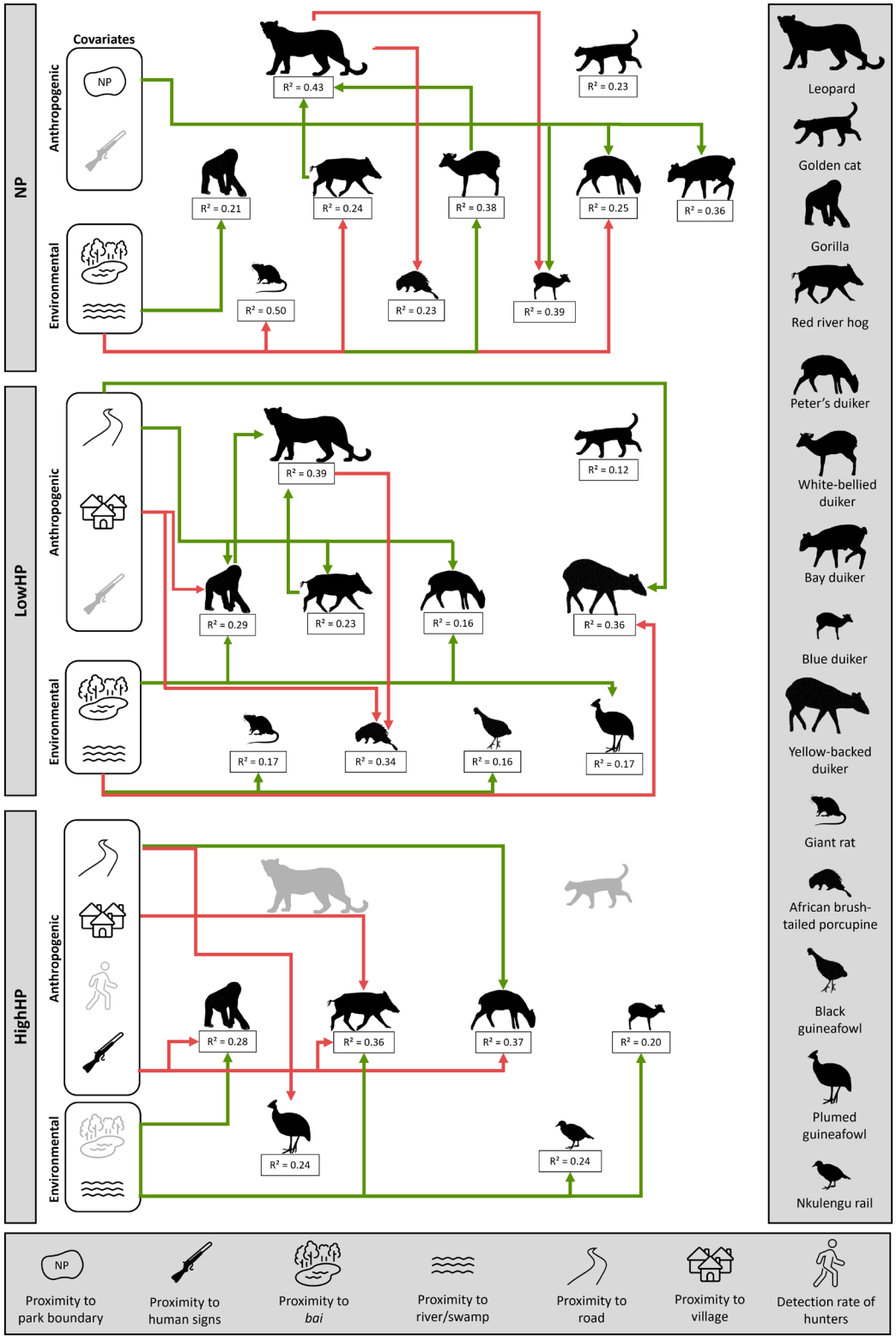

Figure 3. Structural equation models (SEMs) illustrating the trophic structuring of predator–prey interactions and the influence of anthropogenic and environmental covariates on their site use intensity along a gradient of human pressure in Central African forests. The analysis includes three study areas: Nouabale-Ndoki National Park (NP), a logging concession with low human pressure (LowHP), and a logging concession with higher human pressure (HighHP). Only significant pathways ($p < 0.05$) are shown for clarity. Arrows indicate the directionality of the pathway coefficient, with color indicating the nature of the interaction: positive (green) and negative (red). R^2 values are provided for endogenous variables (site use intensity). Prey species with no significant interaction were excluded from the corresponding trophic structure. Models and path coefficients are detailed in the Supporting information.

Table 4. Quantified direct and indirect effects of endogenous predictor variables and anthropogenic covariates on predator and prey species site use intensity across three study areas: Nouabale-Ndoki National Park (NP), a logging concession with low human pressure (LowHP), and a logging concession with higher human pressure (HighHP). '→' denotes the effect of a predictor on an endogenous variable. Only significant ($p < 0.05$) unstandardized pathway coefficients are presented, with associated p-values (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). The total of individual pathway coefficients is reported in the Supporting information.

Direct pathways	Unstandardized coefficients		
Predictor → Response)	NP	LowHP	HighHP
Prey → Predator (bottom–up effects)			
Red river hog → Leopard	0.07***	0.05***	–
White-bellied duiker → Leopard	0.05*	–	–
Gorilla → Leopard	–	0.06*	–
Predator → Prey (top–down effects)			–
Leopard → Blue duiker	−0.08***	–	–
Leopard → Porcupine	−0.23*	−0.26*	–
Anthropogenic variables → Species			–
Distance to park boundary → Peters' duiker	0.09*	–	–
Distance to park boundary → Bay duiker	0.24***	–	–
Distance to park boundary → Blue duiker	0.05*	–	–
Distance to road → Yellow-backed duiker	–	−0.08*	–
Distance to road → Gorilla	–	−0.09**	–
Distance to road → Red river hog	–	−0.11**	–
Distance to road → Peters' duiker	–	−0.07*	−0.19*
Distance to road → Plumed guineafowl	–	–	0.32**
Distance to village → Gorilla	–	0.09*	-
Distance to village → Red river hog	–	–	0.13*
Distance to village → Porcupine	–	0.15*	-
Distance to human signs → Gorilla	–	–	0.32*
Distance to human signs → Red river hog	–	–	0.29*
Distance to human signs → Peters' duiker	–	–	0.42***

Indirect pathways	Unstandardized coefficients		
(Anthropogenic variables → Species 1 → Species 2)	NP	LowHP	HighHP
Distance to road → Gorilla → Leopard	–	−0.005*	–
Distance to road → Red river hog → Leopard	–	−0.006**	–
Distance to village → Gorilla → Leopard	–	0.005*	–

of the species studied were significantly altered in HighHP (Supporting information). Gorillas, red river hogs, Peters' duikers, blue duikers and plumed guineafowl reduced their daytime activity, whereas porcupines showed increased activity closer to sunset (Fig. 4). Despite these shifts, diurnal prey species had higher temporal overlap with hunters in HighHP than with their natural predators in the two other study areas. The red river hog, however, deviated from this trend, with significantly increased nocturnal activity in HighHP, limiting its overlap with hunters.

Discussion

By using a community-focused approach, this study provides, to our knowledge, the first integrated assessment of trophic structures and spatiotemporal organization involving the two largest carnivores and their prey in Central Africa's semideciduous forests, a highly threatened yet understudied wildlife community. Using functional diversity metrics, species co-occurrence, and activity patterns across a gradient of human pressure, we showed that mammal communities differ not only in composition but also in their trophic organization and spatiotemporal structuring. Our findings reveal the complexity and context-dependency of these patterns, with increasing human pressure associated with trophic downgrading, marked by predator loss, and significant shifts in prey abundance, site use and activity patterns, driving reduced functional diversity. Together, these results support the view of humans acting as 'super predators', that tend to be more lethal and frightening to prey than other predators (Darimont et al. 2015, Clinchy et al. 2016).

Shifts in community diversity

We analyzed community structure and diversity across the three study areas, progressing from a broad to a more detailed perspective. At a coarse level, species richness across the three study areas was relatively high compared to other wildlife surveys conducted in Central African forests (Bruce et al. 2018a, Fonteyn et al. 2020), and diversity indices did not indicate significant differences in overall community structure and diversity among areas. However, a more refined analysis revealed significantly lower detection rates of large- and medium-sized species in HighHP, alongside the absence of the two largest predators, the leopard and the golden cat, consistent with our second prediction (P2). This was accompanied by increased detection rates

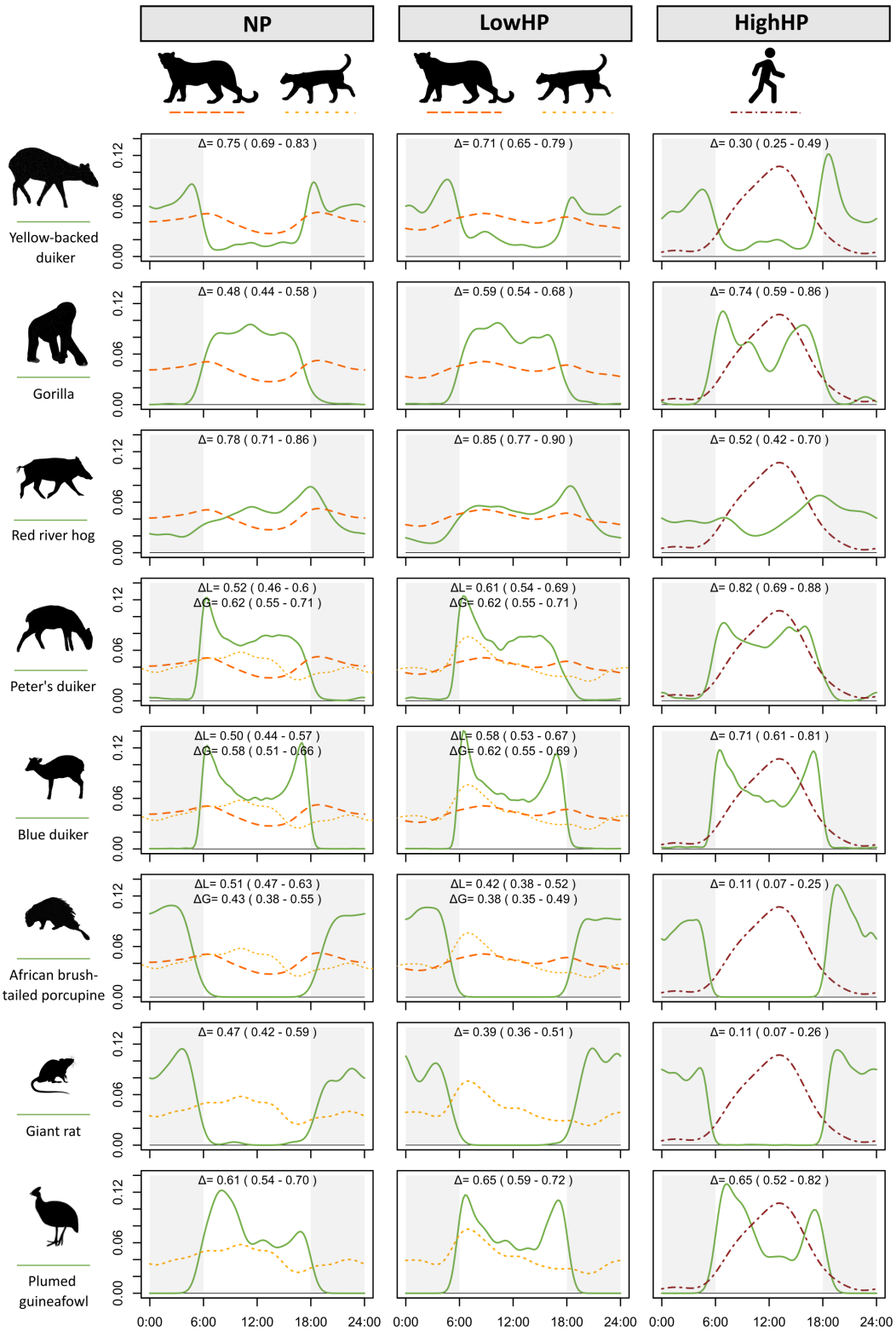

Figure 4. Temporal activity patterns of prey species (solid green line) across three study areas: Nouabale-Ndoki National Park (NP), a logging concession with low human pressure (LowHP), and a logging concession with higher human pressure (HighHP). Activity is shown alongside the leopard (dashed orange line) and the golden cat (dotted yellow line) in NP and LowHP, as well as hunters (dot-dash red line) in HighHP, where predators are absent. Overlap coefficients (with 95% confidence intervals) are provided for each predator–prey (L: leopard, G: golden cat) and hunters-prey pair. The shaded region indicates nighttime hours (18.00–6.00 h). The activity patterns of the remaining prey species are presented in the Supporting information.

of smaller, disturbance-tolerant species, such as porcupines and giant rats, indicative of species turnover and functional reorganization. These patterns are indicative of advanced defaunation, characterized by the decline of human-sensitive species and their replacement by more resilient taxa, leading to simplified assemblages dominated by smaller-sized generalists.

Such findings align with patterns observed in other disturbed tropical forests in Central Africa (Fonteyn et al. 2024, Zwerts et al. 2024), reinforcing the well-established relationship between body size and vulnerability to human pressure (Dirzo et al. 2014, Gallego-Zamorano et al. 2020). From an evolutionary and functional perspective, the release of small generalist species likely reflects the relaxation of top–down predator control and reduced competition with larger frugivores (Benítez-López et al. 2019, Filgueiras et al. 2021). These community shifts may have broader ecological consequences. In Central Africa, 70–90% of tree species rely on large- to medium-sized animals for seed dispersal (Beaune et al. 2013, Evrard et al. 2017). The decline of this guild, coupled with an increased prevalence of smaller seed-eating species such as rodents, is therefore likely to alter plant regeneration patterns and forest composition in HighHP (Effiom et al. 2013, Benítez-López et al. 2019).

Regional evidence further supports our findings, indicating that leopards and golden cats persist in low-impact areas but are absent from more disturbed forests. While sporadically detected in the study FMU in the early 2000s (Mathot and Doucet 2006), neither species was recorded by intensive camera trapping in the area in 2017 (Houngbégnon et al. 2020). At larger spatial scales, both species remain present in relatively undisturbed protected areas, such as Nki National Park and the core of the Dja Faunal Reserve (Fig. 1), but were absent from sectors experiencing higher human pressure (Bruce et al. 2018b, Hongo et al. 2020). Together with our results from HighHP, this pattern supports the view that increasing human pressure promotes local extirpation through a combination of direct persecution (e.g. snaring; Fa et al. 2005), habitat fragmentation (Bahaa-el-din et al. 2015), and prey depletion, identified as a key mechanism in heavily hunted Central African forests (Henschel et al. 2011).

Overall, our findings suggest that human activity within our study area has probably restructured trophic networks both directly, through the local extirpation of species at multiple trophic levels (Abernethy et al. 2013), and indirectly, by altering species interdependencies (Dorresteijn et al. 2015, Kuijper et al. 2016). While some observed patterns are consistent with the framework of human-induced trophic cascades (Smith et al. 2017, Tossens et al. 2024), our results do not provide mechanistic evidence for a cascade sensu stricto. Instead, they more plausibly reflect the combined influence of multiple, overlapping processes acting simultaneously across trophic levels, rather than a single sequential pathway (Montgomery et al. 2019).

Shifts in predator–prey spatiotemporal dynamics

In NP and LowHP, species networks were characterized by a relatively complex spatial organization shaped by an interplay of biotic, environmental and anthropogenic factors, with limited evidence of human-driven impacts on species site use, in line with our first prediction (P1). The interactions between the two focal predators and their prey have remained largely understudied in Central Africa, apart from a few dietary analyses identifying medium-sized ungulates as the preferred prey of leopards (Hayward et al. 2006, Henschel et al. 2011), and small ungulates and rodents as primary prey for golden cats (Bahaa-el-din 2015). In this context, we observed consistent spatial and temporal associations between leopards and red river hogs in both areas where focal predators were present, suggesting a close spatial coupling between leopards and one of their preferred prey species, consistent with bottom–up processes frequently reported in carnivore–prey systems (Burgos et al. 2023, Curveira-Santos et al. 2024). Interestingly, leopard detection rates also appeared to be negatively associated with blue duiker and porcupine site use in one or both of these areas. Although neither species was recorded as a preferred prey item for leopards in Gabon (Henschel et al. 2011), these patterns may be consistent with predator-mediated spatial avoidance or other processes influencing co-occurrence, including behavioral responses to perceived predation risk, a mechanism increasingly recognized across ecosystems worldwide (Moll et al. 2017, Say-Sallaz et al. 2019). By jointly identifying prey availability and predator control as potential structuring forces in low-disturbed areas (P1), our results highlight how the relative balance between bottom–up and top–down forces may contribute to spatial and temporal variation in food-web organization, rather than reflecting a single dominant structuring process (Creel and Christianson 2008, Van Scoyoc et al. 2023).

In contrast, predator–prey spatiotemporal organization in HighHP appeared markedly simplified, as predicted (P2). The absence of leopards and golden cats in this area limited our ability to study their responses at a fine scale. Yet, prey species exhibited apparent behavioral shifts under high human pressure. Spatially, species' habitat use was negatively associated with roads, villages, and human signs in this area, consistent with previous studies identifying proximity to hunters' access points as a significant predictor of defaunation (Vanthomme et al. 2013, Benítez-López et al. 2019, Lhoest et al. 2020). Temporally, most prey species, except rodents and certain ground birds, reduced their diurnal activity, likely a strategy to avoid humans, a response commonly observed across wildlife communities in human-disturbed landscapes (Gaynor et al. 2018, Lee et al. 2024).

Collectively, these patterns suggest that intense human pressure may reorganize the spatiotemporal structure of predator–prey systems by imposing a pervasive and predictable source of risk. Under such conditions, prey behavioral responses may become increasingly decoupled from predator-specific associations and instead converge toward generalized avoidance strategies, consistent with growing evidence that human disturbance simplifies and homogenizes wildlife behavioral organization across communities (Tucker et al. 2018, Van Scoyoc et al. 2023). Such fear-induced behavioral adaptations to human disturbance may weaken

fine-scale ecological processes mediated by species interactions (Bubnicki et al. 2019, Gálvez and Hernández 2022) and have further knock-on effects, such as altered foraging efficiency, antipredator strategies, predation and competition dynamics (Creel and Christianson 2008, Gaynor et al. 2018).

Conservation implications and management strategies

Results from our camera trap surveys in NP and LowHP align with previous research indicating that protected areas and SFM-certified concessions can serve as important refuges for large- and medium-sized mammals (Clark et al. 2009, Bahaa-el-din et al. 2016). However, our findings from the other SFM-certified concession, located in a less remote landscape with higher human population density and hunting pressure, revealed advanced signs of defaunation, resembling patterns observed in non-certified concessions in the Republic of Congo and Gabon (Zwerts et al. 2024). This suggests that, while SFM practices may mitigate some impacts, they do not inherently guarantee wildlife persistence or ecosystem integrity. Instead, conservation outcomes appear to be more strongly driven by the intensity of local human pressure and the broader landscape context in which a concession is embedded.

While LowHP, situated on the periphery of Nouabalé-Ndoki National Park, has benefited from substantial external conservation investment since 1999 through a public-private partnership, HighHP lacks similar long-term support and is likely affected by spillover effects from adjacent logging concessions that do not apply sustainable management principles. In southeastern Cameroon, the finer-scale administrative fragmentation of forest landscapes, relative to the larger, more contiguous management units in northern Congo, likely exacerbates conservation challenges by creating a patchwork of management regimes and limiting coordinated action at the landscape level. This fragmented governance, combined with higher regional human pressure and limited financial resources, may help explain why wildlife survey data from the edge of the Dja Reserve (~80 km from HighHP) showed species richness and relative abundances comparable to those observed in HighHP (Bruce et al. 2018a). Given the lack of pre-exploitation baseline data and direct comparisons with non-certified areas, inferences regarding the effectiveness of SFM certification must remain cautious. Rather than failing to prevent defaunation, SFM practices might have slowed biodiversity loss in an already heavily disturbed landscape with low predator densities (Kehou et al. 2021), reinforcing the idea that both historical and current local human pressures are stronger predictors of wildlife population trends than formal management status alone (Greco et al. 2025).

The contrasting patterns observed between LowHP and HighHP highlight the importance of management strategies that extend beyond individual concessions and explicitly address hunting pressure and habitat connectivity at the landscape scale. Our results therefore support approaches that promote coordination among public and private stakeholders (Edwards et al. 2014), and integrate local communities into management plans, through awareness raising, employment, and sustainable resource initiatives, which are critical for improving long-term conservation outcomes (Clark et al. 2009, Abernethy et al. 2013).

In our study, the leopard and the golden cat were the only IUCN-listed threatened species no longer detected under high human pressure, supporting their potential role as early indicators of defaunation and human-driven cascading effects in Central African forests (Kau et al. 2025). Carnivores, both large (Morrison et al. 2007) and small (Marneweck et al. 2022), are widely recognized as indicators of ecosystem health, given their sensitivity to habitat disturbance. In disturbed landscapes where both felids are already rare or absent, shifts in the biomass distribution and relative dominance of lower trophic-level species may provide alternative, cost-effective signals of functional ecosystem change (Fonteyn et al. 2024). Accordingly, combining predator and prey monitoring across disturbance gradients provides a robust framework for detecting warning signs of ecological degradation and for mitigating the emergence of 'empty forests', where structurally intact ecosystems lose their functional integrity (Abernethy et al. 2013, Benítez-López et al. 2019).

Finally, our study highlights that changes in trophic structure may not be captured by species richness or standard diversity indices alone, emphasizing the value of integrative approaches that assess both diversity and trophic interactions to better diagnose ecosystem responses to anthropogenic disturbance and guide adaptive management (Montgomery et al. 2019).

Study limitations

While providing novel insights into how human pressure is associated with changes in mammal community structure and spatiotemporal organization in Central African forests, our study also highlights key challenges related to data collection, analytical constraints and ecological complexity.

First, grid placement may not fully capture habitat and human pressure heterogeneity, potentially limiting the representativity of our findings at a broader landscape scale. Future studies would benefit from a more systematic stratification of sampling grids across disturbance gradients to improve landscape representativity. Additionally, increasing study area replicates would help assess the broader applicability of our conclusions (Ramage et al. 2013, Zwerts et al. 2024). However, financial, time, safety, and logistical constraints, such as the geographic isolation of study areas, make spatial replication extremely difficult in Central Africa (Lhoest et al. 2024). In addition, it is particularly challenging to find multiple study areas that differ mainly in human pressure while remaining similar in all other ecological characteristics, which further limits our ability to replicate study areas across space.

Second, we excluded certain trophic groups from our analyses due to camera trap detection biases, such as small rodents (<0.5 kg) and arboreal species. Expanding prey detection using complementary methods (e.g. live trapping, molecular diet analyses) would allow for a more comprehensive

assessment of mesopredator–prey interactions and their role in trophic networks.

Third, our use of SEM relies on spatial and temporal co-occurrence patterns as proxies for ecological interactions. While this method has precedent in camera trap studies offering a valuable network-based approach for examining complex ecological relationships (Curveira-Santos et al. 2024, Dyck et al. 2025), such models do not establish causality and do not provide direct measures of interaction strength (Blanchet et al. 2020). Positive or negative associations may therefore reflect not only predator–prey processes, but also shared or opposing responses to unmeasured anthropogenic disturbance or habitat preferences. Although we included some environmental and human-related covariates, it was not feasible to capture all habitat dimensions potentially influencing species distributions in these structurally complex forests. Consequently, unmodelled relationships may persist, notably in HighHP where model fit was borderline (Fisher's C: $p = 0.06$), and some inferred pathways should be interpreted cautiously. One illustrative example is the positive spatial association observed between leopards and gorillas in LowHP. Although gorillas have been documented in leopard diets, likely through occasional predation on juveniles (Henschel et al. 2011), this relationship is more plausibly explained by shared responses to unmeasured ecological factors, such as fine-scale vegetation structure or habitat types favored by both species (e.g. Maranthaceae forests; Picard et al. 2024). This isolated example highlights a key limitation of inferring ecological interactions from co-occurrence patterns alone and underscores the need for cautious interpretation of SEM-derived pathways in complex ecosystems (Sirén et al. 2021, Curveira-Santos et al. 2024). Similarly, temporal overlap between certain species may be driven by other ecological factors (e.g. smaller predators' activity) rather than direct ecological interactions (Prugh et al. 2019).

Nevertheless, in remote and data-poor systems such as Central African tropical forests, where direct observations of interactions and experimental approaches are largely infeasible, spatiotemporal co-occurrence derived from passive monitoring remains one of the most informative and tractable proxies for exploring species interdependencies at the community level. When interpreted cautiously and grounded in ecological knowledge, such patterns provide valuable insights into how trophic organization and species associations may shift under increasing human pressure, while helping to generate testable hypotheses for future, more mechanistic studies.

Conclusion

Our study provides novel baseline insights into how mammal community structure and predator–prey spatiotemporal organization vary along a gradient of human pressure in Central African forests, one of the most biodiversity-rich, yet understudied ecosystems. By jointly examining functional diversity, species co-occurrence and activity patterns, we showed that a human population density of approximately 6.4 inhabitants km^{-2}, combined with high hunting intensity, coincided with major ecological shifts in trophic structure and spatiotemporal organization, including the loss of the two largest predators, severe declines in ungulate populations, and altered prey distributions and activity patterns.

By simultaneously exerting top–down pressure across multiple trophic levels, humans appear to drive trophic downgrading, characterized by reduced functional diversity and community simplification dominated by smaller, generalist species. While our inferences rely on spatial and temporal associations rather than direct measures of interaction strength, the convergence of community-level, spatial, and temporal signals supports the interpretation that humans can act as 'super predators' in Central African forests, with disproportionate effects on mammal communities, impairing body-mass distributions among trophic guilds and overriding natural predator–prey spatiotemporal patterns. The ecological, cascading consequences of such disruptions likely extend beyond the taxa examined in this study, with broader, unmeasured implications for species interactions, forest composition and key ecosystem functions.

Although our work is limited by spatial replication and the constraints inherent to passive monitoring, it offers a transparent analytical framework and testable predictions for future studies across the Congo Basin where conditions allow. More broadly, our findings highlight the urgency of integrating the impact of humans into ecological theory and conservation planning, as management strategies focused solely on species richness or diversity indices may fail to detect significant alterations in trophic structure and ecological interactions. Preserving intact trophic networks across sufficiently large and connected landscapes appears critical for sustaining ecosystem functioning under increasing anthropogenic pressure.

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Author contributions

Sarah Tossens: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Marine Drouilly:** Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Supervision (equal); Validation (equal); Writing – review and editing (lead). **Zoe Woodgate:** Formal analysis (supporting); Writing – review and editing (lead). **Marius Ruwet:** Data curation (supporting); Investigation (supporting); Writing – review and editing (supporting). **Elise Vanderbeck:** Data curation (supporting); Visualization (supporting); Writing – review and editing (supporting). **Simon Lhoest:** Writing – review and editing (supporting).**Cedric Vermeulen:** Writing – review and editing (supporting). **Stéphane Tchakoudeu Kehou:** Writing – review and editing (supporting). **Jean-Louis Doucet:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (supporting); Supervision (equal); Validation (equal); Writing – review and editing (supporting).

Data availability statement

Data are available from Figshare: https://figshare.com/s/faa3d5cc9654441d556c (Tossens et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E. and Maisels, F. 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. – Philos. Trans. R. Soc. B 368: 20120303.

Agostinelli, C. and Lund, U. 2023. R package "circular": circular statistics. – R package ver. 0.5-0, https://CRAN.R-project.org/package=circular.

Ahumada, J. A., Silva, C. E. F., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., McWilliam, A., Mugerwa, B., O'Brien, T., Rovero, F., Sheil, D., Spironello, W. R., Winarni, N. and Andelman, S. J. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. – Philos. Trans. R. Soc. B 366: 2703–2711.

Bahaa-el-din, L 2015. Ecology and conservation of the African golden cat *Caracal aurata*. – PhD thesis, Univ. of KwaZulu-Natal.

Bahaa-el-din, L, Henschel, P., Butynski, T. M., Macdonald, D. W., Mills, D., Slotow, R. and Hunter, L. 2015. The African golden cat *Caracal aurata*: Africa's least-known felid. – Mamm. Rev. 45: 63–77.

Bahaa-el-din, L, Sollmann, R., Hunter, L. T. B., Slotow, R., Macdonald, D. W. and Henschel, P. 2016. Effects of human landuse on Africa's only forest-dependent felid: the African golden cat *Caracal aurata*. – Biol. Conserv. 199: 1–9.

Bassing, S. B., Ho, C. and Gardner, B. 2024a. Anthropogenic activities influence spatiotemporal patterns of predator–prey interactions. – Global Ecol. Conserv. 53: e03017.

Bassing, S. B., Satterfield, L., Ganz, T. R., DeVivo, M., Kertson, B. N., Roussin, T., Wirsing, A. J. and Gardner, B. 2024b. Predator–prey space use and landscape features influence movement behaviors in a large-mammal community. – Ecology 105: e4448.

Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Surbeck, M. and Fruth, B. 2013. Seed dispersal strategies and the threat of defaunation in a Congo forest. – Biodivers. Conserv. 22: 225–238.

Benítez-López, A., Santini, L., Schipper, A. M., Busana, M. and Huijbregts, M. A. J. 2019. Intact but empty forests? Patterns of hunting induced mammal defaunation in the tropics. – PLoS Biol. 17: e3000247.

BirdLife International 2024. BirdLife International. – https://www.birdlife.org/, accessed 8 February 2024.

Blanchet, F. G., Cazelles, K. and Gravel, D. 2020. Co-occurrence is not evidence of ecological interactions. – Ecol. Lett 23: 1050–1063.

Bruce, T., Amin, R., Wacher, T., Fankem, O., Ndjassi, C., Ngo, M., Andrew, B., Hilaire, F. and David, N. 2018a. Using camera trap data to characterise terrestrial larger – bodied mammal communities in different management sectors of the Dja Faunal Reserve, Cameroon. – Afr. J. Ecol. 56: 759–776.

Bruce, T., Ndjassi, C., Lebreton, M., Wacher, T., Fowler, A., Mbobsa, R. B. T. and Olson, D. 2018b. African golden cat and leopard persist in the Dja Faunal Reserve, Cameroon. – Cat News 68: 22–24.

Bubnicki, J. W., Churski, M., Schmidt, K., Diserens, T. A. and Kuijper, D. P. J. 2019. Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. – eLife 8: e44937.

Burgos, T., Salesa, J., Fedriani, J. M., Escribano-Ávila, G., Jiménez, J., Krofel, M., Cancio, I., Hernández-Hernández, J., Rodríguez-Siles, J. and Virgós, E. 2023. Top–down and bottom–up effects modulate species co-existence in a context of top predator restoration. – Sci. Rep. 13: 4170.

Carter, N., Jasny, M., Gurung, B. and Liu, J. 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. – Global Ecol. Conserv. 3: 149–162.

Clark, C. J., Poulsen, J. R., Malonga, R. and Elkan, P. W. 2009. Logging concessions can extend the conservation estate for central African tropical forests. – Conserv. Biol. 23: 1281–1293.

Clinchy, M., Zanette, L. Y., Roberts, D., Suraci, J. P., Buesching, C. D., Newman, C. and Macdonald, D. W. 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. – Behav. Ecol. 27: 1826–1832.

Crawford, D. A., Conner, L. M., Clinchy, M., Zanette, L. Y. and Cherry, M. J. 2022. Prey tells, large herbivores fear the human 'super predator.' – Oecologia 198: 91–98.

Creel, S. and Christianson, D. 2008. Relationships between direct predation and risk effects. – Trend. Ecol. Evol. 23: 194–201.

Curveira-Santos, G., Marion, S., Sutherland, C., Beirne, C., Herdman, E. J., Tattersall, E. R., Burgar, J. M., Fisher, J. T. and

Burton, A. C. 2024. Disturbance-mediated changes to boreal mammal spatial networks in industrializing landscapes. – Ecol. Appl. 34: e3004.
Darimont, C. T., Fox, C. H., Bryan, H. M. and Reimchen, T. E. 2015. The unique ecology of human predators. – Science 349: 858–860.
Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B. and Collen, B. 2014. Defaunation in the Anthropocene. – Science 345: 401–406.
Dorresteijn, I., Schultner, J., Nimmo, D. G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L. and Ritchie, E. G. 2015. Incorporating anthropogenic effects into trophic ecology: predator – prey interactions in a human-dominated landscape. – Proc. R. Soc. B 282: 20151602.
Drouilly, M. and O'Riain, M. 2019. Wildlife winners and losers of extensive small-livestock farming: a case study in the South African Karoo. – Biodivers. Conserv. 28: 1493–1511.
Dyck, M. A., Iosif, R., Promberger–Fürpass, B. and Popescu, V. D. 2025. Dracula's menagerie reloaded: assessing the relative roles of habitat and interspecific interactions in an intact mammalian assemblage using structural equation modeling. – Ecol. Evol. 15: e71381.
Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E. and Laurance, W. F. 2014. Maintaining ecosystem function and services in logged tropical forests. – Trend. Ecol. Evol. 29: 511–520.
Effiom, E. O., Nuñez-Iturri, G., Smith, H. G., Ottosson, U. and Olsson, O. 2013. Bushmeat hunting changes regeneration of African rainforests. – Proc. R. Soc. B 280: 20130246.
Estes, J. A. et al. 2011. Trophic downgrading of planet earth. – Science 333: 301–306.
Evrard, Q., Haurez, B. and Doucet, J.-L. 2017. Le rôle des rongeurs dans la dispersion des diaspores en milieu forestier (synthèse bibliographique). – Biotechnol. Agron. Soc. Environ. 21: 1–14.
Fa, J. E., Ryan, S. F. and Bell, D. J. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. – Biol. Conserv. 121: 167–176.
Fayolle, A., Swaine, M. D., Bastin, J. F., Bourland, N., Comiskey, J. A., Dauby, G., Doucet, J. L., Gillet, J. F., Gourlet-Fleury, S., Hardy, O. J., Kirunda, B., Kouamé, F. N. and Plumptre, A. J. 2014. Patterns of tree species composition across tropical African forests. – J. Biogeogr. 41: 2320–2331.
Filgueiras, B. K. C., Peres, C. A., Melo, F. P. L., Leal, I. R. and Tabarelli, M. 2021. Winner–loser species replacements in human-modified landscapes. – Trend. Ecol. Evol. 36: 545–555.
Fonteyn, D., Fayolle, A., Fa, J. E., Vanthomme, H., Vigneron, P., Vermeulen, C., Malignat, R., Konradowski, B., Noel, M., Okanabene, Y., Dibotty-Di Moutsing, S. A., Dias, S. P., Deniau, C., Cornu, G., Groschêne, M. and Cornélis, D. 2024. Hunting indicators for community-led wildlife management in tropical Africa. – npj Biodivers. 3: 1–9.
Fonteyn, D., Vermeulen, C., Deflandre, N., Cornelis, D., Lhoest, S., Houngbégnon, F. G. A., Doucet, J. L. and Fayolle, A. 2020. Wildlife trail or systematic? Camera trap placement has little effect on estimates of mammal diversity in a tropical forest in Gabon. – Remot. Sens. Ecol. Conserv. 7: 321–336.
Fonteyn, D., Vermeulen, C., Gorel, A. P., Silva de Miranda, P. L., Lhoest, S. and Fayolle, A. 2023. Biogeography of central African forests: determinants, ongoing threats and conservation priorities of mammal assemblages. – Divers. Distrib. 29: 698–712.
Ford, A. T., Goheen, J. R., Otieno, T. O., Bidner, L., Isbell, L. A., Palmer, T. M., Ward, D., Woodroffe, R. and Pringle, R. M. 2014. Large carnivores make savanna tree communities less thorny. – Science 346: 346–349.
Fox, J. and Weisberg, S. 2019. An R companion to applied regression. – Sage.
Galetti, M., Guevara, R., Neves, C. L., Rodarte, R. R., Bovendorp, R. S., Moreira, M., Hopkins, J. B. and Yeakel, J. D. 2015. Defaunation affects the populations and diets of rodents in neotropical rainforests. – Biol. Conserv. 190: 2–7.
Gallego-Zamorano, J., Benítez-López, A., Santini, L., Hilbers, J. P., Huijbregts, M. A. J. and Schipper, A. M. 2020. Combined effects of land use and hunting on distributions of tropical mammals. – Conserv. Biol. 34: 1271–1280.
Gálvez, D. and Hernández, M. 2022. Ecology of fear and its effect on seed dispersal by a neotropical rodent. – Behav. Ecol. 33: 467–473.
Gaynor, K. M., Hojnowski, C. E., Carter, N. H. and Brashares, J. S. 2018. The influence of human disturbance on wildlife nocturnality. – Science 360: 1232–1235.
Gaynor, K. M., McInturff, A. and Brashares, J. S. 2022. Contrasting patterns of risk from human and non-human predators shape temporal activity of prey. – J. Anim. Ecol. 91: 46–60.
Gilbert, N. A., Stenglein, J. L., Pauli, J. N. and Zuckerberg, B. 2022. Human disturbance compresses the spatiotemporal niche. – Proc. Natl Acad. Sci. USA 119: e2206339119.
Grace, J. B. 2008. Structural equation modeling for observational studies. – J. Wildl. Manage. 72: 14–22.
Grantham, H. S. et al. 2020. Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. – Nat. Commun. 11: 5978.
Greco, I. et al. 2025. Landscape-level human disturbance results in loss and contraction of mammalian populations in tropical forests. – PLoS Biol. 23: e3002976.
Gutiérrez-Granados, G. and Dirzo, R. 2021. Logging drives contrasting animal body-size effects on tropical forest mammal communities. – For. Ecol. Manage. 481: 118700.
Hairston, N. G., Smith, F. E. and Slobodkin, L. B. 1960. Community structure, population control, and competition. – Am. Nat. 94: 421–425.
Haswell, P. M., Kusak, J. and Hayward, M. W. 2017. Large carnivore impacts are context-dependent. – Food Webs 12: 3–13.
Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. and Kerley, G. I. H. 2006. Prey preferences of the leopard (*Panthera pardus*). – J. Zool. 270: 298–313.
Henschel, P. 2008. The conservation biology of the leopard *Panthera pardus* in Gabon: status, threats and strategies for conservation. – PhD thesis, Univ. zu Göttingen.
Henschel, P., Hunter, L. T. B., Coad, L., Abernethy, K. A. and Mühlenberg, M. 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. – J. Zool. 285: 11–20.
Hockridge, E. G., Bradford, E. M., Angier, K. I. W., Youd, B. H., McGill, E. B. M., Ngouma, S. Y., Ognangue, R. L., Gibbon, G. E. M. and Davies, A. B. 2024. Spatial ecology, biodiversity, and abiotic determinants of Congo's bai ecosystem. – Ecology 105: e4419.
Hongo, S., Dzefack, Z. C. B., Vernyuy, L. N., Minami, S., Nakashima, Y., Djiéto-Lordon, C. and Yasuoka, H. 2020. Use of multi-layer camera trapping to inventory mammals in rainforests in southeast Cameroon. – Afr. Stud. Monogr. 60: 21–37.
Horion, R., Woodgate, Z. and Drouilly, M. 2024. First insights into the spatio-temporal ecology of sympatric large carnivores in Niokolo-Koba National Park, Senegal. – Oryx 58: 664–675.

Houngbégnon, F. G. A., Cornelis, D., Vermeulen, C., Sonké, B., Ntie, S., Fayolle, A., Fonteyn, D., Lhoest, S., Evrard, Q., Yapi, F., Sandrin, F., Vanegas, L., Ayaya, I., Hardy, C., Le Bel, S. and Doucet, J. L. 2020. Daily activity patterns and co-occurrence of duikers revealed by an intensive camera trap survey across central African rainforests. – Animals 10: 2200.

Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom–up and top–down forces in natural communities. – Ecology 73: 724–732.

Jenny, D. 1996. Spatial organization of leopards *Panthera pardus* in Taï National Park, Ivory Coast: is rainforest habitat a "tropical haven"? – J. Zool. 240: 427–440.

Kau, M., Weckworth, B. V., Li, S., Pires, M. M., Jin, D., Pacifici, M., Rondinini, C., Boitani, L., McCarthy, T. M., Lu, Z., Schaller, G. B., Beissinger, S. R. and Li, J. 2025. Umbrella, keystone, or flagship? An integrated framework for identifying effective surrogate species. – Biol. Conserv. 303: 111025.

Kehou, S. T., Daïnou, K. and Lagoute, P. 2021. The reasons great ape populations are still abundant in logged concessions: environmental drivers and the influence of management plans. – For. Ecol. Manage. 483: 118911.

Kiffner, C., Stoner, C. and Caro, T. 2013. Edge effects and large mammal distributions in a national park. – Anim. Conserv. 16: 97–107.

Kingdon, J. 2015. The Kingdon field guide to African mammals, 2nd ed. – Bloomsbury Publishing.

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K. and Cromsigt, J. P. G. M. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. – Proc. R. Soc. B 283: 20161625.

Laméris, D. W., Tagg, N., Kuenbou, J. K., Sterck, E. H. M. and Willie, J. 2019. Drivers affecting mammal community structure and functional diversity under varied conservation efforts in a tropical rainforest in Cameroon. – Anim. Conserv. 23: 182–191.

Laundré, J. W., Hernández, L., López Medina, P., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K. M., Burke, A. M., Gronemeyer, P. and Browning, D. M. 2014. The landscape of fear: the missing link to understand top–down and bottom–up controls of prey abundance? – Ecology 95: 1141–1152.

Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., Campbell, P. and Ondzeano, C. 2006. Impacts of roads and hunting on central African rainforest mammals. – Conserv. Biol. 20: 1251–1261.

Lee, S. X. T., Amir, Z., Moore, J. H., Gaynor, K. M. and Luskin, M. S. 2024. Effects of human disturbances on wildlife behaviour and consequences for predator–prey overlap in Southeast Asia. – Nat. Commun. 15: 1521.

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution and systematics. – Meth. Ecol. Evol. 7: 573–579.

Lhoest, S., Drouilly, M., Kazaba Kaseya, P., Ngama, S. and Vermeulen, C. 2024. To conserve African tropical forests, invest in the protection of its most diverse wildlife communities. – Conserv. Lett. 17: e13060.

Lhoest, S., Fonteyn, D., Daïnou, K., Delbeke, L., Doucet, J. L., Dufrêne, M., Josso, J. F., Ligot, G., Oszwald, J., Rivault, E., Verheggen, F., Vermeulen, C., Biwolé, A. and Fayolle, A. 2020. Conservation value of tropical forests: distance to human settlements matters more than management in Central Africa. – Biol. Conserv. 241: 108351.

Marneweck, C. J., Allen, B. L., Butler, A. R., Do Linh San, E., Harris, S. N., Jensen, A. J., Saldo, E. A., Somers, M. J., Titus, K., Muthersbaugh, M., Vanak, A. and Jachowski, D. S. 2022. Middle-out ecology: small carnivores as sentinels of global change. – Mamm. Rev. 52: 471–479.

Mathot, L. and Doucet, J.-L. 2006. Méthode d'inventaire faunique pour le zonage des concessions en forêt tropicale. – BFT 287: 59–70.

Meek, P., Fleming, P., Ballard, G., Claridge, A., Banks, P., Sanderson, J. and Swann, D. 2014. Camera trapping: wildlife management and research. – CSIRO Publishing.

Meredith, M. and Ridout, M. 2024. overlap: estimates of coefficient of overlapping for animal activity patterns – J. Agric. Biol. Environ. Stat. 14: 332–337.

Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., Hayward, M. W., Millspaugh, J. J. and Montgomery, R. A. 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. – J. Anim. Ecol. 86: 749–765.

Montgomery, R. A., Moll, R. J., Say-Sallaz, E., Valeix, M. and Prugh, L. R. 2019. A tendency to simplify complex systems. – Biol. Conserv. 233: 1–11.

Morgan, D., Strindberg, S., Winston, W., Stephens, C. R., Traub, C., Ayina, C. E., Ndolo Ebika, S. T., Mayoukou, W., Koni, D., Iyenguet, F. and Sanz, C. M. 2019. Impacts of selective logging and associated anthropogenic disturbance on intact forest landscapes and apes of northern Congo. – Front. For. Global Change 2: 448311.

Morrison, J. C., Sechrest, W., Dinerstein, E., Wilcove, D. S. and Lamoreux, J. F. 2007. Persistence of large mammal faunas as indicators of global human impacts. – J. Mammal. 88: 1363–1380.

Murphy, A., Diefenbach, D. R., Ternent, M., Lovallo, M. and Miller, D. 2021. Threading the needle: how humans influence predator–prey spatiotemporal interactions in a multiple-predator system. – J. Anim. Ecol. 90: 2377–2390.

O'Brien, T. G., Baillie, J. E. M., Krueger, L. and Cuke, M. 2010. The wildlife picture index: monitoring top trophic levels. – Anim. Conserv. 13: 335–343.

Oksanen, J. et al. 2024. vegan: community ecology package – https://vegandevs.github.io/vegan/, https://github.com/vegandevs/vegan.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. – J. Anim. Ecol. 49: 666–685.

Palmer, M. S., Swanson, A., Kosmala, M., Arnold, T. and Packer, C. 2018. Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. – Afr. J. Ecol. 56: 791–803.

Picard, J., Nungi-Pambu Dembi, M. M., Barbier, N., Cornu, G., Couteron, P., Forni, E., Gibbon, G., Lim, F., Ploton, P., Pouteau, R., Tresson, P., van Loon, T., Viennois, G. and Réjou-Méchain, M. 2024. Combining satellite and field data reveals Congo's forest types structure, functioning and composition. – Remot. Sens. Ecol. Conserv. 11: 200–220.

Pires, M. M. and Galetti, M. 2023. Beyond the "empty forest": the defaunation syndromes of Neotropical forests in the Anthropocene. – Global Ecol. Conserv. 41: e02362.

Poulsen, J. R., Clark, C. J., Mavah, G. and Elkan, P. W. 2009. Bushmeat supply and consumption in a tropical logging concession in northern Congo. – Conserv. Biol. 23: 1597–1608.

Preisser, E. L., Bolnick, D. I. and Benard, M. F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. – Ecology 86: 501–509.

Prugh, L. R., Cunningham, C. X., Windell, R. M., Kertson, B. N., Ganz, T. R., Walker, S. L. and Wirsing, A. J. 2023. Fear of large carnivores amplifies human-caused mortality for mesopredators. – Science 380: 754–758.
Prugh, L. R., Sivy, K. J., Mahoney, P. J., Ganz, T. R., Ditmer, M. A., van de Kerk, M., Gilbert, S. L. and Montgomery, R. A. 2019. Designing studies of predation risk for improved inference in carnivore–ungulate systems. – Biol. Conserv. 232: 194–207.
Ramage, B. S., Sheil, D., Salim, H. M. W., Fletcher, C., Mustafa, N. Z. A., Luruthusamay, J. C., Harrison, R. D., Butod, E., Dzulkiply, A. D., Kassim, A. R. and Potts, M. D. 2013. Pseudoreplication in tropical forests and the resulting effects on biodiversity conservation. – Conserv. Biol. 27: 364–372.
Réjou-Méchain, M. et al. 2021. Unveiling African rainforest composition and vulnerability to global change. – Nature 593: 90–94.
Resende, P. S., Viana-Junior, A. B. and Bovendorp, R. S. 2024. A meta-analysis of the effects of anthropogenic disturbances on tropical mammal functional diversity. – Mamm. Rev. 55: e12356.
Ridout, M. S. and Linkie, M. 2009. Estimating overlap of daily activity patterns from camera trap data. – J. Agric. Biol. Environ. Stat. 14: 322–337.
Rovero, F., Martin, E., Rosa, M., Ahumada, J. A. and Spitale, D. 2014. Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. – PLoS One 9: e103300.
Royle, J. A. and Nichols, J. D. 2003. Estimating abundance from repeated presence–absence data or point counts. – Ecology 84: 777–790.
Say-Sallaz, E., Chamaillé-Jammes, S., Fritz, H. and Valeix, M. 2019. Non-consumptive effects of predation in large terrestrial mammals: mapping our knowledge and revealing the tip of the iceberg. – Biol. Conserv. 235: 36–52.
Sirén, A. P. K., Sutherland, C. S., Bernier, C. A., Royar, K. J., Kilborn, J. R., Callahan, C. B., Cliché, R. M., Prout, L. S. and Morelli, T. L. 2021. Abiotic stress and biotic factors mediate range dynamics on opposing edges. – J. Biogeogr. 48: 1758–1772.
Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y. and Wilmers, C. C. 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. – Proc. R. Soc. B 284: 20170433.
Sollmann, R., Mohamed, A., Samejima, H. and Wilting, A. 2013. Risky business or simple solution – relative abundance indices from camera-trapping. – Biol. Conserv. 159: 405–412.
Suraci, J. P., Clinchy, M., Zanette, L. Y. and Wilmers, C. C. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. – Ecol. Lett 22: 1578–1586.
Terborgh, J. and Estes, J. A. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. – Island Press.
Tossens, S., Drouilly, M., Lhoest, S., Vermeulen, C. and Doucet, J. L. 2024. Wild felids in trophic cascades: a global review. – Mamm. Rev. 55: e12358.
Tossens, S., Drouilly, M., Woodgate, Z., Ruwet, M., Vanderbeck, E., Lhoest, S., Vermeulen, C., Kehou, S. T. and Doucet, J-L. 2026. Data from: Humans acting as 'super predators' in Central African forests: trophic downgrading and disruption of predator–prey dynamics. – Figshare, https://figshare.com/s/faa3d5cc9654441d556c.
Tossens, S., Woodgate, Z., Doucet, J.-L., Henschel, P., André, A., Michaux, J. and Drouilly, M. 2026. Density and coexistence patterns of an apex carnivore (*Panthera pardus*) and a mesocarnivore (*Caracal aurata*) in northern Congo forests. – Animals 16: 190.
Tucker, M. A. et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. – Science 359: 466–469.
Van Scoyoc, A., Smith, J. A., Gaynor, K. M., Barker, K. and Brashares, J. S. 2023. The influence of human activity on predator–prey spatiotemporal overlap. – J. Anim. Ecol. 92: 1124–1134.
Vanthomme, H., Kolowski, J., Korte, L. and Alonso, A. 2013. Distribution of a community of mammals in relation to roads and other human disturbances in Gabon, Central Africa. – Conserv. Biol. 27: 281–291.
Woodroffe, R. and Ginsberg, J. R. 1998. Edge effects and the extinction of populations inside protected areas. – Science 280: 2126–2128.
Ziegler, S., Fa, J. E., Wohlfart, C., Streit, B., Jacob, S. and Wegmann, M. 2016. Mapping bushmeat hunting pressure in Central Africa. – Biotropica 48: 405–412.
Zwerts, J. A., Sterck, E. H. M., Verweij, P. A., Maisels, F., van der Waarde, J., Geelen, E. A. M., Tchoumba, G. B., Donfouet Zebaze, H. F. and van Kuijk, M. 2024. FSC-certified forest management benefits large mammals compared to non-FSC. – Nature 628: 563–568.