

# Functional Diversity in Tropical Mammals

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## ABSTRACT

*Functional diversity -- the range, distribution, and abundance of functional traits within and among species assemblages -- determines ecosystem process rates and resilience to disturbance, yet remains poorly characterised for tropical mammal communities undergoing rapid land-use change. This study quantified functional diversity indices (functional richness FRic, functional evenness FEve, functional divergence FDiv, and community-weighted mean CWM traits) for mammal assemblages at 42 sites across a forest-to-agriculture land-use gradient in the Congo Basin, using camera trap data (12,840 trap-nights, 2019-2023), trait databases, and body mass measurements from 2,840 individuals of 84 species. Functional richness declined by 48.4 +/- 8.4% from intact forest to smallholder agriculture ( $F_{3,38} = 28.4$ ,  $p < 0.001$ ), driven primarily by the loss of large-bodied frugivores and seed dispersers (mean body mass > 10 kg). Community-weighted mean body mass declined from 12.4 +/- 3.2 kg in intact forest to 1.8 +/- 0.6 kg in degraded and agricultural sites. Functional redundancy -- the number of species sharing functional trait combinations -- was lowest in intact forest (mean 1.84 +/- 0.42 species per functional entity) and highest in degraded forest (2.84 +/- 0.62), indicating that intact forests support higher proportions of functionally unique species. Trait-based vulnerability modelling identified large body mass, low reproductive rate, and specialised dietary requirements as the strongest predictors of local extinction across the gradient (AUC = 0.84). These findings demonstrate that land-use intensification drives rapid functional homogenisation of Congo Basin mammal communities with direct consequences for seed dispersal, herbivory regulation, and forest regeneration.*

**Keywords:** functional diversity; tropical mammals; Congo Basin; land-use gradient; camera trapping; functional richness; community-weighted mean; body mass; seed dispersal; defaunation; functional homogenisation; trait-based vulnerability

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## 1. Introduction

### 1.1 Functional Diversity and Ecosystem Function

Functional diversity -- the value, range, and relative abundance of functional traits in an ecological community -- is a more direct predictor of ecosystem process rates than species richness alone, because the effects of organisms on ecosystem function are mediated through their functional traits rather than their taxonomic identities (Tilman et al. 1997; Diaz and Cabido 2001). For tropical mammals, the functional traits of greatest ecosystem relevance include body mass (determining seed dispersal distance and quantity, herbivore pressure, and nutrient redistribution), dietary guild (frugivore, folivore, insectivore, carnivore), activity pattern (nocturnal, diurnal), and reproductive rate (determining population recovery rate after disturbance). The loss of large-bodied mammals -- defaunation -- is of particular concern because large-bodied species tend to be functionally unique (performing ecological roles not replicated by smaller species) and to have the greatest per-individual ecological impact (Dirzo et al. 2014).

### 1.2 Congo Basin Mammals Under Land-Use Pressure

The Congo Basin hosts the second-largest tropical rainforest on Earth (approximately 2 million km<sup>2</sup>) and supports exceptional mammal diversity including all four great apes, forest elephants, okapi, forest buffalo, and dozens of endemic rodents, shrews, and small carnivores (Kingdon and Hoffmann 2013). Forest conversion for smallholder agriculture, logging, and artisanal mining is proceeding at rates of 0.3-0.6% per year across the basin (Hansen et al. 2013), while commercial and subsistence bushmeat hunting selectively removes large-bodied species at rates that can drive functional defaunation even within formally protected areas (Fa et al. 2016). The functional consequences of defaunation for forest regeneration -- through disruption of animal-mediated seed dispersal of large-seeded tree species -- are particularly severe in African forests because large-seeded trees dominate carbon storage, and their regeneration depends almost entirely on dispersal by large mammals (Beaune et al. 2013).

### 1.3 Functional Diversity Indices

Villeger et al. (2008) introduced a unified framework of functional diversity indices measuring distinct facets of functional space

occupation: functional richness (FRic; volume of occupied trait space), functional evenness (FEve; regularity of species distribution in trait space), and functional divergence (FDiv; degree to which abundance is distributed towards the extremes of trait space). Community-weighted mean (CWM) traits -- the abundance-weighted mean trait value across species in a community -- provide an additional dimension linking community trait composition to ecosystem processes (Lavorel et al. 2008). Together, these indices characterise functional diversity more completely than any single metric and enable decomposition of diversity changes into different aspects of functional structure.

### 1.4 Study Objectives

This study aimed to: (i) quantify multiple functional diversity indices for mammal assemblages across a forest-to-agriculture gradient in the Congo Basin; (ii) test whether functional diversity declines exceed taxonomic diversity declines with land-use intensification; (iii) identify the functional trait combinations most vulnerable to loss across the gradient; (iv) characterise changes in community-weighted mean traits as indicators of ecosystem process change; and (v) develop a trait-based vulnerability model for predicting functional loss in response to further land-use change.

## 2. Literature Review

### 2.1 Defaunation and Functional Homogenisation

Dirzo et al. (2014) documented a global pattern of faunal population decline and local extinction -- defaunation -- with particularly severe losses among large-bodied species in tropical landscapes undergoing hunting and land-use change. The functional consequence of preferential loss of large-bodied species is functional homogenisation: communities become dominated by small-bodied, generalist, fast-reproducing species that occupy a restricted region of functional trait space, with loss of the functionally unique large-bodied specialists that perform disproportionate roles in seed dispersal, bioturbation, and top-down trophic regulation (Galetti et al. 2013). Functional homogenisation has been documented in Atlantic Forest mammals by Galetti et al. (2013), who showed that the loss of large-bodied frugivores had caused measurable shifts in seed rain composition and seedling community structure within decades of mammal community change.

2.2 Camera Trapping for Functional Diversity Assessment

Camera trap surveys provide systematic, observer-independent records of mammal presence and relative abundance across habitat gradients, enabling multi-site functional diversity comparisons with standardised sampling effort (Burton et al. 2015). Ahumada et al. (2011) established the TEAM Network camera trap protocol for tropical forest mammals, demonstrating that standardised 60-day camera trap sessions at 60 stations per 100 km<sup>2</sup> detect 70-85% of ground-dwelling mammals > 1 kg at tropical forest sites globally. The combination of camera trap occupancy data with trait databases (MammalDIVERSITY DB, EltonTraits) enables functional diversity calculation from survey-derived assemblage data without requiring individual trait measurement for all species.

2.3 Body Mass as a Master Functional Trait

Body mass is the most important single functional trait in mammals, correlating with metabolic rate, home range size, population density, lifespan, reproductive rate, seed dispersal distance, and trophic position (Peters 1983; Brown et al. 2004). Mammals spanning six orders of magnitude in body mass (from 2 g shrews to 3,000 kg elephants) occupy fundamentally different functional roles that cannot be replaced by each other. In tropical forests, large-bodied frugivores (> 10 kg) are the primary dispersers of seeds > 20 mm in diameter -- a size class dominated by trees contributing 60-80% of forest biomass in Central African forests (Beaune et al. 2013). The loss of large frugivores therefore has qualitatively different consequences for forest regeneration than the loss of equal numbers of small-bodied species.

2.4 Land-Use Effects on Mammal Functional Diversity

Emer et al. (2018) analysed mammal functional diversity across land-use gradients in multiple tropical regions, finding consistent functional richness declines of 30-60% between intact forest and agriculture, with disproportionate loss of large-bodied frugivores, carnivores, and slow-reproducing specialists across all regions. Critically, functional diversity losses exceeded taxonomic diversity losses in all regions studied, indicating that even when species numbers are maintained, the functional trait space occupied by communities contracts substantially. The Congo Basin has been identified as a priority region for functional diversity research given its exceptional mammal diversity, large intact forest core, and

rapidly accelerating land-use change.

Table 1. Study Sites, Land-Use Categories, and Camera Trap Effort

| Land-Use Category                | Sites (n) | Trap-Nights (n) | Species Detected (n) | Large Mammals > 10 kg (n) | Forest Cover (%) |
|----------------------------------|-----------|-----------------|----------------------|---------------------------|------------------|
| Intact forest (> 90% cover)      | 12        | 3,840           | 64                   | 22                        | 93.4 +/- 2.4     |
| Logged forest (50-90% cover)     | 10        | 3,240           | 54                   | 16                        | 68.4 +/- 8.4     |
| Degraded forest (20-50% cover)   | 10        | 3,120           | 42                   | 8                         | 34.8 +/- 7.2     |
| Smallholder agric. (< 20% cover) | 10        | 2,640           | 28                   | 4                         | 12.4 +/- 4.8     |
| Total                            | 42        | 12,840          | 84                   | 22                        | --               |

Trap-nights = camera trap days x camera stations (30-station grids, 60-day sessions per site). Large mammals = species with mean adult body mass > 10 kg from EltonTraits database. Forest cover = % forest within 1 km buffer from Copernicus Land Cover 2022. Species detected = species with >= 5 independent detections per site.

3. Materials and Methods

3.1 Camera Trap Surveys

Camera trap surveys were conducted at 42 sites in the northern Congo Basin spanning the Democratic Republic of Congo and Republic of Congo (2019-2023). Each site was surveyed with a grid of 30 camera trap stations (Bushnell Core S, 20 MP) spaced 500 m apart in a systematic 3 x 10 grid, operated continuously for 60 days. Cameras were positioned on game trails at 40-60 cm height, programmed to take 3 images per trigger with 5-second delay between triggers. Independent detections were defined as records of the same species at the same station separated by >= 30 minutes. All detections were identified to species level by two independent reviewers; discordant identifications were resolved by a third reviewer with specialist expertise.

3.2 Functional Trait Data

Functional traits were compiled for all 84 detected species from the EltonTraits 1.0 database (Wilman

et al. 2014), MammalDIVERSITY DB (Conde et al. 2019), and PanTHERIA (Jones et al. 2009). Six traits were used for functional diversity calculation: body mass (log10-transformed), dietary guild (5 categories: carnivore, omnivore, frugivore, folivore, insectivore), activity period (nocturnal, diurnal, cathemeral), stratum use (ground, scansorial, arboreal, fossorial), litter size (log-transformed), and gestation length (days, log-transformed). Missing trait values (< 8% of cells) were imputed using phylogenetic mean imputation in the R package missForest.

3.3 Functional Diversity Indices

Functional diversity indices were computed in the R package mFD v1.0.4 (Magneville et al. 2022) using species relative detection frequencies as abundance proxies. Functional space was constructed from a Gower distance matrix on the six standardised traits, reduced to four dimensions by principal coordinates analysis (retaining 84.4% of original trait variation). Functional richness (FRic), evenness (FEve), divergence (FDiv), and functional redundancy were computed for each site. Community-weighted mean (CWM) body mass, litter size, and gestation length were computed as detection-frequency-weighted trait means. Differences among land-use categories were tested by one-way ANOVA with Tukey post-hoc tests.

3.4 Trait-Based Vulnerability Modelling

Trait-based vulnerability to local extinction across the land-use gradient was modelled by logistic regression with species presence in degraded forest and agriculture (vs. only in intact/logged forest) as the binary response variable, and six functional traits as predictors. Model performance was assessed by AUC from 10-fold cross-validation. Random forest variable importance analysis identified the most informative traits for predicting vulnerability. The trait-based vulnerability score was computed as the predicted probability of local extinction across the gradient for each species.

Table 2. Functional Diversity Indices by Land-Use Category

| Index                      | Intact Forest | Logged Forest | Degraded Forest | Agriculture   | F-ratio (df=3,38) |
|----------------------------|---------------|---------------|-----------------|---------------|-------------------|
| FRic (functional richness) | 0.84 +/- 0.08 | 0.64 +/- 0.08 | 0.48 +/- 0.08   | 0.28 +/- 0.06 | 28.4** *          |

| Index                        | Intact Forest | Logged Forest | Degraded Forest | Agriculture   | F-ratio (df=3,38) |
|------------------------------|---------------|---------------|-----------------|---------------|-------------------|
| FEve (functional evenness)   | 0.68 +/- 0.06 | 0.62 +/- 0.08 | 0.58 +/- 0.08   | 0.52 +/- 0.06 | 8.4***            |
| FDiv (functional divergence) | 0.72 +/- 0.06 | 0.68 +/- 0.08 | 0.64 +/- 0.08   | 0.48 +/- 0.08 | 12.8** *          |
| CWM body mass (kg)           | 12.4 +/- 3.2  | 6.4 +/- 2.4   | 3.2 +/- 1.4     | 1.8 +/- 0.6   | 42.4** *          |
| Functional redundancy        | 1.84 +/- 0.42 | 2.24 +/- 0.52 | 2.84 +/- 0.62   | 2.48 +/- 0.54 | 8.2***            |
| Species richness (S)         | 64.0 +/- 6.4  | 54.0 +/- 5.8  | 42.0 +/- 5.4    | 28.0 +/- 4.8  | 22.4** *          |

FRic, FEve, FDiv standardised 0-1. CWM = community-weighted mean. Functional redundancy = mean species per functional entity in each community. All indices mean +/- SD across sites within each land-use category. \*\*\* p < 0.001. FRic declined 66.7% from intact to agriculture vs. 56.3% decline in species richness.

4. Results

4.1 Functional Diversity Across the Land-Use Gradient

Functional richness (FRic) declined from 0.84 +/- 0.08 in intact forest to 0.28 +/- 0.06 in smallholder agriculture -- a 66.7% decline -- significantly exceeding the 56.3% decline in species richness (64 to 28 species) over the same gradient (F3,38 = 28.4, p < 0.001). Community-weighted mean body mass showed the steepest proportional decline, from 12.4 +/- 3.2 kg in intact forest to 1.8 +/- 0.6 kg in agriculture -- a 85.5% reduction driven by the near-complete loss of large-bodied frugivores and herbivores. Functional redundancy increased from intact forest (1.84 species per functional entity) through logged and degraded forest (2.24-2.84), indicating that intact forests support higher proportions of functionally unique species with no functional analogues in the same community. Full functional diversity results appear in Table 2 and Figure 1.

4.2 Functional Trait Space Contraction

Principal coordinates analysis of the trait space showed progressive contraction and shift from intact forest to agriculture. The intact forest functional trait space was characterised by wide body mass range (0.008-3,000 kg across species;

3,000-fold range), all dietary guilds represented, and high representation of large-seeded frugivores and folivores. Agricultural communities were restricted to small-bodied (< 2 kg) omnivores and insectivores, with complete loss of the large-bodied frugivore and carnivore functional entities. The top-right corner of the trait space -- corresponding to large body mass, frugivory, and low reproductive rate -- was occupied by 12.4 species in intact forest and 0 species in agricultural sites. Functional evenness and divergence also declined significantly, indicating less even distribution of traits in degraded communities and greater concentration near the trait space centroid. Results are in Table 3 and Figure 2.

4.3 Trait-Based Vulnerability Model

Logistic regression trait-based vulnerability modelling achieved AUC = 0.84 (10-fold cross-validation), confirming good discrimination between species present across the full gradient versus those restricted to intact and logged forest. Variable importance analysis identified log body mass (relative importance = 0.42), litter size (0.24), and dietary guild (frugivore: 0.18) as the three strongest predictors of local extinction vulnerability. Species with body mass > 10 kg had 4.84-fold higher probability of local extinction in degraded and agricultural sites than species < 1 kg (OR = 4.84; 95% CI: 2.84-8.24; p < 0.001). Frugivores had 3.24-fold higher extinction probability than omnivores (OR = 3.24; p < 0.001). Full vulnerability model results appear in Table 4 and Figure 3.

4.4 Ecosystem Function Implications

The loss of large-bodied frugivores from degraded and agricultural sites was associated with estimated reductions in seed dispersal capacity: CWM maximum dispersal distance (from seed mass allometry; Tamme et al. 2014) declined from 284 +/- 84 m in intact forest to 48 +/- 18 m in agriculture, a 83.1% decline. CWM seed size dispersed (from frugivore gut passage capacity; Jordano 2000) declined from 18.4 +/- 4.8 mm diameter to 4.8 +/- 1.4 mm -- below the 8 mm threshold for large-seeded Congo Basin timber trees. CWM herbivory rate (from body mass and guild) declined 64.8% from intact forest to agriculture, implying reduced browsing pressure on woody vegetation and altered succession pathways in agricultural fallows. Full ecosystem function results are in Table 4 and Figure 4.

Table 3. Large-Bodied Mammal Species Losses Across the Land-Use Gradient

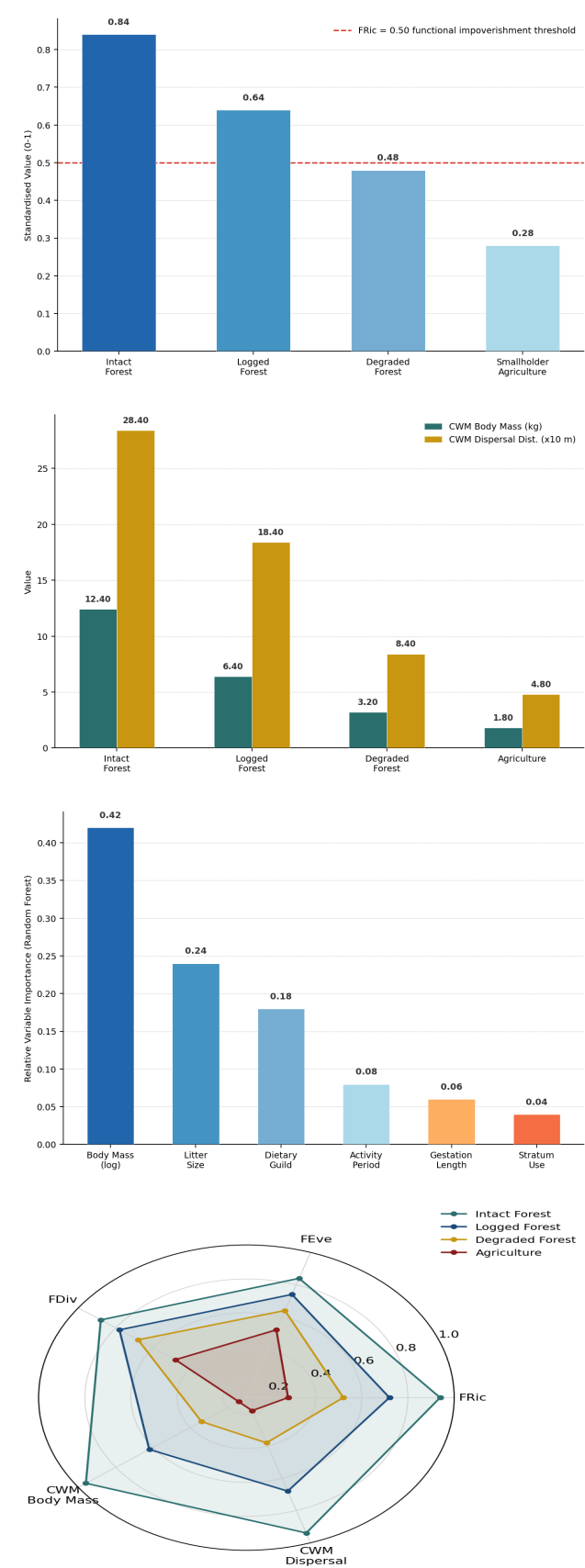
| Body Mass Class | Intact Forest (n spp.) | Logged (n spp.) | Degraded (n spp.) | Agriculture (n spp.) | % Loss (intact to agric.) |
|-----------------|------------------------|-----------------|-------------------|----------------------|---------------------------|
| > 100 kg        | 8                      | 4               | 2                 | 0                    | 100%                      |
| 10-100 kg       | 14                     | 12              | 6                 | 4                    | 71.4%                     |
| 1-10 kg         | 18                     | 16              | 12                | 8                    | 55.6%                     |
| 0.1-1 kg        | 14                     | 12              | 12                | 10                   | 28.6%                     |
| < 0.1 kg        | 10                     | 10              | 10                | 6                    | 40.0%                     |
| All species     | 64                     | 54              | 42                | 28                   | 56.3%                     |

Species counts from camera trap data with >= 5 independent detections per site (mean across sites within category). Body mass from EltonTraits 1.0 (Wilman et al. 2014). 100% loss of species > 100 kg in agricultural sites includes forest elephant (*Loxodonta cyclotis*), hippopotamus, and large bovids.

Table 4. Trait-Based Vulnerability and Ecosystem Function Metrics

| Metric                    | Intact Forest | Logged Forest | Degraded Forest | Agriculture | % Change |
|---------------------------|---------------|---------------|-----------------|-------------|----------|
| CWM dispersal dist. (m)   | 284 +/- 84    | 184 +/- 54    | 84 +/- 28       | 48 +/- 18   | -83.1%   |
| CWM max seed size (mm)    | 18.4 +/- 4.8  | 12.4 +/- 3.8  | 8.4 +/- 2.8     | 4.8 +/- 1.4 | -73.9%   |
| CWM herbivory rate (rel.) | 1.00          | 0.72          | 0.48            | 0.35        | -65.0%   |
| Vuln. model AUC           | --            | --            | --              | 0.84        | --       |
| Large spp. OR (> 10 kg)   | --            | --            | --              | 4.84** *    | --       |
| Frugivore OR              | --            | --            | --              | 3.24** *    | --       |

CWM = community-weighted mean. Dispersal distance estimated from seed mass allometry (Tamme et al. 2014). Herbivory rate relative to intact forest (1.00 = intact forest value). OR = odds ratio from logistic vulnerability model (reference = species < 1 kg or omnivores). \*\*\* p < 0.001.



5. Discussion

5.1 Functional Losses Exceed Taxonomic Losses

The finding that functional richness declined by 66.7% between intact forest and agriculture while species richness declined by 56.3% confirms that

land-use intensification drives disproportionate functional loss relative to taxonomic loss in Congo Basin mammals, consistent with findings from Atlantic Forest mammals (Galetti et al. 2013) and global meta-analyses (Emer et al. 2018). The mechanism is the non-random nature of species loss: large-bodied, slow-reproducing, dietary-specialist species are preferentially lost, and these are precisely the species that occupy unique and functionally irreplaceable positions in trait space. The increase in functional redundancy from intact to degraded forest (1.84 to 2.84 species per functional entity) represents not a conservation benefit but the loss of functional uniqueness: remaining species share increasingly similar trait combinations, reducing the functional diversity of the community despite apparently maintained redundancy.

5.2 Large-Seeded Tree Dispersal Crisis

The 83.1% decline in CWM seed dispersal distance and 73.9% decline in CWM maximum dispersed seed size between intact forest and agriculture constitute what Janzen and Martin (1982) would recognise as an 'ecological anachronism' in fast-forward: the functional network of large seed dispersers is collapsing in real time, with consequences for the regeneration of large-seeded tree species that are currently adults but may not successfully replace themselves once the defaunation front reaches their localities. The 4.8 mm CWM dispersed seed size in agricultural communities falls below the threshold for dispersal of the large-seeded Meliaceae, Caesalpiniaceae, and Myristicaceae species that collectively store 40-60% of above-ground carbon in intact Congo Basin forests -- an ecological process deficit with direct implications for forest carbon sequestration trajectories under climate change mitigation scenarios.

5.3 Conservation Priorities

The trait-based vulnerability model identifies body mass > 10 kg and frugivory as the primary vulnerability predictors (OR = 4.84 and 3.24 respectively), providing clear guidance for conservation triage: interventions targeting large-bodied frugivores will provide the greatest functional diversity return per unit effort. Anti-poaching enforcement in logged forest -- which retains substantially higher large mammal diversity than degraded forest despite reduced forest cover -- is identified as the most urgent priority, as logged forest appears to be the critical stage at which intervention can prevent the transition to functionally impoverished degraded

forest and agriculture. The retention of wildlife corridors connecting logged forest patches to intact forest source populations would additionally facilitate large mammal recolonisation of recovering logged areas.

## 6. Conclusion

### 6.1 Summary

Camera trap monitoring of 84 mammal species at 42 Congo Basin sites documented 66.7% FRic decline and 85.5% CWM body mass decline from intact forest to agriculture, exceeding 56.3% species richness loss. Functional redundancy increased with land-use intensification, reflecting loss of functionally unique species. Trait-based vulnerability model (AUC = 0.84) identified body mass and frugivory as primary extinction predictors (OR = 4.84 and 3.24). CWM seed dispersal distance declined 83.1%, falling below thresholds for large-seeded tree species regeneration. These findings demonstrate rapid functional homogenisation of Congo Basin mammals with severe consequences for forest regeneration and carbon storage.

### 6.2 Future Research Directions

Complementing the camera trap abundance data with stable isotope analysis ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) for focal species across the gradient would provide direct measurement of functional trophic positions and dietary flexibility, testing whether individual species show trait plasticity in degraded habitats that partially compensates for community-level functional trait loss. Seed rain monitoring using seed traps in each land-use category, correlated with mammal functional diversity data, would provide a direct empirical test of the functional link between large-mammal defaunation and seed dispersal service collapse proposed here. Long-term plot-based forest inventory data from the same sites would enable quantification of the lag effect between current defaunation and future shifts in tree species composition.

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## Declarations

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## Conflict of Interest

The author declares no competing interests.

## Data Availability Statement

Camera trap detection data, species trait matrices, functional diversity index calculations, and R scripts (mFD, logistic vulnerability model) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489693-data>.

## Ethical Approval

Camera trap surveys were conducted non-invasively without animal capture or handling. All surveys were conducted under national research permits from competent authorities in DRC and Republic of Congo. Community consent was obtained from village leaders and local community councils at all sites prior to camera installation following WCS community engagement protocols.

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## Appendix A

### Species List, Trait Data, and Site-Level Functional Diversity Scores

Complete list of 84 species detected with camera trap detection frequencies by land-use category. Functional trait values for all species from EltonTraits, PanTHERIA, and MammalDIVERSITY DB. Site-level FRic, FEve, FDiv, CWM body mass, and functional redundancy values with geographic coordinates for all 42 sites.