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# From town to national park: Understanding the long-term effects of hunting and logging on tree communities in Central Africa

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# ABSTRACT

Anthropogenic disturbances are changing the structure and composition of tropical forests worldwide. Multiple disturbances often occur simultaneously in forests. Hunting and logging, for example, are within-forest disturbances that impact vast areas of seemingly intact rainforests. Despite recent work on the individual effects of these disturbances, our understanding of how they interact to influence tree communities is still limited. In northern Republic of Congo, we explored the effects of hunting and logging on tree communities. Over an 8-year period, we monitored 12.552 tree stems (>10 cm diameter-at-breast height) spread over 30 1-ha plots along a gradient of human disturbance to compare the tree diversity between hunted and logged forest, once-logged forest, and protected forest free of both disturbances. Tree density, species richness, and community composition were affected by both hunting and logging. Forest close to human settlements was richer, more heterogenous, and more dynamic in species composition across censuses. In hunted and logged forest, fast-growing secondary species with low shade tolerance replaced old growth species. Comparatively, the once-logged forest had the greatest stem density and intermediate species richness with an increased density of shade-bearing species over time. Both tree species spatial turnover and tree recruitment were greatly affected by proximity to human settlements. A shift towards abiotically dispersed trees and increasing seed predation by rodents near villages can partly explain the differences in tree recruitment across the forest types. The combination of hunting and logging seems to have a greater impact on tree communities than either single disturbance, especially with nearness to villages.

## 1. Introduction

Anthropogenic activities are radically transforming forest ecosystems (Lewis et al., 2015). Worldwide, industrial timber extraction and land-conversion for agriculture are the principal causes of the loss of intact forest landscapes (Gibson et al., 2011; Potapov et al., 2017). In West and Central Africa, the area of protected forests has doubled since 2005 but the area of old-growth forest paradoxically continues to decline, particularly in areas of high population density (Tyukavina et al., 2018; FAO, 2020). Of the remaining forest in Central Africa, 30 to 40% is committed to timber concessions (ca. 44 million hectares; Bayol et al., 2012) opening formerly intact forests to new forms of human exploitation, including hunting (Laporte et al., 2007; Poulsen et al., 2009). Logging and hunting are unlikely to slow in the coming decade in this region (Barlow et al., 2018; FAO, 2020), reinforcing the need to better understand the long-term impacts of these activities on tree species composition and diversity.

Human activities within-forests can have pernicious effects on tropical forest biodiversity, while being difficult to detect and control (Ferreira et al., 2016). Whereas deforestation is readily traceable from space, forest degradation is much more difficult to quantify while having the potential to double biodiversity loss due to deforestation (Barlow et al., 2016). Within-forest disturbance, such as selective logging, generates visible changes in forest structure and species composition (Edwards et al., 2014). By comparison, hunting reduces wildlife populations in forests, but is cryptic in its effects and forests can appear structurally undisturbed (Benítez-López et al., 2017). Together, hunting and logging can transform forest ecosystems (Malhi et al., 2014); thus,

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the challenge is to disentangle the disturbances to quantify their independent and combined effects on forest species diversity and composition (Poulsen et al., 2011).

In recent years, reduced impact logging (RIL) has been embraced in Central Africa as a means of mitigating the collateral negative impacts of wood extraction within logging concessions (Putz et al., 2008). Alone, RIL usually has relatively subtle effects on tree species richness and composition at the community level. Although logging removes trees of species with high commercial value, logged forest shows high species overlap with unlogged forests (Hall et al., 2003; Gibson et al., 2011). Effects of logging tend to be density-dependent, with a positive effect on species richness at low logging intensity, mostly explained by an increase in pioneer and fast growing species in canopy gaps (Martin et al., 2015). Collateral damage during timber harvest can strongly affect species composition. The felling of large trees damages surrounding trees and creates canopy gaps, and construction of skid trails to extract logs from the forest further disturbs the understory (Edwards et al., 2014). Canopy openings from removal of large trees stimulate understory regrowth, facilitating the establishment of fast-growing secondary species and even fast-growing lianas and vines that can choke out local vegetation and slow down ecological succession (Gatti et al., 2014). Heavy machinery employed in logging can also damage the soil seedbank and compact soils, impeding forest regeneration (Hawthorne et al., 2012).

Over the past century, habitat loss and overhunting have driven hundreds of mammal species to extinction (Dirzo et al., 2014). Globally, the abundances of remaining medium- and large-bodied animal species have decreased significantly (Dirzo et al., 2014), with population loss of terrestrial vertebrates occurring at an unprecedented rate (Ceballos et al., 2017). Defaunation creates empty forests that are structurally intact but devoid of wildlife (Redford, 1992). This phenomenon is largely cryptic and occurs over vast forest areas, affecting both humandisturbed and protected landscapes (Harrison et al., 2013). It erodes ecological processes, usually reducing animal-mediated seed dispersal and altering the strengths of seed predation and herbivory (Poulsen et al., 2013; Maicher et al., 2020). Defaunated forests, therefore, tend to contain higher proportions of abiotically-dispersed tree species and reduced proportions of animal-dispersed tree species (Terborgh et al., 2008). In a relatively short-time, defaunation can alter forest composition (Effiom et al., 2013) and structure, increasing the density of saplings as a consequence of reduced herbivory (Harrison et al., 2013; Lamperty et al., 2020) and increased seed-predation (Rosin and Poulsen, 2016).

In this study, we investigate the individual and combined long-term effects of hunting and logging on tree species richness and composition along a gradient of human disturbance. In 2005, we established 30 1-ha plots in lowland semi-evergreen forest in northern Republic of Congo: ten plots in old-growth protected forest, ten plots in once-logged forest mostly free of hunting, and ten plots in forest disturbed by hunting and logging. We address three questions. First, what are the individual and combined effects of hunting and logging on tree diversity and composition? We hypothesize that logged forest will be richer in species than protected forest with the recruitment of secondary tree species following low intensity logging (1-2 stems/ha). We expect hunted and logged forests to shelter distinct tree species assemblages due to higher spatial heterogeneity in species distribution, with a few fast-growing secondary species becoming locally more dominant. Second, what are the environmental factors influencing tree community diversity and composition? Overall, we expect distance from the closest village to be the main factor influencing tree community composition. Compared to the relative effects of hunting and logging disturbances, we expect other factors linked to forest structure, such as pedology, topography, and hydrography, to only weakly affect tree community composition. Third, what are the effects of hunting and logging on tree recruitment? We expect both the direct and indirect effects of hunting and logging to alter tree diversity. Selective logging will directly reduce the number of timber species and open the canopy, while defaunation will decrease sapling

herbivory causing the understory to be saturated by seedlings and saplings of fast-growing secondary species. Logging will indirectly influence tree recruitment, with canopy openings from tree felling, skid trails, collateral damage, and roads promoting the recruitment of fast-growing secondary species. Hunting, on the other hand, will indirectly reduce the density of animal-dispersed tree species in favor of abiotically-dispersed species through a reduction in seed dispersal by large vertebrates. Hunting-induced defaunation will also alter reproductive success of some tree species by increasing rodent density and seed-predation pressure. We expect these changes in the relative recruitment success of tree species to alter forest regeneration.

# 2. Materials and methods

# 2.1. Study site

The study was conducted in northern Republic of Congo in the Nouabalé-Ndoki National Park (NNNP) and the adjacent Kabo logging concession (KLC) (Fig. 1A). Detailed description of the study sites can be found in previous publications (i.e, Clark et al., 2009, 2012, 2013; Poulsen et al., 2009, 2011, 2013). The study area consists of lowland semi-deciduous forest dominated by Euphorbiaceae, Meliaceae, and Annonaceae. Annual rainfall is around 1,500 mm, bimodally distributed between May/June and October, and interrupted by two dry seasons in July and December/February. The average daily temperature varies from 25 °C to 29 °C throughout the year (Harris, 2002).

The NNNP has never been logged and has been protected from hunting since its creation in 1993. The KLC has been logged over the past 50 years (approximately 2 trees/ha) for select timber species (i.e., Entandrophragma cylindricum, Entandrophragma utile, Triplochiton scleroxylon, and Milicia excelsa; Poulsen et al., 2011). Although the area is sparsely inhabited (human density of <1 person/km<sup>2</sup>), the logging economy contributed to the establishment of several permanent settlements along the Sangha River (Elkan et al., 2006). Kabo town, with ca. 4,000 inhabitants, is the largest human settlement of the region. Inhabitants mostly use guns or snares for hunting, which has reduced the abundance of large mammals close to Kabo town (Poulsen et al., 2011). Separately, hunting and logging decrease the density of some animal guilds and increase the density of others in the study area, whereas the combined effects of hunting and logging shift the relative abundance of the animal community away from large animals, such as monkeys, duikers, and apes, toward smaller animals, like squirrels and birds (Poulsen et al., 2011). With a known defaunation gradient and well described tree flora (Harris and Wortley, 2008), the study area provides a unique opportunity to explore the mid- to long-term effects of hunting and logging on tree communities (Poulsen et al., 2011).

#### 2.2. Tree identification

In 2005, we established 30 1-ha plots, with ten plots randomly distributed among three disturbance categories: 1. unhunted and unlogged forest in the NNNP (protected forest); 2. unhunted and logged forest in the KLC (once-logged forest); and 3. hunted and logged forest (hunted and logged forest) in the KLC within ca. 20 km of Kabo village (Fig. 1). In each plot, all trees > 10 cm diameter at breast height (DBH) were measured, tagged, mapped, and identified to species. Three voucher specimens were collected for each tree to allow for identification to species (or finest taxonomical level possible) at the Herbier national du Congo, Brazzaville, and the Edinburgh Botanic Garden. All voucher specimens were identified by a single taxonomist using species names following Harris and Wortley (2008). To control for the effects of logging and hunting on forest dynamics, the plots were re-censused in 2009 and 2013. All trees were remeasured, mortality was recorded, and newly recruited trees  $\geq$  10 cm DBH were tagged, mapped, and identified to species following the same protocol.

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Fig. 1. (A) Map of the Sangha Plot Network study area in northern Republic of Congo, Central Africa. (B) Barplots of the total species richness per census cumulated over the ten 1-ha plots in each forest type. The species mean rank shift (i.e., a quantification of the species reordering between two time points; Collins et al., 2008) between censuses is indicated by the circular arrows on the top of the barplots. The mean shift in rank abundance was higher in both periods in the hunted and logged and the once-logged forests than in protected forest, indicating slower temporal dynamics in protected forest plots with a lower reorganization rate of the species ranks across time.

2.3. Forest characteristics

We characterized the 30 plots with 15 parameters, hereafter *forest characteristics* (summarized in Table A.1 Appendix A). Absence of strong collinearity among individual *forest characteristics* was ensured by using paired scatterplots and Pearson correlation coefficients (with coefficients between predictor variables of  $|\mathbf{r}| < 0.7$ ; Dormann et al., 2013). In addition to the presence or absence of disturbance treatments (*hunting and logging combined* and *logging only*), we recorded *elevation* and *distance from the closest village* and *river* of the plot center using ArcView 3.2. On-site, we recorded the *number of dead trees* and *presence of lianas* in the crown of each tree. The canopy status of each tree was estimated from the ground to determine *the density of emergent, understory, midstory*, and *canopy trees* at each plot.

We also estimated *leaf area index* (LAI) for each plot by averaging values from four hemispherical pictures taken at 30 cm above the ground from the center of each quadrant of the plot. Photographs were taken using a Nikon Coolpix 5000 camera with a Fisheye Converter FC-E8 Nikon lens. To avoid overexposure, pictures were taken early in the morning (06:00–08:00 h), late in the afternoon (16:00–17:30), or on overcast days. Photographs were analyzed using the Gap Light Analyzer 2.0 (Frazer et al., 2001).

Finally, we collected soil samples at three randomly selected locations in each plot, using a soil probe (2.85  $\times$  83 cm) at 15 cm depth. We

weighed the samples after collection (wet mass) and after being air-dried (dry mass). After weighing, we pooled and thoroughly mixed the samples into a single sample for each plot. In the laboratory, the soil characteristics (percentage of sand, clay, and silt), nutrient availability (N, P, K, Al, Ca, Mg, Mn), and pH were analyzed by the IFAS Extension Soil Testing Laboratory (University of Florida). Available cations and P were extracted using the Mehlich III solution (Tran and Simard, 1993), while elemental analysis for the cations and P was done on the extracts by using inductively coupled plasma (ICP) spectroscopy. We extracted N as NH<sub>4</sub> and NO<sub>3</sub><sup>-</sup>, estimating nitrogen by colorimetry using a Technicon II auto-analyzer (SEAL Analytical, Mequon, Wisconsin, USA) and using the Kieldahl method to determine the total N (Hesse, 1971). Soil pH was measured in an Adams-Evans buffer solution made up of one volume of soil diluted in two volumes of water. Subsoil samples were analyzed for soil texture using a hydrometer method (Sheldrick and Wang, 1993). Finally, we summarized variation in soil characteristics into three PCA axes (Fig. A.1 Appendix A) as the last three forest characteristics. The first axis of the soil PCA axis, explaining 43.3% of the variability, corresponds to a gradient of porosity and fertility, where high values correspond to more porous, less organic, fertile soil and low values correspond to higher water retention, organic and fertile soils. The second axis of the soil PCA, explaining 20.8% of the variability, represents a gradient in pH; while the third axis of the soil PCA, explaining 15.5% of the variability, represents a gradient of Fe and soil fertility.

# 2.4. Statistical analyses

Most statistical analyses were performed in R v. 4.0.0 (R Core Team, 2020) and conducted on the 2005 dataset, except when otherwise stated. All redundancy analyses (RDA) were performed in Canoco 5 (ter Braak and Šmilauer, 2012) and assessed by Monte Carlo permutation tests with 9,999 permutations. We first evaluated the strength of the spatial autocorrelation between our plots with multivariate ordination (Šmilauer and Lepš, 2014). We computed RDA on the *forest characteristics* associated with soil characteristics (scores of the *three first PCA axes*), hydrology (*distance from the closest river*), and topology (*elevation*) within each plot, using the forest type as an explanatory variable.

# 2.4.1. Effects of hunting and logging on tree species richness and composition

We compared tree species richness between each forest type using the Chao2 asymptotic species richness estimator with plots as sampling units with the package iNext (Hsieh et al., 2019). We extrapolated the species richness for twice the sample size (i.e., 20 plots) per forest type. We then calculated sampling coverage (i.e., the probability that a newly added tree would belong to an already sampled species) to give the sampling completeness of our surveys.

To explore patterns of  $\beta$ -diversity between plots, tree community composition in each plot was described using nonmetric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity matrices after square-root transformation of tree species abundances. NMDS was performed in Primer-E v6 (Clarke and Gorley, 2006). To then classify individual tree species as specialists or generalists between forest types, we used a multinomial species classification, hereafter referred to as the CLAM test, conducted in the vegan package (Oksanen et al., 2019). Following Oksanen et al. (2019), we used the conservative supermajority specialization threshold of K = 2/3 and an  $\alpha$  of 0.01 divided by the total number of species tested between the two compared forest types.

Finally, we assessed mean rank shift for the different disturbance types across the three censuses using the codyn package (Hallett et al., 2016). The mean shift in rank abundance compares the species-rank distribution abundance between two dates and indicates the degree of species reordering.

# 2.4.2. Environmental factors influencing tree communities

To identify the factors driving the spatial pattern of tree diversity, we used generalized dissimilarity modelling (GDMs) to test the significance of the 15 *forest characteristics*, as well as the effect of *geographic distance between plots* on tree community spatial turnover. We then permuted each environmental variable 500 times, fitting a GDM model for each permutated table and comparing the explained deviance to the deviance of the full model. Statistical significance of each variable was assessed using the bootstrapped p-value of the permuted variables. We retained only statistically significant variables in the final GDM model. GDMs were computed using the gdm package (Fitzpatrick et al., 2020).

We then assessed the effects of the same 15 *forest characteristics* on tree community composition with multivariate ordination (Smilauer and Lepš, 2014). The best set of *forest characteristics* on tree community composition was selected by a forward selection procedure with Bonferroni correction to decrease the risk of type I error (Smilauer and Lepš, 2014). We then computed RDA on the tree community within each plot, using the selected *forest characteristics* as explanatory variables. The log-transformed (n + 1) abundances of individual tree species in each plot were used as the response variable (Smilauer and Lepš, 2014).

# 2.4.3. Effects of hunting and logging on tree recruitment

To determine if certain tree species recruited more often in different forest types, we used partial-RDA on the cohort of trees with < 20 cm DBH (hereafter *recruited trees*), assuming that they represent the most recent recruits within the community at a given census. We used the

forest type (i.e., hunted and logged, once-logged, protected) as an explanatory variable and year of the census as a covariate (i.e., control variable). To then examine if there was a shift in the tree species recruited among forest type across censuses, we used census year as an explanatory variable and forest type as a covariate. The log-transformed (n + 1) abundance of individual tree species <20 cm DBH in each plot was used as the response variable (Šmilauer and Lepš, 2014).

To evaluate how changes in the animal community might affect recruitment, we assigned a dispersal mode (i.e., animal, abiotic, or animal and abiotic dispersal) to each tree species and classified it as representative of primary or secondary succession using the abovementioned CLAM test and the three RDAs. Data on species ecology was compiled from Vivien and Faure (1985), Hawthorne (1995), and Harris (2002), as well as the African Plant Database (version 3.4.0) and from the authors' personal observations.

# 3. Results

From 2005 to 2013, 12,552 trees  $\geq$  10 cm DBH were tagged. Among them, 11,563 trees were identified to species (92.1%), 477 were attributed to morphospecies (3.8%), and 512 trees (4.1%) could not be identified. We discarded the latter from analyses of species richness and species composition (representing 5.7% of the hunted and logged forest, 3.0% of the once-logged forest, and 3.6% of the protected forest trees). The remaining 12,040 trees were identified to 407 (morpho)species (see details in Fig. B.1, Table B.1 Appendix B). No undersampling was detected. The sampling coverage of trees in all forests was very high (>95%; Table B.1 Appendix B), indicating that most tree species present in the three forest types were included in the plots.

Forest types explained well the variation in hydrological, pedological, and topological variations between plots (RDA: all-axes pseudo-F = 6.7, p < 0.001; Fig. A.2, Table A.2 Appendix A) indicating spatial autocorrelation of the plots. The plots in the once-logged forest were at lower elevation and lower distance from rivers than other forest types. However, these differences were very small (Table A.1 Appendix A). Soils in the protected forest were less porous, more organic, and generally more fertile with higher Fe content than the other forest types. Comparatively, plots in the once-logged forest had more porous and generally less fertile soil; whereas soil in the hunted and logged forest plots had the lowest Fe content.

# 3.1. Effects of hunting and logging on tree species richness and composition

At each census, the hunted and logged forest had the highest observed species richness (per plot and in total) among all forest types, followed by the once-logged forest and protected forest (Fig. 1B; Fig. B.2, Table B.1 Appendix B). The estimated species richness followed the same trend for each forest type (Fig. B.2, Table B.1 Appendix B). By contrast, the number of stems  $\geq$  10 cm DBH was highest in the once-logged forest, followed by the hunted and logged and protected forests (Table B.1 Appendix B).

Tree species dominance varied across the three forest types (Fig. B.3 Appendix B). The hunted and logged forest was characterized by a substantially lower density of *Diospyros bipindensis, Strombosia nigropunctata*, and *Grossera macrantha*, and by a higher density of understory, light-gap specialist, and pioneer trees such as *Carapa procera*, *Trichilia rubescens, Trichilia welwitschii*, and *Myrianthus arboreus*. The hunted and logged forest was also associated with a higher species richness of Rubiaceae and Euphorbiaceae (Fig. B.4 Appendix B). The once-logged forest was characterized by a high density of *Celtis mildbraedii* (Fig. B.4 Appendix B). Finally, the protected forest demonstrated a relatively high density of *Grossera macrantha* trees, while having lower species richness of Fabaceae and Malvaceae than other forest types (Fig. B.4 Appendix B).

The relationship of tree community composition changes to

disturbance treatments was confirmed by NMDS (Fig. B.5 Appendix B). Plots from the hunted and logged forest, and especially the plots closest to Kabo village (i.e., plots 1,2, and 3), were the most dissimilar from all other plots. Comparatively, tree communities in the once-logged and protected forests overlapped substantially. The tree community in the once-logged forest had an intermediate  $\beta$ -diversity between plots compared to the two other forest types.

CLAM analyses identified most trees species as generalist or too rare to be classified. However, two species were categorized as specialists of the hunted and logged forest: Myrianthus arboreus and Mallotus oppositifolius (Fig. 2A). Specialists of once-logged forest included Drypetes





Fig. 2. Classification of tree species by CLAM on the original 2005 dataset: (A) hunted and logged versus once-logged forest; (B) once-logged versus protected forest. Only species listed as specialists have been labelled (CEMI = Celtis mildbraedii; DASE = Dasylepis seretii; DUIN = Duvigneaudia inopinata; DRIT = Drypetes ituriensis; GIDE = Gilbertiodendron dewevrei; GRMA = Grossera macrantha; KEBR = Keayodendron bridelioides; MAOP = Mallotus oppositifolius; MYAR = Myrianthus arboreus; PAPE = Pancovia pedicellaris). Dashed lines represent the CLAM thresholds for specialist and generalist classes, and solid lines indicate the threshold at which species were too rare to classify.

ituriensis, Grossera macrantha, and Pancovia pedicellaris compared to the hunted and logged forest (Fig. 2A) and Celtis mildbraedii, Duvigneaudia inopinata, and Keayodendron bridelioides compared to the protected forest (Fig. 2B). Two tree species were categorized as specialists of protected forest: Dasylepis seretii and Gilbertiodendron dewevrei (Fig. 2B).

### 3.2. Environmental factors influencing tree communities

Of the 15 forest characteristics, four influenced tree species spatial turnover: distance from village, density of canopy trees, density of midstory trees, and the third axis of the soil PCA (Fig. 3; Table C.1 Appendix C). In addition, the geographic distance between plots also significantly influenced tree species turnover. Overall, the full GDM model accounted for 77.4% of the deviance in the compositional turnover of trees. The predicted ecological distance and compositional dissimilarity were well-fit with the observed compositional dissimilarity (Fig. 3A). In the order of relative importance, distance from village had the highest importance in the final GDM model (14.6%; Fig. 3B). Turnover rate of tree species sharply increased at short distances from villages, reaching an asymptote 20 km away and remaining constant at farther distances (Fig. 3C). The second and third most important predictors were the *density* of canopy trees (5.7%; Fig. 3B) and the density of midstory trees (5.0%; Fig. 3B). Both steadily increased tree species turnover until 80 and 110 tree stems per plot, respectively (Fig. 3C). At higher densities, the relative contributions of density of canopy and midstory trees to tree species turnover remained constant. The geographic distance between plots was the fourth most important variable in the final model (4.6%; Fig. 3B) confirming the existence of a spatial effect, albeit weak, indicating pseudo-replication across the plots: plots closer to each other had lower tree species turnover, while plots more distant from each other had higher tree species turnover (Fig. 3C). Finally, the score of the third axis of the soil PCA (2.5%; Fig. 3B) also influenced species turnover. Plots with higher iron content and higher general fertility had higher tree species turnover than soil with lower iron content and fertility (Fig. 3C).

In contrast with tree species spatial turnover, three forest characteristics had strong significant effects on tree community composition: distance from the closest village, score of the first axis of the soil PCA, and hunting and logging combined, in order of decreasing relative contribution (RDA: all-axes pseudo-F = 1.7, p < 0.001; Fig. 4C; Table C.2, C.3 Appendix C). The first RDA axis, largely constrained by the distance from the closest village and hunting and logging combined, explained 15.1% of overall species variation. The second axis explained 6.8% of the total variation and was mainly associated with the first axis of the soil PCA where high values correspond to more porous and less organic and fertile soil (Fig. A.1 Appendix A). Thirty-five tree species were especially sensitive to the first axis, having more than a 25% relative contribution to the first axis (Fig. 4A; listed in Table D.2 Appendix D).

#### 3.3. Effects of hunting and logging on tree recruitment

Of the 18-tree species characteristic of forest close to villages, 67% of them are animal dispersed, 22% rely on abiotic dispersion, and 11% are dispersed by both modes (Table D.2 Appendix D). None of the species are reported in the literature as being restricted to old-growth forest and four of them are often found in secondary succession (i.e., Desplatsia chrysochlamys, Mallotus oppositifolius, Myrianthus arboreus, and Ricinodendron heudelotii). Contrastingly, of the 17 species characteristic of forest distant from villages, 88% are animal-dispersed and 12% are abiotically dispersed (Table D.2 Appendix D). None of these species are characteristic of secondary succession, while five of them often characterize old-growth forest (i.e., Dasylepis seretii, Entandrophragma cylindricum, Ongokea gore, Pancovia laurentii, and Strombosiopsis tetrandra).

Forest type significantly affected the composition of recruited trees (partial-RDA: all-axes pseudo-F = 7.5, p < 0.001; Fig. 4; Table D.1 Appendix D), which did not change across censuses (partial-RDA: all-axes pseudo-F = 0.3, p = 1). The first RDA axis was mainly constrained by



Fig. 3. Outputs of the GDM model. (A) Fitted relationship between predicted ecological distance and observed compositional dissimilarity as well as the predicted versus observed biological distance. (B) Variable importance measured as the percent change between the deviance explained by the full model and the percent deviance explained by a model fit with the permuted variable. (C) Fitted functions of observed spatial turnover in composition of trees of  $\geq 10$  cm DBH when all other variables are held constant.

the presence of hunting and logging, explaining 10.7% of overall species variation, while the second RDA axis was constrained by the presence of logging only, explaining 4.4% of the overall species variation (Fig. 4F; Table D.1 Appendix D). In total, we identified 11 tree species especially sensitive to the presence of hunting and logging disturbances (Fig. 4D; listed in Table D.2 Appendix D). Five species were strongly recruited in the hunted and logged forest: Casearia barteri, Celtis adolfi-friderici, Klainedoxa gabonensis, Lannea welwitschii, and Myrianthus arboreus. All these species are known to occur in secondary forests (Table D.2 Appendix D) and are animal dispersed, except Myrianthus arboreus which can be animal or abiotically dispersed. By contrast, six species were more likely to be recruited in protected forest: Dasylepis seretii, Diospyros bipindensis, Diospyros iturensis, Grossera macrantha, Pancovia pedicellaris, and Scottellia klaineana. These species commonly occur in old-growth forests and are animal-dispersed, except Grossera macrantha which can be both animal and abiotically dispersed (Table D.2 Appendix D).

# 4. Discussion

# 4.1. Effects of hunting and logging on tree species richness and composition

In northern Republic of Congo, 50 years of hunting and logging have strongly influenced the tree communities. Unsurprisingly, because of the high species diversity of tropical forests, the three forest types (i.e., hunted and logged, once-logged, and protected forests) exhibited high species overlap with many generalist species. Even so, we identified consistent differences among forest types. Combined, hunting and logging greatly contributed to high tree species richness, mostly explained by an increase in forest heterogeneity and greater  $\beta$ -diversity between plots. Logging alone also increased overall tree species richness, but to a lesser extent than logging combined with hunting, while substantially increasing stem density. Whereas the observed increases in species

richness in the hunted and logged forest and the once-logged forest were predicted, the decrease in the stem density of trees  $\geq 10$  cm DBH with proximity to the village in the hunted and logged forest was not. We interpret this as an effect of hunting additional to logging.

Hunting and logging deeply altered the tree community composition in distinct ways. The once-logged forest was strongly dominated by a few abundant tree species, mostly Celtis mildbraedii, a shade-bearing species in regenerating forests (Sheil et al., 2000; Mwavu and Witkowski, 2009). Comparatively, the hunted and logged forest had a lower density of the most abundant species, including Celtis mildbraedii. Instead, fast-growing secondary species such as Myrianthus arboreus, Mallotus oppositifolius, and Musanga cecropioides that exhibit low shade tolerance established in this forest. This suggests additive effects of hunting and logging on tree community composition. Hunting coupled with logging may have suppressed the regeneration of Celtis mildbraedii in favor of light-loving, fast-growing trees. This increase in the recruitment of fast-growing trees competing for light is consistent with a previous observation from the same plots, where recruited trees in the hunted and logged plots were characterized by lower wood density than the other forest types for the smaller DBH class (Poulsen et al., 2013). Alternatively, several tree species could also be preferentially selected for artisanal timber and construction at proximity from human settlements and be filtered out from the community.

#### 4.2. Environmental factors influencing tree communities

As hypothesized, distance from the closest village was by far the main determinant of tree species composition and spatial turnover, even though weak spatial autocorrelation was detected between plots. Therefore, the pseudo-replicated design of our plots only weakly influenced species spatial turnover, with environmental factors having limited effects on species composition compared to the distance from human settlements. Of the environmental variables, pedological



**Fig. 4.** (A) Biplot of the RDA of the tree taxa ( $\geq 10$  cm DBH) from the 2005 census (only the 35 best fits are shown, corresponding to the number of tree species that had more than a 25% relative contribution to the first axis, representing the gradient of increasing distance from the villages). (D) Biplot of partial-RDA of the recruited tree taxa < 20 cm DBH from all censuses with year of the census as a covariate (only the 11 best fits are shown, corresponding to the tree species that have at least a 25% relative contribution to the first axis, representing the gradient of increasing disturbance). (B, E) Change of the tree diversity through ordination space. (C, F) Projection of the constraining environmental variables. See Table C.2-C.3 Appendix C and Table D.1 Appendix D for all results.

variation most strongly affected tree community composition and spatial turnover, but proximity to the closest village induced far greater species turnover than a simple distance-decay relationship would predict (Soininen et al., 2007). In previous studies, proximity to villages has already been demonstrated as an effective proxy of hunting pressure in Central Africa, being mostly concentrated within 10 km from the closest village (Koerner et al., 2017; Beirne et al., 2019). Similarly, our study identifies a halo of anthropogenic disturbance with high tree species turnover surrounding Kabo village and extending 20 km away.

The increase in forest heterogeneity in the hunted and logged forest, and to a lesser extent in the once-logged forest, is consistent with the scattered nature of selective logging and the centralized nature of hunting. In our study, intensive hunting and logging near the village altered tree dynamics: heavily disturbed forests are more dynamic with a higher level of reorganization between censuses than protected forest. Locally, logging directly reduces the abundance of timber species of high economic value (e.g., *Entandrophragma cylindricum*) and the abundance of tree species with low tolerance for disturbance, while favoring recruitment of generalist species (Martin et al., 2015). Forest plots close to villages may experience different selection pressures due to the removal of medium and large-sized mammals, gradually declining with distance from villages. In addition to hunting and logging, the tree plots closest to Kabo may also have been subjected to artisanal tree extraction for construction of houses and canoes.

#### 4.3. Effects of hunting and logging on tree recruitment

Although our results demonstrate higher temporal dynamics in hunted and logged forest than logged only and protected forest, we cannot conclude that these effects were due to hunting alone. We could not control for the effect of hunting alone because hunted, but not logged forest did not exist in northern Congo – a phenomenon that occurs throughout Central Africa. Moreover, local people also extract wood, fruits, seeds, and other natural resources from the forests near their villages.

Differential rates of seed dispersal and seed mortality might partly explain differences in tree recruitment across forest types. The hunted and logged forest included more abiotically dispersed species, whose relatively small seeds can be dispersed away from parent trees by wind (Nuñez et al., 2019), than protected forest. Previous research in this area suggests that hunting and logging strongly affect plant-animal interactions with potential cascading effects for forest diversity (Poulsen et al., 2013). However, contrary to our expectations, secondary tree species relying on seed dispersal by animals still recruited in the forest close to Kabo (see also Nuñez et al., 2019), although most produce small fruits that could be dispersed by large passerines or rodents (i.e., Casearia barteri, Celtis adolfi-friderici, Lannea welwitschii; but not Myrianthus arboreus). In Central Africa, a large portion of seed mortality is caused by predation by mammals. Filtering of tree recruitment via seed predation can greatly alter the density of established seedlings (Clark et al., 2012; Rosin and Poulsen, 2016). At short distances from villages, defaunation of medium and large mammals often triggers an increase in rodent and squirrel abundances (Effiom et al., 2013; Rosin and Poulsen, 2016; Koerner et al., 2017), likely increasing seed mortality and altering the regeneration of many tree species. While most rodents are seedpredators (Rosin and Poulsen, 2016), some exhibit scatter-hoarding behavior leading to dispersal and germination (Rosin and Poulsen, 2017), perhaps partially explaining why animal-dispersed species continue to be recruited near villages.

### 4.4. Implications for forest conservation

Our results demonstrate that both logging and hunting affect forest composition and diversity. Timber concessions cover immense areas in Central Africa, and therefore logging likely modifies tree species composition and diversity region-wide. Logging also brings people into forests, particularly with the construction of logging towns. Human activities near settlements strongly shift the tree composition away from that in protected forest via multiple pathways. Like the effects of hunting on animal communities (Koerner et al., 2017; Beirne et al., 2019), human disturbance near villages modifies the forest, increasing tree species diversity by conversion of old-growth forest into secondary forest. Without relaxation of human pressure, these forests might remain in a state of secondary forest, with altered ecological processes and lower carbon densities.

### **Data Accessibility**

Data are available on Mendeley Dataset here: Mendeley Data, V1, https://doi.org/10.17632/2jjykccvk4.1.

#### **CRediT** authorship contribution statement

Vincent Maicher: Writing - original draft, Formal analysis. Connie

**Clark:** Conceptualization, Funding acquisition, Investigation, Writing – review & editing. **David Harris:** Conceptualization, Funding acquisition, Data curation, Investigation, Writing – review & editing. **Vincent Medjibe:** Investigation, Writing – review & editing. **John Poulsen:** Data curation, Funding acquisition, Investigation, Writing – original draft, Supervision.

#### **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119571.

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