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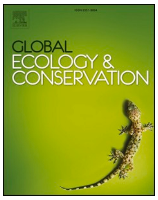

Low-intensity logging alters species and functional composition, but does not negatively impact key ecosystem services in a Central African tropical forest

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ABSTRACT

Selective logging can impact tree composition and the long-term sustainability of forests. Studying the ecological consequences of logging practices is crucial for guiding forest management strategies aiming at maintaining ecological integrity and supporting landscape-level conservation goals. We investigated the consequences of very low-intensity selective logging in multiple tree life stages across a logged forest chronosequence in Gabon. We found that species composition differed between logged and unlogged forests at all life stages (seedlings, saplings, and adults), which were most pronounced in the understory of older forests (logged 10 years prior) compared to unlogged areas. However, logging explained a small portion of the variation in species composition (<3% alone, <8% in combination with habitat). For functional composition, we observed higher wood density in the understory of older logged forests than in unlogged forests. Light-demanding saplings and saplings with animal-dispersed seeds were more prevalent in older logged forests than in unlogged forests. Timber species were less prevalent as seedlings and adults but more prevalent as saplings in logged forests compared to unlogged forests. Our results suggest that very low-intensity logging does not negatively impact key ecosystem services like carbon storage and food availability for frugivores. However, reduced prevalence of timber species may impact logging sustainability. Our study indicates that, when considering best-case scenarios, selectively logged forests have the potential to support conservation goals by offering refugia for biodiversity and maintaining essential ecosystem services. Thus, these forests have

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the potential to complement protected areas and serve as a sustainable alternative to more intensive land use.

Résumé: L'exploitation forestière sélective pourrait avoir un impact sur la composition des arbres et la durabilité à long terme de cette exploitation. L′étude des conséquences écologiques de l′exploitation forestière peut permettre d'améliorer la gestion des écosystèmes forestiers afin de garantir que les forêts exploitées sélectivement conservent leur intégrité écologique et puissent soutenir les objectifs de conservation à l′échelle du paysage. Au Gabon, nous avons étudié les conséquences de l′exploitation sélective à très faible intensité sur plusieurs stades de vie des arbres dans une chronoséquence de forêts exploitées. Nous avons constaté que la composition des espèces différait entre les forêts exploitées et non exploitées à tous les stades de la vie (plantules, jeunes arbres, et adultes). Ces différences se sont montrées plus prononcées dans le sous-étage des forêts exploitées depuis 10 ans par rapport aux sous-étage des forêts non exploitées. Cependant, l′exploitation forestière n′explique qu'une petite partie de la variation de la composition des espèces à tous les stades de la vie (<3% à l′exploitation forestière seule, <8% en combinaison avec l′habitat). En évaluant la composition fonctionnelle, nous avons constaté que les plantules et jeunes arbres des forêts anciennement exploitées avaient une densité de bois plus élevée que dans celui des forêts non exploitées. Les jeunes arbres héliophiles et les graines dispersées par les animaux avaient tendance à être plus prévalent dans le sous-étage des forêts exploitées que dans celui des forêts non exploitées. Les espèces commercialisées étaient moins prévalentes en tant que semis et d′adultes, mais plus prévalent en tant que jeunes arbres dans les forêts exploitées que dans les forêts non exploitées. Nos résultats suggèrent que l′exploitation forestière à très faible intensité na pas d′impact négatif sur les services écosystémiques tels que le stockage du carbone et la disponibilité en nourriture pour les frugivores. Cependant, la prévalence réduite de bois exploitable peut avoir des implications sur la durabilité de l′exploitation forestière. Notre étude indique que l'exploitation forestière modérée constitue une alternative viable face aux méthodes plus intensives. Ces espaces forestiers faiblement exploités peuvent contribuer à la conservation en reliant les zones protégées, en offrant des refuges pour la biodiversité et en maintenant des services écosystémiques essentiels.

1. Introduction

Tropical forests are increasingly affected by human disturbance and extraction (Malhi et al., 2014). In these ecosystems, extractive industries can impact biodiversity and ecosystem function. Very low-intensity selective logging (e.g., the removal of two or fewer trees per hectare) is one type of extractive activity that can balance strict protection and full extractive use, potentially limiting negative impacts to ecosystems whilst also generating income. Forests will not remain unchanged by selective logging, but selectively logged forests can retain meaningful levels of biodiversity, carbon, timber, and ecosystem services (Putz et al., 2012; Edwards et al., 2014; Bousfield et al., 2020), and logged landscapes can harbor intact patches where logging does not directly impact the forest (Putz et al., 2019). Such compromises are becoming important parts of management strategies for biodiversity conservation and sustainable development (Edwards et al., 2010; Putz, 2020; Grünburg et al., 2023). Selectively logged forests that retain high levels of ecological integrity will complement and support protected areas across a landscape by providing connectivity between intact areas. In addition, enabling reasonable economic value to be gained from forests that remain ecologically functional encourages popular support for such policies. However, selective logging does not always have easily predictable impacts on the species and functional composition of forests, which may affect the sustainability of both the ecosystem and its income-generating capacity on longer time scales.

Selective logging can impact forest composition and function in several ways, including indirectly changing forest structure and abiotic conditions, directly removing large reproductive trees, and altering the behavior of animal seed dispersers. First, logging activities have impacts beyond the removal of target trees. Logging gaps and skid trails open up the canopy and clear the understory, resulting in a higher frequency of gap habitats (Asner et al., 2004) and greater light availability (Fauset et al., 2017) in the understory of logged forest compared to undisturbed forest with a closed canopy. The greater environmental heterogeneity in these selectively logged forests likely drives higher spatial heterogeneity in species composition (i.e., beta diversity) because different species are favored under different abiotic conditions (Anderson et al., 2011; Chase et al., 2011).

Further, greater gap frequency and higher understory light in logged forests compared to unlogged forests can benefit species with specific life-history strategies and related functional traits (Baraloto et al., 2012; Döbert et al., 2017; Addo-Fordjour et al., 2020), and impact ecosystem services of logged forests. The species that benefit most from these environmental shifts immediately after logging are typically fast-growing, light-demanding pioneer species (de Carvalho et al., 2017) that tend to have low wood density (Baraloto et al., 2012; Hu et al., 2020) and abiotic seed dispersal (Rahayu et al., 2022; Carvalho et al., 2022), in contrast to the shade-tolerant species that are typically slow-growing and tend to have high wood density and animal-dispersed seeds. Thus, these species may have a competitive advantage and regenerate in higher abundances in early life stages soon after logging.

Moreover, the effect of cutting timber trees is to disrupt the regeneration of these same species. Felling large reproductive individuals not only removes them from the adult tree community but also removes important sources of seeds (Ouédraogo et al., 2018), which may also shift the functional composition of the regenerating tree community (Souza et al., 2021). This change may impact the future success of timber regeneration in logged forests. However, further functional shifts resulting from the removal of timber species' seed sources will depend on the functional composition of the community of timber species. For example, if timber species typically have high wood density and are animal-dispersed, we might expect to see fewer of these species regenerating, affecting ecosystem services such as carbon storage potential and the food availability for frugivores (Carvalho et al., 2022) in logged forests.

Additionally, logging activities may have indirect impacts on the animal community. Certain animals may avoid recently logged forests due to logging noise, human presence, or fallen trees and other woody debris that makes the forest more difficult to navigate (Burivalova et al., 2021). This change in animal behavior may decrease the recruitment of animal-dispersed species and reduce tree damage and/or mortality from herbivory, browsing, and trampling in selectively logged forests. In areas with very low-intensity selective logging, we expect the indirect effects of logging activity on forest heterogeneity and animal behavior to be greater than the direct effect of the removal of timber trees.

Given that the indirect impacts of logging can affect seed dispersal, recruitment, and regeneration, any change in the species and functional composition of a logged forest, and subsequent implications for ecosystem services, should be first evident in the understory rather than in the canopy (Medjibe et al., 2011; SEEF, 2019; Sullivan et al., 2022). However, many studies focus on the impact of logging on adult-sized individuals, missing impacts that may be apparent in earlier life stages.

Finally, we do not know how persistent the effects of selective logging are. The temporary changes to the abiotic environment and regeneration processes that occur immediately after logging could result in only ephemeral changes to the understory community of seedlings and saplings. For example, the heterogeneity induced by canopy gaps and skid trails may rapidly diminish as the forest begins to recover (de Carvalho et al., 2017), as tree canopies grow, and as animals return to the forest and the seeds of shade-tolerant species are dispersed in from adult trees elsewhere. Alternatively, the altered seedling community may represent the first stage of persistent effects that will continue over time to shape the adult tree community. The ultimate composition, structure, and function of logged forests depends on the outcome of these processes many years, decades, and even centuries after logging occurs, and we are far from understanding the long-term effects of selective logging practices.

Research on selective logging in tropical forests has typically focused on larger size classes and one-time measurements of the forest community (Medjibe et al., 2011; Osazuwa-Peters et al., 2015; Umunay et al., 2019). As a result, we are lacking data on how critical ecological processes change in earlier life stages, and information on how these changes persist as a forest recovers over time (White, 1992; Hayward et al., 2021). To better understand the impacts of low-intensity selective logging on tropical forests, we assessed the species and functional composition of seedling, sapling, and adult trees across a logging chronosequence that included areas of unlogged forest, recently logged forest (i.e., one-year-since-logging), and older logged forest (i.e., ten-years-since-logging).

We conducted this study in a lowland tropical forest in Gabon, a country that has very high forest cover (88.5%; Sannier et al., 2016), with much of that forested area designated for logging (approximately 62%; World Resources Institute, 2017). Gabon also has one of the lowest deforestation rates in Central Africa (Karsenty et al., 2016), estimated at a 1.2% decrease in tree cover between 2002–2022 (Global Forest Watch, 2022). Very low-intensity selective logging is understudied in this context. Because selective logging has a massive footprint in Gabon yet appears not to be driving significant deforestation, it is a potentially important model for economic development that can also maintain overall forest cover. If this model can also preserve ecosystem functional integrity and biodiversity, then it is an exciting paradigm for sustainable low-intensity extractive use of tropical forests in the future.

Selective logging currently impacts, and will continue to impact, the majority of the forests in Gabon for the foreseeable future, and is a major industry in the Congo Basin region overall. This study builds on previous work at our study sites, where we found increased heterogeneity in canopy openness and slightly lower sapling stem density in recently logged forests and slightly higher sapling diversity and sapling-sized liana abundance in older logged forests (Sullivan et al., 2022). These previous findings suggest that even at low logging intensities, selective logging can impact understory structure and diversity.

In this present study, we further explore how low-intensity selective logging affects both the forest environment and logging sustainability by examining variation in species composition, functional traits, and timber species in logged forests across a logging chronosequence compared to unlogged forests. Using this study system, we asked (Q1) does low-intensity selective logging alter the species and functional composition of tropical tree communities, and (Q2) do these shifts in composition persist over time?

Because of the very low rate of adult-sized timber tree removal, we expected any effects of low-intensity selective logging to be via regeneration and to be short-lived. Because our chronosequence measured forests up to 10 years post-logging and tropical tree species typically take multiple decades to reach adulthood, we did not expect to see any shifts in regeneration reflected in the adult community. Thus, we predicted that: (i) low-intensity selective logging will impact the species composition of the seedling and sapling community, (ii) the functional composition of the seedling and sapling community following low-intensity selective logging will shift to a greater prevalence of low wood-density, light-demanding, abiotically dispersed, non-timber trees, and (iii) forests logged at low-intensity will recover quickly such that older logged forests will have similar species and functional composition to unlogged forests.

2. Materials & methods

2.1. Study site

We conducted this study in the Société Equatoriale d′Exploitation Forestière (SEEF) logging concession of northwestern Gabon, to the east of the Mbé sector of Monts de Cristal National Park (0°42′41″ N, 10°17′18″ E). The Monts de Cristal landscape is an area of mid-elevation hills covering 20,000 km^2 of evergreen forest. Climate seasonality in Gabon is bimodal, with a more intense dry season in June–August and a less extreme dry season in December–February. More information on the climate, geology, and flora of Monts de Cristal can be found in Sunderland et al. (2004) and Vande weghe (2008). The SEEF concession has areas of selectively logged forest that were logged at different times, as well as areas of unlogged forest. Systematic selective logging began by SEEF in 2000, and logging intensity is very low: studies and reports indicate 0.82–1.6 trees removed per hectare (Medjibe et al., 2011; SEEF, 2019). The logging rate in the SEEF concession is typical across African forests (2 trees per ha^{-1}), but higher logging rates are more common in South America (5–6 trees ha^{-1}) and Asia (8 trees ha^{-1}) (Sist, 2000). Further information about logging history at our study site, such as road density, timber species lists, minimum cutting diameters, and logging history prior to 2000 can be found in Medjibe et al. (2011), SEEF (2019), and Sullivan et al. (2022). We did not observe any signs of older logging (e.g., prior to 2009) where we established plots for this study.

2.2. *Vegetation sampling and experimental design*

In 2018–2019, we set up a total of 80 vegetation plots of 20×20 m to assess community composition across different ages of logged forests and different life stages (Fig. 1A). We used a stratified random sampling method to choose the vegetation plot locations within each logging block in the chronosequence. Each plot contained two 10×10 m sapling subplots and nine 1×1 m seedling subplots (Fig. 1B). We identified, tagged, and measured all trees ≥10 cm DBH in the entirety of each vegetation plot, all saplings and small trees (woody individuals ≥1 cm and <10 cm DBH) in each sapling subplot, all tree seedlings (≤1 m in height) in each seedling subplot. For species that could not be identified in the field, we collected voucher specimens, and botanists from the National Herbarium (L'Herbier National du Gabon) provided determinations for as many species as possible. We established 20 plots in each of two different logging treatments: forest that had been logged one year prior to plot set up (recently logged forest), and forest that had been logged ten years prior to plot set up (older logged forest). We established a further 40 control plots in two unlogged forest areas, with 20 plots in each area (Fig. 1A). For each plot, we took information on habitat by recording elevation in each of the nine seedling plots per plot and used this elevation information to calculate the slope of each plot.

2.3. *Tree traits*

2.3.1. *Wood density*

We compiled wood density information on the taxa from our plots from the Global Wood Database (Chave et al., 2009; Zanne et al., 2009), which contains published wood densities (mass per unit volume) of adult trees. For our dataset, mean wood density was obtained at the lowest specific taxonomic level possible (family = 156 species; genus = 233 species, species = 113 species) because wood density tends to show a phylogenetic signal (Momo et al., 2020). For any species/morphospecies for which there was no information on wood density at the family, genus, or species level, (n = 4 species; 0.2% of adult stems, 3.5% of sapling stems, and 3.5% of seedling stems), we used the mean of the whole tree dataset.

2.3.2. *Life-history strategy, dispersal, and timber*

We compiled information on life-history strategy, dispersal, and timber species status for the taxa in our vegetation plots from the

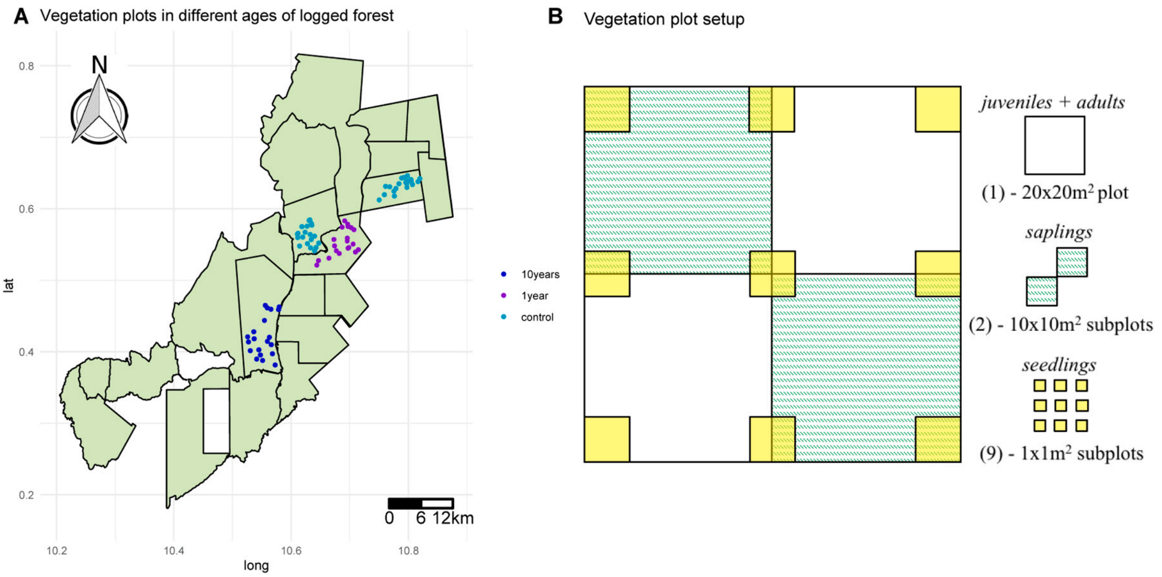

Fig. 1. **(A)** Map showing the location of vegetation plots in recently logged (one year since logging), older logged (ten years since logging), and unlogged (control) treatments in the study concession in the Société Equatoriale d'Exploitation Forestière (SEEF) logging concession of northwestern Gabon, to the east of the Mbé sector of Monts de Cristal National Park. **(B)** Diagram showing the size and number of vegetation plots and subplots. Adult trees ≥10 cm DBH were tagged, measured, and identified in the entirety of each vegetation plot. Saplings and small trees (woody individuals ≥1 cm and <10 cm DBH) were tagged, measured, and identified in each sapling subplot. Seedlings of all trees (≤1 m in height) were tagged, measured, and identified in each seedling subplot.

CoForTraits database (Bénédet et al., 2019) and filled in missing information for our species list based on information from online herbaria (Kew, New York Botanical Gardens, Missouri Botanical Gardens, Herbier du Gabon), floras and published vegetation guides (Burtt et al., 1985; White and Abernethy, 1997; Wilks and Issembé, 2000; Sosef et al., 2010; Meunier et al., 2015) and publications on seed dispersers (Clark et al., 2001; Trolliet et al., 2017).

For life-history strategy, we classified species as shade-tolerant or light-demanding based on categorical classifications from Bénédet et al. (2019). The light-demanding category included both pioneers and long-lived pioneers because both groups require light at early life stages and have faster growth rates than shade-tolerant species (Rüger et al., 2020). For dispersal mode, we classified species as animal dispersed or abiotically dispersed. We compiled a list of timber species harvested within the logging concession from SEEF (2019).

2.4. Statistical analyses

2.4.1. Species composition

To test if low-intensity selective logging alters the species composition of the forest, we first used the *decostand()* function from the R package *vegan* (Oksanen et al., 2022) to produce Hellinger-transformed species-by-plot abundance matrices for all the vegetation plots separately for each life stage (seedlings, saplings, adults) (Legendre and Gallagher, 2001). Then, we created a distance matrix for the vegetation plots for each life stage using an abundance-based Bray–Curtis index (Anderson et al., 2011) using the function *vegdist()* from the R package *vegan* (Oksanen et al., 2022). We tested for between-treatment differences in the species composition across the chronosequence, comparing the central location of composition groups in logged vs. unlogged forests using a PERMANOVA test via the *adonis()* function and using pairwise PERMANOVA post-hoc tests to identify which groups were different from each other (Anderson and Walsh, 2013). We visualized the community composition results with non-metric multidimensional scaling (NMDS) (Kruskal, 1964) using the *ordiplot()* function in the *vegan* package. Because selective logging is carried out in spatially explicit blocks in adherence to legal logging regulations in Gabon, our sample plots within logging treatments are aggregated in space. To better understand how the spatial aggregation of these blocks might impact our composition analyses, we conducted NMDS analyses with the two unlogged areas separated ($n = 20$ plots per unlogged treatment) and checked whether the results were similar.

Additionally, because these logging treatments are spatially aggregated, they may be more similar to each other in terms of habitat, e.g., elevation and slope. To test for impacts of logging on species composition while simultaneously examining the effects (quantified by adjusted R^2 values from linear regression models) of habitat and space, we performed a variance partitioning analysis following Bauman et al. (2019). We used the *decostand()* function from the *vegan* package to produce Hellinger-transformed species-by-plot abundance matrices for each life stage (Legendre and Gallagher, 2001). Then we used the *adespatial* package to create Moran's eigenvector maps (MEMs) derived from a spatial weighting matrix to model spatial structures in community composition. The effect (adjusted R^2) of MEMs corresponded to the space component in the variance partitioning. We used mean elevation and slope of each plot to characterize the habitat and test its effect on community composition (i.e., the habitat component of the variance partitioning). We used logging treatment to test for the effect of logging and time-since-logging on community composition (i.e., the logging component of the variance partitioning). The variance partitioning analyses thus considered the space, habitat, and logging variables simultaneously to quantify the proportion of variation in the community composition data explained by each of these components independently, and by the combined influence of two or more components. We conducted a separate variance partitioning analysis for each life stage (seedlings, saplings, adults).

2.4.2. Comparing functional composition in logged and unlogged forest

To examine if selective logging impacts functional composition and timber species regeneration, we tested for differences in mean

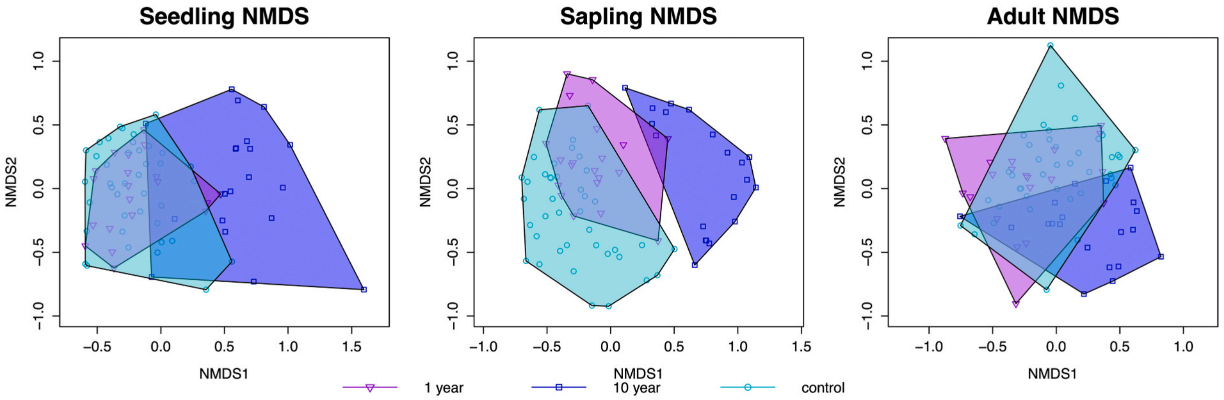

Fig. 2. Differences in composition between 1-year post-logging, 10-years post-logging, and unlogged (control) areas for **(A)** seedlings, **(B)** saplings, and **(C)** adults. Community composition was visualized using the first two axes of a Non-Metric Multidimensional Scaling (NMDS) procedure. Points represent the position of vegetation communities from each plot in multidimensional community space, and polygons group the plots per logging treatment.

wood density and the prevalence of species with differing life history strategy, dispersal mode, and timber status of all tree species in recently logged and older logged forest compared to unlogged forest. For wood density, we calculated the plot-level mean wood density using data on (i) abundance-weighted wood density (i.e., community-weighted mean; CWM) and (ii) species' presence-absence in each 20×20 m plot (i.e., community mean). We then tested for differences in mean wood density per plot by comparing the logged and unlogged forest using linear models (LMs).

For the categorical variables (life-history strategy, dispersal mode, timber status) we calculated the proportion of (i) individuals and (ii) species of light-demanding, animal-dispersed, and timber species in each 20×20 m plot and tested for differences between logged and unlogged forest using generalized linear models (GLMs) with binomial errors. Comparing results based on the proportion of individuals vs. proportion of species per plot allowed us to determine whether differences were being driven by changes in the abundance of species in each group and/or in the gain/loss of species in each group. For all variables, we ran separate models for each life stage. We conducted all analyses in the software environment R 4.1.0 (R. Core Team, 2021).

3. Results

3.1. Composition

3.1.1. Species composition: PERMANOVA

We found significant differences among treatments in the overall species composition of seedlings, saplings, and adults (Fig. 2, Table 1i). In most of the post-hoc pairwise comparisons of the three logging treatments, we found significant differences in composition for each life stage (NMDS, Fig. 2; post-hoc pairwise PERMANOVA, Table 1ii). We observed differences in the composition of all three life stages when we compared the older logged forest (10 yrs) to both the recently logged forest (1 yr) and the unlogged forest (C: control). Additionally, for saplings, species composition was significantly different between the recently logged forest (1 yr) and unlogged forest (C). Overall, our results indicated that there were differences in species composition between logging treatments for seedlings, saplings, and adults, and that the composition differences were strongest in the understory of the older logged forest compared to the recently logged and unlogged forest treatments.

3.1.2. Species composition: logging, space, and habitat

We interpret the results of these analyses with some caution due to our unbalanced design with the unlogged treatments combined (n = 40 plots). However, none of our conclusions changed when we repeated the composition analyses treating the two unlogged blocks as separate groups (Fig. A.1, Table A.1). While the effect of habitat alone explained the highest variation in composition than any other fraction of the variation partitioning (4.56–8.4% across all size classes, Fig. 3), logging explained a small amount of variation in composition across all life stages both alone (0.93–2.62% across all size classes, Fig. 3) and in combination with habitat (1.92–7.55% across all life forms, Fig. 3). Habitat, space and the co-variation between space and logging and space and habitat explained <1% of variation in species composition across all life stages (seedlings, saplings, and adults, Fig. 3). Most of the variation in species composition remained unexplained (≥80% across all size classes, Fig. 3).

3.2. Functional traits and timber species

3.2.1. Wood density

We found significant differences in mean wood density between logged and unlogged forests at the seedling and sapling stages, but not at the adult stage. (Fig. 4, Table A.2). Specifically, mean wood density of individuals was 0.04 g/cm^3 higher in the 10-yr logged forest than in the unlogged forest at both the seedling and sapling stage (Fig. 4A,B; Table A.2). In contrast, mean wood density of sapling species was 0.02 g/cm^3 lower in the 1-yr logged forest compared to the unlogged plots (Fig. 4E; Table A.2).

Table 1

(i) PERMANOVA shows compositional similarity – calculated via Bray-Curtis indices and **(ii)** PAIRWISE PERMANOVA shows which logging treatments are different, for **(a)** seedlings, **(b)** saplings, and **(c)** adults. 1 yr = one year since logging treatment, 10 yrs = ten years since logging treatment, and a C = unlogged (control) treatment.

	i) PERMANOVA						**ii) PAIRWISE PERMANOVA**					
a) Seedlings	*df*	*SS*	*MeanSS*	*F*	*R^2*	*P*		*df*	*SS*	*F*	*R^2*	*P-adj*
Logging treatment	2	2.957	1.479	3.967	0.093	**0.001***	1 yr: 10 yrs	1	1.907	5.044	0.117	**0.003***
Residuals	77	38.704	0.373		0.907		C: 1 yr	1	0.514	1.439	0.024	0.225
Total	79	31.661			1		C: 10 yrs	1	2.158	5.607	0.088	**0.003***
b) Saplings	*df*	*SS*	*MeanSS*	*F*	*R^2*	*P*		*df*	*SS*	*F*	*R^2*	*P-adj*
Logging treatment	2	3.501	1.751	6.475	0.144	**0.001***	1 yr: 10 yrs	1	1.906	7.119	0.158	**0.003***
Residuals	77	20.818	0.270		0.856		C: 1 yr	1	0.750	2.882	0.047	**0.003***
Total	79	24.319			1		C: 10 yrs	1	2.647	9.385	0.139	**0.003***
c) Adults	*df*	*SS*	*MeanSS*	*F*	*R^2*	*P*		*df*	*SS*	*F*	*R^2*	*P-adj*
Logging treatment	2	1.666	0.833	2.574	0.063	**0.001***	1 yr: 10 yrs	1	0.936	2.855	0.070	**0.003***
Residuals	77	24.919	0.324		0.937		C: 1 yr	1	0.488	1.542	0.026	0.21
Total	79	26.585			1		C: 10 yrs	1	1.109	3.384	0.055	**0.003***

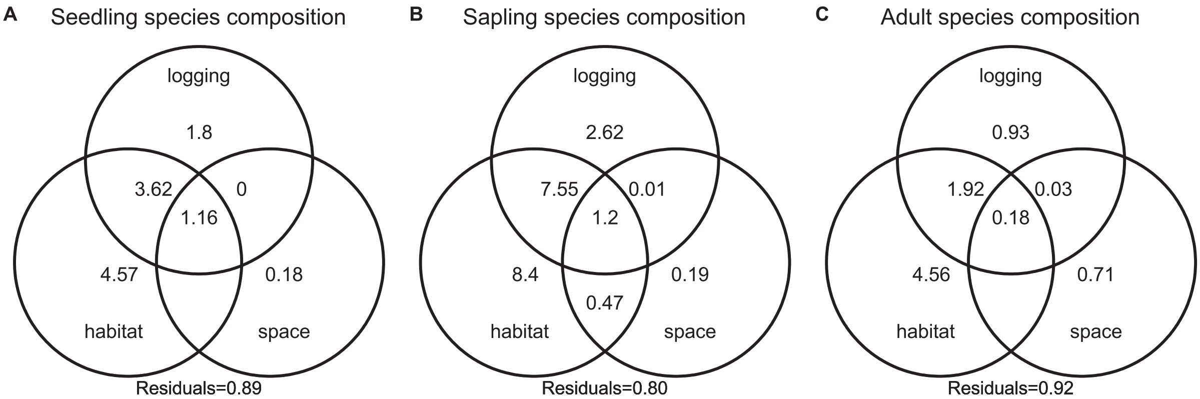

Fig. 3. Venn diagrams show quantification of the variance in community composition data in the species composition of **(A)** seedlings, **(B)** saplings, and **(C)** adults, with respect to the different variables. Numbers within circles show percentages of variation explained by logging, habitat, space, and their interactions. Residuals show the amount of variation unexplained by these variables.

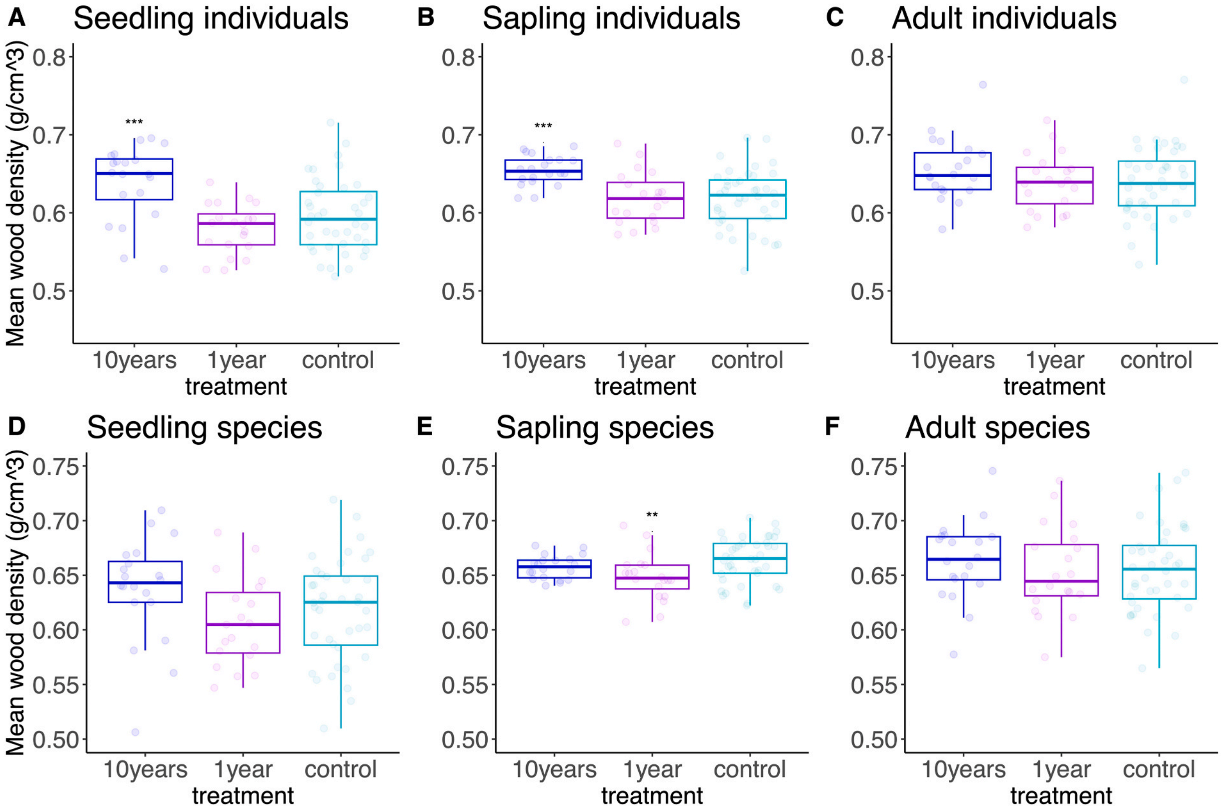

Fig. 4. Mean wood density of 1-year, 10-year, and unlogged plots in a logging chronosequence in Gabon, weighted by individuals **(A, B, C)** or species **(D, E, F)**, for seedlings **(A, D)**, saplings **(B, E)**, and adults **(C, F)**. Points refer to the mean wood density of individuals per 20×20 m plot. Boxes represent inter-quartile range (IQR), lines in the center represent the median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. We used generalized linear models to test for differences across treatments comparing plots in logged treatments to plots in the unlogged plots (Table A.2). Asterisks indicate statistical differences between logged and unlogged plots: *** $P < 0.001$, ** $P < 0.01$.

3.2.2. Life-history strategy

We found significant differences in the proportions of light-demanding individuals in logged vs unlogged forests when looking at saplings and adults, but not seedlings. Additionally, we observed significant differences in the proportions of light-demanding species in logged versus unlogged plots in each size class. Light-demanding species were up to 10.1% less prevalent as seedlings in logged forests compared to unlogged forests, but light-demanding individuals and species were up to 6.1% more prevalent as saplings and up to 11.8% less prevalent as adults in the logged versus unlogged sites (Fig. 5, Table A.3).

3.2.3. Dispersal mode

We found significant differences in the proportions of individuals and species dispersed by animals in logged versus unlogged plots in understory size classes. Animal-dispersed individuals were 10.4% more prevalent as saplings in the older logged forests compared to unlogged sites, but animal-dispersed species were 14.3% less abundant as seedlings and 4.6% less abundant as saplings in the logged compared to unlogged sites (Fig. 6, Table A.4).

3.2.4. Timber status

Finally, we found that seedlings had lower proportions of timber species in recently logged forests compared to unlogged forests, saplings had higher proportions of timber individuals and species in logged forests compared to unlogged forests, and adults had lower proportions of timber individuals and species in older logged forests compared to unlogged forests. Timber species were 3.7% less prevalent as seedlings in recently logged forests compared to unlogged forests. Timber individuals and species were up to 2.3% more prevalent as saplings when comparing logged forests to unlogged forests, and up to 8.1% less prevalent as adults in older logged forests compared to unlogged forests (Fig. 7, Table A.5).

4. Discussion

In this study, we assessed how very low-intensity selective logging impacted the species and functional composition of seedlings, saplings, and adults across a logging chronosequence in a seasonal evergreen tropical forest in Gabon, central Africa. We expected that timber trees and trees with high wood densities, shade-tolerant life-history strategies, and animal dispersal modes would decrease in prevalence in the understory of logged forests compared to unlogged forests in the short term. We did find that logging caused some shifts in the species and functional composition of the forest understory, likely due to the environmental changes in the understory that

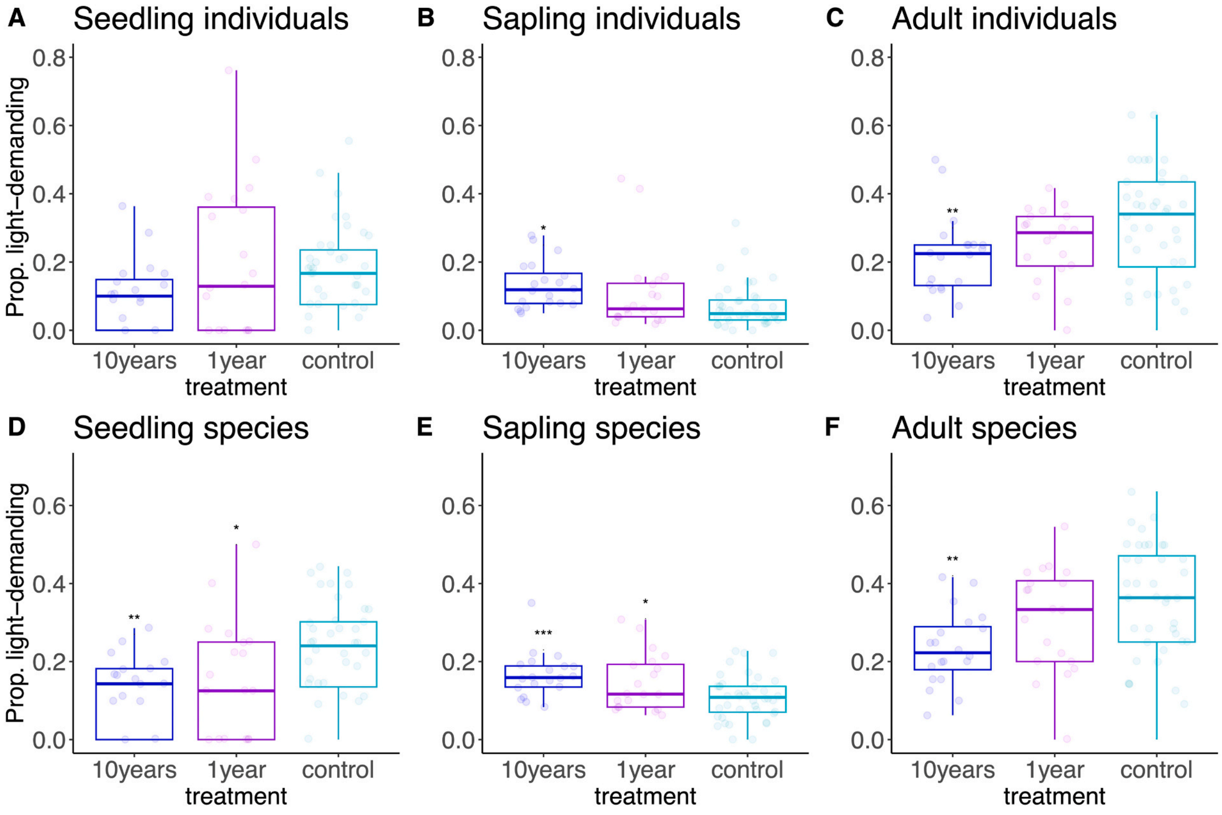

Fig. 5. The proportion of light-demanding trees in 1-year, 10-year, and unlogged (control) plots in a logging chronosequence in Gabon, weighted by individuals **(A, B, C)** or species **(D, E, F)**, for seedlings **(A, D)**, saplings **(B, E)**, and adults **(C, F)**. Points refer to the proportion of light-demanding individuals per 20×20 m plot. Boxes represent inter-quartile range (IQR), lines in the center represent the median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. We used generalized linear models to test for differences across treatments comparing plots in logged treatments to plots in the unlogged (control) plots (Table A.3). Asterisks indicate statistical differences between logged and unlogged plots: *** P < 0.001, ** P < 0.01, * P < 0.05.

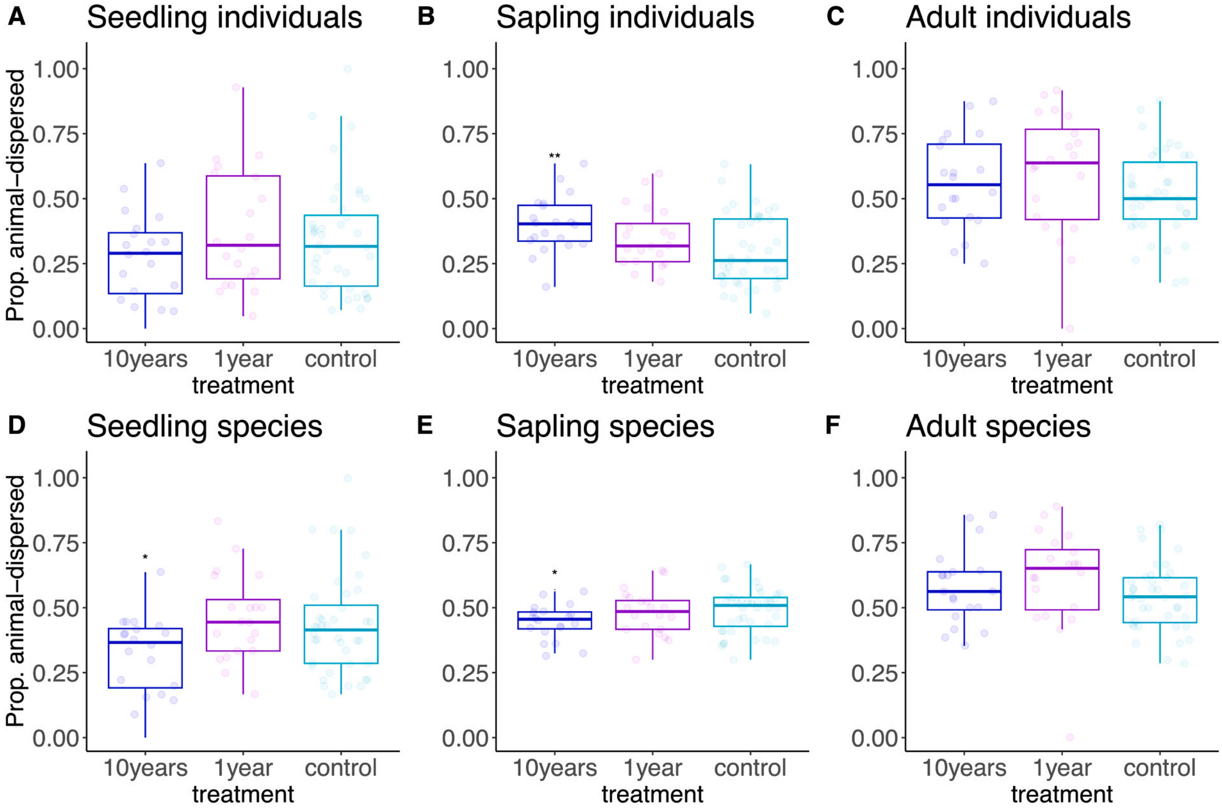

Fig. 6. The proportion of animal-dispersed trees in 1-year, 10-year, and unlogged plots in a logging chronosequence in Gabon, weighted by individuals **(A, B, C)** or species **(D, E, F)**, for seedlings **(A, D)**, saplings **(B, E)**, and adults **(C, F)**. Points refer to the proportion of individuals that are animal-dispersed per 20×20 m plot. Boxes represent inter-quartile range (IQR), lines in the center represent the median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. We used generalized linear models to test for differences across treatments comparing plots in logged treatments to plots in the unlogged (control) plots (Table A.4). Asterisks indicate statistical differences between logged and unlogged plots: ** $P < 0.01$, * $P < 0.05$.

impact regeneration. However, these shifts were small and not always in the expected direction, likely due to the low removal rates of adult trees. These changes appeared to last up to 10 years post-logging, where they were detected in the sapling life stage of the forest. Further inquiry is needed into whether changes will filter up to adult life stages, and how these changes will play out to affect logging sustainability over time periods that are relevant to current logging cycles (25–40 years in these forests).

4.1. Differences in species composition

Because timber removal is sparse in this logging concession, we did not expect to see significant differences in the species composition of adult trees in logged vs. unlogged forests. Instead, we expected any differences in species composition between logged vs. unlogged forests to be evident at early life stages (i.e., seedlings, saplings), because the loss of timber species as seed sources and changes in abiotic conditions would impart a stronger effect on the understory community than the adult community. In line with these predictions, we found differences in the composition of the understory (seedling and sapling) when comparing logged forests to unlogged forests, especially for the older logged forests. We did find some differences in the species composition of adult tree communities between logged and unlogged forests, which likely reflects underlying compositional differences in adult tree communities in these forests that existed prior to logging. These differences in adult tree composition between logged and unlogged forests were smaller than the differences we found in the understory (seedlings and saplings), supporting the idea that logging predominantly impacts early life stages in this system.

We interpret our species composition analyses with caution. Space-for-time experimental designs (i.e., chronosequences) assume that space is an appropriate approximation for time, but this often means that these single snapshots of a community along different points in time are also spatially correlated (Ramage et al., 2013). This spatial clustering could drive differences in composition due to (i) dispersal limitation, (ii) abiotic and environmental differences across the landscape, and (iii) other historical factors (i.e., land use history, human intervention, disease, etc.). We used two different approaches to address spatial clustering in our study. First, we repeated composition analyses with the two spatially separated unlogged plot areas as separate treatments. Results from this analysis indicated that there was a small amount of variation in species composition between the two unlogged forest areas, as we expected;

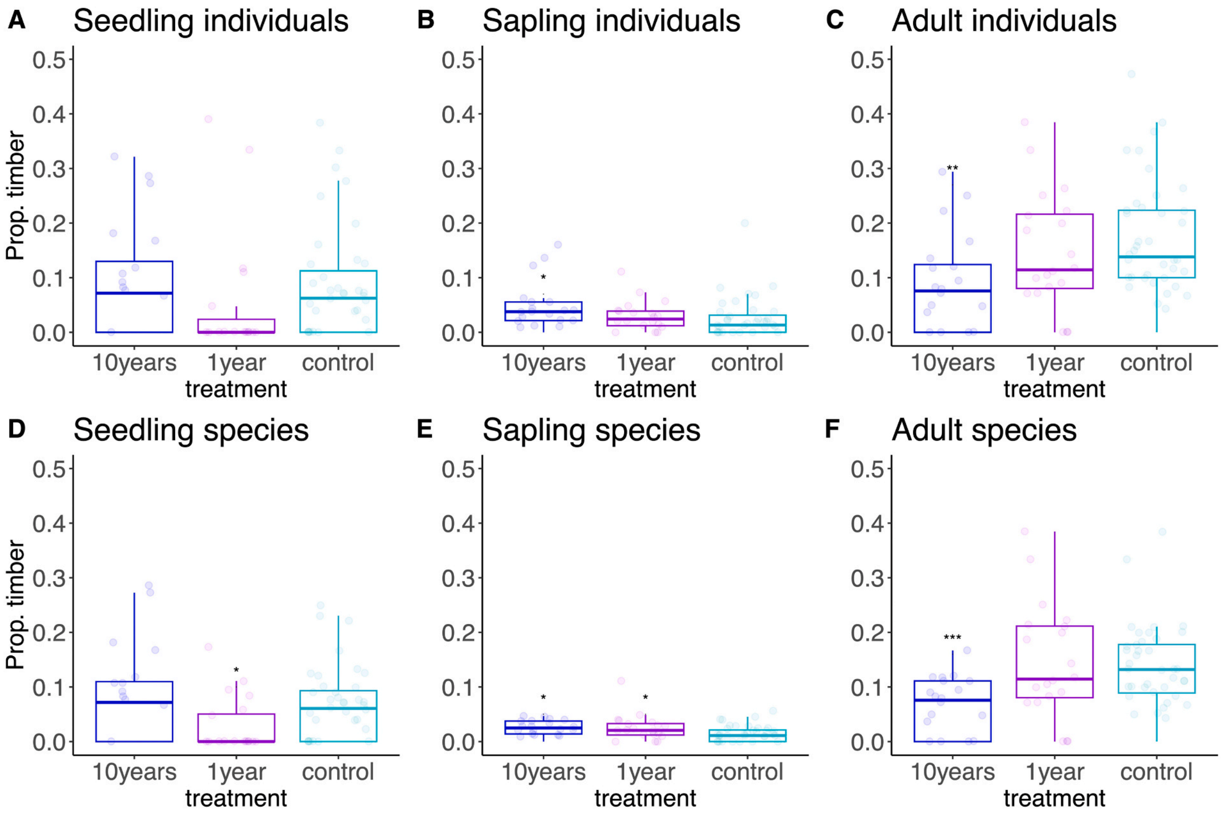

Fig. 7. The proportion of timber trees in 1-year, 10-year, and unlogged (control) plots in a logging chronosequence in Gabon, weighted by individuals **(A, B, C)** or species **(D, E, F)**, for seedlings **(A, D)**, saplings **(B, E)**, and adults **(C, F)**. Points refer to the proportion of timber individuals per 20×20 m plot. Boxes represent inter-quartile range (IQR), lines in the center represent the median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. We used generalized linear models to test for differences across treatments comparing plots in logged treatments to plots in the unlogged (control) plots (Table A.5). Asterisks indicate statistical differences between logged and unlogged plots: *** P < 0.001, ** P < 0.01, * P < 0.05.

however, the results comparing the logged forest treatments with the two different unlogged areas were broadly similar (Fig. A.1, Table A.1). Second, we conducted variance partitioning analyses to quantify how much of the variation in composition was driven by habitat, logging, space, and covariation between these three factors across the chronosequence (Bauman et al., 2019). Much of the variation in community composition that was explained by logging was shared with habitat. At our site, mean elevation was slightly higher in older logged forests, but elevation ranges broadly overlapped, and the mean slope was similar across the three treatment areas; we also did not find any strong differences in climate between logging blocks (Sullivan et al., 2022). Overall, results from these two analyses indicate that logging does explain some of the variation in community composition and that differences between logged vs. unlogged forests are not due to the within-treatment spatial clustering of replicates alone, meaning that spatial autocorrelation is not strongly driving these results.

4.2. Functional composition

Because of increased understory light levels in logged forests, we expected to find a greater prevalence of light-wooded, light-demanding, and abiotically dispersed trees compared to the understory of unlogged forests. As predicted, we observed that light-demanding saplings were more prevalent in older logged forests compared to unlogged forests. However, contrary to our predictions, there were more seedling and sapling individuals with higher wood density in older logged forests compared to unlogged forests. Further, because of the loss or avoidance of animal seed dispersers in forests immediately after logging occurred, we expected to find a greater prevalence of abiotically dispersed trees compared to the understory of unlogged forests. However, contrary to our predictions, we also found that there were higher proportions of animal-dispersed sapling individuals in the older logged forests than in the unlogged forests. Finally, animal-dispersed species in older logged forests were observed at both higher proportions of individual and lower proportions of species, indicating that higher abundances of a few key animal-dispersed tree species may be driving these results.

Other studies that have explored how selective logging impacts functional composition in tropical forests found that logged forests have reduced wood density (Baraloto et al., 2012; Hu et al., 2020) and differences in dispersal mode and life-history strategy (Döbert et al., 2017) compared to unlogged forests. However, in our study, we found conflicting patterns in how these different functional traits respond to selective logging. One of the reasons that we did not observe the patterns we predicted may be because the functional traits associated with timber species and non-timber species were different than we expected (Table A.6, A.7). Specifically, we expected our community of timber species to be typified by higher wood densities and be more likely to be shade-tolerant or animal-dispersed than non-timber species (Rosin, 2014), thus removing timber species seed sources would decrease the prevalence of dense-wooded, shade-tolerant, animal-dispersed species in the understory of the logged forests. However, in our study system, mean wood density was similar for timber and non-timber species (0.63 ± 0.14 g/cm^3 vs. 0.64 ± 0.12 g/cm^3, respectively) and light-demanding species made up 77% of timber species vs. 36% of non-timber species. For both groups, the majority of species were animal-dispersed (56% of timber species and 83% of non-timber species). Thus, our expectations were not in line with the actual functional trait characteristics of the timber species in our plots. In particular, okoumé (*Aucoumea klaineana*), the species prevalently logged in this area, is a long-lived pioneer species with relatively low wood density and is wind dispersed. Many of the other targeted timber species for the forests in Gabon are heliophiles and are likely to have a faster-growing profile than hardwoods that are more commonly harvested in other tropical regions (Rosin et al., 2014, Table A.8, A.9).

Overall, our functional traits results provide evidence about how low-intensity selective logging can have limited adverse impacts on some aspects of the forest, similar to previous studies on logging in Gabon (White, 1992). Increases in high wood density and animal-dispersed trees indicated that ecosystem services such as carbon storage, seed dispersal, and animal food availability may not be negatively affected simply because very low-intensity selective logging removes so few trees. When thinking about the implications of our results for other systems, researchers should carefully consider the species that are locally logged for timber and what their functional characteristics are (Rosin, 2014), as well as local protections for animals (Roopsind et al., 2017), and thus animal dispersal processes, in logging concessions.

4.3. *Timber species*

We expected to find fewer timber trees in the understory of logged forests compared to unlogged forests because of the removal of adult timber tree seed sources. Consistent with this expectation, we found that there was a lower proportion of seedling timber species in recently logged forests and a lower abundance and proportion of adult timber tree species in older logged forests compared to unlogged forests. These results suggest that the removal of adult timber species reduces seed sources, which may reduce timber species regeneration. However, the overall abundance of seedlings of timber species did not differ between logged and unlogged forests, suggesting that at least some timber species can successfully regenerate in logged areas. In both selectively logged and unlogged forests, environmental conditions may hinder some timber species regeneration. This could be the case for okoumé (*Aucoumea klaineana*; Guidosse et al., 2022) and other heliophile timber species that need light early in life, such as azobe (*Lophira alata*), ilomba (*Pycnanthus angolensis*), ozigo (*Dacryodes buettneri*) ozouga (*Saccoglottis gabonensis*), belinga (*Nauclea diderrichii*), and dabema (*Piptadeniastrum africanum*). Because very low-intensity selective logging adds only a few light gaps to the forest, and these light gaps are small, these heliophile timber species may still have a difficult time regenerating in the mostly closed-canopy forest (Fuhr and Delègue, 1999; Karsenty et al., 2018). However, we found that timber species tended to be more abundant and more prevalent in logged forests compared to unlogged forests at the sapling stage, suggesting that a higher richness of timber species is regenerating in selectively logged forests. This could be due to the increased environmental heterogeneity of the forest: perhaps more different types of timber species are found in the sapling layer because the light environment is more heterogeneous. Additionally, our results suggest that the removal of adult timber species can have persistent impacts on the adult community, lasting at least up to a decade after logging occurs.

Multiple timber species were present in all size classes and across all logged and unlogged forest sites (Table A.6). These included several of the most commonly logged taxa (as noted in the SEEF, 2019 report), including abiotically dispersed species such as okoumé, okan, and dabema, and animal-dispersed species such as ilomba, ekoune, and diania (see Table A.7 for timber species traits). Characterizing functional traits of timber species can help us better predict how logging that targets particular timber species with different traits impacts seed sources for different functional groups of trees, and ecosystem services such as carbon storage and animal food availability.

Overall, declines in the regeneration of timber species and a loss of seed sources in logged forests may be concerning for the long-term economic sustainability of even very low-intensity selective logging. Whether timber removal has a positive or negative impact on timber species regeneration at a specific site will be dependent on their initial abundances and logging removal rates, which are both variable across different regions, forest areas, and logging practices (Sist, 2000; Ellis et al., 2019). Because the logging rate in our study concession and across the Congo basin region is very low, timber harvest is more likely to be at sustainable levels compared to harvest levels in other regions (Piponiot et al., 2019). Additionally, the impact of timber removal on timber regeneration is likely variable depending on timber species regeneration requirements (Fayolle et al., 2015). Determining place-specific sustainable timber yields that allow for the successful regeneration of the timber species that are targeted is critically needed to inform management decisions and appropriate forestry policy at national and sub-national levels (Romero and Putz, 2018).

5. Conclusions

A well-managed logging industry is a compromise that can balance economic development and forest protection (Putz et al., 2012; Runting et al., 2019; Ellis et al., 2019). Our results show that very low-intensity logging alters tree species composition in the understory, and that a signature of logging disturbance is retained in the vegetation of the forest understory up to a decade after logging occurs. However, the changes in species composition do not result in functional changes to key ecosystem processes that negatively impact key ecosystem services – such as carbon storage and food availability for animals – in the regenerating tree community. The highest-priority sustainability challenge in even very low-intensity logged forests seems to be the regeneration of timber species (Gourlet-Fleury et al., 2013; Roopsind et al., 2018). Research on the regeneration requirements of timber species would be beneficial to better understand how to successfully manage timber stocks in the long term. Further work is also needed to connect the direct impacts of low-intensity selective logging on wildlife, as our results indicated that the indirect impacts of logging that could affect wildlife (i.e., food availability in logged forests) were not detrimental. Addressing these research gaps would inform forest management and could test the effectiveness of very low-intensity logged forest areas as wildlife corridors to supplement and connect protected areas, such as is promoted by the recent UN Convention on Biological Diversity recognition of OECM areas (CBD, 2018). Low-intensity logging concessions can be managed via different pathways to address conservation concerns outside of formally protected areas and contribute to a variety of different environmental priorities, such as the management of important wildlife species, biodiversity conservation, and carbon finance mechanisms. Our study adds to the body of evidence that managed, low-intensity selectively logged forests can be a middle path between strict protected areas and intensive land use.

CRediT authorship contribution statement

Liza S. Comita: Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Simon A. Queenborough:** Writing – review & editing, Visualization, Supervision, Conceptualization. **Megan K Sullivan:** Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Fabrice Bénédet:** Writing – review & editing, Data curation. **Jason Vleminckx:** Writing – review & editing, Visualization, Formal analysis. **Raoul Niangadouma:** Data curation. **Prince Armel Mouguiama Bissiemou:** Data curation. **Manoushka Ilambi Mayoungou:** Data curation. **Katharine Abernethy:** Writing – review & editing, Supervision, Conceptualization. **Juste Lemeilleur Temba:** Data curation.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the lead author used ChatGPT to suggest edits to the abstract and discussion for conciseness. After using this tool/service, the lead author used the suggestions to edit parts of the abstract and discussion. All co-authors reviewed the content after these edits and take full responsibility for the content of the publication.

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

Data Availability

I have shared the links to the datasets in the main text of the manuscript

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02996.

References

Addo-Fordjour, P., Ofosu-Bamfo, B., Kwofie, F., Akyea-Bobi, N., Rahman, F.A., Amoah, E., 2020. Changes in liana community structure and functional traits along a chronosequence of selective logging in a moist semi-deciduous forest in Ghana. Plant Ecol. Divers. 13, 75–84. https://doi.org/10.1080/17550874.2019.1675095.

Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. 83, 557–574. https://doi.org/10.1890/12-2010.1.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14, 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x.

Asner, G.P., Keller, M., Pereira, J., Rodrigo, Zweede, J.C., Silva, J.N.M., 2004. Canopy damage and recovery after selective logging in Amazonia: field and satellite studies. Ecol. Appl. 14, 280–298. https://doi.org/10.1890/01-6019.

Baraloto, C., Hérault, B., Paine, C.E.T., Massot, H., Blanc, L., Bonal, D., Molino, J.-F., Nicolini, E.A., Sabatier, D., 2012. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. J. Appl. Ecol. 49, 861–870. https://doi.org/10.1111/j.1365-2664.2012.02164.x.

Bauman, D., Vleminckx, J., Hardy, O.J., Drouet, T., 2019. Testing and interpreting the shared space-environment fraction in variation partitioning analyses of ecological data. Oikos 128, 274–285. https://doi.org/10.1111/oik.05496.

Bénédet, F., Doucet, J.-L., Fayolle, A., Gillet, J.-F., Gourlet-Fleury, S., Vincke, D., 2019. African plant traits information database. CoForTraits. https://doi.org/10.18167/DVN1/Y2BIZK.

Bousfield, C.G., Cerullo, G.R., Massam, M.R., Edwards, D.P., 2020. Chapter One - Protecting environmental and socio-economic values of selectively logged tropical forests in the Anthropocene, in: Dumbrell, A.J., Turner, E.C., Fayle, T.M. (Eds.), Advances in Ecological Research. Academic Press, pp. 1–52. https://doi.org/10.1016/bs.aecr.2020.01.006.

Burivalova, Z., Purnomo, Orndorff, S., Truskinger, A., Roe, P., Game, E.T., 2021. The sound of logging: Tropical forest soundscape before, during, and after selective timber extraction. Biol. Conserv. 254, 108812 https://doi.org/10.1016/j.biocon.2020.108812.

Burtt, B.L., Gentry, A.H., Leroy, J.F., 1985. Flore Du Gabon. Muséum National d'Histoire Naturelle, Paris.

de Carvalho, A.L., d'Oliveira, M.V.N., Putz, F.E., de Oliveira, L.C., 2017. Natural regeneration of trees in selectively logged forest in western Amazonia. For. Ecol. Manag. 392, 36–44. https://doi.org/10.1016/j.foreco.2017.02.049.

Carvalho, E.A.R., Hawes, J.E., Haugaasen, T., 2022. Potential losses of animal-dispersed trees due to selective logging in Amazonian forest concessions. Trees For. People 9, 100316. https://doi.org/10.1016/j.tfp.2022.100316.

CBD, 2018. United nations convention on biological diversity: Protected areas and other effective area-based conservation measures. CBD/COP/DEC/14/8. 30 November 2018. https://www.cbd.int/doc/decisions/cop-14/cop-14-dec-08-en.pdf (accessed 12 November 2023).

Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M., Inouye, B.D., 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2, art24. https://doi.org/10.1890/ES10-00117.1.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.

Clark, C.J., Poulsen, J.R., Parker, V.T., 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. Biotropica 33, 606–620. https://doi.org/10.1111/j.1744-7429.2001.tb00219.x.

R. Core Team, 2021. R: A language and environment for statistical computing. Vienna, Austria. https://www.R-project.org/.

Döbert, T.F., Webber, B.L., Sugau, J.B., Dickinson, K.J.M., Didham, R.K., 2017. Logging increases the functional and phylogenetic dispersion of understorey plant communities in tropical lowland rain forest. J. Ecol. 105, 1235–1245. https://doi.org/10.1111/1365-2745.12794.

Edwards, D.P., Gilroy, J.J., Woodcock, P., Edwards, F.A., Larsen, T.H., Andrews, D.J.R., Derhé, M.A., Docherty, T.D.S., Hsu, W.W., Mitchell, S.L., Ota, T., Williams, L.J., Laurance, W.F., Hamer, K.C., Wilcove, D.S., 2014. Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. Glob. Change Biol. 20, 183–191. https://doi.org/10.1111/gcb.12353.

Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhé, M.A., Hamer, K.C., Wilcove, D.S., 2010. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Proc. R. Soc. B: Biol. Sci. 278, 82–90. https://doi.org/10.1098/rspb.2010.1062.

Ellis, P.W., Gopalakrishna, T., Goodman, R.C., Putz, F.E., Roopsind, A., Umunay, P.M., Zalman, J., Ellis, E.A., Mo, K., Gregoire, T.G., Griscom, B.W., 2019. Reduced-impact logging for climate change mitigation (RIL-C) can halve selective logging emissions from tropical forests. For. Ecol. Manag. 438, 255–266. https://doi.org/10.1016/j.foreco.2019.02.004.

Fauset, S., Gloor, M.U., Aidar, M.P.M., Freitas, H.C., Fyllas, N.M., Marabesi, M.A., Rochelle, A.L.C., Shenkin, A., Vieira, S.A., Joly, C.A., 2017. Tropical forest light regimes in a human-modified landscape. Ecosphere 8, e02002. https://doi.org/10.1002/ecs2.2002.

Fayolle, A., Ouédraogo, D.-Y., Ligot, G., Daïnou, K., Bourland, N., Tekam, P., Doucet, J.-L., 2015. Differential performance between two timber species in forest logging gaps and in plantations in Central Africa. Forests 6, 380–394. https://doi.org/10.3390/f6020380.

Fuhr, M., Delègue, M.A., 1999. Silviculture of productive secondary forests in Gabon (Central Africa). In: Sist, P., Sabogal, C., Byron, Y. (Eds.), International Workshop Management of Secondary and Logged-over Forests in Indonesia, Management of Secondary and Logged-over Forests in Indonesia. Centre for International Forestry Research, Bogor, pp. 45–54.

Global Forest Watch, 2022. Gabon. World Resources Institute. https://www.globalforestwatch.org/dashboards/country/GAB/ (accessed 29 Feb 2024).

Gourlet-Fleury, S., Mortier, F., Fayolle, A., Baya, F., Ouédraogo, D., Bénédet, F., Picard, N., 2013. Tropical forest recovery from logging: a 24 year silvicultural experiment from Central Africa. Philos. Trans. R. Soc. B: Biol. Sci. 368, 20120302. https://doi.org/10.1098/rstb.2012.0302.

Grünberg, J., Ghaffariyan, M.R., Jourgholami, M., Labelle, E.R., Kaakkurivaara, N., Robert, R.C.G., Kühmaier, M., 2023. Criteria for assessing the sustainability of logging operations—a systematic review. Curr. For. Rep. 9, 350–369. https://doi.org/10.1007/s40725-023-00198-x.

Guidosse, Q., du Jardin, P., White, L., Lassois, L., Doucet, J.-L., 2022. Gabon's green gold: a bibliographical review of thirty years of research on okoumé (Aucoumea klaineana Pierre). Biotechnol., Agron. Société Et. Environ. 26, 30. https://doi.org/10.25518/1780-4507.19458.

Hayward, R.M., Banin, L.F., Burslem, D.F.R.P., Chapman, D.S., Philipson, C.D., Cutler, M.E.J., Reynolds, G., Nilus, R., Dent, D.H., 2021. Three decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo. For. Ecol. Manag. 488, 119036 https://doi.org/10.1016/j.foreco.2021.119036.

Hu, J., Herbohn, J., Chazdon, R.L., Baynes, J., Vanclay, J., 2020. Silvicultural treatment effects on commercial timber volume and functional composition of a selectively logged Australian tropical forest over 48 years. For. Ecol. Manag. 457, 117690 https://doi.org/10.1016/j.foreco.2019.117690.

Karsenty, A., 2016. The contemporary forest concessions in West and Central Africa: chronicle of a foretold decline? FAO For. Policy Inst. Work. Pap. 34 https://agritrop.cirad.fr/581423/1/Africa%20Report_Karsenty_12%2008%2016.pdf.

Karsenty, A., 2018. Is sustainable logging possible in Africa's dense forest? Bois Forêts Des. Trop. 336, 3–5. https://doi.org/10.19182/bft2018.336.a31615.

Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29, 115–129. https://doi.org/10.1007/BF02289694.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280. https://doi.org/10.1007/s004420100716.

Malhi, Y., Gardner, T.A., Goldsmith, G.R., Silman, M.R., Zelazowski, P., 2014. Tropical forests in the anthropocene. Annu. Rev. Environ. Resour. 39, 125–159. https://doi.org/10.1146/annurev-environ-030713-155141.

Medjibe, V.P., Putz, F.E., Starkey, M.P., Ndouna, A.A., Memiaghe, H.R., 2011. Impacts of selective logging on above-ground forest biomass in the Monts de Cristal in Gabon. For. Ecol. Manag. 262, 1799–1806. https://doi.org/10.1016/j.foreco.2011.07.014.

Meunier, Q., Moumbogou, C., Doucet, J.-L., 2015. Les Arbres Utiles du Gabon. Presses Agronomiques de Gembloux, Gembloux.

Momo, S.T., Ploton, P., Martin-Ducup, O., Lehnebach, R., Fortunel, C., Sagang, L.B.T., Boyemba, F., Couteron, P., Fayolle, A., Libalah, M., Loumeto, J., Medjibe, V., Ngomanda, A., Obiang, D., Pélissier, R., Rossi, V., Yongo, O., Bocko, Y., Fonton, N., Kamdem, N., Katembo, J., Kondaoule, H.J., Maïdou, H.M., Mankou, G., Mbasi, M., Mengui, T., Mofack, G.I.I., Moundounga, C., Moundounga, Q., Nguimbous, L., Ncham, N.N., Asue, F.O.M., Senguela, Y.-P., Viard, L., Zapfack, L., Sonké, B., Barbier, N., PREREDD Collaborators, 2020. Leveraging signatures of plant functional strategies in wood density profiles of African trees to correct mass estimations from terrestrial laser data. Sci. Rep. 10, 2001. https://doi.org/10.1038/s41598-020-58733-w.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Peter Solymos, M.H.H.S., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., O, M, Weedon, J., 2022. vegan: Community ecology package. R package version 2.6-4. https://CRAN.R-project.org/package=vegan.

Osazuwa-Peters, O.L., Chapman, C.A., Zanne, A.E., 2015. Selective logging: does the imprint remain on tree structure and composition after 45 years? Conserv. Physiol. 3, cov012 https://doi.org/10.1093/conphys/cov012.

Ouédraogo, D.-Y., Doucet, J.-L., Daïnou, K., Baya, F., Biwolé, A.B., Bourland, N., Fétéké, F., Gillet, J.-F., Kouadio, Y.L., Fayolle, A., 2018. The size at reproduction of canopy tree species in Central Africa. Biotropica 50, 465–476. https://doi.org/10.1111/btp.12531.

Piponiot, C., Rödig, E., Putz, F.E., Rutishauser, E., Sist, P., Ascarrunz, N., Blanc, L., Derroire, G., Descroix, L., Guedes, M.C., Coronado, E.H., Huth, A., Kanashiro, M., Licona, J.C., Mazzei, L., d'Oliveira, M.V.N., Peña-Claros, M., Rodney, K., Shenkin, A., de Souza, C.R., Vidal, E., West, T.A.P., Wortel, V., Hérault, B., 2019. Can timber provision from Amazonian production forests be sustainable? Environ. Res. Lett. 14, 064014 https://doi.org/10.1088/1748-9326/ab195e.

Putz, F.E., 2020. Science-to-conservation disconnections in Borneo and British Columbia. For. Chron. 96, 20–26. https://doi.org/10.5558/tfc2020-004.

Putz, F.E., Zuidema, P.A., Synnott, T., Peña-Claros, M., Pinard, M.A., Sheil, D., Vanclay, J.K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J., Zagt, R., 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. Conserv. Lett. 5, 296–303. https://doi.org/10.1111/j.1755-263X.2012.00242.x.

Putz, F.E., Baker, T., Griscom, B.W., Gopalakrishna, T., Roopsind, A., Umunay, P.M., Zalman, J., Ellis, E.A., Ruslandi, Ellis, P.W., 2019. Intact forest in selective logging landscapes in the tropics. Front. For. Glob. Change 2. https://doi.org/10.3389/ffgc.2019.00030.

Rahayu, S., Pambudi, S., Permadi, D., Tata, H.L., Martini, E., Rasnovi, S., Nuroniah, H.S., Kindt, R., Nugraha, M., Dewi, S., van Noordwijk, M., 2022. Functional trait profiles and diversity of trees regenerating in disturbed tropical forests and agroforests in Indonesia. For. Ecosyst. 9, 100030 https://doi.org/10.1016/j.fecs.2022.100030.

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., Potts, M.D., 2013. Pseudoreplication in tropical forests and the resulting effects on biodiversity conservation. Conserv. Biol. 27, 364–372. https://doi.org/10.1111/cobi.12004.

Romero, C., Putz, F.E., 2018. Theory-of-change development for the evaluation of forest stewardship council certification of sustained timber yields from natural forests in Indonesia. Forests 9. https://doi.org/10.3390/f9090547.

Roopsind, A., Caughlin, T., Sambhu, H., Fragosa, J.M., Putz, F.E., 2017. Logging and indigenous hunting impacts on persistence of large Neotropical animals. Biotropica 49, 565–575. https://doi.org/10.1111/btp.12446.

Roopsind, A., Caughlin, T.T., Hout, P., Arets, E., Putz, F.E., 2018. Trade-offs between carbon stocks and timber recovery in tropical forests are mediated by logging intensity. Glob. Change Biol. 24, 2862–2874. https://doi.org/10.1111/gcb.14155.

Rosin, C., 2014. Does hunting threaten timber regeneration in selectively logged tropical forests? For. Ecol. Manag. 331, 153–164. https://doi.org/10.1016/j.foreco.2014.08.001.

Rüger, N., Condit, R., Dent, D.H., DeWalt, S.J., Hubbell, S.P., Lichstein, J.W., Lopez, O.R., Wirth, C., Farrior, C.E., 2020. Demographic trade-offs predict tropical forest dynamics. Science 368, 165–168. https://doi.org/10.1126/science.aaz4797.

Runting, R.K., Ruslandi, Griscom, B.W., Struebig, M.J., Satar, M., Meijaard, E., Burivalova, Z., Cheyne, S.M., Deere, N.J., Game, E.T., Putz, F.E., Wells, J.A., Wilting, A., Ancrenaz, M., Ellis, P., Khan, F.A.A., Leavitt, S.M., Marshall, A.J., Possingham, H.P., Watson, J.E.M., Venter, O., 2019. Larger gains from improved management over sparing–sharing for tropical forests. Nat. Sustain. 2, 53–61. https://doi.org/10.1038/s41893-018-0203-0.

Sannier, C., McRoberts, R.E., Fichet, L.-V., 2016. Suitability of global forest change data to report forest cover estimates at the national level in Gabon. Remote Sens. Environ. 173, 326–338. https://doi.org/10.1016/j.rse.2015.10.032.

SEEF, 2019. Bilan d'exploitation AAC 2018. (5,398 ha) UFG2 – UFA2 NZAMALIGUE.

Sist, P., 2000. Reduced-impact logging in the tropics: objectives, principles and impacts. Int. For. Rev. 2, 3–10 https://www.jstor.org/stable/42609931.

Sosef, M.S.M., Florence, J., Wieringa, J.J., 2010. Flore du Gabon, progress and inventories, in: V.H. Jeannoda, V.H., Razafimandimbison, S.G., De Block, P. (Eds.), Flore Du Gabon vol. 40. National Botanic Garden of Belgium, Meise, pp. 465–465.

Souza, A.F., de Ávila, A.L., Araújo, M.M., Longhi, S.J., 2021. Long-lasting effects of unplanned logging on the seed rain of mixed conifer-hardwood forests in southern South America. J. For. Res. 32, 1409–1418. https://doi.org/10.1007/s11676-020-01205-8.

Sullivan, M.K., Biessiemou, P.A.M., Niangadouma, R., Abernethy, K., Queenborough, S.A., Comita, L., 2022. A decade of diversity and forest structure: post-logging patterns across life stages in an Afrotropical forest. For. Ecol. Manag. 513, 120169 https://doi.org/10.1016/j.foreco.2022.120169.

Sunderland, T., Walters, G.M., Issembe, Y., 2004. A preliminary vegetation assessment of the Mbe National Park, Monts de Cristal, Gabon. Cent. Afr. Reg. Program Environ. (CARPE). https://doi.org/10.13140/2.1.2193.6321.

Trolliet, F., Forget, P.-M., Huynen, M.-C., Hambuckers, A., 2017. Forest cover, hunting pressure, and fruit availability influence seed dispersal in a forest-savanna mosaic in the Congo Basin. Biotropica 49, 337–345. https://doi.org/10.1111/btp.12417.

Umunay, P.M., Gregoire, T.G., Gopalakrishna, T., Ellis, P.W., Putz, F.E., 2019. Selective logging emissions and potential emission reductions from reduced-impact logging in the Congo Basin. For. Ecol. Manag. 437, 360–371. https://doi.org/10.1016/j.foreco.2019.01.049.

Vande weghe, P.J., 2008. Monts de Cristal: Les Parcs Nationaux du Gabon. Wildlife Conservation Society, Libreville.

White, L., Abernethy, K., 1997. A guide to the vegetation of the Lopé Reserve. ECOFAC, Libreville.

White, L.J.T., 1992. Vegetation history and logging disturbance: Effects on rain forest mammals in the Lope Reserve, Gabon (with special emphasis on elephants and apes). PhD thesis. University of Edinburgh.

Wilks, C., Issembé, Y., 2000. Guide pratique d'identification: les arbres de la Guinée Equatoriale: Région continentale. CUREF, Bata.

World Resources Institute, 2017. Congo basin forest atlases. http://www.wri.org/our-work/project/congo-basin-forest-atlases.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum. Dryad. https://doi.org/10.5061/dryad.234.