Forest Ecology and Management

A decade of diversity and forest structure: post-logging patterns across life stages in an Afrotropical forest

--Manuscript Draft--

Manuscript Number:	FORECO-D-21-02277R1
Article Type:	Full Length Article
Keywords:	Selective logging; alpha diversity; liana increases; Tropical forest; Gabon
Corresponding Author:	Megan K Sullivan Yale School of Environment New Haven, CT UNITED STATES
First Author:	Megan K Sullivan
Order of Authors:	Megan K Sullivan
	Prince Armel Mouguiama Biessiemou
	Raoul Niangadouma
	Katharine Abernethy
	Simon A. Queenborough
	Liza Comita
Abstract:	Tropical forests are under threat of increasing pressure from income-generating land uses. Selective logging is a compromise that allows use of the land while leaving much of the forest canopy intact across a landscape. However, the ecological impacts of selective logging are unclear, with evidence of positive, negative, and negligible effects on forest structure and diversity. We examined the impact of selective logging on the structure and diversity of evergreen tropical forest in the Monts de Cristal region, a chain of mid-elevation hills in northwestern Gabon. For three size classes (seedling, sapling, and adult) of woody plant species, we tested whether forest structure (canopy openness, stem density, basal area, and relative liana abundances) and diversity were altered in forests that had been logged one year and ten years prior, compared to unlogged forest. In general, we found no large impact of selective logging treatment on the structure and diversity of adult woody plant communities, but the seedling and sapling communities were affected. Compared to unlogged forest, one-year post-logging forest had greater variation in canopy openness and lower sapling stem density. ten-year post-logging forest had higher seedling and sapling species evenness, higher sapling species diversity, and higher relative abundance of sapling-sized lianas compared to unlogged forest. Our results show that key differences between intact and selectively logged forests persist in the understory at least a decade after logging. Overall, these results contribute an additional data point in the literature on selective logging, specifically representing the impacts of very low impact selective logging in Central African forests. Our study highlights the value of exploring selective logging impacts at multiple time periods of recovery, and makes an important contribution to the knowledge Central African managed forests.
Suggested Reviewers:	Robin M Hayward, Master PhD Candidate, University of Stirling r.m.hayward1@stir.ac.uk His phd research is also on selective logging.
	Christopher Baraloto, PhD Professor, Florida International University cbaralot@fiu.edu has worked extensively in tropical logged forests
	Anand M Osuri, PhD moanand@gmail.com Has researched disturbance impacts on tropical forest diversity
	Camille Piponiot, PhD

	CIRAD Camille.piponiot-laroche@cirad.fr Her research focuses on selective logging and carbon in tropical forests
Response to Reviewers:	

1   **Title**:   A decade of diversity and forest structure: post-logging patterns across life stages in an

2   Afrotropical forest

3   Megan K. Sullivan[a,b], Prince Armel Mouguiama Biessiemou[c], Raoul Niangadouma[d], Katharine

4   Abernethy[e, f], Simon A. Queenborough[a], Liza Comita[a,g]

5

6   **Affiliations**

7   a.   School of the Environment, Yale University, New Haven, CT, USA

8   b.   Lewis B and Dorothy Cullman Program, The New York Botanical Garden, Bronx, NY

9   10458, USA

10   c.   Agence Nationale Des Parcs Nationaux, Batterie IV, BP. 20379, Libreville, Gabon

11   d.   Herbier National du Gabon, BP 1156, Libreville, Gabon

12   e.   African Forest Ecology Group, Faculty of Natural Sciences, University of Stirling,

13   Stirling, FK9 4LA, UK

14   f.   Institut de Recherche en Ecologie Tropicale, BP. 13354, Libreville, Gabon.

15   g.   Smithsonian Tropical Research Institute, Box 0843-03092 Balboa, Ancón, Republic of

16   Panama

17   **Running Title:** Selective logging in Northwestern Gabon

18   **Keywords:** selective logging, alpha diversity, liana increases, tropical forest, Gabon

19   **Corresponding author:**

20   Megan Sullivan

21   195 Prospect Street, New Haven, CT, 06511, USA

22   **Email address:** sullivanmks@gmail.com

23   **Abstract**

24   Tropical forests are under threat of increasing pressure from income-generating land uses.

25   Selective logging is a compromise that allows use of the land while leaving much of the forest

26   canopy intact across a landscape. However, the ecological impacts of selective logging are

27   unclear, with evidence of positive, negative, and negligible effects on forest structure and

28   diversity. We examined the impact of selective logging on the structure and diversity of

29   evergreen tropical forest in the Monts de Cristal region, a chain of mid-elevation hills in

30   northwestern Gabon. For three size classes (seedling, sapling, and adult) of woody plant species,

31   we tested whether forest structure (canopy openness, stem density, basal area, and relative liana

32   abundances) and diversity were altered in forests that had been logged one year and ten years

33   prior, compared to unlogged forest. In general, we found no large impact of selective logging

34   treatment on the structure and diversity of adult woody plant communities, but the seedling and

35   sapling communities were affected. Compared to unlogged forest, one-year post-logging forest

36   had greater variation in canopy openness and lower sapling stem density. Ten-year post-logging

37   forest had higher seedling and sapling species evenness, higher sapling species diversity, and

38   higher relative abundance of sapling-sized lianas compared to unlogged forest. Our results show

39   that key differences between intact and selectively logged forests persist in the understory at least

40   a decade after logging. Overall, these results contribute an additional data point in the literature

41   on selective logging, specifically representing the impacts of very low impact selective logging

42   in Central African forests. Our study highlights the value of exploring selective logging impacts

43 at multiple time periods of recovery, and makes an important contribution to the knowledge

44 Central African managed forests.

45

46 **Résumé**

47 Les forêts tropicales sont menacées globalement par les pressions croissantes des

48 aménagements des terres générateurs de revenus. L'exploitation forestière sélective est un

49 compromis qui permet l'utilisation des terres tout en laissant une grande partie de la canopée

50 forestière intacte à travers le paysage. Cependant, les impacts écologiques de l'exploitation

51 forestière sélective ne sont pas clairs, et démontre des preuves d'effets positifs, négatifs et

52 négligeables sur la structure et la diversité des forêts. Nous avons examiné l'impact de

53 l'exploitation forestière sélective sur la structure et la diversité de la forêt tropicale sempervirente

54 dans la région des Monts de Cristal, une chaîne de collines de moyenne altitude au nord-ouest du

55 Gabon. Pour trois classes de taille (les plantules, les jeunes arbres et les arbres adultes), nous

56 avons testé si la structure de la forêt (ouverture de la canopée, densité des tiges, surface terrière

57 et abondance relative des lianes) et la diversité étaient altérées dans les forêts qui avaient été

58 exploitées un an et dix ans auparavant, par rapport à la forêt non exploitée. En général, nous

59 n'avons trouvé aucun impact important d'exploitation forestière sélective sur la structure et la

60 diversité des communautés de plantules et d'adultes, mais la communauté des jeunes arbres a été

61 affectée. La strate de jeunes arbres dans la forêt exploitée depuis dix ans est plus diversifiée et a

62 plus de lianes que la forêt non-exploitée. Les forêts exploitées depuis un an présentent une plus

63 grande variation dans l'ouverture de la canopée et une densité de tiges des jeunes arbres plus

64 faible, et les forêts exploitées sur dix ans présentent une plus grande régularité des plantules et

65 des jeunes arbres, une plus grande diversité de jeunes arbres et des abondances relatives plus

66   élevées de lianes de la taille des jeunes arbres. Nos résultats montrent que les principales

67   différences entre les forêts exploitées intactes et sélectives persistent dans la végétation de sous-

68   bois au moins une décennie après l'exploitation. Dans l'ensemble, ces résultats confirment

69   l'importance des études à long terme sur le rétablissement de la forêt entière après l'exploitation

70   forestière, et confirment l'importance de soutenir des zones forestières intactes dans le paysage

71   d'une zone exploitée de manière sélective.

72

73

74

75   **1. Introduction**

76   Tropical forests contain the majority of terrestrial species diversity but are increasingly impacted

77   by disturbances such as fire, clearing of trees, fragmentation, and selective logging (Lewis et al.,

78   2015). At least 20% of all tropical forests were subjected to selective logging (the practice of

79   cutting and removing trees of selected species and sizes for use as timber) from 2000–2005

80   (Asner et al., 2009) and this proportion is likely to increase (Laurance and Edwards, 2014).

81   However, unlike many other types of income-generating forest disturbance (e.g., clearance for

82   agriculture), selective logging is relatively low impact (Gibson et al., 2011). In a selectively

83   logged forest, the majority of forest area is not damaged directly by logging and the majority of

84   the forest can remain intact (Putz et al., 2019). Thus, selective logging can be viewed as a

85   strategic compromise that allows for economic development and local livelihoods, while also

86   maintaining a landscape of connected forest that contributes to biodiversity conservation, habitat

87   connectivity, and ecosystem function across space and time (Edwards et al., 2014).

88   Understanding the limits at which selective logging remains sustainable is critical to the long-

89   term persistence, diversity, and function of selectively logged tropical forests (Sist et al. 2007,

90   Gourlet-Fleury et al. 2013). It will be a crucial tenet of sustainable use forest management

91   policies, acceptable to the developing nations that harbor the globe's remaining tropical forests.

92   Selective logging activities have direct impacts on forest structure and diversity, as well

93   as on the light environment in the understory. Because large timber species are removed, the

94   number of large trees of these species are lower in logged forest (Senior et al., 2018). This

95   reduction in basal area and stem density of adults can negatively affect long-term carbon stocks,

96   canopy structure, and forest height (Okuda et al., 2019). Disrupting canopy structure and

97   increasing canopy gaps also increases light availability throughout the forest, but especially in

98   the understory (Asner et al., 2004). After large timber species are cut, given enough time,

99   aboveground biomass (AGB) basal area and canopy structure can recover (Gourlet-Fleury et al.,

100   2013; Putz et al., 2012). While populations of the target species do decline after the first cutting

101   cycle, timber yields can be subsequently sustained (Putz et al., 2012). However, the intensity of

102   selective logging is highly variable across the tropics and often coupled with associated

103   degradation and risk of further disturbance, such as fire, clearance, and conversion to agriculture

104   (Edwards et al., 2014). Identifying sustainable timber harvesting thresholds where populations of

105   timber species recover between harvests continues to be a major challenge in tropical forestry

106   (Petrokofsky et al., 2015).

107   When managed well, selectively logged forests can be of high conservation value. Well-

108   managed forests typically retain high levels of biodiversity, carbon storage, and ecosystem

109   function (Putz et al. 2012, Edwards et al., 2014). For example, the impact of selective logging on

110   woody plant species richness appears to be relatively modest (Putz et al., 2012), especially in

111   comparison to other land uses (Gibson et al., 2011). This apparent lack of effect is likely because

112   selective logging is a very patchy disturbance and highly spatially variable. Although direct

113   impacts are diluted and minimal at the scale of the logging concession (Putz et al., 2019), the

114   creation of roads and logging gaps increases heterogeneity in the forest environment, particularly

115   in understory light availability (Asner et al. 2004). This increased spatial heterogeneity in

116   resources may permit the persistence of more species than in untouched old-growth forest by

117   creating more habitats and expanding available niche space (Condit et al., 2002).

118   These apparently small effects of selective logging may have long-term consequences on

119   the structure and function of the forest. The changes in forest structure and diversity that can

120   occur due to selective logging may persist through later life stages of a tree community

121   (Osazuwa-Peters et al., 2015) and affect forest structure and diversity long after selective logging

122   has taken place. More canopy gaps can alter the seedling recruitment patterns of tree species

123   (Pillay et al., 2018), facilitating the success of fast-growing pioneer species that can outcompete

124   shade-tolerant species in high-light areas (Baraloto et al., 2012). The direct and indirect changes

125   to the forest environment induced by selective logging may be particularly beneficial for lianas,

126   which often have a fast-growing, highly competitive life-history strategy. Although in old-

127   growth forest large adult lianas are often associated with large biomass trees (Koerner et al.,

128   2017)—the removal of which by selective logging may at least immediately reduce the

129   abundance of liana species that require emergent trees as hosts—canopy openings (both natural

130   and logging gaps) can promote the proliferation of lianas in tropical forests (Schnitzer et al.,

131   2004). Thus, selective logging often leads to an increase in liana abundance and changes to liana

132   assemblages over time (Addo-Fordjour et al., 2020 & 2021). This increase in lianas may delay or

133   prevent forest recovery, change the trajectory of forest succession, and reduce the carbon storage

134   potential of selectively logged forests (Durán & Gianoli, 2013).

135   Determining how selective logging shapes the structure and diversity of forests therefore

136   requires assessing not only the remaining trees, but also their seedlings and the seedlings of non-

137   tree components such as lianas, across different logging regimes of varying ages. Key ecological

138   processes that act at earlier life stages shape later forest structure and maintain plant diversity

139   (Pillay et al., 2018; Uriarte et al., 2004). Disturbance may have different impacts on different life

140   stages of woody plants (Biwolé et al., 2015) and the growth and survival of seedlings and

141   saplings is dependent on variation in light and biotic interactions that may differ in the post-

142   logging environment (Asner et al., 2004; Darrigo et al., 2018). Thus, assessing patterns in

143   understory size classes of trees and lianas can help predict the structure and function of the

144   logged forests in the future.

145   In the present study, we examine the short- to medium-term effects of selective logging

146   on woody plant diversity and structure in Gabon, the second most-forested country in the world

147   (Sannier et al. 2016). Central Africa contains the second largest contiguous moist tropical forest

148   in the world, harboring rich biodiversity and providing ecosystem services such as carbon

149   storage, rainfall generation, and buffering the effects of climate change (Sosef et al., 2017). Yet,

150   Central Africa plays a key role in the timber industry. For example, in Gabon, forests have been

151   subjected to over 100 years of selective logging, with timber exportation beginning in the 1890s

152   and continuing through the present day. Twenty years ago, Gabon contributed 23% of the timber

153   production from Central Africa (Collomb et al., 2000). By 2017, an estimated two-thirds of

154   Gabonese forests had been affected by logging (Sherif et al. 2018, Table 4, p. 27), increased

155   from c.40% in 1997 (Collomb et al., 2000, Table 1, p. 14). However, forest cover in the country

156   remains very high, at ~86% (Sannier et al. 2016). Because the majority of forests in Gabon are,

157 and will continue to be, affected by selective logging, it is critical to understand how these

158 forests may be altered by and recover following selective logging.

159   In this study, we examined the influence of selective logging on forest structure and

160 diversity of woody plant species in the Monts de Cristal region of northwestern Gabon. We

161 asked:

162   1) How does selective logging affect forest structure (canopy openness, stem density,

163   basal area, liana relative abundance) and tree diversity (species richness and evenness) a

164   year after logging compared with unlogged forest?

165   2) How do these effects vary with life stages (seedling, sapling, adult) and spatial scale?

166   3) Do changes in forest structure and diversity remain evident a decade after selective

167 logging has occurred?

168

2. Materials & Methods

170 *2.1 Study site*

171 We carried out our study in a logging concession in the Monts de Cristal region of northwestern

172 Gabon (0°42′41″ N, 10°17′18″ E) (Fig. 1A, B), adjacent to Monts de Cristal National Park. The

173 Monts de Cristal are a chain of mid-elevation hills occurring over 20,000 km^2, mainly situated

174 between 300–650 m with elevations up to 1000 m, and are covered in evergreen rain forest

175 (Sunderland et al. 2004). Average temperature is 24–26ºC (Sunderland et al. 2004). There is a

176 rainfall gradient in Gabon, with the wettest areas found in the northwest and drier conditions

177 further south and east across the country. In Monts de Cristal, annual rainfall is 2500–3000 mm

178   in the Seni sector of the park, and 2000–2500 mm in the Mbé sector of the park (Vande weghe

179   2008). There is a strong dry season during June–August and a milder dry season in December–

180   February (Vande weghe 2008).

181   The Société Equatoriale d'Exploitation Forestière (SEEF) logging concession is located

182   to the east of the Mbé sector of Monts de Cristal National Park. The SEEF concession includes

183   areas of unlogged forest and areas of selectively logged forest that vary in terms of when they

184   were logged (Fig. 1C). The concession began systematic selective logging in 2000. Logging

185   intensity in the SEEF concession is low: studies from both a decade ago (0.82 trees ha^{-2} removed,

186   Medjibe et al. 2011) and recent reports (0.99–1.6 trees ha^{-2} removed, SEEF 2019) indicate low

187   levels of timber removal. These low levels of selective logging are common across African

188   forests, compared to higher rates of logging in South America (5-6 trees per hectare) and Asia (8

189   trees per hectare) (Sist 2000). Average road density was 6.1m ha^{-1} in zones where logging had

190   occurred. The most common species is *Aucoumea klanieana* Pierre (Burseraceae), commonly

191   known as okoumé. Additionally, 51 timber species are commonly cut by the logging company

192   (Table A1), and the species cut each year vary based on client demand and availability of species

193   as noted in forest inventories prior to cutting (SEEF, 2019). Commonly logged species have

194   minimum cutting diameters of 60–90 cm diameter at 1.3 m above ground (DBH) (SEEF 2019).

195   Logging by other organizations had taken place in this area as early as 1950; however, logging

196   prior to 2000 was sparse and patchy. Previous studies within the concession have noted that there

197   are few signs of past logging, such as cut stumps, graded areas for machines, skid trails, or roads

198   (Medjibe et al. 2011). We did not observe any signs of older logging (e.g., prior to 2000) where

199   we established plots for this study.

200
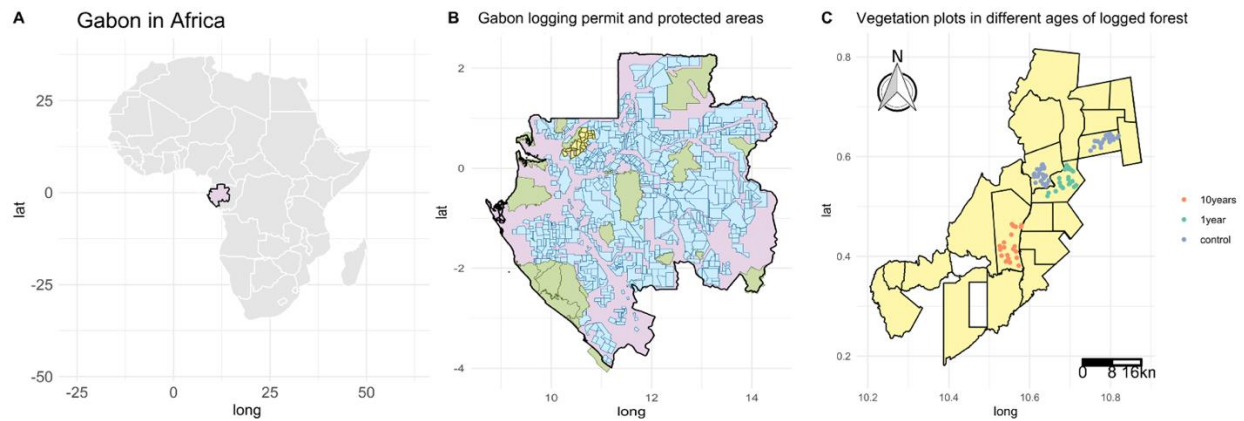
Figure 1. Maps showing the locations of (A) Gabon in Africa, (B) protected areas (in green), logging permit areas (in blue), and the logging concession where the study was conducted (in yellow) in Gabon, and (C) the location of vegetation plots in recently logged (one year since logging), older logged (ten years since logging), and unlogged (control) treatments in the study concession.

2.2 Data collection

To assess the impact of selective logging on forest structure and diversity, we established a total of 80 vegetation plots between September 2018 and October 2019 (Fig. 1C). Each plot was 400 m2 in area (20×20 m). In order to capture the heterogeneous impact that selective logging can have on the forest, we randomly located 20 plots within each of three logging treatment areas: recently logged forest that had been logged approximately one year prior, older logged forest that had been logged ten years prior, and two unlogged forest areas. We measured two separate unlogged areas in order to try and capture some of the natural spatial variation in these forests. For all analyses, we considered the two unlogged areas as a single control treatment. We generated random point sampling schemes based on boundaries of yearly logging blocks using the sp package (Pebesma & Bivand 2005, Bivand et al. 2013).

218   To sample the adult tree community, all free-standing woody stems ≥10 cm DBH were

219   tagged, measured, and identified. For species that were difficult to identify in the field, we

220   collected vouchers and deposited them at the National Herbarium (L'Herbier National du Gabon)

221   who provided determinations for as many species as possible. We also tagged and measured

222   climbing lianas ≥10 cm DBH following Gerwing et al. (2006), though we could not identify

223   many individuals due to the limitations of collecting voucher specimens for lianas where leaves

224   can only be found at the top of the canopy. To sample juvenile trees, saplings, and shrubs, we set

225   up two subplots (10×10 m) nested within each plot. Within these subplots, we tagged, measured

226   DBH, and identified all free-standing woody stems ≥1 cm and <10 cm DBH, and tagged and

227   measured climbing lianas as above. For seedlings, we tagged, measured height, and identified all

228   free-standing woody species and lianas ≥20 cm and ≤1m in height in nine 1×1m2 subplots at 9

229   points (at the four corners, center, and four middle points of each sides) within the main plot. We

230   measured canopy openness at each of the 9 seedling subplots per plot, using a Spherical Crown

231   Densiometer, Concave Model C (Forestry Suppliers, Jackson, MS, USA) (Lemmon, 1956) held

232   level 1m above the ground. Values were averaged to yield one canopy openness value for each

233   adult tree plot.

234   To check for differences among treatments in topography, we measured elevation at each

235   of the 9 seedling subplots per plot, using a Garmin GPSmap 64s device (GARMIN, Olathe, KS,

236   USA) and used the data to calculate slope and mean elevation values for each plot. Values were

237   averaged to yield one elevation value for each adult tree plot. Plots had similar slope across all

238   treatments (mean = 8 m, range = 1–26 m; Kruskal test, p = 0.16; Fig. A1B). Mean elevation was

239   similar in older logged (505m) and unlogged (503 m) forests (Dunn's test, p-adjusted = 0.194),

240   but was slightly higher in recently logged forests (531m) compared to older logged and unlogged

241   forests (Dunn's test, p-adjusted < 0.001 and 0.0001, respectively; Fig. A1A). However, there was

242   broad overlap in elevation values for all three treatments (ranges: older logged, ranges = 464–

243   585m in unlogged, 488–561m in recently logged, and 451–654m in older logged forest). To look

244   at climate differences across sites, we used worldclim data (Fick & Hijmans, 2017) to consider

245   differences in mean annual temperature and mean annual precipitation across sites (Table A2),

246   and found that differences across treatments were small.

247

248   *2.3 Analyses*

249   For each of the three size classes of woody stems (seedlings, saplings, and adults) we compared

250   forest structure and diversity across recently logged (1 year since logging), older logged (10 year

251   since logging), and unlogged forests (see below for details). For seedling and sapling analyses,

252   we pooled the subplot data for each plot. We performed all analyses in R 4.0.2 (R Core Team,

253   2020).

254

255   2.3.1 Forest structure

256   We compared differences in canopy openness, stem density, adult basal area, and liana relative

257   abundance (i.e., number of liana individuals/total number of liana and tree individuals) between

258   recently logged, older logged, and unlogged forests. For metrics that met assumptions of

259   normality and homogeneity of variance, we used ANOVA and post-hoc Tukey's Honest

260   Significant Difference test. For metrics that did not meet those assumptions, we used Kruskal–

261   Wallis H tests and post-hoc Dunn's test. Differences between treatments were considered

262   significant for values of $p < 0.05$.

263

2.3.2 Diversity

Because of the patchy nature of selective logging and the fact that increased heterogeneity may affect species diversity differently at local versus landscape scales, we calculated both plot-level diversity within treatments and also estimated total diversity at the whole treatment level.

We calculated four measures of plot-level diversity using the *vegan* package (Oksanen et al. 2020) in R: observed species richness, individual-based rarefied richness, Shannon's diversity, and Pielou's evenness index. For each diversity metric, we tested for differences among logging treatments using ANOVA and Tukey's HSD or Kruskal–Wallis and Dunn's tests, as noted above.

We estimated treatment-level diversity using the effective number of species (Hill numbers; Chao et al. 2014) separately for seedlings, saplings, and adults. Because common species are more likely to occur in samples of a community and rare species are more likely to have been missed, these diversity estimations use the sampled data to extrapolate to an estimate of the total number of species in a community (Chao et al. 2014). For communities in highly diverse systems, Hill numbers are a better representation of the true diversity than diversity indices that do not take into account sampling effort or abundance information. Additionally, Hill numbers are scalable and are in species units so they are more intuitive to consider when comparing communities (Chao et al. 2014). We used measures of Hill numbers for species richness ($q = 0$) and Simpson's diversity ($q = 2$, the inverse of Simpson concentration) (Gotelli and Chao 2013). We used Chao–Shen corrections to the Hill number indices in order to account for sampling biases due to inadequate or different sample coverage (Chao and Jost, 2012). We then used this information to plot sample-size-based rarefaction and extrapolation (R/E)

286   sampling curves using the *iNEXT* package, and calculated the 95% confidence intervals (CI)

287   using a bootstrap method. (Hsieh et al. 2016). The extrapolation extends up to a maximum

288   sample size of 1000 for seedlings, 4000 for saplings, and 1000 for adults. To assess for

289   differences in estimated diversity between logging treatments, we noted whether the R/E curves

290   overlapped.

291

292   **3.   Results**

293   *3.1 Forest structure*

294   Mean canopy openness was slightly higher in recently logged forest compared to older logged

295   and unlogged forest (9.8% vs 6.6% and 6.2%, respectively) but the differences were ==marginally==

296   ==statistically significant== (Dunn's test, p-adjusted = 0.08; Fig 1A). Compared to unlogged forests,

297   canopy openness was significantly more heterogeneous in recently logged forests (mean sd =

298   5.1, Fig 2B) than in unlogged forests (mean sd = 3.0, Dunn's test, p-adjusted = 0.03) but not than

299   older logged forest (mean sd = 3.1, Dunn's test, p-adjusted = 0.50).
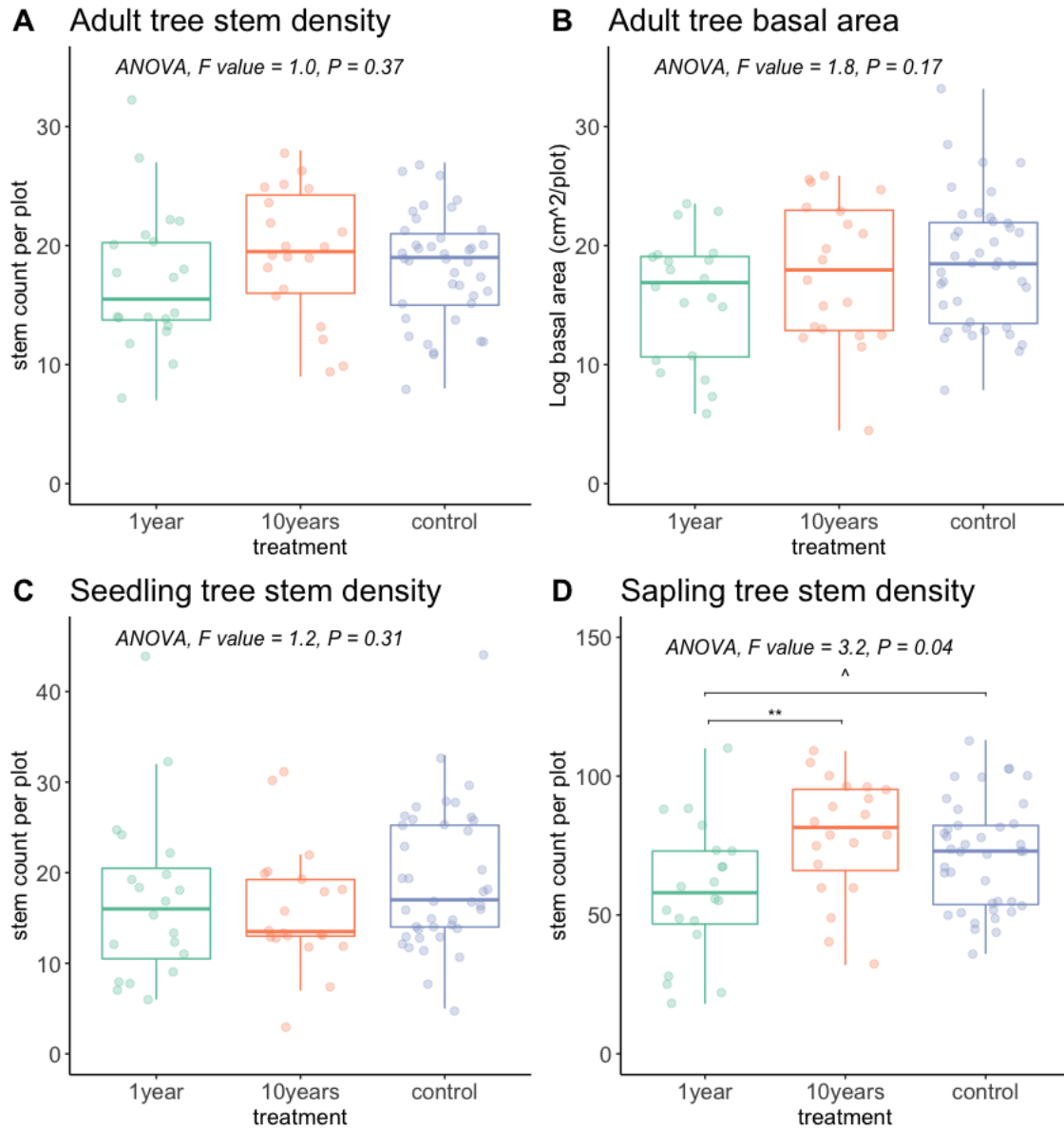
300
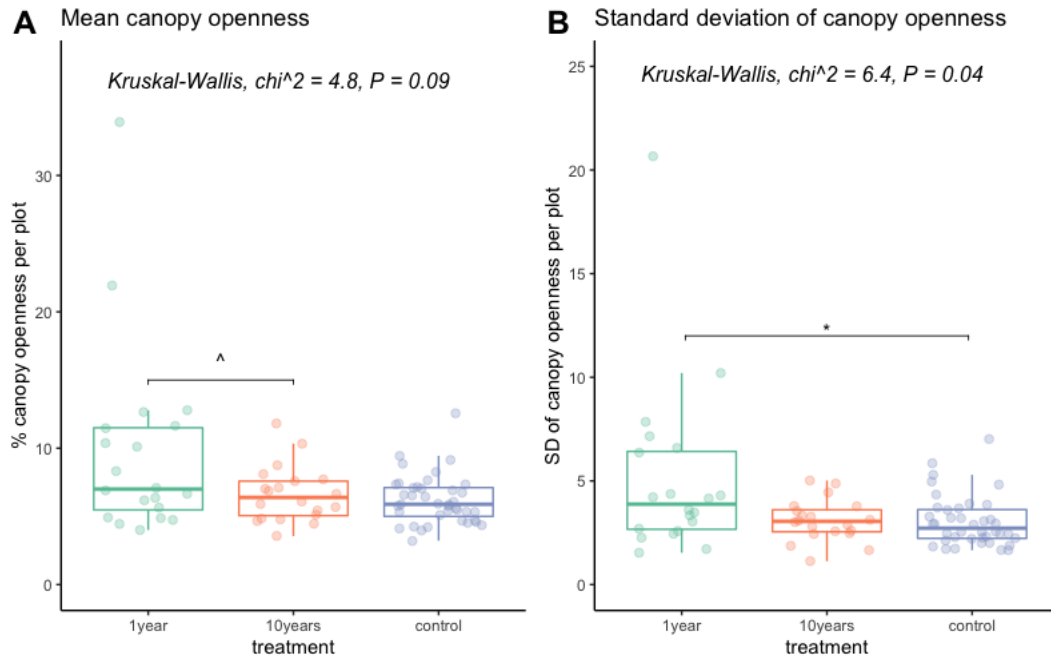
Figure 2. (A) Mean and (B) standard deviation of canopy openness values in 20×20 m forest plots in unlogged areas (blue) compared to areas logged 1 year (green) and 10 years (orange) prior to sampling in the SEEF concession, Monts de Cristal, Gabon. Boxes represent inter-quartile range (IQR), lines in the center represent the median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. Points correspond to 20×20 m forest sampling plots. ^ denotes pairwise comparisons that were marginally significant (0.05<P<0.10) and * denotes pairwise comparisons that were significant at the P<0.05 level based on Dunn's tests.

There were no differences among logging treatments in stem density or basal area of adult-sized trees (Figs. 3A and B), nor for seedling stem density (Fig. 3C). However, sapling stem density varied significantly among treatments (Fig 3D). Recently logged forests had about 13 fewer stems per plot than unlogged forests—a difference just over the 0.05 significance cutoff (Tukey HSD test, p-adjusted = 0.06); and 20 fewer sapling stems per plot than older logged forests, a significant difference (Tukey HSD test, p-adjusted < 0.01).

Figure 3: (A) Stem density for adult trees and (B) tree basal area (only measured in adults), and stem density in C) seedlings and D) saplings in 20×20 m forest forest plots in unlogged areas (blue) compared to areas logged 1 year (green) and 10 years (orange) prior to sampling in the SEEF concession, Monts de Cristal, Gabon. Boxes represent inter-quartile range (IQR), lines in the center repre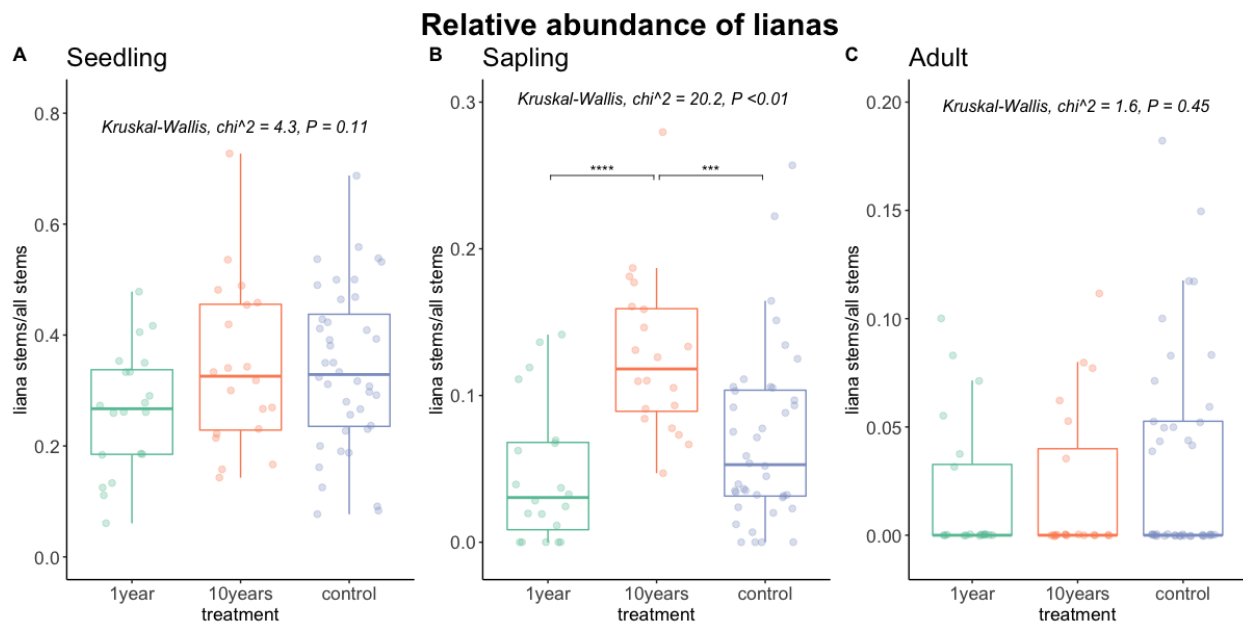sent the median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. Points correspond to 20×20 m forest sampling plots. ** denotes pairwise comparisons that were significant at the P<0.01 level and ^ denotes pairwise comparisons that were marginally significant (0.05<P<0.10) based on Tukey's HSD tests

326   The relative abundance of lianas followed a similar pattern to that of trees. Although

327   lianas were abundant at the seedling stage (often >25% of seedling-sized stems), relative

328   abundance was similar across logging treatments for the seedling and adult tree stages (Fig. 4A

329   and C). However, we saw differences in relative abundance of lianas in sapling-sized stems. In

330   older logged forests, 13% of all sapling-sized stems were lianas, as compared to recently logged

331   forests where only 5% of all sapling-sized stems were lianas (Dunn's test, p-adjusted <0.0001,

332   Fig. 4B), and unlogged forests where 7% of all sapling-sized stems were lianas. (Dunn's test, p-

333   adjusted <0.001, Fig. 4B). Patterns of raw liana abundance followed similar patterns as relative

334   liana abundance (Fig. A2).

335

336

337

338 **Figure 4:** Relative liana abundances for (A) seedlings (B) saplings and (C) adults, in 20×20 m forest forest plots in

339 unlogged areas (blue) compared to areas logged 1 year (green) and 10 years (orange) prior to sampling in the SEEF

340 concession, Monts de Cristal, Gabon. Boxes represent inter-quartile range (IQR), lines in the center represent the

341 median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times

342 IQR. Points correspond to 20×20 m forest sampling plots. *** denotes pairwise comparisons that were significant at

343 the P<0.001 level and **** denotes pairwise comparisons that were significant at the P<0.0001 level based on

344 Dunn's tests.

345

346 **3.2 Diversity**

347 *3.2.1 Plot-level diversity*

348 At the adult stage, plot-level diversity metrics did not differ significantly among logging

349 treatments. Specifically, adult plot-level mean species richness was approximately 11–12 species

350 per plot (Fig. A3C), rarified richness was approximately 5 per plot (Fig. 5C), Shannon's diversity

351 was approximately 2.3 per plot (Fig. A3F), and Pielou's evenness was approximately 0.94 per

352 plot in recently logged, older logged, and unlogged forest (Fig. 5F).

353   In contrast, at the sapling stage, we detected significant differences in diversity metrics

354 between logged and unlogged forest, but only for older logged forest. Specifically, older logged

355 forests had on average 34 sapling species per plot, approximately 11 more sapling species per

356 plot than in recently logged or unlogged forests (observed species richness, Tukey's HSD test, P

357 < 0.0001 for both recently logged and unlogged comparisons, Fig. A3B). Similarly, sapling

358 rarified richness, Shannon diversity, and Pielou's evenness were ca. 21%, 24%, and 1% higher,

359 respectively, in older logged forests compared to unlogged forests (Rarefied richness, Dunn's

360 test, p-adjusted <0.0001 Fig. 5B; Shannon's diversity Tukey's HSD test, p-adjusted < 0.01; Fig.

361 A3E; Pielou's evenness, Dunn's test, p-adjusted <0.01; Fig. 5E). Sapling rarified richness and

362 Shannon diversity were ca. 14% and 21% higher, respectively, in older logged forests compared

363 to recently logged forests (Rarefied richness, Dunn's test, p-adjusted <0.0001 Fig. 5B;

364 Shannon's diversity Tukey's HSD test, p-adjusted <0.001; Fig. A3E).

365   At the seedling stage, observed species richness and Shannon diversity did not differ

366   significantly among logging treatments (Fig. A3A, A3D), and plot-level means seedling

367   observed species richness was approximately 8–10 species per plot across treatments. We found

368   only marginal differences in seedling rarefied richness across logging treatments, with older

369   logged forests having ca. 4% higher seedling rarefied richness than unlogged forests, (Dunn's

370   test, p-adjusted = 0.09; Fig. 5A). However, Pielou's evenness was ca. 5% higher for seedlings in

371   older logger forests than in unlogged forests (Dunn's test, P-adjusted = 0.03; Fig. 5D).

372
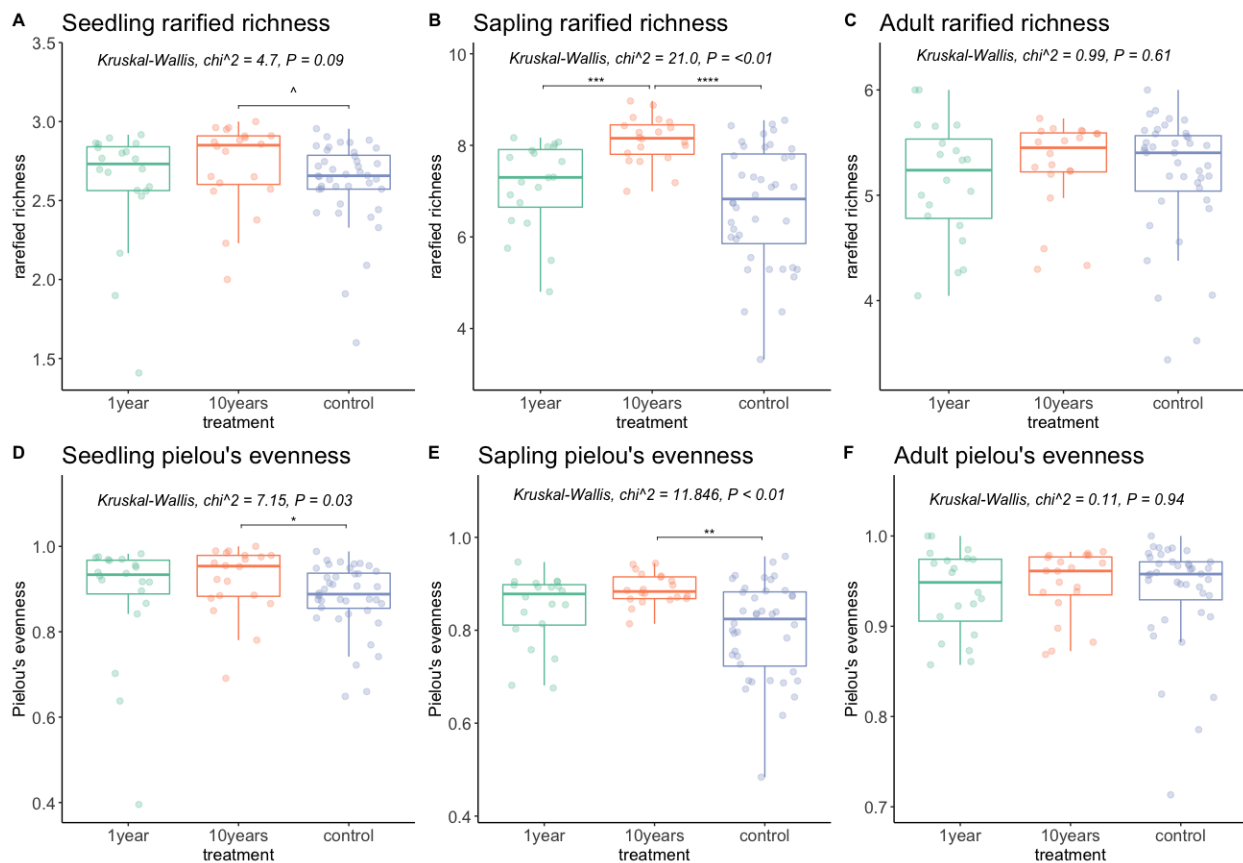
373

374

375   **Figure 5:** Rarefied species richness for (A) seedlings (B) saplings and (C) adults, and Pielou's evenness for (D)

376   seedlings (E) saplings, and (F) adults, in 20×20 m forest sampling plots in unlogged areas (blue) compared to areas

377   logged 1 year (green) and 10 years (orange) prior to sampling in the SEEF concession, Monts de Cristal, Gabon.

378   Boxes represent inter-quartile range (IQR), lines in the center represent the median. Whiskers correspond to the

379   largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. Points correspond to 20×20 m

380   forest sampling plots. ^ denotes pairwise comparisons that were marginally significant (0.05<P<0.10) based on

381   Dunn's tests. * denotes pairwise comparisons that were significant at the P<0.05 level, and ** denotes pairwise

382   comparisons that were significant at the P<0.01 *** denotes pairwise comparisons that were significant at the

383   P<0.001 level, and **** denotes pairwise comparisons that were significant at the P<0.0001 level based on Dunn's

384   tests.

385

386   *3.2.2 Treatment-level diversity estimates*

387   Similar to plot-level diversity patterns, treatment-level diversity estimates using Hill numbers

388   show that, compared to unlogged and recently logged forests, older selectively logged forests

389   had higher estimated species richness (q = 0) and estimated Simpson's diversity (q = 2) for

390   seedlings and saplings, but no difference in adult diversity between logging treatments (Fig. 6,

391   Table A3).

392
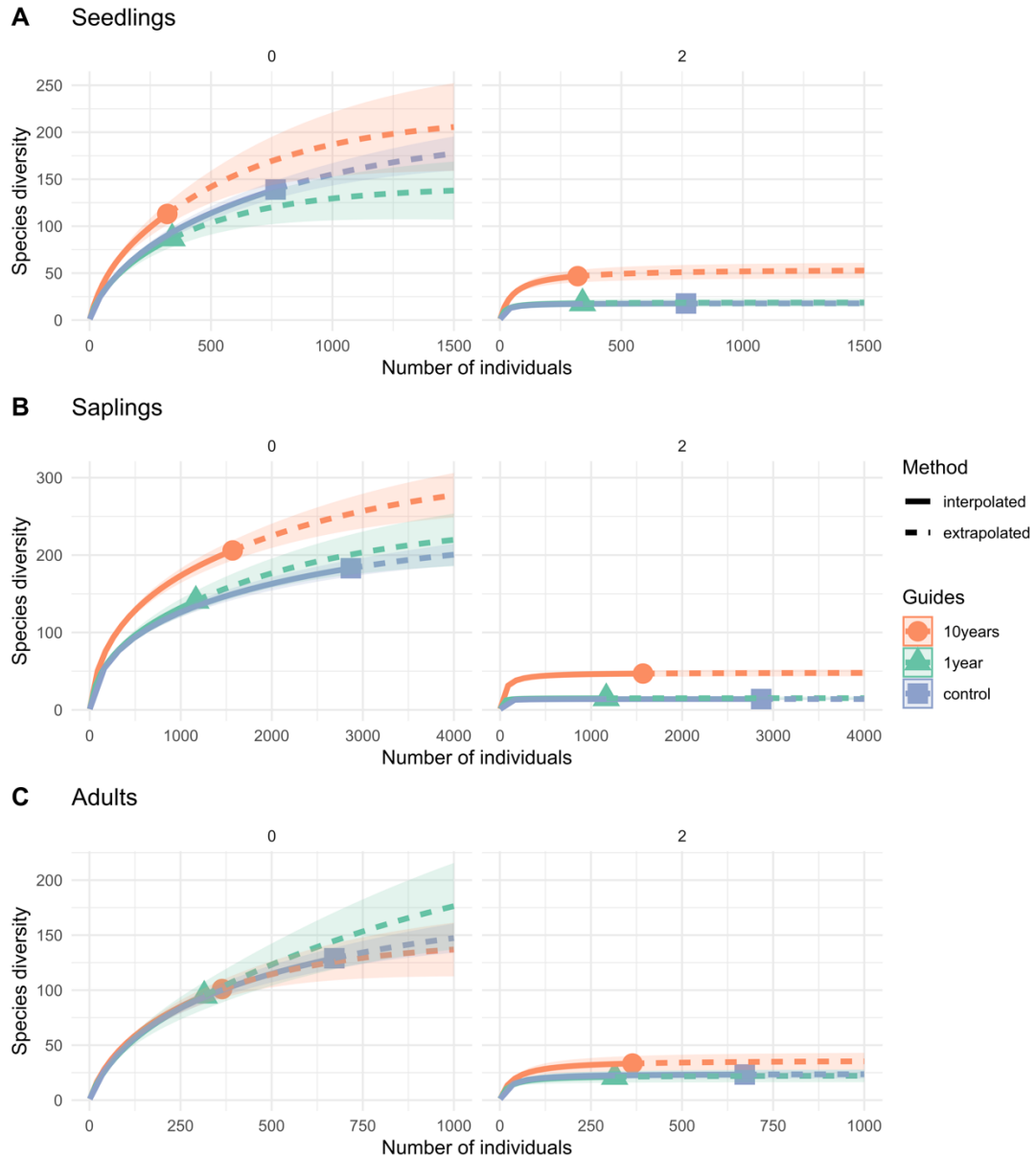
Figure 6: Sample-based rarefaction and extrapolation curves for Hill numbers for A) seedlings, B) saplings, and C) adults, of order: 0 (class richness) and 2 (dominant class richness/Simpson diversity). Solid lines represent curves based on sample data, while dashed lines represent extrapolations. Shaded areas represent the 95% confidence intervals surrounding the rarefaction/estimation curves.

4. Discussion

We assessed how selective logging affected forest structure and diversity, both across ontogenic stages (seedling, saplings, and adults) and ==across different stages of recovery== (recently logged and older logged forests). As expected, given the low intensity of selective logging, we detected no impact of logging on adult tree density or diversity. However, we did find evidence that logging altered composition and diversity in the forest understory, with effects detectable a decade after logging occurred. Most notably, we found a higher relative abundance of sapling-sized lianas in older logged forest compared to unlogged forest. We also found evidence of increased heterogeneity in understory light availability in recently logged forest, but no difference between older logged forest and unlogged forest, suggesting that the impact of logging on understory light availability is short-lived. Logging also had a small positive effect on species diversity: saplings were more diverse in older logged forests, and seedling and sapling communities in older logged forests also had higher species evenness. Whether these results persist and filter up to the adult stage over time will depend on how survival, mortality, and recruitment play out in these forests, and requires further study.

4.1 Selective logging impacts on forest structure:

4.1.1 Adult density and basal area

The low intensity of selective logging in this forest concession was reflected in the fact that adult stem density and basal area were similar across logged and unlogged areas. These results support the claim that low-intensity logging does little to affect tree basal area, and thus selective logging has the potential to foster economic development while maintaining carbon stocks in tropical forests (Gourlet-Fleury et al., 2013; Putz et al., 2012).

424   Consistent with the results for adult tree density and basal area, mean canopy openness

425   was similar in logged and unlogged forests. However, there was higher spatial variation in

426   canopy openness in recently logged forest due to the patchiness of logging effects. This

427   increased spatial heterogeneity in light seems to disappear a decade after logging, indicating a

428   rather short-term change in the forest canopy. Logging gaps can be ephemeral and recovery can

429   happen quite quickly, for example within one year (Asner et al., 2004), though higher numbers

430   of canopy gaps (after 8 years, Rangel Pinagé et al., 2019) and higher light levels (after 45 years,

431   Osazuwa-Peters et al. 2015) may persist in forests for a long time after selective logging has

432   occurred. These contradicting results may depend on logging intensity in the studied

433   concessions, pointing to the importance of characterizing the intensity, frequency, and extent of

434   selective logging using quantifiable metrics when carrying out studies on its impacts on forests.

435

436   *4.1.2 Seedling and sapling densities*

437   As with adult trees, seedling densities were similar across logged and unlogged forests in this

438   concession. In contrast, sapling density was lower in recently logged forests.

439   Logging gaps can increase light levels in the forest understory and can drive an increase

440   in seedling density, since understory plants are typically light limited in tropical forests (Chazdon

441   & Pearcy, 1991). This effect is commonly noted immediately after logging (de Carvalho et al.,

442   2017), although it may be ephemeral, with subsequent declines noted as soon as 10 months after

443   logging has occurred (Duah-Gyamfi et al., 2014). As the canopy recovers, gaps fill in, saplings

444   and lianas grow to block light, and the available light for seedlings will quickly be reduced and

445   both light levels and seedling density levels will return to be similar to pre-logging levels.

446   Because our plots were measured approximately one year after logging, it is possible that our

447   study did not capture this temporary effect.

448   In contrast to seedlings, saplings had lower stem density in recently logged forest. Direct

449   damage to saplings from logging activities, such as damage from falling timber trees, or the

450   creation of skid trails, is likely to be the driver for this change. However, this decline seems to

451   have been ephemeral, as stem density was similar between older logged and unlogged forests.

452   Other studies have noted that the understory structure of logged forests can recover quickly, in as

453   little as 6-7 years (Rangel Pinagé et al. 2019). The rapid recovery of sapling stem density in the

454   decade after logging is likely due to a release of saplings from competition with larger neighbors

455   for both light and below-ground resources (i.e., water, nutrients) (Hubbell et al., 1999). Thus,

456   damage from logging activity can decrease understory plant density in the short term, but also

457   promote subsequent rapid recovery through increased resource availability. Consistent with this

458   scenario, we saw a reduction in sapling density immediately after logging that recovered to pre-

459   logging levels in the older logged forest.

460

461   *4.1.3 Liana relative abundances*

462   Lianas are an important structural component of tropical forests, and shifts in the prevalence of

463   lianas can have consequences for forest structure, dynamics, and function (Marshall et al. 2020).

464   In our study, we found that sapling-sized lianas had higher relative abundances in the older

465   logged forest as compared to unlogged forest, but did not find any other differences in relative

466   liana abundances in the different size classes across different ages of logged forests. Lianas are

467   resilient, fast-growing woody plants that are able to thrive by growing quickly and also by

468   growing quickly in high-light environments, such as tree-fall gaps and forest edges (Barry et al.,

469   2015; Campbell et al., 2018; Schnitzer et al., 2021) and resprouting after they are damaged

470   (Schnitzer et al., 2004). A pattern of clonal stem proliferation of lianas in canopy gaps has been

471   found in other tropical forests (Schnitzer et al., 2021). Because we only see increases in sapling-

472   sized lianas but not in seedlings, this may be a clue that vegetative resprouting is a driver of

473   increased relative liana abundances in logged forests.

474   The higher relative abundance of lianas in the sapling layer of the decade-old logged

475   areas may have profound implications for this forest. Increasing prevalence of lianas may have

476   cascading effects on future forest communities. Lianas can modify the recovery trajectory of

477   logged forests—and larger lianas can also increase canopy cover and restrict understory light

478   (Schnitzer and Bongers, 2002), making it more difficult for some tree species to germinate,

479   survive, and recruit. Increasing liana abundances can also diminish the ability of forests to

480   accumulate and store carbon over time (Durán & Gianoli, 2013; Berenguer et al., 2018), as well

481   as reduce the economic value of forests by causing damage to valuable timber species (Estrada-

482   Villegas and Schnitzer, 2018), making liana densities an important factor to consider and manage

483   in order to protect forest function and value. Indeed, liana removal is a common practice in

484   Reduced Impact Logging (RIL) to deter lianas from colonizing gaps and thriving to the detriment

485   of other tree species (Estrada-Villegas and Schnitzer, 2018), particularly if it is due to vegetative

486   resprouting of damaged larger-sized lianas (e.g., Schnitzer et al. 2021). Following RIL practices

487   that incorporate liana removal from timber trees before or after cutting timber species can protect

488   future timber from damage and reduce the propensity of liana regeneration after the forest is

489   logged (Estrada-Villegas and Schnitzer, 2018; Marshall et al., 2017).

490

491   **4.2 Selective logging impacts on diversity**

492   Due to the low timber extraction rate, selective logging is unlikely to impact adult tree

493   diversity. However, logging-related changes to understory conditions (namely increased

494   patchiness of light availability and altered biotic interactions, such as neighbor competition and

495   insect herbivory) may result in changes to the diversity of seedlings and saplings. Consistent

496   with this, we found no detectable effect of selective logging on adult diversity but higher

497   seedling species evenness and higher sapling species richness and evenness in older logged

498   forest compared to unlogged forests. These results were consistent in both our plot-level analyses

499   (Fig. 5) and treatment-level analyses that estimated community-level species richness and

500   evenness separately for recently logged, older logged and unlogged forests (Fig. 6). These results

501   are in line with other studies that have found that shifts in understory species diversity and

502   evenness can occur after selective logging (Baraloto et al. 2012, De Iongh et al. 2014).

503   Selective logging can modify both the abiotic and biotic environment, which can affect

504   the success of understory species and explain the higher understory richness and evenness found

505   in older logged forests. After logging, as light heterogeneity increases, light-demanding pioneer

506   species in the understory may be more successful than the shade-tolerant later-successional

507   species that usually dominate the low-light understory environment in tropical forests (Gaui et

508   al., 2019). When timber trees are removed and the forest is disturbed by skid trails and road

509   creation, selective logging can heterogeneously change the biotic environment and reduce

510   crowding pressure from other trees. Additionally, at least one study has reported changes in

511   insect herbivory in selectively logged forests (Darrigo et al. 2018). Both of these altered biotic

512   interactions may have consequences for diversity (Uriarte et al. 2004, Forrister et al. 2019).

513   How the simultaneous effects of increased light heterogeneity and altered biotic

514   interactions will play out over time is unclear. Studying understory tree species responses to

515   these phenomena should be prioritized in future studies to better understand how mechanisms of

516   understory diversity are impacted by selective logging. It is important to understand whether

517   changes to understory diversity represent an ephemeral response to short-lived environmental

518   and biotic changes or if they will persist to shape the future adult community in logged forests.

519   With this information, we can predict what future forests will look like and make management

520   decisions about tropical forests.

521

522   Impacts on diversity were negligible or slightly positive in our study. Other studies of

523   selective logging have noted inconsistent effects of selective logging on diversity, including

524   positive, negative, and negligible effects (Gibson et al., 2011; Martin et al., 2015; Putz et al.,

525   2012). These differences are likely because of differences in specific management plans and

526   logging intensity (Putz et al., 2019), the spatial scale of the study (Berry et al., 2008), or time at

527   which diversity is assessed (Clark and Covey, 2012), or because of pre-existing differences in

528   forest type (Surendra et al. 2021). Additionally, logging may play out differently in forests with

529   different land-use histories. Studies have found that past land uses and disturbances can have

530   compound effects on plant communities (Comita et al., 2010), further complicating

531   generalizations about selective logging's impact on biodiversity. Generally, diversity is expected

532   to be reduced at higher logging intensities, smaller spatial scales, and immediately after logging

533   occurs, due to the direct impacts of damage from selective logging. However, diversity is

534   expected to be higher at lower logging intensities, larger spatial scales, and timescales further out

535   from when logging occurs, due to the indirect impacts of increased environmental heterogeneity

536   from selective logging.

537

538

4.3 Caveats and limitations

Our study used space-for-time substitution to explore how selective logging affected forests. This approach has several limitations (Damgaard, 2019). First, it assumes that space is an appropriate approximation for time and that the two different areas in different places are otherwise identical. However, there can be differences in the natural environment and land-use history that affect forest structure and diversity. We believe that our treatment areas are similar because they have similar topographic habitats, no observed signs of differing land-use history, and other studies have noted that soil type is similar across our study area (Chatelin and N'Zoghet, 1964; Gaël et al., 2021). We also tried to address this issue by sampling two unlogged control areas of unlogged forest in order to capture more of the potential natural variation across the landscape. The spatial separation of treatments was limited by the logistics of how logging is carried out; i.e. in spatially-separated yearly logging blocks that must be adhered to according to management planning specifications. Second, space-for-time substitutions use snapshots that do not capture dynamics as well as multi-census studies, because they may miss ephemeral changes over time. Observational studies of change are preferable when possible, particularly long-term studies that document the full range of changes that occur in a logged forest over time. Given that post-logging recovery trajectories play out over the course of several decades and perhaps centuries, such data are unsurprisingly rare.

The use of tree size as a proxy for life stage to determine an individual's likely contribution as adults is an approximation. Because different tree species have different life histories, not all understory trees (seedlings and saplings) will become emergent trees; some will stay as understory trees (e.g. shrub species). Another caveat is that our data on species diversity

561   suggest that we did not observe all species in the community, indicated by the fact that the

562   observed diversity curves did not level off (Fig. 6). This suggests that additional sampling may

563   be needed to capture all species for more robust treatment-level comparisons.

564

565   **5   Conclusions**

566   We found that low intensity selective logging in this evergreen tropical forest concession

567   had minor impacts on forest structure and diversity in the short term: more variable understory

568   light conditions and lower sapling density in recently logged forests suggest that logging

569   activities did cause some changes to understory conditions. While these changes themselves

570   appear to be short-lived, they likely underlie the higher understory diversity and higher relative

571   abundance of liana saplings observed in forest logged 10 years prior. These changes to the forest

572   understory may lead to long-term shifts in forest taxonomic and functional composition.

573   Increases in the prevalence of lianas, in particular, can reduce carbon storage and timber values,

574   and suggest the potential need for management strategies to prevent the 'lianification' (Perring et

575   al., 2020) of forests. Our study is the first that we know of in Gabon to simultaneously consider

576   the effects of selective logging across different life stages and ages of logged forest. Our study

577   highlights the need for long-term studies, combined with data on site-specific selective logging

578   thresholds, cutting diameters, and cutting cycle lengths, to better assess the impacts of selective

579   logging on tropical forests. Better understanding of selective logging impacts is needed to predict

580   what logged forests will look like in the future and to make management decisions that are in

581   line with goals for continued success in protecting both the ecological and economic viability of

582   the forest.

583

584 **Declaration of Competing Interest**

585 The authors declare that they have no known competing financial interests or personal

586 relationships that could have appeared to influence the work reported in this paper.

587

606

Data availability statement

608 The vegetation plot data will be archived by the authors in a digital repository upon acceptance

609 of the manuscript.

610

Common name	family	*scientific name*	minimum cutting diameter
Acajou	Meliaceae	*Khaya ivorensis*	80
Agba/Tola	Fabaceae	*Prioria balsamifera*	80
Aiele	Burseraceae	*Canarium schweinfurthii*	80
Alen/Mambode	Fabaceae	*Detarium macrocarpum*	70
Alep	Irvingiaceae	*Desbordesia glaucescens*	
Alone/Kondroti	Bombacaceae	*Bombax brevicuspe*	70
Andoung 66	Fabaceae	*Bikinia grisea*	70
Andoung Durand	Fabaceae	*Bikinia durandii*	90
Andoung Heitz	Fabaceae	*Aphanocalyx heitzii*	70
Andoung Pellegrin	Fabaceae	*Bikinia pellegrinii*	80
Andoung Testu	Fabaceae	*Bikinia letestui*	90
Azobe	Ochnaceae	*Lophira alata*	80
Bahia/Abura	Rubiaceae	*Hallea ledermannii*	60
Béli	Fabaceae	*Julbernardia pellegriniana*	70
Bilinga	Rubiaceae	*Nauclea diderrichii*	80
Bosse clair	Meliaceae	*Guarea cedrata*	60
Bosse fonce	Meliaceae	*Guarea thompsonii*	70
Dabema	Fabaceae	*Piptadeniastrum africanum*	70
Diania	Ulmaceae	*Celtis tessmannii*	70
Dibetou	Meliaceae	*Lovoa trichilioides*	70
Douka	Sapotaceae	*Tieghemella africana*	90
Doussie blanc	Fabaceae	*Afzelia pachyloba*	70
Ebiara	Fabaceae	*Berlinia bracteosa*	70
Ebiara minkoul	Fabaceae	*Berlinia confusa*	60
Ekop	Fabaceae	*Tetraberliniatubmanian T.bifoliolata*	70
Ekoune	Myristicaceae	*Coelocaryon preussii*	60
Faro (grandes feuilles)	Fabaceae	*Daniellia klainei*	70
Igaganga	Burseraceae	*Dacroydes igaganga*	60
Ilomba	Myristicaceae	*Pycnanthus angolensis*	70
Iroko	Moraceae	*Milicia excelsa*	80
Izombe	Ochnaceae	*Testulea gabonensis*	70
Kevazingo	Fabaceae	*Guibourtia tessmannii*	90
Limbali	Fabaceae	*Gilbertiodendron dewevrei*	70
Longhi abam/rouge	Sapotaceae	*Gambeya lacourtianum*	70
Longhi mbebame/blanc	Sapotaceae	*Gambeya africanum*	70

Moabi	Sapotaceae	*Baillonella toxisperma*	90
Movingui	Fabaceae	*Distemonanthus benthamianus*	70
Niové	Myristicaceae	*Staudtia kamerunensis*	60
Oboto	Clusiaceae	*Mammea africana*	70
Okan	Fabaceae	*Cylicodiscus gabunensis*	90
Okoumé	Burseraceae	*Aucoumea klaineana*	70
Olon	Rutaceae	*Zanthoxylum heitzii*	60
Ossabel	Burseraceae	*Dacroydes normandii*	60
Ovengkol	Fabaceae	*Guibourtia ehie*	70
Ozigo	Burseraceae	*Dacroydes buettneri*	70
Padouk	Fabaceae	*Pterocarpus soyauxii*	80
Pau Rosa	Fabaceae	*Bobgunnia fistuloides*	60
Tali	Fabaceae	*Erythrophleum ivorense/suaveolens*	70
Tchitola	Fabaceae	*Prioria oxyphylla*	70
Tiama blanc	Meliaceae	*Entandrophragma angolense*	80
Tiama noir	Meliaceae	*Entandrophragma congoense*	80

612   **Table A1:** List of timber species with minimum cutting diameters
613
614

|	*10years*	*1year*	*before*	*control*
Precipitation mean (mm)	1059.0	1068.1	1066.0	1080.0
Precipitation SD (mm)	0	5.1289	0	0
Temperature mean (degrees C)	28.100	28.385	28.4	28.3
Temperature SD (degrees C)	0	0.0366	0	0

615   **Table A2:** Mean and standard deviation values of climate variables (mean annual temperature and mean
616   annual precipitation) across treatments (data: worldclim, Fick & Hijmans 2017)
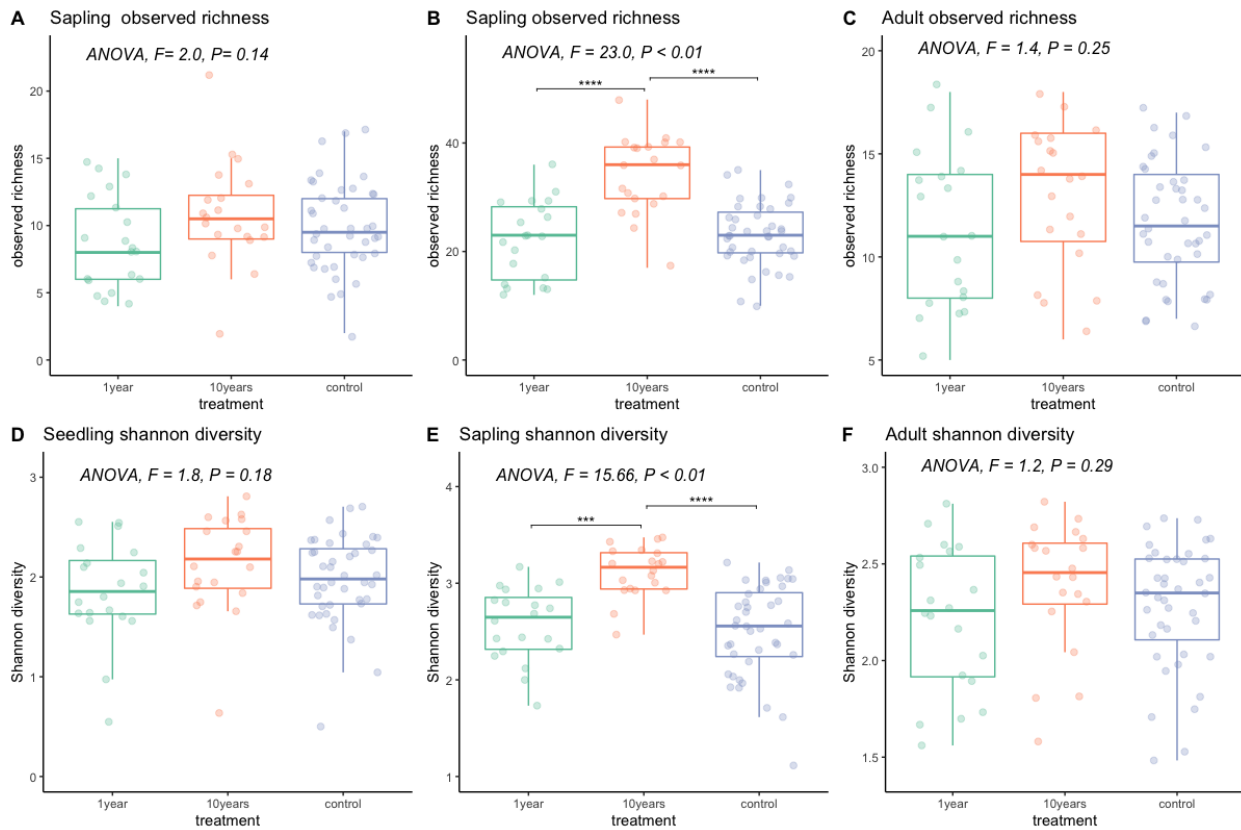617
618
619
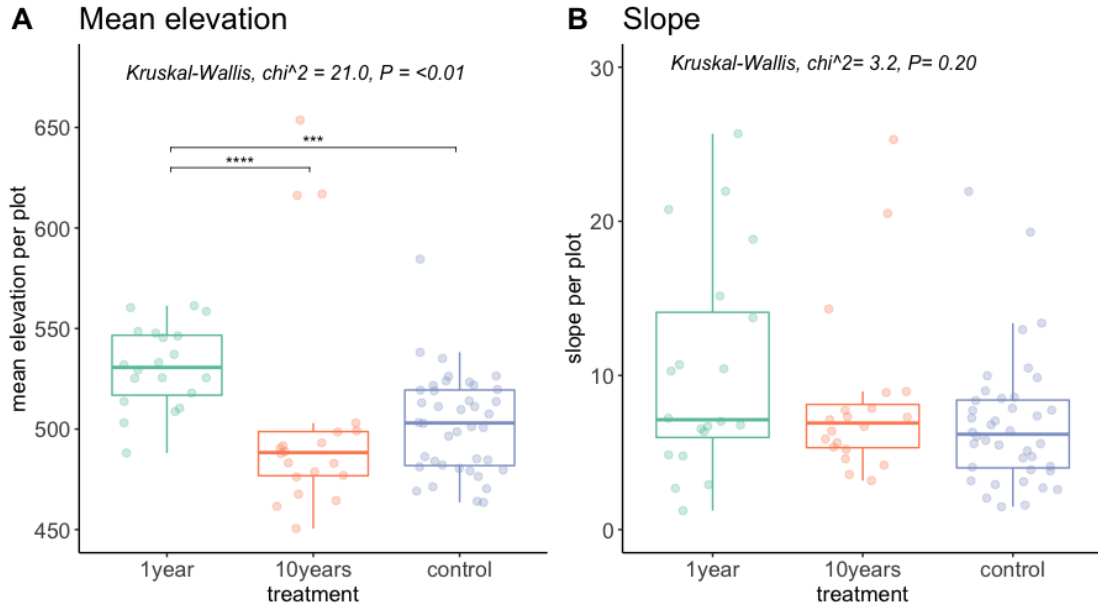
620
621
622 **Figure A1** (A) Mean elevation and (B) slope for in 20×20 m forest plots in unlogged areas (blue)
623 compared to areas logged 1 year (green) and 10 years (orange) prior to sampling in the SEEF concession, Monts de
624 Cristal, Gabon. Boxes represent inter-quartile range (IQR), lines in the center represent the median. Whiskers
625 correspond to the largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. Points
626 correspond to 20×20 m forest ampling plots. *** denotes pairwise comparisons that were significant at the P<0.001
627 level, and **** denotes pairwise comparisons that were significant at the P<0.0001 level based on Dunn's tests.
628
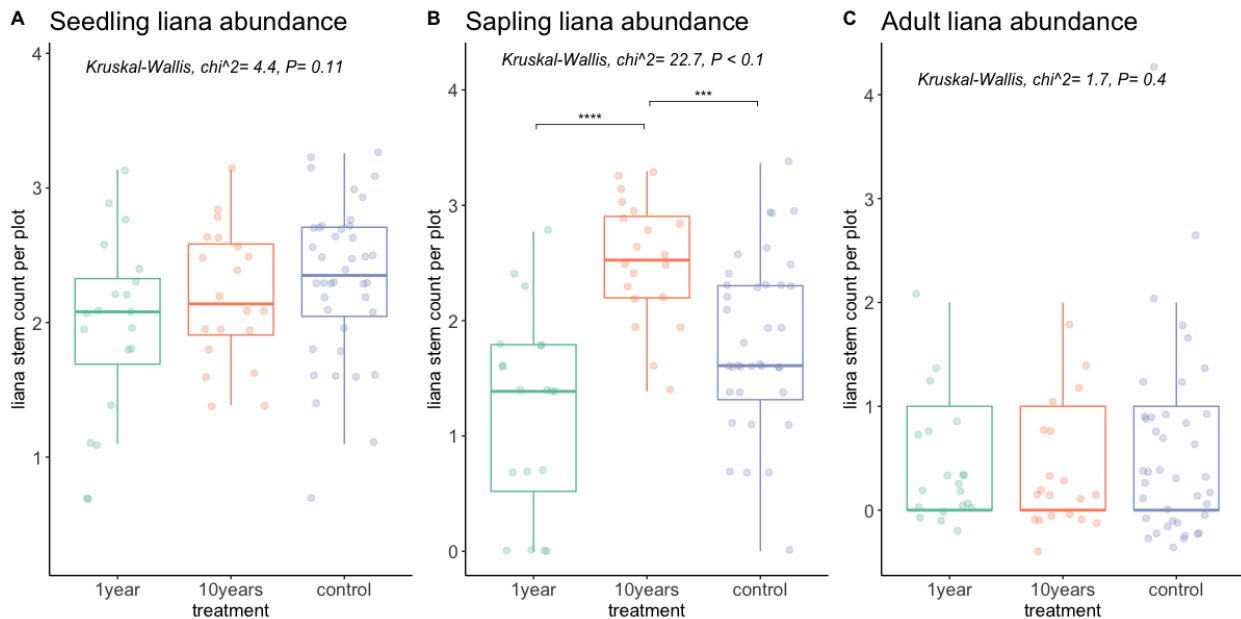
629
630
631 **Figure A2** Absolute liana abundances for (A) seedlings (B) saplings and (C) adults, in 20×20 m forest
632 plots in unlogged areas (blue) compared to areas logged 1 year (green) and 10 years (orange) prior to sampling in
633 the SEEF concession, Monts de Cristal, Gabon. Boxes represent inter-quartile range (IQR), lines in the center
634 represent the median. Whiskers correspond to the largest/smallest value less/greater than upper/lower quartile minus
635 1.5 times IQR. Points correspond to 20×20 m forest sampling plots. *** denotes pairwise comparisons that were

636 significant at the P<0.001 level, and **** denotes pairwise comparisons that were significant at the P<0.0001 level
637 based on Dunn's tests.

638
639
640
641 **Figure A3** Observed species richness for (A) seedlings (B) saplings and (C) adults, and Shannon diversity for (D)
642 seedlings (E) saplings, and (F) adults, in 20×20 m forest plots in unlogged areas (blue) compared to areas logged 1
643 year (green) and 10 years (orange) prior to sampling in the SEEF concession, Monts de Cristal, Gabon. Boxes
644 represent inter-quartile range (IQR), lines in the center represent the median. Whiskers correspond to the
645 largest/smallest value less/greater than upper/lower quartile minus 1.5 times IQR. Points correspond to 20×20 m
646 forest sampling plots. *** denotes pairwise comparisons that were significant at the P<0.001 level, and ****
647 denotes pairwise comparisons that were significant at the P<0.0001 level based on Tukey's HSD tests.

648
649
650   A) Seedlings

Site	Index	Observed Richness	Estimated Asymptote	Estimated s.e.	95% lower confidence interval	95% Upper confidence interval
10years	Species richness	113	218.551	38.777	165.553	324.998
1year	Species richness	87	141.963	23.054	111.969	207.986
control	Species richness	139	203.071	21.79	172.501	261.538
10years	Shannon diversity	72.297	103.007	7.739	87.839*	118.175*
1year	Shannon diversity	37.486	47.059	3.959	39.3	54.818
control	Shannon diversity	44.033	51.047	2.966	45.234	56.86
10years	Simpson diversity	46.758	54.588	5.973	46.758*	66.295*
1year	Simpson diversity	17.867	18.803	1.919	17.867	22.563

control	Simpson diversity	17.649	18.042	1.372	17.649	20.731

B) Saplings

Site	Index	Observed Richness	Estimated Asymptote	Estimated s.e.	95% lower confidence interval	95% Upper confidence interval
10years	Species richness	206	312.895	33.638	264.533	401.216
1year	Species richness	141	244.272	37.352	192.944	346.322
control	Species richness	183	231.773	17.278	207.861	278.686
10years	Shannon diversity	84.141	93.617	2.989	87.759*	99.476*
1year	Shannon diversity	38.647	43.105	2.469	38.647	47.944
control	Shannon diversity	38.573	40.332	1.285	38.573	42.85
10years	Simpson diversity	46.917	48.331	2.442	46.917*	53.117*
1year	Simpson diversity	15.003	15.186	1.06	15.003	17.263
control	Simpson diversity	13.978	14.042	0.552	13.978	15.123

C) Adults

Site	Index	Observed Richness	Estimated Asymptote	Estimated s.e.	95% lower confidence interval	95% Upper confidence interval
10years	Species richness	101	144.903	17.748	121.48	195.115
1year	Species richness	95	250.56	68.342	163.283	449.393
control	Species richness	129	175.011	17.525	151.365	223.657
10years	Shannon diversity	57.062	71.249	4.68	62.076	80.422
1year	Shannon diversity	45.314	64.809	6.985	51.119	78.5
control	Shannon diversity	54.234	62.693	3.617	55.604	69.782
10years	Simpson diversity	33.307	36.561	3.88	33.307*	44.166*
1year	Simpson diversity	21.17	22.624	2.923	21.17	28.352
control	Simpson diversity	23.316	24.118	2.476	23.316	28.972

Table A: Summary of species diversity estimates for (A) seedlings, (B) saplings, and (C) adults. * = CI does not overlap with other CIs of the same index.

References

Addo-Fordjour, P., Boakye, E.K., Rahmad, Z.B., 2021. Logging and topographic effects on tree community structure and habitat associations in a tropical upland evergreen forest, Ghana. J. For. Res. 32, 1361–1372.

Addo-Fordjour, Patrick, 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.

Asner, G.P., Keller, M., Silva, J.N.M., 2004. Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. Glob. Change Biol. 10, 765–783.

Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R. and Emerson, R., 2009. A contemporary asessment of change in humid tropical forests. Conservation Biology, 23(6), pp.1386-1395.

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.

Barry, K.E., Schnitzer, S.A., Breugel, M. van, Hall, J.S., 2015. Rapid liana colonization along a secondary forest chronosequence. Biotropica 47, 672–680.

Berenguer, E., Gardner, T.A., Ferreira, J., Aragão, L.E.O.C., Nally, R.M., Thomson, J.R., Vieira, I.C.G., Barlow, J., 2018. Seeing the woods through the saplings: Using wood density to assess the recovery of human-modified Amazonian forests. J. Ecol. 106, 2190–2203.

Berry, N.J., Phillips, O.L., Ong, R.C., Hamer, K.C., 2008. Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. Landsc. Ecol. 23(8), 915-929.

Biwolé, A. B., Morin-Rivat, J., Fayolle, A., Bitondo, D., Dedry, L., Dainou, K., Hardy, O.J. and Doucet, J. L. 2015. New data on the recent history of the littoral forests of southern Cameroon: an insight into the role of historical human disturbances on the current forest composition. Plant Ecol. Evol., 148(1), 19-28.

Campbell, M.J., Edwards, W., Magrach, A., Alamgir, M., Porolak, G., Mohandass, D., Laurance, W.F., 2018. Edge disturbance drives liana abundance increase and alteration of liana–host tree interactions in tropical forest fragments. Ecol. Evol. 8, 4237–4251.

Chao, A., and Jost, L. Coverage- based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93(12), 2533-2547.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr., 84(1), 45-67.

Chatelin, Y., N'Zoghet, C., 1964. Les sols des massifs cristallins ou cristallophylliens des Monts de Cristal, des Monts de N'Djolé et du chaînon de Lambaréné - Chinchoua. IRD, In : Delhumeau Michel. Etudes pédologiques dans les régions traversées par le projet de voie ferrée Owendo. Office de la Recherce Scientifique et Technique, Mission du Gabon, Service Pedologique. 23.

Chazdon R.L. and Pearcy R.W. 1991. The importance of sunflecks for forest understory plants. BioScience. 41:760–766.

Clark, J.A., Covey, K.R., 2012. Species richness and the logging of natural forests: A meta-analysis. For. Ecol. Manag. 276, 146–153.

Collomb, J.G., Mikissa, J.B., Minnemeyer, S., Mundunga, S., Nzao Nzao, H., Madouma, J., Mapaga J., Mikolo, C., Rabenkogo, N., Akagah, S., Bayani-Ngoye, E., and Mofouma, A. 2000. A first look at logging in Gabon. Report: Global Forest Watch (WRI). ISBN 1-56973-423-2. URL: http://pdf.wri.org/gfw_gabon.pdf

Comita, L.S., Thompson, J., Uriarte, M., Jonckheere, I., Canham, C.D., Zimmerman, J.K., 2010. Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. Ecol. Appl. 20, 1270–1284.

Condit, R., Pitman, N., Jr, E.G.L., Villa, G., Muller-landau, H.C., Losos, E., Hubbell, S.P., 2002. Beta-diversity in tropical forest. Trees. 295, 666–670.

Damgaard, C., 2019. A critique of the space-for-time substitution practice in community ecology. Trends Ecol. Evol. 34, 416–421.

Darrigo, M.R., dos Santos, F.A.M., Venticinque, E.M., 2018. The confounding effects of logging on tree seedling growth and herbivory in Central Amazon. Biotropica. 50, 60–68.

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.

De Iongh, H. H., Kustiawan, W., & De Snoo, G. R. 2014. Structure, composition and diversity of plant communities in FSC-certified, selectively logged forests of different ages compared to primary rain forest. Biodivers. Cons., 23(10), 2445-2472.

Duah-Gyamfi, A., 2014. Natural regeneration dynamics of tree seedlings on skid trails and tree gaps following selective logging in a tropical moist semi-deciduous forest in Ghana. Open J. For., 4(1), 49.

Durán, S. M., & Gianoli, E. 2013. Carbon stocks in tropical forests decrease with liana density. Biol. Lett., 9(4), 20130301.

Edwards, D. P., Gilroy, J. J., Woodcock, P., Edwards, F. A., Larsen, T. H., Andrews, D. J., Derhé, M.A., Docherty, T.D., Hsu, W.W., Mitchell, S.L., Ota, T., Williams, L.J., Laurance, W.F., Hamer, K.C., and Wilcove, D. S. 2014. Land- sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. Glob. Chang Biol., 20(1), 183-191.

Estrada-Villegas, S., Schnitzer, S.A., 2018. A comprehensive synthesis of liana removal experiments in tropical forests. Biotropica 50, 729–739.

Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302-4315.

Forrister, D.L., Endara, M.-J., Younkin, G.C., Coley, P.D., Kursar, T.A., 2019. Herbivores as drivers of negative density dependence in tropical forest saplings. Science. 363, 1213–1216.

Gaël, M.O.R., Neil-Yohan, M., Alexis, N., Jeremy, S., Davi-Lin, M.E., Guirema, A.M., Aubin, O.J., Eric, R., Michel, M.M., 2021. Carbon and nitrogen stocks under various land cover in Gabon. Geoderma Reg. 25, e00363.

Gaui, T.D., Costa, F.R.C., Coelho de Souza, F., Amaral, M.R.M., de Carvalho, D.C., Reis, F.Q., Higuchi, N., 2019. Long-term effect of selective logging on floristic composition: A 25 year experiment in the Brazilian Amazon. For. Ecol. Manag. 440, 258–266.

Gerwing, J. J., Schnitzer, S. A., Burnham, R. J., Bongers, F., Chave, J., DeWalt, S. J., Ewango, C.E., Foster, R., Kenfack, D., Martínez- Ramos, M., Parren, M., Parthasarathy, N.,

748   Pérez-Salicrup, D.R., Putz, F.E., and Thomas, D. W. 2006. A standard protocol for liana
749   censuses. Biotropica. 38(2), 256-261.
750 Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T. A., Barlow, J., Peres, C. A.,
751   Bradshaw, C.J., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are
752   irreplaceable for sustaining tropical biodiversity. Nature. 478, 378–381.
753 Gotelli, N. J., & Chao, A. 2013. Measuring and estimating species richness, species diversity,
754   and biotic similarity from sampling data. Pages 195–211. Encyclopedia of biodiversity.
755   Second edition. Elsevier Ltd. 2nd Edition, Academic Press, Waltham, MA.
756 Gourlet-Fleury, S., Mortier, F., Fayolle, A., Baya, F., Ouédraogo, D., Bénédet, F., Picard, N.,
757   2013. Tropical forest recovery from logging: a 24 year silvicultural experiment from
758   Central Africa. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 368, 20120302.
759   https://doi.org/10.1098/rstb.2012.0302
760 Hsieh, T. C., Ma, K. H., and Chao, A. 2020 iNEXT: iNterpolation and EXTrapolation for species
761   diversity. R package version 2.0.20 URL:http://chao.stat.nthu.edu.tw/wordpress/software-
762   download/.
763 Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J.,
764   Lao, S.L. de, 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a
765   neotropical forest. Science. 283, 554–557.
766 Koerner, S.E., Poulsen, J.R., Blanchard, E.J., Okouyi, J., Clark, C.J., 2017. Vertebrate
767   community composition and diversity declines along a defaunation gradient radiating
768   from rural villages in Gabon. J. Appl. Ecol. 54, 805–814.
769 Laurance, W., Edwards, D., 2014. Saving logged tropical forests. Front. Ecol. Environ. 12,
770   147–147.
771 Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2,
772   314–320.
773 Lewis, S. L., Edwards, D. P., & Galbraith, D. 2015. Increasing human dominance of tropical
774   forests. Science. 349(6250), 827-832.
775 Marshall, A. R., Platts, P. J., Chazdon, R. L., Seki, H., Campbell, M. J., Phillips, O. L., Gereau,
776   R.E., Marchant, R., Liang, J., Herbohn, J., Malhi, Y., and Pfeifer, M. 2020.
777   Conceptualising the global forest response to liana proliferation. Front. for. glob.
778   change., 3, 35.
779 Martin, P.A., Newton, A.C., Pfeifer, M., Khoo, M., Bullock, J.M., 2015. Impacts of tropical
780   selective logging on carbon storage and tree species richness: A meta-analysis. For. Ecol.
781   Manag. 356, 224–233.
782 Medjibe, V.P., Putz, F.E., Starkey, M.P., Ndouna, A.A., Memiaghe, H.R., 2011. Forest Ecology
783   and Management Impacts of selective logging on above-ground forest biomass in the
784   Monts de Cristal in Gabon. For. Ecol. Manag. 262, 1799–1806.
785 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R.,
786   O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H.
787   (2020). vegan: Community Ecology Package. Rpackage version 2.5-7.
788   URL:https://CRAN.R-project.org/package=vegan
789 Okuda, T., Yamada, T., Hosaka, T., Miyasaku, N., Hashim, M., Lau, A.M.S., Saw, L.G., 2019.
790   Canopy height recovery after selective logging in a lowland tropical rain forest. For.
791   Ecol. Manag. 442, 117–123.
792 Osazuwa-Peters, O.L., Chapman, C.A., Zanne, A.E., 2015. Selective logging: does the imprint
793   remain on tree structure and composition after 45 years? Conserv. Physiol. 3, cov012.

Perring, M.P., De Frenne, P., Hertzog, L.R., Blondeel, H., Depauw, L., Maes, S.L., Wasof, S., Verbeeck, H., Verheyen, K., Baeten, L. and Bernhardt-Römermann, M., 2021. "Lianification" or liana invasion–is there a difference?. Front. Ecol. Environ. 19(7), 377-378.

Petrokofsky, G., Sist, P., Blanc, L., Doucet, J.-L., Finegan, B., Gourlet-Fleury, S., Healey, J.R., Livoreil, B., Nasi, R., Peña-Claros, M., Putz, F.E., Zhou, W., 2015. Comparative effectiveness of silvicultural interventions for increasing timber production and sustaining conservation values in natural tropical production forests. A systematic review protocol. Environ. Evid. 4, 8.

Pillay, R., Hua, F., Loiselle, B.A., Bernard, H., Fletcher, R.J., 2018. Multiple stages of tree seedling recruitment are altered in tropical forests degraded by selective logging. Ecol. Evol. 8, 8231–8242.

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, 30.

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. and Palmer, J. 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. Cons. Lett. 5(4), 296-303.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rangel Pinagé, E., Keller, M., Duffy, P., Longo, M., dos-Santos, M., Morton, D., 2019. Long-Term Impacts of Selective Logging on Amazon Forest Dynamics from Multi-Temporal Airborne LiDAR. Remote Sens. 11, 709.

Sannier, C., McRoberts, R.E., Fichet, L-V., 2016. Suitability of Global Forest Change data to report forest cover estimates at national level in Gabon. Remote Sens. Environ. 173, 326–338.

Schnitzer, S.A., DeFilippis, D.M., Visser, M., Estrada-Villegas, S., Rivera-Camaña, R., Bernal, B., Peréz, S., Valdéz, A., Valdéz, S., Aguilar, A., Dalling, J.W., Broadbent, E.N., Almeyda Zambrano, A.M., Hubbell, S.P., Garcia-Leon, M., 2021. Local canopy disturbance as an explanation for long-term increases in liana abundance. Ecol. Lett. 2021 Sept 18.

Schnitzer, S.A., Parren, M.P.E., Bongers, F., 2004. Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. For. Ecol. Manag., Community Ecology and Management of Lianas 190, 87–98.

SEEF. 2019. Bilan d'Exploitation AAC 2018 (5,398 ha) UFG2 – UFA2 NZAMALIGUE. https://opentimberportal.org/operators/100123.

Senior, R. A., Hill, J. K., Benedick, S., & Edwards, D. P. 2018. Tropical forests are thermally buffered despite intensive selective logging. Global Change Biology, 24(3), 1267-1278.

Sherif, K.F., Dore, O., Ochieng, C. 2018. Rapport Stratégique Regional - Développement intégré et durable de la filière bois dans le Bassin du Congo. Groupe de la Banque Africaine de developpment. URL:https://www.afdb.org/en/documents/document/rapport-strategique-regional-developpement-integre-et-durable-de-la-filiere-bois-dans-le-bassin-du-congo-109428

Sosef, M.S.M., Dauby, G., Blach-Overgaard, A., van der Burgt, X., Catarino, L., Damen, T., Deblauwe, V., Dessein, S., Dransfield, J., Droissart, V., Duarte, M.C., Engledow, H.,

840   Fadeur, G., Figueira, R., Gereau, R.E., Hardy, O.J., Harris, D.J., de Heij, J., Janssens, S.,
841   Klomberg, Y., Ley, A.C., Mackinder, B.A., Meerts, P., van de Poel, J.L., Sonké, B.,
842   Stévart, T., Stoffelen, P., Svenning, J.-C., Sepulchre, P., Zaiss, R., Wieringa, J.J.,
843   Couvreur, T.L.P., 2017. Exploring the floristic diversity of tropical Africa. BMC Biol.
844   15, 15.
845 Sunderland, T., Walters, G.M., Issembe, Y. 2004. A preliminary vegetation assessment of the
846   Mbé National Park, Monts de Cristal, Gabon. Central African Regional Program for the
847   Environment (CARPE). DOI: 10.13140/2.1.2193.6321
848 Uriarte, M., Condit, R., Canham, C. D., & Hubbell, S. P. 2004. A spatially explicit model of
849   sapling growth in a tropical forest: does the identity of neighbours matter?. J.
850   Ecol., 92(2), 348-360.
851 Vande weghe, Jean Pierre. 2008. Monts de Cristal: les Parcs nationaux du Gabon. Wildlife
852   Conservation Society (WCS). ISBN: 0982026315.
853
854

Declaration of interests

☒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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRediT author statement

Megan K. Sullivan: conceptualization, methodology, investigation, analysis, writing – original draft, visualization, **Prince Armel Mouguiama Biessiemou**: investigation, **Raoul Niangadouma**: investigation, **Katharine Abernethy**: supervision, writing- review & editing, **Simon A. Queenborough**: supervision, writing- review & editing, **Liza Comita**: supervision, writing- review & editing.