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Concomitant effects of multiple disturbances (logging, fire, biological invasion) on native tree abundances into West Africa's semi-deciduous forests

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ABSTRACT

West African semi-deciduous forests face multiple disturbances directly linked to human activities. A major unknown is the concomitant effects that these disturbances might have on forest communities. We (i) studied the long-term (>30 years) response of 17,038 trees from 207 semi-deciduous forest species to the three disturbances (fire, logging and biological invasion) in a 100-ha experimental set-up, (ii) examined the links between species-specific responses and functional traits related to resource acquisition and to defense strategies, and (iii) listed species vulnerable to local disturbances, in relation to their global vulnerabilities. Our results show that all three disturbances are those with a conservative resource strategy and which invest little in defensive strategies. We found that species that are locally vulnerable to fire are also globally highly threatened species. In the context of West Africa's almost extinct forests, we propose (i) the conservation of the last remaining deciduous forests in West Africa, knowing that opening them to logging simultaneously increases the risk of fire, (ii) the use of native species in reforestation programs to limit the risk of biological invasions, and (iii) the implementation of fire control strategies in conservation and forest restoration policies.

1. Introduction

West African forests are very diverse (Liang et al., 2022; Sabatini et al., 2022), in line with the North-South climatic gradient, and they are ranked among the 25 global biodiversity hotspots (Myers et al., 2000). Unfortunately, this biodiversity is already severely degraded by increasing demands for natural resources and agricultural products in direct relation to high population growth and general increases in living standards (Brandt et al., 2017). The direct consequence is a widespread overexploitation of semi-deciduous forests (Elogne et al., 2023; FAO, 2020). As a result, the deforestation level in West Africa has been estimated at about 83 %, including state-classified forests under protected status (Aleman et al., 2017). An analysis of the main causes of

deforestation highlighted, in descending importance, the expansion of agro-industrial agriculture (coffee, cocoa, oil palm), industrial wood exploitation and charcoal production, infrastructure expansion, mining, and the spread of bushfires (Ouattara et al., 2021; Kouassi et al., 2021). Beyond deforestation *per se*, semi-deciduous forests have historically suffered, and still suffer, numerous degradations directly linked to human activities such as (i) logging, (ii) bushfires and (iii) biological invasions.

Logging began in the 19th century in West Africa. The presence of large volumes of wood seemed inexhaustible to forestry officials and encouraged loggers to exploit the forests excessively. Since the 1980s, the harvesting rules, based on criteria of intensity and frequency of cutting, set by the governments have not allowed for the sustainable

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replenishment of commercial timber stocks, despite the fact that the selective logging of a few individuals per hectare is commonly implemented for the commercial production of timber (Doua-Bi et al., 2021). During selective logging, the removal of individuals preferentially targets tree species with interesting technological properties such as relatively high wood density (Nam et al., 2018). Therefore, selective logging generates changes in the floristic composition of the residual community. A direct consequence of logging trees is the punctual opening of the canopy, which increases the amount of light in the logging gaps, allows colonization by fast-growing pioneer species, a prerequisite for a slower reconstitution of late-successional species (Hérault et al., 2010). Functional trait approach makes it possible to anticipate the response of species to disturbance, with overall, opportunistic species (low density of tissues: wood, leaves and/or roots) that will preferentially colonize the exploitation gap initially, even if, under certain conditions, the bank of young seedlings and saplings of exploited late-successional species can avoid this phase (Mirabel et al., 2021; Mirabel et al., 2020).

Bushfires are a key factor in landscape dynamics in West Africa (Kouassi et al., 2022). Well used and controlled bushfires can be considered as a management tool for agriculture resources (Mbow, 2000). However, in West Africa, uncontrolled fires cause significant damage to both the structure and functioning of the residual forest ecosystems (Swaine, 1992). Why are the West African semi-deciduous forests in particular so prone to fire? Their relatively abundant litter in the understory related to seasonal deciduousness, the duration and intensity of the dry season, and a relatively abundant herbaceous layer are all key factors (Swaine, 1992). After fire, mortality rates of young trees in the understory can vary between 70 and 100 %, even in forests where fire is not so intense (Cochrane and Schulze, 1999). Few young trees are therefore resistant to fire, although the resistance of mature, established trees may be higher and related to certain functional traits. Among the latter, bark and leaf thickness allow, to some extent, to predict the response of bushfire species (Parsons et al., 2015). Tree bark thickness maximizes chances of survival in the face of fire by maximizing cambium protection (Lawes et al., 2012). Leaf thickness also plays a role with thin-leaved species favoring rapid fires consuming a large amount of fuel while ex situ experiments have demonstrated that the least flammable species will have thick, broad leaves (Parsons et al., 2015) even if other thermal and chemical properties may play a role in leaf flammability (Guerrero et al., 2021). The post-disturbance trajectory of forest communities is therefore highly dependent on the structure and functional composition of the assemblage of species that have resisted disturbance (Hérault and Piponiot, 2018).

Biological invasions in West Africa are mainly related to the development of plantations of exotic species for forestry (Bempah et al., 2021). Several exotic species (*Tectona grandis, Gmelina arborea, Cedrela odorata, etc.*) are thus the subject of reforestation programs, and this is at the expense of an investment in native species (Hérault et al., 2020). Due to the absence of competitors and natural predators that could regulate their populations (Forey et al., 2021), exotic species have a direct and negative impact on native species richness and diversity, floristic composition and ecosystem structure and functioning (Pýsek et al., 2012). In the semi-deciduous zone of West Africa, it is fairly well documented that *Cedrela odorata* is a serious threat to the local diversity of forest communities without a clear understanding yet of which native species, and their functional characteristics, are adversely affected (Van der Meersch et al., 2020).

Logging, bushfires and biological invasions constitute, *per se*, three serious disturbances for the residual semi-deciduous forests of West Africa. A major unknown, however, is the concomitant effects that these disturbances might have on forest communities. Multiple disturbances such as logging, fire, and biological invasions can affect the ability of tropical forest trees to recover more than each disturbance alone in several ways. First, when multiple disturbances occur in a short period, they can deplete the resources available to tropical forest trees, making it harder for them to recover (Gunderson, 2000). For instance, logging

can reduce the availability of nutrients in the soil, while fires can destroy the organic matter and reduce water-holding capacity (Certini, 2005). This depletion of resources can limit the growth and recovery of trees and other plant species, making them more vulnerable to subsequent disturbances. Second, multiple disturbances can lead to increased competition between species for limited resources, such as nutrients, water, and light (Violle et al., 2010). For example, after a forest fire, invasive plant species may colonize the area and compete with native tree species for resources, making it harder for the trees to recover (Knelman et al., 2017). Third, some disturbances, such as logging or fire, can physically damage trees, making them more vulnerable to other disturbances (Nepstad et al., 1999). For example, selective logging induce damage on unlogged trees (broken branches, bark removal) that leave those unlogged trees with wounds that can become entry points for pests and diseases, which can further damage the trees and reduce their ability to recover (Pinard and Putz, 1996).

Moreover, ecological systems are complex and the interactions between multiple disturbances can be difficult to predict. For example, considering that the two main consequences of logging are (i) the production of high necromass and (ii) the opening of the stand, it is conceivable that logging both (i) catalyzes the flammability of logged areas (Cochrane and Schulze, 1999) and (ii) facilitates the invasion of exotic species (Veldman et al., 2009).

For this work, we benefited from a unique experiment in semideciduous West Africa, i.e. 100 ha (25 plots of 4 ha) of forest plots established in 1977 that have undergone selective logging (1978), bushfire (1983) and the emergence of an invasive species (1992). This system offers a unique opportunity to evaluate, in the long term and simultaneously, the relative effects of these three disturbances within the same forest stand. The general aim of this study is to investigate the consequences of multiple concomitant disturbances (logging, fire, biological invasion) on native tree abundances, functional characteristics and species vulnerabilities of a West Africa's semi-deciduous forest. Specifically, we ask the following questions: (i) What are the relative effects of past disturbances on general forest community descriptors (forest density, biomass and biodiversity)? (ii) How diverse are the species demographic responses to different disturbances? (iii) Are the specific demographic responses related to the functional characteristics of the species, captured along two major functional axes, *i.e.*, defense strategy and resource acquisition strategy? (iv) Which species are most vulnerable to the three disturbances, and are these local vulnerabilities related to their overall IUCN vulnerability?

2. Materials and methods

2.1. Study Site

The study was conducted in the Téné state-classified forest (between 5°17'32" to 5°29'21"W and between 6°30'51" to 6°31'56"N), a 29,700 ha forest located in the semi-deciduous zone of West Africa, more precisely in the central-western part of Côte d'Ivoire (Oumé department). Semideciduous forest is a type of forest ecosystem characterized by a mix of deciduous and evergreen tree species. In a semi-deciduous forest, some of the tree species shed their leaves during the dry season. Usually, semi-deciduous forests are found between 1200 and 1600 mm of annual rainfall. The Téné classified forest receives an average of 1300 mm of annual rainfall and the average annual temperature is 26 °C (Yedmel et al., 2010). The climate is subequatorial marked by 4 main seasons including 2 dry seasons (December-February, July-August) and 2 rainy seasons (March-June, September-November). The soils are ferralitic (more or less desaturated) or hydromorphic with pseudogley minerals (Bertault, 1992). Within the Téné forest, a permanent experiment of 400 ha was created in 1977 to study the response of the natural forest to logging disturbance (Fig. 1a). The 400 ha (2000 m \times 2000 m) were gridded by trails spaced 400 m apart, delimiting 25 units of 16 ha (400 m \times 400 m) each. In each unit, 4 permanent subplots of 1 ha were



Fig. 1. (a) Location of the study area and of *Cedrela odorata* plantations in the Téné forest (b) Design of the study area, with the mapped soils, the area burned in 1983 and the buffer zones (Van der Meersch et al., 2020).

installed in the center and surrounded by a 100 m wide buffer zone (Fig. 1b).

2.2. Disturbances

Several disturbances have occurred in the experiment over time. Initially, the site was designed to test (in 1978) different logging modalities. Five years after these tests, fire passed over the site (in 1983) and opened up the forest considerably, and this was followed by the arrival (in 1992) of *Cedrela odorata* from the surrounding industrial plantations (Fig. 1a).

2.2.1. Logging

Selective logging took place in 1978 on 15 of the 25 units, with 10 units acting as controls. To quantify the intensity of this selective logging, we used the percentage of basal area that was lost after logging per subplot, hereafter *logging*. This percentage was calculated from forest inventories that were conducted before and after selective logging and varies from 0 % (control subplots) to 43 % (intensively logged subplots).

2.2.2. Fire

The year 1983 was a year of historic drought in Côte d'Ivoire. Large area of forest were burned during several days (Bertault, 1992). Following the fire, field teams were deployed to accurately map the burned and intact areas (Fig. 1b). Mapping of burnt areas was carried out in the field, using the map of large trees already available since 1978. From this mapping, the percentages of area burned by the fire, hereafter *fire*, were calculated, using a geographic information system, in each subplot.

2.2.3. Invasion

Cedrela odorata is a generalist South American species, known to be very invasive outside of its native range. *Cedrela odorata* grows on well-drained soils and can withstand rainfall conditions down to 1000 mm/yr (Paredes-Villanueva et al., 2016). Since 1964, several tests of *Cedrela odorata* performance, from various geographic provenances, have been carried out in Côte d'Ivoire (Dupuy, 1998). Between 1972 and 1990, it was planted near the study site (Fig. 1a) during the reforestation campaigns in the area. Today it is the most important invasive species in the area, accounting for 8 to 46 % of the tree stem density in the forest

subplots (Van der Meersch et al., 2020). We used the subplot density of *Cedrela odorata* to quantify the level of biological invasion experienced by the ecosystem.

2.3. Vegetation data

2.3.1. Tree census

On each of the 100 subplots, all individuals with a diameter at breast height >10 cm were numbered and identified to species. A total of 100 ha were thus inventoried in 2019 that represents 17,038 individuals surveyed and distributed in 207 different native species. In addition to this inventory of native species, we recorded 4434 *Cedrela odorata* trees or about 20 % of the native community. The density of the native tree species in our study area follows a gradient of abundance ranking from species very abundant such as *Triplochiton scleroxylon* (>10 tree.ha⁻¹) to very rare species such as *Cynometra megalophylla* (<0.1 tree.ha⁻¹).

2.3.2. Community descriptors

We estimated three community descriptors X_p (without including *Cedrela* individuals in the calculations):

- *NT_p*, the total stem abundance per ha was calculated by summing all the species abundances in a given subplot *p*.
- *AGB_p*, the aboveground biomass of a given subplot *p* estimated using the BIOMASS package (Réjou-Méchain et al., 2017) with the general equation (without tree height data).
- *SD_p*, the Hill number of the Shannon diversity of a given subplot *p* estimated using the entropart package (Marcon and Hérault, 2015) with bias correction.

2.3.3. Functional traits

For the 48 most abundant local species (83 % of the total stem density), we measured *in the field* four functional traits related to the resource acquisition and defense strategy:

- The resource acquisition strategy (Baraloto et al., 2010a, 2010b) has been estimated using tissue density as a proxy, with a dense tissue reflecting a conservative resource strategy (a low risk of mortality, slow-growth approach that focuses on maximizing the efficiency of resource use) and a light tissue reflecting an opportunistic strategy (a high risk of mortality, fast-growth approach that prioritizes maximizing resource acquisition and investment in the short term). We measured two traits related to leaf tissue density (LMA *i.e.* Leaf Mass per Area in g.m⁻²) and root tissue density (RML *i.e.* Root Mass per unit Length in g.m⁻¹). To the two tissue measured density traits, we added a third one, namely wood density, which is taken from the BIOMASS package database (Réjou-Méchain et al., 2017).
- For the defense strategy, we measured two traits, leaf tissue thickness (LT *i.e.* Leaf Thickness in mm) and bark thickness (BT *i.e.* Bark Thickness in mm). Tissue thickness is a good proxy of defense strategy for plants because thicker tissues protect much better, can physically impede herbivores and pathogens, making it more difficult for them to penetrate and access the valuable resources inside the plant (Kursar and Coley, 2003).

For the field-measured traits, three measurements, according to standard protocols (Pérez-Harguindeguy et al., 2013) were performed on 3 different adult (Diameter at Breast Height > 20 cm) individuals per species, *i.e.* a total of 9 values per species which were averaged and are available on request in the TRY database (DatasetID 546, https://www.try-db.org, Kattge et al., 2020).

2.3.4. IUCN vulnerability categories

For all species inventoried, we queried the IUCN database and classified each species into one of the two main IUCN categories: Threatened and Lower Risk (https://www.iucnredlist.org/). We used the two primary IUCN categories because the numbers of species per secondary category were not sufficient to perform a statistical analysis.

2.4. Data analysis strategy

2.4.1. Community responses

To estimate the relative effect of the three studied past disturbances on common community descriptors X_p , we parameterized a lognormal model (*logN*) that is well adapted to variables defined on R⁺ (Elogne et al., 2023; Van der Meersch et al., 2020).

$$X_p \sim logN(log(\beta_0^X + \beta_1^X) Logging_p + \beta_2^X).Fire_p + \beta_3^X).Invasion_p + \beta_4^X.Soil_p), \sigma^2)$$

with X_p representing the three community descriptors (NT_p , AGB_p or SD_p), β_1 the community response to *Logging*, β_2 the community response to *Fire*, β_3 the community response to *Invasion*, β_4 the control of the soil variability (as the percentage of hydromorphic soils in a given subplot p was highly variable (Fig. 1b), this percentage was used as a covariate to take this variability into account) and σ the dispersion parameter.

2.4.2. Species responses

To estimate the long-term effect of different disturbances on current species abundance, we parameterized a Poisson model that is well adapted to counting variables.

$$N_{sp,p} \sim P(\lambda_{sp,p})$$

where $N_{sp,p}$ is the density of species which describes the abundance level (stem.ha⁻¹) of species *sp* in sub-plot *p*, $\lambda_{sp,p}$ is the parameter of the Poisson model. To study species responses to the three disturbances, we expressed Poisson's lambda as a linear exponential combination of the covariants of interest. The exponential was convenient because lambda is defined over R+ and mathematically cannot take negative values. All covariates were normalized, allowing comparison of the relative response of species between disturbances. In addition, we added the proportion of hydromorphic soils as an explanatory variable to account for this spatial heterogeneity (Fig. 1b) and two random effects, species and subplot, were included in the model to account for these sampling dependencies. The model was written in Stan in a Bayesian framework and inferred using an adapted form of the Monte Carlo Hamiltonian sampler (Carpenter et al., 2017).

 $\lambda_{sp,p} = e^{\left(\vartheta_{1,sp}.Logging_p + \vartheta_{2,sp}.Fire_p + \vartheta_{3,sp}.Invasion_p + \vartheta_{4,sp}.Soil_p + \vartheta_{5,sp} + \vartheta_{6,p}\right)}$

with $\theta_{1,sp}$ the species specific response to *Logging*, $\theta_{2,sp}$ the species specific response to *Fire*, $\theta_{3,sp}$ the species specific response to *Invasion*. The other parameters $\theta_{4,sp}$, $\theta_{5,sp}$ and $\theta_{6,p}$ referred, respectively, to the soil, species and subplot random effects that were nested into normal laws centered on 0 in order to take into account the statistical dependencies due to the design of the experiment. To quantify the importance of the subplot random effect (which is a purely experimental design effect), we compared the goodness of fit (R^2) of the models with (conditional R^2) and without (marginal R^2) the subplot random effect.

2.4.3. Functional responses

Relationships between specific responses and functional characteristics of species were explored using Spearman's correlation coefficients and along two functional axes of interest: defense and resource acquisition strategies.

2.4.4. Species vulnerabilities

To estimate the overall vulnerability of the species to the three disturbances, we had a three step approach:

- We tested the correlation between the specific responses to the different disturbances in pairs using the Spearman correlation coefficient.
- We computed an indicator of local vulnerability to disturbance by species by summing the three specific responses θ_{1.sp}, θ_{2.sp} and θ_{3.sp}.
- We used the non-parametric Wilcoxon test (the choice of the Wilcoxon test is due to the semi-quantitative nature of the global vulnerability variable) to explore the relationships between the specific responses, the local vulnerability and the global vulnerability, the later estimated by the two IUCN primary categories (Threatened and Lower Risk).

3. Results

On the 100 ha inventoried, 17,038 individuals trees from 207 species were inventoried. The abundance of *Cedrela* did not show a direct and clear link, at plot level, with the intensity of fire and logging (Fig. 2).

3.1. Community responses

The total stem abundance *NT* ranged from 82 to 471 trees.ha⁻¹, the aboveground biomass *AGB* ranged from 22 to 510 Mg.ha⁻¹ and the Hill number of the Shannon Diversity *SD* ranged from 2.49 to 57.71 equivalent species. Overall, the effect of the three disturbances on the community descriptors is weak with 2 significant effects out of 9 studied responses (Table 1). These significant effects concern only fire, which caused a decrease in biomass and number of stems, but not on diversity. Invasion tended (not significantly) to have a positive effect on all three community descriptors meaning that the abundance, biomass and diversity of native trees slightly increased with the abundance of *Cedrela odorata*. Finally, it is notable that diversity was not affected significantly by any of the three disturbances studied.

3.2. Species responses

The range of specific responses of the 207 species to disturbances is very wide (the values for the 10 most abundant species are reported in Table 2) and includes, for each of the 3 disturbances, a minor but noteworthy proportion of positive responses. Overall, the distribution of all responses is rather negative (Fig. 3), meaning that abundances of most species are lower in areas of high disturbance. In detail, 55 %, 61 % and 64 % of the species have, respectively, a negative response to logging, fire and invasion. Furthermore, if we consider the most impactful disturbance (*i.e.* the one with the highest θ value) for each species, then we can note that logging is the most impactful for 35.8 % of species, invasion for 33.8 % and fire for 30.4 %.

Regarding the subplot random effects, conditional (0.52) and marginal (0.46) R^2 are very close together indicating that the purely spatial variation in species abundance is of secondary importance.

3.3. Functional responses

Regarding resource acquisition traits, 7 of the 9 relationships explored show negative trends (Fig. 4). Among these 7, 3 are significantly negative (Fig. 4a, d, f), namely the relationships between wood density (WD) and response to logging and fire, and between LMA and response to fire. Therefore, with the exception of invasion, the denser a species' tissues, *i.e.* with a conservative strategy, the more it is disadvantaged by disturbances.

Regarding defense traits, all the relationships explored show positive trends (Fig. 5). Among these, 3 are significantly positive (Fig. 5a, b, f), namely the relationships between leaf thickness and response to logging, and between bark thickness and response to logging and invasion. Therefore, with the exception of fire, the thicker a species' tissues, *i.e.* with a defensive strategy, the more it is advantaged by disturbances.



Fig. 2. Abundances of Cedrela odorata (stems.ha⁻¹) against logging intensity (% of basal area removed) and fire intensity (% of plot area burned).

Table 1

Model parameter values for the response of community descriptors (stand density *NT*, above- ground biomass *AGB*, diversity *SD*) to the three disturbances studied (1-Logging, 2-Fire, 3-Invasion). The median and percentiles (5*th*, 95*th*) of the *a posteriori* distribution of parameters are reported. Distributions significantly different from zero are shown in bold.

Parameters	Median	5th	95 <i>th</i>	
Stem abundance				
β_1^{NT}	-0.33	-15.16	14.74	
β_2^{NT}	-22.66	-38.04	-7.35	
β_3^{NT}	5.76	-7.34	19.98	
Aboveground biomass				
β_1^{AGB}	0.45	-13.62	14.61	
β_2^{AGB}	-28.16	-41.90	-13.99	
β_3^{AGB}	2.45	-8.26	14.39	
Shannon diversiy				
β_1^{SD}	-0.53	-3.22	2.09	
β_2^{SD}	-1.92	-4.59	0.78	
β_3^{SD}	0.56	-1.72	3.06	

3.4. Species vulnerabilities

The correlation matrix between the responses of the different species to the three disturbances shows that these responses are almost uncorrelated (Fig. 6). However, there is a positive, albeit weak, link (R = 0.108) between the response to logging and the response to fire. This link means that the species that are most vulnerable to logging are also those that may be the most vulnerable to fire.

A total local vulnerability index was calculated by summing the species responses to the 3 disturbances. Out of the 207 species inventoried, 147 were assessed by IUCN. These 147 species are divided into 127 Lower Risk and 20 Threatened species. Of these, 14 showed a vulnerability index below 0 and are listed in Table 3. These 14 species include 4 trees of the Meliaceae family that are species of great commercial interest: 3 species from the same genus *Entandrophragma utile* (Sipo), *Entandrophragma cylindricum* (Aboudikro) and *Entandrophragma angolense* (Tiama) as well as 1 African Mahogany species *Khaya anthoteca* (Acajou blanc).

The locally-estimated total vulnerability did not differ between the globally threatened and least concern species, (Fig. 7). However, the local vulnerability to fire and logging differed between the globally threatened and least concern species. In detail, IUCN threatened species are also the most vulnerable to fire in our study, while these same species are the least vulnerable to logging (Fig. 7).

4. Discussion

This study benefits from a unique experiment where the effects of the three most important current disturbances (logging, fire, biological invasion) was tested simultaneously on a West African forest. Moreover, the large size of the stand (100 ha of monitoring) allowed us to estimate the response of a very large number of species (207). Coupled with *in situ*



Fig. 3. Comparative boxplot of the distribution of the 207 species responses (namely $\theta_{1,sp}$ $\theta_{2,sp}$ $\theta_{3,sp}$) to the three studied disturbances (namely 1-Logging, 2-Fire, 3-Invasion).

Table 2

List of 10 most abundances species (genus, species botanical family) with their abundance per hectare (Density) and responses to three studied disturbances (namely 1-Logging, 2-Fire, 3-Invasion).

Genus	Species	Family	Density	1-Logging	2-Fire	3-Invasion
Triplochiton	scleroxylon	Malvaceae	10.76	0.05	-0.03	-0.01
Mansonia	altissima	Malvaceae	10.74	0.05	0.15	-0.22
Trichilia	prieuriana	Meliaceae	10.69	0.05	-0.32	0.05
Nesogordonia	papaverifera	Malvaceae	10.49	-0.20	-0.03	-0.20
Ceiba	pentandra	Malvaceae	10.06	0.03	0.13	0.11
Ricinodendron	heudelotii	Euphorbiaceae	9.44	0.10	0.11	-0.09
Celtis	mildbraedii	Cannabaceae	8.60	-0.13	-0.15	-0.25
Sterculia	rhinopetala	Malvaceae	6.16	-0.12	-0.16	-0.21
Тгета	orientalis	Cannabaceae	5.52	0.73	0.08	-1.18
Celtis	zenkeri	Cannabaceae	5.23	-0.25	-0.16	-0.03



Fig. 4. Resource Acquisition Strategy Relationships between the species responses (namely $\theta_{1,sp}$, $\theta_{2,sp}$, $\theta_{3,sp}$, Y axis square-root scaled) to three studied disturbances (namely 1-Logging, 2-Fire, 3-Invasion) and the species tissue densities (X-axis, WD wood density in g.cm⁻³, Root Mass per unit Length in g.m⁻¹, LMA leaf mass per area in g.m⁻²). Black points are species values and red lines, the overlaid linear regression (confidence intervals in gray) for vizualisation (Spearman correlation coefficient and significance on the top right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

measurements of functional traits for 48 of the most abundant species, we were able to highlight the links between specific responses to disturbances and resource acquisition and defense strategies.

4.1. Community responses

Among the three disturbance studied, fire only had a strong negative effect on the aboveground biomass (AGB) and tree density (NT). It is relatively well known that fire in logged forests have consequences that can last several decades before the ecosystem can recover in terms of forest structure (Berenguer et al., 2014; Maurent et al., 2023). Fire most certainly consumed the dead organic matter from logging residues and any associated nutrients, which is known to constrain tree recruitment and growth, resulting in a long-term reduction in biomass (Durigan et al., 2017). Therefore, Bertault's results showing that, in 1988, fire significantly reduced tree density are still evident 35 years later (Bertault, 1992). Why is the effect of logging not more visible (see for instance, Hiltner et al., 2018, Piponiot et al., 2016) at the community level? One hypothesis is that selective logging, by definition, targets the largest or most mature trees, leaving younger or smaller trees to develop and replace the harvested individuals in the medium term. However, it should be noted that since harvesting has considerably increased light in the understory, this replacement favors pioneer, lightwooded species that are often very competitive, to the detriment of other latesuccessional species (Hérault et al., 2010). Finally, it is surprising that we saw no effect of the three disturbances studied on Shannon diversity.

It is entirely possible that the diversity measured on the scale of our sample is too aggregated to see the effects of disturbance (Baraloto et al., 2012, 2010a). In other words, if the species impacted by the disturbance are offset by other species favored by the disturbance, then the effect on diversity will be zero (Mirabel et al., 2021; Mirabel et al., 2020). It therefore seems essential to analyze each species individually to determine whether, despite the apparent lack of response on diversity, more complex specific responses have occurred.

4.2. Species responses

The impacts of each of the three disturbances studied are still noticeable on current species abundances. However, the general picture is that more recent disturbances had a greater overall effect on abundance, so 55 %, 61 % and 64 % of the species are negatively affected by logging (1978), fire (1983) and biological invasion (post-1992) respectively. Knowing that African forest ecosystems have co-evolved with multiple disturbances for a long time (Aleman et al., 2017), one could ask whether fire and then biological invasion by *Cedrela odorata*, two disturbances that occurred after logging, would have diminished, erased, or blurred the link between logging intensity and species abundances. Our results show that this is not the case and overall our results confirm those obtained in Central Africa, also obtained in the long term (Osazuwa-Peters et al., 2015a, 2015b).

With regard to logging, the very selective choice of (i) first category commercial species with excellent industrial qualities during the



Fig. 5. Defense Strategy - Relationships between the species responses (namely $\theta_{1,sp} \theta_{2,sp} \theta_{3,sp}$, Y axis square-root scaled) to three studied disturbances (namely 1-Logging, 2-Fire, 3-Invasion) and the species tissue thickness (X-axis, LT leaf thickness in mm, BT bark thickness in mm). Black points are species values and red lines, the overlaid linear regression (confidence intervals in gray) for visualization (Spearman correlation coefficients and significance on the bottom right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

intervention and (ii) the largest trees is probably at the origin of this long-term signal, which means, on the other hand, that these commercial species have not yet had sufficient time to recover their pre-logging numbers and this may be why, when we look at the most impactful disturbance per species, logging came out on top. These results are also consistent with the findings of long-term studies in Uganda where regeneration rates of commercial trees remain low even 20 years after logging (Plumptre, 1996).

With respect to fire, it should first be noted that it is widely acknowledged that the consequences of fire are highly dependent on the intensity and duration over which the forest burns (Leonard et al., 2014). At Téné, the mechanism of fire spread in 1983 is known: arrival through buffer zones and then spread from dry biomass accumulated during logging. The fire remained in situ for a long period of 3 to 4 days (Bertault, 1992). We do know that, in semi-deciduous West African forests, intense fires strongly modified the tree community structure with mortality the highest for the small regenerating trees that contain the future large trees (Yedmel et al., 2010). This slow down the forest recovery that can also be linked to the rapid recolonization of burned areas by Marantaceae and Zingiberaceae grasses (Swaine, 1992). The only ecological strategy that could benefit in the medium term from intense fire would be long-lived pioneers (Yedmel et al., 2010), which explains why some species such as Ceiba pentandra or Ricinodendron africanum have a positive response.

The invasion of *Cedrela odorata* remains a relatively recent disturbance compared to the other two disturbances studied. Today, this

species represents 20 % of the floristic composition of the study site and has a negative effect on the abundance of trees that affect the most species. Well-studied in Ghana, *Cedrela odorata* invasion influences nutrient cycling and alters soil functioning through nutrient-rich leaf production in ways that facilitate its invasion (Anning et al., 2017). Beyond its particularly strong competitive power, its high growth rate also allows it to out-compete other slower-growing species (Erskine et al., 2005).

Our results show that these semi-deciduous forest ecosystems in West Africa retain a long-term memory of the disturbances experienced. It is difficult to anticipate a return, in the even longer term, and a complete reconstitution of the initial properties of the ecosystem.

4.3. Functional responses

Overall, the values of the functional traits give a valuable insight into the responses of the 48 species to logging (3 correlated traits), fire (2 traits) and invasion (1 trait).

Regarding resource acquisition strategy traits, the striking signal is that responses to disturbance increase through tissue density decreasing. The classic hypothesis that species with high timber, leaf, and root densities are disadvantaged after disturbance in favor of species with low tissue densities (Hérault et al., 2010) is validated. In fact, these low tissue densities characterize fast-growing pioneer species (Hérault et al., 2011) that are most able to take advantage of new opportunities for resource availability (light, water, nutrients) caused by the combined impacts of logging and fire. These species have the ability to deploy an opportunistic resource acquisition strategy that allows them to rapidly colonize openings and redensify the disturbed ecosystem (Flores et al., 2014; Hogan et al., 2018). Examples include Ricinodendron heudelotii, Carica papaya or Ceiba pentendra, which are well known to thrive after fire (Swaine, 1992). On the other hand, disadvantaged species (with high tissue density) correspond more to understory species, with slow growth, e.g. Diospyros ferrea. These species require a lot of time and shade for their development and a slow growth necessary to produce dense tissues (Mirabel et al., 2018). Finally, these resource acquisition traits did not predict the species responses to invasion by Cedrela odorata. This seems logical because this disturbance is very different from the other two in that it does not alter, directly and immediately, resource availability and thus it makes sense that the resource acquisition traits are not related to species response to Cedrela odorata invasion.

Regarding defense traits, the striking signal is that responses to disturbance increase with tissue thickness The hypothesis that thicker tissues are an effective defense strategy is thus rather validated (Fortunel et al., 2012). (i) For logging, both traits were significantly related to specific response. This is a somewhat surprising result, but it could reflect the fact that the species that benefit the most from logging are those that know how to defend themselves against the various pathogens that develop in disturbed conditions (Sangüesa-Barreda et al., 2015), that have thick leaves that better absorb microclimatic variations (Bongers et al., 2017) and that have a bark that may protect the trees from logging-related damage (Shenkin et al., 2015). (ii) For fire, it is surprising that tissue thickness traits (and in particular bark thickness) are not significantly (even if the relationship is positive) related to the specific response. Indeed, many studies have shown that among bark characteristics, bark thickness is a strong predictor of cambium heating avoidance (Pinard and Huffman, 1997). However, it should be noted that the values of bark thickness are naturally very low in our system (range 0.3-2.1 mm, mean 0.72 mm) compared to those obtained, for example, in an extensive study (Paine et al., 2010) in neotropics (range 0.5-29.0 mm, mean 4.52 mm). (iii) For Cedrela odorata invasion, it is well known that this species develops an aggressive allelopathic strategy towards native species, including the release of chemical compounds that inhibit the growth of neighboring species (Rivas-Torres and Rivas, 2018). It is readily conceivable that species with thin tissue thicknesses have developed fewer protections and are therefore more likely to allow



Fig. 6. Correlation matrix the species responses (namely $\theta_{1,sp}$ $\theta_{2,sp}$ $\theta_{3,sp}$) to three studied disturbances (namely 1-Logging, 2-Fire, 3-Invasion). Histograms of the distribution of each of the species responses on the diagonal running from left to right. Spearman correlation coefficients, at the upper intersection of two variables. Scatter plot of these two variables, at the lower intersection of two variables, the overlaid linear regression (confidence intervals in gray) for visualization.

Table 3

List of 14 species (botanical family, scientific name, vernacular name) that were identified as particularly vulnerable to disturbance in this study and are also classified as Threatened by the IUCN. Species are ordered by decreasing total Vulnerability. Specific vulnerabilities to the three types of disturbance studied are also reported (1-Logging, 2-Fire, 3 Invasion).

Family	Name	Vernacular	1-Logging	2-Fire	3-Invasion	Vulnerability
Simaroubaceae	Gymnostemon zaizou	Zaizou	-4.76	-1.08	-1.49	-7.33
Santalaceae	Okoubaka aubrevillei	Okoubaka	-0.07	-0.27	-4.68	-5.03
Euphorbiaceae	Shirakiopsis aubrevillei	Cocoti	0.51	-2.13	-2.63	-4.25
Fabaceae	Afzelia africana	Lingue	-0.67	-0.78	-1.91	-3.36
Malvaceae	Cola reticulata	Gro	-1.77	-0.42	-0.39	-2.58
Meliaceae	Entandrophragma utile	Sipo	0.46	-1.26	-0.13	-0.94
Meliaceae	Entandrophragma cylindricum	Aboudikro	-0.11	-0.19	-0.61	-0.9
Malvaceae	Nesogordonia papaverifera	Kotibe	-0.19	-0.03	-0.2	-0.43
Fabaceae	Copaifera salikounda	Etimöe	0.17	-0.36	-0.2	-0.4
Meliaceae	Khaya anthotheca	Acajou.blanc	-0.02	-0.28	-0.08	-0.38
Sapindaceae	Placodiscus boya	Boya	1.82	-1.09	-1.1	-0.36
Anacardiaceae	Antrocaryon micraster	Akoua	-0.03	-0.1	-0.04	-0.18
Araliaceae	Cussonia bancoensis	Ringhalla	0.19	0.55	-0.91	-0.18
Meliaceae	Entandrophragma angolense	Tiama	0.59	-0.09	-0.52	-0.01

chemical molecules to penetrate the interior of the tissue and thus diminish the performance of native species.

4.4. Vulnerabilities and lessons for conservation

The positive link (albeit weak) between specific responses to fire and logging creates a double vulnerability that may be worrying. Indeed, it is clear in the studied area that silvicultural interventions carried out before 1978 not only favored the propagation but also the intensity of the 1983 fire (Bertault, 1992). This phenomenon is well known and general in exploited forests which become, after logging, more susceptible to fire by an increase in fuel load is suitable (Cochrane, 2009), a

rapid propagation linked to the higher wind speed in open forest stands (Ray et al., 2005) and a higher risk of fire outbreak linked to the opening of the forest to human activities. It therefore seems appropriate to conserve the last natural forests in West Africa and to bear in mind that opening them to logging automatically increases the risk of fire.

The specific responses to biological invasion by *Cedrela odorata* are not related to responses to other disturbances. It is therefore an ecosystem-independent response that involves specific biological/ ecological mechanisms and is most likely related to specific plant-plant interactions (allelopathy). The good news is that our results do not show any particular relationship between local vulnerability to invasion by *Cedrela odorata* and global vulnerability, as measured by the IUCN list.



Fig. 7. Boxplots of the species responses (namely $\theta_{1,sp}$, $\theta_{2,sp}$, $\theta_{3,sp}$, Y axis squareroot scaled) to the studied disturbances (namely 1-Logging, 2-Fire, 3-Invasion and Total) according to the IUCN categories. *P*-values of the Wilcoxon test between the IUCN categories are reported (ns: not significant). Values above 0 (dashed line) represent a positive impact of the disturbance on species' abundances and negative values a negative impact of species' abundances.

That said, it can be stressed that this invasion represents a major threat to all species. In particular, it is remarkable to note that, despite the recent (1992) arrival of this species in a forest ecosystem, supposedly quite impermeable (Heringer et al., 2020), the effects of this invasion have overtaken the effects of logging and of a major fire. It is therefore very important to limit as much as possible the introduction of alien species in the surroundings of the last natural forests. In this case, *Cedrela odorata* was introduced in monospecific plantations for timber production in the neighbourhood of the study area. Our results show that it is essential to develop, in these situations, alternatives strategies for timber production from native species (Hérault et al., 2020; Kouassi et al., 2023), with the aim of preserving the last natural forests from invasion.

Our total vulnerability index is not related to the global vulnerability categories, as defined by the IUCN. However, we coupled our list of species with total negative vulnerability with the list of IUCN Threatened species to provide a list of priority species for conservation. These species are threatened locally as well as globally and we suggest that conservation actions, as well as a total cessation of logging, should be decided upon by stakeholders. It is notable that species that are globally vulnerable are also the most vulnerable locally to fire disturbance. This result confirms that fire remains, globally as well as locally, the main factor of degradation of forest ecosystems in West Africa, that recurrent fires greatly hinder the normal functioning of forest stands and that this should call for great vigilance in the management of local forest resources in fire zones. As a matter of urgency, the promotion of fire management and control tools should be a priority for conservation policies, with important co-benefits for other biological groups that also suffer from this problem (Hough, 1993). These management measures are a prerequisite for the recovery of forests lost over the past 30 years (Amani et al., 2021, 2022; N'Guessan et al., 2019) and will also promote the growth and multiplication of native species, many of which are of high commercial value (Doua-Bi et al., 2021).

CRediT authorship contribution statement

Marie Ruth Dago: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. Irie Casimir Zo-Bi: Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition. Vincyane Badouard: Investigation, Writing – review & editing. Marco Patacca: Investigation, Writing – review & editing. **Bruno Herault:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Supervision.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Irie C Zo-Bi reports financial support was provided by C2D AMRUGE.

Data availability

Data will be made available on request.

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