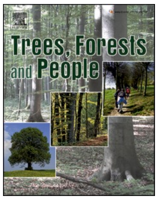
Trees, Forests and People 22 (2025) 101005

Contents lists available at ScienceDirect

Trees, Forests and People

journal homepage: www.sciencedirect.com/journal/trees-forests-and-people



Forest structure recovery around West Africa’s last great rainforest: Modelling complex dynamics in Taï national park

Aya Diane Larissa Houphouët [a,*], Yao Charles Sangne [a], Abdoulaye Diarrassouba [b], Yves Constant Adou Yao [c], Julie Betbeder [d,e], Bruno Hérault [d,e,**]

[a] *Université Jean Lorougnon Guédé, Unité de Formation et de Recherche en Environnement, Daloa, Côte d’Ivoire*
[b] *Office Ivoirien des Parcs et Réserves, Soubré, Côte d’Ivoire*
[c] *Université Félix Houphouët-Boigny, Laboratoire de Botanique, Abidjan, Côte d’Ivoire*
[d] *CIRAD, Forêts et Sociétés, F-34398 Montpellier, France*
[e] *Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France*

ARTICLE INFO

Keywords:
Secondary forest recovery
Bayesian modelling
Forest structure
Passive restoration
Remnant trees
Land-use legacy
Taï national park

ABSTRACT

Tropical secondary forests play a key role in restoring biodiversity and biomass, yet their recovery dynamics remain poorly understood in West Africa, even within protected areas. In Taï National Park, one of the region’s last major rainforests, we modelled forest recovery trajectories in the past agricultural areas to better understand and support effective conservation strategies. We inventoried 118 plots spanning old-growth undisturbed, old-growth disturbed, and secondary forests. Four structural attributes (aboveground biomass, Lorey’s height, quadratic mean diameter, and structural homogeneity) were modelled using a Bayesian framework. We assessed the influence of past land use, disturbance, and environmental factors on recovery rates. Structural attributes recovered at markedly different rates. Structural homogeneity and mean diameter recovered fastest (~20–30 years), followed by height (~30–40 years), while biomass required over a century for near-complete recovery. Recovery was strongly enhanced by the presence of remnant trees and forest connectivity, especially for biomass. In contrast, Marantaceae presence, hydromorphic soils, anthropogenic disturbance, and herbivory slowed recovery. Former cocoa fields showed the highest recovery rates across all attributes, while former gold mining sites exhibited extremely slow regeneration due to severe soil degradation. Our results suggest that forest recovery around Taï National Park will be highly heterogeneous. Cocoa fields with remnant trees offer strong potential for rapid passive recovery, while mined areas may need active restoration. Protecting remnant trees and managing disturbances will be crucial. Overall, passive regeneration holds significant promise, but realistic expectations and adaptive management are essential to support long-term forest resilience in this landscape.

1. Introduction

Tropical forests in West Africa are experiencing rapid and widespread degradation, driven primarily by deforestation and land-use change over the past three decades (Hansen et al., 2013 ; Masolele et al., 2024). Once home to some of the world’s most biodiverse and endemic-rich ecosystems (Myers et al., 2000), these forests are now increasingly fragmented and degraded, leading to significant declines in biodiversity, ecosystem functioning, and carbon storage capacity (Achard et al., 2002). Large-scale agricultural expansion particularly for cocoa cultivation remains the dominant driver of this transformation (Ouattara et al., 2021; Sabas et al., 2020; Sanial et al., 2023), further exacerbated by bushfires, mining logging and population growth (Tchatchou et al., 2015; Alohou et al., 2016). These pressures result in severe ecological consequences, including the release of stored carbon and the disruption of critical ecosystem services (Norris et al., 2010; Oliver et al., 2015).

In many regions, abandoned agricultural lands undergo natural regeneration, initiating secondary succession and giving rise to secondary forests (Chazdon, 2014; Arroyo-Rodríguez et al., 2017; Vancutsem et al., 2021). Unlike primary succession, which occurs on newly formed or barren substrates, secondary succession builds on residual

---

* Corresponding author.
** Corresponding author at: CIRAD, Forêts et Sociétés, F-34398 Montpellier, France.
E-mail addresses: larissahouphouet@gmail.com (A.D.L. Houphouët), bruno.herault@cirad.fr (B. Hérault).

https://doi.org/10.1016/j.tfp.2025.101005
Received 21 July 2025; Received in revised form 10 September 2025; Accepted 11 September 2025

ecological legacies such as developed soils, remnant trees, seed banks and stump shoots (Poorter et al., 2021b). Globally, secondary forests now account for nearly half of all tropical forest cover (Oberleitner et al., 2021) and are increasingly recognized as critical components of climate mitigation strategies due to their substantial carbon sequestration potential (Pan et al., 2011). In contrast to saturated old-growth forests (Hubau et al., 2020), young secondary forests show elevated rates of biomass accumulation in link to structural development in time and successional shifts in species composition (Poorter et al., 2021b). They therefore represent a valuable yet underutilized opportunity for restoring ecosystem functions (Chazdon and Guariguata, 2016; Locatelli et al., 2015).

Although global research on secondary forest recovery is expanding (Martin et al., 2013; Poorter et al., 2016; Matos et al., 2020; Teixeira et al., 2020), West Africa remains critically underrepresented (Amani et al., 2021; N'Guessan et al., 2019). Recent studies from Côte d'Ivoire suggest that secondary forests may recover 50 % of their original biomass within 35 years and up to 80 % in at least 60 years (Amani et al., 2022), although recovery is generally slower than in comparable Neotropical regions (N'Guessan et al., 2019; Norris et al., 2010). Proposed explanations include more intense degradation, reduced animal seed dispersers, and lower landscape connectivity (Titenwi et al., 2025). Despite international policy interest through the Convention on Biological Diversity and REDD+ programs (Alexander et al., 2011) the absence of region-specific studies (but see Titenwi et al., 2025) hampers accurate assessments of forest restoration potential in West Africa (Balvanera et al., 2021).

Biomass recovery during secondary succession is influenced by multiple environmental factors, including land-use history, soil fertility, seed dispersal, forest proximity, and the presence of remnant trees (Peña-Claros, 2003; Poorter et al., 2016; Cecilio Rebola et al., 2021). For example, prior land use can leave long-lasting effects on soil properties and vegetation, influencing regeneration outcomes (Tondoh et al., 2015; Derroire et al., 2016a). Remnant trees and nearby forests serve acts as reservoirs of propagules and habitats for animal seed dispersers - such as birds, bats, and primates that facilitate recolonization (Norden et al., 2009; Arroyo-Rodríguez et al., 2015a; Cuni-Sanchez and Lindsell, 2017). The functional traits of these remnant species, particularly nitrogen fixation capacity, further influence long-term biomass accumulation (Lai et al., 2018). Yet, in regions like Côte d'Ivoire, where faunal communities have been drastically reduced, critical ecological processes such as seed dispersal are disrupted, hindering the spread of late-successional species and slowing tree regeneration (Doughty et al., 2016; Hawes et al., 2020).

Located in southwestern Côte d'Ivoire, Taï National Park offers a compelling case to study forest regeneration dynamics in the region. During the civil conflict in the early 2000s, the park experienced intensified deforestation due to weakened governance and illegal encroachment. Over the past 15 years, however, natural regeneration has taken place across large areas of its degraded margins, creating a mosaic of recovering secondary forests. This landscape provides a valuable setting to investigate how forests recover under varying degrees of past disturbance and environmental conditions. Given the complex interactions between ecological, historical, and anthropogenic variables, this study aims to address three core objectives: (1) To determine the typical rates and trajectories of key forest structure attributes recovery in the Taï National Park? (2) To determine which environmental and historical factors most strongly influence these recovery patterns? (3) To derive key recommendations for guiding effective restoration strategies.

2. Materials and methods

2.1. Study area

Taï National Park (TNP) and the N'Zo Partial Faunal Reserve (RPFN) form a contiguous forest block covering a total area of 536,016 hectares. This forest complex is part of Côte d'Ivoire's protected area network and represents about 25 % of its total protected surface (OIPR, 2020). It is located in the southwest of the country, between the Cavally and Sassandra rivers, spanning latitudes 5°08′ to 6°24′ N and longitudes 6°47′ to 7°25′ W. The region consists of dense, evergreen tropical rainforest under a sub-equatorial climate that is hot and humid year-round (Trochain, 1980). Average annual temperatures range between 25 °C and 27 °C, and mean annual rainfall varies from 1700 mm to 2200 mm (Dimitri et al., 2023). The main study sites include the Djapadji, Soubré, Djouroutou and Taï sectors areas previously affected by human activities. Current and past land uses in these areas include agriculture and artisanal gold mining (Fig. 1).

2.2. Data collection

Sampling plots (0.0625 ha; 25 $m \times$ 25 m) were randomly established within homogeneous vegetation units, as defined in preliminary land-cover maps provided by the Office Ivoirien des Parcs et Réserves (OIPR), while restricting placement to areas that were accessible for field surveys. Plot abandonment age was determined through records provided by OIPR as part of land-use control enforcement operations in the zones concerned. These lands were recovered from various activities, including cocoa plantations, gold mining, and others, with 85 plots abandoned in 2014, 11 in 2013, and the sole earlier exception of 14 in 1998. All woody individuals with a diameter at breast height (DBH) $\geq$ 2.5 cm were identified to species level and measured between September 2023 and July 2024. The inclusion threshold of 2.5 cm DBH was selected to capture the contribution of saplings, which play a pivotal role in the early phases of secondary succession (Swaine and Hall, 1983). A total of 118 plots were inventoried: 7 old-growth undisturbed forest plots (no evidence of logging, corresponding to the original primary forest), 7 old-growth disturbed forest plots (residual fragments located between former cocoa plantations and used by local populations for timber extraction and subsistence resource gathering), and 104 secondary forest plots, the latter predominantly established on former cocoa plantations (91 plots), abandoned artisanal gold mining sites (8 plots) or other land uses (5 plots). These 'other' cases refer to situations where no clear or reliable information was available—for example, the presence of old cocoa tree stumps, signs of former plantations, disturbed forests identified after consultations with local forest agents, or areas affected by slash-and-burn agriculture with full or partial deforestation. Whenever we are not 100 % certain about the previous land use, we classify such situations under the 'Others' category to ensure consistency.

Field assessments also recorded key environmental variables: presence of large mammals (i.e. buffles (*Syncerus caffer*), duikers (*Cephalophus* spp.), elephant (*Loxodonta africana*), chimpanzee (*Pan troglodytes*), and warthog (*Phacochoerus africanus*)), hydromorphic conditions, occurrence of Marantaceae, evidence of human activity and previous land use (Table 1 for details).

For the degree of forest connectivity, we used the 2025 data from the 'Annual Change Collection' of the Tropical Moist Forest (TMF) dataset developed by the European Commission's Joint Research Centre (EC-JRC), which is based on a 34-year Landsat time series (1990–2024) (Vancutsem et al., 2021). The maps provide 30 m resolution information on forest extent, disturbances (deforestation and degradation), and recovery (forest regrowth) for each year. Each disturbance, whether deforestation or degradation, has its own distinct timing and intensity. Deforestation indicates a land cover change from forested to non-forested, whereas degradation refers to temporary disturbances where the area remains predominantly forested, such as selective logging, fires, or extreme weather events like hurricanes, droughts, and blowdowns. Undisturbed forest is defined as closed evergreen or semi-evergreen forest with no disturbance detected throughout the observation period. We created a 'forest-non forest' map considering the

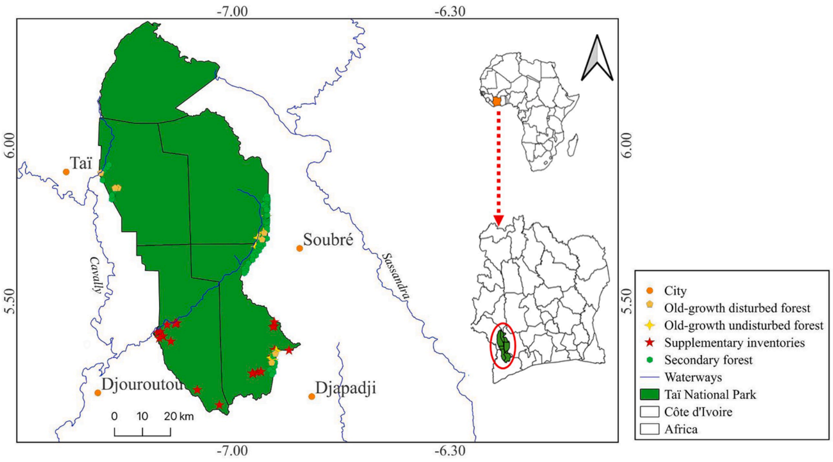


Fig. 1. Location of the study area (© OIPR).

Table 1
Variables considered in the analysis of recovery trajectories of forest structure at the edge of Taï National Park and the main underlying expected effects.

Variable	Description	Unit	Values	Expected effects on recovery trajectories
Previous land use	Former land use of the plot prior to abandonment	/	1 = Cacao plantation, 2 = Gold mining site, 3 = Other	Sites formerly under cocoa recover faster than mined sites due to less severe soil/topsoil damage.
Mammal presence	Number of mammal species detected via indirect signs (dung, feeding traces, footprints)	/	0 = None, 1 = One species, 2 = Two species, 3 = Three species…	Greater mammal (seed-disperser) abundance accelerates recovery via higher seed rain and recruitment.
Soil hydromorphy	Hydromorphic status of soil based on redoximorphic features in surface horizons	/	0 = No-hydromorphic, 1 = Hydromorphic	Poorly drained/hydromorphic soils slow recovery compared to well-drained soils.
Marantaceae	Presence of a dense undergrowth of Marantaceae, generally represented by Thaumatococcus daniellii	/	0 = No Marantaceae, 1 = Marantacae	Dense Marantaceae understory suppresses tree recruitment and slows recovery.
Remnant tree biomass	Biomass of remnant trees. Trees are considered remnant if their current DBH exceeds that expected from 5 cm/year growth since plot abandonment	t/ha	0.00 [0.00; 133.31]	More/larger remnant trees speed recovery by providing propagules and favorable microhabitats.
Human activities	Human activities near the plot (poaching, active agriculture, artisanal gold mining)	/	0 = None, 1 = One activity, 2 = Two activities, 3 = All three	Ongoing human pressure reduces fauna and increases disturbance, slowing recovery.
Forest connectivity	% forest cover within a 250 m radius around the plot center, based on TMF land cover map (2023)	%	15.94 [5.04; 42.19]	Higher connectivity/proximity to intact forest increases propagule flow and speeds recovery.

TMF forest class which has not undergone deforestation or degradation as forest. We then calculated the percentage of landscape (PLAND) metric within buffer zones at two scales (250 m and 1000 m) around the inventory points (Traoré et al., 2024). For each radius, composition metrics were calculated, particularly the plan (the percentage of the buffer area occupied by forest). The effect of these two spatial scales on the dynamics of reconstitution was then compared. Ultimately, the 250 m radius was selected as it correlated better with the observed rates of forest recovery.

To provide a strong reference for advanced recovery states, an additional dataset of supplementary inventories comprising 25 primary forest plots situated in the core of the national park was integrated (Adou Yao and Munoz, 2020). These inventories were conducted between January 1998 and February 2000, with only individuals with DBH ≥ 10 cm censused in these plots.

2.3. Attributes of forest structure

We chose to focus on four key forest structure attributes: Lorey's height, Gini index, mean quadratic diameter, and biomass because together they provide a comprehensive picture of forest recovery. Lorey's height captures vertical structure and canopy development, reflecting forest stratification and light dynamics. The Gini index quantifies structural diversity by measuring the inequality of tree sizes, an important indicator of successional processes and habitat complexity. Mean quadratic diameter represents stand maturity and average tree size, while biomass integrates overall productivity and carbon storage, which are central to ecosystem services and climate regulation. Considering these complementary attributes allows us to evaluate not just how much forest regrows, but how its structure and ecological functions are re-established over time.

2.3.1. Quadratic diameter

The Quadratic Mean Diameter (QMD) is considered more appropriate than the arithmetic mean for characterizing the average size of a group of trees. QMD gives greater weight to larger individuals, thereby providing a better representation of structural dominance. It is commonly used to describe the average tree size within a plot or biotope (Curtis and Marshall, 2000). QMD is calculated as follows:

$$QMD = \sqrt{\frac{\sum_{i=1}^{n}\left(DBH_i^2\right)}{N}}$$

where **DBH** is the diameter at breast height of each tree *i*, derived from circumference measurements collected during field inventories, and **N** is the total number of recorded trees.

2.3.2. Lorey's height

Lorey's height (Hl) weights the contribution of individual trees to stand height by their basal area. It is more stable than an unweighted mean height, as it is less influenced by small trees (Curtis and Marshall, 2000). The formula is as follows:

$$Hl = \frac{\sum_{i=1}^{n} (BA_i \times H_i)}{\sum_{i=1}^{n} BA_i}$$

where BAᵢ is the basal area of each individual tree *i*, and Hᵢ is its corresponding height.

2.3.3. Structural homogeneity

Structural homogeneity of trees was assessed using the Gini index. Although the Gini coefficient is a measure of heterogeneity originally developed to evaluate income and wealth inequality (Sen, 1997), its application has been extended to describe size hierarchies in plant communities (Weiner and Solbrig, 1984). The Gini coefficient (GC) quantifies the inequality of a distribution and is based on the Lorenz curve. Like regularity indices, the Gini index is continuous and bounded within the interval [0,1], with values close to zero indicating a homogeneous population structure, and values approaching one indicating greater size inequality (Cordonnier and Kunstler, 2015; Reich et al., 2022). In this study, the Gini coefficient was applied to the diameter at breast height (DBH) of each individual tree. To facilitate interpretation in terms of structural homogeneity, we used the inverse of the Gini coefficient.

$$GC = 1 - \frac{\sum_{1=1}^{n} (2i - 1 - n)\, DBH_i}{n \sum_{1=1}^{n} DBH_i}$$

where i is the rank of the observed value in ascending order.

2.3.4. Biomass

Aboveground biomass (AGB) of all individuals within each plot was calculated using generic allometric equations that incorporate DBH, tree height, and wood density, implemented through the BIOMASS R package (Réjou-Méchain et al., 2017). Wood density values were retrieved based on species names using the “getWoodDensity” function. The DBH and height values used in the calculations were those measured during the forest inventory. The biomass values of all individuals were summed and scaled to a per-hectare basis.

2.4. Modelling framework

The basic model consists of four likelihood components, corresponding to four types of input data: secondary forests, old-growth undisturbed forests, old-growth disturbed forests, and supplementary inventories (plots where only trees with DBH $\geq$ 10 cm were recorded). This is a simple model that assumes the absolute recovery rate at any given time is proportional to the distance between the current state of the system and its asymptotic value (Maurent et al., 2023). In other words, recovery follows an exponential approach to the asymptote, with the system slowing down as it nears equilibrium, a dynamic commonly observed in forest succession.

2.4.1. Secondary forests

The following model likelihood was used to describe the dynamics of structural and functional attributes over time:

$$X_{p,t} \sim LN\left(\theta_0^X + \left(\left(\theta_{+\infty}^X + \theta_{mar+\infty}^X\right) - \theta_0^X\right) \times \left(1 - e^{\lambda^X t_p}\right), \sigma_X^2\right)$$

where:

- $X_{p,t}$ is the value of ecosystem attribute *X* (aboveground biomass, Lorey’s height, quadratic mean diameter, or structural homogeneity) in plot p at time t;
- θ_0^X is the initial value of *X*, i.e., the value of the attribute at the onset of the recovery process;
- $\theta_{mar+\infty}^X$ represents the effect of the presence of Marantaceae on the asymptotic value of attribute *X*.
- $\theta_{+\infty}^X$ is the asymptotic value of *X*, representing the long-term equilibrium or maximum expected value of the attribute;
- λ^X is the intrinsic recovery rate of *X*, controlling the speed at which the attribute approaches its asymptote;
- *t* is the time since the beginning of recovery for plot *p*;
- σ_X^2 is the variance of the log-normal distribution used to model the variability in *X* among secondary forest plots;

This model describes the non-linear recovery trajectory of structural forest attributes, based on an exponential recovery curve. The attribute increases from its initial value toward an asymptotic value , at a rate governed by λ^X. The model explicitly incorporates the potential influence of Marantaceae-dominated understory on forest recovery, which adjusts the asymptotic level of the attribute.

2.4.2. Old-Growth undisturbed forests

The likelihood is simpler, as there is no explicit recovery time or recovery rate involved; the attributes are assumed to represent a stable asymptotic state. The model is specified as:

$$X_{p,t} \sim LN\left(\theta_{+\infty}^X + \theta_{mar+\infty}^X, \sigma_X^2\right)$$

2.4.3. Old-Growth disturbed forests

The likelihood follows the same framework as that used for old-growth undisturbed forests. In this case, the asymptotic values of each forest attribute are adjusted to account for the effects of anthropogenic disturbances. Specifically, the model allows for the modification of the asymptotic value of each attribute to reflect the potential impact of human activities on forest structure

$$X_{p,t} \sim LN\left(\theta_{dist}^X \times \left(\theta_{+\infty}^X + \theta_{mar+\infty}^X\right), \sigma_X^2\right)$$

where:

- θ_{dist}^X represents the effect of disturbance on the asymptotic value of attribute *X*;

2.4.4. Supplementary inventories

The likelihood follows the same framework as that used for old-growth undisturbed forests. In this case, the asymptotic values of each forest attribute are adjusted to account for the fact that only trees with DBH $\geq$ 10 cm were inventoried

$$X_{p,t} \sim LN\left(\theta_{\geq 10}^X \times \left(\theta_{+\infty}^X + \theta_{mar+\infty}^X\right), \sigma_X^2\right)$$

where:

- $\theta_{\geq 10}^X$ represents the adjustment to the asymptotic value of attribute X to account for the fact that only trees with DBH $\geq$ 10 cm were included in the inventory

Next, we complexified the basic model in order to estimate the recovery rate λ^X for each category of previous land use (a categorical variable), and then used an exponential function to model the effect of continuous explanatory variables (Table 1) on the recovery rates of different ecosystem attributes. An exponential function (Hérault and Piponiot, 2018) was used to model covariate effects because it is always greater than one, as expected for recovery rates. Additionally, all explanatory variables were standardized (i.e., rescaled to a common scale), making it easier to compare their relative effects on recovery rates within and across different forest structure attributes.

$$\lambda^X = \lambda_{land}^X \times e^{\left(\sum_{j=1}^{J} \beta_{COVJ}^X . COV_j^X\right)}$$

where:

- λ^X is the mean recovery rate of attribute X (aboveground biomass, Lorey's height, quadratic mean diameter, and structural homogeneity), estimated for average environmental conditions;
- λ^X_{land} is the recovery rate associated with previous land use for attribute X;
- β^X_{COVJ} is the effect of covariate j on the recovery rate of attribute X;
- COV^X_j is the standardized value of covariate j (e.g., presence of remnant trees, previous land use intensity, soil properties, etc.).

We employed a log-normal likelihood because all the modeled response variables aboveground biomass, Lorey's height, quadratic mean diameter, and structural homogeneity are strictly defined on the positive real line ($R+$) (Maurent et al., 2023). This choice also helps to account for the typically right-skewed distributions observed in these ecological variables (Piponiot et al., 2016). The model was implemented in a Bayesian framework using the Stan probabilistic programming language (Carpenter et al., 2017). Parameter estimation was performed using Hamiltonian Monte Carlo (HMC) with the No-U-Turn Sampler (NUTS), an efficient Markov Chain Monte Carlo (MCMC) algorithm well-suited for high-dimensional models and complex posterior distributions. This approach allows us to fully characterize the uncertainty in parameter estimates and provides robust inference even in the presence of correlated parameters. All models were fitted using four independent Markov chains, each with 5000 iterations, including 2500 iterations for warm-up (burn-in). Convergence of the chains was assessed by examining the potential scale reduction factor and by visually inspecting trace plots for all parameters.

3. Results

The full set of forest inventories included 14,363 individual trees, representing 219 species, 193 genera, and 56 families. After model fitting, the estimated asymptotic values ($\theta^X_{+\infty}$) were: a Gini index of 0.60, a quadratic mean diameter of 13.65 cm, a Lorey's height of 28.48 m, and an aboveground biomass of 616.26 t/ha (Table 2). The presence of Marantaceae ($\theta^X_{mar+\infty}$) reduced the Gini index by −0.02, the mean diameter by −1.67 cm, the Lorey's height by −2.70 m, and aboveground biomass by −151.23 t/ha. Anthropogenic disturbances (θ^X_{dist}) led to a reduction of forest attributes relative to their asymptotic potential. On average, forest structure reached 89 % of the asymptotic value observed in old-growth undisturbed forests. Losses were greater for mean diameter (74 %) and Lorey's height (77 %). Aboveground biomass was especially impacted, with old-growth disturbed forests reaching only 32 % of their asymptotic potential. Including only individuals with DBH ≥ 10 cm ($\theta^X_{\geq 10}$) also influenced the estimated asymptotic values. In these cases, the expected aboveground biomass was 55 % of the total biomass estimated for old-growth undisturbed forests ($\theta \geq 10 = 0.55$). Effects were also notable for other attributes: 2.03 cm for mean diameter, 1.01 m for Lorey's height, and 0.48 for the Gini index.

3.1. Recovery rates and times of attributes

Attributes recover at different rates (Figs. 2 and 3). Structural homogeneity, represented by the Gini index, is the attribute with the shortest recovery time, estimated between 20 and 25 years, and the highest recovery rate ($\lambda = 0.13$). Mean diameter also recovers rapidly ($\lambda = 0.11$), with an estimated recovery time between 20 and 30 years. In comparison, Lorey's height exhibits a slower recovery ($\lambda = 0.09$), requiring 30 to 40 years to reach 95 % of its asymptotic value (Fig. 3). Aboveground biomass shows the lowest average recovery rate ($\lambda = 0.025$) (Table 2 and Fig. 3a). The estimated time required to reach 95 % of its asymptotic value (median = 615 t/ha) exceeds 100 years (Fig. 3b).

3.2. Past land use and recovery rates

Previous land use in cocoa plantations had a clearly positive effect on the recovery rate of all attributes, with median values above zero and a particularly strong effect on the recovery rate of aboveground biomass (Fig. 4). In contrast, former gold mining sites showed a negative effect, especially on biomass recovery.

The "others" land-use category (forest islands, exploited forests) had a generally positive effect on all four attributes studied, with median values above zero.

3.3. Effects of environment on recovery rates

For structural homogeneity (Gini index), both remnant trees (0.03 ± 0.04) and soil hydromorphy (0.05 ± 0.11) had positive effects on the recovery rate, whereas the other variables had significant negative effects (Fig. 5).

For mean diameter, only soil hydromorphy had a positive effect (0.06 ± 0.15), while forest connectivity had a negative effect (−0.11 ± 0.06). The other variables showed no clearly significant effects.

For Lorey's height, only remnant trees had a positive effect on the recovery rate (0.05 ± 0.03). Anthropogenic activities and Animals had very small negative effects (−0.02 ± 0.03 for both).

For aboveground biomass, remnant trees had a strong positive effect on recovery rate (1.33 ± 0.11), followed by forest connectivity, which had a positive but weaker effect (0.06 ± 0.05). In contrast, Activities, Animals, and Hydromorphy all had negative effects on biomass recovery (Fig. 5).

4. Discussion

Before turning to the main discussion on secondary forest regeneration, we first highlight additional patterns observed in our results. This section does not directly address secondary forests—which are the core focus of our study and are presented in detail in the main results—but instead emphasizes broader factors incorporated into our models. These factors help account for variability observed in old-growth disturbed and undisturbed forests, as well as in our sampling protocol (e.g., plots

Table 2

Median and quantiles of the parameters of the basic model for Gini (Structural homogeneity), quadratic diameter, Lorey's height, and aboveground biomass.

Parameters	Gini			Diameter			Height			Biomass		
	Median	5th	95th	Median	5th	95th	Median	5th	95th	Median	5th	95th
$\theta_{+\infty}$	0.60	0.60	0.62	13.43	13.03	14.96	28.33	28.04	29.4	615.95	464.88	769.23
λ	0.13	0.10	0.17	0.10	0.07	0.19	0.08	0.06	0.16	0.025	0.009	0.36
$\theta_{\geq 10}$	0.48	0.45	0.52	2.03	1.82	2.22	1.01	1.00	1.08	0.55	0.40	0.79
$\theta_{mar+\infty}$	−0.02	0.07	0.02	−1.67	−4.02	0.23	−2.70	−7.82	2.56	−151.23	−376.63	214
θ_{dist}	0.89	0.83	0.95	0.74	0.62	0.86	0.77	0.65	0.92	0.32	0.18	0.63
σ	0.13	0.12	0.15	0.20	0.18	0.23	0.17	0.15	0.19	0.36	0.32	0.40

$\theta_{+\infty}$: asymptotic value of the recovery trajectory, λ: mean recovery rate of the attribute,$\theta_{\geq 10}$: effect of considering only large-diameter individuals (DBH > 10 cm) on the asymptotic value,$\theta_{mar+\infty}$: effect of Marantaceae presence on the asymptotic value,θ_{dist}: effect of disturbance on the asymptotic value and σ model error.

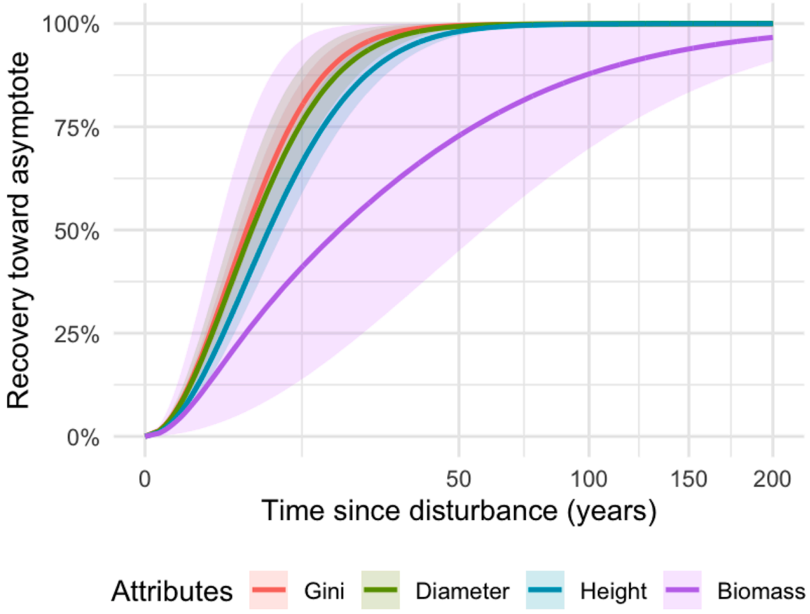
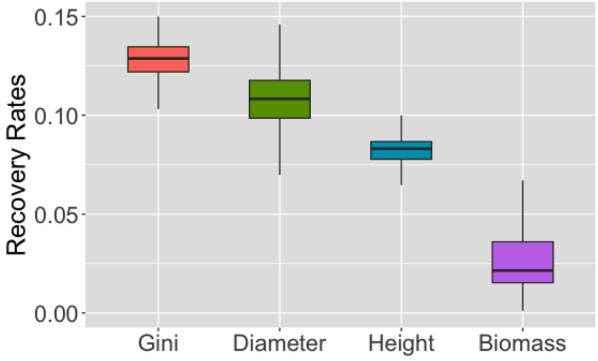
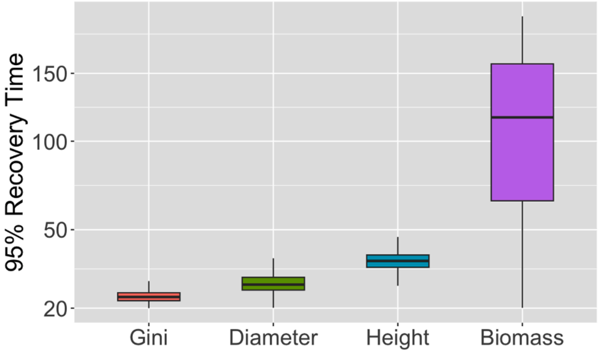


Fig. 2. Secondary-forest recovery trajectories across four attributes from 0 to 200 years since disturbance; time axis uses square-root scale; posterior mean with 95 % credible intervals.



(a)



(b)

Fig. 3. Recovery rate (a) and time to reach 95 % (b) of old-growth forest values for Gini (Structural homogeneity), quadratic diameter, Lorey's height, and aboveground biomass. Each box plot shows the posterior distribution of model-estimated values, where the boxes indicate the interquartile range, the horizontal line marks the median, and the whiskers represent the 95 % credible intervals.

with DBH $\geq$ 10 cm).

First, the presence of Marantaceae is linked to lower values of biomass, mean quadratic diameter, and Lorey's height. This aligns with earlier studies (e.g. Pouteau et al., 2024) showing that dense Marantaceae understories can hinder forest structure by limiting tree regeneration, reducing vertical canopy development, and ultimately lowering overall biomass. In line with these findings, we also observed that hydromorphic soils negatively affect biomass, mean diameter, and mean height recovery rates (Fig. 5). Hydromorphic soils host a distinctive flora adapted to periodic water saturation and often host highly competitive Marantaceae species (Cuni-Sanchez et al., 2016). These form dense monospecific mats that impede regeneration by excluding other plant species. Second, it is unsurprising that old-growth disturbed forests do not reach 100 % of asymptotic reference values, given the historical loss of large trees due to illegal logging. These changes result in lower biomass, reduced canopy height, and altered size distributions (Dago et al., 2023). Finally, when analysing only trees with diameters greater than 10 cm, we observed a reduction in biomass and structural homogeneity (inverse of the Gini index), alongside an increase in mean quadratic diameter and Lorey's height. This outcome reflects a natural shift in averages caused by excluding smaller individuals, which increases inequality in size-based metrics.

Together, these patterns underscore the complexity of forest recovery in this landscape and highlight the value of our modeling framework in disentangling the roles of natural dynamics, disturbance history, and ecological legacies.

4.1. Uneven recovery of forest structural attributes

During secondary forest regeneration, structural attributes recover at different rates. In our study, we identified a clear sequence of recovery among the four attributes analyzed: structural homogeneity (inverse of the Gini index) recovered first, followed by mean quadratic diameter, then Lorey's height, and finally aboveground biomass, which showed the slowest recovery (Table 2). These findings align with Doua-Bi et al. (2021), who reported that tree density, stem volume, and the proportion of large trees recover at different rates. Similarly, Poorter et al. (2021a) showed that forest structure and aboveground biomass in secondary forests follow distinct and asynchronous recovery trajectories.

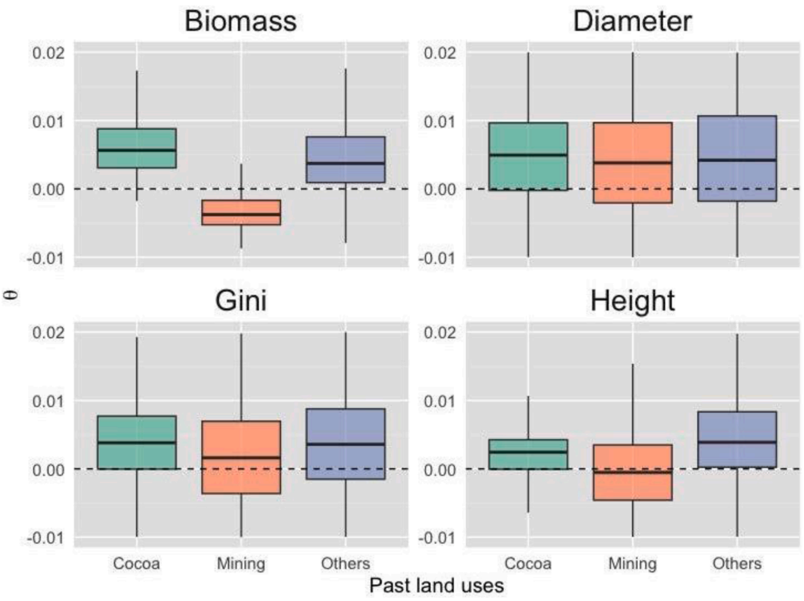


Fig. 4. Effects of previous land use on the recovery rate of Gini (Structural homogeneity), quadratic diameter, Lorey's height, and aboveground biomass. Each box plot shows the posterior distribution of model-estimated values, where the boxes indicate the interquartile range, the horizontal line marks the median, and the whiskers represent the 95 % credible intervals.

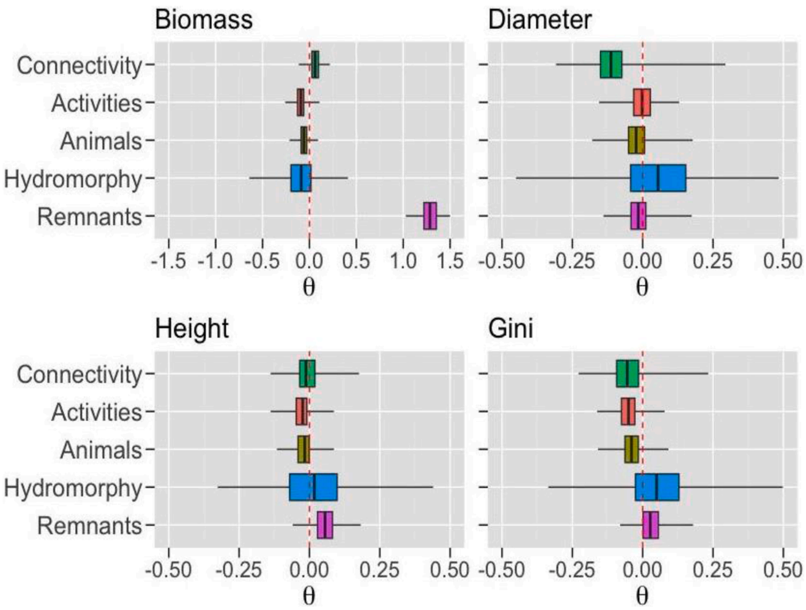


Fig. 5. Effects of environmental variables on the recovery rate of Gini (Structural homogeneity), quadratic diameter, Lorey's height, and aboveground biomass. Each box plot shows the posterior distribution of model-estimated values, where the boxes indicate the interquartile range, the horizontal line marks the median, and the whiskers represent the 95 % credible intervals.

4.2. What explains these differences?

First, the rapid recovery of structural homogeneity reflects an early return to a size distribution of trees similar to that of old-growth undisturbed forests. This pattern is likely driven by pioneer species, which quickly colonize canopy gaps and form relatively uniform cohorts. Their fast growth (Elogne et al., 2023; Mirabel et al., 2019) results in trees with similar diameters during early succession, re-establishing a stable size structure within a few years—a trend also observed in other tropical secondary forests (Poorter et al., 2021a).

Second, in regenerating secondary forests, high light availability promotes radial (diameter) growth over vertical growth. Because young trees face little competition for light, they allocate resources to expanding stem diameter rather than height. Our results are consistent with Collet et al. (2001) and Matsuo et al. (2021), who reported that diameter growth is favored in early-successional, open-canopy environments, while height increases more gradually. Similar dynamics have been observed in West African forests, where early successional communities exposed to high light favor short fast-growing pioneer species (Adou Yao and Muñoz, 2020).

Finally, aboveground biomass recovers much more slowly, as widely documented (Amani et al., 2022; N'Guessan et al., 2019; Poorter et al., 2021a; Titenwi et al., 2025). Several decades are required to reach 90 % of the biomass levels observed in old-growth undisturbed forests (Martin et al., 2013; Poorter et al., 2016; Amani et al., 2022). This is primarily due to the delayed return of large emergent trees—key contributors to carbon storage (Martin et al., 2013; Lindenmayer et al., 2014). As noted by Mukul et al. (2016), these trees often require many decades or even a century to fully recover. Makelele et al. (2021) similarly found that after 60 years of regeneration, only 43 % of aboveground carbon had been restored, largely due to the slow return of large stems. Amani et al. (2022) also estimated that over 50 years may be needed to regain 90 % of old-growth biomass. According to Doua-Bi et al. (2021), the full recovery of these trees can take more than a century.

4.3. *Faster recovery on former cocoa fields compared to mining sites*

Overall, we observed that forest recovery progressed more rapidly on former cocoa fields than on post-mining sites (Fig. 4). This pattern was consistent across all structural attributes analyzed—biomass, diameter, height, and structural homogeneity.

First, the modest positive effect of former cocoa fields on structural homogeneity likely stems from cocoa agroforests retaining elements of the original forest structure (Koffi et al., 2025; Konan et al., 2025a,b). These systems often preserve shade trees (Dago et al., 2025) and remnant individuals that persist after abandonment (Sangne et al., 2015), which help maintain favorable microclimatic conditions. In turn, this supports shade-tolerant species (Kouassi et al., 2023) and promotes a more even tree size distribution within the regenerating stand (Kohl et al., 2024).

Second, the presence of a viable seed bank in former cocoa fields appears to significantly facilitate biomass and structural recovery. Unlike mined areas—where topsoil removal and mechanical disturbance often destroy seed banks—abandoned cocoa fields retain viable seeds in the litter and upper soil layers, accelerating regeneration (Kougbo et al., 2023). This contrast helps explain why vegetation in post-mining landscapes rarely resembles nearby old-growth forests in either structure or composition (Peterson and Heemskerk, 2001).

Third, contrasting soil conditions further explain the divergence in recovery trajectories. Cocoa fields maintain a litter layer enriched with organic matter from leaves and cocoa pods, preserving soil fertility and structure, and supporting root growth and microbial activity. In contrast, mining causes severe soil degradation: topsoil removal eliminates nutrient reservoirs and disrupts physical structure. Albert (2015) showed that such disturbances lead to heavy metal buildup, loss of organic matter, reduced microbial function, and overall fertility decline. Sheoran et al. (2008) also found that essential macronutrients—nitrogen, phosphorus, and potassium—are frequently deficient in mined soils, requiring heavy nutrient inputs for revegetation. Kalamandeen et al. (2020) emphasized that nitrogen depletion is a more critical barrier to forest recovery than mercury contamination. Under these nutrient-poor conditions, tree growth is severely restricted, contributing to the extremely low biomass recovery observed on post-mining sites.

4.4. *Mammals, disturbance, and regeneration*

The interactions between large mammals and anthropogenic disturbances are closely intertwined: increased disturbance typically results in reduced densities of large mammals. Such disturbances negatively impact the recovery of all structural attributes, primarily by disrupting key ecological processes like seed dispersal. Human activities—including hunting and encroachment—displace seed-dispersing animals, many of which are targeted by poachers, thereby limiting dispersal and hindering natural regeneration (Brodie et al., 2009; Markl et al., 2012). In addition, forest loss due to gold mining further reduces mammal diversity and restricts ecosystem recolonization (Boesing et al., 2018; Estavillo et al., 2013; Morante-Filho et al., 2015).

Surprisingly, our results indicate that higher large mammal presence is associated with slower recovery rates across all structural attributes (Fig. 5). This finding contrasts with previous research suggesting that animal activity typically enhances propagule dispersal and accelerates regeneration (Kurten et al., 2015). One possible explanation is that some herbivores and large mammals also hinder regeneration through trampling or browsing of young vegetation. For instance Bulinski and McArthur (1999) showed that browsing significantly reduced seedling growth rates in plantations, while Xu et al. (2023) reported an 89 % reduction in vegetation abundance on restoration sites exposed to herbivores, where plant diversity was suppressed rather than enhanced.

Collectively, these findings underscore the complexity of fauna–vegetation dynamics in regenerating forests. On one hand, anthropogenic pressure diminishes animal-mediated seed dispersal, slowing recovery. On the other, some large mammals may directly inhibit regeneration through physical damage to seedlings. This suggests that an optimal density and composition of animal communities may be needed to balance the positive (dispersal) and negative (herbivory, trampling) effects on forest recovery—a balance that likely remains disrupted in these heavily altered landscapes, where faunal recovery is slow.

In our study, faunal presence was assessed through indirect signs such as footprints, feces, and feeding traces observed during floristic plot inventories. However, this ad hoc method has major limitations. It cannot reliably detect all animal activity, as some individuals may pass through unnoticed or outside survey periods. Consequently, wildlife presence may be underestimated and our results should be taken cautiously. Future studies would benefit from implementing dedicated monitoring protocols, such as camera traps and transect surveys, to provide a more robust and comprehensive assessment of animal activity and diversity.

4.5. *The pivotal role of remnant trees in forest restoration*

A high percentage of surrounding forest exerts a noticeable negative effect on the recovery rate of mean tree diameter and structural homogeneity (Fig. 5). By enabling a large and continuous influx of propagules, it promotes dense, often multi-cohort regeneration. This high density increases both intra- and interspecific competition, which slows individual tree diameter growth—especially during early development—and may hinder the rapid establishment of a stable forest structure (Herault et al., 2010) .

However, this negative effect is largely offset by the presence of remnant trees. Far from being passive survivors of disturbance (Zo-Bi and Hérault, 2023), these trees play a central role in forest recovery (Koffi et al., 2025). They strongly influence growth patterns (Kouassi et al., 2025) and help shape future stand structure. By creating microsites that support accelerated growth, regulating local competition, and providing favorable soil and microclimatic conditions, remnant trees foster diverse developmental niches (Amani et al., 2021; N'Guessan et al., 2019). Their role extends well beyond localized facilitation: they serve as a key source of propagules (Babweteera and Brown, 2009; Derroire, Tigabu, et al., 2016) and act as ecological hubs by attracting seed dispersers such as squirrels and birds, thereby contributing to natural regeneration.

In this context, our findings align with previous research (Arroyo-Rodríguez et al., 2015a; N'Guessan et al., 2019; Titenwi et al., 2025), showing that remnant trees significantly accelerate the recovery of biomass, mean diameter, and height. By facilitating the dispersal of key plant species, especially in fragmented landscapes, these trees serve as critical architects of post-disturbance dynamics. Their presence and distribution also influence the regeneration of late-successional species (Wu et al., 2022), which are essential for long-term forest resilience by enhancing structural complexity, ecological stability, and functional diversity in mature ecosystems.

Thus, even though increased connectivity may slow diameter growth overall, remnant trees play a dominant role in shaping recovery trajectories. By promoting localized growth, supporting functional resilience, and enriching ecosystem structure and biodiversity, remnant trees emerge as key—and in some cases indispensable—levers for forest restoration and sustainable ecosystem functioning.

5. Lessons and recommendations

The future of passive forest recovery around Taï National Park will be shaped by sharp contrasts in past land use, local ecological conditions, and disturbance legacies. Based on observed patterns, the park administration should anticipate highly uneven recovery trajectories across the landscape in the coming decades

- Recovery will be fastest and most complete in former cocoa fields. These areas retain viable seed banks, relatively intact soils, and often remnant trees that act as focal points for regeneration. As a result, they are likely to exhibit rapid gains in structural attributes such as tree size distribution and canopy height, along with a comparatively swift accumulation of biomass. Passive recovery in these areas should be actively supported and closely monitored, as they offer strong potential for contributing to carbon stock restoration.
- By contrast, former mining sites will regenerate extremely slowly. Extensive topsoil removal and severe soil degradation have eliminated critical seed sources and nutrient reservoirs. Even after several decades, these areas are unlikely to develop forest structures resembling old-growth conditions without targeted restoration. The park administration should maintain realistic expectations for these zones and consider long-term monitoring and, if necessary, active interventions to support regeneration.
- Remnant trees are among the most influential factors for accelerating recovery. Their presence enhances biomass accumulation and structural complexity by serving as regeneration nuclei and seed sources. Protecting these trees should remain a central priority in all areas where passive recovery is expected.
- Recovery will be slower in areas dominated by Marantaceae or with hydromorphic soils. Dense understory vegetation and seasonal waterlogging in these zones inhibit tree regeneration and canopy development. These areas will require patience and close observation to determine whether natural regeneration alone is sufficient or if supplemental measures may be needed.
- Wildlife–vegetation interactions will also shape recovery trajectories. While the return of large seed-dispersing animals is ecologically beneficial, high densities of herbivores can impede regeneration through trampling and browsing of young plants. Monitoring these dynamics will be essential to ensure that faunal activity supports, rather than suppresses, vegetation recovery.

Overall, the landscape surrounding Taï National Park will recover heterogeneously. Former cocoa fields and remnant-rich areas are poised to recover most rapidly, showing relatively quick improvements in structure and function. In contrast, post-mining landscapes and hydromorphic zones will lag behind—requiring decades, or even centuries, to approach old-growth conditions. Notably, the recovery of aboveground biomass and large emergent trees—vital for carbon storage and ecosystem resilience—will be slow across all contexts, demanding a long-term perspective.

In conclusion, passive recovery around Taï National Park holds considerable promise, particularly where key ecological legacies remain. However, patience and clear expectations are crucial. The park administration should prepare for a future where forest recovery unfolds at multiple speeds—shaped by past land use and natural dynamics—and where sustained protection of remnant trees and adaptive monitoring are essential to safeguarding long-term ecological integrity.

Funding

This research was made possible through the support of the Moses Mapesa Fellowship for Education and Scientific Research, which aims to promote work conducted in UNESCO World Heritage protected areas. This study was conducted with the financial support from the "Fonds Français pour l’Environnement Mondial" (FFEM) under the "Agence Française de Développement" (AFD) grant Agreement no. CCI 1711.01 D, as part of the Terri4Sol project. The authors would like to thank the management of Taï National Park for their continuous support, both in the field and financially, as well as the forest officers whose availability greatly facilitated the data collection phase.

CRediT authorship contribution statement

Aya Diane Larissa Houphouët: Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Yao Charles Sangne:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Abdoulaye Diarrassouba:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Yves Constant Adou Yao:** Writing – review & editing, Methodology, Data curation. **Julie Betbeder:** Writing – review & editing, Validation, Methodology. **Bruno Hérault:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Bruno Herault reports financial support was provided by French Facility for Global Environment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Supporting dataset is available at https://doi.org/10.5281/zenodo.17091840

References

Achard, F., Eva, H.D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T., Malingreau, J.-P., 2002. Determination of deforestation rates of the world’s humid tropical forests. Science 297, 999–1002. https://doi.org/10.1126/science.1070656.

Adou Yao, C.Y., Munoz, F., 2020. Successional dynamics shape tree diversity in evergreen forests of Côte d’Ivoire, West Africa. J. Trop. Ecol. 1–8. https://doi.org/10.1017/S0266467420000152.

Albert, K.M., 2015. Role of revegetation in restoring fertility of degraded mined soils in Ghana: a review. Int. J. Biodivers. Conserv. 7, 57–80. https://doi.org/10.5897/IJBC2014.0775.

Alexander, S., Nelson, C.R., Aronson, J., Lamb, D., Cliquet, A., Erwin, K.L., Finlayson, C. M., De Groot, R.S., Harris, J.A., Higgs, E.S., Hobbs, R.J., Robin Lewis, R.R., Martinez, D., Murcia, C., 2011. Opportunities and challenges for ecological restoration within REDD+. Restor. Ecol. 19, 683–689. https://doi.org/10.1111/j.1526-100X.2011.00822.x.

Alohou, E.C., Ouinsavi, C., Sokpon, N., 2016. Facteurs déterminants de la fragmentation du bloc forêt classée-forêts sacrées au Sud-Bénin. J. Appl. Biosci. 101, 9618–9633. https://doi.org/10.4314/jab.v101i1.5.

Amani, B.H.K., N’Guessan, A.E., Derroire, G., N’dja, J.K., Elogne, A.G.M., Traoré, K., Zo-Bi, I.C., Hérault, B., 2021. The potential of secondary forests to restore biodiversity of the lost forests in semi-deciduous West Africa. Biol. Conserv. 259. https://doi.org/10.1016/j.biocon.2021.109154.

Amani, B.H.K., N’Guessan, A.E., Van der Meersch, V., Derroire, G., Piponiot, C., Elogne, A.G.M., Traoré, K., N’Dja, J.K., Hérault, B., 2022. Lessons from a regional analysis of forest recovery trajectories in West Africa. Env. Res. Lett. 17. https://doi.org/10.1088/1748-9326/ac9b4f.

Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R., Tabarelli, M., 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research: multiple successional pathways. Biol. Rev. 92, 326–340. https://doi.org/10.1111/brv.12231.

Arroyo-Rodríguez, V., PL Melo, F., Martínez-Ramos, M., Bongers, F.L., Chazdon, R.A., Meave, J., Norden, N.A., Santos, B.R., Leal, I., Tabarelli, M., 2015a. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol. Rev. 92, 326–340. https://doi.org/10.1111/brv.12231.

Babweteera, F., Brown, N., 2009. Can remnant frugivore species effectively disperse tree seeds in secondary tropical rain forests? Biodivers. Conserv. 18, 1611–1627. https://doi.org/10.1007/s10531-008-9546-6.

Balvanera, P., Paz, H., Arreola-Villa, F., Bhaskar, R., Bongers, F., Cortés, S., del Val, E., García-Frapolli, E., Gavito, M.E., González-Esquivel, C.E., Martínez-Ramos, M., Martínez-Yrizar, A., Mora, F., Naime, J., Pascual-Ramírez, F., Pérez-Cárdenas, N., Ugartechea-Salmerón, O.A., Siddique, I., Suazo-Ortuño, I., Swinton, S.M., 2021. Social ecological dynamics of tropical secondary forests. For. Ecol. Manag. 496, 119369. https://doi.org/10.1016/j.foreco.2021.119369.

Boesing, A.L., Nichols, E., Metzger, J.P., 2018. Biodiversity extinction thresholds are modulated by matrix type. Ecography 41. https://doi.org/10.1111/ecog.03365.

Brodie, J.F., Helmy, O.E., Brockelman, W.Y., Maron, J.L., 2009. Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. Ecol. Appl. 19, 854–863. https://doi.org/10.1890/08-0955.1.

Bulinski, J., McArthur, C., 1999. Une étude expérimentale sur le terrain des effets des dommages causés par les mammifères herbivores sur les semis *d'Eucalyptus nitens*. For. Ecol. Manag. 113, 241–249. https://doi.org/10.1016/S0378-1127(98)00430-7.

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., Riddell, A., 2017. Stan: a Probabilistic Programming Language. J. Stat. Softw. 76, 1–32. https://doi.org/10.18637/jss.v076.i01.

Cecilio Rebola, L., Pandolfo Paz, C., Valenzuela Gamarra, L., F.R.P., Burslem, D., 2021. Land use intensity determines soil properties and biomass recovery after abandonment of agricultural land in an Amazonian biodiversity hotspot. Sci. Total Env. 801, 149487. https://doi.org/10.1016/j.scitotenv.2021.149487.

Chazdon, R.L., 2014. Second Growth: the Promise of Tropical Forest Regeneration in an Age of Deforestation. Second Growth. University of Chicago Press.

Chazdon, R.L., Guariguata, M.R., 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48, 716–730. https://doi.org/10.1111/btp.12381.

Collet, C., Lanter, O., Pardos, M., 2001. Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. Ann. For. Sci. 58, 127–134. https://doi.org/10.1051/forest:2001112.

Cordonnier, T., Kunstler, G., 2015. The Gini index brings asymmetric competition to light. Perspect. Plant Ecol. Evol. Syst. 17, 107–115. https://doi.org/10.1016/j.ppees.2015.01.001.

Cuni-Sanchez, A., White, L.J.T., Calders, K., Jeffery, K.J., Abernethy, K., Burt, A., Disney, M., Gilpin, M., Gomez-Dans, J.L., Lewis, S.L., 2016. African savanna-forest boundary dynamics: a 20-year study. PLoS One 11, e0156934. https://doi.org/10.1371/journal.pone.0156934.

Cuni-Sanchez, A., Lindsell, J.A., 2017. The role of remnant trees in carbon sequestration, vegetation structure and tree diversity of early succession regrowing fallows in eastern Sierra Leone. Afr. J. Ecol. 55 (2), 188–197. https://doi.org/10.1111/age.12340.

Curtis, R.O., Marshall, D.D., 2000. Why quadratic mean diameter? West. J. Appl. For. 15, 137–139. https://doi.org/10.1093/wjaf/15.3.137.

Dago, M.R., Zo-Bi, I.C., Badouard, V., Patacca, M., Hérault, B., 2023. Concomitant effects of multiple disturbances (logging, fire, biological invasion) on native tree abundances into West Africa's semi-deciduous forests. Biol. Conserv. 285, 110220. https://doi.org/10.1016/j.biocon.2023.110220.

Dago, M.R., Zo-Bi, I.C., Konan, I.K., Kouassi, A.K., Guei, S., Jagoret, P., Hérault, B., 2025. What motivates West African cocoa farmers to value trees? Taking the 4 W approach to the heart of the field. People Nat. 7 (1), 215–230. https://doi.org/10.1002/pan3.10.754.

Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D.K., Lebrija-Trejos, E., Leiva, J.A., Odén, P.C., Powers, J.S., Rico-Gray, V., Tigabu, M., Healey, J. R., 2016a. Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. Oikos 125, 1386–1397. https://doi.org/10.1111/OIK.03229.

Derroire, G., Tigabu, M., Odén, P.C., Healey, J.R., 2016b. The effects of established trees on woody regeneration during secondary succession in tropical dry forests. Biotropica 48, 290–300. https://doi.org/10.1111/btp.12287.

Dimitri, K.A.Y., Djaha, K., Bénédicte, Y.A.A., Bruno, K.K., Abdoulaye, D., 2023. Diversité des espèces de fruits consommés par les éléphants au Sud du Parc National de Taï (Sud-Ouest. de la Côte d'Ivoire), Journal of Animal & Plant Sciences 55, 10171–10185. https://doi.org/10.35759/JAmPISci.v55-3.1.

Doua-Bi, G.Y.A., Zo-Bi, I.C., Amani, B.H.K., Elogne, A.G.M., N'dja, J.K., N'Guessan, A.E., Hérault, B., 2021. Taking advantage of natural regeneration potential in secondary forests to recover commercial tree resources in Côte d'Ivoire. For. Ecol. Manag. 493, 119240. https://doi.org/10.1016/j.foreco.2021.119240.

Doughty, C.E., Wolf, A., Morueta-Holme, N., Jørgensen, P.M., Sandel, B., Violle, C., Boyle, B., Kraft, N.J.B., Peet, R.K., Enquist, B.J., Svenning, J.C., Blake, S., Galetti, M., 2016. Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. Ecography 39, 194–203. https://doi.org/10.1111/ecog.01587.

Elogne, A.G., Piponiot, C., Zo-Bi, I.C., Amani, B.H., Van der Meersch, V., Hérault, B., 2023. Life after fire-Long-term responses of 20 timber species in semi-deciduous forests of West Africa. For. Ecol. Manage. 538, 120977. https://doi.org/10.1016/j.foreco.2023.120977.

Estavillo, C., Pardini, R., Rocha, P.L.B.D., 2013. Forest loss and the biodiversity threshold: an evaluation considering species habitat requirements and the use of matrix habitats. PLoS One 8, e82369. https://doi.org/10.1371/journal.pone.0082369.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853. https://doi.org/10.1126/science.1244693.

Hawes, J.E., Vieira, I.C.G., Magnago, L.F.S., Berenguer, E., Ferreira, J., Aragão, L.E.O.C., Cardoso, A., Lees, A.C., Lennox, G.D., Tobias, J.A., Waldron, A., Barlow, J., 2020. A large-scale assessment of plant dispersal mode and seed traits across human-modified Amazonian forests. J. Ecol. 108, 1373–1385. https://doi.org/10.1111/1365-2745.13358.

Herault, B., Ouallet, J., Blanc, L., Wagner, F., Baraloto, C., 2010. Growth responses of neotropical trees to logging gaps. J. Appl. Ecol. 47, 821–831. https://doi.org/10.1111/j.1365-2664.2010.01826.x.

Hérault, B., Piponiot, C., 2018. Key drivers of ecosystem recovery after disturbance in a neotropical forest. For. Ecosyst. 5 (1), 1–15. https://doi.org/10.1186/s40663-017-0126-7.

Hubau, W., Lewis, S.L., Phillips, O.L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A.K., Ewango, C.E.N., Fauset, S., Mukinzi, J.M., Sheil, D., Sonké, B., Sullivan, M.J.P., Sunderland, T.C.H., Taedoumg, H., Thomas, S.C., White, L.J.T., Abernethy, K.A., Adu-Bredu, S., Amani, C.A., Baker, T.R., Banin, L.F., Baya, F., Begne, S.K., Bennett, A.C., Benedet, F., Bitariho, R., Bocko, Y.E., Boeckx, P., Boundja, P., Brienen, R.J.W., Brncic, T., Chezeaux, E., Chuyong, G.B., Clark, C.J., Collins, M., Comiskey, J.A., Coomes, D.A., Dargie, G.C., de Haulleville, T., Kamdem, M.N.D., Doucet, J.-L., Esquivel-Muelbert, A., Feldpausch, T.R., Fofanah, A., Foli, E.G., Gilpin, M., Gloor, E., Gonmadje, C., Gourlet-Fleury, S., Hall, J.S., Hamilton, A.C., Harris, D.J., Hart, T.B., Hockemba, M.B.N., Hladik, A., Ifo, S.A., Jeffery, K.J., Jucker, T., Yakusu, E.K., Kearsley, E., Kenfack, D., Koch, A., Leal, M.E., Levesley, A., Lindsell, J.A., Lisingo, J., Lopez-Gonzalez, G., Lovett, J.C., Makana, J.-R., Malhi, Y., Marshall, A.R., Martin, J., Martin, E.H., Mbayu, F.M., Medjibe, V.P., Mihindou, V., Mitchard, E.T.A., Moore, S., Munishi, P.K.T., Bengone, N.N., Ojo, L., Ondo, F.E., Peh, K.S.-H., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Qie, L., Reitsma, J., Rovero, F., Swaine, M.D., Talbot, J., Taplin, J., Taylor, D.M., Thomas, D.W., Toirambe, B., Mukendi, J.T., Tuagben, D., Umunay, P. M., van der Heijden, G.M.F., Verbeeck, H., Vleminckx, J., Willcock, S., Wöll, H., Woods, J.T., Zemagho, L., 2020. Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature 579, 80–87. https://doi.org/10.1038/s41586-020-2035-0.

Kalamandeen, M., Gloor, E., Johnson, I., Agard, S., Katow, M., Vanbrooke, A., Ashley, D., Batterman, S.A., Ziv, G., Holder-Collins, K., Phillips, O.L., Brondizio, E.S., Vieira, I., Galbraith, D., 2020. Limited biomass recovery from gold mining in Amazonian forests. J. Appl. Ecol. 57, 1730–1740. https://doi.org/10.1111/1365-2664.13669.

Koffi, A.B., Tondoh, E.J., Ehouman, E., Freycon, V., Piponiot, C., Amani, B.H., Hérault, B., 2025. Drivers of soil organic carbon recovery during secondary succession along a West African climate gradient. Ecol. Indic. 178, 114073. https://doi.org/10.1016/j.ecolind.2025.114073.

Kohl, T., Niether, W., Abdulai, I., 2024. Impact of common shade tree species on microclimate and cocoa growth in agroforestry systems in Ghana. Agrofor. Syst. 98, 1579–1590. https://doi.org/10.1007/s10457-024-01029-z.

Konan, I.K., N'Guessan, A.E., Dago, M.R., Kouassi, A., N'dja, J.K., Aussenac, R., Hérault, B., 2025a. Maximizing tree diversity in cocoa agroforestry: taking advantage of planted, spontaneous, and remnant trees. Agrofor. Syst. 99 (5), 107. https://doi.org/10.1007/s10457-025-01180-1.

Konan, I.K., N'Guessan, A.E., Kouassi, A., Dago, M.R., N'Dja, J.K., Aussenac, R., Hérault, B., 2025b. Unsung climate guardians: the overlooked role of remnant and spontaneous trees in carbon stocks and gains from tree growth in West African cocoa fields. PLoS One 20 (8), e0328763. https://doi.org/10.1371/journal.pone.0328763.

Kougbo, M.D., Konan, A.S., Dogba, M., Konan, A.P., Malan, D.F., 2023. Possibility of forest reconstitution from soil seed bank of cocoa and rubber farms in eastern Ivory Coast. Int. J. Sci. Res. Updat. 5, 012–022. https://doi.org/10.53430/ijsru.2023.5.1.0197.

Kouassi, A.K., Zo-Bi, I.C., Hérault, B., Konan, I.K., Dago, M.R., Lasbats, B., Aussenac, R., 2025. Tree growth in West African cocoa agroforestry systems: high timber yields and superior performance of natural regeneration. Ann. For. Sci. 82 (1), 1–15. https://doi.org/10.1186/s13595-025-01286-7.

Kouassi, A.K., Zo-Bi, I.C., Aussenac, R., Kouamé, I.K., Dago, M.R., N'guessan, A.E., Hérault, B., 2023. The great mistake of plantation programs in cocoa agroforests–Let's bet on natural regeneration to sustainably provide timber wood. Trees For. People 12, 100386. https://doi.org/10.1016/j.tfp.2023.100386.

Kurten, E.L., Wright, S.J., Carson, W.P., 2015. Hunting alters seedling functional trait composition in a Neotropical forest. Ecology 96, 1923–1932. https://doi.org/10.1890/14-1735.1.

Lai, H.R., Hall, J.S., Batterman, S.A., Turner, B.L., van Breugel, M., 2018. Nitrogen fixer abundance has no effect on biomass recovery during tropical secondary forest succession. J. Ecol. 106, 1415–1427. https://doi.org/10.1111/1365-2745.12979.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., Stein, J. A.R., 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. Conserv. Lett. 7, 61–69. https://doi.org/10.1111/conl.12013.

Locatelli, B., Catterall, C.P., Imbach, P., Kumar, C., Lasco, R., Marín-Spiotta, E., Mercer, B., Powers, J.S., Schwartz, N., Uriarte, M., 2015. Tropical reforestation and climate change: beyond carbon. Restor. Ecol. 23, 337–343. https://doi.org/10.1111/rec.12209.

Makelele, I.A., Verheyen, K., Boeckx, P., Cizungu Ntaboba, L., Mujinya Bazirake, B., Ewango, C., Bauters, M., 2021. Afrotropical secondary forests exhibit fast diversity and functional recovery, but slow compositional and carbon recovery after shifting cultivation. J. Veg. Sci. 32, e13071. https://doi.org/10.1111/jvs.13071.

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Böhning-Gaese, K., 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. Conserv. Biol. 26, 1072–1081. https://doi.org/10.1111/j.1523-1739.2012.01927.x.

Martin, P.A., Newton, A.C., Bullock, J.M., 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proc. R. Soc. B Biol. Sci. 280. https://doi.org/10.1098/rspb.2013.2236.

Masolele, R.N., Marcos, D., De Sy, V., Abu, I.O., Verbesselt, J., Reiche, J., Herold, M., 2024. Mapping the diversity of land uses following deforestation across Africa. Sci. Rep. 14 (1), 1681. https://doi.org/10.1038/s41598-024-52138-9.

Matos, F.A.R., Magnago, L.F.S., Aquila Chan Miranda, C., de Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., da Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S.V., Meira-Neto, J.A.A., Edwards, D.P., 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Glob. Change Biol. 26, 509–522. https://doi.org/10.1111/gcb.14824.

Matsuo, T., Martínez-Ramos, M., Bongers, F., van der Sande, M.T., Poorter, L., 2021. Forest structure drives changes in light heterogeneity during tropical secondary forest succession. J. Ecol. 109, 2871–2884. https://doi.org/10.1111/1365-2745.13680.

Maurent, E., Hérault, B., Piponiot, C., Derroire, G., Delgado, D., Finegan, B., Kientz, M.A., Amani, B.H.K., Bieng, M.A.N., 2023. A common framework to model recovery in disturbed tropical forests: common model for disturbed forest recovery. Ecol. Model. 483. https://doi.org/10.1016/j.ecolmodel.2023.110418.

Mirabel, A., Ouédraogo, D.Y., Beeckman, H., Delvaux, C., Doucet, J.L., Hérault, B., Fayolle, A., 2019. A whole-plant functional scheme predicting the early growth of tropical tree species: evidence from 15 tree species in Central Africa. Trees 33 (2), 491–505. https://doi.org/10.10007/s00468-018-1795-8.

Morante-Filho, J.C., Faria, D., Mariano-Neto, E., Rhodes, J., 2015. Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the brazilian atlantic forest. PLoS One 10, e0128923. https://doi.org/10.1371/journal.pone.0128923.

Mukul, S.A., Herbohn, J., Firn, J., 2016. Tropical secondary forests regenerating after shifting cultivation in the Philippines uplands are important carbon sinks. Sci. Rep. 6, 22483. https://doi.org/10.1038/srep22483.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

N'Guessan, A.E., N'dja, J.K., Yao, O.N., Amani, B.H.K., Gouli, R.G.Z., Piponiot, C., Zo-Bi, I.C., Hérault, B., 2019. Drivers of biomass recovery in a secondary forested landscape of West Africa. For. Ecol. Manag. 433, 325–331. https://doi.org/10.1016/j.foreco.2018.11.021.

Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.-H., Vílchez-Alvarado, B., 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecol. Lett. 12, 385–394. https://doi.org/10.1111/j.1461-0248.2009.01292.x.

Norris, K., Asase, A., Collen, B., Gockowksi, J., Mason, J., Phalan, B., Wade, A., 2010. Biodiversity in a forest-agriculture mosaic – The changing face of West African rainforests. Biol. Conserv. 143, 2341–2350. https://doi.org/10.1016/J.BIOCON.2009.12.032.

Oberleitner, F., Egger, C., Oberdorfer, S., Dullinger, S., Wanek, W., Hietz, P., 2021. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. For. Ecol. Manag. 479, 118580. https://doi.org/10.1016/J.FORECO.2020.118580. –118580.

OIPR, 2020. Plan D'aménagement Et De Gestion du Parc national De Taï (PAG) 2020-2029 (Rapport Stratégique De Planification Environnementale). Abidjan, Côte d'Ivoire.

Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., Proença, V., Raffaelli, D., Suttle, K.B., Mace, G.M., Martín-López, B., Woodcock, B.A., Bullock, J.M., 2015. Biodiversity and resilience of ecosystem functions. Trends Ecol. Evol. 30, 673–684. https://doi.org/10.1016/j.tree.2015.08.009.

Ouattara, T.A., Kouamé, K.F., Zo-Bi, I.C., Vaudry, R., Grinand, C., 2021. Changes in land cover and land use from 2016 to 2019 in south-east côte d'ivoire: impacts of cash crops on forests. Bois For. Trop. 347, 89–104. https://doi.org/10.19182/bft2021.347.a31868.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A Large and Persistent Carbon Sink in the World's Forests. Science 333, 988–993. https://doi.org/10.1126/science.1201609.

Peña-Claros, M., 2003. Changes in forest structure and species composition during secondary forest succession in the bolivian amazon1. Biotropica 35, 450–461. https://doi.org/10.1111/j.1744-7429.2003.tb00602.x.

Peterson, G.D., Heemskerk, M., 2001. Deforestation and forest regeneration following small-scale gold mining in the Amazon: the case of Suriname. Env. Conserv. 28, 117–126. https://doi.org/10.1017/S0376892901000121.

Piponiot, C., Sist, P., Mazzei, L., Peña-Claros, M., Putz, F.E., Rutishauser, E., Hérault, B., 2016. Carbon recovery dynamics following disturbance by selective logging in Amazonian forests. Elife 5, e21394. https://doi.org/10.7554/eLife.21394.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., De Almeida-Cortez, J.S., Cabral, G.A.L., De Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Munõz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., De Oliveira, A.A., Orihuela-Belmonte, E., Penã-Claros, M., Pérez-Garciá, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., Van Breugel, M., Van Der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I. C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214. https://doi.org/10.1038/nature16512.

Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F., Chazdon, R.L., Farrior, C.E., Kambach, S., Meave, J.A., Muñoz, R., Norden, N., Rüger, N., van Breugel, M., Almeyda Zambrano, A.M., Amani, B., Andrade, J.L., Brancalion, P.H.S., Broadbent, E.N., de Foresta, H., Dent, D.H., Derroire, G., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Fantini, A.C., Finegan, B., Hernández-Jaramillo, A., Hernández-Stefanoni, J.L., Hietz, P., Junqueira, A.B., N'dja, J.K., Letcher, S.G., Lohbeck, M., López-Camacho, R., Martínez-Ramos, M., Melo, F.P.L., Mora, F., Müller, S.C., N'Guessan, A.E., Oberleitner, F., Ortiz-Malavassi, E., Pérez-García, E.A., Pinho, B.X., Piotto, D., Powers, J.S., Rodríguez-Buriticá, S., Rozendaal, D.M.A., Ruíz, J., Tabarelli, M., Teixeira, H.M., Valadares de Sá Barretto Sampaio, E., van der Wal, H., Villa, P.M., Fernandes, G.W., Santos, B.A., Aguilar-Cano, J., de Almeida-Cortez, J.S., Alvarez-Davila, E., Arreola-Villa, F., Balvanera, P., Becknell, J.M., Cabral, G.A.L., Castellanos-Castro, C., de Jong, B.H.J., Nieto, J.E., Espírito-Santo, M.M., Fandino, M.C., García, H., García-Villalobos, D., Hall, J.S., Idárraga, A., Jiménez-Montoya, J., Kennard, D., Marín-Spiotta, E., Mesquita, R., Nunes, Y.R.F., Ochoa-Gaona, S., Peña-Claros, M., Pérez-Cárdenas, N., Rodríguez-Velázquez, J., Villanueva, L.S., Schwartz, N.B., Steininger, M.K., Veloso, M.D.M., Vester, H.F.M., Vieira, I.C.G., Williamson, G.B., Zanini, K., Hérault, B., 2021a. Multidimensional tropical forest recovery. Science 374, 1370–1376. https://doi.org/10.1126/science.abh3629.

Poorter, L., Rozendaal, D.M.A., Bongers, F., Almeida, D.J.S., Álvarez, F.S., Andrade, J.L., Arreola Villa, L.F., Becknell, J.M., Bhaskar, R., Boukili, V., Brancalion, P.H.S., César, R.G., Chave, J., Chazdon, R.L., Dalla Colletta, G., Craven, D., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Díaz, García, E., Dupuy, J.M., Durán, S.M., Espírito Santo, M.M., Fernandes, G.W., Finegan, B., Granda Moser, V., Hall, J.S., Hernández-Stefanoni, J.L., Jakovac, C.C., Kennard, D., Lebrija-Trejos, E., Letcher, S. G., Lohbeck, M., Lopez, O.R., Marín-Spiotta, E., Martínez-Ramos, M., Meave, J.A., Mora, F., de Souza Moreno, V., Müller, S.C., Muñoz, R., Muscarella, R., Nunes, Y.R. F., Ochoa-Gaona, S., Oliveira, R.S., Paz, H., Sanchez, Azofeifa, A., Sanaphre-Villanueva, L., Toledo, M., Uriarte, M., Utrera, L.P., van Breugel, M., van der Sande, M.T., Veloso, M.D.M., Wright, S.J., Zanini, K.J., Zimmerman, J.K., Westoby, M., 2021b. Functional recovery of secondary tropical forests. Proc. Natl. Acad. Sci. 118, e2003405118. https://doi.org/10.1073/pnas.2003405118. –e2003405118.

Pouteau, R., Picard, J., Doumenge, C., Brncic, T., Gillet, J.F., Doucet, J.L., Gourlet-Fleury, S., Kimpouni, V., Loumeto, J.J., Pélissier, R., Réjou-Méchain, M., 2024. The puzzling ecology of African Marantaceae forests. Am. J. Bot. 111. https://doi.org/10.1002/ajb2.16320.

Reich, K.F., Kunz, M., Bitter, A.W., Von Oheimb, G., 2022. Do different indices of forest structural heterogeneity yield consistent results? IForest 15, 424–432. https://doi.org/10.3832/ifor4096-015.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. biomass: an r package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol. Evol. 8, 1163–1167. https://doi.org/10.1111/2041-210X.12753.

Sangne, C.Y., Barima, Y.S.S., Bamba, I., N'Doumé, C.-T.A., 2015. Dynamique forestière post-conflits armés de la Forêt classée du Haut-Sassandra (Côte d'Ivoire). VertigO - Rev. Électron. Sci. Env. https://doi.org/10.4000/vertigo.16784.

Sanial, E., Ruf, F., Louppe, D., Mietton, M., Herault, B., 2023. Local farmers shape ecosystem service provisioning in West African cocoa agroforests. Agrofor. Syst. 97 (3), 401–414. https://doi.org/10.1007/s10457-021-00723-6.

Sen, A., 1997. On Economic Inequality. Oxford university press.

Sheoran, V., Sheoran, A.S., Poonia, P., 2008. Soil reclamation of abandoned mine land by revegetation: a review. Int. J. Soil, Sed. Water 3, 13.

Swaine, M.D., Hall, J.B., 1983. Early succession on cleared forest land in Ghana. J. Ecol. 71, 601–627. https://doi.org/10.2307/2259737.

Tchatchou, B., Sonwa, D.J., Ifo, S., Tiani, A.M., 2015. Déforestation Et Dégradation Des Forêts Dans Le Bassin du Congo: État des lieux, Causes Actuelles Et Perspectives. CIFOR.

Teixeira, H.M., Cardoso, I.M., Bianchi, F.J.J.A., da Cruz Silva, A., Jamme, D., Peña-Claros, M., 2020. Linking vegetation and soil functions during secondary forest succession in the Atlantic forest. For. Ecol. Manag. 457, 117696. https://doi.org/10.1016/j.foreco.2019.117696.

Titenwi, P.N., Sainge, M.N., Kargbo, U., Kamara, R.A.S., Musa, A., Kabba, T.M., Buanie, B.K., Njouonkou, A.L., Aruna, E., Sullivan, M.J.P., Leite, A., Cuni-Sanchez, A., 2025. Carbon recovery in secondary forests: insights from three West African countries. For. Ecol. Manag. 575, 122386. https://doi.org/10.1016/J.FORECO.2024.122386. –122386.

Tondoh, J.E., Kouamé, F.N., guessan, Martinez Guéi, A., Sey, B., Wowo Koné, A., Gnessougou, N., 2015. Ecological changes induced by full-sun cocoa farming in Côte d'Ivoire. Glob. Ecol. Conserv. 3, 575–595. https://doi.org/10.1016/J.GECCO.2015.02.007.

Traoré, S., Zo-Bi, I.C., Piponiot, C., Aussenac, R., Hérault, B., 2024. Fragmentation is the main driver of residual forest aboveground biomass in West African low forest-high deforestation landscapes. Trees For. People 15, 100477. https://doi.org/10.1016/j.tfp.2023.100477.

Trochain, J.L., 1980. Ecologie vegetale de la zone intertropicale non desertique.

Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L.E.O.C., Nasi, R., 2021. Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. Sci. Adv. 7, eabe1603. https://doi.org/10.1126/sciadv.abe1603.

Weiner, J., Solbrig, O.T., 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61, 334–336. https://doi.org/10.1007/BF00379630.

Wu, M.M., Liang, Y., He, H.S., Liu, B., Ma, T., 2022. Remnant trees location and abundance play different roles in forest landscape recovery. For. Ecol. Manag. 511, 120154. https://doi.org/10.1016/j.foreco.2022.120154.

Xu, C., Silliman, B.R., Chen, J., Li, X., Thomsen, M.S., Zhang, Q., Lee, J., Lefcheck, J.S., Daleo, P., Hughes, B.B., Jones, H.P., Wang, R., Wang, S., Smith, C.S., Xi, X., Altieri, A.H., van de Koppel, J., Palmer, T.M., Liu, L., Wu, J., Li, B., He, Q., 2023. Herbivory limits success of vegetation restoration globally. Science 382, 589–594. https://doi.org/10.1126/science.add2814.

Yao Sadaiou Sabas, B., Gislain Danmo, K., Akoua Tamia Madeleine, K., Jan, B., 2020. Cocoa production and forest dynamics in ivory coast from 1985 to 2019. Land 9, 524. https://doi.org/10.3390/land9120524.

Zo-Bi, I.C., Herault, B., 2023. Fostering agroforestry? lessons from the republic of Côte d'Ivoire. Bois For. Trop. 356, 99–104. https://doi.org/10.19182/bft2023.356.a37234.