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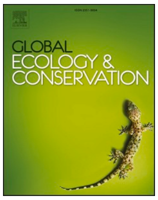

Original research article

Spatio-temporal dynamics of Isoberlinia-dominated woodlands in disturbance-prone landscapes over 15 years

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ABSTRACT

Understanding the impact of productivity and disturbance on vegetation succession is a crucial debate in community ecology, with significant implications for biodiversity conservation. Productivity and disturbance influence species richness and structure, enhancing our understanding of vegetation dynamics and species coexistence over time. Numerous theories, such as the Intermediate Stress Hypothesis, Intermediate Disturbance Hypothesis, and Dynamic Equilibrium Model, have been proposed to explain these mechanisms. However, our understanding of how productivity and disturbance affect the spatio-temporal dynamics of Isoberlinia-dominated woodlands remains limited. We analyzed floristic data from sixteen sites with 64 permanent plots (400 m^2 each) along a south-north precipitation gradient (1112–991 mm per year) over 15 years (2006–2020). We calculated species richness and density for sapling and adult trees, and estimated two main variables: potential productivity using water deficit as a proxy, and disturbance intensity using logging rate. A linear mixed effects model, with plots nested within sites as random variables, was developed to test the effect of potential productivity and level of disturbance on species richness and density, for sapling and adult trees. Our results showed that species richness (SR) and density, for saplings and adult trees decreased over time, regardless of the disturbance and potential productivity gradients. Compared to higher levels of disturbance, low and medium levels of disturbance significantly increase the species richness of saplings and adult trees. In addition, the density of adult trees and saplings decreased over time, but increased with the level of disturbance from high to low. These results suggest that increased disturbance reduces the density of woodland species in favor of invasive species, typically savanna species. Overall, our results are consistent with the Dynamic Equilibrium Model, highlighting the complex interactions between disturbance regimes, productivity gradients, and their effects on species richness within ecosystems. Efficient forest management in Isoberlinia-dominated would avoid the high levels of logging that promote the establishment of invasive species and would maintain the biodiversity of this ecosystem in the long term.

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1. Introduction

Factors shaping vegetation succession have been widely discussed in community ecology (Clements, 1916; Connell, 1978; Doležal et al., 2013; Finegan, 1984; Grime, 1973; Huston, 1979, 2014; Łaska, 2001; McCook, 1994; Meiners et al., 2015; Naudiyal and Schmerbeck, 2018; Noble and Slatyer, 1980; Prach and Walker, 2020, 2011; Sheil, 2001; Van Hulst, 1980). The results of these scientific debates do not adequately integrate strategies to solve environmental and anthropogenic problems (Prach and Walker, 2011). Overall, forest dynamics have been commonly interpreted in a non-equilibrium framework, emphasizing the importance of variability, disturbance regimes and multiple successional pathways (Prach and Walker, 2020; Lindenmayer et al., 2019), rather than in a single-state climax model (Clements, 1916). Although all natural communities probably experience disturbance at some spatial and temporal scale, the role of disturbance in community dynamics has historically been largely overlooked in tropical ecosystems (García Molinos and Donohue, 2011; Sousa, 1984). However, the impact of disturbances on biodiversity remains a critical issue in defining conservation policies for plant communities for the sustainable management of valuable and vital resources and ecosystem services. In community ecology, a wealth of diversity theories have been proposed to explain diversity patterns, focusing on how species richness is influenced by factors such as stress and disturbance (Vonlanthen et al., 2006). Among these concepts, the most widely recognized theories are the "Intermediate Stress Hypothesis (ISH)" and the "Intermediate Disturbance Hypothesis (IDH)" (Huston, 2014), which address how stress and disturbance predict diversity, respectively.

The Intermediate Stress Hypothesis (ISH) is a predominant community ecology theory explaining the relationship between biodiversity and environmental stress. The ISH forecasts maximum species richness at moderate intensities of environmental stress (Grime, 1973; Kammer and Möhl, 2002), and is often interpreted as meaning that at high levels of stress, the site is too harsh for many species to survive, whereas at low levels of stress, the site is favorable and one or a few species dominate through competitive exclusion (Rosenzweig and Abramsky, 1993; Vonlanthen et al., 2006). For Grime (2006), stress is defined as an external constraint which limits biomass production of all or part of the vegetation. Stress can also be determined by resource availability or plant growth rate (Biaou, 2009). Productivity is often used to describe the plants' growth rate (Janousek and Dreitz, 2020), and was measured as net primary productivity, rainfall or evapotranspiration (Biaou, 2009; Mittelbach et al., 2001; Rosenzweig, 1992). On the other hand, the relationship between disturbance and biodiversity has been developed by Connell (1978) and Huston (1979), through the Intermediate Disturbance Hypothesis (IDH). The IDH forecasts that intermediate levels of disturbance produce higher diversity than either very high or very low levels because too little disturbance leads to low diversity through competitive exclusion and too much disturbance eliminates species incapable of rapid re-colonization (Dial and Roughgarden, 1998; Janousek and Dreitz, 2020). Disturbances are perceived as mechanisms for regulating the composition and coexistence of species within a community (Janousek and Dreitz, 2020), and they occur in a variety of forms (Dornelas, 2010; Prach and Walker, 2020; Sousa, 1984), both natural and anthropogenic. In this study, disturbance is defined as all mechanisms which reduce the plant biomass by causing its partial or complete destruction (Battisti et al., 2016; Jentsch and White, 2019; Vonlanthen et al., 2006). Because it does not take into account the variation in ecosystem productivity across sampling locations along a spatial gradient (Huston, 2014, 1994), the IDH was later questioned, and the Dynamic Equilibrium Model (DEM) was proposed by (Huston, 1979) in other to primarily connects both two-dimensional models (IDH and ISH) within a three-dimensional model (Biaou, 2009; Kammer and Möhl, 2002; Loranger et al., 2016).

The Dynamic Equilibrium Model is a synthesis theory of species diversity which suggests that disturbance interacts with the productivity of an ecosystem to affect species richness (Janousek and Dreitz, 2020). The DEM predicts the highest species richness at both intermediate levels of productivity and disturbance (i.e., unimodal relationship) (Janousek and Dreitz, 2020; Kammer and Möhl, 2002; Pollock et al., 1998). However, such interaction between disturbance and productivity could also lead to positive responses (positive correlation of species richness with disturbance in a highly productive environment) or negative (negative correlation of species richness with disturbance in a low productive environment) (Huston, 2014; Kadmon and Benjamini, 2006; Kondoh, 2001). Huston's DEM has been empirically tested for grassland and annual plant communities (During and Willems, 1984; Kammer and Möhl, 2002; Loranger et al., 2016; Osem et al., 2002), bird communities (Janousek and Dreitz, 2020; McWethy et al., 2010), and for other ecological communities (Agard et al., 1996; Cardinale et al., 2006; Rashit and Bazin, 1987; Wolverton et al., 2009), and rarely tested on tree communities especially in tropical areas where environmental conditions are highly variable. Furthermore, empirical evidence for Huston's DEM test on tropical forests is rare, and even less on dry woodlands, in a context where these woodlands were subject to increasing human population growth pressure (land clearance for agriculture, harvesting fuel wood and timber, fire and grazing) (Assédé et al., 2020; Biaou et al., 2021; Moonlight et al., 2020), which leads to vegetation change, both in terms of structure and floristic composition (Kalaba et al., 2013), as well as biodiversity loss (Biaou et al., 2022; Muvengwi et al., 2020).

Traditionally, woodlands ecosystems have been interpreted through the model of forest succession (Clements, 1916). However, savannas, which are often a mosaic of herbaceous and woody vegetation, follow different ecological dynamics that require further attention (Bond and Archibald, 2003). Savannas, particularly in Africa, are known for their ability to maintain a dynamic relationship between woodland and grassland in response to climatic variations and disturbances (Fayolle et al., 2019; Sankaran et al., 2005). In particular, savanna dynamics depend on factors such as fire frequency, grazing regime and drought cycles, which influence plant regeneration and composition (Biaou, 2009; Bond and Keeley, 2005). Rather than considering these woodland ecosystems as a step-in forest succession towards a stable climax, it is more relevant to examine them through the lens of savanna ecology, where complex interactions between disturbance and climate regulate structure and biodiversity (Scholes and Archer, 1997).

The purpose of this study is to test the predictions of these three diversity theories (ISH, IDH and DEM) in the context of Isoberlinia-woodlands distributed along a spatial gradient of productivity, and in disturbance-prone landscapes. Woodlands cover 25 % of Africa's natural vegetation (Biaou, 2009; Mayaux et al., 2004), and are considered in arid and semi-arid tropical ecosystems as a sub-climax formation, in plant succession (Clements, 1916; Prach and Walker, 2020). These tropical dry forests are central to the lives of over 50 million people in Africa (Kiruki et al., 2017) due to their important role in providing ecosystem services (Chidumayo and Marunda, 2010), but have often been neglected in monitoring and modeling (Abbot and Homewood, 1999; Seosaw, 2021), despite the threats to their biodiversity. Understanding monodominant tropical forests' responses under different drivers of change is more important than ever (Muvengwi et al., 2020), and long-term permanent-plot monitoring is regarded as one of the best approaches to monitor biodiversity and ecological phenomena (Gross et al., 2018; Prach and Walker, 2020), in both spatial and temporal scale, because trees have a long lifespan and because changes resulting from post-disturbance succession would be gradual (Vale et al., 2015). In the absence of long-term data (greater than 40 years) (Condit, 1995; Ediriweera et al., 2020; Sheil, 2001), monitoring 64 permanent plots spread over Isoberlinia-woodlands, on a medium-term (2006–2020) is likely to provide insight in this plant community spatio-temporal dynamics as compared to the less than ten years or even intra-year monitoring periods which are frequent in many West African countries.

Drawing upon the three diversity theories (ISH, IDH and DEM), the study hypothesized the following: (i) Species richness is highest at medium levels of disturbance and productivity, both in sapling and in adult trees in the woodlands. It means, that whether we are talking about potential productivity or disturbance, we expect high species richness at the medium level of the gradient, both in sapling and adult trees. The assumption is that species richness will be low at the extremes (low or high) of each gradient; (ii) A high rate of Woodland disturbance will adversely affect adult tree density, but will have a positive effect on the sapling density in response to the disturbance. An implicit prediction is that sapling density will be highest when the level of disturbance is low. Similarly, the density of sapling should increase linearly with productivity within the limits of available resources, partly because individuals can share more resources (Biaou, 2009; Currie, 1991; Rosenzweig, 1968), (iii) Species richness is highest at both medium gradients of productivity and disturbance. In other words, at the extreme levels (low or high) of the gradient of the interaction between disturbance and productivity, we expect disturbance to have a negative effect low-productivity sites and have a positive effect on species richness and species density on high-productivity sites.

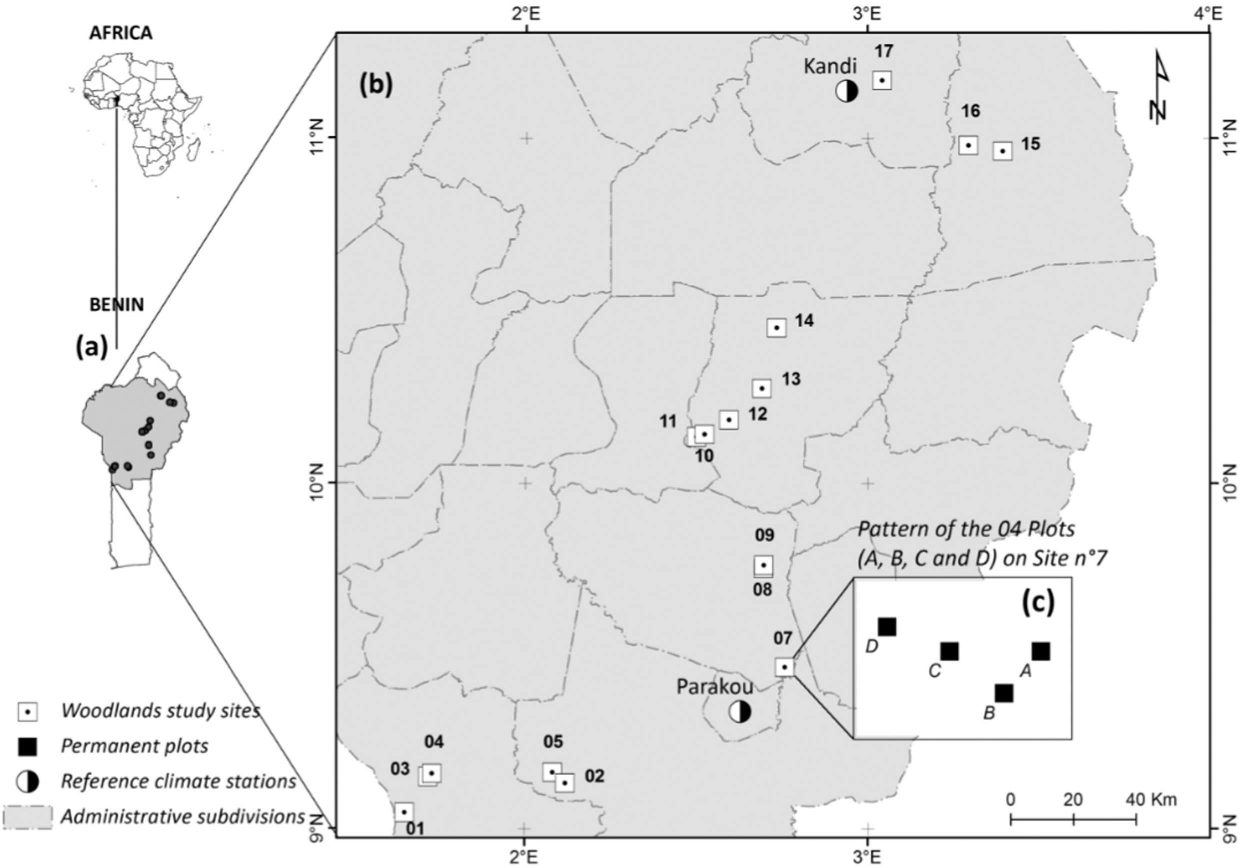

Fig. 1. (a) Location of the study area in Benin; (b) distribution of the 16 *Isoberlinia*-woodlands sites (numbered from 1 to 17; site n°6 is not considered, as historical data are not available); and (c) illustration of the pattern of the 04 permanent plots (A, B, C, D) of site n°7.

2. Materials and methods

2.1. Study area

Our study was conducted in Beninese *Isoberlinia*-woodlands located between 1°45' and 3°45' longitude East, and 9° to 11°30' latitude North (Fig. 1). The study area is marked by a precipitation gradient with increasing aridity from south to north. The climate in the southern part of the study area is Sudano-Guinean, characterized by a progressive merging of the two precipitation peaks into one peak, which indicates a unimodal rainfall regime, and marks the transition towards a typical Sudanian climate. The mean annual rainfall is 1200 mm with a humidity index (IM) varying from 2.7 to 3.9 (Adomou, 2005; Sinsin and Kampmann, 2010). The humidity index of Mangenot (1951) quantifies climatic variables like rainfall, dry season intensity, and air humidity, reflecting water availability. High values (IM $>$ 7.5) indicate hyper-humid climates, while low values (IM $<$ 1) suggest Sahelian dryness. In the northern part of the study area, the climate is Sudanian, characterized by a level of precipitation less than 1150 mm.year-1, a well-defined rainy season from April to October (i.e. 7 months) with rainfall peaking around August/September, and drier conditions with a humidity index less than 2 (Adomou, 2005; Sinsin and Kampmann, 2010). The dominant soil type is tropical ferruginous. The vegetation types primarily included tree and shrub savannas, woodlands, gallery forests, and dry semi-deciduous forests (Biaou, 2009; Hountondji et al., 2013; Sinsin and Kampmann, 2010; Sokpon et al., 2006). Slash-and-burn agriculture dominated by cotton growing, logging of timber wood, harvesting fuel wood, fire and grazing were pointed out as the main anthropogenic disturbances (Hountondji et al., 2013; Zida et al., 2008) that shaping vegetation patterns (Biaou, 2009; Kennedy and Potgieter, 2003).

2.2. Data collection

2.2.1. Sampling design and vegetation monitoring

The study is based on periodic vegetation monitoring data collected over 15 years, from 2006 to 2020, in *Isoberlinia* woodlands in Benin (West Africa). The study design was initially set up in 2003 during a PhD research program (Biaou, 2009), where permanent plots were established on sixteen *Isoberlinia* woodland sites, along a south-north precipitation gradient (from 1112 m to 991 mm per year) to capture the maximum variation in productivity. Each site had four random plots set up at least 25 m apart (Fig. 1). Hence, there were a total of 64 plots of *Isoberlinia* woodlands involved in the study. *Each 400 m^2 plot was established in a 20 m x 20 m orthonormal reference system where the coordinates (Xm, Ym) of each tree were recorded as soon as the plots were established in 2003. These coordinates (X, Y) in metres are used to monitor each tree in the plot. In addition, each tree was marked with red paint at a height of 1.30 m above ground level (breast height) where the DBH is repeatedly measured. These markings are periodically refreshed.* Each of the 64 plots was inventoried annually at the same time of the year (September to October) in 2006, 2010, 2016 and 2020, following the same protocol, to ensure comparability of data collected over time. From the first census in 2006 to the last census in 2020, and within each plot, all woody species equal to or greater than 1.5 m in height (saplings and trees), were identified, marked on the stem or trunk with red paint at 1.3 m above ground level (breast height), their diameter at breast height (DBH) was measured using a standard diameter tape, and their location was mapped for ongoing monitoring. The adult tree is defined as a tree with a DBH equal to or greater than 10 cm (Hogan et al., 2018) and a sapling as young tree with height greater than or equal to 1,50 m and DBH less than 10 cm (Otterstrom et al., 2006). Whenever possible, we identified the species in the field, using local botanical experts and available flora and species lists (Akoègninou et al., 2006; Arbonnier, 2009), but when necessary, specimens were collected for identification or confirmation in the laboratory. APG IV is the nomenclature used to classify plant species.

2.2.2. Climate data at woodlands sites level, and productivity assessment along the rainfall gradient

Based on the geographic coordinates of each woodland plot, we extracted the numerical values of two bioclimatic variables we found to be the most biologically relevant to assess the ecosystem productivity, by using the "extract value by point" function of SDMtoolbox in ArcGis 10.1. These two bioclimatic variables (annual precipitation and annual Potential evapotranspiration) were downloaded from the European Centre for Medium-Range Weather Forecasts (ECMWF) reanalysis v5 (ERA5) (Copernicus Climate Change Service) daily data from 1940 to 2024 (https://cds.climate.copernicus.eu/datasets/reanalysis-era5-land?tab=download). Based on these bioclimatic variables, we assessed the ecosystem potential productivity along the precipitation gradient for each woodland site by using the water deficit as a proxy of potential productivity (Biaou, 2009; Paltineanu et al., 2007). The absolute value of water deficit is used in the study, to facilitate the interpretation of our results, because of the negative value of water deficit in dry ecosystems (Biaou, 2009). The water deficit was calculated as the difference between the annual precipitation (P mm) and the annual Potential evapotranspiration (PET mm): $(P - PET)$.

2.2.3. Woodlands' disturbance assessment

By disturbance, we meant plant biomass destruction (Battisti et al., 2016; Jentsch and White, 2019; Vonlanthen et al., 2006) due to anthropogenic disturbances (or missing trees due to logging) which have led to a change in the density of adult tree compared to the initial state. The level of disturbance was assessed for each plot over successive census years (2006, 2010, 2016 and 2020). To assess anthropogenic disturbance, we focused on logging as a key factor influencing vegetation dynamics. Logging was assessed by plotting for each year of the successive census (2006, 2010, 2016 and 2020) by counting tree stumps cut (trees with DBH $\geq$ 10 cm). Logging intensity was assessed per lot and for 2010, 2016 and 2020 censuses as the ratio $(NS_t/N_0)x100$, where NS_t is the number of tree stumps counted in a given year (2010, 2016 or 2020) and N_0 is the initial number of trees at the time of the first census in 2006. Disturbance intensity was estimated as low if the logging rate was less than 25 %, medium if it was between 25 % and 50 %, and high if it exceeded

50 %.

2.2.4. Diversity indices calculation and the stem density

Data recorded within plots on woody trees $\geq$ 1.50 m in height during the four censuses (2006, 2010, 2016 and 2020) were grouped by genus and family, and into two tree sizes such as adult trees (DBH $\geq$ 10 cm) and sapling (DBH $<$ 10 cm), and the following indices were calculated: species richness, the stem density, and Temporal Beta-diversity Index (TBI). The species richness, i.e. the number of biological species in a particular community (Kondoh, 2001) and the stem density were assessed for adult trees and saplings, for each year of the census, and for each woodland study plot. Species richness was calculated as the number of distinct woody species present in the plot area, and tree density (N) was the number of trees in the 400 m^2 plot. Following Legendre's Temporal Beta-diversity Index (TBI) (Legendre, 2019), we measured the dissimilarity of the species composition on the same plot between an initial survey (T1 i.e. 2006) and a given year survey (T2 i.e. 2010, T3 i.e. 2016, T4 i.e. 2020). We use TBI dissimilarity to assess the changes that have occurred in the woodland's community composition in the same plot through time from repeated census intervals (2006, 2010, 2016 and 2020). The TBI was computed using the package *adespatial* (Dray et al., 2019) in R version 4.1.2 (R Core Team, 2018), based on species abundance data. Moreover, the components species abundance losses and species abundance gains of the TBI dissimilarity were used to analyze the effects of disturbance and potential productivity on the woodlands community, to identify the plots that have changed in composition in exceptional ways, in space-time surveys (Legendre, 2019).

The equations of the TBI dissimilarity and its loss and gain components (Legendre, 2019) were as follows:

$$\mathit{Dissimilarity\ index}(D) = (B + C)/(2A + B + C)$$

$$\mathit{Species\ losses} = B/(2A + B + C)$$

$$\mathit{Species\ gains} = C/(2A + B + C)$$

With:

- A: the part of the abundance of species that is common to the two surveys. It represents the unscaled similarity between the two surveys.
- B: the part of the abundance of species that is higher in Survey 1 than in Survey 2. It is the unscaled sum of species losses between T1 and T2.
- C: the part of the abundance of species that is higher in Survey 2 than in Survey 1. It is the unscaled sum of species gains between T1 and T2.
- (2A + B + C), the denominator of Odum's percentage difference index.

2.3. Data analysis

We tested the effect of disturbance level and potential productivity on biodiversity index and density of tree and sapling separately (separate models), using linear mixed-effects models with package nlme (Pinheiro et al., 2021) of R, with random variable plots nested within sites. The fixed effects were potential productivity, disturbance and year. We included interactions with year because the available predictors were time-dependent. This approach allowed for measurements over time on the same plots, and plots nested within sites. For each of the dependent variables (density and biodiversity index such as species richness, species losses and gains, and dissimilarity), we analyzed three steps: (i) baseline model comprising the random effect and errors covariance structure, (ii) full model including all fixed effects added to the baseline model and (iii) determination of the best modelling approach through the simplification of the full model.

We compared alternate baseline models, with different random effect types and different error covariance structures, using

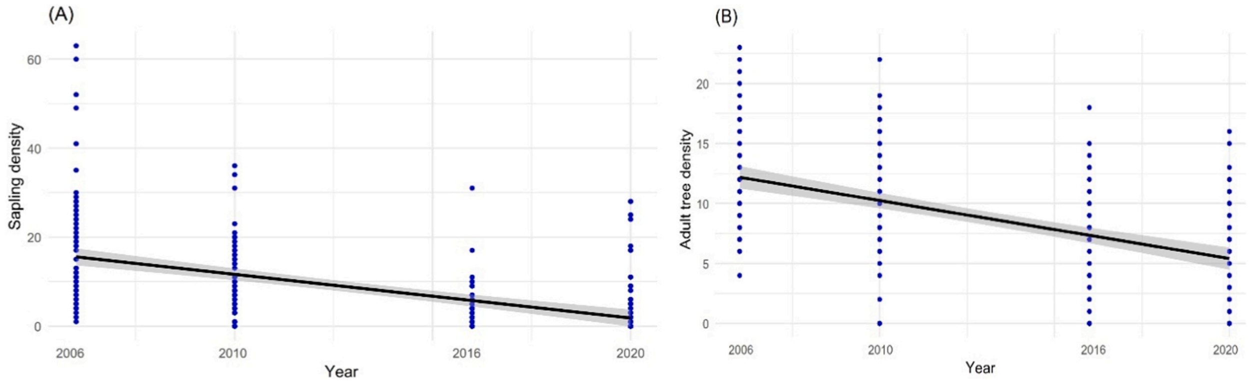

Fig. 2. Trend in sapling density (A) and adult tree density (B) over the years.

likelihood ratio tests to check whether adding more complexity improved the model fit (Ligges, 2009). For both sapling species richness and density, the model was significantly improved with plots nested within sites and the inclusion of a random intercept. We reduced the full model step by step, starting with the removal of the interactions involving variables with the lowest explanatory power as indicated by the hierarchical variance partitioning. At each step of the model simplification, we compared alternate models using the likelihood ratio test with the Anova function and selected the model that significantly improved the model fit with the lowest Akaike information criterion (AIC). We ultimately used the restricted maximum likelihood (REML) method to estimate parameters in the best-fitting model following Pinheiro et al. (2021). Final checking of the best-fitting models indicated that residual errors were reasonably close to a normal distribution. The linear model adequately explained the variation in changes in adult trees and sapling biodiversity indices and stem density.

3. Results

3.1. Changes in Isoberlinia-woodlands plots composition through time

The density of saplings and adult trees decreases significantly over the years (Fig. 2A and B). In addition, the same trend is observed with the TBI statistics for the same period (2006–2020), as shown in Fig. 3, where the red line parallel to and below the green line indicates that density losses by species significantly dominate changes in all woodland's plots between 2006 and 2020.

3.2. Changes in species composition from 2006 to 2020

From 2006 to 2020, 429 tree stems were lost in the woodland plot, while 14 stems (height ≥ 1.50 m and DBH ≥ 10 cm) were gained through recruitment (Table 1). The species with the greatest decline in abundance were: *Isoberlinia spp., Lannea acida* A.Rich.*, Pterocarpus erinaceus* Poir*, Burkea africana, Pericopsis laxiflora* (Benth. ex Baker) Meeuwen*, Vitellaria paradoxa* C.F.Gaertn., *Parinari curatellifolia* Planch. ex Benth.*, Terminalia leiocarpa* (DC.) Baill.*, Uapaca togoensis* Pax*, Margaritaria discoidea* (Baill.) G.L.Webster*, Monotes kerstingii* Gilg*, Maranthes polyandra* (Benth.) Prance*,* and *Entada africana* Guill. & Perr. (Table 1). During the same period (2006–2020), the new conditions created by disturbance (tree logging) have facilitated the emergence of new species in the woodlands, such as *Acacia gourmaensis* A.Chev., *Bridelia ferruginea* Benth., *Ficus sp., Securidaca longepedunculata* Fresen., *Trichilia emetica* (Forssk.) Vahl and *Ximenia americana* L. In addition, *Detarium microcarpum* Guill. & Perr. and *Hexalobus monopetalus* (A.Rich.) Engl. & Diels have been present in the plant community since 2006, but their abundance has increased significantly (Fig. 4).

3.3. Changes in species richness along a disturbance and potential productivity gradient over time

We expected that disturbance and potential productivity would interact on species richness and such interaction may produce a maximum species richness at the medium level of both factors (unimodal relationship), and at the extreme levels, species richness is expected to be positively correlated with disturbance in a highly potential productive environment but negatively correlated with disturbance when potential productivity was low. We found in the sapling woodlands community that time factor (year) had a negative

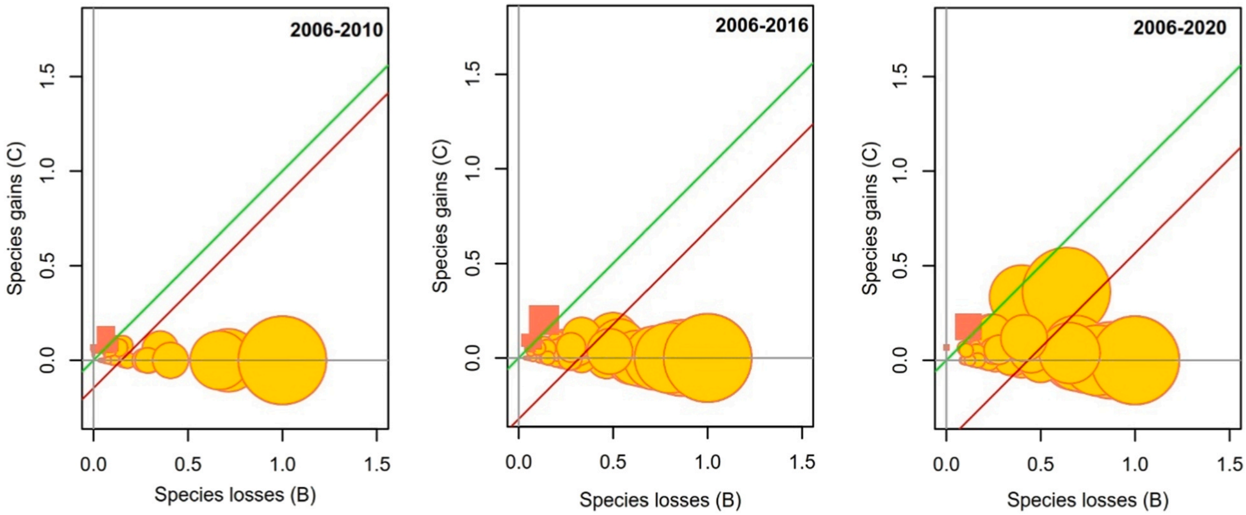

Fig. 3. B-C Plots for density-per-species data from 2006 to 2020**.** The green line (slope 1) represents the line where losses equal gains, and the red line, parallel to and below the green line indicates that, on average, density-per-species losses dominate changes in the entire woodlands over the time step considered. Symbol size is proportional with TBI statistics. Round symbols with a yellow fill represent plots with a loss of species density, while square symbols with a red fill represent plots with an increase in species density. C: species gains; B: species losses.

Table 1
Species (with DBH ≥ 10 cm) that changed significantly in number of stems in the 64 woodlands plots from 2006 (T1) to 2020 (T4).

Species name	Family name	Plot density (400 m^2)		Change in the number of stems
		T1 (2006)	T4 (2020)	T4 - T1
(a) Species whose density has increased significantly				
Hexalobus monopetalus (A.Rich.) Engl. & Diels	Annonaceae	3	7	4
Detarium microcarpum Guill. & Perr.	Fabaceae	4	6	2
Bridelia ferruginea Benth.	Euphorbiaceae	0	2	2
Ximenia americana L.	Olacaceae	0	2	2
Trichilia emetica (Forssk.) Vahl	Meliaceae	0	1	1
Ficus sp.	Moraceae	0	1	1
Securidaca longepedunculata Fresen.	Polygalaceae	0	1	1
Acacia gourmaensis A.Chev.	Fabaceae	0	1	1
(b) Species whose density has decreased significantly				
Isoberlinia spp.	Fabaceae	403	168	−235
Lannea acida A.Rich.	Anacardiaceae	52	18	−34
Pterocarpus erinaceus Poir	Fabaceae	44	12	−32
Burkea africana Hook.	Fabaceae	31	9	−22
Pericopsis laxiflora (Benth. ex Baker) Meeuwen	Fabaceae	22	8	−17
Vitellaria paradoxa C.F.Gaertn.	Sapotaceae	39	29	−10
Parinari curatellifolia Planch. ex Benth.	Chrysobalanaceae	14	4	−10
Terminalia leiocarpa (DC.) Baill.	Combretaceae	18	10	−8
Uapaca togoensis Pax	Euphorbiaceae	8	0	−8
Margaritaria discoidea (Baill.) G.L.Webster	Euphorbiaceae	8	1	−7
Monotes kerstingii Gilg	Dipterocarpaceae	27	10	−7
Maranthes polyandra (Benth.) Prance	Chrysobalanaceae	11	6	−5
Entada africana Guill. & Perr.	Fabaceae	8	3	−5
Total number of tree stems counted		791	362	

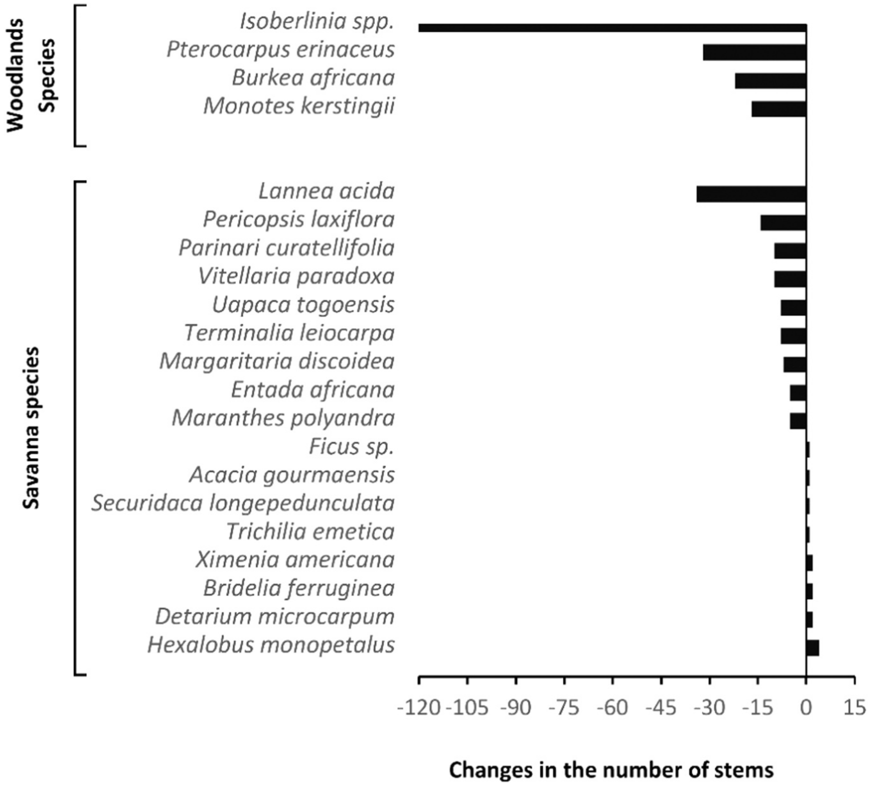

Fig. 4. Species with a significant change in the number of stems (from 2006 to 2020).

significant ($P < 0.001$) effect respectively on sapling and adult tree species richness (Table 2). Compared to higher levels of disturbance, low and medium levels of disturbance significantly increase the species richness of saplings and adult trees (Fig. 5A and B, Table 2). We also found that potential productivity did not directly affect the richness of adult tree species (Table 2). However, the

Table 2
Parameters estimate for change in sapling and adult tree species richness.

Variable	Sapling species richness		Adult tree species richness	
	Estimate	P-value	Estimate	P-value
Independent effects:				
(Intercept)	1.57	0.020	2.52	< 0.001
Year scaled	−1.49	< 0.001	−0.37	0.003
Year scaledˆ2	0.71	< 0.001	-	-
Low disturbance	2.19	< 0.001	2.23	< 0.001
Medium disturbance	1.89	< 0.001	1.66	< 0.001
Potential Productivity scaled	-	-	−0.23	0.508
Low disturbance: Potential Productivity scaled	-	-	0.19	0.385
Medium disturbance: Potential Productivity scaled	-	-	0.68	0.039

Adult tree (tree with DBH $\geq$ 10 cm), and Sapling (tree with DBH $<$ 10 cm and height $\geq$ 1.5 m).

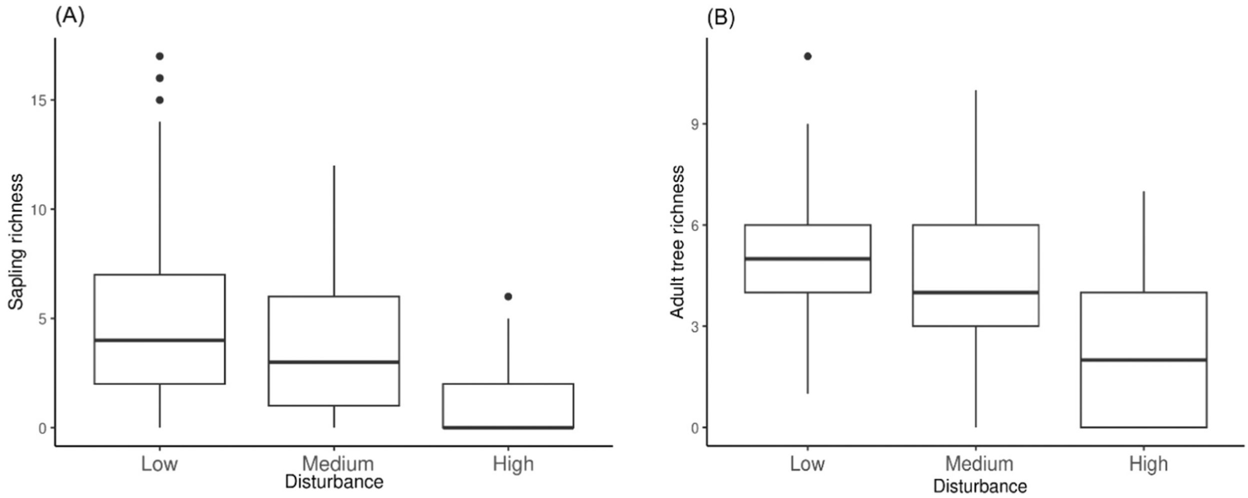

Fig. 5. Effect of disturbance on sapling richness (A) and adult tree species (B). Disturbance reduced sapling and adult tree species richness.

interaction between potential productivity and medium disturbance had a positive and significant effect on the richness of adult tree species (Table 2).

3.4. Changes in species density along a disturbance and potential productivity gradient over time

We expected an increase in sapling density with increasing disturbance. Our results showed a negative and significant effect of time factor (year) on sapling density ($P < 0.001$, Table 3), which meant that over time, there was a decrease in sapling density, i.e. an increase in the sapling species density's losses ($P < 0.001$, Table 3). However, the result showed a significant increase in sapling

Table 3
Parameters estimate for change in species density for sapling and adult trees.

Variable	Sapling species				Adult tree species			
	Density		Density losses		Density		Density losses	
	E	P	E	P	E	P	E	P
Independent effects:								
(Intercept)	3.95	0.029	0.82	< 0.001	4.46	< 0.001	0.67	< 0.001
Year scaled	−3.83	< 0.001	0.22	< 0.001	−1.31	< 0.001	0.05	< 0.001
Year scaledˆ2	-	-	−0.11	< 0.001	-	-	-	-
Low disturbance	6.71	< 0.001	−0.33	< 0.001	6.10	< 0.001	−0.59	< 0.001
Medium disturbance	4.58	0.008	−0.23	< 0.001	4.34	< 0.001	−0.43	< 0.001
Potential productivity scaled	-	-	-	-	-	-	0.04	0.137
Interaction effets:								
Low disturbance: Potential productivity scaled	-	-	-	-	-	-	−0.04	0.030
Medium disturbance: Potential productivity scaled	-	-	-	-	-	-	−0.07	0.010

Adult tree (a tree with DBH $\geq$ 10 cm); Sapling (a tree with DBH $<$ 10 cm and height $\geq$ 1.5 m), E: Estimate; P: Probability value.

density (or decrease in sapling density loss) at low and medium disturbance levels ($P < 0.001$, Table 3, Fig. 6 A) compared to higher disturbance levels. A similar trend was observed for adult trees, with their density decreasing over time ($P < 0.001$, Table 3, Fig. 6B). Sapling and adult tree densities were higher under low and medium disturbances compared to high disturbance levels (Fig. 6). Finally, we found no significant effect of potential productivity on either sapling density or adult tree density. However, when interacting with low and medium disturbances, the potential productivity leads to losses in adult tree density ($P < 0.001$, Table 3)

4. Discussion

Using Huston's Dynamic Equilibrium Model, we explored how disturbance and productivity can affect the species richness of Isoberlinia-dominated woodlands (West Africa), based on permanent plots monitoring over 15 years. Our analyses focused on sapling (individuals with a DBH less than 10 cm and height greater than or equal to 1.50 m) and adult trees (individuals with a DBH greater than or equal to 10 cm). We found that species richness (both for sapling and adult tree) decreased with increasing disturbance levels, suggesting that excessive disturbance can reduce diversity (Sterck et al., 2014). Low to medium disturbance levels lead to greater species richness in saplings and adult trees of Isoberlinia-dominated woodlands, probably by providing heterogeneous environmental conditions that allow species with varied ecological strategies to coexist. Our results suggest that the species richness of sapling is not significantly influenced by disturbance and by the potential productivity. Nevertheless, a significant positive interaction between medium disturbance and potential productivity on species richness was found for adult trees. This may be explained by the fact that the species richness of saplings may be less sensitive to disturbance and potential productivity, due to their ability to rapidly colonize disturbed zones, irrespective of variations in these factors. Adult trees, on the other hand, may benefit more from conditions created by an interaction between moderate disturbance and high productivity. This interaction can favor a diversity of habitats and ecological niches, allowing more adult tree species to coexist. This funding supports the hypothesis that species richness will peak at medium levels of the interaction of disturbance and potential productivity both in the sapling and adult tree of woodlands.

The positive interaction of disturbance and potential productivity on species richness is consistent with others who have shown that the effects of disturbance and productivity on diversity consistently depend on each other and that the direction of their effects (negative or positive) shift between ecosystems of low and high productivity (Huston, 1994; Kondoh, 2001; Proulx and Mazumder, 1998; Scholes et al., 2005; Worm et al., 2002). Peak richness is achieved if disturbance is low or medium and potential productivity is higher, and under these conditions, the trade-off between the species allows the coexistence of more species (Kondoh, 2001). The studied Isoberlinia-dominated woodlands are located in a low-productive environment, and our results support the idea that, in a low or medium-productivity ecosystem, disturbance increases the species richness. An explanation of disturbance and potential productivity interactions on species richness would have to take into account the trade-offs between competitive ability and life-history traits that facilitate species tolerance to disturbance (Kadmon and Benjamini, 2006; Kondoh, 2001). In a low-productivity environment, increasing levels of disturbance are expected to decrease species richness because the environment becomes more constraining to individuals. Thus, following Michalet et al. (2006) and Michalet et al. (2021), we argue that such an environment is favorable to stress-tolerant species that are more abundant than competitive species. Furthermore, we found in the sapling woodlands that time factor (year) had a negative significant effect on sapling species richness, meaning that sapling species richness decreased regardless of disturbance and potential productivity gradient over time. This result shows that, in addition to the time factor, environmental conditions, ecosystem management practices and interspecific competition influence the richness and survival of saplings (Bhadouria et al., 2016; Canham and Murphy, 2017; Hounwanou et al., 2025; Jensen and Löf, 2017).

According to the density parameter, we predicted a decrease in adult tree density and an increase in sapling density at high woodlands disturbance but our data did not support this hypothesis. Contrary to our expectations sapling and adult tree density decreased significantly through the years, but the disturbance effect contributed to a significant increase in both saplings and adult tree abundance. Not surprisingly, the richness of adult trees in a community was strongly determined by the recruitment that took place in the ecological succession process. These results corroborate previous findings that, over time, disturbance strongly determines vegetation dynamics (Biaou, 2009; Gillespie et al., 2000; Lindenmayer et al., 2019). It has also been proposed that a positive disturbance-diversity relationship in a plant community suggests that species are not limited by recruitment, i.e. species are likely to colonize all patches (Cordonnier, 2004). Our results support this idea by showing that low or medium disturbance (logging) promotes the recruitment of new individuals from a sapling that grows into an adult tree.

Disturbances can provide recruitment opportunities (Boisvert-Marsh et al., 2019; Vickers et al., 2014), and could also limit seedling recruitment into the sapling class and sapling recruitment into the adult class, especially at high frequency and intensity of disturbances (Biaou, 2009; Naudiyal and Schmerbeck, 2018). According to Staver et al., (2009), browsing and fire each have an impact on growth, while their combined effect can prevent an increase in tree density. For Walters et al. (2020), a critical height threshold of about 2 m is required for young trees to adults in the face of disturbance. At the 1.5 m height used as a threshold for sapling recruitment in this study, we believe that saplings escape grazing, fire, and the effect of shrubs, and thus have a much greater chance of reaching maturity. Analysis of recruitment quality between 2006 and 2020, indicated that 14 tree stems belonging to eight species (*Acacia gourmaensis, Bridelia ferruginea, Detarium microcarpum, Ficus sp., Hexalobus monopetalus, Securidaca longepedunculata, Trichilia emetica, Ximenia americana*) showed a significant increase and reached tree size in this habitat (Table 3). These species are known to be common species in tropical West African savannas due to their ecology (Akoègninou et al., 2006; Arbonnier, 2009). The emergence of savanna species suggests a strong change in both diversity and structure, indicating that woodlands are being subjected to increasing disturbance. Harvesting of wood for charcoal and timber, conversion of forests to agricultural land due to soil fertility (Dourma et al., 2012; Kiruki et al., 2017; McGregor, 1994; Moonlight et al., 2020) and anthropogenic fragmentation (Biaou et al., 2022; Gross et al., 2018; Hountondji et al., 2013; Petrášová-Šibíková et al., 2017; Waddell et al., 2020) are key factors in plant community dynamics. Therefore,

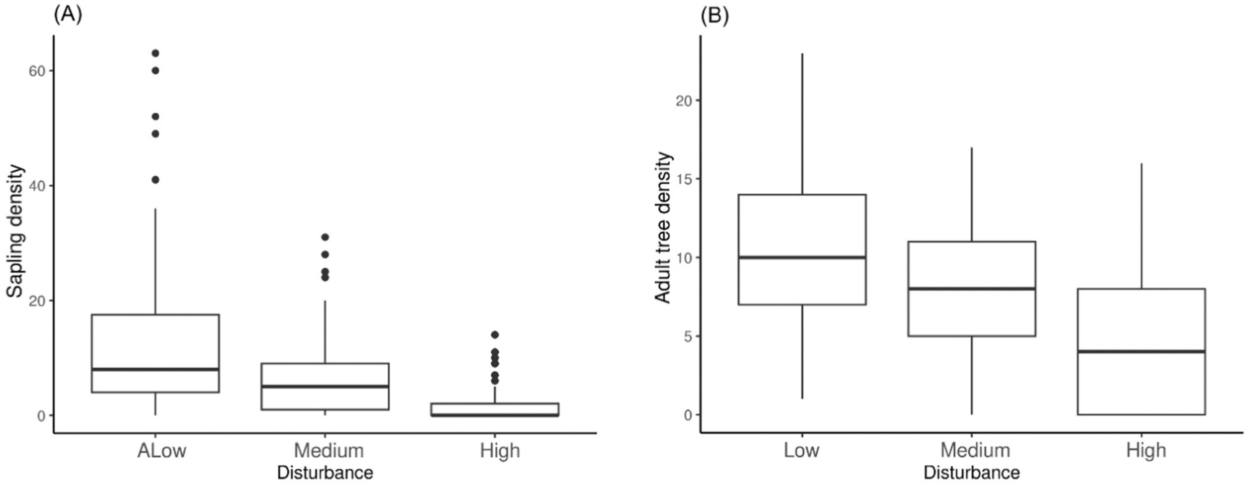

Fig. 6. Effect of disturbance on sapling density (A- 400 m^2) and adult tree species density (B- 400 m^2). Disturbance reduced sapling and adult tree species density.

savanna species are likely to increase in the future in disturbed woodlands due to land-use practices and continued degradation, resulting in changes in the composition and structure of the plant community.

Although the 64 plots studied were spread over a wide area to capture a rainfall gradient, the study remains limited to the Isoberlinia-dominated ecosystem in Benin. This focus limits the generalizability of the results to other tropical forest types or similar ecosystems (Biaou, 2009). Furthermore, anthropogenic disturbances were only assessed during four observation periods (2006, 2010, 2016, 2020), with intervals of several years between surveys. These long intervals could mask the effects of short-term disturbances, especially seasonal variations (Jentsch and White, 2019). The climate variables used, such as precipitation and potential evapotranspiration, are derived from global databases, which may not accurately capture the local microclimates of the study sites. An assessment of ecosystem productivity directly at the scale of individual plots, using methods such as biomass estimation or tree recruitment rates calculations, would have better captured local variation (Chave et al., 2014). In addition, the study focuses primarily on logging as a source of anthropogenic disturbance, excluding other potential factors such as grazing, pruning, barking, fire or land-use change, which also play a key role in vegetation dynamics (Biaou, 2009; Gaoue et al., 2024; Laurance et al., 2014; Sankaran et al., 2005). Furthermore, this study is crucial for tropical ecosystem conservation and management, as it provides long-term data on the dynamics of Isoberlinia woodlands in response to anthropogenic and climatic disturbances. It highlights the influence of human activities, such as logging, on the structure and floristic composition of Isoberlinia woodlands, contributing to a better understanding of the threats to these ecosystems. The results provide a sound basis for developing sustainable management strategies, such as limiting intensive logging, restoring habitats and adapting to climate change, thereby enhancing the resilience of tropical forests.

5. Conclusion

This monitoring study of Isoberlinia woodlands in Benin, West Africa, conducted from 2006–2020, provides important information on the change of these ecosystems over time. The results highlight several significant trends. Firstly, it is clear that the floristic composition of Isoberlinia woodland experienced a substantial change after 2006. This transition is crucial for understanding the dynamics of these ecosystems and may be largely attributed to anthropogenic disturbance. In terms of species richness, we observed a decrease in the species richness of saplings and adult trees over time. This suggests that disturbances hurt the regeneration of saplings, while adult trees appear to have thrived despite these disturbances. Furthermore, the results indicate a complex interaction between disturbance and potential productivity, where the species richness of adult trees is negatively affected by increasing disturbance in a low-productivity environment. This highlights the importance of considering both disturbance and productivity in the management of these ecosystems. Finally, the density of saplings and adult trees also showed interesting trends, with a decrease over time, but a significant increase when the disturbance was low or medium. Our findings provide crucial information for the sustainable management of these valuable Isoberlinia woodlands and underline the need for effective conservation actions to maintain their biodiversity in the face of increasing challenges from environmental degradation.

Ethical Statement

Hereby, I Séverin BIAOU, consciously assure that for the manuscript ‘Spatio-temporal dynamics of Isoberlinia-dominated woodlands in disturbance-prone landscapes over 15 years’ the following is fulfilled:

1) This material is the authors’ original work, which has not been previously published elsewhere.

2) The paper is not currently being considered for publication elsewhere.
3) The paper reflects the authors' research and analysis in a truthful and complete manner.
4) The paper properly credits the meaningful contributions of co-authors.
5) The results are appropriately placed in the context of prior and existing research.
6) All sources used are properly disclosed (correct citation). Literally copying of text must be indicated as such by using quotation marks and giving proper reference.
7) All authors have been personally and actively involved in substantial work leading to the paper, and will take public responsibility for its content.

I agree with the above statements and declare that this submission follows the policies of Solid-State Ionics as outlined in the Guide for Authors and in the Ethical Statement.

Declaration of Competing Interest

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

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Data availability

Data will be made available on request.

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