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Spatiotemporal changes in woody species composition, diversity, and regeneration reveal rapid degradation of a savanna woodland in Blue Nile state, Sudan

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Forests and tree species provide vital resources and ecosystem services, but unsustainable use and disturbances have degraded their ecological integrity. This study assessed forest dynamics in the Elnour Natural Forest Reserve (ENFR) by analyzing species composition, diversity, and natural regeneration in 229 sample plots (1,000 m^2 each) during 2008 and 2021. Over a 13-year period, the Wilcoxon signed-rank test revealed significant temporal changes in several forest structural and regeneration attributes between 2008 and 2021. Tree species decreased from 35 to 19 species and the number of families from 12 to 8. The Fabaceae and Combretaceae remained dominant by contributing over 55% of the species composition. Additionally, mean tree density declined significantly ($W = 582$, $Z = 4.37$, $p < 0.0001$) resulting significant decrease in basal area ($W = 310.50$, $Z = 3.97$, $p < 0.0001$) during this period. Sapling density also differed significantly ($W = 328$, $Z = 2.38$, $p = 0.017$) between the two inventory periods. However, no discernable variation ($W = 11$, $Z = 0.80$, $p = 0.418$) was observed in seedling density between 2008 and 2021. Relative frequency analysis revealed decline in formerly dominant species, including *Vachellia seyal* (14.58 to 14.48%) and *Senegalia senegal* (7.76 to 4.83%) while an increase in disturbance-tolerant shrubs such as *Vachellia oerfota* var. *oerfota* (0.17 to 10.09%) and *Senegalia mellifera* (0.67 to 2.41%). Regeneration status showed marked variation with a fewer species showing good regeneration while many species exhibiting no regeneration, indicating severe recruitment bottlenecks during this 13-year period. The findings highlight an urgent need for targeted conservation measures, sustainable forest management, and assisted regeneration to restore ecological integrity and maintain biodiversity in rapidly degrading dryland forest landscapes of Sudan.

KEYWORDS
anthropogenic disturbance, biodiversity dynamics, climate-driven vegetation change, forest regeneration, savanna woodland, spatial analysis, species composition

1 Introduction

Dryland forests and woodland constitute some of the most extensive terrestrial ecosystems globally and provide essential ecological, economic, and social services to millions of people (Chidumayo, 2010; Agustino et al., 2011; Osewe et al., 2024; Wang et al., 2024). These ecosystems are increasingly threatened by climate change, recurrent drought, land-use change, overgrazing, and unsustainable harvesting practice, resulting in widespread biodiversity loss and ecosystem degradation (Price et al., 2013; Gauthier et al., 2015; Coleine et al., 2024). In Sudan, diverse ecosystems occur within the Sahel-Sudan transition zone, a unique ecotonal region linking the arid Sahel to the more humid savanna systems of sub-Saharan Africa (Lu et al., 2024). This transition zone is characterized by high climatic variability, strong environmental gradients (Mohamed et al., 2024; Adam et al., 2026), and vegetation communities that are particularly sensitive to both anthropogenic disturbances and climate fluctuations (Gauthier et al., 2015; Gogoi and Sahoo, 2018; Gurashi et al., 2024; Musa et al., 2024). Consequently, understanding long-term changes in woody species composition, diversity, and regeneration within these ecosystems is essential for developing effective conservation and restoration strategies.

Forests are crucial for ecological balance and food security, yet information on their valuable ecosystem services is limited, particularly in regions like the Blue Nile State (Abuelbashar et al., 2022; Rajasugunasekar et al., 2023; Serbouti et al., 2023; Musa et al., 2024). Conversely, the region has several natural forest reserves and riverine forests (Musa et al., 2024; Mohammed et al., 2021a), rich in biodiversity of both plants and animals but they face threats from land-use conversion, overexploitation, agriculture expansion, and climate variability. In the Sahel and Sudanese drylands, trees and shrubs are vital for combating desertification and supporting food security and rural livelihoods, especially through cultivation of indigenous fruit trees and agroforestry systems (Lu et al., 2023; Rajasugunasekar et al., 2023) which economically contribute about 50% to household income (Musa et al., 2023).

Understanding species composition, structural dynamics, and regeneration status is essential for assessing forest health and informing conservation strategies (Pokhriyal et al., 2010; Young et al., 2017; Hido et al., 2020; Chetri et al., 2024; Behera et al., 2023; Chepkoech et al., 2024; Masresha et al., 2024; Chettri et al., 2026). Population structure analysis reflects historical disturbance regimes and can help predicts future ecological trajectories (Dereje and Duguma, 2019; Stritih et al., 2024; Zhong et al., 2024). A reverse J-shaped diameter or height class distribution indicates successful regeneration and ecological stability (Lalfakawma et al., 2009; Saxena and Singh, 1984; Tesfaye et al., 2010; Rahman et al., 2019; Gebeyehu et al., 2019; Dibaba et al., 2024). In dryland environments, assessing regeneration status is crucial for understanding vegetation dynamics and informing sustainable forest management (Tesfaye et al., 2010; Yao et al., 2024; Zavala et al., 2024). Effective management requires comprehensive data on regeneration dynamics and their biophysical drivers, which are lacking in Sudan due to political instability, governance gaps, and insufficient support for forest monitoring and restoration practices (Siddig, 2014; Siddig, 2019; Siddig et al., 2019; Yasin and Mulyana, 2022; Yasin et al., 2024).

Sudan's savanna woodland regions, including the Elnour Natural Forest Reserve (ENFR), are home to diverse native species, contributing to their ecological richness (FAO, 2010; IUCN, 2010; Yasin and Mulyana, 2022; Yasin et al., 2024). However, translating national forest conservation goals into management practices is hindered by competing land-use demands, population pressures, and weak forest governance (Ouedraogo et al., 2010; Oke and Jamala, 2013; Vizzarri, 2024; Johansson, 2024; Yasin et al., 2024). These pressures have led to altered fire regimes, shortened fallow periods, and agricultural and livestock encroachment, contributing to biodiversity loss and impaired forest regeneration (Gunawan et al., 2024; Loft et al., 2024; Zhao et al., 2024). Further, the region has experienced significant ecological changes due to civil conflict, agricultural encroachment, wood harvesting, and overgrazing. These human activities, along with natural climatic variability, have altered species composition, compromised biodiversity, and disrupted regeneration cycles. Despite being a protected area, systematic ecological assessments of this reserve are virtually nonexistent, hindering effective conservation and policymaking under frameworks like the Convention on Biological Diversity (CBD) and REDD+ (Osman and Idris, 2012; Ibrahim and Hassan, 2015). On the other hand, inventorying tree species and assessing spatial and temporal variations in forest diversity are essential for understanding ecosystem trends and guiding conservation strategies (Yakubu et al., 2020; Pommerening and Sterba, 2024; Chanachai et al., 2024; Joshi et al., 2024). In addition, local communities' participation in forest management can significantly contribute to biodiversity conservation (Musa and Sahoo, 2023). Despite ENFR's ecological importance and role in supporting biodiversity and local livelihoods, it remains poorly documented compared to other forest ecosystems in Sudan. Research in Sudanese dry forests shows that regeneration is influenced by factors such as grazing intensity, seed availability, microclimatic conditions, edaphic factors (Horner et al., 2010; Osman and Idris, 2012; Yahya et al., 2023; Fatimata et al., 2024) and anthropogenic factors (Mohammed et al., 2021b). However, these studies often have limited temporal scopes and lack spatial detail. Besides, available information is limited to a few localized vegetation assessments, while long-term studies examining changes in woody species composition, diversity, forest structure, and regeneration dynamics using permanent plot data are largely lacking. This scarcity of ecological monitoring data constrains understanding of forest responses to environmental change and limits the development of evidence-based conservation and management strategies for the reserve.

With the advances in geospatial technologies, researchers increasingly rely on these technologies to integrate field data to map species diversity, identify regeneration hotspots, and detect degradation fronts (Alcaras et al., 2024; Charles et al., 2024). These approaches are scalable, cost-effective and highly valuable to supervise the vegetation data across time and space in data-scarce regions like Sudan, where monitoring and reporting are hindered by socio-political and economic constraints. This study examines the spatial distribution and temporal changes in species composition, diversity, and regeneration status in the ENFR over 13 years. The study employed field inventory data and spatial analysis tools, to assess how forest structure and diversity have changed under the current environmental and anthropogenic pressures. Based on ecological theory and previous studies in dryland forest ecosystems, we expected that prolonged anthropogenic disturbances, including tree harvesting and livestock grazing, combined with climatic variability, would lead to declines in woody species diversity, tree density, basal area, and regeneration success over time.

We further expected that disturbance-tolerant species would increase in relative dominance, whereas ecologically sensitive species would decline. Accordingly, this study assessed whether long-term changes in species composition, forest structure, and regeneration dynamics within the ENFR were consistent with these expected patterns of forest degradation. The findings of this study may enhance understanding of dry forest dynamics in Sudan and the broader Sahel and savannah regions of Africa, providing a basis for evidence-based conservation and restoration policies in the ENFR and similar landscapes.

2 Materials and methods

2.1 Study area

This study was conducted in Blue Nile region at Elnour Natural Forest Reserve (ENFR), located between latitudes 11° 48'19 "N and 11° 53' 30" N and longitudes 34° 28'47 "E and 34° 32' 35" E, with distance of 6 km southeast of El Damazin Town and about 3 km east of El Rosaries town (Figures 1A–C). The forest was declared as a reserved forest on June 15, 1959, covering a total area of 4667.17 ha to provide a high degree of protection against poaching and hunting and to support biodiversity conservation. The region's climate is tropical & subcontinental characterized by humid rainy summers and dry winters. The temperature during winter months (December–January) ranges from 16.41 °C to 15.62 °C, while in summer (April and May) ranged between 41.48 °C to 39.91 °C. A significant change in mean daily temperature occurs during the rainy period from June to October due to high humidity. Additionally, rainfall is influenced by South Atlantic and Congo air masses, with minimal impact from the Indian Ocean and precipitation varies between 300 and 700 mm from April to November, peaking from July to September. A study by Harrison and Jackson (1958) classified Sudan's vegetation into various categories, of which ENFR was classified as low rainfall woodland savannah, featuring 55 woody plant species from 36 genera and 18 families (Ibrahim et al., 2014).

The dominant species in the reserve include *Sterculia setigera*, *Combretum hartmannianum*, *Vachellia seyal*, *Terminalia brownii*, *Terminalia laxiflora*, *Anogeissus leiocarpus*, *Balanites aegyptiaca*, *Combretum micranthum*, and *Lannea fruticosa* (Ibrahim and Osman, 2014) while it also harbors many endangered species like *Adansonia digitata*, *B. aegyptiaca*, *Boswellia papyrifera*, *Dalbergia melanoxylon*, *Grewia flavescens*, *Grewia mollis*, *Grewia tenax*, *Philenoptera laxiflora*, *Piliostigma reticulatum*, and *Catunaregam nilotica* (Gibreel et al., 2013). The topography of ENFR is relatively flat, with some depressions in the central and northern clay areas (Fahmi, 2017). The reserve forest soil is classified into two types: dark cracking clay soil, constituting about 64.2% of the forest area (2994.31 ha), and sandy loam to gravelly soil covering 35.8% (1672.86 ha). Moreover, Azaza village is the nearest village to the reserve forest, and is part of the Hamag civil administration under Mayer Obied Abou Shotal. The main tribes

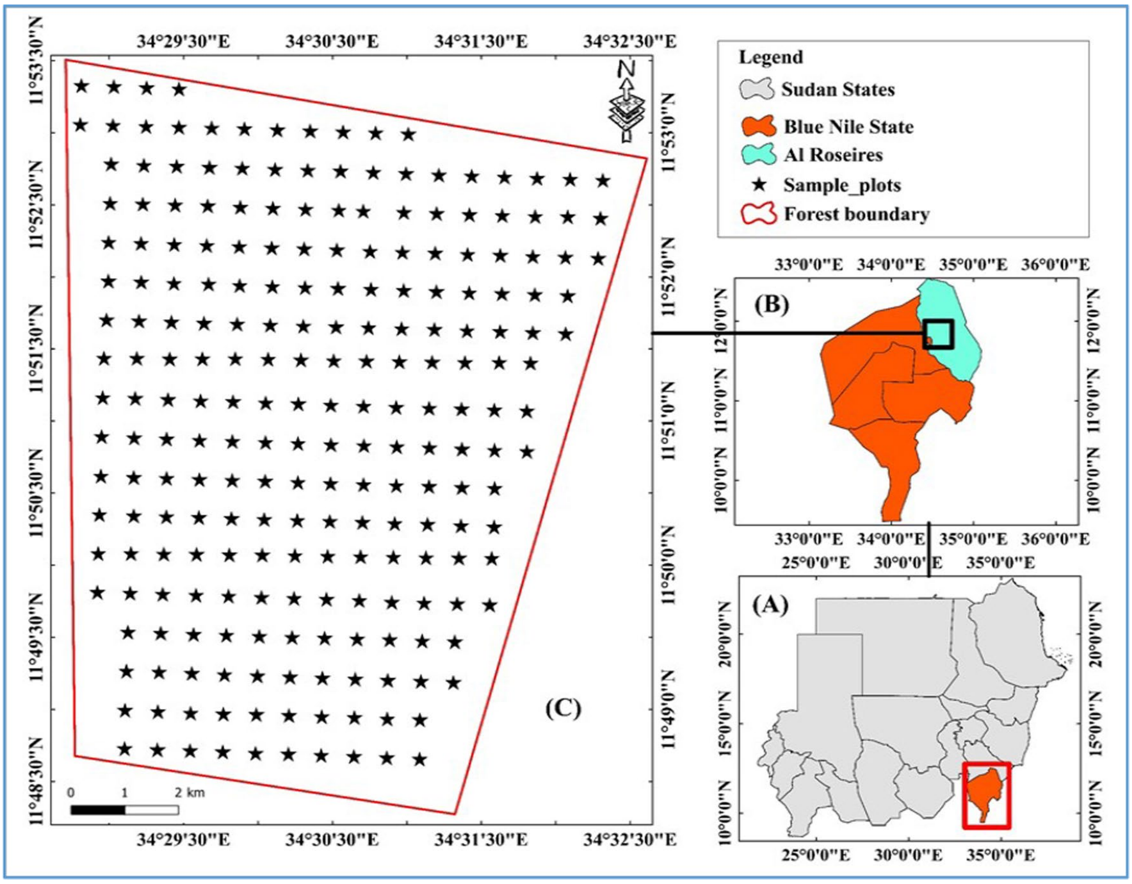

FIGURE 1
Maps showing the location of Blue Nile State in southeastern Sudan **(A)**, location of Elnour Natural Forest Reserve in Blue Nile State **(B)**, and overview of Elnour Natural Forest Reserve with permanent sample plots **(C)**.

inhabiting the area include Kenana (Arab), Rufaa (Arab), Bargo, Masalit, Fallata, Dinka, El Broon, and Tama. The village inhabitants periodically collect dry branches and twigs for firewood, as well as fruits, leaves, barks, and roots for medicine and building materials to support their livelihoods. The forest serves as a grazing area during the dry season from March to May, except in area where new regeneration is established.

2.2 Data collection

To ensure data accuracy on the spatial distribution and temporal dynamics of species composition, diversity, and regeneration status of woody perennials we employed a robust sampling design to provide representative coverage of the 4,667 ha of ENFR. For the purpose, 229 permanent plots (each with radius of 17.84 m containing an area of 1,000 m^2) along 18 transect lines were established in 2008 for monitoring forest vegetation. This sampling intensity represented approximately one plot per 20 ha of forest area and was considered adequate to minimize systematic bias and sampling error to map species distribution and vegetation attributes across the entire landscape. The distance between sample plots, and between transect lines was 100 m and 200 m, respectively. These plots were surveyed first in 2008 and revisited in 2021, allowing for analysis of forest changes under environmental and anthropogenic pressures. During the initial inventory, the geographic coordinates of each plot center were recorded using handheld Garmin GPS receivers, and plot positions were additionally referenced according to transect orientation, inter-plot spacing, and nearby landscape features to facilitate future relocation. In the 2021 resurvey, the plots were relocated using the original GPS coordinates together with the established transect layout and field reference records from the 2008 inventory. The sampling design maintained fixed distances of 100 m between plots and 200 m between transects, which improved relocation consistency and spatial accuracy. GPS measurements during both survey periods had an approximate positional accuracy of ±3–5 m under open-canopy conditions. These combined procedures ensured that the same sampling locations were revisited with high confidence for the spatiotemporal analysis.

All woody plant species within each plot were identified with the help of a professional botanist and were classified into three regeneration classes: seedlings (stem diameter < 3 cm), saplings (≥ 3 cm stem diameter and < 7 cm), and adult trees (diameter at breast height ≥ 7 cm) (Mohammed et al., 2021a; Yasin and Mulyana, 2022). These size-class thresholds were used consistently in both inventory periods and formed the basis for the species-level regeneration assessment, whereby regeneration status (Good, Fair, Poor, or None) was determined from the relative abundance of individuals within the seedling, sapling, and adult classes following Mohammed et al. (2021a) and Maua et al. (2020). Seedlings and saplings were measured at the stem collar due to their small size (Ibrahim and Hassan, 2015; Maua et al., 2020), while adult trees were measured at 1.3 m above ground using calipers, and tree height was estimated using Haga hypsometers (Ouedraogo et al., 2010; Ibrahim et al., 2018). To ensure consistency between inventory periods, species identification and field measurements followed standardized survey protocols and accepted taxonomic references. Field identifications were verified using available floristic literature and expert knowledge of the local flora. Several members of the original inventory team also participated in the 2021 resurvey, further enhancing consistency in plot relocation, species identification, and field measurements. Moreover, to ensure taxonomic accuracy and nomenclatural consistency, all woody plant species names recorded in this study were verified and updated according to the Plants of the World Online (POWO) database maintained by the Royal Botanic Gardens, Kew, and the World Flora Online (WFO) database.[1] Both databases were accessed in June 2026 and used to confirm accepted names, authorship, and synonymy.

Field observations of anthropogenic disturbances, including evidence of tree cutting and livestock grazing, were documented during the surveys to provide contextual information for interpreting observed vegetation changes (Osman and Idris, 2012; Gogoi and Sahoo, 2018). Additionally, we compiled integrated inventory period (2008–2021) climatic data, specifically rainfall and temperature, from the Sudan Meteorological Authority and other sources such as AgERA5 v2.0, NASA POWER, and Climate engine websites. These data were used to provide environmental context for interpreting observed vegetation changes. Formal climate-vegetation correlation analyses were beyond the scope of the present study. The climate record covering 1950–2024 was also used to characterize long-term climatic variability in the region and to provide environmental context for interpreting vegetation changes observed between the two forest inventories.

2.3 Data analysis

Data from the ENFR were statistically analyzed using R and Statistica 13.0 to evaluate variations in natural regeneration and species diversity. Descriptive statistics for tree diameter, height, and density were used to summarize the characteristics and distribution of a forest or woodland. The normality of data distributions was assessed using the Shapiro–Wilk test in Statistica 13.0. However, the ecological significance of each species was quantified using the Importance Value Index (IVI) as the sum of Relative Frequency (RF), Relative Density (RD), and Relative Dominance (RDo), following the method described by Mohammed et al. (2021a). Frequency was computed from the number of plots in which the species occur, density was calculated from the number of individuals per unit area, while the dominance was estimated from tree total basal area. Basal area was computed using standard equations while Relative Abundance (RA) measured the proportional abundance of each species within the sampled plots (Yasin and Mulyana, 2022; Gurashi et al., 2024).

To evaluate regeneration status, tree species were categorized as good, fair, poor, or with no regeneration by analyzing the population densities across three life stages as good regeneration (seedlings>saplings>adults), fair regeneration (seedlings > or ≤ samplings ≤ adults) and poor regeneration (seedling = 0, completely inadequate). These classifications were based on standard population hierarchies (Maua et al., 2020; Mohammed et al., 2021a). Additionally, the three life stages of the tree (seedling, sapling, and adult) densities were calculated by dividing the total number of stems in each category by the sampled area, following the methods by Mohammed et al. (2021a) and Idrissa et al. (2018). Various biodiversity indices were calculated as per the methods given in Table 1. Species richness was calculated by counting distinct species in sampled plots following Ghanbari et al. (2021) and Asbeck et al. (2021). Species were classified following Ogwu et al. (2016) by their Relative Density (RD) to inform conservation strategies: abundant (RD ≥ 5.00), frequent

1 https://powo.science.kew.org/

(4.00 ≤ RD < 5.00), occasional (3.00 ≤ RD < 4.00), rare (1.00 ≤ RD < 3.00), and threatened (RD < 1.00). This analysis clarified species dynamics and regeneration potential in the ENFR under the changing ecological conditions (Table 1).

Prior to statistical analysis, the normality of paired differences between 2008 and 2021 inventories were assessed using Shapiro–Wilk test in Origin Pro software. However, when the data did not satisfy the assumption of normality ($p < 0.05$), the differences during this period in forest structural and regeneration variables were evaluated using the non-parametric Wilcoxon signed-rank test. The statistical test (at $\alpha = 0.05$) was applied to compare mean density of trees, saplings and seedlings and their basal area between the two inventories. To quantify the magnitude of temporal changes, effect sizes (r) were calculated as per Cohen (2013) (Table 1), where Z is the standardized Wilcoxon test statistic and N is the number of paired observations. Effect sizes were interpreted as negligible (< 0.10), small (0.10–0.29), medium (0.30–0.49), and large (≥ 0.50).

The spatiotemporal component of this study was based on repeated measurements of georeferenced permanent plots and comparative assessment of species distribution patterns between 2008 and 2021. Spatial analyses focused on the distribution and relative dominance of woody species across the ENFR landscape using plot-based geographic information and spatial interpolation mapping. We acknowledge that spatial autocorrelation and clustering approaches are more important in landscape ecology because geographically proximate sampling units may exhibit greater similarity than the distance ones. However, we reiterated here that the primary objective of this study was to evaluate the changes in vegetation composition and their attributes across predefined landscape units than to model spatial dependence explicitly. In this study, the sampling plots nevertheless were distributed across the landscape with sufficient interplot distances to minimize spatial dependence. The formal spatial autocorrelation analyses were beyond the scope of the present study and should be employed in future investigations to assess the influence of spatial structure on observed vegetation pattern.

3 Results

3.1 Climate variability over the past 75 years

The climate data showed substantial inter-annual variability during the period (1950 to 2024) based on observed meteorological data for the study region (Figure 2a). Despite this variability, an increasing rainfall trend of +3.481 mm yr.$^{-1}$ ($R^2 = 0.181$) was observed. Rainfall anomalies relative to the 1950–1980 baseline ranged from −60% in earlier decades to +30% in the recent years, with a gradual positive trend of +0.342% yr.$^{-1}$ ($R^2 = 0.164$) (Figure 2b). Maximum temperatures increased steadily over the period, with an overall warming trend of +0.018 °C yr.$^{-1}$ ($R^2 = 0.300$), particularly after the 1970s (Figure 3a). Maximum temperature anomalies showed a strong positive trend of +0.0797% yr.$^{-1}$ ($R^2 = 0.636$), with negative anomalies dominating early decades and positive anomalies reaching up to +5% in the recent years (Figure 3b). Minimum temperatures displayed the most pronounced warming, with a trend of +0.0262 °C yr.$^{-1}$ ($R^2 = 0.519$) and accelerated warming after the late 1990s (from +0.0102 to +0.0274 °C yr.$^{-1}$) (Figure 3c). Minimum temperature anomalies increased consistently throughout the record, with

TABLE 1 Equations used to calculate tree basal area, relative frequency, dominance, and abundance, and Importance Value Index (IVI) of the tree species measured in ENFR.

Equation	Reference
Tree basal area (g) = $\frac{\pi (DBH)^2}{4}$	Ibrahim and Hassan (2015)
Frequency (F) = Presence or absence of the species per site	Mohammed et al. (2021a)
Relative frequency (RF) = $\left(\frac{\text{Tree species frequency}}{\text{Total frequency for all species}}\right) \times 100$	Idrissa et al. (2018)
Dominance (D) = Total basal area of the species	Ibrahim et al. (2015)
Relative dominance (RD) = $\left(\frac{\text{Species dominance}}{\text{Total dominance for all species}}\right) \times 100$	Ibrahim and Osman (2014)
Abundance (A) = Number of trees per area measured	Maua et al. (2020)
Relative abundance (RA) = $\left(\frac{\text{Tree species abundance}}{\text{Total abundance for all species}}\right) \times 100$	Mohammed et al. (2021a)
IVI = Relative frequency + Relative dominance + Relative abundance	Mohammed (2019)
Simpson's Species Diversity index (D) = $\left(\frac{\Sigma n(n-1)}{N(N-1)}\right)$, then 1-D.	Frerebeau (2019)
Margalef species richness index (M) = $\frac{(s-1)}{lnN}$	Gamito (2010)
Species Evenness Index; EH = H/Hmax = $\sum_{i=1}^{s} \frac{piln(pi)}{ln(S)}$	Okpiliya (2012)
Shannon-Weiner diversity index (H′) = $-\Sigma_{i=1}^{s} P_i \ln P_i$	Shannon and Weaver (1949)
Effect size (r) = $\frac{Z}{\sqrt{N}}$	Cohen (2013)

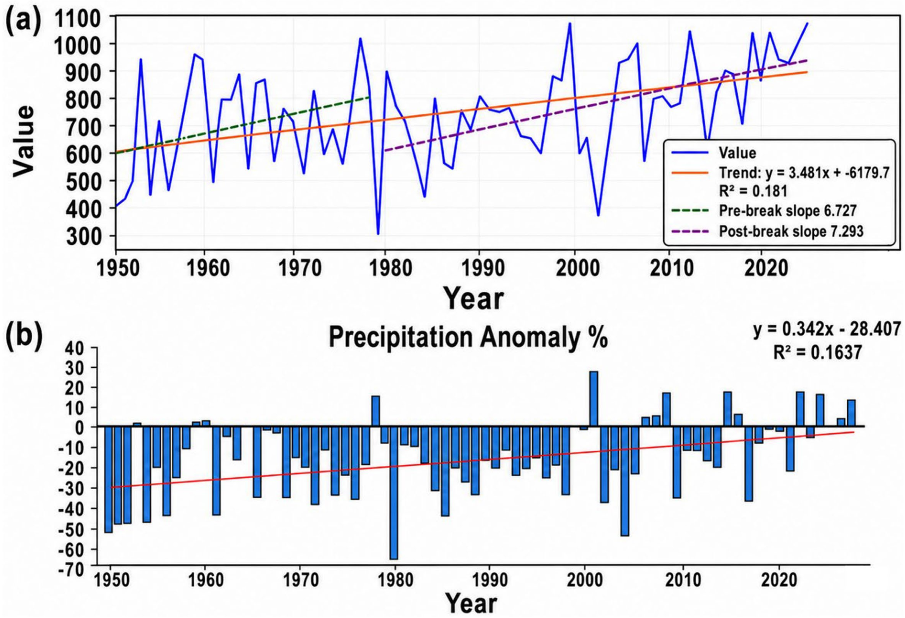

FIGURE 2
Long-term precipitation in study area (1950–2025); **(a)** annual rainfall trend and regime shift analysis and **(b)** long-term precipitation anomalies and trend analysis.

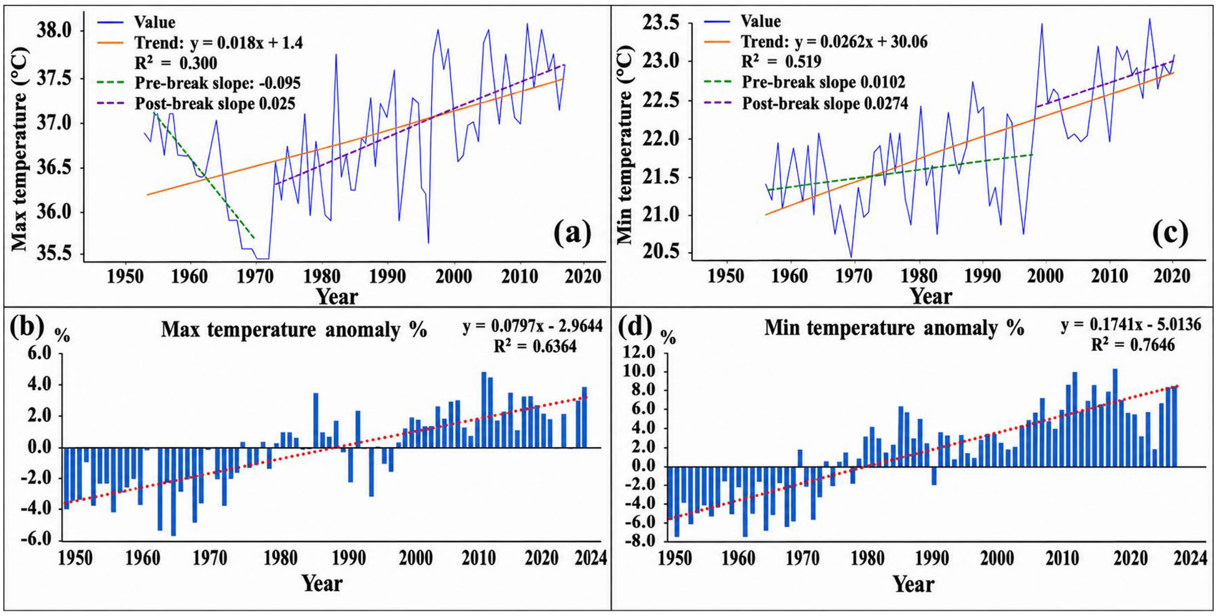

FIGURE 3
Maximum and minimum temperature during period of 1950–2025 in the study area; **(a)** long-term trend and regime shift in annual maximum temperature, **(b)** long-term anomalies and trend in annual maximum temperature, **(c)** long-term trend and regime shift in annual minimum temperature, and **(d)** long-term anomalies and trend in annual minimum temperature (1950–2025).

recent years exceeding +8% relative to the baseline and a trend of +0.1741% yr.$^{-1}$ (R^2 = 0.765) (Figure 3d). Overall, the climate over the past 75 years has shifted toward warmer and slightly wetter conditions, with accelerated warming in both daytime and night-time temperatures and a clear departure from mid-20th century rainfall and temperature patterns. The inclusion of climatic data beyond the inventory period was intended to illustrate long-term trends in rainfall and temperature variability within the region rather than to establish direct climate–vegetation relationships. Climate records for 2025 represent observed meteorological data available at the time of analysis and are not projected values.

3.2 Dynamics of tree species diversity, frequency, and regeneration in the ENFR

The woody species community of the ENFR underwent substantial changes in species composition, abundance, and regeneration between 2008 and 2021. In 2021, a total of 1,498 individual trees

TABLE 2 Number of genera, number of species and relative frequency (RF) of genus and species within identified families in the ENFR in 2008 and 2021.

Family	2008				2021			
	No. of Genera	No. of Species	Genus RF (%)	Species RF (%)	No. of Genera	No. of Species	Genus RF (%)	Species RF (%)
Fabaceae	7	12	28.00	34.29	3	6	23.08	31.58
Combretaceae	2	7	12.00	20.00	3	5	23.08	26.32
Malvaceae	4	4	16.00	11.43	1	1	7.69	5.26
Anacardiaceae	2	2	8.00	5.71	2	2	15.38	10.53
Rhamnaceae	1	2	4.00	5.71	1	2	7.69	10.53
Zygophyllaceae	1	1	4.00	2.86	1	1	7.69	5.26
Rubiaceae	1	1	4.00	2.86	1	1	7.69	5.26
Bignoniaceae	1	1	4.00	2.86	1	1	7.69	5.26
Capparaceae	2	2	8.00	5.71	0	0	0.00	0.00
Ochnaceae	1	1	4.00	2.86	0	0	0.00	0.00
Loganiaceae	1	1	4.00	2.86	0	0	0.00	0.00
Burseraceae	1	1	4.00	2.86	0	0	0.00	0.00
Total	25	35			13	19		

RF, Relative frequency.

representing 19 species across 8 families were recorded in the ENFR. Fabaceae was the most species-rich family with six species, followed by Combretaceae (five species), and Anacardiaceae and Rhamnaceae (two species each). Fabaceae also had the highest abundance (838 individuals), followed by Malvaceae (188 individuals), Zygophyllaceae (160 individuals), Combretaceae (148 individuals), Rhamnaceae (81 individuals), and Anacardiaceae (63 individuals) (Tables 2, 3; Appendix A). In comparison, the 2008 inventory documented 16,979 trees and shrubs, comprising 35 species across 12 families (Table 2). Species richness decreased in most families: Fabaceae and Combretaceae declined from 12 and 7 species in 2008 to 6 and 5 in 2021, respectively, while Anacardiaceae and Rhamnaceae remained constant (Table 2).

Species relative frequency and regeneration patterns also showed marked changes between the inventories. Some dominant species declined, e.g., *Vachellia seyal* (14.58 to 14.48%) and *Senegalia senegal* (7.76 to 4.83%), while increased in *Sterculia setigera* (13.15 to 16.02%) (Appendix A). Several subdominant and rare species, including *V. seyal* var. *fistula*, *S. catechu*, *Dichrostachys cinerea*, and certain *Combretum* and *Grewia* species, were absent in 2021 (Table 3). Disturbance-tolerant species such as *V. oerfota var. oerfota* (0.17 to 10.09%), *S. mellifera* (0.67 to 2.41%), *L. fruticosa* (3.46 to 6.58%), and *Sclerocarya birrea* (0.93 to 1.97%) increased in relative frequency (Appendix A). Overall, ~54% of species declined while ~14% species increased their regeneration capacity; the number of species with "good" regeneration status should be reported based on the final values in Table 3, and 17 species lost their regenerative capacity entirely (Table 3).

3.3 Population structure of woody species in the ENFR

Based on the 2021 inventory, tree diameters at breast height (DBH) ranged from 5.00 to 146 cm, with a mean of 22.83 ± 13.52 cm and tree heights varied from 1.00 to 36.00 m, averaging 7.96 ± 6.04 m (Table 4). In comparison, the 2008 inventory recorded DBH values between 5.00 and 80.00 cm, with a mean of 21.76 ± 11.39 cm, and tree heights from 1.00 to 35.00 m, with a mean of 8.93 ± 6.14 m (Table 4). Additionally, in 2008 DBH ranged from 6 to 10 cm to >41 cm and was strongly skewed toward smaller size classes, however, 6–10 cm class dominated with 32.34% of individuals and less population was recorded in classes > 41 cm (Figure 4a). In 2021, the 6–10 cm class increased to 43.05%, while the 11–15 cm class became the second most abundant category (21.30%) (Figure 4a). Moreover, tree heights in 2008 ranged from 1 to 3 m to 19–21 m and 1–3 m class contained 47.99% of individuals compared to 50.24% in 2021 (Figure 4b).

3.4 Density, IVI and basal area of trees and their conservation status in the ENFR

Both inventories revealed strong interspecific variation in tree density, basal area, and dominance across the ENFR. Mean tree density ranged from 0.17 to 22.93 trees ha^{-1}, while mean basal area varied between 0.00 and 0.35 m^2 ha^{-1} in 2021 compared to 0.04 to 469.21 trees ha^{-1} and 0 to 8.83 m^2 ha^{-1} in 2008, respectively (Table 5). Substantial structural heterogeneity was observed among species. *V. seyal* was the most dominant species, exhibiting the highest mean density (469.21 and 22.93 trees ha^{-1}) resulted in large basal area of 8.83 and 0.35 m^2 ha^{-1} and IVI (125.79 and 71.99) in 2008 and 2021, respectively (Table 5). On the other hand, several other species contributed notably to stand structure in 2021. In 2021, *B. aegyptiaca* showed moderate density (6.99 trees ha^{-1}) and basal area (0.15 m^2 ha^{-1}) but ranked second in dominance with a high IVI (53.16) compared to *S. setigera* with an IVI of 43.18 in 2008 (Table 5). In contrast, several species recorded in 2008 were absent in 2021, indicating their possible local extirpation. The shift in conservation status of many species from 2008 to 2021 indicated a critical crisis of biodiversity status in the ENFR (Table 5).

TABLE 3 Vegetation species type, presence, frequency, and regeneration status in ENFR in 2008 and 2021.

Family	Species	Vernacular names	Type	Presence		Regeneration status			
				2008	2021	RF (%) 2008	Reg.	RF (%) 2021	Reg.
Anacardiaceae	*Lannea fruticosa* (Hochst. ex A. Rich.) Engl.	Leyun/ or Ghallub	Shrub	✓	✓	3.46	Poor	6.58	Good
	Sclerocarya birrea (A. Rich.) Hochst.	Humeid	Tree	✓	✓	0.93	Poor	1.97	Good
Bignoniaceae	*Stereospermum kunthianum* Cham.	Khashkash Abiad	Tree	✓	✓	0.76	Poor	0.88	None
Burseraceae	*Boswellia papyrifera* (Caill.) Hochst.	Trag Trag	Tree	✓	-	0.25	Poor	0	None
Capparaceae	*Maerua angolensis* DC.	Shagar ElZaraf	Shrub	✓	-	0.25	Poor	0	None
	Capparis decidua (Forssk.) Edgew.	Tundub	Shrub	✓	-	0.59	Poor	0	None
Combretaceae	*Anogeissus leiocarpus* (DC.) Guill. & Perr.	Sahab/or seilk	Tree	✓	✓	3.46	Poor	4.83	Fair
	Terminalia laxiflora Engl.	Subagh/or Darut	Tree	✓	✓	2.95	Poor	3.51	Poor
	Terminalia brownii Fresen.	Subagh/or Shaf	Tree	✓	✓	2.28	Good	2.85	Fair
	Combretum hartmannianum Schweinf.	Habeel Al Gabal	Tree	✓	✓	7.67	Good	7.46	Poor
	Combretum aculeatum Vent.	Habeel Shehait	Shrub	✓	-	1.26	Good	0	None
	Combretum molle R. Br. ex G. Don	Habeel Khrisha Kabeira	Tree	✓	-	2.19	Good	0	None
	Combretum glutinosum Perr. ex DC.	Habeel Khrisha	Tree	✓	✓	1.43	Good	1.97	Good
Fabaceae	*Vachellia seyal* (Delile) P. J. H. Hurter	Talih Ahmar/ or Talih	Tree	✓	✓	14.58	Good	14.48	Good
	Vachellia seyal var. fistula (Schweinf.) Kyal. & Boatwr.	Sufar Abiad	Tree	✓	-	13.66	Fair	0	None
	Senegalia catechu (L.f.) P. J. H. Hurter & Mabb.	Kakamoot	Tree	✓		4.13	Fair	0	None
	Senegalia senegal (L.) Britton	Hashab	Tree	✓	✓	7.76	Good	4.83	Poor
	Dichrostachys cinerea (L.) Wight & Arn.	Kadad	Shrub	✓	-	3.37	Poor	0	None
	Senegalia mellifera (Vahl) Seigler & Ebinger	Kitir	Shrub	✓	✓	0.67	Fair	2.41	Good
	Vachellia oerfota var. oerfota.	Laut	Shrub	✓	✓	0.17	Poor	10.09	Good
	Philenoptera laxiflora (Guill. & Perr.) Roberty	Khashkash Azrag	Tree	✓	✓	1.01	Good	1.1	Poor
	Dalbergia melanoxylon Guill. & Perr.	Abnos/ or Babanos	Tree	✓	-	0.42	Poor	0.66	Good
	Cassia arereh Delile	Al Gaga	Tree	✓	-	0.08	Poor	0	None
	Tamarindus indica L.	Aradaib	Tree	✓	-	0.08	Poor	0	None
	Piliostigma reticulatum (DC.) Hochst.	Kharub	Shrub	✓	-	0.08	Good	0	None
Loganiaceae	*Strychnos innocua* Delile	Um Bukheisa	Shrub	✓	-	0.34	Good	0	None

(Continued)

TABLE 3 (Continued)

Family	Species	Vernacular names	Type	Presence		Regeneration status			
				2008	2021	RF (%) 2008	Reg.	RF (%) 2021	Reg.
Malvaceae	*Sterculia setigera* Delile	Tartar	Tree	✓	✓	13.15	Poor	16.02	Fair
	Grewia tenax (Forssk.) Fiori	Guddeim	Shrub	✓	-	0.51	Good	0	None
	Grewia flavescens Juss.	Guddeim Abou Dlouae	Shrub	✓	-	0.17	Good	0	None
	Adansonia digitata L.	Tabaldi (Gongulis)	Tree	✓	-	0.25	Poor	0	None
Ochnaceae	*Ochna afzelii* R. Br. ex Oliv.	Lessan El kalib	Shrub	✓	-	0.25	Good	0	None
Rhamnaceae	*Ziziphus spina-christi* (L.) Desf.	Siddir/or Nabag	Tree	✓	✓	1.69	Poor	4.39	Good
	Ziziphus abyssinica Hochst. ex A. Rich.	Siddir Al Feel	Shrub	✓	✓	1.52	Poor	3.51	Good
Rubiaceae	*Catunaregam nilotica* (Stapf) Tirveng.	Shidr el Marfein	Shrub	✓	✓	1.18	Poor	2.19	Fair
Zygophyllaceae	*Balanites aegyptiaca* (L.) Delile	Hegleeg (Laloub)	Tree	✓	✓	7.5	Poor	10.75	Poor

Symbols (✓) mean present, absent (−), RF: relative frequency, Reg: regeneration.

TABLE 4 Summary statistics of growth variables in ENFR.

Variables	2008		2021	
	DBH (cm)	Height (m)	DBH (cm)	Height (m)
Maximum	80.00	35.00	146.00	36.00
Minimum	5.00	1.00	5.00	1.00
Mean	21.76	8.93	22.83	7.96
SD	11.39	6.14	13.52	6.04

The Wilcoxon signed-rank test revealed significant temporal changes in several forests' structural and regeneration attributes between 2008 and 2021 (Table 6). Mean tree density declined significantly over the study period ($W = 582$, $Z = 4.37$, $p < 0.0001$), with a large effect size ($r = 0.74$), indicating substantial changes in stand structure. Basal area also decreased significantly ($W = 310.50$, $Z = 3.97$, $p < 0.0001$), with a large effect size (r = 0.67), reflecting a considerable reduction in woody biomass and forest structural complexity (Table 7). Sapling density differed significantly between the two inventory periods ($W = 328$, $Z = 2.38$, $p = 0.017$), with a medium effect size ($r = 0.40$). In contrast, seedling density did not show any significant variation between 2008 and 2021 ($W = 11$, $Z = 0.80$, $p = 0.418$), and the associated effect size was small ($r = 0.14$) (Table 6).

Marked shifts were also observed in relative density (RD) of the species between the inventories. The statistics showed significant ecological shift between 2008 and 2021, the proportion of abundant species surged from 11.43 to 42.11% where a few dominant species outperform others (Table 7). The "Frequent" species absent in 2008 accounted for 5.26% population in 2021, while "occasional" species increased from 5.71 to 31.58% of the population. "Rare" species during this period increased from 8.57 to 21.05%, whereas "threatened" species, which constituted 74.29% in 2008, were no longer recorded in 2021, likely due to local extirpation or population decline below detectable levels (Table 7). Despite reductions in species richness, diversity indices showed contrasting trends. The Shannon–Wiener diversity index (H′) increased from 1.56 in 2008 to 2.21 in 2021, and Simpson's diversity index increased from 0.58 to 0.82, indicating a more even distribution of individuals among the remaining species (Table 7). Species evenness similarly increased from 0.44 to 0.75, while the Margalef species richness index declined from 3.49 to 2.46, consistent with losses in taxonomic richness. The index of dominance decreased from 0.42 to 0.18, reflecting reduced dominance by formerly abundant species (Table 7).

3.5 Spatial distribution and species composition patterns in the ENFR

The spatial distribution of species reveals notable changes between 2008 and 2021 in the ENFR. In 2008, *V. seyal* was seen occupying large continuous areas across the reserve, followed by *S. setigera* and *Combretum* species, while other taxa such as *T. laxiflora* and *A. leiocarpus* were sparsely distributed (Figure 5a). In 2021, the distribution of *V. seyal* became more fragmented, while several less important species such as *V. oerfota* var. *oerfota*, *S. mellifera*, *L. fruticosa*, and *D. melanoxylon* increased in their relative density and spatial coverage, reflecting adaptive responses to disturbance (Figure 5b). Concomitantly, the disturbance-tolerant species such as *B. aegyptiaca* and *Z. spina-christi* showed wider distribution in 2021 in the ENFR (Figure 5b).

4 Discussion

The observed changes in forest structure, species composition, and regeneration documented in this study provide empirical evidence from repeated inventories of permanent plots. Interpretations regarding the underlying drivers of these changes are based on field observations and ecological patterns reported in previous studies and should therefore be considered indicative rather than direct evidence of causality.

4.1 Climate variability and its influence on tree regeneration in the ENFR

Long-term climatic trends in the ENFR provide important context for interpreting the observed changes in tree regeneration and population structure between 2008 and 2021. The persistence of high seedling abundance alongside a pronounced decline in saplings and adult trees suggests that climatic factors interact strongly with anthropogenic pressures to shape regeneration outcomes. Although long-term rainfall records indicate a minor increase in annual precipitation, the pronounced inter-annual variability in rainfall, characterized by alternating wet and dry years, likely created unstable conditions for successful seedling recruitment beyond early establishment stages (Díaz et al., 2021; Cueva-Ortiz et al., 2020; Martini et al., 2022). Seed germination may be favored during episodically wet years, explaining the relatively stable seedling numbers recorded in both inventories, whereas subsequent dry spells can severely limit seedling survival and transition into the sapling stage (Volis, 2024; Denton et al., 2024; Stone et al., 2025; Copeland et al., 2025). Several studies reported that microclimatic variables such as soil temperature and moisture are the key factors controlling early seedling growth at the forest floor (Mohammed et al., 2025a; Musa et al., 2025; Musa et al., 2026). The sustained increase in minimum temperatures may enhance seed germination rates and prolong the growing season, creating conditions initially favorable for seedling establishment. However, concurrent increases in maximum temperatures intensify evaporative demand and soil moisture loss, exposing young plants to heat and drought stress. Such conditions disproportionately affect saplings and juveniles with shallow root systems, offering a plausible explanation for the sharp decline in sapling density observed in 2021. Similar regeneration bottlenecks linked to warming and rainfall variability have been widely documented in dryland and savanna forest ecosystems (Hankin et al., 2025; Lalor et al., 2023; Crockett and Hurteau, 2024; Petrie et al., 2023).

The interaction between climate variability and species-specific functional traits appears to have favored disturbance- and drought-tolerant taxa, such as *V. oerfota var. oerfota*, *S. mellifera*, *B. aegyptiaca*, and *Z. spina-christi*, which showed increased relative seedling density and importance. In contrast, species requiring more stable moisture conditions or longer recovery periods exhibited reduced regeneration and declining dominance. Over time, these selective pressures are likely to drive compositional shifts, reduce functional diversity, and reinforce structural simplification (van Der Sande et al., 2023; de Oliveira et al., 2024; Chaturvedi et al., 2024). These findings highlight the importance of incorporating climate-informed management strategies, such as protecting regeneration niches, reducing grazing pressure during drought years, and promoting assisted regeneration of vulnerable species, to enhance forest resilience and ensure sustainable regeneration under ongoing climate change.

4.2 Trends of structural variables of the ENFR

The variations in DBH classes of the woody species in the ENFR for both inventories highlight the persistence of large individuals and active recruitment of smaller trees. The forests were characterized by a predominance of trees in smaller DBH classes, a structural feature commonly observed in tropical forests, where juvenile and sub-adult stems dominate stem counts (Adekunle and Olagoke, 2008; Adekunle et al., 2013; Akindele, 2013; Aigbe et al., 2014). The relatively low number of trees with larger DBH (> 41 cm) is largely attributed to selective logging and harvesting of mature individuals for fuelwood, timber, and other uses, as previously documented in similar tropical forest ecosystems (Hadi et al., 2009). The observed distribution of diameter and height classes reflects both the horizontal and vertical structure of the ENFR, but the strong decline in saplings and adult trees suggests that recruitment may be insufficient to maintain mature forest structure (Adekunle et al., 2013). Moreover, the presence of large trees is a key indicator of mature forest conditions, contributing to canopy complexity, biomass storage, and ecological stability (Adekunle and Olagoke, 2008; Aigbe et al., 2014).

4.3 Trends in species composition, diversity, regeneration, and IVI

The ENFR experienced a marked decline in tree species richness and family representation between 2008 and 2021. Despite this reduction, the reserve maintained relatively high taxonomic diversity, characteristic of dryland forest ecosystems (Okey et al., 2022; Mohammed et al., 2021a). Anacardiaceae, Combretaceae, Fabaceae, and Rhamnaceae remained the most prevalent families, although both species richness and family representation decreased, indicating ongoing biodiversity erosion. Regional comparisons reveal substantial variability in tree diversity across similar ecosystems. For instance, Jebel Elgarri forest, Blue Nile State, Sudan, recorded only 14 species (Dafa-Alla et al., 2022), while the Tozi tropical dry forest in Sinnar State contained just four species from two families (Yasin and Mulyana, 2022). Conversely, higher richness has been observed in Abu Gadaf Natural Reserve, Sudan (47 species from 20 families, Mohammed et al., 2021a) compared to ENFR. These differences largely reflect variations in ecological conditions and the intensity of anthropogenic pressures such as grazing, logging, and land-use conversion (Yeom and Kim, 2011; Gogoi and Sahoo, 2018; Liu et al., 2024). The dominance of the Fabaceae is known for nitrogen-fixing capacity and rapid regeneration, mirrors patterns in Nigerian and Sudanese tropical forests (Mukhtar, 2002; Edet et al., 2012; Aigbe et al., 2014). These traits likely contributed to its persistence despite anthropogenic disturbances. Nevertheless, prolonged pressure has reduced Fabaceae species richness, highlighting that even disturbance-tolerant taxa have thresholds beyond which their resilience is exceeded (Abdou et al., 2016; Hasoba et al., 2025).

The inferential analysis also supported the observed long-term degradation of the ENFR. Mean tree density and basal area declined significantly between 2008 and 2021, with large effect sizes ($r = 0.74$ and 0.67, respectively), indicating substantial reductions in stand structure and woody biomass. Sapling density also decreased significantly ($r = 0.40$), suggesting impaired recruitment into intermediate size classes. These findings align with Johnson et al. (2011) and Musa et al. (2026) who reported that seedling mortality of tree species is

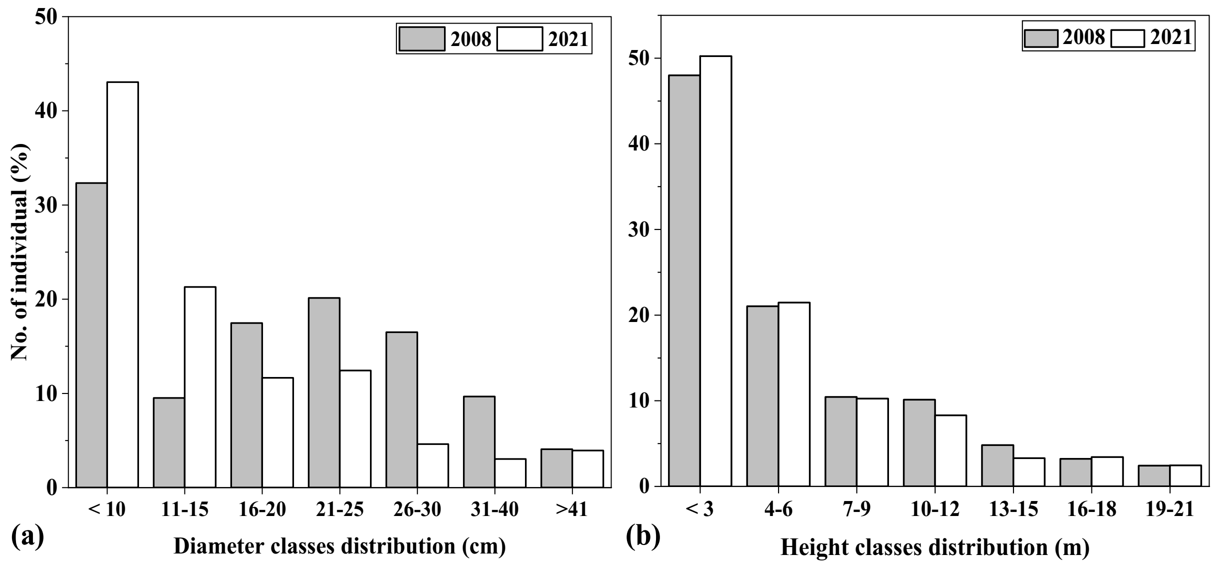

FIGURE 4
Size-class distribution of woody species in the ENFR (2008 and 2021): **(a)** Diameter at breast height (DBH) classes distribution of individual trees and **(b)** Height classes distribution of individual trees.

usually higher during the early development stage. In contrast, seedling density did not differ significantly between the two inventory periods ($p = 0.418$), and the associated effect size was small ($r = 0.14$). This apparent stability in seedling abundance, despite marked declines in saplings and mature trees, suggests that seed germination and initial establishment are still occurring within the reserve. However, the transition from seedlings to larger size classes appears to be constrained, likely resulting in a regeneration bottleneck. Such patterns are commonly observed in degraded dryland forests where grazing pressure, moisture stress, competition, fire, or other disturbances reduce seedling survival and recruitment into sapling and adult stages (Mohammed et al., 2025b). Consequently, stable seedling numbers should not be interpreted as evidence of successful regeneration, but rather as an indication that recruitment failure occurs after the seedling stage. The Shannon–Wiener diversity index increased from 1.56 in 2008 to 2.21 in 2021, a more even distribution among the remaining species following the decline of formerly dominant taxa (Gamito, 2010; Okpiliya, 2012; Dafa-Alla et al., 2022; Gurashi et al., 2024; Chepkoech et al., 2024). However, this increase should be interpreted cautiously because it occurred alongside substantial declines in species richness, tree density, basal area, and regeneration success. Therefore, reliance on diversity indices alone may mask ongoing ecological degradation and underestimate biodiversity loss in dryland forests.

The IVI further highlights shift in forest structure and species dominance over time. *V. seyal* remained the most dominant species, yet its IVI declined from 2008 to 2021, reflecting substantial reductions in density and basal area. *S. senegal*, and *A. pilosum* also experienced significant IVI declines, indicating diminished ecological influence. In contrast, disturbance-tolerant species such as *B. aegyptiaca*, *V. oerfota* var. *oerfota*, and *Z. spina-christi* increased in relative importance, demonstrating partial resilience under anthropogenic pressure. Several species recorded in 2008 were absent in 2021, suggesting local extirpation or severe population decline. Overall, these trends indicate structural simplification, reduced forest resilience, and the economic implications of selective tree removal, emphasizing the need for targeted conservation of both dominant and lesser-represented species, alongside assisted regeneration to restore forest complexity and long-term ecosystem stability (Mohammed et al., 2021a; Musa et al., 2024; Maua et al., 2020; Vizzarri, 2024). An important implication of these findings is that diversity indices alone may not adequately reflect ecosystem condition in degrading dryland forests. Although Shannon and Simpson diversity indices increased between 2008 and 2021, these changes occurred simultaneously with substantial declines in species richness, tree density, basal area, and regeneration success. The increase in diversity indices primarily reflects a more even distribution of the remaining species rather than an improvement in biodiversity. Consequently, reliance on diversity indices without considering species richness and structural attributes may mask ongoing ecological degradation and underestimate biodiversity loss.

4.4 Trend in species conservation status between 2008 and 2021

The analysis of tree species inventories from 2008 and 2021 highlights pronounced temporal shifts in relative density (RD), diversity, and conservation status within the ENFR, reflecting both disturbance impacts and natural regeneration dynamics. In 2008, *V. seyal* dominated the forest with a high relative density, classifying it as abundant, consistent with patterns observed in Sudanese dryland forests where *Vachellia and Senegalia* species often exert strong structural and functional control (Osman and Idris, 2012; Mohammed et al., 2021a). In 2021, while *V. seyal* remained the most dominant species, its RD declined, indicating substantial reductions in population size likely driven by selective harvesting, fuelwood collection, and livestock browsing. Similar trends have been frequently reported in semi-arid woodlands across East Africa and Sudan (Ibrahim and Hassan, 2015; Musa et al., 2024). Several species, including *V. seyal var. fistula*, *S. catechu*, *C. aculeatum*, and *G. flavescens*, were no longer detected in 2021, suggesting local extirpation or severe population collapse. This pattern aligns with findings from dry forests and savanna ecosystems in Ethiopia (Gebeyehu et al., 2019), Kenya (Maua et al., 2020), and Benin

TABLE 5 Tree Species density, basal area, and importance value index in the ENFR in 2008 and 2021.

Species	2008				2021			
	MD	MBA	IVI	CBRD	MD	MBA	IVI	CBRD
Senegalia mellifera	0.74	0.01	0.93	Threatened	1.66	0.01	7.09	Abundant
Vachellia oerfota var. oerfota	0.13	0	0.19	Threatened	8.78	0.13	25.32	Abundant
Senegalia catechu	13.28	0.26	10.31	Rare	0	0	0	-
Senegalia senegal	42.4	2.35	19.8	Abundant	2.53	0.25	15.12	Abundant
Vachellia seyal	469.21	8.83	125.79	Abundant	22.93	0.35	71.99	Abundant
Vachellia seyal var. fistul	27.73	0.31	20.11	Occasional	0	0	0	-
Adansonia digitata	0.13	0.03	0.66	Threatened	0	0	0	-
Anogeissus leiocarpus	5.24	0.24	5.6	Threatened	1.66	0.06	9.4	Occasional
Balanities aegyptiaca	17.73	0.24	10.02	Rare	6.99	0.15	53.16	Abundant
Boswellia papyrifera	0.13	0	0.32	Threatened	0	0	0	-
Capparis decidua	0.57	0.01	0.88	Threatened	0	0	0	-
Cassia arereh	0.04	0	0.11	Threatened	0	0	0	-
Catunaregam nilotica	0.09	0	0.22	Threatened	0	0	0	-
Combretum aculeatum	3.8	0.09	1.82	Threatened	0	0	0	-
Combretum glutinosum	2.75	0.05	1.89	Threatened	0.7	0.01	5.35	Occasional
Combretum hartmannianum	28.3	1.24	12.56	Occasional	2.1	0.05	10.78	Rare
Combretum molle	4.06	0.08	2.76	Threatened	0	0	0	-
Dalbergia melanoxylon	1.09	0.14	1.49	Threatened	0.26	0	3.3	Rare
Dichrostachys cinerea	44.24	0.87	14.65	Abundant	0	0	0	-
Grewia flavescens	0.44	0	0.57	Threatened	0	0	0	-
Grewia tenax	0.35	0	0.47	Threatened	0.44	0	1.63	Abundant
Lannea fruticosa	4.59	0.04	4.5	Threatened	1.83	0.02	10.29	Rare
Maerua angolensis	0.13	0.01	0.37	Threatened	0	0	0	-
Ochna afzelii	0.26	0.01	0.43	Threatened	0	0	0	-
Philenoptera laxiflora	0.61	0	0.86	Threatened	0.17	0	1.26	Rare
Piliostigma reticulatum	0.04	0	0.11	Threatened	0	0	0	-
Sclerocarya birrea	1.14	0.02	1.53	Threatened	0.92	0.03	6.8	Frequent
Sterculia setigera	48.78	2.32	43.18	Abundant	8.21	0.19	44.88	Abundant
Stereospermum kunthianum	2.4	0.07	2.58	Threatened	0.7	0.01	5.57	Occasional
Strychnos innocua	0.22	0	0.43	Threatened	0	0	0	-
Tamarindus indica	0.04	0	0.14	Threatened	0	0	0	-
Terminalia brownii	3.01	0.06	4.38	Threatened	0.92	0.02	5.72	Occasional
Terminalia laxiflora	4.45	0.16	5.06	Threatened	1.09	0.02	5.29	Occasional
Ziziphus abyssinica	2.75	0.19	2.03	Threatened	1.05	0.04	5.62	Occasional
Ziziphus spina-christi	10.57	0.23	3.32	Rare	2.49	0.1	11.28	Abundant
Total	741.44	17.88			65.41	1.44		

MD, Mean density (no. of individual ha^{-1}); MBA, Mean basal area (m^2 ha^{-1}); IVI, Importance value index; CBRD, Classification based on relative dominance.

(Assogbadjo et al., 2010), where disturbance-sensitive species with low reproductive capacity or high exploitation value are disproportionately lost under sustained anthropogenic pressure (Siddig, 2019). Such losses reduce functional redundancy and compromise ecosystem resilience, particularly for species that provide critical habitat or cultural and economic services. Conversely, disturbance-tolerant species showed marked increases in RD, reflecting ecological plasticity and the ability to exploit altered competitive environments. Collectively, the results reveal a dynamic restructuring of the ENFR tree community; historically dominant species are declining, disturbance-tolerant taxa are gaining prominence, and overall diversity is moderately increasing. While this demonstrates the forest's partial resilience, the simultaneous loss of sensitive species underscores ongoing ecological vulnerability. The findings emphasize the urgent need for targeted

TABLE 6 Wilcoxon signed-rank test comparing woody species structural and regeneration variables between the 2008 and 2021 inventories in the ENFR.

Variable	W-value	Z-value	*p*-value	Effect size (r)
Mean number of tree (density ha^{-1})	582.00	4.37	< 0.0001	0.74
Mean number of seedling (ha^{-1})	11.00	0. 80	0.418	0.14
Mean number of sapling (ha^{-1})	328.00	2.38	0.017	0.40
Basal area (m^2 ha^{-1})	310.50	3.97	< 0.0001	0.67

TABLE 7 Summary of stand structural variables and diversity indices in the ENFR in 2008 and 2021.

Growth variables and diversity indices	2008	2021
Number of families	12	8
Genera	25	13
Number of tree species	35	19
Mean density (tree ha^{-1})	741.44	65.41
Number of trees	16,979	1,498
Mean number of seedlings (ha^{-1})	361.79	360.92
Mean number of saplings (ha^{-1})	239.78	28.17
Total basal area of all species (m^2 ha^{-1})	17.88	1.44
Mean basal area of species (m^2 ha^{-1})	0.51	0.04
Abundant (relative density; RD ≥ 5)	4 (11.43%)	8 (42.11%)
Frequent (4.00 ≤ RD ≥ 4.99)	–	1 (5.26%)
Occasional (3.00 ≤ RD ≥ 3.99)	2 (5.71%)	6 (31.58%)
Rare (1.00 ≤ RD ≥ 2.99)	3 (8.57%)	4 (21.05%)
Threatened/ Endangered (0.00 < RD ≤ 1)	26 (74.29%)	–
Shannon–Wiener [Diversity index (H)]	1.56	2.21
Margalef's index (species richness)	3.49	2.46
Species evenness index (E_H)	0.44	0.75
Simpson's species diversity index	0.58	0.82
Index of dominance	0.42	0.18

conservation interventions, including protection of declining and economically important species, regulation of selective harvesting, and assisted regeneration, to maintain ecosystem functionality, structural complexity, and long-term resilience (FAO, 2010; Siddig et al., 2019; Vizzarri, 2024; Yasin et al., 2024).

4.5 Spatial distribution and species composition patterns in the ENFR

The spatial distribution maps and dominance charts for 2008 and 2021 reveal marked changes in tree species composition and spatial patterns across the ENFR. In 2008, *V. seyal* overwhelmingly dominated the forest, with dense, widespread distribution across the reserve, followed by *S. setigera* and *Combretum* species, reflecting a relatively simple species hierarchy. Fewer species were widespread, and many taxa, such as *T. laxiflora* and *A. leiocarpus*, were localized, indicating a patchy distribution pattern typical tropical dry forests affected by environmental heterogeneity and selective use (Osman and Idris, 2012; Ibrahim and Hassan, 2015). In 2021, species composition became more heterogeneous, with previously minor or rare species, including *V. oerfota* var. *oerfota*, *S. mellifera, L. fruticosa*, and *D. melanoxylon,* increasing in relative density and spatial presence. While *V. seyal* remained dominant, its relative importance declined, and previously abundant species like *Combretum* species and *S. senegal* were reduced, reflecting selective harvesting and anthropogenic pressure. The emergence of *Z. spina-christi* and *B. aegyptiaca* as more prominent species demonstrates the resilience of disturbance-tolerant taxa under ongoing ecological stress (Mohammed et al., 2021a; Musa et al., 2024).

The spatial maps further show that areas dominated by historically abundant species are contracting, while patches of mixed species composition are increasing, suggesting shifts toward more fragmented and heterogeneous forest structure. This fragmentation can affect ecological processes such as seed dispersal, regeneration, and habitat provision for fauna, potentially reducing forest resilience and ecosystem functionality (Assogbadjo et al., 2010; Vizzarri, 2024). Overall, these patterns highlight both the decline of historically dominant species and the adaptive response of disturbance-tolerant species. Management implications include prioritizing conservation of declining species, promoting assisted regeneration, and maintaining connectivity between forest patches to preserve species diversity and ecosystem function (Ahmed and Desougi, 2014; Wilfahrt et al., 2023).

4.6 Study limitations

We acknowledge that in this study potential spatial autocorrelation among neighboring plots was not explicitly evaluated. Therefore, the reported patterns should be interpreted as reserve-scale trends rather than statistically independent spatial observations. The regeneration assessment was based on species-level population structure rather than plot-level regeneration classifications; therefore, spatial mapping of regeneration status across the reserve was not possible. Future monitoring efforts should incorporate plot-level regeneration metrics to support spatial analyses of regeneration patterns, recruitment success and environmental factors controlling regeneration dynamics. In addition, the systematic transect sampling design used in this study may introduce spatial dependence among plots, which was not formally tested. Future studies should incorporate spatial statistical approaches and spatial autocorrelation analyses to account for potential non-independence among sampling units and improve inference regarding forest structure and dynamics.

5 Conclusion

The present study demonstrates that the ENFR has undergone substantial structural and compositional degradation between 2008

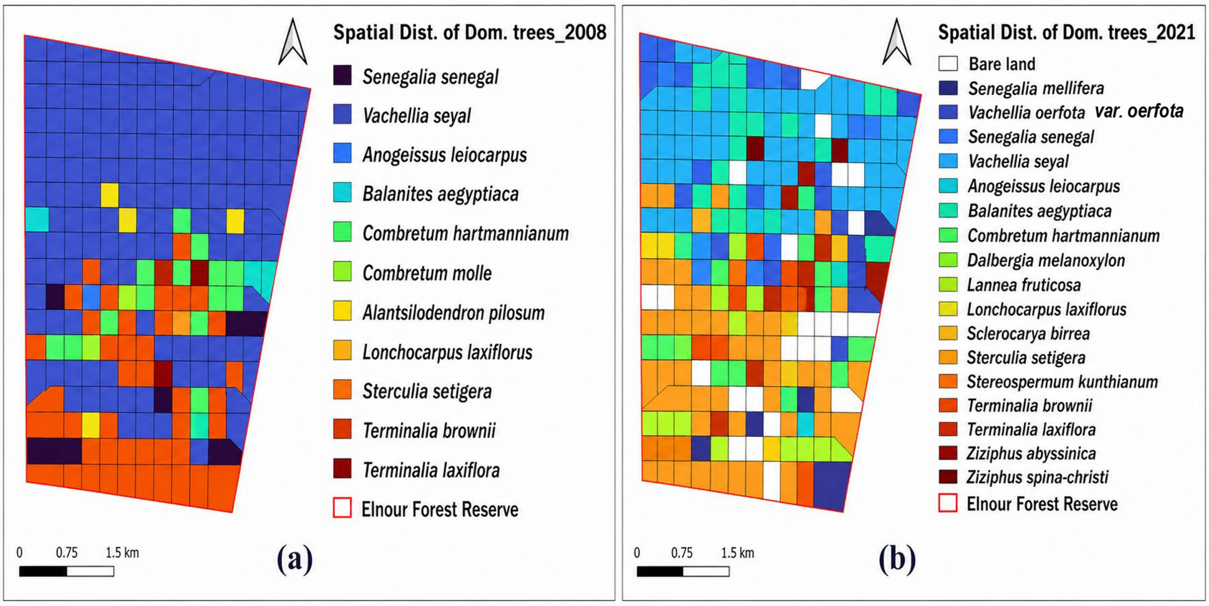

FIGURE 5
Spatial distribution of dominant tree species in the ENFR: **(a)** dominant species in 2008 and **(b)** dominant species in 2021.

and 2021. Tree density significantly declined from 741.4 to 65.4 trees ha^{-1}, representing a reduction of approximately 91%, while species richness decreased from 35 to 19 species (46% decline). Total basal area also significantly reduced from 17.88 to 1.44 m^2 ha^{-1}, corresponding to a reduction of approximately 92%. Although seedling abundance remained relatively stable, the drastic reduction in sapling and adult trees indicates severe regeneration bottlenecks and limited recruitment into mature size classes. The forests were increasingly dominated by a few disturbance-tolerant species, while previously recorded taxa in 2008 were absent in 2021, suggesting local population decline or extirpation. The observed increase in diversity indices despite declining species richness highlights the importance of interpreting biodiversity metrics collectively, as increased species evenness may conceal substantial losses in forest composition, structure, and ecological integrity. These findings highlight the urgent need for targeted conservation interventions in the ENFR. Management efforts should prioritize strict regulation of illegal tree cutting reduction of uncontrolled grazing pressure, and protection of regeneration hotspots, particularly during drought periods. Assisted natural regeneration and enrichment planting programs should focus on vulnerable native species that showed major declines including *S. senegal*, *S. setigera*, *C. hartmannianum*, and other ecological important taxa. Long-term monitoring using permanent georeferenced plots should be maintained to track vegetation recovery and assess the impacts of climate variability and anthropogenic disturbance. In addition, community-based forest management strategies and climate-adaptive restoration approaches are essential to enhance ecosystem resilience, restore forest structural complexity, and conserve biodiversity in the ENFR under the current environmental change.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

EY: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. HG: Data curation, Writing – review & editing. AS: Visualization, Writing – review & editing. FM: Formal analysis, Visualization, Writing – review & editing. US: Visualization, Writing – review & editing. KC: Supervision, Writing – review & editing.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2026.1835477/full#supplementary-material

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