Methodological Integration for Enhanced Analysis of the Structure of Forest Patches in Western Africa

Inaugural dissertation
of the Faculty of Science,
University of Bern

presented by

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From Igis, Graubünden

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Summary

Tropical forests are increasingly threatened by deforestation, fragmentation, and degradation, primarily driven by agriculture, logging, and fire. In Western Africa, thousands of small and isolated forest patches persist in agriculture-dominated landscapes. Although often unprotected, these forests provide essential ecosystem services such as biodiversity conservation, carbon storage, and the supply of resources like timber and bushmeat, while also holding cultural and spiritual significance. Safeguarding them requires a deeper understanding of their ecological functioning, as well as innovative monitoring approaches and consideration of local socio-economic realities.

However, knowledge about the structure of these forests—an essential ecological feature—is limited. Forest structure determines whether a forest is composed of large versus small trees, how canopy layers are organized, and whether gaps dominate the canopy. Such attributes are directly linked to forest biomass and carbon sequestration, both of which are key indicators of ecological functioning. This thesis contributes to closing this knowledge gap by analyzing the structure, aboveground biomass (AGB), and tree species richness of tropical forest patches across Western Africa. The research focused on nine forest patches in Togo, Benin, Nigeria, and Cameroon, based on 121 forest plots with tree inventories and species identifications.

The results revealed relatively intact forest structure and high aboveground biomass (85–260 Mg/ha), as well as the presence of several vulnerable and endangered tree species such as *Afzelia bipindensis* and *Guibourtia tessmannii*. At the same time, the forest patches showed pronounced edge effects: degradation was most visible near the edges, while more intact zones were confined to the core. Structural metrics—including basal area, canopy height, species richness, complexity, and tree vitality—increased with distance from the edge. In highly isolated patches, edge effects also reduced AGB and wood density. AGB values in the studied community forests were lower than those in nearby officially protected areas, underscoring the importance of conservation measures beyond formal reserves.

Beyond describing ecological conditions, this thesis advances methodological innovation for forest assessment. A terrestrial laser scanner (TLS) was tested to estimate AGB and compared with manual inventories. While both methods produced moderately correlating results, challenges remained due to sensor occlusion and the lack of species-specific wood density data. In addition, unmanned aerial vehicles (UAVs) equipped with LiDAR and multispectral sensors enabled fine-scale disturbance mapping, complementing ground-based information on forest structure and vitality. Together, these tools demonstrate how emerging technologies can improve monitoring of fragmented tropical forests.

Finally, the thesis integrates social dimensions to contextualize ecological findings. Through 328 interviews with regular forest users, it examined local perceptions of forest integrity and forest-related activities such as hunting and logging. Results revealed contrasting perspectives: in intensively used areas, degradation was often not perceived as a major concern, whereas communities maintaining sacred forests showed strong awareness of threats such as fire and illegal logging. Forests near urban centers exhibited higher exploitation pressure, and interviewees frequently reported declining forest areas and the disappearance of key species. These insights highlight the role of cultural traditions and socio-economic contexts in shaping both forest condition and conservation prospects.

Taken together, the results highlight that Western Africa's remaining forest patches retain important ecological value—relatively intact structures, high biomass stocks, and threatened species—yet remain highly vulnerable to edge effects and human pressure. To safeguard their ecological and social value, this thesis recommends conservation strategies such as establishing buffer zones to reduce edge degradation, reconnecting fragments with habitat corridors, and integrating socio-economic approaches into forest management. By combining ecological analysis, methodological innovation, and social perspectives, the thesis advances knowledge on tropical forest functioning and provides tools and strategies for their sustainable management.

Keywords: Aboveground biomass, Carbon, Degradation, Edge effects, Fragmentation, Forest use, Perceptions, Structural complexity, Tree species

Résumé

Les forêts tropicales sont de plus en plus menacées par la déforestation, la fragmentation et la dégradation, principalement sous l'effet de l'agriculture, de l'exploitation forestière et des incendies. En Afrique de l'Ouest, des milliers de petits fragments forestiers isolés subsistent dans des paysages dominés par l'agriculture. Bien que souvent non protégées, ces forêts fournissent des services écosystémiques essentiels tels que la conservation de la biodiversité, le stockage du carbone et l'approvisionnement en ressources comme le bois et le gibier, tout en revêtant une importance culturelle et spirituelle. Les protéger nécessite une compréhension approfondie de leur fonctionnement écologique, ainsi que des approches de suivi innovantes et la prise en compte des réalités socio-économiques locales.

Cependant, les connaissances sur la structure de ces forêts — une caractéristique écologique essentielle — restent limitées. La structure forestière détermine si une forêt est composée principalement de grands ou de petits arbres, comment les strates de la canopée sont organisées et si les trouées dominent la couverture forestière. Ces attributs sont directement liés à la biomasse aérienne (BA) et à la séquestration du carbone, deux indicateurs clés du fonctionnement écologique. Cette thèse contribue à combler cette lacune en analysant la structure, la biomasse aérienne (BA) et la richesse en espèces d'arbres des fragments forestiers tropicaux d'Afrique de l'Ouest. La recherche s'est concentrée sur neuf fragments forestiers situés au Togo, au Bénin, au Nigeria et au Cameroun, à partir de 121 parcelles forestières avec inventaires d'arbres et identification des espèces.

Les résultats ont révélé une structure forestière relativement intacte et une biomasse aérienne élevée (85–260 Mg/ha), ainsi que la présence de plusieurs espèces d'arbres vulnérables et menacées telles que *Afzelia bipindensis* et *Guibourtia tessmannii*. En même temps, les fragments forestiers ont montré des effets de lisière prononcés : la dégradation était la plus visible près des bords, tandis que des zones plus intactes étaient confinées au cœur des fragments. Les indicateurs structurels — notamment la surface terrière, la hauteur de la canopée, la richesse en espèces, la complexité structurale et la vitalité des arbres — augmentaient avec la distance par rapport à la lisière. Dans les fragments fortement isolés, les effets de lisière réduisaient également la biomasse aérienne et la densité du bois. Les valeurs de BA dans les forêts communautaires étudiées étaient inférieures à celles des zones protégées officielles à proximité, soulignant l'importance de mesures de conservation au-delà des réserves formelles.

Au-delà de la description des conditions écologiques, cette thèse fait progresser l'innovation méthodologique pour l'évaluation forestière. Un scanner laser terrestre (TLS, *terrestrial laser scanner*) a été utilisé pour estimer la BA et comparé aux inventaires manuels. Bien que les deux méthodes montrent une corrélation moderée, des difficultés subsistent en raison de l'occultation des capteurs et du manque de données de densité du bois spécifiques aux espèces. De plus, des véhicules aériens sans pilote (UAV, *unmanned aerial vehicle*) équipés de LiDAR et de capteurs multispectraux ont permis de cartographier les perturbations à fine échelle, complétant les informations obtenues au sol sur la structure et la vitalité forestières. Ensemble, ces outils démontrent comment les technologies émergentes peuvent améliorer le suivi des forêts tropicales fragmentées.

Enfin, la thèse intègre des dimensions sociales pour contextualiser les résultats écologiques. Grâce à 328 entretiens avec des usagers de la forêt, elle a examiné les perceptions locales de l'intégrité forestière et les activités forestières telles que la chasse et l'exploitation du bois. Les résultats ont révélé des perspectives contrastées : dans les zones à forte exploitation, la dégradation n'était souvent pas perçue comme un problème majeur, tandis que les communautés maintenant des forêts sacrées montraient une forte conscience des menaces telles que les incendies et l'exploitation illégale. Les forêts situées à proximité des centres urbains présentaient une pression d'exploitation plus élevée, et les interviewés signalaient fréquemment un recul des surfaces forestières et la disparition d'espèces clés. Ces observations mettent en évidence le rôle des traditions culturelles et des contextes socio-économiques dans la détermination de l'état des forêts et des perspectives de conservation.

Dans l'ensemble, les résultats montrent que les fragments forestiers restants d'Afrique de l'Ouest conservent une valeur écologique importante — structures relativement intactes, stocks élevés de biomasse et espèces menacées — mais restent très vulnérables aux effets de lisière et aux pressions humaines. Pour préserver leur valeur écologique et sociale, cette thèse recommande des stratégies de conservation telles que l'établissement de zones tampons pour réduire la dégradation en bordure, la reconnexion des fragments par des corridors écologiques et l'intégration d'approches socio-économiques dans la gestion forestière. En combinant analyse écologique, innovation méthodologique et perspectives sociales, la thèse fait progresser la connaissance du fonctionnement des forêts tropicales et fournit des outils et stratégies pour leur gestion durable.

Mots-clés: Biomasse aérienne, Carbone, Complexité structurelle, Dégradation, Effets de lisière, Espèces d'arbres, Fragmentation, Perceptions, Utilisation des forêts

Zusammenfassung

Tropische Wälder sind zunehmend durch Abholzung, Fragmentierung und Degradierung bedroht, hauptsächlich verursacht durch Landwirtschaft, Holzeinschlag und Feuer. In Westafrika bestehen in von Landwirtschaft dominierten Landschaften noch tausende kleine und isolierte Waldfragmente. Obwohl diese Wälder oft ungeschützt sind, erbringen sie essenzielle Ökosystemleistungen wie den Erhalt der Biodiversität, die Kohlenstoffspeicherung sowie die Bereitstellung von Ressourcen wie Bauholz und Wildfleisch und haben gleichzeitig kulturelle und spirituelle Bedeutung. Ihr Schutz erfordert ein tieferes Verständnis ihres ökologischen

Funktionierens sowie innovative Monitoring-Ansätze und die Berücksichtigung lokaler sozioökonomischer Realitäten.

Allerdings sind die Kenntnisse über die Struktur dieser Wälder — ein wesentliches ökologisches Merkmal — begrenzt. Die Waldstruktur bestimmt, ob ein Wald hauptsächlich aus grossen oder kleinen Bäumen besteht, wie die Schichten der Baumkronen (Kronendachstrukturen) organisiert sind und ob Lücken die Baumkronen dominieren. Diese Merkmale stehen in direktem Zusammenhang mit der oberirdischen Biomasse (AGB, *aboveground biomass*) und der Kohlenstoffspeicherung, die beide zentrale Indikatoren für das ökologische Funktionieren darstellen. Diese Dissertation trägt dazu bei, diese Wissenslücke zu schliessen, indem sie die Struktur, die AGB und die Artenvielfalt von Bäumen in tropischen Waldfragmenten Westafrikas analysiert. Die Untersuchung konzentrierte sich auf neun Waldfragmente in Togo, Benin, Nigeria und Kamerun, basierend auf 121 Waldparzellen mit Baum-Inventur und Artenbestimmungen.

Die Ergebnisse zeigten eine relativ intakte Waldstruktur und eine hohe oberirdische Biomasse (85–260 Mg/ha), sowie das Vorkommen mehrerer gefährdeter und bedrohter Baumarten wie *Afzelia bipindensis* und *Guibourtia tessmannii*. Gleichzeitig wiesen die Waldfragmente ausgeprägte Randeffekte (*edge effects*) auf: Degradierung war besonders an den Waldrändern sichtbar, während intakte Bereiche im Kern der Fragmente lagen. Strukturmetriken — einschliesslich Baumgrundfläche, Kronenhöhe, Artenvielfalt, strukturelle Komplexität und Baumvitalität — nahmen mit zunehmender Entfernung vom Waldrand zu. In stark isolierten Fragmenten reduzierten die Randeffekte zusätzlich die AGB und die Holzdichte. Die AGB-Werte in den untersuchten Gemeinschaftswäldern lagen unter denen der nahegelegenen offiziell geschützten Gebiete, was die Bedeutung von Schutzmassnahmen über formelle Reservate hinaus unterstreicht.

Über die Beschreibung ökologischer Bedingungen hinaus leistet diese Dissertation einen Beitrag zur methodischen Innovation in der Waldbewertung. Ein terrestrischer Laserscanner (TLS, *terrestrial laser scanner*) wurde zur Schätzung der AGB eingesetzt und mit manuellen Inventaren verglichen. Obwohl beide Methoden stark korrelierende Ergebnisse lieferten, bestanden weiterhin Herausforderungen aufgrund von Sensorverschattungen (*occlusion)* und fehlender artspezifischer Holzdichtedaten. Zusätzlich ermöglichten unbemannte Luftfahrzeuge (UAVs, *unmanned aerial vehicles*) mit LiDAR- und Multispektralsensoren die Kartierung von Störungen auf feiner Skala, wodurch die bodengestützten Informationen über Waldstruktur und Vitalität ergänzt wurden. Zusammen zeigen diese Technologien, wie moderne Methoden die Überwachung fragmentierter tropischer Wälder verbessern können.

Schliesslich integriert die Dissertation soziale Dimensionen, um die ökologischen Ergebnisse zu kontextualisieren. Durch 328 Interviews mit Waldnutzenden wurden lokale Wahrnehmungen der Waldintegrität und waldbezogener Aktivitäten wie Jagd und Holzeinschlag untersucht. Die Ergebnisse zeigten kontrastierende Perspektiven: In intensiv genutzten Gebieten wurde Degradierung oft nicht als ernsthaftes Problem wahrgenommen, während Gemeinden, die heilige Wälder pflegen, ein starkes Bewusstsein für Bedrohungen wie Feuer und illegalen Holzeinschlag zeigten. Wälder in der Nähe städtischer Zentren waren stärkerer Nutzung ausgesetzt, und die Befragten berichteten häufig über rückläufige Waldflächen und das Verschwinden wichtiger Arten. Diese Erkenntnisse verdeutlichen die Rolle kultureller Traditionen und sozioökonomischer Kontexte bei der Bestimmung des Waldzustands und der Aussichten für den Naturschutz.

Zusammenfassend heben die Ergebnisse hervor, dass die verbleibenden Waldfragmente Westafrikas eine bedeutende ökologische Wertigkeit besitzen — relativ intakte Strukturen, hohe Biomassebestände und bedrohte Arten —, jedoch weiterhin stark anfällig für Randeffekte und menschlichen Druck sind. Um ihren ökologischen und sozialen Wert zu sichern, empfiehlt diese Dissertation Schutzstrategien wie die Einrichtung von Pufferzonen zur Reduzierung der Randdegradierung, die Wiedervernetzung von Fragmenten durch Habitatkorridore und die Integration sozioökonomischer Ansätze in die Waldbewirtschaftung. Durch die Kombination ökologischer Analysen, methodischer Innovationen und sozialer Perspektiven erweitert die Dissertation das Wissen über das Funktionieren tropischer Wälder und liefert Werkzeuge und Strategien für deren nachhaltige Bewirtschaftung.

Stichworte: Baumarten, Degradierung, Fragmentierung, Kohlenstoff, Oberirdische Biomasse, Randeffekte, Strukturelle Komplexität, Wahrnehmungen, Waldnutzung

I. Acknowledgments

"We are like continents in the sea, or like trees in the forest. The mahogany and the kapok may whisper to each other with their leaves…But the trees also commingle their roots in the darkness underground, and the continents also hang together through the ocean's bottom. Just so there is a continuum of cosmic consciousness, against which our individuality builds but accidental fences, and into which our several minds plunge as into a mother-sea or reservoir." Adapted from William James, 'Essays and Lectures' (1909)

Like almost everything in life, this PhD is the result of enabling circumstances in time and space, shaped by the people who supported me at crucial moments. First, I want to thank Amelie Kreuzer for pointing out this PhD position, she set this entire journey in motion. I am deeply grateful for the support of my family. My brother, Simon Hepner, encouraged me to think twice about the statistical tests I applied in this work. My mother continuously supported me, even if she may not have fully understood the point of writing hundred pages of text in four years. She also made sure we planned regular holidays, which helped to clearing my mind and gave me the chance to explain my research in plain Swiss German. My father, Klaus Hepner, undoubtedly sparked my curiosity for the natural sciences. Even 30 years after university, he could still recall every plant by its Latin name. Sadly, he left us in 2024, may he rest in peace and read this thesis from another world. My sister, Naemi Hepner, deserves thanks for organizing family reunions and trips to beautiful natural places. Finally, I am especially grateful to my wonderful girlfriend, Lisa Niederauer. As a neurologist at the university hospital, she tirelessly demonstrated what true hard work looks like. She showed patience (and even interest) during my mock presentations, let me go when I traveled for summer schools and fieldwork, and welcomed me with open arms when I returned.

This thesis was conducted at the University of Bern, where I was fortunate to benefit from the expertise of various institutions and individuals. The statistics consulting service and the Data Science Lab helped me navigate challenges related to error propagation and Python scripts. I am grateful for the support of key people at the Institute of Geography, for example Saliba Saliba, Marlis Röthlisberger-Zaugg, Nicole Sarbach-Schumacher, and Carmen Theler, who provided me with a computer, a chair, and a desk, and ensured that my expenses, salary, and working hours were properly managed.

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II. Preface

From a small village in the Swiss Alps to even smaller villages in Western Africa. Like many Swiss people, I was not particularly interested in Africa for a long time and did not think and know much about it. However, during my master's at the University of Lausanne, I came across a thesis advertisement about agriculture in Côte d'Ivoire. After a quick Google search to locate Côte d'Ivoire on the map and listening to a few songs by Magic System, I decided to go for it. I spent a few months there, and after overcoming the initial cultural shock, I began to appreciate the spicy food, the hospitality of the people, the lush landscapes, and the relaxed working atmosphere. I was into it.

That experience made it impossible to resist applying for this PhD position, which promised exciting fieldwork in Togo, Benin, Nigeria, and Cameroon—countries one does not typically visit as a tourist, but whose realities I was eager to explore. Of course, a PhD is not just about fieldwork. It is an abstract and often unpredictable journey, difficult to fully grasp from the outside. During an adventurous mountaineering tour to the Piz Scerscen in the Grisons, I chose the unknown and decided to move to Bern and conduct this PhD.

The PhD was conducted in the Land Systems and Sustainable Land Management unit at the Institute of Geography at the University of Bern. It was part of the SUSTAINFORESTS project (2021-2026), funded by the European Research Council (grant agreement No. 101001200).
Looking back, I am grateful for this enriching experience, full of learning opportunities and inspiring people. These four years have passed quickly, and I am happy to present the outcome in this thesis.

1. Introduction

1.1 Historical context

Humans began living in African tropical forests around 60,000 years ago and later colonized tropical forests on other continents (Lewis et al., 2015; Scerri et al., 2022). For much of history, people relied on forests for food, shelter, and energy (Vantomme, 2011). Early impacts included megafauna extinctions, such as stegodonts and gomphotheres, which altered forest structure (Lewis et al., 2015). The loss of such keystone species also led to changes in forest structure and composition (Lewis et al., 2015; Malhi et al., 2013, 2014). Around 6000 years ago, agriculture reduced forest cover locally (Lewis et al., 2015). These small-scale, low-impact human–forest interactions persist today among uncontacted tribes (Gerstner, 2019; Vantomme, 2011). However, most societies progressively modified forests to increase productivity for human benefits (Wunder, 2001). European colonization in Africa around 1800 further transformed forests through commercialization and systematic exploitation (Kitunda, 2025; Uzu et al., 2022). Most accessible forests were first logged and then converted to agriculture (Ashton & Hall, 2011; Knoke & Huth, 2011; Potapov et al., 2021; Wunder, 2001). Modern machinery has made exploitation increasingly efficient (Grigorev et al., 2020).

Today, in the Anthropocene (Crutzen, 2002), only a fraction of tropical forest remains, facing compounding threats from climate change and biodiversity loss (Lewis et al., 2015). Competing claims complicate management: local communities depend on resources like bushmeat and firewood (Heinimann et al., 2017; Lewark, 2022; Neuenschwander et al., 2015), while global institutions push for conservation and carbon storage (Convention on Biological Diversity (CBD), 2021; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2022; International Union for Conservation of Nature (IUCN), 2022; United Nations, 2015). Meanwhile, governments, corporations, and elites often prioritize short-term profits (Baruah, 2017; Ruiz Pérez et al., 2005).

As resource demands grow, land-use conflicts intensify, particularly between agriculture and forest preservation (Günter et al., 2011). Scientists warn that tropical forests may be nearing ecological tipping points, shifting to savannah-like states (Malhi et al., 2014; Sullivan et al., 2020; Zemp et al., 2017). Yet opportunities remain: up to 0.9 billion hectares of unforested land could support natural regeneration, aiding climate mitigation and ecosystem restoration (Bastin et al., 2019). These long-term and contemporary dynamics shape not only the extent of tropical forests but also their structure, biomass, and species richness, as well as how local people perceive and interact with them.

As the uses and values of forests have shifted over time, so too have forest research questions and their corresponding methods (Chen et al., 2022). Early inventories focused on describing forest stands and estimating timber, but over time methods became increasingly systematic, accurate, and representative (Asrat & Tesfaye, 2013; Murtiyoso, Cabo, et al., 2024). Since the mid-20th century, forest research has progressively expanded from timber-focused measurements to broader ecological assessments, incorporating statistical design, growth and yield modeling, and biodiversity monitoring (Burkhart et al., 2019).

1.2 Current approaches in forest research

Recent decades have seen a rapid technological transformation of forest research. Among the most important advances is terrestrial laser scanning (TLS), which enables highly detailed mapping of forest structure by capturing the three-dimensional spatial distribution of vegetation (Calders et al., 2020). TLS point clouds can be used to derive tree height, volume, and biomass, as well as canopy architecture and deadwood (Krisanski et al., 2021; Wilkes et al., 2023). Mobile and aerial systems, including UAVs and airborne laser scanning, extend point cloud acquisition across larger areas, while satellite missions such as ESA's BIOMASS launched in 2025 promise global insights into aboveground biomass (Brede et al., 2019; European Space Agency, 2025). Beyond measurement, point clouds are increasingly used to build digital twins for management simulations (Holm & Schweier, 2024), to perform radiative transfer modeling linking structural and spectral data (Calders et al., 2018), and to generate synthetic forests that reduce the need for extensive field sampling (Feng et al., 2025). Novel UAV designs even mimic animal flight or perch silently in canopies, opening new opportunities for biodiversity monitoring (Chang et al., 2020; Kirchgeorg & Mintchev, 2022; Ramezani et al., 2017).

Each method for studying forests has strengths and limitations. Manual inventories provide highly accurate measurements of individual trees and ecological details, forming essential ground-truth data, but they are labor-intensive and restricted to small areas. TLS offers precise three-dimensional mapping of forest structure and biomass yet is similarly limited in spatial extent. UAVs allow flexible and relatively cost-effective data collection across intermediate scales, though dense canopies or complex terrain can constrain their use. Satellite remote sensing provides global and temporal coverage, but at coarser spatial resolution, making fine-scale structural analysis challenging. Beyond technological tools, local knowledge and perceptions give crucial insights into disturbances, resource use, and ecosystem dynamics that are invisible from remote sensing, though they may reflect subjective or culturally influenced views.

Integrating these approaches—combining solid ground-truth data from manual inventories, TLS precision, UAV flexibility, satellite reach, and local ecological knowledge—offers a holistic and robust understanding of forest structure, biomass, species richness, and disturbance dynamics. This multi-scale, multi-perspective framework underpins the approach of the present study, linking high-resolution measurements with broader ecological patterns and local perceptions.

1.3 Forest research in the African context

Most forest research is conducted and funded in developed countries such as the USA, China, and in Europe (Aleixandre-Benavent et al., 2017; Aznar-Sánchez et al., 2018; Chen et al., 2022; Y. Song & Zhao, 2013), while tropical forests remain comparatively less studied. The Brazilian Amazon dominates the literature about tropical forests, with long-term studies on deforestation, fragmentation, and restoration (e.g., Asner et al., 2005; Fearnside, 2005; Laurance et al., 2002). In contrast, Africa—especially Western Africa—has been severely neglected, with only a handful of published studies and limited grey literature (Ashton & Hall, 2011; North et al., 2020). Structural barriers such as scarce funding and research capacity contribute to this gap (Ighodaro & Igbinedion, 2020; North et al., 2020). Here, the term *Western Africa* refers to both the Guinean forests of West Africa and the ecologically similar Lower Guinea forests extending into Cameroon.

Yet African tropical forests are globally significant. They make up about 30% of the world's tropical forests and differ from Amazonian and Asian forests in structure, biomass, and species richness (Lewis et al., 2013, 2015). For example, African forests host fewer species and trees per hectare but store more biomass due to longer carbon residence times. Megafauna extinction was less severe than elsewhere, and elephants still play a key role in shaping forest composition. These forests are also highly vulnerable to shifting cultivation and agricultural expansion, with 47 million hectares lost between 2003 and 2019 (Heinimann et al., 2017; Potapov et al., 2021). Climate change adds further uncertainty: while dieback is projected for many tropical forests, shifts in the West African Monsoon could even expand forest potential in parts of the Sahel, though sparse meteorological data limit model reliability (Lenton et al., 2008; Réjou-Méchain et al., 2021).

Despite their global importance, ecological data on African tropical forests remain scarce, particularly regarding forest structure and biomass. This lack of baseline knowledge constrains both conservation strategies and climate models. Research is urgently needed as rapid population growth, urbanization, and economic development increase pressure on natural resources. With Africa's population projected to double by 2050 , the demand for forest products and land is expected to intensify, making a better understanding of forest structure, biomass, species richness, and local perceptions of forest ecology particularly pressing (Grinin & Korotayev, 2023).

1.4 Forest patches in Western Africa

In the last decades, Western Africa has faced very high rates of tropical deforestation (Hansen et al., 2013; Poorter et al., 2004; Schelhas & Greenberg, 1996) and the countries of Togo, Benin, Nigeria, and Cameroon are no exception. These countries host thousands of small, isolated forest patches in fragmented, agriculture-dominated landscapes (Wingate et al., 2022, 2024), which are crucial for biodiversity conservation, carbon storage, and resources such as timber and bushmeat (Neuenschwander et al., 2015). The persistence of these patches is uncertain, given widespread agricultural expansion, associated deforestation, and the lack of formal protection (Akinyemi & Ifejika Speranza, 2022; Mintah et al., 2024; Poorter et al., 2004). Small and primary forests are particularly vulnerable to large-scale land-cover change (Wingate et al., 2024). Their continued existence highlights the challenges of balancing environmental values with human development in regions under high land-use pressure (Ifejika Speranza et al., 2019). Moreover, these patches are often overlooked in both research and policy design (Meyfroidt et al., 2018; Mintah et al., 2024). It is likely that larger forest blocks, such as the Congo Basin, will also become increasingly fragmented due to ongoing land-use changes (Fischer et al., 2021) with significant consequences for biodiversity and other ecosystem services (Blockhus et al., 1992). Studying the dynamics of fragmented landscapes in Western Africa thus provides valuable insights into the potential future of the Congo Basin.

1.5 Scientific gaps and problem statement

1.5.1 Understanding ecological functioning in tropical forests

Tropical forests play a key role in global ecological functioning, supporting biodiversity, regulating climate, and storing large amounts of carbon (Ameray et al., 2021). Forest structure is an important proxy for forest resilience and integrity, as it correlates with indicators such as biodiversity, productivity, carbon storage, and microclimate regulation (Coverdale & Davies, 2023). However, despite its importance, forest structure and its links to forest degradation and fragmentation remain insufficiently quantified in many regions, particularly in Western Africa, restricting our capacity to assess forest integrity and detect patterns of degradation and resilience.

Aboveground biomass (AGB) estimation represents a second major gap. Although tropical forests store around 80% of terrestrial aboveground carbon, with roughly half of tree biomass consisting of carbon (Ghazoul & Sheil, 2010), accurately estimating AGB remains challenging. Uncertainties are especially high in fragmented landscapes, such as those found across Western Africa (Araza et al., 2022). These uncertainties limit our ability to determine whether forests act as net carbon sinks or sources (Mitchard, 2018), despite the fact that climate models rely heavily on precise AGB estimations (Chave et al., 2019).

Finally, the ecological consequences of anthropogenic disturbances on tree species compositions in these forests are not well understood. The spatial patterns of disturbance and edge effects remain largely unknown, as does their impact on alpha and beta diversity, even though these forests harbor near-threatened, vulnerable, and endangered species such as *Anonidium mannii, Afzelia bipindensis,* and *Guibourtia tessmannii*.

1.5.2 Testing new methods to improve capturing forest conditions

Monitoring tropical forests, whether large tracts or small patches, is inherently challenging due to their vast extent, inaccessibility, and structural complexity. Traditional approaches, such as manual inventories and allometric equations, are prone to systematic biases, limiting the accuracy of AGB estimations (Calders et al., 2022) This thesis addresses these limitations by advancing the use of TLS in tropical forests. For the first time in this region, TLS is systematically applied to not only quantify structural complexity but also to compare biomass as estimated by manual inventories and TLS respectively.

At the same time, more remote sensing technologies offer promising opportunities to improve forest monitoring. Unmanned aerial vehicles (UAVs) have emerged as effective tools for assessing forest health (Ecke et al., 2022; Torresan et al., 2017), yet their potential remains underexplored in Western Africa. In particular, UAV LiDAR has never been combined with multispectral data to evaluate forest patches in this region. By fusing these datasets, this thesis develops an integrated disturbance index for contiguous forest areas, which can be validated against ground-based observations of forest degradation. This approach provides a more comprehensive understanding of forest conditions than ground-based surveys alone.

1.5.3 Social dimensions of ecological forest conditions

The social dimensions of deforestation and degradation—how local communities use, perceive, and manage forests—remain insufficiently studied, even though millions of people depend on tropical forests for their livelihoods (Lewark, 2022). In Western Africa, the persistence of forest patches directly reflects community practices, placing local people at the forefront of either degrading or conserving forests. Yet no comparative research has systematically examined these dynamics across Togo, Benin, Nigeria, and Cameroon.

Addressing this gap is crucial, since ecological measurements and local perceptions capture different but complementary realities. Structural complexity, AGB, and diversity provide objective indicators of degradation and resilience, but they cannot reveal how forests are experienced, valued, or managed on the ground. Conversely, local perceptions highlight pressures and disturbances that may not be immediately detectable in ecological data, but they can be subjective, shaped by cultural and economic contexts. Linking the two perspectives therefore adds explanatory depth: it helps clarify mismatches (e.g., when forests perceived as degraded still retain ecological integrity, or when intact-looking forests are already under pressure) and supports more robust, socially grounded management strategies.

This thesis addresses these gaps by analyzing forest structural complexity along edge–core gradients, providing AGB data at both tree and plot levels, and examining alpha and beta diversity across forest patches in Western Africa. New methods are tested by comparing AGB estimates from manual inventories and TLS, and by integrating LiDAR and multispectral data from UAVs. The social dimensions are addressed by combining interview data with socio-economic and ecological measurements, thereby embedding objectively measured forest conditions within the lived realities of local communities.

1.6 Research objectives of the PhD

Building on these gaps, this thesis, embedded in the interdisciplinary *SUSTAINFORESTS* project, addresses them through five corresponding papers. The research focuses on nine forest patches in Togo, Benin, Nigeria, and Cameroon, spanning the Guinean Savanna and the Guineo-Congolian zone (Dinerstein et al., 2017; Tappan et al., 2016). Accordingly, the thesis is guided by the following research questions:

1.6.1 Understanding ecological functioning in tropical forests

Paper 1: Degradation effects on forest structure

1. How does the stand structural complexity index (SSCI) vary with fragmentation, connectivity, canopy openness, tree height, basal area, number of tree stems, and tree species richness?
   - We expect that SSCI increases with high connectivity, low fragmentation, low canopy openness, a high number of tall trees, a high basal area, a high tree stem density, and high tree species richness.
2. How do edge effects impact the SSCI of forest patches?
   - We expect that SSCI decreases toward forest edges.
3. How does the *in situ* measured SSCI of the forest patches compare with the corresponding ecological reference value?
   - We expect intact forest patches where *in situ* measured SSCI equal the corresponding ecological reference value.

Paper 2: Aboveground biomass in small forest patches measured with TLS

1. What is the current AGB and carbon in the studied forest patches and how is it spatially distributed?
   - We expect that the amounts and spatial patterns of AGB and carbon vary across the forest patches, indicating environmental and disturbance gradients.
2. Which forest characteristics correlate most with AGB?
   - We expect basal area, tree height, and wood density to correlate most with AGB.
3. How does the AGB of these patches compare with that of other forests in the region?
   - We expect to find lower AGB in isolated forest patches as compared to larger forest areas, due to edge effects.

Paper 3: Disturbance effects on tree species diversity

1. How does alpha diversity of tree communities vary in relation to both anthropogenic disturbances and bioregion types?
   - We expect variation in tree community-alpha diversity along the bioregion types and disturbance gradients.
2. How does beta diversity vary among tree communities in forest patches across the Guineo-Sudanian and Guineo-Congolian bioregions?
   - Tree beta diversity increases with spatial distance between forest patches.
3. What are the effects of disturbance intensity and bioregion type on tree stand structure in forest patches?
   - Tree stand parameters (e.g., tree density and basal area) are negatively correlated with disturbance gradients, mainly due to selective logging of timber species and forest fires.

1.6.2 Testing new methods to improve capturing forest conditions

Paper 2: Aboveground biomass in small forest patches measured with TLS

4. How does AGB estimated from manual inventory compare to AGB obtained by TLS?
   - We expect that AGB obtained by TLS will show a positive correlation with AGB derived from manual inventories across forest patches.

Paper 4: Integrating LiDAR and multispectral UAV data

1. How can structural properties, derived from UAV LiDAR data and spectral vegetation indices from UAV multispectral imagery, be used to assess the current state of the forest?
   - Structural and spectral metrics, derived from UAV LiDAR and multispectral imagery, can effectively characterize spatial variation in forest condition.
2. How can an Integrated Disturbance Index (IDI) be generated using principal component analysis (PCA) of correlated structural and spectral vegetation indices?
   - An Integrated Disturbance Index (IDI) generated via PCA of structural and spectral metrics can capture gradients of forest disturbance.
3. How can the IDI be used to delineate low, medium, and high disturbance levels to identify forest areas that require immediate conservation action?
   - The IDI can reliably classify forest areas into low, medium, and high disturbance levels to support conservation prioritization.

1.6.3 Integrating social perspectives and measured values of forest conditions

Paper 5: Forest use and its perceptions

1. To what extent do forest use patterns differ across forests with varying socio-cultural, economic, and ecological contexts?
   - Forest use is expected to be dominated by the collection of non-timber forest products across all sites, with minor differences possibly linked to observable site characteristics, such as governance rules (e.g., sacred forests) or ecological conditions (e.g., swamp vs. semi-deciduous forests).
2. How do perceptions of forest use impacts differ across sites with varying socio-cultural, economic, and ecological contexts?

- Logging and fire are expected to be widely perceived as degrading forests across sites, while perceptions of other activities (e.g., agriculture, charcoal production, NTFP collection) are expected to show greater variability depending on measurable or describable contextual factors, such as forest type, local restrictions, and community norms.

3. How are pressure on forests and perceived and measured forest degradation interrelated?
   - Forests under greater pressure of use (e.g., logging, hunting, weak governance) are expected to show higher measured degradation. These pressures are also likely to shape local perceptions, such that observable degradation corresponds with community perceptions.

2. Methods

This thesis was conducted between 2021 and 2025. I began by reviewing the literature to identify knowledge gaps and become familiar with specific methods. I then participated in fieldwork to collect data, followed by analyzing the data and integrating the results with existing datasets such as satellite imagery. The findings were connected with the literature and published. Finally, I and the rest of the research team returned to the field communities to share results and discuss conclusions and potential next steps. This mixed-methods approach led to three first-authored and two second-authored scientific papers.

2.1 Pre-fieldwork

2.1.1 Literature review

A large body of open access scientific knowledge is available through the internet and academic libraries. To familiarize myself with the topic, I conducted keyword searches using various platforms, including Web of Science, Scopus, Google Scholar, and the Swiss university library database (swisscovery.ch). A proposal was formulated, indicating the knowledge gaps and outlining the strategy to fill these gaps in the given PhD-period. To keep pace with scientific advances, I sporadically searched for new papers in my research topics. I used the reference management software Zotero (Digital Scholar, 2025) for reading and citing scientific texts.

2.2 Fieldwork

In 2022 and 2023, four PhD colleagues, the principal investigator, and I (consequently called "we") conducted fieldwork in nine forest patches across Togo, Benin, Nigeria, and Cameroon (Figure 1). These sites were selected from a larger pool of 420,446 identified forest patches, which are formally unprotected and isolated within the agricultural landscape (Wingate et al., 2022, 2024). The nine sites were chosen to represent different ecological and cultural contexts, encompassing *terra firme* and swamp forests, agroforestry systems, and several sacred forests, spanning both the Guinean Savanna and Guineo-Congolian zones. The individual sites were Koui, M'poti, Agou, Ewè-Adakplamè (also known as Kouvizoun sacred forest Adakplamè-Ewè), Hlanzoun, Iko, Ikot, Mbangassina, and Ngam-Kondomeyos.

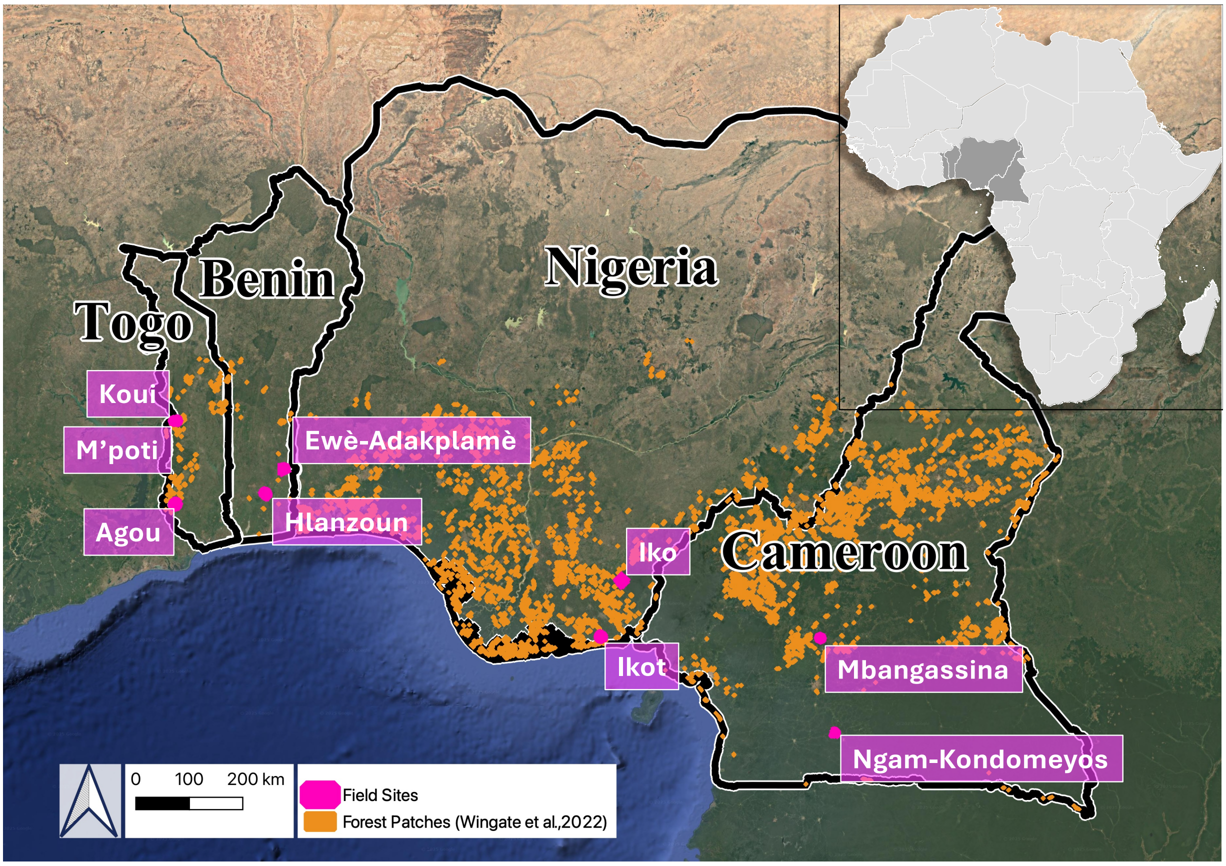

Figure 1 Map of the studied countries Togo, Benin, Nigeria, and Cameroon in Western Africa. We chose nine field study sites from 420'446 identified forest patches, which are formally unprotected and isolated in the agricultural landscape (Wingate et al., 2022, 2024). Koui and M'poti are close to each other and shown as one dot.

A range of methods were applied in and around forest patches, integrating both quantitative and qualitative metrics, with different methods complementing and validating each other (Figure 2).

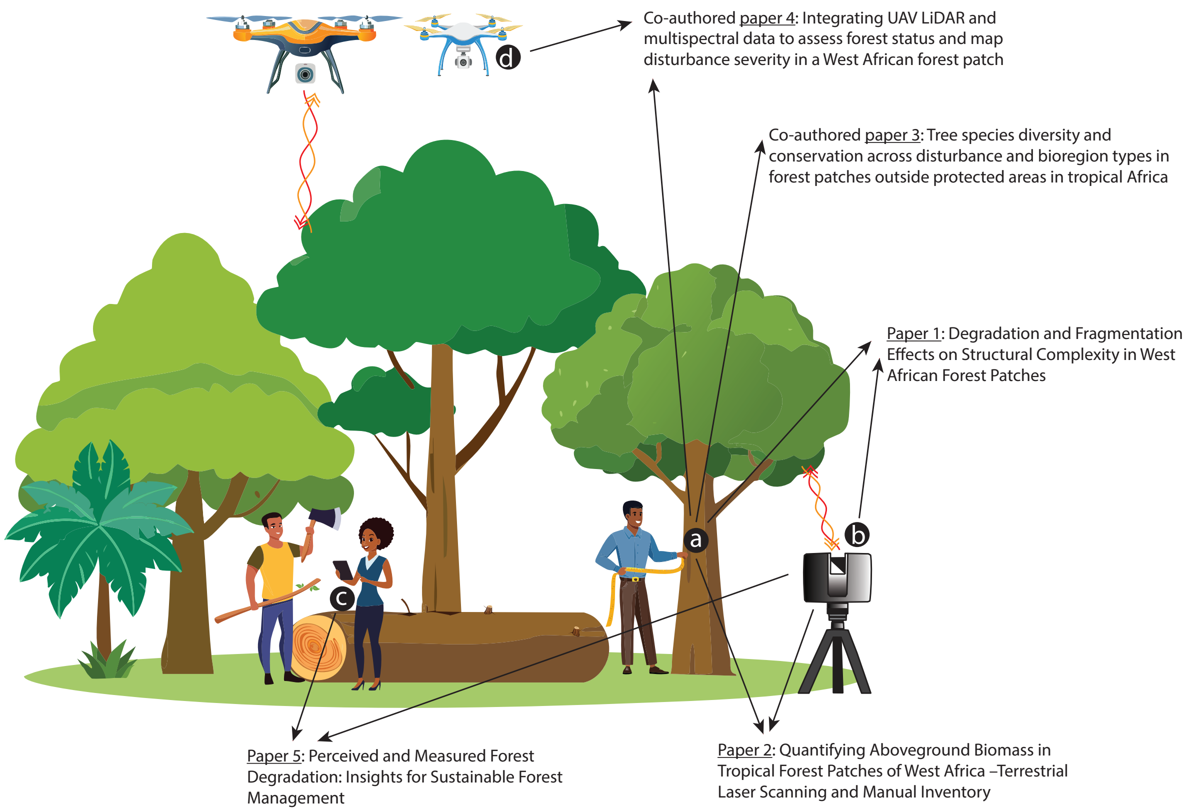

Figure 2 To obtain data on the ecological conditions and underlying management dimensions of forest patches, various methods were applied to get more complete insights and compensate limitations of single methods. The methods included a) manual forest inventories, b) terrestrial laser scanning, c) unmanned aerial vehicles, and d) interviews with regular forest users.

2.2.1 Sampling plots

Forest inventories use well-defined sampling strategies with representative plots to generalize findings to the whole forest (Food and Agriculture Organization of the United Nations (FAO), 2011). In tropical forests, where biomass and other characteristics vary greatly across space (Grussu et al., 2016), robust sampling is essential (Asrat & Tesfaye, 2013). Plots—small, spatially restricted areas—are established according to research goals, forest type, accessibility, and constraints such as time and budget (Food and Agriculture Organization of the United Nations (FAO), 2008; Grussu et al., 2016; Paul et al., 2019). For this study, we used square plots of 50 × 50 m, with 25 × 25 m subplots (Paper 2, Figure 2), as this size is practical to set up (Duncanson et al., 2021) and sufficiently representative for biomass estimations (Chave et al., 2019). We applied a simple random sampling strategy to ensure plots were well distributed across each forest (Ravindranath & Ostwald, 2008), using the “random points in a polygon” function in a geographic information system (QGIS Development Team, 2023). To avoid spatial autocorrelation, we enforced a minimum distance of 50 m between sample plots in a forest. This setup allowed us to capture the gradient from forest edge to core. At each selected location, we confirmed that the plot area exhibited relatively homogeneous forest composition before data collection.

2.2.2 Traditional forest inventory

A forest inventory involves collecting quantitative and qualitative data on trees within a defined area (Asrat & Tesfaye, 2013). For this study, we included all living trees with a diameter at breast height (DBH) greater than 10 cm in the manual inventory. We measured i) DBH using a measuring tape, ii) estimated tree height using a clinometer, and iii) identified the tree species with the help of local botanists and national herbaria. This standardized approach aligns with established guidelines (Asrat & Tesfaye, 2013; Duncanson et al., 2021; Food and Agriculture Organization of the United Nations (FAO), 2008, 2011; Phillips et al., 2021; Ravindranath & Ostwald, 2008). The ecology field team typically consisted of six members. One person measured DBH and identified tree species, another estimated tree height, and a third recorded the data in a handwritten table. In addition, one team member operated the terrestrial laser scanner, another collected soil data, and a local guide supported the team in orienteering in the forest (Figure 3). Immersing oneself in the field to collect ecological data is essential for understanding nature, exchanging knowledge, and grounding research beyond office-based work (Soga & Gaston, 2025).

Figure 3 The ecology field team gathered at a huge kapok tree (Ceiba pentandra) in the sacred forest of Koui. Photo taken by local guide from Koui (name unknown).

2.2.3 Terrestrial laser scanning (TLS)

We used a FARO Focus M70 terrestrial laser scanner, which emits laser pulses and detects returns from distances of up to 70 meters. While TLS does not replace traditional forest inventories, it provides valuable complementary data, particularly for assessing forest structure and biomass (Chave et al., 2019; Newnham et al., 2015). To analyze forest structure (Figure 4a), we performed five single scans per plot—one in each corner and one in the center (Ehbrecht et al., 2017, Paper 1: Figure 2). For aboveground biomass estimation and to generate detailed three-dimensional point clouds, we carried out multiple overlapping scans in a continuous chain in subplots of 25 x 25 m (Duncanson et al., 2021; Tao et al., 2021; Wilkes et al., 2017). The resulting point clouds (Figure 4b) were processed, co-registered, and segmented using FARO Scene (FARO Technologies Inc., 2023), R (R Core Team, 2024), CloudCompare (Girardeau-Montaut, 2023), and the Python-based FSCT algorithm (Krisanski et al., 2021). TLS offers new insights into the complex tropical forest ecosystems, with untapped research potential, scanning protocols yet to be standardized, and very few studies conducted in Africa (Calders et al., 2020; Coops et al., 2025; Momo et al., 2018).

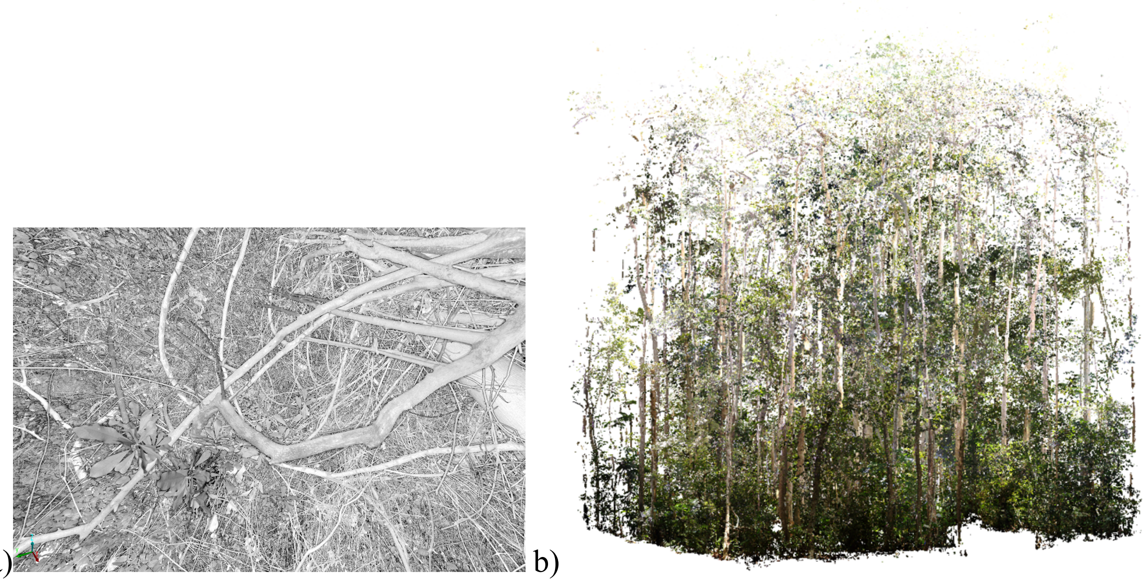

Figure 4 a) Black and white photo taken with the terrestrial laser scanner (TLS) in a single-scan approach in a corner of a plot in Ewè-Adakplamè, Benin with dense understory. b) Real-colored point cloud as product of the multi-scan approach in the swamp forest of Hlanzoun, Benin.

2.2.4 Unmanned aerial vehicles (UAVs)

UAVs, commonly known as drones, allow for the collection of forest data beyond plot-level measurements. UAVs can capture high-resolution spatial metrics across entire forest patches within just a few days, effectively bridging the gap between detailed ground-based inventories and broader satellite-based observations. In this study, we employed two UAVs (DJI, Shenzen, China); one equipped with a light detection and ranging (LiDAR) sensor (DJI Matrice 300 RTK) and the other with a multispectral sensor (DJI Phantom 4 Multispectral). Mapping fine-scale forest disturbance severity, by integrating LiDAR and multispectral data has rarely been documented for Western African forests (e.g., Iheaturu et al., 2024).

2.2.5 Interviews

The forest patches are actively managed and used by local communities, who often depend on the ecosystem services these forests provide. Through a large household survey (n=1956; Tabi Eckebil et al., submitted), we identified regular forest users (n=328) and conducted interviews to understand their forest uses and perceptions of forest conditions. Research assistants translated responses from local languages into French or English. The perspectives of local forest users has only been poorly studied and understanding local realities deserves more research attention since it directly drives forest conservation and degradation respectively (Lewark, 2022).

2.3 Post-fieldwork

2.3.1 Data analysis and statistics

The data used in this thesis are predominantly quantitative, enabling the application of a wide range of statistical analyses. All analyses were conducted in R (R Core Team, 2024), using a consistent statistical framework across studies. Commonly used packages included *dplyr* (Wickham et al., 2023) and *tidyr* (Wickham et al., 2024) for data wrangling, *ggplot2* (Wickham, 2016) for visualization, and *lme4* (Bates et al., 2015) for fitting linear mixed-effects models, among others. These models were primarily employed to account for the non-independence of observations, particularly due to the nested structure of plots within individual forest patches. While the specific model formulations, standardized effect sizes (e.g., r-values), and significance levels (p-values) are detailed in the individual papers, this unified analytical approach underpins the synthesis of results across studies.

2.3.2 Remote sensing and spatial analysis

Thousands of satellites orbit the Earth, continuously contributing to environmental and socio-economic data. Many satellite-derived products are open-access and readily available through platforms such as Google Earth Engine (Gorelick et al., 2017) making satellite imagery a key source of information at large spatial and temporal scales. In this thesis, I extracted key explanatory variables from satellite imagery, such as population density (Bondarenko et al., 2020), a relative wealth index (Chi et al., 2022), canopy heights (Lang et al., 2023), and fire frequency (Chuvieco et al., 2018). In addition, I used QGIS (QGIS Development Team, 2023) to conduct various spatial analyses with vector and raster data, such as calculating the shortest distance from each plot to the forest edge and extrapolating AGB estimates from sampled plots to entire forest patches. Using multiple data sources and methods strengthen corresponding results by evening out weakness of single methods.

2.3.3 Science communication

In addition to scientific publications, we shared our research through various science communication formats. I produced a 20-minute film on our fieldwork in rural Western Africa (available at the project homepage: sustainforests.giub.unibe.ch). We also used virtual reality goggles (HTC Vive Pro) to enable users explore the tropical forests virtually. Hovering through these forests and hearing the ambient forest sounds creates an immersive experience that helps users connect with these remote environments. Furthermore, we published regular blog posts on the project homepage and contributed to newsletters such as that of the Swiss Society for African Studies to communicate our work beyond the academic sphere.

Finally, we returned to the same communities where we had collected data and organized result-exchange workshops. These included scientific presentations for academics, practitioners, and political representatives, as well as workshops with local communities and accessible science communication through public posters. We also visited primary and secondary schools to present our work to children—the next generation of forest and land users—and provided puzzles and memory games to support playful learning and environmental awareness. In addition, we revisited the forests, which allowed us to ground-truth our data and critically reflect on our interpretations, models, and conclusions.

Overview of research papers

The resulting research outputs have been submitted as five papers in corresponding journals (Table 1).

Table 1 Overview of research outputs as scientific papers. Each paper contributes to one or two of three chapters. Chapter abbreviations: E: Understanding Ecological Functioning in Tropical Forests, M: Testing New Methods to Improve Capturing Forest Conditions, S: Integrating social perspectives and measured values of forest conditions.

Nr	Contribution to chapter	Title	Authors	Journal	Status
1	E	Degradation and Fragmentation Effects on Structural Complexity in West African Forest Patches Short: Degradation effects on forest structure	Hepner, S., Agonvonon, G. A., Ehbrecht, M., Iheaturu, C., Azihou, A. F., & Ifejika Speranza, C.	Biotropica	Published (2025)
2	E; M	Aboveground Biomass in Seven Tropical Forest Patches of Western Africa: Comparison of Manual Inventory and Terrestrial Laser Scanning Short: Aboveground biomass in small forest patches measured with TLS	Hepner, S., Agonvonon, G. A., Kükenbrink, D., Iheaturu, C., Azihou, A. F., Sinsin, B., & Ifejika Speranza, C.	Annals of Forest Science	Submitted (2025)
3	E	Tree Species Diversity and Conservation across Disturbance and Bioregion Types in Forest Patches outside Protected Areas in Tropical Africa Short: Disturbance effects on tree species diversity	Agonvonon, G. A., Hepner, S. Iheaturu, C. J., Azihou, F. A., Sonwa D. J., Bisong F. E., Anwana E. D., Koudouvo K., Sinsin B. A., Fischer M. & Ifejika Speranza, C.	Forest Ecology and Management	Published (2025)
4	M	Integrating UAV LiDAR and Multispectral Data to Assess Forest Status and Map Disturbance	Iheaturu C. J., Hepner S., Batchelor J. L., Agonvonon G. A.,	Ecological Informatics	Published (2024)

		Severity in a West African Forest Patch Short: Integrating LiDAR and multispectral UAV data	Akinyemi F. O., Wingate V. R. & Ifejika Speranza, C.		
3	S	Perceived and Measured Forest Degradation in West Africa: Insights for Sustainable Forest Management Short: Forest use and its perceptions	Hepner, S., Tabi Eckebil, P. P., Mintah, F., Azihou, A. F., Sinsin, B., Fischer, M. & Ifejika Speranza, C.	Trees, Forests and People	Published (2025)

The central tenet of this thesis is that the widespread deforestation and the persistence of isolated forest patches must be understood to allow an informed and sustainable forest management. This requires understanding ecological processes in tropical forest patches. Subsequently, new methods must be developed and tested to improve ways of capturing forest conditions. Additionally, the ecology of these forest patches is not an isolated natural phenomenon but is directly affected by peoples' management and forest use. Therefore, the social dimension of the ecological forest conditions, including local perceptions must be studied as well (Figure 5), calling for methodological integration.

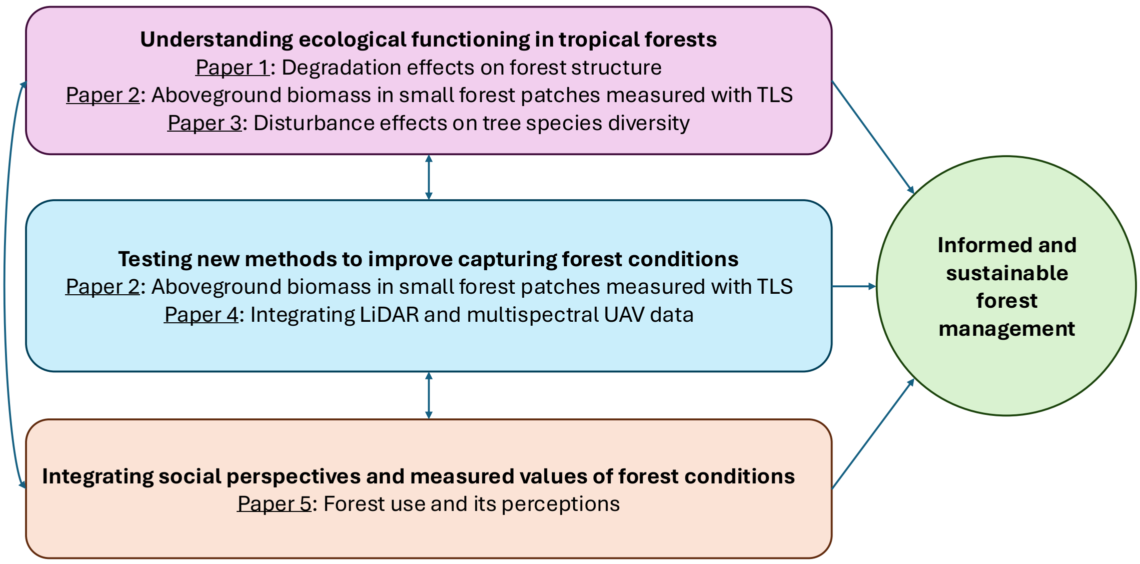

Figure 5 Conceptual framework of the five papers structured into three chapters informing sustainable forest management.

3. Key insights and conclusions

3.1 Understanding ecological functioning in tropical forests

Our studies provide several insights into the ecological functioning of tropical forest patches in Western Africa, with a particular focus on structural complexity, biomass storage, species diversity, and the role of disturbances:

Paper 1: Degradation and Fragmentation Effects on Structural Complexity in West-African Forest Patches

- Structural complexity increases with distance to forest edge.
- Edge effects are pronounced in isolated forest patches with low connectivity.
- Spatial variation of structural complexity in forests patches indicate disturbances.
- Structural complexity below the ecological reference indicates forest degradation.

Paper 2: Aboveground Biomass in Seven Tropical Forest Patches of Western Africa: Comparison of Manual Inventory and Terrestrial Laser Scanning

- Aboveground biomass (AGB) increases from forest edge to forest interior.
- AGB did not correlate with tree species richness or wood density.
- AGB in these unprotected forest patches was lower than in protected forests nearby.

Paper 3: Tree species diversity and conservation across disturbance and bioregion types in forest patches outside protected areas in tropical Africa

- Alpha diversity and stem density increase along Sudanian-Guineo-Congolian transects.
- Within-forest environmental heterogeneity does not affect the stand composition.
- Anthropogenic disturbances decrease along the forest patch edge-interior gradient.
- Anthropogenic disturbances adversely impact tree community diversity and structure.
- Sustainable management of the forests should include a triad zoning approach.

Forest Structure: We confirmed that a higher stand structural complexity index (SSCI) is associated with lower forest fragmentation and reduced canopy openness. However, SSCI did not show significant relationships with connectivity, tree height, basal area, stem density, or species richness. Importantly, distance to forest edges strongly influenced SSCI, canopy openness, basal area, and tree density, highlighting the pervasive role of edge effects.

Among the seven studied forest patches, five exhibited SSCI values close to their potential, indicating that they remain structurally intact. In contrast, the forests of Ewè-Adakplamè and Ikot scored significantly below their potential SSCI, classifying them as degraded.

Biomass and Carbon Storage: We confirmed that aboveground biomass (AGB) and carbon storage vary both across and within forest patches, reflecting underlying environmental and disturbance gradients. AGB values were higher in formally protected and typically larger forests than in unprotected, smaller patches subject to stronger edge effects. Moreover, AGB increased with distance from forest edges, emphasizing the importance of intact forest cores as carbon reservoirs.

Our results also contribute to the debate on the link between species richness and AGB. We found that AGB correlates with uncorrected species richness but not with richness adjusted through rarefaction and extrapolation. This suggests that while diverse forests can be highly productive, biomass accumulation also depends on the presence of large, heavy-wooded tree species.

Tree Species Diversity Patterns: Tree alpha diversity varied with both bioregion and anthropogenic disturbance. Diversity increased along the Sudanian–Guineo–Congolian rainfall gradient, confirming rainfall as a key driver of species richness. Beta diversity increased with spatial distance between forest patches emphasizing the need to conserve multiple patches to capture the full spectrum of diversity.

Disturbances such as logging, fires, agricultural encroachment, and invasive species primarily reduced tree density near edges rather than directly affecting species richness. Logging pressure was especially evident for large trees (>50 cm DBH) near forest edges.

Overall, the studied patches host 15–30% of the tree species found in their respective countries, with ~10% classified as near-threatened, vulnerable, or endangered. This highlights their disproportionate conservation value despite their small size.

Disturbances and Edge Effects: Edge effects include increased wind exposure, wind throw, altered species composition, more frequent fires, and heightened anthropogenic pressures. These effects were strongest in isolated patches with little surrounding vegetation, underscoring the need for buffer zones and green corridors to maintain forest integrity and prevent long-term collapse at the landscape scale.

Management and Conservation Implications: Our findings reveal that formal protection is strongly associated with higher AGB and greater structural integrity, even when enforcement is incomplete. Governance structures, such as defining minimum felling diameters, formalizing land use and management, and promoting equitable resource-sharing, are essential to maintain forest functions.

3.2 Testing new methods to improve capturing forest conditions

Paper 2: Aboveground Biomass in Seven Tropical Forest Patches of Western Africa: Comparison of Manual Inventory and Terrestrial Laser Scanning

- AGB obtained from manual inventory and terrestrial laser scanning correlated moderately.

Paper 4: Integrating UAV LiDAR and multispectral data to assess forest status and map disturbance severity in a West African forest patch

- Fused UAV LiDAR and multispectral data to map forest status and disturbance severity.
- Derived an integrated disturbance index through principal component analysis.
- The integrated disturbance index outperformed individual sensors used alone.
- The method can enable tailored conservation interventions, thereby optimizing resource allocation.

Validation of Biomass Estimates: We confirmed that AGB values derived from TLS correlate moderately with those obtained through manual inventory. Using both approaches provides a valuable cross-validation, since AGB estimation is inherently uncertain. Interestingly, in our study, a manual inventory conducted by three people was faster than scanning the same plots with a FARO Focus M70, reflecting the practical challenges of TLS in dense tropical forests.

Multi-Sensor Forest Assessment: Structural and spectral metrics derived from UAV LiDAR and multispectral imagery effectively characterized spatial variation in forest condition, as demonstrated by the disturbance severity map of Ewè-Adakplamè. The fusion of data streams from LiDAR and multispectral sensors revealed aspects of forest status that neither source could capture alone, underscoring the importance of multi-sensor integration.

LiDAR data showed that 95% of trees were below 20 m, while the maximum canopy height reached 48 m, indicating a stunted forest well below its potential height and vertical stratification. Meanwhile, multispectral imagery revealed low vegetation indices (e.g., GNDVI), suggesting stress linked to nutrient deficiency or drought. Integrating these complementary perspectives reduces blind spots and provides a more complete picture of forest integrity.

Spatial Mapping and Management Applications: The resulting high-resolution disturbance maps highlight spatial patterns of degradation caused by logging, agricultural encroachment, and fires. Such maps provide essential information for targeted interventions, including enrichment planting in canopy gaps and establishing corridors between nearby forest fragments. This is particularly valuable when resources for forest management are limited and must be allocated efficiently. Field-based observations of anthropogenic disturbances served as ground truth to validate UAV-derived maps, strengthening confidence in their use for guiding conservation, sustainable use, and restoration measures.

3.3 Integrating social perspectives and measured values of forest conditions

Paper 5: Perceived and Measured Forest Degradation in West Africa: Insights for Sustainable Forest Management

- Collection of non-timber forest products is the main forest activity.
- Logging, fires, and agriculture are largely perceived as driving forest degradation.
- Forest uses are similar across forests, but perceptions of forest use impacts vary.
- Locally perceived forest degradation is not always in line with pressure on forests.
- High socio-economic pressure is captured in increased measured forest degradation.

Forest Use Activities: Across the studied sites, the collection of non-timber forest products (NTFPs) was the most widespread activity, followed by hunting and logging. These dominant activities were consistent regardless of socio-cultural (sacred vs. non-sacred), economic (low vs. intermediate wealth), or ecological (semi-deciduous vs. moist forest) contexts. Importantly, NTFP use is not associated with large-scale forest damage, suggesting that it can support livelihoods while maintaining forest integrity.

Perceptions of Degradation: Contrary to claims that the narrative of forest degradation is primarily a foreign construct (Amanor, 2004; Fairhead & Leach, 1996), many local forest users acknowledged the negative impacts of logging, fire, and agriculture. However, our results reveal a mismatch between forest uses that contribute to degradation and local perceptions of degradation. In Ikot (Nigeria), where logging and fire are widespread, these practices were not considered degrading—likely because they are normalized and no intact forest remains for comparison. By contrast, in Koui (Togo), where a sacred forest is strictly protected, the community expressed strong concern over potential damage, reflecting the forest's deep cultural and religious significance. These cases illustrate how psychosocial factors, traditions, and reference points shape local perceptions of forest integrity.

Socio-economic pressure and governance: Forests facing the highest socio-economic pressure—where many people exploit forest resources in a small area—showed the greatest values of measured degradation. Proximity to cities likely intensifies this same pressure by increased demand and purchasing power for these forest resources. However, the extent of degradation ultimately depends on governance: where management rules are effectively implemented, respected, and supported by communities, governance can buffer these pressures. Sustainable forest management in the region therefore hinges on governance systems that are both effective and trusted.

3.4 Overall key insights

Tropical forests are structurally complex and subject to multiple interacting disturbances, making comprehensive assessment challenging. In this thesis, we applied complementary methods—manual forest inventories, TLS, UAV LiDAR and multispectral imagery, and interviews with local forest users—to capture ecological and social dimensions of forest structure, biomass, species richness, and disturbances across nine forest patches in Western Africa. While two of the seven papers explicitly compared single-method versus multi-method approaches, demonstrating the added value of methodological integration, the main goal was to leverage multiple approaches in combination to obtain a robust, multi-scale understanding of forest conditions. This integrative perspective was essential to identify patterns of edge effects, anthropogenic pressures, and mismatches between perceived and measured forest degradation, and to contextualize ecological findings within local socio-cultural realities.

The five papers collectively examined forest structure from different perspectives: TLS captured detailed 3D structural complexity (e.g., SSCI), manual inventories measured tree size distributions, UAVs enabled high-resolution, centimeter-scale mapping of larger forest areas, and interviews documented local knowledge about trees, including culturally significant and large individuals, as well as temporal changes in forest structure over the past decade. Across studies, anthropogenic disturbances consistently altered forest structure, a pattern also observed globally, particularly in fragmented landscapes (Bentsi-Enchill et al., 2022; Chaudhury et al., 2022; Schwartz et al., 2017). Forest structure was tightly linked to disturbances, both influencing and responding to the ecosystem's disturbance regime and resilience (Mitchell et al., 2023).

Edge effects emerged as a pervasive factor: forests near edges were less intact than cores, with reduced structure, lower AGB, diminished vitality, and fewer trees, particularly where local use was higher and natural vulnerability was greater. Fragmentation can intensify these effects, threatening carbon storage, successional stages, tree architecture, and wood anatomy (Nunes et al., 2023; Ordway & Asner, 2020; Silva Da Costa et al., 2020; Tabarelli et al., 2008).

3.5 Relevance and novelty

The relevance of this PhD lies in filling critical knowledge gaps for tropical forests in Western Africa, a region that remains comparatively under-studied. The findings are important because they both align with global observations and generate region-specific insights: they document biodiversity and forest structure in poorly studied landscapes, provide ground-truth data to improve satellite-based AGB estimates, and reveal patterns of degradation, edge effects, and structural complexity. In this way, the work establishes a foundation for further studies in Western African tropical forests, current and future analogous landscapes worldwide through a "space-for-time" perspective and strengthens the evidence base for informed forest policy and management.

Its novelty stems from the generation of new high-resolution data and the application of innovative methods. By applying TLS for the first time across forests in Togo, Benin, Nigeria, and Cameroon, this work provides structural insights that were previously unavailable. Several forest patches were mapped for the first time, and some methodological approaches were pioneered within the project (cf. Iheaturu et al., 2025; Wingate et al., 2022, 2023, 2024). Together, these advances contribute both new knowledge and methodological innovation to the field of tropical forest research.

3.6 Outlook

3.6.1 Future research

The work conducted in this PhD has significantly advanced our understanding of the selected forest patches, opening an avenue for further research.

Methods & Technology: Future steps could begin at the finest scale by climbing trees to scan canopies, which can reduce occlusion and provide unprecedented detail on canopy architecture, leaf distribution, and canopy biodiversity (D'hont et al., 2025; Lowman et al., 2013). At slightly larger scales, TLS captures dense point clouds near the sensor, and integrating these with data from UAVs (Coops et al., 2025; Terryn et al., 2022) allows sensors above and below the canopy to complement each other, revealing more comprehensive forest structure (Schneider et al., 2019). Moving to even larger spatial scales, airborne laser scanning (e.g., from planes) can expand insights across landscapes.

Tools for segmenting point clouds continue to improve, and future research could explore recently developed algorithms that promise to increase the accuracy of segmentation (e.g., Wielgosz et al., 2024; Wilkes et al., 2023; Xiang et al., 2024) and tailor these for African forest characteristics. Further research could focus on segmentation of point clouds into smaller units, such as individual leaves (Song et al., 2025) and tree species identification based on point clouds (Åkerblom et al., 2017; Puliti et al., 2025). Accurate, tree-wise point clouds could also be used to refine allometric equations (Clark & Kellner, 2012).

Biomass & Carbon: A critical challenge in future research will be validating different methods for estimating forest AGB. Since forest AGB is never directly measured but estimated with varying accuracy (Réjou-Méchain et al., 2019), perfect validation data remains elusive. Quantifying uncertainty from start to finish is an ongoing challenge (Chave et al., 2004; Réjou-Méchain et al., 2019). To improve the accuracy of standing carbon estimates, additional wood density data (Clark & Kellner, 2012) and wood carbon concentrations (Martin et al., 2018) will be needed. Looking ahead, it will also be important to expand carbon research beyond aboveground biomass to include belowground pools (roots, soils) and necromass (deadwood, litter), and other essential life elements such as nitrogen and phosphorus.

Monitoring & Visualization: Based on our research, a monitoring system could be established to measure forest characteristics over time (e.g., Coops et al., 2025), providing insights into the dynamics of forest patches under various climate change and governance scenarios. Creating virtual forest environments based on measured data could enhance decision-making and help visualize forest development (Holm & Schweier, 2024; Murtiyoso, Holm, et al., 2024). Standardized monitoring protocols could also contribute to validating satellite imagery (Chave et al., 2019), such as that from the recently launched BIOMASS satellite (European Space Agency, 2025).

Biodiversity & Genetics: Further topics to be explored include biodiversity, genetics, and economics. Biodiversity hotspots are predicted for Western African forests, but samples remain limited (Bâ et al., 2012; Lücking et al., 2014; Wagner, 2019). Small life forms, such as insects, lichens, and fungi, are essential for ecosystem functions like organic matter processing and nutrient cycling (Crespo-Pérez et al., 2020), yet their roles in forest fragments remain largely unknown.

Forest fragmentation and the spatial isolation of patches also affect genetic diversity. Trees have high genetic diversity due to their longevity, but reduced pollinator mobility limits cross-pollination, leading to decreased diversity (Finkeldey, 2011). This diversity is often underestimated but is critical for adaptation to climate change (cf. Aguirre-Gutiérrez et al., 2025; Dawson et al., 2014; Finkeldey, 2011).

Economics: From a socio-economic perspective, forests can be seen as a portfolio of land-use options (Knoke & Huth, 2011). In tropical regions, forests are often perceived as low-profit land-use areas and converted into agriculture (Pouliot et al., 2012; Wunder, 2001). How forests can be managed sustainably—ecologically, socially, and economically—remains an open question (Knoke & Huth, 2011; Kotru & Sharma, 2011) with solutions likely to emerge locally (Garrett et al., 2024; Gbedomon et al., 2016).

Resilience & Thresholds: Gaining a deeper understanding of the thresholds of resilience in small forest remnants remains crucial. Future studies should examine conditions under which regeneration becomes unlikely (Ghazoul et al., 2015), the longevity of trees and forests under changing land use and climate (cf. Aguirre-Gutiérrez et al., 2025), and how spatial configuration influences ecological pressures at the forest edge.

3.6.2 Call to action

From a social-ecological perspective, the findings of this PhD highlight the urgent need to integrate ecological and community considerations in forest management. Quantifying AGB and carbon stocks in forest patches provides a strong evidence base for initiatives such as carbon compensation programs, which could support both conservation and local livelihoods (Jones, 2024; Turia et al., 2022). However, the dynamics and risks of introducing financial incentives must be carefully evaluated, and programs should follow standardized guidelines to ensure additional and sustainable carbon storage (McDonald et al., 2023).

Interview data revealed that local perceptions and forest-use practices vary widely: communities maintaining sacred forests were highly aware of degradation risks, whereas areas with intensive resource use often undervalued forest integrity. These insights suggest that interventions—such as promoting non-destructive forest-related activities—should be tailored to community context, building on existing knowledge, traditions, and economic realities.

The ecological findings also point to structural vulnerabilities in the forests. Edge effects, fragmentation, and localized degradation indicate that sustainable management should include measures such as establishing buffer zones, reconnecting fragmented habitats, and restoring degraded areas (Bastin et al., 2019; Ebreg & De Greve, 2000; Zeller et al., 2020). Integrating these measures with socio-economic strategies can enhance both ecological resilience and community engagement. Implementation will require careful planning, particularly under conditions of limited financial resources and governance constraints. Together, these evidence-based recommendations demonstrate how high-resolution ecological data, innovative methods, and social insights can guide targeted conservation actions, ensuring the long-term preservation of Western Africa’s tropical forest patches.

4. Reflections

4.1 Strengths and limitations

The research conducted during this PhD as part of the SUSTAINFORESTS project contributes valuable data to a region that is often underrepresented in scientific forest studies. The four countries—Togo, Benin, Nigeria, and Cameroon—are frequently overlooked in global data collections. Despite the challenging conditions, working in these countries and providing open-access data for the global community is a key strength of this project.

Strengths: A team of seven researchers, each focusing on a specialized topic, worked on the same forest patches within the same time frame. The complementarity of expertise was invaluable in understanding forest dynamics from multiple perspectives. This approach was supported by a wide range of methods, including manual forest inventories, TLS, UAV, qualitative and quantitative interviews, satellite imagery, and literature reviews. The team included members from both the studied countries and Switzerland, fostering an international and intercultural working environment that enhanced our understanding of contexts in both the global North and South.

Limitations: As Heraclitus (6th-5th century BC) observed, "One cannot step into the same forest twice." Forests are dynamic systems undergoing cyclical processes (Binkley, 2021; Ghazoul et al., 2015). A key limitation of this PhD is that field data were collected only once during the dry season. Aside from historical satellite imagery and interviews about past and future changes, our ecological dataset represents a snapshot in time, reflecting the time- and resource-intensive nature of fieldwork. We revisited sites during the results exchange campaign, which allowed us to ground-truth and reassess interpretations, but systematic long-term data remain lacking.

Another limitation is sampling scale**.** We gathered data from nine forests, with an average of twelve plots per forest. While adequate for representation, larger datasets would improve statistical explanatory power (Ferretti et al., 2024), and allow for broader extrapolation.

In terms of methods and technology, we applied cutting-edge but affordable tools for our project. More advanced TLS and UAV systems with higher point cloud density could have provided richer data in less time. Our methodological choices reflected a careful balance between financial constraints, expert advice, and field realities.

Finally, gender bias must be acknowledged: 90% of interview insights are based on male respondents. In the studied societies, males often speak for the household, but this social pattern may have limited female perspectives on forest management.

4.2 Positionality

I was born and raised in Switzerland, one of the wealthiest countries on earth (Federal Department of Foreign Affairs (FDFA), 2024). My skin color resembles white, and I identify as male, both attributes are usually associated with privileges. Over the course of my life, I have spent just 1.5 years in tropical developing countries, with a maximum of six months during the fieldwork for this PhD. I am keenly aware that I cannot fully grasp the realities faced in these places, due to significant economic, cultural, and linguistic differences. For example, I have never depended on forests for my livelihood and tend to view them mainly for their aesthetic value. I do not fully understand the concept of Vodún, sacred forests, and the associated worldviews. I recognize my tendency to compare Western African forests and forest management practices with those in Switzerland, which is not necessarily adequate.

My presence in Western Africa often drew attention. People frequently assumed I was leading the project and associated me with money and power due to my skin color. This is understandable, given the historical legacy of colonization and the slow process of decolonization, as well as the persistent imbalances of wealth and power. I did not conduct interviews myself, nor was I involved in the initial negotiations with communities to avoid distorting the presentation of our project and the ongoing negotiations. While I appreciated integrating myself into local societies by adapting to customs and learning the basics of the local language, I am aware of my privileges, such as access to funding, mobility, and education.

Beyond personal reflection, I also participated in workshops on positionality and the 'theory of change' (Belcher et al., 2020). In these settings, we actively examined how our own positions, interests, and assumptions influenced both research processes and outcomes. This collective engagement led to the development of a manuscript (Ifejika Speranza et al., submitted), further formalizing these considerations.

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5. Scientific papers

5.1 Paper 1: Degradation and Fragmentation Effects on Structural Complexity in West African Forest Patches

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Degradation and Fragmentation Effects on Structural Complexity in West-African Forest Patches

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ABSTRACT

Tropical forests face alarming rates of deforestation and degradation, driven mainly by agricultural land expansion. West Africa is particularly affected by widespread forest fragmentation, leaving behind isolated forest patches in an agriculture-dominated landscape. Forest fragmentation and isolation can impact forest structural complexity, biomass, and species richness through various edge effects. The consequent loss of biodiversity and ecosystem services is expected to be more prominent in small and fragmented forests and closer to forest edges. We used terrestrial laser scanning to investigate patterns of forest structural complexity in 84 plots across seven forest patches in Togo, Benin, Nigeria, and Cameroon. We quantified forest structure using the stand structural complexity index (SSCI) and related it to tree species composition, distance to edge, and the modeled potential SSCI of primary forests as an ecological reference value to identify forest degradation. Spatial variability of SSCI within forest patches and plots indicates various areas of disturbance, ultimately accumulating to forest degradation. The overall trend suggests an increase in structural complexity, tree height, basal area, and tree species richness with increasing distance to the edge. However, these correlations were only significant for some of the forest patches analyzed. Comparison with the ecological reference value showed significant deviations for two forests, indicating degradation of forest structural integrity. Our results confirm and challenge theories of ecological dynamics in tropical forest patches in West Africa. Quantifying structural integrity helps to locate degradation and preserve the last remaining forest patches crucial for biodiversity, climate regulation, and forest products.

RÉSUMÉ

Les forêts tropicales sont confrontées à des taux alarmants de déforestation et de dégradation, principalement dus à l'expansion des terres agricoles. L'Afrique de l'Ouest est particulièrement touchée par la fragmentation généralisée des forêts, qui laisse derrière elle des îlots forestiers isolées dans un paysage dominé par l'agriculture. La fragmentation et l'isolement des forêts peuvent avoir un impact sur la complexité structurelle des forêts, la biomasse et la richesse des espèces par le biais de divers effets de lisière. La perte de biodiversité et de services écosystémiques qui en résulte devrait être plus importante dans les petites forêts fragmentées et plus proches des lisières. Nous avons utilisé le scanneur laser terrestre pour étudier les schémas de complexité structurelle des forêts dans 84 placeaux réparties sur sept îlots forestiers au Togo, au Bénin, au Nigéria et au Cameroun. Nous avons quantifié la structure forestière à l'aide de l'indice de complexité structurelle des peuplements (ICSP) et l'avons associé à la composition des espèces d'arbres, à la distance à la lisière et à l'ICSP potentiel modélisé des forêts primaires en tant que valeur de référence écologique pour identifier la dégradation forestière. La variabilité spatiale de l'indice de complexité structurelle des peuplements au sein des placeaux et des îlots forestiers indique diverses zones de perturbation, qui aboutissent finalement à la dégradation de la forêt. La tendance générale suggère une augmentation de la complexité structurelle, de la hauteur des arbres, de la surface terrière et de la richesse des espèces d'arbres à mesure que l'on s'éloigne de la lisière. Toutefois, ces corrélations n'étaient significatives que pour certaines des îlots forestiers analysées. La comparaison avec la valeur écologique de référence a révélé des écarts significatifs pour deux forêts, ce qui indique une dégradation de l'intégrité structurelle de la forêt. Nos résultats confirment et remettent en question les théories de la dynamique écologique dans les îlots forestiers tropicale en Afrique de l'Ouest. La quantification de l'intégrité structurelle aide à localiser la dégradation et à préserver les dernières îlots forestiers cruciales pour la biodiversité, la régulation du climat et les produits forestiers.

1 | Introduction

1.1 | Forest Loss, Fragmentation, and Persisting Patches in West Africa

Tropical forests are being cleared at alarming rates globally (Schelhas and Greenberg 1996; Hansen et al. 2013; Poorter et al. 2021), with annual deforestation rates estimated at 0.5% (Achard et al. 2014). In West Africa, forests have declined to 20%–50% of their 1900-extent (Poorter et al. 2004). Amani et al. (2021) identify expanding agriculture driven by human population growth as a primary cause. Forested areas are not only shrinking but also fragmented into smaller patches (Taubert et al. 2018). In Africa, the number of forest fragments, split from larger blocks, increased by 45% to 64% million between 2000 and 2010 (Fischer et al. 2021). This exponential increase of ever smaller forest fragments will soon reach a critical point where a collapse and complete disappearance of forest patches could occur (Taubert et al. 2018). Fragmentation of forest patches has negative effects on biodiversity due to decreased habitat area, decreased connectivity, and increased edge effects (Hill and Curran 2003; Ibáñez et al. 2014; Taubert et al. 2018).

Nonetheless, thousands of small forest patches (<1000 ha) persist in isolation across the landscape. In Togo, Benin, Nigeria, and Cameroon alone, over 400,000 patches have been detected (Wingate et al. 2023). These patches, ranging from 0.5 and 1000 ha large, have at least 30% canopy cover and trees taller than 5 m (Food and Agriculture Organization of the United Nations (FAO) 2016; Wingate et al. 2022). The remaining forest patches are vital for their ecosystem services. Local communities rely on forest products such as timber, fuelwood, medicinal plants, and bushmeat (Poorter et al. 2004), and some patches are valued and protected for religious purposes (Alohou et al. 2016, 2017). Furthermore, these forest patches are crucial for biodiversity conservation (Poorter et al. 2004; Lewis et al. 2015). Vulnerable tree species such as *Afzelia africana* Sm. Ex Pers. and *Brachystegia nigerica* Hoyle & A.P.D. Jones and endangered and endemic species such as the red-bellied monkey (*Cercopithecus erythrogaster* Gray) are found only in West Africa's remaining forest patches (IUCN 1998, 2016, 2019; Neuenschwander et al. 2015). As long as these patches have an intact structure, they play important roles in regulating plant and zoonotic diseases and local climates (Sintayehu 2018). However, knowledge about the structural characteristics of forest patches in West Africa is limited.

1.2 | Structural Complexity of Forests

The intricate complexity of forests is crucial for their resilience to disturbances and their capacity to support biodiversity. Several indices have been developed to describe plant material distribution in three-dimensional space (Coverdale and Davies 2023). We use the stand structural complexity index (SSCI) to quantify heterogeneity in plant material distribution patterns (Ehbrecht et al. 2017). This index calculates the area and dimensions of free space between a laser scanner and the nearest plant material in various angles (Ehbrecht et al. 2017). SSCI increases with greater diversity of tree sizes and crown complementarity (see figure 1 in Ehbrecht et al. 2021). It is time-efficient for assessing forest structure, and a global model of potential SSCI of primary forests serves as an ecological reference value (Ehbrecht et al. 2021). By subtracting the in situ measured SSCI from this ecological reference value, we can quantify forest structural integrity. In the absence of a clear and standardized definition of forest degradation (Ghazoul et al. 2015), we define forest degradation as a simplification of forest structure compared to the ecologically potential forest structural complexity. Consequently, a degraded forest exhibits lower biodiversity and a reduced capacity to provide ecosystem services than the environmental conditions would allow.

Each forest stand has a unique structure shaped by environmental, biological, and legacy factors (Mitchell et al. 2023). Structural complexity correlates well with (i) faunal biodiversity, including mammals, birds, and invertebrates, (ii) forest productivity, carbon storage, canopy height, greenness, and successional stage, (iii) microclimate regulation, and (iv) species interactions and animal movement (Coverdale and Davies 2023). Stand structural complexity is also linked to forest resilience to disturbances (Seidel and Ammer 2023), which is crucial for isolated forest fragments in West Africa. The spatial pattern of forest structure can indicate forest integrity, identify disturbed areas (Ghazoul et al. 2015), and vary between forest edge and forest interior.

1.3 | Edge Effect and Tropical Forest Structure

Fragmentation, the division of forest blocks, causes forest patches to shrink and become more isolated (Harris 1984), exponentially increasing edge lengths and the area affected by edges. Edge effects that alter forest structure depend on contrasts with surrounding land cover, spatial extent, and edge age (Harper et al. 2005). Natural edge effects include increased air and soil temperature, more sunlight, increased wind exposure, more frequent fires, and altered species composition, which can extend several hundred meters into the forest (Harper et al. 2005; Laurance and Peres 2006). Anthropogenic resource extraction is more pronounced near edges than in the forest interior, exacerbating natural edge effects (Olupot and Chapman 2006). Unsustainable exploitation of forest resources decreases forest structural integrity by (i) slashing and burning, which opens the forest and creates gaps, (ii) logging, which reduces plant material, (iii) targeted logging of specific species, hindering their reproduction, (iv) overhunting seed-dispersing animals, impeding the survival of corresponding tree species (Peres and Palacios 2007), and (v) trampling and soil compaction by livestock, hampering regeneration (Faria et al. 2009). Tabarelli et al. (2008) report lower tree densities, reduced tree diversity, fewer large trees, and fewer saplings close to forest edges, leading to decreased stand structural complexity.

Despite rapidly increasing fragmentation and its ecological consequences (Fischer et al. 2021; Harper et al. 2005), few studies have compared edge effects on forest structure (Echeverría et al. 2007; Nguyen et al. 2023) and the impact of distance to edge has not been analyzed using the well-established SSCI. Quantifying edge effects on forest structural complexity reveals the severity of fragmentation on forest structural integrity. This study aims to enhance our understanding of the structural complexity of small, edge-influenced forest patches in West Africa and their links to forest degradation. We pose the following questions:

1. How does the stand structural complexity index (SSCI) vary with fragmentation, connectivity, canopy openness, tree height, basal area, number of tree stems, and tree species richness?
    - We expect that SSCI increases with high connectivity, low canopy openness, a high number of tall trees, a high basal area, a high tree stem density, and high tree species richness but decreases with fragmentation.
2. How do edge effects impact the SSCI of forest patches?
    - We expect that SSCI decreases toward forest edges.
3. How does the in situ measured SSCI of the forest patches compare with the corresponding ecological reference value?
    - We expect intact forest patches where in situ measured SSCI equal the corresponding ecological reference value.

2 | Methods

2.1 | Study Area

Two moist semideciduous forests (1. Koui, 2. Ewè-Adakplamè), two swamp forests (3. Hlanzoun (also known as Lokoli), 5. Ikot), and three moist forests (4. Iko, 6. Mbangassina, 7. Ngam-Kondomeyos) were selected across Togo, Benin, Nigeria, and Cameroon (Figure 1). According to (Dinerstein et al. 2017), the selected forest patches in Togo and Benin fall within the Tropical and Subtropical Grasslands, Savannas, and Shrublands biome, while those in Nigeria and Cameroon align with the Tropical & Subtropical Moist Broadleaf Forests. (Tappan et al. 2016) refers to the forests in Togo and Benin as Guinean Savanna and those in Nigeria and Cameroon as part of the Guineo-Congolian zone. These forests are a subset of those identified by Wingate et al. (2022) and contribute to ground truthing satellite image-based archetypes in Wingate et al. (2023). The seven forests allow us to answer the research questions along a latitudinal gradient and gain insights from different administrative units.

These forest patches, surrounded by agriculture, agroforestry, and wetlands, have persisted since at least 1975 despite being formally unprotected and threatened by anthropogenic land use change (Table 1; Hansen et al. 2013; Wingate et al. 2022). Forest regrowth is negligible (Potapov et al. 2022). Annual precipitation ranges from 1000 to 1300 mm in the Guinean Savanna and from 1500 to 3000 mm in the Guineo-Congolian zone. Annual temperatures average between 22°C and 28°C (Hijmans et al. 2005) and the forests are located at elevations of 15 to 700 m above sea level (Jarvis et al. 2008). These forests host over 300 different tree species, and the most frequent are *Alstonia congensis* Engl. (Apocynaceae), *Coelocaryon botryoides* Vermoesen (Myristicaceae), and *Treculia africana* Decne Ex Trécul (Moraceae).

Most people in the surrounding areas live on < 1$ per day, have only basic formal education, and depend on forest products such as timber, fuelwood, bushmeat, and medicinal plants (Neuenschwander et al. 2015). Population growth is high, life expectancy averages 59 years (United Nations, Department of Economic and Social Affairs (UNDESA), Population Division 2022), and most people work in the agricultural sector. Governance structures often face challenges from corruption (Ighodaro and Igbinedion 2020) and regional land uses are poorly mapped and documented. Consequently, sustainable forest management is rarely prioritized, maintaining high pressure on forest resources.

2.2 | Data Collection

Between September 2022 and March 2023, we established 84 plots (50×50 m^2) across seven forest patches, with a minimum separation of 50 m between plots (Figure 2). The number of sampled plots per forest varied from 6 to 20, depending on forest patch size, forest heterogeneity, resource constraints, and security issues. In some cases (e.g., sacred forests), access to sacred areas was restricted. Based on remote sensing analysis and local knowledge, we believe our sampling effectively captured the features of the studied forests.

Five single scans (resolution: 43.7 Mpts, 0.035°/pt) were taken per plot using a terrestrial laser scanner (TLS, FARO M70), positioned on a tripod at the corners and center of each plot. The TLS emitted laser beams in 360° horizontal and 300° vertical directions. The laser beams reflected off plant material, such

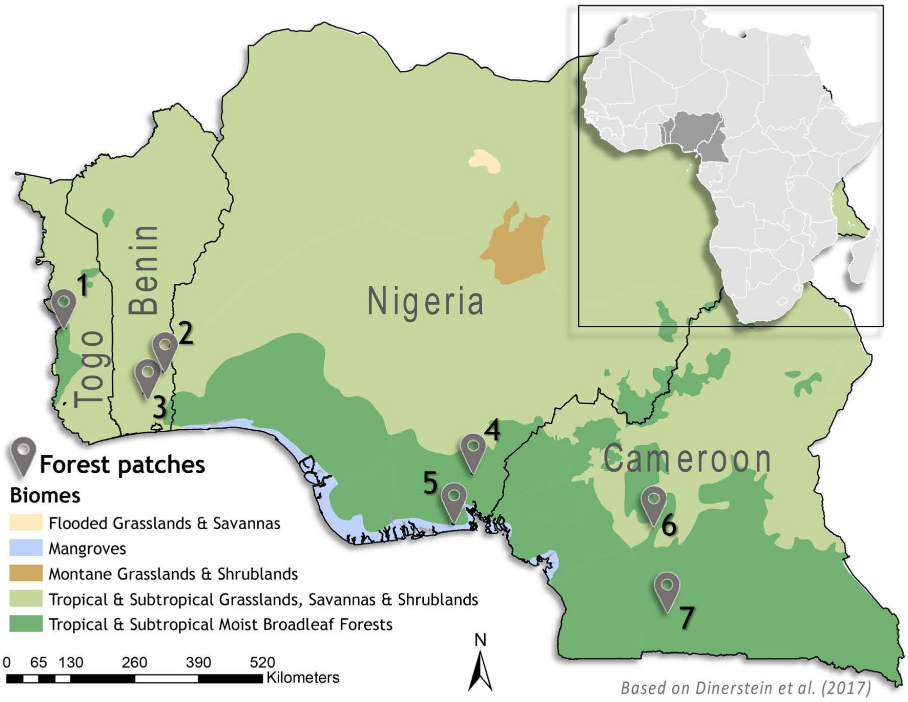

FIGURE 1 | Locations of the seven selected forest patches, where forest structural integrity was assessed by measuring stand structural complexity with terrestrial laser scanning. The forest patches are in the Tropical & Subtropical Grasslands, Savannas & Shrublands (light green) and the Tropical & Subtropical Moist Broadleaf Forests (dark green) of Togo, Benin, Nigeria, and Cameroon in Africa (marked gray in the inset map). 1. Ewè-Adakplamè, 2. Hlanzoun, 3. Koui, 4. Iko, 5. Ikot, 6. Mbangassina, 7. Ngam-Kondomeyos.

as leaves, branches, and stems, and were received by the TLS (Figure 3). Each reflected and received laser beam is saved as a point with its position information. Concurrently, we surveyed all trees with a diameter at breast height (DBH) ≥10 cm, measuring DBH with a tape and identifying species together with local botanists and national herbaria.

2.3 | Data Analysis

2.3.1 | Forest Structural Complexity Analysis

In the SCENE software (version 2023.0.1, FARO Technologies Inc. 2023), the scan data were downsampled by a factor of 4 and exported in .xyz format. The stand structural complexity index (SSCI) was calculated by constructing polygons of open space around the scanner position, connecting points where plant material reflected the laser beams. SSCI is defined as

$$\mathrm{SSCI} = \mathrm{MeanFrac}^{\ln(\mathrm{ENL})}$$

where MeanFrac refers to the mean of the fractal dimension index of 1280 polygons surrounding the scanner, derived from the perimeter and area of these polygons. ENL refers to the effective number of layers, quantifying 20 cm voxels filled with plant material in 1 m layers from the scanner to the canopy top (Ehbrecht et al. 2017). The higher the number of canopy layers, the denser the canopy packing, and the more heterogeneous the plant material distribution, the higher is the resulting SSCI (see also Ehbrecht et al. 2016, 2017). SSCI, canopy openness, and maximum tree height were calculated using the code from Ehbrecht et al. (2017) in R (version 2023.06.0, R Core Team 2019). In QGIS (version 3.28.7-Firenze, QGIS Development Team 2023) GPS positions were merged with SSCI values for the plots. The Shapiro–Wilk test was used in R to assess data distribution; correlations between SSCI and other forest characteristics were tested, and a one-way analysis of variances (ANOVA) was applied to determine significant differences between the forests. Linear mixed-effects models were applied to account for the random effects of the individual forests (single factor), utilizing the lme4 and lmerTest R-packages (Bates et al. 2015; Kuznetsova et al. 2017). Among four tested variations (fixed intercept and fixed slope, fixed intercept and varying slope, varying intercept and fixed slope, varying intercept and varying slope) the model with the lowest Akaike information criterion was retained (Bozdogan 1987) and model fit was assessed by Restricted Maximum Likelihood (REML). Ehbrecht et al. (2021) modeled a global distribution of potential SSCI by extrapolating values from 279 scanned plots with various environmental datasets from other studies. This dataset (spatial resolution: 30 arc sec), indicating the potential SSCI under current environmental conditions without human influences, served as a baseline and ecological reference for quantifying forest degradation.

TABLE 1 | Characteristics of the seven forest patches studied in Togo, Benin, Nigeria, and Cameroon. The column headers without sources indicate own measurements and field observations.

Nr.	Country	Forest name	Coordinates (WGS 84, Latitude/ Longitude)	Measured forest area (ha)	Number of plots	Vegetation type	Governance type	Soil (International Union of Soil Sciences (IUSS) Working Group World Reference Base for Soil Resources (WRB) 2015)	Surrounding landcover
1	Togo	Koui	0°43′12″/8°15′36″	20	6	Moist semideciduous forest	Sacred, traditionally protected forest	Acrisol	Settlement/ Agriculture/Savanna
2	Benin	Ewè-Adakplamè	2°34′12″/7°28′12″	220	18	Moist semideciduous forest	Sacred, traditionally protected forest, contested ownership	Acrisol/Lixisol	Settlement/ Agriculture/Savanna
3		Hlanzoun (also known as Lokoli)	2°15′36″/7°3′36″	680	20	Swamp forest	Sacred, traditionally protected forest	Acrisol/Gleysol/ Lixisol	Settlements/ Agriculture/Wetlands
4	Nigeria	Iko	8°15′0″/5°35′24″	1160	14	Moist forest	Community-based forest management	Acrisol	Agriculture/ Agroforestry
5		Ikot	7°53′24″/4°39′36″	1120	11	Swamp forest	Family-owned forest	Acrisol/Cambisol/ Fluvisol	Settlement/ Agriculture/Water
6	Cameroon	Mbangassina	11°35′24″/4°38′24″	160	7	Moist forest	Family-owned forest	Ferralsol	Agriculture/ Agroforestry
7		Ngam-Kondomeyos	11°49′48″/3°2′24″	400	8	Moist forest	Community-based forest management	Ferralsol	Wetlands/ Agroforestry

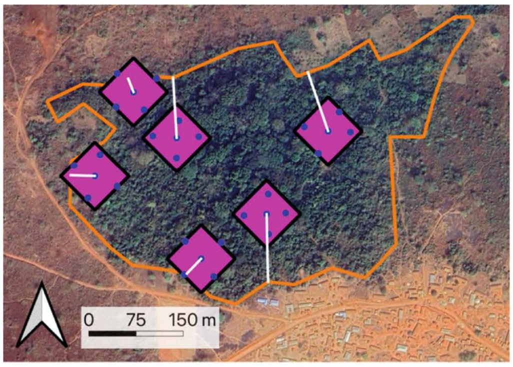

FIGURE 2 | Sampling plots distributed in the forest of Koui, Togo, to study forest structural complexity. Blue points indicate scan positions, white lines indicate distance to edge, pink squares symbolize study plots, and the orange line demarcates the forest patch. Maps of all the forests are available in the Data S1.

2.3.2 | Forest Edges Analysis

The seven forests were either never mapped before, mapped at a coarse scale inadequate for forest edge analysis (spatial resolution of 90 m by Wingate et al. 2022), or mapped using different methods years ago (Dan 2009; Houngnon et al. 2021). In Google Earth Engine (Gorelick et al. 2017), a supervised classification was performed with Sentinel S2 imagery for the period between March 1st 2022 and March 1st 2023 to differentiate between forest and non-forest areas. For Iko and Ikot, Landsat 8 provided better results due to nearby agroforestry and plantations. The analysis achieved high overall accuracies (OA) of 0.92 (Koui), 1 (Ewé-Adakplamé, Hlanzoun), and 0.96 (Iko, Ikot). However, for Mbangassina and Ngam-Kondomeyos, which are embedded in agroforestry and wetlands, supervised classification with satellite data was inaccurate (OA: 0.58, see Code S1.3). Consequently, GPS data of a tracked walk along the forest edge were used to determine the forest perimeter. In QGIS (QGIS Development Team 2023), the 'shortest line between features'-function was employed to calculate the distance between each plot and the forest edge.

The fragmentation index per forest was calculated by dividing the area within 100 m of the edge by the total forest area (Fischer et al. 2021). Thus, a greater area near the edge results in a higher fragmentation index, which ranges from 0 to 1. Connectivity was determined by assessing tree cover within a 1 km buffer surrounding the forests. A higher number of trees in this buffer indicates greater connectivity, signifying that the forest patch is less isolated. Connectivity is expressed in percent.

2.4 | Tree Composition

The number of trees (> 10 cm DBH) per plot was scaled up to a per-hectare basis for comparison purposes. The diameter at breast height was used to calculate total basal area for each plot, serving as a proxy for standing tree volume and aboveground biomass (Slik et al. 2010). Tree species richness was assessed by counting the number of different tree species per plot, adjusted for the number of trees, using rarefaction and extrapolation methods (Chao et al. 2014) implemented in the iNEXT R-package (Hsieh et al. 2024). Among the 342 tree species identified across the seven forests, 15 (4%) were classified only to the genus level.

3 | Results

3.1 | Characterization and Variation of Forest Structure of the Seven Forest Patches in Togo, Benin, Nigeria, and Cameroon

The calculated fragmentation index ranged from 0.2 in Ngam-Kondomeyos to 0.8 in the very small (20 ha) forest of Koui, and the larger (220 ha) but disturbed forest of Ewè-Adakplamè (Figure S1, panel 1). Forest fragmentation index decreased, and connectivity increased toward the equator and the Congo basin. While Koui and Ewè-Adakplamè were rather isolated in a landscape with few trees around the forests, Mbangassina was embedded in agroforestry, and Ngam-Kondomeyos was surrounded by agroforestry and wetlands, leading to a high connectivity (Figure S1, panel 2). The ecological characteristics of the two groups of climate-mediated vegetation (moist semideciduous forest and moist forest) and the group of soil-mediated vegetation (swamp forest) were well distinguishable (Figure S1, panels 3 to 9) and several parameters correlated with latitude. Koui and Ewè-Adakplamè had lower SSCI, higher openness, lower canopy height, lower maximum stem diameters, lower total basal area, fewer trees, and fewer tree species per plot compared with Ikot, Mbangassina, and Ngam-Kondomeyos. The swamp forests of Hlanzoun and Ikot were characterized by smaller trees (once only reaching 13 m height), smaller diameters, and fewer species (once only reaching 4 species, Figure S1, panels 5, 6, 9).

Stand structural complexity index correlated significantly negatively with fragmentation ($r = -0.86$, $p < 0.05$), but not with connectivity ($r = 0.59$, $p = 0.16$, Figure S2). Further, SSCI and canopy openness had a negative correlation ($t = -6.64$, $p < 0.001$). No significant effects on SSCI were found for tree heights, basal area, number of trees per hectare, and tree species richness (Figure 4). Surprisingly, SSCI decreased with the number of trees in Mbangassina ($r = -0.83$, $p < 0.05$) when analyzed by itself.

3.2 | Impact of Edge Effect on Forest Structure, Tree Height, and Canopy Openness

Across all the forests, several structural parameters were significantly related to distance to edge (Figure 5). SSCI, basal area, and number of trees per hectare increased significantly, while canopy openness decreased toward the forest interior. No significant trend was found for tree height and species richness.

For individual forests, SSCI did not increase significantly with distance to edge. However, Hlanzoun ($n = 20$) showed significant edge effects in canopy height ($r = 0.62$, $p < 0.005$) and basal area ($r = 0.56$, $p < 0.05$). Koui ($n = 6$) showed significantly more tree species richness toward the forest interior ($r = 0.93$, $p < 0.01$). Ewè-Adakplamè ($n = 18$) showed a significantly higher number of trees toward the forest interior ($r = 0.48$, $p < 0.05$) and higher tree species richness close to the edge ($r = -0.77$, $p < 0.001$). Iko,

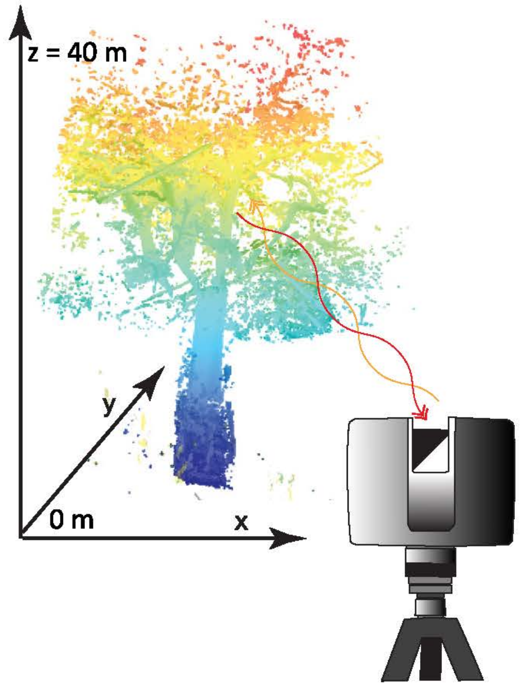

FIGURE 3 | The terrestrial laser scanner emits laser beams, which are reflected by trees and received again by the scanner, allowing detailed measurements of forest characteristics. The color gradient shows the tree height (*z*-axis) from blue (0 m) to red (40 m).

Ikot, Mbangassina, and Ngam-Kondomeyos did not show significant edge effects. Among the seven forests, Ewè-Adakplamè had a significantly high standard deviation of SSCI ($SD = 1.2$, $p < 0.05$) and SSCI ranged between 2.7 and 7.8 across this forest.

3.3 | Comparing Measured SSCI With Potential SSCI

The measured SSCI of the forest plots correlated moderately ($r = 0.46$, $p < 0.001$) with the modeled and potential ecological reference value by Ehbrecht et al. (2021, Figure 6). However, Ewè-Adakplamè ($\Delta = -1.3$, $p < 0.001$) and Ikot ($\Delta = -1.7$, $p < 0.001$) were significantly below the ecological reference value. Measured SSCI ranged between 3 and 8 and thus varies more per forest than the modeled SSCI ranging between 5 and 8 (Figure 6).

4 | Discussion

4.1 | Forest Characteristics Reflect Vegetation Types and Biomes

We report results from a field campaign in tropical forest patches across Togo, Benin, Nigeria, and Cameroon, where we investigated forest stand structural complexity in field plots using terrestrial laser scanning and traditional field inventories. We can confirm our hypothesis that the higher the SSCI, the lower the forest fragmentation index and the lower the canopy openness. However, the relationship between SSCI and connectivity, tree height, basal area, tree stem density, and tree species richness is not significant, highlighting the challenges of inferring and generalizing ecological functions from TLS-based structural metrics (Coverdale and Davies 2023). Our data align partially with previously published trends, such as increasing structural complexity with more precipitation toward the equator (Ehbrecht et al. 2021).

However, in the secondary forest of Mbangassina, SSCI decreases with more trees per plot. This contradicts the basic assumption behind SSCI stating that the more plant material, the higher the SSCI is (Ehbrecht et al. 2017). Successional stages and disturbance legacies may create a dense understory, captured by the TLS but excluded in the tree inventory that only captures trees with > 10cm DBH. Additional data on stand age, remnant trees, and disturbance history might help explain the unexpected negative relationship between SSCI and the number of trees.

4.2 | Impact of the Edge Effect on Forest Structure

Distance to the edge significantly affects SSCI, canopy openness, basal area, and number of trees, confirming our hypothesis of edge effects across diverse forest patches and management types (Harper et al. 2005; Laurance and Peres 2006). Our results suggest gradual edge effects within 600 m from the forest edge, while Ordway and Asner (2020) report effects within 200 m, and Nguyen et al. (2023) only beyond 200 m. Forest edge effects are complex and vary with species composition, topography, and current and past environmental conditions (Ibáñez et al. 2014).

Smaller, fragmented forests with relatively more area close to the edge show stronger and steeper gradients in structural parameters toward the interior. Additive effects from several edges (Harper et al. 2005), the form and age of edges, and the surrounding landscape play important roles, which are hard to disentangle (Ghazoul and Sheil 2010; Nguyen et al. 2023). In Koui, Ewè-Adakplamè, and Hlanzoun, at least one structural variable correlated with distance to edge, likely due to low connectivity and high isolation. Forests embedded in agroforestry with a higher connectivity (> 50%) show no significant edge effects, highlighting the importance of landscape connectivity (Zeller et al. 2020).

Surprisingly, in Ewè-Adakplamè, the number of trees increases toward the forest interior, while tree species richness decreases toward the interior. The plots close to the edge are therefore sparser but more diverse. Edge effects can alter tree composition, promoting pioneer species and suppressing shade-tolerant species (Faria et al. 2009; Harper et al. 2005). Ewè-Adakplamè's advanced fragmentation state (Map S1.3) and overlapping edge effects could explain these patterns.

Spatial variability of SSCI is high in Ewè-Adakplamè, due to disturbances like fire, logging, cattle trampling by livestock,

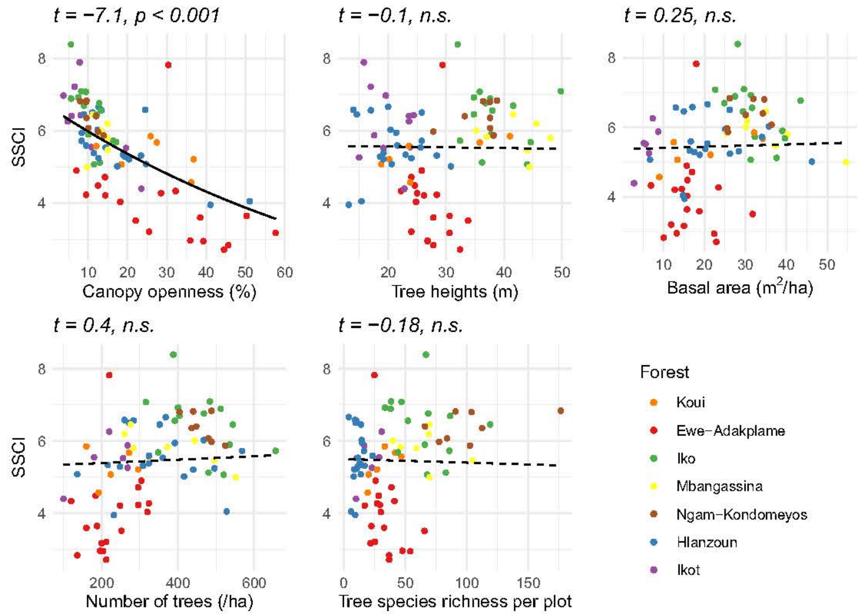

FIGURE 4 | The relationship between stand structural complexity index (SSCI, y-axis) and canopy openness, tree heights, basal area, number of trees, and tree species richness (*y*-axis) is shown for plots across seven forest patches (colors). The characteristics of moist semideciduous forests (Koui, Ewè-Adakplamè), moist forests (Iko, Mbangassina, Ngam-Kondomeyos), and swamp forests (Hlanzoun, Ikot) are often clustered. n.s. indicates nonsignificant relationship.

hunting pressure on seed-dispersing animals, invasive species (e.g., *Chromolaena odorata* (L.) R.M.King & H. Rob.), and liana infestations (Houngnon et al. 2021; field observations). These disturbances alter forest structure, thereby increasing SSCI variation. However, species loss and neophytes may also homogenize forest structure (Ghazoul et al. 2015). Small-scale disturbances may go undetected between plots, while large-scale disturbances affecting the whole forest require temporal data.

4.3 | Forest Structural Integrity

Our data allows to assess forest structural integrity by comparing measured SSCI with the potentially highest SSCI of a primary forest in the same place (Ehbrecht et al. 2021). Deviations between measured SSCI and ecological reference value arise because of model limitations or when the forests are recovering from disturbances. The ecological reference value has a spatial resolution of 30 arc sec and was built in 2020. Therefore, local features, such as swamps, or spatio-temporal dynamics, such as regeneration, are not considered or simplified. The ecological reference value does not account for human management, and we can conclude that deviations between measured SSCI and the model are mainly due to anthropogenic disturbances when found on a large spatial scale (Korom et al. 2022). Of the seven assessed forest patches, five have an SSCI close to their potential. This confirms our hypothesis that these forests are structurally intact.

However, the forest of Ewè-Adakplamè is significantly below its potential. Indeed, Ewè-Adakplamè is highly fragmented (0.8, Map S1.3) and not well connected (20%). Several fires reduced its area in the last 20 years (Chuvieco et al. 2018; Wingate et al. 2022) with losses peaking in the last 3 years (Wingate et al. 2024). Contested forest ownership negatively affects forest management and, with illegal charcoal production, increases pressure on forests. These issues, linked with social, economic, and political insecurities and open conflicts, can accelerate forest degradation (Kouassi et al. 2022).

The forest of Ikot is significantly below its potential SSCI. This could be due to the high demand for fuelwood from the population of the neighboring communities and the city of Eket. Half a million people live in the 10 km surrounding Ikot forest (World pop.org, 2020) and demand for fuelwood is particularly high because fuelwood alternatives are not fully accessible in many low-income societies (Ebe 2014). The deviation between measured and potential SSCI could also be explained by an overestimation of the potential SSCI. Potential SSCI in the region of Ikot is modeled with increased uncertainty (95% confidence interval >1, Ehbrecht et al. 2021).

The forests with an SSCI close to the ecological reference value are often not easily accessible. Inaccessibility can result from (i) topography, as seen in Hlanzoun and Ngam-Kondomeyos, where wetlands and rivers prevent easy access to the forest and its resources, (ii) religious restrictions, as in Koui, where the sacredness of the forest is well-respected and some parts

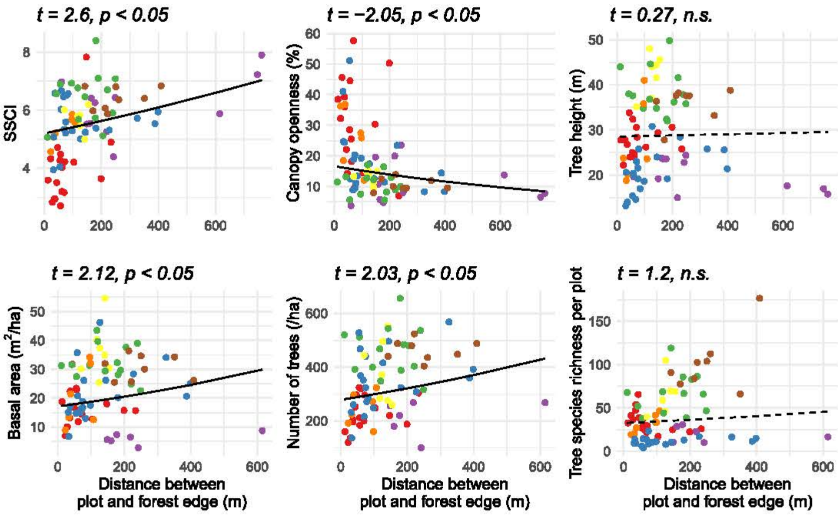

FIGURE 5 | Several structural parameters, such as SSCI, basal area, and number of trees (*y*-axis) increase significantly with distance to the forest edge (*x*-axis) in plots across seven forest patches (colors). Canopy openness decreases significantly with distance to the forest edge. The relationship is not significant for tree heights and tree species richness per plot.

are not accessible at all, and (iii) limited infrastructure, as in Iko and Mbangassina, where deteriorated roads and long distances to economic centers limit forest exploitation. These findings align with studies reporting higher forest integrity where access is restricted by topography (Freitas et al. 2010), religion (Lynch et al. 2018), and infrastructure (Ahrends et al. 2010).

We used the ecological reference value (Ehbrecht et al. 2021) to assess forest structural integrity. Skewed DBH distributions, missing DBH classes, or particular thresholds in canopy openness and basal area can also indicate forest degradation (Vásquez-Grandón et al. 2018). However, our data do not show such patterns, and thresholds must be set based on intact reference forests in the same edaphoclimatic zone. The absence of large commercially valuable trees near the edge suggests logging pressure (Ali and Wang 2021; Korom et al. 2022). However, in West Africa, large trees are sometimes explicitly retained, domesticated, and used for medicinal and religious purposes (Atindehou et al. 2022; Fairhead and Leach 1996; Nkouam et al. 2017), and pressure on commercial tree species varies with market dynamics.

4.4 | Applying Insights From Forest Structural Integrity

Our data provide ground truth for satellite remote sensing products. Wingate et al. (2023) grouped Koui and Hlanzoun in an archetype, characterized by frequent, severe disturbances, and high biomass loss (2010–2018). However, our TLS analysis shows both forests are structurally intact, and few disturbances were observed. Field data like ours are essential to validate remote sensing products, enabling spatial extrapolation of insights.

Our results suggest that various governance types can manage forests sustainably. Community-based management (e.g., Ngam-Kondomeyos), family-owned (e.g., Mbangassina), and sacred and traditionally protected forests (e.g., Koui) maintain intact forest structures. However, when governance is disregarded (Ewè-Adakplamè) or demand and exploitation exceed sustainable levels (Ikot), forests degrade, independent of governance type.

4.5 | Study Limitations

Forest structure can indicate disturbances and degradation. However, forest structure is shaped by internal dynamics (e.g., species competition) and perturbations of different spatio-temporal extents (Ghazoul and Sheil 2010). Assessing full degradation requires data on seedbanks and seed viability under future climatic scenarios (Ghazoul et al. 2015). Since our data were collected once, they offer limited temporal representativity given forests' daily and yearly cycles (Binkley 2021) and the long-term climate change. Spatial representativity is also constrained by natural (e.g., swamps) and religious barriers (e.g., sacredness). Local edaphic conditions, potentially impacting forest structure, were not considered. Still, our study provides valuable data and fills a key knowledge gap about the structural complexity of forest patches in West Africa.

5 | Conclusions

Terrestrial laser scanning was applied in seven tropical forest patches across Togo, Benin, Nigeria, and Cameroon, alongside traditional forest inventory data, to enhance our understanding of

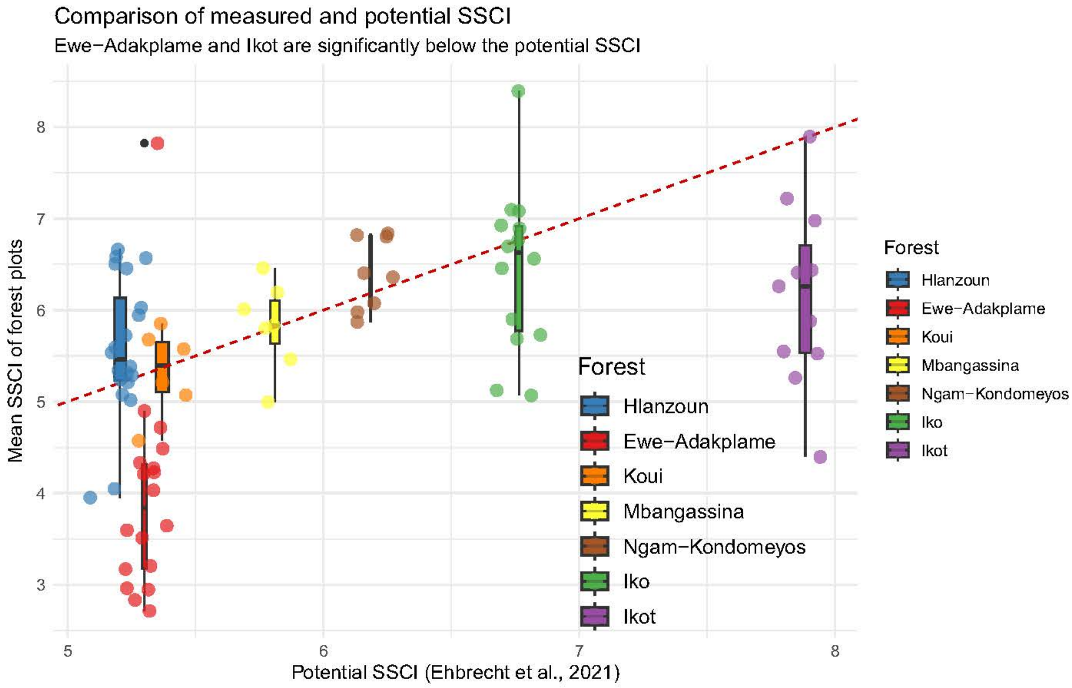

FIGURE 6 | Comparison of the potential stand structural complexity index (SSCI) used as ecological reference value on the *x*-axis and the in situ measured SSCI on the *y*-axis. Boxplots describe the distribution of points (plots in the field), which are both colored according to the forest. The dashed red line indicates where measured and potential SSCI correspond. Ewè-Adakplamè (red) and Ikot (purple) are significantly below their potential SSCI (red line).

tropical forest fragmentation and ecological dynamics in this understudied region. The forests are Koui (Togo), Ewè-Adakplamè and Hlanzoun (Benin), Iko and Ikot (Nigeria), and Mbangassina and Ngam-Kondomeyos (Cameroon). Climate- and soil-mediated forests exhibited forest characteristics like canopy height, basal area, and species richness that vary by biome and latitude. Surprisingly, in Mbangassina, forest structural complexity correlated negatively with the number of trees, likely due to specific successional stages and legacy effects. Edge effects on canopy openness, tree height, basal area, and tree species richness were found in highly isolated forests, but not in forests that are embedded in agroforestry or wetlands. Small, fragmented forests had steeper gradients of characteristics with distance to edge, possibly due to additive and overlapping edge effects. Comparison with the potential SSCI revealed that Ewè-Adakplamè and Ikot are structurally degraded, most likely because of unsustainable management and overexploitation of forest resources. The detected edge effects call for connecting isolated forest patches and establishing buffering zones around forests; that is, to buffer edge effects. Furthermore, assessing forest integrity helps prioritize conservation projects, which is increasingly important amidst rapid land use change and forest degradation in West Africa. Future research should also address the temporal aspects of forest degradation and socio-economic contexts driving poor forest governance and unsustainable management that lead to forest degradation.

Author Contributions

S.H. and C.I.S. designed the study, C.I.S. acquired funding, S.H., G.A.A., C.I., and C.I.S. collected field data, S.H. analyzed the data and wrote the manuscript, and C.I.S., C.I., M.E., and A.F.A. reviewed the manuscript.

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Conflicts of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Data Availability Statement

The data that support the findings of this study are openly available in Boris at https://boris-portal.unibe.ch/handle/20.500.12422/204410.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

5.2 Paper 2: Aboveground Biomass in Seven Tropical Forest Patches of Western Africa: Comparison of Manual Inventory and Terrestrial Laser Scanning

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Aboveground Biomass in Seven Tropical Forest Patches of Western Africa: Comparison of Manual Inventory and Terrestrial Laser Scanning

Key message

Aboveground biomass (AGB) increases from forest edge to forest interior in small forest patches of Western Africa. In plots of 0.25 ha, AGB did not correlate with tree species richness or wood density. AGB in these unprotected forest patches was lower than in protected forests nearby. AGB obtained from manual inventory and terrestrial laser scanning correlated moderately.

Abstract

Context

Tropical forests are disappearing and fragmenting, raising concerns about their role as biodiversity habitats and carbon sinks. In Western Africa, small, unprotected forest patches amidst agricultural lands provide vital ecosystem services like carbon storage. However, accurately measuring aboveground biomass remains challenging, and terrestrial laser scanning (TLS) might become an accurate, non-destructive method.

Aims

This study explores AGB, its spatial distribution and relationships with ecological determinants, and compares AGB estimated from manual inventory with those from TLS.

Methods

We established 109 plots and inventoried 9591 trees across seven forests in Togo, Benin, Nigeria, and Cameroon. AGB was obtained from allometric equations using diameter and tree heights as well as from segmented point clouds. Plot-level AGB was extrapolated to the entire forest.

Results

AGB in forest patches ranged from 85 to 259 Mg/ha, which is lower than in nearby protected forests. Forests close to the equator have generally higher AGB, and most forests showed reduced AGB and wood density close to forest edges. AGB showed no correlation with wood density, structural complexity, and tree species richness. AGB estimations by manual inventory and TLS correlated moderately.

Conclusion

Our findings highlight the value of ground-based methods and the need to connect and protect forests as carbon reservoirs.

Keywords: Allometric equation, Automatic point cloud segmentation, Edge effects, Forest fragmentation, Tree species richness, Wood density

1. Introduction

1.1 Forest loss, fragmentation, and persisting patches in Western Africa

Tropical forests are being cleared globally at alarming rates (Schelhas and Greenberg 1996; Hansen et al. 2013; Poorter et al. 2021). In Western Africa, more than 80% of the 1900 forest extent has been lost, mainly due to the growing human population clearing forests for agriculture (Aleman et al. 2017; Curtis et al. 2018; Amani et al. 2021; Akinyemi and Ifejika Speranza 2022). In addition to deforestation, large contiguous forests have been fragmented into numerous small patches (Taubert et al. 2018; Traoré et al. 2024; Wingate et al. 2022). Between 2000 and 2010 the number of forest fragments increased by 42% in Africa (Fischer et al. 2021). Fragmented areas are particularly affected by forest loss (Dangbo et al. 2020) and remaining forest patches are vulnerable to edge effects, such as fire, desiccation, and altered species composition (Hill & Curran, 2003; Ibáñez et al. 2014; Laurance, 2004; Taubert et al. 2018).

Despite this deforestation trend, thousands of small forest patches (<1000 ha) persist in isolation across the Western African landscape and in Togo, Benin, Nigeria, and Cameroon alone over 400,000 patches have been detected in the Guineo-Congolian forest and the Guinea Savanna zones (Wingate et al. 2023). These patches, ranging between 0.5 and 1000 ha, are characterized by trees exceeding 5 m in height and a canopy cover greater than 30% (Food and Agriculture Organization of the United Nations (FAO) 2016; Wingate et al. 2022). They are crucial for biodiversity conservation and climate regulation including carbon storage and sequestration (Lewis et al. 2015).

1.2 Aboveground biomass (AGB)

Tropical forests store the majority of terrestrial aboveground carbon and are central to climate mitigation and biodiversity conservation (Chave et al. 2019a; Ameray et al. 2021). Aboveground biomass (AGB), largely contained in woody compartments of trees (Williams et al. 2013), is therefore a key parameter for assessing greenhouse gas emissions, timber management, and ecosystem services. International initiatives such as REDD+ (Reducing Emissions from Deforestation and forest Degradation and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries), the Kunming-Montreal Global Biodiversity Framework, and other funding schemes require robust estimates of AGB to monitor commitments and guide management (Food and Agriculture Organization of the United Nations (FAO) and United Nations Environment Programme (UNEP) 2020; Convention on Biological Diversity (CBD) 2021; International Union for Conservation of Nature (IUCN) 2022; Turia et al. 2022).

In Western Africa, however, most AGB studies have concentrated on large, formally protected forest blocks or a few commercially important species (Basuki et al. 2009; Chenge and Osho 2018; Aabeyir et al. 2020; Atsri et al. 2020; Arouna et al. 2021). Small and unprotected forest patches remain underrepresented, despite their abundance and ecological importance (Wingate et al. 2023). These patches are particularly exposed to edge effects, including higher tree mortality, windthrow, and fire, which can substantially reduce biomass (Laurance et al. 1997, 2000; Ordway and Asner 2020; Giancola et al. 2024). Structural changes, such as reduced tree height for a given diameter (Nunes et al. 2023), and the loss of large animal seed dispersers (Lewis et al. 2015) further contribute to lower AGB compared to continuous forests.

Understanding AGB in small forest patches is therefore crucial. They may serve as analogues of the future landscape if fragmentation continues (Tabarelli et al. 2008; Taubert et al. 2018a), and their carbon dynamics will determine whether they act as persistent carbon sinks or as sources of emissions. Yet, temporal trends of AGB in these fragments remain poorly understood and contested (Wingate et al. 2023). In addition, little is known about how the biomass of these small forest patches compares with that of other nearby forests in the region, whether larger, formally protected, or similar in size and management, although this contrast is central for evaluating their role in regional carbon budgets.

1.3 Challenges of quantifying aboveground biomass

Quantifying AGB in tropical forests is notoriously difficult due to high species richness, variable tree allometries, and the presence of very large individuals (Hemp et al. 2017; Cazzolla Gatti et al. 2022; Calders et al. 2022). While destructive harvesting remains the most accurate method (Ketterings et al. 2001), it is rarely feasible, and indirect approaches such as manual inventories and remote sensing are commonly used (Clark and Kellner 2012). However, inventorying even a single hectare of tropical forest is logistically demanding and expensive (Chave et al. 2019a; ForestPlots.net et al. 2021), and such efforts remain scarce in Western Africa (Harris et al. 2021). Satellite-derived biomass maps provide valuable regional and global coverage, but their accuracy is limited by the paucity of representative ground data and by strong structural heterogeneity in Afrotropical forests (Chave et al. 2019a; Araza et al. 2022). These limitations are particularly acute in small forest patches, which are often excluded from large-scale inventories and misclassified by coarse-resolution remote sensing products. As a result, current maps show discrepancies of more than 150 Mg ha^{-1} in Western Africa (Araza et al. 2022), and the biomass of small patches remains largely unvalidated.

Emerging technologies such as terrestrial laser scanning (TLS) offer a promising complement to manual inventories. TLS captures forest structure in three dimensions, providing accurate estimates of tree size and canopy height without destructive sampling (Calders et al. 2020; Terryn et al. 2024). While TLS has been tested in temperate and Amazonian forests, its application in Western Africa is minimal and absent from Togo, Benin, and Nigeria (Momo et al. 2018, 2020). Forest patches are a particularly relevant test case, as they combine high floristic diversity, structural heterogeneity, and strong edge effects within small areas, posing both logistical challenges and opportunities for TLS validation. Moreover, comparing the AGB of these patches with other regional forests can clarify whether small remnants store carbon proportionally or show systematic differences across the landscape.

To shed light on aboveground biomass and its quantification in these understudied ecosystems, we address the following questions:

1. What is the current AGB and carbon in the studied forest patches and how is it spatially distributed?

- H: We expect that the amounts and spatial patterns of AGB and carbon vary across the forest patches, indicating environmental and disturbance gradients.

2. Which forest characteristics correlate most with AGB?

- H: We expect basal area, tree height, and wood density to correlate most with AGB.

3. How does the AGB of these patches compare with that of other forests in the region?

- H: We expect to find lower AGB in isolated forest patches as compared to larger forest areas, due to edge effects.

4. How does AGB estimated from manual inventory compare to AGB obtained by TLS?
   - H: We expect that AGB obtained by TLS will show a positive correlation with AGB derived from manual inventories across forest patches.

To address this knowledge gaps, we focused on seven forest patches in Togo, Benin, Nigeria, and Cameroon, spanning diverse forest types and ecological conditions.

1.4 Study area

These patches represent both Tropical and Subtropical Grasslands, Savannas, Shrublands, and Moist Broadleaf forests (Fig. 1; Dinerstein et al. 2017; see Table A1 for details). These remnants include semi-deciduous forests (Koui and Ewè-Adakplamè), soil-mediated swamp forests (Hlanzoun, also known as Lokoli, and Ikot), and moist forests (Iko, Mbangassina, and Ngam-Kondomeyos). Together, they capture a broad ecological gradient and taxonomic diversity, with frequent tree families such as Moraceae (e.g., *Treculia africana* Decne Ex Trécul), Fabaceae (e.g., *Gilbertiodendron dewevrei* (De Wild.) J.Léonard), and Myristicaceae (e.g., *Pycnanthus angolensis* (Welw.) Warb.).

Despite lacking formal protection, these forest patches have persisted since at least the 1970s, surrounded today by croplands, agroforestry systems, and wetlands (Hansen et al. 2013; Wingate et al. 2022). They span pronounced environmental gradients: mean annual precipitation ranges from 1000 to 1300 mm in Koui, Ewè-Adakplamè, and Hlanzoun, and from 1500 to 3000 mm in Iko, Ikot, Mbangassina, and Ngam-Kondomeyos; mean annual temperatures lie between 23 and 28 ° C (Hijmans et al. 2005). Elevations extend from 15 m above sea level in Ikot to 700 m in Ngam-Kondomeyos (Jarvis et al. 2008). Soil types predominantly include Acrisols, Lixisols, and Ferralsols, with Gleysols and Fluvisols occurring in the swamp forests (International Union of Soil

Sciences (IUSS) Working Group World Reference Base for Soil Resources (WRB) 2015). Including such ecologically diverse sites strengthens the spatial coverage of AGB assessments across Western Africa (Lewis and Pickavance 2024) and provides essential ground-truthing data for satellite-based forest archetypes (Wingate et al. 2023).

[Insert Fig. 1 here]

2. Methods

2.1 Data collection

Between September 2022 and March 2023, we installed 109 plots each measuring 50 x 50 m across seven forest patches, following plot size recommendations by Chave et al. (2004) and Duncanson et al. (2021). Within each patch, plots were distributed randomly, constrained by a minimum inter-plot distance of 50 m, accessibility, and human security considerations. To ensure representativeness, plots were located in internally homogeneous areas (avoiding canopy gaps or abrupt changes in vegetation structure, composition, and topography). Depending on forest patch size (20–1160 ha), we installed 6–21 plots per forest to ensure representative coverage.

The manual forest inventory included all trees with a diameter at breast height (DBH) ≥ 10 cm. Smaller trees, dead logs, lianas, and palms were disregarded in the manual inventory since they contribute little to AGB (Ali et al. 2019c; Atsri et al. 2020; Duncanson et al. 2021). The position of each tree was taken with a handheld GPS (Garmin GPSMAP 66i). While occasional device readings suggested a precision of around ±3 m, actual horizontal accuracy likely varied with canopy density, generally falling within the 5–10 m range (Garmin Ltd. 2025). DBH was measured with a diameter tape (0.1 cm precision), individual tree height was estimated with a clinometer, and tree species were identified with local botanists and later confirmed in national herbaria.

While various methods exist for installing subplots within a main plot (Bechtold and Scott 2005), we established a 25 × 25 m subplot in a random corner of each plot (see subplot level 1 in Food and Agriculture Organization of the United Nations (FAO), 2004). This approach facilitated orientation in the dense forests, as two subplot sides coincided with measuring tapes from the main plot, and the four subplot corners were already marked with colored poles. Within each subplot, all trees were tagged with unique numbers and registration markers (FARO Technologies Inc. 2017). We scanned the subplot with a terrestrial laser scanner (FARO M70) with 24.2 MPts, 0.044°/pt, and color mode, which took ca. 4.5 min/scan. We followed a continuous chain, always scanning the markers twice to allow subsequent co-registration (Wilkes et al. 2017; Martin-Ducup et al. 2021; Tao et al. 2021). Depending on forest density, we conducted approximately 30 scans per subplot, with scan positions spaced around 6 meters apart (Fig. 2). Additionally, we took five single scans in the corner and the center of the plots to quantify the stand structural complexity index (SSCI, Ehbrecht et al. 2017; Hepner et al. 2025). Scans were only taken when there were no rain, no wind, and no moving people close to the scanner.

[Insert Fig. 2 here]

2.2 Data analysis

2.2.1 Manual inventory data

In total, 9,591 individual trees of 369 different species were identified. 281 trees (3%) of 25 genera (7%) could only be identified to the genus. To calculate AGB of these trees, the BIOMASS-package (Réjou-Méchain et al. 2017) was run (see also Mo et al. 2023; Ploton et al. 2020) in R (version 2023.06.0, R Core Team, 2023). Due to the potential inaccuracy of tree heights measured with a clinometer, we applied a local allometric model (log2, residual standard error *(RSE)* = *4.96 m*) to adjust the estimates (Réjou-Méchain et al. 2017). Species-specific wood densities from the Global Wood Density Database (Zanne et al. 2009) were assigned to 5,062 trees (53%), genus-averaged densities to 3,011 trees (31%), and plot averages to 1,518 trees (16%). We applied the pantropical allometric equation by Chave et al. (2014), which is commonly used in tropical AGB studies (Cuni-Sanchez et al. 2021; Davies et al. 2021; Zemp et al. 2023, equation 1):

$AGB_m = 0.0673 * (\rho D^2 H)^{0.976}$ (equation 1),

where AGB_m = aboveground biomass (kg) from manual inventory, ρ = wood density (g/cm^3), D = diameter at breast height (cm), and H = tree height (m).

Subsequently, a Monte Carlo test was applied to quantify error propagation and corresponding credibility at the plot level (2.5% and 97.5%, Fig. A1). AGB_m was converted to carbon by the factor 45.6% (±0.2), which is the mean for tropical angiosperms (Martin et al. 2018). Species richness was standardized for differences in tree abundance among plots using individual-based rarefaction and extrapolation (Chao et al. 2014) implemented in the iNEXT R-package (Hsieh et al. 2024). Further, species richness was estimated from species–abundance data (stem counts per plot) with datatype = "abundance" and q = 0, providing rarefied, extrapolated, and asymptotic richness values with associated standard errors. To test the relationships between ecological determinants of aboveground biomass (AGB), including basal area, tree height, wood density, tree species richness, number of trees, SSCI, and canopy openness, we applied linear mixed-effects models. This approach accounted for the random effects of individual forests as a single factor, using the lme4 and lmerTest R packages (Bates et al. 2015; Kuznetsova et al. 2017). We evaluated four model variations: fixed intercept and fixed slope, fixed intercept and varying slope, varying intercept and fixed slope, and varying intercept and varying slope. The model with the lowest

Akaike information criterion (AIC) was retained (Bozdogan 1987) and model fit was assessed using Restricted Maximum Likelihood (REML).

2.2.2 Extrapolation from plot to forest

We estimated forest-wide AGB by extrapolating AGB_m from the 109 plots (50 x 50 m) using its relationship with canopy height. First, in QGIS (version 3.28.7-Firenze, QGIS Development Team, 2023) the minimum bounding geometry function was applied to the coordinates of individual trees to determine the position and orientation of each corresponding 50 x 50 m plot (0.25 ha). Then, zonal statistics was used to get the mean and median of satellite-obtained canopy height (Lang et al. 2023) and normalized difference vegetation index (NDVI) of the corresponding period (Planet Labs PBC 2022) for each plot. In R (R Core Team 2023), correlations were tested between AGB_m and satellite-obtained canopy height and NDVI. AGB_m correlated stronger with median canopy height ($r=0.8$, $p<0.001$) than with NDVI and mean canopy height. This suggests that the median better reflects typical canopy structure by reducing the influence of rare emergent trees that may inflate the mean canopy height.

As with the linear mixed-effects models to examine relationships between AGB and ecological determinants (chapter 2.2.1), we use such to analyze the relationships between AGB_m and canopy height. Again, we tested four variations (fixed intercept and fixed slope, fixed intercept and varying slope, varying intercept and fixed slope, varying intercept and varying slope) of single-factor linear mixed-effects models with forests treated as the random factor (Kuznetsova et al. 2017). The model with the lowest Akaike information criterion was retained (Bozdogan 1987) and model fit was assessed by Restricted Maximum Likelihood (REML). The retained model had a varying intercept and a fixed slope and allowed to extrapolate AGB_m beyond the sampled plots (equation 3):

$$AGB_m = 33.2071 * \exp(0.0504 * Height_L) \qquad \text{(equation 3)},$$

where AGB_m = aboveground biomass (Mg/ha) obtained from manual forest inventory and $Height_L$ = median of canopy height (m) per plot obtained from (Lang et al. 2023, *t=5.1, p<0.001*). Based on the relationship between plot-AGB_m and satellite-obtained canopy $Height_L$, we could extrapolate AGB from the plots to the whole forest patch using raster calculator in QGIS (QGIS Development Team 2023). The spatial resolution of the plots (50 x 50 m) was maintained and the aligned raster data could later be used to generate difference maps with the AGB map by Harris et al. (2021, *r=0.6, p<0.001*).

In QGIS (QGIS Development Team, 2023), we used zonal statistics to sum AGB and calculate its mean and standard deviation per forest. These values then fed into the error propagation calculation for converting AGB to carbon: (equation 4, (Goodman 1960)):

$$\sigma_{AGB*Carbon} = \sqrt{(\sigma^2_{AGB} + \mu^2_{AGB})(\sigma^2_{Carbon} + \mu^2_{Carbon}) - (\mu^2_{AGB} * \mu^2_{Carbon})} \qquad \text{(equation 4)},$$

where $\sigma_{AGB*Carbon}$ is the standard deviation of the product of our estimated AGB and the carbon conversion factor as quantified by Martin et al. (2018), σ^2_{AGB} is the variance of AGB, μ^2_{AGB} is the squared mean of AGB, σ^2_{Carbon} is the variance of carbon (0.002), and μ^2_{Carbon} is the squared mean of carbon (0.456) (Martin et al. 2018). Total AGB uncertainty per forest was calculated as (equation 5, adapted from Taylor (1997)):

$$\sigma_{sumAGBforest} = \sigma_{AGBPerPixel} * \sqrt{\frac{n}{1+2*r(d)}} \qquad \text{(equation 5)},$$

where $\sigma_{sumAGBforest}$ is the uncertainty of the total AGB per forest, $\sigma_{AGBPerPixel}$ is the uncertainty of AGB per 50 x 50 m pixel, *n* represents the number of pixels per forest, and *r(d)* is the correlation coefficient of a pixel with its eight immediate neighboring pixels corresponding to a 50 m radius. The distance of 50 m was chosen during field data collection and applied in the analysis to avoid biases due to spatial autocorrelation. Finally, we validated extrapolated AGB by comparing it with input plot data using a Wilcoxon test (Bauer 1972; R Core Team 2023). We compiled published AGB data from the same or nearby forests to compare isolated patches with larger, differently managed, and differently estimated forest tracts.

2.2.3 Terrestrial Laser Scanning (TLS) data

TLS-data from 86 subplots were processed, and co-registered in SCENE (version 2023.1.0, FARO Technologies Inc., 2023). We generated 50 point clouds, each consisting of 167 million points on average with a mean point error of 22 mm. In 36 subplots, scan registration failed due to very dense understory vegetation, hindering automatic merging of adjacent scans. In seven subplots, we did not identify tree species and therefore had no corresponding wood densities, leading to the number of 43 completely analyzed subplots.

The point clouds were processed in Forest Structural Complexity Tool (FSCT), which is sensor-agnostic and known for high accuracy (Krisanski et al. 2021; Boroujeni et al. 2024). We segmented the point clouds automatically in ground, leaf, and stem points, isolated individual trees, and fitted cylinder for tree volume estimation (Krisanski et al. 2021; Fig. A2). Visual inspection of the segmented point clouds was performed in CloudCompare (Girardeau-Montaut 2023).

The output of FSCT was filtered by DBH ≥10 cm and circumference completeness index (CCI) ≥0.3 (Krisanski et al. 2021), to align with the manual inventory and reduce noise (Fig. 3). The CCI measures the completeness of a scanned circular object, such as a stem or branch. Apparent stems scanned only from one side were excluded as noise. These filters were confirmed as best fit by an analysis of Euclidean distance between the manual inventory data and FSCT output and on average 60% of the originally detected 'trees' were filtered out this way. Wood density for each FSCT subplot was derived from the manual inventory by assigning species-specific wood densities and calculating a basal-area–weighted mean. Basal area was computed for each tree as $\pi * (\frac{\mathrm{DBH}}{2})^2$, and subplot-level mean wood density was obtained by weighting species wood densities by their relative basal area contributions. This mean wood density was then applied to the TLS-derived stem volumes to convert them into subplot-level aboveground biomass (AGB_{TLS}). Correlations were used to compare forest characteristics estimated by manual inventory and TLS. Analysis of variance (ANOVA) was used to detect peculiarities across forest patches.

[Insert Fig. 3 here]

Based on five scans per plot, we calculated the stand structural complexity index (SSCI, Ehbrecht et al. 2017). This index constructs polygons of open space around the scanner position, connecting points where plant matter reflected the laser beams. SSCI is defined as (equation 2):

$$SSCI = MeanFrac^{\ln(ENL)} \quad \text{(equation 2)},$$

where $MeanFrac$ refers to the mean of the fractal dimension index of 1280 polygons surrounding the scanner, derived from the perimeter and area of these polygons. ENL refers to the effective number of layers, quantifying 20 cm voxels filled with plant material in 1 m layers from the scanner to the canopy top (Ehbrecht et al. 2017). SSCI is powerful in quantifying the three-dimensional forest structure and high structural complexity is typically associated with greater ecosystem functioning (Coverdale and Davies 2023).

3. Results

3.1 AGB and carbon in the seven studied forest patches

Addressing research question 1, we quantified AGB and carbon in seven forest patches (Table 1). AGB_m ranged from 85 Mg/ha in Ikot to 199 Mg/ha in Ngam-Kondomeyos, corresponding to 39

Mg/ha and 91 Mg/ha carbon. The smallest forest Koui (18 ha) stored 351 Mg AGB and the largest forest Iko (1163 ha) stored 44,812 Mg AGB.

[Insert Table 1 here]

3.1.1 Spatial patterns of AGB within forests

A linear mixed-effects model with log-transformed AGB, distance from the forest edge as a fixed effect and forest as a random intercept *(lmer(log(AGB) ~ distance + (1 | Forest)))*, showed that AGB$_m$ increased toward forest interiors (*t=2, p<0.005*). However, distances from plot to forest edge and AGB$_m$ were significantly different between forests (*ANOVA, p<0.001, Fig. 4*). Across forests, Hlanzoun (r=0.2, p<0.001), Iko (r=0.06, p<0.05), and Ikot (r=0.2, p<0.001) showed edge effects of increasing AGB$_m$ toward the forest interior.

[Insert Fig. 4 here]

Separate linear mixed-effects models with distance from the forest edge as a fixed effect and forest as a random intercept suggested that diameter (*t=3, p<0.005*), tree height (*t=3, p<0.005*), and wood density (*t=4, p<0.001*) increased toward the forest interior. Log-transformations were applied to diameter and tree height to improve model fit, while wood density was modeled on the original scale. Tested individually the forests of Hlanzoun and Ikot showed the same edge effects. For wood density alone, the relationship is significant in Koui (*r=0.13, p<0.01*), Iko (*r=0.08, p<0.001*), and Mbangassina (*r=0.07, p<0.05*).

Wilcoxon test comparing field-estimated and extrapolated AGB per plot indicates that the extrapolation from plot to forest using satellite-obtained canopy height is accurate for Koui, Ewè-Adakplamè, and Hlanzoun. However, it slightly overestimates AGB in Iko and Ngam-Kondomeyos, while underestimating AGB in Ikot.

3.2 Ecological determinants of AGB

In addressing research question 2, we note that AGB_m is composed of wood volume and wood density. Accordingly, we found strong correlations between AGB_m and both basal area (*t=6, p<0.001*) and tree height (*t=4.8, p<0.001*). However, AGB_m did not show a significant correlation with wood density.

AGB_m and tree species richness were both low in the swamp forests (Ikot, Hlanzoun) and the moist semi-deciduous forests (Koui, Ewè-Adakplamè) and high in the moist forests toward the equator (Iko, Mbangassina, Ngam-Kondomeyos). AGB_m and tree species richness did not correlate (Fig. A3). AGB_m correlated well with the number of tree stems (DBH>10 cm, *t=2.8, p<0.01*), the standard deviation of tree height (*t=7.36, p<0.001*) but neither with stand structural complexity (SSCI) nor with canopy openness. Interestingly, wood density is higher in shorter trees (*t=-2.3, p<0.05*) but no correlation was found with the number of trees, tree height variability, SSCI, nor canopy openness.

3.3 Comparing AGB

3.3.1 Regional AGB comparison

Addressing research question 3, we compared our AGB estimations of isolated forest patches with published AGB data from forests in the same region. Our AGB estimations are mostly lower than comparable forest sites in the same regions (Table 2).

[Insert Table 2 here]

3.3.2 Comparing AGB from manual inventory and TLS

To address research question 4, we compared manual tree inventory and TLS-data from 43 subplots (25 x 25 m). There were several significant, moderate correlations between forest characteristics estimated by manual inventory and TLS, such as the number of detected trees, tree height, and AGB (Table 1). Manual inventory detected more trees and estimated DBH and AGB higher and tree heights lower than TLS.

[Insert Table 3 here]

AGB as estimated by manual inventory and TLS correlated moderately (*$r=0.4$, $p<0.01$,* Table 1*)*. Manual inventory estimated AGB higher than TLS in 30 of 43 plots (Fig. 5). Differences between AGB_m and AGB_{TLS} ranged from -93% to + 136%. According to an ANOVA, the discrepancies between AGB_m and AGB_{TLS} as well as the amount of noise in TLS point clouds were evenly distributed across the forests.

[Insert Fig. 5 here]

4. Discussion

4.1 AGB and carbon in seven studied forest patches

We confirm the hypothesis that amounts and spatial patterns of AGB and carbon vary across and within the forest patches, indicating environmental and disturbance gradients. AGB in the sampled forests was higher in the biome of moist broadleaf forest compared to the ones in the savanna, grasslands, and shrublands (see Fig. 1). This coincides with global gradients of precipitation and water availability, which is, besides soil fertility, elevation, and disturbances, a main driver of

AGB (Chave et al. 2019), generally leading to higher AGB toward the equator (Lewis et al. 2013). Soil water saturation in swamp forests (Hlanzoun, Ikot) appeared to act as a chronic stressor, limiting aboveground biomass and tree species richness (see also Koponen et al. 2004; Rodríguez-González et al. 2010).

4.1.1 Spatial patterns of AGB within forests

We used AGB_m for plot-to-forest extrapolation, since manual inventory covered bigger areas than TLS (see 2.1) and detected more trees than TLS (see 3.3.2). We can confirm the hypothesis that AGB varies across the different forest patches, indicating disturbance gradients. In fact, extrapolation of our plot-based measurements revealed edge effects in AGB. This is in line with literature (Chaplin-Kramer et al. 2015; Laurance et al. 1997; Mo et al. 2023; Ordway & Asner, 2020) and particularly expressed in isolated forest patches such as Koui, Ewè-Adakplamè, Hlanzoun, and Ikot with few trees in 1 km surrounding (connectivity < 30%, Hepner et al. 2025). Reasons can be the altered microclimate with more and stronger winds, higher temperatures, and more risk of desiccation, which leads to altered species composition and forest structure close to edges (Chaplin-Kramer et al. 2015; Laurance et al. 1997). High prevalence of anthropogenic fires also add to lower AGB close to edges (Chaplin-Kramer et al. 2015) which is the case in Koui, Ewè-Adakplamè, and Iko (Chuvieco et al. 2018). These effects can affect tree architecture, which additionally decreases AGB close to forest edges (Nunes et al. 2023).

Edge effects in tree diameter, tree height, and wood density were not visible in Ewè-Adakplamè and Ngam-Kondomeyos. Ewè-Adakplamè is likely to be too fragmented to show clear edge gradients, while Ngam-Kondomeyos has a high connectivity (=90%, Hepner et al. 2025), and surrounding trees can buffer edge effects. In four of seven forests, wood density was lower in trees close to edges. Edges promote fast-growing, light-demanding pioneers which invest less resources in wood robustness and density and are therefore lighter-wooded (Ghazoul and Sheil 2010; Nunes et al. 2023). Tree species, exposed to a new edge, can also adapt wood structure and density to reduce desiccation risk (Silva Da Costa et al. 2020). In the swamp forest of Hlanzoun, growth rate in the forest interior is likely to be limited by chronic soil water saturation from the Hlan-river (Rodríguez-González et al. 2010), leading to higher wood densities. Generally, flooding constrains tree growth and survival of most species strongly. However, comparable data from Western African floodplains are lacking (Yamanoshita et al. 2001; Koponen et al. 2004; Parolin and Wittmann 2010; Smith et al. 2022).

4.2 Ecological determinants of aboveground biomass

We can confirm the hypothesized correlation between AGB and basal area, and AGB and tree height. However, despite wood density being a fundamental factor for AGB, our data show no such correlation. Wood density and tree volume are largely uncorrelated, and control AGB independently (Phillips et al. 2019). Therefore, high wood density can compensate low wood volume and vice versa to a certain degree. High wood density is associated with slow-growing, shade-tolerant trees which invest more resources in structurally robust stems (Ghazoul and Sheil 2010). Indeed, our data show higher wood density in shorter trees. However, no such correlation was found, neither with the number of trees in a plot, SSCI, nor canopy openness. Wood density depends on several small-scale factors such as tree genetics and edaphic conditions (Phillips et al. 2019). It is important to note that carbon concentration is negatively related to wood density and varies between tree species (Martin et al. 2018; Mo et al. 2024). Wood densities and corresponding carbon concentrations of African trees are yet to be studied in more detail.

In our 0.25 ha plots, AGB did not correlate with tree species richness. This is consistent with other studies in similar plot sizes and environments (Ali et al. 2016; ForestPlots.net et al. 2021; Cuni-Sanchez et al. 2021). However, Sullivan et al. (2017) and Dyola et al. (2022) found such correlation in smaller plots of 0.04 ha. While niche complementarity theory suggests that higher species richness enhances biomass through resource use efficiency accumulations (Ali et al. 2019a), factors like past disturbances (Mitchard, 2018) and current climate stressors may obscure the relationship between AGB and tree species richness (Yang et al. 2024).

The relationship between AGB and forest structure is not entirely clear. This study found correlations between AGB and the number of trees, tree heights, and height variability, but not with stand structural complexity as defined by Ehbrecht et al. (2017). While it seems intuitive that more tree stems would correlate with higher AGB, this is not necessarily the case (Lewis et al. 2013) as few large trees can offset the AGB of many small ones (Ali et al. 2019b). Lang et al. (2023) confirmed a correlation between AGB and tree height. Structurally complex forests are known to capture light more efficiently, pack canopy denser, and store more carbon (Coverdale and Davies 2023). Ali et al. (2019b) identify stand structural complexity, based on DBH and tree height variance, as a key biotic factor influencing AGB, with tree species richness contributing to AGB through greater size variability and complexity. However, Ehbrecht et al. (2021) found no correlation between SSCI and basal area, a proxy for AGB, highlighting that the bidirectional relationship between forest structural complexity and AGB requires further research (Coverdale and Davies 2023).

4.3 Comparing AGB

4.3.1 Regional AGB comparison

Confirming our hypothesis, AGB is higher in formally protected and often larger forests as compared to the formally unprotected small forest patches, which are exposed to various edge effects. The discrepancy in the Hlanzoun forest is considerable. In fact the numbers, published by Biah et al. (2024) are two to four times higher than ours. This might be because they include trees using the DBH threshold of >5 cm, while we use >10 cm. However, Atsri et al. (2020) show that the choice of minimum diameter size (≥5 cm or ≥10 cm) does not significantly affect AGB estimates in Togolese forests. In fact, the biggest 1% of trees are more important than the 99% remaining smaller tress in driving tropical AGB (Ali et al. 2019b) and small trees contribute only little to biomass, especially in high AGB forests, such as tropical ones (i.e., 10% biomass contribution by trees with DBH <10 cm in a forest with AGB >175 Mg/ha, Duncanson et al. 2021; Schroeder et al. 1997). Biah et al. (2024) identified eight dominant species, while we differentiate between 30 species in the Hlanzoun swamp forest. Also, Biah et al. (2024) use a generic factor to expand stem biomass to aboveground biomass (Intergovernmental Panel on Climate Change (IPCC) 2006), with the background that swamp vegetation has its very own architecture due to chronic water logging (e.g., more stems per tree (Rodríguez-González et al. 2010) and fewer large diameter stems (Lewis et al. 2013)). Further, while we use a spatial resolution of 50 x 50 m, Biah et al. (2024) simplify the forest structure by assuming homogenous AGB on areas >550 ha. Our study can rely on two, correlating methods to estimate aboveground biomass, with TLS as a traceable method. Our AGB-numbers compare well to the numbers by Lewis et al. (2013), where they compare 260 forests across tropical Africa and report lower AGB in swamp forests as compared to *terra firme* ones. The discrepancies show that published AGB numbers are still diverging and highlight the need for more research on AGB measurement methodologies.

The AGB-map by Harris et al. (2021) generally showed good correlation with our estimations. However, in swamp forests (Hlanzoun, Ikot) and forests surrounded by agroforestry (Mbangassina, Ngam-Kondomeyos) differences ranged between -89 and +147 Mg/ha (Fig. 6). Forests are dynamic systems with AGB varying interannually and over the years (Chave et al. 2019; Harris et al. 2021).

Our study focuses on small and formally unprotected forest fragments. It is likely that edge effects, low landscape connectivity, and anthropogenic disturbances constrain the accumulation of higher AGB stocks (Laurance et al. 1997). In degraded forests, such as Ewè-Adakplamè and Ikot (Houngnon et al. 2021; Hepner et al. 2025), where logging is prevalent, AGB is below its potential.

[Insert Fig. 6 here]

4.3.2 Comparing AGB from manual inventory and TLS

We can confirm that the AGB obtained by manual inventory correlates with AGB from TLS. However, manual inventory showed practical advantages over the TLS campaign, e.g., manual inventory allowed us to census forest faster (12 person-days/ha) compared to TLS (16 person days/ha) and manual inventory succeeded in all plots, while registration and segmentation of our TLS-data were only successful in 60% of the scanned plots. Tropical forests with dense and complex structures are still hard to scan and to segment automatically (Martin-Ducup et al. 2021) and objective methods to evaluate point cloud quality and accuracy for tree volume reconstruction is yet to be developed (Momo et al. 2018; Demol et al. 2022). In some cases, leaves, lianas, and epiphytes covered the stem making it impossible to be detected correctly by TLS and only clearing could increase point cloud quality (Burt et al. 2018). However, our data showed no evidence that AGB_m and AGB_{TLS} are more similar in open and structurally simple forests, or in the case of taller trees. Estimating AGB becomes more difficult for manual inventories and TLS when forests are denser, and trees are taller and uncertainty of AGB estimations increase with higher AGB (Fig. A1). While Demol et al. (2022) observe better performance of TLS in tall trees, Momo Takoudjou et al. (2018) warn about increased occlusion due to complex shapes and crown overlaps in large trees. Due to poor tree isolation in FSCT, no allometric equations were developed from TLS-data (Fig. A2b). Efforts to identify tree species from point clouds are underway (Åkerblom et al. 2017; Puliti et al. 2025), but not yet reliably working, in particular in tropical forests. Currently, TLS does not replace manual inventory since species identification is required to attribute corresponding wood density, which can vary considerably.

Based on the number of trees detected, we chose the manual inventory as the reference data for AGB-calculation via allometric equations. Due to a lack of species-specific allometric equations from this region (GlobAllomeTree 2024), and because region-specific allometric equations (Feldpausch et al. 2012) performed worse than the pantropical equation by Chave et al. (2014), we opted for the latter. Choosing one allometric equation simplifies reality by neglecting tree morphological plasticity (Calders et al. 2022) and induces uncertainty by limited calibration data and questionable representativity (Demol et al. 2022). It is suggested that allometric equations perform particularly weak in dense, complex forests (Gonzalez de Tanago et al. 2018) and in large trees (Burt et al. 2018; Calders et al. 2022; Disney et al. 2018). Our data showed no correlations between tree form (DBH, height) and number of trees per plot, SSCI, and tree species richness. Still, tree allometry is likely to depend on forest stand structure and environmental conditions, which is not captured by a single allometric equation (Loubota Panzou et al. 2021; Sullivan et al. 2017).

Felling and weighting trees is the only accurate method to measure AGB directly (Clark and Kellner 2012; Chen et al. 2015). However, this destructive approach is not an option in partly sacred and vulnerable small forest patches. Therefore, using more than one method to estimate biomass is adequate and balances discrepancies, strengths and weakness of each method, which are often uncritically seen as “ground truth” (Réjou-Méchain et al. 2019). Overcoming the known limitations of allometric equations (Calders et al. 2022; Réjou-Méchain et al. 2019) could be solved by new powerful (mobile) laser scanners that scan faster and therefore allow more scanning positions and reduce occlusion. New algorithms (e.g., Xiang et al. (2024; Wielgosz et al. (2024)), which are trained on manual segmentations of these forests, could also help to overcome the bottleneck of correctly and automatically segmenting trees (Calders et al. 2022) and become less dependent on allometric equations when estimating AGB.

4.4 Broader implications

This study contributes exact estimates of AGB and carbon on a tree-scale with manual inventory and TLS. In view of climate change and fast forest fragmentation (Fischer et al. 2021), data from understudied regions with landscapes vulnerable to land cover change are urgent. In fact, accurate data of tree species richness and AGB are requested by several globally relevant organizations (e.g., Convention on Biological Diverstity (CBD), 2021; Group on Earth Observations Biodiversity Observation Network (GEO BON) & bioDISCOVERY, 2022; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2022; International Union for Conservation of Nature (IUCN), 2022; United Nations, 2015; United Nations, Climate

Change, 2024) to address planetary crises of climate change, land degradation, and biodiversity loss. Combining more than one method to estimate AGB is advisable since each method has its strengths and weaknesses.

4.5 Limitations

Our data are one-time estimations of AGB, based on assumptions such as the validity of a single pantropical allometric equation. Quantifying accuracy and precision of data requires direct measurements (felling and weighting trees) and replication (Clark and Kellner 2012), which was not an option in the seven forest patches, some of which are sacred and protected due to their spiritual and cultural significance. Further, our results rely on wood densities and wood carbon concentrations, which are only poorly quantified for the Western African region. Moreover, we used tree-based data of AGB, summed up in plots, located by GPS, to be extrapolated with satellite-obtained pixel-wise canopy height data. Uncertainty can be introduced by trees on the plot edge (e.g. trunk is inside plot, but crown is outside) and inaccurate GPS-signal (usually ±3 m) and being propagated (Réjou-Méchain et al. 2019). Considering more error sources complicates definite AGB quantification (Chen et al. 2015), however some potential errors (i.e., allometric equations) can also be flattened out over the vast amount of sampled trees and plots (Réjou-Méchain et al. 2019).

The strong correlation between plot AGB and canopy height by Lang et al. (2023) enabled us to extrapolate AGB values across entire forests. However, potential errors may arise because the canopy height data is from 2020, while our AGB measurements were conducted two to three years later. The canopy height data show a typical standard deviation of nine meters, which is consistent across sites but slightly higher in Hlanzoun and Mbangassina compared to Ikot. Once available, airborne LiDAR and local canopy models are likely to be more accurate than the canopy height by Lang et al. (2023) (Schwartz et al. 2023).

Soil fertility can drive AGB (Ghazoul and Sheil 2010; Ali et al. 2019a, b), however, soil data on a 50 m spatial resolution were not available. In a study in a fragmented landscape of Western Africa, soil characteristics was next to landscape connectivity in explaining AGB (Traoré et al. 2024). Information about current and previous forest management could also explain the measured AGB (Lewis et al. 2015; Lindsell & Klop, 2013), which however is yet to be evaluated.

4.6 Outlook

Further research needs to focus on i) extensively sampling wood density and carbon concentration of tropical tree species (Réjou-Méchain et al. 2019), ii) developing powerful laser scanners that reduce point cloud occlusion in complex forests (see also Abegg et al. 2017), iii) fusing point cloud data of terrestrial and aerial laser scanners to reduce occlusion in tree crowns (see Zhou et al. 2023), iv) developing more accurate segmentation and tree isolation algorithms to overcome dependence on static allometric equations and to create more representative and dynamic allometric equations (Calders et al. 2022), and v) expand pool wise carbon estimations to whole carbon and elements cycles including belowground, soil, atmospheric, fungal, microbial, herbal and faunal pools (see Ashton et al. 2012). Further field studies, such as ours, will be crucial for calibration and validation of satellite data, which are becoming increasingly important and more accurate in estimating forest AGB (Calders et al. 2022a; European Space Agency 2025).

5. Conclusion

Forest patches, when undisturbed, serve as important carbon reservoirs and hotspots of tree species diversity. Our results show that wood density and aboveground biomass (AGB) increase toward forest interiors, although they are not directly correlated. These edge effects are particularly pronounced in isolated forest patches, highlighting the need for ecological connectivity through buffer zones, forest corridors, and agroforestry systems around small patches to support sustainable management. Formal protection of forest patches further enhances their potential to store AGB.

At the global scale, carbon maps remain uncertain, especially for swamp forests and forests embedded in agroforestry landscapes. To address this gap, this study evaluates the performance of manual forest inventory and terrestrial laser scanning (TLS) for estimating AGB in tropical forest patches. We find that manual inventory is more effective in detecting trees than TLS in tropical complex forests. By providing plot-level data from the understudied Western African region, our work supports both climate and ecological modeling efforts.

6. Appendix

6.1 Tables

Table A1 Characteristics of the seven forests patches studied in Togo, Benin, Nigeria, and Cameroon. The column headers without sources indicate own measurements and field observations. This table partly overlaps with the one presented in {Hepner et al. 2025}

Nr.	Country	Forest name	Plots abbreviation	Coordinates (WGS 84, Latitude / Longitude)	Measured forest area (ha)	Number of plots	Vegetation type	Soil (International Union of Soil Sciences (IUSS) Working Group World Reference Base for Soil Resources (WRB) 2015)	Surrounding landcover
1	Togo	Koui	Kou	0° 43' 12" / 8° 15' 36"	18	6	Moist semi-deciduous forest	Acrisol	Settlement / Agriculture / Savanna

2	Benin	Ewè-Adakplamè	Ada	2° 34' 12" / 7° 28' 12"	218	20	Moist semi-deciduous forest	Acrisol / Lixisol	Settlement / Agriculture / Savanna
3		Hlanzoun (also known as Lokoli)	Lok	2° 15' 36" / 7° 3' 36"	676	20	Swamp forest	Acrisol / Gleysol / Lixisol	Settlements / Agriculture / Wetlands
4	Nigeria	Iko	Iko & Owa	8° 15' 0" / 5° 35' 24"	1163	18	Moist forest	Acrisol	Agriculture / Agroforestry
5		Ikot	Eke	7° 53' 24" / 4° 39' 36"	1116	12	Swamp forest	Acrisol / Cambisol / Fluvisol	Settlement / Agriculture / Water
6	Cameroon	Mbangassina	Mbi	11° 35' 24" / 4° 38' 24"	145	12	Moist forest	Ferralsol	Agriculture / Agroforestry
7		Ngam-Kondomeyos	San	11° 49' 48" / 3° 2' 24"	399	21	Moist forest	Ferralsol	Wetlands / Agroforestry

Due to practical circumstances during fieldwork, we also included the two forests of Iko and Ikot in Nigeria, which are slightly larger than the threshold of 1000 ha we set for small forest patches.

6.2 Figures

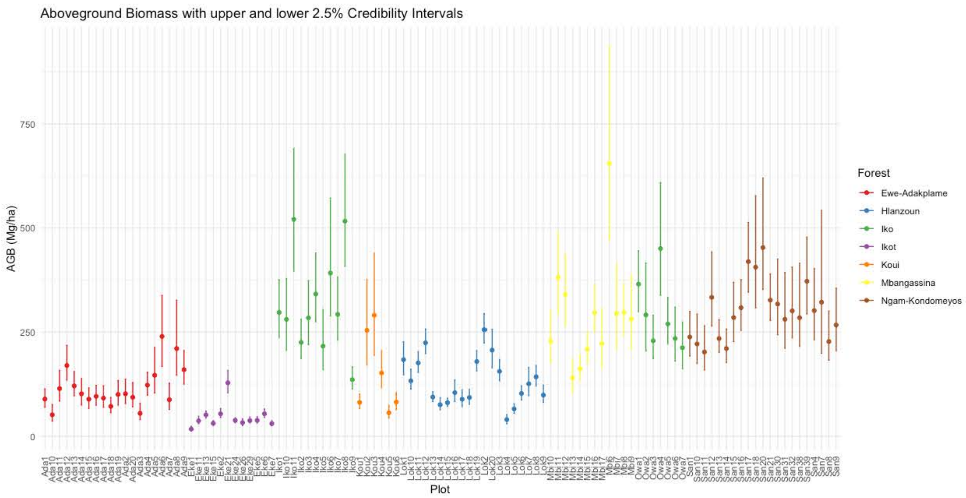

Fig. A1 *The higher AGB (i.e. in the moist forests of the Guineo-Congolian zone, in Iko (green), Mbangassina (yellow), Ngam-Kondomeyos (brown)), the higher is uncertainty of its estimation as quantified by the Monte-Carlo method*

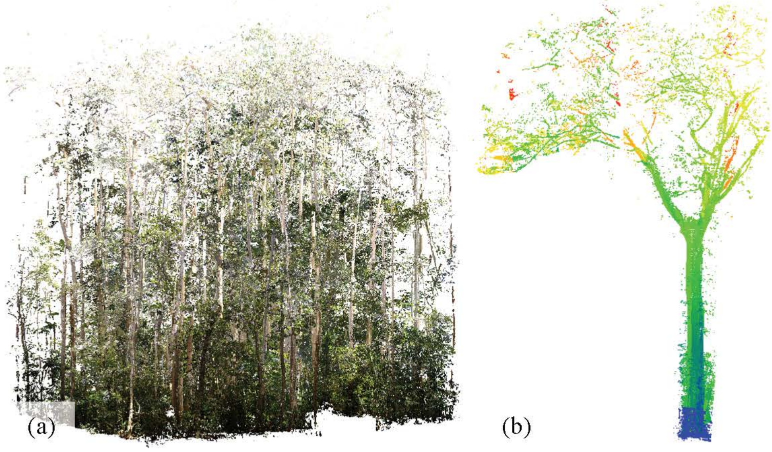

Fig. A2 *(a) Plot point clouds (25 x 25 m) were segmented in ground, leaves, and stem points by FSCT (Krisanski et al. 2021). (b) Tree isolation from plot point cloud is imperfect, shown by different tree IDs respectively colors assigned to one single tree. Tree isolation is particularly challenging in overlapping crowns*

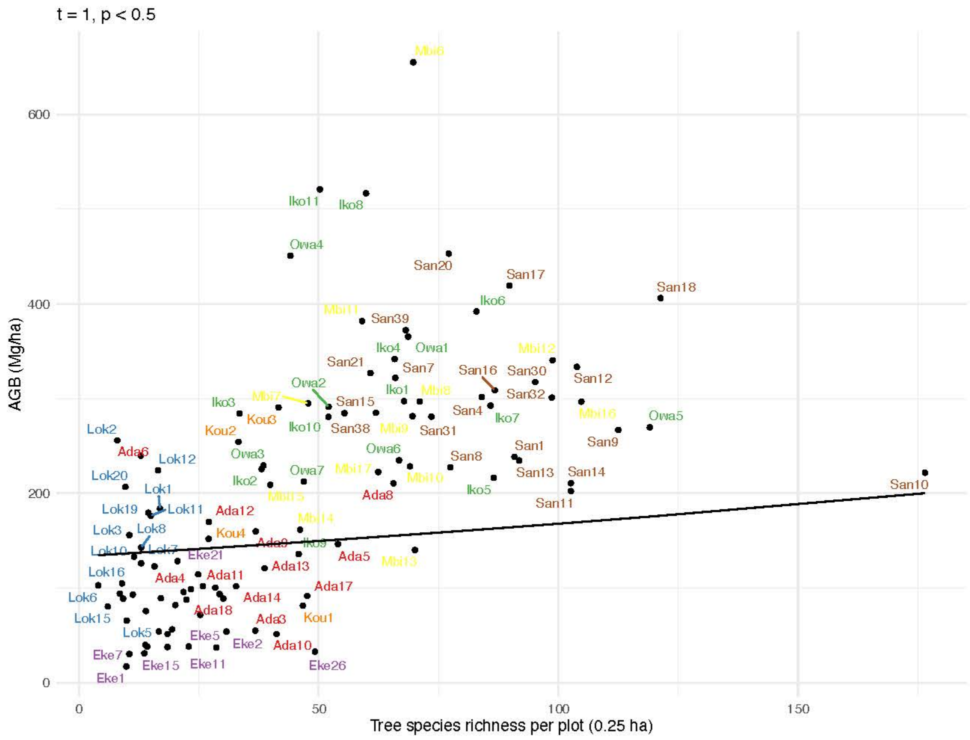

***Fig. A3** Linear mixed-effects model of tree species richness and AGB (Mg/ha) per plot (0.25 ha). Swamp forests have lower tree species richness and AGB, and both increases toward the equator. When controlling for the forests, there is no significant relationship between AGB and tree species richness*

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Tables

Table 1 Forests vary in area, AGB per ha, carbon content, and total AGB storage. Means are accompanied by standard deviations in brackets. AGB per hectare depends on forest type (lower in swamp forests i.e. Ikot), forest integrity (lower in degraded forests i.e. Ewè-Adakplamè) and increases toward the equator. Mean AGB in the plots was often higher than mean AGB in the whole forest since we did not sample forest gaps with tree cover <10%

Forest	Area (ha)	Mean AGB per plot (Mg/ha)	Mean AGB per forest (Mg/ha)	Mean carbon per forest (Mg/ha)	Total AGB per forest (Mg)
Koui	18	153 (±98)	116 (±42)	53 (±19)	1969 (±224)
Ewè-Adakplamè	218	116 (±48)	104 (±17)	44 (±8)	22,818 (±321)
Hlanzoun	676	131 (±58)	108 (±31)	52 (±14)	73,006 (±1011)
Iko	1163	309 (±106)	188 (±41)	86 (±19)	218,849 (±1835)
Ikot	1116	46 (±28)	85 (±23)	39 (±10)	94,392 (±962)
Mbangassina	145	293 (±134)	259 (±43)	118 (±20)	37,492 (±663)
Ngam-Kondomeyos	399	301 (±69)	207 (±28)	94 (±13)	83,051 (±713)

Table 2 AGB as estimated in this study by manual inventory is usually lower than comparable studies from nearby forests

Forest patch	AGB_m this study (Mg/ha)	AGB comparison value (Mg/ha)	Description of comparison forest	Forest size (ha)	Reference
Koui	116	209	Closed canopy forest Fazao Malfakassa National Park, 13 km distance	192,000	(Atsri et al. 2020)
		129	Dense forest in same ecological zone	604,000	(Dangbo et al. 2020)
		104	Sabi sacred forest, 100 km distance	240	(Lynch et al. 2018)
		131	Kala sacred forest, 100 km distance	500	(Lynch et al. 2018)
Ewè-Adakplamè	104	829	Lama forest reserve, 75 km distance	4780	(Biah et al. 2024)
Hlanzoun	108	488	Intact parts of same Hlanzoun forest (also known as Lokoli swamp forest)		(Biah et al. 2024)
		199	Disturbed parts of same Hlanzoun forest (also		(Biah et al. 2024)

			known as Lokoli swamp forest)		
Iko	188	223	Intact forests with little or no human disturbances in Cross River State	729,000	(Amuyou et al. 2022)
		107	Disturbed forests with signs of logging, fire, agriculture in Cross River State	729,000	(Amuyou et al. 2022)
Mbangassina	259	421	Belabo Sub-Divion, Lom & Djeren forest management unit, 200 km distance	4,590	(Chimi et al. 2018)
Ngam-Kondomeyos	207	401	Dja Biosphere Reserve, 100 km distance	526,000	(Djuikouo et al. 2010)

Table 3 Mean and standard deviations of key parameters compared between manual forest inventory and TLS per subplot. Correlations are mostly moderate. The p-values are expressed with asterisks (: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$)*

Mean (and standard deviation) in subplots	Manual forest inventory (n trees = 1,109)	TLS (n trees = 897)	Spearman correlation
Number of trees	26 (±10)	21 (±13)	0.4 **
DBH (cm)	26 (±6)	20 (±5)	0.4 *

Max DBH (cm)	72 (±30)	44 (±23)	0.1
Tree height (m)	16 (±1)	19 (±7)	0.5 ***
Max tree height (m)	25 (±4)	29 (±11)	0.7 ***
AGB (Mg)	15 (±11)	9 (±5)	0.4 *

Caption of figures

Fig. 1 *Seven forest patches were selected in the Tropical & Subtropical Grasslands, Savannas & Shrublands (light green) and the Tropical & Subtropical Moist Broadleaf Forests (dark green) of Togo, Benin, Nigeria, and Cameroon, in Western Africa. 1. Koui, 2. Ewè-Adakplamè, 3. Hlanzoun, 4. Iko, 5. Ikot, 6. Mbangassina, 7. Ngam-Kondomeyos*

Fig. 2 *Scan sampling strategy in plots of 50 x 50m with subplot of 25 x 25 m. Distances and number of trees not to scale*

Fig. 3 *Workflow showing the initial selection of forest patches, the establishment of plots to collect data, and subsequent data analysis to compare AGB obtained by manual inventory and TLS respectively*

Fig. 4 *Maps of the forest patches showing the spatial distribution of AGB (Mg/ha) and the plots of forest inventory (white). In Koui, AGB was higher in the interior lying in a topographic depression with likely more water availability. In Ewè-Adakplamè, the forest was strongly fragmented, and high AGB persisted only in the former forest interior. In Hlanzoun, AGB increased significantly toward the interior ($r=0.1$, $p<0.001$), where there was more water saturation but less edge effects and accessibility. However, in the southern part of the forest, water saturation suppresses AGB both in the interior and along the edge, where it transitions into a wetland. In Ikot, AGB increased slightly toward the interior ($r=0.2$, $p<0.001$), however, visual inspection suggests that AGB decreased with proximity to the periodically rising Kwa Ibo River in Ikot. In Iko ($r=0.06$, $p<0.05$), Mbangassina, and Ngam-Kondomeyos, AGB was homogenously distributed with some local decreases where humans logged in the past. Background from Google Maps*

Fig. 5 *Comparison of AGB estimation per plot (n=43) by manual inventory with allometric equations (x-axis, AGB_m) and TLS with FSCT (y-axis, AGB_{TLS}). The red line shows where x and y-axis correspond. Plots are colored according to seven forests (Ada = Ewè-Adakplamè, Eke = Ikot, Iko and Owa = Iko, Kou = Koui, Mbi = Mbangassina, Lok = Hlanzoun, San = Ngam-Kondomeyos)*

Fig. 6 *Difference maps between Harris et al. (2021) and this study, showing AGB difference (Mg/ha) in seven Western African forests. Blue color means higher estimations; orange color means lower estimations by Harris et al. (2021) compared to this study.*

White squares show plot location. Differences are low and homogenously distributed in Koui, Ewè-Adakplamè, and Iko. Differences for the whole forest are notable in Hlanzoun, Ikot, Mbangassina, and Ngam-Kondomeyos. Background from Google

Figures

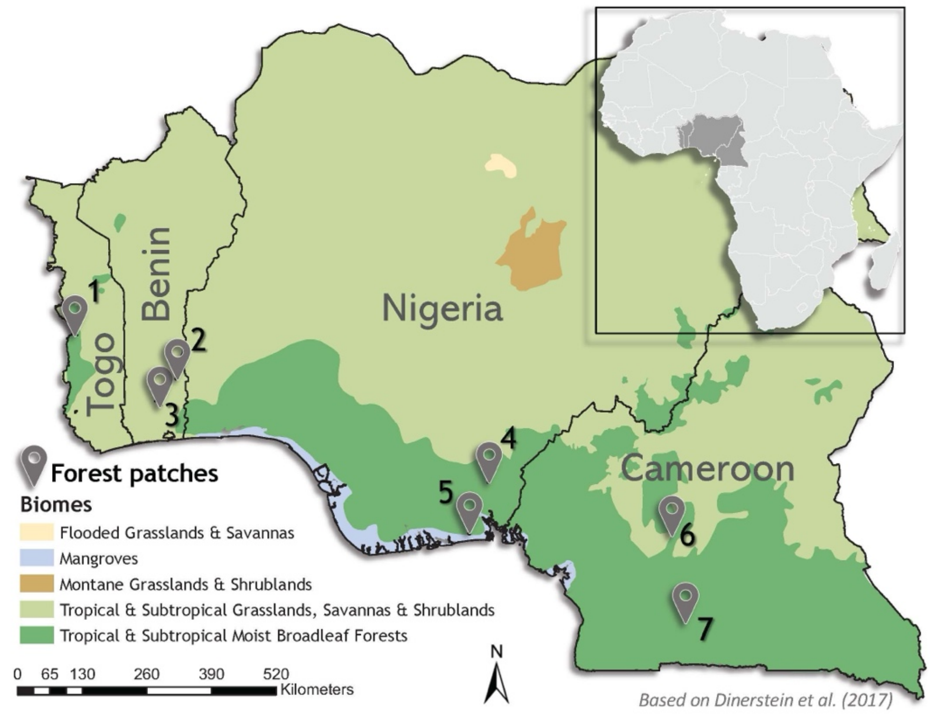

Fig. 1

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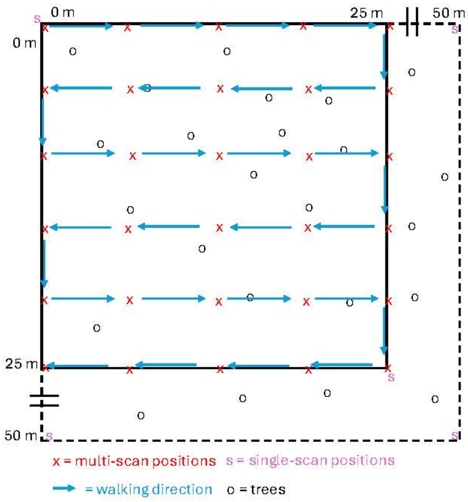
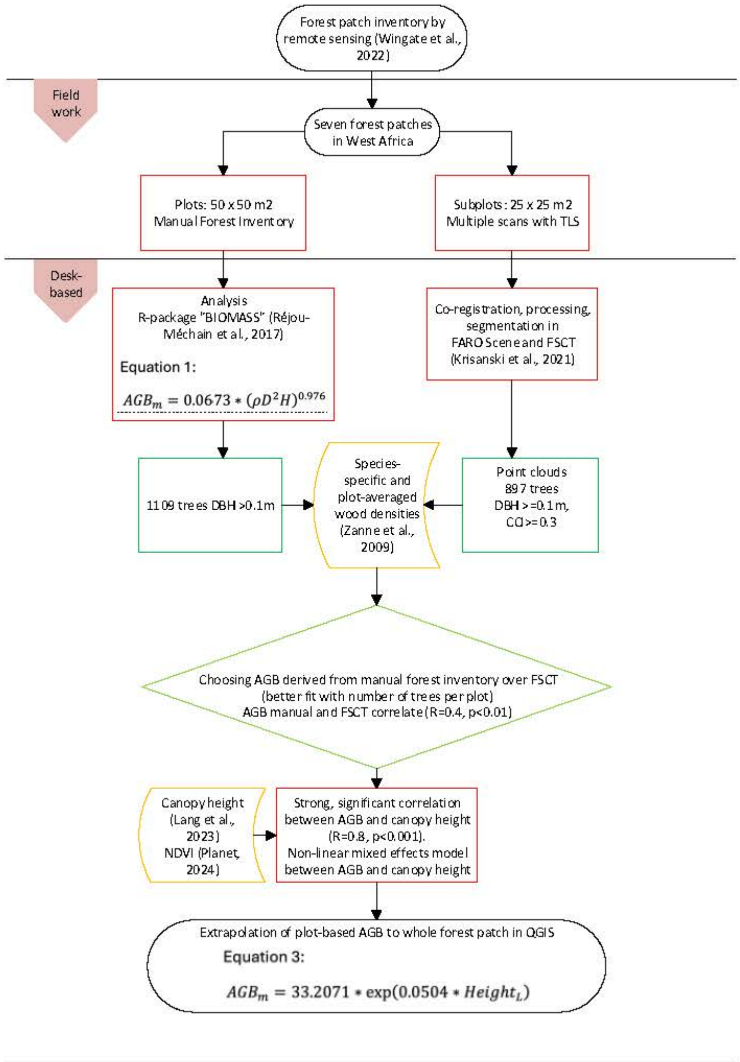


1053

1054 *Fig. 2*

49



Forest patch inventory by remote sensing (Wingate et al., 2022)
Field work
Seven forest patches in West Africa
Plots: 50 x 50 m2
Manual Forest Inventory
Subplots: 25 x 25 m2
Multiple scans with TLS
Desk-based
Analysis
R-package "BIOMASS" (Réjou-Méchain et al., 2017)
Equation 1:
$AGB_m = 0.0673 * (\rho D^2 H)^{0.976}$
Co-registration, processing, segmentation in FARO Scene and FSCT (Krisanski et al., 2021)
1109 trees DBH >0.1m
Species-specific and plot-averaged wood densities (Zanne et al., 2009)
Point clouds
897 trees
DBH >=0.1m,
CCI>=0.3
Choosing AGB derived from manual forest inventory over FSCT
(better fit with number of trees per plot)
AGB manual and FSCT correlate (R=0.4, p<0.01)
Canopy height (Lang et al., 2023)
NDVI (Planet, 2024)
Strong, significant correlation between AGB and canopy height (R=0.8, p<0.001).
Non-linear mixed effects model between AGB and canopy height
Extrapolation of plot-based AGB to whole forest patch in QGIS
Equation 3:
$AGB_m = 33.2071 * \exp(0.0504 * Height_L)$

Fig. 3

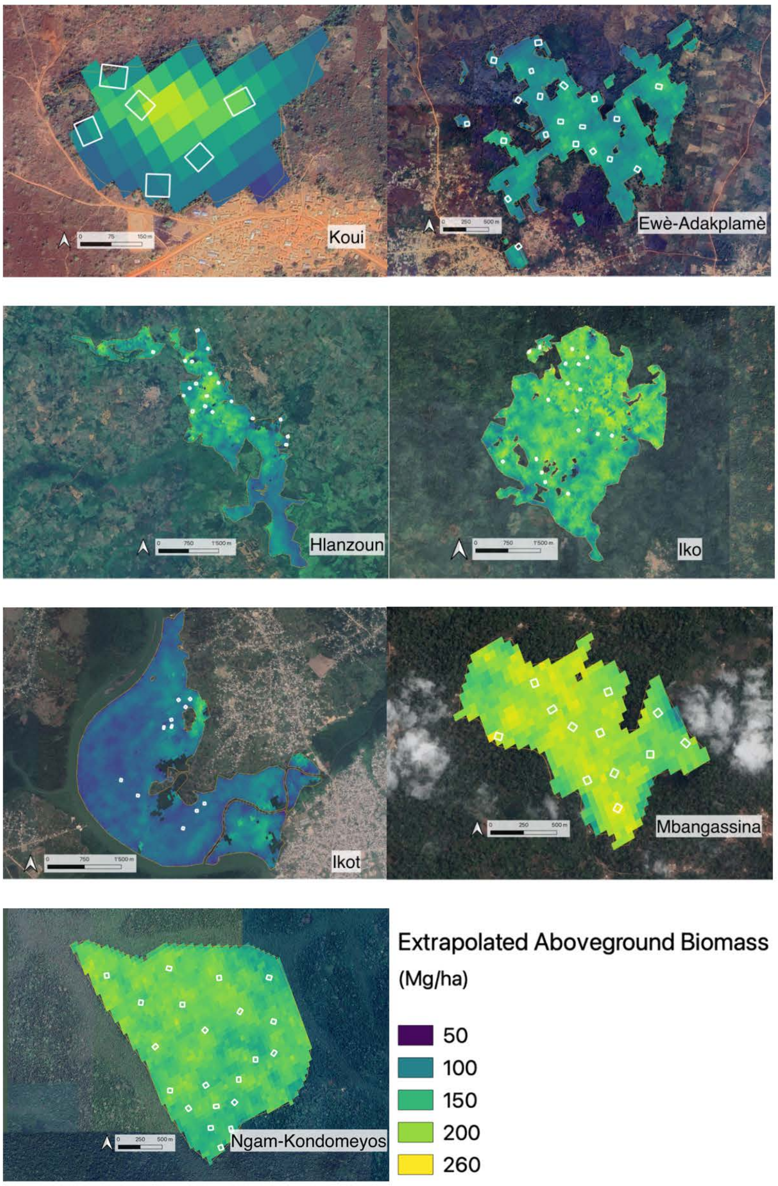

Koui
Ewè-Adakplamè
Hlanzoun
Iko
Ikot
Mbangassina
Ngam-Kondomeyos
Extrapolated Aboveground Biomass
(Mg/ha)
50
100
150
200
260

Fig. 4

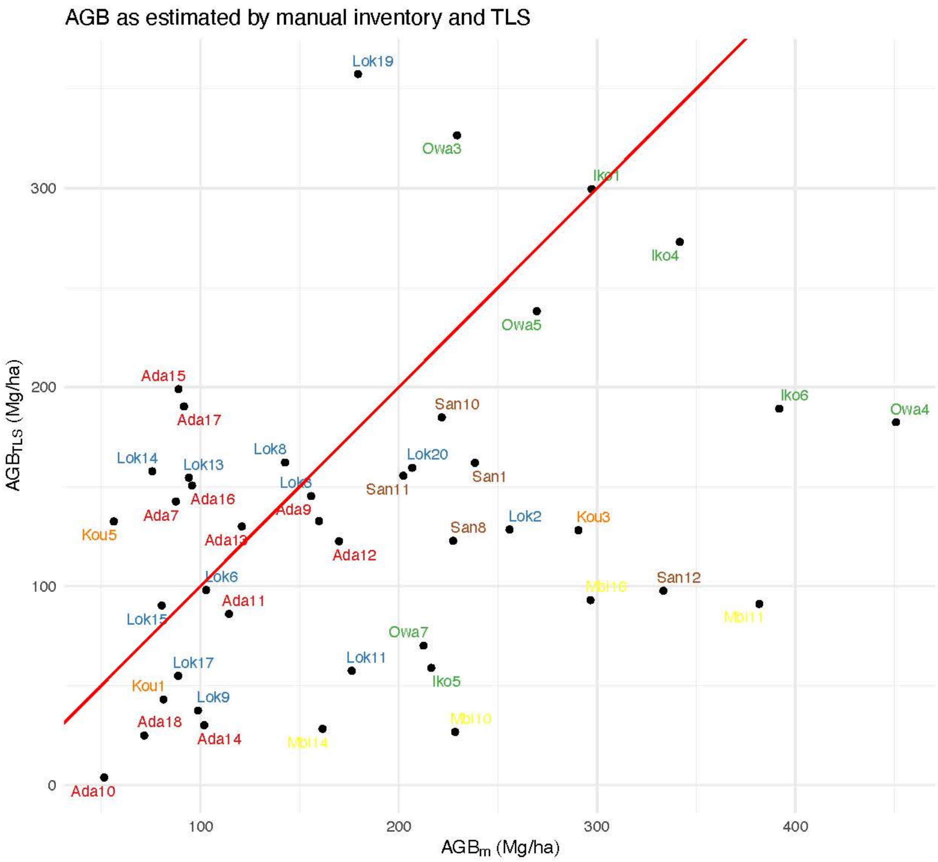

AGB as estimated by manual inventory and TLS
AGB_TLS (Mg/ha)
AGB_m (Mg/ha)
0
100
200
300
400
Lok19
Owa3
Iko1
Iko4
Owa5
Ada15
Ada17
Iko6
Owa4
San10
Lok14
Lok13
Lok8
Lok20
San1
Ada16
San11
Ada7
Ada9
Lok2
Kou3
San8
Kou5
Ada13
Ada12
Lok6
San12
Ada11
Lok15
Owa7
Lok17
Lok11
Kou1
Iko5
Lok9
Ada18
Ada14
Ada10

Fig. 5

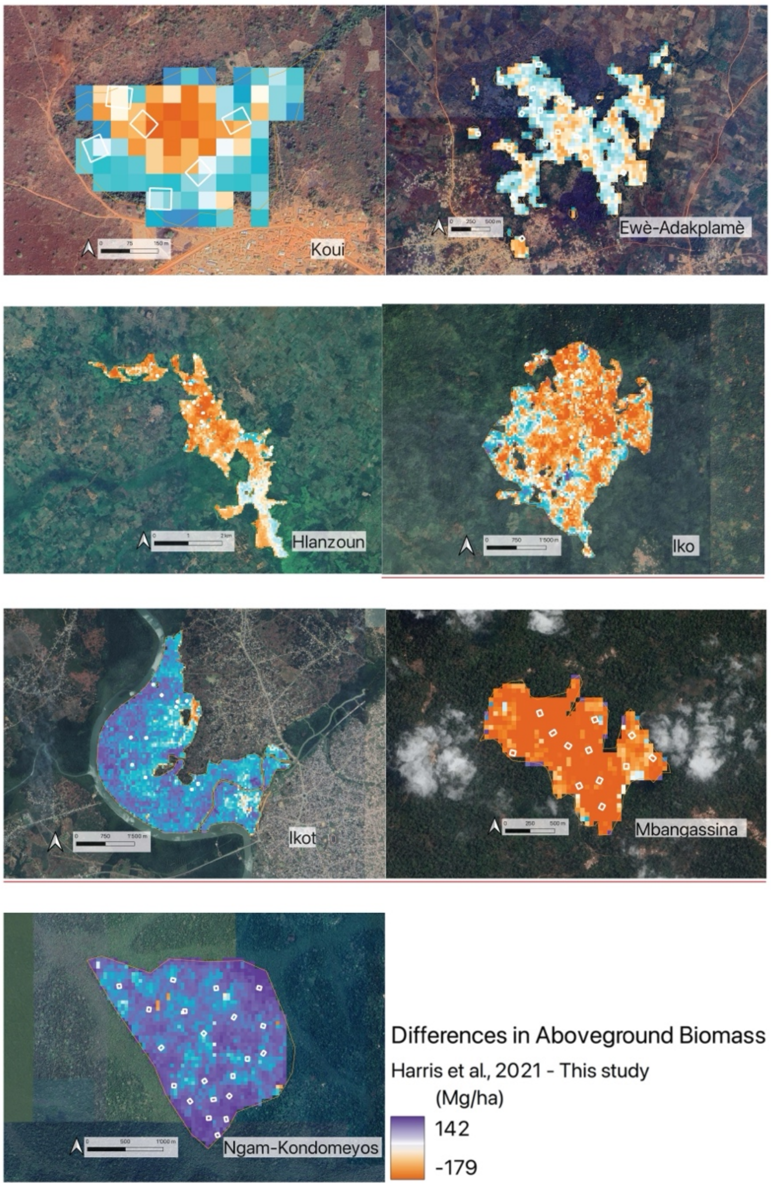

Koui
Ewè-Adakplamè
Hlanzoun
Iko
Ikot
Mbangassina
Ngam-Kondomeyos
Differences in Aboveground Biomass
Harris et al., 2021 - This study
(Mg/ha)
142
-179

Fig. 6

5.3 Co-authored paper 3: Tree species diversity and conservation across disturbance and bioregion types in forest patches outside protected areas in tropical Africa

Authors: Agonvonon, G. A., Hepner, S. Iheaturu, C. J., Azihou, F. A., Sonwa D. J., Bisong F. E., Anwana E. D., Koudouvo K., Sinsin B. A., Fischer M. & Ifejika Speranza, C.

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Tree species diversity and conservation across disturbance and bioregion types in forest patches outside protected areas in tropical Africa

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ABSTRACT

In West and Central Africa, most forest patches lie outside protected areas and are managed by local communities who depend on their ecosystem services. Yet, their role in conserving tree diversity under varying bioregions and disturbance pressures remains poorly documented. We investigated tree community diversity and structure in nine forest patches across the Guineo-Sudanian and Guineo-Congolian bioregions using 121 plots (2500 m^2 each) along edge-interior gradients. We recorded anthropogenic disturbances (wildfire, logging, agriculture, invasive plants, footpaths) and measured the diameter at breast height (DBH) for all trees $\geq$ 10 cm. We identified 382 tree species, of which ~10 % are globally threatened. Despite their small size, the patches contribute 15–33 % of national tree species richness in the four countries studied. Tree density and basal area were consistently lower than reference values from nearby protected forests, ranging from 186 to 422 stems.ha^{-1} and 12.36–23.17 $m^2.ha^{-1}$ in the Guineo-Sudanian, and 263–476 stems.ha^{-1} and 12.20–34.75 $m^2.ha^{-1}$ in the Guineo-Congolian. Alpha diversity was higher in the Guineo-Congolian than in the Guineo-Sudanian, and beta diversity was generally high among forest patches. Disturbances were concentrated at forest edges and negatively affected tree structure and composition, irrespective of ownership. Our findings show that small, unprotected forest patches make a disproportionate contribution to national and regional tree diversity but remain vulnerable to disturbances. Strengthening customary rights and inclusive governance under "Other Effective area-based Conservation Measures" (OECMs), coupled with locally adapted forest zoning, could enhance both biodiversity conservation and community livelihoods.

1. Introduction

Forests play a critical role as ecosystems, supporting diverse life forms and providing essential services to humanity, including climate regulation, food, and timber (Brandon, 2014; Houghton et al., 2015). However, forest conservation faces significant challenges due to unsustainable land-use practices (Guz and Kulakowski, 2021). In tropical regions, deforestation has led to the fragmentation of once-continuous forests into numerous small forest patches (Taubert et al., 2018). These patches are especially prevalent in forest-agricultural landscapes

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across West and Central Africa (Djagoun et al., 2022; Wingate et al., 2022).

The conservation of forest patches, both small and large, in biodiversity-rich areas like the tropics is widely recognised as crucial for maintaining biodiversity and ecosystem services (Arroyo-Rodríguez et al., 2022). Small forest patches, although often more vulnerable to habitat loss and biodiversity decline due to their size and isolation (Hansen et al., 2020a), can serve as biodiversity hotspots and provide critical ecosystem services, even in fragmented landscapes (Decocq et al., 2016; Wintle et al., 2019). Empirical studies have shown that, when aggregated in size, small patches may even harbour more species than a few large patches (Fahrig, 2020; Riva and Fahrig, 2023). Furthermore, a synthesis on forest biodiversity conservation in human-modified landscapes suggested that optimal landscape scenarios for forest-dwelling species should contain at least 40 % forest cover, with a substantial proportion composed of dispersed small forest patches (Arroyo-Rodríguez et al., 2020), underscoring their key role in biodiversity conservation.

Globally, biodiversity, including forests and trees, remains threatened (Pereira et al., 2020; Rivers et al., 2023). Thus, major targets of the Kunming-Montreal Global Biodiversity Framework include ensuring that by 2030, at least 30 % of degraded terrestrial areas are effectively restored and 30 % of terrestrial areas, especially those critical for biodiversity and ecosystem functions and services, are effectively conserved, sustainably used, and managed (Convention on Biological Diversity, 2022). While there is evidence that conservation areas that combine nature protection, cultural values and sustainable use could offer similar potential to strictly-protected areas for animal conservation (Vimal et al., 2021), little is known about their tree community structure. Moreover, in West and Central Africa, there is still limited evidence on the importance of small forest patches outside protected areas as habitats for diverse tree species.

While there are nearly 73,300 tree species globally (Cazzolla Gatti et al., 2022), consistent patterns of common tree species and tree species abundance distributions are observed across tropical continents, despite their distinct biogeographic, climatic, and anthropogenic histories (Cooper et al., 2024). On the other hand, studies have evidenced high turnover among tropical forests due to environmental factors such as rainfall, topography, and soil nutrients, which influence the spatial distribution of tree species (De Cáceres et al., 2012; Fayolle et al., 2014a, b; Marshall et al., 2021; Ringelberg et al., 2023). In tropical African forests, Sosef et al. (2017) estimated tree species richness to be circa 3000, and these forests exhibit high conspecific negative density dependence, which contributes to maintaining high tree diversity (Kalyuzhny et al., 2023). Despite these insights, a gap remains in understanding how geographically distinct assemblages of tree communities, hereafter bioregion types (Droissart et al., 2018), and forest management types influence the conservation of tree communities across forest patches.

The high demand for certain tree species and the challenges related to sustainable forest management in tropical Africa (Fischer et al., 2020) have led to the overexploitation of native forest resources, particularly timber trees, for local use and local and international trade (Hills et al., 2022; Uzu et al., 2022). In addition, land-use change for agriculture represents a major driver of forest loss in the region, often accompanied by logging and wildfire (Jellason et al., 2021). Consequently, tree community composition and structure are shifting, particularly in the remaining forest patches that are shrinking in size in the landscape. This underscores the need for a deeper understanding of how anthropogenic disturbances affect both tree community-alpha and -beta diversity in such tropical forests.

The responses of biodiversity to forest disturbances have been extensively studied (Bowd et al., 2021). However, these responses vary depending on the taxa examined and the methodologies used (Almeida-Rocha et al., 2020). While several studies have explored the combined effects of various anthropogenic disturbances on tree populations (Zébazé et al., 2023; Wu et al., 2025; Dossou et al., 2025), relatively few have investigated their impacts on tree communities as complex ecosystems, particularly in West and Central African forests. Additionally, how these effects vary across bioregions remains unclear. This research gap is partly due to the challenges of quantifying forest disturbances, which differ in intensity, frequency, and spatial distribution (Orwig et al., 2022).

Understanding the impacts of anthropogenic disturbances on tree communities in tropical forests is challenging, as these disturbances often occur as discrete or localised events. For example, selective logging tends to be sporadic and patchy in tropical forests, which are also affected by other disturbances such as fire and agricultural expansion (Assede et al., 2023). To fully understand how these combined disturbances impact tree communities, it is essential to use methods that can quantify and integrate the effects of multiple disturbance types (DellaSala et al., 2025).

In this study, we address how bioregions and anthropogenic disturbances affect tree community diversity and structure in tropical forest patches outside protected areas in West and Central Africa. Specifically, we aimed to: i) estimate the alpha diversity of tree communities in relation to both disturbances and bioregions; ii) assess beta diversity variation among tree communities in the forest patches in the Guineo-Sudanian and Guineo-Congolian bioregions; and iii) analyse the effects of disturbances and bioregion types on tree stand structure in the forest patches.

It is posited that: i) variation in tree community diversity among forest patches will be influenced by both bioregion and anthropogenic disturbances; ii) tree beta diversity (measured as inverse of Jaccard similarity) will increase with the spatial distance between forest patches; and iii) tree stand parameters (e.g., density and basal area) will be negatively correlated with disturbance gradients, primarily due to selective logging of timber trees (i.e., specific species harvested for their wood, Hills et al., 2022) and forest fires.

2. Methods

2.1. Study area

This study focuses on nine forest patches located outside protected areas across West and Central Africa, in the Guineo-Sudanian and Guineo-Congolian bioregions. These were Agou (Togo), Elavagnon-Todji (Togo), Koui (Togo), Hlanzoun (also known as Lokoli swamp forest; Benin), and Kouvizoun Adakplamè-Ewè, hereafter Kouvizoun (Benin), in the Guineo-Sudanian bioregion; and Iko (Nigeria), Ikot (Nigeria), Mbangassina (Cameroon), and Ngam-Kondomeyos (Cameroon) in the Guineo-Congolian bioregion (Fig. 1a and Table 1). The forest patches were selected from a remote sensing-based inventory of tropical forest patches in West and Central Africa (Wingate et al., 2022). In their dataset, forest patches were defined as areas with more than 30 % tree cover, with trees taller than 5 m. For this study, forest patches with sizes ranging from 0.36 km^2 to circa 10 km^2 were selected based on geographically distinct assemblages of tree communities (bioregion types) in West and Central Africa (Fig. 1a and Table 1). In the bioregions (Guineo-Sudanian and Guineo-Congolian), nine forest patches that are natural vegetation were selected by accounting for the variation in anthropogenic disturbances, mostly related to the forest ownership (forests with private ownership and forests that are managed by community organizations) (Table 1). Local communities manage these forest patches, which are in agricultural landscapes. Agriculture is the main income source of the communities and is characterized by slash-and-burn subsistence crop farming, teak and oil palm plantations in the Guineo-Sudanian bioregion, and primarily cacao, banana and oil palm plantations in the Guineo-Congolian bioregion. There is high population growth (2.6–3 % per year) and a high agricultural expansion (3–7 % per year) in the study area (CILSS, 2016), all accelerating forest fragmentation and associated habitat loss for wildlife. Meanwhile, the

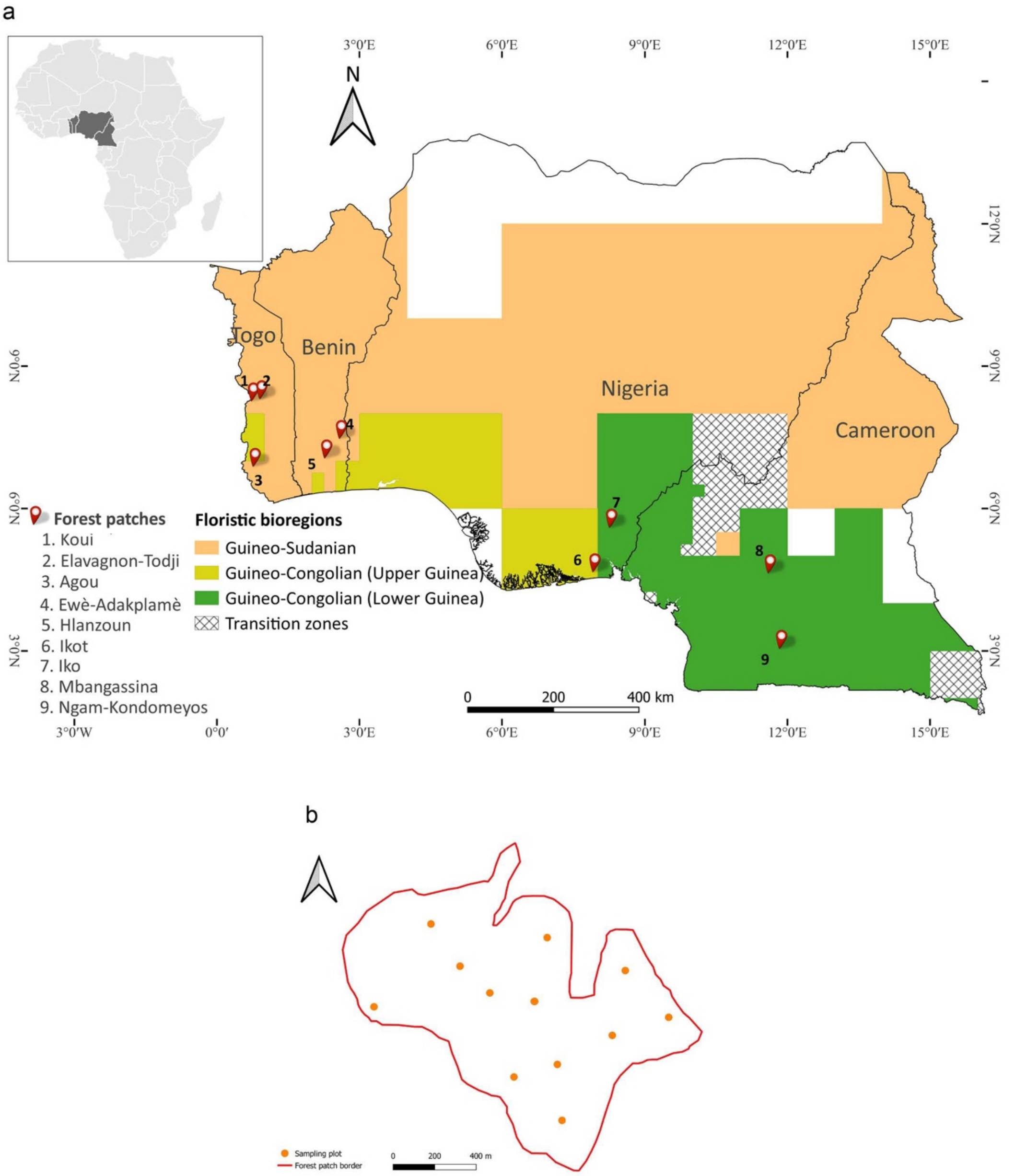

Fig. 1. Study area showing **(a)** the nine study forest patches in the Guineo-Sudanian and Guineo-Congolian (Upper Guinea and Lower Guinea) bioregions of tropical Africa. Floristic bioregions were adapted from biogeographical regionalization of tropical Africa (Droissart et al., 2018). The random-sampling plot design (the sample size varies across forests) is illustrated for the Mbangassina forest patch (127.42 ha) in the Guineo-Congolian region **(b)**. *Map lines delineate study areas and do not necessarily depict accepted national boundaries.*

Table 1
Characteristics of the selected forest patches outside protected areas in tropical Africa. Ownership types were PCS (Private or community sacred) and CNS (Community non-sacred); vegetation types were dense forest, SDDF (semi-deciduous dense forest), Woodland, and YSDF (Young secondary dense forest). Bioregion classification follows the biogeographical regionalization of tropical Africa (Droissart et al., 2018), while the soil classification follows Jones et al. (2013) and Nkwunonwo et al., (2020), and soils were F (Ferralitic), Cs (Clayey in swamp soil), R (Rocky) and FC (Ferralitic with concretion). The mean annual rainfall data (1981–2010) were extracted from Karger et al. (2017).

Country	Forest[a]	Main vegetation type	Ownership	Area (ha)	Bioregion	Plots[b]	Mean distance (m) between plots	Soil	Mean altitude (m)	Mean annual rainfall (mm)
Togo	Koui (1)	Woodland	PCS	35.95	Guineo-Sudanian	6	220.12	FC	666	1653
Togo	Elavagnon-Todji (2)	Woodland	PCS	226.28	Guineo-Sudanian	4	677.32	R	654	1552
Togo	Agou (3)	SDDF	PCS	1100.32	Guineo-Sudanian	7	2108.25	R	595	1402
Benin	Kouvizoun (4)	SDDF	PCS	276.60	Guineo-Sudanian	20	994.30	F	177	1160
Benin	Hlanzoun (5)	SDDF	PCS	701.56	Guineo-Sudanian	20	1399.74	Cs	24	1062
Nigeria	Ikot (6)	YSDF	CNS	715.71	Guineo-Congolian	12	1386.64	Cs	16	2916
Nigeria	Iko (7)	Dense forest	CNS	1082.31	Guineo-Congolian	19	1624.34	FC	196	2444
Cameroon	Mbangassina (8)	YSDF	PCS	127.42	Guineo-Congolian	12	635.12	F	507	1590
Cameroon	Ngam-Kondomeyos (9)	Dense forest	CNS	381.99	Guineo-Congolian	21	1045.05	F	688	1610

[a] value in bracket indicates forest label as in Fig. 1a
[b] plots are squared and 0.25 ha each

forests provide timber, firewood, medicinal plants, and edible fruits to the populations (CILSS, 2016). The climax vegetation across the selected forests consists of semi-deciduous dense forest in the Guineo-Sudanian bioregion and evergreen rainforest in the Guineo-Congolian bioregion (White, 1983; Houngnon et al., 2021). The mean annual rainfall varies between 1000–1600 mm and 1600–2900 mm per bioregion, while the elevation ranges from 24 to 666 m a.s.l. and from 16 to 688 m a.s.l., respectively, across selected forest sites (Table 1). The soils were either ferralitic or rocky in the climax forests, and hydromorphic clayey in the two swamp forests (Hlanzoun in the Guineo-Sudanian and Ikot in the Guineo-Congolian, Table 1).

2.2. *Data collection*

2.2.1. *Sampling design*

In total, 121 plots were established across the nine forest patches (Table 1). Each plot measured 50 m x 50 m, with 4–21 plots per forest, spaced at least 200 m apart. These plots were distributed along an edge-to-interior gradient in the forests (Table 1, Fig. 1b). The initial design of establishing forest-plots according to the forest size was adapted to field circumstances (e.g., treeless areas within forests, rocky outcrops, constrained access due to sacredness, conflict, and security). Thus, the number of plots per forest did not directly scale with forest size due to varying degrees of disturbance and vegetation cover. In several patches, large areas were devoid of trees due to past wildfires or dominated by non-forest vegetation. These treeless areas were excluded from sampling, as our study focused specifically on tree community structure and diversity. Consequently, the number of plots per forest reflects both forest size and the extent of tree-covered habitat (Table 1).

2.2.2. *Tree community data collection*

In each plot, the species name and the diameter at breast height (DBH) of all tree stems with DBH $\geq$ 10 cm were recorded. We collected and identified voucher specimens of non-identified tree species in herbaria located at the University of Abomey-Calavi in Benin, the University of Uyo in Nigeria, and the University of Yaoundé I in Cameroon. For this study, a modified definition of tree by the IUCN's (International Union for Conservation of Nature) Global Tree Specialist Group (GTSG) was adapted, and trees were referred to as woody plants with usually a single stem growing to at least 2 m height and at least 10 cm of DBH, or if multi-stemmed, then at least one vertical stem 10 cm in DBH (Cazzolla Gatti et al., 2022). Tree species taxonomy followed the Angiosperm Phylogeny Group IV (The Angiosperm Phylogeny Group, 2016).

2.2.3. *Disturbance characterization of forest tree communities*

Before conducting a within-forest sampling, various forms of anthropogenic disturbances were recorded in the forest. These include fire outbreaks, tree logging, footpaths, agriculture, and invasive alien plant occurrences. We used these disturbances to establish a disturbance gradient in each forest (Table 2), following the methodology of Mohandass et al. (2017) and DellaSala et al. (2025).

We calculated a disturbance index per plot through the following steps: (i) first, the relative impact of each disturbance type was estimated per plot. For each disturbance type, we considered values across all 121 plots, and calculated the relative impact in a plot as the ratio of the value recorded in that plot to the maximum plot-level value observed among all plots (Table 2); and (ii) second, we computed the disturbance index for each plot by adapting the disturbance impact factor approach (Sagar et al., 2003; Mohandass et al., 2017). This involved summing the relative impacts of all disturbance types recorded in the plot (Table 2). Although the disturbance variables had different units, scaling each to a relative value between 0 and 1 for each disturbance type across plots (Table 2) ensured comparability before summing them.

This disturbance impact factor is a proxy for common anthropogenic disturbances that are assumed to affect the species composition and structure (Niang et al., 2024). The strength of this index lies in its ability to integrate multiple disturbance types, and similar approaches have been utilized in assessing direct human impacts on plant communities (Sagar and Singh, 2006; Mohandass et al., 2017). By assuming an equal impact of each disturbance type on tree communities, we minimized potential bias, as anthropogenic disturbances in tropical forests typically exert severe effects (Assede et al., 2023). Additionally, our focus on tree communities with diameters above 10 cm ensured consistency in the assessment: the temporal effect of disturbance does not influence the output of this study as it affects tree communities in the long term through regeneration processes (Leverkus et al., 2020; Chapagain et al., 2021).

Table 2
Estimation of the disturbance impact factor in the Kouvizoun Adakplamè-Ewè forest patch. Each value in the columns (Footpath, Invasive species, Forest fire, and Agriculture) represents the relative impact of a specific disturbance type in the corresponding plot. The relative impact was calculated as the ratio of the observed value in the plot to the maximum value recorded across all plots (see Section 2.2.3). Footpath was measured as the total length (in m) of human-made paths or trails within each plot. Tree cutting was recorded as the number of cut stumps observed. Invasive species, fire, and agriculture disturbances were recorded as the percentage of the plot area affected. The overall disturbance impact factor is the sum of all relative disturbance impacts recorded in each plot.

Plot	Footpath / Trails	Tree cutting / Lopping	Invasive alien species	Fire	Overall disturbance impact factor
1	0.58	0.03	0	0	0.61
2	0	0.03	0.02	0.05	0.1
3	0	0.11	0.31	0.75	1.17
4	0	0.03	0.01	0.01	0.05
5	0.41	0.03	0.08	0.01	0.53
6	0	0.03	0	0.01	0.04
7	0	0.03	0.46	0	0.49
8	0	0.03	0	0	0.03
9	0	0.14	0	0	0.14
10	0	0.08	0	0	0.08
11	0	0.03	0.38	0	0.41
12	0	0.03	0.02	0.75	0.8
13	0	0.03	0	0.35	0.38
14	0	0.03	0.92	0.6	1.55
15	0.66	0.03	0	0.95	1.64
16	0	0.03	1	1	2.03
17	0	0.03	0.23	0.8	1.06
18	0	0.03	0.23	0.4	0.66
19	0	0.03	0.23	0.1	0.36
20	1	0.14	0	0	1.14

2.3. Analyses

2.3.1. Assessing drivers of anthropogenic disturbances in the forest patches

To investigate the effect of forest patch characteristics on the disturbance occurrence in the forests, a generalized linear mixed-effects model (GLMM) was used by applying the '*lmer*' function from the R package 'lme4' (Bates et al., 2015). The response variable was the quantified anthropogenic disturbance (overall disturbance impact factor) in each plot, while predictors were the distance from the centre of plot to the forest edge, the plot ownership, and the forest site in which the plot was sampled (random effect). For statistical analysis, we excluded the four plots from the Elavagnon-Todji forest (Table 1) due to insufficient replication along the edge-to-interior gradient, caused by limited forest cover. Similarly, the bioregion variable was not included in the model, as its effect was already accounted for by the forest variable.

2.3.2. Forest patches' alpha diversity metrics

The tree taxonomic diversity in the study forests was estimated using Hill numbers (Hill, 1973). Hill diversity was chosen for its ability to measure alpha diversity in ways that are easy to interpret and to facilitate comparisons across sites, even with unbalanced sample sizes (Roswell et al., 2021). Hill diversity is defined as follows:

$$^{q}D = \left(\sum_{i=1}^{s} p_i^{q}\right)^{1/1-q} \quad (1)$$

where D is the Hill diversity, s the number of species, p_i the relative abundance of the species i $(i = 1, 2, \ldots, s)$ in the community. For $q = 0$, ^{0}D refers to the species richness (the count of species equally, regardless of their relative abundance). For $q = 2$, ^{2}D refers to the inverse of the Simpson index and is interpreted as the effective number of dominant species in the community. When $q = 1$, Eq.1 is undefined but its limit as q tends to 1 is the exponential of the Shannon index, referred to as Shannon diversity (Chao et al., 2014):

$$^{1}D = \lim_{q \to 1} {}^{q}D = \exp\left(-\sum_{i=1}^{s} p_i \log p_i\right) \quad (2)$$

In this case ^{1}D counts the species in proportion to their abundances, and is interpreted as the effective number of common species in the community (Hsieh et al., 2016).

To facilitate comparison among tree community data from the nine forest patches, the sample completeness (Chao et al., 2014) was first performed (Fig. A. 1a and b). The coverage, which is a measure of how completely a community has been sampled, was chosen as it has been proven more effective for biodiversity comparisons between sites, rather than the equal sample size method (Roswell et al., 2021). The coverage-based standardization was done using the '*iNEXT*' function from 'iNEXT' R package (Hsieh et al., 2016). The '*estimateD*' function was then used to estimate three diversity metrics, namely: species richness, Shannon diversity and the inverse of Simpson index (Eq.1) at 90 % equal coverage (see Fig. A. 1a and b). These analyses were done by separating the swamp forests (Ikot and Hlanzoun, Fig. 1a) from the non-swamp ones (i.e., climax forests) for comparison purpose, since they have different ecological conditions.

2.3.3. Tree community composition among forest patches

We assessed beta diversity, that is the variation in tree species composition between pairs of forest patches, using the Jaccard similarity index (Chao et al., 2005):

$$J = \frac{A}{A + B + C} \quad (3)$$

where A is the number of species common to both sites, B is the number of species occurring in the first site but not in the second, and C is the number of species occurring in the second site but not in the first.

The Euclidean distance (d) between pairs of forest patches was measured using QGIS version 3.22.7 (QGIS Development Team, 2022). To test the relationship between beta diversity and forest isolation, we applied a Mantel test (Pearson correlation, 9999 permutations) between the Jaccard similarity and Euclidean distance matrices using the 'vegan' package in R (Oksanen et al., 2022).

To assess within-forest change in tree species composition in relation to the disturbance and distance to forest edge, the function '*adonis*' of the 'vegan' R package (Oksanen et al., 2022) was used. The dissimilarity matrices were derived from Bray-Curtis distance measures (Bray and Curtis, 1957). The disturbances were first categorized as high and low, while the variable distance to forest edge was categorized into core and edge. Within-forest tree assemblage in relation to these variables was represented by performing non-metric multidimensional scaling (Kruskal, 1964) on the dissimilarity matrix.

2.3.4. Forest tree communities' structural characterization

The tree diameter distribution in each forest patch was estimated using the Weibull distribution. We chose the Weibull distribution due to its flexibility in fitting various diameter distribution data, particularly from forest patches that undergo various disturbances and ecological conditions (Teimouri et al., 2020).

To assess how forest management, the spatial heterogeneity in the forests, and the bioregion types affected the tree species richness and the structure of tree communities, we applied a linear multiple regression analysis where tree species richness and tree stand structural parameters (i.e., density, basal area, mean and maximum values of DBH, and mean geometric diameter) were dependent variables. The studies by Sagar and Singh (2006), and Korhonen et al. (2023) indicate that these variables are suitable metrics to demonstrate how the anthropogenic disturbances observed in different plots may have influenced the stand structure of the tree communities. The regression's predictors were: the disturbance impact factor (estimated disturbance impact in each plot, Table 2), the edge distance (Euclidean distance from the centre of each plot to the nearest edge of the forest in which the plot was sampled), the protection (ownership status of the plot), and the bioregion from which the plot was sampled (Droissart et al., 2018). We included forest-level covariates such as vegetation type and mean altitude to control for potential site-level confounding factors.

All statistical analyses were conducted in R 4.3.2 (R Core Team, 2023).

3. Results

3.1. Patterns of anthropogenic disturbances among forest patches

Agriculture, footpaths, tree cutting and lopping, wildfire and related invasive alien species proliferation (mainly *Chromolaena odorata* (L.) R. M.King & H.Rob.) were the main common disturbances occurring in the selected forests outside protected areas. The mean disturbance impact varied from 0.003 to 0.95 in community non-sacred forests and from 0.01 to 0.66 in the private or community sacred forests (Table 1). GLMM results indicated that anthropogenic disturbances decreased significantly with increasing distance from the forest edge to the interior ($p < 0.05$), while plot ownership had no significant effect (Table 3). The low marginal R^2 (0.04) suggests that fixed effects alone explained a small portion of the variation in disturbances. In contrast, the higher conditional R^2 (0.48) indicates that a substantial proportion of the variance was explained by the model overall, highlighting the influence of site-level or landscape-level factors represented by the random effect (forest site).

3.2. Tree taxonomic diversity and assemblages across forest patches in the Guineo-Sudanian and Guineo-Congolian bioregions

A total of 382 tree species belonging to 55 families were recorded across the nine forest patches in the Guineo-Sudanian and Guineo-Congolian (Upper Guinea and Lower Guinea) transects (Table 4, Appendix A.1). In the Guineo-Sudanian forests, Fabaceae, Apocynaceae, Malvaceae, Meliaceae, and Moraceae were the most abundant families, whereas Myristicaceae, Moraceae, Annonaceae, Burseraceae, and Dichapetalaceae dominated in the Guineo-Congolian. Dominant tree assemblages included *Pycnanthus angolensis*, *Desbordesia glaucescens*, *Staudtia kamerunensis*, *Piptadeniastrum africanum*, and *Santiria trimera* in Guineo-Congolian sites, and *Ceiba pentandra*, *Albizia glaberrima*, *Alstonia congensis*, *Spondianthus preussii*, *Antiaris toxicaria*, and *Ficus* spp. in Guineo-Sudanian sites (Table 4).

Diversity indices (tree species richness and Shannon diversity) were consistently higher in the Guineo-Congolian than in the Guineo-Sudanian bioregion (Table 4, Fig. 2a and b). Plot-level richness ranged from 14 to 22 tree species in Guineo-Sudanian climax forests and from 36 to 49 tree species in Guineo-Congolian climax forests. Swamp forests showed lower tree species richness (9 and 14 species per 0.25 ha in Hlanzoun and Ikot, respectively).

Table 3
Generalized Linear Mixed Model (GLMM) showing the effects of type of forest patch ownership and distance from the forest edge on the strength of anthropogenic disturbances. Marg. R^2 is the Marginal R^2 and represents the proportion of variance explained by the fixed effects (Ownership and edge distance), and Cond. R^2 is the Conditional R^2, which represents the proportion of variance explained by both fixed and random (forest) effects. The coefficient for the modality (OwnershipCNS) describes how the community- and non-sacred based ownership differ from the private or community-sacred one. By including the random intercepts for forest, forest-level covariates likely to affect the results were controlled by the model.

GLMM Model: Disturbance ~ Protection + Edge distance + (1 | Forest)						
Fixed factors	Marg. R^2	Cond. R^2	Coefficient	Std. Error	t value	p
Intercept	0.04	0.48	0.31	0.17	2.92	< 0.05
OwnershipCNS			−0.15	0.28	−0.67	0.52
Edge distance (m)			−0.0003	0.0001	−1.98	< 0.05

3.3. Effects of disturbances and bioregions on alpha diversity in the forest patches

The linear multiple regression showed that bioregional factors significantly influenced the tree species richness among the forest patches ($p < 0.05$; Table 5), while the effects of disturbances on tree species richness were not significant ($p > 0.05$; Table 5). Further, the variation in altitude and vegetation types explained the tree species richness across plots, with higher values in the rainforest plots than in the other vegetation types ($p < 0.05$; and Adj. $R^2 = 0.88$; Table 5). These environmental effects on the tree species richness align with the observed differences in dominant families and assemblages (Table 4).

3.4. Variation in tree community composition among forest patches

The similarity in tree species composition among forest patches was generally low (Jaccard index < 0.5), and showed no significant relationship with spatial distance between forest patches (Mantel test, r = -0.04, $p < 0.66$). The similarity in tree species composition remained low between the swamp forests and climax forests, irrespective of their spatial isolation (Fig. 3). These compositional differences reflect the contrasting dominant assemblages (Table 4), highlighting strong bioregional signatures in species pools.

For all forest patches, the Adonis tests revealed that there were no significant effects of the disturbance or distance from forest edge (edge effect) on within-forest tree community composition (p-values > 0.05; see appendix, Fig. A.2a and b).

3.5. Effects of disturbance and bioregions on tree community structure

For all forest patches in the Guineo-Sudanian and Guineo-Congolian bioregions, the curve of the probability density function was right-skewed (shape >1, see appendix, Fig. A.3), indicating a high density of trees for smaller diameter classes, and fewer trees for diameter classes above 50 cm. On average, tree density and basal area were higher in Guineo-Congolian than in Guineo-Sudanian forests, and lowest in swamp forests (Fig. 2c and d). Compared with reference values reported from nearby old-growth forests, the studied patches show reduced but still substantial stand structure, underscoring their ecological value as buffers for biodiversity loss outside protected areas (Table 4).

The linear multiple regression indicated that the bioregion in which the plot was located did not significantly explain the tree density, nor the basal area ($p > 0.05$, Table 5). This was due to confounding factors such as altitude and vegetation, which explained the variation in tree density across plots in the two bioregions ($p < 0.05$, Table 5). Regarding the variable disturbance, the regressions showed that forest disturbance negatively affected all structural parameters, including the tree density, which increased significantly along the gradient from forest edge to interior ($p < 0.05$, Table 5).

3.6. Contribution to national floras and threatened tree species in West and Central Africa

Despite their small size, the sampled forest patches (4648.14 ha in total) make a disproportionately high contribution to tree conservation at the national scale. They harbour between 15 % and 30 % of the known tree flora of Togo, Benin, Nigeria, and Cameroon, and between 5 % and 38 % of the globally threatened tree species in these countries (Table 6). Notably, globally threatened taxa such as *Khaya grandifoliola* (VU), *Nesogordonia papaverifera* (VU), *Mansonia altissima var. altissima* (EN), and *Afzelia africana* (VU) were locally abundant in some forest

Table 4
Forest-level structure, diversity, and dominant taxa for each patch compared to nearby primary vegetation. Tree species richness is given as the total number of species, with mean plot-level richness ± standard error in parentheses. Shannon diversity (H'), tree density (stems.ha^{-1}), and basal area (m^2.ha^{-1}) are means ± SE across plots (0.25 ha each). The threatened species follow the IUCN Red List categories (VU Vulnerable, EN Endangered; IUCN, 2025).

Forests (bioregion)	Tree species richness	Shannon diversity (H')	Tree density (stems. ha)	Basal area (m^2.ha)	Dominant tree species	Dominant family	Threatened species	References
Agou (GS)	70 (22 ± 3.51)	2.41 ± 0.26	422 ± 50.84	23.17 ± 03.24	*Tabernaemontana pachysiphon*; *Albizia glaberrima*; *Voacanga africana*; *Margaritaria discoidea*	Apocynaceae; Fabaceae; Apocynaceae; Phyllanthaceae	*Afzelia africana* (VU); *Khaya grandifoliola* (VU); *Vitellaria paradoxa* (VU); *Pterocarpus erinaceus* (EN)	This study
Reference forest (primary vegetation)	-	3.96	767	27.99 ± 25.58	-	-	-	Dangbo et al., (2020)
Elavagnon-Todji (GS)	32 (14 ± 2.02)	2.31 ± 0.15	186 ± 28.77	12.36 ± 02.17	*Aubrevillea kerstingii*; *Khaya grandifoliola*; *Sterculia tragacantha*; *Lecaniodiscus cupanioides*	Fabaceae; Meliaceae; Malvaceae; Sapindaceae	*Khaya grandifoliola* (VU)	This study
Reference forest (primary vegetation)	-	4.62	679.6 ± 315.9	25.6 ± 10.2	-	-	-	Wala et al., (2012)
Koui (GS)	42 (18 ± 1.15)	2.44 ± 0.10	245 ± 25.85	20.45 ± 04.36	*Khaya grandifoliola*; *Trilepisium madagascariense*; *Aubrevillea kerstingii*; *Sterculia tragacantha*	Meliaceae; Moraceae; Fabaceae; Malvaceae	*Khaya grandifoliola* (VU); *Khaya senegalensis* (VU); *Lophira alata* (VU); *Pterocarpus erinaceus* (EN)	This study
Reference forest (primary vegetation)	-	4.62	679.6 ± 315.9	25.6 ± 10.2	-	-	-	Wala et al., (2012)
Kouvizoun (GS)	70 (18 ± 0.78)	2.43 ± 0.06	222 ± 16.02	17.59 ± 01.43	*Englerophytum oblanceolatum*; *Triplochiton scleroxylon*; *Celtis prantlii*; *Dialium guineense*	Sapotaceae; Malvaceae; Cannabaceae; Fabaceae	*Afzelia africana* (VU); *Nesogordonia papaverifera* (VU); *Mansonia altissima var. altissima* (EN); *Pterocarpus erinaceus* (EN)	This study
Reference forest (primary vegetation)	-	2.6	212.5 ± 7.02	34.79 ± 6.46	-	-	-	Bonou et al., (2009); Alohou et al., (2017)
Hlanzoun (GS)	30 (9 ± 0.46)	1.47 ± 0.08	350 ± 25.07	21.74 ± 02.05	*Alstonia congensis*; *Spondianthus preussii*; *Ficus trichopoda*; *Anthocleista vogelii*	Apocynaceae; Phyllanthaceae; Moraceae; Gentianaceae	-	This study
Reference forest (primary vegetation)	-	3.24	620	44.9	-	-	-	Djossa et al., (2010)
Ikot (GC)	38 (14 ± 1.32)	1.90 ± 0.10	263 ± 25.68	12.20 ± 04.76	*Coelocaryon botryoides*; *Mitragyna ciliata*; *Anthocleista vogelii*; *Pachylobus klaineanus*	Myristicaceae; Rubiaceae; Gentianaceae; Burseraceae	-	This study
Reference forest (primary vegetation)	-	2.66	541 ± 29	34.3 ± 0.40		-	-	Asinwa et al., (2018); Igu and Marchant, (2018)
Iko (GC)	144 (36 ± 1.54)	2.99 ± 0.06	448 ± 22.74	32.45 ± 01.94	*Treculia africana*; *Tapura africana*; *Dialium pachyphyllum*; *Pycnanthus angolensis*	Moraceae; Dichapetalaceae; Fabaceae; Myristicaceae	*Cola gigas* (VU); *Englerodendron obanense* (VU); *Entandrophragma cylindricum* (VU); *Nesogordonia papaverifera* (VU); *Pterygota macrocarpa* (VU); *Pycnanthus microcephalus* (VU); *Sterculia oblonga* (VU); *Terminalia ivorensis* (VU); *Guibourtia tessmannii* (EN); *Mansonia altissima var.*	This study

(*continued on next page*)

Table 4 (*continued*)

Forests (bioregion)	Tree species richness	Shannon diversity (H')	Tree density (stems. ha)	Basal area (m^2.ha)	Dominant tree species	Dominant family	Threatened species	References
							altissima (EN); *Prioria balsamifera* (EN)	
Reference forest (primary vegetation)	-	2.87	714 ± 24	37.6 ± 0.41	-	-	-	Asinwa et al., (2018)
Mbangassina (GC)	129 (36 ± 1.59)	3.19 ± 0.12	333 ± 30.98	34.20 ± 02.77	*Trilepisium madagascariense; Sterculia rhinopetala; Drypetes leonensis; Trichilia tessmannii*	Moraceae; Malvaceae; Putranjivaceae; Meliaceae	*Afzelia africana* (VU); *Afzelia bipindensis* (VU); *Diospyros crassiflora* (VU); *Entandrophragma cylindricum* (VU); *Khaya grandifoliola* (VU); *Nesogordonia papaverifera* (VU); *Pterygota macrocarpa* (VU); *Sterculia oblonga* (VU)	This study
Reference forest (primary vegetation)			498–573	31.7–32.4		-	-	Fobane et al., (2024)
Ngam-Kondomeyos (GC)	194 (49 ± 0.98)	3.51 ± 0.03	476 ± 12.26	34.75 ± 01.61	*Meiocarpidium oliverianum; Staudtia kamerunensis; Desbordesia glaucescens; Pycnanthus angolensis*	Annonaceae; Myristicaceae; Irvingiaceae; Myristicaceae	*Afzelia africana* (VU); *Afzelia bipendensis* (VU); *Anopyxis klaineana* (VU); *Baillonella toxisperma* (VU); *Calpocalyx heitzii* (VU); *Diospyros crassiflora* (VU); *Entandrophragma candollei* (VU); *Entandrophragma cylindricum* (VU); *Entandrophragma utile* (VU); *Khaya grandifoliola* (VU); *Khaya ivorensis* (VU); *Nesogordonia papaverifera* (VU); *Pterygota bequaertii* (VU); *Sterculia oblonga* (VU); *Guibourtia tessmannii* (EN)	This study
Reference forest (primary vegetation	-	4.43	263	28.36 ± 28.86	-	-	-	Mbobda et al., (2018)

patches.

4. Discussion

4.1. Forest disturbance characterization

The major types of disturbance recorded in our study (selective logging, agricultural expansion, and wildfire) were consistent with trends observed across tropical Africa, where rapid population growth has resulted in increased agricultural pressures, often characterized by slash-and-burn practices, including wildfire and logging (Laurance et al., 2014). These disturbance types were also previously identified as key drivers of land-use and land-cover changes across tropical Africa (Brandt et al., 2018; Assede et al., 2023). The anthropogenic disturbance types were concentrated at forest edges, as the GLMM results showed a significant decrease in disturbance intensity with increasing distance from the forest edge towards the forest interior. Distance to the forest edge is a well-known predictor of the intensity and magnitude of edge effects (Willmer et al., 2022), and our findings are consistent with previous studies documenting pronounced edge effects in tropical forests (Muposhi et al., 2016; Beche et al., 2022). However, the GLMM suggested that anthropogenic disturbances in the forests were further influenced by potential confounding factors such as land use histories or disturbance legacies that might have influenced the observed patterns.

Forest ownership type, although assumed to influence anthropogenic disturbance, did not significantly affect disturbance occurrence, which is generally high for all forests in our study. This suggests that forest patches outside protected areas are vulnerable to disturbance, regardless of ownership status. This shows that both protected and unprotected forests in tropical Africa are impacted by human activities, contributing to forest fragment shrinkage and loss (Muposhi et al., 2016; Hansen et al., 2020a). These results highlight the urgent need for stronger governance frameworks to ensure sustainable management of these forest patches, to mitigate further degradation and ease pressure on the remaining natural forests in the Congo basin (Hansen et al., 2020b). Future studies that assess disturbances over time will be essential for understanding how these pressures influence tree functional composition and ecosystem resilience (Bongers et al., 2009).

4.2. Tree community composition within forest patches

We followed a phytogeographical gradient to assess alpha and beta diversity among tree communities under various disturbances in West and Central Africa. As hypothesized, species diversity metrics increased from Guineo-Sudanian to Guineo-Congolian forests. This relationship could be explained by the gradient in rainfall from the Guineo-Sudanian to the Guineo-Congolian bioregions and has been confirmed in a global study on vascular plants where rainfall was identified as a major driver of alpha diversity (Sabatini et al., 2022), which aspect is also related to the variation in our bioregion types (Fayolle et al., 2014a,b; Marshall et al., 2021; Davies et al., 2023). The climax forest patches in our study were more diverse than the swamp forests, likely because the tree communities in swamp forests are dominated by specialized species adapted to flooding, which results in lower diversity (Lopez and Kursar, 2003).

4.3. Variation of tree species diversity across forest patches

Regarding beta diversity across forest patches, we hypothesised that tree communities would exhibit high beta diversity, with the inverse of Jaccard similarity increasing as the spatial distance between forest patches increased. This hypothesis was only partially supported: although tree species similarity among forest patches was generally low, there was no significant correlation between the Jaccard similarity (J) and the Euclidean distance (d). Variations in environmental factors such as rainfall (Ringelberg et al., 2023) and topography (De Cáceres et al.,

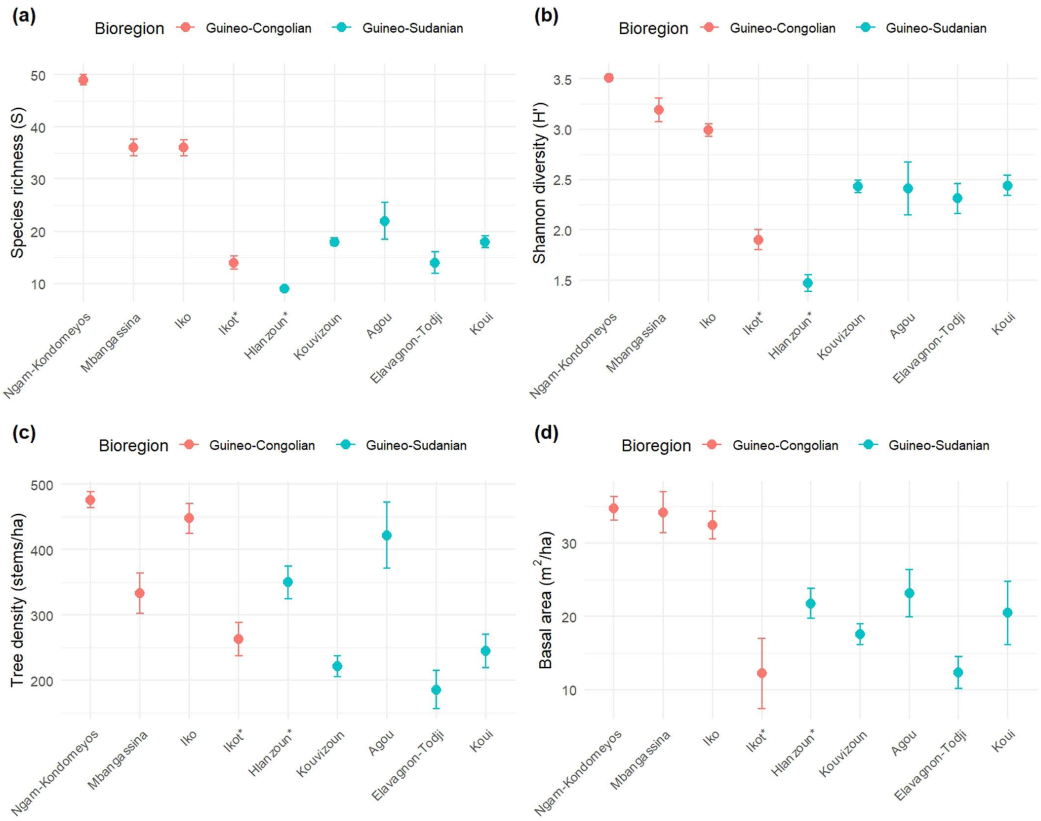

Fig. 2. Stand-level diversity and structure across forest patches. Points show forest means; whiskers are ± SE across 0.25 ha plots. Colours denote bioregion. Asterisked forests (Ikot*, Hlanzoun*) are swamp habitats. Panels indicate (**a**) species richness (S), (**b**) Shannon diversity (H'), (**c**) tree density (stems.ha^{-1}), and (**d**) basal area (m^2.ha^{-1}).

Table 5
Linear multiple regressions showing the effects of bioregions and site characteristics (disturbance and distance to forest edge) on tree stand composition and structure. The model in each case follows the formula: *Dependent variable ~ Bioregion type + Vegetation + Altitude + Distance to forest edge + Disturbance*. References were Guineo-Sudanian and Rainforest respectively for the variables *bioregion types* and *vegetation* across models.

Dependent variables		Tree species richness		Tree density (stems. ha)		Basal area (m^2.ha)		Mean geometric diameter (cm)		Max DBH of non-timber tree (cm)		Max DBH of timber tree (cm)	
Predictors		Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p
Bioregion type (Guineo-Sudanian)		−4.428	< 0.05	−4.444	0.899	1.430	0.65	3.303	< 0.05	−1.483	0.85	19.918	0.09
Distance to forest edge		−0.001	0.41	0.084	< 0.05	0.001	0.65	−0.002	0.19	0.003	0.67	−0.009	0.46
Disturbance		−1.364	0.23	−48.655	< 0.05	−9.502	< 0.05	−3.483	< 0.05	−20.007	< 0.05	−10.539	0.15
Altitude		0.026	< 0.05	0.103	< 0.05	0.007	< 0.05	−0.001	0.55	0.033	< 0.05	0.014	0.31
Vegetation (Rainforest)	YSF[a]	−11.803	< 0.05	−110.731	< 0.05	−6.071	0.05	0.726	0.62	9.815	0.22	−38.787	< 0.05
	OSF[b]	−9.166	< 0.05	−100.759	< 0.05	6.381	0.11	3.660	0.06	38.215	< 0.05	−1.913	0.89
	W[c]	−26.765	< 0.05	−196.143	< 0.05	−15.909	< 0.05	−2.011	0.36	−4.495	0.711	−54.931	< 0.05
	SDDF[d]	−16.186	< 0.05	−77.442	0.06	−8.704	< 0.05	−0.212	0.90	5.267	0.593	−55.141	< 0.05
Adj. R^2		0.88		0.45		0.48		0.15		0.31		0.29	

[a] YSF = Young Secondary Forest;
[b] OSF = Old Secondary Forest;
[c] W = Woodland;
[d] SDDF = Semi-deciduous Dense Forest

	Forests	Similarity in tree species composition: Agou	Elavagnon-Todji	Koui	Kouvizoun	Iko	Mbangassina	Ngam-Kondomeyos	Hlanzoun*	Ikot*
Euclidean distance (km)	Agou	**1**	0.22	0.25	0.20	0.08	0.12	0.06	0.13	0.06
	Elavagnon-Todji	149.75	**1**	0.42	0.15	0.04	0.08	0.04	0.08	0.09
	Koui	150.01	4.74	**1**	0.14	0.05	0.07	0.05	0.10	0.08
	Kouvizoun	207.17	214.88	220.79	**1**	0.1	0.11	0.05	0.06	0.02
	Iko	838.22	875.31	883.84	659.56	**1**	0.29	0.29	0.03	0.11
	Mbangassina	1225.49	1263.22	1269.38	1047.18	382.42	**1**	0.38	0.03	0.07
	Ngam-Kondomeyos	1298.64	1354.35	1360.21	1137.05	483.49	176.03	**1**	0.02	0.07
	Hlanzoun*	163.77	208.70	213.72	54.50	677.72	1066.08	1147.64	**1**	0.06
	Ikot*	824.61	880.56	886.33	663.56	106.13	409.09	470.02	672.71	**1**

Fig. 3. Matrix showing the relationship between the similarity in tree species composition (above diagonal) and the distance between forest patches (below diagonal). For each forest patch, shading gradients in grey (climax forests) or blue (swamp forests) along the cells on either side of the diagonal represent the gradient in distance (below diagonal) and Jaccard index (above diagonal), respectively. Forests marked with an asterisk (Hlanzoun* and Ikot*) are swamp forests, while those without an asterisk (Agou, Elavagnon-Todji, Koui, Kouvizoun Adakplamè-Ewè, Iko, Mbangassina, and Ngam-Kondomeyos) are climax forests.

Table 6
Contribution of sampled patches (4648.14 ha in total) to national tree floras and threatened tree species pools. Values in parentheses are percentages of national totals (BGCI, 2024; IUCN, 2025).

Parameters	Benin	Togo	Nigeria	Cameroon
Sampled area across forest patches (ha)	10	4.25	7.75	8.25
Tree species richness	573	446	1280	2048
Tree species recorded	188 (32.81 %)	138 (30.94 %)	284 (22.19 %)	299 (14.60 %)
Threatened tree species	26	16	165	451
Threatened tree species recorded	7(26.92 %)	6(37.50 %)	22 (13.33 %)	23(5.10 %)

2012) are expected to affect the tree species distribution between the two bioregions (Guineo-Sudanian and Guineo-Congolian) included in our study. However, the absence of a significant relationship between Jaccard similarity and spatial distance may partially reflect the limited number of forest patches (nine) assessed. Furthermore, our beta diversity estimates did not partition total dissimilarity into turnover and nestedness components (Baselga, 2010), which constrains detailed mechanistic interpretation.

For all forests, we did not observe a clear pattern of change in within-forest tree species composition related to either the distance from the forest edge or the level of plot disturbance. This lack of a pattern may be attributed to the small size of the forest patches, where limited spatial variation could obscure potential effects. While edge effects on tree communities in forest patches may be subtle in the short term (Gonçalves-Souza et al., 2025), further research should focus on long-term monitoring and consider adjacent land use. Likewise, trees sampled in our study may have been established before the observed disturbances. Another plausible explanation is that soil nutrient variation within each forest, rather than distance to the edge or disturbance levels, could be driving tree species composition (John et al., 2007). To better elucidate these dynamics, future studies should explore how soil nutrient variations correlate with both distance from forest edge and disturbance gradients. Additionally, long-term monitoring of the disturbances and assessing their effect on the tree community functional properties will contribute to a better understanding of potential changes in the tree community composition (Carreño-Rocabado et al., 2012). Finally, our analysis did not account for natural biotic and abiotic disturbances, such as drought, insect outbreaks, or pathogen proliferation, which are likely to intensify with global climate change. These factors could be critical in shaping within-forest tree community composition (Seidl et al., 2017), warranting further investigation.

4.4. Tree community structure

The effects of disturbances on tree stand structure supported our hypothesis as the structural parameters, especially tree density and basal area, were all negatively and significantly affected by forest disturbance. This is due to the selective logging of both timber and non-timber trees. The diameter distribution of trees in the forest patches exhibited an inverse-J curve, which is characteristic of healthy forests with active regeneration. However, the scarcity of trees with diameters exceeding 50 cm across the two bioregions underscores the intense logging pressure on mature trees in the forests. In contrast, primary forests in the region typically show a higher prevalence of trees exceeding 50 cm DBH (Bonou et al., 2009; Fayolle et al., 2014a,b; Adjonou et al., 2017; Akwaji and Onah, 2023). Although the tree communities contain a high proportion of regenerating individuals, ongoing anthropogenic disturbances jeopardize the long-term persistence of mature size classes and may ultimately erode both functional diversity and overall biodiversity (Zambrano et al., 2020; Maua et al., 2020).

The fact that the diameter of non-timber trees was affected by anthropogenic disturbances, highlights the pressure on timber resources in these unprotected forests. With the scarcity of timber trees, which are valued for their high-quality wood (Hills et al., 2022), "non-timber" tree species (though generally of lower wood value), are now targeted for uses such as charcoal production and crafting (Mensah et al., 2022). Together, these findings underscore how disturbances alter both structure and resource use trajectories, with implications for long-term functional diversity. Overall, our findings reveal that the forest edge effect predominantly influences tree density, with a notable increase in density observed as distance from the forest edge increases. This is consistent with various studies of edge influence on vegetation, where significant differences in forest structure were reported between forest edge and interior (Franklin et al., 2021; Hepner et al., 2025). The spatial pattern observed in our study suggests that forest patches outside protected areas, already under anthropogenic pressure, may continue to shrink over time due to edge effects (Edwards et al., 2019; Hepner et al., 2025). Moreover, the altitude and vegetation types significantly influenced most of the assessed structural parameters. This aligns with the observed patterns in alpha diversity, indicating that biophysical differences play a crucial role in shaping the tree communities within these disturbed forest patches. We found that anthropogenic disturbance has a strong negative effect on the forest structural parameters. As a result, tree density and basal area in the studied forests were lower than the reference values in the nearby old-growth vegetation. Given that these disturbance-types are likely to persist under current management systems for forest patches outside protected areas (Edwards et al., 2019), assessing the impacts of other forms of disturbance (e.g., defaunation) on tree community functional diversity will be critical for informing long-term management strategies (Gardner et al., 2019).

4.5. Implications for tree conservation and the management of forest patches

Although small, these nine forest patches collectively harbour 15 % of total African tree species richness (Sosef et al., 2017). This underscores the conservation value of these small, isolated forest patches. At the national level, these forest patches contribute significantly to the tree flora, housing at least 30 %, 32 %, 22 %, and 15 % of the total tree species in Togo, Benin, Nigeria, and Cameroon, respectively (BGCI, 2024). In terms of threatened species conservation, these patches are also critical, providing habitats for at least 37 %, 27 %, 13 %, and 5 % of the threatened tree species in these countries (Table A.1; BGCI, 2024; IUCN, 2025). For instance, the Kouvizoun Adakplamè-Ewè forest in Benin is the sole habitat for species like *Mansonia altissima var. altissima* (EN) and *Nesogordonia papaverifera* (VU) (Houngnon et al., 2021), which highlights the unique conservation value of these areas. *Khaya grandifoliola* (VU) is also abundant in the Agou forest patch in Togo.

Despite their importance, current management frameworks fail to prevent severe anthropogenic disturbances, such as agricultural encroachment, selective logging, and wildfire across forests. Although the cultural protection systems associated with forests can positively influence their persistence (Mintah et al., 2024), our study shows that they are not sufficient to safeguard the long-term persistence of tree communities in forest patches managed by local communities. Effective engagement of local communities and stakeholders in management strategies is essential to mitigate these pressures. One potential pathway is the designation of these forests as "Other Effective area-based Conservation Measures (OECMs), as proposed by the Convention on Biological Diversity (CBD) (Hansen et al., 2020b). OECMs offer flexible governance models that empower local communities to manage resources while ensuring conservation outcomes. Given the importance of these forest patches for local livelihoods, it is critical to establish governance structures that balance resource use with conservation goals. Key steps could include assessing the minimum felling diameter of timber trees, evaluating the sustainability of harvesting non-timber forest products (Sokpon and Biaou, 2002; De Mello et al., 2020), and promoting participatory conservation efforts, particularly for threatened tree species.

The results showed that nearby forest patches are not necessarily more similar than distant ones, indicating that effective in-situ conservation strategies must encompass multiple patches across different bioregions. Since these patches are managed by local communities, fostering a network of forest governance involving various stakeholders is crucial for their long-term persistence. Our findings of strong edge effects on stand structure further highlight the need for spatially differentiated management. In this context, local communities could implement a zoning approach, including core conservation areas, buffer zones, and resource-use areas. This could reduce edge-driven degradation while supporting local livelihoods. Unlike formal Man and Biosphere Reserves, which are typically applied within protected area frameworks, such zoning could be adapted under OECMs-type arrangements to strengthen customary rights and local governance. Experiences from community forest concessions in the Maya Biosphere Reserve, Guatemala, show that rights-based zoning can maintain forest cover while generating local benefits when accompanied by clear tenure, monitoring, and accountability mechanisms (Sundberg, 2003; Monterroso and Barry, 2012; Radachowsky et al., 2012). Adapting these lessons to the West and Central African context would mean formal recognition of customary tenure, co-defined conservation zones to protect interior habitats, and regulated buffer and use zones to sustain wood and non-timber forest products.

Moreover, forest restoration initiatives should also prioritise enhancing the structural integrity of forest edges in terms of tree density, diversity, and composition, as this could limit further forest loss. To achieve a balance between biodiversity conservation and livelihoods, it is essential to create landscapes with at least 40 % forest cover (Arroyo-Rodríguez et al., 2020). This could involve maintaining isolated forest patches alongside timber plantations and sustainable agricultural practices (Rocha-Santos et al., 2016; Arroyo-Rodríguez et al., 2020). Such an approach is critical to meeting the 2030 targets of the CBD (Convention on Biological Diversity, 2022). Engaging local communities in growing fast-growing tree species for timber and other uses is also crucial. Given the high failure rate of restoration projects, prioritizing the use of native and threatened species rather than the exotic ones in restoration efforts, can significantly improve success rates (Bartholomew et al., 2023). Sustainable forest management in tropical Africa must involve all stakeholders, including local communities, customary authorities, forest resource collectors, and government institutions (Uzu et al., 2022). Finally, legal frameworks that support inclusive governance and equitable resource-sharing are essential for the long-term persistence of these forest patches.

5. Conclusions

This study demonstrates that forests outside protected areas are indispensable for conserving tree diversity in West and Central Africa. Despite their small size, they contribute substantially to national floras and threatened species pools. Our findings indicate that effective conservation cannot rely on single sites but should instead encompass networks of forest patches across bioregions. Current governance frameworks leave these forests vulnerable to anthropogenic pressure, particularly logging, agriculture, and wildfire, which degrade stands and erode large-tree populations, especially near edges. Customary-based governance proved insufficient to secure the long-term persistence of tree communities in these forests outside protected areas. We therefore recommend combining (i) formal recognition of these forests as critical biodiversity habitats, with (ii) strengthening customary rights through inclusive governance, and (iii) implementing zoning approaches with core conservation, buffer, and resource-use areas. Embedding such measures into national strategies will sustain local livelihoods while safeguarding irreplaceable biodiversity.

CRediT authorship contribution statement

Georges Alex Agonvonon: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Samuel Markus Hepner:** Writing – review & editing, Investigation. **Chima Jude Iheaturu:** Writing – review & editing, Investigation. **Akomian Fortuné Azihou:** Writing – review & editing, Methodology, Conceptualization. **Denis Jean Sonwa:** Writing – review & editing. **Francis Ebuta Bisong:** Writing – review & editing. **EnoAbasi Deborah Anwana:** Writing – review & editing. **Koffi Koudouvo:** Writing – review & editing. **Brice Brice Augustin Sinsin:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Markus Fischer:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Chinwe Ifejika Speranza:** Writing – review & editing, Supervision, Project administration, Methodology, Data curation, Conceptualization, Funding acquisition.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123314.

Data availability

Data will be made available on request.

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5.4 Co-authored paper 4: Integrating UAV LiDAR and multispectral data to assess forest status and map disturbance severity in a West African forest patch

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Integrating UAV LiDAR and multispectral data to assess forest status and map disturbance severity in a West African forest patch

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ABSTRACT

Unmanned aerial vehicle (UAV) technologies have emerged as promising tools to improve forest ecosystem assessments. These technologies offer high-resolution data that can significantly enhance evaluations of forest structure, condition, and disturbance severity. UAV sensors such as LiDAR and multispectral provide complementary information about forest attributes, capturing structural and spectral details, yet their integration for comprehensive forest assessment remains understudied. In this paper, we explored the potential of combining UAV LiDAR and multispectral data to assess the disturbance severity of a West African forest patch (Benin). We developed an integrated disturbance index (IDI) that fuses structural properties from LiDAR data and spectral characteristics from multispectral vegetation indices through principal component analysis (PCA). This allowed us to delineate low (> 0.65), medium (0.35–0.65), and high (< 0.35) forest disturbance levels. We applied the IDI to the 560-ha Ewe-Adakplame relict forest in Benin, West Africa, and achieved 95 % overall accuracy in disturbance detection, outperforming both LiDAR-only (80 %) and multispectral-only (75 %) approaches. The IDI revealed that 23 % of the forest area has experienced low disturbance, while 28 % and 49 % face medium and high disturbance levels, respectively. These findings indicate that more than three-quarters of this relict forest exhibits medium to high levels of disturbance, underscoring the urgent need for tailored conservation strategies to strengthen forest resilience. This method's ability to differentiate disturbance levels can inform resource allocation, prioritize conservation efforts, and guide the development of site-specific management plans. The integration of UAV LiDAR and multispectral data demonstrated here has potential for application across diverse tropical forest patches, providing an effective means to monitor forest health, assess disturbance severity, and support data-driven decision-making in forest conservation and sustainable management.

1. Introduction

Anthropogenic disturbance factors such as wildfire, logging, and agricultural expansion are driving widespread fragmentation and degradation of tropical forests across West Africa (Dago et al., 2023). These disturbances alter forest structure, composition, and function, leading to a loss of biodiversity and ecosystem services (Malhi et al., 2014). Restoration efforts like the African Forest Landscape Restoration Initiative (AFR100) aim to reverse these negative impacts by restoring degraded forests and enhancing forest resilience (Mansourian and Berrahmouni, 2021). However, the success of such initiatives depends on access to reliable information about the current condition and structure (hereafter status) and disturbance severity of the threatened forests. This data can then be used to target areas for intervention, develop targeted restoration approaches based on disturbance levels, and effectively allocate resources for ecological recovery.

While traditional field assessments of forest status provide critical localized information, they are limited in spatial coverage. Only a small fraction of the forest area can be covered because manual field data collection is time- and labor-intensive and is constrained by accessibility to remote areas of dense vegetation (Butler et al., 2016; Zellweger et al., 2014). These challenges restrict field sampling to discrete plots, further limiting the wider characterization of forest status and the identification of areas that have undergone disturbance. Furthermore, standardizing

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traditional field assessment methods across different regions and forest types poses significant challenges. While standardization aims to ensure consistency, variations in sampling protocols, measurement techniques, and data collection practices may persist (Gschwantner et al., 2016). If not adequately addressed, these variations can lead to data discrepancies, making it challenging to compare and integrate information from different sources.

The recent proliferation of high-resolution satellite systems presents new opportunities to help overcome field data constraints, offering the potential for standardized, wide-area coverage of forests (Popkin, 2016; Rahimi et al., 2024; Reiche et al., 2016). However, persistent data gaps, mainly due to cloud and cloud shadow contamination in optical satellite images, pose challenges for monitoring West African forests (Hackman et al., 2017). Compared to other tropical regions, West Africa has a scarcity of publicly accessible, cloud-free, high-resolution optical and radar data (Pospichal and Crewell, 2011). This shortage of such imagery limits satellite-based monitoring of West African forests. Bridging this gap with other means to acquire high-resolution data could complement traditional field assessments in forest conservation and restoration efforts (Aleman et al., 2018).

Emerging unmanned aerial vehicle (UAV) technologies offer a promising approach to acquiring high-resolution images to complement satellite systems and field-based methods for monitoring tropical forests. The possibility to mount different types of sensors on UAVs (e.g., RGB cameras, multispectral sensors, and light detection and ranging (LiDAR) scanners) provides fine-scale spectral imagery and three-dimensional (3D) structural data comparable to intensive traditional field-based assessments (Berie and Burud, 2018). However, some pressing questions remain regarding optimizing UAV technologies for forest monitoring (Ecke et al., 2022). For example, what analysis techniques best integrate disparate data streams like spectral imagery and LiDAR point clouds to maximize ecological insight? What workflows enable scalable and reproducible forest monitoring frameworks? Addressing these questions through UAV applications could potentially bridge significant knowledge gaps, such as characterizing the extent and levels of forest disturbance while providing high-quality and timely data.

Several studies have demonstrated the value of UAVs for assessing forest structure, species composition, and condition (Ecke et al., 2022; Wallace et al., 2012; Zlinszky et al., 2015). For example, research has shown the ability of UAV LiDAR to quantify various forest structural parameters, such as canopy height, gap fractions, diameter at breast height (DBH), canopy density, and rumple (Cao et al., 2019; Seidl et al., 2012; Swayze et al., 2021). Additionally, passive UAV multispectral imagery has been employed to assess forest health (Fraser and Congalton, 2021) and detect patterns of forest disturbance (Minařík and Langhammer, 2016).

To date, few studies have assessed the potential of integrating UAV LiDAR and multispectral or hyperspectral data for tropical forest assessments. For example, Vaglio Laurin et al. (2014) integrated airborne LiDAR and hyperspectral data using partial least squares regression models with field measurements to estimate above-ground biomass in African tropical forests, while de Almeida et al. (2021) fused UAV-borne hyperspectral and LiDAR data to monitor diversity and structure in restored tropical forests.

This study explored the potential of integrating UAV-based LiDAR and multispectral data to evaluate forest status and map disturbance severity in the Ewe-Adakplame Relict Forest (EARF) in Benin. We employed a static approach to assess the severity of forest disturbance, providing a snapshot of current conditions. Three specific objectives were pursued as follows: (i) derive structural properties from UAV LiDAR data and spectral vegetation indices (VIs) from UAV multispectral imagery to assess the state of the forest; (ii) generate an Integrated Disturbance Index (IDI) using principal component analysis (PCA) of correlated structural and spectral VIs; and (iii) delineate low, medium, and high disturbance levels based on the IDI to identify areas requiring immediate conservation action.

Our study goes beyond the limitations of traditional field plot sampling by providing comprehensive, centimeter-level spatial coverage of the forest from UAV data. The IDI promises a more nuanced understanding of forest disturbance levels, exceeding simple binary classifications. This approach can be upscaled using satellite-based LiDAR and multispectral observations for large-scale tropical forest restoration efforts during the United Nations Decade on Ecosystem Restoration (2021–2030).

2. Materials and methods

2.1. Study site

This study was conducted in the EARF, a 560-ha semi-deciduous forest fragment located in the Ketou District of southeastern Benin, West Africa (Fig. 1). This remnant forest patch falls within the Guinean region, which lies south of the Sudanian region (CILSS, 2016). The climate is subequatorial with a bimodal rainfall pattern. The main rainy season occurs from April to late July. This rainy season is characterized by relatively heavy rainfall, ranging from an average of 80 mm in April to a peak of 280 mm in July, the rainiest month. There is a shorter, less intense rainy period from September (100 mm) to November (20 mm). However, the average annual precipitation ranges from 900 to 1300 mm, which is lower than that typical for the Guinean region (Adomou et al., 2006). The mean annual temperature ranges from 24 to 37 °C. There is a long plant-growing season spanning 240 days. The EARF harbors high levels of biodiversity, with about 185 vascular plant species documented, including range-restricted species typical of Upper Guinean forests (Houngnon et al., 2021). However, as with most forests in Benin, the fragment faces significant human pressures, such as agricultural expansion and illegal logging (Oloukoi et al., 2006), that is causing a decrease in the size and connectivity of natural habitats, leading to a severe loss of local biodiversity (Houngnon et al., 2021).

2.2. UAV multispectral and LiDAR data

We conducted the UAV surveys on two different dates to optimize data quality. Multispectral data were collected during the less intense rainy season (7–17 October 2022) when vegetation is still vibrant, enhancing the capture of spectral signatures related to plant health. LiDAR data, on the other hand, were collected during the dry season (27–29 December 2022) when reduced leaf cover enables clearer penetration of laser pulses for detailed canopy structure. The multispectral data was collected using a DJI Phantom 4 Multispectral UAV (DJI, Shenzhen, China) with real-time kinematic (RTK) with six 1/2.9" Complementary Metal Oxide Semiconductor (CMOS) sensors for visible and multispectral imaging. The surveys were conducted between 9 am and 3 pm under clear, sunny skies with low wind speeds and minimal cloud cover (less than 5 %). The UAV was flown at 150 m above ground level (AGL) with 80 % forward overlap and 65 % side overlap, capturing 43,404 nadir images at 8 cm/pixel ground sample distance (GSD).

For the LiDAR data, we used a DJI Matrice 300 RTK (DJI, Shenzhen, China) with a Zenmuse L1 laser scanning system. We conducted the flights under favorable weather conditions, similar to those used for the multispectral surveys. We used a scan mode flight pattern with 80 % forward overlap and 65 % side overlap at an altitude of 100 m AGL and a mapping speed of 6 m/s. The L1 system scanned at 160 kHz, recording up to three returns per pulse and generating a point cloud with a density of 317 $\pm$ 114 (mean + SD) ppm^2, of which 85.3 % were first returns.

2.3. Field data

Ground-based measurements were conducted in the same period as the UAV flights to validate the UAV-derived products. Twenty sample plots (Fig. 1) of 0.25 ha were selected using stratified random sampling to capture varying forest conditions. All trees $\geq$10 cm DBH within each

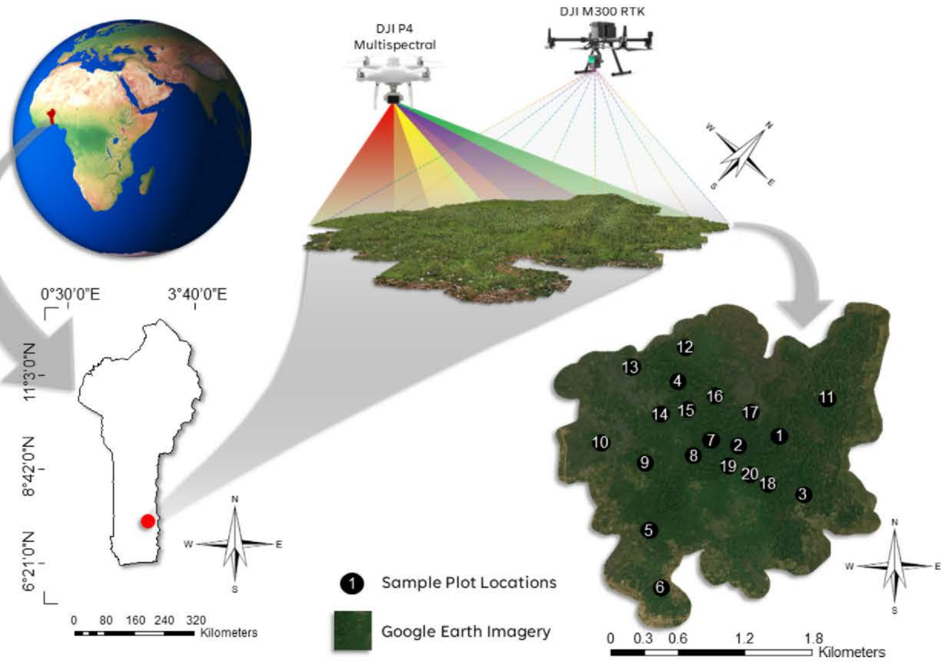

Fig. 1. Study area and study design. Upper left - The location of Benin Republic in West Africa (in red); bottom left - Map of Benin Republic showing the location of EARF (red dot); Upper right - UAV multispectral and LiDAR setup over the field site, EARF; bottom right - Google Earth Image of EARF showing the 20 forest inventory plot locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

plot were recorded, and tree heights were measured using a Suunto clinometer to characterize tree height distributions.

Signs of anthropogenic disturbances (Fig. 2) were assessed per plot, including fire (charcoal/scorch marks), logging (stumps), trails, agricultural encroachment, dead trees, canopy gaps, lianas/vines, and understory density as indicators of forest disturbance.

2.4. Multispectral data processing

The raw multispectral images captured by the DJI Phantom 4 Multispectral RTK UAV in blue (475 nm), green (560 nm), red (668 nm), red edge (717 nm) and near-infrared (NIR) (840 nm) bands were downloaded in georeferenced TIFF (GeoTIFF) format and referenced to the World Geodetic System 1984 (WGS84) Universal Transverse Mercator (UTM) zone 31 N coordinate system. These images were processed using Agisoft Metashape Professional software (version 2.0.2, Agisoft LLC, St. Petersburg, Russia), employing structure-from-motion (SfM) photogrammetry techniques to generate an orthomosaic. After photo alignment and dense 3D point cloud generation, a digital surface model (DSM) was reconstructed from the point cloud, camera positions, and orientations. Each band's orthomosaic was radiometrically calibrated using Metashape's "Calibrate Reflectance" tool with the "Sun sensor" option (Manfreda et al., 2018). No image filtering or minimum look angle constraints were applied to preserve the structural details of the vegetation (Anders et al., 2019).

2.4.1. Calculation of vegetation indices

To assess the health and condition of the forest canopy, we calculated five key vegetation indices (VIs) using the raster calculator within Agisoft Metashape Professional software. The selected VIs include the Green Normalized Difference Vegetation Index (GNDVI) (Gitelson and Merzlyak, 1998), Enhanced Vegetation Index (EVI) (Jiang et al., 2007), Soil Adjusted Vegetation Index (SAVI) (Huete, 1988), Normalized Difference Red Edge (NDRE) (Barnes et al., 2000), and Leaf Chlorophyll Index (LCI) (Datt, 1999). These indices were chosen based on the available spectral bands from the multispectral imagery and their common usage in vegetation studies (see Table 1).

These specific VIs were selected because they provide complementary information for assessing tropical forest health and disturbance levels. For instance, GNDVI measures the contrast between the green and NIR bands and is less affected by chlorophyll absorption than the traditional Normalized Difference Vegetation Index (NDVI). By reducing chlorophyll sensitivity, the GNDVI can better capture structural properties like foliage density and gap fractions related to disturbance factors such as deforestation, fires, storms, or insect infestations that impact forest health (Gitelson and Merzlyak, 1998). EVI complements the GNDVI's ability to capture structural properties in tropical vegetation by adjusting for background influences from tropical soils and atmospheric variation, providing a robust characterization of productivity in high-biomass tropical forests (Huete, 2012). SAVI improves NDVI by minimizing soil influences in tropical systems. Specifically, SAVI adjusts NDVI based on soil brightness factors using an L parameter (soil brightness correction factor) set to 0.5 for intermediate canopy density (Huete, 1988). This minimizes the false variability introduced by contrasting soil hues in heterogeneous tropical landscapes. By accounting for soil brightness, SAVI enables reliable characterization of canopy density and condition, which are crucial for monitoring tropical forest health.

NDRE can further enhance our understanding of vegetation stress and deterioration by isolating the red edge band to detect early pigment loss and leaf senescence, which is useful for mapping the gradual decline of tropical forest canopies (Zarco-Tejada et al., 2013). Such decline

Fig. 2. Evidence of anthropogenic disturbance in EARF: (a) A maize plot visibly encroaching into the adjacent forest, (b) A felled tree along a foot trail showing scorch marks, (c) A freshly cut down tree stump, probably logged for its timber, (d) Scorch marks at the base of a still-standing tree, suggesting it survived a fire. Photo credit: Samuel Hepner and Georges A. Agonvonon.

Table 1
Formulas for the VIs used.

Vegetation Indices	Abbreviation	Formula	Reference
Green Normalized Difference Vegetation Index	GNDVI	(NIR – G)/(NIR + G)	(Gitelson and Merzlyak, 1998)
Leaf Chlorophyll Index	LCI	(NIR – RE)/(NIR + R)	(Datt, 1999)
Soil Adjusted Vegetation Index	SAVI	((NIR - R)/(NIR + R + L)) * (1 + L)	(Huete, 1988)
Normalized Difference Red Edge	NDRE	(NIR – RE)/(NIR + RE)	(Barnes et al., 2000)
Enhanced Vegetation Index without the blue band	EVI	2.5 * ((NIR – R)/(NIR + 2.4 * R + 1))	(Jiang et al., 2007)

G is the green band, R is the red band, RE is the red edge band, L is the soil brightness correction factor, and NIR is the near-infrared band.

could be in the form of a reduction in leaf area, chlorophyll content, and overall canopy density, resulting from various stress factors like drought, nutrient deficiency, pest infestations, or anthropogenic disturbance factors like fire or logging. Lastly, LCI estimates chlorophyll content, offering high sensitivity to early stages of tropical forest stress from factors such as disease, insects, or nutrient deficiency (Daughtry et al., 2000). Taken together, these indices provide a more comprehensive view of the health and vitality of tropical forests.

2.5. LiDAR data processing

The raw LiDAR data was downloaded and imported into DJI Terra software (version 4.1.0) for initial processing. The point cloud density was set to 100 % to retain all points. The output coordinate system was defined as WGS84 UTM zone 31 N before initiating the automated calibration. The point cloud effective distance parameter was kept at 250 m, and the "Optimize Point Cloud Accuracy" option was enabled. The cleaned point cloud was then exported in LAS (LASer) format.

LAStools software (rapidlasso GmbH, version 2023.03.30) was then used to generate a pit-free canopy height model (CHM) from the LAS point cloud (Khosravipour et al., 2014). First, the raw LAS point cloud was classified into ground and non-ground returns using the *lasground* algorithm. Next, a digital terrain model (DTM) representing ground elevation was interpolated to 10 cm resolution from classified ground returns using the *las2dem* algorithm. Finally, the CHM was produced by calculating the height above ground for the first returns with the *lasheight* algorithm and subtracting the DTM (Mielcarek et al., 2018) (Eq. (1)).

$$CHM = Z_{first\ return} - DTM \tag{1}$$

Where CHM is the canopy height model, $Z_{first\ return}$ is the elevation of the first return LiDAR points, and DTM is the digital terrain model representing ground elevation.

2.5.1. Generation of forest structural metrics

We utilized LAStools to derive key canopy structural metrics identified in other studies for distinguishing forest structural conditions: 95th percentile canopy height (H_{95}), canopy cover density, gap fraction, and canopy surface rumple. These canopy metrics serve as indicators of vertical and horizontal complexity, which reflect the impacts of disturbances on forest ecosystems as they progress through succession and development stages (Jucker et al., 2018).

The H_{95} represents the maximum vertical stature and indicates forest maturity and structural complexity (Parker and Russ, 2004). In intact tropical forests, values typically exceed 30 m, while lower values signal stunted growth from disturbances like logging (Sheffield et al., 2021). Canopy cover density quantifies horizontal canopy closure by calculating the proportion of laser pulses reflected by vegetation above 2 m height relative to the total number of pulses (Jennings et al., 1999). Dense, multi-layered intact tropical forests exhibit high canopy cover density approaching 100 %, whereas disturbed, fragmented forests have lower values, often below 80 % (Olsoy et al., 2014). The gap fraction metric complements canopy cover density by quantifying vertical porosity as the ratio of pulses penetrating through canopy gaps to the ground (Zhao et al., 2011). Lower gap fractions below 15 % characterize structurally complex forests with multi-strata obstructing light penetration, while higher values typify disturbed, open canopies. Finally, the rumple index measures 3D canopy surface roughness as the ratio of canopy area to ground area, ranging from 1 for a flat, uniform canopy to 8 for a highly complex surface (Seidl et al., 2012). Intact forests exhibit higher rumple values, typically above 3, due to their structural heterogeneity across multiple canopy layers, whereas severely disturbed forests have lower rumple closer to 1 (Kane et al., 2010).

2.6. Data fusion and disturbance mapping analysis

To map the disturbance severity across the forest area, we integrated multispectral and LiDAR UAV datasets. We developed an IDI framework (Fig. 3) to identify disturbed conditions. These disturbed conditions were characterized by coincident low vegetation index values from the multispectral data and reduced canopy structural metrics derived from the LiDAR data, such as decreased canopy height and density, as well as increased canopy gaps, when compared to the expected characteristics of an undisturbed, intact forest canopy.

To enable this integrated analysis, we resampled the 10 cm resolution LiDAR-derived CHM to match the 8 cm resolution of multispectral orthomosaics using nearest-neighbor interpolation in ArcGIS Pro® (Esri Inc., Version 3.2.1). The CHM was then co-registered with the multispectral bands by manually identifying 30 common ground control points (GCPs) and applying a polynomial warp transformation for georectification (Han et al., 2019). This alignment enabled pixel-level analysis. We calculated the five VIs — GNDVI, EVI, SAVI, NDRE, and LCI — from the co-registered multispectral bands described in Section 2.4.1. Spearman correlation analysis assessed relationships between LiDAR-derived canopy height and spectral VIs, identifying significant correlations at $p < 0.05$. Finally, we used PCA to integrate the LiDAR and spectral (VIs) variables into a composite disturbance index (Eq. (2)). PCA condensed these indicators into ordered principal components (PCs), explaining the decrease in variance. The first principal component (PC1) explains the largest portion of the variance in the correlated variables, making the PC1 raster an effective proxy for the IDI.

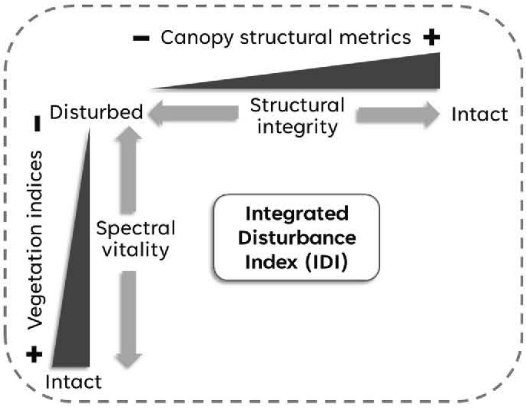

Fig. 3. Integrated Disturbance Index (IDI) framework for mapping forest disturbance. The framework integrates canopy structural metrics derived from LiDAR data and spectral vitality indicators captured by vegetation indices.

$$PC1 = a_1X_1 + a_2X_2 + \ldots + a_nX_n \quad (2)$$

Where a is the component loading or weight for each variable, X is the original correlated variable, and n is the number of significantly correlated variables.

The PC1 raster was classified into categorical disturbance classes using a combination of K-means clustering and knowledge-based reclassification. We initially tested different numbers of clusters (k = 2 to 5) in the K-means algorithm (Table S1). After visual inspection of the resulting maps and consideration of the interpretability and practical utility for forest management, we determined that three clusters provided a balance between simplicity and the ability to capture meaningful variations in forest conditions.

The K-means clustering with k = 3 was applied to the PC1 values, identifying natural groupings within the data. These clusters were then reclassified into specific disturbance categories (low, medium, and high) based on prior knowledge of the relationships between PC1 values, VI values, and canopy structure metrics. To refine the boundaries between disturbance classes, we examined the distribution of PC1 values within each cluster and adjusted the thresholds to align with notable breaks or inflection points in the data distribution. The final thresholds for the three disturbance classes were defined as follows:

1. Low Disturbance: PC1 values >0.65
2. Medium Disturbance: $0.35 <$ PC1 values ≤ 0.65
3. High Disturbance: PC1 values ≤ 0.35

These thresholds were further validated through field observations and comparison with the high-resolution UAV RGB imagery to ensure they accurately reflected on-the-ground conditions. Areas with low PC1 values (≤ 0.35) were characterized by low VI values and reduced canopy structure (e.g., low canopy heights and high gap fractions). These regions were classified as high disturbance zones, reflecting severe disturbances with significantly reduced vegetation cover and structural integrity. Conversely, areas with high PC1 values (> 0.65), supported by high VI values and intact canopy structure (e.g., tall canopy heights and low gap fractions), were classified as low disturbance zones, indicating healthy forest conditions. These zones were distinguished by their robust vegetation cover and structural integrity. Intermediate PC1 values ($0.35 <$ PC1 ≤ 0.65) were classified as medium disturbance zones, representing partial canopy damage or other disturbances that may have impacted forest structure and health while retaining some vegetation cover and canopy integrity.

2.7. Accuracy assessment

We assessed the disturbance map's accuracy by comparing it to field observations from 20 ground plots. In each plot, we recorded disturbance indicators such as signs of fire, logged tree stumps, human trail density, agricultural encroachment, liana proliferation, dead tree density, canopy gaps, and vegetation cover. Based on these indicators, each plot was classified into low, medium, or high disturbance (Table 2).

For each field plot, we extracted the proportions of pixels classified as Low, Medium, and High disturbance levels from the PC1 raster and compared these to the field-based disturbance class. For instance, a field plot classified as high disturbance should have a higher proportion of pixels classified as high disturbance in the PC1 raster. By aggregating and comparing the disturbance classes within each plot to the field reference, we evaluated the accuracy of the fused LiDAR-multispectral dataset and the derived disturbance index.

We also compared the field-based disturbance classes with individual LiDAR and spectral metrics to determine if the data fusion improved disturbance detection accuracy. Accuracy metrics such as overall accuracy (OA), user's accuracy (UA), and producer's accuracy (PA) were calculated to quantify performance against the field reference data (Congalton and Green, 2019).

Table 2
Field-based classification of disturbance levels based on the percentage of the plot affected.

Disturbance level	Percentage of plot affected	Description
Low Disturbance	<15 %	Minimal or no signs of disturbance, such as the absence of fire scars, stumps, human trails, agricultural encroachment, liana proliferation, dead trees, and canopy gaps. Likely represents intact or relatively undisturbed forest conditions.
Medium Disturbance	15 % - 30 %	Moderate levels of disturbance indicators, such as scattered stumps, a few human trails, moderate liana infestation, and some canopy gaps. May have experienced selective logging, localized agricultural activities, or other low-to-moderate disturbance events that have impacted the forest structure and health to some degree.
High Disturbance	> 30 %	Extensive evidence of disturbance, including widespread fire scars, numerous stumps, dense human trails, extensive agricultural encroachment, heavy liana proliferation, high densities of dead trees, and significant canopy gaps. Likely represents areas that have undergone severe anthropogenic disturbances or natural disturbances, leading to deterioration of the forest structure and condition.

3. Results

3.1. Forest structural and spectral characteristics and their relationships

The LiDAR-derived CHM revealed the spatial distribution of canopy heights across the 560-ha forest area (Fig. 4). The CHM also revealed areas of closed tall forest canopy, lower stature vegetation, and canopy gaps. Furthermore, the structural metrics derived from the CHM revealed that the H_{95} for the 560-ha study area was below 20 m. The canopy cover density averaged 0.56, and correspondingly, the overall canopy gap fraction was 0.44. Lastly, the rumple index averaged 2.54.

The VIs derived from the co-collected multispectral bands provided complementary spectral information about the forest's health. Fig. 5 reveals diverse spatial patterns and variability of the vegetation conditions across the forest, with areas of high index values (typically >0.6) and low index values (generally below 0.3) clearly visible. The GNDVI ranged from -0.50 to 0.92 (Fig. S1a), with a high mean of 0.69 (± 0.10 standard deviation), exceeding the typical high-value threshold of 0.6. The EVI exhibited higher variability, averaging 0.74 (± 0.14) across the full observed range of -0.29 to 0.95 (Fig. S1b), again highlighting regions with values exceeding 0.6. SAVI values spanned from -0.29 to 0.63 (Fig. S1c), with a mean of 0.26 (± 0.06), indicating substantial areas below the low index benchmark of 0.3. The NDRE had a mean of 0.23 (± 0.11), with values ranging from -0.50 to 0.75 (Fig. S1d), mostly exhibiting low index values below 0.3. Lastly, the LCI had an average of 0.34 (± 0.08), with a wider range of -0.81 to 0.73 (Fig. S1e), indicating considerable areas with values below 0.3.

The correlation matrix (Fig. 6) shows the correlation coefficients (r) quantifying the relationships between CHM and the VIs. The CHM exhibited positive correlations with all VIs. The strongest correlations were observed with NDRE ($r = 0.709$), LCI ($r = 0.693$), and SAVI ($r = 0.657$). While still significant ($p < 0.05$), the correlations with GNDVI ($r = 0.604$) and EVI ($r = 0.650$) were slightly weaker in comparison.

3.2. Data fusion and disturbance mapping

The PCA integrated the LiDAR and spectral VIs into a composite disturbance index. The variable-PCA-biplot (Fig. 7a) illustrates the contribution of each variable to the overall data variation. The scree plot

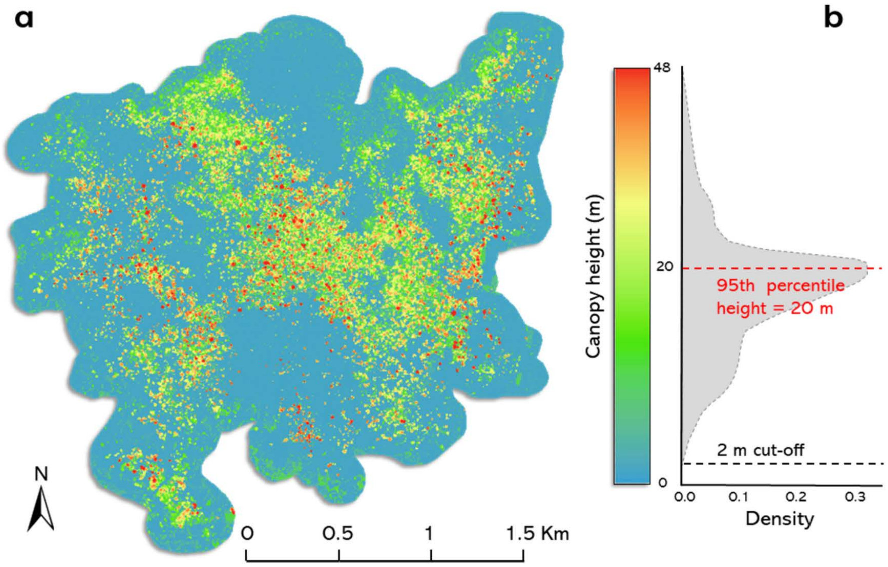

Fig. 4. (a) Top view of the canopy height model (CHM), with heights below 2 m removed to exclude understory vegetation and ground returns, (b) Distribution of canopy heights above 2 m.

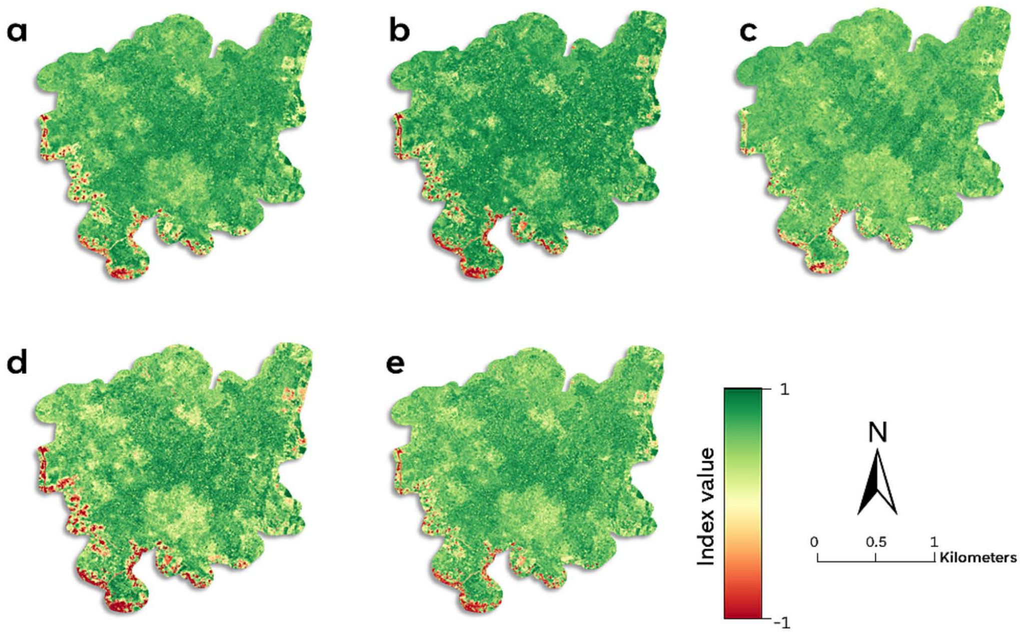

Fig. 5. Spatial distribution of VIs derived from the UAV multispectral data, including (a) GNDVI, (b) EVI, (c) SAVI, (d) NDRE, and (e) LCI. Areas of healthy vegetation are represented by dark green hues. In contrast, regions of stressed vegetation exhibit a gradient that transitions from light green to yellow and ultimately to red, reflecting varying degrees of vegetative stress. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

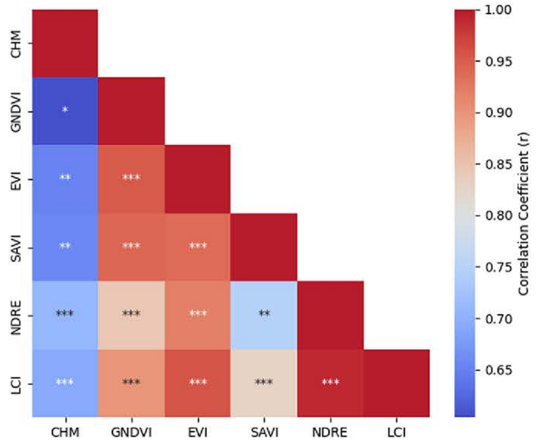

Fig. 6. Spearman's correlation matrix between LiDAR and spectral metrics. The correlation values are ranked from 0.6 to 1, where 0.6 to 0.7 means moderate positive correlation, and 0.8 to 1 indicates a strong positive correlation. The p-value significance levels are "*" 0.05, "**" 0.01, and "***" 0.001.

(Fig. 7b) indicates that PC1 accounted for the majority (75.7 %) of the variance in the original disturbance metrics, while PC2 explained 23.5 % of the variance. As shown in Fig. 7c, EVI, CHM, and GNDVI had the highest loadings and contributed most significantly to PC1, while SAVI, NDRE, and LCI loaded more heavily onto PC2. Fig. 7d further details the contributions of the variables specifically to PC1.

Fig. 8 shows the resulting categorical high-resolution (8 cm) disturbance map from the classified PC1 raster (IDI), delineating zones of disturbance severity. Analysis of this map revealed that 49 % (275.75 ha) of the 560-ha forest fell into the high disturbance category, 28 % (154.16 ha) was classified as medium disturbance, and the remaining 23 % (130.09 ha) was categorized as low disturbance.

3.3. *Accuracy assessment*

The accuracy assessment revealed that combining LiDAR and multispectral data for IDI classification achieved an OA of 95 %, outperforming individual sensors used alone. For instance, LiDAR-derived CHM achieved an OA of 80 %, while spectral VIs alone reached an OA of 75 %. Fig. 9a shows the confusion matrix, which highlights the alignment between the classified IDI and field measurements. For all disturbance classes, both PA and UA of the IDI exceeded 85 %. Conversely, the LiDAR CHM exhibited lower accuracy, particularly in the medium disturbance class, where PA and UA were 71.43 % (Fig. 9b). Similarly, spectral VIs demonstrated lower performance in the medium disturbance class, with a PA of 71.43 % and UA of 62.50 %. For the high disturbance class, spectral VIs had a PA of 62.50 % and a UA of 71.43 % (Fig. 9c). The proportions of pixels classified in each disturbance category for each of the 20 field plots are provided in Table S2.

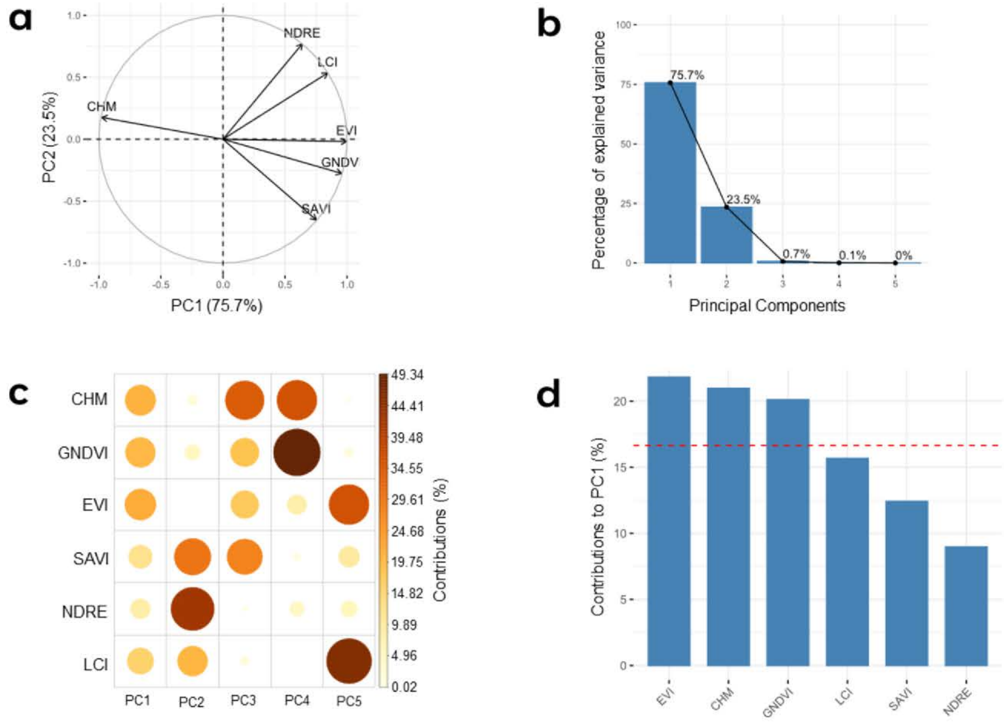

Fig. 7. (a) Variable PCA-biplot showing the contribution of variables in data variation, (b) Scree plot showing the percentage of explained variance by the principal components, (c) Contributions of the variables to the PCs, (d) Contributions of variables to PC1 in percentages. The red dashed line indicates the expected average contribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

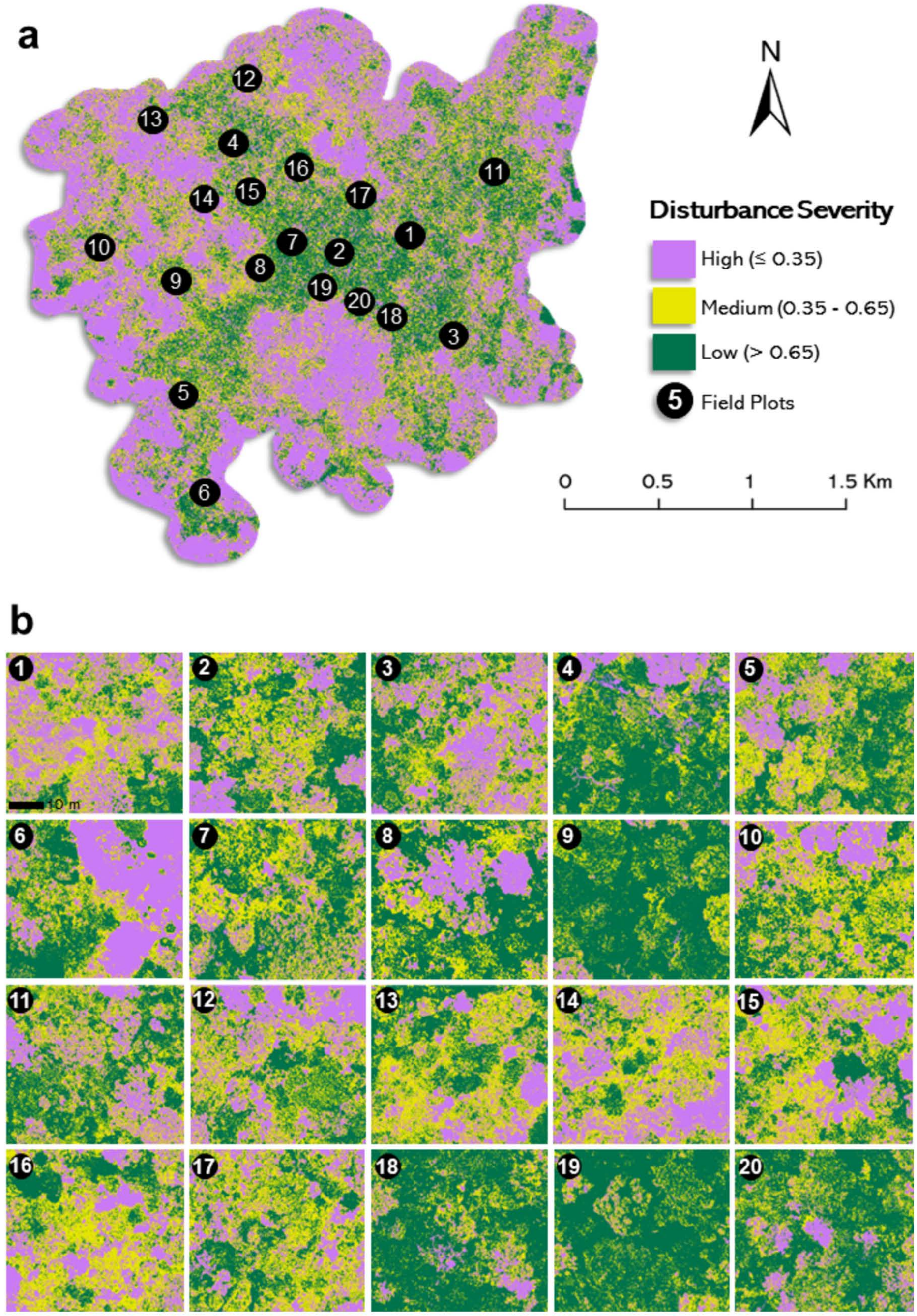

Fig. 8. (a) Categorical disturbance map derived from the IDI showing high, medium, and low disturbance zones; (b) Zoomed-in disturbance maps for the 20 field plots, highlighting localized disturbances.

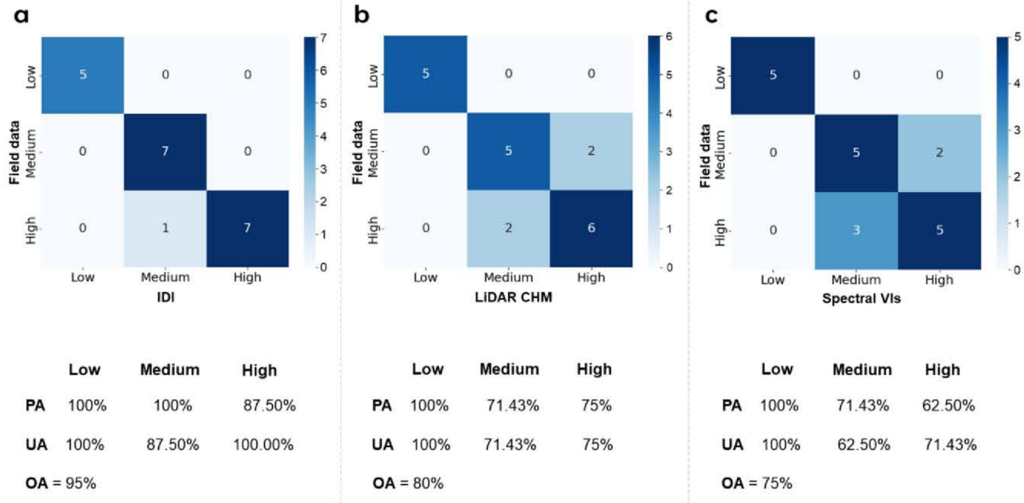

Fig. 9. Confusion matrices and performance metrics for disturbance severity classification with the different datasets: (a) IDI, (b) LiDAR CHM, (c) Spectral VIs.

4. Discussion

Our UAV LiDAR and multispectral data fusion approach showed a strong potential for assessing the status and disturbance severity of tropical forest fragments. By combining LiDAR-derived structural metrics with multispectral VIs through PCA, we achieved a comprehensive and accurate characterization of forest disturbance. To our knowledge, this is the first study to combine UAV LiDAR and multispectral data to evaluate the status and disturbance severity across a West African tropical forest.

4.1. Forest structural and spectral characteristics and their relationships

The structural properties quantified through the LiDAR-derived CHM provided insights into the 3D structure and vertical complexity of the forest. The relatively low H_{95} (20 m) compared to the maximum height of 48 m observed in the study area suggests a generally low overall forest stature. While a definitive reference threshold for mature West African forests is not available, this relatively low value suggests the overall forest stature is generally low compared to what would be expected in a mature undisturbed tropical forest (Vaglio Laurin et al., 2014). This low stature likely results from the logging of large trees, which has hindered the forest's ability to attain its full structural complexity and vertical stratification.

Further evidence of disturbance is reflected in the relatively open canopy structure, with a canopy cover density of only 56 % and a high gap fraction of 44 %. These results corroborate the findings of Dupuis et al. (2023), who associated open, gapped canopy conditions with anthropogenic disturbances. The average rumple index of 2.54 indicates a low degree of canopy surface roughness, which is perceived as a sign of disturbance. These structural characteristics suggest that past disturbances may have simplified vertical stratification and created a smoothened canopy surface across this forest.

The spectral VIs offered complementary insights into forest health and productivity interacting with structural development. The positive correlations between canopy height and VIs like EVI, NDRE, and LCI confirm that taller, more complex forest stands exhibit higher canopy moisture content, chlorophyll concentrations, and photosynthetic activity (Huete, 2012). However, the considerably low values observed in spectral indices like SAVI, NDRE, and LCI suggest potential deterioration in canopy moisture, leaf pigments, and photosystems across different parts of the forest. The low VI values observed in areas with relatively high biomass and greenness during the less intense rainy season may indicate localized disturbances such as selective logging, which can impact forest structure while leaving surrounding vegetation largely intact (Cazzolla Gatti et al., 2015).

While GNDVI is more sensitive to canopy density and adjusted greenness, it might not always be directly proportional to canopy height. This could explain why its relationships with canopy height were not as strong as those observed for indices like NDRE and LCI, which are more directly related to the canopy's structural characteristics and biophysical properties. Previous studies have shown that canopy structure and vertical complexity can significantly influence indices like NDRE and LCI more than greenness-based indices like GNDVI (Huete, 2012; Zou and Mõttus, 2017). Additionally, the weaker relationships between the indices and canopy height could be attributed to potential variability arising from vegetation stress factors, such as moisture availability or nutrient deficiencies, which may not be directly linked to canopy height but can affect greenness and density measures (Vélez et al., 2023).

4.2. Data fusion and disturbance mapping

The disturbance characterized by the data fusion approach reflects aspects of the tropical forest status that neither the multispectral nor LiDAR data streams can independently capture. The intrinsic structural properties derived from LiDAR cannot detect subtle declines in moisture content, photosynthetic productivity, and chlorophyll concentration, which often precede visible structural changes in vegetation (Both et al., 2019). For instance, our results showed that using LiDAR data alone had a UA of only 71.43 % for mapping medium disturbance areas, likely missing early signs of stress or deterioration not yet manifested in structural changes. Similarly, relying solely on multispectral data had a PA of 71.43 % for medium disturbance, potentially overlooking emerging patterns in forest structure signaling disturbance, such as canopy thinning, gap formation, or changes in vertical complexity (Souza et al., 2005). An example could be a selectively logged area where the canopy structure has been altered, but the remaining vegetation may still appear spectrally similar to an undisturbed forest.

Combining structural and spectral metrics through PCA provides a more comprehensive understanding of forest status. Among the variables integrated into PC1 (IDI), EVI, CHM, and GNDVI exhibited the highest loadings. Since GNDVI and EVI had slightly weaker correlations with CHM compared to NDRE, SAVI, and LCI, which are more closely related to structural characteristics of the canopy, they provided complementary information better suited for capturing vegetation spectral vitality. The complementary nature of these metrics enables the detection of both structural deteriorations captured by the LiDAR-derived CHM and declining spectral vitality reflected in VIs like EVI and GNDVI.

The accuracy assessment of this approach showed that it aligns more closely with field-based observations of disturbance, indicating its improved performance for disturbance characterizations. This integrated method reveals not only canopy structural damage or pigment loss but also serves as an indicator of potential threats to interconnected ecological processes that regulate forest function, such as nutrient cycling, water balance, and energy exchange. These processes are susceptible to disruptions caused by disturbances (Nepstad et al., 2008). By identifying areas exhibiting signs of stress or deterioration through the combined structural and spectral signals, it is possible to take management action to prevent further decline.

4.3. Implications for sustainable forest management

The spatial patterns of forest disturbance mapped in this study provide critical information to guide sustainable forest management responses focused on conservation, sustainable use, and restoration. Evidence from the field observation points to anthropogenic disturbances like timber harvesting, agricultural expansion, and uncontrolled fires as key factors degrading forest structure and condition. These findings align with previous studies that have highlighted the severe implications of such disturbances for forest sustainability if not properly managed. For instance, Barlow et al. (2016) found that anthropogenic disturbances, particularly fire and logging, have caused widespread degradation of Amazon forests, with negative impacts on carbon storage, biodiversity, and other ecosystem services. Their study highlights the urgent need for sustainable forest management practices to mitigate these disturbances. Similarly, Lewis et al. (2015) reported that human activities, such as deforestation, selective logging, and fragmentation, are major drivers of forest degradation in the tropics, leading to significant losses in biomass and biodiversity. They emphasize the importance of implementing conservation strategies and sustainable land-use practices to preserve the integrity of these ecosystems.

The IDI developed in this study provides a more detailed understanding of the forest conditions, allowing for management interventions to be tailored according to disturbance severity. This targeted approach helps avoid inadequate interventions in highly disturbed areas and overly aggressive actions in minimally affected areas, thereby ensuring efficient allocation of limited conservation resources. The spatial detail of the IDI also allows for the identification of disturbance agents and potential remedies, informing contextualized sustainable forest management policies. For example, areas mapped as high disturbance (49 % of the forest) face immediate risks of ecological transformation away from natural forest states. In these zones, urgent action is needed to protect the remaining habitat quality and sustain biodiversity, carbon storage, and other ecosystem services vital for sustainable management (Barlow et al., 2016). This calls for interventions that limit further anthropogenic pressures, such as illegal logging, which has been detected in this zone. While local community efforts to deter such degrading activities exist in the region, they have only partially succeeded (Abdul Aziz et al., 2024). This highlights the need for additional strategies to enhance forest protection. Furthermore, to aid the recovery of these highly disturbed areas, implementing assisted natural regeneration through silvicultural practices could be beneficial (Brancalion et al., 2019).

Similarly, 28 % of the forest categorized as medium disturbance requires continued monitoring to avoid further decline in forest vitality. Prioritizing the conservation of proximal intact forest areas can help buffer these partially degraded zones against encroaching edge effects (Bakarr and Abu-Bakarr, 2022). Enrichment plantings to boost understory diversity could also strengthen the resilience of these forests against potential invasive species colonization following disturbance (Yeong et al., 2016). For the areas mapped as low disturbance (23 % of the forest), active conservation is needed to maintain these zones as propagule reservoirs capable of facilitating recovery in disturbed regions (Sloan et al., 2016). Conducting biodiversity surveys to map species distributions in relation to degradation levels can inform sustainable management plans. Co-management with government entities can support community-based arrangements to protect suitable habitats harboring endangered flora and fauna likely persisting in these intact forest refugia. Connecting such refugia through habitat corridors could enable climate-adaptive species migrations as climate change impacts accelerate (Heller and Zavaleta, 2009). Opportunities for carbon finance programs like REDD+ aimed at reducing emissions from deforestation may incentivize continued conservation in these low-disturbance zones (Andoh et al., 2022).

4.4. Limitations and future research direction

This study utilized data collected during a single period for each sensor type (LiDAR and multispectral), which allowed us to evaluate the current state of the forest and identify areas of concern for targeted conservation efforts. While this snapshot provides valuable insights, some limitations warrant discussion. First, our study did not capture changes over time, which restricts our understanding of how the forest evolves and recovers (i.e., forest successional pathways and dynamics). To fully comprehend the impacts of disturbances on these pathways, a multi-temporal approach would be essential and could be a worthwhile direction for future research. This will involve acquiring regular UAV LiDAR and multispectral data across wet and dry seasons over multiple years. Such a temporal dataset would not only enhance the characterization of disturbance severity on forest successional pathways but also quantify post-disturbance recovery rates. By capturing the temporal dimension, researchers could model tropical forest stability regimes and their responses to different disturbance types and severities, providing a more holistic understanding of these complex ecosystem processes. This approach would complement the findings of the present study and offer insights into the long-term trajectories of forest recovery and resilience.

Additionally, future studies should consider employing LiDAR sensors optimized for multi-return recording to expand the suite of structural variables that can be derived from the data. Since 85 % of the LiDAR returns in this study were first pulses, the sub-canopy vegetation structure was not fully captured, limiting the characterization of vertical complexity within the forest profile from the canopy to the understory layers. By leveraging multi-return LiDAR systems, additional metrics related to the vertical distribution of vegetation elements below the canopy could be extracted, providing a more comprehensive representation of the 3D forest structure (Hancock et al., 2019; Leitold et al., 2014). This enhanced structural information could improve the ability to assess ecosystem health and biodiversity across different vertical strata. The sub-canopy layers play a crucial role in supporting diverse plant and animal communities (Goetz et al., 2007). For instance, Müller et al. (2018) demonstrated that LiDAR-derived vertical forest structure metrics are strong predictors of bird species richness in temperate forests. Similarly, Simonson et al. (2014) found that the structural complexity of the understory, as measured by LiDAR, was positively associated with bat species diversity in tropical forests.

Lastly, expanding the applicability of the UAV-derived disturbance mapping methodology to larger spatial scales is a critical next step toward advancing the understanding of forest disturbance patterns. Future research could explore integrating high-resolution satellite imagery and airborne LiDAR data with UAV data, enabling the extrapolation of localized findings to national and regional levels (Lima et al., 2019). Hyper-spectral satellites, such as the German Environmental Mapping and Analysis Program (EnMAP) and the Italian PRecursore IperSpettrale della Missione Applicativa (PRISMA), provide finer spectral resolution, potentially improving the detection of subtle changes in forest health and composition (Transon et al., 2018). Moreover, space-borne LiDAR systems like Global Ecosystem Dynamics Investigation (GEDI) offer opportunities for large-scale, 3D forest structure assessment (Dubayah et al., 2020). By combining GEDI's global coverage with the fine-scale detail from UAV-LiDAR, we could develop more robust models of forest structure and biomass across vast areas. This multi-scale, multi-sensor approach can potentially improve the assessment and management of forest resources. It could provide a more comprehensive view of forest dynamics, from individual tree-level changes captured by UAVs to landscape and regional patterns observed by satellites. Such integrated methodologies would equip decision-makers with powerful tools to implement effective conservation and restoration strategies, monitor progress toward national and international forest management goals, and better understand the complex interactions between local disturbances and larger-scale forest health trends.

5. Conclusions

This study demonstrated the effectiveness of fusing UAV LiDAR and multispectral data to enhance tropical forest disturbance mapping. By integrating structural metrics from LiDAR with spectral metrics through PCA, we achieved a more comprehensive and accurate characterization of forest disturbance compared to using either dataset alone. The resulting IDI proved effective in delineating gradations of disturbance—low, medium, and high—across the forest. This stratification enables forest managers to implement interventions specifically tailored to the degree of disturbance, optimizing the use of limited conservation resources. Field observations linked the mapped disturbances to anthropogenic drivers like logging, agriculture expansion, and fires, informing targeted mitigation strategies. The novelty of this research lies in the complementary integration of structural and spectral indicators, providing a better understanding of tropical forest ecosystem health. By presenting an accessible framework for fusing UAV LiDAR and multispectral data, this study paves the way for the widespread implementation of advanced disturbance mapping techniques. This supports evidence-based conservation strategies crucial for safeguarding vulnerable tropical forests in the face of accelerating global changes and anthropogenic pressures.

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CRediT authorship contribution statement

Chima J. Iheaturu: Writing – original draft, Writing – review & editing, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Samuel Hepner:** Writing – review & editing. **Jonathan L. Batchelor:** Writing – review & editing. **Georges A. Agonvonon:** Writing – review & editing. **Felicia O. Akinyemi:** Writing – review & editing, Supervision. **Vladimir R. Wingate:** Writing – review & editing, Supervision. **Chinwe Ifejika Speranza:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2024.102876.

Data availability

The codes used in this study are available at doi:https://doi.org/10.5281/zenodo.13844840.

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5.5 Paper 5: Perceived and Measured Forest Degradation in West Africa: Insights for Sustainable Forest Management

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Perceived and measured forest degradation across Western Africa: Insights for sustainable forest management

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ABSTRACT

Tropical forests face fragmentation, degradation, and conversion, leading to biodiversity loss, reduced carbon storage, and diminished ecosystem services. While local populations depend on forest products, the intensity of these extractions can lead to forest degradation. This paper examines the interplay between socio-economic pressure, perceived and measured forest degradation, and the insights to be gained for informed forest management.

A survey of 1956 respondents was conducted across seven forests in Togo, Benin, Nigeria, and Cameroon, from which 328 forest users were identified who regularly work in one of the seven studied forests. In semi-structured questionnaires, we asked about forest uses and perceptions of corresponding impacts on forest integrity. We integrated spatially explicit demographic and governance data (forest pressure) with interview-based insights (perceived degradation) and quantitative assessments of forest structural complexity (measured degradation).

Most forest users gather non-timber forest products, though hunting and logging were also important activities. Generally, forests affected by logging and fire, or conversion to agriculture, were perceived as degraded. Further, the disappearance of large, old trees, different plant and animal species, and the loss of forested areas were observed over the years. However, perceptions did not always reflect forest uses. The community with the highest pressure on forests was least concerned about forest degradation, while people near strictly protected and sacred forests were most concerned. The different relationships between local perceptions, measurable forest degradation, and pressure on forest resources need to be considered to guide sustainable forest management and reduce ongoing forest degradation and biodiversity loss in Western Africa.

1. Introduction

1.1. Persistence and degradation of isolated forest patches in Western Africa

Tropical forests are being cleared at an unprecedented pace across the globe (Hansen et al., 2013; Poorter et al., 2021; Schelhas and Greenberg, 1996). In Western Africa, over 80 % of the forest cover present in 1900 has been lost, primarily due to agricultural expansion driven by population growth (Akinyemi and Ifejika Speranza, 2022; Aleman et al., 2017; Amani et al., 2021; Curtis et al., 2018). This deforestation has, particularly in the rainforest zone, fragmented large, continuous forests into numerous small patches that now characterize much of the Western African landscape (Dangbo et al., 2020; Taubert et al., 2018; Wingate et al., 2022). In Togo, Benin, Nigeria, and Cameroon alone, more than 400,000 forest patches have been identified (Wingate et al., 2022). These patches, while critical for biodiversity conservation, climate regulation, and ecosystem services (Lewis et al., 2015), face significant threats from edge effects such as fire, desiccation, and species extinctions (Hill and Curran, 2003; Ibáñez et al., 2014; Laurance, 2004).

Clearing rainforests not only contributes to the current ecological crisis but also poses a significant social and economic challenge (Lewark, 2022). Millions of people live in or near tropical forests, many of whom are among the poorest and rely on forest resources for their livelihoods (Lewark, 2022; Lewis et al., 2015; Rietbergen, 1993). Over generations,

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forest-dependent communities have developed complex silvicultural practices rooted in their deep connection with the forest, yet these practices are often poorly documented and not well understood by scientists and policymakers (Shanley et al., 2016). While originally sustainable, many of these practices are no longer viable due to growing pressures (Lewark, 2022). Overexploitation of forest resources, driven by increasing demands from both rural and urban populations and enhanced access to markets and the monetary economy, contributes to forest degradation as well as forest loss (Lewark, 2022; Malhi et al., 2013).

1.2. Framing forest degradation

Forest degradation is not univocally defined, but it generally refers to the simplification of forest structure, the reduction of biodiversity, and the decline in the capacity of a forest to provide ecosystem services compared with an intact reference forest (Ghazoul et al., 2015; Hepner et al., 2025; Vásquez-Grandón et al., 2018). In contrast, deforestation denotes a change in land use that results in the permanent reduction of tree canopy cover below 10 % (Food and Agriculture Organization of the United Nations (FAO), 2020a, 2020b). Unlike deforestation, degradation does not necessarily involve a complete loss of tree cover; rather, it describes the biophysical alterations caused by damaging human activities, which may unfold over long periods and become evident only gradually and subtly (Vásquez-Grandón et al., 2018). Understanding forest degradation, therefore requires not only an assessment of the actual and reference ecological state given current environmental conditions, but also attention to its social-ecological context (Schulze et al., 2019), including how forests are used (Putz, 2011), and how local communities perceive forest conditions (Ihemezie et al., 2021). The social-ecological context includes the interplay of broader social, cultural, political, and economic factors and drives forest conservation and degradation, respectively (Ihemezie et al., 2022). In many developing countries, a plethora of economic incentives leads people to degrade forests (Ihemezie et al., 2022; Vásquez-Grandón et al., 2018). However, intrinsic and relational values can also lead to forest conservation (Ihemezie et al., 2021).

1.2.1. Forest uses and their roles in forest degradation

Forest uses often sustain livelihoods but, when unsustainable, such as overharvesting timber, can result in forest degradation and loss (Lewark, 2022; Vásquez-Grandón et al., 2018). In multi-purpose forests, sustainable management depends on minimizing impacts on other uses; otherwise, conflicting and unsustainable practices can lead to forest degradation (Schulze et al., 2019). In Western Africa, communities depending on forests for their livelihoods use them in diverse ways—including harvesting non-timber forest products, timber, fuelwood, and charcoal, hunting bushmeat, and engaging in religious practices—often with overlapping impacts that compromise forest integrity (Asner, 2009; Johns, 2004; Malhi et al., 2014).

Forest products are often categorized under **Non-Timber Forest Products (NTFP)**, which include firewood, fruits, fodder, fiber, and food (Lewark, 2022; Prasad, 1999; Pretzsch, 2014). Alternatively, these products are sometimes framed as Non-Wood Forest Products (NWFP), explicitly excluding wood (Muir et al., 2020). Most NTFP are harvested sustainably (Corlett, 2016), but frequent harvesting and harmful practices such as overexploitation can lead to forest degradation and local species extinction (Johns, 2004; Rietbergen, 1993; Shanley et al., 2016).

Timber is the most widely traded and controversial forest product (Barbier et al., 2019; Rietbergen, 1993). The selective removal of high-value timber species, a practice known as high-grading, has several cascading effects on forest ecosystems, including gap formation and reduced structural complexity (Asner, 2009). Although selective logging can provide short-term employment and income, it often facilitates forest access, increases hunting pressure, accelerates fragmentation, and ultimately contributes to deforestation (Johns, 2004; Lewis et al., 2015; Malhi et al., 2014).

In Sub-Saharan Africa, **fuelwood and charcoal**, which are the most important energy sources (Leach and Mearns, 1993; Sola et al., 2019), have also contributed to forest degradation and deforestation (Sedano et al., 2016; Williams and Anghelea, 2021). Fuelwood sourced from forests represents a substantial biomass removal, with uncertain effects on nutrient and carbon cycles but a possible reduction in forest flammability (Malhi et al., 2014; Morton, 2007).

In recent years, fire frequency and spatial extent have increased significantly (Malhi et al., 2014; Shlisky et al., 2009), making it a major driver of forest degradation in Western Africa (Dago et al., 2023; Goldammer, 2016). Yet, **fire** has been used for millennia to manage tropical forests (Goldammer, 2016; Tacconi et al., 2006). It is employed to enhance soil fertility and increase crop yields, control pests and weeds, and facilitate hunting (Amoako and Gambiza, 2022).

Forests are important sources of **bushmeat and fish**, which are primary sources of protein for many subsistence societies (Brashares et al., 2004; Lewark, 2022; Shanley et al., 2016). However, defaunation significantly impacts forest ecosystems by breaking trophic chains and altering plant dissemination (Lewis et al., 2015; Malhi et al., 2014). Fish depletion and impacts of artisanal fishing in seasonally inundated forests remain largely unknown in Western Africa.

Forests are also used for non-material services, such as for **religious practices**. Western Africa is home to the animistic religion Vodún (Alohou et al., 2016). While the conservation of forests and trees is not a central tenet of the Vodún religion (Fournier, 2011; Nyamweru and Sheridan, 2008), there are thousands of sacred forests in Western Africa with intact plant communities, high biodiversity, and substantial aboveground biomass (Kossi et al., 2021; Lynch et al., 2018). However, traditional woodcuttings and forest burnings for the religious interpretation of smoke signals can also lead to forest degradation (Kokou and Sokpon, 2006; Kossi et al., 2021). Thus, it is important to understand the social-ecological contexts of forest degradation.

1.2.2. The social-ecological context of forest degradation

Individual use of forest resources has localized impacts, but pressures at the forest scale are largely determined by broader socio-economic conditions (Geist and Lambin, 2002). In many African rural areas, livelihoods depend heavily on subsistence farming and forest products such as fuelwood and timber, with limited market access and mechanization further reinforcing this dependence (Neuenschwander et al., 2015; Sulaiman et al., 2017; Van Vliet and Nasi, 2008).

1.2.2.1. Pressure on forests. Land and forest degradation arises from the interaction of social, ecological, and institutional factors that together shape human pressure on forest ecosystems. While a larger population near forests does not always result in greater degradation (Agrawal, 1995; Wardell et al., 2003), it often does so, as higher population density tends to increase demand for forest resources and pressure on forest integrity (Mertens and Lambin, 2000; Mon et al., 2012; Ryan et al., 2017; Zhao et al., 2006). In this study, we adopt the assumption that population size generally correlates with forest use intensity. The number of users entering forests to extract resources directly affects the rate of exploitation, and even when resources are renewable, additional users raise the likelihood of exceeding the forest's carrying capacity (De, 2012). Excessive logging and hunting can disrupt forest structure and ecological processes, including water and carbon cycling and animal population dynamics (Lewis et al., 2015; Malhi et al., 2014). Infrastructure such as roads and tools like chainsaws further accelerate degradation by improving access and extraction efficiency (Ahrends et al., 2010). The **ecological setting** modulates these dynamics. Larger forests can buffer pressure more effectively than smaller ones, while **isolation**—the ratio of forest to non-forest area in the immediate surrounding (Hepner et al., 2025)—captures how unique or exposed a forest is within its landscape context. More isolated forests often face higher pressure due to limited alternative resource areas. Similarly, **fragmentation**—the proportion of forest area close to an edge (Fischer et al., 2021; Hepner et al., 2025)—increases accessibility and vulnerability, creating a feedback loop in which human use generates more edges, which in turn attract further use (Olupot and Chapman, 2006). Moreover, smaller and more fragmented forest patches typically have reduced capacity to regenerate or recover from disturbances and are more likely to disappear over time compared to larger, less fragmented forests (Wingate et al., 2024). Finally, **governance** mediates how human and ecological factors translate into actual pressure (cf. Fasona et al., 2019). Governance structures—ranging from prohibited or sacred access to family- or community-based management (Mintah et al., in prep.)—can either restrict or enable forest use. Together, population demand, types of use, ecological context, and governance determine how strongly human activities shape forest degradation.

1.2.2.2. Perceived forest degradation. While forest use and resource extraction generally lead to measurable alterations in the ecosystem, these changes are subjectively perceived by forest users (Fernández-Llamazares et al., 2015). Perceptions of forest degradation depend on socio-economic status, interests, and the perceived benefits from forests (Hasanah et al., 2019; Ihemezie et al., 2022). For instance, when land conversion from forest to non-forest generates economic profits, users may view it as land valorization rather than degradation, despite the objective loss of forest ecosystem services (Hasanah et al., 2019; Ihemezie et al., 2022). Since forest changes can occur gradually and over timescales that are difficult for people to perceive (Binkley, 2021), perceptions of degradation often deviate from measured forest change. Communities tend to notice tangible signs such as the decline of valuable timber species, the need to walk longer distances or purchase timber that is no longer available nearby, lengthening dry seasons and delayed rains, or increased time and effort needed for hunting due to declining wildlife (cf. Hermans-Neumann et al., 2016). Yet many forms of degradation remain unreported, including the loss of already rare species, subtle shifts in forest structure, or changes in less valued species that are not perceived as relevant to local livelihoods (cf. Binkley, 2021; Food and Agriculture Organization of the United Nations (FAO), 2011). Perceptions of degradation are particularly important among local users, since they directly influence forest use and management (Adenle et al., 2022; Fernández-Llamazares et al., 2015; Tadesse and Teketay, 2017; Tesfaye et al., 2012). While perceptions shape how people act, measurable indicators remain essential to assess ecological change directly.

1.2.2.3. Measured forest degradation. Forest degradation is often a slow and subtle process, making it challenging to detect directly through observation and remote sensing (Jiménez-Rodríguez et al., 2022; Reygadas et al., 2019). Nevertheless, it can be assessed indirectly using specific indicators, such as biodiversity loss, biomass decline, and simplification of forest structural complexity (Ghazoul et al., 2015; Hepner et al., 2025). Forest structural complexity refers to the three-dimensional arrangement of forest and tree components and can be measured using terrestrial laser scanning (Ehbrecht et al., 2017). It is strongly correlated with ecosystem functioning, productivity, biodiversity, and overall forest integrity (Coverdale and Davies, 2023). High structural complexity typically indicates intact, resilient forest ecosystems (Coverdale and Davies, 2023; Ehbrecht et al., 2017) with minimal human impact (Johns, 2004; Poore, 2013; Shanley et al., 2016; Willim et al., 2019), though some forest types are naturally less complex (e.g., tropical savanna and woodlands; Ehbrecht et al., 2021). In general, structural complexity that is substantially lower than the natural reference for a given forest type is a key indicator of degradation (Hepner et al., 2025). Comparing actual and reference structural complexity provides a rapid, objective assessment of degradation.

Finally, integrating the forest's social-ecological context, actors' perceptions, and objective measures such as structural complexity provides a more comprehensive understanding of forest degradation. This integration highlights the need for management approaches that bring these dimensions together.

1.3. Addressing degradation through sustainable forest management

To address forest degradation and balance forest use with conservation, sustainable forest management (SFM) has been proposed (Corlett, 2016). SFM refers to "*the process of managing permanent forest land to achieve one or more clearly specified objectives of management with regard to the production of a continuous flow of desired forest products and services without undue reduction in its inherent values and future productivity and without undue undesirable effects on the physical and social environment*" (International Tropical Timber Organization (ITTO), 2006, p. 12).

SFM represents a compromise between different values, as defined by various interest groups (Lewark, 2022) and can help slow forest degradation (Knoke, 2016). However, social, economic, and ecological sustainability often conflict (Lewark, 2022), and management decisions cannot rely solely on objective measures such as forest structural complexity (Ehbrecht et al., 2017; Hepner et al., 2025). Effective management must also consider the perceptions of forest users, which may diverge from measured conditions and vary across social groups (Meijaard et al., 2013; Taddese et al., 2020).

By integrating multiple perspectives—social-ecological context, user perceptions, and objective indicators—SFM can be both ecologically sound and socially legitimate (Colfer, 2005; Reed, 2008). This paper thus provides insights for SFM by comparing pressure on forests with perceived and measured forest degradation. We examine seven forest patches in the agricultural landscapes of Togo, Benin, Nigeria, and Cameroon, a poorly studied region with diverse social-ecological conditions, including both sacred and non-sacred sites. We pose the following research questions and hypotheses:

1. To what extent do forest use patterns differ across forests with varying socio-cultural, economic, and ecological contexts?
   - H: Forest use is expected to be dominated by the collection of non-timber forest products across all sites, with minor differences possibly linked to observable site characteristics, such as governance rules (e.g., sacred forests) or ecological conditions (e.g., swamp vs. semi-deciduous forests).
2. How do perceptions of forest use impacts differ across sites with varying socio-cultural, economic, and ecological contexts?
   - H: Logging and fire are expected to be widely perceived as degrading forests across sites, while perceptions of other activities (e.g., agriculture, charcoal production, NTFP collection) are expected to show greater variability depending on measurable or describable contextual factors, such as forest type, local restrictions, or community norms.
3. How are pressure on forests and perceived and measured forest degradation interrelated?
   - H: Forests under greater pressure of use (e.g., logging, hunting, weak governance) are expected to show higher measured degradation. These pressures are also likely to shape local perceptions, such that observable degradation corresponds with community perceptions.

2. Methods

2.1. Study site

2.1.1. Ecological characterization of forests

We selected seven forest patches in Togo, Benin, Nigeria, and Cameroon, in the two biomes of the 'Tropical and Subtropical Grasslands, Savannas, Shrublands', and the 'Moist Broadleaf Forests' (Fig. 1; Dinerstein et al., 2017; see Table A1 for details). These sites include

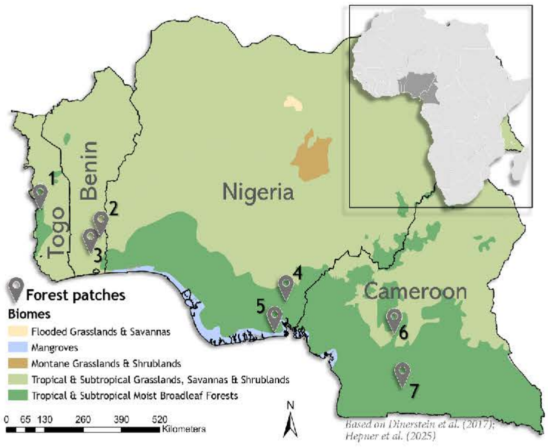

Fig. 1. Forest management practices of seven forest patches were studied in the Tropical & Subtropical Grasslands, Savannas & Shrublands (light green) and the Tropical & Subtropical Moist Broadleaf Forests (dark green) of Togo, Benin, Nigeria, and Cameroon, in Africa (marked grey in the inset map). 1. Koui, 2. Ewè-Adakplamè, 3. Hlanzoun, 4. Iko, 5. Ikot, 6. Mbangassina, 7. Ngam-Kondomeyos.

semi-deciduous forests (1. Koui and 2. Ewè-Adakplamè, also known as Kouvizoun sacred forest Adakplamè-Ewè), swamp forests (3. Hlanzoun, also known as Lokoli, and 5. Ikot), and moist forests (4. Iko, 6. Mbangassina, and 7. Ngam-Kondomeyos), ranging from 20 to 1160 ha. Precipitation varies between 1000 and 1300 mm in Koui, Ewè-Adakplamè, and Hlanzoun, and from 1500 to 3000 mm in Iko, Ikot, Mbangassina, and Ngam-Kondomeyos, with annual temperatures averaging between 23 and 28 °C (Hijmans et al., 2005). Common tree families in these forests include Moraceae (e.g., *Treculia africana*), Fabaceae (e.g., *Gilbertiodendron dewevrei*), and Myristicaceae (e.g., *Pycnanthus angolensis*). The selected forests build on previous studies (Hepner et al., 2025; Wingate et al., 2022, 2023, 2024), contributing to a more comprehensive understanding of Western African forest patches.

2.1.2. *Socio-economic characterization of forest communities*

Most people living in the areas surrounding these forests earn less than $1 per day, have limited formal education, and rely on forest resources such as timber, fuelwood, bushmeat, and medicinal plants (Food and Agriculture Organization of the United Nations (FAO) & United Nations Environment Programme (UNEP), 2020; Neuenschwander et al., 2015). Based on the Relative Wealth Index (Chi et al., 2022), these communities are economically modest, ranging from −0.6 in Mbangassina to 0.3 in Ikot. While this does not indicate extreme poverty (−1), it is typical for low- and middle-income countries and affects daily life: residents may have limited access to household assets, reliable electricity, transportation, clean water, sanitation, and waste management (Chi et al., 2022; Rutstein and Johnson, 2004).

These socio-economic conditions contribute to a high pressure on forests, which is further amplified by (i) rapid population growth (United Nations, Department of Economic and Social Affairs (UNDESA), Population Division, 2022), (ii) economic inequalities (Goers et al., 2012), (iii) widespread corruption in governance structures (Ighodaro and Igbinedion, 2020), and (iv) insecure land tenure, poor mapping and documentation of land uses, and resulting land disputes (Ewane et al., 2015; Kouassi et al., 2022). Consequently, sustainable forest management is rarely prioritized.

Forest governance and ownership vary across sites, and we differentiate four types based on rules of access and use (Mintah et al., in prep.). These rules define who can enter the forest and what activities are permitted within it, both of which strongly influence degradation dynamics.

Type 1 corresponds to forests where both access and use are completely prohibited due to sacredness, as in Koui. Women are not allowed to enter at all, and only initiated men may enter on explicit invitation to perform religious rituals; otherwise, no one enters or uses the forest.

Type 2 represents partially sacred forests, where some areas are restricted (completely protected) and others are accessible for limited use. On certain days, no one may enter the forest, but for most of the year, men and women, including non-initiated individuals, can access non-sacred parts, while sacred sections remain strictly protected (e.g., Ewè-Adakplamè, Hlanzoun).

Type 3 encompasses family-managed forests, where access and use are controlled by individual family lineages. Only family members can enter and manage their plots according to lineage-specific rules (e.g., Ikot, Mbangassina).

Type 4 corresponds to community-managed forests, which are generally the most accessible: members of the local community are allowed to enter and use forest resources according to communal rules (e.g., Iko, Ngam-Kondomeyos).

In practice, these classifications are not absolute: not all users comply fully with customary rules, and governance arrangements may change over time. Ownership disputes are rare, occurring only in Ewè-Adakplamè, where they indirectly weaken compliance with access and use regulations as belief systems evolve. Day-to-day governance and enforcement largely depend on local institutions, customary arrangements, and their interplay with formal government structures.

Most people in these communities work in agriculture, which constitutes the dominant land use surrounding these forest patches, along with croplands and agroforestry systems. These land-use patterns interact with forest governance: sacred and community-managed forests tend to have stricter rules on clearing or logging (Kossi et al., 2021), whereas family-owned forests may experience more variable land-use pressure depending on family practices (see also Nath et al., 2018). Despite the lack of strong formal protection, these forest patches have persisted since at least 1975, surrounded by croplands, agroforestry, and wetlands (Hansen et al., 2013; Wingate et al., 2022).

2.2. Data collection

Between September 2022 and March 2023, we conducted a household survey with 1956 randomly selected households in 22 villages near the seven forests in Togo, Benin, Nigeria, and Cameroon, based on Cochran's sample size for an unknown population size (Cochran, 1977). From this sample, 328 individuals (15 %) reported that they regularly use the forest and are familiar with its current condition. We therefore administered our questionnaire to these respondents (see Supplementary Information for the questionnaire).

Surveys were carried out by members of our research team, supported by assistants from local universities and forest ministries, using the software Epicollect5 (Aanensen et al., 2009). Interviews were conducted in local languages and later translated into English. Questions were typically posed in a closed-ended format with predefined answer options, followed by open-ended prompts that allowed respondents to elaborate freely (Table 1). To ensure clarity, the concept of forest degradation was translated into practical interview questions (e.g., disappearance of tree species) and distinguished from deforestation, which was assessed through questions on forest area or canopy cover change. All respondents were informed about the purpose of the survey and gave their consent to participate.

The final sample of 328 respondents represented 17 ethnic groups, with up to six ethnic groups per forest (Table 2). Age ranged from 20 to 65 years, with most interviewees being over 40 and having lived near the forests for more than a decade (Figs. A1 and A2). Only 9 % of respondents were women, reflecting local norms where men typically speak for the household. Most respondents reported subsistence uses of forest resources (fuelwood, wild foods, medicinal plants), while some also mentioned commercial activities such as bushmeat and timber sales.

Table 1
Examples from the questionnaire with alternating closed-ended and open questions. Closed-ended questions offered predefined answers (shaded grey), while open questions allowed free elaboration (white background). Questions 1–4 focus on forest degradation (e.g., impacts of logging, species disappearance), while questions 5–6 address deforestation (forest area change). The questionnaire is available as supplementary information.

Questions	Answers
1. What is the impact of logging on forest integrity?	• Strong negative impact • Low negative impact • No impact • Low positive impact • Strong positive impact
2. Explain the impact of logging	• E.g., less trees • E.g., hotter temperatures • E.g., it is forbidden to log trees • E.g., the forest becomes more open
3. Do you know any tree species that disappeared?	• Yes • No
4. Which tree species disappeared?	• E.g., Mahogany • E.g., Iroko
5. Did the forest area change in the last 10 years?	• Yes, it increased • Yes, it decreased • No, it did not change
6. Explain your answer about the forest area change in the last 10 years.	• E.g., Forest area changed due to logging and farming. • E.g. The forest boundaries remain the same.

2.3. Data analysis

All interview data were cleaned in Microsoft Excel (Microsoft Corporation, 2024) and analyzed using R (R Core Team, 2024). Given the varying number of interviews per forest, we primarily worked with relative values.

2.3.1. Pressure on forests

Population pressure on finite resources is a key contextual factor for quantifying pressure on forests (Francesconi et al., 2022). To capture this, we developed a composite indicator of forest pressure for each site based on the following equation and suited to isolated and formally unprotected forest patches:

$$\text{Pressure on forests} = Iso * Pop + Frag * Users + Gov * Harm \quad (1)$$

where:

- **Iso (isolation)** = ratio of forest to non-forest area within a 10 km buffer surrounding each forest (Hepner et al., 2025), describing how isolated the forest patch is in the landscape. Forests with few surrounding trees are assumed to experience higher pressure (Table 3).
- **Pop (population density)** = population living within 10 km of the forest (Bondarenko et al., 2020) divided by forest area (ha), reflecting the local demand on forest resources.
- **Frag (fragmentation)** = ratio of forest area within 100 m of the edge to total forest area (Fischer et al., 2021; Hepner et al., 2025), as edge areas are generally easier to access and exploit (Olupot and Chapman, 2006).
- **Users** = population that regularly uses the forest divided by forest area (ha), based on household surveys in the corresponding communities (Garekae et al., 2017; Jha et al., 2022; Pinheiro et al., 2016; Sambrook et al., 1999).
- **Gov (governance)** = one of four classes based on accessibility and user rules (Mintah et al., in prep.): 1 = prohibited access & sacred, 2 = partial access & sacred, 3 = family-based management, 4 = community-based access.
- **Harm (harmful activities)** = proportion of users engaged in potentially environmentally harmful activities (logging and hunting).

The weights (Iso, Frag, Gov) amplify or buffer human pressures. Higher Iso values indicate greater isolation, where forests are surrounded by less tree cover and thus represent rarer, more sought-after resources in the landscape. Higher Frag values denote greater fragmentation, where a larger proportion of forest area lies close to edges—zones that are more accessible, ecologically exposed, and often the first to be exploited (Olupot and Chapman, 2006). Gov represents access regulation, with lower values corresponding to restricted or sacred access and higher values to more open, community-based use. Together, these factors modulate the strength of human pressure: isolation can concentrate demand, fragmentation enhances accessibility, and governance determines the degree to which access is controlled or extraction permitted.

The model follows an additive logic in which human pressure results from the combined influence of population density, user intensity, and harmful activities. Each of these factors is weighted multiplicatively by its corresponding modifier (*Iso, Frag, Gov*) to reflect that the impact of human presence depends on ecological and institutional context. Multiplication can yield zero values after min–max normalization, which is acceptable and meaningful, as it represents minimal pressure under favorable conditions (e.g., low population or restricted access and use).

We explored alternative weighting schemes to check the robustness

Table 2
Respondents' characteristics for each studied forest community.

Forest	Respondents interviewed (n)	Villages interviewed (n)	Ethnicities interviewed (n)	Males : females interviewed (%)
Koui	3	1	1	100 : 0
Ewè-Adakplamè	11	2	2	100 : 0
Hlanzoun	35	3	3	71: 29
Iko	176	4	5	93 : 7
Ikot	80	6	1	95 : 5
Mbangassina	14	4	6	85 : 15
Ngam-Kondomeyos	9	2	1	1000

of results. The chosen configuration, with *Iso* and *Frag* ranging from 0 to 1 and *Gov* from 1 to 4, was retained as it provided realistic gradients of pressure and reflects the mediating role of governance in how social and ecological factors translate into actual forest use. Empirical evidence shows that governance, while operating through diverse pathways and impacts, often weighs more heavily on forest outcomes than demographic or biophysical drivers, through its effects on enforcement, tenure, and institutional capacity (Fischer et al., 2020; Nolte et al., 2013). The higher weighting assigned to harmful users (1–4) acknowledges their disproportionately direct impact on forest integrity compared to broader population presence or general forest users.

To ensure comparability across forests and reduce the influence of differences in scale and units, we applied a min–max normalization (range 0–1) to the *Pop, Users*, and *Harm* variables before applying the equation (Table 4). The equation builds on similar approaches integrating demographic and spatial data with insights from household interviews (Garekae et al., 2017; Jha et al., 2022; Pinheiro et al., 2016; Sambrook et al., 1999). Iso was extracted in Google Earth Engine (Gorelick et al., 2017) within a 10 km buffer around each forest, chosen as a reasonable walking distance for carrying forest products. Population within 10 km of each forest was derived from spatially explicit census data (Bondarenko et al., 2020) in QGIS (QGIS Development Team, 2023). Forest areas were delineated from forest/non-forest classifications of satellite imagery (Hepner et al., 2025). Variables for regular forest users and harmful activities (logging and hunting) were informed by household surveys in corresponding communities.

After calculating Eq. (1), we compared the resulting pressure values across the seven forests to facilitate site-level interpretation (Table 5). Finally, we assessed the relationship between forest pressure and both perceived and measured degradation using a Pearson correlation test (R Core Team, 2024).

2.3.2. *Determination of forest uses*

Respondents were individuals who regularly work in the forest. They were asked to report their main forest activities, including the collection of NTFPs, hunting, logging, fishing, religious practices, and other uses. Multiple activities could be selected. Activities considered illegal, such as charcoal production, were not asked about directly, but perceptions of their impacts were captured elsewhere in the survey. A heat map was then generated to visualize the distribution of activities across the different forest sites.

2.3.3. *Perceptions of forest use impacts and degradation*

Respondents were asked to classify the perceived impact of specific forest uses on forest integrity using five categories, ranging from 'strong negative' to 'strong positive' impact. The relative contributions of 'low negative' and 'strong negative impact' to the whole spectrum were used to define 'perceived degradation'. To determine whether perceptions differed significantly across communities and users' main activities, we applied a G-test (Agresti, 2007), which is a likelihood-ratio test for categorical data assessing the independence of variables in contingency tables, implemented via the DescTools package (Signorell, 2025). In addition, respondents reported observed signs of degradation, for example the loss of certain species.

2.3.4. *Measured forest degradation*

Forest uses may impact forest integrity and contribute to measurable forest degradation. To define measured degradation, we relied on the difference between actual and reference stand structural complexity as presented in Hepner et al. (2025; Table A2). In that framework, forest degradation and fragmentation are related to structural complexity, with reference values derived from the potential structural complexity modeled by Ehbrecht et al. (2021). This model extrapolates structural attributes from primary forests and predicts the maximum stand structural complexity index (SSCI) achievable under the specific edaphoclimatic conditions of a given location in the absence of human interference. The predictions are spatially explicit at 30 arcseconds (~100 m) resolution, so that each forest patch in our study has its own reference value reflecting local potential conditions.

This reference represents the most complex forest structure achievable under current natural conditions without human interference and thus serves as a benchmark for ecological integrity. Actual structural complexity was quantified using the SSCI, which captures the heterogeneity in the three-dimensional distribution of plant material based on terrestrial laser scans (Ehbrecht et al., 2017).

Forest integrity and degradation are therefore expressed along a continuous range, represented by the difference between actual and reference SSCI values. Negative differences indicate structural simplification relative to the potential reference—i.e., degradation—while values closer to zero suggest higher integrity. For interpretative purposes, we classify stands with substantially negative deviations as degraded and those within the expected reference range as intact. In this study, "intact forest" refers specifically to stands that are not structurally degraded relative to the modeled reference SSCI; it does not necessarily imply a pristine or old-growth state, nor does it encompass other ecological dimensions such as biodiversity or ecosystem functioning, which are beyond the scope of this analysis.

3. Results

3.1. *Forest uses*

The seven forest patches are managed in non-industrial, predominantly manual ways, with minimal use of small machinery like chainsaws. Most people collect non-timber forest products (NTFP, 50 %), while hunting (15 %) and logging (13 %) are also important activities (Fig. 2). Main activities did not differ significantly across forests. In the swamp forest of Hlanzoun, fishing (26 %) is a key activity, while in the sacred forest of Koui, eco-guardian duties ('Others', 67 %) and religious activities (33 %) are important.

NTFP primarily include fuelwood, along with fruits and medicinal plants. The "Others" category includes mainly agricultural activities (46 %), and to a minor degree, trading of forest products, and work as eco-guard. Hunters mainly target mammals, such as small antelopes (e.g., Duiker: *Cephalophus* sp.) and rodents (e.g., rat: *Thryonomys* sp.), but also birds and snakes.

While most people do not actively plant trees, roughly 30 % of respondents plant trees (mainly in Ngam-Kondomeyos, Ewè-Adakplamè, and Ikot). These respondents plant economically valuable species

Table 3
Factors (a, c, d) exert pressure on a forest area (b). Pressure intensity is modulated by three weights: Iso (0–1; 0 = embedded within surrounding forests, 1 = isolated in a treeless landscape), Frag (0–1; 0 = low fragmentation, 1 = high fragmentation with extensive edge areas), and Gov (1–4; 1 = limited accessibility and use, 4 = high accessibility and use).

Forest	(a) Population in 10 km surrounding the forests (Lloyd et al., 2017; WorldPop, 2018)	(b) Area (ha)	(c) Population that regularly uses the forest (n)	(d) Population engaged in logging and hunting (n)	Iso: Isolation	Frag: Fragmentation	Gov: Governance / accessibility (low to high)
Koui	3350	20	3	0	0.69	0.8	1
Ewe-Adakplame	29,200	220	11	6	0.83	0.78	2
Hlanzoun	30,600	680	35	9	0.82	0.49	2
Iko	4000	1160	176	38	0.51	0.33	4
Ikot	488,250	1120	80	49	0.76	0.28	3
Mbangassina	16,300	160	14	3	0.38	0.46	3
Ngam-Kondomeyos	5650	400	9	3	0.12	0.2	4

Table 4
Min–max normalization (0–1) was applied to allow comparison of socio-ecological variables across different forest sites.

Forest	Pop: a/b: min-max normalized	Users: c/b: min-max normalized	Harm: e/c: min-max normalized
Koui	0.38	0.99	0.00
Ewè-Adakplamè	0.30	0.21	0.89
Hlanzoun	0.10	0.22	0.42
Iko	0.00	1.00	0.35
Ikot	1.00	0.38	1.00
Mbangassina	0.23	0.50	0.35
Ngam-Kondomeyos	0.02	0.00	0.54

Table 5
Weighted factors are summed up for the final indicator of forest pressure with a theoretical range of 0 (minimal pressure) to 6 (maximal pressure).

Forest	Iso * Pop	Frag * Users	Gov * Harm	Sum of indicators: forest pressure
Koui	0.26	0.79	0.00	1.05
Ewè-Adakplamè	0.25	0.17	1.78	2.19
Hlanzoun	0.08	0.11	0.84	1.03
Iko	0.00	0.33	1.41	1.74
Ikot	0.76	0.11	3.00	3.87
Mbangassina	0.09	0.23	1.05	1.37
Ngam-Kondomeyos	0.00	0.00	2.18	2.18

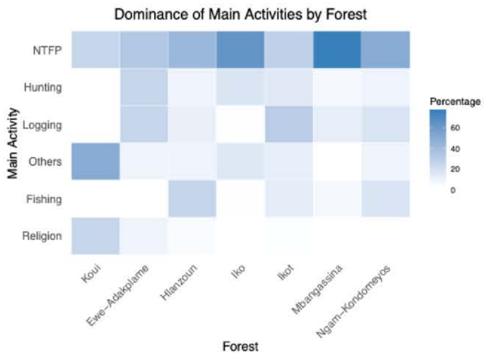

Fig. 2. The heat map shows the seven forests on the x-axis and six different main activities on the y-axis. Multiple answers were allowed. Most forest users (n 328) collect non-timber forest products (NTFP) across all the forests. In the prohibited access, sacred forest of Koui, Togo, logging, hunting, and fishing are forbidden. The respondents who ticked 'Others' explained that they work in agriculture, as traders of forest products, and as eco-guardians. In Iko, Mbangassina, and Ngam-Kondomeyos, religion was not mentioned as a forest activity. Main activities did not significantly differ across forests.

outside of forests, such as palms for palm wine production (e.g., *Raphia vinifera*), fruit trees (e.g., *Irvingia gabonensis*), and timber trees (e.g., *Tectona grandis*). Some also plant trees to mark land boundaries.

3.2. Perceptions of forest use impacts and signs of degradation

Perceptions of forest use impacts differ significantly ($p < 0.001$) across forests. In total, two-thirds of the interviewees perceive logging (61 %) and fire (60 %) as having a strong negative impact on the forests (Fig. 3). Agriculture (35 %) is also perceived negatively by about one-third of respondents, while charcoal production, fuelwood extraction,

Fig. 3. Respondents of seven forests ($n = 328$) were asked about their perception (five classes) of six different activities, which can impact and eventually degrade forests. Activities such as logging and fire are mostly perceived as having a negative impact (red, on top) on forests, as compared to fuelwood and NWFP collection (dark grey and green, below). Note that fire is not a forest use directly, but its practice facilitates other uses, such as logging, agriculture, and hunting. Communities on the left side of the x-axis (e.g., Koui) frequently report strong negative impacts across forest uses as compared to those on the right side of the x-axis (e.g., Ikot). Perceived impacts of forest practices differ significantly across forests ($p < 0.001$).

and NTFP collection are widely regarded as having little or no impact. In Koui, two of three respondents perceive strong negative impacts from logging, fire, agriculture, and charcoal production. In Ewè-Adakplamè, however, logging is mostly perceived as having only low to moderate negative impacts. In the two swamp forests of Hlanzoun and Ikot, most respondents do not perceive any of the uses as having strong negative effects. In Ikot, 42 % of respondents even consider agriculture to have a positive impact, reflecting the central role of farming in local livelihoods. Perceptions of impacts do not differ significantly across respondents' main activities.

Beyond these perceptions, respondents also reported concrete signs of degradation. Across all sites, the most cited indicators were the disappearance of large, old trees (78 %), the loss of valuable timber species such as *Milicia excelsa, Khaya grandifolia*, and *Diospyros* sp. (71 %), and the disappearance of wildlife such as forest elephants (*Loxodonta cyclotis*), lions (*Panthera leo*), and chimpanzees (*Pan troglodytes*) (78 %). These signs were reported by the majority in nearly every forest. Respondents frequently associated these changes with logging, farming, and hunting, noting that timber and bushmeat have become harder to access and more costly.

Some signs of degradation were site-specific. In the Cameroonian forests of Ngam-Kondomeyos (89 %) and Mbangassina (64 %), invasive plants were a notable concern, whereas they were hardly mentioned elsewhere. Insect decline was reported by fewer respondents overall (26 %), but was pronounced in Koui (66 %), Mbangassina (64 %), and Ngam-Kondomeyos (50 %).

In addition to signs of degradation, the loss of forest area was also mentioned. In Ewè-Adakplamè and Ngam-Kondomeyos, all respondents (100 %) reported a decrease in forest area, while in Hlanzoun, only 29 % did so, with many perceiving no change (37 %) or even expansion (34 %). In Ikot, some respondents likewise reported stability (16 %) or an increase (24 %).

Taken together, communities most often perceive logging and fire as the most harmful uses, and report signs of forest degradation in the form of tree and animal losses, with variation across sites reflecting social-ecological conditions such as livelihood reliance on agriculture, restrictions on forest use, and ecosystem type.

3.3. Pressure on forests and perceived and measured forest degradation

The relationship between **pressure on forests and perceived impacts** of forest uses shows no statistically significant correlation (Fig. 4). Descriptively, however, communities with high pressure, that is, large populations in relation to the forest area and many loggers and hunters, do not perceive their forest uses as degrading (e.g., Ikot swamp forest, Nigeria), whereas communities with lower pressure and stricter restrictions express greater concern about degradation (e.g., Koui sacred forest, Togo).

When contrasting **pressure and measured degradation** on forests, there is a strong, negative, and significant correlation (Fig. 5). Most forests have low pressure and remain intact. However, Ewè-Adakplamè and Ikot have a high pressure, with for example, more than 50 % of the forest users engaged in logging and hunting. In these two cases, forest structure is significantly below its potential and therefore the two forests are considered as degraded.

When contrasting **perceived and measured degradation,** no consistent pattern emerges (Fig. 6). In some cases, perception aligns with measured degradation (e.g., Ewè-Adakplamè), while in others it does not (e.g., Ikot, low perceived degradation but high measured degradation).

Taken together, only pressure on forests and measured degradation correlate, while pairs involving perceived degradation do not. The three dimensions converge in some forests (e.g., Ewè-Adakplamè) but diverge in others (e.g., Ikot, Koui). These patterns suggest that, despite broad similarities in forest uses across sites, perceptions vary with socio-economic conditions and local governance, influencing how communities recognize and report degradation.

4. Discussion

4.1. Forest uses and forest degradation

Forest activities range from extractive uses, such as hunting and logging (Fig. 2), to conservation practices like the maintenance of sacred forests. As expected from our first hypothesis, the collection of NTFPs is the most widely conducted activity among forest users, followed by hunting and logging. Despite socio-cultural (e.g., sacred vs. non-sacred), economic (e.g., low vs. intermediate wealth), and ecological (e.g., semi-deciduous vs. moist forest) differences between the studied forest sites, the dominant activities of forest users do not differ significantly. Some forests (e.g., Ewè-Adakplamè and Ikot) are located near cities, where communities have comparatively higher economic resources; these sites also show more logging and hunting, with consequences on measured forest degradation. Hunters provide communities with bushmeat (except in Koui), a vital protein source in rural Africa (Benjamin-Fink, 2019), often tied to cultural values (Dounias and Ichikawa, 2017).

Forest uses and management are shaped by (i) cultural habits (Fa et al., 2002; Van Vliet and Nasi, 2008), (ii) available technologies (Putz

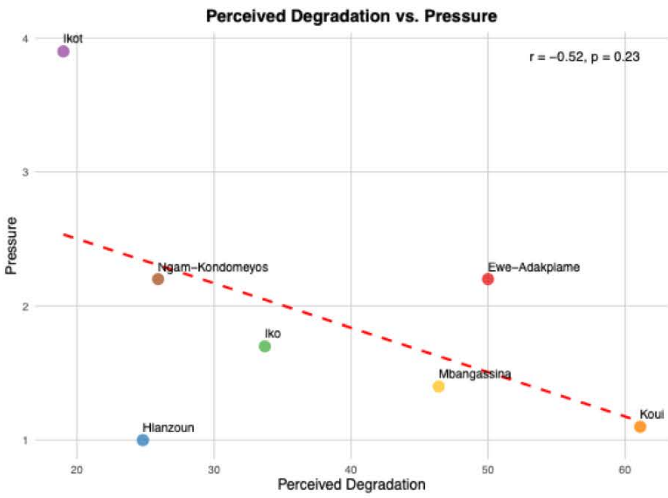

Fig. 4. Perceived degradation does not correlate with pressure on the forest.

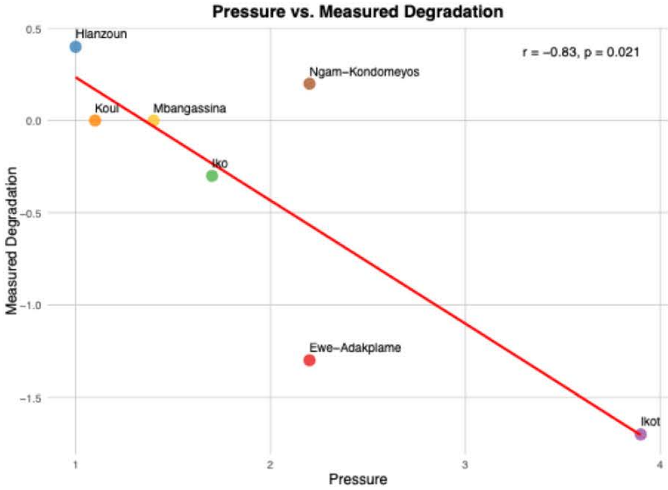

Fig. 5. Strong, negative, and significant correlation between forest pressure and measured degradation. Pressure reflects the intensity of forest use, and measured degradation denotes the gap between observed and potential forest structure, with lower (more negative) values indicating greater degradation.

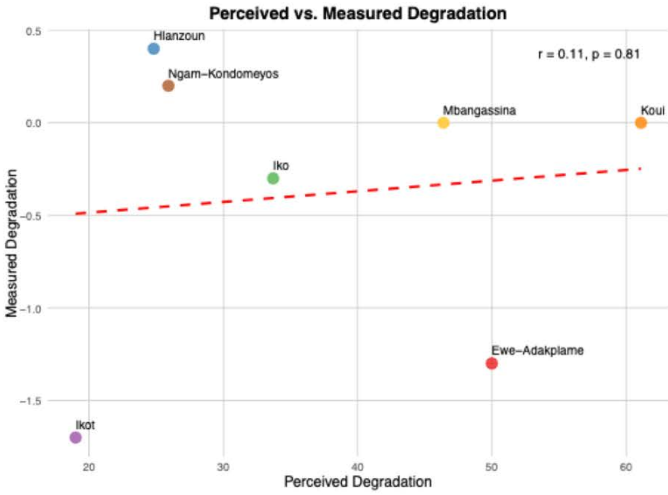

Fig. 6. Perceived and measured forest degradation do not correlate. In the top left corner (e.g., Hlanzoun) and bottom right corner (e.g., Ewè-Adakplamè), perceived and measured forest degradation match. However, in the bottom left corner (e.g., Ikot) and top right corner (e.g., Koui), perceived and measured forest degradation do not match.

et al., 2000), (iii) governance (Kishor and Belle, 2004; Zoysa and Inoue, 2008), (iv) livelihood alternatives (Banerjee and Madhurima, 2013; De, 2012), and (v) market dynamics (Lewark, 2022). Uses often overlap: charcoal production requires prior logging, fire facilitates logging, agriculture, and hunting. These overlapping uses have reciprocal ecological consequences: intensive logging can displace wildlife and reduce hunting success, while heavy hunting can deplete seed-dispersing animals, affecting future timber availability (Lewis et al., 2015). In Koui's sacred forest, religious practices prohibit extractive uses such as fishing, hunting, and logging.

Although most people engage in extractive uses, only few actively restore formerly forested areas by planting trees, mainly in Ngam-Kondomeyos, Ewè-Adakplamè, and Ikot. Cultivating fruit trees can attract wildlife, promoting seed dispersal and indirectly supporting bushmeat hunting (Levis et al., 2018). Tree planting can decrease pressure on forests by providing nearby timber or fruits (Hermans-Neumann et al., 2016), but it requires secure land tenure (Shepherd et al., 1993), which is often contested (Kouassi et al., 2022). Forest use patterns can also change over time due to workforce migration (Lewark, 2022) or the introduction of new actors with greater financial power. For example, a Beninese forest has seen the introduction of honey production and ecotourism by an NGO (Gbedomon et al., 2016).

4.2. Perceptions of forest use impacts and signs of degradation

Perceptions of the impacts of forest uses differ across sites but not across respondents' main activities. Logging and fire are widely perceived as strongly degrading forests (about 60 % of respondents), reflecting shared environmental awareness, while perceptions of agriculture, charcoal production, and NTFP collection vary across sites, influenced by forest type, customary restrictions, and community norms. Although respondents' activities (e.g., eco-guardians, hunters, or NTFP collectors) did not significantly affect perceptions, it remains plausible that such roles shape awareness, as individuals more involved in forest protection may perceive threats differently.

Respondents largely perceived forest area loss over recent years, partly due to fire, which is supported by remote sensing (Aleman et al., 2017; Chuvieco et al., 2018; Hansen et al., 2013; Wingate et al., 2022, 2024). However, forest decline is not limited to outright loss: forests are often degraded before they disappear completely, a process that may not be visible to outsiders or detectable from satellite imagery (Iheaturu et al., 2025). For example, respondents reported little change in forest area in Hlanzoun between 2010 and 2020, whereas Biah et al. (2024) indicate that much of the intact forest has been degraded. The negative impacts of forest uses are also reflected in the disappearance of large, old trees, both in the sampled forests and in surrounding areas (Atindehou et al., 2022). Fewer large, old trees also contribute to a decline in forest structural complexity and aboveground biomass (Ali et al., 2019; Ali and Wang, 2021).

Similarly, the absence of large animals can limit aboveground biomass, as many large-bodied vertebrates disperse large-seeded trees that store a substantial share of carbon; their loss can reduce forest carbon stocks by up to ~3 % (Chanthorn et al., 2019; Lewis et al., 2015). Our results suggest that most large animals have disappeared from all the sampled forests. Large animals and top predators are typically the first species to be displaced and extirpated as human populations grow (Chanthorn et al., 2019; Lewis et al., 2015). Large-bodied animals often cause economic losses by feeding on crops or attacking humans and livestock, which may explain why some of the interviewed individuals express relief at their absence. Human-wildlife conflicts are common in different parts of Africa, particularly where human populations and corresponding land use expand (Benjamin-Fink, 2019).

Invasive plant species do not appear to be a major concern across the sampled forests. It is possible that people have become accustomed to invasive species or even utilize them for their beneficial attributes (e.g., *Chromolaena odorata* for medicinal use, Omokhua et al., 2016), and therefore do not perceive them as symptoms of forest degradation. Still, in Cameroon, more than 60 % of respondents considered invasive plants problematic (e.g., *Osteospermum* sp.). Whether an invasive species is perceived as delaying forest recovery or, conversely, as providing agronomic or medicinal benefits is largely a matter of perspective and context (Juru et al., 2024; Omokhua et al., 2016; Tchiengue et al., 2013).

Although the global decline of insect populations is a recognized threat (Wagner et al., 2021) and deforestation is a well-established driver of insect decline (Wagner, 2019), only a minority of respondents in our case study sites reported declines in insect populations. Interestingly, insect decline was noted in Koui (the best-protected forest in our sample) and in Mbangassina and Ngam-Kondomeyos, which correspond to the most connected forests, highlighting the need for further research and potentially reflecting differences in the environmental awareness and observations of respondents. In Western Africa, specific instances of insect decline have been documented (Dendi et al., 2023; Olatoye et al., 2024), but data remain sparse (Wagner, 2019), and more work is needed to disentangle the interactions between deforestation and degradation in shaping insect populations. By contrast, in Zimbabwe, climate change has promoted insect outbreaks that damaged forest trees (Mataruse et al., 2023). Other tree diseases were not perceived as a significant issue in the sampled forests, possibly due to their high species diversity (Bosu et al., 2019).

4.3. Pressure on forests and perceived and measured forest degradation

Although forest uses are similar across sites, perceptions of their impacts differ. A negative tendency—though not statistically significant—exists between **pressure** (population density and proportion engaged in logging and hunting) **and perceived degradation**. This indicates that intensive forest use is not always recognized as harmful, leading us to reject parts of the third hypothesis. Differing value priorities likely explain these patterns: in Koui (Togo), sacred forests foster relational values that outweigh utilitarian considerations (Ihemezie et al., 2021), whereas in Ikot (Nigeria), instrumental values dominate, allowing intensive use without perceived degradation (Ihemezie et al., 2021, 2022).

Such mismatches can create feedback loops. In high-use sites like Ikot, resource depletion can increase value and drive further exploitation. In restricted forests like Koui, spiritual and ecosystem services reinforce traditional conservation practices. Cognitive and social mechanisms, including shifting baseline syndrome (Fernández-Llamazares et al., 2015), cognitive dissonance (balancing the belief that the forest is well-protected with awareness of harmful practices; Harmon-Jones & Mills (2019)), and cultural and institutional reinforcement (Kasperson et al., 1988; Renn, 2011), further shape local perceptions of degradation.

Measured degradation largely aligns with pressure and governance contexts. In Ewè-Adakplamè and Ikot, high pressure coincides with advanced degradation, whereas Hlanzoun and Koui maintain higher integrity due to restricted access, and Ngam-Kondomeyos and Mbangassina benefit from large forest areas and resource availability outside forests. Disputes over land tenure and local conflicts can exacerbate pressure, as seen in Ewè-Adakplamè, where forest loss is accepted for more profitable land use (cf. Hasanah et al., 2019).

Governance is context-dependent. What effectively preserves forests in one site (e.g., strict sacred-forest rules in Koui) may not work elsewhere. Under high pressure, governance levels can erode gradually—restricted regimes can shift toward more open access (2 → 4 in Ewè-Adakplamè; 3 → 4 in Ikot)—whereas strengthening governance, such as re-sacralization or tighter restrictions, is considerably more difficult, particularly with the spread of Christianity and Islam (Alohou et al., 2017; Mintah et al., 2024; Neuenschwander and Adomou, 2017). Together, these results emphasize that forest condition emerges from a complex interplay of ecological conditions, human pressure, governance, landscape context, and local perceptions, rather than from single factors, even though wealth disparities may modulate pressure (higher relative wealth index in Ewè-Adakplamè and Ikot; Chi et al., (2022)).

The relationship between **perceived and measured forest degradation** differs across sites. While in Ewè-Adakplamè, perceived and measured degradation coincide, in Ikot and Koui, perception and measured forest degradation do not consistently align. These patterns underscore the importance of integrating local perceptions with ecological measurements to fully understand forest change in its social-ecological context. While we explored the relationships between pressure on forests and perceived and measured forest degradation, no strong correlations or clear patterns emerged, likely due to the limited sample size and the inherent complexity of social-ecological dynamics.

4.4. Implications for sustainable forest management

Forest degradation is a complex, wicked problem with no one-size-fits-all solution that simultaneously enables livelihoods and conserves forests (Nikolakis and Innes, 2020; Pouliot et al., 2012). Strong traditional management systems, such as sacred forests, can promote conservation, foster personal responsibility, enhance environmental knowledge, and reduce careless behaviors (Kingbo et al., 2022;

Maleknia et al., 2024).

Respondents highlighted the need for forest guards and stronger institutions to facilitate landscape and land-use planning (cf. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2018; Lewis et al., 2015) and coordinate reforestation (Kouassi et al., 2021), though corruption can undermine these efforts (Ighodaro and Igbinedion, 2020). Region-specific socio-bioeconomies supporting sustainable livelihoods are essential (Garrett et al., 2024). For instance, honey production and ecotourism can generate income without immediate forest degradation (Gbedomon et al., 2016) and biodiversity or carbon credits could be explored for Western African forests (Jones, 2024).

Critically, local **perceptions of degradation** are central for effective SFM. Both Ikot and Ewè-Adakplamè experience high human pressure and show signs of degradation, yet only Ewè-Adakplamè respondents perceive this as such. This divergence illustrates that governance and conservation effectiveness depend not only on ecological conditions but also on how local users recognize and interpret forest change. Without such recognition, attempts to halt degradation and deforestation are unlikely to succeed.

4.5. Limitations

The extensive number of household interviews ($n = 1956$) represents approximately 3 % of the population living within 10 km of the seven studied forest patches (around 580,000 people, Bondarenko et al., 2020). Of all the interviewed people, roughly 15 % ($n = 328$) answered specific questions related to forest management practices and ecology, indicating that they frequently enter the forest and understand its dynamics. While we are confident that these numbers provide representative insights (margin of error ±5 % at 95 % confidence interval, Eq. (2)), 91 % of our interviewees were male, reflecting local norms where men are considered household heads. As forest tasks are often gender-specific (e.g., firewood collection by women; Lewark, 2022; Sinasson et al., 2017), some responses may reflect household-level perspectives rather than individual experiences.

We conducted the surveys once in each village during the dry season. Responses might differ if the same questions were asked in another spatial and temporal setting (Rietbergen, 1993). Prior to the surveys, we carefully reviewed question wording with local scholars experienced in fieldwork. Nevertheless, some questions may have been phrased in ways unfamiliar to interviewees, potentially causing misunderstandings. Interviews are inherently subjective, and responses—particularly regarding individual perceptions—may depend on socio-economic and political circumstances, as well as the specific benefits respondents derive from the forests. Sensitive or illegal practices such as charcoal production were not asked about directly, as these would likely have been underreported, and our insights on this activity therefore remain indirect. However, no obvious outliers were found during data cleaning. Increasing the number of studied forests could provide more robust statistical insights and reveal additional nuances between different forest archetypes (Wingate et al., 2023).

5. Conclusion

Across all forests, the use of non-timber forest products predominates, confirming that livelihoods are closely tied to forest resources despite ecological and cultural differences. Perceptions of forest use impacts converge on logging and fire as the main drivers of degradation, but their intensity and direction vary with local governance and livelihood dependence. The expected alignment between pressure, perceived, and measured degradation is only partial: while physical degradation corresponds to higher use pressure, it does not necessarily match local perceptions. This divergence reflects how social-ecological contexts and shifting baselines shape people's understanding of forest change.

Integrating these three dimensions reveals that forest degradation is not solely an ecological process but also a social one, mediated by access, norms, and governance. Sustainable management therefore, requires coupling biophysical assessments of degradation with the social dimensions of forest use and perception. Strengthening locally embedded governance systems—such as sacred forest protection—alongside context-specific livelihood strategies offers pathways to balance forest conservation and human well-being.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the first author used ChatGPT (OpenAI) to assist with improving clarity, readability, and language. The authors have reviewed and edited all content and take full responsibility for the published work.

CRediT authorship contribution statement

Samuel Hepner: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Paule Pamela Tabi Eckebil:** Writing – review & editing. **Frank Mintah:** Writing – review & editing. **Akomian Fortuné Azihou:** Writing – review & editing. **Brice Sinsin:** Writing – review & editing, Supervision. **Markus Fischer:** Writing – review & editing, Supervision. **Chinwe Ifejika Speranza:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships, which may be considered as potential competing interests: the European Research Council grant (No. 101001200) was awarded to Prof. Chinwe Ifejika Speranza, who is the principal investigator of the project. Samuel Hepner, Paule Pamela Tabi Eckebil, and Frank Mintah were employed under this grant but did not receive the funding directly. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2025.101061.

Annex

Figs. A1, A2, Tables A1, A2.

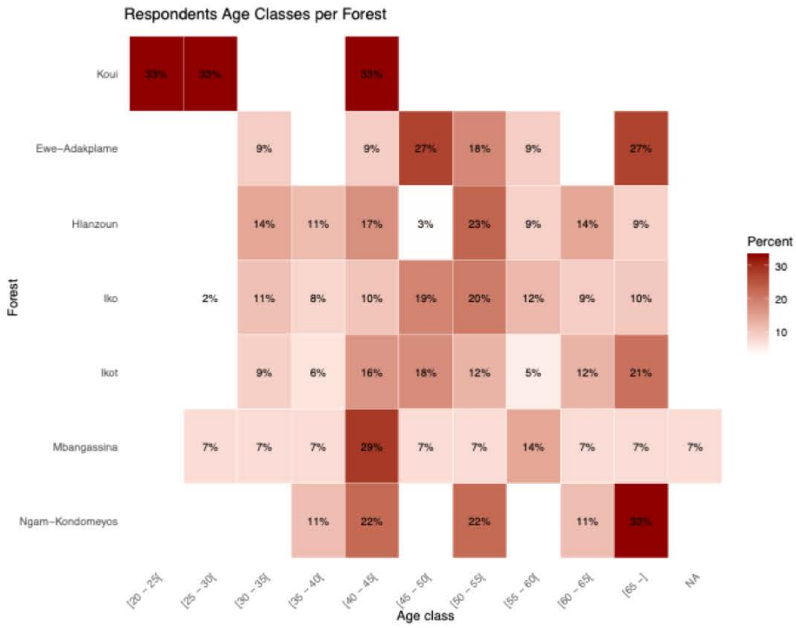

Fig. A1. The age of respondents (n 328) spans the whole society from 20 to over 65 years old.

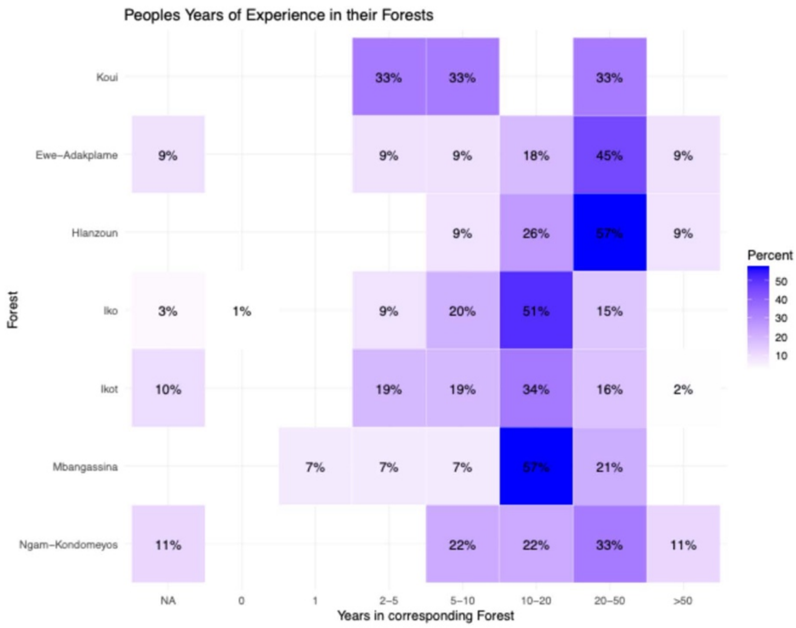

Fig. A2. Most respondents (n = 328) have spent more than 10 years living close to their respective forest.

Table A1
Characteristics of the seven forests patches studied in Togo, Benin, Nigeria, and Cameroon (Hepner et al., 2025). Soil type is based on International Union of Soil Sciences (IUSS) Working Group World Reference Base for Soil Resources (WRB) (2015).

Country	Forest name	Coordinates (WGS 84, Latitude / Longitude)	Vegetation type	Soil	Surrounding landcover
Togo	Koui	0° 43′ 12″ / 8° 15′ 36″	Moist semi-deciduous forest	Acrisol	Settlement / Agriculture / Savanna
Benin	Ewè-Adakplamè (also known as Kouvizoun sacred forest Adakplamè-Ewè)	2° 34′ 12″ / 7° 28′ 12″	Moist semi-deciduous forest	Acrisol / Lixisol	Settlement / Agriculture / Savanna
	Hlanzoun (also known as Lokoli)	2° 15′ 36″ / 7° 3′ 36″	Swamp forest	Acrisol / Gleysol / Lixisol	Settlements / Agriculture / Wetlands
Nigeria	Iko	8° 15′ 0″ / 5° 35′ 24″	Moist forest	Acrisol	Agriculture / Agroforestry
	Ikot	7° 53′ 24″ / 4° 39′ 36″	Swamp forest	Acrisol / Cambisol / Fluvisol	Settlement / Agriculture / Water
Cameroon	Mbangassina	11° 35′ 24″ / 4° 38′ 24″	Moist forest	Ferralsol	Agriculture / Agroforestry
	Ngam-Kondomeyos	11° 49′ 48″ / 3° 2′ 24″	Moist forest	Ferralsol	Wetlands / Agroforestry

Table A2
Ecological data describing the studied forest patches from Hepner et al. (2025). Forest structure is considered degraded in Ewè-Adakplamè and Ikot, since the actual structural complexity is significantly (***) below its potential.

Forest	Actual stand structural complexity index	Reference stand structural complexity	Forest structural integrity (actual - reference ssci)	Total Tree Species Richness
Koui	5.3 (±0.5)	5.4	0	42
Ewe-Adakplame	4 (±1.2)	5.3	−1.3 ***	70
Hlanzoun	5.6 (±0.8)	5.2	0.4	30
Iko	6.5 (±0.9)	6.8	−0.3	143
Ikot	6.2 (±1)	7.9	−1.7 ***	38
Mbangassina	5.8 (±0.5)	5.8	0	129
Ngam-Kondomeyos	6.4 (±0.4)	6.2	0.2	194

Data availability

Data will be made available on request.

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6. Declaration of authorship

Declaration of consent

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Supervisor: Prof. Dr. Chinwe Ifejika Speranza, Prof. Dr. Brice Sinsin, Prof. Dr. Markus Fischer

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