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Restoring forest structure, biodiversity and ecosystem function in the West African humid tropics: secondary versus plantation forests

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Academic Dissertation

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ABSTRACT

Deforestation and forest degradation in the tropics has resulted in the depletion of vital forest resources and services, the near eradication of suitable habitats for forest fauna and flora, and the impoverishment of human populations reliant on forest ecosystems. The rapid and concerning pace of deforestation in tropical regions calls for urgent and pragmatic steps to tackle the root causes and rehabilitate or restore degraded and deforested landscapes. The aim of the study was to evaluate the effectiveness of old, unmanaged forest plantations compared to similar-aged secondary forests in restoring forest stand structure, floristics and diversity of vascular plants, and important ecological functions with reference to neighbouring primary forests. In addition, timber value was estimated and compared among the three forest types.

The research was conducted across 11 sites within Ghana's moist and wet climatic/forest zones. Systematic random sampling of 93 plots each measuring 20m × 20m with nested subplots measuring 5m x 5m for saplings and 2m x 2m for ground vegetation was undertaken.

Forty-two years after establishment and/or abandonment, both the plantation and secondary forests showed structural attributes comparable to those of the primary forests. Nevertheless, the plantation recorded much higher bole volume and basal area compared to the secondary forests. The secondary, plantation and primary forests exhibited considerable overlap in terms of floral composition, with the presence of several rare and restricted-range species. A significant proportion of primary forest vascular plant species, namely 60% and 77%, were identified in the secondary and plantation forests, respectively. The diversity of plant species, as quantified by the Shannon-Wiener Diversity Index (H') and Simpson Index (S), showed no significant variation between primary (H'=3.07, S = 0.91) and secondary (H'=2.95, S = 0.87) or plantation (H'=2.85, S = 0.87) forests. Generally, the primary and secondary forests exhibited higher species richness than the plantations. The mean above-ground carbon stocks of the plantations (159.7 ± 14.3 Mg ha-1) was found to be similar to that of the primary forests (173.0 ± 25.1 Mg ha-1), but both were much higher than the secondary forests (103.4 ± 12.0 Mg ha-1).

Soil pH levels in the wet sites were much lower, ranging from 4.2 to 4.6, compared to moist sites, which had pH levels ranging from 4.6 to 5.4. Soil physicochemical properties, carbon stocks, fertility, microbial activity, and litter decomposition measurements across the different forest types within the climatic zones were similar. Nevertheless, significant differences were observed between climatic zones. Contrary to results of earlier tropical studies, we observed higher litter decomposition rates in the moist compared to the wet zone, which experiences higher annual rainfall, especially for the recalcitrant carbon fraction of the litter. Relatedly, soil microbial biomass and microbial population were significantly greater in the moist compared to the wet zone. Mean soil carbon stocks (0 - 50 cm) was significantly higher in the wet (106.8 $Mgha^{-1}$) compared to the moist (56.9 $Mgha^{-1}$), with mean site values ranging from 51.16 $Mgha^{-1}$ to 122.84 $Mgha^{-1}$.

The mean timber stumpage value of plantations was $8577 per hectare, compared to primary and secondary forests, which were $3112 and $1870 per hectare, respectively.

Tropical forest plantations established on long rotations under low-intensity management regimes, and secondary forests can evolve into forest systems that exhibit structural complexity, floristic diversity, ecological functionality, and self-sustainability, akin to primary forests. Such forest plantations and secondary forests constitute viable pathways for the restoration of deforested landscapes and climate change mitigation, while potentially providing landowners with moderate financial returns through selective timber harvesting.

Keywords: above-ground carbon stocks, soil organic carbon, litter decomposition, basal area, conservation value, timber stumpage value

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LIST OF ORIGINAL ARTICLES

This dissertation is based on the following three original research articles published in peer-reviewed journals, which are referred to by their Roman numerals in the text.

I. Brown, H.C.A., Berninger, F.A., Larjavaara, M., Appiah, M. (2020). Above-ground carbon stocks and timber value of old timber plantations, secondary and primary forests in southern Ghana. Forest Ecology and Management 472, article id 118236. https://doi.org/10.1016/j.foreco.2020.118236

II. Brown, H.C.A., Appiah, M. and Berninger, F.A. (2022). Old timber plantations and secondary forests attain levels of plant diversity and structure similar to primary forests in the West African humid tropics. Forest Ecology and Management 518, article id 120271. https://doi.org/10.1016/j.foreco.2022.120271

III. Brown, H.C.A., Appiah, M., Quansah, G, W., Adjei, E. O., and Berninger, F. (2024). Soil carbon and bio-physicochemical properties dynamics under forest restoration sites in southern Ghana. Geoderma Regional 38, article id e00838. https://doi.org/10.1016/j.geodrs.2024.e00838

Hugh C. A. Brown is fully responsible for the summary of this doctoral thesis.

I. Hugh C. A. Brown Conceptualized and planned the study together with co-authors. Hugh C. A. Brown supervised the field investigations together with M. Appiah with support of technical field crew. Hugh undertook statistical analyses, drafted original manuscript and together with co-authors reviewed and edited manuscript.

II. Hugh C. A. Brown Conceptualized and planned the study together with co-authors. Hugh C. A. Brown supervised the field investigations together with M. Appiah with support of technical field crew. Hugh C.A. Brown and F. Berninger undertook statistical analyses. Hugh drafted original manuscript and together with co-authors reviewed and edited manuscript.

III. Hugh C. A. Brown Conceptualized and planned the study together with co-authors. Hugh C. A. Brown supervised the field investigations together with E. Adjei and G. Quansah with support of technical field crew. E. Adjei and G. Quansah supervised laboratory work. Hugh C.A. Brown together with E. Adjei and F. Berninger drafted original manuscript and together with co-authors reviewed and edited manuscript.

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ABBREVIATIONS

AGB	Above-ground Biomass
AGC	Above-ground Carbon stocks
DBH	Diameter at Breast Height
ECEC	Effective Cation Exchange Capacity
GHI	Genetic Heat Index
IVI	Importance Value Index
SOC	Soil Organic Carbon
TBI	Tea Bag Index

1 INTRODUCTION

1.1 Background

The importance of forests as crucial repositories of biodiversity, regulators of climate, and providers of ecosystem goods and services are well-recognized (Aerts & Honnay, 2011). Yet, these biodiverse ecosystems are under considerable threat, particularly in the tropics, where forest degradation and deforestation rates are alarmingly high (Cazzolla Gatti et al., 2015). The degradation of these ecosystems significantly reduces biodiversity, impacting ecosystem functioning and services (López-Bedoya et al., 2022). In the West African tropics, one of the regions most affected by deforestation and forest degradation, these impacts are more pronounced. N'Guessan et al. (2019) highlighted how these phenomena affect forest structure and biodiversity, leading to losses in above-ground biomass. This loss, in turn, disrupts the forests' ability to store carbon, an essential function for climate regulation.

In light of these grave challenges, the restoration of forests has become a prominent area of emphasis in efforts to conserve biodiversity and mitigate the effects of climate change. Aerts and Honnay (2011) emphasized the importance of restoring not just the tree cover but the whole forest structure, biodiversity, and ecosystem functions. They suggested that both secondary forests, which regenerated naturally following disturbances, and plantation forests, which were artificially established, play crucial roles in forest restoration. However, a key debate remains over the effectiveness of secondary forests versus plantation forests in restoring forest structure, biodiversity, and ecosystem functions. While both serve as practical approaches to reforestation, their ability to restore and sustain the biodiversity and ecosystem functions of the original forest ecosystems vary. This thesis contributes to this ongoing debate by comparing the effectiveness of secondary and plantation forests in restoring forest structure, biodiversity, and ecosystem functions in the West African humid tropics.

Despite the growing attention on forest restoration, the effectiveness of different forest restoration approaches in recovering biodiversity and ecosystem services remain a contentious issue. Brockerhoff et al. (2013) underscored the role of plantation forests, such as those of eucalypt in the provision of ecosystem services and conservation of local biodiversity. They argued that these plantations, if managed appropriately, could contribute significantly to conserving and enhancing biodiversity at the landscape level. On the contrary, Hua et al. (2022) identified trade-offs associated with different forest restoration approaches. They asserted that while plantation forests could support the recovery of certain ecosystem functions such as carbon sequestration and storage, they often fall short in supporting biodiversity recovery. This limitation presents a significant problem considering that biodiversity is integral to the resilience and functioning of ecosystems. Consequently, there is a critical need to understand the trade-offs, similarities and differences between these different forest restoration approaches, which appear to be the main methods of forest restoration in the tropics. Identifying the more effective approaches, depending on the context, for restoring forest structure, biodiversity, and ecosystem functions in Ghana, and by extension, the West African humid tropics is therefore crucial for guiding restoration strategies and policies in the region.

1.2 Objectives

1.2.1 General Objective

This research aimed to assess the efficacy of secondary forests compared to plantation forests in the restoration of forest structure, biodiversity, and ecosystem functions, specifically with reference to primary forests within the West African humid tropics.

1.2.2 Specific Objectives

1. To compare the vascular plant diversity levels in secondary and plantation forests.
2. To assess the structural differences between secondary and plantation forests.
3. To evaluate the ecosystem functions (e.g., carbon sequestration, soil physicochemical properties, microbial activity and litter decomposition) of secondary and plantation forests.
4. To compare the above forest ecosystem attributes (1 – 3) for plantation and secondary forests with that of reference primary forests.
5. To determine and compare timber values of the three forest types (plantation, secondary and primary forests).

1.3 Research Questions

1. What are the biodiversity levels in secondary and plantation forests?
2. How does the forest structure differ between secondary and plantation forests?
3. How do the ecosystem functions, such as carbon sequestration, soil physicochemical properties, microbial activity and litter decomposition compare between plantation and secondary forests?
4. How do the above parameters (1 – 3) for plantation and secondary forests compare with reference primary forests?
5. What are the implications of these differences for forest restoration strategies in the West African humid tropics?
6. How does timber values of the plantation and secondary forests compare with that of reference primary forests?

1.4 Significance of the Study

Forest restoration is a critical component of global strategies to halt biodiversity loss, combat climate change, and enhance ecosystem services. The importance of this study lies in its comparative evaluation of secondary and plantation forests, two key forest restoration approaches, in the context of the West African humid tropics. Firstly, the outcomes of the study shed light on the role of the wet and moist climatic zones and forest types on carbon stocks (Study I, III), an essential component of climate regulation. Using insights from Nero and Opoku's (2022) study on *Cedrela odorata* plantations in Ghana, this research explored how these factors affected carbon sequestration in both secondary and plantation forests.

Secondly, by addressing the resilience and functioning of ecosystems in tropical rainforests, as studied by Keller (2023), this research provided much-needed data on the impacts of the two forest restoration approaches on key ecosystem functions and recovery of biodiversity (Study I, II, III). Understanding these differences is crucial for devising effective strategies to enhance the resilience and functioning of these ecosystems. Finally, this study contributed to expanding corpus of research about the significance of tropical secondary forests in landscape restoration. The study expanded upon the findings of Bieng et al. (2021) to provide valuable insights into the capacity of secondary forests in the West African humid tropics to contribute to forest landscape restoration (Study I, II, III). In sum, this study has significant implications for forest restoration strategies and policies in the region. It provides practical insights for policymakers, forest conservationists and restoration practitioners, and local communities aiming to restore degraded landscapes, conserve biodiversity, and enhance ecosystem services in the West African humid tropics.

1.5 Scope

This research was conducted in Ghana's wet and moist climatic/forest zones; nevertheless, the results have broad implications for the West African humid tropics, owing to similarities in climate, vegetation, culture, socioeconomic situations, and human influences. The area has abundant resources in flora and fauna but is endangered by deforestation and forest degradation. According to Soh et al. (2019), habitat loss has impacted biodiversity and lowered the quantity and quality of ecosystem services. This comparative research investigates, compares and provides insight into how secondary and plantation forests might assist in restoring forest structure, biodiversity, and ecosystem functioning in deforested and degraded forest landscapes in West Africa's humid tropics.

2 THEORETICAL FRAMEWORK

The theoretical foundation of this study is established by a comprehensive analysis and synthesis of prior research conducted on passive forest restoration (secondary forests) and active forest restoration (forest plantations) in tropical regions, with specific focus on forest structure, biodiversity, and ecosystem functions. The research questions were formulated by examining the significant findings, controversies, and knowledge gaps in the relevant literature. This study investigated the significance of secondary and plantation forests in preserving biodiversity, examining their structural attributes and ability to sequester and store carbon and perform other ecological functions. Furthermore, this dissertation examines the trade-offs, similarities and differences between the two forest restoration strategies, along with an analysis of their implications for forest restoration efforts in the West African humid tropics.

2.1 Forest Restoration and Restoration Success

Elliott et al. (2013) defined forest restoration as "actions to re-establish ecological processes, which accelerate recovery of forest structure, ecological functioning, and biodiversity levels to those typical of climax forest,". The Society for Ecological Restoration (SER) defines ecological restoration as “…the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed". The SER generally recognizes three broad strategies for ecological restoration – natural regeneration, assisted regeneration and reconstruction approaches. Natural regeneration approach is employed where damage is relatively low and preexisting biota is able to recover following the cessation of the agents or causes of degradation. Assisted regeneration, on the other hand, is undertaken at sites of intermediate or high degradation that requires both removal of causes of degradation and further active interventions to correct abiotic damage and trigger biotic recovery. A reconstruction approach is employed when damage is high and causes of degradation need to be removed or reversed, and all biotic and abiotic damage corrected, where all or majority of its desirable biota have to be reintroduced (McDonald et al., 2016). According to Gann et al. (2019) ecological restoration seeks to move an altered or degraded ecosystem onto a path of recovery that permits adaptation to local and global changes, as well as the persistence and evolution of its component species. Even though there appears to be no universal definition of ecological restoration (Jørgensen 2013), the international forestry community agrees that forest degradation is a loss or reduction in the quality of forest structure, composition, function, or processes (Convention on Biological Diversity [CBD], 2002; Simula, 2009; FAO, 2011; Lamb et al., 2012). Conversely, forest restoration can be described as the process of improving the quality or recovery of forest structure, composition and function or processes, along a continuum of naturalness (Stanturf et al., 2014a).

Stanturf et al., (2014a) identified four restoration paradigms – revegetation, ecological restoration, functional restoration and forest landscape restoration. They emphasized that the four paradigms can be differentiated based on their goal, or measure of restoration success. Maginnis and Jackson (2007) define Forest Landscape Restoration (FLR) as "a process that aims to regain ecological integrity and enhance human well-being in deforested or degraded forest landscapes". FLR therefore, unlike the other paradigms, seeks restoration of not only ecological integrity but also enhancement of human well-being and livelihoods, thus integrating natural and social science. The International Union for the Conservation of Nature (IUCN) and the World Resources Institute (WRI) succinctly explained that successful FLR reverses environmental degradation, strengthens the resilience of landscapes, secures forest-based livelihoods, and optimizes ecosystem goods and services to meet the changing needs of society (IUCN and WRI 2014).

It has not always been easy defining the desired endpoint of forest restoration initiatives or what constitutes restoration success (Cortina & Vallejo, 2004; Ruiz-Jaen & Aide, 2005; Stanturf et al., 2014b). SER lists six essential ecosystem attributes that can be used to characterize reference ecosystems and evaluate and monitor the recovery at restoration sites. These include physical conditions, lack of hazards, species composition, ecosystem function, structural diversity, and external exchanges (Gann et al., 2019). These six attributes broadly correspond to the three generally accepted ecological attributes of restored forests relative to the reference ecosystem: vegetation structure, species diversity and abundance, and ecological processes, which are frequently used to classify indicators or variables of ecosystem condition in the literature (Noss, 1990; Aronson et al., 1993; Ruiz-Jaén & Aide, 2005; Wortley et al., 2013; Gatica-Saavedra et al., 2017). There is a growing consensus that incorporating socio-economic attributes or indicators will enhance the assessment of restoration success (Gann & Lamb, 2006; Egan & Estrada, 2013; Shackelford et al., 2013; Li et al., 2017; Alba-Patino et al., 2021). In a review of forest landscape restoration practice, Mansourian et al. (2017) emphasized the need for restoration success to focus more on a scale of impact than the scale of effort and concluded that forest restoration should be viewed as a tool for achieving human and ecological objectives as opposed to an end in itself. In determining restoration success, the question has been whether to look back to pre-disturbance conditions; to potential future ecosystem conditions considering the likely impact of global change on the ecosystem in question; or to use the existing conditions of nearby ecosystems that have not experienced disturbance and are in relatively pristine condition as a reference or endpoint. Forest landscape restoration (FLR) defines success as "a functioning landscape that meets the livelihood needs of local communities and provides ecosystem services" (Maginnis & Jackson, 2005; Lamb et al., 2012; Stanturf et al., 2014a; Mansourian et al., 2017). Ecological restoration seeks a return to a historic pre-disturbance state (SER, 2004). FLR expands the scope of restoration from specific sites to the entire landscape, with the explicit inclusion of meeting societal needs.

In contrast, functional restoration anticipates the future with gradual adaptations to a changed climate and other conditions propelling global change, while intervention ecology seeks transformative adaptation to future conditions (Hobbs et al., 2011; Kates et al., 2012). Restoration ecology however, focuses on restoring the sustainability of landscape-level ecosystem processes rather than historical compositions and structures (Choi, 2007; Stanturf et al., 2014a). Clewell and Aronson (2007) state that an ecosystem is restored when it is "self-organizing, self-sustaining, and capable of self-maintenance”. Gann et al. (2019) and Young et al. (2022) acknowledge that self-organization and resilience are essential characteristics of a restored ecosystem.

In light of ongoing global change and climate variability, and their effects on ecosystems, the aim of restoring to a pre-disturbance state appears highly improbable or impossible (Harris et al., 2006). Therefore, it is more pragmatic to pursue the best available contemporary or existing reference condition of nearby undisturbed ecosystems (Cortina & Vallejo, 2004; Hobbs & Cramer, 2008; Stanturf et al., 2014b). A recent meta-analysis of 400 restoration studies spanning 1900 to May 2013 across various ecosystems found that 79% used contemporary reference sites (Jones et al., 2018). SER has recently reevaluated its earlier position and now emphasizes that reference models should be based on contemporary reference sites (Gann et al., 2019). This study is principally an ecological restoration assessment and therefore adopted the SER criteria to evaluate the restoration success of naturally regenerated (passive) and plantation forests (active) using contemporary reference sites (primary forests). However, acknowledging the growing importance of socio-economic benefits in evaluation of forest restoration success, additionally, timber value of the forest types was estimated and compared.

2.2 Overview of Forest Restoration Efforts Globally

The United Nations has declared 2021 – 2030 as the UN Decade on Ecosystem Restoration, aimed at rallying member states to halt the degradation of ecosystems, and restore them to achieve global goals. Forest restoration initiatives have acquired substantial momentum on a global scale as the role of forests in climate regulation, biodiversity conservation, and the provision of ecosystem services has been increasingly recognised (Stanturf & Mansourian, 2020). Pursuant to achieving these global forest restoration goals, forest landscape restoration has emerged as a critical strategy, focusing on restoring ecological integrity on a landscape scale and improving human well-being. Diverse initiatives, such as the Bonn Challenge, which seeks to bring under restoration 350 million hectares of degraded and deforested landscapes by 2030, clearly demonstrates the global commitment to forest restoration. To support the achievement of the Bonn Challenge, some regional blocks have initiated countryled forest restoration efforts, for example; AFR100 (the African Forest Landscape Initiative) which aims to bring 100 million hectares of land in Africa into restoration by 2030, and Initiative 20x20, a Latin American and Caribbean effort aimed at protecting and restoring 50 million hectares of forests, farms, pasture and other landscapes also by 2030 (Suding et al., 2015; Chazdon et al., 2017; Stanturf & Mansourian, 2020). Achieving these ambitious goals, however, requires a nuanced comprehension of forest regeneration processes, which are typically complex and context-dependent (Hanbury-Brown et al., 2022). Both primary and restored forests play a crucial role in sustaining global biodiversity (Brown et al., 2022, Wang et al., 2022). Ulyshen et al. (2023) emphasize the critical significance of forests to global pollinator diversity, which is essential for sustaining plant biodiversity and enhancing pollination in adjacent agricultural lands. Therefore, forest restoration efforts, while primarily aimed at recovering forest ecosystems, also have significant spillover benefits for surrounding landscapes.

In addition, forests produce distinct microclimates that can mitigate the effects of climate change. De Frenne et al. (2021) highlight the role of forest microclimates in buffering species against climatic extremes, thereby contributing to climate change resilience at both local and global scales. This reinforces the urgency of forest restoration efforts in light of the escalating effects of climate change. Forests provide various ecosystem services, such as water regulation and watershed protection, carbon sequestration, and soil fertility enhancement, which are essential for human well-being and sustainable development. A scientometric review by Xie et al. (2020) reveals a developing body of research on land ecosystem services, highlighting their significance for directing forest restoration efforts. Therefore, the global state of forest restoration is characterized by increasing efforts to restore degraded and deforested lands, driven by the vital role of forests in climate regulation, conservation of biodiversity, and provision of ecosystem services. However, the complexity of forest regeneration processes necessitates context-specific restoration strategies informed by a nuanced understanding of these processes and the numerous functions and services that forests provide.

2.3 The Importance of Forest Structure, Biodiversity and Ecosystem Functions

Forest structure, biodiversity, and ecosystem functions are intricately linked and jointly contribute to the overall health and resilience of forest ecosystems. Forest structure, characterized by elements such as tree density, height, basal area and canopy cover, plays a critical role in regulating ecosystem functions. LaRue et al. (2019) demonstrated that structural diversity is a crucial predictor of ecosystem function, with structurally diverse forests typically exhibiting higher productivity, more significant carbon sequestration, and increased resilience to disturbances. Biodiversity, which encompasses the variation of life at dimensions ranging from DNA to species to ecosystems, is central to the functioning and sustainability of forests. According to Yuan et al. (2020), biodiversity above and below ground regulates multiple ecosystem functions, including nutrient cycling, carbon sequestration, and disease resistance. These highlight the significance of biodiversity conservation in forest restoration efforts.

Ecosystem functions are the chemical, physical and biological processes or characteristics that contribute to an ecosystem's self-maintenance, such as primary production, nutrient cycling, and decomposition. They are the foundation of ecosystem services; the benefits humans derive from ecosystems. These services include timber and non-timber forest products, climate regulation and disease control, and recreational and spiritual benefits (Watson et al., 2019). Evaluations of ecosystem services, such as the one conducted by Canedoli et al. (2020) in a protected mountain area, highlights the interconnectedness of forest structure, biodiversity, and ecosystem functions. For example, the study discovered a strong correlation between soil organic carbon stock, an essential function of ecosystems, and biodiversity in alpine forests and grasslands. In the context of forest restoration, the significance of forest structure, biodiversity, and ecosystem functions is emphasised further. According to Hua et al. (2022), various restoration strategies can affect biodiversity and ecosystem services, with potential trade-offs between the two. For example, fast-growing plantation forests can rapidly sequester carbon but may have less biodiversity than slower-growing secondary forests. Understanding these trade-offs is essential for the design of effective and sustainable forest restoration strategies.

2.4 The West African Tropics: Forest Structure, Biodiversity, and Ecosystem Functions

The West African tropics host a diverse range of forest ecosystems, which are critical hotspots for biodiversity and provide numerous ecosystem services. However, these ecosystems face significant threats, such as unsustainable agricultural land use practices, urbanisation, and habitat degradation from other land uses, thus affecting forest structure, biodiversity, and ecosystem functions (Balima et al., 2020; Tiando et al., 2021). Agricultural land use, especially the conversion of forests to farmland, has been demonstrated to substantially reduce plant biodiversity and carbon storage in the region (Balima et al., 2020). Rapid urbanization in the region's coastal areas has also resulted in substantial land use and land cover changes, impacting the quality of ecosystem services (Tiando et al., 2021). The effects of these modifications are evident in the structure and function of forests. Ali (2019) emphasizes the significance of forest stand structure to ecosystem functioning and calls for additional research to address future challenges posed by anthropogenic change. Changes in forest structure may impact ecosystem services, such as carbon sequestration, water regulation, and habitat provision, which can have socioeconomic repercussions (Camarretta et al., 2020).

These land-use changes imperil biodiversity and ecosystem functions by degrading tropical habitats (Soh et al., 2019). The conservation and restoration of these ecosystems is essential to preserve biodiversity and ecosystem services. Ola and Benjamin (2019) evaluated biodiversity and ecosystem service incentives in West African forests, watersheds, and wetlands. These included community-based conservation, sustainable land management, and payments for ecosystem services. Agroforestry techniques also promise to integrate agricultural production with biodiversity conservation and the provision of ecological services. Gupta et al. (2023) investigated soil biodiversity and litter decomposition in tropical Asia and Africa, and the viability of agricultural expansion in these regions.

2.5 Secondary versus Plantation Forests

Secondary forests are naturally regenerated forests re-established following a significant disturbance such as logging, wildfire, or agricultural use (Biró et al., 2022). Reflecting the local environmental conditions, the extent of the disturbance, and the length of time since the disturbance, the species composition and forest structure of these forests are typically highly variable. Over time, secondary forests can recover a significant portion of primary forests' biodiversity and ecosystem functions. For instance, Abbas et al. (2019) discovered that the richness of species and composition in a tropical secondary forest approached those of the original primary forest over 70 years of succession. Similarly, Garrido et al. (2021) reported diverse lichen communities in the mid-elevations of secondary forests of Costa Rica 14 years after pasture abandonment, indicating the recovery of epiphytic biodiversity.

Plantation forests, on the other hand, are usually characterised by cultivating one or a few tree species, typically non-native, for commercial purposes such as timber or fibre production. Due to their low structural complexity and often unsuitable habitat for native species, these forests tend to have less biodiversity than primary or secondary forests. However, they can provide essential ecosystem services, such as carbon sequestration, soil erosion control, and timber provision. However, for plantation forests to truly serve as a viable pathway to forest restoration and support appreciable levels of biodiversity, they must be managed less intensively and selectively logged rather than clear cut, with natural regeneration allowed in the understory.

2.6 Gaps in Current Research

Secondary and plantation forests in the tropics are still poorly understood, particularly in the West African tropics with very few published forest restoration studies. Even fewer comparative studies of forest plantations and secondary forests have been published across the tropics. In addition, most of these tropical forest restoration studies are based on sites less than 20 years old (Bonner et al., 2013). It is therefore challenging to predict with certainty later development of such early successional sites. The paucity of well-designed tropical restoration projects that are old enough to support the needed fine-tuning between ecological theory and practice presents a huge challenge for forest restoration practitioners (Weiher, 2007; Temperton, 2007). Longitudinal studies of biodiversity, forest structure, and ecosystem processes in secondary and plantation forests are lacking. Some studies have followed secondary forest regeneration across decades (Abbas et al., 2019), while others have investigated the potential of forest plantations to contribute to biodiversity conservation (Wang et al., 2022), but more extensive studies that include additional ecological variables and socio-economic factors are needed. Long-term research is crucial to understanding forest recovery and its drivers (Gupta et al., 2023).

2.7 Study framework

Based on the reviewed literature, the study was designed to assess restoration success based on Elliott et al.'s, (2013) definition of forest restoration. Therefore, vegetation structure, plant species composition and diversity, and ecological functioning were identified as the key forest ecosystem attributes for evaluating restoration success (SER 2004; Stanturf et al., 2014a; Stanturf et al., 2014b; Prach et al., 2019). Subsequently, appropriate ecological indicators and metrics were selected to enable an objective assessment. Table 1 summarizes the study framework.

Table 1: Framework of study highlighting key ecosystem attributes to be assessed and related restoration success indicators and metrics

Forest Ecosystem Attribute	Ecological Indicators	Metrics
Vegetation Structure	Tree canopy	percentage canopy cover
	Vertical Structure	total height, dominant height, bole volume
	Horizontal Structure	basal area, DBH, stem density
Composition / Diversity of vascular plants	Species diversity	diversity indices, evenness, species richness, similarity indices
	Floristic composition	species abundance, importance value index, distribution of guilds and life-forms
	Conservation value	Genetic Heat Index (GHI), IUCN Conservation Ratings
Function	Carbon sequestration / primary productivity	above-ground biomass and carbon stocks, soil organic carbon, soil carbon stocks
	Nutrient cycling	soil pH, soil C: N, soil nutrient levels, ECEC,
	Decomposition	litter decomposition rate (k), microbial population, microbial biomass C

In addition to the ecological attributes in Table 1, we assessed the potential financial returns from timber sales from each of the three forest types by estimating their respective standing timber values by calculating the timber stumpage values.

3 MATERIALS AND METHODS

3.1 Study area

The research was carried out within portions of five lowland forest reserves (below 300 masl) within the wet and moist climatic zones of the Western and Eastern Administrative Regions respectively, in Ghana (Study I, II, III) (Figure 1). The soils of the wet zone are principally Xanthic Ferralsols. These soils are generally acidic in nature with low nutrient content and low cation exchange capacity (CEC), with a clay assemblage primarily composed of kaolinite and sequioxides, with low levels of base cations. The soils of the moist zone are primarily Haplic Acrisols, which are strongly weathered acid soils. They tend to have a sandy-loamy surface soil and accumulation of low-activity clay with low base saturation and low nutrient content (FAO, 1998; WRB, 2015).

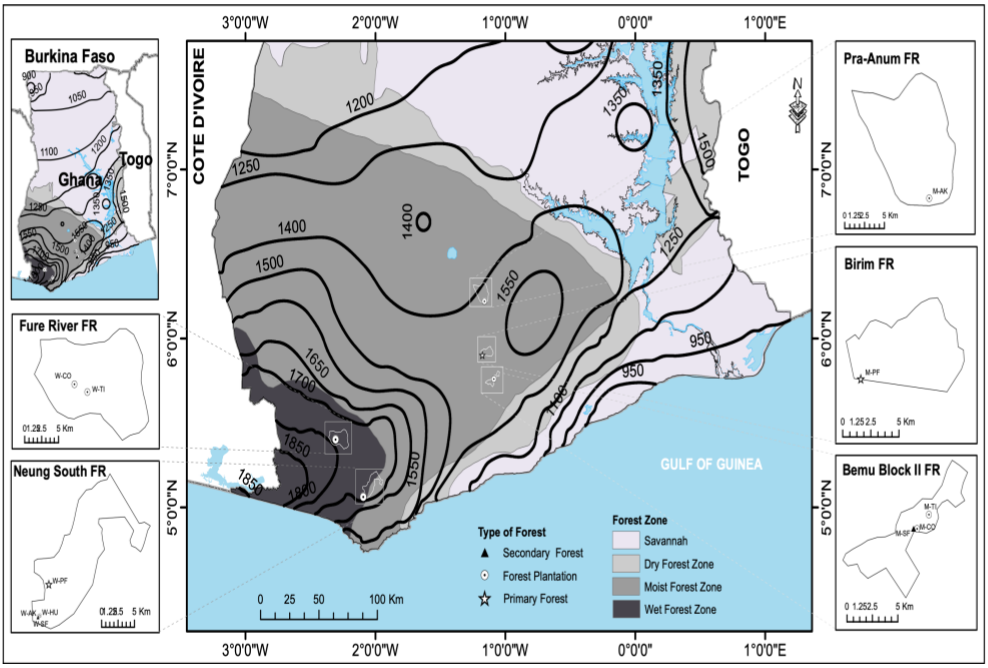

Figure 1. Map of Ghana highlighting location of the five (5) forest reserves and 11 study sites (adapted from Brown et al., 2020).

Eleven sites were selected and demarcated with a total of ninety-three 20m x 20m plots established across the 11 study sites. These are the same study sites reported by Brown et al. (2020). The eleven sites were coded as follows:

In the Moist Zone (5 Sites):

M-AK: *Aucoumea klaineana* plantation

M – CO: *Cedrela odorata* plantation

M – TI: *Terminalia superba* plantation

M – SF: secondary forest

M – PF: primary reference forest

In the Wet Zone (6 Sites):

W – AK: *Aucoumea klaineana* plantation

W – CO: *Cedrela odorata* plantation

W – TI: *Terminalia superba* plantation

W – TU: *Tarrietia utilis* plantation

W – SF: secondary forest

W – PF: primary reference forest

Old (at least 40 years old) unmanaged forest plantation sites with no record of thinning, harvesting or wildfires since abandonment were selected. Nearby or adjoining similar-aged failed plantation sites or areas cleared for plantation development under the Taungya System which were cultivated with food crops and abandoned to naturally regenerate were selected. The closest pristine primary forests with no physical evidence of human disturbances (i.e., logging, farming, etc.) within each of the two climatic zones was selected. The selected plantation and secondary forests sites have similar ages (42 – 47 years) since abandonment, and located in fairly close proximity (e.g., in the moist zone; M-CO and M-SF are adjoining sites, while in the wet zone; W-AK, W-TU, and W-SF are adjoining sites) within each of the two climatic zones. The exotic and native species timber plantations were established and maintained for approximately three years and then abandoned, while the secondary forest stands were cleared around the same time that the forest plantations were developed and abandoned after three years of cultivation of food crop farms. At the time of data collection none of the forest plantations had been thinned or harvested and there was no record or evidence of timber harvesting within the secondary forests. A detailed description including locations of the study sites is provided in Table 2. Detailed land-use history, plantation establishment techniques and site selection criteria are the same as reported by Brown et al. (2020) (Study I).

Table 2. The location, age of stands and climatic parameters of the study sites

Forest Reserve (Gross area in km²)	Study Site Code	Latitude/ Longitude	Study Site	Year Planted	Study Site Size (ha)	No. of 20x20m plots sampled	Avg. Annual Precipitation[a] (mm)	Avg. Annual Temp[a]. (°C)	Avg. Dry Months/ Yr[b]
Primary Forest (Reference)									
Birim (39)	M-PF	05°54'11.3" N 01°10'32.6" W	Primary Forest	N/A	37	10	1521	26.2	2
Neung South (113)	W-PF	05°05'53.7" N 02°04'42.3" W	Primary Forest	N/A	25	10	1722	26.0	1
Secondary Forest									
Bemu (Block II) (43)	M-SF	05°45'41.5" N 01°05'27.4" W	Secondary Forest	1976*	5	8	1569	26.0	2
Neung South (113)	W-SF	05°03'46.8" N 02°05'36.0" W	Secondary Forest	1972*	10	9	1706	26.1	1
Forest Plantations									
Pra-Anum (123)	M-AK	06°13'19.2" N 01°09'34.1" W	*Aucoumea klaineana*	1971	3	8	1459	26.3	2
Bemu (Block II) (43)	M-CO	05°45'41.5" N 01°05'15.7" W	*Cedrela odorata*	1974	7	9	1569	26.0	2
Neung South (113)	W-AK	05°03'51.7" N 02°05'32.8" W	*Aucoumea klaineana*	1971	2	7	1706	26.1	1
Fure River (158)	W-CO	05°24'17.1" N 02°18'22.7" W	*Cedrela odorata*	1976	2.32	7	1779	26.3	1
Bemu (Block II) (43)	M-TI	05°46'16.2" N 01°04'38.4" W	*Terminalia ivorensis*	1974	3	8	1573	26.0	2
Neung South (113)	W-TU	05°03'54.0" N 02°05'26.3" W	*Tarrietia utilis*	1971	6.37	8	1706	26.1	1
Fure River (158)	W-TI	05°23'48.4" N 02°17'21.0" W	*Terminalia ivorensis*	1971	7.24	9	1779	26.3	1

Modified from Brown et al. 2020

[a] Interpolated average rainfall and temperature data: 1970–2000 (WorldClim, version 2)
[b] Dry month (< 60 mm rainfall per month) in accordance with the Köppen Climate Classification System for Tropical climates

* Year site was abandoned

Figure 2. 47-year-old *Tarrietia utilis* plantation (W-TU) in the Nueng South Forest Reserve in the wet climatic zone in southern Ghana

Figure 3. 44-year-old *Terminalia ivorensis* plantation (M-TI) within the Bemu (block II) Forest Reserve in the moist climatic zone in southern Ghana.

3.2 Data collection

The research used a random sampling approach. Grid lines were drawn across the sites and points of intersection selected as plot positions. The study plot design is an adaptation of the modified Whittaker plot design (Stohlgren et al., 1995) and the nested-intensity plot design developed by Barnett and Stohlgren (2003) which are used for assessing plant diversity. The study design incorporated different size plots within a larger plot to accommodate various size classes and plant life-forms. A total of ninety-three plots were delineated, with dimensions of 20 metres by 20 metres. The dimensions of main plots within the research area were 20 m x 20 m. Each main plot had a smaller subplot with dimensions of 5 metres by 5 metres, positioned at its centre. There were five minor subplots, each measuring 2 metres by 2 metres with four of them positioned at the four corners of the 20m x 20m plot and the fifth in the middle of a 5 m x 5 m subplot (Study II) (Figure 4). The 2m x 2m subplots were used to assess ground vegetation and seedlings, the 5m x 5m subplots were used to assess saplings, lianas, shrubs and small trees with DBH 2 – 9.9 cm. the 20m x 20m plots were used to assess trees, large lianas and other woody perennials with DBH ≥ 10cm.

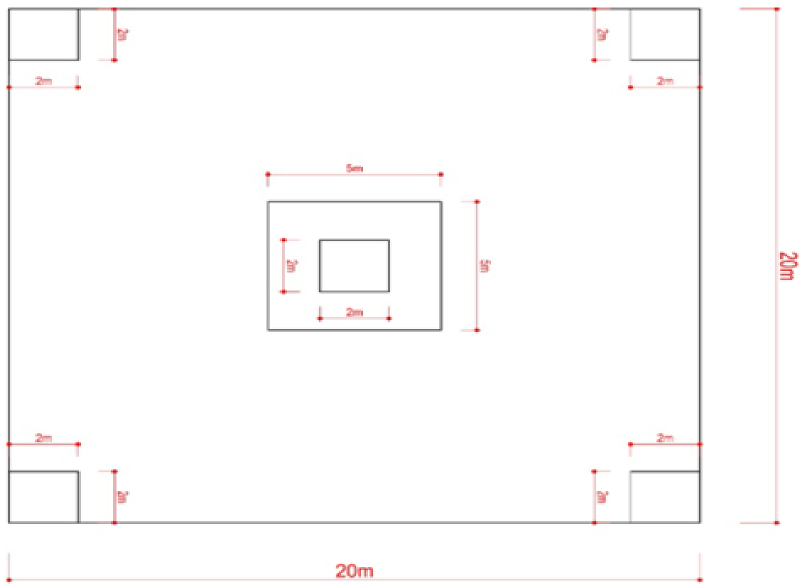

Figure 4. Sample Plot Design used in the study (Brown et al., 2022)

3.2.1 Vegetation

The collection of field data took place from February to June 2018. All woody perennial plants, including lianas, that had a diameter at breast height (DBH) of at least 10cm were identified and measured at a height of 1.3m above the ground or just above the point of convergence of buttress (where the point of convergence is higher than 1.3m) within the 20m x 20m plots. The measurements were taken using diameter tapes or a Spiegel Relaskop (usually for buttress trees where the point of measurement was beyond reach).

The measurement of the merchantable height of all timber trees with DBH of at least 30 cm was conducted using a Nikon Forestry Pro laser rangefinder and a Spiegel Relaskop. The height measurement extended up to a top diameter of 20 cm; which is comparable to the minimum diameter of the small end of a sawlog. In the 5 m × 5 m subplots, all saplings, shrubs, lianas, and vines with DBH ranging from 2 cm to 9.9 cm were identified and labelled. The measurement of the DBH was conducted using diameter tapes, as described in the studies by da Silva et al. (2002) and McMahon & Parker (2015). DBH measurements were obtained at a distance of 1.3 metres from the main rooting position for both vines (herbaceous climbing plants) (Kokou et al., 2002) and lianas (woody climbing plants) (Pearson et al., 2005; Gerwing et al., 2006, Brown et al., 2020). All seedlings, saplings, herbs, grasses, vines, and ferns with DBH less than 2 cm were identified and quantified within the 2 m x 2 m subplots. The plants were identified by plant taxonomists affiliated with the CSIR-Forestry Research Institute of Ghana. The vertical structure of the forest was characterised by the height of trees/ vegetation, which was categorised as follows: forest floor or ground layer (less than 5 m), understorey (5-19.9 m), lower canopy (20-29.9 m), upper canopy (30-40 m), and emergent trees (> 40 m) (Addo-Fordjour et al., 2009).

Figure 5. Research field team using a diameter tape to measure the diameter of a buttressed 47-year-old *Aucoumea klaineana* tree located within a plantation in the Neung South Forest Reserve (W-AK) in the wet climatic zone.

The measurement of canopy cover was conducted using the GRS Densitometer, as described by Brown et al. (2022). The estimation of canopy cover followed the methods established by Stumpf (1993). Measurements were taken at grid points that were spaced 5 metres apart along linear transects within the 20 m × 20 m plots. A total of twenty-five sample measurements were obtained in each 20m x 20m plot (Ganey & Block, 1994). Each data point measurement was documented.

3.2.2 Soil

Field data was obtained between May and July of the year 2018. A screw auger was used to collect composite soil samples at two separate soil depths (0 - 20 cm; 20 - 50 cm). For soil bio-physicochemical examination, the soil samples were taken at three points along the diagonal of the research plots (20m x 20m). The nutrient analysis samples were aggregated into one sample for the various soil depths per research plot. In contrast, the bulk density samples were taken separately using the core sampler at the same soil depths.

The top composite soil samples (0 - 20 cm) were split into two sections. One half was saved for physicochemical study, while the other was utilised for microbiological analysis. The Soil Research Institute of Ghana conducted soil analysis. The microbiological analysis samples were maintained at four (4) °C. Every soil sample site was georeferenced.

Cores for soil bulk density determination were collected randomly at two points along the diagonal of the research plots at two separate soil depths (0 - 20 cm; 20 - 50 cm).

3.2.3 Litter decomposition

Following the Tea Bag Index (TBI) protocol (Keuskamp et al., 2013), Lipton Green and Rooibos tea bags were weighed and incubated in pairs at a depth of 8 cm. Before the tea bags were buried, they were dried at 70 °C until their weight was constant. At each of the eleven study sites, between 100 and 120 tea bags were buried in the ground 8 cm deep for six months, starting in May 2018. After that, a sample pair of tea bags was taken every month. The collected bags were cleaned and dried at 70 degrees Celsius until their weight stayed constant.

3.3 Data analysis

Given the scarcity of comparable aged unmanaged timber plantation sites and corresponding secondary forest sites within the two zones, randomly selected plots within the study sites were treated as replicates, as documented by Griscom et al. (2011), Amazonas et al. (2011), and Garcia et al. (2016).

3.3.1 Species diversity

Estimating the Species Richness Index (S) included quantifying the number of species inventoried inside the designated plots. The Shannon-Wiener Species Diversity Index was used to assess the plant species diversity within the forest types. According to Gimaret-Carpentier et al. (1998) and Parthasarathy et al. (2001), the Shannon-Wiener Index (H) may be computed using the following formula:

The equation;

$$H = \sum[(pi) \times In(pi)] \quad (1)$$

represents the calculation of entropy, where H is the entropy value and $\sum[(pi) \times In(pi)]$ represents the summation of the product

Where:

The variable "Pi" denotes the percentage of the whole sample a specific species represents. To calculate the proportion of individuals belonging to species i, dividing the number of individuals of species i by the total number of samples is necessary.

S represents the number of species, which is equivalent to species richness.

The equation Hmax = ln(S) represents the maximum achievable level of diversity.

The equation for evenness may be expressed as the ratio of the observed heterozygosity (H) to the maximum possible heterozygosity (Hmax).

The Simpson Index (D) and Evenness Index (E) were used to assess species dominance and distribution evenness (Magurran, 1998). The Simpson Diversity Index was calculated using the formula

$$Ds = 1\text{-}\Sigma i\ (pi2) \qquad (2)$$

where Ds is the Simpson Index. In order to get a clear representation of species domination, the value of D′ is calculated as the complement of Ds, where Ds represents the Simpson Diversity Index. It is known that the Simpson Diversity Index exhibits a negative correlation with biodiversity. As proposed by Pielou in 1966, the equation for evenness is defined as the ratio of the Shannon-Wiener diversity index (H') to the logarithm of the number of species (s) contained in the sample. The Importance Value Index (IVI) calculation at the family level included the summation of relative density, relative frequency, and relative basal area or dominance, as described by Addo-Fordjour (2009) and Tavankar and Bonyad (2015). The IVI values range from 0 to 300 (Allaby, 2015).

The evaluation and comparison of pairwise similarity in species composition across the three forest types were conducted using both Jaccard's Similarity Index (JSI) and SØrensen's Similarity Index (SSI). The calculation of similarity indices was performed in the following manner: SSI is calculated as the ratio of the number of shared species (M) to the sum of M and the total number of unique species (N) in the comparison pair. On the other hand, JSI is calculated as the ratio of M to the sum of M and N.

According to Hawthorne (1996), a guild may be described as a grouping of plant species that exhibit comparable ecological characteristics and lifestyles. In accordance with Hawthorne’s classification, vascular plant species identified in this study were grouped into the following guilds: shade-bearers (SB), non-pioneer light-demanders (NPLD), pioneers (P), and swamp (SW). The study used the Kruskal-Wallis H-test to assess the presence of statistically significant disparities in the distribution of plant life-forms and guilds across various forest types.

The authors Hawthorne and Abu-Juam (1995), Gordon et al. (2004), and Tchouto et al. (2006) used the Genetic Heat Index (GHI), a quantitative measure of conservation, to assess the conservation significance of forest stands. According to the definition provided by Gordon et al. (2004), the GHI is a comparative metric that assesses the frequency of unusual or geographically limited plant species within a given sample. A high GHI represents a location relatively rich in rare or restricted-range plant species. Consequently, any loss or degradation of such a region would significantly deplete genetic resources. The conservation classes include a range of GHI values, as Hawthorne (1996) described. These values include deficient conservation value (50 >GHI), low conservation value (50 < GHI < 100), moderate conservation value (100 < GHI < 150), high conservation value (150 < GHI < 200), and very high conservation value (GHI > 200). The GHI computation was conducted using the Star Ratings assigned to each species, which categorises them based on their rarity in Ghana and globally, considering the species' ecological and taxonomic characteristics. The accompanying weights used in this computation are shown in Table 3.

Table 3. Species conservation categories and corresponding Genetic Heat Index (GHI) for plant species in Ghana.

Star Category	GHI Weight	Comments
Black Star (BK)	27	The species are endemic to Ghana or are close to being so. They occur infrequently internationally and in Ghana. Existing populations of these species require immediate conservation measures.
Gold Star (GD)	9	The species are relatively uncommon globally and locally. These are uncommon and endangered in Guinean and Guineo-Congolian forest endemics. Ghana must take action to protect these species.
Blue Star (BU)	3	The species are Guineo-Congolian and Guinean forest endemics, fairly common in the tropics but rare in Ghana, or vice versa. It might be in Ghana's interest to protect these species.
Scarlet Star (SC)	1	These particular species are not uncommon, although they face significant challenges due to over-exploitation. In order to encourage sustainable use, it is essential to curb or control exploitation. The importance of protection across many scales cannot be overstated.
Red Star (RD)	1	These species are widespread in the tropics, but currently under pressure from high level of exploitation. Need careful control and some tree by tree and area protection.
Pink Star (PK)	1	These species are widespread and moderately exploited.
Green Star (GN)	0	These are common Guineo-Congolian and Guinean, pantropical and tropical species. They are not under pressure and there are no current conservation concerns.

Modified from Hawthorne and Abu-Juam (1995), Hawthorne (1996) and Tchouto et al. (2006)

Additionally, the IUCN Red List of Threatened Species database was used to identify threatened, endemic, and rare species (Study II).

The Genetic Heat Index (GHI) for each site was determined as follows:

GHI = [((BK x BK weight) + (GD x GD weight) + (BU x BU weight) + (RD x RD weight) + (GN x GN weight))/ (BK + GD + BU + RD + GN)] x 100; (3)

where BK = number of black star species; GD = number of gold star species; BU = number of blue star species; GN = number of green star species; and RD = number of red, scarlet, and pink star species.

3.3.2 Forest structure

3.3.2.1 Basal Area

Using DBH data, the basal area of each plot (20 m x 20 m) and subplot (5 m x 5 m) was determined (m^2/ha). The Tree basal area (BAtree) was calculated as follows:

BAtree (m^2) = (DBH/200)2 X 3.142 (4)

where DBH is in centimetres and π is 3.142 (Wong & Blackett, 1994; Appiah, 2013; Bettinger et al., 2016).

3.3.2.2 Dominant height

It is the arithmetic mean height of the 100 trees with the greatest diameter within a hectare (West, 2009). Therefore, the average total height of the four largest-diameter (DBH) trees was used to determine the dominant height per plot (0.04 hectares).

3.3.2.3 Stem density

Stem density was estimated as the total count of all stems with DBH $\geq$ 2cm at the plot-level, and expressed as count per unit area (stems / ha).

3.3.2.4 Bole volume

Bole volume of woody perennials ($\geq$ 2 cm DBH) was calculated using the tree inventory data (DBH and total height) using the tree volume equation reported by Wong and Blackett (1994) for the Moist Forest Zone in Ghana:

$\log_{10} Y = \log_{10} (0.0003494) + 2.287 \times \log_{10} (X)$ (5)

where X is DBH (cm), Y represents tree bole volume (m^3).

3.3.2.5 Canopy cover

Percentage canopy cover per plot was determined as the mean of the 25 individual point estimates per plot (20mx20m) recorded using the GRS Densitometer.

3.3.3 Ecological function

3.3.3.1 Above-ground biomass and carbon stocks

DBH and total height were used to estimate the above-ground biomass (AGB), using the pantropical allometric equation developed by Chave et al. (2014) with three variables, i.e., total tree height, DBH and wood density:

$$AGB = 0.0673 \text{ x } (\rho D^2 H)^{0.976} \quad (6)$$

where D is diameter at breast height (cm), H is total tree height (m), ρ is wood density (g cm^{-3}), and AGB is the estimated above-ground biomass (kg).

AGB for shrubs, and lesser-known tree species with no data on their wood densities was estimated using the allometric equation of Henry et al. (2010), developed from studies undertaken in the moist forest zone in Ghana:

$$AGB = 0.30 \text{ x } D^{2.31} \quad (7)$$

Allometric equation of Schnitzer et al., (2006) was used for lianas as follows:

$$AGB = \exp\,[-1.484 + 2.657\ \text{In}(D)] \quad (8)$$

The AGB was converted to carbon mass (carbon stocks) by applying the carbon fraction of dry matter conversion factor of 0.465 recommended for tropical angiosperms (Martin et al. 2018).

3.3.3.2 Soil physicochemical properties

3.3.3.2.1 Soil pH

The measurement of soil pH was conducted using a 1:2.5 soil-water solution that was thoroughly mixed and allowed to settle overnight. The pH was determined using a glass electrode pH metre (H19017 Microprocessor) using the methodology outlined by Blakemore et al. (1987).

3.3.3.2.2 Soil organic carbon concentration

Soil organic carbon concentration was determined following the methods (modified dichromate oxidation method) of Walkley-Black as described by Nelson and Sommers (1982).

3.3.3.2.3 Soil carbon stocks

Soil carbon stock, in soil organic carbon per unit area, for sample plot (sp) stratum (i) was determined using the equation:

CSOCsp,i = CSOCsample,sp,ix BDsample,sp,ix Depsample,sp,i x 100:
(9)
where:

CSOCsp,i, =	Carbon stock in soil organic carbon for sample plot sp, stratum i, (Mg C ha-1).
CSOCsample,sp,i =	Soil organic carbon of the sample in sample plot sp, stratum i, determined in the laboratory in g C/100 g soil (fine fraction <2 mm).
BDsample,sp,i =	Bulk density of fine (<2 mm) fraction of mineral soil in sample plot sp, stratum i, determined in the laboratory in g fine fraction cm^{-3} total sample volume.
Depsample,sp,i =	Depth to which soil sample is collected in sample plot sp in stratum i (cm)
sp =	1, 2, 3 … Pi sample plots in stratum i
i =	1, 2, 3 … M strata

3.3.3.2.4 Particle size distribution

Distribution of the particle size was established using the Bouyoucos hydrometer method (Bouyoucos, 1962), with sodium hexametaphosphate and sodium bicarbonate (Calgon) as dispersing agents.

3.3.3.2.5 Soil bulk density

The soil bulk density was established by calculating the dry soil mass per unit volume (core sampler volume). Dry mass was obtained by dehydrating soil samples at 105°C for 48 hours, following Gradwell and Birrell (1979).

3.3.3.3 Litter decomposition and soil microbial activity

3.3.3.3.1 Soil Microbial Population

To evaluate the enzymatic activity of microorganisms, the total microbial population in the soil samples was obtained by quantifying the bacterial and fungal populations. The quantification of fungal and bacterial populations was conducted using the spread and pour plate procedures, as described by Black (1965).

3.3.3.3.2 Microbial biomass

The soil samples underwent fumigation, and the subsequent extraction of carbon, nitrogen, and phosphorus in 0.5M K2SO4 solution from the fumigated soils was used to determine the quantities of phosphorus, nitrogen and carbon present in the soil's microbial biomass. This estimation method was derived from the one proposed by Jenkinson (1988).

Litter decomposition is an important ecological phenomenon that contributes significantly to nutrient cycling and organic matter turnover within ecosystems.

In this study, a linear random mixed effect model was used to examine the association between the natural logarithm of the residual proportion of tea and several factors, including tea type, climatic zone, and incubation. The model incorporated a random intercept for variability.

At the outset, our intention was to calculate the Tea Bag Index (TBI) as proposed by Keuskamp et al. (2013). However, we found that the decomposition rates observed at our research locations do not align well with the underlying assumptions used in the aforementioned computations. As a result, the double exponential decomposition model, which serves as the foundation for the TBI, was used in an indirect manner.

$$w_{ij} = L(T)e^{(k_1+\kappa_{1i})t_{ij}} + (1 - L(T))e^{k_2(R)t_{ij}} + \epsilon_{ij}$$

(10)

Where w_{ij} is the proportion of litter remaining. L(T) is the fraction of labile carbon in the tea bag (0.842 for Green and 0.552 for Rooibos tea, and t_{ij} is time (days). k_1 and $k_2(R)$ are the decomposition substances for labile and recalcitrant carbon fractions. $k_2(R)$ depends on the climatic zone. κ_{1i} is a plot-wise random effect on k_1. Values of κ_{1i} are normally distributed with a mean of 0. And ε_{ij} is the error for plot i and observation j. The presented model is the best model based on the Akaike information criteria (AIC) of several different constellations of random factors and fixed factors (e.g., making k_1 dependent on the climatic zone).

3.3.3.3.4 Influence of the rate of decomposition on soil carbon stocks

Pearson correlation coefficient (r) was estimated to confirm the linear relationship between the rate of decomposition of recalcitrant carbon material, k_2 and labile carbon fraction k_1 (equation 10) with carbon content of forest soils.

$$r = \frac{\Sigma(X-\overline{X})(Y-\overline{Y})}{\sqrt{\Sigma(X-\overline{X})^2}\sqrt{(Y-\overline{Y})^2}}$$

Where, $\overline{X}$ - mean of X variable
$\overline{Y}$ - mean of Y variable

(11)

3.3.4 Timber value

3.3.4.1 Timber volume

During the inventory, the recorded estimated merchantable height values were adjusted by deducting a stump height of 0.5m. In the case of buttressed trees, the deduction was made based on the buttress height.
The calculation of timber volume (Vt) was performed using the following formula:

$Vt = (0.00007857 \times D^2) \times Hm \times 0.6093$ (12)

The variable Hm represents the merchantable height, which excludes the height of the stump or buttress, D represents diameter at breast height (cm).

3.3.4.2 Timber stumpage value

Timber stumpage value was calculated based on the formula prescribed by the Timber Resources Management and Legality Licensing Regulations, 2017 (LI 2254) of the Republic of Ghana. This formula is based on market conditions or current demand, timber prices and forest inventory levels or estimated resource life of timber species. Therefore, the stumpage value (StV) calculated is as follows:

$$StV = 0.35 \times FOB \times StR \times Vt \tag{13}$$

where the factor 0.35 represents the average sawlog-lumber recovery rate;
FOB is the free-on-board value of air-dried lumber (September 2018); StR is Stumpage Rate which is an estimate for market demand and forest inventory levels of the species.

3.3.4.3 Net Present Value (NPV)

Net Present Value (NPV) was computed for the restoration sites (plantation and secondary forests). NPV analyses were undertaken as follows:

$$NPV = \sum_{t=0}^{n} \frac{R_t}{(1+i)^t} \tag{14}$$

where:
R_t = net cash inflow – outflows during a single period t
i = discount rate
t = number of years
(Jagerson 2022)

3.3.5 Statistical analyses

Descriptive statistics were computed for the whole of the 93 research plots and used to conduct both one-way and two-way analysis of variance (ANOVA). Q-Q plots were used to assess the normality of the residuals. Dependent variables investigated in this study include diameter at breast height, basal area, total tree height, dominant height, merchantable tree height, canopy cover, stem density, above-ground carbon stocks, timber volume, timber value, plant species richness, plant species diversity, genetic heat index (GHI), soil carbon stocks, carbon-nitrogen ratio (C:N ratio), pH, litter decomposition rate, bulk density, microbial population, and microbial biomass C. The independent factors in this study were the forest type (plantation, secondary, and primary forests) and forest/ climatic zones (moist and wet). Two-way factorial analysis of variance was employed to concurrently examine the impact of the two independent factors on the dependent variables.

Independent-samples t-test was used to compare the mean values of woody recruits between the forest plantation and secondary forest sites for the dependent variables of above-ground carbon stocks, basal area, timber volume, and timber value. The Games-Howell test was used for post-hoc analysis due to the confirmation of uneven error variances by the estimated Levene statistic. The diversity indices in the vegan function were computed using the R programming language (Oksanen et al., 2020). The remaining statistical analyses were conducted using R version 4.1 and IBM SPSS Statistics version 28.

4 RESULTS

4.1 Floristic Composition and Species Diversity

4.1.1 Floristic Composition

A total of 14 315 vascular plants belonging to 530 species, 323 genera and 92 families were enumerated within 3.72 ha across the 11 study sites. A total of 1839 individuals had DBH ≥10 cm., 662 had DBH ranging between 2 – 10 cm, and 11 814 had DBH below 2 cm (Study II). At the species level 192 had DBH ≥ 10 cm; 148 had DBH between 2 - 9.9 cm, while 442 species had DBH below 2 cm. At the family level, 83 were found in plantations, 69 in secondary forests, and 81 in primary forests. Out of the 323 genera identified, 271 were in plantations, 189 in secondary, and 227 in primary forests. Seven plant life-forms were also recorded namely trees, lianas, shrubs, vines, herbs, grasses and ferns (Study II).

The percentage species occurrence of the seven plant life-forms recorded across the forest types was found to be comparable (Kruskal-Wallis test, $H(2) = 0.999$, $P = .607$). The most dominant plant life-form was trees in all the forest types, followed by lianas (Table 4). The most species-diverse family was Fabaceae with 62 species, comprising the following subfamilies: Caesalpinioideae, Papilionoideae, and Mimosoideae. Other major species-diverse families recorded included; Annonaceae (21), Apocynaceae (29), Euphorbiaceae (17), Malvaceae (25), and Rubiaceae (49).

Table 4. Species occurrence of the seven (7) plant life-forms identified in the three studied forest types (secondary, plantation and primary forests)

Plant Life-form	**Forest type**					
	Plantation		**Primary**		**Secondary**	
	Number of species	Spp. occurrence (%)	Number of species	Spp. occurrence (%)	Number of species	Spp. occurrence (%)
Fern	11	2	7	2	3	1
Grass	4	1	2	1	3	1
Herb	25	6	18	5	19	7
Liana	104	25	80	24	53	20
Shrub	46	11	36	11	32	12
Tree	215	51	172	52	147	55
Vine	17	4	16	5	11	4
Total	**422**	**100**	**331**	**100**	**268**	**100**

4.1.1.1 Canopy tree assemblage

A total of 117 species of emergent and canopy trees were identified at the 11 study sites. A total of 9, 17, and 10 emergent tree species were identified in the primary, plantation and secondary forests respectively, with 30, 25, and 15 upper canopy tree species and 44, 64, and 37 lower canopy tree species recorded respectively (Study II).

4.1.2 Successional Status / Guilds

Generally, the primary forests had significantly more shade-bearers than the other two forest types, both of which showed comparable proportions (see Table 5). Plantations exhibited a greater prevalence of pioneer species than secondary and primary forests. The sapling stratum had a significantly greater number of shade-tolerant species compared to the tree stratum across all forest types, with this trend being most prominent in the forest plantations (see Table 5). There were no significant differences in the pattern of distribution of successional groupings (guilds) across the forest types (Kruskal-Wallis test, H (2) = 1.830, p = .401).

Table 5. Distribution (%) of plant guilds within the study sites

	Forest Type	**Plant Guild**			
		Non-pioneer light demander **(NPLD)**	**Pioneer**	**Shade-bearer**	**Swamp**
All (Trees, saplings, seedlings/ground vegetation)	Plantation	31.5	19.4	46.2	2.9
	Primary	20.6	10.3	67.6	1.5
	Secondary	44.5	9.4	45.5	0.6
Trees	Plantation	26.6	39.1	32.2	2.1
	Primary	22.8	15.8	59.0	2.4
	Secondary	32.2	16.2	48.4	3.2
Saplings	Plantation	16.5	13.8	67.8	1.9
	Primary	15.7	6.3	78.0	0.0
	Secondary	18.3	6.7	75.0	0.0
Ground Vegetation	Plantation	32.3	19.6	45.2	2.9
	Primary	20.8	10.5	67.2	1.5
	Secondary	45.5	9.5	44.4	0.6

4.1.3 Regeneration of trees in the plantations

About 85% of trees (DBH ≥ 10 cm) enumerated in the plantations was naturally regenerated. Approximately, 15% of trees were planted (TI – 7.4%, TU – 9.2%, CO – 17.1%, AK – 28.9%). It was observed that the planted trees had relatively larger diameters compared to the recruits, and contributed about 42% to overall stand basal area (TI – 34.6%, TU – 15.4%, CO – 41.5%, AK – 57.1%)

4.1.4 Plant Species Diversity

The plantations had a substantially lower level of plot-wise richness (mean ± standard error of mean (SEM): 42.9 ± 1.00) compared to the secondary (48.1 ± 1.90) and primary (48.7 ± 1.70) strata $F(2, 89) = 5.942$, $P < 0.01$). Nevertheless, the elimination of the AK stands (Plantation No-AK) from the analysis eradicated the disparities in richness (Table 6).

Pielou's evenness index is a measure used in ecology to quantify the evenness or equitability of species abundance. The evenness of the overall plant strata in the three forest types, namely plantations, primary forests, and secondary forests, had comparable values of 0.76 ± 0.01, 0.79 ± 0.02, and 0.76 ± 0.02, respectively. However, statistically significant differences were noted in the tree stratum (DBH ≥ 10 cm) between the forest plantation stands and the two other forest types ($F(2, 89) = 5.942$, $p < 0.01$).

Table 6. Average species diversity, richness and evenness recorded in the study sites in southern Ghana. Letters indicate Games-Howell post-hoc test results comparing diversity variables between forest types. Means with the same letters are not significantly different ($\alpha = 0.05$). Standard error of the means (SEM) in parentheses.

		Forest Type			
Diversity Indices		**Primary**	**Secondary**	**Plantation**	**Plantation (No-AK)**
Shannon					
	Trees	2.43^{a} (0.16)	$2.40^{a,b}$ (0.17)	1.79^{c} (0.09)	$2.19^{b,c}$ (0.07)
	Saplings	1.32^{a} (0.12)	1.36^{a} (1.13)	1.36^{a} (0.07)	1.34^{a} (0.08)
	Seedlings	2.96^{a} (0.10)	2.86^{a} (0.11)	2.75^{a} (0.06)	2.76^{a} (0.07)
	All (Trees, Saplings, seedlings)	3.07^{a} (0.10)	2.95^{a} (0.11)	2.85^{a} (0.06)	2.87^{a} (0.07)
Simpson					
	Trees	0.89^{a} (0.05)	$0.88^{a,b}$ (0.06)	0.71^{c} (0.03)	0.84^{b} (0.01)
	Saplings	0.66^{a} (0.05)	0.68^{a} (0.05)	0.68^{a} (0.03)	0.68^{a} (0.03)
	Seedlings	0.90^{a} (0.02)	0.87^{a} (0.02)	0.87^{a} (0.01)	0.87^{a} (0.02)
	All (Trees, Saplings, seedlings)	0.9^{a} (0.02)	0.88^{a} (0.02)	0.87^{a} (0.01)	0.88^{a} (0.02)
Richness					
	Trees	13.35^{a} (1.04)	13.60^{a} (1.13)	9.87^{b} (0.62)	$12.10^{a,b}$ (0.60)
	Saplings	4.50^{a} (0.46)	4.59^{a} (0.49)	4.80^{a} (0.27)	4.61^{a} (0.30)
	Seedlings	35.25^{a} (1.72)	35.94^{a} (1.87)	32.38^{a} (1.03)	32.34^{a} (1.25)
	All (Trees, Saplings, seedlings)	48.70^{a} (1.70)	48.10^{a} (1.90)	42.9^{b} (1.00)	$44.60^{a,b}$ (1.25)
Evenness (Pielou)					
	Trees	0.95^{a} (0.03)	0.93^{a} (0.04)	0.80^{b} (0.02)	$0.89^{a,b}$ (0.01)
	Saplings	0.96^{a} (0.02)	0.96^{a} (0.01)	0.92^{a} (0.01)	0.92^{a} (0.01)
	Seedlings	0.83^{a} (0.02)	0.80^{a} (0.03)	0.79^{a} (0.01)	0.80^{a} (0.02)
	All (Trees, Saplings, seedlings)	0.79^{a} (0.02)	0.76^{a} (0.02)	0.76^{a} (0.01)	0.76^{a} (0.01)

No significant differences were observed in the overall diversity of forest types as determined by the Shannon-Weiner index (H'), $F(2, 89) = 1.667$, $p = 0.194$ and the Simpson index, $F(2, 89) = 0.7594$. Statistically significant differences were observed only in the analysis of the tree stratum (Shannon-Weiner: $F(2, 89) = 10.275$, $p < 0.001$; Simpson: $F(2, 89) = 9.076$, $p < 0.001$). There were no significant differences observed in the sapling and ground vegetation layers.

The primary forest stands exhibited a superior overall species richness compared to the other stands. The TU and AK stands were the worst overall performers, with the secondary forest, CO and TI stands being intermediate (Figure 6A). The primary forest exhibited similar superior performance in species accumulation at the tree and seedlings/ground vegetation layer, but not in the sapling stratum where the CO stands clearly out-performed all others. (Figures 6B, 6C, 6D).

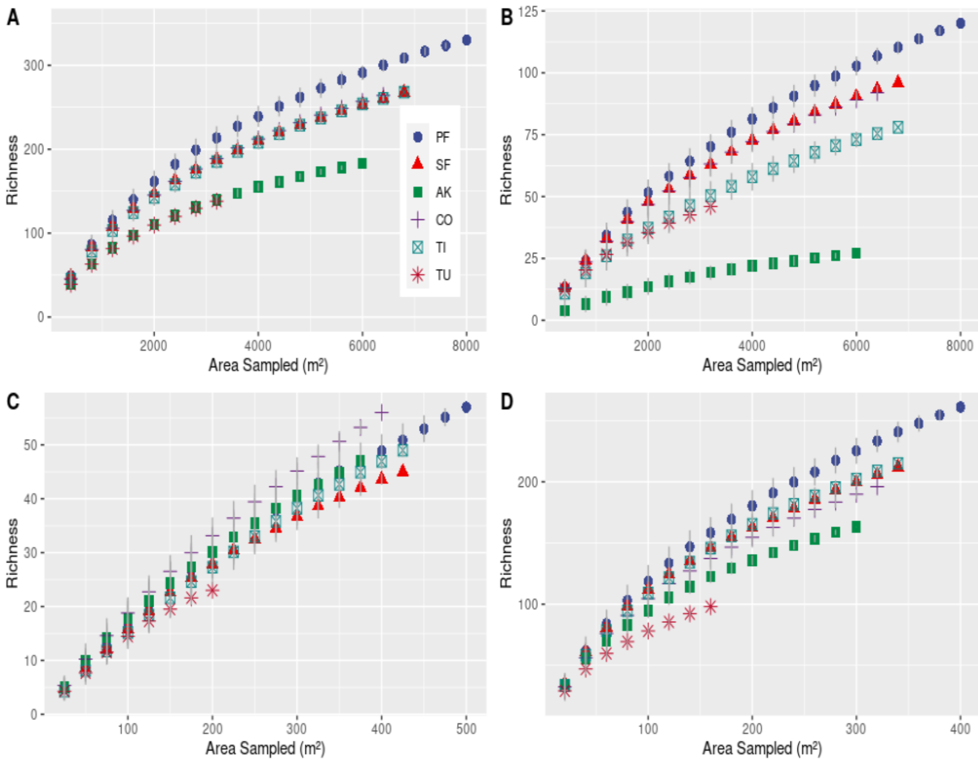

Figure 6. Species accumulation curves in southern Ghana for (A) all plant strata, (B) trees (DBH ≥10 cm), (C) saplings (10 cm >DBH ≥ 2 cm), and (D) ground vegetation/seedlings, using the area sampled as a metric of sampling effort. The x-axis shows the sampled area, while the y-axis reflects the number of species. AK- *Aucoumea klaineana*, CO- *Cedrela odorata*, TI - *Terminalia ivorensis* TU - *Tarrietia utilis*, PF - Primary Forest, SF - Secondary Forest. (Adapted from Brown et al., 2022)

4.1.5 Similarity

Overall, the primary forest shared more plant species with the plantations (254 spp.) than the secondary forest (197 spp.) (Figure 7A). This was true for the tree, sapling, and seedling/ground vegetation layers (Figure 7). At the tree level, the observed variations were much less.

According to the Jaccard Similarity Index (JSI), Sørensen's Similarity Index (SSI) values for paired primary-secondary, primary-plantation, and plantation-secondary for all plants were more than 0.5, signifying 49%, 51%, and 47% of mutually comparable species, respectively (Table 7). The seedling stage showed the fewest shared species in pairwise comparisons, with SSI values less than 0.5.

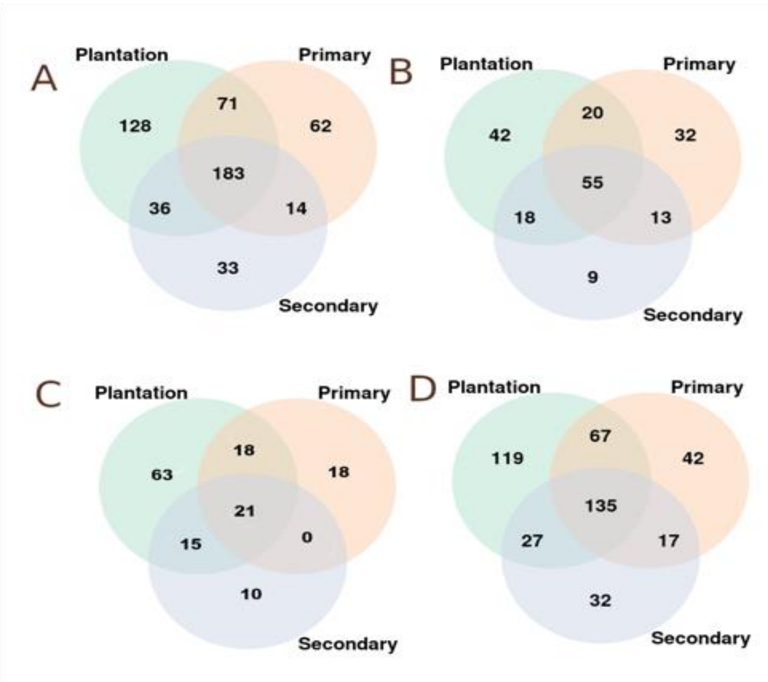

Figure 7. The number of species and shared species in the three forest types. Estimates were based on the following plant strata: (A) all plant strata, (B) trees (DBH ≥ 10 cm), (C) saplings (10 cm >DBH ≥ 2 cm), and (D) ground vegetation/seedlings (DBH < 2cm). (Brown et al., 2022)

Table 7. Pairwise comparison of species composition using the Sørensen's Similarity Index (SSI) and Jaccard Similarity Index (JSI) for the studied forest types in Ghana. (Brown et al., 2022)

Pairing of Forest Types	**Similarity Indices**	
	SSI	**JSI**
All Plants		
Primary x Secondary	0.66	0.49
Primary x Plantations	0.68	0.51
Plantation x Secondary	0.56	0.47
Trees		
Primary x Secondary	0.63	0.49
Primary x Plantations	0.59	0.41
Plantation x Secondary	0.63	0.46
Saplings		
Primary x Secondary	0.41	0.25
Primary x Plantations	0.45	0.28
Plantation x Secondary	0.44	0.28
Seedlings / Ground Vegetation		
Primary x Secondary	0.5	0.47
Primary x Plantations	0.66	0.49
Plantation x Secondary	0.58	0.4

4.1.6 Conservation Value

The Genetic Heat Index (GHI) analysis indicates that conservation value is generally lower in the moist relative to the wet climatic zone across the 11 study sites in Ghana (Figure 8).

Expectedly, the green star species was the majority category in all three forest types. The percentage of species with high conservation value (black, gold, blue) was greatest in the primary forest compared to the other forest types (Figure 9). Conversely, the secondary forest contained the greatest percentage of species with high timber value (scarlet, red, and pink).

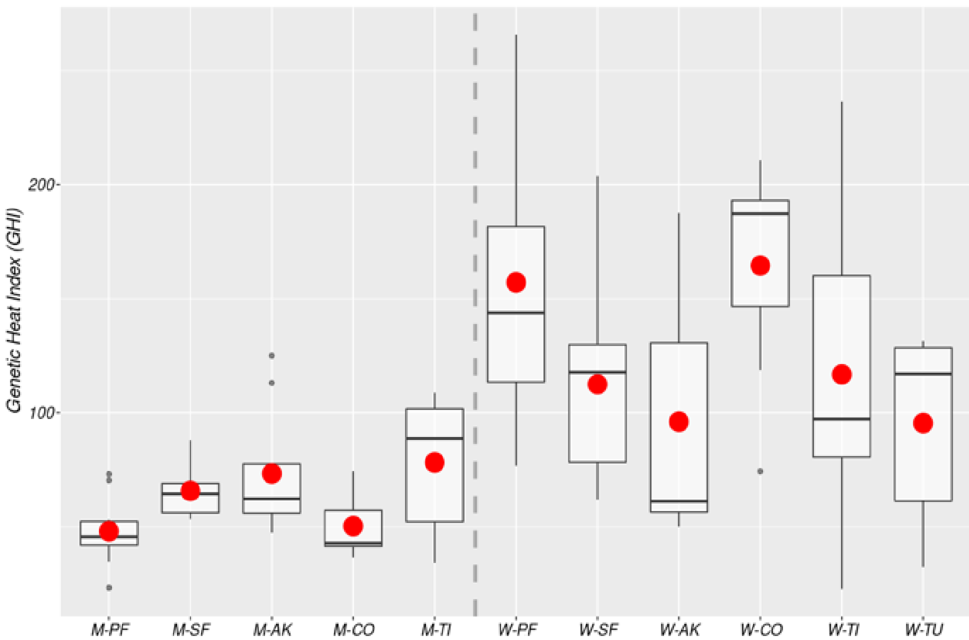

Figure 8. Mean Genetic Heat Indices measured at the 11 research locations within southern Ghana's wet and moist climatic zones. (In the Wet Zone, W-PF denotes primary forest, W-SF denotes secondary forest, W-AK denotes *Aucoumea klaineana* plantation, W-CO denotes *Cedrela odorata* plantation, W-TI denotes *Terminalia ivorensis* plantation, and W-TU denotes *Tarrietia utilis* plantation. In the Moist Zone, M-PF = primary forest, M-SF = secondary forest, M-AK = A. *klaineana* plantation, M-CO = C. *odorata* plantation, M-TI = T. *ivorensis* plantation)

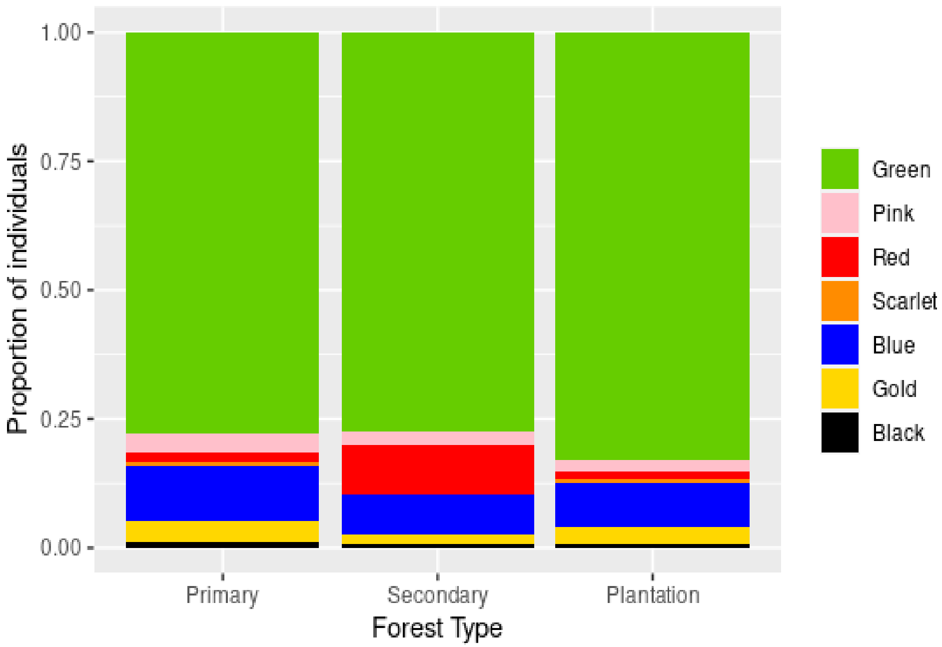

Figure 9. Relative composition of star species categories within the studied forest types in Ghana.

In Study II, a comprehensive inventory was conducted in the three forest types, documenting 132 species of high conservation value, including 79 trees, 19 shrubs, 24 lianas, five vines, and five herbs. The species inventoried were those categorised as Vulnerable (VU) or higher on the IUCN Conservation Scale or designated as 'Blue Star' or above on Hawthorne's Conservation Scale of rare or restricted-range species (Study II). 69, 64, and 96 of these species were identified within the primary, secondary, and plantation forests, respectively.

4.2 Forest Structure

No statistically significant variations were observed in stem density, canopy cover, dominant height, and total tree height across the three forest types, as shown in Table 8. The forest plantations exhibited significantly greater average DBH ($F(2, 89) = 6.323$, $p < 0.01$), bole volume ($F(2, 89) = 3.609$, $p < 0.05$) and basal area ($F(2, 89) = 3.476$, $p < 0.05$) compared to the secondary forest.

Dominant height and basal area across the study sites show a fairly good plot-level spread, indicating vertical (using dominant height), and horizontal (using basal area) structural complexity within the primary, secondary and plantation forests (Fig. 10).

The diameter class distribution within the plantation and secondary forests follows a Reverse-J curve (Fig. 11), which is akin to that of an uneven-aged primary or natural forest stand (Bettinger et al., 2016), indicating similar horizontal structure among the three forest types. The trees in the plantation and primary forests had substantially larger diameters than those in the secondary forests (Fig. 11).

Table 8. Mean values of key forest structural characteristics of secondary, plantation, and primary forests in southern Ghana. Letters qualitatively denote Games-Howell post-hoc test results comparing forest stand structural variables between forest types. Means with the same letters are not significantly different (α = 0.05). Standard error of mean, 1 SEM.

Forest Structural Parameter	Plantation	Secondary	Primary
Mean Canopy Cover (%)	85.5^{a} (0.6)	85.2^{a} (1.1)	85.0^{a} (0.9)
Mean DBH (cm)	18.4^{a} (0.4)	16.6^{b} (0.7)	18.1^{a,b} (0.7)
DBH Range (cm)	(2–120)	(2–79)	(2–126.5)
Mean Tree Height (m)	15.7^{a} (0.2)	15.6^{a} (0.4)	14.9^{a} (0.4)
Height Range (m)	(2–48)	(2–52)	(2–50)
Mean Dominant Height (m)	29.3^{a} (0.9)	26.9^{a} (1.7)	26.6^{a} (1.6)
Mean Basal Area of Trees/Shrubs/Saplings (m^2 ha^{-1})	37.8^{a} (2.3)	24.8^{b} (4.3)	34.0^{a,b} (3.9)
Mean Basal Area of Trees (m^2 ha^{-1}) Basal Area Range (m^2 ha^{-1})	33.8^{a} (2.3) 5–105	21.8^{b} (4.2) 11–39	30.2^{a,b} (3.8) 11–63
Mean Stem Density (ind. ha^{-1})	3581.2^{a} (171.6)	2954.4^{a} (311.5)	3000.0^{a} (287.2)
Mean Stem Density (ind. ha^{-1})	502.6^{a} (18.9)	507.3^{a} (34.3)	460^{a} (31.6)
Mean Bole Volume (m^3)	478.7^{a} (34.6)	285.1^{b} (62.8)	443.3^{a} (57.9)
Mean Bole Volume (m^3)	448.9^{a} (34.5)	264.3^{b} (62.7)	416.2^{a} (57.8)

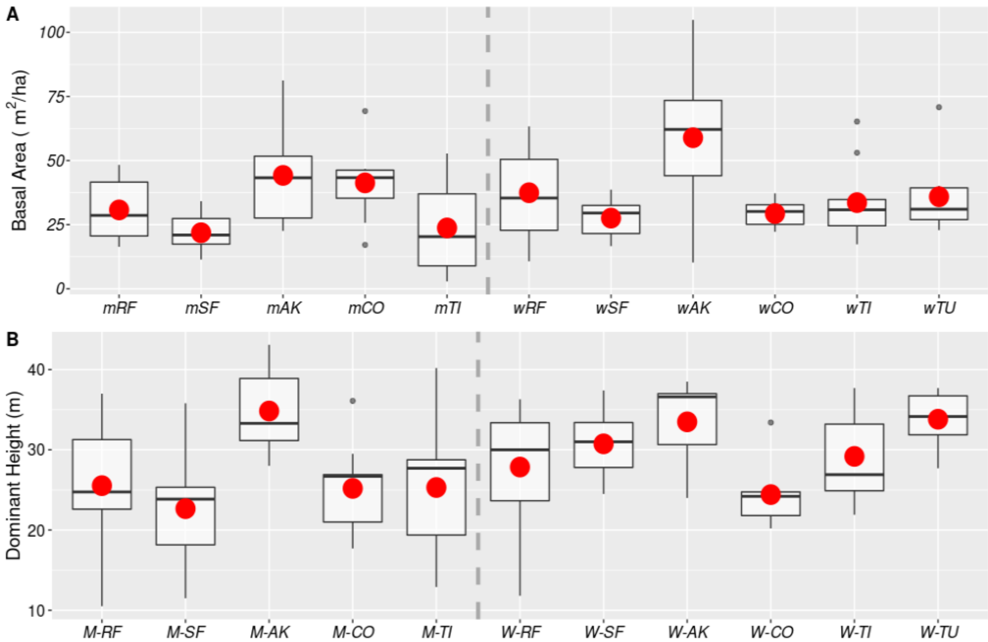

Figure 10. Plot-level mean basal area and tree dominant height across the 11 study sites in southern Ghana (Mean values are represented by red dots)

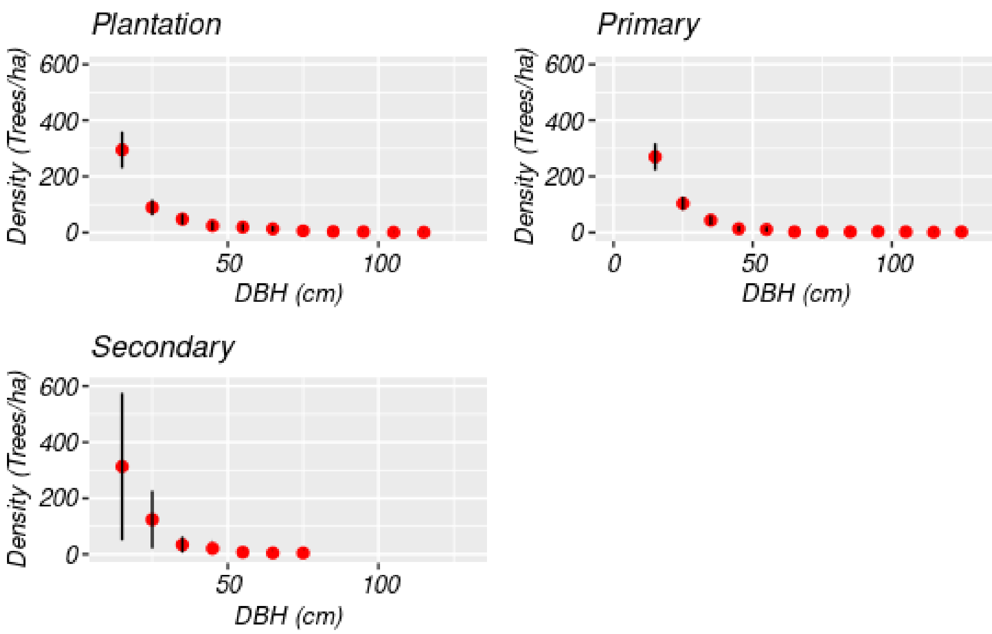

Figure 11. Distribution of tree diameters (DBH ≥ 10 cm) among the three forest types at the research sites in southern Ghana (Means are depicted by red dots, with bars denoting one standard deviation).

Table 9. Mean above-ground carbon stocks of the three forest types

Parameter	Forest Type		
	Plantation	Primary	Secondary
Above-ground carbon stocks (Mg ha^{-1})			
Mean	159.7^{a}	173.0^{a}	103.4^{b}
Std. error of mean (SEM)	14.3	25.1	12.3

4.3 Ecological functioning / Processes

4.3.1 Above-ground biomass and carbon stocks

Letters indicate Games-Howell post-hoc test results comparing carbon stocks between forest types: means with identical letters are not statistically different ($\alpha = 0.05$).

Analysis of variance (ANOVA) was used to examine the impact of forest types (plantation, secondary, and primary forests) on above-ground carbon stocks (AGCs). No statistically significant differences in above-ground carbon stocks (AGCs) were observed between plantations and primary forests. Nevertheless, it is essential to note that both plantation and primary forests had significantly greater above-ground carbon stocks (AGCs) in comparison to secondary forests ($F(2, 87) = 3.892$, $p < 0.05$), as shown in Table 9.

Distribution and level of carbon stock accumulation in the two forest zones for the forest types are shown in Fig. 12. The spread of AGC in the wet zone plantations shows a strong positive skew, indicating a higher frequency of high value scores, thus resulting in the mean score being much higher than the median. On the contrary, the primary forest values from both the wet and moist zones show the reverse.

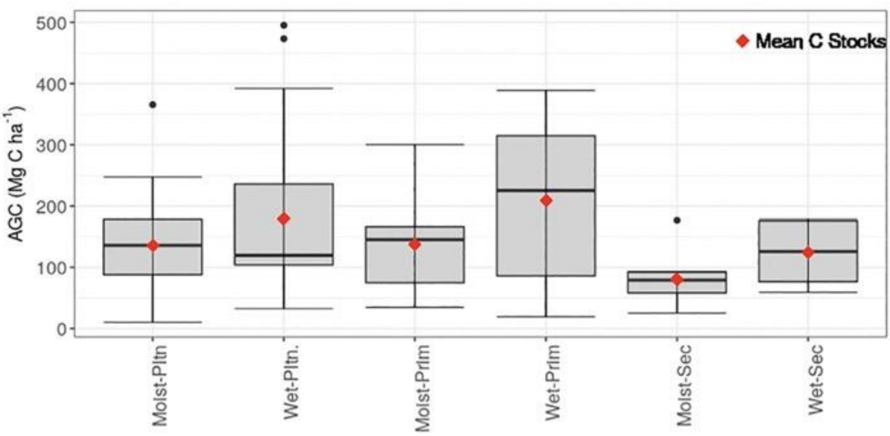

Figure 12. Above-ground carbon stocks (AGC) in the two distinct climatic zones (wet and moist) across the three forest types (plantation, secondary and primary forests).

4.3.2 Soil bio-physicochemical properties

The findings of the soil bio-physicochemical studies are succinctly presented in Table 10. In general, sites within the wet zone had significantly lower pH levels ($F(1, 70) = 41.119$, $p < 0.001$), with higher acidity, and lower base saturation. The moist zone sites had statistically higher microbial population compared to the wet ($F(1, 41) = 29.064$, $p < 0.001$). The data were log-transformed to fulfil the normality assumptions. Whereas the mean microbial population in the moist zone was 300 10^3 g^{-1}, that of the wet was only 0.34 10^3 g^{-1}. Microbial biomass carbon was higher in the moist zone ($F(1, 45) = 6.608$, $p < 0.05$). The wet zone exhibited notably significantly higher soil organic carbon ($F(1, 70) = 62.670$, $p < 0.001$) and carbon stock ($F(1, 70) = 51.742$, $p < 0.001$) levels than the moist zone. The wet zone exhibited greater carbon-to-nitrogen (C: N) ratios, with notable variations seen across different sites within the zones, such as TI and AK. Except for notable variations across climatic zones, no discernible distinctions were seen across sites and forest types within these zones. Furthermore, the combined effect of the climatic zone and forest type did not provide statistically significant interactions.

Table 10. Soil bio-physicochemical properties, for 0-50 cm depth of the three forest types across the two climatic zones. Numbers in parentheses represent standard errors of means, 1 SEM. Letters represent Tukey post-hoc test results, means with the same letters are not statistically different (α = 0.05)

Soil Parameter	Study Sites										
	M-AK	M-CO	M-TI	M-SF	M-PF	W-AK	W-CO	W-TI	W-HU	W-SF	W-PF
pH	5.13^{b,d} (0.171)	5.34^{c,d} (0.197)	5.43^{d} (0.183)	4.72^{a,d} (0.197)	4.95^{a,d} (0.153)	4.25^{a} (0.197)	4.52^{a,b,c} (0.183)	4.35^{a,b} (0.161)	4.44^{a,b} (0.171)	4.39^{a,b} (0.183)	4.55^{a,b,c} (0.153)
Org Carbon (%)	0.740^{b,d} (0.141)	0.940^{a,c,d} (0.162)	0.730^{a,b} (0.150)	0.830^{a,c} (0.126)	0.713^{a,c} (0.126)	1.384^{a,c,e} (0.162)	1.465^{c,e} (0.150)	1.371^{b,c,e} (0.133)	1.627^{d,e} (0.141)	1.493^{c,e} (0.150)	1.879^{e} (0.126)
Total Nitrogen (%)	0.0698^{a} (0.0129)	0.0817^{ab} (0.0149)	0.0691^{a} (0.0138)	0.0760^{ab} (0.0149)	0.0670^{a} (0.0115)	0.1163^{a,c} (0.0149)	0.1351^{bc} (0.0138)	0.1147^{a,c} (0.0121)	0.1385^{b,c} (0.0129)	0.1254^{b,c} (0.0138)	0.1690^{c} (0.0115)
Soil C stocks	51.16^{a,b} (6.98)	65.30^{a,b} (4.60)	53.75^{a,b} (7.61)	61.54^{a} (9.74)	49.44^{a} (6.21)	91.48^{c} (5.31)	97.87^{a,b} (11.93)	81.12^{a,b} (9.99)	118.98^{c} (8.73)	103.33^{b} (14.98)	122.84^{c} (15.45)
C/N ratio	9.97^{a} (0.364)	11.38^{a,c} (0.420)	10.11^{a,b} (0.389)	10.73^{a,c} (0.420)	10.27^{a,b} (0.325)	11.96^{b,c} (0.420)	11.46^{a,c} (0.389)	11.99^{c} (0.343)	11.88^{b,c} (0.364)	11.64^{ac} (0.389)	11.50^{a,c} (0.325)
Soil MB C	43.1^{a} (23.2)	210.6^{d} (20.7)	223.9^{b,c} (32.8)	170.7^{b,d} (23.2)	92.0^{a,b,c} (20.7)	59.2^{a,b} (23.2)	142.9^{a,b} (23.2)	100.2^{a,b,c} (20.7)	83.8^{a,b} (23.2)	90.9^{a,b,c} (26.8)	70.7^{a,b} (20.7)
Log (Tot Mic. Pop.) (CFU/g)	12.58^{c,d} (0.453)	11.86^{b,d} (0.405)	11.33^{a,d} (0.523)	10.79^{a,d} (0.523)	12.89^{d} (0.405)	10.30^{a,b} (0.453)	10.77^{a,b,c} (0.453)	10.79^{a,b,c} (0.453)	9.74^{a} (0.453)	10.35^{a,b} (0.405)	10.37^{a,b} (0.453)
Ca (Cmol (+) kg^{-1})	2.192^{c} (0.242)	2.139^{b,c} (0.280)	2.320^{c} (0.259)	1.439^{a,c} (0.280)	2.148^{c} (0.217)	0.783^{a} (0.280)	1.439^{a,c} (0.259)	0.943^{a,b} (0.228)	0.893^{a} (0.242)	1.008^{a,b} (0.259)	0.929^{a} (0.217)
Mg (Cmol (+) kg^{-1})	1.494^{b} (0.227)	1.006^{a,b} (0.262)	1.129^{a,b} (0.214)	1.362^{a} (0.262)	1.081^{a} (0.203)	0.420^{a,b} (0.262)	0.694^{a,b} (0.242)	0.680^{a,b} (0.214)	0.368^{a} (0.227)	0.548^{a,b} (0.242)	0.538^{a,b} (0.203)
K (Cmol (+) kg^{-1})	0.110^{a} (0.028)	0.0720^{a} (0.032)	0.136^{a} (0.030)	0.0150^{a} (0.032)	0.144^{a} (0.032)	0.055^{a} (0.032)	0.075^{a} (0.030)	0.054^{a} (0.026)	0.0117^{a} (0.028)	0.141^{a} (0.030)	0.080^{a} (0.025)
Na (Cmol (+) kg^{-1})	0.051^{a} (0.43)	0.030^{a} (0.050)	0.043^{a} (0.046)	0.033^{a} (0.050)	0.051^{a} (0.039)	0.052^{a} (0.050)	0.073^{a} (0.046)	0.072^{a} (0.041)	0.122^{a} (0.043)	0.151^{a} (0.046)	0.106^{a} (0.039)
P (mg kg^{-1})	4.74^{a} (1.22)	3.91^{a} (1.41)	3.61^{a} (1.31)	6.25^{a} (1.41)	5.46^{a} (1.09)	5.46^{a} (1.41)	2.60^{a} (1.31)	2.39^{a} (1.15)	5.06^{a} (1.22)	5.22^{a} (1.31)	3.90^{a} (1.09)
TEB ((Cmol (+) kg^{-1})	3.85^{d} (0.388)	3.25^{a,d} (0.448)	3.63^{c,d} (0.415)	2.94^{a,d} (0.448)	3.42^{b,d} (0.347)	1.31^{a} (0.448)	2.28^{a,d} (0.415)	1.75^{a,b} (0.366)	1.50^{a} (0.388)	1.85^{a,b,c} (0.415)	1.65^{a} (0.347)
ECEC (Cmol (+) kg^{-1})	4.85^{b} (9,362)	4.12^{a,b} (0.418)	4.50^{a,b} (0.387)	4.24^{a,b} (0.418)	4.55^{a,b} (0.324)	2.90^{a} (0.418)	3.66^{a,b} (0.387)	3.29^{a,b} (0.341)	2.99^{a} (0.362)	3.34^{a,b} (0.387)	3.29^{a,b} (0.341)
Ex. Acidity (Cmol (+) kg^{-1})	1.006^{a,b} (0.119)	0.872^{a} (0.137)	0.870^{a} (0.127)	1.300^{a,b} (0.137)	1.128^{a,b} (0.106)	1.587^{b} (0.137)	1.383^{a,b} (0.127)	1.537^{b} (0.112)	1.495^{b} (0.119)	1.499^{b} (0.127)	1.393^{a,b} (0.106)
BS (%)	77.7^{d} (3.83)	73.3^{b,d} (4.43)	77.4^{d} (4.10)	64.9^{a,d} (4.43)	72.2^{c,d} (3.43)	44.5^{a} (4.43)	57.6^{a,b,c} (4.10)	51.5^{a} (3.62)	50.3^{a} (3.83)	53.3^{a,b} (4.10)	54.0^{a} (3.43)
Sand (%)	77.2^{c,d} (1.99)	74.5^{c,d} (2.30)	77.9^{d} (2.13)	79.7^{d} (2.30)	77.5^{d} (1.78)	54.9^{b} (2.30)	57.5^{b} (2.13)	51.5^{a} (1.88)	56.5^{b} (1.99)	67.8^{c} (2.13)	44.8^{a} (1.78)
Silt (%)	8.10^{a,b} (1.37)	9.47^{a,c} (1.59)	6.46^{a} (1.47)	8.73^{a,c} (1.59)	9.88^{a,c} (1.23)	14.73^{b,c} (1.59)	25.2^{d} (1.47)	33.07^{e} (1.30)	14,95^{c} (1.37)	12.51^{a,c} (1.47)	25.2^{d} (1.23)
Clay (%)	14.8^{a,b} (1.42)	16.1^{a,b} (1.64)	15.6^{a,b} (1.52)	11.5^{a} (1.64)	12.6^{a} (1.27)	30.4^{c} (1.64)	17.3^{a,b} (1.52)	15.4^{a,b} (1.34)	28.6^{c} (1.42)	19.7^{b} (1.52)	30.0^{c} (1.27)

4.3.3 Litter decomposition

4.3.3.1 Decomposition rates of Green and Rooibos tea

Figure 13 shows that generally, the rate of decomposition of Green tea was higher compared to Rooibos tea, with little differences between sites. Analyses of linear mixed models confirm that the interactions between climate and remaining litter mass is significant for Rooibos tea but not for Green tea (Table 11).

The analysis of the double exponential decomposition model showed that the decomposition of the recalcitrant carbon fraction (k_2) was significantly lower in the wet climatic zone compared to the moist (Figure 14B). The decomposition of the labile fraction was similar between the two zones (Table 12, Figure 14A).

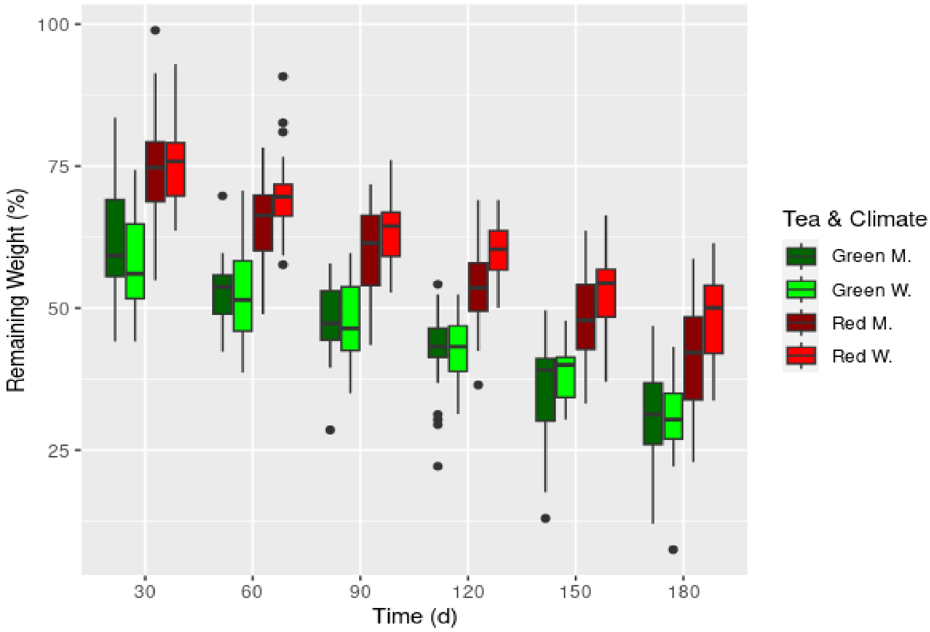

Figure 13. Weight remaining (%) in the tea bags as a function of the incubation period (days). Dark shades denote the moist climatic zone and lighter shades, the wet climatic zone, green represents Green tea and red, Rooibos tea.

Table 11. Results of a mixed model on the decomposition of Green and Rooibos tea in teabags. Results of a model ($\log(w)=a + b_1t+b_2C+b_3tC+\beta+\varepsilon$). Where $\log(w)$ is the logarithm of the proportion of tea litter remaining at time t, t is the time, C is climate, a, b1, b2, b3 are fixed parameters, β is a normally distributed random effect with a mean of 0 and ε is a normally distributed residual error with a mean of 0.

	Green tea	Rooibos tea
a(Intercept)	-0.340 (0.043) ***	-0.1811 (0.0296) ***
b_1(time)	-0.00478 (0.00028) ***	-0.00389 (0.00016) ***
b_2(Climate Wet)	-0.0658 (0.0589) ns	0.00095 (00.0402) ns
b_3 Time x Climate	0.00070 (0.00037) ns	0.000879 (0.00022) **
β Random intercept (std)	0.136	0.107
ε Error (std)	0.162	0.0947

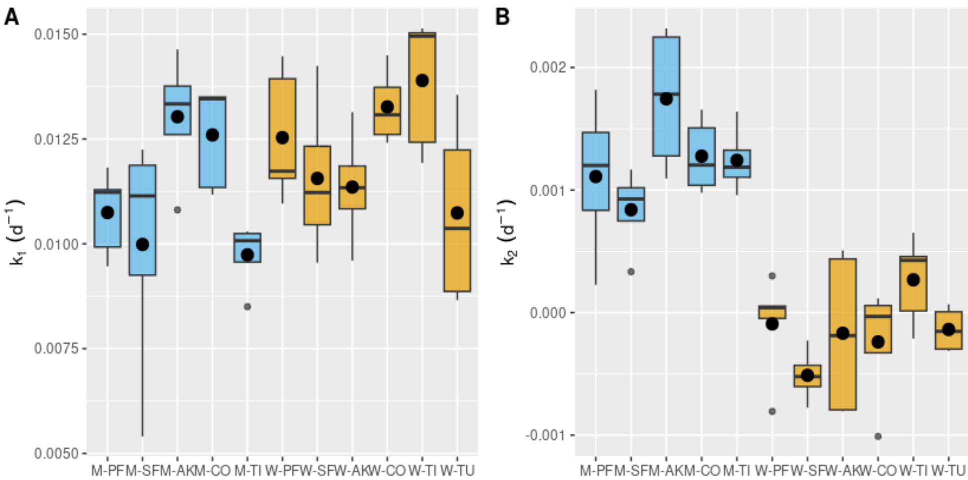

Figure 14. Decomposition rates for labile carbon (k_1) (d^{-1}) and recalcitrant carbon (k_2) (d^{-1}) at the 11 study sites across the two climatic zones. Values were estimated using equation-10 using non-linear mixed effects models.

Table 12. Results of the non-linear mixed model for the decomposition of tea based on equation-10. P values for all fixed parameters (k_1 = decomposition of labile carbon fraction; k_2 = decomposition of recalcitrant carbon fraction) were significant. Numbers in parenthesis represent standard errors of the means.

Fixed effects	Wet Climatic Zone	Moist Climatic Zone	P value for differences between climatic zones
k1	0.0123(0.0008)	0.0113 (0.0006)	0.22
k2	-0.00013 (0.00036)	0.00123 (0.000028)	<0.001
Random effects	Standard deviation		
κ1	0.00231		
κ2	0.00073		
ε	0.086		

4.3.3.2 Influence of the rate of decomposition on soil carbon contents

The soil carbon content was negatively correlated with the decomposition rate of the recalcitrant carbon fraction as measured by the parameter k_2. Pearson's correlation revealed that sites with a higher rate of decomposition of recalcitrant carbon had lower soil carbon contents ($r(40) = -0.65$, $p<0.001$). Site-wise rates of decomposition were calculated from equation 1 as the sum of the fixed and the random factor (e.g., $k_2 + \kappa_2$), there was however, no relationship between the rate of decomposition of labile carbon on the carbon stocks ($r(40) = -0.14$, $p = 0.37$).

4.4 Timber value

The value of standing timber in plantations was substantially greater than in primary and secondary forests. However, timber value in the primary forest was greater than in the secondary forest, even though the differences were not statistically significant (Table 13).

Table 13. Comparison of timber volume and values per hectare of the three forest types in the study (Std. error of mean, 1SEM in brackets)

Parameter	**Forest Type**		
	Plantation	Primary	Secondary
Mean timber volume (m^3 ha^{-1})	338 (41) [a]	294(50) [a,b]	167(38) [b]
Mean timber stumpage value (US\$ ha^{-1})	8577 (1441) [a]	3112(809) [b]	1870 (548) [b]

Letters represent Games-Howell post-hoc test results comparing standing timber volume and value variables between forest types: means with the same letters are not significantly different ($\alpha = 0.05$).

5 DISCUSSION

This thesis introduces an exclusive dataset from unmanaged forest plantations established 42 to 47 years ago. These plantations were abandoned around three years after establishment due to unforeseen economic and management challenges. The dataset also includes secondary forests of comparable age. Forest ecologists have often viewed secondary forests as relatively simple, unstable, and poorly organised systems, possessing little conservation value. In contrast, primary forests are considered as ecosystems that optimize complexity, diversity, and stability (Lugo, 2009). The old plantations examined in this research closely align with Lugo's (1997) notion of "self-design," which entails the delicate equilibrium between human intervention and the inherent ability of ecosystems to self-design. In this specific instance, the management of young forest plantation stands is neglected, allowing for the passive encroachment of native recruits in their understories. The reforestation sites in question, which have remained untouched by human intervention for over forty years and have effectively facilitated the establishment of diverse native plant species in their understorey, including certain rare and restricted-range species of significant conservation importance, and some of which have over the period, reached the canopy layers (as observed in Studies I and II), are anticipated to serve as valuable restoration models not only in the West African Tropics but also in other tropical regions. In this thesis, it has been shown that these plantations can provide modest financial returns for landowners and contribute to sustainable livelihood by selectively harvesting a proportion of the initially planted timber species (Study I). An examination of such old restoration sites has the potential to provide valuable insights that may contribute to the advancement of knowledge and application of forest restoration in tropical regions.

Utilizing the study framework outlined in Table 1, this research demonstrates that monoculture forest plantations and secondary forest regrowth can develop into self-organized and self-sustaining forest ecosystems. These ecosystems exhibit floristic diversity, structural complexity, and functional attributes such as energy and nutrient flow, biomass production, and decomposition of organic matter. Notably, these characteristics are similar to those found in the reference primary forests. This conclusion is supported by the findings of Study I, II, and III, conducted about four decades following abandonment.

5.1 Species composition

The study demonstrates a notable amount of plant species recovery in both secondary forests (66%) and abandoned timber plantations (77%) after 42 years, as compared to the reference primary forest (Study II). Furthermore, threatened and commercially valuable native timber species (scarlet star species) such as *Milicia excelsa* (Welw.) C.Berg, *Nauclea diderrichii* (De Wild. & T.Durand) Merrill, *Mansonia altissima* (A.Chev.) A.Chev., *Lovoa trichilioides* Harms, and *Daniellia ogea* (Harms) Holland, identified in the restoration sites rather than the primary forests, underscores the capacity of these sites to enhance biodiversity conservation at the landscape level. The variability in the pace of regeneration of indigenous plant species in tropical abandoned farmlands or plantations is contingent upon factors such as the specific environment, proximity to sources of propagules, and the intensity of previous land use (Chazdon 2003, 2008; Holl, 2007). The origins of these propagules in the context of this study are expected to be primarily from seed dispersal mechanisms such as avian and mammalian (particularly bats) seed rain, wind dispersal, and ballochory. However, it is also possible, albeit less probable, that the propagules could have been contributed by the soil seed bank and vegetative growth from stumps and other plant parts (Swaine & Hall, 1983).

The secondary and plantation forest sites are situated fairly close to one another, and at comparable distances from existing residual forests. These sites have similar land-use histories and have been abandoned for similar lengths of time, ranging from 42 to 47 years. The principal distinction between the previous management approaches for the two forest types is that while the plantations were established through direct planting and in some cases under an agro-forestry scheme i.e., Taungya, using high-value timber tree species, primarily long-lived pioneers, and were cultivated together with food crops for 3-4 years before being abandoned; the secondary forests were actively cultivated for agricultural food crops during a similar time frame before being abandoned.

The conditions present at the time of abandonment, characterised by partially shaded areas with plantations having a stocking of approximately 400 young trees per hectare, and the farms with predominantly plantain stems with stocking ranging from 2500 to 4000 stems per hectare, may have played a role in facilitating the successful regeneration of non-pioneer light demanders (31.5% for plantations and 44.5% for secondary forests) and shade-bearers (46.2% for plantations and 45.5% for secondary forests) in the understorey (Study II). Nevertheless, when considering all groups of vegetation (including trees, saplings, and ground vegetation), it was observed that the reference forests had a significantly higher percentage (67.6%) of shade-tolerant species compared to the restoration sites (Study II). This difference likely reflects the greater age and maturity of the primary forests, established for centuries, in contrast to the restoration sites that have only existed for approximately four decades.

The observed similarity in the relative composition of plant guilds across the three forest types at the sapling stratum suggests that the future replacement of older canopy trees and emergents is expected to result in a cohort that closely resembles the reference forest. The observed similarity in the proportion of life-forms across the three forest types supports the notion that composition has been largely restored in the plantation and secondary forests.

An analysis of the composition of the naturally regenerated canopy and emergent tree species, presumed to have been among the first group of colonizers in the restoration sites, reveals that animals dispersed a significant proportion of these species. Specifically, 56% and 57% of canopy and emergent tree species in the plantations and secondary forests are animal-dispersed, in contrast to 65% in the primary forests. It was also observed that the wind-dispersed tree species accounted for 33% and 38% of the total in the plantations and secondary forests, respectively, while in the primary forests, this percentage was 23%. Non-pioneer light demanders and shade-bearers were prevalent in the canopy layer with 65% and 66% identified in the plantations and secondary forests respectively, while in the primary forest, they constituted 73% of the tree population. The proportion of pioneer tree species found in the canopies of plantation and secondary forests (32% and 28%, respectively) was much higher compared to the primary forest (18%). Notably, 41 (63%) out of the total of 65 canopy tree species found in the primary forests were shared with the restoration sites. The mix of different plant guilds in the canopy and emergent layers of the restoration sites appear to indicate a pattern of succession that aligns with Horn's theory of competitive hierarchy (Horn, 1976). According to this theory, the initial cohort of invading species, including both pioneer and primary species, gradually diminishes due to the competitive exclusion of pioneers, particularly those with shorter lifespans. This decline is partially offset by a slow but persistent accretion of new primary (shade tolerant) species over time (Swaine & Hall, 1983). According to Suganuma and Durigan (2015), it is anticipated that the percentage of shade-tolerant, animal-dispersed tree species will steadily rise over time unless there are significant disruptions that result in abnormally large gaps in the restoration sites.

5.2 Vegetation Structure

Recurrent disturbances and the succession process perpetually influence the structure of forests. The dynamics of disturbance and succession take place at many scales in space and time. Changes in the intensity and frequency of disturbances may impact the pattern of succession and the resulting structural features of forests (Doyle, 1981). Structural composition and heterogeneity significantly impact species richness and biodiversity in a region (Connell, 1978; Brokaw & Scheiner, 1989; Franklin et al., 2002). After forty years after its abandonment, the plantation and secondary forests saw significant development, resulting in forest stands that exhibit vertical and horizontal structural complexity similar to the uneven-aged primary forests (Figures 10 and 11). The research evaluated many essential indicators of forest structure, including stem density, tree basal area, height, and canopy cover. These metrics were found to have been effectively restored in the secondary and plantation forests, as shown in Study II. However, it should be noted that the bole volume was comparatively smaller in the secondary forest, as shown in Table 8. The forest plantations exhibited a more rapid restoration of key forest structural characteristics, such as basal area, bole volume, and DBH, compared to the secondary forests (Table 8).

Additionally, the forest plantations have a greater abundance of larger diameter trees (DBH> 50 cm) compared to the secondary forests. Diameter at breast height (DBH) of trees over 100 cm was evident in both plantation and primary forests, but absent within the secondary forest. It is anticipated that primary and plantation forests, due to their considerably higher horizontal structural complexity than secondary forests, would provide a more diverse range of possible niches and habitats for species. The significantly larger basal area and bole volume, both of which serve as reliable indicators of ecosystem productivity, in the plantations compared to the secondary forests of the same age, provide evidence of better growth or biomass accumulation.

The observed robust growth of both the plantation and secondary forests, along with their intricate structural characteristics and diverse array of plant species and life-forms resembling those found in long-established primary forests, unequivocally showcases their capacity as feasible alternatives for tropical forest restoration.

5.3 Forest ecosystem functions

The consensus among scholars is that the restoration of multiple and stable forest functions necessitates the inclusion of diverse tree species assemblages, encompassing both multi-species and functional diversity (Balvanera et al., 2006; Aert & Honnay, 2011; Cardinale et al., 2012; Mascaro et al., 2012; Zhang et al., 2012; Jochum et al., 2020; Bongers et al., 2021). Given the established correlation between plant diversity and ecosystem functioning, numerous forest restoration initiatives in tropical regions have focused on cultivating diverse tree species to establish multi-species stands to enhance ecosystem productivity and functioning (Rodrigues et al., 2009; Lamb, 2018). Monocultures, however, have been widely regarded as having limited ecological advantages, which may be justified. The results of this research, which corroborate results of some previous research on forest restoration (e.g., Lugo 1992; Ashton et al., 1997; Keenan et al., 1997; Lugo, 1997; Pryde, 2015), appear to validate the paradoxical concept articulated by Lugo (1997). This concept involves the counterintuitive practice of establishing monoculture forest plantations on degraded land to facilitate the regeneration of diverse and ecologically complex forests. This study provides clear evidence that the restoration sites, which have experienced over four decades of abandonment, exhibit structurally complex and floristically diverse stands (Study II). These sites are successfully sequestering carbon and accumulating biomass (Study I), recycling soil nutrients and restoring soil fertility (Study III), maintaining optimal microbial populations and activity, and also facilitating litter decomposition (Study III). Notably, the soil carbon stocks within these restoration sites are comparable to those found in primary forests within the respective climatic zones (Study III).

The soil organic carbon (SOC) storage is heavily influenced by the equilibrium between the influx of plant material and the depletion of SOC via decomposition (Jobbágy & Jackson, 2000). The findings from the investigation of soil bio-physicochemical properties and litter decomposition suggest that the disparities seen in soil parameters evaluated are influenced mainly by the contrasting conditions between the moist and wet climatic zones. The differences across locations were often discernible, although they were less significant than the variances between climatic zones. The observed variations in decomposition rates and soil organic carbon may be attributed to the disparities in soil chemistry, which are influenced by climatic factors, particularly mean annual rainfall. The findings above are substantiated by the seminal pantropic research conducted by Marín-Spiotta and Sharma (2013) across more than 400 reforested areas and tree plantations. Their study determined that climate exerted a more substantial influence on the variability of soil organic carbon in successional and plantation forests compared to previous land use or forest age. Previous research on tropical ecosystems has shown evidence that higher average yearly rainfall is associated with an increased rate of litter decomposition (Cleveland et al., 2006; Wielder et al., 2009; Anaya et al., 2012). In contrast, Yu et al. (2019) posited that the pace of litter decomposition is influenced by the distribution rather than the amount of annual rainfall. In this study, however, higher decomposition rates were observed in the moist compared to the wet zone which experiences higher annual rainfall. This could possibly be a result of lower pH (higher acidity) in the wet zone which negatively impacted microbial population and activity (Růžek et al. 2021; Shen et al., 2021). It is notable that the differences were larger for the decomposition of the recalcitrant fraction of the litter than for the labile fraction (Fig. 14B). Standard models of soil organic matter assume that litter is composed of different fractions that differ in their recalcitrance in a way that the rate of decomposition of the recalcitrant fractions is particularly important for soil organic matter formation (Jenkinson 1990). Other factors are, of course, the rates of litter production. Lloyd et al. (1999) modelled carbon storage as the product of productivity and carbon residence time. The idea explains our observations of soil organic carbon storage. Assuming that litter production is related to standing biomass we showed that soil carbon storage is proportional to both standing above ground biomass and the rate of decomposition of recalcitrant litter.

5.4 Timber value

Timber plantations are typically established and managed to maximise timber volume, quality and value, generating a financial return for the landowner and/or investor. The monoculture plantations of the four timber species (*Tarrietia utilis*, *Terminalia ivorensis*, *Cedrela odorata*, *Aucoumea klaineana*) included in this study, which were aged between 42 and 47 years, were not subjected to any silvicultural interventions such as understorey competition removal, thinning, pruning, or application of fertiliser or soil amendments approximately three years after initial planting. The plantations exhibited notably higher standing timber volume compared to the secondary forests, whereas no significant difference was found between the plantations and primary forests. The timber stumpage value in the plantations (US$8555 ha^{-1}) was found to be significantly higher compared to the primary (US$3112 ha^{-1}) and secondary (US$1870 ha^{-1}) forests. The primary reason for the greater timber value of the plantations may be the deliberate cultivation of timber tree species with well-established market demand and value. These planted species accounted for roughly 55% of the total volume of standing timber (DBH) ≥ 30cm). Plot 1 in the A. klaineana stand (W-AK1) recorded the highest standing timber value of US$51,499 per hectare. This value was obtained from the 20 m × 20 m plot with ten timber trees, all A. klaineana, resulting in a density of 250 stems per hectare. These findings provide insight into the possible benefits of a well-managed A. klaineana plantation stand that is four decades old. The highest timber value in the case of the secondary forests was obtained in M-SF2 in the moist zone with a value of US$7740 ha^{-1}

At a concessionary discount rate of 2% per annum applied over the 40-year period, and the costs for establishing and maintaining the plantations estimated at US$2300 per hectare over the first three years (Zahawi & Holl, 2009; Brown & Kollert, 2017), and no cost assigned to the secondary forest, the net present value (NPV) for the timber plantations per hectare is US$1641, while that of the secondary forests is US$863. However, when discount rates are increased to 3% or higher, the secondary forests' NPV is higher, provided the cost of management for the secondary forests remains zero. Previous research have however, recommended assigning costs towards passive restoration in order to account for the expenses associated with monitoring and protection against grazing and wildfires, particularly during the early stages of establishment (Janzen, 2002; Birch et al., 2010; Zahawi et al., 2014). The NPV values obtained in this study align with previous economic research on forest landscape restoration under the framework of Initiative 20x20. This initiative is a regionally-led endeavour to restore 20 million hectares of land in Latin America and the Caribbean by 2020, as documented by Vergara et al. (2016).

The findings of this study suggest that timber plantations that are established at wide spacing (e.g., 5 m × 5 m), could provide a favorable microclimate for the growth of native woody plants in both the lower and upper canopy while additionally providing positive economic outcomes. The financial analysis results provide a strong rationale for implementing long-term passive restoration strategies, particularly in areas that do not require much financial investments for monitoring and protection during the initial stand development. Providing such landowners with long-term financing at concessionary interest rates to support reforestation or forest restoration initiatives could make these projects financially appealing as viable land-use alternatives that integrate conservation efforts with economic benefits and livelihood improvements. Including payments for forest ecosystem services, such as watershed protection, carbon sequestration, and biodiversity conservation, will significantly enhance the feasibility of such projects.

6 CONCLUSIONS AND RECOMMENDATIONS

There is a pressing need to implement measures aimed at restoring forest landscapes that have suffered degradation and deforestation worldwide, with particular emphasis on tropical regions. Fortunately, there is increasing recognition globally regarding the consequences of forest degradation and deforestation on biodiversity, climate change, and human welfare. As a result, policymakers around the world are making commitments to ambitious restoration goals through various regional and global initiatives. Therefore, these restoration projects must be informed by current research and best practices to optimize allocation of scarce financial resources towards restoration initiatives. It is essential to ensure that restoration initiatives are not just focused on ecological goals but also prioritize the improvement of livelihoods for populations reliant on forests, and landowners. This approach is essential in order to mitigate the potential for project failure.

Based on the established study framework and the subsequent selection of ecological indicators to assess the success of restoration efforts, our findings unequivocally indicate that four decades after abandonment, the restoration sites have effectively achieved a state comparable to that of the reference site in terms of forest structure, composition/diversity, and function. Furthermore, it can be seen that the restoration sites satisfy the criteria proposed by Clewell and Aronson (2007) for classifying restored ecosystems. These criteria include the ability of the ecosystem to exhibit self-organization, self-sustainability, and self-maintenance.

This research has provided evidence that naturally regenerating sites or secondary forests and passively managed forest plantations, can serve as effective methods for restoring forest structure, composition, diversity, and various ecological functions (such as carbon sequestration and biomass accumulation, litter decomposition, and soil fertility conservation) within deforested landscapes. This restoration process occurs through the passive colonization of the understorey by native woody recruits, as demonstrated in Study I and II. This phenomenon is particularly pronounced when the restoration sites are located near remnant forest areas since these patches assist the dissemination of seeds and other propagules. In addition, the restoration sites created favorable conditions that facilitated the regeneration and preservation of primary forest plant diversity, which in this study is used as a proxy for biodiversity. These included shade-tolerant species, often referred to as late-successional plant species and some rare and restricted-range plant species. Furthermore, the implementation of these two restoration pathways has the potential to generate economic benefits for landowners. This can be achieved through low-intensity selective logging of timber trees, as demonstrated in Study I. Additionally, Study II highlights the enhanced availability of non-timber forest produce including medicinal plants, and also presents promising opportunities for landowners to receive payments for ecosystem services rendered by the restoration sites.

The findings of the study indicate that timber plantations exhibit more significant biomass buildup and climate mitigation potential, as well as higher timber value and structural characteristics, in comparison to secondary forests (Study I & II). However, Study II also showed notable similarities in plant diversity, composition, and conservation value between the two restoration types and the reference forests.

In the context of restorative plantings or forest plantation projects with dual commercial and conservation objectives in the tropics, we propose utilizing the following model: which involves planting suitable fast-growing timber tree species at relatively wide spacing, with stocking density typically ranging from 400 to 650 stems per hectare. These planted trees are managed for three to four years to establish a canopy. Subsequently, the stands are left unmanaged, except for protection measures against wildfires, cattle grazing, and encroachment, thus allowing for the passive conversion of the stands into more natural ecosystems. Alternatively, passive restoration through natural regeneration coupled with protection of sites from the agents of degradation or deforestation is another option. These two methods are considered cost-effective and viable alternatives for restoring deforested tropical landscapes.

Additionally, governments should consider adopting policies that impose legal obligations on commercial forest plantation owners to allocate permanently a certain proportion of their land holdings (e.g., 5 - 10%) for forest restoration or conservation objectives. These areas may consist of degraded or deforested land that can naturally regenerate (fallow) or sections within existing plantations that could be left to natural processes or managed less intensively. An example of low-intensity management could involve selectively thinning high-value timber trees at low-intensity, thereby providing financial benefits to the owner of the plantation. This thinning process would result in small gaps in the canopy, like the natural disturbances in tropical forests, which have the potential of promoting the colonization of the understorey by non-pioneer woody plants. With regards to the reported global coverage of plantation forests, which is approximately 131 million hectares (FAO & UNEP, 2020), the implementation of such an approach has the potential to immediately put under conservation a substantial portion of these existing forest plantations. Furthermore, governments could provide various incentives to private owners of forest plantations such as; provision of long-term concessionary loan facilities, enhancing the availability of consulting and extension services, and streamlining access to markets for ecosystem services and other value chains.

In highly intricate ecosystems, such as the humid tropical forests, characterised by a wide array of interspecies interactions and reciprocal influences between the environment and organisms, it is improbable for research of this kind to comprehensively examine or evaluate all the features, components and interrelationships within the system. Hence, specific ecological indicators and proxies are employed to facilitate the assessment of restoration efficacy or success; a crucial aspect in establishing endpoints or objectives within the realm of ecological restoration. It is crucial to underscore that the primary focus of biodiversity conservation in the tropics should consistently revolve around preserving and safeguarding natural forests, ensuring their integrity remains intact and shielded from the many factors that contribute to degradation and deforestation. In the context of production tropical forests, such as logging concessions, sustainable forest management practices must be implemented, including low-impact logging practices, and protection of ecologically sensitive areas or areas of high conservation value, and keystone species within the timber concessions. However, when forest landscapes experience degradation, destruction, alteration, or conversion to alternative uses, it is important to possess the knowledge and tools required to intervene or provide assistance to facilitate their recovery.

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