The Ecological Functions of Congo Basin Ecosystems and Basin-Wide Carbon Cycle

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B.-I. Inogwabini et al. (eds.), *Resilience and Sustainability in the Congo Basin*,
https://doi.org/10.1007/978-3-032-02023-9_10-1

Abstract

The Congo Basin, spanning over 3.7 million km^2 across Central Africa, plays a critical role in regulating global climate, sustaining biodiversity, and supporting regional livelihoods. We explore the ecological functions of the Congo Basin ecosystems, emphasizing their role in the carbon cycle. We synthesize current knowledge on biogeochemical processes, carbon stocks, species interactions, and biodiversity patterns, while highlighting key data gaps and research needs. The region's forests, soils, wetlands, and aquatic systems together form one of the world's most significant carbon sinks, with unique characteristics, including high megafaunal density, extensive peatlands, and relatively low deforestation rates, shaping its contributions to carbon sequestration and climate regulation. We detail carbon cycle dynamics across lowland, montane, flooded, and savanna ecosystems and underscore the vast belowground carbon storage in the Cuvette Centrale peatlands. Patterns of alpha and beta tree species diversity affect ecosystem function and resilience, with plant functional traits playing a key role in nutrient

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cycling and productivity. Species such as forest elephants influence forest structure and carbon storage through seed dispersal and disturbance. Moreover, strong land-atmosphere feedbacks mean that evapotranspiration from the Congo Basin's tropical forests plays a key role in shaping regional rainfall patterns. Land use and climate change pose growing threats to these functions, potentially triggering regime shifts and biodiversity loss. Ultimately, the Congo Basin remains underrepresented in ecological research and monitoring despite its global importance. Enhanced field-based and remote sensing efforts are urgently needed to inform integrated conservation and climate change mitigation strategies that account for both carbon dynamics and biodiversity.

Keywords

Central Africa · Peatlands · Evapotranspiration · Biodiversity · Land use change · Nutrient cycling

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Introduction

The Congo Basin plays a critical role in global climate regulation; biodiversity conservation; climate change mitigation via carbon sequestration in trees, mineral soils, and peatlands; regional water cycling; local energy production (e.g., hydropower); and staple and cash crops and medicine provisioning. Spanning over 3.7 million km^2 across six countries in Central Africa, Congo Basin ecosystems, illustrated broadly in Fig. 1, act as a major carbon sink, absorbing vast amounts of atmospheric carbon dioxide and mitigating climate change. The region's extensive river network, including the Congo River, supports hydrological cycles and land-atmosphere interactions that influence local, regional, and global climate systems. The Congo Basin is also home to an extraordinary array of flora and fauna, including endemic and endangered species such as forest elephants (*Loxodonta cyclotis*), bonobos (*Pan paniscus*), and okapis (*Okapia johnstoni*), making it one of the most biodiverse regions on Earth. Interactions between the Congo Basin's forests, biodiversity, and biogeochemical and hydrological cycles yield emergent ecosystem functions that underpin many services on which people depend. The Congo Basin provides resources directly to over 75 million people in local communities, including Baka, Bayaka, Bagyele, and Bantu communities, who rely on Congo Basin forests and rivers for food, medicine, and cultural practices. Billions

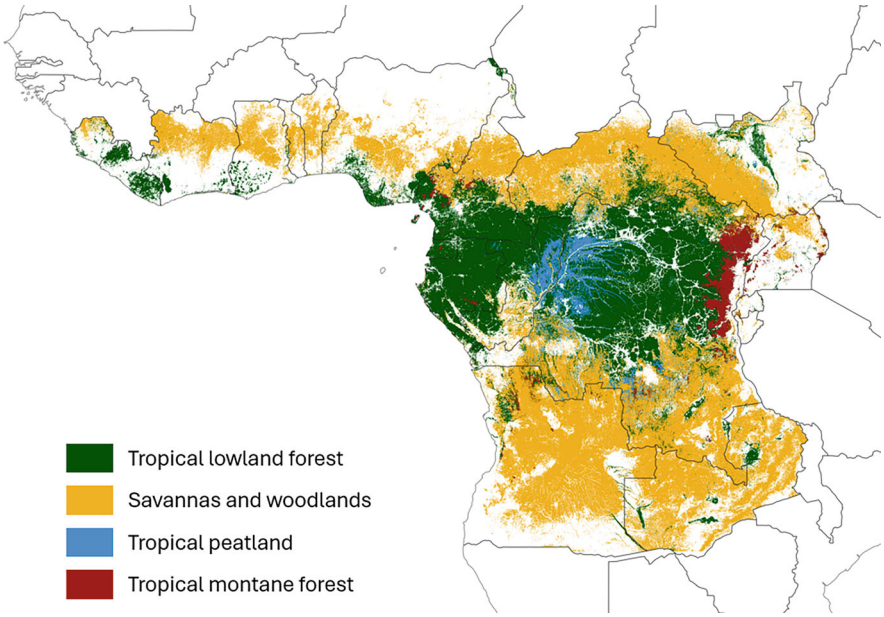


Fig. 1 Map of ecosystem types across the Congo Basin. Map created based on a reclassification of land cover CCI maps by ESA. Tropical moist forest below 800 masl was considered tropical lowland forest, while tropical moist forest above 800 masl was considered tropical montane forest (consistent with Cuni-Sanchez et al. 2021)

of people worldwide depend on the region's multifold services indirectly. Understanding the many interconnected functions of the Congo Basin ecosystem—its carbon sequestration, water regulation, biodiversity support, and socioeconomic contributions—is essential for developing strategies that ensure its stability and resilience for future generations. In this chapter, we focus on these interactions through the lens of the Congo Basin carbon cycle.

Congo Basin Ecosystem Functions

Interconnections Between Forests, the Atmosphere, Soil, Freshwater, and Biogeochemical Cycles in the Congo Basin

Congo Basin ecosystem functions, including carbon cycling, result from complex interactions between soils, vegetation and wildlife, the atmosphere, and the cycling of water and nutrients. While these dynamics play out in all tropical forest regions, several unique aspects of the Congo Basin contribute to the region's ecosystem functions (Atyi 2022; Malhi et al. 2013; White et al. 2013; White 2021). Compared to other tropical forest regions, the Congo Basin has a higher average elevation, lower annual precipitation, a sweeping range of mixed deciduous-evergreen vegetation, and historically lower rates of land cover change (Parmentier et al. 2007; Ernst et al. 2013). In addition, the abundance of megafauna in Africa is suggested to be one of the major drivers of intercontinental differences in forest structure between the Congo Basin and the Amazon (Blake et al. 2009).

Terrestrial Biogeochemical Fluxes

The African continent contributes to about 70% of global burned area and about half of global fire carbon emissions, with most biomass burning occurring within savannah regions (Chen et al. 2010; Ramo et al. 2021). These fires release nitrogen (N) and phosphorus (P) into the atmosphere that is subsequently transported by winds to the Congo Basin, contributing significantly to nutrient translocation within the region (Bauters et al. 2018, 2021a). In total, the Congo Basin forests receive approximately 18.2 kg N ha^{-1} yr^{-1} as wet deposition, with additional dry deposition via canopy interception (Bauters et al. 2018), while secondary forests have been shown to receive up to 3.1 ± 1.4 kg P ha^{-1} yr^{-1} from wet and dry deposition (Bauters et al. 2021a). Model simulations indicate that phosphorus deposition has significantly influenced aboveground carbon sequestration within the Congo Basin, which is more phosphorus-limited than nitrogen-limited (Du et al. 2020; Goll et al. 2023). However, land cover and land use changes also alter nutrient cycling in the region. Repeated clearing can lead to declines in plant-available N and P in the topsoil, but it mainly reduces soil cation stocks (Bauters et al. 2017, 2021b). This is due to the mobility of cations in the soil, as well as the high fraction of cations locked up in the aboveground woody biomass (Bauters et al. 2022a). Regrowing secondary forests

cycle an increasing amount of N and P deposition through a more efficient dry deposition filtering (Bauters et al. 2021a; Makelele et al. 2022). Therefore, along succession, forests in the region are potentially increasingly cation-limited (e.g., calcium) (Bauters et al. 2022b). In combination with the vulnerability of these cations in the fate of land use change, further research is needed to determine the role of cations in sustaining forest productivity in both old-growth as well as secondary forests.

Aquatic Biogeochemical Fluxes

The Congo River exports the second largest amount of terrestrial carbon to the ocean after the Amazon, mostly sourced from the region's humid lowland forests (Coynel et al. 2005; Spencer et al. 2016; Drake et al. 2023). In total, the Congo River exports 2 MtC yr^{-1} of particulate organic carbon (POC), 12 MtC yr^{-1} of dissolved organic carbon (DOC), and 4 MtC yr^{-1} of dissolved inorganic carbon (DIC), while outgassing between 133 and 177 MtC yr^{-1} of carbon to the atmosphere, although there remain large uncertainties in this particular carbon flux (Seyler et al. 2005; Coynel et al. 2005; Drake et al. 2018; Komba et al. 2024; Moustapha et al. 2022; Spencer et al. 2016; Wang et al. 2013; Aufdenkampe et al. 2011; Raymond et al. 2013). Seasonal variations in POC and DOC exports are largely hydrologically driven (Coynel et al. 2005; Drake et al. 2023; Hemingway et al. 2017). While many studies have focused on assessing sediment and carbon fluxes from the main stem of the Congo River at Kinshasa-Brazzaville (Coynel et al. 2005; Seyler et al. 2005; Wang et al. 2013; Lambert et al. 2016; Spencer et al. 2016; Hemingway et al. 2017; Kurek et al. 2022), studies investigating fluxes at smaller tributaries and sub-basins reveal contrasting within-watershed biogeochemical characteristics (Lambert et al. 2016; Borges et al. 2019; Bouillon et al. 2012, 2014; Coynel et al. 2005; Mann et al. 2014; Upstill-Goddard et al. 2017; Drake et al. 2019, 2020, 2023; Spencer et al. 2010; Baumgartner et al. 2022), largely driven by terrestrial ecosystem structure and to some extent hydrology (Mann et al. 2014). The Cuvette Centrale peatland complex additionally plays an important role in changing the composition of sediments and flow, storing large amounts of sediment from upstream while likely altering the amount of organic material from C3 vegetation passing through the Congo River headwaters (Datok 2021; Hemingway et al. 2017; Molliex et al. 2019; Laraque et al. 2009).

Climate and land use changes are impacting aquatic biogeochemical fluxes in several ways. Land use changes from deforestation are altering the sources of dissolved organic matter and concentrations of DOC, POC, and DIC (Battin et al. 2023; Drake et al. 2019, 2024), with increases in flooding frequency and duration associated with land use changes increasing carbon exports (Bradshaw et al. 2007). Carbon and nutrient balances are also affected by changing storm severity and frequency. Storm events in the region have increased in extent and intensity since the 1980s (Raghavendra et al. 2018; Alber et al. 2021) and are projected to continue on this track (Fotso-Nguemo et al. 2018), which has the potential to increase suspended sediment exports, as well as dissolved nutrients (Baumgartner et al. 2022, 2023).

Land-Atmosphere Interactions

The contribution of evapotranspiration to precipitation over land affects both local and regional climate, as evaporated moisture can travel thousands of kilometers in the atmosphere (Theeuwen et al. 2023; van der Ent and Savenije 2011). Recent studies suggest that the Congo Basin relies heavily on evapotranspiration to provide atmospheric moisture for rainfall via moisture recycling (Worden et al. 2021; Baker and Spracklen 2022; Sorí et al. 2022), while also providing moisture for areas downwind, including nearby agricultural regions that are primarily rainfed (Nyasulu et al. 2024; van der Ent et al. 2010; Te Wierik et al. 2024). Deforestation and degradation can significantly disrupt this key ecosystem process by decreasing evapotranspiration. For example, deforestation from 2003 to 2017 was observed to have an impact on moisture recycling and ultimately result in lower precipitation in the Congo Basin (Smith et al. 2023). However, these impacts have been more extensively studied in Amazonian tropical forests compared to the Congo and would benefit from further research in the region (Zemp et al. 2017; Xu et al. 2022; Staal et al. 2018, 2020; Flores et al. 2024).

Species Interactions

Animals, especially large herbivores and frugivores, can impact tree growth and forest structure via seed dispersal, forest disturbance, nutrient cycling enhancement, and other animal-mediated ecosystem processes in the Congo Basin (e.g., Malhi et al. 2022). A unique example of the region lies in the interaction between African forest elephants and large-seeded tree species. African forest elephants disperse the most intact large seeds across the longest distances (tens of kilometers) and from the highest diversity of plants (Blake et al. 2009; Poulsen et al. 2021). In addition to their seed dispersal impact, elephant trampling and herbivory decrease forest stem density, which can alter light and water availability as well as the spatial partitioning of resources, resulting in forests with fewer trees that tend to be larger-statured and higher wood density species (Berzaghi et al. 2019, 2023; Deblauwe et al. 2025). Vegetation demographic modeling suggests that forest elephant disturbances—typical around 0.5–1 elephants km^{-2}—increase AGB by 26–60 tons (t) C ha^{-1} (Berzaghi et al. 2019). However, this can simultaneously decrease forest net primary productivity (NPP) as larger and slower-growing trees dominate. Critically, the African forest elephant population is declining rapidly due to overhunting and habitat fragmentation (Blake et al. 2009; Poulsen et al. 2013; Maisels et al. 2013). Increasing the population to ~201,000 elephants over the next 30 years could create a carbon sink of 109 tC (Berzaghi et al. 2022). Much work is needed on this topic to understand the many ways that animal species interact with trees and forest ecosystems more broadly to influence the carbon cycle. For example, areas with higher gorilla abundances have been shown to correspond to forests with 27.5 tC ha^{-1} higher carbon stocks, while this relationship was not observed for chimpanzees, although the generalizability of this result and its underpinning mechanisms require improved understanding (Vale et al. 2024).

Congo Basin Carbon Stocks and Productivity

Recent work suggests that C dynamics in old-growth forests in the Congo Basin diverge from those in the more extensively studied and better characterized Amazonian tropical forests (Hubau et al. 2020). Although the mechanisms underpinning these divergent patterns have yet to be conclusively determined, there is strong evidence that the two largest tropical forests differ in forest structure (Banin et al. 2012; Lewis et al. 2013) and species composition (Slik et al. 2018). Additionally, the African tropics experience a drier average climate compared to the Amazon, with bimodal seasonality along the equator (Guan et al. 2015; Nicholson 2022), and substantially higher atmospheric nutrient deposition resulting from biomass burning on the continent (Bauters et al. 2018, 2021a).

Recent bottom-up work based on forest inventory plot data demonstrated that C uptake and emissions from African forests amount to some of the largest fluxes globally (Pan et al. 2024). Top-down findings from the Orbiting Carbon Observatory-2 model intercomparison project (OCO-2 MIP) showed net carbon sinks over the Congo Basin, which contrasted with net carbon sources over northern tropical Africa (Byrne et al. 2023). Signals of the Congo Basin's net biosphere exchange (NBE) from 2009 onwards also indicate a persistent carbon sink that contrasts with large sources of emissions in the western and eastern parts of tropical Africa (Palmer et al. 2019), although net CO_2 emissions were temporarily observed by OCO-2 (a contrast from the typical sink) over the region following the 2015/2016 El Niño, possibly owing to increased respiration resulting from heightened temperatures (Liu et al. 2017). In contrast, repeated forest census observations in the Congo Basin showed a persistent carbon sink during that same El Niño event, with no significant reduction in carbon gains from tree growth or increase in carbon losses from tree mortality (Bennett et al. 2021).

Large uncertainties remain related to the individual effects of the above drivers on the Congo Basin C sink (Ciais et al. 2011). Despite the role of tropical forests as the highest contributors to gross primary productivity, carbon sequestration, and natural methane emissions, tropical forest regions have the fewest research plots and flux towers (Baldocchi 2020; Schimel et al. 2015), and only limited efforts currently focus on the monitoring of GHG fluxes in the region. Very few comprehensive datasets exist that have reasonable spatiotemporal resolution for forest floor GHG fluxes (Barthel et al. 2022; Daelman et al. 2024). Additionally, only one flux tower exists in the entire Central African humid tropical forest biome (Sibret et al. 2022).

Below, we review what is currently known about carbon stocks and fluxes across the lowland, flooded, and montane forests, as well as savannas, woodlands, peatlands, and freshwater systems in the Congo Basin (Fig. 2).

Lowland Forests

The carbon sink in live aboveground biomass in intact African tropical forests has been stable for the past three decades. As such, intact forests in the region act as a net C sink, sequestering approximately 0.66 tC ha^{-1} $yr.^{-1}$ (Hubau et al. 2020). Forest inventory data and long-term carbon studies had previously estimated a stock change

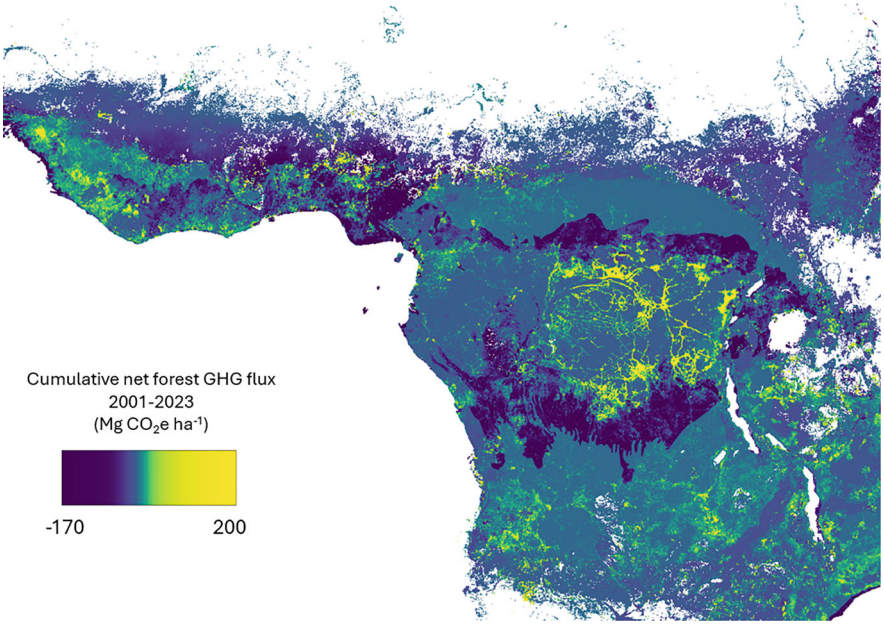


Fig. 2 Net annual forest-related GHG fluxes across the Congo Basin, summing per-pixel emissions over 2001–2023 from forest disturbance and removals associated with forest regrowth or with undisturbed forests. Positive fluxes represent emissions from the ecosystem to the atmosphere; negative fluxes represent removal from the atmosphere to the ecosystem. (Data source: Harris et al. (2021))

of 0.94 tC ha^{-1} $yr.^{-1}$ in intact African tropical forests from 2000 to 2007, totaling 482 MtC yr^{-1} (Pan et al. 2024). Field studies suggest that Central African forests may be more resilient to changing climatic conditions and may offer a longer-term carbon sink compared to other tropical forests (Hubau et al. 2020; Bennett et al. 2021). From 2001 to 2019, the Amazon region (5.14 million km^2) was a weak net carbon sink (-0.03 GtC yr^{-1}), with gross uptake (-0.4 GtC yr^{-1}) and gross emissions (0.3 GtC yr^{-1}). In contrast, the smaller African Congo Basin (2.98 million km^2) was a considerably stronger carbon sink (-0.17 GtC yr^{-1}), despite having similar gross uptake rates(-0.3 GtC yr^{-1}). The magnitude of gross emissions in the Congo Basin (0.14 GtC yr^{-1}) was approximately half of the emissions in the Amazon (Harris et al. 2021). However, satellite remote sensing studies that encompass not only forests, but also agricultural, urban, and aquatic systems, indicate that Central African forests are just as sensitive to climate anomalies as the Amazon (Liu et al. 2017; Palmer et al. 2019). In addition, future projections for the region from Earth system models remain highly uncertain, largely due to the lack of historic climate data and resultant low confidence projections of future climate (Brando et al. 2019).

On average, African tropical forests store roughly 180–195 tC ha^{-1} in aboveground biomass, which is notably higher than East or West African forests and

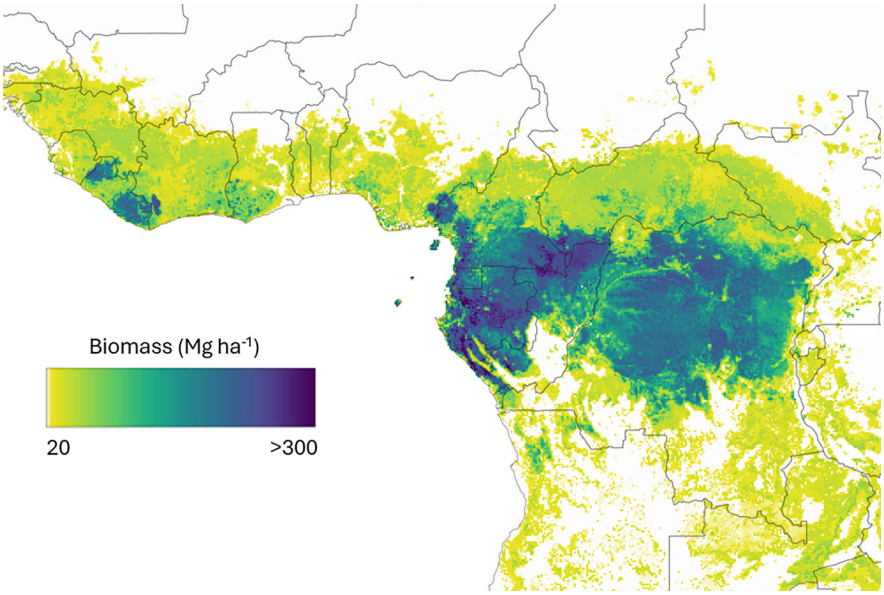


Fig. 3 Biomass distribution across the region. Values lower than 20 t ha^{-1} were masked. (Data source: Xu et al. (2022))

comparable to Bornean forests (Lewis et al. 2013). A relatively small percentage of species, around 1.5%, accounts for half of the regional aboveground carbon storage, exhibiting a pattern of "biomass hyperdominance" similar to the Amazon (Bastin et al. 2015; Cooper et al. 2024). Although uncertainty and variation between regional estimates of aboveground carbon stocks exist (e.g., Mitchard 2018), general patterns have emerged in recent years (Fig. 3).

Spatial variation in carbon stocks within the Congo Basin is driven by a complex interplay of environmental, geographical, biological, and historical factors. Climate plays a significant role, with the maximum temperature showing a negative effect on aboveground carbon (AGC; Sullivan et al. 2020). Rainfall seasonality also exhibits a negative relationship, with more carbon stored in less seasonal forests. Relatedly, light conditions play an important role, particularly in western Central Africa, where extensive low-level cloud cover during the dry season leads to a light-deficient climate but enhances the quality of light via increased diffuse irradiance, enabling evergreen forests to thrive, despite low mean annual rainfall (Philippon et al. 2019). Nutrient availability and soil properties like topsoil organic carbon and soil potassium can also influence above- and belowground carbon allocation, further adding to the complexity of spatial carbon stock variation (Bauters et al. 2019a; Bukombe et al. 2022; Doetterl et al. 2015; Gourlet-Fleury et al. 2011; Philippon et al. 2019).

Finally, C fluxes from deforestation, degradation, and regrowth are becoming increasingly important in the region's overall C balance (Noon et al. 2021). Over the past three decades (1990–2019), tropical deforestation offset approximately

two-thirds of the gains provided by the global forest carbon sink (2.2 ± 0.5 GtC yr^{-1}; Pan et al. 2024). Unlike South America and Southeast Asia, shifting cultivation is the main driver of land use change in Central Africa (Gillet et al. 2016; Tyukavina et al. 2018; Van Vliet et al. 2012; Curtis et al. 2018). The Congo Basin is projected to experience a fourfold increase in human population by the end of this century before stabilizing (Gerland et al. 2014), which, in combination with the prevailing shifting and subsistence cultivation system, is already accelerating deforestation (Tyukavina et al. 2018; Kleinschroth et al. 2019) and has the potential to make Central Africa the future land use change hotspot. Importantly, however, different countries in the region are undergoing distinct trends. In the DRC and Cameroon, for example, deforestation has been accelerating over the past several decades, shifting their trajectories increasingly away from high forest, low deforestation countries to deforestation frontiers (Tyukavina et al. 2018; Shapiro et al. 2021; Biswas et al. 2025). In contrast, Gabon and the Republic of Gabon remain high forest, low deforestation countries, with distinct regrowth dynamics associated more with logging disturbances (Heinrich et al. 2023; Biswas et al. 2025). Understanding the regrowth trajectories of secondary forests following disturbance is essential to project future land cover changes, regional forest productivity, tree species distributions, and C cycle-climate feedbacks (Anderson-Teixeira et al. 2021). Widely varying post-disturbance forest regrowth trajectories that span 60 to 200 years have been reported in the Congo Basin (Makelele et al. 2021) and West Africa (Amani et al. 2022), underscored by the large variation in global C sink estimates in regrowing forests (Pugh et al. 2019). For example, estimates from 1990 to 2000 vary from 1.2 to 1.6 GtC yr^{-1} using bookkeeping methods (Pan et al. 2024; Houghton et al. 2012) and 0.4 to 0.6 GtC yr^{-1} based on global vegetation models (Shevliakova et al. 2009; Kondo et al. 2018).

Montane Forests

African tropical montane forests, defined as forests located ≥800 m above sea level (a.s.l.), have a mean AGC stock of 149 tC ha^{-1}, which is significantly higher than previously thought (Cuni-Sanchez et al. 2021). The mean AGC stock in these forests is comparable to lowland forests in Africa (Lewis et al. 2013) but about 70% and 32% higher than averages from plot networks in Neotropical montane (Spracklen and Righelato 2014; Vilanova et al. 2018; Álvarez-Dávila et al. 2017) and lowland (Sullivan et al. 2020) forests, respectively. African montane forests are characterized by low stem density but a high abundance of large trees (Lewis et al. 2013; Cuni-Sanchez et al. 2021), trees >70 cm diameter contributing substantially to AGC stocks.

The high AGC stock of African montane forests is a pervasive, albeit unexpected, phenomenon across a wide environmental gradient (Cuni-Sanchez et al. 2021), with montane forests generally assumed to have lower AGC stocks than lowland forests due to decreased temperature, cloud immersion, soil waterlogging, and nutrient-limited soils, which reduce productivity. However, AGC, stem density, and the density of large stems are not significantly related to elevation but rather increase with annual precipitation and decrease with soil fertility (Cuni-Sanchez et al. 2021).

Montane forests with elephants were found to have lower AGC stocks (Cuni-Sanchez et al. 2021).

Since 2000, approximately 8000 km^2 of old-growth African montane forest have been lost, critically threatening this carbon stock (Cuni-Sanchez et al. 2021). The Democratic Republic of the Congo, Uganda, and Ethiopia have experienced the highest losses. Studying carbon dynamics in montane regions is crucial for enhancing our understanding of the factors affecting carbon storage, which requires establishing permanent plots in both disturbed and undisturbed forests to gain deeper insights into tree biomass dynamics (Imani et al. 2021).

Savannas and Woodlands

Forest-savanna woodlands in sub-Saharan Africa play a pivotal role in carbon dynamics and sustain the livelihoods of approximately 150 million people (Demol et al. 2024; Dewees et al. 2010; Frost 1996). The most well-studied savanna woodland systems in the Congo Basin are the Miombo woodlands, spanning ~2.5 million km^2. In the Congo Basin, Miombo woodlands occur primarily in the southern DRC, forming a transitional zone between the dense humid tropical forests and more open savanna ecosystems, characterized by distinct wet and dry seasons, nutrient-poor soils, and a dominance of *Brachystegia*, *Julbernardia*, and *Isoberlinia* species (Ryan et al. 2016). Despite their ecological significance, they face increasing pressures from agricultural expansion, logging, and changing fire regimes (Demol et al. 2024; Pelletier et al. 2018; Ryan et al. 2016).

Carbon stocks in Miombo woodlands vary widely, influenced by land use history, fire frequency, climatic conditions, and conservation approach (Bulusu et al. 2021; Gumbo et al. 2018; Shelukindo et al. 2014; Walker and Desanker 2004). AGC stock estimates across the biome for undisturbed Miombo range from 28 to 63 tC ha^{-1} (Bulusu et al. 2021) and 1 to 95 tC ha^{-1} (Gumbo et al. 2018). In contrast, recovering Miombo shows lower AGC stocks, with estimates averaging 19 ± 16.8 tC ha^{-1} (Bulusu et al. 2021). Recent estimates using lidar for total aboveground carbon storage across Africa's Miombo woodlands are estimated at approximately 3.7 GtC and suggest that conventional methods may underestimate carbon sequestration potential (Soka and Nzunda 2014; Demol et al. 2024).

A defining characteristic of Miombo woodlands is their capacity for rapid regeneration after disturbances and thus rapid AGC recovery, primarily through coppicing (Syampungani et al. 2015). AGC recovery rates range between 0.98 and 1.42 tC ha^{-1} yr^{-1} for agriculture and charcoal fallows, respectively, and vary with recovery age and disturbance type (Chidumayo 2013; Kalaba et al. 2012, 2013). Chronosequence studies find that C stocks between old-growth Miombo and 20–30-year-old fallows do not significantly differ, suggesting that these woodlands can recover aboveground carbon storage in as little as 20 years (Kalaba 2013; Williams et al. 2008). There is also increasing evidence that African tropical forests and savannas can exist as alternative stable states, with transitions influenced by climate, fire regimes, and historical land use (Aleman et al. 2020; Hirota et al. 2011). While precipitation plays a role, fire seems to be a key driver—frequent burning maintains savannas by limiting tree recruitment, while fire suppression allows forests to expand

(Staver et al. 2011). Paleoecological and floristic data suggest these biomes have remained distinct over long timescales, with minimal species overlap (Aleman et al. 2020). As climate change and human activities intensify, understanding these dynamics is crucial for predicting biome shifts and guiding conservation efforts (Hirota et al. 2011).

Peatlands and Flooded Forests

Seasonally and permanently flooded forests are extensive within the Congo Basin (Verhegghen et al. 2012; Dargie et al. 2017; Sonwa et al. 2022), storing ~103–191 tC ha^{-1} of AGC (Ifo et al. 2019; Djuikouo et al. 2010). Some studies report similar AGC in flooded forests to *terra firme* (Ifo et al. 2019; Djuikouo et al. 2010), while Lewis et al. (2013) reported relatively lower AGC in flooded forests. The central depression of the Congo Basin, known as the Cuvette Centrale, contains seasonally flooded and swamp forests that have an average AGC of 104 tC ha^{-1} (Xu et al. 2022). However, the Cuvette Centrale peatlands contain a substantial amount of belowground carbon, with a median estimate of 29 GtC (Crezee et al. 2022). This represents approximately 28% of the world's tropical peat carbon, which is a significant increase in the estimate from an earlier study, now revised to between 26 and 32 GtC (Dargie et al. 2017). Peat depths average 2.4 ± 1.6 m, with a maximum of 6.4 m.

The Cuvette Centrale peatland complex is the largest in the tropics, covering an area of 167,600 km^2. The peatland carbon is not evenly distributed and is found in different geomorphological settings, including rainfed interfluvial basins and river-influenced areas with low nutrient status, where peat has accumulated over thousands of years, beginning around 10,600 years ago (Dargie et al. 2017). The DRC holds ~20 GtC, and the Republic of the Congo stores ~9 GtC (Crezee et al. 2022). These belowground peat carbon stocks are enormous when compared to aboveground forest carbon, with the peat carbon equivalent to approximately 82% and 238% of each country's aboveground forest carbon stock, respectively. The mean carbon density within these peatlands is estimated at 1712 ± 634 tC ha^{-1}, with some areas reaching a maximum of 3970 tC ha^{-1} (Crezee et al. 2022), which is about nine times the mean carbon stored in the aboveground live tree biomass of African tropical moist forests (Crezee et al. 2022). Despite the vast quantity of carbon stored in these peatlands, only 8% (2.4 GtC) is within nationally protected areas. Logging, mining, and palm oil concessions overlie 26% of the total carbon stocks or 7.4 GtC, and hydrocarbon concessions cover almost the entire peatland complex, highlighting their vulnerability to land use change.

Biodiversity and Ecosystem Functions

Below, we discuss diversity patterns of tree species as they relate to ecosystem function. See Chapters ▶ "The Evolution of Congo Basin Ecosystem Diversity", ▶ "Human Influence on Current Status of Biodiversity of the Congo Basin", and ▶ "Opportunities and Potential for Sustainable Development" for more detailed reporting on other aspects of floral and faunal diversity.

α-Diversity for Critical Areas of the Congo Basin

Alpha diversity, i.e., site-specific species diversity, in Congo Basin forests is a result of complex ecological interactions, historical biogeography, and anthropogenic influences (Couvreur et al. 2021). While tropical forests worldwide share a common physiognomy, African tropical forests stand out in cross-continental comparisons (Richards 1973). The "odd man out" hypothesis was developed to explain this phenomenon and describes three features: (1) the relative paucity of the African flora, (2) the wide distribution of African species, and (3) the sparseness of certain plant groups in Africa. Evidence now abounds to support the relative paucity of African tropical flora, including plot-level comparisons of alpha diversity between the Neotropics and Afrotropics (Parmentier et al. 2007) and across all three tropical regions (Slik et al. 2015). Tropical Africa is home to an estimated 4500–6000 tree species, substantially less than the Amazonian or Indo-Pacific regions, yet still significant in terms of endemism and functional diversity (Slik et al. 2015). While flora are approximately four times less diverse in tropical Africa than the Neotropics, the same families are the most species-rich (notably, Fabaceae) (Silva de Miranda et al. 2022). The wide distribution of African species is confirmed by low species turnover, evidenced by the relatively rapid accumulation and saturation of species along accumulation curves (Slik et al. 2018), with many tree species occurring across the entire Guineo-Congolian region (White 1983). The seminal work of Frank White on African vegetation and its spatial organization has since been confirmed by numerous empirical analyses (e.g., Küper et al. 2004; Linder et al. 2001, 2012; Droissart et al. 2018). Finally, several plant groups are sparse in Africa, with a notable example being palms. For example, tree-like palms are ubiquitous in the Neotropics but rare in the African tropics, which is dominated more by tree-climbing palms (Muscarella et al. 2020).

In relative terms, Africa hosts around 15% of the number of tree species that exist globally (Gatti et al. 2022). This diversity is not evenly distributed, with local hotspots of richness and endemism occurring, such as the Albertine Rift (Orme et al. 2005), recognized early on by White (1983) as the regional mosaic of Lake Victoria. Lower Guinea is especially rich in tree species diversity, with wet evergreen forests in Gabon hosting enormous plant diversity (Texier et al. 2022). In contrast, the inner Congo Basin, in the Sangha River interval between the two subcenters of endemism, is depauperate (White 1983) and is thought to be a former savanna corridor (Maley 2001, 2002).

A key characteristic of tree diversity in the Congo Basin is the presence of monodominant stands, particularly those dominated by *Gilbertiodendron dewevrei*, described by Gerard (1960) in northern Congo and observed across the Sangha River interval (Fayolle et al. 2014b) and eastward to Ituri (Hart et al. 1989; Hart 1995). Monodominance is generally recognized as occurring when a single tree species dominates >50% of the stems in a forest stand (ter Steege et al. 2019; Makana et al. 2011). The mechanism leading to this dominance has long eluded researchers (Hart et al. 1989; Torti et al. 2001; Peh et al. 2011; Bauters et al. 2019a). Recent work suggests that ectomycorrhizal association might enable *Gilbertiodendron* trees to

access nutrients directly from the soil organic matter, subsequently promoting nutrient limitation for co-occurring species (Hall et al. 2020). These forests, while structurally complex, exhibit lower alpha diversity due to the competitive exclusion of other tree species.

Anthropogenic disturbances, including selective logging, agriculture, and shifting cultivation, have profound effects on alpha diversity. Secondary forests recovering from these disturbances exhibit rapid increases in species richness and functional trait diversity, often reaching near-old-growth levels within six decades (Makelele et al. 2021). However, full recovery of floristic composition is much slower, with old-growth forests continuing to harbor unique assemblages of species that do not easily re-establish in disturbed areas (Makelele et al. 2021; Bauters et al. 2019b). Alpha diversity in the Congo Basin forests reflects both ecological and evolutionary processes, shaped by natural environmental gradients and increasingly modified by human activities. Maintaining this diversity requires an integrated conservation approach that considers species richness, functional traits, and the ecological roles of common and rare species.

β-Diversity Across Critical Areas of the Congo Basin

Beta diversity, which measures species turnover across different sites or communities, is a key determinant of Congo Basin forest biodiversity patterns. It reflects the degree of species differentiation between habitats and is shaped by historical biogeography, environmental gradients, and anthropogenic pressures (Duivenvoorden et al. 2002). Strong floristic discontinuities exist across the region, with species composition varying significantly along climatic and edaphic gradients (Réjou-Méchain et al. 2021; Picard et al. 2024). One of the most pronounced biogeographic divides is located at the Albertine rift that separates the dry, moist, and wet forests of West and Central Africa (the entire Guineo-Congolian region) from the upland and coastal forests of East Africa (Fayolle et al. 2014b). This major floristic discontinuity has also been characterized for savannas (Fayolle et al. 2019). Described decades ago by White (1983), this discontinuity has subsequently been challenged and reconfirmed by multiple studies (Küper et al. 2004; Linder et al. 2005, 2012; Droissart et al. 2018).

On average, African tropical forests are exposed to drier and more seasonal climates compared to tropical forests on other continents (Guan et al. 2015). Across tropical Africa, climate (e.g., seasonal drought) shows strong spatial variations (White 1983), with many species having evolved toward specialized climatic niches (Gorel et al. 2022). Recent analyses indicate that climate is a primary driver of beta diversity in the region (Fayolle et al. 2014a, b; Réjou-Méchain et al. 2021), distinguishing the Congo Basin from other tropical forests where soil properties exert a stronger influence on species turnover (Réjou-Méchain et al. 2021; Fayolle et al. 2012; Vleminckx et al. 2020). Strong variation between function and floristic turnover exists, for example, from equatorial areas with a low water deficit to areas with a high-water deficit toward the limits of the tropics (Réjou-Méchain et al. 2021), areas with high evapotranspiration rates (e.g., the northern limit of Central African forests), and areas with a cool and light-deficient dry season (e.g., coastal Gabon). In

general, rainfall seasonality, maximum temperature, and evapotranspiration rates seem to be particularly important in structuring tree communities in the Congo Basin, with drier regions supporting different species assemblages than wetter areas. Functional beta diversity (i.e., variation in species traits between sites) further underscores the complexity of forest composition in the region. While floristically distinct forest types exist, they often exhibit functional convergence, meaning that different species may occupy similar ecological niches in response to comparable environmental conditions. This redundancy in functional traits can buffer ecosystems against disturbances but also highlights the need to preserve both taxonomic and functional diversity to ensure long-term ecosystem stability (Réjou-Méchain et al. 2021).

Functional Properties of Biodiversity

Functional diversity, i.e., the value and range of the functional traits of the organisms in a given ecosystem, in African tropical forests, is a critical aspect of their resilience, productivity, and capacity to provide ecosystem services. Based on pan-tropical modeled estimates of functional richness and divergence, these forests exhibit functional trait variation driven by environmental gradients, disturbance regimes, and long-term evolutionary processes (Aguirre-Gutiérrez et al. 2022). Functional diversity appears to play a key role in ecosystem stability, influencing carbon storage, nutrient cycling, and the ability of forests to withstand climatic fluctuations (Day et al. 2014; Aguirre-Gutiérrez et al. 2019). The functional contribution of large, rare tree species, with a unique combination of functional traits, is particularly significant, as they likely affect ecosystem functioning more than smaller trees (Kearsley et al. 2019).

An additional key feature of African tropical flora is deciduousness (Loubota Panzou et al. 2018). The proportion of deciduous stems varies across the Congo Basin (Réjou-Méchain et al. 2021), and its response to climate was found to be mediated by the geological substrate in the Sangha River Interval. Recent work shows that phylogenetic constraints and climate shape drought-related traits in African tropical trees, with leaf habit responses to climate mediated by tree height and wood density (Gorel et al. in press JEcol).

Integrating functional diversity with carbon storage in conservation and restoration is critical (Achieng et al. 2023). In the Congo Basin, secondary forests recover functional diversity within six decades of shifting cultivation, yet carbon stocks and species composition rebound more slowly, with specialist species often missing (Makelele et al. 2021). Successional studies also show shifts from acquisitive to conservative traits, especially in nitrogen-related leaf traits that affect nutrient cycling and productivity (Bauters et al. 2019b). Frequent disturbances further deplete soil nutrients and alter functional composition (Bauters et al. 2021b). Maintaining functional diversity is thus crucial for ecological integrity and adaptation, with future work needed linking field traits with remote sensing and models to assess long-term impacts of climate change and land use.

Changing Biodiversity and Ecosystem Function: Dynamics and Drivers

Climate change and land use changes are significantly impacting ecosystem function and biodiversity in the Congo Basin. Both interpolated gridded climate datasets (Tsalefac et al. 2015; Dezfuli 2017; Nicholson et al. 2018, 2019; Mabrouk et al. 2022) and satellite products (Diem et al. 2014; Zhou et al. 2014) report a lengthening of the dry season in Central Africa over the last few decades, starting between 1990 and 2000 (Malhi and Wright 2004; Saatchi et al. 2013; Zhou et al. 2014; Nicholson et al. 2018). Multiple independent precipitation and satellite-derived vegetation datasets show that the dry season length increased by 6–10 days per decade from 1988 to 2013 due to an earlier dry season onset and a delayed dry season end (Kasongo et al. 2023; Jiang et al. 2019). Coincidentally, wet and dry extreme events are expected to become more frequent and more severe in the region (Fotso-Nguemo et al. 2018; Kendon et al. 2019; Karam et al. 2022).

A hotter and more seasonal climate may have important consequences for Congo Basin forest composition, carbon sequestration, and ecosystem functioning more broadly. Such shifts have led to species composition turnover in West Africa (Fauset et al. 2012; Aguirre-Gutiérrez et al. 2020) and in the drier parts of the Amazon (Esquivel-Muelbert et al. 2019), with drought-tolerant (deciduous) species replacing trees adapted to wetter conditions. Although no field studies exist for Central Africa, satellite data show a long-term decline in Congo Basin forest greenness, likely from a canopy shift toward more deciduous species (Zhou et al. 2014). Long-term and systematic monitoring of both forest species composition and climate across the Congo Basin is necessary to develop early warning systems for ecosystem degradation and regime shifts.

Synthesis

The Congo Basin plays a vital role in global climate regulation and biodiversity conservation and acts as a major carbon sink by sequestering carbon through its forests, soils, and peatlands. Unique characteristics, such as high megafauna density, unique vegetation types, and low deforestation rates compared to other tropical continents, shape the region's emergent ecosystem functions. Soil properties, biogeochemical cycles, and aquatic fluxes interact with the Congo River, exporting carbon, while peatlands store immense belowground carbon reserves. Biodiversity drives ecosystem processes, with elephants enhancing seed dispersal and carbon sequestration. Climate change and land use shifts threaten these functions, with deforestation reducing carbon stocks and altering water cycles. As climate pressures intensify, further research into ecosystem dynamics will be crucial for maintaining the region's resilience. Forthcoming advances in remote sensing technologies offer a powerful means to map forest composition, estimate biomass, and detect degradation at fine scales, helping to address gaps in carbon cycle dynamics in the region, although doing so depends on continued and expanded large-scale in situ monitoring (Bossy et al. 2025). Safeguarding its stability requires integrated conservation

strategies that address these interconnected dynamics, including, for example, both carbon sequestration and functional biodiversity.

Competing Interest Declaration The author(s) has no competing interests to declare that are relevant to the content of this manuscript.

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