ABOVEGROUND CARBON STOCKS AND SINKS IN RECOVERING TROPICAL FORESTS

DANIELA REQUENA SUAREZ

Propositions

1. The inclusion of disturbed and recovering forests in climate change mitigation policies should not be stalled by limited data availability.
   (this thesis)

2. Integrating remote sensing and forest plot data is essential to improve forest carbon sink estimations.
   (this thesis)

3. There is no such thing as an "independent" researcher because collaboration is beneficial and necessary.

4. The applicability of environmental science outputs is hindered by its Anglocentrism.

5. Minorities in science experience systemic exclusion disguised as impostor syndrome.

6. The only way to effectively address climate change is to tackle structural inequalities at a global scale.

7. Menstrual cycles can be leveraged for personal productivity.

Propositions belonging to the thesis, entitled

Aboveground carbon stocks and sinks in recovering tropical forests

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Summary

Tropical and subtropical forests have many valuable roles, one of them within the carbon cycle. Within this cycle they are an essential terrestrial component, functioning as carbon reservoirs and sinks. The importance of (sub)tropical forests in climate change mitigation has been highlighted in recent climate change policies, such as the Paris Agreement, with signatory countries working towards a robust monitoring of their forest carbon stocks and sinks. Additionally, efforts to enhance forest carbon sinks through the restoration of degraded land has been highlighted by the Bonn Challenge, with currently more than 70 pledges in 60 countries underway.

Until recently, large-scale assessments and country-level reporting of forest carbon stocks and sinks have been relying on coarse estimates provided in 2006 by the Intergovernmental Panel on Climate Change (IPCC). However, these estimates were based on a handful of studies per global ecological zone (also known as *ecozone*), did not provide methods for their derivation nor measures of uncertainty, and did not distinguish between forest successional stages.

Furthermore, little is known about the drivers of variations in carbon stocks and sinks across (sub)tropical forests, particularly in forests with limited forest plot data availability. In this respect, insights for variations in forests and woodlands in the African dry tropics and in forests recovering from recent disturbance remains limited. Understanding how forest carbon stocks and sinks vary is essential for monitoring greenhouse gas (GHG) fluxes as well as for improving forest conservation and restoration endeavours.

Over time, research on (sub)tropical forest carbon stocks and sinks has progressed, as well as country-level monitoring efforts to improve forest GHG reporting. This has led to the increase in availability of forest plot data. Simultaneously, large-scale remote sensing products have become available and region-specific methods for the monitoring of forest disturbance/recovery dynamics have improved over time. Thus, the opportunity to combine forest plot data with remote sensing to evaluate carbon stocks and sinks in (sub)tropical forests at different stages of recovery arises.

The overall aim of this thesis is to integrate forest plot data with remote sensing to contribute towards understanding and quantifying aboveground forest carbon stocks (aboveground biomass; AGB) and sinks (aboveground biomass change; ΔAGB) in (sub)tropical forests. More specifically, this thesis has the objectives of (1) improving estimations of (sub)tropical aboveground forest carbon stocks and sinks under varying disturbance types for GHG reporting and of (2) understanding the drivers of aboveground carbon stocks and sinks in recovering forests in the (sub)tropics.

Chapter 2 provides a refinement of the IPCC 2006 default aboveground biomass (AGB) estimates for natural forests in (sub)tropical forest ecozones. This chapter used forest plot data from over 25 thousand plots in natural forests as well as a global AGB map for areas where no forest plot data was available. AGB estimates were calculated per continent, ecological zone, and successional forest type (younger secondary, older secondary and old-growth forests), and provided a measure of uncertainty. Refined default values generally reflected the large-scale climatic gradients in the tropics, with higher AGB in wetter areas. Furthermore, as expected, AGB was generally higher in old-growth forests than in secondary forests, and higher in older secondary than in younger secondary forests. This chapter provides a reproducible approach to facilitate future refinement, and encourages targeted efforts to establish permanent plots in areas with data gaps.

Chapter 3 provides a refinement of the IPCC 2006 default aboveground biomass change (ΔAGB) rates for natural forests in (sub)tropical forest ecozones by incorporating available plot data in secondary, old-growth and managed/logged forests. This chapter incorporated ΔAGB data available from 2006 onwards, comprising 176 chronosequences in secondary forests and 536 permanent plots in old-growth and managed/logged forests located in 42 countries in Africa, North and South America and Asia. ΔAGB rates were generated for younger secondary forests, older secondary forests and old-growth forests, following the same definition as per Chapter 2. This chapter provides a traceable refinement of the IPCC 2006 default ΔAGB rates for (sub)tropical forests and identifies areas for which more research on ΔAGB is required.

Chapter 4 addresses the need for understanding variations of AGB in recovering tropical forests in the African dry tropics along gradients in environmental conditions and human use. For this purpose, AGB data from 1,958 National Forest Inventory (NFI) plots covering Tanzania's forests and woodlands were integrated with spatial datasets and regional remote sensing analysis. For the latter component, Landsat-derived satellite time series of forest cover probability were used to divide NFI plots into recovering forests (areas recovering from deforestation for less than 25 years) and established forests (areas consistently defined as forests for at least 25 years), and to detect the year of forest establishment for recovering forests. In decreasing order of importance, AGB in recovering forests unexpectedly decreased with water availability, increased with surrounding tree cover and time since establishment, and decreased with elevation, distance to roads, and soil phosphorus content. AGB in established forests unexpectedly decreased with water availability, increased with surrounding tree cover, and soil nitrogen content, and decreased

with elevation. AGB in recovering forests increased by 0.4 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ during the first 20 years following establishment. These results can serve as the basis of carbon sink estimates in south-eastern African recovering tropical forests and woodlands, and aid in forest landscape restoration planning.

Chapter 5 explores the degree of disturbance in Peru's Amazonian forests; evaluates the effect of disturbance on AGB, tree species diversity and their recovery towards undisturbed levels; and identifies the main environmental and human use drivers of AGB, biodiversity and their recovery. This was done through the integration of AGB and tree species data from 1,847 NFI plots covering the Peruvian Amazonia with spatial datasets and regional remote sensing analysis. For the latter component, Landsat-derived Normalized Difference Moisture Index (NDMI) spatio-temporal cubes, in combination with a local phenological baseline were employed to distinguish time and intensity of disturbance for all NFI plot locations. Disturbance intensity had a negative effect on AGB and tree species diversity as well as their recovery. Time since disturbance had a positive effect on AGB and on similarity in species composition with undisturbed levels. While gradients in environmental conditions and human use affected AGB and its recovery, this was not evident for tree diversity and its recovery, nor its similarity in species composition. Following disturbance, forests in the Peruvian Amazonia can act as partial carbon sinks: during the first 20 years after disturbance AGB increases at an overall rate of 4.05 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$. This chapter highlights the need to consider disturbance intensity and subsequent recovery in forest GHG reporting for forest-based mitigation endeavours.

The results of this thesis contribute towards improving estimations of forest carbon stocks and sinks under varying disturbance types and by evaluating the effects of gradients in environmental conditions and human use on aboveground carbon stocks and sinks in tropical and subtropical forests. Moving forward, conscientious collaborations that leverage available forest plot data and employ novel remote sensing techniques to monitor forest dynamics will be required to fill new and persistent knowledge gaps.

Resumen

Los bosques tropicales y subtropicales tienen muchos roles valiosos, uno de ellos dentro del ciclo de carbono. Dentro de este ciclo son un componente terrestre esencial, actuando como reservas y sumideros de carbono. La importancia de los bosques tropicales y subtropicales en la mitigación del cambio climático se ha destacado en políticas como el Acuerdo de París, con países signatarios trabajando para monitorear reservas y sumideros de carbono forestal. Adicionalmente, la mejora de los sumideros de carbono forestal mediante la restauración de tierras degradadas ha sido destacada en el Desafío de Bonn, con más de 70 compromisos en 60 países en curso.

Hasta hace poco, las evaluaciones a gran escala y los informes nacionales sobre las reservas y sumideros de carbono se basaban en estimaciones proporcionadas en 2006 por el Grupo Intergubernamental de Expertos sobre el Cambio Climático (IPCC, por sus siglas en inglés). Sin embargo, estas estimaciones se basaron en un número limitado de estudios por zona ecológica global (también conocida como *ecozona*), no proporcionaron métodos para su derivación ni medidas de incertidumbre, y no distinguieron entre etapas sucesionales del bosque.

Además, poco se sabe acerca de los factores que influyen las variaciones en las reservas y sumideros de carbono en bosques tropicales y subtropicales, particularmente en bosques con disponibilidad limitada de datos de campo. En este sentido, los conocimientos sobre las variaciones en los bosques secos africanos y en los bosques en proceso de recuperación de perturbaciones recientes siguen siendo limitados. Comprender cómo varían las reservas y los sumideros de carbono en zonas forestales es esencial para monitorear los flujos de gases de efecto invernadero (GEI), así como para mejorar los esfuerzos de conservación y restauración de bosques.

Con el tiempo, la investigación sobre las reservas y sumideros de carbono en bosques tropicales y subtropicales ha progresado, así como las capacidades nacionnales de monitoreo para la elaboración de informes de GEI. Esto ha resultado en un aumento de la disponibilidad de datos provenientes de parcelas forestales. Al mismo tiempo, se han puesto a disposición nuevos productos de sensoramiento remoto de gran escala y los métodos para el seguimiento de la dinámica de perturbación/recuperación de los bosques a nivel regional han mejorado. Por lo tanto, surge la oportunidad de combinar los datos

de las parcelas forestales con sensoramiento remoto con el fin de evaluar las reservas de carbono y los sumideros en bosques tropicales y subtropicales bajo diferentes estados de recuperación.

El objetivo general de esta tesis es integrar los datos de las parcelas forestales con sensoramiento remoto para contribuir con la comprensión y cuantificación de los reservorios de carbono por encima del suelo (biomasa aérea; AGB, por sus siglas en inglés) y sumideros (cambio de biomasa aérea; ΔAGB) en bosques tropicales y subtropicales. Específicamente, los objetivos de esta tesis son (1) mejorar las estimaciones de las reservas y sumideros de carbono de los bosques tropicales y subtropicales bajo diferentes tipos de perturbaciones para la elaboración de informes de GEI y (2) comprender los factores influyentes de las reservas y sumideros de carbono en bosques bajo diferentes estados de recuperación.

El **Capítulo 2** proporciona un refinamiento de las estimaciones de biomasa aérea del IPCC propuestas en el 2006 para bosques naturales en ecozonas forestales tropicales y subtropicales. Este capítulo utilizó datos de más de 25 mil parcelas en bosques naturales, así como un mapa global de biomasa aérea para áreas donde no se disponía de datos de parcelas forestales. Las estimaciones de biomasa aérea se calcularon por continente, ecozona y estado sucesional del bosque (secundarios jóvenes, secundarios viejos y maduros), y proporcionaron una medida de incertidumbre. Los valores refinados en este estudio reflejan los gradientes climáticos a gran escala en los trópicos, con mayores valores de biomasa aérea en zonas con mayor humedad. Además, como era de esperarse, la biomasa aérea fue generalmente mayor en bosques maduros que en bosques secundarios, y mayor en bosques secundarios viejos que en bosques secundarios jóvenes. Este capítulo proporciona una metodología reproducible para facilitar el refinamiento futuro, además de alentar esfuerzos dirigidos para establecer parcelas permanentes en zonas con información limitada.

El **Capítulo 3** proporciona un refinamiento de las tasas de cambio de biomasa aérea (ΔAGB) propuestas por el IPCC en 2006 para bosques naturales en ecozonas de bosques tropicales y subtropicales mediante la incorporación de datos de parcelas provenientes de bosques secundarios, maduros y bajo uso forestal. Este capítulo incorporó datos de Δ AGB disponibles desde 2006 en adelante, que comprenden 176 cronosecuencias en bosques secundarios y 536 parcelas permanentes en bosques primarios y bosques bajo uso forestal ubicados en 42 países de África, América del Norte, América del Sur y Asia. Las tasas de ΔAGB se generaron para los bosques secundarios jóvenes, secundarios viejos y maduros siguiendo la misma definición del Capítulo 2. Este capítulo proporciona un refinamiento reproducible de las tasas de ΔAGB para los bosques tropicales y subtropicales e identifica áreas para las cuales se requiere más investigación sobre ΔAGB.

El **Capítulo 4** aborda la necesidad de comprender las variaciones de biomasa aérea en bosques tropicales en recuperación en los trópicos secos africanos a lo largo de gradientes en condiciones ambientales y actividad antrópica. Con este fin, los datos de biomasa aérea de 1,958 parcelas del Inventario Nacional Forestal de los bosques y zonas boscosas de Tanzania se integraron con datos espaciales y análisis regionales de sensoramiento remoto. Para este último componente, se utilizaron series de tiempo de probabilidad de cobertura forestal derivadas de imágenes Landsat para dividir las parcelas en bosques en recuperación (áreas que se establecieron durante menos de 25 años) y en bosques establecidos (áreas definidas consistentemente como bosques durante al menos 25 años), y para detectar el año de establecimiento de los bosques en recuperación. En orden decreciente de importancia, la biomasa aérea en bosques de recuperación disminuyó inesperadamente con la disponibilidad de agua, aumentó con la cobertura de arbórea circundante y con el tiempo desde el establecimiento, y disminuyó con la elevación, la distancia a los caminos y el contenido de fósforo del suelo. La biomasa aérea en los bosques establecidos disminuyó inesperadamente con la disponibilidad de agua, aumentó con la cobertura arbórea circundante y con el contenido de nitrógeno del suelo, y disminuyó con la elevación. La biomasa aérea en bosques en recuperación aumentó en 0.4 $\mathrm{Mg\,ha^{-1}\,año^{-1}}$ durante los primeros 20 años posteriores al establecimiento. Estos resultados pueden servir como base para las estimaciones de los sumideros de carbono en los bosques y zonas boscosas en recuperación de África del sudeste, y ayudar en la planificación de la restauración del paisaje forestal.

El **Capítulo 5** explora el grado de perturbación en los bosques amazónicos de Perú; evalúa el efecto de la perturbación en la biomasa aérea y en la diversidad de especies arbóreas y su recuperación hacia niveles no perturbados; e identifica los principales factores ambientales y de actividad antrópica que influyen los niveles de biomasa aérea y biodiversidad y la recuperación de ambas. Este estudio se desarrolló mediante la integración de datos de biomasa aérea y especies arbóreas 1,847 subparcelas del Inventario Nacional Forestal y de Fauna Silvestre que cubren la Amazonía peruana en conjunto con datos espaciales y sensoramiento remoto. Para este último componente, se emplearon cubos espacio-temporales de Índice de Humedad de Diferencia Normalizada (NDMI, por sus siglas en inglés), derivados de imágenes Landsat, en combinación con una línea de base fenológica local para distinguir el tiempo y la intensidad de la perturbación para todas las ubicaciones de las subparcelas. La intensidad de la perturbación tuvo un efecto negativo en biomasa aérea y la diversidad de especies arbóreas, así como en su recuperación. El tiempo transcurrido desde la perturbación tuvo un efecto positivo en biomasa aérea y en la similitud de composición de especies en bosques no perturbados. Si bien los gradientes en las condiciones ambientales y de actividad antrópica influyeron en los niveles de biomasa aérea y su recuperación, no fue el caso para la diversidad de árboles y su recuperación ni para su similitud en composición de especies. Después de la perturbación, los bosques de la Amazonía peruana pueden actuar como sumideros parciales de carbono: durante los primeros 20 años después de una perturbación, la biomasa aérea aumenta en una tasa de 4.05 $\mathrm{Mg\,ha^{-1}\,año^{-1}}$. Este capítulo destaca la necesidad de considerar la intensidad de la perturbación y la posterior recuperación en la elaboración de informes de GEI para los esfuerzos de mitigación de cambio climático.

Los resultados de esta tesis contribuyen a mejorar las estimaciones de las reservas y sumideros de carbono forestal bajo diferentes tipos de perturbaciones y a evaluar los efectos de los gradientes en condiciones ambientales y de actividad antrópica en las reservas y sumideros de carbono sobre el suelo en zonas tropicales y subtropicales. En el futuro, se requerirán de colaboraciones que aprovechen la información disponible en parcelas forestales y empleen nuevas técnicas sensoramiento remoto para monitorear la dinámica forestal con el fin de llenar nuevas y persistentes brechas de conocimiento.

Contents

Chapter 1

Introduction

1.1 Forests and the global carbon cycle

Forests are essential ecosystems. They provide the world with a variety of ecosystem services, such as the production of food and resources for humans and non-human organisms, the regulation of the water cycle and of soil erosion processes, as well as the capacity to harbour biodiversity within them (Brockerhoff et al., 2017). Furthermore, forests have provided humans not only with provisioning and regulating services, but also with intangible benefits, such as reduction of stress levels and promotion of well-being (Millennium Ecosystem Assesment, 2005), as well as being a source of inspiration, traditional knowledge, and identity to surrounding communities (Daniel et al., 2012).

However, forest-human relationships are not unidirectional. As we have steadily entered into the Anthropocene, the increase of human activities have started to affect forests and other natural ecosystems (Guz and Kulakowski, 2020). These activities have led to rising emissions of greenhouse gases (GHG) to the atmosphere, the most important of them being carbon dioxide (CO_2). The increase of GHG emissions is resulting in rising temperatures, the impacts of which can already be seen in forests (Slot and Winter, 2016; Sullivan et al., 2020).

While GHG emissions into the atmosphere is a relatively new concept for humans, plants have been acquainted with GHGs for millions of years. Ever since plants were in their initial evolutive stages, as cyanobacteria in water, they have played a role in the global carbon (C) cycle, by synthesising nutrients from CO_2 and water (Badger and Price, 2003). Presently, CO_2 levels in the atmosphere have been regulated by water and land carbon reservoirs and sinks.

It is estimated that the amount of carbon present in the terrestrial vegetation is of the same order of carbon in the atmosphere (Houghton, 2007). Forests are an essential element of the terrestrial component of the global carbon cycle (Pan et al., 2011), as they assimilate and store carbon at greater amounts than other vegetation types. Inside forests, trees fixate CO_2, which is afterwards either released back into the atmosphere through respiration or used for growth in biomass of trees and saplings. In this respect, forests naturally play two roles in the terrestrial carbon cycle: through the biomass they store they function as reservoirs of carbon stocks, and through their tree growth and recruitment they can also function as carbon sinks from the atmosphere (Brown and Lugo, 1982). In addition, as forests are currently being intensively used around the world, emitting CO_2 from deforestation and degradation into the atmosphere, they have acquired a third role in the global carbon cycle, acting as carbon sources (Malhi et al., 2002).

Among all natural forests globally, forests in the tropics and subtropics are considered a crucial component of the terrestrial carbon cycle. Tropical and subtropical forests have a global extent of 2,330 million hectares, and from 2000-2019, considering their role as

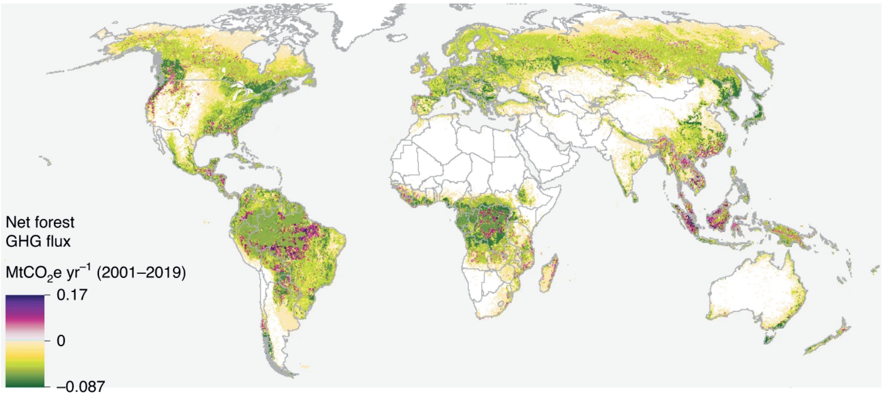

Figure 1.1: Net annual forest greenhouse gas (GHG) fluxes for 2001-2019, taken from Harris et al., 2021

carbon reservoirs, sinks and sources, have had a net annual carbon flux of approximately -2.35 $GtCO_2e\,year^{-1}$, 30.6% of net GHG fluxes across all forests (Harris et al., 2021). By functioning as net sinks of CO_2, (sub)tropical forests are essential mitigating components of the effects of climate change (Figure 1.1).

1.2 Forest-related climate change and restoration commitments

During the last decades, the mitigating role of tropical forests has been highlighted on international climate change and restoration agendas. In 1992, the United Nations Framework Convention on Climate Change (UNFCCC) was opened for signatures (UN General Assembly, 1994). The need to stabilise GHG concentrations in the atmosphere was emphasised in this convention, partially through the sustainable management and conservation of forest carbon reservoirs and sinks. Until now, a total of 197 countries have signed and ratified this convention, and in 2015 UNFCCC parties signed the Paris Agreement, a legally binding international treaty on climate change (UNFCCC, 2015). Among other commitments, this treaty requires signatory nations to monitor as well as enhance their forest carbon sinks and reservoirs.

For the UNFCCC parties it is necessary to quantify and understand current (sub)tropical forest carbon sources, stocks and sinks, as well as identify ways in which stocks and sinks can be enhanced. For these purposes, the Intergovernmental Panel on Climate Change (IPCC) supports the UNFCCC by providing monitoring guidelines as well as up-to-date scientific information on GHG emissions and removals from land use, land use change and forestry (LULUCF). The IPCC also supports data-limited countries by providing a reporting framework as well as default which can be used in absence of national data.

Another legally-binding pledge is the Bonn Challenge, which was launched by the International Union for Conservation of Nature (IUCN) and the government of Germany (IUCN, 2011). The Bonn Challenge aims to tackle water and food security while contributing to climate change commitments through the restoration of degraded and deforested forest lands. By May 2021, more than 70 pledges in 60 countries had committed to the Bonn Challenge, and are currently in the process of restoring over 210 million hectares of deforested or degraded forests (www.bonnchallenge.org/progress). To track restoration commitments, a systematic framework called the Bonn Challenge Barometer was established (Dave et al., 2017). In it, one of the required indicators is the estimation of CO_2 removed from the atmosphere by restored forests.

Estimates of (sub)tropical forest-based CO_2 emissions from deforestation and degradation have improved over time (De Sy, 2016); for example, a recent study has been able to estimate gross CO_2 emissions annually (Harris et al., 2021). On the other hand, estimating (sub)tropical forest carbon stocks and sinks remains a challenge. This challenge is underscored by the extent and large regional variability of (sub)tropical forest structure and species composition, and therefore variability in their magnitude as carbon stocks and sinks (Harris et al., 2021; Pan et al., 2011).

1.3 Regional variations of (sub)tropical forest carbon stocks and sinks

The variation of carbon stocks and sinks in (sub)tropical forests is in part due to biogeographic and climatic variation. Forest carbon stocks tend to be higher in areas with high water availability (Becknell et al., 2012; Chave et al., 2014; Poorter et al., 2015), lower maximum temperatures (Sullivan et al., 2020), low altitude (Girardin et al., 2014), and on fertile soils (Quesada et al., 2012). In addition, forest carbon stocks tend to be higher in areas with high tree stem density, tree size and higher species diversity (Baraloto et al., 2011; Poorter et al., 2015). The carbon sink capacity of (sub)tropical forests is also subject to environmental factors. Resource availability (i.e. water availability and soil nutrient availability) influences the capacity of a forest to function as carbon sink (Chazdon et al., 2016). Increased atmospheric levels of CO_2 in the atmosphere have also been linked with an increased tropical forest sink capacity (Hubau et al., 2020; Lewis et al., 2004; Luo, 2007).

Forest successional stage also influences the carbon stocks and sinks in a given forest (Chazdon, 2014; Poorter et al., 2016). Younger forest stands tend to have lower carbon stocks, but through their rapid stem growth and recruitment their carbon sink capacity is high. On the other hand, while older forest stands tend to have higher carbon stocks, their growth and recruitment ability is lower, therefore their carbon sink capacity is lower when compared to younger forest stands.

Understanding how, why and where carbon stocks and sinks vary in the (sub)tropics is of great importance when assessing the role of these forests in climate change mitigation. Many uncertainties remain on how forest carbon stocks and sinks vary along environmental gradients and degrees and types of disturbance; disentangling the individual effects of these factors remains a challenge.

1.4 Effects of forest disturbance on carbon stocks and sinks

In addition to biogeographical and climatic factors, forest disturbance and recovery also affect carbon stocks and sinks. Disturbance can be human (i.e. human-induced fires, clear-cut or logging) or natural (i.e. wildfires, droughts or hurricanes). Disturbances also vary along an intensity gradient, ranging from lower levels of disturbance intensity, which do not result in a major loss of forest structure (i.e. forest degradation) to higher levels of disturbance intensity, which result in a complete or near-complete loss of forest (i.e. deforestation). As expected, (sub)tropical forests that have experienced disturbances to their forest structure, hereafter referred to as *disturbed forests*, have lower forest carbon stocks as disturbance intensity and frequency increase (Berenguer et al., 2014; Chazdon, 2003; Espírito-Santo et al., 2014).

Undisturbed forests, also commonly referred to as old-growth forests, are forests that have no signs of recent high disturbance. It is estimated that 24% of tropical forests and 2% of subtropical forests are considered undisturbed (Mercer, 2015). It is very likely that undisturbed forests have had past disturbances over time (Cole et al., 2014; Ellis et al., 2021) while maintaining a seemingly-intact forest structure.

Recently, the extent of undisturbed forests has been decreasing through deforestation and degradation. The latter process has led to the increase of disturbed forests (Lewis et al., 2015; Potapov et al., 2017). It is estimated that 30% of existing tropical forests and 40% of existing subtropical forests considered as degraded (Mercer, 2015). Due to the extent, importance and vulnerability of disturbed forests, disturbed forests need to be integrated into GHG monitoring frameworks (Bustamante et al., 2016).

1.5 Forest recovery from disturbance

After a disturbance, a disturbed forest can have the potential to recover, through the growth of remaining trees and/or the recruitment of new trees (Chazdon, 2014). This potential is underpinned by a forest's resilience, which is defined here as the ability of a forest to recover after a disturbance event. Recovery by natural forest regeneration through tree recruitment and by tree growth in disturbed forests leads to an increase in forest biomass (Anderson-Teixeira et al., 2013; Chazdon, 2014; Lugo and Brown, 1992; Rozendaal et al., 2017), giving the opportunity for recovering disturbed forests to act as carbon sinks.

Secondary forests, which are forests recovering from major, stand-replacing disturbances, can have high carbon sink capacities. The carbon sink potential of secondary forests has been assessed mostly in the Americas (Anderson-Teixeira et al., 2016; Chazdon et al., 2016; Poorter et al., 2016). Furthermore, the carbon sink potential of recovering logged forests has also been assessed in South America (Rutishauser et al., 2015) and in Central Africa (Gourlet-Fleury et al., 2013). Future projections regarding the carbon sink potential of recovering forests in the coming years have been performed at continental and global scales (Chazdon et al., 2016; Cook-Patton et al., 2020).

In addition to the factors mentioned in Section 1.3, several additional factors can influence carbon stocks and sinks in recovering disturbed forests. Type and intensity of disturbance, frequency of previous disturbances, as well as ongoing disturbances and previous land use are thought to influence the carbon sink capacity of secondary forests (Chazdon, 2003). For example, in central Amazonia, the history and intensity of previous land-use has shown to affect forest carbon sinks: forests growing on heavily-used land decrease their carbon sink capacity (Jakovac et al., 2015). In Ivory Coast, rates of forest recovery in secondary forests were affected by previous land use and by the presence of remnant trees (N'Guessan et al., 2019). In Central and South America, the carbon sink potential of secondary forests increases with water availability and soil fertility (Poorter et al., 2016).

Forest recovery from disturbance plays an important role in the carbon cycle (Frolking et al., 2009; Mitchard, 2018). However, the assessment of variations of carbon stocks and sinks due to biogeographical and climatic gradients have been mostly constrained to undisturbed forests or secondary forests; we currently do not know whether carbon stocks and sinks in other types of recovering disturbed forests present similar relationships. In addition, while there are several studies focusing on recovering forests in the Americas, much less is known in other (sub)tropical regions.

1.6 From trees and biomass to hectares and carbon

Due to the complexities of factors that can affect carbon stocks and sinks in (sub)tropical undisturbed and disturbed forests, their quantification is riddled with uncertainties (Harris et al., 2021; Le Quéré et al., 2016). Therefore, attempting to do so requires building on several years of knowledge in tropical forest ecology, collaborating with research networks that estimate and study carbon stocks and sinks at different locations whilst employing similar methodologies (ForestPlots.net et al., 2020; Pennington and Baker, 2021)

To obtain forest carbon stocks and sink estimates for a given site, tree-by-tree biomass is estimated in ground forest plots. According to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories (IPCC, 2006), forest biomass is assessed by measuring 5 carbon pools: aboveground live biomass (AGB), belowground biomass (BGB), dead wood, litter and soil biomass. Given that AGB is the biomass pool more straightforward to measure and more susceptible to be affected by forest degradation (Berenguer et al., 2014; Gibbs et al., 2007; Houghton, 2005), the majority of studies on tropical forest carbon stocks provide at least estimations of AGB.

1.6.1 Measuring forest carbon stocks

Estimating tree-level AGB (in Mg) relies on forest plot data and allometric models. Forest plot data often consists of, but is not restricted to, tree diameter at breast height (DBH, in cm), total tree height (H, in m), and tree species identification for wood specific gravity (in $\mathrm{g\,cm^{-3}}$), as well as forest type (Chave et al., 2005). These data are used in allometric models, which are regression models formulated at pantropical, continental, regional, or species-specific level. Allometric models are constructed based on harvested trees which have been weighed. Recent advancements in remote sensing, such as terrestrial laser scanning (TLS) currently can be implemented in the elaboration of regional allometric models while reducing the number of harvested trees needed (Lau et al., 2019; Momo Takoudjou et al., 2018). Given the difficulties of measuring tree height in closed-canopy forests, as well as the observed dependence of H to DBH, most allometric models require DBH measurements only. Information on wood specific gravity can be obtained from global wood density databases at species or genus level, thus information on a tree's species or genus is necessary.

Plot-level AGB (in $\mathrm{Mg\,ha^{-1}}$) is calculated as the sum of tree-level AGB estimates (in Mg) per plot size (in ha). The size of plots can vary greatly: in this thesis, forest plot sizes range from 0.001 to 42 ha. To represent large areas of forests, we expect better plot-level estimates in larger plots (Hernández-Stefanoni et al., 2018; Mauya et al., 2015). However, better estimations of AGB are also dependent on the number and distribution of plots in a forest, thus the approach of only measuring large plots is logistically unfeasible and would be more difficult to extrapolate across larger scale. In this respect, plot size and number of plots have to be decided according to feasibility in the field (Tomppo et al., 2014).

1.6.2 Measuring forest carbon sinks

While forest carbon stocks require static AGB estimates, quantifying forest carbon sinks requires the introduction of a temporal component. By estimating AGB estimates at different times in a given forest stand, we can obtain rates of AGB change (ΔAGB, in $\mathrm{Mg\,ha^{-1}\,year^{-1}}$). ΔAGB can be obtained directly through the remeasurement of permanent plots over time, or indirectly, through the use of AGB chronosequences. The chronosequence approach requires multiple plots with different stand ages or years since disturbance in a given location. ΔAGB is then estimated from these plots arranged along a temporal gradient (Walker et al., 2010).

By requiring fieldwork only at one point in time, chronosequences enable the estimation of ΔAGB without relying on remeasurements over a longer time-span. This is advantageous particularly for disturbed forests, as these forests can be susceptible to recurrent disturbances (Schwartz et al., 2017). Thus, the majority of studies on forest carbon sinks on disturbed forests are based in AGB chronosequences. Currently, a few studies using permanent plots have been carried out in disturbed forests (Berenguer et al., 2014; Gourlet-Fleury et al., 2013; Rozendaal and Chazdon, 2015; Rutishauser et al., 2015), providing insights in the processes of forest recovery. However, given the predominance of chronosequence data for the assessment of ΔAGB in disturbed forests, the majority of large-scale studies rely mainly on chronosequence data.

1.6.3 Who measures forest plots?

Currently, undisturbed forests remain the most studied forests in the tropics, with several research networks carrying out long-term studies within them for decades (Davies et al., 2021; ForestPlots.net et al., 2020). Disturbed forests have also been extensively studied in the pantropics (Becknell et al., 2012; Chazdon et al., 2016; Poorter et al., 2016; Rozendaal et al., 2019; Sist et al., 2015), with plot networks located mostly in North and South America.

Parallel to this, countries with (sub)tropical forests have also been striving to quantify their forest carbon stocks and sinks at national scale. Forest monitoring capacities have greatly improved recently, with many national forest inventories (NFI) underway (Nesha et al., 2021). NFIs strive to provide a representative snapshot of a country's forests by consistently sampling their forests and employing a consistent methodology throughout.

The design and execution of NFI plots strive to optimise the accuracy of their biomass estimates with the economical and logistical viability of a national-scale project (Tomppo et al., 2008). Because of this, NFI plots tend to be smaller than plots in research networks, but higher in number.

1.7 Current data and knowledge gaps and needs for GHG reporting

National GHG reporting of CO_2 fluxes in forest stands is limited by AGB and ΔAGB data availability. The IPCC GHG reporting guidelines propose three levels of reporting complexity, also known as Tiers. Tiers are based on data availability, from reporting based on default rates (Tier 1), to national-and-regional-level reporting based on ground data (Tiers 2 and 3). Until the 2019 Refinement of the 2006 IPCC GHG Guidelines (IPCC, 2019), IPCC Tier 1 default estimates of AGB and ΔAGB in (sub)tropical natural forests relied on estimates proposed in 2006 (IPCC, 2006), which were based on a handful of local studies around the (sub)tropics. These default estimates did not distinguish between forests over 20 years of age undisturbed forests, thus grouping undisturbed forests with older secondary forests. In addition, other types of disturbed forests besides secondary forests were not included in these estimates.

Today, more countries with (sub)tropical forests are reporting at higher levels of complexity, thus national forest AGB and ΔAGB reporting is consistently moving towards higher Tiers (Nesha et al., 2021; Romijn et al., 2015). Currently, many NFIs in the tropics are on their first round of measurement, and while their estimations of AGB are greatly improving in detail, ΔAGB cannot be derived from one round of NFI data alone. Therefore, countries either use Tier1 ΔAGB default rates or do not report on their forest carbon sinks at all.

While the IPCC GHG Inventory Guidelines provide a framework for reporting on undisturbed and secondary forests, recovering disturbed forests which are not secondary forests are not included (Bustamante et al., 2016; Pearson et al., 2017). This is most likely due to data availability, as extensive AGB measurements in forests at varying degrees of disturbance and recovery are not available. This lack of data availability also affects research on disturbed forests in the (sub)tropics. Currently, we do not know what environmental or human use factors shape AGB in disturbed forests, and if disturbed forests at large scales are recovering in biomass.

1.8 Addressing knowledge gaps through data integration

Understanding how AGB and ΔAGB in (sub)tropical forests are affected by disturbance and recovery, as well as how they vary along gradients of environmental conditions and human use is essential for two reasons. First, it allows for a better quantification of forest carbon stocks and sinks (Houghton et al., 2015). Second, this knowledge can serve as an ecological basis for forest conservation and restoration (IPBES, 2018). In this respect, understanding why and how the recovery of disturbed forests varies across large scales can help us identify disturbed forest land whose recovery would result in high carbon sinks and protect forest areas with low carbon sink capacities from disturbance (Poorter et al., 2016).

Over the last decades, AGB data from forest plots has become increasingly available in (sub)tropical forests. Research consortia have established measurement protocols and best practices, and have made their data publicly available. In addition, AGB and ΔAGB data from various networks have been integrated into datasets which can be publicly accessed (Anderson-Teixeira et al., 2018b; ForestPlots.net et al., 2020). At the same time, national forest monitoring efforts have increased: by 2020, approximately 57% of countries in the tropics were using NFI data (Nesha et al., 2021).

However, assessing and monitoring disturbed forests and their recovery in the (sub)tropics currently face additional challenges. Given their vulnerability to continued disturbance, recovering disturbed forests are difficult to monitor (Bustamante et al., 2016; Mitchard, 2018). In addition, information on their initial or ongoing disturbance is often not available, or has to be obtained from additional sources, such as interviews with local people or by analysing satellite imagery (Chazdon, 2014).

Advancements in remote sensing increased the level of forest monitoring in the (sub)tropics. Global datasets of forest cover and its change have been made publicly available, and are being updated over time (Hansen et al., 2013). Until recently, the detection of forest disturbances had been limited to the detection major disturbances, yet current advancements are enabling the detection of minor disturbances (DeVries et al., 2015a; Espírito-Santo et al., 2014; Hamunyela et al., 2020; Herold et al., 2011). Furthermore, advancements in the detection of forest recovery and forest establishment have also been made (Hansen et al., 2013; Sexton et al., 2016). This new range of remote sensing methods allow us to observe forest disturbances and recovery across large scales.

Existing knowledge gaps on (sub)tropical forest carbon stocks and sinks can be addressed by leveraging the increase of forest plot data availability with new remote sensing products and analysis. Thus, integrating forest plot AGB and ΔAGB data with remote sensing opens the opportunity of assessing disturbance and recovery, as well as their effect on carbon stocks and sinks, at large scales.

1.9 Research objectives

The overall objective of this PhD thesis is to integrate forest plot data with remote sensing to contribute towards understanding and quantifying aboveground forest carbon stocks (AGB) and sinks (ΔAGB) in (sub)tropical forests. More specifically, this thesis has the following research objectives:

- **R.O.1** Improve estimations of (sub)tropical aboveground forest carbon stocks and sinks under varying disturbance types for GHG reporting.
- **R.O.2** Understand the drivers of aboveground carbon stocks and sinks in recovering forests in the (sub)tropics.

1.10 Thesis overview

This PhD thesis is divided into 6 chapters. **Chapter 1**, which you are now reading, provides a brief introduction into the current state of knowledge regarding aboveground forest carbon stocks and sinks, current research gaps and possibilities to address them. The following four chapters seek to answer both research objectives by leveraging AGB forest plot data from different sources with remote sensing products and analysis, considering varying environmental and human use gradients and providing AGB and ΔAGB estimates at different scales. Figure 1.2 provides a conceptual overview of how Chapters 2 through 5 relate to R.O.1 and R.O.2.

Chapter 2 provides a refinement of the IPCC 2006 default AGB values for natural forests in (sub)tropical forest ecozones. This is done by incorporating AGB data from forest plots, and deriving separate estimates for young secondary forests, older secondary forests and for old-growth (i.e. undisturbed) forest. For areas where plot data is not available, remote-sensing datasets are used to estimate default values. Furthermore, areas with limited forest AGB data are identified.

Chapter 3 provides a refinement of the IPCC 2006 default ΔAGB rates for natural forests in (sub)tropical forest ecozones by incorporating available plot data in secondary, old-growth and managed/logged forests. Rates are derived from permanent forest plots and AGB chronosequences. Updated ΔAGB rates are provided for younger secondary forests, old secondary and old-growth (undisturbed) forests. Furthermore, areas with limited forest ΔAGB data are identified.

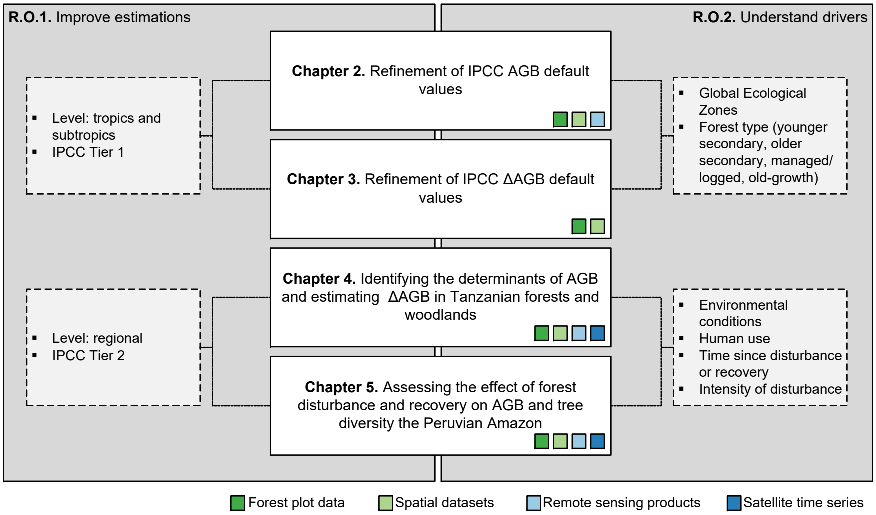

Figure 1.2: Conceptual overview of Chapters 2 through 5. Use of forest plot data, spatial datasets, remote sensing products and remote sensing analyses are presented in green, light green, light blue and blue, respectively.

Chapter 4 integrates NFI plot data covering Tanzania's forests and woodlands with spatial datasets and remote sensing analyses to identify the determinants (or drivers) of AGB. Furthermore, Landsat-derived time series of forest cover probability are used to divide NFI plots into established and recovering forests. For recovering forests, time since forest establishment is used as a quantitative indicator to assess ΔAGB and therefore the carbon sink capacity of Tanzania's recovering forests.

Chapter 5 integrates AGB and tree diversity data from Peru's NFI with Landsat-derived NDMI (Normalised Difference Moisture Index) time series and spatial datasets to evaluate the degree of recent forest disturbance in Peruvian Amazonia, as well as the potential effects of disturbance, environmental conditions and human use on AGB and tree diversity in disturbed forests, and on their potential recovery towards undisturbed forest levels.

Lastly, **Chapter 6** summarises the main findings and results from the previous four chapters, and provides a detailed overview into how they contribute towards the two specific research objectives of this thesis. Subsequently, it provides a reflection and outlook, laying out recommendations on the potential next steps towards a better understanding of (sub)tropical aboveground forest carbon stocks and sinks.

Chapter 2

Aboveground forest biomass varies across continents, ecological zones and successional stages: Refinement of IPCC default values for tropical and subtropical forests

This chapter is based on:

D. M. A. Rozendaal, D. Requena Suarez, V. De Sy, V. Avitabile, S. Carter, C. Y. Adou Yao, E. Alvarez-Dávila, K. Anderson-Teixeira, A. Araujo-Murakami, L. Arroyo, B. Barca, T.R. Baker, L. Birigazzi, F. Bongers, A. Branthomme, R. J. W. Brienen, J. Carreiras, R. C. Gatti, S. C. Cook-Patton, M. Decuyper, B. DeVries, A. B. Espejo, T. R. Feldpausch, J. Fox, J. G. P. Gamarra, B. W. Griscom, N. Harris, B. Hérault, E. N. Honorio Coronado, I. Jonckheere, E. Konan, S. M. Leavitt, S. L. Lewis, J. Lindsell, J. Kassi N'Dja, A. E. N'Guessan, B. Marimon, E. T. A. Mitchard, A. Monteagudo Mendoza, A. Morel, A. Pekkarinen, O. L. Phillips, L. Poorter, L. Qie, E. Rutishauser, C. M. Ryan, M. Santoro, D.S. Silayo, P. Sist, J. W. F. Slik, B. Sonké, M. J. P. Sullivan, G. V. Laurin, E. Vilanova, M. M. H. Wang, E. Zahabu, and M. Herold (in preparation). "Aboveground forest biomass varies across continents, ecological zones and successional stages: Refinement of IPCC default values for tropical and subtropical forests"

Abstract

For monitoring and reporting on forest carbon stocks and fluxes, many countries in the (sub)tropics rely on default values of forest aboveground biomass (AGB) from the Intergovernmental Panel on Climate Change (IPCC) Guidelines for National Greenhouse Gas (GHG) Inventories. Default IPCC aboveground biomass values have not been updated since 2006, and are an estimate of average forest AGB per continent and ecological zone. The 2006 default values were based on limited plot data available at the time, methods for their derivation were not fully clear, and no distinction between successional stages was made. As part of the 2019 Refinement to the IPCC Guidelines for GHG Inventories, we updated the 2006 default AGB values for (sub)tropical forests based on AGB data from >25,000 plots in natural forests and a global AGB map when no plot data were available. We calculated refined AGB default values per continent, ecological zone, and successional forest type (younger secondary, older secondary and old-growth forests), and provided a measure of uncertainty. Aboveground biomass in (sub)tropical forests varied by up to more than an order of magnitude across continents, ecological zones, and successional forest types. Our refined default values generally reflected the large-scale climatic gradients in the tropics, with higher AGB in wetter areas. AGB was generally higher in old-growth forests than in secondary forests, and higher in older secondary (regrowth >20 years old and degraded/logged forests) than in younger secondary forests (≤20 years old). Refined default values for tropical old-growth forest were generally similar to the previous 2006 default values, but 4.0 to 7.7-fold lower for younger secondary forests, thus using the refined values will strongly alter estimated carbon stocks and fluxes. We provide a reproducible approach to facilitate future refinement, and we encourage targeted efforts to establish permanent plots in areas with data gaps.

2.1 Introduction

Tropical forests contain two-thirds of the total global terrestrial biomass (Pan et al., 2013), but these forests and their carbon stocks are rapidly disappearing due to land use conversion (FAO, 2020). Accurate and current data on forest biomass are required for environmental policies and to inform management practices (Herold et al., 2019). In the Paris Climate Agreement, countries have agreed to promote climate change mitigation, for example by avoiding emissions from deforestation and forest degradation. Countries in the (sub)tropics can benefit from Reducing Emissions from Deforestation and forest Degradation and forest enhancements (REDD+) programs by maintaining and increasing their forest carbon stocks, but are required to monitor forest carbon stocks and fluxes, following IPCC good practice guidance for national greenhouse gas accounting (IPCC, 2006).

Various methods for reporting on forest carbon stocks and fluxes can be applied, depending on the technical and financial capacity of a country (IPCC, 2006). Reporting can be done (1) at the Tier 1 level, based on IPCC default values of forest aboveground biomass (AGB) and net biomass change per continent and ecological zone in combination with maps of land cover (for distinguishing secondary and old-growth forest); (2) at the Tier 2 level when national-level data are available for estimating values for standing biomass and biomass change and land use; or (3) at the Tier 3 level, which requires a higher level of detail such as biomass estimates based on a national forest inventory, repeated measurements from plots to estimate biomass change, and/or the use of process-based models (IPCC, 2006). The availability of recent national forest inventory data is limited in the tropics (Romijn et al., 2015), thus IPCC default values are, in absence of more detailed data, widely used for carbon pool reporting, technical assessments (e.g. UNFCCC reviews), global assessments (e.g. FAO Forest Resources Assessment) and by researchers e.g. Achard et al., 2014. In 2015, 84 out of 99 tropical countries were still reporting carbon pools at the Tier 1 level (Romijn et al., 2015).

IPCC AGB default values have been specified for natural forests per continent and global ecological zone (IPCC, 2006). By distinguishing continents, biogeographical variation in forest structure and species composition is considered. For example, AGB of tropical forests is higher in parts of Africa and Asia than in most of South America (Sullivan et al., 2017). Similarly, because rainfall has a strong, positive effect on AGB (Becknell et al., 2012; Slik et al., 2013; Sullivan et al., 2020), IPCC AGB defaults were reported for different climatic zones. Despite their wide use, the 2006 IPCC default AGB values have shortcomings. AGB is also strongly influenced by other factors, such as anthropogenic disturbance, which is not captured by a single default value per continent and ecological zone. For secondary forests that regrow after complete forest clearance, for example on abandoned agricultural land, AGB increases with stand age (Rozendaal et al., 2017), and is typically lower in old-growth forests (Poorter et al., 2016). Similarly, forests that are not completely cleared, but degraded, for example through selective logging, have a lower AGB compared to old-growth forests (Berenguer et al., 2014; Longo et al., 2016; Rutishauser et al., 2015).

Because of limited data availability at the time, the 2006 AGB default values were based on only a few data sources. Moreover, it is not clear how they were defined or estimated (Langner et al., 2014), and not all data sources were traceable (see IPCC, 2003; IPCC, 2006). Moreover, no consistent measure of uncertainty was included, since default values consisted either of a single value with a range, a single value only, or a range only. As such, it was not possible to account for uncertainty in carbon stock estimates. Since 2006, a large amount of high-quality AGB data from forests in (sub)tropical forests have become available. Recently, research networks have published AGB values from forest plots in old-growth forests (Brienen et al., 2015a; Lewis et al., 2013; Qie et al., 2017; Sullivan et al., 2017), and logged forests (Rutishauser et al., 2015) across the tropics, and for secondary forests in Latin America (Poorter et al., 2016). In addition, global datasets of forest AGB values have been made available (Anderson-Teixeira et al., 2018b; Cook-Patton et al., 2020), and countries in the tropics are establishing NFIs. Average forest-biome specific AGB values have been published (Pan et al., 2013), as well as recovery rates for secondary forests across the tropics (Anderson-Teixeira et al., 2016), but these values were not taken up by the IPCC yet.

In this study, we refined the IPCC 2006 default AGB values for natural forests in both the tropics and the subtropics, as part of the 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories (IPCC, 2019). We provide a rigorous, reproducible refinement by (1) incorporating suitable AGB data from forest plots that have become available since 2006; (2) providing separate estimates for successional forest types; and (3) including a measure of uncertainty. We primarily relied on AGB data from forest plots, despite the increasing availability of pantropical and global remote-sensing datasets of forest AGB, because pixel-level uncertainty remains high (Herold et al., 2019). We used a new remote-sensing dataset of AGB (Santoro et al., in review) to estimate default values for areas where plot data were not available. We facilitate future refinement by documenting the approach for deriving the 2019 AGB default values, and by identifying areas with limited data on forest AGB where data collection should be prioritized.

2.2 Methods

2.2.1 Aboveground biomass data from forest plots

We compiled AGB data from plots in natural forests in the tropics and subtropics from (1) data from published studies, including studies from research networks and global databases; and (2) national forest inventory programs (NFIs). We included plots from traceable sources only, thus with a literature reference and known geographical location (coordinates). Large-scale research networks that monitor the structure and dynamics of tropical old-growth (Lewis et al., 2013; Malhi et al., 2002) and degraded forests (e.g. Rutishauser et al., 2015), or that measure forest recovery on abandoned agricultural land (e.g. Poorter et al., 2016), generally collect detailed information on the disturbance history and/or the stand age of the plots. For plots that are established as part of NFIs, in a consistent way across a wide range of environmental conditions, such information is generally lacking. We particularly targeted plot data from NFIs in Africa and Asia, because for North and South America (hereafter *the Americas*) more plot data from published studies were available.

Census years of the included plots varied widely, but most measurements (96% of all plots) were done after the year 2000. If a plot was repeatedly measured, only the most recent census was used. The minimum size of included trees was at least 10 cm diameter at breast height (DBH), or above deformity in the case of buttresses, with trees identified to the finest taxonomic resolution possible. For regrowing forests, the minimum DBH was generally 5 cm (Anderson-Teixeira et al., 2018b; Poorter et al., 2016), because smaller trees comprise a substantial part of AGB (Hughes et al., 1999). Most studies estimated tree biomass based on DBH, wood density, and in some cases tree height, based on general allometric equations for tropical trees (Chave et al., 2005; Chave et al., 2014; Feldpausch et al., 2012). If aboveground carbon was reported instead of AGB, the aboveground carbon value was divided by the IPCC AGB to aboveground carbon conversion factor of 0.47 for conversion to AGB. If another conversion factor was used in the original source, we used the original conversion factor.

2.2.2 Successional forest types

We followed IPCC guidance for calculating default AGB values per continent (Africa, the Americas, Asia), per global ecological zone (FAO, 2012), and successional forest type. Global ecological zones were defined as broad, climatic forest types, with an exception for mountain systems (here referred to as *montane forests*) that were classified based on altitude only (FAO, 2012). Five global ecological zones were included for the tropics (rainforests, moist forests, dry forests, shrublands, montane forests), and four for the subtropics (humid forests, dry forests, steppe, montane forests). Three successional forest types were distinguished: (1) old-growth forests, which we defined as forests with no record of human disturbance in the past 100 years (Anderson-Teixeira et al., 2016; Poorter et al., 2016), thus secondary forests >100 years old were regarded as old-growth forests; (2) older secondary forests >20 and ≤100 years old, including forests regrowing on abandoned agricultural land, and degraded (including logged) forests; and (3) younger secondary forests ≤20 years old.

Plots with information on disturbance history were assigned to a successional forest type based on stand age for secondary forests, or disturbance history for degraded forests. If plots lacked information on disturbance history, we included them as secondary forests if they fell outside of two remote-sensing products that we used as a proxy for old-growth forests: a map of intact forest landscapes (Potapov et al., 2017) and a map of hinterland forests (Tyukavina et al., 2016). Intact forest landscapes are large (≥500 km^2), contiguous forest areas with no human activity based on spatial data and visual interpretation of remote sensing data (Potapov et al., 2017). Hinterland forests occur in areas where there is no recent remotely-sensed evidence of disturbance (≥12 years), at >1 km distance to a recent, stand-replacement forest disturbance, and they have an area of at least 100 km^2 (Tyukavina et al., 2016). For plots classified as secondary forest based on this method, we did not distinguish between younger and older secondary forests. We did not classify plots that fell within intact forest landscapes or hinterland forests as old-growth forest, since both intact forests and hinterland forests may experience some degree of human disturbance that is not detected in the remote-sensing data.

2.2.3 Calculation of default values based on forest plot data

Default values were calculated per continent, ecological zone, and successional forest type if plot data were available. The methodology depended on the successional forest type, and on the number of available plots (Figure 2.1). For old-growth forests, default values were calculated as the weighted mean across all plots, weighted by the square root of plot size, to account for the large variation in plot size (Brienen et al., 2015a; Requena Suarez et al., 2019; Rutishauser et al., 2015). Only old-growth plots with information on disturbance history were included, to guarantee that they were not subject to anthropogenic disturbance. Default values for old-growth forest were calculated if at least ten plots with information on plot size were available (Figure 2.1a).

For secondary forests in the Americas, the size of most individual plots was unknown. Therefore, default values for secondary forests were expressed as average AGB per 0.5-degree grid cell, instead of a plot-size weighted mean. As such, we accounted for spatial clustering of plots, and avoided overrepresentation of locations with many plots. We used 0.5-degree grid cells, because one 0.5-degree grid cell generally included one research site with chronosequence plots for secondary forests (Poorter et al., 2016). Per continent, ecological zone, and successional forest type, we first calculated average AGB per grid cell, and then averaged these to obtain the default value. If plot data with information on disturbance history were available for at least five grid cells for both younger and older secondary forests, default values for both younger and older secondary forests were calculated (Figure 2.1b). If AGB data were available for secondary forest plots for at least five grid cells, with or without information on disturbance history, we calculated default values for all secondary forests together (Figure 2.1b).

For continents and ecological zones for which not sufficient plot data were available to distinguish successional forest types, we calculated a single default value per continent and ecological zone to represent all successional forest types, if plot data (with or without information on disturbance history) were available for at least five grid cells (Figure 2.1c). We made three exceptions to our general methodology. First, for tropical dry forests in Africa, we did not distinguish successional forest types. These forests are subject to heavy anthropogenic use (McNicol et al., 2018), thus successional stages cannot be clearly distinguished. Second, for tropical dry forests in Asia, we also included a default value for all successional forest types together although plot data were available for three grid cells only, because we preferred to use plot data (36 plots) over an estimate from a biomass map. Third, for old-growth subtropical forests in Asia, we included a grid cell mean instead of a plot-size weighted mean (Table 2.1), because plot sizes were unknown.

In total, we included 2,318 plots for the Americas, 22,279 plots for Africa, and 1,291 plots for Asia (Figure 2.2). A total of 3,880 plots with information on disturbance history was included, with an average plot size of 2.9 ha (range: 0.001-42 ha). Plots were typically one hectare or larger for old-growth forests (Sullivan et al., 2017) and logged forests (Rutishauser et al., 2015), and on average 0.1 ha for regrowing forests (Poorter et al., 2016). Plot-level AGB was included, but for some datasets AGB estimates were based on multiple plots at the same location (Anderson-Teixeira et al., 2018b; Slik et al., 2015). In total, 22,008 plots without information on disturbance history were included. These generally small plots were mostly from NFIs, and had an average plot size of 0.1 ha (range: 0.01-1.85 ha). Overall, most plots were from tropical forests (25,681 plots in total), while only 207 plots were included in subtropical forests (Figure 2.2).

2.2.4 Calculation of default values for continents and ecological zones without plot data

For combinations of continent and ecological zone for which no plot data were available, we calculated AGB default values based on an AGB map (Figure 2.1c). For the tropics across the three continents, for just 3% of the total area default values were map-based estimates, compared to 50% of the area for the subtropics. Nevertheless, for the three

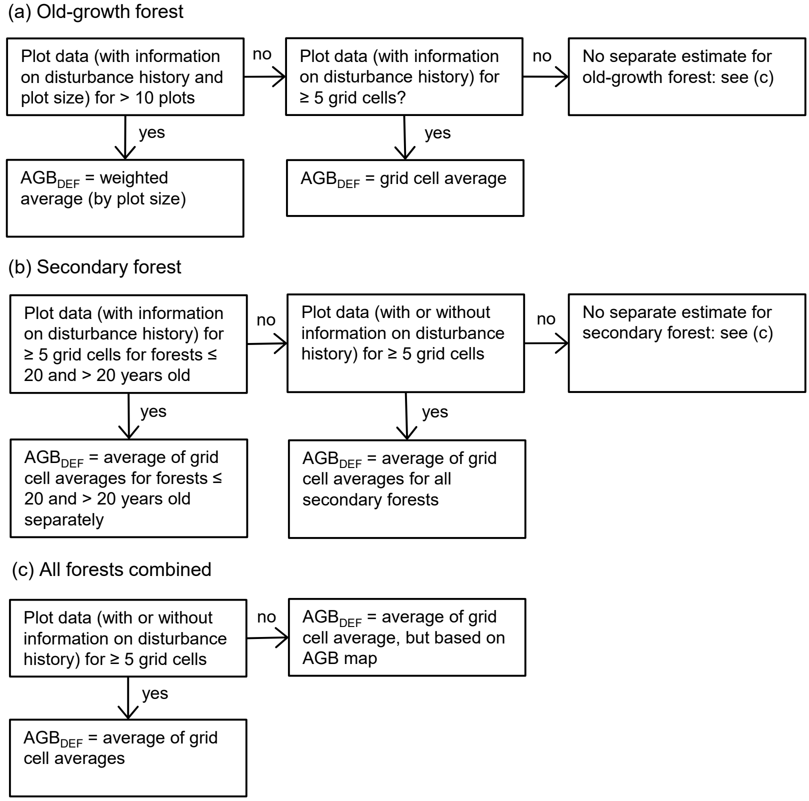

Figure 2.1: Overview of the methodology for the calculation of the refined 2019 IPCC default values for aboveground biomass (AGB_{DEF}). (a) Methodology for old-growth forests; (b) Methodology for secondary forests; (c) Methodology for all forests combined.

included continents, the tropics comprise a larger area, and for the two large ecological zones in subtropical Asia, humid forests and montane forests, plot data were used (Figure 2.2). We used a global, 100-m resolution AGB map for the year 2010 (Santoro et al., in review), because AGB estimates for tropical forests from this map were more accurate than values from pantropical AGB maps (Santoro et al., in review). Based on a comparison with plot data, AGB estimates up to 200 and 300 Mg ha^{-1} are unbiased for the tropics and subtropics, respectively (Santoro et al., in review). We calculated mean AGB and the standard deviation per 0.25-degree grid cell per continent and ecological zone, not distinguishing successional forest types. Non-forest areas, i.e. areas with <10% tree cover in 2010 (Hansen et al., 2013), and plantations (Harris et al., 2019) were excluded. To assess whether results were influenced by grid cell size, we repeated the analysis for 0.1-degree

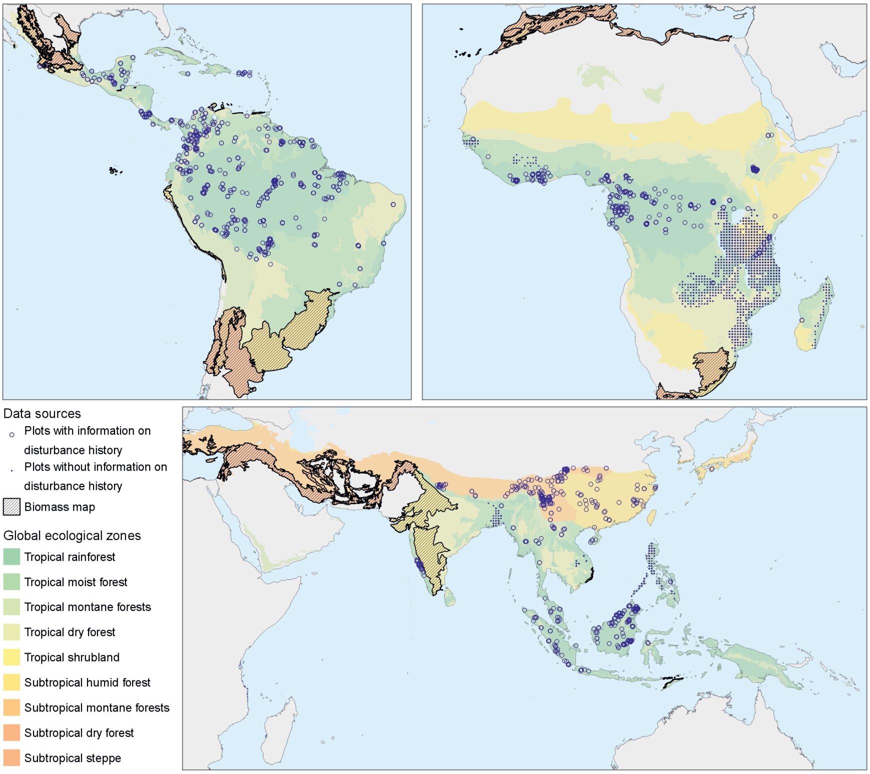

Figure 2.2: Overview of locations of plots with information on disturbance history and plots without information on disturbance history (mostly data from National Forest Inventories), as well as the FAO global ecological zones for which the refined default biomass values were estimated based on a global biomass map.

grid cells. Results for both grid cell sizes were similar, therefore we included the default values calculated for 0.25-degree grid cells. All analyses were conducted in R 3.4.3 (R Core Team, 2017).

2.3 Results

Aboveground biomass in tropical forests varied by up to more than an order of magnitude across continents, ecological zones, and successional forest types based on the included plots (Figure 2.3). For old-growth tropical forests in the Americas, our new, refined IPCC 2019 AGB default values decreased from rainforests (307.1 $\mathrm{Mg\,ha^{-1}}$), to moist forests (187.3 $\mathrm{Mg\,ha^{-1}}$), to dry forests (127.5 $\mathrm{Mg\,ha^{-1}}$), and the default value for montane forests

(195.0 Mg ha^{-1}) was close to the value for moist forests. Similarly, for the African tropics, the AGB default value for old-growth tropical rainforest was higher (404.2 Mg ha^{-1}) than for tropical moist forest (236.6 Mg ha^{-1}). For tropical shrublands on all continents, refined default values were lowest (38.3-71.5 Mg ha^{-1}; Table 2.1), although successional forest types were not distinguished. For subtropical forests in Africa and the Americas across all successional forest types, refined default values were highest for dry forest, unexpectedly, followed by humid forests and steppe based on the AGB map. For subtropical Asia, nevertheless, refined default values were higher in humid forests than in dry forests, based on plot data (Table 2.1). As expected, we found that, overall, AGB was highest in old-growth forests, followed by older secondary forests, and lowest in younger secondary forests for ecological zones in the tropics and subtropics for which plot data for these successional forest types were available (Figure 2.3; Table 2.1).

Table 2.1: Refined 2019 IPCC aboveground biomass (AGB) default values per continent, ecological zone and successional forest type. The mean, standard deviation (SD), and the median are indicated; the mean and SD are included in the refined IPCC defaults (IPCC, 2019). Method refers to the method of calculating the refined default values. Median AGB values were not included for old-growth data for continents and ecological zones when default values were based on a plot-size weighted mean. America includes both North and South America. The IPCC refers to montane forests as 'mountain systems'; old-growth forests are included as 'primary' forests (IPCC, 2019). YSF = young secondary forest (≤20 years old); OSF = older secondary forest (>20 years old); SF = all secondary forests; OGF = old-growth forest; All = all successional forest types. Weighted indicates AGB default values calculated as a plot-size weighted average, grid cell indicates that the default values was calculated based on 0.5-degree grid cell means, and AGB map indicates that the default value was derived from a global map of aboveground biomass (Santoro et al., in review)

Ecological zone	Continent	Forest type	Mean AGB (Mg ha^{-1})	SD (Mg/ha^{-1})	Median AGB (Mg ha^{-1})	Method	# plots	# grid cells	Ref.
Tropical rainforest	Africa	OGF	404.2	120.4		Weighted	451		[1-12]
		OSF	212.9	143.1	141.6	Grid cell	97	9	[5-7, 11, 13-16]
		YSF	52.8	35.6	56.3	Grid cell	83	9	[9-11, 14, 15, 17]
	America	OGF	307.1	104.9		Weighted	487		[3, 4, 9, 10, 18-21]
		OSF	206.4	80.4	208.3	Grid cell	328	26	[9, 10, 22-28]
		YSF	75.7	34.5	67.1	Grid cell	513	23	[9, 10, 14, 22, 23, 28-32]
	Asia	OGF	413.1	128.5		Weighted	192		[3, 4, 9, 10, 33-35]
		OSF	131.6	20.7	131.6	Grid cell	94	5	[9, 10, 36, 37]

Table 2.1 continued from previous page

		YSF	45.6	20.6	50.6	Grid cell	88	7	[9, 10, 37-39]
Tropical moist forest	Africa	OGF	236.6	104.7		Weighted	25		[1, 2, 16]
		SF	72.8	36.4	64.2	Grid cell	7530	52	[9, 10, 16, 40-47]
	America	OGF	187.3	94.0		Weighted	106		[3, 4, 9, 10, 18-21]
		OSF	131.0	54.2	112.4	Grid cell	185	17	[9, 10, 22-26]
		YSF	55.7	28.7	44.7	Grid cell	353	17	[9, 10, 22, 23, 25, 26]
	Asia	All	67.7*	93.4	31.9	Grid cell	322	36	[9, 10, 35, 48-50]
Tropical dry forest	Africa	All	69.6	47.5	59.7	Grid cell	9410	47	[1, 2, 43, 44, 51-53]
	America	OGF	127.5	72.6		Weighted	12		[18-21]
		OSF	118.9	81.3	121.1	Grid cell	72	6	[9, 10, 22, 23, 54]
		YSF	32.2	24.2	32.1	Grid cell	44	5	[9, 10, 22, 23, 54, 55]
	Asia	All	184.6**	144.5	161.6	Grid cell	36	3	[9, 10, 35, 48, 56]
Tropical shrubland	Africa	All	48.4	45.8	37.2	Grid cell	2626	17	[44, 57, 58]
	America	All	71.5	46.4	62.5	AGB map		216	[59]
	Asia	All	38.3	33.0	27.1	AGB map		1458	[59]

Table 2.1 continued from previous page

Tropical montane forest	Africa	All	190.0	131.2	218.9	Grid cell	2057	46	[1-4, 9, 10, 42-44, 47, 53, 60-68]
	America	OGF	195.0	95.6		Weighted	83		[3, 4, 9, 10, 18-21]
		OSF	184.4	111.0	177.7	Grid cell	21	8	[9, 10, 22, 23, 26, 69]
		YSF	75.9	51.1	74.9	Grid cell	114	8	[9, 10, 22, 23, 26, 69, 70]
	Asia	OGF	433.5***	147.5		Weighted	23		[3, 4, 9, 10, 34, 35]
		SF	66.4	61.0	48.5	Grid cell	329	19	[9, 10, 50, 71-73]
Subtropical humid forest	Africa	All	54.1	20.6	52.4	AGB map		203	[59]
	America	All	84.5	42.9	91.5	AGB map		3986	[59]
	Asia	OGF	323.0	157.7	281.3	Grid cell	29	11	[9, 10]
		SF	258.4	128.1	243.7	Grid cell	31	14	[9, 10]
Subtropical dry forests	Africa	All	65.2	27.1	60.2	AGB map		650	[59]
	America	All	115.9	46.2	110.8	AGB map		330	[59]
	Asia	All	70.9	26.2	75.6	AGB map		223	[59]
Subtropical steppe	Africa	All	50.5	23.9	47.0	AGB map		147	[59]
	America	All	44.0	26.0	39.8	AGB map		2797	[59]
	Asia	All	41.6	24.7	39.9	AGB map		400	[59]
Subtropical montane forest	Africa	All	35.1	22.2	26.8	AGB map		681	[59]
	America	All	74.6	40.1	64.6	AGB map		1835	[59]
	Asia	OGF	250.2	59.4	247.5	Grid cell	115	17	[9, 10]
		SF	155.2	41.7	166.5	Grid cell	32	14	[9, 10]

Table 2.1 continued from previous page

*A default value of 155.3 Mg ha^{-1} based on Pan et al. (2013) can be considered instead. The IPCC AGB to aboveground carbon conversion factor of 0.47 was used to derive total biomass. Belowground biomass is included in this estimate.
**A default value of 112.8 Mg ha^{-1} based on Pan et al. (2013) can be considered instead. Note that the IPCC AGB to aboveground carbon conversion factor of 0.47 was used to derive total biomass. Belowground biomass is included in this estimate.
***A default value of 195.0 Mg ha^{-1} based on the default value for old-growth montane forest in the Americas can be considered instead.

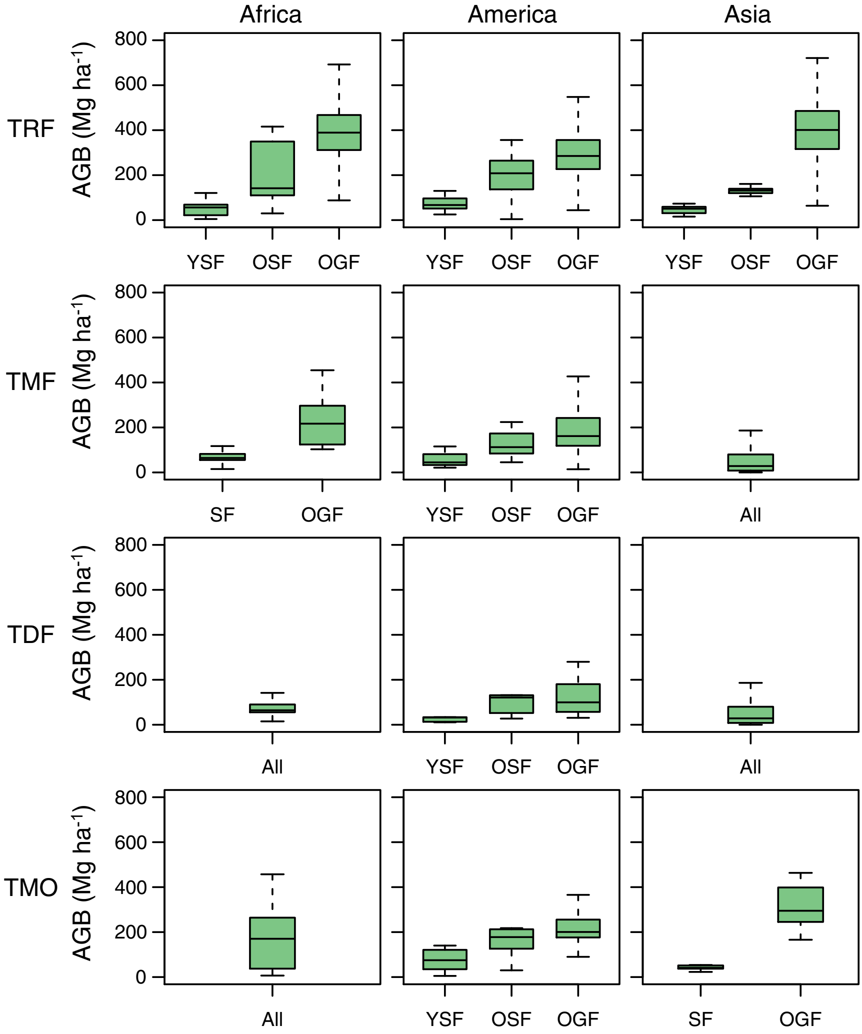

Figure 2.3: Aboveground biomass (AGB) per successional forest type, for each continent and ecological zone. For secondary forests, grid cell averages were included; for old-growth forest AGB for each plot (here not weighted for plot size). Boxes include the 25th and 75th percentile; the horizontal line indicates the median. TRF = tropical rainforest; TMF = tropical moist forest; TDF = tropical dry forest; TMO = tropical montane forest. YSF = younger secondary forest ($\leq$20 years old); OSF = older secondary forest (>20 years old); SF = all secondary forests; OGF = old-growth forest; All = all successional forest types.

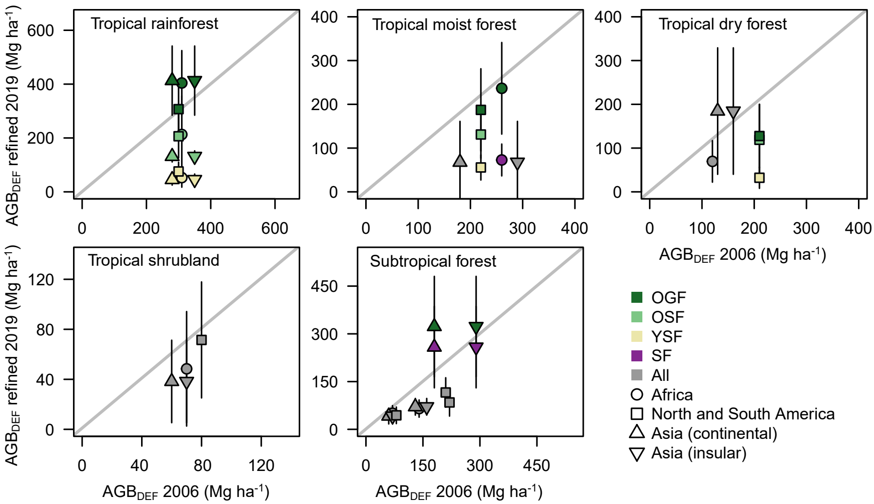

Figure 2.4: Comparison between the refined 2019 (with standard deviation) and previous (2006) default biomass values (AGB_{DEF}) for the three continents, per ecological zone and successional forest type. For Asia, 2006 AGB_{DEF} is indicated for both continental and insular Asia. (Sub)tropical montane forests were excluded because in 2006 only a range was included, not an estimate of average biomass. For AGB_{DEF} 2006, no distinction between successional forest types was made. YSF = younger secondary forest ($\leq$20 years old); OSF = older secondary forest (>20 years old); SF = all secondary forests; OGF = old-growth forest; All = all successional forest types.

For tropical moist and tropical dry forest across all successional forest types in Asia, refined default values were unrealistically low and high, respectively. Similarly, for old-growth tropical montane forest in Asia, the default value was higher than the one for tropical rainforest on the same continent. These unrealistic values may either be a result of a low number of included plots, or where a single default value across successional forest types was included, plots may have represented largely one successional forest type. In these cases, we recommend using alternative values (Table 2.1), either the value for another continent, or a general estimate across all successional forest types based on (Pan et al., 2013).

Across continents, our refined default values for tropical old-growth rainforests, moist forests, dry forests, and for shrublands of all successional forest types together were generally close to the previous, 2006 IPCC default values (Figure 2.4). In contrast, for tropical secondary forests, refined default values were consistently lower than the 2006 values, with for younger secondary forests, 4.0 to 7.7-fold lower values (Figure 2.4). For subtropical forests, refined default values were generally lower than the 2006 default values, except for subtropical humid forests in Asia that were higher than the 2006 default values for continental Asia (Figure 2.4). Across all continents and ecological zones for tropical and subtropical forests, standard deviations of the refined default values were large, indicating large spatial variation in AGB within ecological zones (Figure 2.4; Table 2.1).

2.4 Discussion

2.4.1 Refined IPCC AGB default values

We found large variation in AGB across continents, ecological zones, and successional forest types. Our refined default values generally reflect the large-scale climatic gradients in the tropics. Forest biomass generally increases from drier to wetter forests because of a longer growing season and higher water availability (Poorter et al., 2017; Sullivan et al., 2020), which was reflected in the refined default values for tropical old-growth forests, as they increased from dry, to moist, to rainforests (Table 2.1). In addition, tropical forest biomass decreases with elevation because of decreasing temperatures (Girardin et al., 2010). Our refined default estimates were partly consistent with this pattern, as the default value for tropical montane forests was lower than the one for tropical rainforests in the Americas (Table 2.1).

Where possible, we provided refined AGB default values per successional forest type, differentiating between younger and older secondary forests. For all continents and ecological zones for which we were able to distinguish between secondary and old-growth forests, AGB was lower in secondary forests than in old-growth forests, and increased from younger to older secondary forests as forests regrow and vegetation biomass builds up, in agreement with ecological first principles and previous analyses for tropical forests (Anderson-Teixeira et al., 2016; Martin et al., 2013; N'Guessan et al., 2019; Poorter et al., 2016).

Our refined default AGB values were generally consistent with the IPCC 2006 default values for old-growth tropical rainforests and tropical moist forests, but were lower than previous values for secondary forests and for all successional forest types combined, with the strongest deviations for younger secondary forests (Figure 2.4). These results suggest that IPCC 2006 default values for at least tropical rainforests and moist forests were largely defined based on old-growth forests (Langner et al., 2014), and stress the importance of differentiation by successional forest type. By specifying separate default values for younger secondary, older secondary, and old-growth forests, we better reflect the reality of twenty-first century tropical forests, as secondary forests are estimated to account for 30% of the forest area in the tropics (Pan et al., 2011).

Our refined default values provide a more realistic estimate of forest carbon stocks when only IPCC default AGB and AGB change values in combination with information on land cover can be applied for carbon accounting (Tier 1 level). Using IPCC 2006 values almost certainly led to overestimated carbon stocks for many countries, because they reflected values for old-growth forests. Moreover, IPCC default values of net rates of AGB change (ΔAGB) have also been refined recently, with overall rates 30% lower than the 2006 default values (Requena Suarez et al., 2019). Taken together, refined estimates for both AGB and net AGB change will improve national estimates of forest carbon stocks and fluxes.

2.4.2 Recommendations for future refinement

In our effort, we included the available, high-quality data to provide refined default values, but data gaps remain (Figure 2.5). We recommend future refinement by incorporating AGB data for ecological zones and successional forest types that are currently undersampled, or for which data from plots with information on disturbance history were not available. The availability of AGB data from forest plots strongly varied across continents and ecological zones, with data gaps for secondary forests in Africa and Asia, and for subtropical forests in general (Figure 2.2; Table 2.1). Particularly in Africa, shifting cultivation is common (Heinimann et al., 2017). Overall, availability of plot data with information on disturbance history was low for the drier areas in Africa, parts of Asia, and subtropical forests on all continents (Figure 2.5). This may be because dry forests in Africa are commonly used (McNicol et al., 2018), which complicates determining their disturbance history. Nevertheless, targeting collection of data from plots, along with detailed information on their disturbance history in these areas should be a priority, although on a per-area basis tropical moist and wet forests in Africa and the Americas remain also relatively undersampled (Figure 2.5). Establishing permanent forest plots is essential, for accurate estimation of both AGB and AGB change over time, for all successional forest types (ForestPlots.net et al., 2020). For future refinement, we also recommend distinguishing successional stages in more detail, as the three successional forest types represent broad categories. Particularly, older secondary forests could be divided into degraded/logged forests and regenerating forests after complete removal of vegetation (e.g., slash-and-burn agriculture), because they are subject to distinct levels of disturbance with differential impacts on carbon stocks (Berenguer et al., 2014).

Our refined default values are well-suited for Tier 1 level reporting, along with the refined IPCC default values for net biomass change (Requena Suarez et al., 2019), but for Tier 2 and 3 level reporting other approaches would be needed for more accurate national estimation of carbon stocks. Within ecological zones, there was large variation in AGB (as indicated by the large SD), probably because of large variation in environmental conditions within each ecological zone. We recommend to account for variation in environmental conditions within ecological zones to increase precision in AGB estimates, as several climatic and edaphic factors influence tropical forest AGB. In old-growth tropical forests, AGB varies with climate and soil fertility (e.g. Poorter et al., 2016; Quesada et al., 2012;

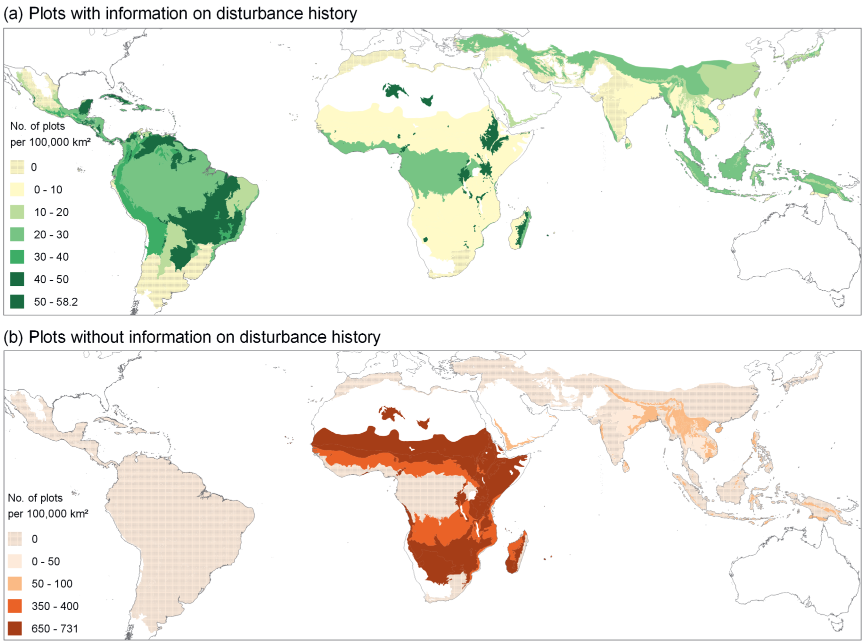

Figure 2.5: Number of plots per 100,000 km_2 of natural forests per ecological zone. Natural forest areas per ecological zone were based on Schulze et al., 2019. (a) Plots with information on disturbance history; (b) Plots without information on disturbance history.

Sullivan et al., 2020). For regrowing forests, AGB could be modelled as a function of stand age and climate, as these drive much of the variation in AGB in regrowing forests (Cook-Patton et al., 2020; Poorter et al., 2016), and soil fertility. In regrowing forests, including dry, moist, and wet tropical forests, in Latin America, such an approach has been applied on a continental scale (Chazdon et al., 2016), but for Africa and Asia such information is lacking. Moreover, effects of forest cover in the landscape matrix (Bonner et al., 2013) and previous land-use (Jakovac et al., 2021) on AGB in regrowing forests should also be considered. Similar approaches could be explored for degraded/logged forests, although quantifying forest disturbance levels for large areas remains challenging.

AGB maps based on remotely-sensed data are increasingly becoming available for the tropics, but uncertainty at the pixel level is still very high, particularly for high-biomass tropical forests (Herold et al., 2019), which limits their use in greenhouse gas inventories. Integrating NFI data with remote-sensing products may be an alternative approach for monitoring impacts of land-use change on AGB over large areas, as NFIs have large geographical coverage, and should be further explored in the future (Bustamante et al., 2016; Herold et al., 2019).

2.5 Conclusions

We provided a rigorous refinement of the 2006 IPCC AGB default values for (sub)tropical forests by integrating plot data from multiple sources to derive the refined 2019 AGB default values. Instead of a single default value per continent and ecological zone, we included separate values for younger and older secondary forests, and for old-growth forests. For ecological zones for which no plot data were available, we used a global AGB map to estimate default values; for the tropics, this was done for a negligible part of the three continents. We now also consistently account for uncertainty by including the standard deviation for all refined default values. While we provide a rigorous update to the previous default values, data gaps remain. High-quality data from well-distributed permanent forest plots is essential to fill these data gaps. We provide a reproducible approach to derive AGB default values to facilitate future refinement efforts. These refined AGB default values will aid in more accurate monitoring of forest carbon stocks and dynamics in (sub)tropical forests.

2.6 Supporting information

2.6.1 Appendix 1

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Chapter 3

Estimating aboveground net biomass change for tropical and subtropical forests: Refinement of IPCC default rates using forest plot data

This chapter is based on:

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Abstract

As countries advance in greenhouse gas (GHG) accounting for climate change mitigation, consistent estimates of aboveground net biomass change (ΔAGB) are needed. Countries with limited forest monitoring capabilities in the tropics and subtropics rely on IPCC 2006 default ΔAGB rates, which are values per ecological zone, per continent. Similarly, research into forest biomass change at a large scale also makes use of these rates. IPCC 2006 default rates come from a handful of studies, provide no uncertainty indications and do not distinguish between older secondary forests and old-growth forests. As part of the 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories, we incorporate ΔAGB data available from 2006 onwards, comprising 176 chronosequences in secondary forests and 536 permanent plots in old-growth and managed/logged forests located in 42 countries in Africa, North and South America and Asia. We generated ΔAGB rate estimates for younger secondary forests ($\leq$20 years), older secondary forests ($>$20 years and up to 100 years) and old-growth forests, and accounted for uncertainties in our estimates. In tropical rainforests, for which data availability was the highest, our ΔAGB rate estimates ranged from 3.4 (Asia) to 7.6 (Africa) Mg ha^{-1} year^{-1} in younger secondary forests, from 2.3 (North and South America) to 3.5 (Africa) Mg ha^{-1} year^{-1} in older secondary forests, and 0.7 (Asia) to 1.3 (Africa) Mg ha^{-1} year^{-1} in old-growth forests. We provide a rigorous and traceable refinement of the IPCC 2006 default rates in tropical and subtropical ecological zones, and identify which areas require more research on ΔAGB. In this respect, this study should be considered as an important step towards quantifying the role of tropical and subtropical forests as carbon sinks with higher accuracy; our new rates can be used for large-scale GHG accounting by governmental bodies, nongovernmental organizations and in scientific research.

3.1 Introduction

Signatory nations of the Paris Agreement agreed to report on greenhouse gas (GHG) emissions and removals for climate change mitigation efforts (UNFCCC, 2015). Reporting requires providing the UNFCCC with reliable estimates of anthropogenic CO_2 emissions based on anthropogenic activity data and removals based on ecosystem- level GHG fluxes. In this respect, forest ecosystems are a central terrestrial component of the global carbon (C) cycle, storing roughly half of terrestrial C (Bonan, 2008) and generally acting as C sinks (Houghton, 2007). Tropical and subtropical forests account for approximately 70% of the world's gross forest C sink (Pan et al., 2011), and through their conservation and restoration, they have the potential to partially offset CO_2 anthropogenic emissions (Houghton et al., 2015). Thus, accounting for GHG removals from the atmosphere through tropical and subtropical forest C sinks is of utmost importance.

Countries with tropical and subtropical forests can benefit from climate change mitigation policies through land restoration initiatives and Reducing Emissions from Deforestation and Forest Degradation (REDD+) schemes as a way to conserve and enhance their forest C sinks. These initiatives and schemes require monitoring, reporting and verification systems to account for forest C pools and fluxes (Turnhout et al., 2017) and should follow IPCC good practice guidelines (IPCC, 2003; IPCC, 2006).

Due to the complexity of these ecosystems, as well as the often limited national forest monitoring capacities within the tropics, there are scarce country-specific data on C sinks in natural forests. Thus, tropical countries rely heavily on default values (Tier 1) specified in the IPCC guidelines (IPCC, 2006), rather than using country-specific data (Tier 2) or higher level methods such as repeated measurements in permanent plots (Tier 3). For example, for forest C pool reporting of tropical countries by 2015, 84 out of 99 countries were reporting at only Tier 1 level (Romijn et al., 2015).

IPCC 2006 Tier 1 forest C pools and sinks in natural forests are characterized in part as aboveground live tree biomass (AGB) and rates of aboveground net biomass change (ΔAGB). In this context, ΔAGB is defined as the balance between annual rates of AGB gain (productivity and recruitment) and loss (mortality) over time and per unit area. IPCC 2006 Tier 1 default ΔAGB rates consist of single values and/or ranges (IPCC, 2006, Table 4.9) which provide spatially coarse estimates of ΔAGB across global ecological zones (FAO, 2012). Besides being widely used by countries for C reporting (FAO, 2015a; FAO, 2015b; Romijn et al., 2015), these default rates are also commonly used in research on forest biomass change and forest C fluxes (Achard et al., 2014; Viglizzo et al., 2011). To provide a thorough characterization of natural forest C sinks, IPCC 2006 default ΔAGB rates can be used together with other Tier 1 default values — such as AGB, belowground biomass (BGB) to AGB ratios — and loss estimates of AGB by anthropogenic activities. Natural forest C sink estimates are used alongside planted forest C sink estimates, which can then be combined with spatially explicit information such as forest cover and its change over time, as well as land-use maps, to provide globally consistent estimates of AGB and BGB (e.g., Ruesch and Gibbs, 2008) and of changes in forest C pools (e.g., Petrescu et al., 2012).

While influential, IPCC 2006 default ΔAGB rates require improvement, since they incorporate only a fraction of the currently available forest plot data. Since the first compilation of these rates, new and expanding databases have greatly enlarged the amount of readily available and high-quality tropical and subtropical forest plot data (Anderson-Teixeira et al., 2016) In addition, the IPCC 2006 default tables do not provide measures of variation, which is why the uncertainty of estimates cannot be characterized based on their values. Furthermore, there is no information on how these values were selected or derived, or how representative they are of the forests they describe.

Finally, IPCC 2006 default ΔAGB rates divide natural forest stands into above and below 20 years, which is a broad classification that does not account for known age-related variation in secondary forests — which are naturally regenerated forest stands that regrow after natural or anthropogenic disturbances. Younger secondary forests have high ΔAGB rates (Anderson-Teixeira et al., 2016; Poorter et al., 2016) which then decrease over the course of forest succession (Chazdon et al., 2007; Houghton, 2005) until the stand reaches a mature (further referred to as old-growth) state in which ΔAGB slows down. Old-growth forests may locally fluctuate between AGB gains and losses over time (Brienen et al., 2015a; Chambers et al., 2013; Phillips et al., 1998) but most old-growth tropical forest has on average contributed a net sink (e.g., Espírito-Santo et al., 2014; Lewis et al., 2009; Pan et al., 2011). Since ΔAGB rates are expected to vary over the course of succession, secondary forests over 20 years should be disaggregated from old-growth forest stands.

Managed and/or logged forests can also have high ΔAGB rates, since timber extraction and silvicultural treatments partially open the forest canopy, increasing the ΔAGB rate in the remaining stand (Rutishauser et al., 2015). Until recently, managed/logged forests have been largely overlooked when quantifying the contribution of tropical and subtropical forests to the global terrestrial C sink, even though they represent approximately 20% of the world's humid tropical forests (Asner et al., 2009b).

In this study, as part of the 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories (IPCC, 2019) we refine the IPCC 2006 default ΔAGB rates in tropical and subtropical ecological zones. In the interest of facilitating the scientific use and future update of these default rates, we (a) incorporate newly available data on secondary, old-growth and managed/logged forests; (b) disaggregate forests over 20 years into older secondary and old-growth forests; (c) derive ΔAGB rate estimates in a clear, rigorous and reproducible manner; and (d) identify areas where better ΔAGB data are needed.

3.2 Methods

3.2.1 Data compilation

We compiled AGB (Mg ha^{-1}; linked with stand age) and ΔAGB (Mg ha^{-1} year^{-1}) data from existing plot networks, databases and primary scientific literature on natural, as opposed to planted, forest stands (Anderson-Teixeira et al., 2018a; Anderson-Teixeira et al., 2018b; Anderson-Teixeira et al., 2016; Brienen et al., 2015a; Cook-Patton et al., 2020; Lewis et al., 2009; Poorter et al., 2016; Qie et al., 2017; Rutishauser et al., 2015) in global tropical and subtropical ecological zones (hereafter referred to as *ecozones*) as defined by FAO, 2012. Additional studies not present in these databases were obtained through a review of studies in the Web of Science (v.5.26.2). Data were only included if they were present in a peer-reviewed source, within the main text, as part of a table or as supplementary material. All data had to be georeferenced for aggregation by continent (North and South America, Africa or Asia) and ecozone. Following IPCC guidelines, studies with sites in continental United States were excluded from this compilation.

We divided forest plot data based on stand age or the presence of anthropogenic intervention. Following the methodology by Poorter et al., 2016, we included data from secondary forests stands up until 100 years. These data were then divided into younger secondary forests (≤20 years; as per the IPCC 2006 values) and older secondary forests (>20 years), based on their stand age or on the time since the last anthropogenic disturbance. Forest stands with no record of anthropogenic disturbance for at least the past 100 years were regarded as old-growth forests. Forest stands with anthropogenic interventions resulting in partial stand disturbance such as silvicultural treatments or selective logging were regarded as managed/logged forests (Sist et al., 2015).

In old-growth and managed/logged forests, ΔAGB is monitored mainly through repeated measurements of permanent plots (Brienen et al., 2015a; Chave et al., 2008; Lewis et al., 2009; Muller-Landau et al., 2014; Qie et al., 2017; Sist et al., 2015), while the study of ΔAGB in secondary forests relies mostly on chronosequences (Chazdon et al., 2007; Chazdon et al., 2016; Poorter et al., 2016). A chronosequence consists of static measurements (i.e. AGB) of plots under similar environmental conditions that differ in their age since abandonment. Chronosequences use, therefore, a space-for-time substitution to estimate long-term successional change without monitoring individual plots over long time periods, and provide a critical data source given the large practical challenges to monitoring recovering forests for many decades.

Secondary forest chronosequences consisted of AGB or C (Mg ha^{-1}) plots at different stand ages per chronosequence site. For North and South America, only chronosequences with ≥3 chronosequence plots were included to generate site-specific AGB–stand age relationships. For Asia and Africa, where fewer data were available, proximate sites (<1.5°

in Africa and $<4.0°$ in Asia) in the same ecozone were grouped and treated like single chronosequences. This permitted us to include data from 18 sites in Asia and nine sites in Africa which contained only one or two plots each.

For old-growth forests and managed/logged forests, we included ΔAGB (or ΔC) rates from permanent plots. For ΔAGB rates $\mathrm{Mg\,ha^{-1}\,year^{-1}}$, each plot had at least one ΔAGB value based on two consecutive measurements (one census interval) of the same plot. When aboveground C (or aboveground ΔC) was reported, we converted these values to AGB or ΔAGB by dividing them by the conversion factor cited in the original source, if given, or the IPCC conversion factor of 0.47.

For all forest types, plot-level AGB values were calculated in the original sources by aggregating tree-level AGB within each plot. Tree-level AGB was estimated based on diameter at breast height, tree height (if available) and species-specific wood density. The set of allometric equations (Chave et al., 2005; Chave et al., 2014; Feldpausch et al., 2012; Talbot et al., 2014) used in the original sources were carefully selected to account for climatic factors such as different levels of precipitation and bioclimatic stress.

3.2.2 Calculation of ΔAGB rates per forest type

ΔAGB rates were derived separately for younger secondary forests, older secondary forests, old-growth forests and managed/logged forests. For younger and older secondary forests, a mixed-effects modelling framework was applied to model AGB as a function of stand age (fixed effect) and chronosequence sites (random effect). For this, we used the *lme4* package (Bates et al., 2015) in R v.3.4.0 (R Core Team, 2017). Stand age was ln-transformed to account for the nonlinear increase in AGB with stand age. Subsequently, plot AGB for each chronosequence was modelled as a function of stand age, including a random intercept and slope (Figure 3.1a).

For younger and older secondary forests, site-specific models, that is, models with a site-specific intercept and slope based on the random effects, were used to derive ΔAGB rates per chronosequence. For younger secondary forests, we did so by predicting AGB at 20 years and then dividing this value by 20 to obtain the ΔAGB rate (Figure 3.1a; slope of the red line). As such, we assumed a linear increase in AGB over the first 20 years of succession, which has been observed in some secondary tropical forests (Alves et al., 1997; Saldarriaga et al., 1988). This assumption is not always accurate (e.g. when some biomass remains following disturbance or when succession is delayed), and our calculated rates, therefore, will not always accurately represent instantaneous ΔAGB rates for stands $\leq$20 years. However, this approach yields rate estimates that should provide, on average, unbiased average estimates over the first 20 years of forest regrowth when applied in a bookkeeping context. For older secondary forests, AGB was predicted at 20 years (or the youngest age after 20 years) and at the maximum stand age available. Following this,

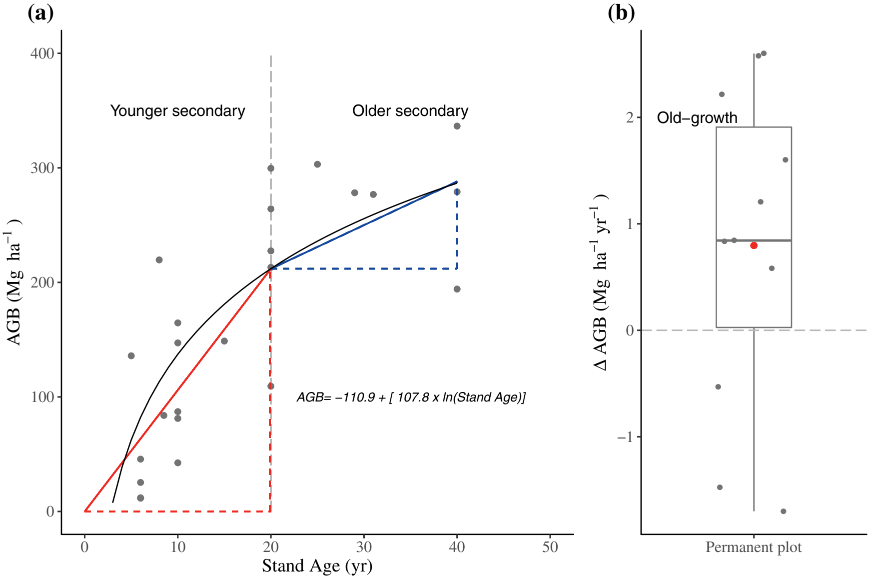

Figure 3.1: Examples of (a) an aboveground biomass (AGB)–stand age relationship in a given chronosequence in a secondary forest and (b) ΔAGB rates in a given permanent plot in an old-growth forest. In (a), grey dots indicate AGB plot values. ΔAGB rates are calculated by obtaining two slopes per growth curve (the black curve): one for younger secondary forests (0–20 years; red line) and another one for older secondary forests (20 years to the maximum age available at a given site; blue line). In (b), grey dots indicate ΔAGB rates derived from consecutive census in a given plot, with the red dot showing the mean value across censuses for that plot

site-specific ΔAGB rates were calculated by subtracting AGB at 20 years from AGB at the maximum stand age, then dividing it by the difference in stand age (Figure 3.1a; slope of the blue line).

For old-growth forests and for managed/logged forests, permanent plots from which ΔAGB rates were obtained were treated as single sites. ΔAGB rates were weighted according to total monitoring period and plot size, following the weighting procedures determined in the original sources (Brienen et al., 2015b; Lewis et al., 2009; Qie et al., 2017; Rutishauser et al., 2015) unless all plots in an ecozone presented the same monitoring period and plot size, such as for plots in managed/logged forests in Africa (Gourlet-Fleury et al., 2013). For permanent plots with two or more census intervals and two or more ΔAGB rates derived from these, we used the mean ΔAGB rate (Figure 3.1b).

3.2.3 Derivation of IPCC default ΔAGB rates

To derive IPCC ΔAGB default rates, site-specific ΔAGB rates were averaged per continent, ecozone and forest type (younger secondary, older secondary and old-growth). Following IPCC requirements, data from managed/logged forest data, when available, were combined with the older secondary forest type. Default ΔAGB rates were calculated for categories (i.e. combinations of continent, ecozone and forest type) with sufficient data only ($\geq$2 chronosequences or permanent plots per category). For younger and older secondary forest categories, we included standard deviations (SD) and confidence intervals (CI; 95%) as measures of variation. For old-growth forest categories, we calculated the weighted SD and bootstrapped CI (95%, 1,000 repetitions with replacement).

For categories with insufficient data, we used default rates from the same ecozone and forest type from another continent. If default rates from the other two continents were available, we chose the value that more closely aligned with the default value(s) of a different forest type in the ecozone and continent of interest. If no data were available across all three continents, we recommended using the IPCC 2006 default rates. For the latter cases, we did not differentiate between old-growth forests and secondary forests >20 years, per the IPCC 2006 default rates. Categories with recommended rates can be found in Appendix 1. For ecozones with sufficient data for secondary forests but insufficient data for old-growth forests, only default rates for secondary forests were derived (e.g. tropical moist forests in Africa, Table 3.1).

3.3 Results

3.3.1 Data availability

Overall, we assembled a database of 176 chronosequences (consisting of 1,924 plots) of secondary forests and 536 permanent plots (1,324 census intervals) of old-growth or managed/logged forests. Within chronosequences, younger secondary forests were better represented than older secondary forests (65.7% and 34.3% of plots respectively). Of all permanent plots, the majority were located in old-growth forests (79.1%, 1,212 census intervals in total), as opposed to managed/logged forests (20.9%, 112 census intervals in total).

For secondary forests, 43.8% of the chronosequences were situated in North and South America (excluding continental United States), 15.3% in Africa and 40.9% in Asia. For permanent plots in old-growth forests, 64.6% of plots were situated in North and South America, 18.6% in Africa and 16.7% in Asia. For permanent plots in managed/logged forests, 75% of plots were situated in North and South America and 25% in Africa. Overall

67.6% of chronosequences and 100% of permanent plots were situated in tropical, as opposed to subtropical ecozones (Figure 3.2).

In North and South America, of 77 chronosequences, 27.3% had >20 plots, 19.5% had between 11 and 20 plots and 53.2% had ≤10 plots. In Africa, of 27 chronosequences, 7.4% had >20 plots, 22.2% had between 11 and 20 plots and 70.4% had ≤10 plots. In Asia, of 72 chronosequences, 2 had >20 measurements each, 3 had between 11 and 20 measurements and the remaining majority (93.1%) had ≤10 plots.

3.3.2 Default ΔAGB rates per IPCC forest type

We derived new default ΔAGB rates for natural forests per continent, ecozone and forest type (Table 3.1). Across all continents and ecozones, our default ΔAGB rates for younger secondary forests were higher than for older secondary forests, which in turn were higher than rates for old-growth forests. In tropical rainforests, default rates for all forest types were higher in Africa than in North and South America and Asia. In tropical mountain systems, default rates for younger secondary forests were also higher in Africa than in the other continents (Table 3.1). Default ΔAGB rates in old-growth forests ranged from -0.7 (-0.1, 1.9) in tropical mountain systems in Asia to 1.3 (0.5, 2.1) $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ in tropical rainforests in Africa. In individual census intervals, negative rates were reported for all ecozones and continents, but default rates for old-growth forests tended to be significantly positive and especially so where sufficient sample size was available to assess change with a high degree of confidence (Table 3.1).

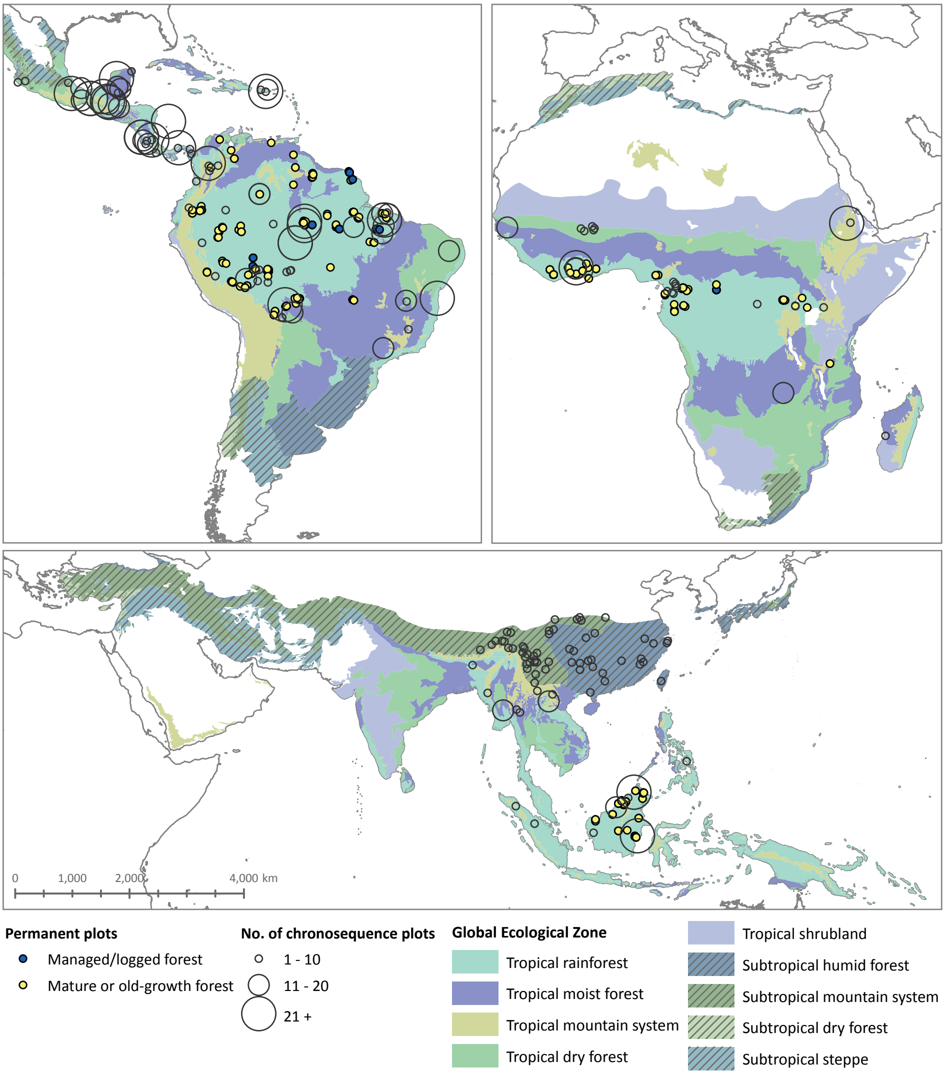

Figure 3.2: Distribution of chronosequences and permanent plots. Coloured areas show the extent of global ecological zones (according to FAO, 2012) included in this study; subtropical ecozones are hatched. Chronosequences are indicated with hollow circles; symbol size varies with the number of plots per chronosequence. Permanent plots are indicated with blue (managed/logged forests) and yellow (old-growth forests) circles

Table 3.1: Refined default aboveground net biomass change (ΔAGB) rates

Ecological Zone	Continent	Forest type[a]	ΔAGB ($Mg\,ha^{-1}\,year^{-1}$) Mean ΔAGB	Median ΔAGB	SD	CI (95%)	No. of chronosequences and/or permanent plots
Tropical rainforest	Africa	YS	7.6	3.5	5.9	4.6, 10.6	15
		OS	3.5	1.9	3.3	1.5, 5.5	10
		OG	1.3	1.7	3.5	0.5, 2.1	77
	North and South America	YS	5.9	5.0	2.5	5.1, 6.7	42
		OS	2.3	2.1	1.1	2.0, 2.6	39
		OG	1.0	0.9	2.0	0.6, 1.4	248
	Asia	YS	3.4	2.1	3.9	0.5, 6.3	7
		OS	2.7	2.7	3.1	-1.6, 7.0	2
		OG	0.7	0.8	2.2	0.1, 1.3	66
Tropical moist forest	Africa	YS	2.9	2.9	1.0	1.5, 4.3	2
		OS	0.9	0.9	0.7	-0.1, 1.9	2
	North and South America	YS	5.2	4.5	2.3	4.2, 6.2	21
		OS	2.7	2.2	1.7	1.9, 3.5	18
		OG	0.4	0.8	2.1	-0.7, 1.5	19
	Asia	YS	2.4	2.4	0.3	2.0, 2.8	2
Tropical dry forest	North and South America	YS	3.9	3.1	2.4	2.0, 5.8	6

Table 3.1 continued from previous page

		OS	1.6	1.5	1.1	0.6, 2.6	5
Tropical mountain system	Africa	YS	5.5	5.5	6.8	-3.9, 14.9	2
	North and South America	YS	4.4	4.0	1.6	3.1, 5.7	6
		OS	1.8	1.5	0.8	1.0, 2.6	4
		OG	0.5	0.1	1.9	-0.9, 1.9	6
	Asia	YS	2.9	2.9	0.1	2.8, 3.0	5
		OS	1.1	1.2	0.4	0.7, 1.5	5
		OG	-0.7	-0.3	3.1	-3.2, 1.8	5
Subtropical humid forest	Asia	YS	2.5	2.2	0.8	1.7, 3.3	4
		OS	1.0	0.7	0.9	0.4, 1.6	8
Subtropical mountain system	Asia	YS	2.5	2.5	0.03	2.5, 2.5	2
		OS	0.5	0.4	0.3	0.3, 0.7	12

Note: Forest types include younger secondary forests (YS), older secondary forests (OS) and old-growth forests (OG). Refined IPCC default ΔAGB rates consist of mean ΔAGB and SD. See Appendix 1 for a complete version of the table that includes recommended rates for categories without data.

[a] IPCC-defined forest type categories are "Secondary ≤20 years" (younger secondary forests), "Secondary>20 years" (older secondary forests) and "Primary" (old-growth forests).

3.3.3 Comparison with IPCC 2006 default rates in selected ecozones

We compared our refined rate estimates to previous IPCC 2006 default ΔAGB rates for three ecozones (tropical rainforests, tropical moist forests and tropical mountain systems) with the highest data availability, and for which default rates were derived across all continents for at least one forest type.

For younger secondary forests, our refined rate estimates were lower than the IPCC 2006 default rates for forests <20 years old, with the exception of tropical mountain systems in North and South America (1 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ higher) and Africa (2 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ higher).

Our refined rates for the new forest types (older secondary forests and old-growth forests) that replaced forests >20 years old partially aligned with IPCC 2006 default rates (Figure 3.3). In all cases, our rates for old-growth forests were more conservative (i.e. smaller net positive gains) than the IPCC 2006 default rates for all forests >20 years old. For older secondary forests, our rates in North and South America and in Africa were higher than the IPCC 2006 default rates for forests >20 years old, with the exception of tropical rainforests in North and South America (0.8 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ lower; Figure 3.3a) and tropical moist forests in Africa (0.4 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ lower; Figure 3.3e). In Asia, our rates for older secondary forests were lower than for the IPCC 2006 default rates previously calculated separately for insular and continental areas (Figure 3.3c,f,i). The distinction between insular and continental rates for Asia is residual from the IPCC 2006 rates and was not continued in our estimates, due to limited data availability. Across all forest types, standard deviations tended to be higher for rates obtained from forest categories with fewer sites. For example, in tropical rainforests, the SD for younger secondary forests in Africa (15 sites) was more than double the SD for the same forest category in North and South America (42 sites).

3.3.4 ΔAGB rates per forest type for selected ecozones

In secondary forests, AGB–stand age relationships varied strongly between continents and ecological zones (Figure 3.4). A complete list of AGB–stand age relationships for secondary forests can be found in Appendix 2. Across all continents, tropical rainforests (Figure 3.4a,b,c) showed the highest ΔAGB rates in comparison with other ecozones. In North and South America, where data availability was highest, AGB at 20 years varied from 88.7 $\mathrm{Mg\,ha^{-1}}$ (tropical mountain system) to 118.9 $\mathrm{Mg\,ha^{-1}}$ (tropical rainforest). Variation was stronger in Africa, where AGB after 20 years ranged from 57.3 $\mathrm{Mg\,ha^{-1}}$ (tropical moist forest) to 151.2 $\mathrm{Mg\,ha^{-1}}$ (tropical rainforest). Asia showed lower variation within ecological zones, with AGB after 20 years ranging from 47.1 $\mathrm{Mg\,ha^{-1}}$ (tropical moist forest) to 68.8 $\mathrm{Mg\,ha^{-1}}$ (tropical rainforest).

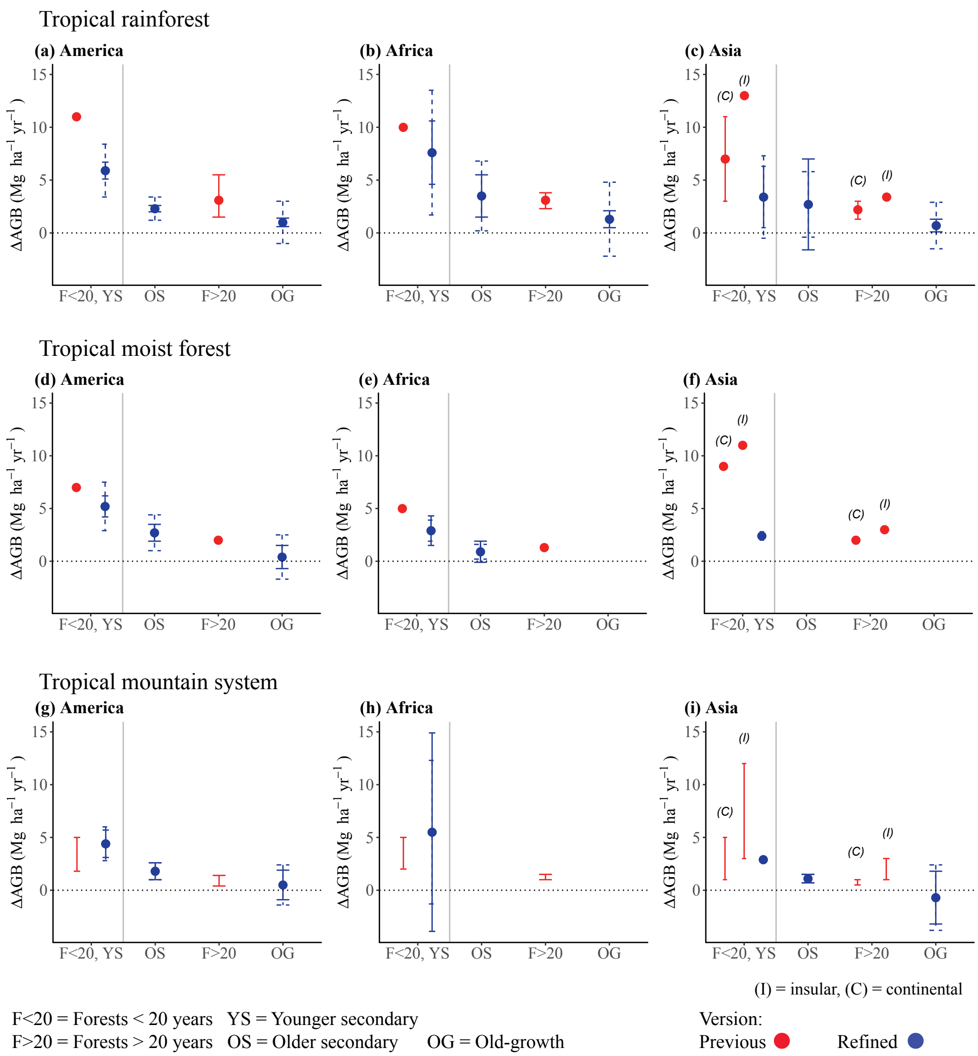

Figure 3.3: Comparison of previous IPCC 2006 default aboveground net biomass change (ΔAGB) rates with refined default rates per continent and forest type in tropical rainforests (a, b, c), tropical moist forests (d, e, f) and tropical mountain systems (g, h, i). Previous (in red) ΔAGB rates (Mg ha^{-1} year^{-1}) were divided into forests ≤20 years and forests >20 years old. Our refined (in blue) ΔAGB rates are divided into younger secondary forests, older secondary forests and old-growth forests. Vertical continuous lines represent ranges for previous default rates and CI (95%) for refined default rates, and vertical dashed lines represent SD. For Asia, previous rates were divided into continental and insular values. The grey vertical line divides forests ≤20 years and younger secondary forests from the other forest types

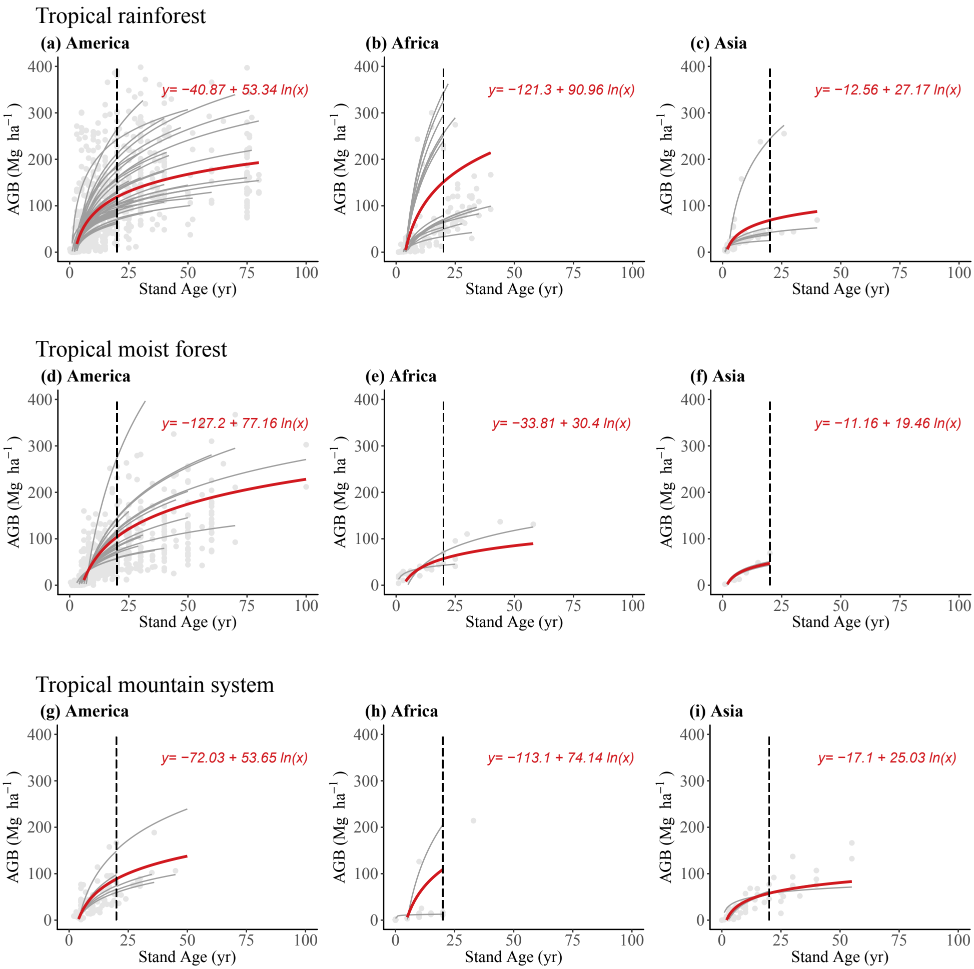

Figure 3.4: Relationships between aboveground biomass (AGB) and stand age in tropical rainforests (a, b, c), tropical moist forests (d, e, f) and tropical mountain systems (g, h, i) for secondary forests. AGB plots and chronosequences are represented in grey dots and grey curves respectively. Overall relationships between AGB and stand age for each ecozone are presented in red. The dashed vertical line divides the graph into younger secondary (≤20 years) and older secondary (>20 years) forests. Data from managed/logged forests were not included in this figure. For other ecozones, data were not available across all three continents

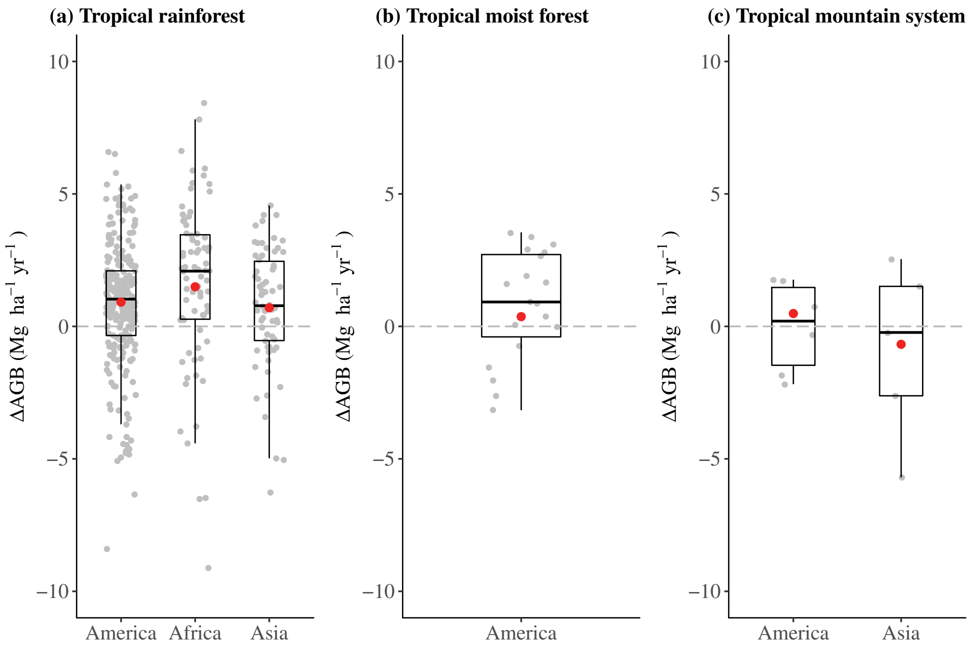

Figure 3.5: Aboveground net biomass change (ΔAGB) rates in old-growth (a) tropical rainforests, (b) tropical moist forests and (c) tropical mountain systems. Plot-specific ΔAGB rates are represented in grey. Red dots represent the mean ΔAGB rate per ecozone. Two values (-16.24 and -10.84) in tropical rainforests in Africa were excluded from (a)

For old-growth forests, mean ΔAGB rates were positive with the exception of tropical mountain systems in Asia (Figure 3.5c). Site-specific negative ΔAGB rates were present across all three ecozones. In such cases, negative rates indicate a period in which biomass loss by mortality has exceeded biomass accumulation by growth and recruitment over a period of time. Mean rates in old-growth tropical rainforests were highest in Africa, followed by North and South America, then Asia (Table 3.1). Mean rates in tropical mountain systems ranged from -0.7 Mg ha^{-1} year^{-1} in Asia to 0.5 Mg ha^{-1} year^{-1} in North and South America. In North and South America, old-growth tropical moist forests showed the lowest rate (0.4 Mg Mg ha^{-1} year^{-1}) in comparison with the rates obtained for old-growth forests in the other two ecozones (Table 3.1).

For managed/logged forests, ΔAGB rates were available only for tropical rainforests in North and South America and in Africa and for tropical moist forests in North and South America. For tropical rainforests (Figure 3.6a), the mean rate in Africa was more than twice as high as the mean rate in North and South America. In America, managed/logged forests in tropical rainforests had a higher mean rate than tropical moist forests (2.8 and 0.7 Mg ha^{-1} year^{-1} respectively).

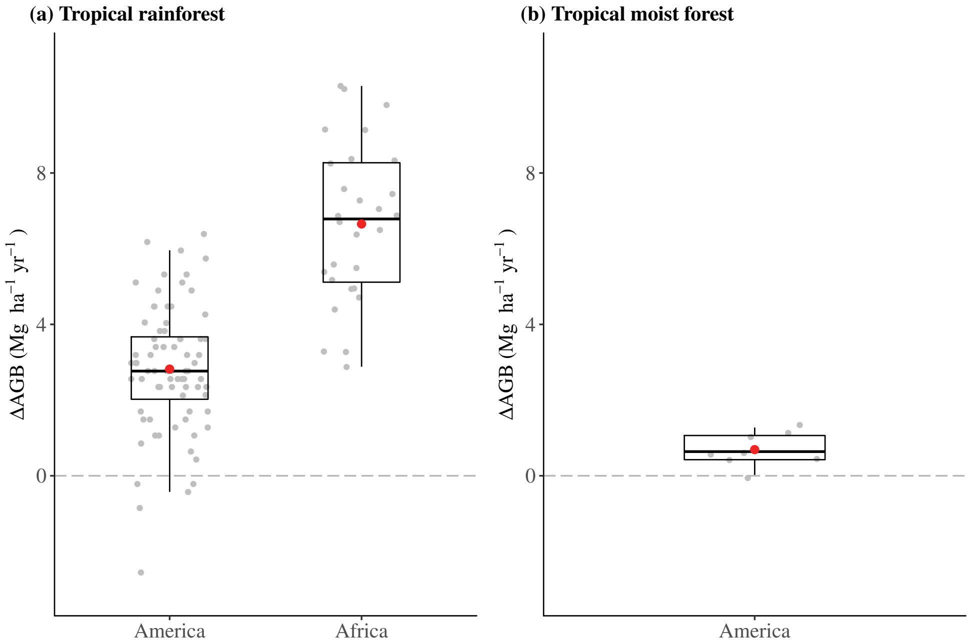

Figure 3.6: Aboveground net biomass change (ΔAGB) rates in managed/ logged (a) tropical rainforests and (b) tropical moist forests. Plot-specific ΔAGB rates are represented in grey. Red dots represent the mean ΔAGB rate per ecozone

3.4 Discussion

3.4.1 Refined IPCC default ΔAGB rates across forest types

Our refined rates were on average 30% smaller than the IPCC 2006 default rates, indicating that the use of the latter may overestimate forest C sequestration. Our rates for younger secondary forests were 30.1% smaller than the IPCC 2006 rates for forests <20 years old. Our rates for older secondary forests were on average neither smaller nor larger than the IPCC 2006 rates for forests >20 years old. Rates for old-growth forests, however, where on average 79.4% smaller than the IPCC 2006 rates for forests >20 years old. Thus, disaggregating older secondary forests and old-growth forests from the previous category of forests >100 years has provided us with more nuanced default rates.

Standard deviations per continent and ecozone ranged from 0.03 to 6.8Mg ha^{-1} year^{-1} in younger secondary forests, from 0.3 to 3.3 in older secondary forests and from 1.9 to 3.5 in old-growth forests. The large variability in SDs is partly due to the limited amount of sites or plots in many categories, which can result in a low SD if all chronosequences or plots are under similar site conditions. On the other hand, high SDs are not an unexpected result from combining plot measurements from forests that differ in their composition and site-specific factors. This variability can be observed in tropical mountain systems, for which more chronosequences and permanent plots are needed. Due to the variability in forests within ecozones, SDs and confidence intervals in categories with a limited number of sites should be used with caution, as these values would likely change with the addition of more sites.

Our refined rates can be used for entire ecozones per forest type, therefore, they are suitable for Tier 1 calculations. These rates should only be used in the absence of country-specific emission/removal factors (Tier 2) and/or local and detailed ΔAGB data (Tier 3; IPCC, 2006). Tropical countries reporting at Tier 1 level, but with substantial or highly uncertain estimates of AGB and ΔAGB in their natural forests, should strive to collect country-level data to report at higher tier levels.

Our methodology can be further refined for Tier 2 and Tier 3 calculations by accounting for deviations resulting from within-ecozone variation due to site conditions such as climate (e.g. precipitation, temperature), soil fertility, species composition, the presence of remnant trees and previous land use, all of which influence ΔAGB (Chazdon, 2014; Feldpausch et al., 2004; N'Guessan et al., 2019; Poorter et al., 2016; Rozendaal et al., 2017). Similarly, given the variability in ΔAGB across forest succession, forest types could be further disaggregated into smaller age classes, in particular among older secondary forests.

While our study focuses only on the C pool of living biomass and its change in natural forests, countries with a substantial amount of planted forests should also consider them when describing this pool at Tier 1 level. Default values and methods for planted forests are included in the 2006 IPCC Guidelines (IPCC, 2006), and have also been updated in the 2019 Refinement (IPCC, 2019). Furthermore, other C pools, such as dead organic matter or soil organic matter, should also be accounted for when estimating total forest C pools and sinks. Methods for estimating these pools are included in the 2006 IPCC Guidelines, and have also been partly updated in the 2019 Refinement.

3.4.2 Methodological implications

Secondary forests — use of chronosequences

For secondary forests, we derived ΔAGB rates from chronosequences, an approach that is typically applied to estimate AGB accumulation during secondary forest succession (e.g. Feldpausch et al., 2007; Poorter et al., 2016). However, this approach has limitations. By substituting space for time, we assume that all measurements have been affected in the same way by biotic and abiotic conditions (Johnson and Miyanishi, 2008), which may not be the case. To obtain actual ΔAGB rates in secondary forests in future refinements, long-term monitoring through repeated measurements of secondary forest plots is needed. While this has been carried out in some sites (e.g. Chazdon et al., 2007; Feldpausch et al., 2007; Rozendaal et al., 2017), such data were not available for many sites thus far, and data that were available deviated from chronosequence predictions in some sites (Feldpausch et al., 2007).

The compiled chronosequences consisted mostly of plots in stands below 20 years of age; thus, estimates for older secondary forests rely on less data. Furthermore, of all plots in older secondary forests, only 19.4% had stand ages over 60 years. Because of these limitations in data availability, we decided to not extend the modelled AGB–stand age relationships beyond the maximum age available per ecozone (Appendix 2) instead of extending these relationships until the cut-off at 100 years. The rates obtained for older secondary forests will have an upward bias; as more data in older secondary forests become available, in particular in stands over 60 years old, ΔAGB estimates in older secondary forests should be further refined.

As expected, ΔAGB estimates in young secondary forests were higher compared to old-growth forests. There is high C sequestration potential in secondary forests through reforestation and forest restoration (Chazdon et al., 2016); however, due to their vulnerability and rapid turnover, as well as a lack of mechanisms for their conservation (Vieira et al., 2014), secondary forests remain vulnerable to deforestation and degradation.

Old-growth and Managed/logged forests — use of permanent plots

In old-growth forests, site-specific ΔAGB rates spanned from positive to negative values. Site-specific positive rates may occur in stands recovering from past disturbance and/or in response to global change processes such as changes in atmospheric CO_2 concentration or N deposition (Lewis et al., 2004; Luo, 2007). Site-specific negative rates may account for particular periods when biomass loss was higher than biomass gain due to stochastic processes such as tree mortality resulting from natural gap phase dynamics, or due to exceptional and/or repeated droughts and climate variability (Brienen et al., 2015a; Feldpausch et al., 2016; Phillips et al., 2009; Qie et al., 2017). The plot-to-plot variability makes it clear that large sample sizes are needed in order to better constrain old-growth ecosystem biomass trajectories. While our results indicate that old-growth forests are on average small C sinks per unit area, they become a significant component of the planetary carbon balance due to their large extent and for large amounts of biomass they store (Pan et al., 2011).

In managed/logged forests, an overwhelming majority of sites (95.5%) had positive site-specific ΔAGB rates. Similar to old-growth forests, the few sites in managed/logged forest with negative rates are associated with stochastic events such as tree mortality (Rutishauser et al., 2015). High positive site-specific rates are expected from managed/logged sites, as they are obtained from remaining stands after logging. These rates do not account for released C by logging or silvicultural practices, which can vary depending on the type of logging techniques (Putz et al., 2008).

Given the growing extent of tropical forests with constant anthropogenic disturbances (Lewis et al., 2015), further research should be done on ΔAGB in managed/logged forests, particularly in relation to the effects of different types of logging practices. Once more data on this forest type become available, it will be possible, and advisable, to disaggregate estimates for managed/ logged forests from older secondary forests.

Furthermore, more plots in degraded forests are necessary to understand how degradation affects ΔAGB. Currently, our estimates do not account for level of degradation. There are studies that focus on the effects of forest degradation on AGB (Berenguer et al., 2014; Chaplin-Kramer et al., 2015); but effects on ΔAGB remain largely unknown and should be further explored. For this reason, countries with a large extent of degraded forests should consider our estimates as a first step, and account for the effect that degraded forests may have on ΔAGB through the establishment and monitoring of plots in degraded forests.

3.4.3 Improving ΔAGB data availability

Data availability varied across ecozones and continents (Figure 3.7). More data were available in tropical ecozones than in subtropical ecozones, and the latter had better data availability in Asia in comparison to the other continents. There were no chronosequences nor permanent plots available in subtropical dry forests or subtropical steppes in any of the continents. In addition, there were no data available for tropical shrublands and subtropical humid forests in North and South America, subtropical humid forests and subtropical mountain systems in Africa and tropical shrublands in Asia.

To derive large-scale estimates, a high number of chronosequences and permanent plots per ecozone is recommended to ensure representative estimates (Muller-Landau et al., 2014; Phillips et al., 2016; Poorter et al., 2016). Even though tropical rainforests had higher chronosequence and permanent plot densities across all continents, these densities are still relatively low (6.2, 4.7 and 4.3 chronosequences and permanent plots per 100,000 km^2 of natural forests in North and South America, Africa and Asia respectively). Given the extent of natural forests in tropical forest ecozones, their high inherent C sequestration potential (particularly in secondary forests) and their vulnerability to global change, more carefully positioned plots are needed to enhance the long-term monitoring of these forests at different successional stages. On the other hand, natural forests in ecozones with lower density of chronosequences and permanent plots should also be prioritized in future research (Figure 3.7; Appendix 3). For example, little is known about ΔAGB

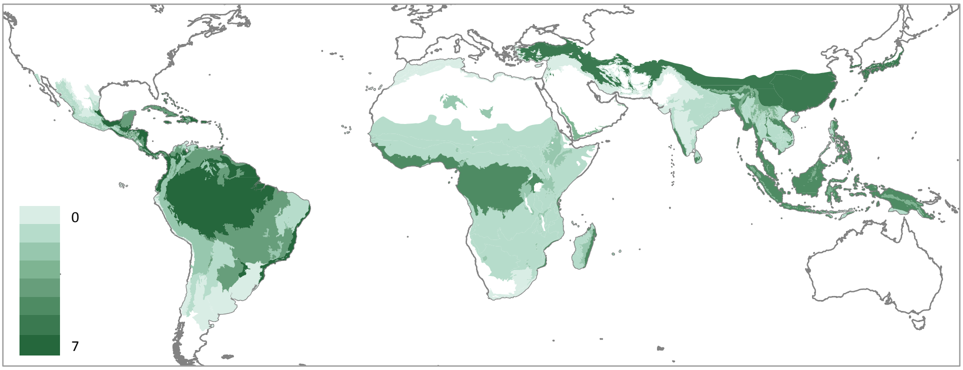

Figure 3.7: Chronosequence and permanent plot density per 100,000 km^2 of natural forests in tropical and subtropical ecozones. Extent of natural forests were obtained from Schulze et al., 2019 and combined with FAO, 2012 to obtain coarse estimates of natural forest area per ecozone. A full list of chronosequence and plot density can be found in Appendix 3

in low-biomass forests in tropical shrublands, even though this ecozone accounts for a substantial land area in Africa (approximately 5.95×1012 km^2).

The various threats to tropical forests posed by global change processes themselves means that it would be naïve to simply assume that past records are likely to be a good guide to future behaviour of these forests (e.g. Cavaleri et al., 2015): the future C balance of tropical and subtropical forests under a changing climate remains unknown. There is, however, already some evidence that these sinks are threatened by global change pressures and have been declining recently in some regions (Brienen et al., 2015a; Qie et al., 2017). Expanded and careful long-term monitoring with permanent plots will be needed to understand the changing carbon dynamics of the world's tropical and subtropical forests.

3.4.4 Future possibilities for improvement

To make use of more field data, AGB plots without stand age could be used in conjunction with a reliable stand age map to derive ΔAGB estimates. There have been advances in the elaboration of stand age maps (e.g. Poulter et al., 2018); however, such maps are currently not available in the resolution nor certainty required. Furthermore, disaggregating ΔAGB as a result of natural forest dynamics from forest degradation remains a challenge (Bustamante et al., 2016; Mitchell et al., 2017).

For categories for which rates could not be derived due to insufficient data, there is promise in using remote sensing (RS) data to monitor ΔAGB at a large scale. This could be achieved through consistent monitoring of forest cover change and biomass change at high spatial and temporal resolutions. Current global or pantropical RS products provide valuable information regarding forest cover gain or biomass change, but do so at medium-to-low spatial resolutions (e.g. Song et al., 2018) and for one particular time period instead of annually (e.g. Hansen et al., 2013). For example, the aboveground C density change map of Baccini et al., 2017 accounts for net change from 2003 until 2014, and, due to its methodology and low spatial resolution, does not distinguish between C density change from natural forest dynamics or from anthropogenic processes such as deforestation and degradation.

Evolving initiatives on AGB estimation such as the Global Ecosystem Dynamics Investigation mission (Dubayah et al., 2014), which aims to provide periodic AGB density estimates at a global scale, will facilitate our access to spatially explicit and multitemporal AGB estimates. In addition, interdisciplinary approaches that integrate AGB and ΔAGB plot data with RS data from the start will prove to be useful for future updates.

3.5 Conclusions

As part of the 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories (IPCC, 2019), we provide a rigorous refinement of the Tier 1 IPCC 2006 default ΔAGB rates for tropical and subtropical forests by incorporating forest plot data that have become available since the publication of the IPCC 2006 default rates. Our refined rates disaggregate forests >20 years old into older secondary forests and old-growth forests, and provide measures of variation to account for their uncertainty. These new rates can be used for large-scale C accounting by governmental bodies, nongovernmental organizations and in scientific research. Due to their spatial coarseness, these rates are not recommended for project-level monitoring. We present a clear, simple and reproducible approach to derive these rates, and have identified the ecozones for which more research is needed; therefore, these rates can be further refined as more data become available. In this respect, this study should be considered as an important step forward towards quantifying the role of tropical and subtropical forests as C sinks at large scales with higher accuracy.

3.6 Supporting information

3.6.1 Appendix 1

Default rates of aboveground net biomass change (ΔAGB; in Mg ha^{-1} year^{-1}). Forest types consist of old-growth (OG), older secondary forests (OS) and younger secondary forests (YS).

Ecological Zone	Continent	Forest Type[a]	ΔAGB (Mg ha^{-1}yr^{-1}) Mean	SD	Observation	References
Tropical rainforest	Africa	OG	1.3	3.5		[1, 2]
		OS	3.5	3.3		[3-8]
		YS	7.6	5.9		[3-7, 9]
	North and South America	OG	1	2		[2, 10, 11]
		OS	2.3	1.1		[3, 4, 12-15]
		YS	5.9	2.5		[3, 4, 6, 12-14]
	Asia	OG	0.7	2.2		[2, 16]
		OS	2.7	3.1		[3, 4, 17]
		YS	3.4	3.9		[3, 4, 17-19]
Tropical moist forest	Africa	OG	0.4	NA	Different region	
		OS	0.9	0.7		[20, 21]
		YS	2.9	1.0		[20, 21]
	North and South America	OG	0.4	2.1		[2, 10, 11]
		OS	2.7	1.7		[3, 4, 12, 13, 15, 22]
		YS	5.2	2.3		[3, 4, 12, 13, 22]
	Asia	OG	0.4	NA	Different region	
		OS	0.9	NA	Different region	

		YS	2.4	0.3		[3, 4]
Tropical dry forest	Africa	OG	-	-		
		OS	1.6	NA	Different region	
		YS	3.9	NA	Different region	
	North and South America	OG	-	-		
		OS	1.6	1.1		[12, 13]
		YS	3.9	2.4		[12, 13, 23]
	Asia	OG	-	-		
		OS	1.6	NA	Different region	
		YS	3.9	NA	Different region	
Tropical shrublands	Africa	OG *	0.9 (0.2-1.6)	NA	2006 IPCC values	[24]
		OS*	0.9 (0.2-1.6)	NA	2006 IPCC values	[24]
		YS	0.2-0.7	NA	2006 IPCC values	[24]
	North and South America	OG *	1.0	NA	2006 IPCC values	[24]
		OS*	1.0	NA	2006 IPCC values	[24]
		YS	4.0	NA	2006 IPCC values	[24]
	Asia (continental)	OG *	1.3 (1.0-2.2)	NA	2006 IPCC values	[24]
		OS*	1.3 (1.0-2.2)	NA	2006 IPCC values	[24]
		YS	5.0	NA	2006 IPCC values	[24]
	Asia (insular)	OG *	1.0	NA	2006 IPCC values	[24]
		OS*	1.0	NA	2006 IPCC values	[24]
		YS	2.0	NA	2006 IPCC values	[24]
Tropical mountain system	Africa	OG	0.5	NA	Different region	
		OS	1.8	NA	Different region	
		YS	5.5	6.8		[25-27]
	North and South America	OG	0.5	1.9		[2, 10, 11]
		OS	1.8	0.8		[3, 4, 12, 13]
		YS	4.4	1.6		[3, 4, 12, 13, 22]

	Asia	OG	-0.7	3.1		[2, 16]
		OS	1.1	0.4		[3, 4, 28, 29]
		YS	2.9	0.1		[3, 4, 28-30]
Subtropical humid forest	Africa	OG	-	-		
		OS	1.0	NA	Different region	
		YS	2.5	NA	Different region	
	North and South America	OG	-	-		
		OS	1.0	NA	Different region	
		YS	2.5	NA	Different region	
	Asia	OG	-	-		
		OS	1.0	0.9		[3, 4, 31]
		YS	2.5	0.8		[3, 4, 31]
Subtropical dry forest	Africa	OG *	1.8 (0.6-3.0)	NA	2006 IPCC values	[24]
		OS*	1.8 (0.6-3.0)	NA	2006 IPCC values	[24]
		YS	2.4 (2.3-2.5)	NA	2006 IPCC values	[24]
	North and South America	OG *	1.0	NA	2006 IPCC values	[24]
		OS*	1.0	NA	2006 IPCC values	[24]
		YS	4.0	NA	2006 IPCC values	[24]
	Asia (continental)	OG *	1.5	NA	2006 IPCC values	[24]
		OS*	1.5	NA	2006 IPCC values	[24]
		YS	6.0	NA	2006 IPCC values	[24]
	Asia (insular)	OG *	2.0	NA	2006 IPCC values	[24]
		OS*	2.0	NA	2006 IPCC values	[24]
		YS	7.0	NA	2006 IPCC values	[24]
Subtropical steppe	Africa	OG *	0.9 (0.2-1.6)	NA	2006 IPCC values	[24]
		OS*	0.9 (0.2-1.6)	NA	2006 IPCC values	[24]
		YS	1.2 (0.8-1.5)	NA	2006 IPCC values	[24]
	North and South America	OG *	1.0	NA	2006 IPCC values	[24]

		OS*	1.0	NA	2006 IPCC values	[24]
		YS	4.0	NA	2006 IPCC values	[24]
	Asia (continental)	OG *	1.3 (1.0-2.2)	NA	2006 IPCC values	[24]
		OS*	1.3 (1.0-2.2)	NA	2006 IPCC values	[24]
		YS	5.0	NA	2006 IPCC values	[24]
	Asia (insular)	OG *	1.0	NA	2006 IPCC values	[24]
		OS*	1.0	NA	2006 IPCC values	[24]
		YS	2.0	NA	2006 IPCC values	[24]
Subtropical mountain system	Africa	OG	-	-		
		OS	0.5	NA	Different region	
		YS	2.5	NA	Different region	
	North and South America	OG	-	-		
		OS	0.5	NA	Different region	
		YS	2.5	NA	Different region	
	Asia	OG	-	-		
		OS	0.5	0.3		[3, 4, 32]
		YS	2.5	0.03		[3, 4, 32]

*Recommendation based on IPCC 2006 rates for forests > 20 years
[a] IPCC-defined forest type categories are "Primary" (old-growth forests), "Secondary >20 years" (older secondary forests) and "Secondary ≤20 years" (younger secondary forests)

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3.6.2 Appendix 2

Ecozone AGB ($Mg\,ha^{-1}\,year^{-1}$) — Stand age relationships for secondary forests

Ecozone	Continent	Equation	Max age
Tropical rainforest	Africa	AGB= -121.3 + {90.96 x ln(Age)}	40
	North and South America	AGB= -40.87 + {53.34 x ln(Age)}	80
	Asia	AGB= -12.56 + {27.17 x ln(Age)}	40
Tropical moist forest	Africa	AGB= -33.81 + {30.4 x ln(Age)}	58
	North and South America	AGB= -127.2 + {77.16 x ln(Age)}	100
	Asia*	AGB= -11.16 + {19.46 x ln(Age)}	20
Tropical dry forest	North and South America	AGB= -104.26 + {60.54 x ln(Age)}	70
Tropical mountain system*	Africa*	AGB= -113.1 + {74.14 x ln(Age)}	63
	North and South America	AGB= -72.03 + {53.65 x ln(Age)}	50
	Asia	AGB= -17.1 + {25.03 x ln(Age)}	55
Subtropical humid forest	Asia	AGB= -142.43 + {64.47 x ln(Age)}	100
Subtropical mountain system	Asia	AGB= -88.94 + {46.64 x ln(Age)}	100

*Model only applicable for younger secondary forests.

3.6.3 Appendix 3

Number of chronosequences and permanent plots per 100,000 km^2 of natural forests in tropical and subtropical ecozones[a].

Ecological Zone	Continent	No. of permanent plots	No. of chronosequences	Number of permanent plots and chronosequences per 100,000 km^2 of natural forests
Tropical rainforest	Africa	105	16	4.68
	North and South America	324	42	6.20
	Asia	66	7	4.29
Tropical moist forest	Africa	2	2	0.21
	North and South America	27	21	3.07
	Asia	0	2	0.45
Tropical dry forest	Africa	0	5	0.39
	North and South America	1	7	0.82
	Asia	0	1	0.32
Tropical shrubland	Africa	0	1	0.26
	North and South America	0	0	0
	Asia	0	0	0
Tropical mountain system	Africa	0	3	1.05
	North and South America	6	6	1.82
	Asia	5	6	2.25
Subtropical humid forest	Africa	0	0	0.00
	North and South America	0	0	0.00
	Asia	0	24	5.14
Subtropical dry forest	Africa	0	0	0
	North and South America	0	0	0
	Asia	0	0	0
Subtropical steppe	Africa	0	0	0
	North and South America	0	0	0
	Asia	0	0	0
Subtropical mountain system	Africa	0	0	0
	North and South America	0	1	0.48
	Asia	0	32	5.85

[a]Extent of natural forests were obtained from Schulze et al. (2019) and combined with FAO (2012) to obtain coarse estimates of natural forest area per ecozone.

Chapter 4

Variation in aboveground biomass in forests and woodlands in Tanzania along gradients in environmental conditions and human use

This chapter is based on:

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Abstract

Disturbed African tropical forests and woodlands have the potential to contribute to climate change mitigation. Therefore, there is a need to understand how carbon stocks of disturbed and recovering tropical forests are determined by environmental conditions and human use. In this case study, we explore how gradients in environmental conditions and human use determine aboveground biomass (AGB) in 1958 national forest inventory (NFI) plots located in forests and woodlands in mainland Tanzania. Plots were divided into recovering forests (areas recovering from deforestation for $<$25years) and established forests (areas consistently defined as forests for $\geq$25 years). This division, as well as the detection of year of forest establishment, was obtained through the use of dense satellite time series of forest cover probability. In decreasing order of importance, AGB in recovering forests unexpectedly decreased with water availability, increased with surrounding tree cover and time since establishment, and decreased with elevation, distance to roads, and soil phosphorus content. AGB in established forests unexpectedly decreased with water availability, increased with surrounding tree cover, and soil nitrogen content, and decreased with elevation. AGB in recovering forests increased by 0.4 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ during the first 20 years following establishment. Our results can serve as the basis of carbon sink estimates in African recovering tropical forests and woodlands, and aid in forest landscape restoration planning.

4.1 Introduction

Tropical forests store approximately 55% of the world's forest carbon (C) stocks, acting as C sinks through a positive balance of tree growth, recruitment and mortality (Pan et al., 2011). While forest C stocks and sinks in the tropics have primarily been studied in structurally intact, undisturbed forests in humid ecosystems (Brienen et al., 2015a; Hubau et al., 2020; Qie et al., 2017), disturbed and recovering forests are both increasing in extent (Aide et al., 2013; Lewis et al., 2015). Given their rapid growth, recovering forests have higher instantaneous C sink capacities per unit area in comparison with capacities in old-growth forests under similar conditions (N'Guessan et al., 2019; Poorter et al., 2016; Rutishauser et al., 2015).

African tropical forests and woodlands cover approximately 636 million ha, are inhabited by approximately 284 million people (FAO, 2018; FAO, 2020), and experience disturbances followed by recovery (McNicol et al., 2018; Mitchard and Flintrop, 2013). African forests and woodlands are partial sources of income and act as safety nets for rural and semirural communities in situations of poverty, economic instability, and/or under the effects of climate change (Chomitz, 2007; Djoudi et al., 2015). Due to their vast extent, their unique composition and their ability to support surrounding human and non-human populations, while at the same time being under constant use, understanding the role that African forests and woodlands have in climate change mitigation is of utmost importance.

The determinants of C stocks in disturbed and recovering tropical forests and woodlands in Africa remain mostly understudied (Becknell et al., 2012; Marunda and Bouda, 2010; Pennington et al., 2018; Schimel, 2010). Forest C stocks are often estimated by measuring standing aboveground biomass (AGB; Mg ha^{-1}), which in undisturbed forests is determined mainly by local environmental conditions. Across undisturbed forests and woodlands in Africa, AGB is likely to be higher in areas with low elevation and gentle slopes (Ensslin et al., 2015; Yohannes and Soromessa, 2015), high levels of water availability throughout the year (Becknell et al., 2012; Ensslin et al., 2015) and on older, fertile soils (Lewis et al., 2013) In disturbed and recovering forests, AGB is additionally influenced by natural or human disturbances. AGB tends to be higher under lower intensities of human activities such as wood extraction, land conversion (Bonner et al., 2013; McNicol et al., 2018; Pelletier et al., 2017), and when not affected by forest fires (Ryan and Williams, 2011; Tarimo et al., 2015). In addition, AGB in recovering forests is expected to increase with time since forest establishment (N'Guessan et al., 2019; Pelletier et al., 2018; Requena Suarez et al., 2019).

Large-scale efforts such as national forest inventories (NFIs) have the potential to identify which environmental conditions and degrees of human use are associated with AGB across large areas in forest ecosystems in Africa. NFIs provide valuable in situ observations of AGB, covering broad gradients in environmental conditions and degrees of human use, and can therefore be used for this purpose. Although NFIs seldom provide a quantitative metric of disturbance or recovery of their plots, through the use of validated methodologies of forest cover change detection using time series of satellite images (Feng et al., 2016; Hamunyela et al., 2020; Lembani et al., 2019; Sexton et al., 2016; Sexton et al., 2015; Sexton et al., 2013), it is possible to estimate time since forest establishment in recently recovered forests. The integration of AGB estimated from NFI plots, spatial datasets of environmental conditions and human use (including time since establishment) opens the opportunity to identify the major determinants of AGB stock in disturbed and recovering forests across large scales.

In this study, we use an extensive NFI dataset across Tanzania's forests and woodlands—consisting mainly of open and closed woodlands, including miombo woodlands and degraded forests—–and integrate it with spatial datasets to identify the determinants of AGB. Tanzanian forests are currently under use throughout the country (URT, 2016), with fuelwood and charcoal use contributing to 92% of the country's energy consumption (Malimbwi and Zahabu, 2009). At the same time, efforts for their sustainable management have been underway for at least three decades (Blomley et al., 2011), as well as forest conservation, through the establishment of protected areas in 36% of its mainland area (Gizachew et al., 2020). Understanding how AGB varies along gradients in environmental conditions and human use can aid forest landscape restoration planning in Tanzanian forests and woodlands as well as in similar ecosystems in other areas.

Here, we use forest cover time series to divide forest plots into established and recovering forests. For recovering forests, we used time since forest establishment—derived from satellite time series—–as a quantitative indicator to assess AGB recovery and therefore the C sink capacity of Tanzania's recovering forests. We hypothesize that (a) AGB is higher in areas with low elevation and gentle slopes, with high levels of water availability, in fertile soils, and with low intensity of human use, and that (b) AGB in recently recovering forest plots increases with time since forest establishment, and therefore that recovering forests act as partial C sinks.

4.2 Methods

To test our hypotheses, we used a mixed-effects modelling approach to identify the main environmental and human use determinants of AGB in Tanzania's forests, which we divided into recovering and established forests. For this study, we define *recovering forests* as areas with forests or woodlands that have been regrowing for less than 25 years, and *established forests* as areas that have been consistently defined as forests or woodlands for at least the last 25 years. We used the same covariations for environmental and human use to test the first hypothesis (determinants of AGB at a specific point in time) in both types of forests. Additionally, for recovering forests, we tested the second hypothesis (effect of time on AGB) through the inclusion of time since forest establishment.

4.2.1 Study site and forest plot data

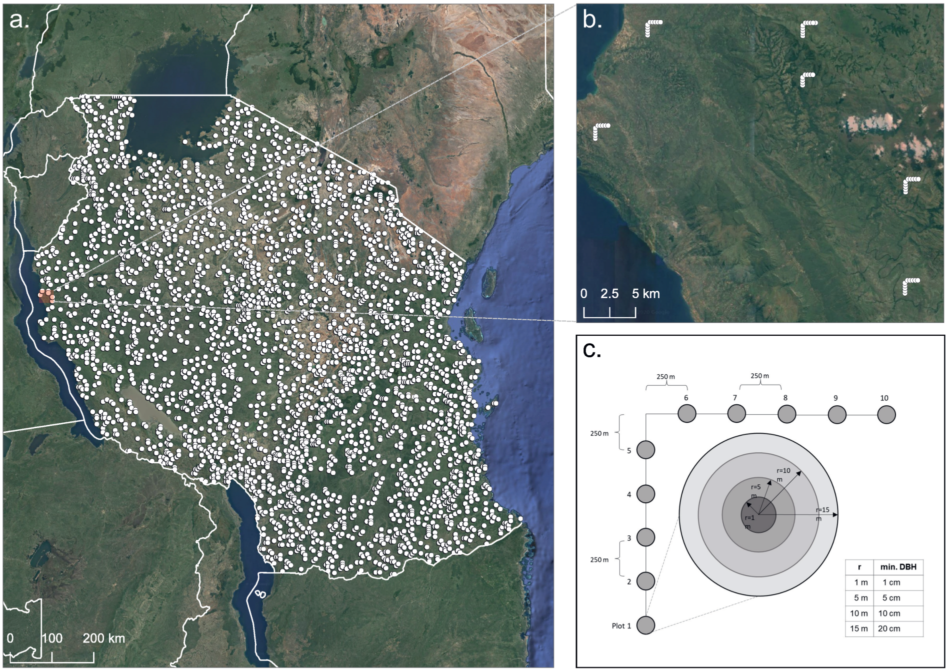

Figure 4.1: Distribution of NAFORMA clusters and plots. (a) White dots represent the cluster locations in Tanzania, (b) close-up of clusters (red inset in (a)) in which individual plots can be distinguished, and (c) NAFORMA cluster and plot design.

Forest plots were measured across Tanzania (Figure 4.1a) from 2010 until 2012 as part of the NAFORMA (National Forest Monitoring and Assessment of Tanzania Mainland) project led by the Tanzania Forest Services Agency, in collaboration with the FAO-Finland forestry programme (TFS, 2015). A stratified sampling design was followed to account for variability in forests and land use (Tomppo et al., 2014). Forest plots were arranged in L-shaped clusters of up to ten plots (average=9.5), with 250 m between plots (Figure 4.1b-c). A total of 30,382 plots grouped in 3,208 clusters were measured as part of the inventory, including plots outside forests and woodlands.

NAFORMA uses circular forest plots of 0.0707 ha (Figure 4.1c). Within these plots, the total height (H; in m) and diameter at breast height (DBH; in cm) of all trees with a

DBH above 1, 5, 10 or 20 cm— based on sub-plot radii of 1, 5, 10 and 15 m, respectively (Figure 4.1c)—were measured. Species-specific or regional allometric equations were used to calculate tree-level volume (m^3) (Haule and Munyuku, 1994; Malimbwi, 1987; Malimbwi et al., 2000; Malimbwi et al., 1998). Tree-level AGB (Mg) was calculated by multiplying tree-level volume estimates with species-specific or regional wood densities (TFS, 2015). These values were used to estimate total AGB ($\mathrm{Mg\,ha^{-1}}$) per plot. We included 16,630 plots in natural forests and woodlands, and excluded plots located in plantations, mangroves, bushlands, grasslands, cultivated land and inland water areas. In order to include a plot in the analysis, AGB estimates had to be >0 and <400 $\mathrm{Mg\,ha^{-1}}$ to exclude plots with AGB values higher than those expected in undisturbed closed-canopy forests (Brown and Gaston, 1995; Lewis et al., 2013).

4.2.2 Estimation of time since establishment

The time since establishment (in years) of each forest plot was determined based on a time-series analysis of Landsat multispectral imagery. Time since establishment was estimated by detecting changes in the probability of forest cover derived from the estimate and uncertainty of tree-canopy cover (Sexton et al., 2016; Sexton et al., 2013) at plot locations based on the full Landsat image archive at the time—from 1984 to 2018. For this region, pixels with >10% tree cover were defined as forest. This threshold was chosen due to the predominance of low-biomass tropical forests and woodlands in the study area, coinciding with Tanzania's definition of 'forest' (URT, 2016). With this threshold, we generated a forest reference baseline corresponding to 2018, and plots in locations that did not exceed the threshold in 2018 were excluded from further analysis. Year of forest gain at each plot location was detected through a kernel analysis of a time-series of forest-cover, expressed as the probability of the class forest in a given pixel in a given year. A kernel spanning 7 years, including 3 years before and 3 years after a given year, was run retrospectively through the series beginning in 2018. The mean and variance of forest probabilities in before- and after-kernel samples around the focal year (i.e. the year in which forest probability surpassed 50%) were calculated, and the difference between groups was tested using a variant of the two-sample z-test. If a statistically significant ($p < 0.05$) difference was identified between the two ascending groups, the focal year was labelled as forest gain. If multiple significant gains were detected in the series, the location was labelled with the year of most recent gain. Plots in locations for which forest gain was detected during the study period were regarded as recovering forests, and plots in locations for which the forest probability was over 50% throughout the whole period were regarded as established forests.

For plots in recovering forests, the establishment year was assumed to occur 2 years prior to the detection of forest gain. Time since forest establishment was calculated by subtracting the year of forest establishment from the year in which the plot of the given location was measured (i.e. measurement year). Two additional criteria were applied for recovering forest plots: first, the plot needed to have been measured at least one year after the year of forest establishment; second, we included plots for which the probability of forest gain was at least 20%.

4.2.3 Environmental and human use predictors

To test the effect of topography, water availability, soil fertility and degree of human use on AGB in the selected forest plots, we gathered ten relevant environmental and human use predictors for all plot locations (Table 4.1). Due to the extent of the study area, plots spanned broad gradients in environmental conditions and human use.

The effect of topography was evaluated through elevation (m) and slope (°) extracted or calculated from the shuttle radar topography mission digital elevation model (Jarvis et al., 2008) at 90 m resolution. To evaluate effects of water availability, we extracted climatic water deficit (CWD; in mm $year^{-1}$) from (Chave et al., 2014) at a resolution of 2.5′, defined as the sum of the differences between monthly rainfall and monthly evapotranspiration in the months where evapotranspiration exceeded rainfall, thus only in periods of water deficit. To evaluate the effect of soil fertility, we included nitrogen (N) and phosphorus (P) soil content data at 0–30 cm depth (in ppm) from (Hengl et al., 2017) at a resolution of 250 m.

To test for the effect of human use, we included metrics of surrounding tree cover, forest accessibility and fire disturbances. We calculated the percent surrounding tree cover in the landscape based on percent tree cover data for 2010 (%), which was extracted from Hansen et al., 2013 at 30 m spatial resolution within radius of 500 m of the plots' locations. Degree of forest accessibility was included as distance of plots to roads and settlements. This was done by calculating the Cartesian distance (in km) to the nearest primary, secondary or tertiary road and to the nearest city, village or town using road and settlement vector data for Tanzania (OpenStreetMap Contributors, 2019). To account for the effect of fire, we evaluated intensity of fire disturbances (Chidumayo, 1997; Kennard et al., 2002; Trapnell, 1959) through the inclusion of average fire duration per month which was extracted for the 2003–2012 period from Andela et al., 2019 at 500 m resolution.

Predictors were extracted or calculated in R v.3.4.0 (R Core Team, 2017), using the *raster*, *spatialEco*, and *rgeos* packages (Bivand and Rundel, 2017; Evans, 2018; Hijmans, 2019). Four plots with unrealistically high soil N (n=1; 5505 ppm) and soil P (n=3; 2260–2455 ppm) content were excluded from further analysis.

Table 4.1: Environmental and human use predictors for the NAFORMA forest plots. Time since establishment was derived from this study only for plots in recovering forests.

Code	Variable	Unit	Min	Max	Mean	SD	Original Source	Original spatial resolution
yrs_since_est	Time since establishment (only for recovering forests)	yr	3.0	26.0	13.0	7.4	this study	-
elevation	Elevation	m	13.0	2123.0	1108.8	393.8	Jarvis et al (2008)	90 m
slope	Slope	°	0.0	17.2	1.4	2.1	Jarvis et al (2008)	90 m
CWD	Climatic Water Deficit	mm y^{-1}	-1312.5	-372.0	-891.4	156.1	Chave et al (2014)	2.5′
soilP	Total phosphorus (P) content of the soil fine earth fraction for 0-30 cm depth	ppm	73.0	1163.0	255.8	123.5	Hengl et al (2017)	250 m
soilN	Total nitrogen (N) content of the soil fine earth fraction for 0-30 cm depth	ppm	373.0	2336.0	811.7	284.8	Hengl et al (2017)	250 m
tree_cover	Surrounding tree cover in 2010 (500m radius)	%	3.3	65.9	26.7	10.0	Hansen et al (2013)	30 m
dist_roads	Distance to nearest road	km	0.0	121.2	23.5	23.8	OpenStreetMap-Contributors (2019)	-
dist_settl	Distance to nearest settlement	km	0.2	78.5	21.7	15.2	OpenStreetMap-Contributors (2019)	-
fire_duration	Average fire duration per month	days	0.0	11.8	4.3	1.9	Andela et al (2019)	500 m

4.2.4 Statistical analysis

To identify the determinants of AGB in recovering and established forests, we modelled plot-level AGB (in $Mg\,ha^{-1}$) for recovering and established forests separately as a function of elevation, slope, CWD, soil P content, soil N content, surrounding tree cover, distance to roads, distance to settlements and average fire duration using a linear mixed-effects model. An interaction between CWD and average fire duration was included, in line with (Lehmann et al., 2014) who describe a strong relationship between water availability and fires affecting biomass in African sparse woodlands. For recovering forests, we additionally included time since establishment, which was ln-transformed to account for the non-linear AGB increase over time. The aforementioned predictors were included as fixed effects, and plot clusters were regarded as random effects, for which random intercepts were included. Model performance was evaluated using Akaike's information criterion and model fits were evaluated based on their marginal (fixed-effects only) and conditional (fixed and random effects) R^2 (Nakagawa and Schielzeth, 2013). All predictors were standardised by subtracting the mean and dividing the difference by 1 SD (Gelman and Hill, 2007) to compare effect sizes. We used the *lme4* package (Bates et al., 2015) to fit mixed-effects models in R.

4.3 Results

4.3.1 Spatial distribution and stand age of forest plots

A total of 1479 plots in recovering forests and 479 plots in established forests were included in the analysis (Figure 4.2). Thirty-nine percent of the plots were located within 10 km of a road and 27.4% of the plots were located within 10 km of a human settlement (Figure 4.2a). Recovering forests comprised a similar percentage of the total number of plots within 10 km of roads and settlements (40.0% and 28.1%,respectively) as plots in established forests (36.1% and 25.3%, respectively).

For plots in recovering forests, time since establishment varied from 1 to 24 years (Figure 4.2c), with the majority (54.2%) established 1–10 years before field measurement. The majority (88.5%) of AGB values for recovering and established forests did not exceed 100 $Mg\,ha^{-1}$. The overall mean AGB for established forests (56.0 $Mg\,ha^{-1}$) was 0.5 $Mg\,ha^{-1}$ higher than for recovering forests.

4.3.2 Environmental and human use determinants of AGB

AGB varied along environmental and human use gradients in both recovering and established forests. In recovering forests (Figure 4.3a), in decreasing order of importance, AGB

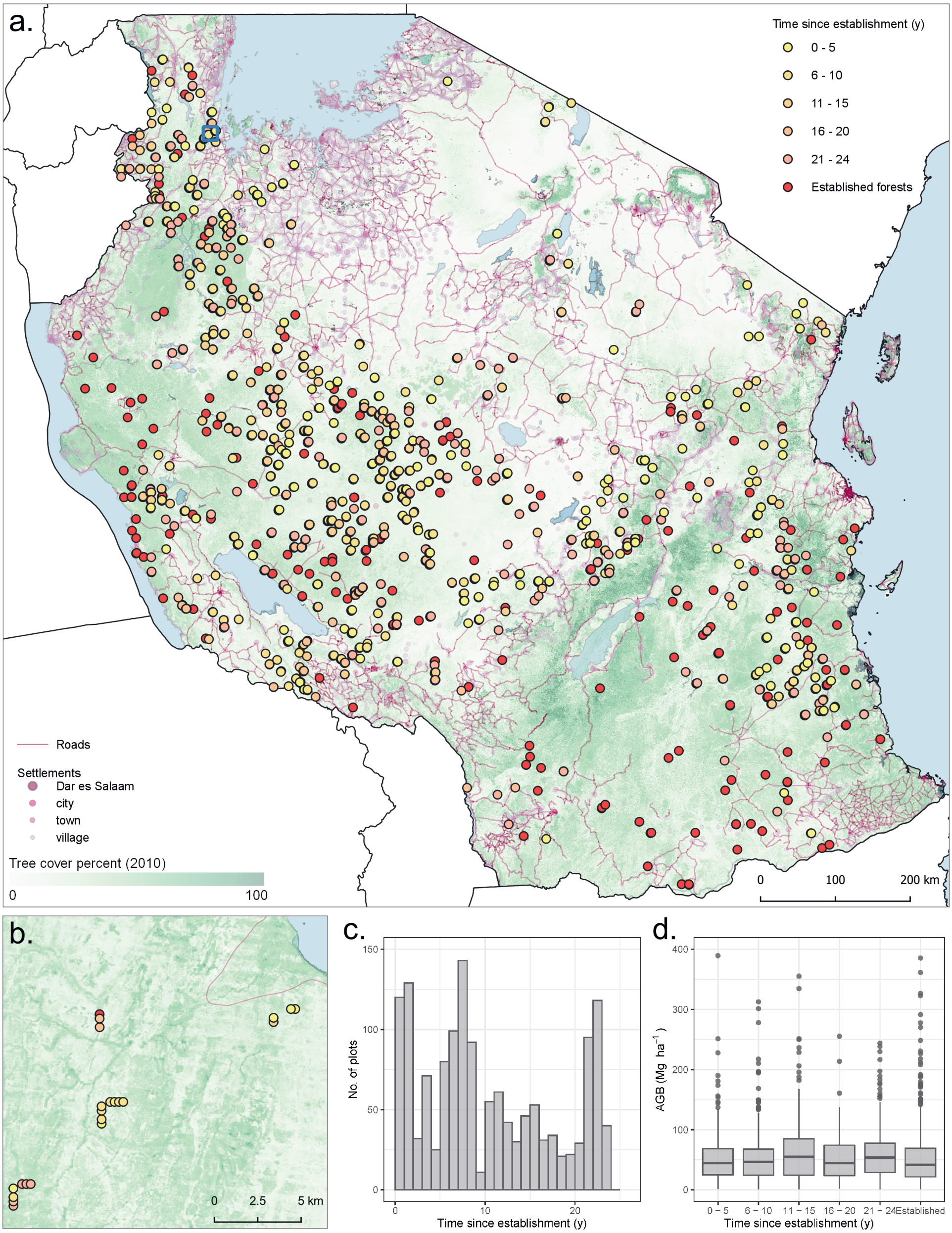

Figure 4.2: Stand age and AGB distribution of forest inventory plots in Tanzania. (a) Spatial plot distribution, (b) close-up of plot composition per cluster at a given location (blue inset in (a)), (c) distribution of inventory plots in recovering forests per time since establishment and (d) plot-level AGB per time since establishment category.

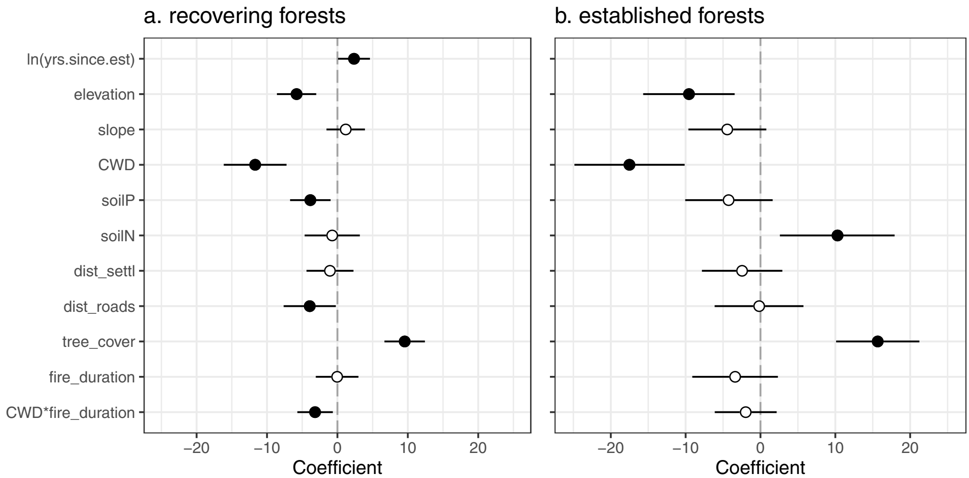

Figure 4.3: Effects of environmental and human use determinants of AGB in Tanzanian forests. Effects of all predictors tested for (a) recovering forests and (b) established forests. Time since establishment was not considered in established forests. Standardised coefficients of the predictors' effects and confidence intervals (95%) are indicated. Significant responses are indicated with filled symbols; non-significant responses with open symbols.

decreased with increasing CWD, increased with higher percentages of surrounding tree cover, decreased with elevation, distance to roads, soil P content, with the interaction between CWD and average fire duration, and increased with time since forest establishment. In established forests (Figure 4.3b), in decreasing order of importance, AGB decreased with increasing CWD, increased with surrounding tree cover and with soil N content, and decreased with elevation. The effects of slope, distance to settlements and average fire duration were not significant for either forest category. The marginal (fixed effects only) and conditional (both fixed and random effects) R^2 were 0.08 and 0.24, respectively, for the model describing recovering forests and 0.10 and 0.19 for the model describing established forests.

The effects of CWD, elevation and surrounding tree cover were significant and similar in direction in both recovering and established forests (Figure 4.4a-c). The unexpected negative effect of CWD on AGB, which suggests that lower water deficit results in lower AGB, was the largest absolute effect in both forest categories, followed by the expected effects of surrounding tree cover (positive) and elevation (negative).

In recovering forests, the effect of time since forest establishment was small yet significant (Figure 4.4d). Based on the predicted AGB at 1 and 20 years after forest establishment, and keeping all other predictors constant, the overall AGB recovery rate during the first 20 years was 0.4 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$.

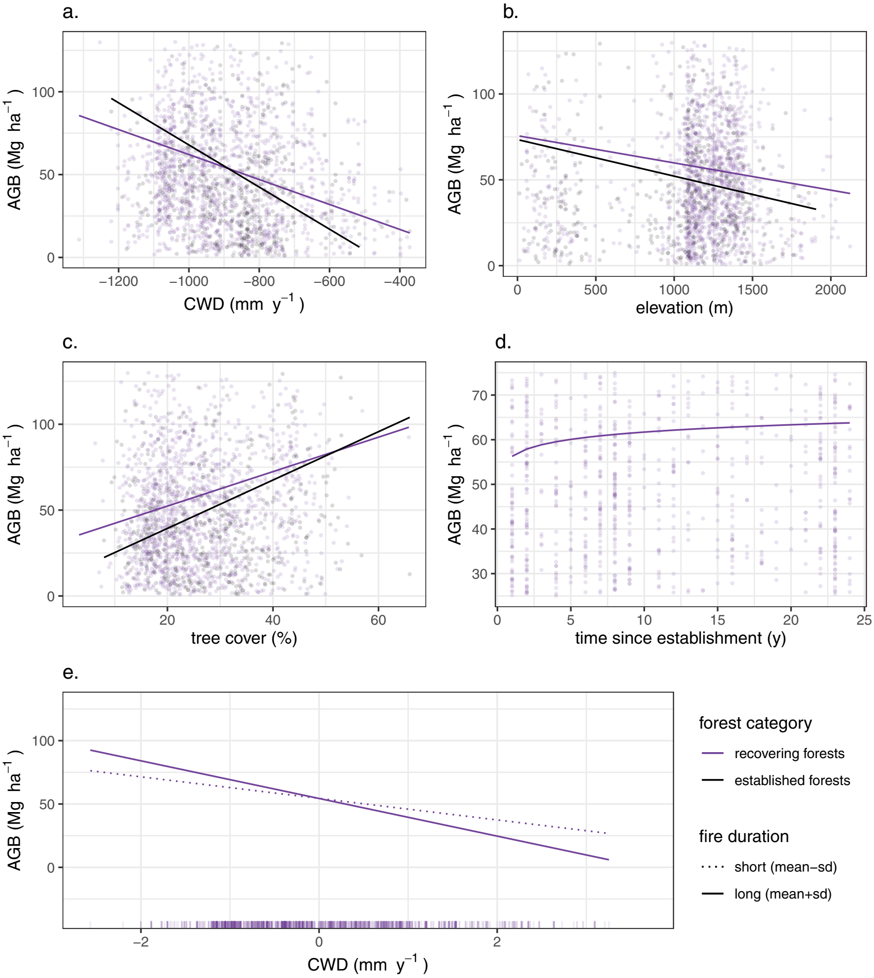

Figure 4.4: Observed and predicted AGB values in relation to individual effects (a)–(d) and interactions (e) in Tanzanian forests. The effect of (a) CWD, (b) elevation and (c) tree cover on AGB in recovering and established forests are indicated as purple and black lines, respectively. The effect of (d) years since forest establishment on AGB was only observed in recovering forests. Symbols represent original AGB values in recovering (purple) and established (black) forests. (e) Effect of fire duration on AGB-CWD relationships are shown for long (mean + SD; continuous line) and short (mean - SD; dotted line) fire duration in recovering forests, original CWD values are included at the bottom of the panel. Note the different y-axis range for (d). For all panels, other predictors were kept constant at the mean.

4.4 Discussion

4.4.1 Environmental and human use determinants of AGB in Tanzanian forests

Forests and woodlands in Tanzania occur mostly in areas with highly seasonal rainfall, and are subject to dryland-specific ecological, environmental and anthropogenic dynamics (Timberlake et al., 2010). Because of this, AGB values in this study greatly varied, aligning with AGB estimates for miombo forests, which overlap with the western part of the Tanzanian forest area covered in this study, which range from 1.3 to 95.7 $\mathrm{Mg\,ha^{-1}}$ (Gumbo et al., 2018), and with AGB estimates in seasonally dry tropical dry forests in Africa, which range from 39 to 334 $\mathrm{Mg\,ha^{-1}}$ (Becknell et al., 2012). The aforementioned studies evaluated how climate and disturbance affect AGB in these regions, but they are complicated by combining limited plot data from different methodologies. The spatial extent and methodological consistency of the NAFORMA dataset allowed consistent evaluation of AGB stocks along environmental and human use gradients.

For both recovering and established forests, the selected environmental and human use predictors determined less than 24% and 19% of the variation, respectively. Among these predictors, AGB was most strongly determined by, unexpectedly, a negative effect of CWD. While dry periods are a major AGB-limiting factor (Eamus, 1999), the negative effect of CWD on AGB in both forest categories, surprisingly, suggests that seasonality characterised by very dry periods might positively influence AGB. This might be due to increasing periods of water deficit inhibiting the proliferation of herbaceous species, which could potentially limit forest establishment in dry forests and woodlands (Bhadouria et al., 2017; Vieira and Scariot, 2006); however to test this hypothesis, more studies on the initial stages of forest establishment are needed. Moreover, given that, overall, effects of environmental conditions and human use evaluated in this study were weak, additional research on determinants of AGB is needed. The significant interaction between CWD and fire duration in recovering forests suggests that tree establishment in recovering forests might be positively affected by recurrent, longer fires and very dry periods. This interaction was not significant for established forests, and while fires might benefit seedling establishment (Khurana and Singh, 2001), consistently recurring fires ultimately simplify the composition of a forest community (Vieira and Scariot, 2006), causing further forest degradation.

As expected, elevation had a negative effect on AGB for both forest categories. The effect of slope, on the other hand, was not significant. While Tanzania has broad elevational gradients across its territory, gentle slopes are common, with steeper slopes mostly found in the Eastern Arc Mountains, which transect Tanzania from northeast to southwest. The great majority of plots (93.2%) used in this study had a slope of 0°–5°, suggesting that small changes in gentle slopes have little to no effect on AGB.

The effect of soil fertility, which we hypothesised to be positive, varied for both recovering and established forests, suggesting that higher AGB is found in recovering forests on soils with lower P content and in established forests on soils with higher N content. While the positive effect of soil N content on AGB was expected (Davidson et al., 2007), this was not observed for recovering forests, indicating that AGB during the first years is not significantly determined by the amount of soil N. Soil P content, considered a limiting nutrient in tropical forests growing on weathered soils (Ceccon et al., 2006; Davidson et al., 2007; Murphy and Lugo, 1986), had a negative effect on AGB in recovering forests. Soils may have weathered, and/or further degraded due to lack of soil moisture, current and previous land use, recurrent resource extraction, constant herbivory and recurrent human-induced fires. Furthermore, recent local studies have suggested that AGB stocks are more strongly related to soil hydromorphy rather than to soil fertility (Gourlet-Fleury et al., 2011). Lastly, these confounding relationships could be a consequence of using gridded spatial predictions for assessing soil nutrient effects, as opposed to using field data, which were not available.

Overall, our results reveal a complex underlying relationship between human activity and forest recovery, which has been reported previously in African forests and woodlands (Timberlake et al., 2010). For both forest categories, the predictor of human use which mainly drove AGB was surrounding tree cover, an indicator of the extent of land conversion. This is expected, as the presence of nearby forests benefits tree establishment through natural regeneration and tree growth; however, high rates of degradation and deforestation in African woodlands (McNicol et al., 2018) limit this effect. In recovering forests, distance to roads had a negative effect on AGB, suggesting that forest recovery tends to occur in more accessible areas (Malimbwi et al., 2005). Land conversion is often done through induced fires, which on their own did not have a significant effect on either recovering or established forests.

Other determinants, for which no spatially explicit information was available are influencing forest recovery and degradation in Tanzania's forests. The effect of herbivory, be it by wildlife or livestock, could provide insight into tree establishment and mortality (Sankaran et al., 2013), tree cover and forest structure (Asner et al., 2009a), as well as competition with herbaceous (grass) species (Riginos, 2009). Megafauna has also been linked to the proliferation of fires (Foster et al., 2020) and competition with herbaceous species (Bhadouria et al., 2017). Prevalence of natural regeneration through tree resprouting, common in dry forest ecosystems (Ewel, 1980; Timberlake et al., 2010), and its interaction with constant human use (Vieira and Scariot, 2006), might also provide insight into recovery from degradation. Finally, local information on previous land use preceding forest establishment, as well as current levels of forest use, both of which have proven to determine AGB stocks in miombo forests (Jew et al., 2016; Pelletier et al., 2017), could also provide insight into the varying levels of AGB in both recovering and established forests.

4.4.2 AGB recovery in Tanzanian recovering forests

Time since establishment had a significant, positive effect on AGB in recovering forests, indicating that, even though recovering forests in Tanzania experience disturbance, through biomass accumulation over time they can act as partial C sinks. Our estimate (0.4 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$) is comparable to, albeit lower than, local estimates obtained through repeated remeasurements in permanent plots in the woodlands of south-eastern Africa. For example, coppiced miombo woodland in Mutupa, Zambia, evaluated during 1982–1988, had a mean annual increment (MAI) of 1.97 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ (range: 0.41– 2.91 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$) for woodlands aged 3–29 years (Chidumayo, 1990). In miombo woodlands in Kitulangalo, Tanzania, for the period of 3 years (1996– 1999), MAI was estimated as 2.35 $\mathrm{m^3\,year^{-1}}$ (Malimbwi et al., 2005), which roughly translates to 1.18 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$. In Kilwa, Tanzania, regrowing forests after land disturbance accumulated AGB at a rate of 0.83 $\mathrm{Mg\,C\,ha^{-1}\,year^{-1}}$ (McNicol et al., 2015a). A recent national study of vegetation change for all forests and woodlands in Zambia (Pelletier et al., 2018) estimated annual biomass gain rates of 1.17 $\mathrm{Mg\,C\,ha^{-1}\,year^{-1}}$ (mean) and 0.31$\mathrm{Mg\,ha^{-1}\,year^{-1}}$ (median). While our rate is lower, it accounts for varying types of disturbance during recovery, such as fires and extraction of wood, which is not fully the case in the aforementioned studies, which either account for specific disturbances, or select sites with no signs of disturbance after abandonment.

Our AGB accumulation rate estimate was one-tenth as large as the 2019 continent-level IPCC Tier 1 estimate for African recovering tropical dry forests (3.9$\mathrm{Mg\,ha^{-1}\,year^{-1}}$) which is based on values estimated for Central and South American dry forests due to limited data availability in Africa; however it aligns with AGB accumulation estimates suggested for African recovering tropical shrublands (0.2–0.7 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$) (IPCC, 2019). Continent-level estimates, which are being used for national greenhouse gas reporting of C sinks, are based on a limited number of locations in tropical dry forests and woodlands, with a major gap in Africa (Requena Suarez et al., 2019). Region-level estimates are usually based on sites with recovery pathways with little to no disturbance during the first years, and while this could be a common pathway for recovering humid forests (Chazdon et al., 2007; N'Guessan et al., 2019), this is not the case for African recovering dry forests and woodlands, which are under constant use. While reporting on the C sinks in African dry forests and woodlands, recurrent disturbance of recovering forests must be taken into consideration.

4.4.3 Methodological implications and next steps

Given the predominance of low-biomass, sparse forests and woodlands in the study area, the use of dense time series to detect forest cover gain is challenging. Nevertheless, Landsat-derived dense time series have been used before in this region for detection of forest cover change (Hamunyela et al., 2020; Lembani et al., 2019). The Tanzanian NFI plot size (15 m radius; 0.0707 ha) and spacing within clusters (250 m) allowed us to derive this metric per plot; however we can expect some error estimating AGB due the small plot size (Kachamba et al., 2017; Tomppo et al., 2008), as well as the pixel-level uncertainty in forest establishment year.

For recovering forests, we used a space-for-time substitution to estimate AGB recovery. This chronosequence approach has been used elsewhere in the tropics (Chazdon et al., 2007; N'Guessan et al., 2019; Poorter et al., 2016) and, since it requires plots to be measured only at a single point in time, it is a practical way to estimate AGB recovery without having to remeasure forest plots over several decades. In this study, we have employed this approach by detecting time since establishment in forest plot locations, thus deriving information on time since recovery based on 1479 plots embedded in 543 clusters treated as chronosequences.

Chronosequences require having field AGB measurements at known times since major disturbances or abandonment. Time has to be estimated in a precise, consistent, and straightforward manner, and usually relies on interviews with land owners or occasionally on aerial images (Chazdon et al., 2007; Piotto et al., 2009; Ruiz et al., 2005). This greatly limits the number of forest plots that can be used, as many forest plots do not have information on the beginning of recovery or on land use history, unless they have been measured for the main purpose of studying recovery or regrowth. However, as remote sensing technologies improve, and satellite image archives become available, monitoring forest cover dynamics over several years enables the use of forest plots measured for different purposes, for which time since establishment in recovering forests is unknown. With this, using the first round of NFIs to assess forest recovery across large scales becomes possible. Since NFIs strive to systematically sample large forest areas, they are a valuable source of on-the-ground data, which, in combination with satellite time series, can be utilised to study AGB stocks in recovering forests at a national scale. Studies that use remeasured NFIs, such as the case of Pelletier et al., 2018, offer the opportunity to examine AGB accumulation into more detail.

Satellite-based estimates of time since forest establishment, critical to assess forest recovery, can be applied to other forest inventories for which no field data on stage of recovery is available. As countries refine their estimates of forest C stocks through the implementation of NFIs, satellite time series can serve as an alternative method for repeated measurements over time to estimate C sinks in recovering forests. Many countries with (sub)tropical forests have recently conducted, or are currently in the process of designing or carrying out NFIs (Romijn et al., 2015), generating large-scale field data which could be appropriate for this approach.

4.5 Conclusions

AGB in Tanzanian forests and woodlands is partially determined by gradients in environmental conditions and human use. We found that, in spite of constant use, recovering forests have the potential to act as partial C sinks through biomass accumulation. In this respect, recovering forests in Tanzania have a climate change mitigating value, in addition to the already-essential ecosystem services that they provide to surrounding communities. Carefully planned ecosystem restoration, designed with awareness of the particularities of forest and woodland ecosystems in Africa, could assist with climate change mitigation and sustainable development. In this respect, considering only environmental determinants such as climate and topography is not enough; human use determinants of biomass, such as forest accessibility and degree of forest use, must be taken into account to provide a comprehensive picture of the potential of forest and woodland restoration.

More generally, while integrating plot data and spatial data remains a challenge, we have demonstrated how combining these data sources improves analysis of forest recovery and forest-related climate change mitigation activities. This offers new pathways to integrate forest information in national assessments and planning for climate change mitigation actions. In this respect, large-scale ecological questions which merge environmental and human contexts can be answered through the combination of national field endeavours, satellite time series and spatial datasets.

Chapter 5

Forest disturbance and recovery in Peruvian Amazonia

This chapter is based on:

D. Requena Suarez, D. M. A. Rozendaal, V. De Sy, M. Decuyper, N. Málaga, P. Durán Montesinos, A. Arana Olivos, R. De la Cruz Paiva, C. Martius, and M. Herold (in preparation) "Forest disturbance and recovery in Peruvian Amazonia"

Abstract

Amazonian forests function as reservoirs of carbon stocks and carbon sinks, contributing to climate change mitigation. While they continuously experience disturbance and recovery, the extent and degree of disturbance remains unknown, as well as their potential recovery of biomass and diversity. Here, we evaluate the degree of recent forest disturbance in Peruvian Amazonia, as well as the potential effects of disturbance, environmental conditions and human use on biomass and tree diversity in disturbed forests. For this purpose, we integrate data on biomass and tree diversity from forest plots from Peru's National Forest Inventory (NFI) with remotely-sensed monitoring of forest dynamics, finding that roughly 15.3% of Peruvian Amazonia has experienced at least one human or natural disturbance event since 1984, based on disturbances detected from Landsat-derived Normalized Difference Moisture Index (NDMI) time series. Disturbance intensity — estimated as the difference in NDMI at the time of disturbance and its phenological baseline — has a negative effect on aboveground biomass (AGB) and tree species diversity as well as their recovery towards undisturbed levels. Furthermore, time since disturbance has a positive effect on AGB and similarity in species composition with undisturbed forests. While AGB and its recovery varied along gradients in environmental conditions and human use, this was not evident for tree diversity and its recovery, nor its similarity in species composition. Following disturbance, forests in Peruvian Amazonia can act as partial carbon sinks: during the first 20 years after disturbance AGB increases at an overall rate of 4.05 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$. We recommend disturbance intensity and subsequent recovery to be considered in forest GHG reporting for forest-based mitigation endeavours. Our study highlights the potential of combining recent tropical country NFI forest plot data with satellite time series for the study of forest disturbance, recovery and their impacts on biomass and biodiversity.

5.1 Introduction

Tropical forests are a major terrestrial component of the carbon cycle, functioning as carbon reservoirs and sinks (Pan et al., 2011). Over the last 20 years, it is estimated that tropical forests in the Amazon Basin have been functioning as a net carbon sink of approximately -0.1 Gt CO_2e year^{-1}, considering removals from forest growth and emissions from deforestation and other disturbances (Harris et al., 2021). This estimate suggests that, while the forests in the Amazon Basin are being affected by deforestation and other disturbances, overall they are actively removing CO_2 from the atmosphere, and therefore contributing to climate change mitigation. This mitigating role is underpinned by the rich biodiversity found in Amazonian natural forests, making them resilient to disturbances and climate change (Levine et al., 2016; Thompson et al., 2009).

Tropical forests constantly experience disturbance. Disturbances can be natural (e.g. droughts or wildfires), human (e.g. human-induced fires, clear-cuts or selective logging), or a combination of both. For example, droughts can be the result of climate change related to human activities elsewhere on the planet (Van Loon et al., 2016). At the same time, disturbances vary along an intensity gradient, ranging from low disturbance intensity, leading to partial reductions of forest biomass (i.e. degradation), to high disturbance intensity, leading to complete forest removal (i.e. deforestation). A recent study based on remote sensing data suggests that from 1995 to 2017, over 17% of the extent of the Amazon rainforest biome had been recently disturbed, roughly equating to 1,036,700 km^2 (Bullock et al., 2020b).

After a disturbance, forests generally have the ability to recover in terms of biomass and biodiversity, towards pre-disturbance levels or alternative states (Anderson-Teixeira et al., 2013; Didham et al., 2005). Disturbance and recovery dynamics are an essential component of forest ecology, and natural and human disturbances are predominant across large forest landscapes (Bullock et al., 2020b; Espírito-Santo et al., 2014; Phillips et al., 2009). Secondary forests, which are forests that recover after high-intensity, stand-replacing disturbances, have the potential to recover in biomass and biodiversity (Chazdon, 2014; Poorter et al., 2016; Rozendaal et al., 2019). In a similar manner, forest stands recovering from lower-intensity disturbances, such as logged forests, also recover in biomass (Avila et al., 2018; Rutishauser et al., 2015). However, both carbon stocks and biodiversity in disturbed forests as well as their recovery remain largely ignored in the Amazon Basin (Bustamante et al., 2016), particularly within climate change mitigation schemes such as REDD+ (Berenguer et al., 2014; Edwards et al., 2010; Gardner et al., 2012; Sasaki et al., 2011), which currently only accounts for secondary and undisturbed forests (IPCC, 2019).

Furthermore, we currently do not know to what extent environmental conditions and human use as well as type and intensity of disturbance have an effect on biomass, biodiversity, and their recovery across disturbed forests in the Amazon Basin. In managed, logged and secondary forests, disturbance intensity has a negative effect on biomass and biodiversity (Avila et al., 2018; Gibson et al., 2011; Rutishauser et al., 2015; Vidal et al., 2016). In logged and secondary forests, time since disturbance has a positive effect on biomass (Heinrich et al., 2021; Meli et al., 2017; Poorter et al., 2016; Rutishauser et al., 2015) as well as on biodiversity (Rozendaal et al., 2019). In secondary forests, biomass is driven by environmental conditions, generally increasing with higher levels of water availability and soil fertility (Heinrich et al., 2021; Li et al., 2017; Poorter et al., 2016) and decreasing with higher intensities of previous and current land use and by higher levels of human accessibility (Chazdon, 2003; Crk et al., 2009; Jakovac et al., 2015). In undisturbed and degraded forests, slope and distance to nearest forest edge also had a positive effect on biomass (Berenguer et al., 2014). In parallel, biodiversity in secondary forests increases with higher levels of surrounding forest cover, as well as with higher levels of water availability (Rozendaal et al., 2019). Understanding how biomass and biodiversity, as well as their recovery, vary along environmental gradients and human use conditions in disturbed forests in general could shed further light on the mitigating role of disturbed forests in the Amazon Basin.

The main challenge of assessing forest disturbance and recovery in the Amazon Basin lies in data availability. When permanent plots in seemingly-undisturbed and logged forests experience disturbances, such as logging, fire or droughts, repeated measurements of these plots have shed light on the effects of disturbance on biomass accumulation (Berenguer et al., 2018; Phillips et al., 2009; Rutishauser et al., 2015). A robust and representative setup of permanent forest plots in disturbed forests in the Amazon Basin would enable the study of forest recovery from disturbance occurring at varying times and intensities, while at the same time accounting for the effect of broad gradients in environmental conditions and human use. While several efforts are currently underway (Laurance et al., 2011; Málaga et al., 2021; Poorter et al., 2016; Sist et al., 2015), such information does not fully capture fine-scale variations in disturbance intensity as well as gradients in environmental conditions and human use.

In the tropics, national forest-monitoring capabilities have greatly improved in quality and extent over the last years: 62 countries used national forest inventory (NFI) data obtained within the last 10 years for GHG reporting, and when possible report at higher levels (i.e. Tiers) of complexity (Nesha et al., 2021). One of these countries, Peru, is currently carrying out an NFI led by its Forest and Wildlife Service (SERFOR). Using a consistent methodology, Peru's NFI plots are a representative sample of the country's forests, covering broad environmental and human use gradients. While qualitative information on the degree of human and natural disturbances has been gathered, quantitative information on the time or intensity of these disturbances is still unavailable.

Remote sensing has come to enable the study of forest disturbance and recovery across large scales. While remote sensing analysis has enabled the detection of major disturbances (i.e. deforestation), detecting other minor disturbances (i.e. degradation) has been a recurrent challenge for the forest monitoring community (DeVries et al., 2015a; Herold et al., 2011). Dense satellite time series have proved useful in the detection of small-scale disturbances, including forest degradation (Bullock et al., 2020a; Bullock et al., 2020b; DeVries et al., 2015a; DeVries et al., 2015b; Hamunyela et al., 2020). However, these methodologies require an initial training period to establish an undisturbed forest baseline and detect only one disturbance event, therefore not fully capturing longer-term forest change dynamics. Recent remote sensing methods (Decuyper et al., in review) have shown that it is possible to continuously monitor forest change dynamics, both disturbances and regrowth, by using nearby forests throughout the entire period as a reference baseline. The integration of these advancements in remote sensing with consistent plot data provides the opportunity to assess forest disturbance and recovery across large scales (Bustamante et al., 2016; Requena Suarez et al., 2021).

In this study, we evaluate the degree of recent forest disturbance in Peruvian Amazonia, as well as the potential effects of disturbance, environmental conditions and human use on biomass and tree diversity in disturbed forests, as well as their recovery. We address the following research questions:

1. What is the degree of forest disturbance of Peruvian Amazonia?
2. In recently-disturbed forests, how do disturbance intensity and time since disturbance influence biomass, biodiversity and their recovery?
3. What are the main environmental and human use drivers of biomass, biodiversity and their recovery in disturbed forests?

We integrate forest plot data from Peru's NFI with remote sensing analysis of forest dynamics to assess the degree forest disturbance (natural and human) and potential recovery in aboveground biomass and tree species diversity. Furthermore, we assess effects of disturbance intensity, time since disturbance, environmental conditions and human use on aboveground biomass, tree species diversity (based on species' relative abundance), and on recovery in aboveground biomass, tree species diversity and species composition (i.e. similarity in species composition with undisturbed forests) towards values found in undisturbed forests.

5.2 Methods

To address our research questions, we (1) calculated aboveground biomass and species diversity for all NFI plots in Peruvian Amazonia; (2) employed dense satellite time-series analysis to categorise plots into disturbed and undisturbed forests, obtaining disturbance intensity and time since disturbance for the former category for the period of 1984-2019; (3) estimated the recovery of AGB *(AGB (%r))* and species diversity *(species diversity (%r))*, as well as similarity in species composition between disturbed and undisturbed forest plots; and (4) applied a mixed-effects modelling framework to assess the effect of disturbance intensity and time since disturbance, as well as the effects of environmental conditions and human use, on biomass, biodiversity and their recovery in disturbed forests in Peruvian Amazonia.

5.2.1 Forest plot data

Forest plot data is part of the Peruvian National Forest and Wildlife Inventory, which is currently being carried out by SERFOR. We include only data measured from 2013 until 2019. Forest plots were distributed in four forest strata in Peruvian Amazonia: lowland forests, accessible montane forests, inaccessible montane forests, and tropical wetlands (Figure 5.1a). L-shaped clusters (Figure 5.1b; referred to as "plots" by SERFOR), consisting of rectangular or circular plots (referred to as "subplots" by SERFOR), were distributed throughout these categories. In lowland forests, plots were rectangular, had an area of 0.1 ha and a minimum between-plot spacing of 75 m between them. In the remaining strata, plots were circular, with an area of 0.05 ha and a minimum spacing of 30 m between them.

In clusters with rectangular plots, the minimum diameter at breast height (DBH) of measured trees was 10 cm for all plots. Clusters with circular plots, on the other hand, had a minimum DBH of 5 or 10 cm; for these plots, we included only circular plots with a minimum DBH of 10 cm. For all plots the DBH of all trees over the minimum DBH were measured and their respective taxonomic identification was recorded.

5.2.2 Estimation of disturbance intensity and time since disturbance

For the purpose of this study, we define disturbed forests as forests with at least one natural or human disturbance detected during the study period (from 1984 until the year of field measurement) and undisturbed forests as forests with no disturbance detected during the study period. Disturbance intensity and time since disturbance were obtained through satellite time series analysis of Landsat-derived Normalized Difference Moisture Index (NDMI) spatio-temporal cubes, which is explained in detail below. We chose NDMI for the evaluation of disturbance, due to its high sensitivity to canopy moisture content (Jin and Sader, 2005), and previous results of disturbance-regrowth detection in forests in Peruvian Amazonia (DeVries et al., 2015a). Due to the nature of our method, we were unable to classify forest disturbance types, and thus did not differentiate between natural and human disturbances.

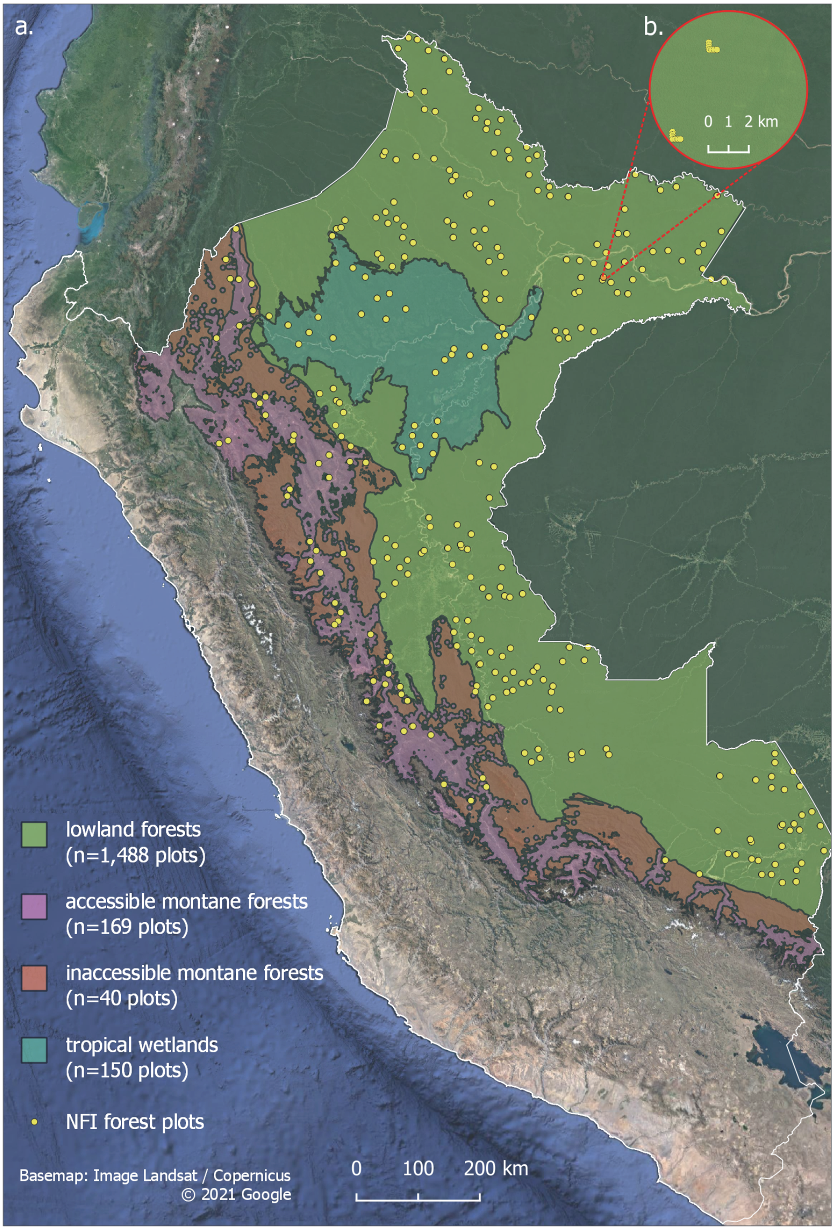

Figure 5.1: Map of the included plots and an overview of plot design. (a) Distribution of plots in lowland forests, accessible montane forests, inaccessible montane forests, and tropical wetlands in Peruvian Amazonia. (b) Inset of map showing the L-shaped disposition of clusters.

Disturbance intensity and time since disturbance were determined for all plots using Anomaly Vegetation Change Detection (coined AVOCADO; Decuyper et al., in review). This approach uses spatio-temporal cubes in a given area derived from satellite imagery and a delimitation of an undisturbed forest patch located within the given area to construct the reference forest phenology. Through the generation and comparison with a local reference baseline, pixel-level anomalies aided the detection of forest disturbance over the entire study period.

Normalized Difference Moisture Index (NDMI) spatio-temporal cubes using the entire Landsat archive at the time (1984-2019) were pre-processed, and downloaded from Google Earth Engine for a 6.5 km × 6.5 km area around each cluster. To select reference undisturbed forests, we used historical imagery available in Google Earth Pro for each area of interest to demarcate forest patches with no apparent disturbance over the entire study period. By using the full Landsat time-series for the reference forest, and by making use of the flexibility of kernel density estimations, we created a robust forest reference phenology for every cluster.

The year of the most recent disturbance was determined for all plot locations, with any detection occurring in or after the year in which a plot was measured excluded from further analysis. Plots with seemingly no natural or human disturbances detected from 1984 until the year of measurement were classified as undisturbed forests, while plots with at least one detection of natural or human disturbance were classified as disturbed forests. Disturbance intensity was calculated as the absolute difference between the reference NDMI value and the NDMI value at the time that the most recent disturbance was detected (ΔNDMI). Time since disturbance (in years) was calculated as the number of years between the latest disturbance and the year of plot measurement.

5.2.3 Estimation of AGB and tree species diversity and their recovery

To evaluate biomass and its recovery, we calculated AGB and percent recovery of AGB towards values found in undisturbed forest (hereafter *AGB (%r)*). Tree-level measurements of DBH and species-specific wood density (WD) were used to calculate AGB, using the pantropical allometric equation of Chave et al. (2014). Wood density was extracted from the Global Wood Density (GWD) database (Chave et al., 2009; Zanne et al., 2009). This was done in R v.3.6.1 (R Core Team, 2019), using *BIOMASS* (Réjou-Méchain et al., 2017). To evaluate the relative recovery of AGB in disturbed forest plots towards undisturbed forest levels, we calculated AGB (%r). AGB (%r) is the percentage of AGB present in a disturbed forest plot in comparison with undisturbed forest plot(s) in the same cluster. If more than one undisturbed forest plot was present within the same cluster, AGB (%r) was calculated using the average of AGB in all undisturbed forest plots in that cluster.

AGB (%r) was not calculated for disturbed forest plots in clusters with no undisturbed forest plots.

To evaluate biodiversity and its recovery, tree species data were used to calculate the Shannon Index (hereafter *species diversity*; i.e. species identity and abundance), and its percent recovery towards undisturbed forest levels (hereafter *species diversity (%r)*). For species diversity, we calculated the Shannon Diversity Index for all plots in R using *vegan* (Oksanen et al., 2019). Similar to AGB (%r), species diversity (%r) was derived to evaluate the relative recovery of species diversity in disturbed forest plots towards undisturbed forest levels. Species diversity (%r) is the percentage of species diversity present in a disturbed forest plot in comparison with undisturbed forest plot(s) in the same cluster. If more than one undisturbed forest plot was present within the same cluster, species diversity (%r) was calculated using the average value of species diversity in all undisturbed forest plots in that cluster. Species diversity (%r) was not calculated for disturbed forest plots in clusters with no undisturbed forest plots.

In addition, biodiversity recovery was further evaluated through the inclusion of similarity in species composition between disturbed and undisturbed forests. For this, we calculated Chao's dissimilarity index (Chao et al., 2004), which uses species abundance information to identify shared species between two locations and evaluate how dissimilar these locations are in species composition. This index was obtained between each disturbed forest plot and each undisturbed forest plot in the same cluster using *vegan*, obtaining dissimilarity values ranging from 0 to 1, which we then subtracted from 1 to obtain similarity values. Mean similarity values were considered for disturbed plots with more than one undisturbed plot in the same cluster. As with AGB (%r) and species diversity (%r), similarity in species composition was not calculated for disturbed forest plots in clusters with no undisturbed forest plots.

5.2.4 Additional data on environmental conditions and degree of human use

To identify the main environmental and human use drivers of AGB, AGB (%r), species diversity, species diversity (%r) and similarity in species composition, we included predictors of climate, topography, soil and human use for all plot locations (Table 5.1). The effect of climate was evaluated by including Climatic Water Deficit (CWD, in mm year^{-1}; Chave et al., 2014), which is the annual evaporative demand during dry months, and thus includes both precipitation and temperature during dry periods. The effect of topography was evaluated by including slope (°), calculated from SRTM elevation data (Jarvis et al., 2008). Soil fertility was assessed by including total Nitrogen (N) content, through extracted gridded predictions from SoilGrids250m 2.0 (in g kg^{-1}; ISRIC, 2020). In line with previous studies (Poorter et al., 2016; Requena Suarez et al., 2021; Rozendaal et al., 2019), we

Table 5.1: Summary of environmental and human use predictors for all disturbed forest plots

Covariate	unit	min.	max.	mean	SD	Original source
Climatic water deficit (CWD)	mm year^{-1}	-588.5	0	-111.7	124.1	Chave et al., 2014
Slope	°	0.0	15.5	1.7	3.4	Jarvis et al., 2008
Total nitrogen (N) content	g kg^{-1}	223.0	608.0	335.3	88.9	ISRIC, 2020
Surrounding tree cover	%	31.7	100.0	92.0	9.8	Hansen et al., 2013
Distance to nearest navigable waterway or road	km	0.0	27.2	5.8	6.7	OpenStreetMap Contributors, 2020, Schielein, 2017

included surrounding tree cover and human accessibility as proxies for degree of human use. Surrounding tree cover was calculated as the mean percent tree cover in 2010 (Hansen et al., 2013) within a 5 km radius around each plot. Accessibility was calculated as the Euclidean distance (km) of each plot to the nearest navigable waterway (Schielein, 2017) or road (OpenStreetMap Contributors, 2020). Predictor values were extracted or calculated for all plot locations using *raster*, *spatialEco* and *rgeos* (Bivand and Rundel, 2017; Evans, 2018; Hijmans, 2019) in R.

5.2.5 Statistical analysis

To identify the drivers of AGB, AGB (%r), species diversity, species diversity (%r) and similarity in species composition, we employed linear mixed-effects models using *lme4* and *lmerTest* (Bates et al., 2015; Kuznetsova et al., 2017) in R. For all five models, we included disturbance intensity, time since disturbance, CWD, slope, soil N content, surrounding tree cover and distance to nearest road or navigable waterway as fixed effects. Time since disturbance was ln-transformed for AGB and AGB (%r), to account for the nonlinear increase in AGB and AGB (%r) over time. Plot clusters were included as random effects, to account for the effect of proximity between plots within a cluster. Predictors were standardised and model fits were evaluated based on the conditional (fixed and random effects) and marginal (only fixed effects) R^2 (Nakagawa and Schielzeth, 2013).

5.3 Results

5.3.1 Levels of disturbance

Out of all plots considered in this study (1,847), 280 plots were in areas with detected previous disturbance (Figure 5.2a-c). Disturbance intensity ranged from 0.04 to 0.62

ΔNDMI, with 74.3% of plots with a disturbance intensity of up to 0.2 ΔNDMI (Figure 5.2b). The majority of disturbed forest plots in disturbed (239, 85.4%) had one disturbance event, 38 plots had 2 events and 3 plots had 3 events of disturbance during the study period. Time since the latest disturbance in these plots ranged from 1 to 34 years, with a mean of 14.7 years (Figure 5.2d).

Overall, mean AGB and species diversity and variation therein were lower in disturbed forest plots than in undisturbed forest plots. Mean AGB (Figure 5.3a) in disturbed forest plots was 149.3 Mg ha^{-1} (SD=138.0), approximately 57.5% of the mean biomass in undisturbed forest plots, which was 259.6 Mg ha^{-1} (SD=198.0). Species diversity (Shannon Index) in disturbed forests was 0.8 lower of what was observed in undisturbed forests, with a mean value of 1.9 (SD=0.9) in comparison to 2.7 (SD=0.5) in undisturbed forest plots (Figure 5.3c).

For 205 disturbed forest plots, there was at least one undisturbed forest plot in the same cluster, which enabled evaluating percent recovery compared to undisturbed forest values (%r). When compared to nearby undisturbed forest plots (i.e. within the same cluster), disturbed forests had on average 99.6% of the AGB (%r) (Figure 5.3b) and 91.7% of the tree diversity (%r) (Figure 5.3d) of undisturbed forests, and a 0.3 similarity in species composition with undisturbed forests (1-Chao's Index, Figure 5.3e).

5.3.2 Effects of disturbance intensity and time since disturbance on AGB and species diversity

Our results show that there is a significant negative effect of disturbance intensity on AGB and species diversity (Figure 5.4a-c). For an increase in ΔNDMI of 0.01, AGB decreased at a rate of 1.7 Mg ha^{-1}, from 205.9 to 107.3 Mg ha^{-1}, equating to 79.3% and 41.3% of mean values in undisturbed forests (boxplot in Figure 5.4b). Species diversity (calculated as Shannon Index) decreased by 0.01 for an increase in ΔNDMI of 0.01, decreasing from 2.3 to 1.5, equating to 85.7% and 56.9% of mean species diversity values in undisturbed forests (boxplot in Figure 5.4d).

The effect of time since disturbance was significant for AGB (Figure 5.4b). For disturbed forest plots, rates of AGB change (ΔAGB) were 6.6 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$, during the first 10 years after disturbance, slowing to 1.7 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ between 11 to 20 years after disturbance, 1.0 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ between 21-30 years, and 0.8 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ between 31-34 years after disturbance. According to our AGB model, and keeping all other variables constant at the mean, AGB at 34 years since disturbance would be 217.5 $\mathrm{Mg\,ha^{-1}}$, 83.8% of AGB expected in undisturbed forests. There was no effect of time since disturbance for species diversity (Figure 5.4d), indicating that species diversity did not increase with time during the first 34 years since disturbance.

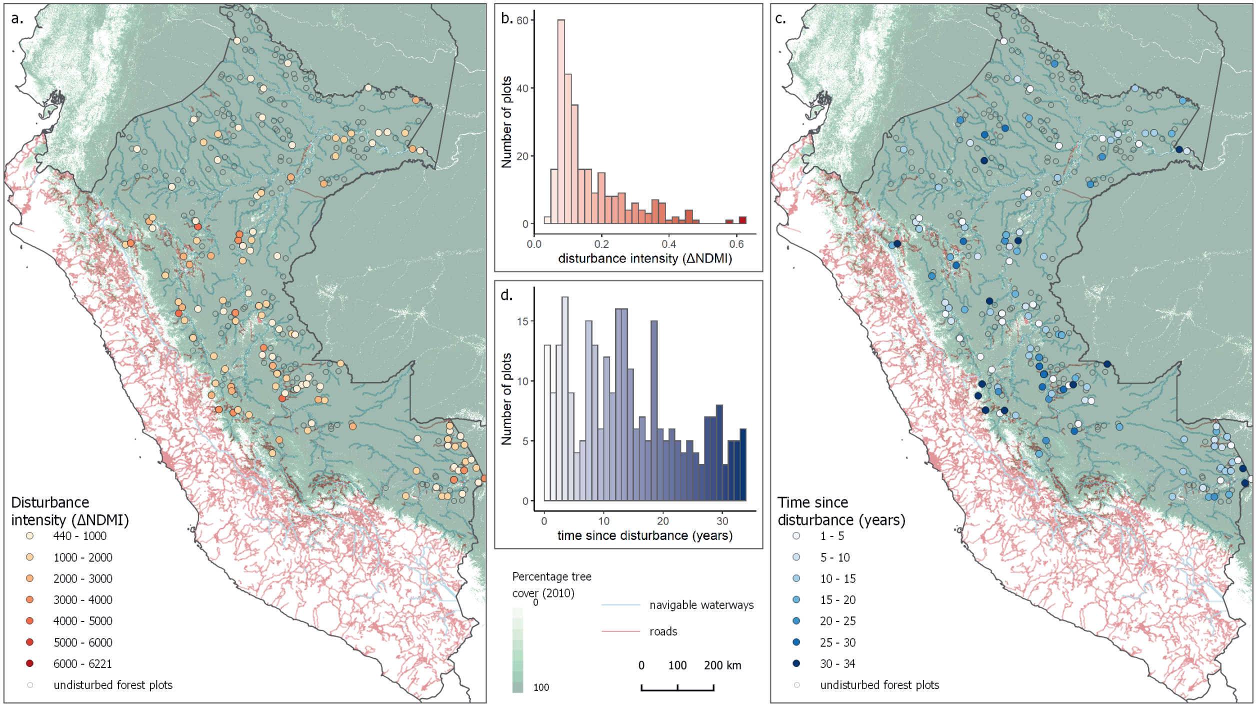

Figure 5.2: Levels of disturbance of NFI plots. Distribution (a) and number of plots (b) per disturbance intensity (ΔNDMI); and distribution (c) and number of plots (d) per time since disturbance (years). In (a) and (c), undisturbed forest plots are shown as hollow circles; navigable waterways (Schielein, 2017) and roads (OpenStreetMap Contributors, 2020) are indicated with blue and red lines, respectively; and 2010 percentage tree cover (%) from Hansen et al. (2013) is displayed in green.

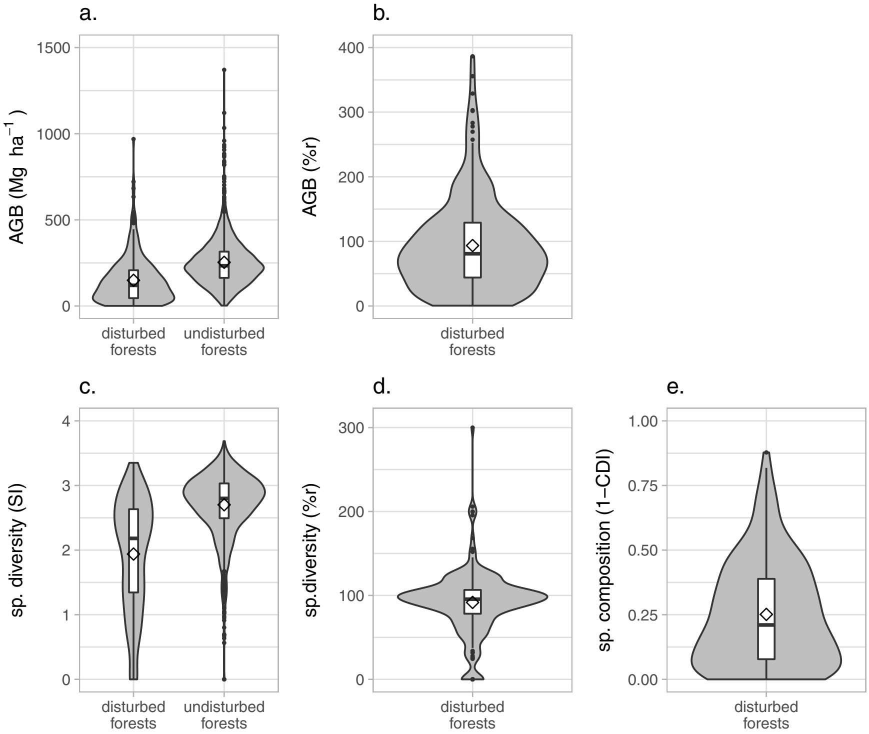

Figure 5.3: (a) Aboveground biomass (AGB), (b) its recovery (AGB (%r)), (c) species diversity (Shannon Index, SI), (d) its recovery (species diversity (%r)), and (e) similarity in species composition (1-CI, Chao's Dissimilarity Index subtracted from one) in disturbed and undisturbed forest plots. AGB values for three plots in undisturbed forests plots (3,025.5 3,383.2 and 4,028.9 Mg ha^{-1}) are not shown in (a), but included in further analysis. For (a) and (c), we include all disturbed (n=280) and undisturbed (n=1,567) forest plots; for (b), (d) and (e), we only include disturbed forest plots (n=205) with at least one undisturbed forest plot in its cluster.

The effect of disturbance intensity and time since disturbance on AGB (%r), species diversity (%r) and species composition towards undisturbed forest levels varied. AGB (%r) was significantly affected by disturbance intensity, but not by time since disturbance (Figure 5.5a-b). For disturbance intensity, AGB (%r) decreased by 1.6% for an increase in ΔNDMI of 0.01, decreasing from 111.1% to 17.9% of AGB in undisturbed forests across the range in disturbance intensity that we observed.

Species diversity (%r) was significantly driven by disturbance intensity, but not by time since disturbance (Figure 5.5c-d). For an increase in ΔNDMI of 0.01, species diversity (%r) declined by 0.8%, with values decreasing from 99.6% to 56.1%. Similarity in species

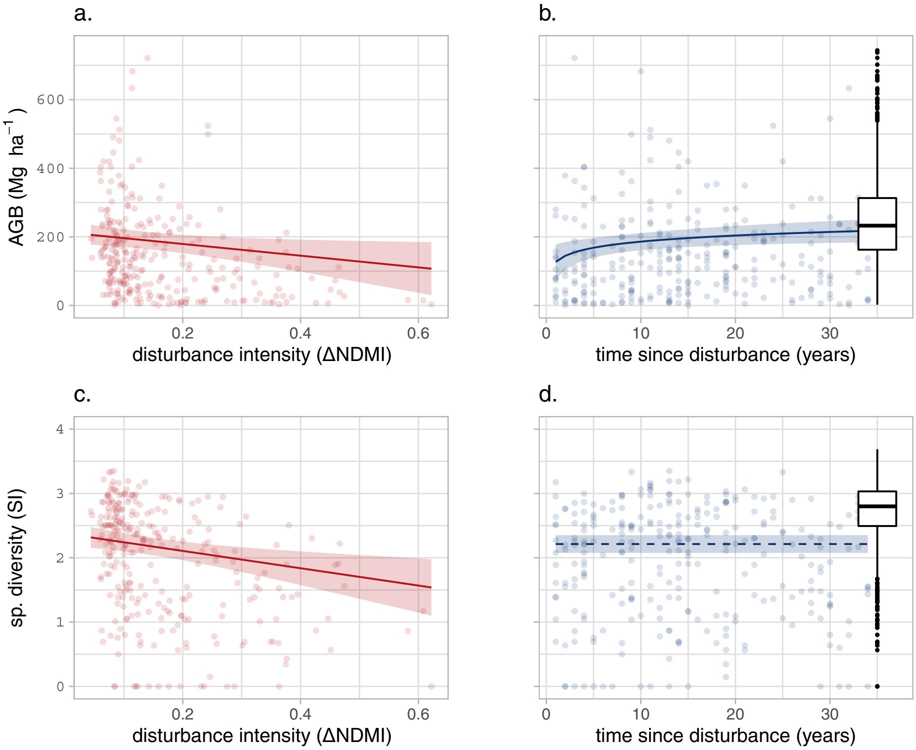

Figure 5.4: Effect of disturbance intensity and time since disturbance on aboveground biomass (AGB; a and b) and tree species diversity (Shannon Index SI; c and d) in disturbed forest plots. Solid lines indicate significant effects, dashed lines indicate non-significant effects, and bands indicate confidence intervals (CI, 95%). Boxplots represent values in undisturbed forest plots. For all panels, all other predictors were kept at the mean.

composition was significantly driven by time since disturbance (Figure 5.5f), but not by disturbance intensity (Figure 5.5e). Similarity in species composition increased by 0.003 per year since disturbance, increasing in total from 0.25 to 0.35 from 1 to 34 years since disturbance.

5.3.3 Effects of environmental conditions and human use

AGB was significantly and associated, in order of increasing importance, negatively with disturbance intensity, and positively with time since disturbance, CWD and surrounding tree cover (Figure 5.6a). In the same order, AGB (%r) was significantly, negatively associated with disturbance intensity and positively with CWD and slope (Figure 5.6b). Neither soil N content nor distance to nearest waterway or road were significantly associated

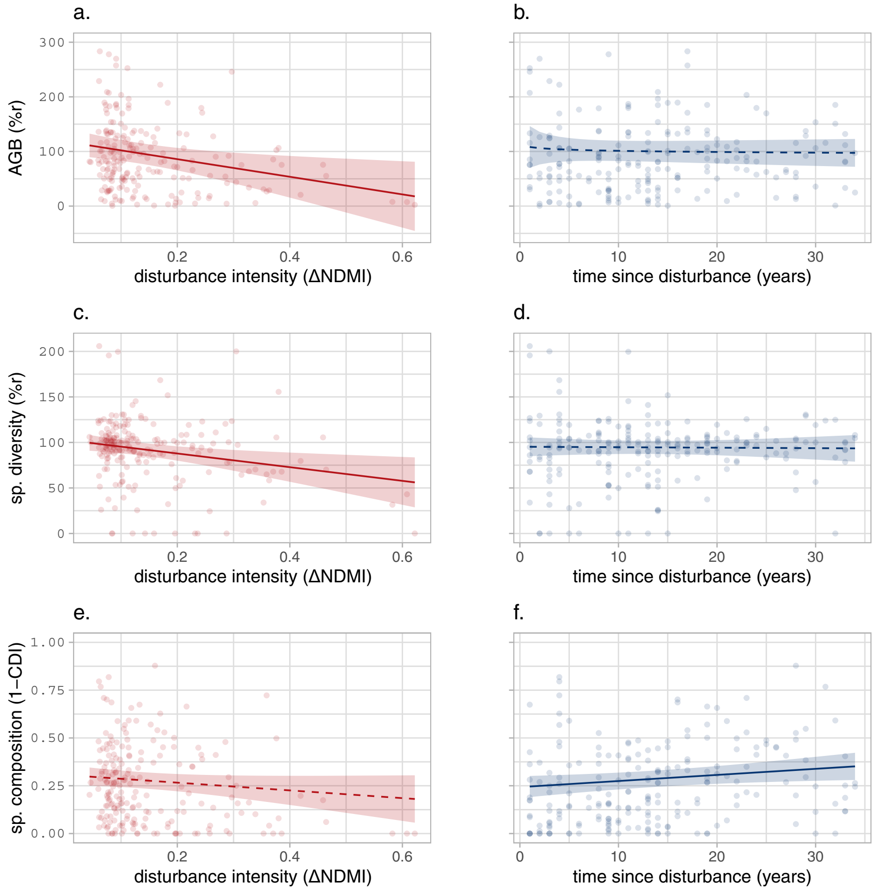

Figure 5.5: Effect of disturbance intensity and time since disturbance on (a and b) AGB (%r), (c and d) species diversity (%r), and (e and f) species composition (1-CI, Chao's Dissimilarity Index subtracted from one) in disturbed forest plots. Disturbance intensity and time since disturbance values are indicated in red and blue, respectively. Percent recovery values (%r) of 205 disturbed forest plots were obtained in comparison to at least one undisturbed forest plot in the same cluster. Solid lines indicate significant effects, dashed lines indicate non-significant effects, and bands indicate confidence intervals (CI, 95%). For all panels, all other predictors were kept at the mean.

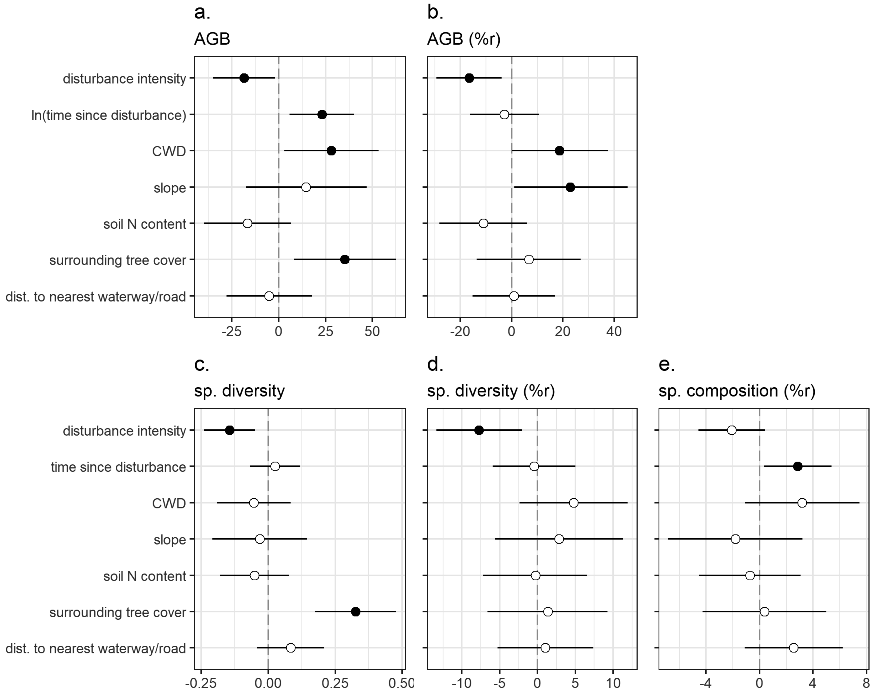

Figure 5.6: Effects of environmental conditions and human use on AGB, AGB (%r), species diversity, species diversity (%r) and similarity in species composition for disturbed forests. (a) AGB and (b) AGB (%r), (c) species diversity and (d) species diversity (%r) (e) similarity in species composition. Significant predictors are shown as filled, black symbols; non-significant predictors are shown as open symbols. Whiskers represent confidence intervals (CI, 95%).

with either AGB nor AGB (%r). Species diversity was significantly associated positively to surrounding tree cover and negatively to disturbance intensity (Figure 5.6c). Species diversity (%r) was associated only to disturbance intensity (Figure 5.6d). Similarity in species composition was associated only positively with time since disturbance (Figure 5.6e).

The amount of variation explained by the predictors (fixed effects) varied. For AGB and AGB (%r), large part of the variation was explained by cluster-to-cluster variation, as fixed and random effects together explained 51.3% and 45.8% of the variation; on the other hand, fixed effects explained 14% and 6% of the variation, respectively. Similarly, large part of the variation in species diversity and species diversity (%r) was explained by cluster-to-cluster variation, as fixed and random effects together explained 54.7% and 26.2% of the variation, while fixed effects only explained 27.6% and 5.2%, respectively.

Variation in similarity in species composition was explained for 64.3% by fixed and random effects, and for 10.9% by the fixed effects only.

5.4 Discussion

In this study we have quantified the extent and degree of forest disturbance in Peruvian Amazonia, and assessed the influence of disturbance intensity and time since disturbance on aboveground biomass and tree diversity. Furthermore, we looked into the environmental and human use drivers of biomass and diversity in tropical disturbed forests.

5.4.1 Extent and degree of disturbance

We found that 280 of the evaluated forest plots evaluated were located in forests recovering from recent human or natural disturbances, with 73.9% of them presenting a disturbance intensity lower than 0.2 ΔNDMI (Figure 5.2) By roughly extrapolating our results to the reported forest extent of 2019 (Plataforma Geobosques, 2021), taking into consideration the forest types defined by SERFOR, 15.3% of Peruvian Amazonia, roughly equating to 104,171 million km^2, has experienced natural and/or human disturbances at least once since 1984. This percentage is similar to values reported by (Bullock et al., 2020b) who found that between 1995 and 2017, 17% of natural forests in the Amazon Basin had been disturbed. Our results include disturbed forests recovering from intense disturbances (i.e. deforestation) as well as less-intense disturbances (i.e. selective logging, droughts). In this respect, since our detection of disturbance does not differentiate between human and natural disturbances, we account for the combined effect of human pressures (e.g. logging) as well as climate change on natural forests (e.g. droughts; Easterling and Apps, 2005; Fischlin et al., 2009).

On average, AGB in disturbed forest plots was 57.5% of AGB in undisturbed forest plots. This is comparable with two studies in the Peruvian and in the Brazilian Amazon Basin that found that on average disturbed forests stored 40% less aboveground carbon than undisturbed forests (Berenguer et al., 2014; Málaga et al., 2021). Species diversity (Shannon Index) in disturbed forest plots was lower than what was observed in undisturbed forests, generally in line with findings of Gibson et al., 2011. Large variation in AGB and species diversity was observed for both disturbed and undisturbed forest plots, most likely linked with the limitations of working with a high number of small plots across large scales (McRoberts and Tomppo, 2007; Requena Suarez et al., 2021).

5.4.2 Effect of disturbance intensity

The range of disturbance intensity was broad (Figure 5.2b): the high frequency of lower disturbance intensity values in disturbed forest plots suggests that minor disturbances (i.e. forest degradation) were the more predominant disturbance events. Values of tree diversity support this: while species diversity indices in disturbed forests were overall lower than in undisturbed forests (Figure 5.3), when compared to nearby undisturbed forests, diversity values in disturbed forests were relatively high (91.7% of values for undisturbed forests).

Disturbance intensity had a significant, inverse effect on both AGB and AGB (%r) (Figures 5.4-5.5); higher disturbance intensity leads to a greater decline in AGB and AGB (%r), up to 41.3% and 17.6% of their undisturbed levels, respectively. This coincides with previous studies in logged forests in the region (Avila et al., 2018; Rutishauser et al., 2015; Vidal et al., 2016), where silvicultural practices with low disturbance intensities, such as selective logging or reduced-impact logging, resulted in forests with higher remaining biomass compared to forests under higher-impact silvicultural practices, such as conventional logging.

Disturbance intensity also negatively influenced species diversity and species diversity (%r), with lowest values of 56.9% and 56.1%, respectively. Our results coincide with studies in logged forests under silvicultural practices of varying intensities (Putz et al., 2012), and studies on effects of disturbance in human-disturbed forests (Gibson et al., 2011). While not explored here, many studies looked into the effects of human disturbances on diversity in various animal taxa (Barlow et al., 2016; Burivalova et al., 2014; França et al., 2017; Gibson et al., 2011; Mant et al., 2014; Moura et al., 2013; Perry et al., 2016), showing that higher disturbance intensities lead to higher reductions in biodiversity when compared with undisturbed levels. Assessments of taxa more sensitive to disturbances can provide insights into the effect of minor disturbances, such as selective logging, which cannot be fully captured by evaluating only tree species (Gibson et al., 2011; Putz et al., 2012).

5.4.3 Effect of time since disturbance

Time since disturbance had a significant effect on AGB, but this effect was not present for AGB (%r). The effect of time on AGB suggests that, overall, after disturbance forest have the ability to act as partial carbon sinks through their recovery over time, but unexpectedly, this effect was not captured when compared to nearby undisturbed forests (AGB (%r)). This could be due to the high AGB variability in undisturbed forest plots (Figure 5.3a), which was somewhat constrained by the cluster average of undisturbed plots within the same cluster only as reference value. However, at the lowest disturbance intensity AGB (%r) was still over 100%, suggesting that this constraint was not fully achieved. Additionally, while no disturbance was detected for undisturbed plots since 1984, undisturbed forest plots could still be recovering from disturbances prior to 1984. Small NFI plot size might have also had an effect on the high AGB variability in undisturbed plots, thus affecting the comparison between disturbed and undisturbed plots. In addition, continued minor disturbances could be ongoing, undetectable to remote sensing analysis: for example, qualitative NFI data on disturbance in lowland forests showed that 65.8% of all NFI plots had signs of human disturbance, and that 34.2% had signs of natural disturbance (SERFOR, 2019). While insightful, as this qualitative data did not provide the exact time of disturbance, its inclusion in this study was not feasible.

Until now, large-scale studies of ΔAGB in disturbed forests had not been carried out in Peruvian Amazonia. During the first twenty years after disturbance, ΔAGB rates were 4.1 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$. Our rate is consistently lower compared to rates found in forests recovering from stand-replacing disturbances, such as secondary forests: 31% lower than the 2019 IPCC rate for young secondary forests in North and South America (5.9 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$; IPCC, 2019; Requena Suarez et al., 2019), 34% lower than for Neotropical secondary forests (5.9 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$; Poorter et al., 2016), and 33% lower than for secondary forests in western Brazil (6.0 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$; Heinrich et al., 2021). When comparing to ΔAGB in forests recovering from forest degradation, this result is consistently greater: 52% larger than in logged forests across the Brazilian Amazon (2.7 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$; Rutishauser et al., 2015) and 309.1% and 71.6% larger than in forests under conventional logging and reduced-impact logging respectively in Para, Brazil (1.0 and 2.4 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$; Vidal et al., 2016). While previous studies have looked at ΔAGB rates in secondary forests or degraded forests, we have quantified ΔAGB in forests recovering disturbances ranging in intensity and representative for a large forest area. In this respect, we provide a broader context of the carbon sink role of disturbed forests in Peruvian Amazonia.

Our results do not show an effect of time since disturbance on species diversity nor its recovery (species diversity (%r). Time since disturbance only had a significant effect on recovery in species composition, which increased up to 0.35 at 34 years since disturbance. Across Neotropical secondary forests, Rozendaal et al. (2019) also found a slow increase of species composition over time, as well as Meli et al. (2017), pantropically. On the other hand, the effect of time since disturbance on diversity and diversity recovery was not significant. This could be due to the generally short time since disturbance in disturbed forest plots in our study (mean: 14.7 years), as recovery of species richness is a slower process than biomass recovery (Martin et al., 2013; Meli et al., 2017), often taking more than 50 years to recover following major disturbances (Rozendaal et al., 2019). It could also be due to the type of disturbances: tree diversity in disturbed forests is similar to diversity in undisturbed forests, indicating that overall the disturbances did not strongly affect diversity. For example, while diversity loss and subsequent recovery is evident in secondary forests that regrow after major disturbances (Martin et al., 2013; Rozendaal et al., 2019), logged forests retain their diversity (Edwards et al., 2014; Gibson et al., 2011).

5.4.4 Effects of climate, topography, soil and human use

AGB and AGB (%r) were significantly related to Climatic water deficit (CWD), suggesting that higher values of AGB and AGB (%r) in disturbed forests are expected in areas with higher water availability during dry periods. This relationship has been observed in mature, logged and secondary natural forests in the Amazon (Álvarez-Dávila et al., 2017; Heinrich et al., 2021; Poorter et al., 2016; Poorter et al., 2017; Sullivan et al., 2017). Slope, which ranged from 0 to 19° in the studied plots (Table 5.1), had only a positive significant effect on AGB (%r). Other possible drivers, such as distance to nearest waterway or road, did not have a significant effect on either AGB, diversity, nor their recovery. The mean distance to nearest navigable waterway or road was 5.8 km (Table 5.1) which could be why we did not find an effect. Similarly, our results suggest that soil nitrogen content —a proxy for soil fertility —had no significant effect on AGB nor AGB (%r). Previous studies have shown AGB to be positively related to soil fertility in undisturbed forest (Sullivan et al., 2017), though this effect has not been consistently observed in secondary nor disturbed forests (Poorter et al., 2016), which are studies which also used gridded soil data. Surrounding tree cover had a significant positive effect on AGB but not on AGB (%r). This was unexpected, as surrounding forests are thought to foster the natural regeneration process by acting as a source of propagules, necessary for tree recruitment (Chazdon, 2003; Rocha et al., 2016). However, 88.2% of disturbed forest plots had a surrounding forest cover of 80% or more within a 5 km radius, suggesting that there was just little variation in tree cover across the included plots, thus no effect on AGB (%r).

While our results show a clear influence of environmental conditions and human use on AGB and AGB (%r), this was not the case for species diversity, species diversity (%r), nor similarity in species composition. Our results partially coincide with results from Rozendaal et al. (2019), which found no effect of soil fertility on species diversity and its recovery, but an effect of water availability on species diversity. While we did not observe an effect of water availability on diversity or its recovery, this could be due to specific characteristics of our study region, which does not cover large areas of seasonally dry forests. Surrounding tree cover had a positive effect on species diversity, but not on species diversity (%r) nor on similarity in species composition. This was unexpected, but could be due to the consistently high tree cover percentages (Table 5.1). Similar to AGB and AGB (%r), no effect of soil N content nor distance to nearest waterway or road was observed on species diversity, species diversity (%r) nor similarity in species composition.

5.4.5 Integration of NFI forest plots and remote sensing

Previously, no large scale study of forest disturbance and recovery using forest plot data has been performed in Peruvian Amazonia. By combining consistent data on biomass and diversity from forest plots with remote sensing of forest dynamics, our results offer insight into the extent of disturbed forests, their aboveground biomass and tree diversity and recovery therein, as well as their variation across environmental and human use gradients. These insights are much-needed, not only for enhancing ecological understanding, but also for climate-change mitigation efforts (Bustamante et al., 2016). From this perspective, NFIs in combination with remote sensing are a valuable source of data, providing a snapshot of a country's forests. NFI data is valuable not only for GHG reporting and national forest management practices, but also for ecological research, as they provide forest plot data representative of large areas, while employing a consistent methodology throughout (see Requena Suarez et al., 2021). As time passes and the Landsat archive increases in time, analyses of forest disturbance frequency and intensity, and recovery will be possible at a longer temporal scale. Moreover, as detection methods of forest disturbance improve, we might be able to assess forest recovery from different disturbance types. Finally, as countries advance in tropical forest monitoring (Nesha et al., 2021) and more NFIs become available, the opportunity to assess disturbance and recovery in other regions arises.

5.5 Conclusions and implications

Our results show that approximately 15.3% of Peru's Amazon forests have experienced at least one disturbance event since 1984. In disturbed forests, disturbance intensity has a significant negative effect on AGB and tree species diversity, as well as on their recovery towards undisturbed levels. There was an evident effect of time since disturbance on AGB, as well as on similarity in species composition to undisturbed forests. While water availability increased standing AGB stocks, and its recovery towards undisturbed forest levels, effects of water availability were not evident for tree diversity nor its recovery.

Following disturbance, tropical forests in Peruvian Amazonia can act as partial carbon sinks: during the first 20 years after a disturbance, AGB increases at an overall rate of 4.05 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$. As a way forward, we recommend forest-based mitigation endeavours to be cognizant of the role of disturbance intensity on forest biomass and biodiversity and their recovery over time. For human disturbances, disturbance intensity can be reduced through the implementation of sustainable forest management practices. The role of natural forest recovery for climate change mitigation has been highlighted in the tropics (Cook-Patton et al., 2020; Harris et al., 2021) and particularly in the Amazon Basin (Heinrich et al., 2021; Poorter et al., 2016; Rutishauser et al., 2015). However, disturbed forests and their recovery are often overlooked in mitigation policies (Bustamante et al., 2016; Edwards et al., 2010), as is the role of biodiversity in climate change mitigation (Gardner et al., 2012). In this respect, large-scale analyses of biomass and diversity in disturbed forests, as well as their recovery, are an important step towards including disturbed forests and their recovery in climate change mitigation policies.

Chapter 6

Synthesis

This thesis contributed towards the aim of understanding and quantifying aboveground forest carbon stocks and sinks in tropical and subtropical forests. More specifically, it has contributed towards improving estimations of (sub)tropical aboveground forest carbon stocks and sinks under varying disturbance types for GHG reporting (R.O.1) and towards understanding the drivers of aboveground carbon stocks and sinks in recovering forests in the (sub)tropics (R.O.2).

The following chapter consists of two sections: Section 6.1 summarises how Chapters 2 through 5 have contributed towards achieving both research objectives and compares the methodologies employed and results obtained therein. Section 6.2 reflects on what has been done in the aforementioned chapters and provides an outlook into future research opportunities and ways of collaboration.

6.1 General discussion

Chapters 2 through 5 have addressed both research objectives through the integration of different forest plot and remote sensing data. They have focused on different levels of study, considering the effect of different disturbance types and intensities, and have assessed the effect of different potential drivers of aboveground forest carbon stocks (Figure 6.1).

Overall objective: Integrate forest plot data with remote sensing to contribute towards understanding and quantifying aboveground forest carbon stocks (AGB) and sinks (ΔAGB) in (sub)tropical forests.

	Chapter 2	**Chapter 3**	**Chapter 4**	**Chapter 5**
R.O.1: Improve estimations of (sub)tropical aboveground forest carbon stocks and sinks under varying disturbance types for GHG reporting.				
Forest plot data	Research plots and NFI plots	Research plots	NFI plots	NFI plots
Remote sensing data	Global remote sensing products	Global remote sensing products	Satellite time series and spatial datasets	Satellite time series and spatial datasets
Level of study	Tier 1 (Sub)tropics	Tier 1 (Sub)tropics	Tier 2 National (Tanzania)	Tier 2 National (Peruvian Amazon)
R.O.2: Understand the drivers of aboveground carbon stocks and sinks in recovering forests in the (sub)tropics.				
Disturbances	Major and minor disturbances (secondary and managed/logged forests)	Major and minor disturbances (secondary and managed/logged forests)	Major and minor disturbances (recovering and established forests)	Major and minor disturbances (disturbed and undisturbed forests)
Drivers	▪ Time since establishment	▪ Time since establishment	▪ Time since establishment ▪ Environmental conditions ▪ Human use	▪ Time since disturbance ▪ Disturbance intensity ▪ Environmental conditions ▪ Human use

Figure 6.1: Summary of the overall and specific research objectives and comparison of the types of forest plot and remote sensing data used as well as assessed disturbance type and drivers in Chapters 2 through 5 of this thesis.

Chapters 2 and 3 focused on natural forests in tropical and subtropical ecozones in North and South America, Africa and Asia. On the other hand, Chapters 4 and 5 were done at national scales, focusing on forests and woodlands across mainland Tanzania and on tropical humid forests in Peruvian Amazonia. Due to the different levels of study, spatial scale and availability of data, various methods were used to integrate ground and remote sensing data.

6.1.1 Improving estimations for forest-related GHG reporting (R.O.1)

Chapters 2 and 3 had the main purpose of refining the 2006 IPCC Tier 1 default values of AGB and ΔAGB in natural forests in (sub)tropical ecozones. In this respect, four key improvements were made.

The first improvement was the development of clear, consistent methodologies which use forest plot data. Prior to this, IPCC Tier 1 default values were based on a handful of studies per ecological zone (Gibbs et al., 2007; Langner et al., 2014). The results of both chapters highlight how forest plots measured for research purposes can be used for Tier 1 reporting and monitoring of forest carbon stocks and sinks, be it for national-level reporting to the UNFCCC as well as for large-scale forest GHG flux studies (Baker et al., 2020; ForestPlots.net et al., 2020; Gibbs et al., 2007). In Chapter 2, the inclusion of NFI plots was done in the absence of research plots. Since NFI plots lacked information on their forest age (i.e. years since establishment) or successional stage (i.e. secondary forests, degraded forests, old-growth forests), this information was derived from two global remote sensing products (Potapov et al., 2017; Tyukavina et al., 2016). In addition, for areas in which plot data was limited, a global biomass map (Santoro et al., in review) was used to estimate AGB. Our results highlight the current importance of having available forest plot data for Tier 1 estimates as well as the benefits of using remote sensing products in areas with limited plot availability. Our methodologies can be used for future refinements as more data becomes available.

The second improvement was the addition of uncertainty estimates to Tier 1 values. Prior to this, Tier 1 estimates and rates had no measures of uncertainty, and thus the effects of bioclimatic gradients and forest types within ecological zones were not accounted for (Gibbs et al., 2007). In both chapters uncertainties for our default values were high, indicating high variability in AGB and ΔAGB in (sub)tropical ecozones. This is not unexpected, as ecozones are broad forest categories that comprise ranges in species composition, environmental conditions and disturbance. However, ecozones are a useful way of categorizing forest ecosystems for the calculation of large-scale GHG fluxes in the absence of Tier 2 or Tier 3 data. The inclusion of high uncertainties add therefore extra nuance into Tier 1 defaults, highlighting the complexities of (sub)tropical forest ecosystems.

The third improvement was the inclusion of forest successional stages for Tier 1 reporting. Prior to this, AGB values were included for all successional forest types together, and ΔAGB in older secondary forests and old-growth forests had been grouped together. Thus, the use updated Tier 1 defaults will result in more realistic estimations, as they now account for forest succession. Similar to the use of ecozones, the categorisation of forests into younger secondary (≤20 years), older secondary (>20 years) and old-growth forests is broad, albeit fit-for-purpose, as one of the main objectives of Tier 1 defaults is to be used in areas with limited regional data. Chapter 3 employed AGB chronosequences to estimate ΔAGB in both younger and older secondary forests. This approach was useful as it gave ecozone-explicit ΔAGB curves (Chapter 3, Supporting information) which can be used to calculate ΔAGB for particular times since establishment, if needed. As expected, results show that AGB increases and ΔAGB decreases with forest age, therefore these categories provide a higher level of detail in Tier 1 reporting.

The fourth improvement was the inclusion of managed and logged forests. Even though forests under human use are increasing in extent in the (sub)tropics (Lewis et al., 2015), they are seldom accounted for in forest GHG monitoring and reporting, mostly due to limited data availability (Bustamante et al., 2016; Edwards et al., 2010; Gardner et al., 2012; Gibbs et al., 2007; Sasaki et al., 2011). In both chapters, forest plot data for managed and logged forests were included within the older secondary forest category. Ideally, Tier 1 default values for managed and logged forests should be accounted for separately; however these forests are currently not accounted for in the IPCC GHG Guidelines nor do they have enough forest plot data available to derive robust estimates and rates. Chapters 2 and 3 therefore provide an initial step towards their inclusion in Tier 1 level reporting and for large-scale forest GHG analysis.

Chapters 4 and 5 assessed AGB and ΔAGB in recovering forests and woodlands in Tanzania and in disturbed forests in Peruvian Amazonia, respectively. Until now, large-scale estimates had been lacking for both recovering dry forests and woodlands in south-eastern Africa, as well as disturbed forests in Peruvian Amazonia. Both chapters made use of NFI plot data and satellite time series, obtaining results that could be used at national Tier 2 level of IPCC reporting (Gibbs et al., 2007). Satellite time series analysis was performed for all NFI plot locations to derive time since establishment (Chapter 4) or time and intensity of disturbance (Chapter 5). In addition, available spatial data on climate, soil fertility, human accessibility and surrounding forest cover were used to account for environmental gradients and variation in human use.

One major difference between Chapters 2-3 and Chapters 4-5 is that, while Chapters 2-3 focused mainly on secondary and old-growth forests, Chapters 4-5 focused on recovering and disturbed forests, which encompass both secondary and degraded forests. By leveraging NFI plots with remote sensing analyses, forests and woodlands were assessed at national (Chapter 4) and regional (Chapter 5) levels, providing estimates that better reflect the

Table 6.1: Comparison of AGB ($\mathrm{Mg\,ha^{-1}}$) and ΔAGB ($\mathrm{Mg\,ha^{-1}\,y^{-1}}$) values from the 2006 IPCC GHG Guidelines and obtained in this thesis.

Africa												Forests and woodlands in Tanzania *(Chapter 4)*				
2006 IPCC Tier 1 default values and rates						2019 Refined IPCC Tier 1 default values and rates *(Chapters 2 and 3)*										
Ecozone	Forest type	AGB	SD	ΔAGB	SD	Ecozone	Forest type	AGB	SD	ΔAGB	SD	Ecozone	Forest type	AGB	SD	ΔAGB
Tropical dry forest	All forests	120 (120-130)	-	-	-	Tropical dry forest	All	69.6	47.5	-	-	Open and closed woodlands	Recovering	55.5	43.6	0.4
	$\leq$20 years	-	-	2.4 (2.3-2.5)	-											
	>20 years	-	-	1.8 (0.6-3.0)	-											
Tropical shrubland	All forests	70 (20-200)	-	-	-	Tropical shrubland	All	48.4	45.8	-	-		Established	56.0	54.3	-
	$\leq$20 years	-	-	0.2-0.7	-											
	>20 years	-	-	0.9 (0.2-1.6)	-											

North and South America												Peruvian Amazonia *(Chapter 5)*				
2006 IPCC Tier 1 default values and rates						2019 Refined IPCC Tier 1 default values and rates *(Chapters 2 and 3)*										
Ecozone	Forest type	AGB	SD	ΔAGB	SD	Ecozone	Forest type	AGB	SD	ΔAGB	SD	Ecozone	Forest type	AGB	SD	ΔAGB
Tropical rainforest	All forests	300 (120-400)	-	-	-	Tropical rainforest	Younger secondary	75.7	34.5	5.9	2.5	Tropical rainforests, montane forests and wetlands	Disturbed	149.3	138	4.1
	$\leq$20 years	-	-	11	-		Old secondary	206.4	80.4	2.3	1.1					
	>20 years	-	-	3.1 (1.5-5.5)	-		Old growth	307.1	104.9	1	2		Un-disturbed	259.6	198	-

reality of forests across large areas. In Tanzania, 75.5% of NFI plots in natural forests were recently recovering, while in Peruvian Amazonia 15.2% of NFI plots were considered as recently disturbed. In Chapter 2, for African tropical dry forests and shrublands, refined Tier 1 AGB defaults were provided for all forests types (Table 6.1), due to the recurrence of human use (McNicol et al., 2018). These results therefore call for reflecting on how representative the IPCC forest types are across (sub)tropical forests, and the need to account for forests that are neither secondary nor old-growth in large-scale forest GHG analyses.

Chapter 4 provides much-needed insights on ΔAGB rates in south-eastern Africa, resulting from the knowledge gap identified in Chapter 3 (Table 6.1). The ΔAGB rate derived in Chapter 4 falls within the range of 2006 IPCC values for tropical shrublands in forests $\leq$20 years, which is based on a single study in Burkina Faso (Nygård et al., 2004). The methods developed in Chapter 4 also allowed for the differentiation between recovering and established forests, with AGB estimates and uncertainties similar to the Tier 1 AGB values in African tropical dry forests shrublands obtained in Chapter 2. The AGB estimates obtained in Chapters 2 and 3, however, were much lower than the 2006 IPCC AGB default values; the use of the refined estimates will result in lower but more realistic estimates of aboveground forest carbon stocks and sinks. 2006 IPCC defaults were based on the 2003 IPCC Good Practice Guidance (IPCC, 2003) and did not distinguish between successional forest types. Since no references were provided for the 2003 AGB default estimates, the reason of this difference cannot be traced back.

Chapter 5 assessed the extent and degree of disturbance in forests Peruvian Amazonia, providing AGB and ΔAGB estimates for disturbed and undisturbed forests. Until now, there have been only local studies of anthropogenic forest disturbance and recovery in Peruvian Amazonia (Cutire Tinta and Ramirez Chávez, 2017; Hergoualc'h et al., 2017; Málaga et al., 2021; Quintero Cardozo et al., 2020; Schwartz et al., 2017). Thus, large-scale studies of forest disturbance in the Amazon Basin are greatly needed. Since disturbed forests in Chapter 5 comprise secondary and degraded forests, the ΔAGB estimates obtained in this study are not directly comparable to Tier 1 default AGB and ΔAGB rates. Nevertheless, the ΔAGB rate for disturbed forests falls between our Chapter 3 estimates for younger and older secondary forests in tropical rainforests (Table 6.1), suggesting that disturbed forests consist partially of forests recovering from major disturbances such as secondary forests. In the case of seemingly-undisturbed forest plots in Chapter 5, even though these plots cannot be completely categorised as undisturbed, their AGB estimates and uncertainty are in line with Tier 1 AGB values provided in Chapter 2 for old-growth tropical rainforests in the Americas, as well as with the 2006 IPCC AGB range (Table 6.1). For the assessment of old-growth tropical rainforests, permanent plots in research networks such as RAINFOR provide long-term monitoring of AGB and ΔAGB, spanning over several decades, can be used to provide Tier 2 values in old-growth forests in Peruvian Amazonia (Vicuña Miñano et al., 2019).

Chapter 3 provides, for the first time, appropriate Tier 1 ΔAGB values for old-growth rainforests in North and South America. Prior to this, the IPCC 2006 ΔAGB rates for rainforests over twenty years were mistakenly obtained from coarse wood productivity rates in old-growth forest plots in Neotropical forests (Malhi et al., 2004). Coarse wood productivity is defined as the rate in which carbon is fixed into aboveground coarse woody biomass structures, and does not account for processes such as AGB loss due to mortality. Because of this, the 2006 IPCC ΔAGB rates for forests over 20 years are 34.7% and 210% larger than what Chapter 3 estimated for older secondary and old-growth forests, respectively. In 2004, a parallel study carried out in a subset of the plots of Malhi et al 2004 estimated ΔAGB for the Amazon Basin, obtaining a ΔAGB rate of 0.98 $\mathrm{Mg\,ha^{-1}\,y^{-1}}$ (Baker et al., 2004), similar to the rate proposed for old-growth forests in Chapter 3.

In summary, Chapters 2 and 3 have provided updated Tier 1 AGB values and ΔAGB rates, while Chapters 4 and 5 have provided estimates which can be used for Tier 2 reporting and that were not available until now. Methodological approaches for the integration of forest plot data and remote sensing varied in accordance to data availability, levels of study, and forest type of interest. The use of available global remote sensing products was predominant in the Chapter 2, while for the Chapters 4 and 5 the use of satellite time series for all NFI plot locations was performed. Our Tier 1 AGB and ΔAGB estimates can be improved over time, as Chapters 2 and 3 provide a framework that can be updated in the near future. Chapters 4 and 5 showcase how NFIs can be leveraged towards developing Tier 2 estimates, even when permanent forest plots are lacking in disturbed forests. The data integration approach followed in Chapters 4 and 5 can be used with other NFI data, which is increasingly becoming available (Nesha et al., 2021). Furthermore, results from Chapters 4 and 5 highlight the limitations of using Tier 1 IPCC forest types; as more data becomes available, it is essential to include disturbed or degraded forests in large-scale analysis of forest carbon stocks and sinks in the subtropics.

6.1.2 Understanding the drivers of AGB in disturbed forests across large scales (R.O.2)

In this thesis, the integration of forest plot data with remote sensing has allowed for the evaluation of the causes of variation in AGB and ΔAGB across forests in the (sub)tropics. In Chapters 2 and 3, variations of AGB based on disturbance or forest establishment were broadly disaggregated into IPCC-defined forest types. Both chapters mostly relied on available research plot data, which mainly consisted of secondary and old-growth forests.

Currently, research plots are limited in the African dry forests as well as in disturbed forests in Peruvian Amazonia; therefore, the integration of NFI plot data with remote sensing in Chapters 4 and 5 allowed for the exploration of the main drivers of AGB in both regions. Due to their high number, methodological consistency and broad coverage, NFI plots are ideal to explore the potential effect of fine-scale variations in environmental conditions and human use on AGB in (sub)tropical forests. Moreover, integrating NFI plot data with satellite time series analysis allowed for the assessment of the effects of forest recovery (Chapter 4) as well as time since disturbance and disturbance intensity (Chapter 5). In this respect, the potential effects of time since establishment or disturbance, disturbance intensity and variations in environmental conditions and human use were evaluated for recovering forests (Figure 6.1). Furthermore, Chapter 5 looks into the effects of these potential drivers on tree species diversity and its recovery. In the Neotropics, tree species diversity has been linked to increased carbon storage (Poorter et al., 2015) and its link to climate change makes the study of biodiversity and its recovery essential for forest-based mitigation practices (Otto-Portner et al., 2021).

Understanding which conditions result in higher levels of biomass and tree species diversity in forests recovering from disturbances is essential for forest conservation and restoration planning. Forests with slow or inexistent recovery rates can be prioritised for conservation, whereas areas with conditions that could foster high recovery rates could be prioritised for landscape restoration activities. In addition, to understand current levels of AGB in recovering forests, it is essential to look into the effects of disturbance intensity. Understanding these effects can lead to better predictions of current levels of AGB in recovering disturbed forests, which would result in better large-scale forest carbon stock estimates.

Assessing the effect of time

Across all chapters the effect of time on AGB stocks was evaluated. Chapters 2 and 3 estimated AGB values and ΔAGB rates through the classification of time since major disturbance. In Chapter 2, this classification was done by disaggregating younger secondary forests, older secondary forests and old-growth forests. This was done either by using research plot data in secondary and old-growth forests or by inferring the successional forest type of NFI plots through the use of global spatial datasets (Potapov et al., 2017; Tyukavina et al., 2016). As expected, AGB values increased with time (Figure 2.3), from younger secondary to old-growth forests.

In Chapter 3, to obtain ΔAGB rates in secondary forests, forest age data from research forest plots in secondary forests was used (Anderson-Teixeira et al., 2016; Cook-Patton et al., 2020; Poorter et al., 2016). With this information, growth curves were estimated for each individual site, up to the maximum forest age available (Figure 3.4). This allows for the estimation of AGB in secondary forests at a given forest age, and for the derivation of ΔAGB for a given period. As expected, ΔAGB decreased with time (Figure 3.3). In old-growth forests, permanent forest plots were used (Brienen et al., 2015a; Lewis et al., 2009; Qie et al., 2017), which directly estimate ΔAGB for each plot.

While both Chapter 4 and Chapter 5 integrate NFI plot data with satellite time series, Chapter 4 centres on forest establishment while Chapter 5 centres on forest disturbance. Thus, Chapter 4 looks directly at AGB recovery, while Chapter 5 relies on comparing AGB and tree species diversity in disturbed forest plots with nearby undisturbed forest plots to estimate AGB recovery.

Due to the objectives of both chapters, as well as differences in forest ecozones and climate – in particular water availability – the remote sensing approaches differed. Chapter 4 used Landsat-derived time series of forest cover probability, while Chapter 5 used Landsat-derived NDMI time series. While NDMI time series works well in humid forest ecosystems, capturing minor and major disturbances, dry forest ecosystems characterised by strong seasonality make the use of NDMI challenging (Decuyper et al., in review). Thus, for dry forest ecosystems with mostly sparse canopies, Chapter 4 opted for an algorithm based on forest cover probability using a threshold of 10% tree cover. While detecting forest establishment proved to be challenging, as this tends to be a gradual process, this approach was chosen since one of the main objectives of Chapter 4 was to evaluate recovery. Conversely, given that Chapter 5 focused on disturbed forests in a region with high water availability, the use of NDMI time series was selected. In this respect, a cautious selection of the remote sensing approach, in line with the study objectives and local context, has to be carried out prior to its integration with forest plot data.

In Chapter 4, a significant positive effect of time since forest establishment was observed for recovering forests and woodlands in Tanzania. This result suggest that recovering forests and woodlands in this region are overall accumulating AGB after a disturbance, and therefore on a whole are acting as partial carbon sinks. Previously, local studies have been carried out in similar regions (Chidumayo, 1990; Malimbwi et al., 2005; McNicol et al., 2015b), though for forests recovering from particular disturbances. The insights provided in Chapter 4 apply to Tanzanian forests and woodlands as a whole, thus accounting for varying types of disturbance such as fuelwood extraction, grazing or the recurrence of fires. Insights derived from these chapter can be used in national forest GHG reporting as well as in carefully-designed ecosystem restoration plans.

Chapter 5 evaluated the effect of time since disturbance on AGB and tree species diversity, as well as their potential recovery towards undisturbed levels. Time since disturbance had a significant positive effect on AGB in recovering disturbed forests. This result suggests that, overall, recently disturbed forests in Peruvian Amazonia are accumulating AGB over time through their recovery. Until now only local studies in recovering disturbed forests had been carried out in Peruvian Amazonia (Hergoualc'h et al., 2017; Málaga et al., 2021). There was a positive significant effect on the similarity of species composition between disturbed and nearby undisturbed forests, suggesting that after disturbance these forests have the capacity to recover in species composition towards undisturbed levels. When looking at AGB recovery and species diversity and its recovery, however, there was no effect of time since disturbance. This lack of effect could be due to the small NFI plot size, which in this case ranged from 0.05 to 0.1 ha. Overall, Chapter 5 provides much-needed insights into the role of disturbed forests in Peruvian Amazonia and their recovery towards undisturbed levels. These insights can be used both for conservation of existing disturbed forests as well as for restoration planning.

Higher ΔAGB rates were observed in disturbed forests in Peruvian Amazonia compared to recovering forests and woodlands in Tanzania. Lower ΔAGB rates in Tanzanian recovering forests and woodlands, which mainly consist of closed and open woodlands, are in line with what one would expect in south-eastern African dry tropics. Tanzanian woodlands are characterised by strong seasonality in water availability, recurrence of fires and ongoing human use. Higher ΔAGB rates in disturbed forests in Peruvian Amazonia are consistent with our estimates in Chapter 3 for tropical rainforests, and could be due to a larger extent of secondary forests in the Amazon Basin followed by lower levels of ongoing minor disturbance (Bullock and Woodcock, 2021; Chazdon et al., 2016), in combination with relatively high levels of water availability throughout the year. While the classification of secondary forests is useful in contexts where regeneration following complete forest removal is common, imposing this classification on all (sub)tropical forest ecosystems, particularly dry forests and woodlands, while not accounting for varying degrees of disturbance intensities and the presence of ongoing disturbance will ultimately not yield realistic estimates.

Effects of disturbance intensity

Throughout all four chapters, disturbance intensity was included, though at different levels of detail. Chapters 2 and 3 included mostly major disturbances, by mainly considering secondary forests and old-growth forests. In Chapter 4, disturbance intensity was not directly assessed, though effect of human accessibility as a proxy for human disturbance was implicit in both established and recovering forests.

Chapter 5 assessed the effect of disturbance intensity on AGB and tree species diversity, finding it to be a strong negative driver of AGB and tree species diversity, as well as their recovery towards undisturbed levels. The detection of disturbance intensity in NFI plot locations offers a glimpse into the extent and degree of disturbed forests in Peru. By using NDMI anomalies as a proxy for disturbance intensity, Chapter 5 assesses the gradual effect of disturbance intensity on AGB and tree species diversity. The need to look at forest disturbance as a gradient has been previously suggested (Ryan et al., 2012), particularly for the assessment of overall levels of disturbance across large areas. In this respect, this chapter's results can be applied to Peru's national reporting of forest carbon stocks and sinks, by offering estimates on disturbance intensity and its effects on carbon stocks. Furthermore, our methodology can be extended to other areas where a high number of forest plots are available, such as other countries in the tropics currently finishing their NFIs (Bustamante et al., 2016).

Effects of environmental and human use conditions

For both recovering and established forests and woodlands in Chapter 4 and for disturbed forests in Chapter 5, the effect of climate was evaluated through the inclusion of climatic water deficit (CWD). In Chapter 5, CWD had a significant positive effect on AGB and its recovery towards undisturbed forest levels, as hypothesised. The effect of water availability on AGB has been observed before in secondary (Heinrich et al., 2021; Poorter et al., 2016) as well as undisturbed forests (Álvarez-Dávila et al., 2017; Sullivan et al., 2017), thus our results confirm this for recovering forests. On the other hand, in Chapter 4 the direction of the effect of CWD on AGB was contrary to the initial hypothesis. This unexpected result offers insight into ongoing research gaps. Currently, research on the variation of carbon stocks in African woodlands – and in general on dry forests and savannahs in the tropics – remains limited, with varying ecological processes among continents (Dexter et al., 2018; Lehmann et al., 2014).

The confounding effects of soil fertility on AGB in Chapter 4 and the absence of effects of soil fertility on AGB and its recovery in Chapter 5 suggest that the use of gridded spatial predictors provides may not fully represent reality. Gridded soil predictions have been used in other studies, with weak or no effects (Poorter et al., 2016; Poorter et al., 2015). In this respect, as gridded predictions of soil characteristics continue to improve over time, a more in-depth evaluation of other soil characteristics – such as soil hydromorphy – might provide insights into the role of soils on AGB in recovering forests.

Surrounding tree cover, which was used as a proxy for land use conversion, was significantly positively related to AGB in both chapters. These results highlight the importance of including information on current or previous human use when assessing forest ecosystems at large scales. While recovering forest plots in Tanzania (n=1,479) had on average 26% (SD=9.5) surrounding tree cover in a radius of 500 meters, disturbed forest plots in disturbed forests in Peruvian Amazonia (n=280) had a much higher average of 92% (SD=9.8) surrounding tree cover in a radius of 5,000 meters. Surrounding trees can act as sources of propagules, and therefore can contribute to AGB accumulation as well as to diversity recovery, depending on the diversity of surrounding forests. In Chapter 5, a positive effect of tree cover was observed for species diversity, but not for its recovery. This could be due to the overall high levels of surrounding tree cover in disturbed forests plots in the study region, or due to the lack of information of tree species diversity within a plot's surrounding tree cover.

For both chapters, open-source anthropogenic data was used (OpenStreetMap Contributors, 2019; 2020) as well as a dataset of potential navigable rivers for Chapter 5 (Schielein, 2017). While these potential drivers rendered weak or no significant effects on AGB, species diversity or their recovery in Chapter 5, this could be due to the generally high accessibility levels of most forest NFI plots in both chapters. To guarantee feasibility, the design and distribution of NFI plots must carefully consider the time required to get to each plot cluster (Tomppo et al., 2014).

Chapters 3 and 4 provide a first attempt at combining NFI plots with available spatial datasets to analyse how environmental conditions and human use affect AGB in recovering and disturbed forests. The representability and high number of NFI plots have enabled working with consistent ground data, which is very limited to come by. However, this approach has the challenge of working with clustered plots of small sizes. On one hand, small plots have the disadvantage of increasing the uncertainty of AGB estimates (Mauya et al., 2015). On the other hand, due to their spacing and small size, they can be combined with high-resolution remote sensing data in a straightforward manner.

6.2 Reflection and Outlook

6.2.1 Increasing research plot availability in (sub)tropical forests

Quantifying carbon stocks and sinks in (sub)tropical forests is imperative for their inclusion in climate change policy. In addition, assessing what local factors influence a forest's ability to store and sequester carbon can provide insights for forest-based mitigation through restoration. For many decades, research plots in undisturbed and disturbed forests have been monitored using similar measuring protocols, and the data therein have been made publicly accessible. This increased accessibility of research plot data has enabled intercontinental studies of carbon stocks and sinks in undisturbed (Hubau et al., 2020; Sullivan et al., 2017) and disturbed forests (Cook-Patton et al., 2020). Chapters 2 and 3 of this thesis have integrated existing forest plot data to update IPCC GHG Tier 1 Guidelines, and have provided a transparent methodology that can be updated as more forest plot data becomes available.

Chapters 2 and 3 have also contributed towards understanding where forest plot data gaps remain (Figures 2.5 and 3.7), mostly located in the subtropics and dry tropics. Currently, in addition to existing permanent plots in tropical humid forests, efforts to establish new permanent monitoring plots in areas with limited forest monitoring are underway. Future projects such as SECO (blogs.ed.ac.uk/seco-project/) seek to monitor carbon stocks and sinks in tropical dry forests and woodlands, with adapted protocols for the setup of permanent plots (Moonlight et al., 2021). Funding long-term monitoring projects is challenging due to current financing schemes in academia, which are often linked to short-term outputs. To address this, climate change research agendas should invest in the long-term continuation of forest monitoring in permanent plots (ForestPlots.net et al., 2020).

6.2.2 Leveraging NFI plots

An additional source of plot data which often goes untapped for research in forest ecology is NFI plots in countries with (sub)tropical forests. In recent years, new NFI data in (sub)tropical forests have become available: by 2020, 57 out of 99 countries with (sub)tropical forests were making use of NFI data in their forest GHG reporting, 11 of which were using NFIs measured from 2015 onwards (Nesha et al., 2021). Among other purposes, NFIs are carried out to monitor carbon stocks in a countries forests, seeking to adequately sample and represent large forest areas.

While NFI plot data have been used in previous studies in (sub)tropical forests (Chaves et al., 2020; Pelletier et al., 2018; Pelletier et al., 2017; Soehartono and Newton, 2000), its combination with satellite time series remains limited. In this respect, Chapters 4 and 5 provide a novel data integration approach in which NFI plot data can be combined with remote sensing analysis and spatial datasets to address large-scale ecological questions. With several NFIs currently underway, this approach can be used to explore persistent data gaps in forest ecology.

In addition, re-measured NFI plots offer the opportunity of directly measuring ΔAGB (Pelletier et al., 2018). This, in combination with information on previous land use and disturbance history derived through remote sensing could offer the possibility of looking at variations of ΔAGB in the near future. As NFIs enter their second round of measurements, they can be leveraged for this purpose.

6.2.3 Advancements in remote sensing of forest dynamics

In recent years, new techniques for the detection of forest dynamics have been developed. In parallel, the Landsat archive has been increasing in length of time, providing consistent land cover information at medium spatial resolution (approx. 30 m) for over 35 years.

Globally, attempts to detect changes in AGB from forest degradation — something that is currently needed (Bustamante et al., 2016; Herold et al., 2011; Mitchard, 2018) — using satellite images have been carried out in the last years (Baccini et al., 2017). Also, attempts to detect forest regrowth and forest age have been carried out globally (Besnard et al., under review; Hansen et al., 2013). There are still many improvements to be made in the global mapping of ΔAGB and forest dynamics (Hansen et al., 2019; Mitchard, 2018; Tropek et al., 2014), as current estimates cannot be directly combined with ground data for the purpose of analysing ΔAGB, as they are either too coarse (Baccini et al., 2017; Besnard et al., in review) or focus on particular time periods of regrowth (Hansen et al., 2013). However, as these methods improve over time it might be possible to analyse forest dynamics with global remote sensing products at a large scale.

At regional scales, locally-calibrated satellite time series can be used to detect forest disturbance and recovery in tropical humid forests as well as dry forests and woodlands (Bullock and Woodcock, 2021; DeVries et al., 2015a; Hamunyela et al., 2020; Sexton et al., 2016). Chapters 4 and 5 made use of these methods to assess the effect of forest disturbance and recovery. However, some questions remain unanswered. For example, current remote sensing algorithms such as AVOCADO (Decuyper et al., in review) do not distinguish between human and natural disturbances, thus the effects of human-induced land conversion and logging were not addressed separate from natural disturbances in either chapter. Advances in this direction will enable the exploration of the effects of disturbance type across large regions. In addition, even though the remote sensing analysis used in Chapter 5 was able to provide number of disturbance events per plot, 85.4% of disturbed plots had only one disturbance event, thus inhibiting the assessment of the effect of frequent disturbances. Figure 6.2 shows the number of disturbances per disturbed forest

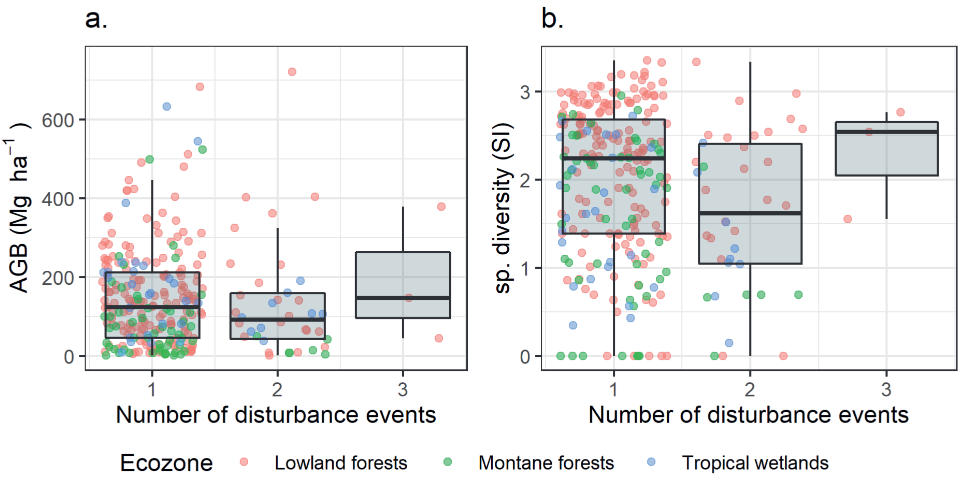

Figure 6.2: Aboveground biomass (a) and Shannon diversity index (b) in disturbed NFI plots in Peruvian Amazonia per number of disturbance events detected. Disturbed NFI plots with 1 (n=239 plots), 2(n=38 plots) and 3 (n=3 plots) disturbance events across lowland forests, montane forests and tropical wetlands in Peruvian Amazonia.

plot and, though no results could be derived due to the limited number of NFI plot data in disturbed forests with more than one disturbance, visually a decrease in biomass can be observed.

New spaceborne missions focused on satellite-based AGB estimation are underway. Since 2019 and for a scheduled period of two years, the GEDI mission (Dubayah et al., 2020) will provide Light Detection and Ranging (LIDAR) measurements of canopy height and vertical structure. These measurements are currently being calibrated and validated against coinciding airborne laser scanning and ground plot data (Dubayah et al., 2020; Silva et al., 2018). Parallel to this, since its launch in 2018 ICESat-2 has been collecting photon counting LIDAR data, with the purpose of measuring canopy height and structure; though, for the purpose of estimating forest height and structure in tropical forests its combination with GEDI data is advised (Neuenschwander and Pitts, 2019). BIOMASS and NISAR, both expected to be launched in 2022, are expected to provide wall-to-wall Synthetic Aperture Radar (SAR) data, with the objective of monitoring canopy height to estimate forest AGB and detect forest disturbance (Kellogg et al., 2020; Quegan et al., 2019). From the ground up, forest plots will actively serve as a baseline for calibration and validation of these products (Chave et al., 2019). These new advancements could make the assessment of AGB along gradients in environmental conditions and human use possible in areas for which no research plots or NFI pots are available.

6.2.4 Near-future opportunities to understand and quantify (sub)tropical forest carbon stocks and sinks

Recent increase in ground and satellite data availability, as well as improvements in the detection and mapping of forest dynamics and AGB are currently underway. In this thesis, Chapters 2 through 5 have shown how data integration can aid in the understanding and quantifying forest carbon stocks and sinks, with the purpose of providing a more realistic estimate of the contribution of (sub)tropical forests in climate change mitigation.

Harris et al. (2021) recently developed a data-integration framework to estimate net GHG fluxes in natural forests, combining ongoing monitoring efforts, one of which being the results obtained in Chapter 3. However, degraded forests were not included in this framework, since at the time of the study this kind of information was very limited. As we gain a better understanding of (sub)tropical forest carbon stocks and sinks in degraded forests, such data-integration frameworks can be refined in the near future to account for these forest types. Bustamante et al. (2016) reflects on the need of assessing forest degradation and recovery at large scale by relying on a combination of ground data and remote sensing.

Currently, IPCC Tier 1 estimates provided in Chapters 3 and 4 are coupled with high uncertainties, as they strive to represent large forest areas with high variability according to local factors. As countries advance in forest monitoring, it is expected that they will shift towards higher Tiers of GHG reporting (Gibbs et al., 2007; Nesha et al., 2021), and thus disaggregate forests according to local forest ecozones and presence of disturbance. Current collaborations between research institutes and government are underway (Petersen et al., 2018), as research-led integrated forest monitoring is being adopted in the tropics. Maintaining open communication lines between research and governments is necessary to guarantee the integration of new information into national forest GHG reporting.

Identifying and understanding drivers of AGB and ΔAGB in (sub)tropical forests is an essential next step to not only reduce uncertainties in GHG reporting, but to support the design and implementation of research-based forest conservation approaches needed to achieve the climate change mitigation potential of (sub)tropical forests. In this respect, spatially-explicit data on potential environmental and human use drivers is increasingly becoming available. Data on climatic variables (Chave et al., 2014; Fick and Hijmans, 2017), soil characteristics (Hengl et al., 2017; ISRIC, 2020), tree cover (Hansen et al., 2013), fire size and duration (Andela et al., 2019), and human accessibility (OpenStreetMap Contributors, 2019; 2020) are constantly improving. This currently enabled large-scale studies centred on understanding the effect that environmental conditions and human use have on AGB and ΔAGB in Chapters 4 and 5, as well as other studies (Becknell et al., 2012; Cook-Patton et al., 2020; Heinrich et al., 2021; Toledo et al., 2011). One of the main drivers that was not included due to limited spatial data availability was previous land use.

Previous studies suggest that the type and length of previous land use is a determinant of AGB recovery, with long and intense forms of land use negatively impacting ΔAGB (Jakovac et al., 2021; N'Guessan et al., 2019; Wandelli and Fearnside, 2015). Currently, the automatic detection of land use following forest removal is not straightforward, though this is currently being improved (Masolele et al., in review). This improvement could make the analysis of the effects of land use history on AGB in forests regrowing on abandoned land possible in the future.

Other methodological approaches are being carried out to spatially predict AGB and ΔAGB, particularly in secondary forests. For example, Cook-Patton et al. (2020) — from which ground data in secondary forests was obtained in part for Chapter 3 – spatially predicted ΔAGB for younger secondary up to 30 years, using forest age and 66 environmental covariates using Random Forest (RF), a machine learning algorithm. This approach is best used when the main purpose is to develop a model with high predictability, and is less centred on understanding the relationships between the covariates and variable of interest.

6.2.5 Current and future opportunities for collaboration

Generation of knowledge on carbon stocks and sinks in (sub)tropical forests requires ongoing collaboration. Forest plot networks have proven to be essential to study forest ecosystems, providing ground measurements used to track changes in carbon stocks and sinks over time (ForestPlots.net et al., 2020). Meanwhile, national forest monitoring efforts in countries with (sub)tropical forests have been increasing (Nesha et al., 2021). Parallel to this, a series of ongoing and planned spaceborne missions are and will be producing remote sensing data that, when combined, will result in improved estimates of carbon stocks and sinks as well as improved detection of forest dynamics (Hansen and Loveland, 2012; Herold et al., 2019; Reiche et al., 2016; Silva et al., 2021; Song et al., 2017).

In order to advance the current state of knowledge on forest carbon stocks and sinks in the (sub)tropics, ongoing collaboration is indispensable. Forest ground data is essential for the validation and calibration of AGB and ΔAGB remote sensing data, as it provides information that cannot be derived from space, such as wood density or tree species (Chave et al., 2019; Mitchard et al., 2014). Conversely, remote sensing can aid in the spatial planning of NFIs, as well as provide information on forest dynamics for the analysis of forest plot data (Bustamante et al., 2016; Chambers et al., 2007; Espírito-Santo et al., 2014; McRoberts and Tomppo, 2007). In this respect, guaranteeing collaboration for the study of (sub)tropical forests requires developing and maintaining integrated forest monitoring frameworks, sharing leadership roles among researchers in the global north and those in (sub)tropical countries, as well as ensuring long-term financing mechanisms

(Baker et al., 2019; Baker et al., 2020; Bustamante et al., 2016; ForestPlots.net et al., 2020).

Furthermore, collaboration is necessary not only within academia, but also between research and policy. Currently, the inclusion of new ecological knowledge in climate change policy is not straightforward. It is subject to extent of personal networks and understanding of policy processes (Oliver and Cairney, 2019). To influence climate change policy, opportunity windows have to be identified on an ongoing basis, relying on ongoing links between researchers, practitioners and policy makers (Baker et al., 2020; Rose et al., 2020).

As recent international agreements for climate change mitigation come into force (Turnhout et al., 2017), better knowledge of tropical forest carbon stocks and sinks, particularly related to disturbance and recovery, will become more essential (Houghton et al., 2015). Moving forward, conscientious collaboration will be required to fill new and persistent knowledge gaps.

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About the author

Daniela Requena Suarez was born on March 16, 1991 in Lima, Peru. Though she grew up mainly in the capital, she spent many summers with her family in San Jerónimo de Tunán and la Oroya, Junín, where she enjoyed the two best things that the Peruvian Andes have to offer: natural landscapes and pachamanca. During her childhood, both of her parents nurtured her love of nature, art and travelling, which is believed to be one of the main reasons why she ended up deeply interested in the natural sciences.

Following her interest in nature, Daniela pursued a Bachelors in Forestry at Universidad Nacional Agraria la Molina (UNALM) in Lima from 2008 until 2013. During these years she had the opportunity to travel throughout Peru, studying tropical forests in detail, and specialising in tropical forest ecology and conservation. These skills were put to test on her first job at Consultores Asociados en Naturaleza y Desarrollo (CANDES), where she started as a field assistant and worked her way up to leading her own field team. During this period, Daniela had the opportunity to travel to the Peruvian Andes and Amazonia for extended periods of time. This period was also her first encounter with remote sensing, assisting in the interpretation of high-resolution images of Andean peatlands.

Her interest in research made her get in touch with UNALM professor Carlos Llerena, who suggested she follow a Masters at Oxford University. Thus, Daniela applied to the MSc in Biodiversity, Conservation and Management offered by the School of Geography and the Environment (SoGE). To fund her MSc studies, she was granted the BCM Award and the ITTO Fellowship Award. During her MSc studies she continued specialising in tropical forest ecology and conservation, carrying out a thesis on shihuahuaco (*Dipteryx* spp.) seed collection in Ucayali, Peru, under the supervision of Constance McDermott and Aoife Bennett and financed by Fauna & Flora International's Global Trees Campaign Master's Bursary.

After completing her MSc studies, Daniela stayed in Oxford working as a postgraduate research assistant at the Ecosystems Lab, under the supervision of Cécile Girardin and Yadvinder Malhi. In parallel, she also carried out an research internship at Botanic Gardens Conservation International (BGCI) under the supervision of Malin Rivers, where she assisted in the Red-Listing of tree species in the Canary Islands and Amazonia. During this time, Daniela's interest in tropical forest ecology and conservation heightened.

Pursuing a PhD in tropical forest ecology was a logical next step, so when Daniela saw an PhD position on forest ecology and remote sensing offered by Wageningen University & Research (WUR) and by the Center for International Forestry Research (CIFOR) —organisations whose work she had been admiring for a long time —she immediately applied. She was warmly welcomed by Martin Herold, Niki De Sy and Danaë Rozendaal at the Laboratory of Geo-Information Science and Remote Sensing, where she had a head-first encounter with remote sensing of tropical forests. Daniela's PhD thesis titled "Aboveground carbon stocks and sinks in recovering tropical forests", which you are now reading, is part of CIFOR's Global Comparative Study. During her PhD research, she has led several successful international collaborations and has presented her research in international conferences and symposia. In addition, as part of the PE&RC PhD Council, she has organised several activities, including PE&RC's 2019 symposium.

Daniela's current interests still lie in tropical forest ecology and conservation. She is deeply interested in using remote sensing in combination with field data to analyse disturbance-recovery dynamics of tropical forests and to address existing knowledge gaps through collaborative approaches. Following her PhD defence, she will stay at Wageningen University & Research as a post-doctoral researcher for a few months, as she carefully plans her next steps.

Peer-reviewed Journal Publications

Harris, N. L., D. A. Gibbs, A. Baccini, R. A. Birdsey, S. de Bruin, M. Farina, L. Fatoyinbo, M. C. Hansen, M. Herold, R. A. Houghton, P. V. Potapov, **D. Requena Suarez**, R. M. Roman-Cuesta, S. S. Saatchi, C. M. Slay, S. A. Turubanova, and A. Tyukavina (2021). "Global maps of twenty-first century forest carbon fluxes". *Nature Climate Change*. DOI: 10.1038/s41558-020-00976-6.

Requena Suarez, D., D. M. Rozendaal, V. De Sy, D. A. Gibbs, N. L. Harris, J. O. Sexton, M. Feng, S. Channan, E. Zahabu, D. S. Silayo, A. Pekkarinen, C. Martius, and M. Herold (2021). "Variation in aboveground biomass in forests and woodlands in Tanzania along gradients in environmental conditions and human use". *Environmental Research Letters* 16.4, 44014. DOI: 10.1088/1748-9326/abe960.

Requena Suarez, D., D. M. Rozendaal, V. De Sy, O. L. Phillips, E. Alvarez-Dávila, K. Anderson-Teixeira, A. Araujo-Murakami, L. Arroyo, T. R. Baker, F. Bongers, R. J. Brienen, S. Carter, S. C. Cook-Patton, T. R. Feldpausch, B. W. Griscom, N. Harris, B. Hérault, E. N. Honorio Coronado, S. M. Leavitt, S. L. Lewis, B. S. Marimon, A. Monteagudo Mendoza, J. Kassi N'dja, A. E. N'Guessan, L. Poorter, L. Qie, E. Rutishauser, P. Sist, B. Sonké, M. J. Sullivan, E. Vilanova, M. M. Wang, C. Martius, and M. Herold (2019b). "Estimating aboveground net biomass change for tropical and subtropical forests: Refinement of IPCC default rates using forest plot data". *Global Change Biology* 25.11, 3609–3624. DOI: 10.1111/gcb.14767.

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Pérez Chaves, P., **D. Requena Suarez**, C. Lozano Alvarez, and J. Rosero Alvarado (2013). "Dendrocronología aplicada para fijación de carbono en plantaciones de teca (Tectona grandis) en el Fundo La Génova, Junín - Perú". *Xilema* 26.1, 35–41. DOI: 10.21704/X.V26I1.613.

Other Scientific Publications

Requena Suarez, D., D. M. Rozendaal, V. De Sy, C. Martius, E. Zahabu, D. S. Silayo, A. Pekkarinen, D. A. Gibbs, N. L. Harris, J. O. Sexton, S. Channan, M. Feng, P. Durán Montesinos, A. Arana Olivos, R. De la Cruz Paiva, M. Decuyper, N. Malaga, and M. Herold (2020). "Using National Forest Inventories (NFIs) and remote sensing to unravel drivers of C stocks and sinks in tropical forests". In: *BES Festival of Ecology*.

Requena Suarez, **D.**, D. M. A. Rozendaal, V. De Sy, O. L. Phillips, E. Álvarez-Dávila, K. Anderson-Teixeira, A. Araujo-Murakami, L. Arroyo, T. R. Baker, T. Bongers, R. J. W. Brienen, S. Carter, S. Cook-patton, T. R. Feldpausch, B. Griscom, N. Harris, B. Herault, E. N. Honorio Coronado, S. M. Leavitt, S. L. Lewis, B. S. Marimom, A. Monteagudo Mendoza, J. Kassi N'dja, A. E. N'Guessan, L. Poorter, L. Qie, E. Rutishauser, P. Sist, B. Sonké, M. J. P. Sullivan, E. Vilanova, M. M. H. Wang, C. Martius, and M. Herold (2019a). "Estimating above ground net biomass change in tropical and subtropical forests". In: *XXV IUFRO World Congress, Pesquisa Florestal Brasileira*, v. 39 217–218.

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (4.5 ECTS)

- Tropical forest cover gain and carbon sequestration for climate change mitigation

Post-graduate courses (9.6 ECTS)

- Global comparative study on REDD+ Workshop; CIFOR (2017)
- Geocomputation using free and open source software; Spatial Ecology (2018)
- Global comparative study on REDD+ Workshop; CIFOR (2018)
- Geostatistics; PE&RC (2018)
- The Art of Modelling; PE&RC (2019)
- Peru National REDD+ Workshop; CIFOR (2020)

Invited review of (unpublished) journal manuscript (2 ECTS)

- Scientific Reports: tropical forest carbon stock estimation (2019)
- Environmental Development: tropical forest carbon stocks and sinks (2020)

Competence strengthening / skills courses (7.1 ECTS)

- Essentials of scientific writing and presenting; Wageningen in'to Languages (2017)
- Project time and management; PE&RC (2017)
- Scientific publishing; PE&RC (2017)
- Scientific writing; Wageningen in'to Languages (2019)
- Scientific artwork; WGS (2019)

- Reviewing a scientific manuscript; WGS (2020)
- Career perspectives; VLAG (2020)

Scientific integrity/ethics in science activities (0.6 ECTS)

- Scientific integrity; WIAS (2018)

PE&RC Annual meetings, seminars and the PE&RC weekend (2.4 ECTS)

- PE&RC First year's weekend (2017)
- WGS PhD Workshop Carousel (2018)
- PE&RC Day (2018)
- PE&RC Day (2019)
- PE&RC Midterm weekend (2019)

National scientific meetings, local seminars, and discussion groups (4.6 ECTS)

- Treub symposium; the Netherlands (2017)
- Discussion group - climate – forests – food; the Netherlands WUR (2017-2018)
- Global landscapes forum; Germany (2018)
- Workshop on remote sensing and forest monitoring; the Netherlands (2018)
- Discussion group R users meeting; the Netherlands (2018-2019)
- Workshop on earth observations and terrestrial carbon cycling; the Netherlands (2019)
- Seminar on performance assessment of forest-based climate change mitigation initiatives; the Netherlands (2020)
- Frontiers in forest monitoring: research horizons for global forest watch; online (2020)
- Geo for Good Summit; online (2020)
- Seminar: estimation for AGB change in (sub)tropical forests; Peru (2020)
- FTA Science conference; online (2020)
- GEO-INPE Webinars on Brazil's forest monitoring systems; online (2021)

International symposia, workshops and conferences (5.6 ECTS)

- IUFRO World Congress; Brazil (2019)
- Festival of Ecology; online (2020)

Committee work (3.5 ECTS)

- PE&RC PhD Council (2018-2021)

BSc/MSc thesis supervision (3 ECTS)

- Jos Westdijk: deriving the underlying variables behind AGB on ground across African moist tropical forests (2021)

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