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

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Supplementary material for this article is available online

Abstract

For monitoring and reporting forest carbon stocks and fluxes, many countries in the tropics and subtropics 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 forest AGB values originated from 2006, and are relatively crude estimates of average values 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 2006 IPCC Guidelines for GHG Inventories, we updated the default AGB values for tropical and subtropical forests based on AGB data from >25 000 plots in natural forests and a global AGB map where no plot data were available. We calculated refined AGB default values per continent, ecological zone, and successional stage, and provided a measure of uncertainty. AGB in tropical and subtropical forests varies by an order of magnitude across continents, ecological zones, and successional stage. Our refined default values generally reflect the climatic gradients in the tropics, with more AGB in wetter areas. AGB is generally higher in old-growth than in secondary forests, and higher in older secondary (regrowth >20 years old and degraded/logged forests) than in young secondary forests (⩽20 years old). While refined default values for tropical old-growth forest are largely similar to the previous 2006 default values, the new default values are 4.0–7.7-fold lower for young secondary forests. Thus, the refined values will strongly alter estimated carbon stocks and fluxes, and emphasize the critical importance of old-growth forest conservation. We provide a reproducible approach to facilitate future refinements and encourage targeted efforts to establish permanent plots in areas with data gaps.

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). 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 tropics and subtropics 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 Intergovernmental Panel on Climate Change (IPCC) good practice guidance for National Greenhouse Gas (GHG) accounting (IPCC 2006, 2019).

Various methods for reporting on forest carbon stocks and fluxes can be applied, depending on the technical and financial capacity of a country. Reporting can be done (a) at the tier 1 level, based on IPCC default values of forest aboveground biomass (AGB) and net AGB change per continent and ecological zone in combination with maps of land cover (for distinguishing secondary and old-growth forest); (b) at the tier 2 level when national-level data are available for estimating values for standing biomass and biomass change and land use; or (c) at the tier 3 level, which requires a higher level of detail such as biomass estimates based on a national forest inventory (NFI), repeated measurements from plots to estimate biomass change, and/or the use of process-based models (IPCC 2006, 2019). The availability of recent NFI data, or publicly available forest plot data in general, is limited in the tropics (Romijn *et al* 2015, Liang and Gamarra 2020), 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 forest 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 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 forest age (Rozendaal *et al* 2017, Anderson-Teixeira *et al* 2021), and is typically lower than 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, Rutishauser *et al* 2015, Longo *et al* 2016).

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, 2006). Moreover, no consistent measure of uncertainty was included, since default values consisted of either a single value with a range, a single value only, or a range only. As such, accurately accounting for uncertainty in carbon stock estimates was not possible. Since 2006, a large amount of high-quality AGB data from tropical forests have become available. Recently, research networks have published AGB values from plots in old-growth forests (Lewis *et al* 2013, Brienen *et al* 2015, 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, databases of forest AGB values have been made available (Anderson-Teixeira *et al* 2018, Cook-Patton *et al* 2020), and countries in the tropics are establishing their own 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, Cook-Patton *et al* 2020), 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 GHG Inventories (IPCC 2019). We provide a rigorous, reproducible refinement by (a) incorporating suitable AGB data from forest plots that became available between 2006 and 2019; (b) providing separate estimates for successional stages; and (c) including a measure of uncertainty. We primarily relied on AGB data from forest plots, despite the increasing availability of pan-tropical and global remote-sensing-based datasets of forest AGB, because uncertainty of local AGB estimates (i.e. at the pixel-level) remains high (Herold *et al* 2019). We used a new remote-sensing dataset of AGB (Santoro *et al* 2021) 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. Methods

2.1. AGB data from forest plots

We compiled AGB data from plots in natural forests in the tropics and subtropics from (a) data from published studies, including studies from research networks and global databases; and (b) 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 (Malhi *et al* 2002, Lewis *et al* 2013, Anderson-Teixeira *et al* 2015, ForestPlots.net *et al* 2021) and degraded/logged 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 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. Although the census year varied, by including recent data and by distinguishing successional stages, our AGB estimates represent average current AGB levels in tropical and subtropical forests. 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 (Poorter *et al* 2016, Anderson-Teixeira *et al* 2018), because smaller trees comprise a substantial part of AGB (Hughes *et al* 1999). This means that we may have slightly underestimated AGB in old-growth forests. Nevertheless, trees between 5 and 10 cm dbh contribute little to AGB in old-growth forests, with a 1.178 times higher AGB for tropical dry forests when including trees between 5 and 10 cm dbh, but only a 1.033 and 1.020 times higher AGB for tropical moist and wet forests, respectively (Poorter *et al* 2015). We included aboveground live tree biomass, thus trees smaller than the minimum dbh, shrubs, lianas, herbs, necromass and belowground biomass were not included. For one dataset, dead trees were included as well, but this dataset comprised less than 1% of the total number of plots that was included from NFIs.

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, 2014, Feldpausch *et al* 2012). If aboveground carbon was reported instead of AGB, the aboveground carbon value was divided by the IPCC 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. Successional stages

We calculated default AGB values per continent (Africa, the Americas, Asia), per global ecological zone (FAO 2012), and successional stage. 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; appendix A (available online at stacks.iop.org/ERL/17/014047/mmedia)). 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 stages were distinguished: (a) 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; (b) older secondary forests >20 and ⩽100 years old, including forests regrowing on abandoned agricultural land, and degraded (including logged) forests; and (c) young secondary forests ⩽20 years old. Plots with information on disturbance history were assigned to a successional stage based on stand age for secondary forests, or disturbance history for degraded/logged forests. If plots lacked information on disturbance history, we determined the successional stage based on remote-sensing products (Tyukavina *et al* 2016, Potapov *et al* 2017, appendix B).

2.3. Calculation of default values based on forest plot data

Default values were calculated per continent, ecological zone, and successional stage if plot data were available. The methodology depended on the successional stage, and the number of available plots (figure 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* 2015, Rutishauser *et al* 2015, Requena Suarez *et al* 2019). 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 per continent and ecological zone (figure 1(a)).

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° 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° grid cells, because one 0.5° grid cell generally included one research site with chronosequence plots for secondary forests (Poorter *et al* 2016). Per continent, ecological zone, and successional stage, 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 young and older secondary forests, separate default values for both young and older secondary forests were calculated (figure 1(b)). 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 1(b)).

For continents and ecological zones for which not sufficient plot data were available to distinguish successional stages, we calculated a single default value per continent and ecological zone to represent all successional stages, if plot data (with or

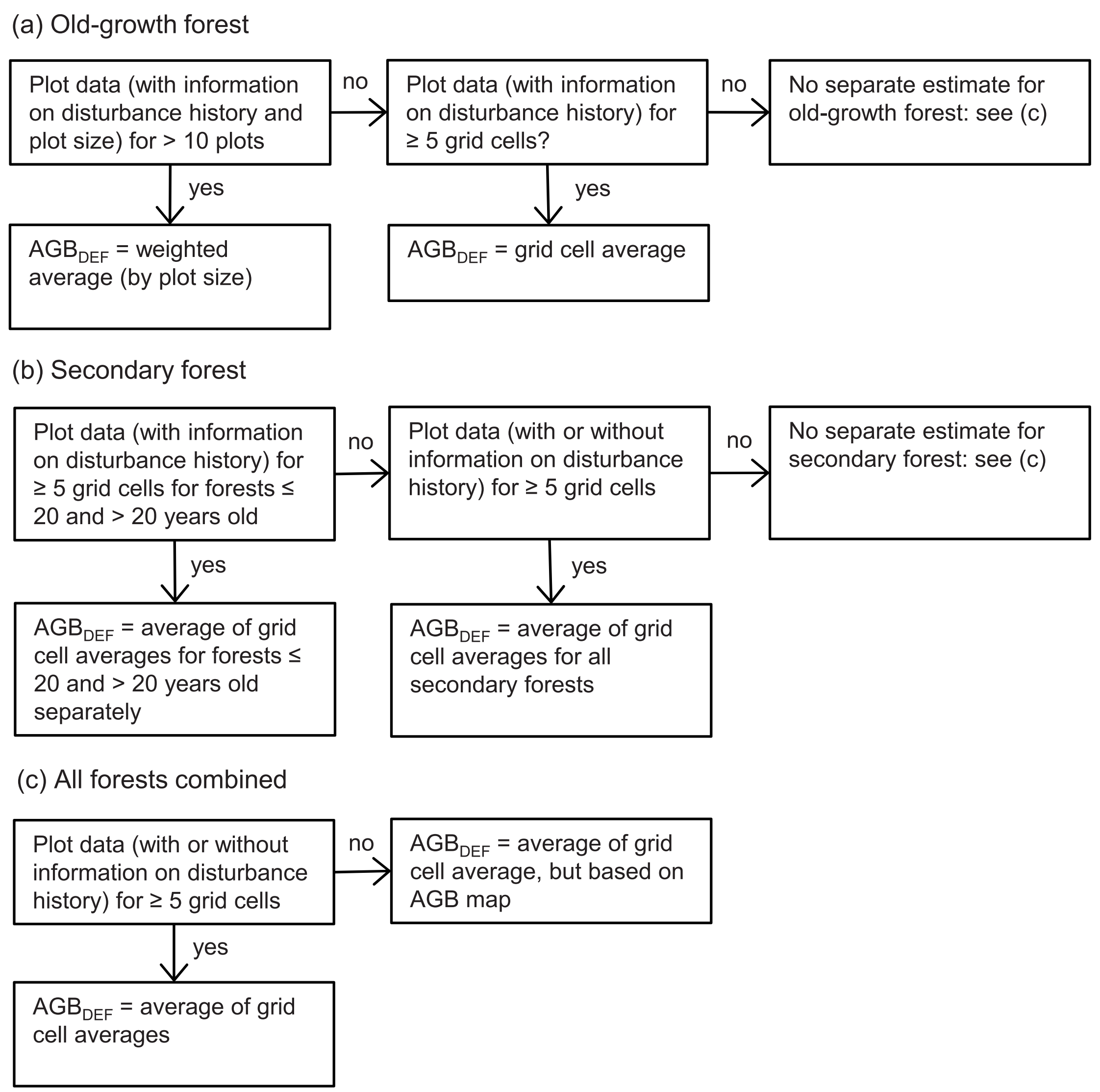

Figure 1. Overview of the methodology for the calculation of the refined 2019 IPCC default values for AGB$_{DEF}$. (a) Methodology for old-growth forests; (b) methodology for secondary forests; (c) methodology for all forests combined.

without information on disturbance history) were available for at least five grid cells (figure 1(c)). 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 1(c), appendix B). We made three exceptions to our general methodology. First, for tropical dry forests in Africa, we did not distinguish successional stages, although plot data were available per successional stage. These disturbance-adapted ecosystems are subject to chronic and acute disturbances (natural and anthropogenic; McNicol *et al* 2018), thus successional stages cannot be meaningfully distinguished. Second, for tropical dry forests in Asia, we also included a default value for all successional stages 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 remote sensing-derived biomass map. Third, for old-growth subtropical forests in Asia, we included a grid cell mean instead of a plot-size weighted mean (table 1), because plot sizes were unknown.

In total, we included 2318 plots for the Americas, 22 279 plots for Africa, and 1291 plots for Asia (figure 2). A total of 3880 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 (Slik *et al* 2015, Anderson-Teixeira *et al* 2018). 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).

Table 1. Refined 2019 IPCC AGB default values per continent, ecological zone and successional stage. The mean, 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 stages. Weighted indicates AGB default values calculated as a plot-size weighted average, grid cell indicates that the default values were calculated based on 0.5° grid cell means, and AGB map indicates that the default value was derived from a global AGB map (Santoro *et al* 2021). References are included in appendix D.

Ecological zone	Continent	Successional stage	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]
		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[a]	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[b]	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]
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[c]	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]

[a] 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.

[b] 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.

[c] 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.

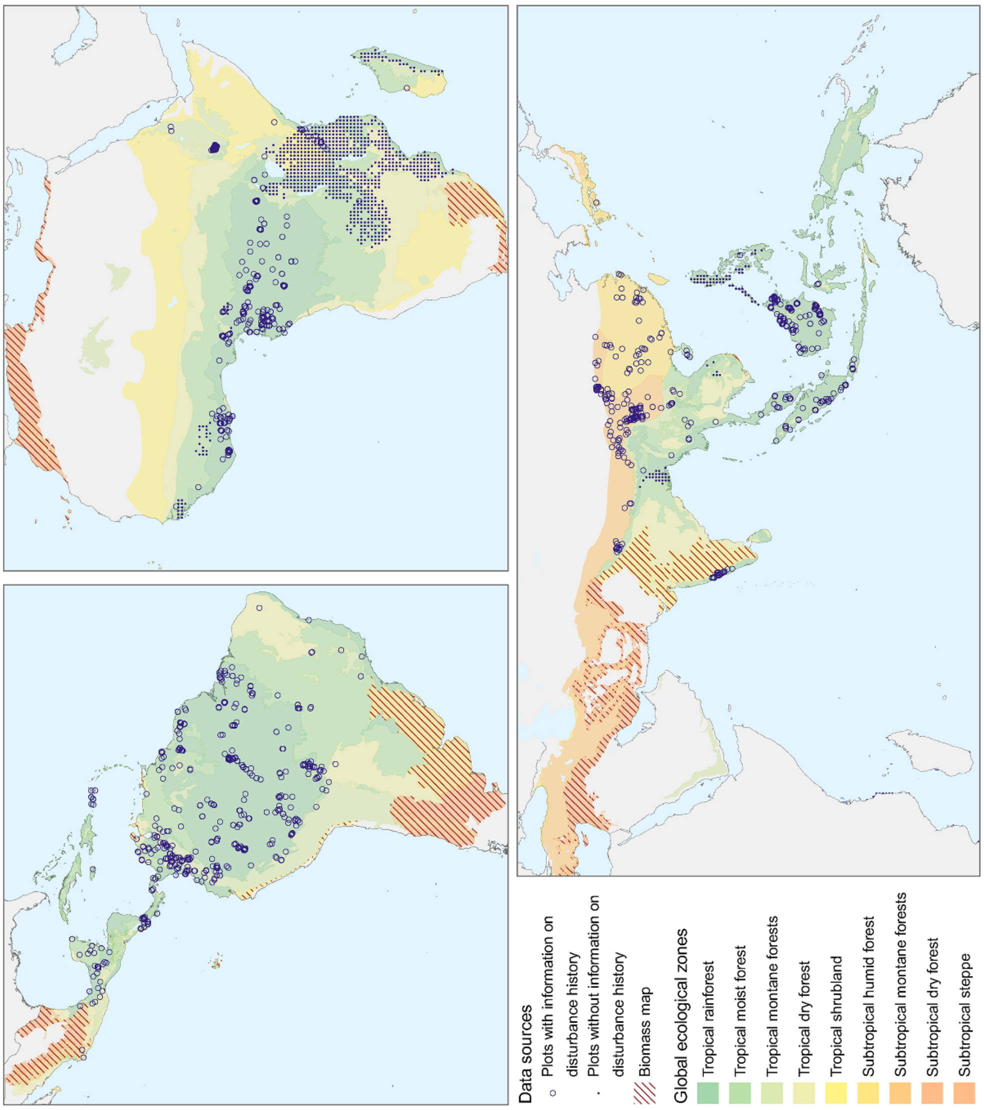

Figure 2. Overview of locations of plots with information on disturbance history and plots without information on disturbance history (mostly data from NFIs), as well as the FAO global ecological zones (FAO 2012) for which the refined default biomass values were estimated based on a global biomass map.

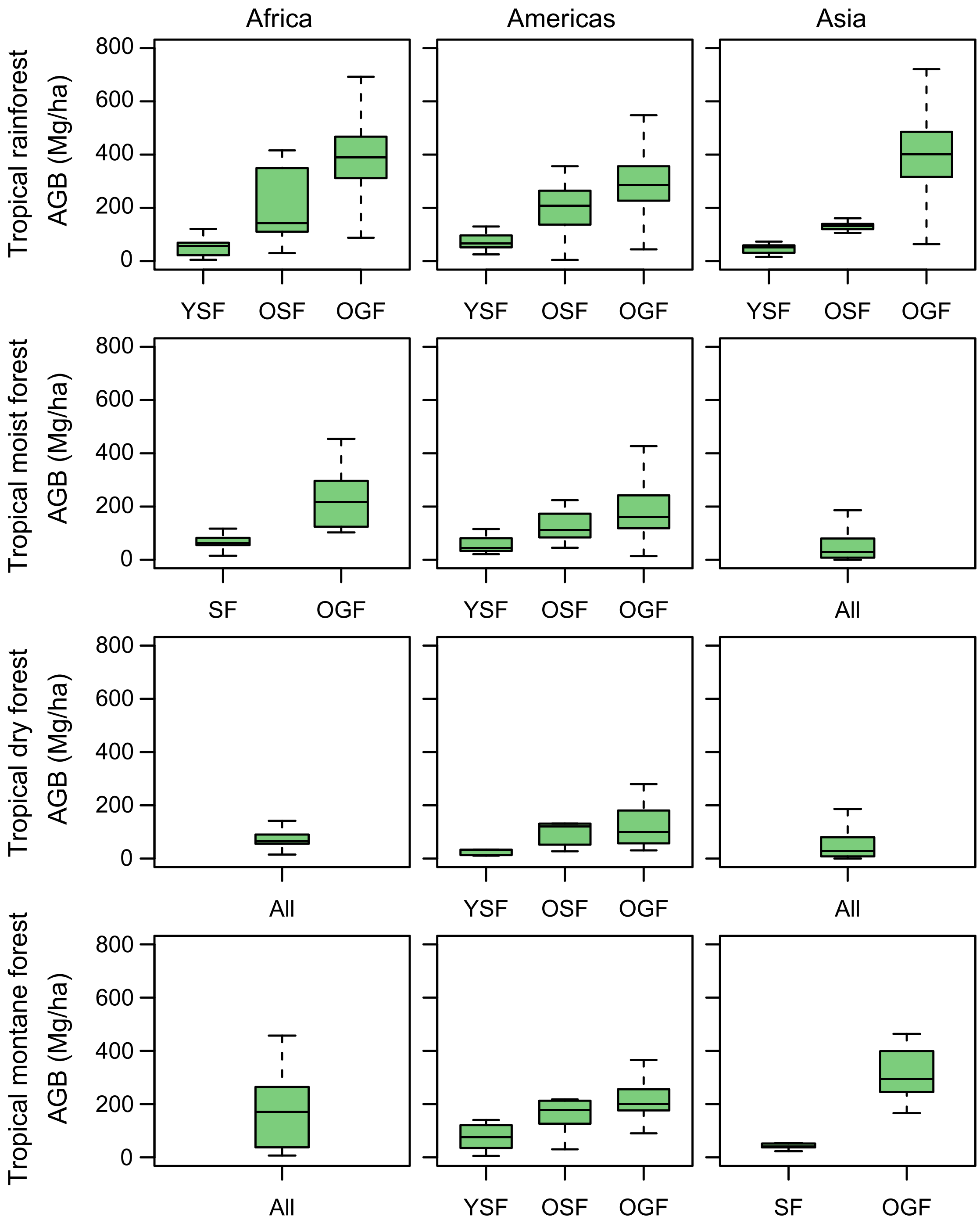

Figure 3. AGB per successional stage, for each continent and ecological zone. For secondary forests, grid cell averages were included; for old-growth forest, AGB for each plot (here not weighted for plot size). Boxes include the 25th and 75th percentile; the horizontal line indicates the median. YSF: young secondary forest (⩽20 years old); OSF: older secondary forest (>20 years old); SF: all secondary forests; OGF: old-growth forest; All: all successional stages.

3. Results

AGB in tropical forests varied by an order of magnitude across continents, ecological zones, and successional stages based on the included plots (figure 3). For old-growth tropical forests in the Americas, our new, refined IPCC 2019 AGB default values decreased from rainforests (307.1 Mg ha^{-1}), to moist forests (187.3 Mg ha^{-1}), to dry forests (127.5 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 than for tropical moist forest. For tropical shrublands on all continents, refined default values were the lowest (38.3–71.5 Mg ha^{-1}; table 1), although successional stages were not distinguished. For subtropical forests in Africa and the Americas across all successional stages, refined default values were highest for dry forests, unexpectedly, followed by humid forests and

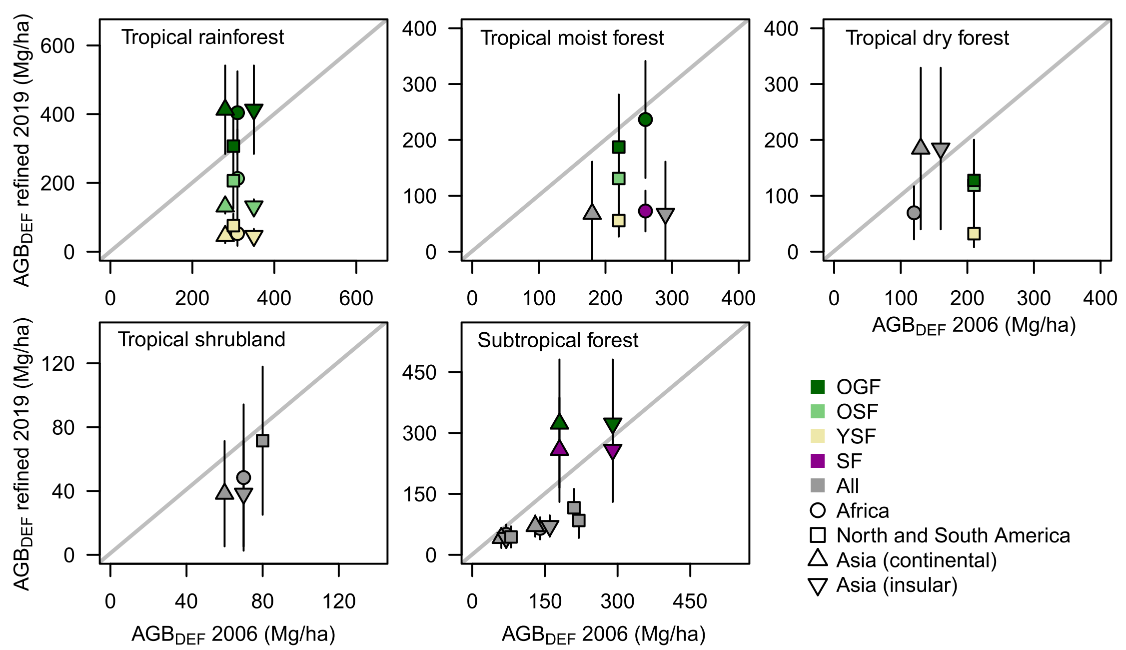

Figure 4. Comparison between the refined 2019 (with SD) and previous (2006) default biomass values (AGB_{DEF}) for the three continents, per ecological zone and successional stage. For Asia, 2006 AGB_{DEF} is indicated for both continental and insular Asia. Tropical and subtropical montane forests were excluded because in 2006 only a range was included, not an estimate of average biomass. For AGB_{DEF} 2006, no distinction between successional stages was made. 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 stages.

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 1). As expected, we found that, overall, AGB was highest in old-growth forests, followed by older secondary forests, and lowest in young secondary forests for ecological zones in the tropics and subtropics for which plot data per successional stage were available (figure 3, table 1).

Across all successional stages in tropical Asia, refined default values were unrealistically low for moist forest and high for dry forest. 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 stages was included, plots may have largely represented one successional stage. In these cases, we recommend using alternative values (table 1), either the value for another continent, or a general estimate across all successional stages 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 stages together were generally close to the previous values, with a range from 45% lower to 48% higher than the 2006 IPCC default values (figure 4). In contrast, for tropical secondary forests, refined default values were consistently lower than the 2006 values, with for young secondary forests, 4.0–7.7-fold lower values (figure 4). For subtropical forests, refined default values were generally slightly lower than the 2006 default values, except for default values for subtropical humid forests in Asia that were higher than the 2006 default values for continental Asia (figure 4). Across all continents and ecological zones for tropical and subtropical forests, standard deviations (SDs) of the refined default values were on average 55% (range: 16%–138%) of the refined default value (figure 4, table 1). Thus, uncertainty in the refined default values was large, indicating large variation in AGB within ecological zones.

4. Discussion

4.1. Refined IPCC AGB default values

We found large variation in AGB across continents, ecological zones, and successional stages. 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 also reflected in the refined default values for tropical old-growth forests, as they increased from dry, to moist, to rainforests (table 1). In addition, tropical forest biomass decreases with elevation (Leuschner *et al* 2007, 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 1).

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

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 stages combined, with the strongest deviations for young secondary forests (figure 4). These results suggest that IPCC 2006 default values for at least tropical rainforests and moist forests were largely defined based on data from old-growth forests (Langner *et al* 2014), and stress the importance of differentiation by successional stage. By specifying separate default values for young secondary, older secondary, and old-growth forests, the reality of 21st century tropical forests is better reflected. In Latin America, for example, secondary forests account for 41% of the forest area (Chazdon *et al* 2016), and are expected to expand in area.

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 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.

To be able to apply the refined default values, countries need to distinguish successional stages per ecological zone. For countries that do not have information on the extent of young, older, and old-growth forests per ecological zone, for example from a NFI, we recommend to largely follow the approach of Harris *et al* (2021) for delimiting these successional stages based on remote-sensing products (appendix C).

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 5). With the refined default values, we provided the SD of the default values as a measure of uncertainty, which indicates AGB variation among plots, but does not include the uncertainty of the plot-level AGB estimates. We included both plots from research networks and NFIs. While NFI plots are usually established following a probability sampling design (e.g. Tomppo *et al* 2014), the design of a research plot network depends on the specific objectives of the research project, and may not cover spatial variation in environmental conditions, or plots may, for example, be established in locations that are easily accessible. We preferably included data from research networks for which detailed information on disturbance history was included, but for some default values solely based on NFI plots, the disturbance history was estimated based on remote-sensing products. In addition, the variation in allometric equations used for the biomass estimates may have introduced additional uncertainty, as biomass estimates vary with the allometric equation used (Chave *et al* 2004).

We recommend future refinement by incorporating AGB data for ecological zones and successional stages 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, table 1). 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 5). This may be because most 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 5). Establishing permanent forest plots is essential, for accurate estimation of both AGB and AGB change over time, for all successional stages. For future refinement, we also recommend distinguishing successional stages in more detail, as the three included stages represent broad categories. Particularly, older secondary forests could be divided into degraded/logged forests and regenerating forests after complete removal of vegetation (e.g. shifting cultivation), 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

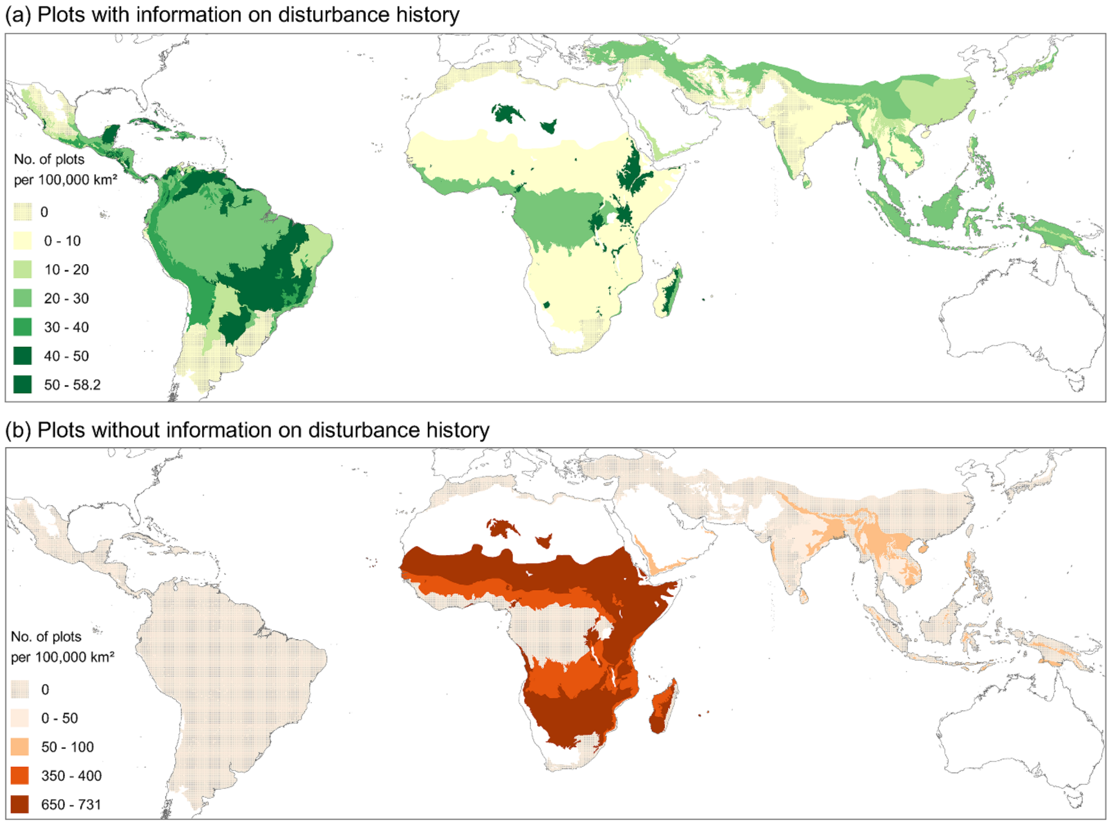

Figure 5. Number of plots per 100 000 km^2 of natural forests per ecological zone. Natural forest areas per ecological zone were based on Schulze *et al* (2019). We recommend targeted data collection in areas with low sampling intensity, particularly to increase the number of plots with information on disturbance history. (a) Plots with information on disturbance history; (b) plots without information on disturbance history.

ecological zone. We recommend accounting 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. Quesada *et al* 2012, Poorter *et al* 2017, Sullivan *et al* 2020). For regrowing forests, AGB could be modeled as a function of stand age and climate, as these drive much of the variation in AGB in regrowing forests (Poorter *et al* 2016, Cook-Patton *et al* 2020), 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 intensity (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 pixel-level uncertainty is still very high, particularly for high-biomass tropical forests (Herold *et al* 2019), which limits their use in GHG 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 (Requena Suarez *et al* 2021), as NFIs have large geographical coverage, and should be further explored in the future (Bustamante *et al* 2016, Herold *et al* 2019).

5. Conclusion

We provided a rigorous refinement of the 2006 IPCC AGB default values for tropical and subtropical 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 young 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 SD 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 tropical and subtropical forests.

Data availability statement

The data generated and/or analyzed during the current study are not publicly available for legal/ethical reasons but are available from the corresponding author on reasonable request.

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