



Original Research Article

Aboveground biomass in secondary montane forests in Peru: Slow carbon recovery in agroforestry legacies



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ABSTRACT

Andean tropical montane forests (TMF) are hotspots of biodiversity that provide fundamental hydrological services as well as carbon sequestration and storage. Agroforestry systems occupy large areas in the Andes but climatic pressures, market volatility and diseases may result in agroforestry abandonment, promoting secondary succession. Secondary forests are well-adapted and efficient carbon sinks whose conservation is vital to mitigate and adapt to climate change and to support biodiversity. Little is known, however, about how secondary TMF recover their aboveground biomass (AGB) and composition after abandonment. We established a 1.5 ha plot at 1780 masl on a 30-year old abandoned agroforestry and compared it against two control forest plots at similar elevations. Agroforestry legacies influenced AGB leading to far lower stocks ($42.3 \pm 5.4\text{--}59.6 \pm 7.9 \text{ Mg ha}^{-1}$ using allometric equations) than those expected after 30 years ($106 \pm 33 \text{ Mg ha}^{-1}$) based on IPCC standard growth rates for secondary montane forests. This suggests a regional overestimation of mitigation potentials when using IPCC standards. Satellite-derived AGB largely overestimated our plot values ($179 \pm 27.3 \text{ Mg ha}^{-1}$). Secondary growth rates ($1.41\text{--}2.0 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for $\text{DBH} \geq 10 \text{ cm}$) indicate recovery times of ca. 69 to 97 years to reach average control AGB values ($137 \pm 12.3 \text{ Mg ha}^{-1}$). This is 26 years above the average residence time of montane forests at our elevation (71 ± 1.91 years) suggesting a non-recovery or far slower recovery to control AGB values. Three variables appear to define this outcome compared to the control plots: lower DBH ($15.8 \pm 5.9 \text{ cm}$ vs $19.8 \pm 11.0 \text{ cm}$), lower basal area (12.67 ± 0.7 vs $28.03 \pm 1.5 \text{ m}^2 \text{ ha}^{-1}$) and higher abundance of lighter-wood tree genera (0.46 ± 0.10 vs $0.57 \pm 0.11 \text{ gr cm}^3$) such as *Inga*, a common shade-tree in Andean agroforests. With 3.2 million hectares committed to restoration, Peru needs to target currently neglected TMF recovery schemes to support biodiversity, water and carbon storage and fulfill its international commitments.

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1. Introduction

The Andes are global hotspots of biodiversity but are also historically characterized by high rates of land use change (Myers et al., 2000). Adding to other human impacts, climate change is known to be rapidly acting in the Andes through a variety of factors. Above-mean rising temperatures (Bradley et al., 2006) are expected to force species elevation shifts (Fadrique et al., 2018; Tito et al., 2020). Accelerated glacier melting (Masiokas et al., 2020; Rabatel et al., 2012), an increase in ENSO-related tropical extreme events (Cai et al., 2014) and alterations in cloud condensation levels (Fadrique et al., 2018; Halladay et al., 2012; Ruiz et al., 2012) are associated with drought/flood events (Espinoza et al., 2020; Fraser, 2012; Poveda et al., 2020) and fire (Oliveras et al., 2014a; Roman-Cuesta et al., 2014); overlaid on decadal and interdecadal drought patterns in the Central Andes (Segura et al., 2016). This poses extreme social, economic and ecological challenges, not only for the Andean montane biome itself but for its interdependent ecosystems, such as the Amazon basin to the east and the Pacific coastal desert valleys on the west, whose hydrologies are highly dependent on the Andean Water Towers (Espinoza et al., 2020; Mark et al., 2017; Poveda et al., 2020; Vuille et al., 2008).

Tropical Montane Forests (TMF) in the Andes are disproportionately important in providing hydrological services and supporting biodiversity and endemism (Bruijnzeel et al., 2011; Young and León, 2000). Their role in carbon sequestration is now better understood (Cruz-del-Amo et al., 2020; Girardin et al., 2010, 2014; Malhi et al., 2017; Moser et al., 2011; Yepes et al., 2015, 2016) with the largest contribution coming from soil carbon storage (Calderón-Loor et al., 2020; Oliveras et al., 2014b; Roman-Cuesta et al., 2011; Vásquez et al., 2014; Zimmermann et al., 2010). In spite of their importance, Andean TMF remain poorly monitored, without a national or an international system properly registering their land use dynamics (e.g. deforestation/degradation/regeneration). In Peru, a vegetation map produced by the Ministry of Environment (MINAM, 2015) suggested a total area of tropical Andean forests (500–3500 masl) of 12.2 million hectares in 2011, which represented ca. 21% of the total forested land in the country's 73.3 million hectares (MINAM, 2011). Driven by road building, timber extraction, agricultural expansion and fires, deforestation has been advancing in montane forests (Aide et al., 2019; Bax and Francesconi, 2018). For Peru, Bax and Francesconi (2018) estimated that 23% (44,200 km²) of the initial extent of the tropical Andean forest biome had already been deforested by 2017.

Within the tropical montane forests in the Andes, agroforestry systems such as shade coffee and tea occupy large areas, and are the main source of income for many farmers through highly valuable agricultural exports (Aide et al., 2019; Jha et al., 2014; Tulet, 2010). It is estimated that by 2018 these activities involved 608,332 ha in Peru (FAO, 2020). Several studies have assessed biomass stocks in tropical agroforestry systems as ranging between 34.8 and 145 Mg ha⁻¹ (Hergoualc'h et al., 2012; Kalita et al., 2020; Solis et al., 2020; Somarriba et al., 2013; Soto-Pinto et al., 2009). However, few studies have considered the composition and carbon recoveries of secondary TMF that derive from the abandonment of agroforestry activities (Grau et al., 2004; Marciano-Vega et al., 2002; Raymundo et al., 2018). A secondary forest is understood as “forests regenerating largely through natural processes after significant human and/or natural disturbance of the original forest vegetation” (Chokkalingam and de Jong, 2001). Secondary succession may turn into a common pathway in montane agroforestry systems given climatic pressures, market price volatility, and plant-diseases (Jha et al., 2014; Tulet, 2010). Thus, between 1980 and 2000, one million hectares of coffee plantations were abandoned globally (Jha et al., 2014) and although some of those areas may change to other land uses, many are left fallow. The actual transitions and fate of abandoned agroforestry systems in the Andes is unknown. However, in Peru, MINAM (2009) reported ca. 1.4 million hectares of anthropogenic secondary forests in the tropical Andes for 2000.

Due to their unassisted establishment, secondary forests act as a cost-efficient nature-based solution (IUCN, 2020), well adapted to local environmental conditions and providers of multiple ecosystem services (Chazdon and Guariguata, 2016; Crouzeilles et al., 2017; Griscom et al., 2020). In terms of carbon sequestration, secondary forests are known for higher productivity rates than older successional stages (up to eleven times more than old-growth forests) (Poorter et al., 2016; Requena-Suarez et al., 2019). In spite of their importance, carbon dynamics of secondary forests in montane regions remain less studied with a large research-bias towards lowland Amazon forests (Barbosa et al., 2014; Chazdon et al., 2016; Poorter et al., 2016). Some research exists for carbon recovery pathways in burned tropical montane cloud forests in Peru (Oliveras et al., 2014a,c; Roman-Cuesta et al., 2011) but fewer data exist on carbon and species recovery of secondary montane forest, particularly deriving from abandoned agroforestry systems in the Andes.

Since most of these Andean agroforestry systems use shade trees to regulate microclimate and provide services to the plantation (Jha et al., 2014; Tulet, 2010), their contribution to biodiversity and their expected rapid regrowth can make them attractive for conservation finance under carbon markets (e.g. NDCs, REDD+, Verified Carbon Standards (VCS)) with biodiversity co-benefits (e.g. Climate, Community and Biodiversity (CCB) standards). Additional opportunities arise under the UN Decade of Restoration, and Initiative 20 × 20: <https://initiative20x20.org/> (part of the Bonn Challenge: <https://www.bonnchallenge.org/>), where Latin American Governments aim to restore 52 million hectares of degraded land by 2030 (Declaración de Buenos Aires, 2018). The Peruvian Forestry Service (SERFOR) has set a goal to restore 3.2 million hectares, of which 2 million hectares target commercial plantations and 1.2 million hectares will focus on degraded land (Román et al., 2018). While degraded land in Peru has so far not included degraded forests, SERFOR promotes secondary forest growth as part of their restoration strategies (Román et al., 2018). This provides an opportunity to promote adaptation and mitigation activities throughout Peru's highly relevant Andean montane forests.

Latin America is well positioned to benefit from services, such as carbon removal, provided by secondary growth forests (Chazdon et al., 2016), but adequate monitoring and accounting are needed (Busch et al., 2019; Cook-Patton et al., 2020). Most data on secondary vegetation in Latin America relies on satellite tracking of deforestation, however, additional ground data is essential to validate forest condition and their projected carbon dynamics. In this study we assess and monitor a 30-year old secondary TMF in an abandoned agroforestry tea plantation, at 1,780 masl, located in the La Convención province, Cuzco, Peru.

Our study aims to answer the following questions: i) what are the structure and species composition of a secondary TMF after 30 years of abandonment?, ii) what are the aboveground biomass (AGB) and approximate growth rates of this Andean montane agroforest system?, iii) how is the estimation of AGB variability within this forest system affected by the scale of data aggregation (from species to biome) and methodological choices (e.g. allometric equation vs satellite data)?, iv) How do our secondary forests compare with primary control forests?, and finally, v) what are the opportunities for secondary TMFs to contribute to Peru's restoration commitments under the Initiative20×20 and in Peru's NDC commitments under the UNFCCC?.

2. Materials and methods

2.1. Study site

TMF in Peru are more abundant on the eastern slopes of the Andes, on an elevation range of 500–3500 masl (MINAM, 2015, 2016; Young and León, 2000). Our secondary montane forest is located at 1780 masl in La Convención province, Cuzco Region, in southern Peru (Fig. 1, Table 1). It has a mean annual temperature of 18.4 °C, annual rainfall of 1852–2100 mm (1972–2014) with a rainy season during the months of May to September (CESEL Ingenieros, 2013; Manz et al., 2016). Our plot was established on a 30-year abandoned tea plantation (as informed by the landowner), in a west-facing flat terrace, in the Convencion Valley, in an area known as Yanayaco, in

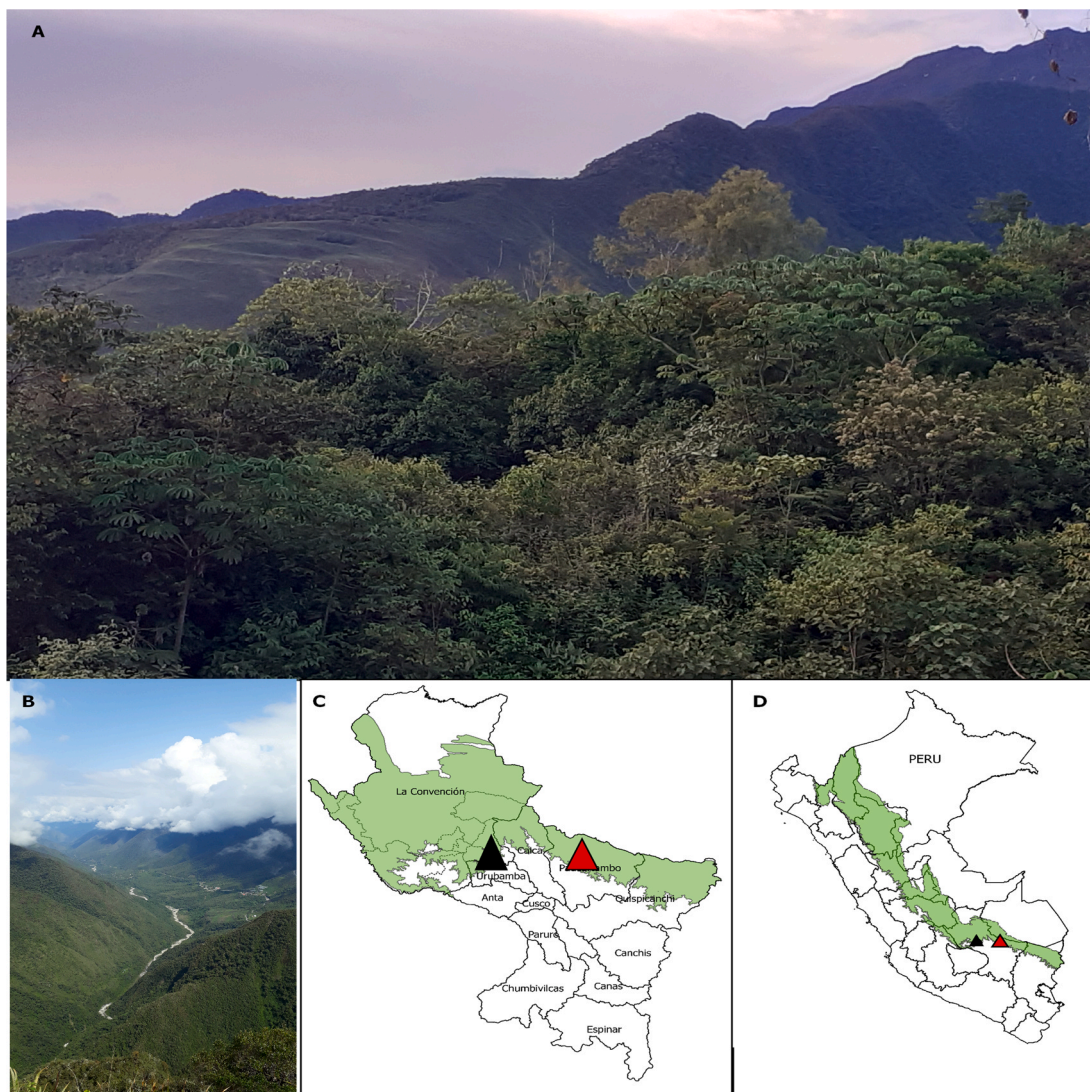


Fig. 1. Study sites: Tropical montane secondary agroforest at the Huayopata district (black triangle) and control sites at the Challabamba district (red triangle). A) Tropical montane secondary agroforest plot; B) Huayopata District, La Convencion, Cuzco, Peru; C) The Cuzco Region with study sites marked; D) Distribution of Tropical Andean Montane forest in Peru (green shading). Photos credit: Vicky Huaman Quellon & Susan Aragón. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Summary of site characteristics for the secondary and control tropical montane forest in the Huayopata and Challabamba districts (SP1 = San Pedro 1, TU-8 = Trocha Union 8). Data from: Malhi et al. (2017); CESEL Ingenieros (2013); TRMM Manz et al. (2016).

	Secondary TMF	Primary TMF	
	Yanayaco	SP-1	TU-8
Elevation (masl)	1780	1750	1885
Latitude (S)	12° 59' 42"	13° 2' 49"	13° 4' 16"
Longitude (W)	72° 31' 16"	71° 32' 31"	71° 33' 18"
Plot area (hectares)	1.52	1.52	1
Number of subplots (20×20m)	38	38	25
Aspect	W	W	W
Mean annual air temperature (C°)	18.4°	17.4°	18.0°
Rainfall (mm.year ⁻¹)	2100	5302	2472
Soil organic layer (cm)	40	32	30

the Huayopata District. This district has been Peru's main tea producer in the 20th century, with a maximum of ca. 2500 ha dedicated to its cultivation at its peak in 1977 (Dueñas, 1997). The valley has suffered extensive deforestation for tea and coffee plantations and also for firewood and timber extraction (landowner pers. comm.). First tea plants were established in 1913, but large-scale commercialization started in 1943 (Dueñas, 1997). Traditionally, tea and coffee has been grown in a multistrata agroforestry system with trees such as *Inga* spp. for soil fertilization and shade (Ehrenbergerová et al., 2016; Solis et al., 2020). Overstory is cleared to an optimal density and tea plants are pruned to approximately 0.5–1 m height, for easier collection. Tea plants left unpruned can reach up to 9–15 m in their natural range, India (Hall, 2000). Due to market changes, deregulation of tea imports, mismanagement and rural emigration, large scale tea cooperatives have gone bankrupt since the mid 1990s and the area under active tea cultivation had been reduced to 1,500 ha in 2017 with 1,000 hectares having been abandoned or dedicated to other uses (MINAGRI, 2020).

As primary forests were not available in Huayopata, we selected a set of intensively studied montane forests in our range of elevation as the control-undisturbed primary forest. These plots are part of an elevation gradient along the Kosñipata Valley, in the Challabamba district, that covers well preserved forests that ranges from the Amazon (300 masl) to the Andes (3400 masl) (Malhi et al., 2010; Salinas et al., 2011). Mean annual temperatures in the Kosñipata Valley ranged between 17.4 and 18.8 °C and annual precipitation between 2472 and 5300 mm year⁻¹ (Huaraca Huasco et al., 2014; Malhi et al., 2017), being cooler and rainier than our location at Huayopata (Table 1).

2.2. Site selection and replication limitations

With Peru lacking a national secondary forest map, we relied on Google Earth to search for deforested areas in the mid-1980s or 1990s that had returned to forest by 2000 and persisted until 2020. This led to 30-year secondary forests and this age was settled for our study. The Google Earth-identified secondary forests were visited and we interviewed the owners to learn about their forest histories (time since deforestation = secondary forest age, drivers of deforestation/degradation, land tenure, and future use). This approach led us to the Huayopata district, and to its abandoned tea-plantations, where we installed a 1.5 hectare plot. The valley was highly impacted and replication, while desirable, became very difficult. Replication was conditioned by the following factors: forests had to match the 30-year age restriction, which excluded replication along a chronosequence. Moreover, the replicated plots had to be located in the same elevation range and affected by the same drivers of deforestation (e.g. the abandoned tea plantation). All these conditions, together with very fragmented forests remaining in the valley, the time consuming way of locating secondary forests and their owners, as well as the COVID pandemic-mediated closure of most montane valleys in 2020, made true replication very difficult. Alternatively, we focused on representativeness. We thus targeted secondary forests that were representative of a predominant land use in the montane region in Peru. Agroforestry systems are extensive in Peru's Tropical Montane Forests, covering 608,332 ha in 2018 (FAO, 2020). And while coffee is far more predominant than tea, they both are shade crops (90% for coffee) (Jha et al., 2014), with *Inga* spp. predominately used as a shade tree (Tulet, 2010).

2.3. Field measurements

Our study falls within a paired-sample analysis with a control-treatment approach (where control is the "primary forest" understood as a non-disturbed forest and the treatment is a secondary forest of known age). We contrast carbon stocks in primary vs secondary forests to estimate recovery times and we compare forest diversity and abundance in both primary and secondary forests in the Andes.

Our treatment plot, the secondary forest, was a 1.5-hectare plot with 38 subplots (20 × 20 m each) established in January 2020 (wet season). We used the RAINFOR-GEM protocols for AGB measurements (Marthews et al., 2015). All stems ≥ 2 m height and DBH ≥ 10 cm were tagged, its DBH measured with a diametric tape, and its height (h) with a laser Nikon rangefinder (mean of two measurements per tree). In order to assess the contribution of smaller trees, we sampled six subplots for trees ≥ 2 m of height and DBH between 2 and 10 cm. Species were identified by field botanists to family or genera taxa and to their species level whenever possible. Botanical material was collected for identification in the Herbarium.

While this research relies on one treatment plot only, and focuses exclusively on aboveground biomass, its representativeness and the lack of existing data on carbon stocks in secondary montane forests in the Andes of Peru, makes it a valuable contribution.

Our control plots are part of intensively studied primary forests along an elevation gradient in the Kosñipata Valley. Data inventorying runs every 4 years since 2003, for all trees. We used data from the last census (2017). Data is accessible at the RAINFOR-GEM repository: Forestplot.org (Lopez-Gonzalez et al., 2011). Plot data collection for the control plots also followed the RAINFOR-GEM protocols (Marthews et al., 2015).

2.4. Estimating AGB and growth rates

As biomass uncertainty highly depends on its aggregation level, we estimated AGB at different scales: 1) at the plot, ecosystem, and biome levels through allometric equations, and 2) at the landscape level through biomass remote-sensed products. We also applied IPCC standard growth rates for secondary montane forests in Latin America to estimate stocks after 30 years. We used the residence time from a primary TMFs (71 ± 1.91 years) in the valley of Kosñipata for the same altitudinal level (Girardin et al., 2010; Malhi et al., 2017).

2.4.1. Allometric equations

At the plot level (trees $DBH \geq 10$ cm), we used 32 species-specific allometric equations through a literature search including proxy-species (e.g. species of the same genera that occur in montane forests) and from the Global Allometric Tree repository (<http://www.globallometree.org>). At the ecosystem level, we searched for montane forest allometric equations in the Andes (Alvarez et al., 2012; Sierra et al., 2007; Valle et al., 2011). For the moist forest biome level we used generic pan-tropical equations from Chave et al., (2005, 2014), and Brown et al. (1989) (with the formulation of Pearson et al., 2005). Please refer to Supplementary Material 1 (SM1) for all the equations. Since ecosystem and biome equations were not meant to estimate agroforestry species, these species were calculated with their species-specific equations and later added to the ecosystem and moist biome estimates. All AGB values were then area-corrected to offer Megagrams per hectare. For the control plots, we applied Chave et al. (2014) moist biome equation to estimate AGB. For understorey biomass (2 to 10cm DBH) we used Chave et al. (2014) moist biome equation and species-specific equations for species not considered in Chave's equations (e.g. agroforestry species) (see Section 2.4.4). Growth rates were estimated as the ratio between the AGB at the plot level and the number of years under growth (30 years).

For allometric equations that included wood density (WD), we assigned each tree with its species-specific WD, from the World WD Database and the literature (Chave et al., 2009; Van Breugel et al., 2011; Zanne et al., 2009). When the WD at the species level was not available, we then assigned average values for their genera and/or family levels. For individuals without botanical identification ($n = 31$ out of 885 trees in our secondary TMF plot) we used the average WD for the plot, as implemented on the R-package BIOMASS (Réjou-Méchain et al., 2017).

2.4.2. Remote sensing

For the landscape AGB estimates we relied on four biomass products which derived from satellite data merged with ground data: i) Aboveground live woody biomass density (Baccini et al., 2017) at 30 m pixel resolution with 2000 as the base-year, ii) Pantropical biomass map (Avitabile et al., 2016) at 1000 m resolution with 2000 as the base-year, iii) GlobBIOMASS (Santoro et al., 2018) with 100 m resolution and 2010 as the base-year, and iv) CCI Forest AGBiomass (Santoro and Cartus, 2019), with 100 m spatial resolution and 2017 as base-year. Given that our secondary and control plots did not match exactly the satellite pixel grid, we averaged the biomass values of all the pixels that overlapped each plot and expressed the variability as standard deviation from the mean. We used QGIS (QGIS Developmental team, 2018) to run raster analyses.

2.4.3. IPCC-derived AGB

To calculate the AGB in our 30-year abandoned secondary TMF plot, we used Requena-Suarez et al. (2019) growth estimates for North and South American young secondary montane forests ≤ 20 years (4.4 ± 1.6 Mg ha⁻¹), for 20 years and added 10 years of growth using the estimate for secondary montane forests > 20 years (1.8 ± 0.8 Mg ha⁻¹).

2.4.4. Tree categories

To avoid applying the allometric equations out of their intended range of species, we classified the trees in our secondary TMF plot into three groups: i) montane forest species, ii) agroforestry species, and iii) early successional species, based on the literature and field observation (Farfan-Rios et al., 2015; Martinez-Camilo et al., 2018; Lohbeck, 2010). We used control plot data to identify montane species (e.g. *Alchornea*, *Weinmannia*, *Alnus*, etc), and to identify light wood density species that were not naturally part of TMF at our elevation (or that are present in far lower densities in the control sites) (e.g. *Ficus* and *Cecropia*). Agroforestry species included those associated with human cultivation (e.g. as lemon, avocado, zapote, tea, loquat, etc, as found in our plot) and those under forest management, such as *Ingas* for shade and soil fertilization (see SM1 for the list of species and their categories).

2.4.5. Uncertainties and variability

We estimated the variability of AGB expressed as the standard deviation of the mean at the plot level by bootstrapping (1000 runs without replacement) using the R-package boot (v.1.3–20) in R 3.5.3 (R Core Team, 2019; Canty and Ripley, 2017)

Table 2

Structure and composition of the secondary and control TMF plots for trees with DBH ≥ 10 cm. The species for the secondary montane forest are disaggregated into montane forest species, early successional species, and agroforestry species (mainly *Cecropia ssp* and *Ficus spp*). DBH: diameter at 1.30 m, H: height, WD: Wood density, BA: Basal area.

	Yanayaco (Secondary TMF)				Kosñipata (Primary TMF)	
	All	Montane forest	Early successional	Agroforestry	SP1	TU8
Elevation (masl)	1780				1750	1885
N (stems)	866	491	192	152	1003	1082
Plot area (ha)	1.52				1.52	1
Species	35	23	6	6	181	128
Genera	32	22	5	6	84	61
Families	26	19	4	6	48	39
BA (m ² .ha ⁻¹)	12.67 \pm 0.7	6.43 \pm 0.3	4.08 \pm 0.7	1.83 \pm 0.2	28.03 \pm 1.5	29.41 \pm 1.5
DBH (cm)	15.8 \pm 5.9	15.1 \pm 5.1	18.7 \pm 7.9	14.6 \pm 4.7	19.8 \pm 11.0	17.3 \pm 6.8
H (m)	10.1 \pm 2.8	9.7 \pm 2.2	12.4 \pm 3.1	8.9 \pm 2.3	10.7 \pm 3.9	9.9 \pm 3.5
WD (g.cm ⁻³)	0.46 \pm 0.10	0.47 \pm 0.07	0.31 \pm 0.04	0.57 \pm 0.03	0.57 \pm 0.11	0.57 \pm 0.13
Most common species	<i>Alchornea latifolia</i> , <i>Inga punctata</i> , <i>Cecropia angustifolia</i> , <i>Inga edulis</i> , <i>Ocotea longifolia</i>	<i>Alchornea latifolia</i> , <i>Inga punctata</i> , <i>Nectandra coriacea</i> , <i>Ocotea longifolia</i> , <i>Clethra obovata</i>	<i>Cecropia angustifolia</i> , <i>Ficus spp</i> , <i>Trema micrantha</i> , <i>Urera caracasana</i>	<i>Inga edulis</i> , <i>Eriobotrya japonica</i> , <i>Persea americana</i>	<i>Cyathea spp.</i> , <i>Tapirira spp.</i> , <i>Pseudolmedia rigida</i> , <i>Guatteria glauca</i> , <i>Mollinedia lanceolata</i>	<i>Cyathea lechleri</i> , <i>Clethra revoluta</i> , <i>Myrcia rostrata</i> , <i>Tapirira spp.</i> , <i>Alzatea verticillata</i>
Most Common families	Euphorbiaceae, Fabaceae, Lauraceae, Moraceae				Cyatheaceae, Lauraceae, Anacardiaceae, Moraceae, Melastomataceae, Monimiaceae, Fabaceae, Annonaceae, Rubiaceae	Cyatheaceae, Myrtaceae, Clethraceae, Clusiaceae, Alzateaceae, Anacardiaceae, Aquifoliaceae, Lauraceae, Rubiaceae

3. Results and discussion

3.1. Structure and composition of secondary montane agroforests in the Andes

Our 1.5-hectare secondary TMF was far less diverse (35 species, 32 genera, and 26 families) than the control plots (e.g. 181 species, 84 genera and 48 families) (Table 2). Most abundant in our secondary TMF were montane early successional species like *Alchornea latifolia* (n = 220) followed by the agroforestry species *Inga punctata* (n = 97) and *I. edulis* (n = 51), and the non-montane early successional species *Cecropia angustifolia* (n = 76) and *Ficus spp* (n = 57). *Inga spp* is traditionally used for shade in tea and coffee agroforests in Tropical America (Ehrenbergerová et al., 2016; Hall, 2000; Solis et al., 2020) and its structural, and carbon, legacies remain strong 30 years after abandonment. The most abundant families in our secondary forest represented light wood density taxa: Euphorbiaceae, Fabaceae, Lauraceae and Moraceae (mean WD=0.46 ± 0.10 g cm⁻³), which contrasted with the higher wood density taxa in the control plots: Cyatheaceae, Lauraceae, Anacardiaceae, Moraceae, Myrtaceae and Clethraceae, (mean WD =0.57 ± 0.11 g cm⁻³) (Table 2). Structure-wise, the overstory of our secondary montane agroforest was dominated by the early successional group (mainly *Cecropia spp* and *Ficus spp*) with a mean height of 12.4 ± 3.1m and a mean diameter of 18.7 ± 7.9 cm. However, the largest group contributing to basal areas was secondary montane forest species (6.43 m² ha⁻¹), mainly due to a higher number of stems (n = 491) (Table 2). The understory, with 1141 stems of DBH between 2 and 10 cm, corresponding to 31 Species, 31 Genera and 25 Families (Table 3) (Fig. 2a, c, e) was dominated by agroforestry species, especially in the lowest diametric class (2–5 cm DBH) where tea plants were most abundant (Fig. 2c). Montane forest species are present as saplings and in the lower diametric class of trees (10–15 cm DBH) (Fig. 2b). This suggested an ongoing but very slow compositional change where montane forest species remained suppressed by the high density of remaining tea plants in the understory even after 30-years of abandonment. From the 1141 saplings recorded in the understory plots, tea (*Camellia sinensis*) was the most abundant (n = 639), followed by montane forest species such as *Alchornea latifolia* (n = 71), *Vernonia patens* (n = 60) and *Ocotea spp* (n = 36) (refer to SM1 for more species). Abandoned tea plants reached heights of up to 4 m and diameters of 17 cm DBH, growing taller in spite of the closed canopy (Fig. 2b).

Compared to the secondary TMF, undisturbed control plots had similar mean tree heights (10.7 ± 3.9 vs 10.1 ± 2.8 m) but higher DBH (17.3 ± 6.8 vs 15.8 ± 5.9 cm) and higher WD (0.57 ± 0.11 vs 0.46 ± 0.10 g.cm⁻³) (Table 2). While a more humid and cooler climate in Kosñipata clearly played a role in the species composition and structure of the control plots, the observed differences can be mainly attributed to different levels of human interventions at both sites.

Structure-wise, the persistence of certain agroforestry species in our plot (particularly tea) might control the structural recovery of the secondary montane forest by suppressing its growth. Persistent structure legacies have also been found in fragmented lowland Amazonian forests 22 years after disturbance (Almeida et al., 2019). Composition-wise, the persistence and dominance of agroforestry species after abandonment has been recorded by other researchers in abandoned shade coffee plantations in Puerto Rico (Marcano-Vega et al., 2002) and Brazil (Raymundo et al., 2018). In those cases, secondary montane forests still had a distinctive agroforest-related composition and structure compared to secondary forests recovering from pastures, even after 40–60 years of abandonment, with a higher alfa diversity in abandoned shade coffee than sun coffee plots (25 vs.15) (Marcano-Vega et al., 2002). Some of the agroforestry species used in the tea plantation for shade (e.g. *Inga edulis*, *Inga punctata*) occur in TMF at our elevation (1780 masl), but at lower densities than observed in the control plots. With more than 300 species, the neotropical genus *Inga* has been important to humans over millennia (Dawson et al., 2008). In the case of *Inga edulis*, its fruit has long promoted its expansion through human semi-domestication (Clement, 1999; Clement et al., 2010; Dawson et al., 2008; Pennington, 1997). Other agroforestry species included fruit trees such as avocado, loquat, lemon tree and zapote, which have persisted after 30 years of abandonment confirming the large resilience of agroforestry trees in tropical landscapes, as identified in 500-year post-Conquest abandoned ‘anthropic’ forest landscapes in fluvial and interfluvial plains in the Amazon Basin (Roosevelt, 2013).

Species-wise, one of the most striking differences between our control and secondary forests, was the absence of tree-ferns in our secondary agroforest, although they were present outside the plot, in less disturbed areas. Tree ferns are a common feature of the undisturbed forests at our elevation.

Table 3

Structure and composition of Yanayaco secondary TMF for trees with DBH between 2 and 10 cm. The secondary montane forest is disaggregated into montane forest, early successional, and agroforestry (mainly tea: *Camellia sinensis*) species. Mean ± SD for DBH: diameter at 1.30 m, H: Height, WD: Wood density, BA: Basal area.

	All species	Montane Forest species	Early successional species	Agroforestry species
Species	31	18	5	8
Genera	31	18	5	8
Families	25	17	4	6
N (stems)	1141	389	53	670
BA (m ² . ha ⁻¹)	6.71 ± 2.2	3.19 ± 1.4	0.44 ± 0.4	2.80 ± 2.1
DBH (cm)	3.9 ± 1.5	4.7 ± 1.9	4.8 ± 1.8	3.4 ± 0.9
H (m)	4.7 ± 1.6	5.4 ± 1.8	5.0 ± 1.6	4.2 ± 1.3
WD (g cm ⁻³)	0.52 ± 0.08	0.48 ± 0.10	0.44 ± 0.12	0.55 ± 0.02
Most common species	<i>Camellia sinensis</i> , <i>Alchornea latifolia</i> , <i>Vernonia patens</i> , <i>Ocotea spp.</i> , <i>Psycotria spp.</i>	<i>Alchornea latifolia</i> , <i>Vernonia patens</i> , <i>Ocotea spp.</i> , <i>Psycotria spp.</i> , <i>Clethra obovata</i>	<i>Palicourea spp.</i> , <i>Cecropia angustifolia</i> , <i>Trema micrantha</i> , <i>Urera caracasana</i>	<i>Camellia sinensis</i> , <i>Coffea arabica</i> , <i>Citrus sinensis</i> , <i>Inga edulis</i>

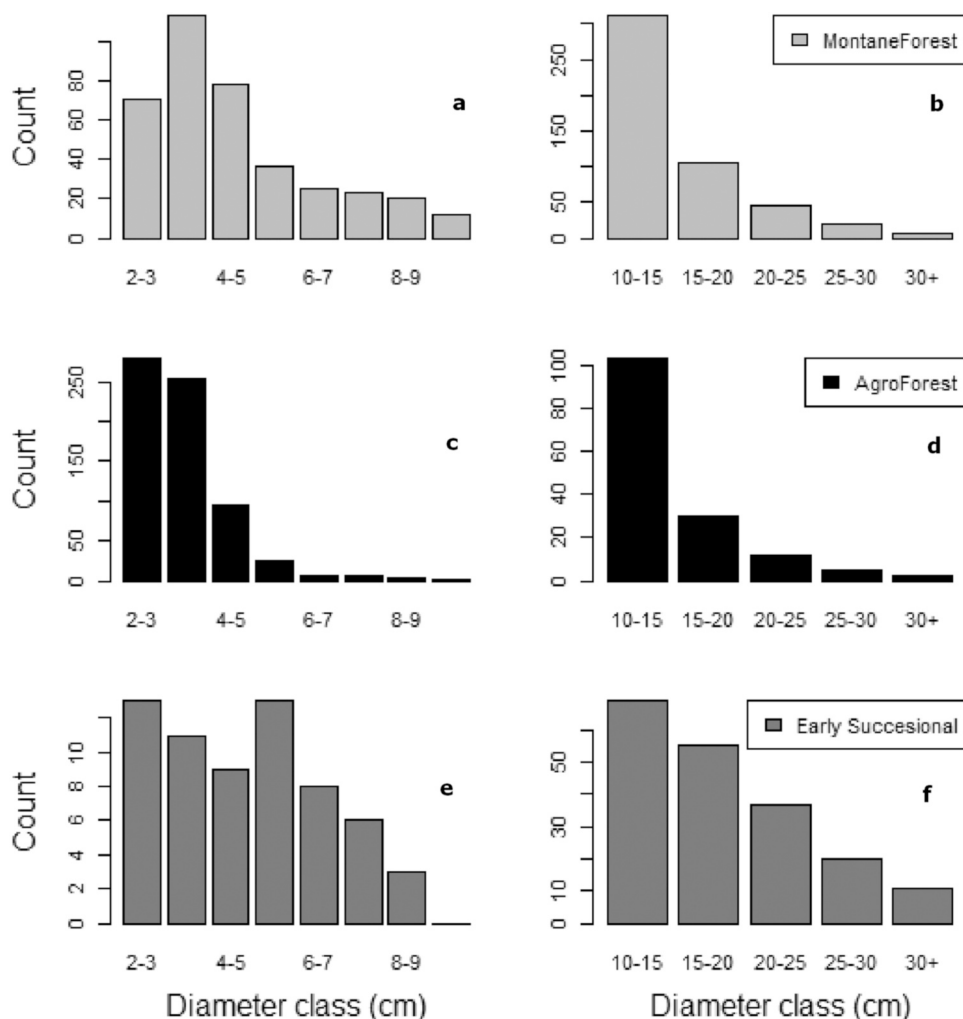


Fig. 2. Diametric distribution of trees with $h \geq 2$ m and DBH between 2 and 10 cm (a,c,e), and trees with DBH ≥ 10 cm (b,d,f). The smallest diametric classes (2–5 cm DBH) were dominated by the agroforestry species: tea (*Camellia sinensis*).

Another highlight of our research was the evidence of high Andean endemism, where climate, disturbance types, histories and intensities, soil parent material and fertility promote very different species compositions in nearby valleys, even though they may have similar structures. Thus, our secondary TMF shared only a few species with our old-growth controls (6% for species-level and 34% for genera-level), raising some warnings on out-of-valley comparability. Some of the early successional species such as *Cecropia* and *Ficus* were present in both secondary and control plots, but responded to different disturbance types (landslides and/or canopy gaps in the control plots) (Clark et al., 2016) than agroforestry abandonment (see SM1 for the species list).

3.2. AGB estimates and growth rates

Variability in AGB is high in TMF, due to large environmental and topographic gradients (Malhi et al., 2010; Spracklen and Righelato, 2014; Young and León, 2000). However, the level of aggregation (from plot to landscape) and the methodological choice to estimate AGB also play major roles. Along this line, our research showed higher biomass estimates with greater aggregation levels. The most conservative estimates were at plot level (species-specific) $42.3 \pm 5.4 \text{ Mg ha}^{-1}$, followed by the averaged ecosystem and biome levels ($59.6 \pm 7.9 \text{ Mg ha}^{-1}$). Remote sensing offered the most liberal estimates (mean $179 \pm 27.3 \text{ Mg ha}^{-1}$) with a four-fold increase over plot level values (Table 4). Satellite-derived data have been reported to overestimate AGB compared to field values (Mitchard et al., 2014; Réjou-Méchain et al., 2019). For optical sensors this partly relates to a poor correlation between the chosen optical variables (leaf area index, greenness index, canopy cover) and biomass estimates (Mitchard et al., 2014; Réjou-Méchain et al., 2019). For active sensors (i.e. radar and lidar) further sources of uncertainty are edge effects, geolocation and instruments errors (Rödig et al., 2019). Acquisition angles and topographically complex areas such as montane terrain can also reduce estimates accuracy (Barbosa et al., 2014; Réjou-Méchain et al., 2019).

Table 4

Aboveground biomass (AGB) estimates for our secondary and control tropical montane forests (TMF) in the Andes, at different scales (from plot level to landscape level) using different approaches (*allometric equations*: at the species level and at the ecosystem (Alvarez et al., 2012; Valle et al., 2011); and pantropical level (Brown et al., 1989; Chave et al., 2005, 2014); *remote sensing* for the landscape level. San Pedro (SP1) and Trocha Union (TU8) are the control plots at 1750 and 1885 masl, in the nearby Kosñipata Valley.

	AGB (Mg. ha ⁻¹) Mean ± SD		
	Secondary TMF	Primary TMF	
	Yanayaco	SP1	TU8
Species level			
Species specific	42.3 ± 5.4		
Ecosystem and biome level			
Valle et al. (2011)	57.3 ± 8.1		
Alvarez et al. (2012)	45.3 ± 5.4		
Brown et al. (1989)	86.4 ± 12.4		
Chave et al. (2005)	66.3 ± 8.5		
Chave et al. (2014)	42.7 ± 5.5	139.8 ± 10.7	134.1 ± 6.1
Average	59.6 ± 7.9	137 ± 12.32	
Landscape level: Remote sensing estimates			
Aboveground Live Woody Biomass (Baccini et al., 2017)	220.7 ± 16.6	214.6 ± 34.2	152.6 ± 14.6
Pantropical Biomass (Avitabile et al., 2016)	185.2 ± n/a	325.2 ± n/a	280.7 ± n/a
GLOBBIOMASS (Santoro et al., 2018)	149.3 ± 48.9	116.5 ± 15.9	194.5 ± 32.8
CCI - AGBiomass (Santoro and Cartus, 2019)	160.8 ± 25.6	137.8 ± 8.8	107.5 ± 7.5
Average	179 ± 27.3	191.2 ± 119.8	

TMF controls showed a three-fold higher mean AGB ($137 \pm 12.32 \text{ Mg ha}^{-1}$) than our secondary agroforest estimates at the plot and biome levels. Three variables explain these lower AGB values: lower DBH ($15.8 \pm 5.9 \text{ cm}$ vs $19.8 \pm 11.0 \text{ cm}$), lower basal area (12.67 ± 6.3 vs $28.03 \pm 1.5 \text{ m}^2 \text{ ha}^{-1}$) and higher abundance of lighter-wood genera (0.46 ± 0.10 vs $0.57 \pm 0.11 \text{ gr cm}^{-3}$) such as *Alchornea*, *Cecropia*, *Inga*, *Ficus* (Table 2).

In relation to standard growth rates, our allometry-based AGB offered far lower values than those expected after 30 years using IPCC's growth rates for secondary montane forests in the American continent ($106 \pm 33 \text{ Mg ha}^{-1}$) (Table 4). This difference is driven by lower growth rates in our secondary TMF ($1.41\text{--}2.0 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for $\text{DBH} \geq 10 \text{ cm}$) than those suggested by the IPCC (4.4 ± 1.6 forests ≤ 20 years), (Requena-Suarez et al., 2019). The composition, structure, and understory suppression legacies of our agroforestry plot may be behind our lower AGB estimates compared to IPCC predictions. They would also explain the slower than expected recovery time to reach the control AGB values. Thus, if we conservatively apply our growth rates from the first 30 years to the entire period, we

Table 5

Reference AGB values for montane and agroforestry systems. When available, mean ± SD are shown. *AGB for Kosñipata Valley plots was recalculated in this study based on the 2017 census.

Reference	Country	Forest type	Altitude (m)	AGB (Mg/ha)
Girardin et al. (2010);Malhi et al. (2017); this study*	Kosñipata Valley, Peru	Old growth	1750 (SP1)	139.8 ± 10.7
			1855 (TU8)	134.1 ± 6.1
			2020 (TU7)	92.4 ± 8.3
			2250 (TU6)	166.4 ± 11.4
Moser et al. (2011)	Ecuador	Old growth	1890	163.2
			2380	94.6
Cruz-del-Amo et al. (2020)	Peru	Old growth	1900–2100	184.4 ± 64.1
	Ecuador		1900–2100	186.1 ± 107.9
Gonzalez et al. (2014)	Peru	Old growth	1291	196 ± 22.6
		Secondary	2000	80.0 ± 14.1
Valle et al. (2011)	Colombia	Secondary (3–10 yr)	550–1700	43.3
		Secondary (10–20 yr)		99.5
		Secondary (>20 yr)		180.8
Peña and Duque (2013)	Colombia	Secondary forest (18 years)	1280–1330	86.3 ± 1.0
		Old growth	1000–2000	156.6 ± 41.6
Alvarez et al. (2012)	Colombia	Secondary(1–5 yr)	2250	16.0
		Secondary(12–15 yr)		55.0
		Secondary(>40 yr)		68.7
Ehrenbergerová et al. (2016)	Peru	Shade Coffee	1550	60.6 ± 6.4
	Peru	Shade Coffee (Inga)	500–800	34.8 ± 8.4
Solis et al. (2020)		Shade Coffee (Polyculture)	960–1050	97.0 ± 13.4
			1000	92.6
Soto-Pinto et al. (2009)	Mexico	Shade coffee (Inga)	1180	50.4 ± 0.8
Hergoualc'h et al. (2012)	Costa Rica	Shade coffee (Inga)	1180	50.4 ± 0.8
Somarriba et al. (2013)	Central America	Shade cacao	300–1700	98.4 ± 49.4
Kalita et al. (2020)	India	Tea agroforest < 10 yr	450–1100	67.0 ± 3.4
		Tea agroforest 10–20 yr		84.6 ± 6.7
		Tea agroforest > 20 yr		85.9 ± 9.0

would need ca. 69–97 years to reach the average AGB value in the control plots ($137 \pm 12.3 \text{ Mg ha}^{-1}$) (Table 2). On the higher end of the estimate, this recovery time would already be 26 years above the average residence times of Andean montane trees at our elevation range, which is 71 ± 1.91 years (at 1855 masl) (Girardin et al., 2010; Malhi et al., 2017). This suggests an unlikely recovery of the original AGB or a far longer time period to achieve it.

While our results do not invalidate estimates made by Requena Suarez et al. (2019), which rely on old and young secondary montane forests mostly based in Mesoamerica and Colombia, with higher precipitation than ours, they highlight the need for caution into their application to predict mitigation potentials out of their original range. Similarly, other legacies such as recurrent droughts have also been reported to reduce AGB recoveries in secondary lowland Amazonian forests, compared to IPCC growth rates for those ecosystems (Elias et al., 2020; Smith et al., 2020). In addition to the impact of agroforestry legacy, the compounded effects of drought and fire in the region (Oliveras et al., 2014c; Roman-Cuesta et al., 2014), are most likely also influencing regrowth in our plot.

An important highlight from our agroforestry legacy research was the role of small trees (DBH between 2 and 10 cm) in the total AGB value. Thus, the understory contributed with ca. 20% of the total AGB in our secondary montane agroforest ($10.8 \pm 7.0 \text{ Mg ha}^{-1}$) (Supplementary Material 2). Besides the important role of the understory into explaining the current structural and AGB legacy of the overstory, it also strongly contributes to the total AGB in the plot. This high contribution has been highlighted by several authors in secondary forest succession (Memiaghe et al., 2016; Puc Kaul et al., 2019; Spracklen and Righelato, 2016) and suggests the need to include small tree monitoring ($2 \geq \text{DBH} < 10 \text{ cm}$) when evaluating AGB in secondary forests.

3.3. Comparison with other montane forests

Compared to other agroforestry systems, our secondary montane agroforest ranked low at $42.3 \pm 5.4 \text{ Mg ha}^{-1}$ vs 50.4 to 98.4 Mg ha^{-1} (Ehrenbergerová et al., 2016; Kalita et al., 2020; Solis et al., 2020; Somarriba et al., 2013; Soto-Pinto et al., 2009). It also ranked low when compared with similarly-aged TMF in the Andes and in other tropical sites (68 to 189 Mg ha^{-1}) (Peña and Duque, 2013; Spracklen and Righelato, 2016; Valle et al., 2011) (Table 5). Our plot was more similar, however, to younger secondary montane forests (ca. 10 year-old in the Colombian Andes) (Valle et al., 2011) (43.3 Mg ha^{-1}), with the caveat that precipitation is much higher there. Compared to other old growth undisturbed Andean forests (156.6 – 196 Mg ha^{-1}), our control forests ranked also slightly lower ($137 \pm 12.3 \text{ Mg ha}^{-1}$), making our biomass comparisons conservative (Table 5). What can account for the low AGB of this secondary succession? Besides a somewhat drier climate, we think that the persistence of *Camellia sinensis* (tea plant) in the understory and of agroforestry shade trees in the overstory may be the reason. Tea plants are known to have well developed root systems and are capable of surviving for very long time under closed canopies (Kalita et al., 2016, 2020); without mechanical removal, it can be difficult for other plants to establish and thrive. The dominance of *Camellia sinensis* may have affected tree species composition in our secondary agroforest, leading to the dominance of light WD early successional species, while montane forest species remained small in the understory. This has also been the case with other secondary forests (Marcano-Vega et al., 2002; McCulloh et al., 2011; Schwartz et al., 2020). Moreover, farmers may have not completely abandoned their plantations, and still clear them from time to time in order to maintain the tea plants, hoping for a revival of the tea industry in the valley. Farmers in the area, point out to an absence of better agricultural alternatives and they still want to reinvest in tea or coffee if prices get better.

3.4. AGB variability due to methodological choices and spatial aggregation scales

Methodological choices influence AGB estimates. Equations that only rely on DBH (e.g. Brown et al., 1989) tend to be more liberal and can offer up to 50% higher estimates of AGB than equations that also include WD and height (Chave et al., 2014) (in our case 86.4 ± 12.4 vs $42.7 \pm 5.5 \text{ Mg ha}^{-1}$) (Table 4). WD changes along the succession through changes in species composition. While mostly ignored, these changes affect AGB stocks estimates and accumulation rates through time (Baker et al., 2004; Lohbeck, 2010). WD is highly conserved phylogenetically (Baker et al., 2004) and species identification is fundamental for accurate estimations of AGB.

AGB values also differed at the ecosystem and biome level, since allometric equations differ substantially from each other (Alvarez et al., 2012; Brown et al., 1989; Chave et al., 2005, 2014). Most equations have been developed for primary forest (e.g. H-DBH and DBH-Biomass relations) and their use in secondary forests must be evaluated carefully. In agroforests this allometry can be highly modified due to the management that farmers provide to the shade tree. Moreover, the use of ecosystem and biome equations must comply with the species and DBH thresholds used to calibrate the equations. Their out-of-range use may lead to AGB biases (Chave et al., 2014).

Although the use of multi-species models is favored on the premise that tree-level errors will average out on plot and landscape scales, this uncertainty is rarely assessed for forest stands and forests across landscapes. The spatial variation in AGB across forests represents another important source of uncertainty and determines the intensity of landscape sampling required to obtain confidence in stand- and landscape-level AGB estimates (Clark and Clark, 2000; Sierra et al., 2007). This is especially important for the validation of remote sensing products that estimate AGB at larger scales. Likewise, the preference, by farmers, for certain useful species such as *Inga spp.* can skew the species composition of a plot and its AGB estimates.

At the landscape level, there are a myriad of problems that can affect remote sensing estimates of AGB. Including the heterogeneity of topography and montane forests' vegetation types, cloud persistence, co-registration problems, pixel size and reflectance saturation issues in tropical forests (Réjou-Méchain et al., 2019; Rödig et al., 2019). One of the bottlenecks of remote-sensed AGB products is the way models relate the scarce field data available to calibrate and validate remote sensing variables. Biomass errors propagate from the plot level up to the landscape level estimates. However, the reduction of errors along this propagation chain is still poorly developed (Réjou-Méchain et al., 2019); although controlling for the geolocation of the reference datasets, reducing the temporal mismatch and the stratification of areas with homogeneous errors have significantly increased the accuracy of biomass maps (Avitabile et al., 2016).

3.5. Potential of secondary forest contributions to climate change mitigation in Peru

While highly uncertain, MINAM (2009) reported that approximately 29% of the deforested area in Peru until 2000, was covered by secondary forest (Che Piu and Menton, 2013), of which at least 1,412,714 ha (68%) occurred in TMF-containing Regions (MINAM, 2009). Secondary forests have been reported to sequester carbon at higher rates through faster growth (Poorter et al., 2016), which makes them attractive for climate change mitigation activities (Griscom et al., 2020), combined with fundamental co-benefits (biodiversity and water) (Rozendaal et al., 2019; Seddon et al., 2020). Moreover, secondary forests have higher rates of success than expensive and poorly adapted afforestation and reforestation initiatives (Chazdon and Guariguata, 2016). However, secondary forests remain fully ignored under Latin American land management initiatives and international UN commitments.

In the case of Peru, secondary forests could help achieve the country's commitments under the UNFCCC through FREL-REDD+ and under NDC adaptation and mitigation targets. Moreover, Peru has pledged to restore 3.2 million hectares by 2030 under the Initiative 20 × 20. Of those, 2 million will be restored through commercial plantations. The remaining 1.2 million hectares will restore areas with water erosion, overgrazing, soil compaction, agrochemical contamination and salinization (Initiative 20 × 20 barometer: Peru). While forest degradation is not targeted as degraded land under their Initiative 20 × 20 commitments, Peru considers "natural reforestation" (sic) and agroforestry as restoration pathways (Román et al., 2018). This opens some opportunities for secondary forests under Landscape Restoration practices. Peru's commitments under FREL-REDD+ and NDCs are in the process of being resubmitted, however, in their previous commitments (UNFCCC, 2016), secondary forests were not explicitly included. Current NDCs revisions are moving towards more explicit forest activities than the original vague 30% emission reduction target (GTM-NDC, 2018; Supplementary Material 3). However, as has happened in the past, Amazonian ecosystems get Peru's full attention, while efforts shy away from TMFs, which bear a large importance for adaptation, mitigation and the provision of critical services such as biodiversity conservation, water provision and carbon sequestration. Incentives for montane forest management including the protection of secondary forest regrowth urgently need more visibility and finance.

4. Conclusions

Although we have examined only one secondary forest plot in comparison with primary forests plots, the trends and dynamics are strong enough to suggest a high effect of agroforestry legacy species in AGB stocks, pointing to three structural variables affecting aboveground carbon stocks compared to the control plots: lower DBH (15.8 ± 5.9 cm vs 19.8 ± 11.0 cm), lower basal area (12.67 ± 0.7 vs 28.03 ± 1.5 m² ha⁻¹) and higher abundance of lighter-wood genera (0.46 ± 0.10 vs 0.57 ± 0.11 gr cm³) such as *Inga*, a common shade-tree in Andean agroforests. As seen in other tropical forest research, agroforestry legacies show a long-term persistence in terms of composition and structure that highly affects carbon storage and sequestration of the newly established secondary montane forests.

Our results are important for Peru, as agroforestry systems (including coffee and tea) cover 608,332 ha and are vulnerable to abandonment due to rural emigration, market price volatility, pests and warming temperatures. There is, moreover, few data available on the composition, structure and carbon recovery of secondary Tropical Montane Forests in the Andes, especially those deriving from agroforestry abandonment. Our results show that, in spite of the optimism for the Natural Climate Solutions associated with secondary forests, the mitigation potentials of our agroforestry-derived secondary TMF were three times lower than those estimated from IPCC values for South America montane forests. This can lead to overestimating Andean mitigation potentials under international commitments such as Peru's NDCs and Initiative 20 × 20, however, high endemism and the water capture and retention potential of these forest increase their overall ecological service value. If mitigation and adaptation by secondary TMF is to be promoted, the assisted removal of the agroforestry understories may be needed to accelerate its compositional, structural and carbon recoveries towards old growth TMF.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01696](https://doi.org/10.1016/j.gecco.2021.e01696).

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