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Forest biomass stocks and dynamics across the subtropical Andes

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Abstract

Forest biomass plays an important role in the global carbon cycle. Therefore, understanding the factors that control forest biomass stocks and dynamics is a key challenge in the context of global change. We analyzed data from 60 forest plots in the subtropical Andes (22–27.5° S and 300–2300 m asl) to describe patterns and identify drivers of aboveground biomass (AGB) stocks and dynamics. We found that AGB stocks remained roughly constant with elevation due to compensating changes in basal area (which increased with elevation) and plot-mean wood specific gravity (which decreased with elevation). AGB gain and loss rates both decreased with elevation and were explained mainly by temperature and rainfall (positive effects on both AGB gains and losses). AGB gain was also correlated with forest-use history and weakly correlated with forest structure. Mean annual temperature and rainfall showed minor effects on AGB stocks and AGB change (gains minus losses) over recent decades. Although AGB change was only weakly correlated with climate variables, increases in AGB gains and losses with increasing rainfall—together with observed increases in rainfall in the subtropical Andes—suggest that these forests may become increasingly dynamic in the future.

Abstract in Spanish is available with online material

KEYWORDS
biomass dynamics, biomass stocks, forest structure, forest-use history, montane forests, rainfall, temperature

1 | INTRODUCTION

FORESTS REPRESENT THE LARGEST ABOVEGROUND CARBON STOCK AMONG TERRESTRIAL ECOSYSTEMS and play an important role in the global carbon cycle (Le Quéré et al., 2016). Tropical and subtropical forests account for approximately 70% of the global forest carbon sink (Pan et al., 2011) and exhibit substantial inter-annual variation in carbon storage, largely driven by temperature and moisture (Wang et al., 2014). Biomass stocks and dynamics depend on environmental conditions (i.e., resource availability) and on forest attributes in terms of quantity (e.g., stem density, basal area) and quality (i.e., functional traits of the community) (Lohbeck, Poorter, Martínez-Ramos, & Bongers, 2015; Poorter et al., 2017). In tropical forests, stocks of aboveground biomass (AGB) have been mainly related to forest structure and species composition (Baker et al., 2004; Lewis et al., 2013; Malhi et al., 2006) and to a lesser extent to temperature, rainfall, soil fertility, and topography (Clark & Clark, 2000, Valencia, Condit, Muller-Landau, Hernandez, & Navarrete, 2009, Álvarez-Dávila et al. 2017). Regional patterns of basal area and plot-mean wood specific gravity have explained more than 80% of AGB variation across tropical forests

(Baker et al., 2004; Baraloto et al., 2011; Poorter et al., 2017), which is expected because AGB is inherently related to tree diameter and wood specific gravity. However, structural parameters may differ in their relationships with environmental variation (e.g., climate) and disturbance (Zhang et al., 2015). Thus, a variety of forest structure and AGB patterns may emerge across environmental gradients, with implications for AGB stocks and dynamics at the regional scale.

Forest structure and species composition change along elevation gradients across montane forests. In general, stem density and basal area increase, and tree height decreases from lowland to high-montane forests (Clark, Hurtado, & Saatchi, 2015; Girardin, Farfan-Rios, et al., 2014). Species composition has shown continuous variation across these complex environmental gradients (Fahey, Sherman, & Tanner, 2016), and it is possible to distinguish altitudinal vegetation zones (e.g., Kessler, 2000). AGB stock does not show clear patterns along elevation in tropical montane forests. It may increase (Alves et al., 2010, Cuni-Sanchez et al. 2017), decrease (Girardin et al., 2010; Kitayama & Aiba, 2002; Miyamoto, Sato, Arana Olivos, Clostre Orellana, & Rohner Stornaiuolo, 2018; Raich, Russell, Kitayama, Parton, & Vitousek, 2006), or remain relatively constant along altitudinal transects (Culmsee, Leuschner, Moser, & Pitopang, 2010; Imani et al., 2017; Peña, Feeley, & Duque, 2018; Unger, Homeier, & Leuschner, 2012). On the other hand, rates of AGB productivity decrease with elevation, and the causal factors proposed for explaining this pattern include temperature limitation of physiology (Kitayama & Aiba, 2002), limitation in nutrient uptake (Bruijnzeel, 2004), and cloud cover (Girardin, Malhi, et al., 2014). Structural patterns of forest recovery from disturbance also affect AGB productivity in tropical montane forests (Peña et al., 2018).

Andean forests have been identified as one of the most important hotspots of global biodiversity (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000; Rahbek et al., 2019), and these forests provide important ecosystems services, such as climate regulation (Jarvis & Mulligan, 2011) and carbon storage (Spracklen & Righelato, 2014). The interaction between abiotic factors and forest recovery related to land-use change vary across latitudes and elevations, leading to differences in forest structure and productivity between the tropical and subtropical Andes (Báez et al., 2015). Although many studies have analyzed patterns of AGB stocks and dynamics across tropical Andean forests (e.g., Unger et al., 2012, Girardin, Malhi, et al., 2014, Girardin, Farfan-Rios, et al., 2014, Miyamoto et al., 2018, Peña et al., 2018, Vilanova et al., 2018), no studies to date have quantified these patterns in the subtropical Andes.

In this paper, we use inventory data from 60 forest plots (45 of them with two censuses), distributed along elevation (300–2300 m) and latitudinal (22–27.5° S) gradients in the subtropical Andean forests of Argentina, to quantify patterns in AGB stocks and dynamics in the subtropical Andes. The forest plots represent well-conserved and mature forests, although historical human practices, such as seasonal cattle grazing (hereafter, "grazing") and selective logging have occurred in some plots. We analyze patterns of AGB stocks and AGB dynamics (i.e., AGB change and its components: AGB gain due to growth and recruitment, and AGB loss due to mortality) along elevation and latitudinal gradients. Also, we quantify how AGB stocks and dynamics depend on environmental factors (i.e., climate variables and forest-use history) and forest structural parameters (basal area, stem density of large trees, and plot-mean wood specific gravity). We test the hypotheses that AGB stocks and AGB dynamics are positively related to temperature (Girardin et al., 2010; Sullivan et al., 2020) and water availability (Álvarez-Dávila et al. 2017), and that AGB dynamics are related to forest structure (Lohbeck et al., 2015; Poorter et al., 2017).

2 | METHODS

Andean forests of northwest Argentina represent the southernmost extension of Neotropical montane forests (Cabrera & Willink, 1980). In this part of the Andes, climate is defined as subtropical, with a marked dry season (April-October) and occasional frost during cold months (Brown, Grau, Malizia, & Grau, 2001). Mean annual temperature decreases from 21.5°C to 11.5°C along the altitudinal gradient, and rainfall ranges from 800 to more than 2000 mm annually, being higher on slopes with eastern exposures (Arias & Bianchi, 1996). In addition, water input through fog interception may be as important as direct rainfall in low- and high-montane forests (Hunzinger, 1997). Based on floristic composition, three forest types are differentiated along the elevation gradient: premontane forest from *ca*. 400 to 800 m asl; low-montane forest from *ca*. 800 to 1,500 m asl; and high-montane forest from *ca*. 1,500 to 2,500 m asl; montane grasslands occur above tree line (Brown et al., 2001). Besides forest conversion to agriculture in the lowlands, grazing and selective logging have been the principal human activities in these montane forests during the last centuries (Brown et al., 2001).

2.1 | Forest inventory plots

Plots were established between 300 and 2,300 m asl, and between 22° and 27.5° S (Figure S1) to cover the wide environmental variation of the subtropical Andes (e.g., temperature, rainfall, slope, and aspect). Plot establishment and measurement were performed between 2002 and 2017 (Table S1), and followed standardized protocols for Andean forests (Osinaga-Acosta et al., 2014). We analyzed inventory data from 60 permanent plots, 45 of them measured twice with a mean of 6.6 years between censuses (29 plots with 4–6 years between census 1 and 2, and 16 plots with 9–10 years between census 1 and 2). The 60 plots include 53 1-ha plots (51 rectangular plots of 20 × 500 m and two square plots of 100 × 100 m), four 0.4-ha plots (two 40 × 100 m and two 20 × 200 m), two 0.24-ha plots (40 × 60 m), and one 6-ha plot (200 × 300 m). All stems with diameter at 1.3 m height (diameter at breast height, DBH) ≥ 10 cm were marked, identified, and DBH measured. These inventoried stems included single-stemmed trees, as well as stems

of multi-stemmed individuals that forked below 1.3 m height. We marked and measured a total of 28,983 stems belonging to 154 species. Nearly all trees were identified to the species level, with 0.38% of individuals identified to the genus level, and 0.12% of individuals unidentified.

Plots were established in well-conserved and mature forests. However, some plots have occasional grazing; this does not seem to reduce forest biomass but may affect species composition after decades of forest use (Blundo et al., 2018). In addition, some plots had low-intensity selective logging prior to the initial census. Forests in this region with low-intensity logging largely recover to their pre-logging condition, in terms of forest structure and species composition, within 20 years (Blundo, Malizia, & González-Espinosa, 2015). In summary, 48 out of 60 plots were old-growth forests (28 with grazing and 20 without), and 12 out of 60 plots were forests with low-intensity logging (>20 years since the last selective logging) (Table S1).

For each plot, we obtained climatic data at 1-km resolution from the CHELSA database (Karger et al., 2017). To describe the climate gradient in terms of environmental energy and water availability, we used mean annual temperature (MAT), temperature seasonality (TS), annual rainfall, and rainfall seasonality (RS). We obtained wood specific gravity (WSG) for 74% of species using local databases (Easdale, Healey, Grau, & Malizia, 2007, INTI-CITEMA 2007; https://www.inti.gob.ar/publicaciones/descargac/365), and we used an international database when local data were unavailable (Chave et al., 2006). For unidentified individuals, we used the plot-mean WSG value (see details below) of the plot where that individual occurred.

We calculated plot-level basal area, stem density of large trees, and plot-mean WSG to describe forest structure of each plot. Basal area of individual trees was calculated as: $BA = \pi/4 \times DBH^2$. Tree-level BA values (m^2) were summed to estimate plot-level BA (m^2/ha). Stem density of large trees (SD50) is the density of all stems ≥ 50 cm in DBH measured in the plot (stem/ha). Plot-mean WSG (WSGµ) in each plot was calculated by weighting the WSG of each species (g/cm^3) by its plot basal area.

AGB was estimated from the equation developed by Chave et al. (2014) for cases where tree height was unavailable (as is this case): $AGB = \exp(-1.803 - 0.976 \times E + 0.976 \times \ln(WSG) + 2.673 \times \ln(DBH) - 0.0299 \times (\ln(DBH))^2)$. The environmental factor E was calculated from plot-level climate variables as follows: $E = (0.178 \times \text{Temperature seasonality} - 0.938 \times \text{Climatic Water Deficit} - 6.61 \times \text{Precipitation seasonality}) \times 10^{-3}$). We extracted the Climatic Water Deficit index from Chave et al. (2014) (http://chave.ups-tlse.fr/pantropical_allometry.htm). Tree-level AGB values (Mg biomass) were summed to estimate plot-level AGB (Mg biomass/ha).

To quantify AGB dynamics within each plot, we calculated plot-level AGB change, AGB loss, and AGB gain (Mg biomass/ha/yr). AGB change = $(AGB_2 - AGB_1)/T$, where AGB_1 and AGB_2 are AGB at the time of the first and second measurements, respectively, and T is the census interval (years). AGB loss (due to tree mortality) is the AGB of trees alive at time 1 but dead at time 2, annualized by T. Finally,

based on the formula for AGB dynamics, $AGB_2 = AGB_1 + (\text{AGB gain} - \text{AGB loss}) \times T$, we obtained annualized AGB gain (due to tree recruitment and growth), as: AGB gain = $(AGB_2 - AGB_1)/T + \text{AGB loss}$.

2.2 | Data analysis

We calculated Spearman rank correlations (ρ) to evaluate relationships among spatial variables (i.e., elevation, latitude), climate variables (i.e., MAT, TS, annual rainfall, RS), forest structure variables (i.e., BA, SD50, WSGµ), AGB stocks, and AGB dynamics variables (i.e., AGB change, ABG gain, and AGB loss). To determine which environmental variables (i.e., climate variables and forest-use history) were related to AGB stocks, and which environmental and forest structure variables were related to AGB gain and loss, we fitted a series of nested generalized linear models (GLM). First, we evaluated the relationship between spatial variables (elevation and latitude) and AGB stocks, AGB gain, and AGB loss (i.e., Null model versus Spatial model, where "Null" refers to an intercept-only model). Second, to test the hypothesis that AGB stocks and AGB dynamics are positively related to temperature and water availability, we compared the spatial model with each climate variable (i.e., Spatial model versus Spatial + Climate model). Then, to evaluate if forest structure variables (i.e., BA, SD50 and WSGµ) explain additional variance in AGB gain and AGB loss, we compared the spatial + climate model with each forest structure variable (i.e., Spatial + Climate model versus Spatial + Climate + Forest structure model). Finally, we analyzed the effects of forest-use history (i.e., old-growth forests, old-growth forests with grazing, and forests with past logging) on AGB stocks, AGB gain and AGB loss. We used the Gaussian family in all models, and we log-transformed AGB gain and AGB loss to normalize variables. Comparisons between nested models were performed with likelihood ratio tests. All analyses were performed in R (R Core Team 2020).

3 | RESULTS

Forest structure showed clear patterns along the environmental gradient of subtropical Andean forests, in which temperature decreases and rainfall seasonality (RS) increases with elevation (Table S2). Basal area increased with elevation and increased slightly with latitude, and WSGµ decreased with elevation and with latitude (Figure 1a-b, Table S2). AGB stocks remained relatively constant along the elevation gradient and increased with latitude (Figure 1c, Table S2). The mean AGB stock was 324 Mg biomass/ha, and the range was 140 to 522 Mg biomass/ha. The latitudinal trend in AGB stocks was significant (Table 1) with a slight increase of AGB stocks toward southern forests (310 ± 12 Mg biomass/ha in northern plots; 376 ± 23 Mg biomass/ha in southern plots; ± values are standard error). AGB stock was correlated with basal area (ρ = 0.61) and stem density of large trees (SD50; ρ = 0.71), but not correlated with WSGµ (Figure 1d-f). AGB stock was not significantly related to climate variables or forest-use history (Table 1).

Mean AGB gain (recruitment plus growth) was 4.9 Mg biomass/ha/yr (range 1.2 to 12.1 Mg biomass/ha/yr), and mean AGB loss was 5.0 Mg biomass/ha/yr (range 0.9 to 15.7 Mg biomass/ha/yr). Mean AGB change was −0.1 Mg biomass/ha/yr (range −9.9 to 6.4 Mg biomass/ha/yr). AGB change was relatively constant along elevation and latitudinal gradients (Figure 2a), and none of the climate or forest structure variables were correlated with AGB change (Table S2). AGB gain and AGB loss decreased along altitudinal gradient (Figure 2b-c). Elevation explained 18% of AGB gain variance, and 12% of AGB loss variance (Table 1). When climate variables were added to the elevation model, mean annual rainfall had the highest explanatory power for both AGB gain and loss (Table 1). MAT did not significantly improve the elevation models for AGB gain or loss, but the strong negative correlation between MAT and elevation (Table S2) suggests a role for MAT in the elevation effect. Forest structure also contributed to explaining variance in AGB gain: including SD50 (density of trees with DBH ≥ 50 cm) in the model increased the explained variation from 24% to 29%, a marginally significant improvement ($p = .06$; Table 1). By itself, SD50 was negatively but not significantly correlated with AGB gain (Table S2). Forest structure did not significantly increase variance explained in AGB loss. Finally, forest-use history significantly improved the model for AGB gain, with grazing and past logging both leading to reduced AGB gain (Figure 2b, Table 1). Forests with a history of grazing and logging also appeared to have reduced AGB

loss rates (Figure 2c), but these effects were not significant in the AGB loss model (Table 1).

4 | DISCUSSION

We analyzed patterns of forest structure and their correlations with AGB stock and AGB dynamics across environmental gradients in the subtropical Andean forests in Argentina. We found that the pattern of increasing basal area and stem density of large trees, and decrease in WSGμ, resulted in a relatively constant AGB stock along the altitudinal gradient. Temperature and rainfall explained significant variation in AGB gain and loss, but not in AGB stocks. Forest structure explained some of the variation in AGB dynamics, with AGB gain decreasing with increasing the density of large trees. Finally, forest-use history did not explain differences in AGB stocks or loss rates, but rates of AGB gain in undisturbed old-growth forest were higher than in forests with grazing or past logging.

4.1 | Forest structure along subtropical Andes

AGB stocks in subtropical Andean forests were not strongly related to elevation or climate variables. Temperature and water availability may drive large changes in forest structure and species composition along
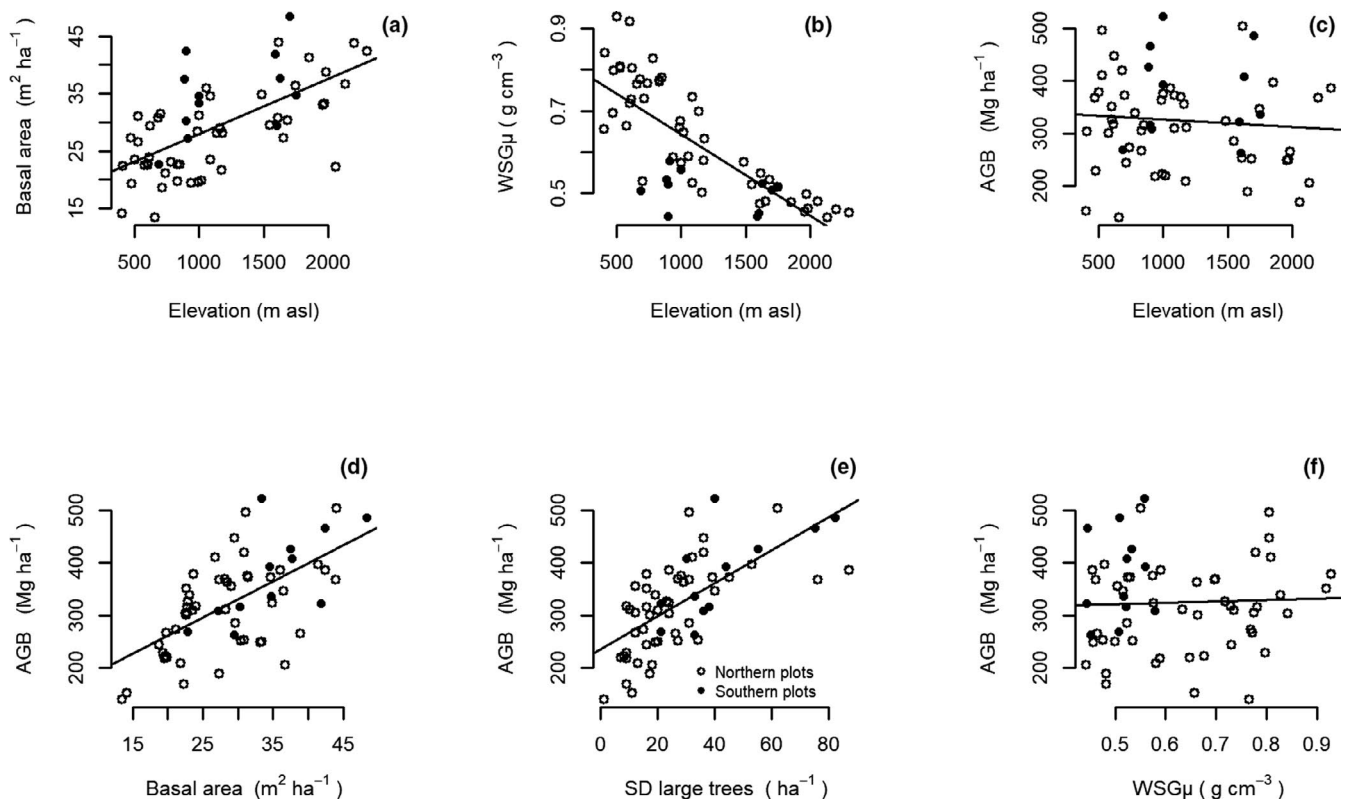

FIGURE 1 Altitudinal and latitudinal patterns of forest structure in 60 forest plots across the subtropical Andes (a-c), and associations between forest structure variables and AGB stocks (d-f). WSGμ = plot-mean wood specific gravity; AGB = aboveground biomass; *SD* large trees = stem density of trees with DBH ≥ 50 cm

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TABLE 1 Summary of comparisons between nested models of aboveground biomass (AGB) stocks and AGB gain and loss rates

Model	AIC	~ 1	~ Lat	~ Elev	~ Elev + Rain	~ Elev + Rain +SD50	Pseudo R^2
AGB stocks							
~ 1	710.7						
~ Elevation	712.3	0.51					
~ Latitude	708.2	0.03					0.07
~ Latitude + Elevation	709.7		0.46				
~ Latitude + MAT	709.5		0.41				
~ Latitude + Rain	708.7		0.21				
~ Latitude + TS	710.2		0.77				
~ Latitude + RS	710.1		0.69				
~ Latitude + FUH	707.9		0.12				
AGB gain							
~ 1	210.2						
~ Elevation	203.4	0.003					0.18
~ Latitude	212.2	0.88					
~ Elevation + MAT	204.8			0.42			
~ Elevation + Rain	201.8			0.05			0.24
~ Elevation + TS	205.4			0.79			
~ Elevation + RS	205.2			0.63			
~ Elevation + Rain +BA	203.8				0.83		
~ Elevation + Rain +WSGμ	203.6				0.66		
~ Elevation + Rain +SD50	200.5				0.06		0.29
~ Elevation + Rain +SD50 + FUH	198.1					0.04	0.39
AGB loss							
~ 1	230.4						
~ Elevation	226.5	0.02					0.12
~ Latitude	232.4	0.98					
~ Elevation + MAT	228.5			0.89			
~ Elevation + Rain	223.8			0.03			0.21
~ Elevation + TS	228.5			0.96			
~ Elevation + RS	224.4			0.04			0.19
~ Elevation + Rain + BA	224.3				0.23		
~ Elevation + Rain +WSGμ	225.3				0.46		
~ Elevation + Rain + SD50	224.6				0.28		
~ Elevation + Rain + FUH	225.7				0.35		

Note: Each row in the table represents a different model for AGB stocks, gain, or loss. The first column indicates the explanatory variables included in the model, with "~1" (intercept-only) being the null model. The remaining columns give the AIC (Akaike information criterion), the description of the nested models used for the Likelihood Ratio tests (*p*-values are indicated for each test), and the Pseudo-R^2 for significant models ((Null Deviance – Residual Deviance)/ Null Deviance × 100).

Abbreviations: MAT, mean annual temperature; Rain, annual rainfall; TS, temperature seasonality; RS, rainfall seasonality; BA, basal area; WSGμ, plot-mean wood specific gravity; SD50, stem density of large trees (≥50 cm DBH); FUH, forest-use history.

elevation gradients (Fahey et al., 2016), and different patterns of forest structure have been reported across tropical montane forests. Clark et al. (2015) suggested that elevational transects from warm and wet lowland forests to cool and dry montane forests may show different patterns in forest structure than elevational transects from warm and dry lowland forests to cool and moist montane forests. Therefore,

different altitudinal patterns of forest structure and species composition may combine to yield different trends in AGB stocks across tropical montane forests, for example, increasing, decreasing, or constant AGB with elevation. For example, in the Peruvian Andes, the lack of trend in basal area with elevation suggests that AGB decline is driven by reduced tree height with increasing elevation (Girardin, Farfan-Rios,
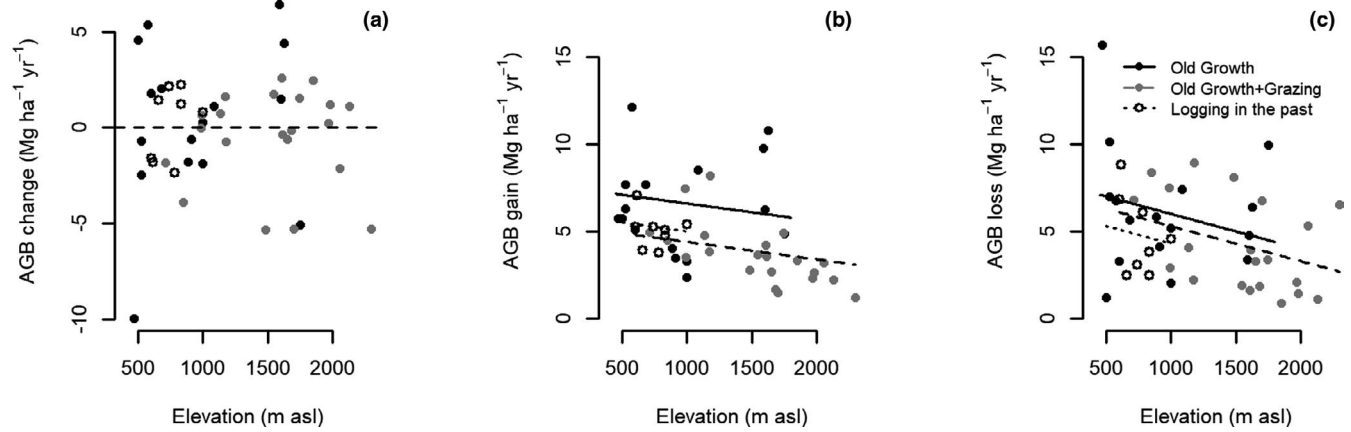
FIGURE 2 Altitudinal and latitudinal patterns of AGB change (a), AGB gain (b), and AGB loss (c), classified by forest-use history in 45 remeasured forest plots across the subtropical Andes

et al., 2014). In contrast, in tropical montane forests of Indonesia, canopy height decreased as basal area increased with elevation, such that AGB stocks were relatively constant along the elevation gradient (Culmsee et al., 2010). In the subtropical Andes, we found compensating changes across elevation in basal area and species composition (in terms of community-mean wood specific gravity, WSGμ); that is, low basal area and high WSGμ in premontane forests resulted in an AGB that was similar to that in high-montane forests with high basal area and low WSGμ. A similar trade-off between forest structure and species composition has previously been reported in tropical montane forests (Culmsee et al., 2010).

In our study area, the decreasing WSGμ with increasing elevation may be related to the biogeographic origins of trees species. Premontane forests (high WSGμ) share a high fraction of species with seasonal tropical forests, such as Caatinga and Atlantic coastal forests in Brazil (Werneck, Costa, Colli, Prado, & Sites, 2011), in which WSG of trees tends to be higher than 0.7 g/cm³ on average (Chave et al., 2006). In contrast, high-montane forests (low WSGμ) have a high fraction of species of austral and boreal origin (e.g., *Podocarpus* and *Alnus*; Brown et al., 2001) that have low WSG (~0.5 g/cm³). Little is known about patterns of wood density of species along elevation gradients (Clark et al., 2015), and to our knowledge, only Chave et al. (2006) have reported a decrease in species WSG with increasing elevation in the central Andes. We found the same pattern in the southern Andes.

4.2 | Drivers of forest dynamics

In our study, AGB gain and loss rates were highest in premontane forests around 500 m asl, where temperature was highest. Elevation is a complex gradient along which several biotic and abiotic factors are correlated (Ashton, 2003; Kitayama, 1992). Although elevation and MAT were correlated with AGB gain and loss (Table 1 and Table S2), unmeasured variables (such as fog, light incidence, and relative humidity) that vary with elevation may also play a role in determining AGB gain and loss rates. Elevation explained 18% of AGB gain and 12% of AGB loss, with both rates decreasing with elevation (and increasing with MAT). Rainfall, which was not significantly

correlated with elevation in our study, also explained additional variation in AGB gain and loss (both positively correlated with rainfall).

We hypothesized that forest structure would affect AGB gain and loss; however, neither of these rates was strongly correlated with forest structure variables. The only significant forest structure variable in our multiple regression models was the stem density of large trees (SD50), which increased with elevation (Table S2) and explained about 5% of AGB gain (increasing the model R^2 from 24% to 29%; Table 1). Rates of biomass growth increase with tree size in many species (Stephenson et al., 2014), but it is well known that tree growth rates often decrease with elevation (Coomes & Allen, 2007; Rapp et al., 2012). In our study, AGB gain decreased with elevation even though large trees were relatively abundant in high-montane forests. AGB gain was positively correlated with WSGμ in our study (Table S2). That is, AGB gain was relatively high in premontane forests (low elevation and high WSGμ). Poorter et al. (2017) reported that high plot-mean WSG increases AGB gain, and they argue that high stand-level WSG indicates dominance of shade-tolerant trees with less volumetric growth. In premontane forests, tree species with high WSG and high rates of DBH growth are canopy dominants (e.g., *Anadenanthera colubrina*, *Myracrodruon urundeuva*, and *Myroxylon peruiferum*, Blundo et al., 2015). Our results suggest that the main determinants of AGB dynamics (gain and loss rates) are abiotic variables (e.g., MAT and/or other factors that covary with elevation), but forest structure and species composition may also affect AGB dynamics to some degree.

4.3 | Forest-use history in subtropical Andean forests

Our forest plots were established in mature forests with minimal disturbance and, to the extent possible, represent the original subtropical Andean forest vegetation. None of the forests included in this study were recovering in post-agriculture areas. In comparison with the tropical Andes, in which the reported AGB stocks range from 150 to 250 Mg biomass/ha (e.g., Girardin, Farfan-Rios, et al., 2014; Peña et al., 2018; Vilanova et al., 2018), we found that subtropical

Andean forests had 320 to 370 Mg biomass/ha. Subtropical Andean forests had AGB stocks that were similar as subtropical forests outside the Andes, such as subtropical Atlantic forests in South America (Blundo et al., 2018; Vieira et al., 2008). The abundance of species with high wood specific gravity may contribute to the high AGB stocks of subtropical forests. Tree species composition (and therefore community-mean WSG) differed between tropical and subtropical Andean forests, due to the influence of different floristic regions (Malizia et al., 2020).

Subtropical Andean forests have a long history of use, spanning more than 2000 years of documented occupation (Ortiz, Ramos, & Alavar, 2017) that has intensified over the last 200 years (Brown et al., 2001). Selective logging and grazing are the principal human activities in these subtropical montane forests that do not involve total deforestation. Forest-use history in our plots did not affect AGB stocks along the elevation gradient; however, plots established in undisturbed old-growth forests had higher rates of AGB gain than old-growth forests with grazing. Few studies have evaluated the effects of this historical human practice on forest structure and dynamics at the community level, but the change in species composition may be partially explained by cattle presence (Blundo, Malizia, Blake, & Brown, 2012). Cattle presence does not seem to reduce AGB stock but leads to changes in species composition after decades of forest-use, for example, increased abundance of some understory species (Malizia, Easdale, & Grau, 2013) or increased abundance of evergreen species (Blundo et al., 2018). Additional studies about the effects of this historical human influence would lead to a better understanding of forest dynamics in the subtropical Andes.

4.4 | Study limitations and conclusions

The capacity to evaluate the effect of climate in this study was limited to some extent by lack of data on climate factors that can be important in montane forests, for example, cloud cover, water input from fog, and solar irradiance. Also, without plot-level instrumentation available, we relied on a global climate product, which may be especially error-prone in mountainous regions. Another limitation of our study concerns the area and time-period (60 total plots; 45 remeasured with a mean census of interval of 6.6 years). Most of the 60 plots were 1 ha in size, and six plots were smaller than 1 ha. Even in the 1-ha plots, the stochastic nature of mortality (e.g., the death of a single large tree, or the absence of canopy mortality during a census interval) could create variance that is not representative of the broader landscape (Chambers et al., 2013). Increasing the sampled area and/or time-period should allow for more robust estimates of AGB stocks and dynamics.

Despite the above limitations, our results provide the first quantification of AGB stocks and rates of AGB gain and loss for a complete elevation gradient across subtropical Andean forests. Over recent decades, mean rainfall and rainfall variability have both increased in northwest Argentina (Ferrero & Villalba, 2019). Our results suggest that both AGB gain and loss rates will increase if the rainfall trends observed over recent decades continue into the future. This implies the potential for increasing dynamism of subtropical Andean forests. The potential impacts of this dynamism on ecosystem properties (e.g., species diversity; Phillips, Hall, Gentry, Sawyer, & Vásquez, 1994) are the important topic for future research.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.