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Carbon sequestration rates indicate ecosystem recovery following human disturbance in the equatorial Andes

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Abstract

Few studies exist that document how high-elevation Andean ecosystems recover naturally after the cessation of human activities and this can limit the implementation of cost-effective restoration actions. We assessed Andean forest (Polylepis stands) and páramo grassland recovery along an elevation gradient (3,600–4,350 m.a.s.l.) in the Yanacocha Reserve (Ecuador) where natural recovery has been allowed since 1995. Within the Yanacocha Reserve in 2012 and 2014 the aboveground biomass (AGB), aboveground necromass (AGN) and belowground biomass (BGB) carbon (C) stocks were measured and C sequestration rates calculated as proxy of ecosystem recovery. The soil organic carbon (SOC) stock to 36-cm depth was also quantified during the 2012 survey. To explore potential drivers of spatiotemporal variation of the forest and páramo C stocks they were related to abiotic and biotic variables. Andean forest C stocks were influenced mainly by disturbance history and tree-species composition. Páramo C stocks’ spatial variation were related to the elevation gradient; we found a positive significant trend in páramo AGB-C stocks with elevation, whereas we found a significant negative trend in AGN-C stocks. Likewise, significant temporal changes were found for AGB-C and AGN-C stocks. Net increases in AGB-C stocks were the largest in the Andean forest and páramo, 2.5 Mg C ha$^{-1}$ year$^{-1}$ and 1.5 Mg C ha$^{-1}$ year$^{-1}$ respectively. Carbon sequestration rates were partly explained by environmental variables. In the Andean forest, plots with low dominance of Baccharis padifolia were observed to present higher AGB-C and lower BGB-C sequestration rates. In the páramo, higher sequestration rates for AGB-C were found at higher elevations and associated with higher levels of growth-forms diversity. Temporal changes in BGB-C stocks on the contrary were non-significant. Our results indicated that terrestrial aboveground C sequestration rates might be an appropriate indicator for assessing Andean forest and páramo recovery after human disturbance.
Introduction

High-elevation tropical Andean ecosystems, such as woodlands dominated by the genus *Polyplepis* (hereafter Andean forest) and grass dominated páramo, are of paramount importance due to the economic and ecosystem services they provide [1–3]. These services include diverse and unique biodiversity [4, 5], carbon (C) storage [6–11], and water provision for direct human consumption, irrigation and hydropower generation [8]. However, large areas of the Andean forest and páramo in the Ecuadorian Andes have been degraded by a diverse array of human land-uses including: overgrazing, fire, timber extraction, introduction of exotic species and agricultural activities [8, 12–15].

In the high Andes, ecosystem services, including terrestrial C storage, and threats to those services, are intrinsically interlinked [15–17]. Aerial and belowground C stocks vary greatly along the Andean forest and páramo gradient with the ratio between aboveground biomass (AGB) and soil organic carbon (SOC) decreasing at higher elevations. Typical AGB-C stocks for forest over 3,500 m.a.s.l. (meters above sea level) range between 38–83 Mg C ha\(^{-1}\) [18, 19], whereas for páramo these values can be around 4 and 17 Mg C ha\(^{-1}\) [20, 21]. Aboveground necromass (AGN) C stocks have been measured considering land use and vegetation cover mainly in forests [9, 22, 23], but the effect of other abiotic (e.g. elevation) variables have not been assessed in páramo ecosystems. Belowground biomass (BGB) C stocks, have been rarely reported for páramo and no clear trend with elevation has previously been documented [7]. High relative humidity, low temperatures and volcanic ash deposition reduce decomposition rates in páramo and Andean forest soils resulting in increases in the SOC stock in the organic layers [24]. Different environmental and anthropic factors may influence C allocation in the different pools of high elevational gradients. For example, in Andean forests selective logging coupled with annual burning events results in ecosystem degradation including reduction in C stock, forest fragmentation and species loss [19]. While in páramo, areas of extensive cattle grazing and associated burning events have homogenized the vegetation (i.e. reduced growth-forms diversity) and resulted in a decrease in AGB and BGB-C stocks [12, 25–27]. Furthermore, in páramo ecosystems consecutive fires and persistent grazing have shown to decrease AGB production [28, 29]. Yet, grazing and burning may have effects on the SOC stock of both páramo and Andean forest ecosystems [1, 8, 14].

Recognition of the societal value of high Andean ecosystems and their ecosystem services, together with the current threat they face due to ongoing land-use change, have led to an increased global awareness of the need to restore the functionality of regional threatened ecosystems to secure human wellbeing [30]. Yet, our understanding on how tropical mountain ecosystems recover from land-use disturbance is still limited, particularly in areas experiencing natural recovery over long periods.

Secondary tropical forest, previously converted into pasture land-use, have been shown to recover vegetation structure and biomass to pre-disturbance levels over an 80-year period [31]. AGB accumulation in recovering secondary forests has been reported to be 5, 3 and 1 Mg C ha\(^{-1}\) year\(^{-1}\) over the first 5–7, 20 and 80 years of succession respectively [32–35]. Yet, these studies focused on mountain forest of low and mid altitudes whereas high Andean montane forest studies over 3,700 m.a.s.l., particularly in *Polylepis* stands, are very rare. The few available studies (e.g. [19, 36]) are based on chrono-sequence designs (synchronic approach) instead of diachronic approaches in which non-linear secondary succession dynamics can be assessed. To the best of our knowledge there are no published studies assessing ecosystem recovery of *Polylepis* forests using repeated surveys of the same sites.

Natural recovery of páramo vegetation is a slow process, involving diverse ecosystem responses [37, 38]. For example, in *Calamagrostis* spp. dominated páramos AGB-C stocks
recovered to its original state five years after a burning event [12]. However, this process could take longer depending on the frequency and intensity of fire events, grazing, original degree of disturbance of the ecosystem, and on the local climatic (i.e. precipitation, humidity, wind velocity and temperature) conditions [12, 39, 40]. Furthermore, natural recovery may be slower at higher elevations [12] and for sites dominated by few species, such as páramo tussock grasses of the genus *Calamagrostis* [29, 41].

Two major knowledge gaps limit our understanding of C storage dynamics in recovering high Andean ecosystems at local scales [18, 42]. The first one is the scarcity of research on the natural recovery process for different C pools along environmental (e.g. elevation) gradients using repeated surveys in the same region. Secondly, although different studies have addressed the natural recovery in C stocks in high Andean ecosystems, primarily páramo, after a disturbance [12, 19, 39, 43–45], only a handful of them have included ancillary variables for explaining C-dynamics during secondary succession [7, 27, 43, 46, 47].

In this paper we seek to improve the understanding of the natural recovery of terrestrial C stocks in both high-elevation Andean forest (> 3,700 m.a.s.l.) and páramo. To do this we provide a comprehensive assessment of AGB, AGN, BGB, and SOC stocks in Andean forest and páramo (northwestern Ecuador) 23 years after grazing, firewood extraction and fire regimes ceased. We use biomass-C sequestration rates as a proxy to infer the recovery status of the ecosystem [29, 41, 48, 49], and tested three hypotheses: (i) Páramo aboveground C stocks (AGB and AGN) and elevation have an inverse relationship, whereas belowground C stocks (BGB and SOC) has no response to increases in elevation; (ii) C sequestration rates for AGB and AGN, in both Andean forest and paramo, are higher than those for BGB; and (ii) areas at lower elevation exhibit higher rates of C sequestration.

**Materials and methods**

**Study area**

The research was conducted in the Yanacocha Reserve (Ministry of Environment Research permit:004–15 IC-FLO-DNB/MA), owned by the Jocotoco foundation. The Yanacocha Reserve has 1,200 ha of extension, which 960 ha are covered by montane evergreen forest and 240 ha by páramo; it is located 5 km northwest of Quito (0.13˚ S, 78.58˚ W) and is underlain by the Pichincha volcanic complex. The study area (50 ha, 3,600–4,350 m.a.s.l.; Fig 1) located in a glacial valley, characteristic of the high Andes, has been heavily influence by Quaternary volcanic activity, ~ 1,100–2,000 years ago [50, 51]. The slope angle within the study area is highly variable (from 5° to 26°).

Soils within the Yanacocha Reserve study area are Andosols, typical of the high Andes [52]. Preliminary information obtained from soil pits within the study area (one pit in forest and two in páramo) showed that soils contained well-defined layers of volcanic ash intercalated with the organic layers. The topsoil layer in both forest and páramo was found to vary from 15 to 18 cm depth containing more than 7% of soil organic matter (SOM); it was also composed of litter and an array of fine, medium and coarse roots. The organic layers below the volcanic layers were found to be of similar thickness than those in the topsoil, although the proportion of root biomass was found to decrease with increase in depth. Roots were present up to 155 cm in forest and 55 cm depth in páramo.

The lower elevation limit of the study area within the Yanacocha Research is ca. 3,600 m.a.s.l., about 300 m below the upper forest line. At the upper forest line, the species composition is characterized by non-deciduous trees like *Polylepis pauta*, *Gynoxys acostae*, *Escallonia myrtilloides*, *Baccharis padifolia*, *Columellia oblonga* and *Buddleja incana* [53]. The páramo starting at 3,900 m.a.s.l. is characterized by grass species like *Calamagrostis intermedia*, shrubs like...
Pernettya prostrata, and herbs like Hieracium frigidum or Lachemilla orbiculata. At higher elevations the dominant growth-forms shift from grasses to sclerophyllous shrubs (including Chuquiraga jussieui, Loricaria thuyoides and Baccharis caespitosa) and, prostrated herbs and cushions mats (including Werneria nubigena, Xenophyllum humile, and Plantago rigida) [54]. Both forest and páramo ecosystems in the Yanacocha Reserve have a history of human disturbance [55]. Extensive cattle grazing combined with annual burning events transformed the area and almost obliterated the shrubby elements of the páramo, and reduced the upper forest line to at least 100 meters in the most exposed areas of the reserve. Selective logging and firewood extraction degraded the Yaconcha Andean forest (personal communication with local inhabitants). However, most human activities (grazing, fire and logging) ceased in 1995 when the reserve was created, leaving the ecosystems to naturally recover (personal communication with local inhabitants). Unfortunately, there are no records of C stocks and species or growth-forms composition along the elevation gradient at the time of the cessation of human activities.

The climate of the Yanacocha Reserve is typical of high tropical mountains areas [56]. Average hourly temperature values over a 24-hour cycle from November 2013 to October 2014 show a more pronounced variation than the monthly average variation, e.g. air temperature at
10 cm aboveground can vary by 2–10˚C in one day (Fig 2B) compared with monthly variations, of 6.5–8˚C (Fig 2A). Soil temperature, at 10 cm in depth, is comparably stable through both daily and yearly cycles (6.5–8˚C daily, 6.7–7.7˚C yearly).

**Experimental design**

Two censuses were conducted to quantify the spatiotemporal increases of terrestrial biomass C stocks, as a proxy for ecosystem recovery. The baseline was determined during the months of June to December of 2012, and the second census was conducted during the same months in 2014. Within the 50-ha study area of the Yanacocha Reserve thirty-nine square permanent plots (sample units) of 10 x 10 m size were established. Ten plots were located in the forest and twenty-nine in the páramo. The plots were deployed in a stratified random design, where each ecosystem was considered as a stratum. We used a preliminary C stocks’ census in páramo and a forest inventory for defining the number of plots to be deployed in the field. The number of plots for each ecosystem was calculated as follows: \( n = \frac{(n_s - 1) \times (t) \times (SD) \times (E)}{2} \) [57], where \( n \) is the sample size; \( n_s \) the number of sub-sampling units, four in this case; \( t \) the sample statistic from the t-distribution for the 95-percent confidence level; \( SD \) the standard deviation of the sample; and, \( E \) the allowable error or the desired half width of the confidence interval. Páramo plots were differentiated by elevation, i.e. plots located between 3,900–4,100 m.a.s.l. and plots located between 4,100–4,300 m.a.s.l. The elevation range over which the plots were deployed was designed to capture the gradual transition from the páramo to the superpáramo ecosystem [58, 59].

The permanent plots were established facing north, and the corners and center were marked with PVC tubes. Inside each plot the following variables were measured: elevation, coordinates of the center of the plot, slope angle, aspect, AGB, AGN (ground litter and detritus), BGB and SOC in a depth increment of 18 and 36 cm. Each permanent plot was sampled using the Calderón, Romero-Saltos [55] protocol designed to sample terrestrial C stocks destructively through time but with minimum long-term impact. The design provides 12 possible sub-sampling positions in two concentric circles (Fig 3). For each census four sub-
sampling units (each 50 x 50 cm) were randomly selected in a cross formation, two from the inner and two from the outer circle. The same procedure was performed for the re-census but with the previously sampled positions excluded from possible selection, i.e. the same positions could not be sampled twice allowing the C stocks to recover in the measured pools.

### Field methods

**Aboveground biomass sampling.** A nondestructive inventory was conducted inside each permanent forest plot for all stems with diameter at breast height (DBH) ≥ 5 cm. To develop site-specific allometric biomass equations, 36 trees from different diameter classes, DBH 5.5–23.3 cm, were collected outside the permanent plots. Trees of four species were harvested based on their prevalence inside the permanent plots: *Polylepis pauta* (21 individuals), *Baccharis padifolia* (4 individuals), *Escallonia myrtilloides* (5 individuals) and *Gynoxis acostae* (6 individuals). Measurements of trunk diameter and total height were recorded for each tree before harvest. Trunks were harvested from the base of the trunk. Trunk material, branches and foliage were cut in small fragments for laboratory processing. Wood density was estimated by taking wood cores from the trunk using an increment borer [60].

In páramo, a treeless ecosystem, the AGB of the grasses and shrubs was collected inside each of the four sub-sampling unit within each permanent plot; the crowns and existent stems were harvested, weighted and packed for laboratory processing.
Aboveground necromass, belowground biomass and soil sampling. In páramo and forest, AGN, BGB and SOC, were sampled in the same four sub-sampling units within each plot. First, AGN was collected manually leaving the sub-sampling area free of dead vegetation (Ho and H1 horizons were removed), then two soils samples were extracted with a borer, in two depths 0–18 and 18–36 cm from the A horizon. To define the depths of measurement three soil pits were dug along the gradient where soil horizons were visually identified and their depth measured. Eight soil samples, four at each depth, per permanent plot were taken for the analysis of BGB fine roots, ≤ 2 mm, and SOC. We set the 2 mm threshold for separating fine and coarse roots following accepted definitions used by other ecological studies in high Andean and tropical ecosystems [9, 22, 61, 62]. Despite that coarse roots were not considered, the inclusion of a threshold allowed us to compare our BGB results between ecosystems.

SOC was only analyzed in the first census and was assumed to not change significantly over the two years of the study [63].

Vegetation and soil coverage. Growth-form and substrate cover was assessed inside each sub-sampling unit in the plots located in páramo to characterize responses of terrestrial C stocks to functional diversity and soil substrate, following the GLORIA protocol [64]. Following an adapted version of the growth-form classification defined by Ramsay and Oxley [56], the percentage cover of each growth-form and substrate was also visually estimated in each plot. Growth-forms were defined as rosette (including stem, basal and acaulescent rosette), tussock, cushion, shrub (upright and prostrate shrub), herb (erect and prostrate), erect grass and cespitose grass. Substrate types were defined as rock, scree, bare soil, aboveground decomposing necromass and bryophytes-lichens.

Laboratory analyses

Fresh samples (live and dead vegetation, roots and soil) were weighted in the field following collection before they were taken to the laboratory for dry weight quantification. AGB, AGN and BGB samples were dried at 60˚C in an oven until stable weight was reached.

SOM was estimated by loss-on-ignition method; the soil samples (roots and rocks were manually separated) were heated at 350˚C for 24 h and weighted to quantify the percentage of SOM. We used Kopecky’s rings to collect undisturbed soil cores for determining their bulk density. The soil samples were dried in an oven at 105˚C for about 18–24 hours [65]. Prior to these analysis (except bulk density), roots were manually extracted from soil cores during 60 min time following the Metcalfe [66] protocol. Sampled roots were rinsed in water to remove soil particles, oven dried at 60˚C in the lab until constant mass was reached, and then weighted.

The immersion method was used to determine the wood density of the core samples [60], these were plunged in water for two hours, then oven-dried to 60˚C until a stable weight was obtained (around two days).

Data analyses

Allometric biomass equations. For forest plots, we developed mixed-species allometric models to estimate AGB using trunk diameter, total height and wood density as predictors (see S1 Appendix). Different linear and nonlinear regressions models were tested. Best-fit model was selected by comparing the Bayesian information criterion (BIC), the Akaike information criterion (AIC), the coefficient of determination (R^2) and the Root mean squared error (RMSE). The first two criteria penalize the number of parameters used in the regression [67], the R^2 coefficient is the proportion of the AGB variance explained by the model, and the RMSE shows the sum of all regression errors. These four criteria provide enough information.
to evaluate the performance of the regression model [68]. Based on these analyses, a nonlinear regression model was developed to estimate the AGB in the forest of the Yanacocha Reserve using only the trunk diameter (cm) (to reduce intrinsic errors in the field estimation of tree height) (Equation 1) \( \text{AGB} = 0.041 \times (\text{DBH})^{2.56}, R^2 = 0.919 \), as predictor variable (further details are presented in S1 Appendix).

**Calculation of carbon stocks.** To estimate the mean AGB, BGB, AGN and SOC C-stocks for each permanent plot, the values of all the samples per C pool were averaged. The C stocks were then estimated as 50% of the dry weight of AGB, AGN and BGB pools [69, 70]. Forest AGB for each permanent plot was estimated using the trunk diameter allometric biomass equation derived for the forest (Equation 1). The "Van Bemmelen" factor (= 1.724) was used to convert SOM into SOC [71, 72] as no local information on SOC was available. The prevalence of growth-forms and substrate cover in the four sub-sampling units of the páramo plots were averaged to obtain a mean value for each permanent plot. Growth-form cover was used to calculate a diversity index, Shannon-index, for each plot [73].

Carbon stocks were extrapolated to Mg C ha\(^{-1}\) and averaged to estimate their mean values (and their standard deviation) by ecosystem and along the elevation gradient.

**Carbon sequestration rates.** Since mean C stocks of both censuses came from the same permanent sampling units (non-independent), a paired t-tests with unequal variances were performed between censuses to assess significant differences of C stocks on each pool. Normality of the data was first checked using a Shapiro-Wilk test [74].

An ordination analysis was performed to characterize C variation responses to biophysical variables (besides elevation), such as slope, growth-form diversity measured with a Shannon-index, soil substrate (only organic matter, and bryophytes and lichens were used in the analysis as most of the substrates were zero) and species abundances (only for forest). A distance-based redundancy analysis (db-RDA) was performed, since the explanatory and response variables were expected to have a linear relationship, on the environmental, log-transformed, and response variables [75]. This analysis was done separately for the páramo and for the Andean forest, because the set of environmental variables expected to control C sequestration rates was different for each case. For the Andean forest, the basal area per species was calculated to determine how much variation in the C stocks at the plot scale could be explained by tree community composition. Manhattan distance was used to interpret the influence of environmental variables on C stocks variations [75], and the adjusted \( R^2 \) (\( R^2\)-adj) for assessing the proportion of the C stocks variance explained by the independent variables and penalized by the number of parameters included in the model that do not improve its performance. All the statistical analyses were conducted in R [76], code included in the ‘vegan’ package was used to perform the ordination analyses [77].

**Results**

**Carbon stocks of the different pools from Andean forest and páramo**

There were significant differences between the 2012 and 2014 for AGB and AGN-C stocks (Fig 4A1, 4B1, 4A2 and 4B2). AGB-C content in the Andean forest was 34 (±22) and 39 (±24) Mg C ha\(^{-1}\) in 2012 and 2014 respectively. We found an increase in the number of individuals recruited, and the total number of individuals, in each DBH class of trees in 2014, except for the 2.5–4.9 and the 5–10.9 cm classes that experienced a subtle decrease in number of individuals (Table 1). Furthermore, a small increase in DBH among all trees was observed between the two censuses, 0.5 cm (t = 1.853, p = 0.033). Similarly, we recorded increases in all the tree DBH classes, and by 0.1–1.3 cm among plots. DBH did not increase in one plot (t = -0.0922, p = 0.537) (Fig 5). The relatively high variation in plot-based AGB was influenced principally
Carbon sequestration rates in recovering Andean ecosystems

A) Forest

\[ t = -6.004, p\text{-value} = 0.0002 \] **

B) Páramo

\[ t = -3.96, p\text{-value} = 0.0004 \] **

1) AGB

\[ t = -2.227, p\text{-value} = 0.053 \] *

\[ t = -2.559, p\text{-value} = 0.015 \] *

2) AGN

\[ t = -0.736, p\text{-value} = 0.481 \text{ ns} \]

\[ t = -1.396, p\text{-value} = 0.173 \text{ ns} \]

3) BGB(0–36 cm)

4) SOC (0–36 cm)

Census 2012 2014
by the DBH profile of trees in each plot (see S1 Fig). Only half of the Andean forest plots had trees with DBH greater than 20 cm, mostly *Polylepis pauta*, which contributed more than 35% to the AGB. On the other hand, young trees with DBH of 5–10 cm, which represented 27–96% of the individuals in a plot, contributed nearly 17% to the total forest AGB in both years. Furthermore, the DBH profile of the plots without large adult trees (DBH > 20 cm) was highly heterogeneous and dominated by juvenile trees (DBH < 5 cm) (see S1 Table).

AGB was the smallest C pool in páramo, 4 (2012) and 7 (2014) Mg C ha$^{-1}$, whereas the largest pool was SOC, 113 Mg C ha$^{-1}$. Páramo AGB-C stocks increased with elevation ($p = 2.02 \times 10^{-6}$, $R^2 = 0.57$). AGN was the smallest C pool in the forest, ca. 4 and 7 Mg C ha$^{-1}$ for the 2012 and 2014 sampling, respectively. In the páramo, the AGN-C pool decreased slightly as elevation increased ($p = 0.04$, $R^2 = 0.14$) (Fig 6A).

Non-significant differences between samplings were found in BGB-C stocks in the Andean forest and páramo. BGB-C stocks had a mean value of 11 Mg C ha$^{-1}$ in 2012 and 12 Mg C ha$^{-1}$ in 2014 in forest ($t = 0.7358$, $p = 0.4806$), whereas in páramo these values were higher in 2012, 14 Mg C ha$^{-1}$, and lower, 11 Mg C ha$^{-1}$, in 2014 ($t = 1.398$, $p = 0.1731$) (Fig 4A3 and 4B3). Interestingly, we found a significant increase of páramo’s BGB-C stocks along the elevational gradient. However, 74% of the variance in BGB-C stocks was not explained by the elevation ($p = 0.004$, $R^2 = 0.26$) (Fig 6B). SOC stock in the Andean forest at 0–18 cm depth was higher than that at 18–36 cm depth, i.e. 38 vs. 26 Mg C ha$^{-1}$ in 2012. SOC in páramo did no vary along the elevational gradient ($p = 0.63$, $R^2 = 0.009$) (Fig 6B).

AGN had the higher relative increase in both ecosystems, 84% in the forest and 202% in the páramo. Similarly, the AGB–C stock presented the highest absolute increase in both ecosystems: 5 and 3 Mg C ha$^{-1}$ in the Andean forest and páramo, respectively. On average, the absolute relative variation in C stocks, not including SOC, in páramo was higher than in the Andean forest, 89 and 48% respectively.

Effects of biotic and abiotic variables on carbon sequestration rates

The db-RDA conducted to assess the effect of the biotic and abiotic variables over the differences in biomass and necromass-C stocks showed two distinctive behaviors in the forest model and in the páramo model. For the forest model the $R^2$-adj coefficient was 0.29, i.e. more than 70% of the C stocks variance was not explained by the included variables. Only *Baccharis padifolia* was significant to the model, influencing BGB gains (Table 2). Plots with higher DBH are ordinated in the top right quadrant of the biplot presenting higher AGB gains (Fig 7A).

Table 1. Individuals distribution by diameter classes in 2012 and 2014 of the Yanacocha Reserve Andean forest plots (n = 10).

| Diameter class (cm) | # Individuals | Average trunk diameter (cm) (±1 SD) |
|---------------------|--------------|------------------------------------|
|                     | 2012 | 2014 | 2012 | 2014 |
| 2.5–4.9             | 329  | 276  | 3.5 (±0.7) | 3.6 (±0.6) |
| 5–10.9              | 214  | 209  | 6.9 (±1.5) | 7 (±1.5) |
| 11–20.9             | 72   | 80   | 14.4 (±2.6) | 14.5 (±2.7) |
| >21                 | 15   | 16   | 25.1 (±3.4) | 25.3 (±3.6) |
| Total               | 630  | 581  |       |       |

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AGN gains could not be explained with the employed environmental variables because of their non-significance in the model. We did not include elevation as an ancillary variable as the gradient in the forest is too short to identify an effect of this variable over the C differences in all the analyzed pools.

In the páramo model the $R^2$-adj was 0.32; nonetheless, the Elevation, Organic matter and Shannon-index were significant to the model (Table 2). These three variables ordered half of the plots in two quadrants, upper right quadrant and left lower quadrant (Fig 7B). Elevation and Shannon-index are directly correlated with higher AGB gains (plots located above 4,200 m.a.s.l.). On the other side, less diverse plots located at lower elevations with high organic matter contents (plots located between 3,938–4,160 m.a.s.l., see S2 Appendix) presented lower gains in AGB but higher gains in BGB. The other two variables: slope and bryophytes-and-lichens’ percentage coverage had a small influence on AGN gains.

Discussion

We have quantified biomass and necromass-C stocks in 2012 and 2014 in the Andean forest and páramo in the Yanacocha Reserve. In the 2012-census the total average C stock estimated for the Yanacocha Reserve was 132 Mg C ha$^{-1}$ with the SOC (0–36 cm depth) pool being the largest terrestrial C stocks in the páramo, 113.4 Mg C ha$^{-1}$, and Andean forest, 63.4 Mg C ha$^{-1}$,
respectively. Increases between 2012 and 2014 in AGB-C stocks were observed to be the largest, with a mean 1.5 Mg C ha\(^{-1}\) increase both in the forest and páramo.

These overall data demonstrate that the Yanacocha Reserve has acted as a C sink in the AGB C pools over the studied period. However, spatial and temporal variation between ecosystems and carbon pools was also observed. In Andean forest C stocks were influenced mainly by disturbance history and on the tree-species composition, whereas in páramo spatial variation C stocks were related to the elevation gradient in most of the pools, partially confirming

Fig 6. 2012 C stocks variation in the elevational páramo gradient. A) Aboveground C pools (AGB, green circles, and AGN, black diamonds); b) Belowground C pools (BGB, yellow triangles, and SOC, brown squares). For visualization purposes y-axis is presented in a log-10 scale.

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Table 2. Loads, eigenvalues and significance level of the distance-based RDA including the environmental variables analyzed for testing the influence over carbon stock differences for both ecosystems, Andean forest and páramo.

| Model     | Environmental variables       | Loads          | Permutation test |
|-----------|-------------------------------|----------------|-----------------|
| Andean forest |                                |                |                 |
|           | db-RDA1                       | db-RDA2        | F               | Pr(>F)          |
| Baccharis padifolia |                            | -0.97          | 3.9347          | 3.305           | 0.04 |
| Escallonia myrtilloides |                        | -0.183         | 0.763           | 0.641           | 0.61 |
| Gynoxys acostae |                                | -0.525         | 0.256           | 0.215           | 0.917 |
| Polylepis pauta |                                | -0.263         | 2.244           | 1.885           | 0.154 |
| Eigenvalue |                                | 4.12           | 2.508           |                 |      |
| Proportion explained |                        | 57.3           | 34.9            |                 |      |
| $R^2$     |                                | 0.61           |                 |                 |      |
| $R^2$-adjusted |                           | 0.29           |                 |                 |      |
| Páramo    |                                |                |                 |
| Elevation |                                | 0.5398         | 36.522          | 5.724           | 0.004 |
| Slope     |                                | -0.5678        | 9.464           | 1.483           | 0.244 |
| Organic matter |                        | -0.3399        | 30.359          | 4.758           | 0.014 |
| Shannon-index |                      | 0.2308         | 27.516          | 4.312           | 0.012 |
| Bryophytes and lichens |                  | -0.4024        | 12.15           | 1.904           | 0.156 |
| Eigenvalue |                                | 0.874          | 0.637           |                 |      |
| Proportion explained |                        | 31.42          | 22.87           |                 |      |
| $R^2$     |                                | 0.44           |                 |                 |      |
| $R^2$-adjusted |                           | 0.32           |                 |                 |      |

Bold values represent maximum load values, grey boxes represent the statistically significant variables to each model.

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Fig 7. Biplots of distance-based redundancy analyses of the environmental and carbon stock differences for A) Andean forest and B) páramo. Response variables (carbon stock differences) and sites are presented in red and blue text respectively. Andean forest plots, green circles, below 3,900 m.a.s.l; the size of the circle is relative to the plot’s mean trunk diameter in the first census. Páramo plots represented with a diamond are located above 4,100 m.a.s.l and with a square between 3,900–4,100 m.a.s.l.

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our first hypothesis. Temporal variation in AGB and AGN between the two years (2012–2014) suggests that the C sequestration rates were higher in the aboveground pools and were associated with higher elevations and plant functional diversity, confirming our second hypothesis and contrary to our third hypothesis.

**Carbon stocks’ spatial variation**

The spatial patterns of C stocks along the páramo elevation gradient, partially confirmed our first hypothesis. However, contrary to expectations, we found a positive significant increase in páramo AGB-C stocks with elevation, whereas we found a significant opposite trend in AGN-C stocks (Fig 6A). The shift along the elevation gradient in vegetation composition explained the majority of the spatial variance in AGB-C and AGN-C stocks, whereas variations in BGB-C stocks were, only, partially dependent on elevation. We found no changes in SOC-C stocks with elevation. This lack of change is likely to be because the elevational range studied (3,900–4,250 m.a.s.l.) was not sufficient to capture a major change in soil climate which is thought to be the major driver of variation in SOC-C stocks [78]. Yet, the significant changes of most C-pools along the elevation gradient in the Páramo, suggests the relevance of elevation as a primary factor controlling spatial patterns of carbon allocation across time.

On average, in 2012 the páramo stored more C (138.7 ± 32.8 Mg C ha$^{-1}$) than the forest (112 ± 26.8 Mg C ha$^{-1}$) mainly due to differences in the size of the SOC pool (0–36 cm depth) (Fig 4A4 and 4B4). The finding that páramo ecosystems store more carbon than Andean forest was in line with previous studies [47, 78]. The total average C value reported here (125.4 Mg C ha$^{-1}$) is somewhat lower than the value reported by Gibbon, Silman [47] across a similar, non-disturbed, transition in the Eastern Peruvian Andes (161 Mg C ha$^{-1}$) and may reflect the different disturbance histories (Fig 8A1).

Carbon stock allocation was different between the forest and the páramo at Yanacocha. While nearly 57% of the C stock in the Andean forest was allocated to the SOC pool, this allocation was higher in the páramo, 82%, in line with other studies [9, 79]. Previous studies (this included) indicate that the SOC pools in the páramo and in the Andean forests store at least 50% of the total C stock [18, 19, 47], and potentially as much as ca. 90% [80].

**AGB-C stocks**

AGB-C stocks values found in both forest (33.7 Mg C ha$^{-1}$) and páramo (4 Mg C ha$^{-1}$) ecosystems in the Yanacocha Reserve are at the lower end of values reported from other studies [23, 80], probably related to the early successional stage of the Andean forest after land-use change in combination with the high elevation where it is located (Fig 8A1 and 8B1). For instance, the majority of measured trees across the 10 plots had a DBH < 10 cm and stored only 17% of the total AGB-C stock found in the Yanacocha forest (Table 1). Conversely, studies reporting higher AGB-C stocks [10, 18, 19, 47] than the Yanacocha Reserve were located at lower elevations, had less human impact, and affected by different local environmental factors (Fig 8A1). Taken together with previous studies, our results suggest that low elevation range, gentle slopes and an homogeneous precipitation throughout the year appear to be major contributors to higher forest AGB-C stocks. However, methodological factors, e.g. plot size and employed allometric equations, used for measuring AGB-C might be influencing the variation in the reported AGB-C stocks across studies. The specific effects of these factors can be found elsewhere in the literature [81–84].

Average páramo AGB-C stocks found at Yanacocha (5.7 Mg C ha$^{-1}$) were lower when compared with undisturbed cases (i.e., 17.4 Mg C ha$^{-1}$), and similar to those reported in studies developed in degraded páramo ecosystems (i.e., 4 Mg C ha$^{-1}$; Fig 8B1). Furthermore, we found
a significant increase of AGB-C stocks with elevation, as opposed to expected, partially explained by the plot's vegetation composition (Fig 6 and Fig 8B1). A gradual shift in the dominance of growth-forms, from tussock grasses to prostrate and erect shrubs, at mid-elevation range, to cushion matts and basal-rosettes at high elevations (see S2 Appendix). Stem-rosettes and tussock grasses, both showing positive relationship with higher AGB-C stocks, were also the dominant growth-forms in the Colombian locations reporting high AGB-C stocks (Fig 8B1). The differences in human impacts among higher and lower plots could also explain the
increased AGB-C stocks along the elevation gradient; it is possible that plots at higher elevations were less disturbed by human use. When compared to other studies, higher páramo AGB-C stocks were related to undisturbed study cases and located in a lower elevation range (3,450–4,100 m.a.s.l.), whereas lower AGB-C stocks were primary related to land use impacts and differences in the vegetation composition (e.g. dense tussock grasses vs. stem-rosettes (Fig 8B1)).

AGN-C stocks
AGN-C stocks in the Yanacocha Reserve forest (4.2 Mg C ha\(^{-1}\) in 2012) were lower than in the páramo (7.3 Mg C ha\(^{-1}\) in 2012), and within the range reported in other studies (Fig 8A2 and 8B2). Apparently, from the few available cases, AGN-C stocks are controlled primary by land use disturbance regimes. A peak in the AGN-C stocks has been reported in recovered forests with mid-range values of the AGB distribution [85]. Beyond that peak, as AGB-C increases, the proportion of AGN-C decreases. Thus, we expect that over the years, as AGB-C stocks increases, the opposite will occur with the AGN-C stocks.

In the Yanacocha páramo the AGN-C stock was higher than values previously reported for similar ecosystems (Fig 8B2). Higher C stock values of AGN found in our study could be related to the dominance of tussock grasses in the majority of the páramo plots (see S2 Appendix). According to Monteiro, Hilbrunner [86] high necromass and litter values are particularly characteristic of tussock graminoids such as those that are the dominant growth-form in the lower and middle section of our study area. The dominance of tussocks in the páramo at Yanacocha likely reflects the characteristic vegetation successional stage after the suppression of fire and grazing disturbance [12, 16, 21].

BGB-C stocks. BGB-C stocks, excluding coarse roots, were the only stocks that did not differ between ecosystems (t = 1.1986, p = 0.238). An average of 12 Mg C ha\(^{-1}\) was found in both Andean forest and páramo. The Andean forest BGB-C stocks at Yanacocha (11 and 12 Mg C ha\(^{-1}\) in 2012 and 2014 respectively) are in the range of other reported values for equivalent sites, 5–15 Mg C ha\(^{-1}\) (Fig 8A3). However, previously published BGB-C stock values for páramo grasslands report considerably lower values (0.5–3.1 Mg C ha\(^{-1}\)) than that found at Yanacocha (Fig 8B3). The differences in BGB-stocks along the elevational gradient in the páramo are likely due to methodological constraints and their intrinsic uncertainty. For instance Gibbon, Silman [47] used a mean root to shoot ratio for estimating the C stocks in roots, which might underestimate the BGB-C stocks. Other causes may be related with plant composition, e.g. the Eynden [26] study was performed in puna grasslands dominated by Calamagrostis spp. containing more AGB-C than BGB-C stocks. Albeit methodological constraints, our results of the BGB-C stocks suggests that the potential for BGB root pools to be a more important one in many high-elevation systems than previously reported. Improved methods such as including coarse roots (> 2 mm) and continuous monitoring could help elucidate this critical knowledge gap.

SOC stocks. The SOC stocks (0–36 cm depth) at the Yanacocha Reserve, 112 and 139 Mg C ha\(^{-1}\) for the Andean forest and páramo respectively, were similar to previous studies (Fig 8A4 and 8B4) [10, 50, 61, 87]. The difference between forest and páramo at Yanacocha is likely exacerbated by the historical fire events that are known to have occurred in the forest. Román-Cuesta, Salinas [45] reported differences in SOC in burned and unburned forests in the Southern Peruvian Andes. The low SOC stocks associated with past fire events indicates that the detrimental impact of burning on terrestrial ecosystem C storage may have a long below-ground legacy. Aside from the importance of fire, several other environmental factors are known to affect SOC (i.e. land cover, temperature, moisture and radiation) but those specific factors
where not assessed in this study [8, 78, 88]. Further studies are needed to understand the effects that microhabitat conditions have over SOC stocks.

**Carbon stocks temporal change due to natural recovery.** We recorded significant differences in C stocks between both years in both ecosystems, with AGB and AGN-C stocks in 2014 being higher than those in 2012. Similarly, our results suggest that C sequestration rates are higher in the AGB and AGN, in comparison with BGB along the Yanacocha Reserve elevational gradient, confirming our second hypothesis.

**Aboveground-C stocks' recovery.** AGB-C increases in the Yanacocha Reserve were observed both in the forest and in the páramo ecosystems (Fig 4A1 and 4A2). The AGB-C increase rate was 2.5 Mg C ha\(^{-1}\) year\(^{-1}\) in the forest (see S3 Appendix) similar to those reported in recovering secondary forests in Ecuador, 2.9 Mg C ha\(^{-1}\) year\(^{-1}\) [19]. Within the Yanacocha Andean forest increased C-sequestration rates were generally associated with more mature (large diameter class) trees, i.e. the highest AGB-C sequestration rates were observed in forest plots that already had on average large diameter trees (Fig 5). The RDA result evidenced that higher AGB-C uptake was related to the tree composition of each plot. Those plots with dominance of *Polylepis pauta* and lower prevalence of *Baccharis padifolia* had a positive relationship with higher AGB-C gains. These results suggest the importance large-statured trees, community species composition and their abundances in controlling C of dynamics as previously reported for high tropical and lowlands forests [84,89–92]. Further explanation of these differential sequestration rates may be related to the recent heterogeneous human impact that each plot experienced. We infer that as time passes, and consequently more trees mature, the natural regeneration process in the Andean forest of the Yanacocha Reserve will lead to higher and similar C sequestration rates among plots. Even so, our observation of a positive relationship between trees size and C sequestration rates requires further research combined with a pro-longed monitoring period that can provide more insights on the natural recovery dynamics of this ecosystem.

AGB-C increase rates in the Yanacocha páramo, 1.5 Mg C ha\(^{-1}\) year\(^{-1}\) (see S3 Appendix), are towards the upper end of C sequestration rates reported by other authors, 0.8–1.5 Mg C ha\(^{-1}\) year\(^{-1}\). Contrary to our third hypothesis, higher AGB-C gains occurred mainly within plots with a relatively high functional diversity and at higher elevations (Fig 7A). A similar relationship of increasing C sequestration with high diversity observed in studies of temperate grasslands [49] might be applicable to the páramo, suggesting the importance of growth-form functional diversity in ecosystem functionality. The correlation between AGB-C sequestration rates and altitude in the Yanacocha páramo might be also related to decreasing human impact with increasing elevation [93]. The gains in AGB-C in the Yanacocha Reserve, are similar to rates observed in moderately degraded grassland ecosystems, suggesting an intermediate stage of recovery of the páramo at higher elevations. The link between higher AGB sequestration rates and decreasing disturbance within the páramo may indicate that natural (passive) regeneration techniques likely represent a very effective strategy for regaining AGB in degraded areas, and that intervention that stimulates successional vegetation dynamics leading to an increase in growth-form diversity could accelerate the process further.

AGN-C stocks' increases were found for the Andean forest and páramo in the Yanacocha Reserve. By comparing 2012 with 2014 census data the same significant gain rate was recorded for both ecosystems, 1.3 Mg C ha\(^{-1}\) year\(^{-1}\). AGN-C gains in Yanacocha forest are related to those plots dominated by *Polylepis pauta* and *Escallonia myrtilloides* (Fig 7A). In the páramo of Yanacocha, higher sequestration rates in AGN-C were found in páramo’s plots located at flat terrain sites with low coverage of bryophytes and lichens. Yet, the net positive increment in AGN-C among years, in both ecosystems (2.6 Mg C ha\(^{-1}\)), may reflect a positive trend towards a less disturbed ecosystem.
Belowground biomass C stocks’ recovery. The BGB-C (0–36 cm depth) compartment did not present a clear trend between the two censuses within the Yanacocha Reserve. Increases in BGB-C stock values in the Andean forest (0.65 Mg C ha\(^{-1}\) year\(^{-1}\)) and negative values in the páramo (-1.3 Mg C ha\(^{-1}\) year\(^{-1}\)) were not significant. The rate of BGB-C sequestration observed in the Yanacocha forest is within the range of previous studies [7], albeit these results are the first one to report on fine roots BGB-C dynamics above 3,800 m.a.s.l. in *Polylepis* stands. The ordination result showed a clear trend in which the plots dominated by *Baccharis padifolia* evidenced higher BGB-C increments to the plots dominated by *Polylepis pauta*. This finding suggests different C accumulation rates in the root system among dominant species. Plots dominated by *Baccharis padifolia* suggest an earlier successional stage of the forest to those dominated by *Polylepis pauta* that are indicative of a more mature successional stage of the forest.

Negative differences in BGB-C stocks in the Yanacocha páramo were predominantly in the plots located above 4,200 m.a.s.l. suggesting limitations in our sampling method. Since we did not measure coarse roots (≥ 2 mm diameter), we suspect finest roots (< 2 mm) might be under sampled resulting in an underestimation of BGB pool, particularly in plots dominated by coarse-root growth-forms such as shrubs and basal rosettes. Consequently, additional data are required in order to clarify the factors that drive spatiotemporal trends in BGB-C. Additionally, improving the sampling methodology to include coarse roots as well as include an analysis of short-term turnover in root biomass could help strengthen the sampling protocol, and reduce the uncertainty related to páramo BGB productivity.

Conclusions

The C stocks across the elevational gradient of the Yanacocha reserve were considerably lower (mean 125 Mg C ha\(^{-1}\)) than those reported for undisturbed sites in similar ecosystems. The lower C stocks in Yanacocha Reserve are likely the legacy of the cattle grazing, fires and timber extraction that occurred in the reserve 23 years ago. Despite the multi-decadal impact of past human activity, the observed C sequestration rates (2.5 Mg C ha\(^{-1}\) year\(^{-1}\) and 1.5 Mg C ha\(^{-1}\) year\(^{-1}\) in forest and páramo, respectively) suggest a gradual recovery of C stocks is underway. Carbon sequestration rates in the Yanacocha reserve were positive in both forest and páramo ecosystems and indicate that the aboveground pools are recovering faster than the belowground pools. In the Andean forest, higher accumulation rates in AGB were found in plots with a prevalence of mature trees, whereas in the páramo grasslands the temporal variations were explained by a combination of elevation and plant functional diversity. Higher gains of páramo AGB-C were observed at higher elevations in plots with high levels of growth-forms diversity.

AGN accumulation rates were found to be increasing in páramo plots located in flat terrain irrespective of their altitudinal position, whereas higher BGB accumulation rates were associated with páramo plots located at lower elevations. C stocks allocation in aboveground and belowground compartments in the high Andean indicates that the preservation of the SOC pool is of paramount importance if ecosystems are to be managed to maximize their potential C stocks. Furthermore, we expect that over the long term the Yanacocha Reserve will keep acting as an aboveground C sink with AGB values reaching similar values as those reported for less degraded Andean ecosystems.

To our knowledge, the results presented here are some of the first to quantify C stocks and their temporal variation using repeated surveys of the same sites in degraded high Andean ecosystems. These findings help to elucidate the natural environmental factors driving the dynamics in high Andean C stocks. The design and implementation of low-cost restoration strategies
in Andean forests and páramos may include cost-benefit analyses considering biomass accumulation rates for human assisted and natural restoration processes, taking into account the degree of disturbance, the landscape context and the local environmental variables to maximize the ecological and environmental benefits expected from restoration actions. As our results suggest the use of biomass allocation and productivity as functional indicators may provide insight to the process of assessing ecosystem recovery along environmental and temporal gradients. However, a longer period of continuous monitoring will improve our results and provide a more robust dataset upon which guide restoration actions to contribute to secure environmental services, including climate change mitigation.

Supporting information

S1 Fig. Community structure for each Andean forest plot by diametric class and species frequency for the first (FC) and second (SC) censuses of the Yanacocha Reserve. (DOCX)

S1 Table. Number of tree individuals and average trunk diameter for each Andean forest plot for the first (FC) and second (SC) censuses of the Yanacocha Reserve. (DOCX)

S2 Table. Average C-stock (± 1 standard deviation) for the first and second censuses (italics) in Mg C ha⁻¹ in the Andean forest and páramo of the Yanacocha Reserve, Pichincha, Ecuador. Cells bordered with thick lines represent non-significant differences in compartments between censuses (95% confidence level and p ≥ 0.05). Shaded cells represent non-significant differences in compartments between habitats (95% confidence level and p ≥ 0.05). In all the cases, a t-test was used. FC: First Census; SC = Second Census. (DOCX)

S1 Appendix. Multispecies allometric equations to estimate Andean forest aboveground biomass. (DOCX)

S2 Appendix. (XLSX)

S3 Appendix. (XLSX)

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References

1. Farley KA, Bremer LL, Harden CP, Hartsig J. Changes in carbon storage under alternative land uses in biodiverse Andean grasslands: implications for payment for ecosystem services. Conservation Letters. 2013; 6(1):21–7.

2. Buytaert W, Cuesta-Camacho F, Tobón C. Potential impacts of climate change on the environmental services of humid tropical regions. Global Ecology and Biogeography. 2011; 20(1):19–33. https://doi.org/10.1111/j.1466-8238.2010.00585.x

3. Buytaert W, De Bièvre B. Water for cities: The impact of climate change and demographic growth in the tropical Andes. Water Resources Research. 2012; 48(8). https://doi.org/10.1029/2011wr011755

4. Sklenář P, Hedberg I, Cleef A. Island biogeography of tropical alpine floras. Journal of Biogeography. 2014; 41(2):287–97. https://doi.org/10.1111/jbi.12212

5. Gentry AH. Patterns of diversity and floristic composition in Neotropical Montane Forests. Biodiversity and conservation of neotropical montane forests 1995. p. 103–26.

6. Malhi Y, Silman M, Salinas N, Bush M, Meir P, Sattatchi S. Introduction: Elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Glob Chang Biol. 2010; 16:5.

7. Moser G, Leuschner C, Hertel D, Graefe S, Soethe N, lost S. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. Glob Chang Biol. 2010; 17(6):2211–26.

8. Buytaert W, Celleri R, De Bièvre B, Cisneros F, Wyseure D, Deckers J, et al. Human impact on the hydrology of the Andean páramos. Earth-Science Reviews. 2006; 79(1):53–72.

9. Girardin C, Aragão L, Malhi Y, Huaraca Huasco W, Metcalfe D, Durand L, et al. Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. Global Biogeochemical Cycles. 2013; 27(1):252–64.

10. Moser G, Röderstein M, Soethe N, Hertel D, Leuschner C. Altitudinal changes in stand structure and biomass allocation of tropical mountain forests in relation to microclimate and soil chemistry. Gradients in a tropical mountain ecosystem of Ecuador: Springer; 2008. p. 229–42.

11. Tonneijck F, Jansen B, Nierop K, Verstraten J, Sevink J, Lange LD. Carbon stocks and stabilization mechanism in volcanic ash soils in natural Andean ecosystem of northern Ecuador2009. 182 p.

12. Ramsay P, Oxley E. Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. Plant Ecology. 1996; 124(2):129–44.

13. Vanacker V, Vanderschaege M, Govers G, Willems E, Poesen J, Deckers J, et al. Linking hydrological, infinite slope stability and land-use change models through GIS for assessing the impact of deforestation on slope stability in high Andean watersheds. Geomorphology. 2003; 52(3):299–315. https://doi.org/10.1016/S0169-555X(02)00263-5.

14. Poulenard J, Podwojewski P, Janeau J-L, Collinet J. Effects of tillage and burning on hydrodynamic properties of volcanic ash soil in Ecuadorian páramos. Catena. 2001; 45:185–207.

15. Podwojewski P, Poulenard J, Zambrana T, Hofstedé R. Overgrowing effects on vegetation cover and volcanic ash soil properties in the páramo of Llangahua and La Esperanza (Tungurahua, Ecuador) 2002. 45–55 p.

16. Keating PL. Fire ecology and conservation in the high tropical Andes: Observations from northern Ecuador. Journal of Latin American Geography. 2007:49–62.

17. Marengo JA, Pabón JD, Díaz A, Rosas G, Ávalos G, Montealegre E, et al. Climate Change: Evidence and Future Scenarios for the Andean Region. Climate change effects on the biodiversity of the tropical Andes: an assessment of the status of scientific knowledge. Paris, Francia2011.

18. Girardin C, Malhi Y, Aragão L, Mamani M, Huaraca Huasco W, Durand L, et al. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. Glob Chang Biol. 2010; 16(12):3176–92.
19. Fehse J, Hofstede R, Aguirre N, Paladines C, Kooijman A, Sevink J. High altitude tropical secondary forests: a competitive carbon sink? Forest Ecology and Management. 2002; 163(1):9–25.

20. Ramsay P, Oxley ERB. An assessment of aboveground net primary productivity in Andean grasslands of central Ecuador. Mountain Research and Development. 2001; 21(2):161–7.

21. Hofstede R, Castillo M, Osorio C. Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. I. Aboveground vegetation. Arctic and Alpine Research. 1995:1–12.

22. Hofstede R, Rossenaar AJ. Biomass of grazed, burned, and undisturbed Paramo Grasslands, Colombia. II. Root mass and aboveground: Belowground ratio. Arctic and Alpine Research. 1995:13–8.

23. Leuschner C, Moser G, Bertsch C, Röderstein M, Hertel D. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. Basic and Applied Ecology. 2007; 8(3):219–30.

24. Buytaert W, Deckers J, Dercon G, De-Bièvre B, Poesen J, Govers G. Impact of land use changes on the hydrological properties of volcanic ash soils in South Ecuador. Soil use and management. 2002; 18:7. https://doi.org/10.1079/SUM20011107

25. Keating PL. Chronically disturbed páramo vegetation at a site in southern Ecuador. Journal of the Torrey Botanical Society. 2000:162–71.

26. Mvd Eynden. Effects of fire history on species richness and carbon stocks in a Peruvian puna grassland, and development of allometric equations for biomass estimation of common puna species: Norwegian University of Life Sciences; 2011.

27. Hofstede R, Chillo E, Sandovals E. Vegetative structure, microclimate, and leaf growth of a tussock grass species, in undisturbed, burned and grazed conditions. Vegetatio. 1995; 119(1):53–65.

28. Margarel R. On certain unifying principles in ecology. The American Naturalist. 1963; 97(897):357–74.

29. Tilman D, Reich PB, Knops JM. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature. 2006; 441(7093):629. https://doi.org/10.1038/nature04742 PMID: 16738658

30. Chazdon RL, Brancalion PH, Lamb D, Laestadius L, Calmon M, Kumar C. A policy-driven knowledge agenda for global forest and landscape restoration. Conservation Letters. 2017; 10(1):125–32.

31. Martin PA, Newton AC, Bullock JM. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proc R Soc B. 2013; 280(1773):20132236. https://doi.org/10.1098/rspb.2013.2236 PMID: 24197410

32. Silver W, Ostertag R, Lugo A. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restoration ecology. 2000; 8(4):394–407.

33. Spracklen D, Righelato R. Tropical montane forests are a larger than expected global carbon store. Biogeosciences. 2014; 11(10):2741–54.

34. Spracklen DV, Righelato R. Carbon storage and sequestration of regrowing montane forests in southern Ecuador. Forest Ecology and Management. 2016; 364:139–44.

35. Peña MA, Duque A. Patterns of stocks of aboveground tree biomass, dynamics, and their determinants in secondary Andean forests. Forest Ecology and Management. 2013; 302:54–61.

36. Román-Cuesta R, Salinas N, Asbjornsen H, Oliveras I, Huaman V, Gutiérrrez Y, et al. Implications of fires on carbon budgets in Andean cloud montane forest: The importance of peat soils and tree resprouting. Forest Ecology and Management. 2011; 261(11):1987–97.

37. Horn SP, Kappelle M. Fire in the páramo ecosystems of Central and South America. Tropical fire ecology: Springer; 2009. p. 505–39.

38. Suárez E, Medina G. Vegetation structure and soil properties in Ecuadorian páramo grasslands with different histories of burning and grazing. Arctic, Antarctic, and Alpine Research. 2001:158–64.

39. Farley KA. Grasslands to tree plantations: forest transition in the Andes of Ecuador. Annals of the Association of American Geographers. 2007; 97(4):755–71.

40. Adler PB, Morales JM. Influence of environmental factors and sheep grazing on an Andean grassland. Journal of Range Management. 1999:471–81.

41. Tilman D, Isbell F, Cowles JM. Biodiversity and ecosystem functioning. Annual review of ecology, evolution, and systematics. 2014; 45.

42. Oliveras I, Eynden M, Malhi Y, Cahuana N, Menor C, Zamora F, et al. Grass allometry and estimation of above-ground biomass in tropical alpine tussock grasslands. Austral ecology. 2014; 39(4):408–15.

43. Minaya V, Corzo G, Romero-Saltos H, van der Kwast J, Lantinga E, Galarraga-Sánchez R, et al. Allitudinal analysis of carbon stocks in the Antisana páramo, Ecuadorian Andes. Journal of Plant Ecology. 2015; 9(5):553–63. https://doi.org/10.1093/jpe/rtv073

44. Abreu Z, Liambi LD, Sarmiento L. Sensitivity of soil restoration indicators during Páramo succession in the high tropical Andes: chronosequence and permanent plot approaches. Restoration Ecology. 2009; 17(5):619–27.
45. Román-Cuesta RM, Salinas N, Asbjornsen H, Oliveras I, Huaman V, Gutiérrez Y, et al. Implications of fires on carbon budgets in Andean cloud montane forest: The importance of peat soils and tree resprouting. Forest Ecology and Management. 2014. https://doi.org/10.1016/j.foreco.2014.07.032

46. Peña E, Zúñiga O, Peña J. Accounting the carbon storage in disturbed and non-disturbed tropical Andean ecosystems. Planet Earth 2011—Global Warming Challenges and Opportunities for Policy and Practice: InTech; 2011.

47. Gibbon A, Silman MR, Malhi Y, Fisher JB, Meir P, Zimmermann M, et al. Ecosystem Carbon Storage Across the Grassland—Forest Transition in the High Andes of Manu National Park, Peru. Ecosystems. 2010; 13(7):1097–111. https://doi.org/10.1007/s10021-010-9376-8

48. Aronson J, Floret C, Floc'h E, Ovalle C, Pontanier R. Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. I. A View from the South. Restoration ecology. 1993; 1(1):8–17.

49. Tilman D, Downing JA. Biodiversity and stability in grasslands. Nature. 1994; 367(6461):333–51.

50. Tonneijck F, Hageman J, Sevink J, Verstraten J. Tephra stratification of volcanic ash soils in northern Ecuador. Geoderma. 2008; 144:17.

51. García-Aristizábal A, Kumagai H, Samaniego P, Mothes P, Yepes H, Monzier M. Seismic, petrologic, and geodetic analyses of the 1999 dome-forming eruption of Guagua Pichinchana volcano, Ecuador. Journal of volcanology and geothermal research. 2007; 161(4):333–51.

52. Tonneijck F, Jansen B, Nierop K, Verstraten J, Sevink J, Lange LD. Towards understanding of carbon stocks and stabilization in volcanic ash soils in natural Andean ecosystems of northern Ecuador. European Journal of Soil Science. 2010; 61:15.

53. Jørgensen PM, Ulloa CU. Seed plants of the high Andes of Ecuador: a checklist. AAU Reports. 1994; 34:1–443.

54. Cuesta F, Muriel P, Llambí LD, Halloy S, Aguirre N, Beck S, et al. Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes. Ecography. 2017; 40(12):1381–94.

55. Calderón M, Romero-Saltos H, Cuesta F, Báez S. Monitorio de contenidos y flujos de carbono en gradientes altitudinales altoandinos. Quito-Ecuador: CONDESAN; 2013.

56. Ramsay P, Oxley E. The growth form composition of plant communities in the ecuadorian páramos. Plant Ecology. 1997; 131:20.

57. Pearson T, Brown S, Birdsey R. Measurement Guidelines for the Sequestration of Forest Carbon. USDA Forest Services Northern Global Change research Program, 2007.

58. Sklenár P, Balslev H. Geographic flora elements in the Ecuadorian superpáramo. Flora—Morphology, Distribution, Functional Ecology of Plants. 2007; 202(1):50–61.

59. Sklenár P, Ramsay PM. Diversity of zonal páramo plant communities in Ecuador. Diversity and Distributions. 2001; 7(3):113–24. https://doi.org/10.1046/j.1472-4642.2001.00101.x

60. Chave J. Medición de densidad de madera en árboles tropicales. Manual de campo. PAN-AMAZONIA, 2006.

61. Graefe S, Hertel D, Leuschner C. Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. Biotropica. 2008; 40(5):536–42.

62. Mathews T, Metcalfe D, Malhi Y, Phillips O, Huaraca W, Riutta T, et al. Measuring tropical carbon forest carbon allocation and cycling: A RAINFOR-GEM field manual for intensive census plots (v2.2). Manual, Global Ecosystems Monitoring network. 2012.

63. Lal R. Sequestration of atmospheric CO2 in global carbon pools. Energy & Environmental Science. 2008; 1(1):15. https://doi.org/10.1039/b809492f

64. Pauli H, Gottfried M, Lamprecht A, Niessner S, Rumpf S, Winkler M, et al., editors. The GLORIA field manual—standard Multi-Summit approach, supplementary methods and extra approaches. 5th edition. ed: GLORIA-Coordination, Austrian Academy of Sciences & University of Natural Resources and Life Sciences, Vienna.; 2015.

65. Carter M. Relative measures of soil bulk density to characterize compaction in tillage studies on fine sandy loams. Canadian Journal of Soil Science. 1990; 70(3):425–33.

66. Metcalfe D. Cálculo de dinámicas de raíz en ecosistemas tropicales. Manual de campo. RAINFOR, 2007.

67. Picard N, Saint-André L, Henry M. Manual for building tree volume and biomass allometric equations: from field measurement to prediction. Food and Agricultural Organization of the United Nations, 2012.

68. Chave J, Andalo C, Brown S, Cairns M, Chambers J, Eamus D, et al. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia. 2005; 145(1):87–99. https://doi.org/10.1007/s00442-005-0100-x PMID: 15971085
69. Pearson T, Walker S, Brown S. Sourcebook for lan use, land-use change and forestry Projects. Winrock International, Bio Carbon Fund, 2005.

70. IPCC. Guidelines for National Greenhouse Gas Inventories. IPCC, 2006.

71. Jain TB, Graham RT, Adams DL. Carbon to organic matter ratios for soils in Rocky Mountain coniferous forests. Soil Science Society of America Journal. 1997; 61(4):1190–5.

72. Waksman SA, Stevens KR. A critical study of the methods for determining the nature and abundance of soil organic matter. Soil Science. 1930; 30(2):97–116.

73. Biswas SR, Mallik AU. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology. 2010; 91(1):28–35. https://doi.org/10.1890/08-0887.1 PMID: 20380192

74. Sokal RR, Rohlf FJ. Biometry: the principles and practice of statistics in biological research 2nd edition. 1981.

75. McCune B, Grace JB, Urban DL. Analysis of ecological communities: MJM software design Glendenen Beach, OR; 2002.

76. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2015.

77. Oksanen J, Blanchet G, Kindt R, Legendre P, Minchin P, O’Hara B, et al. Vegan: Community Ecological Package. 2012.

78. Zimmermann M, Meir P, Silman M, Fedders A, Gibbon A, Malhi Y, et al. No Differences in Soil Carbon Stocks Across the Tree Line in the Peruvian Andes. Ecosystems. 2009: 13.

79. Zimmermann M, meir P, Bird MI, Malhi Y, Ccahuana AJQ. Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient. European Journal of Soil Science. 2009; 60(6):895–906. https://doi.org/10.1111/j.1365-2389.2009.01175.x

80. Vásquez E, Ladd B, Borchard N. Carbon storage in a high-altitude Polylepis woodland in the Peruvian Andes. Alpine botany. 2014; 12(1):71–5.

81. Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J. Measuring net primary production in forests: concepts and field methods. Ecological Applications. 2001; 11(2):356–70.

82. Feldpausch TR, Banin L, Phillips OL, Baker TR, Lewis SL, Quesada CA, et al. Height-diameter allometry of tropical forest trees. Biogeosciences. 2011; 8(5):1081–106. https://doi.org/10.5194/bg-8-1081-2011

83. Feldpausch TR, Lloyd J, Lewis SL, Brienen R, Gioor E, Mendoza AM, et al. Tree height integrated into pan-tropical forest biomass estimates. Biogeosciences Discussions. 2012;9(3).

84. Peña MA, Feeley KJ, Duque A. Effects of endogenous and exogenous processes on aboveground biomass stocks and dynamics in Andean forests. Plant Ecology. 2018; 219(12):1481–92.

85. Palace M, Keller M, Hurtt G, Frolking S. A Review of Above Ground Necromass in Tropical Forests. In: Sudarshana P, Nageswara M, Soneji J, editors. Tropical Forests. Croacia: INTECH; 2012. p. 38.

86. Monteiro JAF, Hillbrunner E, Körner C. Functional morphology and microclimate of Festuca orthophylla, the dominant tall tussock grass in the Andean Altiplano. Flora-Morphology, Distribution, Functional Ecology of Plants. 2011; 206(4):387–96.

87. Rhoades C, Eckert G, Coleman D. Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador. Ecological Applications. 2000: 9.

88. Körner C. The use of ‘altitude’ in ecological research. Trends in ecology & evolution. 2007; 22(11):569–74.

89. Poorter L, van der Sande MT, Arets EJ, Acsarrunz N, Enquist BJ, Finegan B, et al. Biodiversity and climate determine the functioning of Neotropical forests. Global ecology and biogeography. 2017; 26 (12):1423–34.

90. Cuni-Sanchez A, Pfeifer M, Marchant R, Calders K, Serensen CL, Pompeu PV, et al. New insights on above ground biomass and forest attributes in tropical montane forests. Forest Ecology and Management. 2017; 399:235–46.

91. Venter M, Dwyer J, Dieleman W, Ramachandra A, Gillieson D, Laurance S, et al. Optimal climate for large trees at high elevations drives patterns of biomass in remote forests of Papua New Guinea. Glob Chang Biol. 2017; 23(11):4873–83. https://doi.org/10.1111/gcb.13741 PMID: 28566838

92. Hemp A, Zimmermann R, Remmele S, Pommer U, Berauer B, Hemp C, et al. Africa’s highest mountain harbours Africa’s tallest trees. Biodiversity and conservation. 2017; 26(1):103–13.

93. Hofstede R. Effects of livestock farming and recommendations for management and conservation of paramo grasslands (Colombia). Land Degradation & Development. 1995; 6(3):133–47.