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Non-destructive allometric estimates of above-ground and below-ground biomass of high-mountain vegetation in the Andes

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Abstract
Aim: Studies that monitor high-mountain vegetation, such as paramo grasslands in the Andes, lack non-destructive biomass estimation methods. We aimed to develop and apply allometric models for above-ground, below-ground and total biomass of paramo plants.

Location: The paramo of southern Colombia between 1°09′N and 077°50′W, at 3,400 and 3,700 m a.s.l.

Methods: We established 61 1-m² plots at random locations, excluding disturbed, inaccessible and peat bog areas. We measured heights and basal diameters of all vascular plants in these plots and classified them into seven growth forms. Near each plot, we sampled the biomass from plants of abundant genera, after having measured their height and basal diameter. Hence, we measured the biomass of 476 plants (allometric set). For each growth form we applied power-law functions to develop allometric models of biomass against basal diameter, height, height x basal diameter and height x basal area. The best models were selected using AICc weights. Using the observed and predicted plant biomass of the allometric set we calculated absolute percentage errors using cross-validation. The biomass of a plot was estimated by summing the predicted biomass of all plants in a plot. Confidence limits around these sums were calculated by bootstrapping.

Results: For groups of <20 plants the biomass predictions yielded large (>15%) errors. Applying groups that resembled the 1-m² plots in density and composition, the errors for above-ground and total biomass estimates were <15%. Across all plots, we obtained an above-ground, below-ground and total plot biomass of 329 ± 190, 743 ± 486 and 1011 ± 627 g/m² (mean ± SD), respectively. These values were within the range of biomass estimates obtained destructively in the tropical Andes.

Conclusions: In new applications, if target vegetation samples are similar regarding growth forms and genera to our allometric set, their biomass might be predicted applying our equations, provided they contain at least 50–100 plants. In other situations, we would recommend gathering additional biomass measurements from local plants to evaluate new regression equations.

Keywords
basal diameter, Colombia, grassland, growth form, paramo, plant height
1 | INTRODUCTION

Biomass is the main indicator of C allocation at different levels of community organization and therefore essential to estimate the global C balance (Flombaum & Sala, 2007). In ecosystems, plant biomass has been used as a predictor of primary productivity and plant response to disturbances and climate change (TerHorst & Munguía, 2008; Nafus, McClaran, Archer, & Throop, 2009). Monitoring programmes to study the effects of human impact or climate change on plant communities, such as those developed for the Andes of South America (Báez et al., 2014; Cuesta et al., 2012, 2017), demand reliable and non-destructive estimation methods to estimate above-ground and below-ground biomass in permanent plots. In these studies multispecies biomass estimation methods are a prerequisite to efficiently deal with species-rich plant communities (Chave et al., 2005; Oliveras, Van der Eyden et al., 2014). However, biomass estimates of high-mountain vegetation are usually obtained applying destructive harvesting methods (Beekman & Verweij, 1987; Hofstede, Mondragon, & Rocha, 1995; Liu, Liu, Gong, Wang, & Sun, 2014; Montilla, Monasterio, & Sarmiento, 2002; Nie, Yang, Yang, & Zhou, 2016; Ramsay & Oxley, 2001; Smith & Klinger, 1985; Tol & Cleef, 1992). Allometric equations have been widely used to estimate the biomass of plant communities in a non-destructive way, but mostly in the context of lowland forest studies (Kerkhoff & Enquist, 2006; Zianis & Mencuccini, 2004).

The biomass of the vegetation of the high mountains of the northern Andes, also called paramo (Luteyn, 1992), is a key factor controlling the supply of drinking water and the retention of C, which are crucial environmental services for the human population (Harden, Hartsig, Farley, Lee, & Bremer, 2013; Molina et al., 2007; Ochoa-Tocachi et al., 2016). Paramo grasslands in Ecuador and Colombia are generally characterized by a low nutrient availability, low temperatures and a wet climate (Luteyn, 1992). In these paramo environments, the productivity and decomposition occur at low rates, and plant growth is constrained (Hofstede et al., 2014; Körner, 2003). Plant species in paramo show a large variety of growth forms to cope with these harsh environmental conditions (Hedberg & Hedberg, 1979; Ramsay & Oxley, 1997). This variation in growth forms reflect different mechanisms of C assimilation that ultimately influence size-mass relationships used in allometric regression techniques of biomass estimation (Cáceres, Lliambi, & Rada, 2015; Dorrepaal, 2007).

With this in mind, the aims of our study were to: (1) develop and evaluate non-destructive multispecies allometric models for above-ground, below-ground and total biomass of paramo plants arranged according to their growth form, and (2) show the applicability of these models by estimating the biomass of paramo vegetation sampled in a series of small plots.

2 | METHODS

2.1 | Study sites

The study sites were located at Cumbal (0°56′N, 077°50′W), Ovejas-Tauso (1°09′N, 77°20′W) and Paja Blanca (0°59′N, 077°37′W), at elevations between 3,400 and 3,700 m a.s.l. These areas represent high Andean ecosystems in Nariño, southern Colombia (Appendix S1). The areas have a yearly rainfall between 900 and 2,000 mm and the monthly rainfall is relatively low from Jul to Sept (Solarte-Cruz et al., 2007). Above 3,200 m these locations are covered by paramo vegetation (Luteyn, 1992). Frequently found vascular plant species belong to Blechnum, Carex, Espeletia, Distertzigma, Oreobolus, Paspalum, Azorella, Jamesonia, Calamagrostis and Festuca. The areas are sparsely inhabited by farmer families, who mainly use their land for agriculture (potato), charcoal production (Delgado et al., 2007) or extensive grazing by cattle.

2.2 | Field data

In 2013 and 2014, we established a total of 61 plots of 1 m² in paramo vegetation that had been undisturbed by human activities for at least 10 years, as witnessed by the lack of signs of soil removal, agriculture or burning. Plot locations were randomly selected, but we excluded sites with inaccessible terrain conditions (e.g., steep slopes or ravines) and peat bogs. In each plot, we counted the number of individuals of each vascular plant species. Clonally-growing plants were defined as a plant clump of continuous cover that was spatially separated from neighbouring clumps of the same species (Johnson, Johnson, & West, 1988). Unidentified plant species were collected for taxonomic identification at the herbarium of the Universidad de Nariño. Nomenclature followed Tropicos (2016). We classified the species into seven growth forms, each of which is widespread in paramo vegetation (Cleef, 1978; Hedberg & Hedberg, 1979; Pedraza-Peñalosa, Betancur, & Franco-Rosselli, 2004): basal rosettes, caulirosettes, cushion, herbs, sedges/grasses (non-tussock forms), shrubs and tussocks. For each species in a plot we measured the plant height and basal diameter of all individuals. Plant height was measured as the length from the soil surface to the apical leaf using a tape measure (±0.1 cm). Basal diameter was measured within 0.5 cm from the soil surface, using callipers (±0.01 cm) for basal rosettes, cushion, herbs and sedges/grasses, and a diameter tape (±0.1 cm) for tussocks and caulirosettes.

2.3 | Plants used for the allometric regression models ("allometric set")

At each plot we established a list of the most abundant genera that collectively represented >80% of all vascular plants in the plot. From these genera, we selected three plants that occurred outside the plot but within a distance of 3 m from the plot boundary. After measuring the height and the basal diameter of each of these plants, we harvested their above-ground and below-ground biomass. We defined biomass as plant tissues belong to living organs following Körner (2003). Biomass did not include necromass, which we defined as tissue from organs that showed 100% decay but that were still attached to the plant. Furthermore, the above-ground biomass in our study included leaves, stem or culm, but reproductive organs were excluded. To collect the roots, we carefully excavated each plant following the direction of the root system, by manually...
digging into the soil to a depth of 1 m. For some plants, it was necessary to extract an entire volume of soil in order to keep secondary and tertiary roots attached (Sierra-Escobar & Mora-Osejo, 1994). In the laboratory we separated the above-ground necromass from the above-ground biomass. We washed the roots in a sieve to remove any soil material. We did not distinguish between living roots or dead roots; so all roots were treated as below-ground biomass. Finally, we weighed all biomass samples using an analytical balance (Ohaus PA214; ±0.0001 g), after having dried them at 70°C until constant weight.

2.4 | Allometric regression models

We hypothesized the existence of allometric scaling relationships between plant biomass and each of four single predictor variables: basal diameter, plant height, the virtual rectangular area described by the product of plant height and basal diameter, and the virtual cylindrical volume described by the product of plant height and basal area, with basal area defined as \( \pi \times (\text{basal diameter})^2/4 \) (Johnson et al., 1988). Using the information from the allometric set, we tested these allometric relationships applying simple power-law functions \( Y = aX^b \). We fitted these functions using log-linear ordinary least square regression analysis, i.e., applying linear least square regression after log transforming both sides of the equation \( \ln Y = \ln(a) + b \ln(X) \). We assumed a log-normally distributed, multiplicative error structure of our allometric data sets (Xiao, White, Hooten, & Durham, 2011). We ran these models considering plants from each growth form separately. For each allometric model, we report the percentage relative standard error (PRSE) of the model parameters \( \text{PRSE} = 100 \times [\text{SE}/|\text{parameter}|] \), residual standard error (RSE), adjusted \( r^2 \) (\( r^2_{\text{adj}} \)), AICc (second-order variant of AIC adjusted to correct for small sample bias; Burnham & Anderson 2010) and AICc weight (Burnham & Anderson 2010). PRSE values >20 indicate that parameter estimates become less reliable (MJM Software, Gleneden Beach, OR, US.; Sileshi, 2014). Model selection was based on AICc weights (Burnham & Anderson 2010; Sileshi, 2014), calculated using R package MuMIn (v 1.15.6; R Foundation for Statistical Computing, Vienna, at). Selected models were validated on the basis of residual plots, outliers and influential points (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

2.5 | Biomass prediction of individual plants

Applying the selected models we predicted the above-ground, below-ground and total biomass of individual plants. These plant biomass predictions \( (B_{\text{final}}) \) were back-transformed into arithmetic units using the exponential function as follows:

\[
B_{\text{final}} = \exp(B_{\text{fit}}) \times \text{CF}
\]

with CF as a correction factor (Baskerville, 1972; Chase et al., 2005) calculated as,

\[
\text{CF} = \exp\left(\frac{(\text{RSE})^2}{2}\right)
\]

in which RSE was the residual standard error of the selected allometric model.

2.6 | Prediction errors

To examine bias in the biomass estimation (i.e., any systematic under- or overestimation compared to the true biomass), we regressed the log-transformed observed biomass vs the biomass predictions \( (B_{\text{fit}}) \) of the plants in the allometric set (Piñeiro, Perelman, Guerschman, & Paruelo, 2008). We further used the observed and predicted biomass \( (B_{\text{final}}) \) from individual plants or groups of plants of the allometric set to calculate absolute percentage errors (Sileshi, 2014), as follows:

\[
\text{Absolute percentage error} = 100 \times \frac{\text{abs}(\text{observed biomass} - \text{predicted biomass})}{\text{observed biomass}}
\]

The absolute percentage errors were calculated by means of cross-validation (James, Witten, Hastie, & Tibshirani, 2013), i.e., by holding out a subset of \( k \) randomly picked plants from the allometric set, estimating the regression equation coefficients with the remaining plants using the selected model, and applying those regression results to predict the biomass of the hold-out set. Prediction errors based on
cross-validation tend to have an upward bias if the group size (k) becomes large (Fushiki, 2011). For this reason we also report the absolute percentage errors calculated without cross-validation, i.e., using predicted biomass values estimated with regression results obtained from all plants of the allometric set. These errors have a downward bias (Fushiki, 2011). Finally, we estimated the 95% upper and lower prediction intervals around the biomass prediction of single plants observed in the plots (i.e., not belonging to the allometric set), according to the method supplied by Sokal and Rohlf (1995).

2.7 | Plot biomass

We calculated plot biomass by summation of the plant biomass estimates (B\text{final}) of all plants recorded in a plot. We bootstrapped the plant biomass estimates in each plot to calculate a 95% non-parametric confidence interval around the plot biomass (applying the R package “bootstrap”). For this, we used bias-corrected and accelerated (BCa) confidence limits (Efron & Tibshirani, 1993). These confidence intervals were divided by the plot biomass to obtain their relative width.

We qualitatively compared our plot biomass values with results from multi-species biomass estimations of high-mountain vegetation elsewhere. In addition, we evaluated how the number of plant biomass predictions that were obtained by extrapolation affected the relative width of the bootstrapped confidence intervals around the plot biomass estimates. We did this because we expected that in new studies, in which our regression equations are used, some plant measurements may fall outside the range observed in our allometric set. We also expected that in new studies the vegetation composition may differ substantially from our allometric set. Therefore, we explored how the relative width of the confidence intervals around the plot biomass values depended on the Bray-Curtis dissimilarities (Legendre & Legendre, 1998) between each plot and the allometric set, quantified on the basis of plant counts regarding growth forms or genera. For correlation analysis we used the Spearman rank (r_{s}) coefficient. All statistical analyses were done in R software 3.2.4.

3 | RESULTS

3.1 | Measurements of plants from the allometric set

The allometric set consisted of 476 plants, distributed over 31 genera (Appendix S2). In this set, tussocks were most abundant (144 plants) and basal rosettes least (14 plants; Table 1). On average, tussock plants had the highest plant height (37.7 ± 14.4 cm; ±SD), and caulirosettes the highest basal diameter (2.9 ± 1.4 cm) and total biomass values (30.8 ± 24.0 g; Table 1).

3.2 | Model selection

For the above-ground, below-ground and total biomass of basal rosettes and tussocks, the allometric regression models with the highest relative likelihood (as expressed by the AICc weights; Burnham &
Figure 1: Relationships between observed and predicted biomass of plants from the allometric set. The dashed lines represent the line $y = x$. In the left corner of each diagram, the 95% confidence intervals of the intercept and slope of the linear regression of the log-transformed observed plant biomass against the log-transformed predicted plant biomass.
Anderson 2010) were those with the product of basal diameter and plant height (i.e., the rectangle) as descriptor (Appendix S3). The biomass of cushion plants was best modelled using their basal diameter. Regarding the other growth forms, several descriptors yielded relatively high AICc weights. The biomass was well modelled using rectangle or volume regarding caulirosettes; height and rectangle in the case of herbs; diameter (clearly for above-ground and total biomass) and rectangle (for below-ground biomass) for sedges/grasses; and volume and rectangle regarding shrubs. For several growth forms, the PRSE values of models that were ultimately selected for biomass prediction (Table 2; Appendix S3) were well above 20.

3.3 | Biomass predictions of plants from the allometric set

The intercept and slope of the regressions of observed vs predicted biomass (Figure 1) did not differ significantly from 0 to 1, respectively, indicating that the fitted biomass values were in principle reliable (Sileshi, 2014). Biomass predictions of single plants from the allometric set yielded absolute percentage errors that were generally well above 100% (Figure 2). Summing the predicted biomass over several plants, however, reduced the error. Applying similar group sizes, the errors for below-ground biomass were about two to three times larger than those obtained for above-ground and total biomass. For plant groups composed of several growth forms, applying for each growth form a number of plants that corresponded to the mean growth form density (rounded off to zero) across all plots, we obtained cross-validated absolute percentage errors of 14 ± 10.0% (mean ± SD for 100 randomizations) for above-ground biomass, 27 ± 23.0% for below-ground biomass, and 12 ± 10.2% for total biomass. Without cross-validation these errors were 11 ± 10.3%, 24 ± 18.0%, and 10 ± 9.0%, respectively.

3.4 | Plant observations in the plots

On average, a 1-m² plot contained 86 (±50.7) plants (Appendix S4). Shrubs and tussock plants were most frequently observed (in 60 and 59 plots, respectively), followed by caulirosettes (51 plots), herbs (46), cushions (41), sedges/grasses (41) and basal rosettes (34). In all plots together, we recorded 5,521 plants distributed over 64 genera, which was twice the number of genera found in the allometric set. However, most of the more abundantly occurring genera in the plots were also part of the allometric set. For example, of the 24 genera that were registered with 50 plants or more in all plots combined, 21 were included in the allometric set. The Bray-Curtis dissimilarity between a plot and the allometric set was 0.71 ± 0.14; 0.37, 0.97 (mean ± SD; minimum, maximum) for growth forms, and 0.78 ± 0.11; 0.47, 0.97 for genera. Individual plots contained 3.6 ± 4.3 plants with heights above the maximum plant height seen in the allometric set, and 8.4 ± 13.5 plants with heights below the minimum height in that set (Appendix S4). For basal diameter, these values were 10.7 ± 11.7 and 9.1 ± 12.0, respectively.

3.5 | Plot biomass

Plot biomass values ranged between 21 and 785 g/m² for above-ground biomass, 4 and 1,878 g/m² for below-ground biomass, and 25 and 2,530 g/m² for total biomass. Averaging the plot biomass values yielded a mean of 329 ± 190 g/m² for above-ground biomass, 743 ± 486 g/m² for below-ground biomass, and 1,011 ± 627 g/m² for total biomass. The mean relative width of the 95% bootstrapped confidence intervals around the plot biomass estimates (Figure 3) was 72 ± 40% for above-ground biomass, 90 ± 43% for below-ground biomass, and 80 ± 41% for total biomass. These relative widths were not correlated, or were negatively correlated, with the number of plants that showed a height of basal diameter exceeding the range of the allometric set (Appendix S4). However, they did show a fairly strong and positive association with the Bray-Curtis dissimilarities regarding growth forms (r values between 0.35 and 0.52; Appendix S4). Thus, stronger differences between plots and the allometric set regarding growth form or genus composition reduced the precision of the plot biomass estimates.

4 | DISCUSSION

Our study is the first to use allometric regression modelling to estimate above-ground, below-ground and total biomass of multispecies vegetation samples in high-mountain vegetation (Table 3). The across-plot averages for above-ground and below-ground biomass recorded in our field area were within the range of biomass estimates obtained hitherto in the tropical Andes (Table 3) or in tropical and temperate biomes elsewhere (Appendix S5). These results suggest that our allometric modelling approach has potential application to estimate the biomass of high-mountain vegetation in the tropical Andes and elsewhere.

Compared to the standard practice of destructive biomass estimations in high-mountain environments, our method has several advantages. (1) Non-destructive biomass estimation methods greatly facilitate studies of biomass change in vegetation through time. These studies are highly needed for ecosystem monitoring programmes, such as those developed in the Andes of South America that focus on paramo restoration (Cabrera & Ramirez, 2014; MADS 2015) or paramo responses to global change (Báez et al., 2014; Cuesta et al., 2017). (2) Our biomass values were based on the entire spectrum of vascular species in the plots, and therefore yield an optimal approximation of biomass production of paramo vegetation (Körner, 2003). Allometric modelling approaches have been used in the tropical Andes, but only for biomass estimates of particular growth forms, such as tussocks (Minaya et al., 2016; Verweij, Kok, & Budde, 2003), caulirosettes (Torres, Peña, Zuñiga, & Peña, 2012), basal rosettes (Minaya et al., 2016), shrubs (Torres et al., 2012) or cushion forms (Minaya et al., 2016). (3) We separated plants according to growth form in order to optimize the biomass estimation. Growth forms exist because plants apply different mechanisms of assimilation (Cáceres et al., 2015; Dorrepaal, 2007). Hence, plants
FIGURE 2  Absolute percentage error (%) of the predicted biomass summed over k randomly picked plants from the allometric set. Shown are the mean ± SD (vertical bars) of 100 randomizations. Notice that some SD bars are too long to fit in the graph. Solid lines connect mean errors found in the hold-out set using cross-validation (James et al., 2013). Dashed lines connect mean errors found in the so-called training set, obtained without cross-validation. Axis scales may change between the graphs. To promote visual comparisons, dotted lines show error levels of 15% (lower line) and 20% (upper line).
Continuous horizontal line in each plot is the across-plot mean, representing the bootstrapped 95% confidence intervals. The biomass is presented in order of increasing plot biomass. Vertical lines come with the estimates and, moreover, the complexity involved to quantify these errors. Our allometric approach yielded large uncertainties around biomass estimates of groups with 20 plants or less (Figure 2, Appendices S4–S5). Errors around biomass estimates of single plants are largely the consequence of added effects of uncertainties related to plant measurements, model selection and model allometry (Chave et al., 2004). Fortunately, the errors of biomass estimates aggregated for groups of plants tended to cancel out. Indeed, for groups that mirrored the plots regarding plant density and growth form composition, we obtained cross-validated absolute percentage errors below 15% for above-ground and total biomass. We illustrate the importance of obtaining a trustworthy estimate of the error with an example (based on Sokal & Rohlf, 1995). Assuming an experimental treatment on paramo vegetation using small open-top chambers to artificially increase the temperature (mimicking global warming) applying small, manageable plots that contain 100 plants. To be able to detect an expected treatment effect of 20% biomass increase at a probability of 5% with a power of 80%, this experiment would need at least 17 treatment and 17 control plots, if the allometrically estimated plot biomass had uncertainty of 20%. The bootstrapped confidence intervals around the plot means, which were derived from regression results applied to newly measured plants in the plots, also provided uncertainties for sample sizes that match the number of plants we found in 1-m² plots. Due to the exponential allometric models we applied, the upper prediction intervals tended to be larger than the lower intervals (Figure 3). However, assuming that the bootstrapped prediction intervals were normally distributed around the estimated plot biomass and applying a t-value of 2, the average widths of the 95% bootstrapped confidence intervals around the plot biomass estimates (which were between 72%, 90% and 80% for above-ground, below-ground and total plot biomass, respectively), would roughly correspond to standard errors around the mean plot biomass of 18%, 23% and 20%. Across the 61 plots, the landscape-scale from particular growth forms likely share similar size–mass relationships, for which reason we assume that allometric modelling performs better if growth forms are treated separately. (4) We only used plant height and basal diameter as basic predictors. Measuring these variables can be applied easily to all plants regardless of their growth form, which promotes the repeatability of our field method. Our results thus contribute to achieving the much needed standardization of non-destructive biomass estimation of high-mountain vegetation (Oliveras, Van der Eynden et al., 2014). Plant height and basal diameter have been used before to estimate biomass for tussocks (Guevara, Gonnet, & Estevez, 2002; Oliveras, Girardin et al., 2014) and shrubs (Ali et al., 2015). We refrained from using canopy diameter as suggested by others (Guevara et al., 2002; Oliveras, Girardin et al., 2014; Oliveras, Van der Eynden et al., 2014). Basal diameter can be measured more precisely than canopy diameter, especially for paramo growth forms such as prostrate shrubs and cauliflores. (5) Our study showed that potentially useful estimates of below-ground biomass can be obtained on the basis of above-ground predictors (Niklas, 2005). Environmental conditions typically occurring in paramo, such as low temperatures, high radiation and strong winds, favour relatively strong C investment in below-ground organs (Körner, 2003; Patty, Halloy, Hiltbrunner, & Körner, 2010). Because the below-ground biomass in paramo vegetation is relatively large, it is important to include this information in ecosystem studies (Ma, Yang, He, Zeng, & Fang, 2008; Niklas, 2005). Below-ground biomass estimates are much needed to understand and predict the dynamics of regional and global C cycles (Ma et al., 2008; Scurluck & Hall, 1998). However, our method also comes with important limitations. Allometric biomass estimation methods require meticulously measuring predictor values of individual plants, which is far more time-consuming than destructively harvesting plot biomass, especially in non-forest vegetation. Using 1-m² plots (a plot size commonly used in monitoring programmes of high-mountain vegetation; e.g., Cuesta et al., 2017), our field method seemed feasible. If larger plot sizes are applied, the above-ground biomass might perhaps be more efficiently assessed by means of proxies like plant cover (e.g., Cáceres et al., 2015). Compared to destructive methods, the most important limitations of allometric methods are the uncertainties that inevitably come with the estimates and, moreover, the complexity involved to quantify these errors. Our allometric approach yielded large uncertainties around biomass estimates of groups with 20 plants or less (Figure 2, Appendices S4–S5). Errors around biomass estimates of single plants are largely the consequence of added effects of uncertainties related to plant measurements, model selection and model allometry (Chave et al., 2004). Fortunately, the errors of biomass estimates aggregated for groups of plants tended to cancel out. Indeed, for groups that mirrored the plots regarding plant density and growth form composition, we obtained cross-validated absolute percentage errors below 15% for above-ground and total biomass. We illustrate the importance of obtaining a trustworthy estimate of the error with an example (based on Sokal & Rohlf, 1995). Assuming an experimental treatment on paramo vegetation using small open-top chambers to artificially increase the temperature (mimicking global warming) applying small, manageable plots that contain 100 plants. To be able to detect an expected treatment effect of 20% biomass increase at a probability of 5% with a power of 80%, this experiment would need at least 17 treatment and 17 control plots, if the allometrically estimated plot biomass had uncertainty of 20%. The bootstrapped confidence intervals around the plot means, which were derived from regression results applied to newly measured plants in the plots, also provided uncertainties for sample sizes that match the number of plants we found in 1-m² plots. Due to the exponential allometric models we applied, the upper prediction intervals tended to be larger than the lower intervals (Figure 3). However, assuming that the bootstrapped prediction intervals were normally distributed around the estimated plot biomass and applying a t-value of 2, the average widths of the 95% bootstrapped confidence intervals around the plot biomass estimates (which were between 72%, 90% and 80% for above-ground, below-ground and total plot biomass, respectively), would roughly correspond to standard errors around the mean plot biomass of 18%, 23% and 20%. Across the 61 plots, the landscape-scale
uncertainty of the mean plot biomass values showed a coefficient of variation of 58%, 65% and 62% for above-ground, below-ground and total plot biomass, respectively. This variability is probably controlled for partially by effects of the environment (e.g., soil, elevation) and vegetation dynamics or land-use history, a topic not further elaborated here. In comparison, Chave et al. (2004) reported a landscape-scale coefficient of variation of 23% in the case of biomass estimates of tropical forest plots in Panama.

In view of the above, it is evident that it depends on the research question and the associated sampling design of new studies whether or not our allometric equations can be applied meaningfully. In situations where the growth form or genera composition of target vegetation samples is broadly similar to our allometric set (e.g., showing Bray-Curtis dissimilarities matching those of the plots in our study), the application of our regression equations should yield uncertainties resembling the errors we found, provided the target samples contain at least 50 plants for above-ground and total biomass and 100 plants for below-ground biomass. Considering the biogeographic affinities among paramo regions, we would expect that such conditions might be fulfilled in paramos located in Nariño, Macizo Colombiano and the Central Cordillera in Colombia (Londoño, Cleef, & Madriñan, 2014), or in paramos of northern Ecuador (Cuesta, Báez, Muriel, & Salgado, 2014; Moscol & Cleef, 2009). If the composition of growth forms or genera of such sufficiently large target samples becomes more different, larger uncertainties can be expected.

For studies that need to non-destructively estimate the biomass of target samples containing 50 plants or less, we would recommend improving the allometry by extending the size of our allometric set (Appendix S2) with measurements of biomass and predictor values of local plants, followed by renewed regression analyses and subsequent model selections. Increasing the number of plants in the allometric set likely reduces the influence of outliers on the RSE, which decreases the prediction errors. In such situations, the allometric set might preferably be expanded with information from growth forms with PRSE values >20 (Appendix S3). Chave et al. (2004) recommended constructing allometric equations for biomass estimation of tropical forests on the basis of at least 100 trees. In our current allometric set only tussocks reached that threshold. In all cases, great care must be taken to measure biomass and predictor values of plants with optimal accuracy.

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**TABLE 3** Average above-ground and below-ground biomass of paramo vegetation in the tropical Andes. If available, the SD is added in parentheses.

<table>
<thead>
<tr>
<th>Country</th>
<th>Location</th>
<th>Method</th>
<th>Above-ground biomass (g/m²)</th>
<th>Below-ground biomass (g/m²)</th>
<th>Elevation (m a.s.l.)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecuador</td>
<td>Daldal</td>
<td>Destructive</td>
<td>815 (30)</td>
<td>133 (117)</td>
<td>3,750–4,000</td>
<td>Ramsay &amp; Oxley (2001)</td>
</tr>
<tr>
<td>Ecuador</td>
<td>Mazar Reserve</td>
<td>Destructive</td>
<td>2,020 (600)</td>
<td>No data</td>
<td>3,453</td>
<td>Bremer, Farley, Chadwick, &amp; Harden (2016)</td>
</tr>
<tr>
<td>Colombia</td>
<td>Laguna Verde</td>
<td>Destructive</td>
<td>603 (122)</td>
<td>1,212</td>
<td>3,600</td>
<td>Lutz &amp; Vader (1987)</td>
</tr>
<tr>
<td>Colombia</td>
<td>Laguna Verde</td>
<td>Destructive</td>
<td>197 (42)</td>
<td>886.3 (81)</td>
<td>3,620</td>
<td>Beekman &amp; Verweij (1987)</td>
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<td>Cruz Verde</td>
<td>Destructive</td>
<td>107 (26)</td>
<td>2.4 (0.9)</td>
<td>3,300–3,400</td>
<td>Cardozo &amp; Schnetter (1976)</td>
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<td>Chingaza</td>
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<td>1,725 (486)</td>
<td>No data</td>
<td>3,670</td>
<td>Tol &amp; Cleef (1992)</td>
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<td>1,327 (693)</td>
<td>4,000</td>
<td>Rossenaar &amp; Hofstede (1992)</td>
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<td>Rocha &amp; Mondragon (1994)</td>
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<td>245 (117)</td>
<td>3,530–4,700</td>
<td>Smith &amp; Klinger (1985)</td>
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<td>Barnola &amp; Montilla (1997)</td>
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<td>329 (190)</td>
<td>743 (486)</td>
<td>3,400–3,600</td>
<td>This study</td>
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