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# Root biomass and production by two cushion plant species of tropical high-elevation peatlands in the Andean páramo

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## SUMMARY

High-elevation peatlands in the Andes are receiving increasing attention for their biodiversity and their high rates of carbon accumulation. However, the ecology of these peatlands and the environmental factors that control their carbon dynamics remain under-studied. Here we report on the patterns of root biomass productivity and turnover rates for two cushion plant species (*Distichia muscoides*, *Plantago rigida*) that commonly dominate high-elevation peatlands (>4200 m a.s.l.) in the Andean páramo landscape of Northern Ecuador. Root biomass for *P. rigida* ranged from 680 to 864 g m<sup>-2</sup> and was approximately 40 % higher than for *D. muscoides* (507–620 g m<sup>-2</sup>). In contrast, root production was almost twice as high for *D. muscoides* (2000–2800 g m<sup>-2</sup> yr<sup>-1</sup>) than for *P. rigida* (1030–1080 g m<sup>-2</sup> yr<sup>-1</sup>). These patterns resulted in high root turnover rates, especially for *D. muscoides* (0.98–1.90 yr<sup>-1</sup>). Below-ground productivity (as C) at our sites conservatively ranged from 0.55 to 1.5 kg m<sup>-2</sup> yr<sup>-1</sup>, representing approximately 30 % of the estimated total productivity for these species, which only accounts for root production down to 50 cm depth. These high productivity rates are in accordance with the extremely high rates of carbon accumulation that have been reported for high-elevation peatlands of the Andes.

**KEY WORDS:** Cayambe-Coca NP, Chakana, Ecuador, *Distichia muscoides*, *Plantago rigida*, root turnover

## INTRODUCTION

The high-elevation peatlands of the tropical Andes are well known for the high diversity of their plant communities (Cooper *et al.* 2010, Schmidt-Mumm & Vargas Rios 2012) and their regional importance in water supply and regulation (Mosquera *et al.* 2015). In Northern Ecuador, for example, the páramo environment (high-elevation complex with several vegetation types occurring above ~3200 m a.s.l.) is dotted with numerous peatlands that cover up to 23 % of the landscape and store carbon in excess of 2000 Mg ha<sup>-1</sup> (Chimner & Karberg 2008, Benavides *et al.* 2013; Hribljan *et al.* 2016, 2017), with a prominent contribution of low-stature cushion plants, especially at higher elevations (> 4200 m a.s.l.).

Fine-root production has been extensively studied in boreal/temperate northern regions and is recognised as a key process in the accumulation of soil carbon (McCormack *et al.* 2015). In the case of peatlands, typical rates are highly variable, ranging from 50 to 1000 g m<sup>-2</sup> yr<sup>-1</sup> depending on factors such as the type of vegetation, latitude, water table level and soil nutrient content (Saarinen 1996, Murphy *et al.* 2009, Murphy & Moore 2010, Bhuiyan *et al.* 2017). However, for tropical high-elevation peatlands,

where plant community structure and climate can be very different, there is virtually no information concerning rates of root production and its contribution to carbon dynamics.

Peatlands dominated by cushion plants (e.g. *Distichia* spp, *Plantago rigida*, *Oreobolus* spp.) are common in the páramo landscape of the Northern Andes. In particular, peatlands occurring above 4100 m a.s.l. in Northern Ecuador tend to be dominated by *P. rigida* and *Distichia muscoides*, with an increasing dominance of *D. muscoides* towards higher elevations (Bosman *et al.* 1993). It is likely that these cushion plants are aerenchymatous, i.e., they transport oxygen to their roots, enabling the roots to grow into submerged, anoxic peat. Although the adaptation has not been confirmed in these particular species, it is common in other *Plantago* species (Striker *et al.* 2007) and in other neotropical Juncaceae (the family of *D. muscoides*; Balslev 1996). The adaptation permits significant root production and contributions of new organic matter deeper in the peat, along with the potential for oxidation. Hence, in order to understand the processes driving peat accumulation and turnover, it is essential to have knowledge of the biomass, distribution and production of cushion plant roots.



Páramo peatlands accumulate carbon (C) at extremely high rates and can store up to  $2123 \pm 308$  Mg ha<sup>-1</sup> (Hribljan *et al.* 2016, 2017). However, there is very little information about the role that different species play in the process of carbon accumulation and its response to environmental conditions. Moreover, to our knowledge there is no available information on root production and turnover rates for the species that dominate these peatlands. This information is crucial in terms of future modelling of possible effects of climate change on the functioning of high-elevation Andean peatlands. Here we report on a study of root production and turnover rates in the two dominant cushion-forming species of two páramo peatlands in Northern Ecuador.

## METHODS

We studied two páramo peatlands located at 4200 and 4300 m a.s.l. in the Cayambe-Coca National Park, Northern Ecuador (0° 18.847' S, 78° 11.352' W; Figure 1). This landscape is part of the Chakana

volcano, a 50 km long Pleistocene caldera that lies 50 km to the east of Quito (Hall & Mothes 2008). Characterised by a complex topography which bears the signs of volcanic activity and glacial erosion, the area is dominated by typical páramo vegetation covering the steep slopes of the mountains and dotted by multiple peatlands that occupy almost 25 % of the landscape (Hribljan *et al.* 2017). Mean annual precipitation in the area reaches 1500 mm at an elevation of 4100 m a.s.l., and mean air temperature is 6.8 °C. As is common in páramo ecosystems, air temperature at our study site exhibits wide daily variations with mean monthly minimum and maximum temperatures of 2.5 °C and 9.2 °C, respectively. On average, temperatures below freezing occurred on ten days per year between 2008 and 2020 (<http://sedc.fonag.org.ec/reportes/consultas/>).

The two peatlands that we studied are dominated by *P. rigida* and *D. muscoides*, which together cover 60–70 % of the surface area of each site. *D. muscoides* tends to dominate portions of the peatlands with higher water table, while *P. rigida* can occur throughout the peatlands but tends to show



Figure 1. Study sites located in the páramos of Cayambe-Coca National Park (Northern Ecuador), on cushion plant dominated peatlands at (A) 4300 m a.s.l. and (B) 4200 m a.s.l. Panels C and D depict the ingrowth bags that were used to measure root production.

higher coverage in areas with slightly lower water tables and can even occur outside of the wetlands. The remaining vegetation is composed of a matrix of mosses (e.g. *Breutelia* and *Campylopus* species), grasses and herbs (e.g. *Cortaderia sericantha*, *Castilleja nubigena*) and scattered shrubs (e.g. *Loricaria thuyoides*, *Diplostephium rupestre*). These peatlands have high water tables with three-year average depths (below ground surface) of  $6.7 \pm 1.7$  cm for the site at 4300 m, and  $3.5 \pm 0.7$  cm for the site at 4200 m.

### Root biomass

In November 2016, core samples (0–50 cm) were taken at the centres of four randomly selected individuals of each species, at each of the two sites (16 samples in total). The samples were extracted with an open-face auger and stored in the laboratory at 4 °C until processing. In the laboratory, each core was cut into 10 cm sections and individual roots from each section were hand-picked, dried in an oven at 65 °C, then weighed. Roots from each core section were ashed in a muffle furnace for five hours at 550 °C, and all results are presented as ash-free dry mass. Our data probably underestimate root biomass as very fine roots are difficult to sample with this method.

### Root production

Root production was estimated at each site following a modification of the ingrowth bag method (Neill 1992, Laiho *et al.* 2014). Ingrowth bags were made from plastic garden mesh with a mesh size of 1.5 cm, assembled as cylinders of length 60 cm and diameter 3.8 cm with a circular piece of the same mesh capping one end. To fill the ingrowth bags, we collected peat from a peatland located in the buffer zone of the Antisana Ecological Reserve, 10 km to the south of our study site. The peat was transported to the laboratory, sun-dried, and laid on blankets where we carefully removed all visible roots. Each ingrowth bag was filled with an amount of root-free peat to achieve a bulk density of  $0.2\text{--}0.3$  g cm<sup>-3</sup>, consistent with values that have been reported for these sites (Hribljan *et al.* 2016, 2017). In order to avoid the possibility of peat falling through the holes in the mesh, the root-free peat was weighed, rewetted, and then carefully placed in the ingrowth bags to a height of 50 cm, thus leaving 10 cm of headspace in each bag to facilitate installation and recovery (Figure 1).

Between September and October 2017, a total of 36 ingrowth bags were installed. At each site, 18 ingrowth bags were deployed at the centres of nine cushions of *D. muscoides* and nine cushions of *P. rigida*. Plants for ingrowth bag installation were

chosen only based on the availability of well-developed individuals in which we could be sure that new roots would come from the selected species. Installation was performed using a soil corer as described by Laiho *et al.* (2014) and the ingrowth bags were left to incubate in the field for 14 months (427 days). After this period the ingrowth bags were carefully extracted, transported to the laboratory, and processed as described above for root biomass. Based on the biomass of new roots extracted from each 10 cm section of the ingrowth bags, root production is reported as ash-free dry mass (g m<sup>-2</sup> yr<sup>-1</sup>), by converting our values to an annual production rate.

### Root turnover

Root turnover (RT) was calculated as:

$$RT = \frac{\text{Annual belowground production}}{\text{Maximum belowground standing crop}} \quad [1]$$

As suggested by (Gill & Jackson 2000), we transformed our values of mean root biomass (mean belowground standing crop; MBSC) to maximum belowground standing crop (MxBSC) with the equation:

$$MxBSC = 0.45 * \text{belowground production} + MBSC \quad [2]$$

With this definition of root turnover, a value of 1.0 yr<sup>-1</sup> means that all the roots produced by the plant die and are replaced within one year.

### Statistical tests

We compared root biomass, root production and proportional root allocation by depth between species and sites using mixed models; with core as random effects nested in site, and species, site and depth as fixed effects. Total production was estimated with standard least squares, with species and site as fixed effects. All analyses were carried out in JMP Pro 14 (SAS Inc).

## RESULTS

Total root biomass at our sites ranged from 500 to 860 g m<sup>-2</sup> in the top 50 cm of the soil profile (Table 1). At both sites, total root biomass was approximately 40 % greater for *P. rigida* than for *D. muscoides*, a marginally significant difference ( $p = 0.051$ ; Table 2). At the more elevated site (4300 m), mean total root biomass reached  $507 \pm 44$  g m<sup>-2</sup> for *D. muscoides*, and  $864 \pm 27$  g m<sup>-2</sup> for *P. rigida*, while corresponding values at 4200 m were  $620 \pm 125$  g m<sup>-2</sup> and  $680 \pm 140$  g m<sup>-2</sup> for *D. muscoides* and *P. rigida*, respectively, although these site

Table 1. Mean root standing stock, root production, and root turnover rate in cushion plants of *Distichia muscoides* and *Plantago rigida* at two peatland sites at different elevations (4200 and 4300 m a.s.l., respectively) in the páramos of Northern Ecuador. Numbers in parentheses: standard error of the mean. For biomass, four samples were taken from each species at each site. For root production, nine ingrowth bags were installed for each species at each site.

Site (a.s.l.)	Depth (cm)	<i>Distichia muscoides</i>				<i>Plantago rigida</i>			
		Mean root biomass (g m <sup>-2</sup> )	Mean root production (g m <sup>-2</sup> yr <sup>-1</sup> )	Modelled max. root biomass (g m <sup>-2</sup> )	Root turnover (yr <sup>-1</sup> )	Mean root biomass (g m <sup>-2</sup> )	Mean root production (g m <sup>-2</sup> yr <sup>-1</sup> )	Modelled max. root biomass (g m <sup>-2</sup> )	Root turnover (yr <sup>-1</sup> )
4300 m	0–10	56.4 (21)	746.2 (220)	392.2	1.90	110.5 (8)	373.4 (57)	278.6	1.34
	10–20	169.9 (61)	896.9 (95)	573.5	1.56	341.2 (34)	318.6 (109)	484.6	0.66
	20–30	149.9 (34)	467.0 (64)	360.1	1.30	190.5 (24)	245.0 (101)	300.8	0.81
	30–40	126.8 (21)	445.4 (68)	327.2	1.36	174.9 (32)	96.8 (12)	218.5	0.44
	40–50	78.1 (15)	267.9 (85)	198.6	1.35	105.0 (28)	155.2 (80)	174.9	0.89
	Totals	507.7 (44)	2722.2 (206)			864.9 (27)	1087.1 (239)		
4200 m	0–10	64.9 (12)	425.0 (63)	256.1	1.66	195.6 (35)	277.7 (39)	320.6	0.87
	10–20	142.9 (26)	625.9 (143)	424.5	1.47	185.6 (25)	256.9 (90)	301.2	0.85
	20–30	150.7 (41)	477.0 (88)	365.4	1.31	165.3 (48)	197.0 (49)	254.0	0.78
	30–40	161.0 (51)	280.1 (42)	287.1	0.98	76.4 (17)	142.3 (30)	140.4	1.01
	40–50	100.7 (24)	200.9 (49)	191.1	1.05	76.6 (19)	165.2 (45)	150.9	1.09
	Totals	620.3 (125)	2008.9 (229)			680.3 (140)	1039.2 (178)		

Table 2. Fixed effect results of full factorial mixed models performed on (A) root biomass, and (B) root production. Fixed effects: species, site, depth. Random effects: core in site.

	Source	# parameters	D.F. numerator	D.F. denominator	F ratio	Prob.> F
A: Root biomass	site	1	1	10.8	0.425	0.5278
	species	1	1	10.8	2.245	0.1626
	site×species	1	1	10.8	0.782	0.3957
	depth	4	4	42.1	12.457	<0.0001
	site×depth	4	4	42.1	2.904	0.0329
	species×depth	4	4	42.1	4.789	0.0028
	site×species×depth	4	4	42.1	2.058	0.1035
B: Root production	site	1	1	23.0	4.344	0.0484
	species	1	1	23.0	22.059	<0.0001
	site×species	1	1	23.0	3.105	0.0913
	depth	4	4	92.0	13.138	<0.0001
	site×depth	4	4	92.0	1.663	0.1652
	species×depth	4	4	92.0	3.166	0.0174
	site×species×depth	4	4	92.0	1.646	0.1693

differences were not significant (Table 2). For both species, root biomass was concentrated in the top 30 cm of the soil profile, especially for *P. rigida*, which had more than three-quarters of its roots in this layer ( $77 \pm 2.8$  % for *P. rigida* vs.  $61 \pm 3$  % for *D. muscoides*). However, vertical biomass distribution among depths differed between species (species×depth,  $p = 0.0028$ ), with greater *P. rigida* biomass near the surface compared with *D. muscoides*, but no difference at depth.

Productivity was significantly higher in *D. muscoides* than in *P. rigida*, with more than double the rate for *D. muscoides* ( $2000\text{--}2800$  g m<sup>-2</sup> yr<sup>-1</sup>) vs. *P. rigida* ( $1030\text{--}1080$  g m<sup>-2</sup> yr<sup>-1</sup>;  $p < 0.001$ ; Table 1, Figure 2). In both species, 70–79 % of total root productivity occurred within the top 30 cm of the soil profile (Figure 2). However, the species differed in their depth allocation patterns of biomass production (species×depth,  $p = 0.017$ ; Figure 2) with a biomass production peak for *D. muscoides* at 10–20 cm but a more-or-less monotonic decline in root production with depth for *P. rigida*. For both species, non-zero root production at 50 cm and the decline of production with depth strongly suggests that additional unmeasured root production occurred below that depth.

Root turnover (RT) rates were high, especially in the top 20 cm of the soil (Table 1). For *D. muscoides*, RT ranged from 1.9 to 1.3 yr<sup>-1</sup> at 4300 m, and from 1.6 to 0.98 yr<sup>-1</sup> at 4200 m. Corresponding values for *P. rigida* were approximately 1.7 times lower than those for *D. muscoides*, ranging from 1.34 to 0.44 yr<sup>-1</sup> at 4300 m and from 1.1 to 0.44 yr<sup>-1</sup> at 4200 m (Table 1).

## DISCUSSION

Mountain peatlands in the páramo have been largely under-studied and only recently are being recognised as an important component of the tropical Andean landscape with a distinct role in providing critical ecosystem services such as water supply (Mosquera *et al.* 2015). On a unit area basis, these peatlands can store as much carbon in their peat (more than 2000 Mg ha<sup>-1</sup> for average depth 6 m) as a tropical rain forest stores in its biomass (Hribljan *et al.* 2017), and they contribute significantly to water quality and regulation (Mosquera *et al.* 2015). They have also been shown to accumulate carbon at very high rates (Chimner & Karberg 2008, Benavides *et al.* 2013, Hribljan *et al.* 2016), but the controls behind these processes and their relation to vegetation have not been explored.

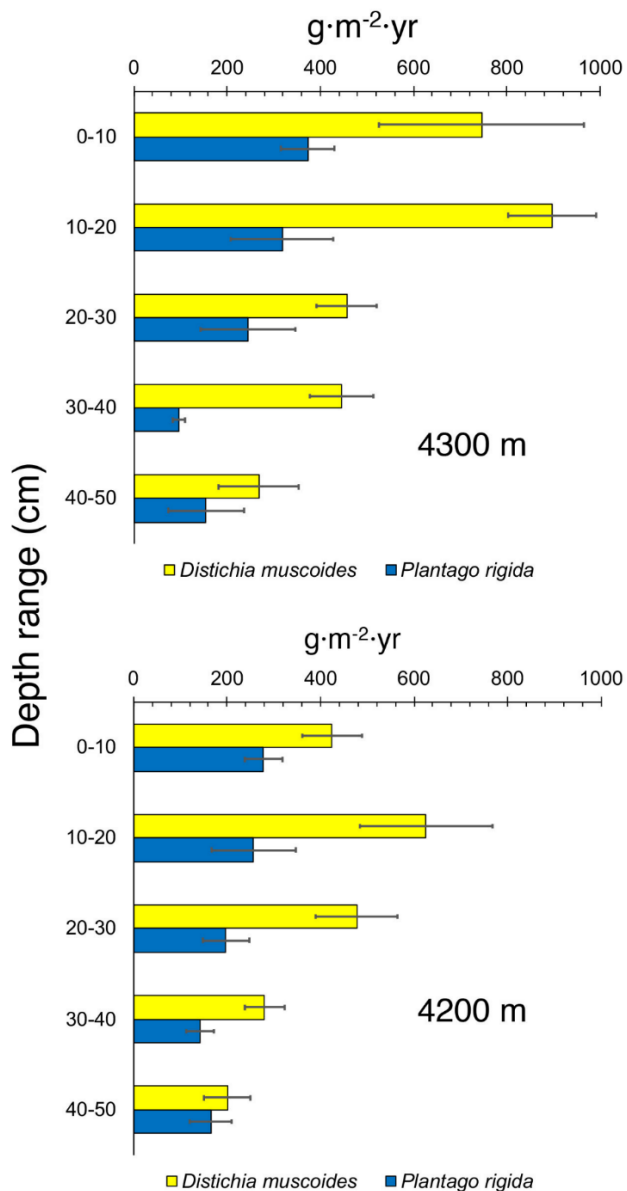


Figure 2. Patterns of root production in cushion plants of *Distichia muscoides* and *Plantago rigida* at two peatland sites at elevations of 4200 and 4300 m a.s.l. in the páramos of Northern Ecuador. Each bar represents the mean and standard error of nine samples.

Root production at our sites varied between  $1039 \pm 178$  and  $2722 \pm 206$   $\text{g m}^{-2} \text{yr}^{-1}$  for the 0–50 cm layer, and was considerably higher than common values reported in the literature which range from 1 to  $1424 \text{ g m}^{-2} \text{yr}^{-1}$  (Table 3; (Murphy *et al.* 2009, Murphy & Moore 2010, Laiho *et al.* 2014, Bhuiyan *et al.* 2017). The much higher root production at our sites could be due to two main factors. On one hand, our results might represent the upper end of the range of potential root production at our sites, because our ingrowth bags were located at the centres of the

cushion plants where root density and production are probably at their maxima. On the other hand, most published information on root production comes from temperate, markedly seasonal ecosystems. In this context, the high rates of root production that we reported might be a result of the constant productivity of the vegetation which proceeds year-round in the equatorial climate that characterises our sites (Sánchez *et al.* 2017). This high productivity is consistent with the elevated rates of carbon accumulation that have been reported for peatlands in the páramo and puna landscape of the high Andes of Colombia, Ecuador and Bolivia (Chimner & Karberg 2008, Benavides *et al.* 2013; Hribljan *et al.* 2014, 2016).

Root biomass and production varied also between species. In general, mean root biomass for *P. rigida* was 1.4 times higher than for *D. muscoides*, but the opposite was true for annual root production which was almost twice as high for *D. muscoides* than for *P. rigida*. We hypothesise that this difference in productivity could be due to *D. muscoides* being more closely adapted than *P. rigida* to the flooding conditions and shallow water table that characterise the wet centres of these peatlands. Although both *D. muscoides* and *P. rigida* are dominant at our study sites, their distributions are usually segregated, with *D. muscoides* occupying areas with persistent flooding and shallower water table while *P. rigida* tends to occupy the outskirts of the peatland, even extending onto adjacent well-drained soils where the species is common. This hypothesis needs further exploration through additional studies on the morphology, anatomy and physiology of these species, which could help us to better characterise the spatial patterns of carbon accumulation and species distribution in these ecosystems. Given the observed segregation of the species along elevation (Bosman *et al.* 1993) and water table gradients, future studies should explore the effects of environmental variation on the patterns of root production and biomass.

Root turnover rate at our sites was high, especially for *D. muscoides*. Typical values for peatlands in temperate regions range from  $0.2$  to  $0.7 \text{ yr}^{-1}$  (Saarinen 1996, Finer & Laine 1998, Gill & Jackson 2000, Bhuiyan *et al.* 2017), whereas corresponding values for the 0–20 cm layer at our sites ranged from  $1.5$  to  $1.9 \text{ yr}^{-1}$  for *D. muscoides* and from  $0.6$  to  $1.3 \text{ yr}^{-1}$  for *P. rigida*. Although we could not find comparable information for other tropical high elevation peatlands, similar values have been reported for a premontane forest in Venezuela ( $2.0 \text{ yr}^{-1}$ ), a tropical montane forest in Southern Ecuador ( $0.7$  to  $1.3 \text{ yr}^{-1}$ ), and other tropical ecosystems across the world (Priess *et al.* 1999, Gill & Jackson 2000, Graefe *et al.*

Table 3. Examples of root production estimates from the literature. The list does not represent a systematic review and is included only for the purpose of comparison.

Study organisms	Root production (g m <sup>-2</sup> yr <sup>-1</sup> )	Peatland type	Citation
Trees	53–262	Temperate-boreal lowland bog	Iversen <i>et al.</i> 2018
Shrubs	3–60	Temperate-boreal lowland bog	Iversen <i>et al.</i> 2018
Sedges	1–10	Temperate-boreal lowland bog	Iversen <i>et al.</i> 2018
Shrubs	25.4 ± 4.4	Boreal lowland bog	Korrensalo <i>et al.</i> 2018
Sedges	21.6 ± 6.2	Boreal lowland bog	Korrensalo <i>et al.</i> 2018
Total	47.0 ± 7.6	Boreal lowland bog	Korrensalo <i>et al.</i> 2018
Total	220 ± 163	Southern boreal fen (wet)	Mäkiranta <i>et al.</i> 2018
Total	168 ± 79	Southern boreal fen (dry)	Mäkiranta <i>et al.</i> 2018
Total	48 ± 41	Northern boreal fen (wet)	Mäkiranta <i>et al.</i> 2018
Total	120 ± 99	Northern boreal fen (dry)	Mäkiranta <i>et al.</i> 2018
Total	1424 ± 170	Northern boreal fen	Saarinem 1996
Forest Bog	221 ± 24	Boreal forested peatland	Bhuiyan <i>et al.</i> 2017
Forest Fen	512 ± 57	Boreal forested peatland	Bhuiyan <i>et al.</i> 2017
<i>D. muscoides</i>	2000–2800	Tropical mountain peatland	This study
<i>P rigida</i>	1030–1080	Tropical mountain peatland	This study

2008). Essentially, the values that we report here mean that, on average, it takes 8–10 months for all the root biomass to be replaced which suggests high productivity and high mortality rates. As previously mentioned, the productivity and turnover rates are high if compared to other peatland ecosystems but would help to explain the fast pace at which these peatlands have accumulated carbon (Chimner & Karberg 2008, Hribljan *et al.* 2016). Of course, other factors driving peat accumulation outside the scope of the present study, including higher rates in other input terms (e.g. annual aboveground production), or lower rates in loss terms (e.g., mineralisation of peat and leaching of DOC) could also explain the high rates of peat accumulation. Future studies would be needed to parse the relative importance of root production vs. these other terms in driving peat accumulation.

Lacking the thick mats of *Sphagnum* and other mosses that contribute most of the carbon in many temperate/boreal peatlands, the cushion plant dominated peatlands of the high Andes constitute a completely different peatland system which we are just beginning to understand. A previous study in the Bolivian Andes showed that *Distichia*-dominated peatlands have one of the highest rates of above-

ground net primary production, sequestering C at 1.5–4.0 kg m<sup>-2</sup> yr<sup>-1</sup> (Cooper *et al.* 2015). Transforming our root production values to their C equivalents, based on the equation used by Cooper *et al.* (2015), belowground productivity at our sites ranges from 0.55 to 1.5 kg m<sup>-2</sup> yr<sup>-1</sup>. If we assume that our sites have similar aboveground values to those reported by Cooper *et al.* (2015), we arrive at total net productivity values (as C) between 2 and 5.5 kg m<sup>-2</sup> yr<sup>-1</sup>. This tentative estimate is conservative, because, based on the production at 50 cm and the decline of production with depth, unmeasured root production is likely to have occurred below 50 cm. Even this conservative estimate is high, and consistent with the extremely high carbon storage capacity that has been reported for these peatlands (Hribljan *et al.* 2016), but it also highlights their potential sensitivity and the need to better understand these systems in the context of current climate change.

Finally, our study suggests that páramo peatlands dominated by cushion plants might have different patterns of biomass allocation. Temperate mountain sedge peatlands had an average root production (as C) of 0.129 kg m<sup>-2</sup> yr<sup>-1</sup>, contributing ~60 % of the total NPP (Chimner & Cooper 2003). Fifty percent of the root production was found in the top 10 cm and



75 % was in the top 20 cm, although roots were found at the bottoms of the ingrowth root cores. Similarly, the C content of fine root biomass production measured in a tropical lowland forested peatland in Micronesia ranged from 0.097 to 0.161 kg m<sup>-2</sup> yr<sup>-1</sup> and 80 % of the roots were found in the top 15 cm (Chimner & Ewel 2005). This equates to roughly 10 % of the total NPP of the forested peatland. In contrast, roots at our study sites account for ~35 % of the total production. These differences in the proportion of production allocated to roots could result from intrinsic dissimilarities in morphology and allocation patterns between cushion plants, sedges and other functional groups. But they could also point to more complex patterns related to the lack of seasonality, as well as to the younger soils that predominate in the high Andes and their influence on nutrient content. These mechanisms and the resulting patterns of carbon accumulation remain unexplored in the páramo landscape, with its heterogeneous matrix of peatlands, and offers an excellent system for future studies looking at the functional ecology of high-elevation tropical peatland species. However, as noted above, the root production estimate for these species is conservative. Root production below the water table, to depths of a metre or more, has been found in other aerenchymatous cushion plants (Fritz *et al.* 2011) and sedges (Moore *et al.* 2002), so production estimates for deeper roots are needed to confirm the proportional allocation of production in these species.

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## AUTHOR CONTRIBUTIONS

Conceptualisation, methodology and data curation: ES and SCH; data analysis: ES, RCH and EL; project administration: SCH; funding acquisition and writing

(original draft): ES; writing (review and editing): ES, SCH, RCH, EL.

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