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Andean grasslands are as productive as tropical cloud forests

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Abstract

We aim to assess net primary productivity (NPP) and carbon cycling in Andean tropical alpine grasslands (puna) and compare it with NPP of tropical montane cloud forests. We ask the following questions: (1) how do NPP and soil respiration of grasslands vary over the seasonal cycle? (2) how do burning and grazing affect puna productivity? (3) if the montane forest expands into the puna, what will be the resulting change in productivity? The study sites are located at the South-eastern Peruvian Andes; one grassland site and the forest sites are in Wayqecha biological station, and another grassland site in Manu National Park. At each grassland site, we selected a burnt and an unburnt area, installed unfenced and fenced transects in each area, and monitored above-ground productivity (NPP_{AG}), below-ground productivity (NPP_{BG}) and soil respiration (R_s) for 2 yr. In the forest, we monitored NPP_{AG} , NPP_{BG} and R_s for 2–4 yr. Grassland NPP varied between 4.6 ± 0.25 (disturbed areas) to 15.3 ± 0.9 $Mg\ C\ ha^{-1}\ yr^{-1}$ (undisturbed areas) and cloud forest NPP was between 7.05 ± 0.39 and 8.0 ± 0.47 $Mg\ C\ ha^{-1}\ yr^{-1}$, while soil carbon stocks were in the range of 126 ± 22 to 285 ± 31 $Mg\ C\ ha^{-1}$. There were no significant differences on NPP between the puna and forest sites. The most undisturbed site had significantly higher NPP than other grassland sites, but no differences were found when relating grazing and fire at other sites. There were lower residence times of above-ground biomass compared to below-ground biomass. There was a strong seasonal signal on grassland NPP_{AG} and NPP_{BG} , with a shift on allocation at the beginning of the austral summer. High elevation tropical grasslands can be as productive as adjacent cloud forests, but have very different carbon cycling and retention properties than cloud forests.

 Online supplementary data available from stacks.iop.org/ERL/9/115011/mmedia

Keywords: tropical alpine wetlands, above-ground productivity, below-ground productivity, fire, grazing, disturbances, puna

Introduction

Alpine grasslands in the tropical Andes extend from the treeline (around 2500–3500 m elevation) to more than 4800 m a.s.l., (Román-Cuesta *et al* 2014), occupying around 470 000 km^2 (Tovar *et al* 2013). The physiognomy of this tropical alpine vegetation varies within and between regions,



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but the different physiognomies share some features, like similar topography and similar growth forms of the dominant tussocks, usually from the genera *Calamagrostis*, *Scirpus* and *Festuca*. Another common feature is their long history of human disturbance. The tropical Andes have been inhabited since prehistorical times (Chepstow-Lusty *et al* 1996), and its tropical alpine grasslands have been extensively used for agriculture and grazing (Sarmiento and Frolich 2002, Bustamante 2006, Bustamante and Bitencourt 2007). Some authors have defined these landscapes as cultural landscapes rather than natural in most of the alpine treeline (Laegaard 1992). Over the last decades, however, human activities in these highland ecosystems have increased and intensified drastically (e.g. Buytaert *et al* 2011, Farley *et al* 2013, Lutz *et al* 2013). These grasslands are increasingly used for intensive cattle grazing, afforestation with exotic species, cultivation and human occupation (Buytaert *et al* 2006). In addition to the increasing direct human pressures, climate change is also expected to significantly alter the composition and function of Andean ecosystems. There has been a mean increase in temperature of 0.15 °C per decade over the period 1950–1994 (Vuille *et al* 2003). Climate projections for the tropical Andes predict an increase between 4 and 5.5 °C temperature increase by 2100 (A2-B2 scenarios, Urrutia and Vuille 2009). Andean tropical montane cloud forest (TMCF) plant species may migrate upslope in response to future climate warming (Feeley *et al* 2011), but land-use on the highland grasslands could hamper species and whole-biome migration and favour large population declines in the area (Feeley and Silman 2010). However, if conservation strategies promoting upward migration of forest tree species were successful, Andean grasslands would still be threaded by a progressive encroachment of montane forest tree species.

Forest–grassland ecotones are particularly fascinating ecological natural laboratories, with a number of ecological questions directly challenging the current state of modern ecology and their vulnerability to global change. Despite the increasing number of studies looking at the stability of these systems (e.g. Urrego *et al* 2011, Lutz *et al* 2013), there have been few efforts comparing the adjacent forests and grasslands, either in the Andes (Zimmermann *et al* 2010, Gibbon *et al* 2010), or elsewhere (Reich *et al* 2001). A suite of recent studies have described in detail the carbon cycle of Andean montane cloud forests (Girardin *et al* 2010, 2013, Huaraca Huasco *et al* 2014), including woody, canopy and fine root productivity. However, there are very few studies addressing productivity of Andean grasslands (Ramsay 1992, Carilla *et al* 2011). Andean grasslands, like other natural grasslands, play a significant but poorly recognized role in the global carbon cycle, having been omitted from major grasslands studies (for example Lieth 1978, Parton *et al* 1993, 1995, Scurlock and Hall 1998, Scurlock *et al* 2002, FAO 2005). However some recent studies have highlighted their importance in terms of carbon storage (Ramsay and Oxley 2001, Piñeiro *et al* 2009a, Zimmermann *et al* 2010, Gibbon *et al* 2010).

Here we present the first systematic study of above- and below-ground net primary productivity (NPP) in tropical

alpine grasslands (hereafter referred to as *puna*), and compare it to NPP of two nearby TMCFs. We ask the following questions: (1) how do the components of NPP and soil respiration of these high-elevation grasslands vary over the seasonal cycle? (2) if anthropogenic changes continue, what will be the resulting change in productivity? (3) if the montane forest expands into the puna, what will be the resulting change in productivity?

Material and methods

Site description

The study was carried out in two puna and two TMCF sites in the South-eastern Peruvian Andes. The first puna site was located at approximately 3085 m a.s.l. in Wayqecha Biological Station (W, 13°18'S, 71°58'W), in the South-western buffer area of Manu National Park (MNP) (figure 1). The second puna site was located in Acjanaco (A, 13°17'S, 71°63'W), at approximately 3450 m a.s.l., inside the Southern extent of the Western border of MNP (a world heritage site, figure 1). The TMCF sites were located near the Wayqecha Biological Station, at Esperanza (ESP, 13°11'S, 71°35'W, 2825 m a.s.l.) and Wayqecha (WAY-01, 13°11'S, 71°35'W, 3025 m a.s.l.). Both forest plots were located near the upper limit of the cloud forest treeline, where the forest makes a sharp transition to puna vegetation.

In Wayqecha, main annual rainfall was ca. 1560 mm, with a dry season from May to August/September (figure S1). Mean annual air temperature was ca. 11.8 °C, with <5 °C diurnal and season variation around this mean (Girardin *et al* 2013). In Acjanaco, mean annual rainfall was ca. 760 mm, also with a dry season from May to August/September (figure S1). Mean annual air temperature was ca. 6.8 °C with less than 2 °C diurnal and seasonal variation (figure S1).

A more detailed site description and local meteorology is provided in supplementary information (SI) and figure S1, available at stacks.iop.org/ERL/9/115011/mmedia.

Experimental set up

At each puna site, a burnt and an unburnt area were selected. In the Acjanaco site (Site A), the burnt area was located near to the outer limits of the park where it is delimited by the path that stopped the spread of a fire in 2005. Before the 2005 fire, the area had not been burnt since the mid-70s. The unburnt area was located within the park boundaries. In the Wayqecha site (Site W), the burnt area had burnt in 2003, and we do not have information about the disturbance history before 2003. The burnt areas in both sites were at approximately 20 m from the TMCF timberline, but the unburnt sites were at least 200 m from the treeline.

At each puna area, we set up four transects of 30 m, and in each transect eight 2×2 m plots were delineated. Two transects were fenced to exclude any grazing activity, and the two other transects were left unfenced. Site W unfenced areas

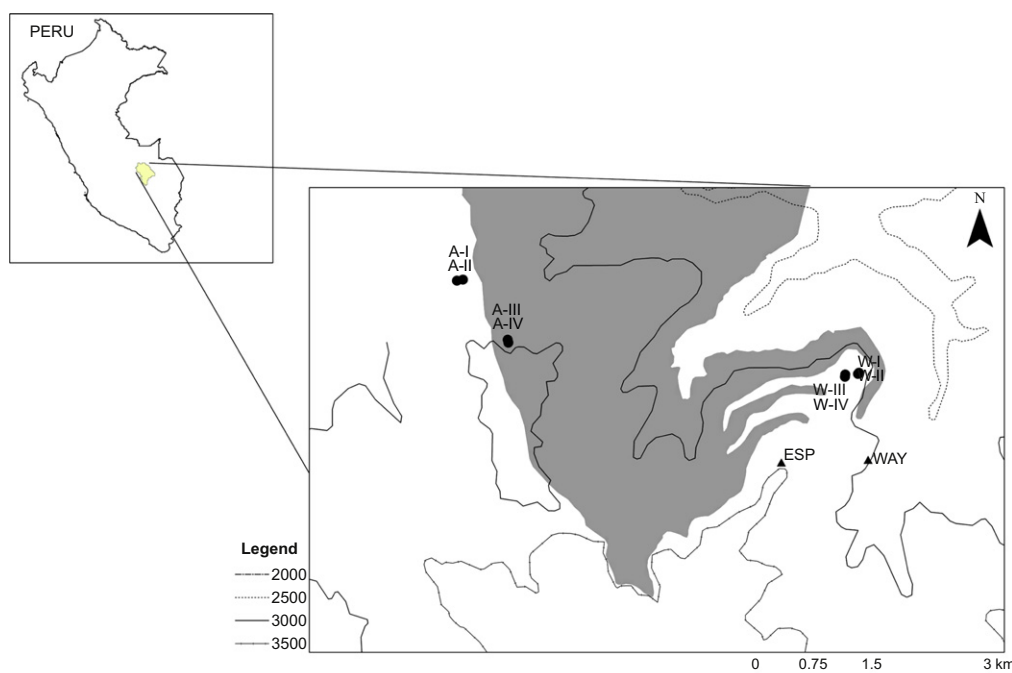


Figure 1. Localization of the puna plots (A-I, A-II, A-III, A-IV in Acjanaco, W-I, W-II, W-III, W-IV in Wayqecha, table 1) and the forest plots (ESP: Esperanza, WAY: Wayqecha). The shaded area corresponds to Manu National Park.

Table 1. Description of the study areas and most common species (on a basal area basis) at each site. Numbers in brackets indicate percentage contribution to the total basal area of the site. Fire indicates the date of last fire, and grazing indicates grazing pressure.

Area	Site	Fire	Grazing	Species (% of total BA in the area)
A-I	A	2005	Low	<i>Calamagrostis longearistata</i> (74); <i>Festuca dolichophylla</i> (12); <i>Scirpus rigidus</i> (9); 6 spp (5)
A-II	A	2005	No	<i>Calamagrostis longearistata</i> (65); <i>Festuca dolichophylla</i> (14); <i>Scirpus rigidus</i> (13); <i>Juncus bufonius</i> (2); 6 pp (5)
A-III	A	No	Low	<i>Calamagrostis longearistata</i> (57); <i>Scirpus rigidus</i> (20); <i>Cortaderia jubata</i> (11); <i>Disterigma pernettyoides</i> (4); <i>Luzula racemosa</i> (3); <i>Festuca dolichophylla</i> (2); 6 spp (3)
A-IV	A	No	No	<i>Calamagrostis longearistata</i> (62); <i>Luzula racemosa</i> (11); <i>Juncus bufonius</i> (10); <i>Festuca dolichophylla</i> (8); <i>Scirpus rigidus</i> (8); 5 spp (1)
W-I	Way	2003	Moderate	<i>Ageratina cuscoensis</i> (33); <i>Calamagrostis longearistata</i> (21); <i>Scirpus rigidus</i> (17); <i>Halenia weddelliana</i> (11); <i>Festuca dolichophylla</i> (5); <i>Hesperomeles spp</i> (3); <i>Werneria nubigena</i> (2); <i>Senecio burkatii</i> (1); 7 spp (7)
W-II	Way	2003	No	<i>Calamagrostis longearistata</i> (50); <i>Ageratina cuscoensis</i> (22); <i>Scirpus rigidus</i> (16); <i>Festuca dolichophylla</i> (8), <i>Halenia weddelliana</i> (2); 2 spp (2)
W-III	Way	No	Moderate	<i>Ageratina cuscoensis</i> (47); <i>Calamagrostis longearistata</i> (30); <i>Scirpus rigidus</i> (14); <i>Vaccinium floribundum</i> (4); <i>Festuca dolichophylla</i> (2); 5 spp (3)
W-IV	Way	No	No	<i>Ageratina cuscoensis</i> (48); <i>Calamagrostis longearistata</i> (54); <i>Scirpus rigidus</i> (17); <i>Festuca dolichophylla</i> (4); <i>Werneria nubigena</i> (2); 5 spp (5)
WAY	Way 3025 m	No	No	<i>Weinmannia crassifolia</i> (27); <i>Clusia flaviflora</i> (13); <i>Clusia alata</i> (11); <i>Clethra cuneata</i> (6); <i>Weinmannia bangii</i> (5); <i>Weinmannia reticulata</i> (5); <i>Hesperomeles ferruginea</i> (5); <i>Prunus integrifolia</i> (4)
ESP	Esp 2028 m	No	No	<i>Weinmannia bangii</i> (35); <i>Clusia trochiformis</i> (17); <i>Prunus integrifolia</i> (9.2); <i>Meliosma frondosa</i> (4); <i>Weinmannia crassifolia</i> (4), <i>Myrsine coriacea</i> (4), <i>Symplocos reflexa</i> (3)

were classified as *Moderate grazing*, and Site A unfenced areas as *Low grazing* intensity. Both fenced Site A and W areas were classified as *No grazing* (table 1). Data were collected between August 2010 and October 2012.

The forest plots are 1 ha plots, divided in twenty 20 × 20 m subplots. The methods for collecting data from the forest sites on biomass, productivity and respiration components are described in detail in Girardin et al (2013). Data

from the TMCF plots were collected between 2007 (WAY-01) or 2009 (ESP-01) and December 2011.

Above-ground productivity (NPP_{AG})

In the puna sites, each plot was divided in 0.25 m² sub-plots and, every two months, all above ground biomass in one sub-plot was clipped and oven dried to dry weight. NPP_{AG} was

calculated as the amount of dry biomass produced between harvesting periods. The amount of dead biomass between sampling periods was negligible. Similarly, the amount of litterfall production in these systems is negligible, as most of the dead material remains attached to the tussocks (Oliveras *et al* 2014). C content was considered to be 50% following previous studies in the area (Gibbon *et al* 2010, Oliveras *et al* 2014).

In the forest sites, all major components of NPP_{AG} were measured as described in Girardin *et al* (2013). However, several components NPP_{AG} were only measured on an annual basis. As a result, our estimates of NPP_{AG} seasonality are based on equation (1) and our estimates of annual NPP_{AG} were based on equation (2):

$$NPP_{AG,seasonal} = NPP_{ACW \geq 10} + NPP_{canopy}, \quad (1)$$

$$NPP_{AG} = NPP_{ACW \geq 10} + NPP_{ACW < 10} + NPP_{canopy} + NPP_{CWD}, \quad (2)$$

$NPP_{ACW > 10}$ is the productivity of above-ground coarse wood for trees with a diameter at base height above or equal to 10 cm (measured every three months), $NPP_{ACW < 10}$ is the productivity of above-ground coarse wood for trees with a diameter at base height between 2.5 and 10 cm (measured once a year), NPP_{canopy} is litterfall measured from the leaves, flowers, fruits and twigs collected in litterfall traps every two weeks plus the proportion of litterfall lost to herbivory (estimated on an annual timescale) and NPP_{CWD} is the productivity of coarse woody debris, measured every three months.

Below-ground productivity (NPP_{BG})

Below-ground fine root productivity was determined using the ingrowth core technique (Vogt *et al* 1998), following the methodology described by Metcalfe *et al* (2007), that provides estimates of root production per unit area and time ($Mg\ ha^{-1}\ yr^{-1}$). These were 30 cm depth cores of root-free soil surrounded by mesh bags in which roots were allowed to grow over a set period of time (two months for puna and three months for forest sites). Fine roots were manually removed using a method that corrects for underestimation of fine root biomass (Girardin *et al* 2010). Sampled roots were rinsed in water to remove soil particles, oven dried at 70 °C in the lab until constant weight.

In the puna sites, four ingrowth cores were installed in the plots in August 2010 and sampled every two months, while twenty ingrowth cores were installed in the TCMFs sites in May 2007 and were measured every three months. No fine root stock data are available for ESP.

Soil respiration

Measurements of soil CO_2 efflux (R_s) were made using an Infra-red Gas Analyser (EGM-4 and SRC-1 chamber, PP Systems, Hitchin, 155 UK), following Metcalfe *et al* (2007). Two months prior to the initiation of the measurements plastic collars were inserted into the soil at each measurement

location, to a depth of approximately 2 cm, to ensure a good seal between the IRGA chamber and soil. At all R_s measurement locations, instantaneous measurements of volumetric soil moisture (CS616 probe, Campbell Scientific, Loughborough, UK) and soil temperature (Testo 926 probe, Testo, Hampshire, UK) were taken at a soil depth of 0.3 m.

In the puna sites, measurements were made every two months at 4 points per transect, over the period 2010–2012. In TCMF sites, soil respiration was monitored through monthly measurements of total soil respiration in 25 regularly spaced permanent collars in each plot, over the period 2007–2011 (WAY) and 2009–2011 (ESP) as described in Girardin *et al* (2013).

Soil carbon stocks

At each transect of the puna sites, we took three soil samples at 0–30 cm depth. Each sample was processed following the methodology of Zimmermann *et al* (2010). Each sample was oven dried at 60 °C to constant mass, and the dry mass was quantified. The samples were crushed and sieved to 2 mm to remove stones, and measured again to quantify the soil bulk density (i.e. the stone-free dry weights divided by the sampling volumes corrected for the stone volume. A sub-sample was ground and analysed for C with a Carlo Erba Elemental Analyser (Milano, Italy) at the University of Saint Andrews (UK). Soil C stocks were calculated according to the soil densities and SOC stocks of the whole profile averaged to site values. In the TCMF sites, soil carbon stocks were estimated using soil cores to 67 cm depth and analysed following Quesada *et al* (2011) (CA Quesada, personal communication 20 September 2013).

Total NPP

In the puna sites, we considered total NPP (NPP) as the sum of the above-ground and below-ground biomass.

Residence times (Tr)

Above- and below-ground residence times were estimated by dividing the biomass stock by the rate of production: this assumes that the biomass stock is in approximate equilibrium, and not substantially aggrading or degrading. Above-ground residence in the forest plots accounted for leaves only.

Data analysis

Differences between areas were analysed using one-way ANOVA and TukeyHSD post-hoc tests (Sokal and Rohlf 1995), after testing for normality and homogeneity of variances. Seasonal differences and differences between areas in NPP_{AG} , NPP_{BG} , NPP_{Total} and R_s were explored through repeated-measures ANOVA using the *ezANOVA* function on R.3.0.2 (R Development Core Team 2013).

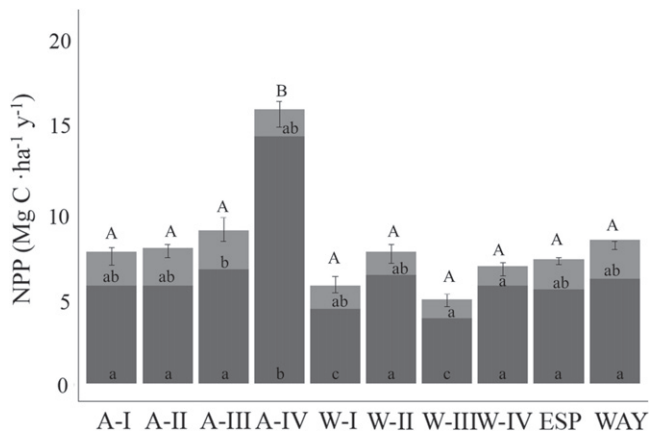


Figure 2. Annual net primary productivity (NPP) in the studied puna (A, W) and forest sites (WAY, ESP). Dark grey bars represent NPP_{AG}, light grey bars indicate NPP_{BG}. I and II are burnt plots (III and IV are unburnt plots), I and III indicate grazed plots (II and IV are ungrazed plots). Refer to table 1 for further details. Letters inside the boxes indicate significant differences between areas for each NPP type; capital letters indicate significant differences on total NPP between areas.

Results

Productivity

Annual productivity. Total NPP_{AG} was higher in the Acjanaco sites ($7.8 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) than in the Wayqecha sites ($4.9 \pm 0.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, $P < 0.001$, figures 2 and S2). Total annual NPP_{AG} was highest in the undisturbed area A-IV and lowest in the moderately grazed areas W-I and W-III, (figure 2, table S1). The forest sites had, on average, a slightly lower NPP_{AG} than the puna sites ($5.6 \pm 0.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ versus $6.3 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for forest and puna sites, respectively) but the difference was not significant ($P = 0.52$).

NPP_{BG} varied within the range of $1.3\text{--}2.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (figure 2, table S1), being significantly higher in Acjanaco than in Wayqecha (3.8 ± 0.4 and 2.4 ± 0.2 respectively, $P < 0.001$, table S1). NPP_{BG} was significantly lower in the W-III and W-IV areas ($P < 0.001$). NPP_{BG} averaged $1.42 \pm 0.41 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in the TMCF sites, with no significant differences between puna and forest sites.

Total average annual puna NPP at Acjanaco ($9.6 \pm 1.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) was significantly higher than NPP at Wayqecha ($5.9 \pm 0.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, $P < 0.001$, figure 2), although only the undisturbed area A-IV, was significantly higher than any of the other areas ($P < 0.001$, table S1, figure 2). There were no significant differences on NPP between the puna and forest sites (averaging $7.54 \pm 0.61 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ between the two plots, $P = 0.075$).

Seasonal patterns. There were significant seasonal patterns in puna NPP_{AG} ($P < 0.001$), NPP_{BG} ($P < 0.001$), NPP ($P < 0.001$) and R_s ($P < 0.001$, figure 4). All puna areas followed the same seasonal pattern with a peak of NPP_{AG} at the beginning of the rainy season (October), followed by a

shift in allocation from NPP_{AG} to NPP_{BG}. NPP followed a similar seasonal pattern as NPP_{AG}, and contributed to more than 60% of NPP for most part of the year. However, NPP_{BG} contributed to 50–80% of NPP at the beginning of the rainy season. The undisturbed A-IV area consistently had the highest NPP_{AG} and the lowest NPP_{BG} throughout the year (figure S2). The A site had more NPP_{AG} than the W site throughout the year, but the difference between puna sites was larger from July to October (figure 3), whilst the largest difference in NPP_{BG} was from January to May (figure 3), resulting on higher NPP in the A site throughout the year (figure 3).

Seasonality in the forest sites was less marked than in the puna sites (figure 3). Both forest sites showed an increase in NPP_{AG} at the end of the dry season (September–October, figure 3), followed by a shift in allocation from above- to below-ground onset of the rainy season (November–December). The proportional allocation of total NPP to above-ground components was highest (80%) at the onset of the dry season (May, figure 3).

Stocks

In the puna sites, the total average above-ground (AG C) and below-ground carbon stocks (BG C) were $3.7 \pm 2.1 \text{ Mg C ha}^{-1}$ and $2.8 \pm 0.2 \text{ Mg C ha}^{-1}$ respectively. All areas had similar AG C stocks ($3.4 \pm 0.1 \text{ Mg C ha}^{-1}$ on average) excepting the undisturbed area A-IV, which had the highest AG C stocks ($5.9 \pm 0.5 \text{ Mg C ha}^{-1}$), followed by the unburnt, low-intensity grazed area A-III ($P < 0.001$, figure 4, table S1). The burnt areas in A (A-I and A-II) had lower AG C stocks than the unburnt A areas (table S1). As would be expected, the forest sites had much higher AG C stocks because of their woody component, averaging $75.6 \text{ Mg C ha}^{-1}$ over the two plots (figure 3, Girardin *et al* 2013).

Average puna BG C stocks were estimated at $2.8 \pm 0.2 \text{ Mg C ha}^{-1}$, slightly lower than AG C stocks ($3.8 \pm 1.0 \text{ Mg C ha}^{-1}$), and forest BG C were estimated at $7.24 \text{ Mg C ha}^{-1}$ (WAY-01), over a soil depth of 0–30 cm.

The average puna soil C stock in the Acjanaco sites ($253 \pm 25 \text{ Mg C ha}^{-1}$) was significantly higher than puna soil C stock for the Wayqecha sites ($P < 0.001$, table S1). A-II and A-IV were the areas with the highest soil C stocks (figure 3), and W-I and W-IV the areas with the lowest C stocks.

Soil respiration

Total R_s in the A puna sites was significantly lower than in W sites ($3.4 \pm 0.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ versus $3.7 \pm 0.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, $P < 0.001$, table S1), but lower R_s rates occurred from March to July only (figure 3). There were also significant differences on R_s between the puna areas ($P < 0.001$), with R_s at A-I, A-III and W-IV being significantly lower than in the other puna areas (table S1, figure S2). The forest sites had significantly higher R_s than the puna sites ($P < 0.001$, figure 3, table S1).

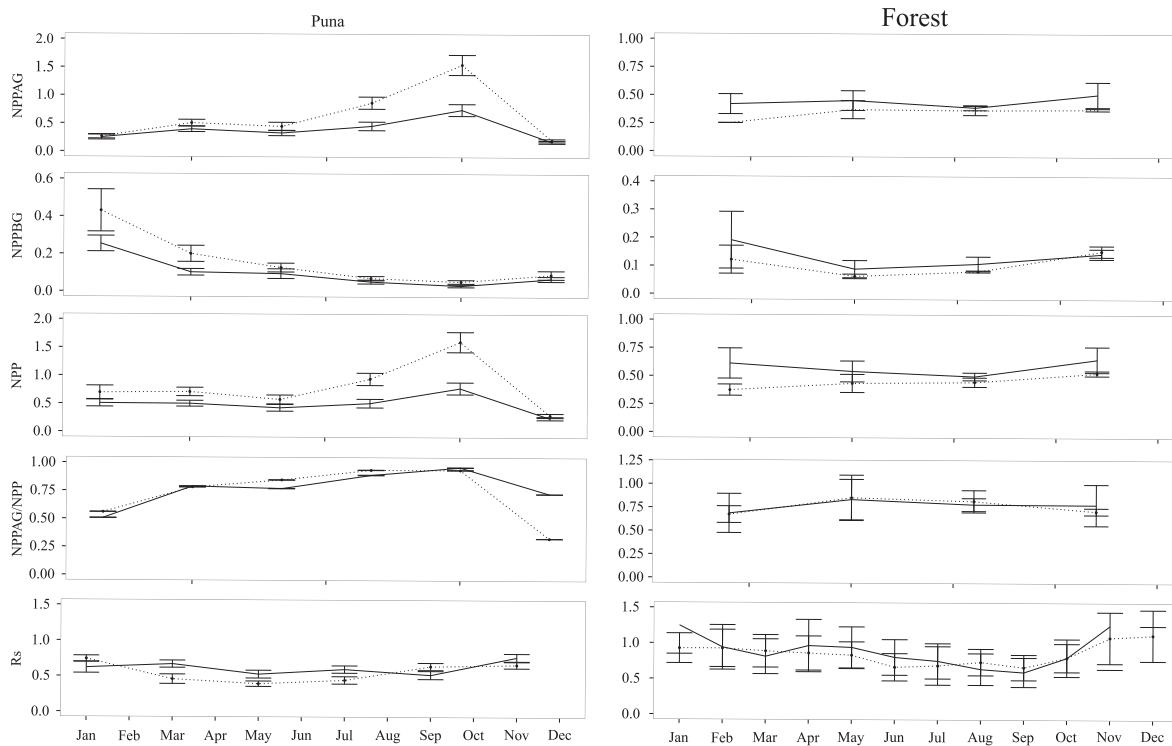


Figure 3. Seasonal variation in above-ground productivity (NPP_{AG}), below-ground productivity (NPP_{BG}), total net primary productivity (NPP), the above ground NPP fraction NPP_{AG}/NPP , and soil respiration (R_s) in the puna (left panels, dashed line Wayqecha site, solid line Acjanaco site) and in the forest (right panels, dashed line Wayqecha, solid line Esperanza). Error bars indicate standard errors. Values are expressed in $Mg\ C\ ha^{-1}\ month^{-1}$. Please note that graphs scales are different.

Residence time

In the puna the residence times of the AG C stocks (T_{rag}) varied between approximately six months and 1 yr (table 2), but differences between puna areas were not significant ($P=0.250$). Residence times of leaves in the forest plots was significantly higher than for puna sites ($P<0.001$), varying between 2 and 3 yr.

Residence times of BG C stocks (T_{rbg}) were significantly higher than T_{rag} ($P=0.0014$), and varied between 1 and 2.8 yr (table 2). T_{rbg} in the A site was significantly lower than W site ($P<0.001$), with A-IV having the lowest T_{rbg} and W-III and W-IV the highest.

Discussion

Previous studies on the productivity of tropical alpine Andean grasslands are scarce, and have only provided above-ground values of NPP for puna/páramo grasslands (Ramsay 1992, Hofstede *et al* 1995, Ramsay and Oxley 2001). This is the first study to provide a comprehensive description of above- and below-ground productivity in the tropical alpine Andean grasslands, and to show that they behave as extremely dynamic ecosystems with productivity rates comparable to those of their neighbouring montane forests (question 3). NPP is dominated by above-ground productivity, and there is a marked seasonal shift in carbon allocation (question 1). We also found that undisturbed sites were more productive than

disturbed sites, although we did not find a strong effect of fire and grazing over NPP (question 2) and the disturbed sites may have lost some above-ground biomass though grazing.

There is a seasonal shift in above-ground and below-ground carbon allocation, and seasonal patterns on soil respiration

Grasslands and savannas are known to be highly productive systems (Scurlock and Hall 1998, Grace *et al* 2006). In our study region, our results corroborate previous findings by showing high NPP_{AG} productivity rates: Ramsay (1992) and Ramsay and Oxley (2001) reported 4.0 and 5.12 $Mg\ C\ ha^{-1}\ yr^{-1}$ in páramo fields above 3750 m a.s.l. respectively, which is within the range of the values reported in this study. In terms of different components of NPP, we found much higher NPP_{AG} compared to NPP_{BG} , likewise most other grassland types worldwide (Scurlock *et al* 2002, Grace *et al* 2006).

In the puna sites we found a shift in carbon allocation from above-ground to below-ground at the end of the austral spring (November). Maximum NPP_{AG} occurred at the end of the austral winter (September), while other studies in NW Argentina have found peaks of mountain grassland productivity during the summer months (Carilla *et al* 2011). During the austral winter, the study area receives the highest radiation rates of the year (figure S1) and it records the maximum intra-diurnal variability in radiation (Rapp and Silman 2012). High radiation rates and first rains in September may stimulate the flush of new leaves on tussocks.

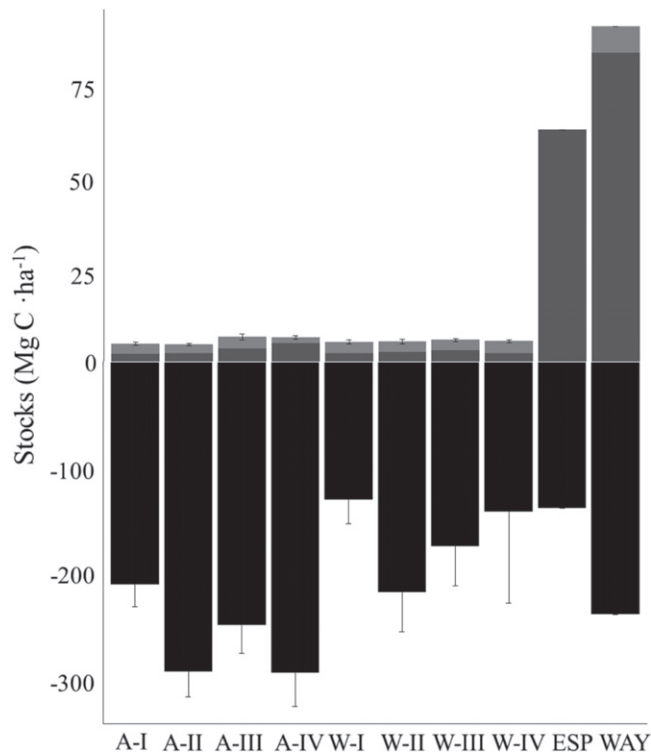


Figure 4. Above-ground carbon (dark grey), below-ground carbon (light grey) and soil carbon (black) stocks in the studied puna (A, W) and forest sites (WAY, ESP). I and II are burnt plots (III and IV are unburnt plots), I and III indicate grazed plots (II and IV are ungrazed plots). Refer to table 1 for further details. Error bars represent standard error. Graph scaling between above-ground and below-ground stocks is different.

Table 2. Residence times of above-ground and below ground carbon stocks in years. T_{rag} = residence time of above-ground biomass (in puna) and leaves (in forest sites), T_{rbg} = residence time of below-ground biomass.

Area	T_{rag}	T_{rbg}
A-I	0.55 ± 0.04	1.50 ± 0.29
A-II	0.56 ± 0.04	1.14 ± 0.15
A-III	0.71 ± 0.10	1.44 ± 0.26
A-IV	0.42 ± 0.04	1.05 ± 0.18
W-I	0.74 ± 0.08	2.43 ± 0.45
W-II	0.56 ± 0.05	2.30 ± 0.45
W-III	1.05 ± 0.10	2.85 ± 0.36
W-IV	0.57 ± 0.03	2.84 ± 0.41
ESP	1.96 ± 0.23	—
WAY	2.52 ± 0.18	3.78 ± 0.81

Once the new leaves are grown and productive, the tussocks appear to invest more in the production of new roots. We find little seasonality in NPP_{AG} in the forest plots. This may be explained by a seasonal shift in allocation from leaf production to woody production during the dry to wet seasonal transition. NPP_{ACW} increases as NPP_{canopy} decreases, resulting in little seasonality of the sum of above-ground components. Individually, each above-ground component shows evidence of seasonality in NPP (Girardin *et al* in press). For

soil respiration, in contrast, there was moderate seasonality in the forest but little seasonality in the puna. In the forest sites soil respiration seasonality is primarily driven by heterotrophic respiration (Heinemeyer *et al* 2007, Zimmermann *et al* 2009, Girardin *et al* 2013). The increase in heterotrophic respiration during the rainy season in forests (Girardin *et al* 2013) may be explained by higher litterfall incidence and accumulation of litterfall material on the dry season, which is then decomposed during the rainy season. Conversely, autotrophic respiration remains fairly constant throughout the year (Girardin *et al* 2013). The lack of seasonality in soil respiration in the puna may be explained by the fact that litterfall is negligible, as all dead material remains attached to the tussocks and either accumulates or decays *in situ* (Ramsay 1992, Oliveras *et al* 2014). This results in less seasonal input of fresh material for heterotrophic soil respiration.

Residence times in below-ground biomass in the puna was twice as long as those for above-ground biomass. These grassland soils are partly waterlogged, which would contribute to longer residence time than forest roots residence time, by slowing root mineral uptake (Girardin *et al* 2010, Wang *et al* 2013). Soil carbon stocks in the puna are in the same range (137 ± 84 to 285 ± 31 Mg C ha⁻¹) as soil carbon stocks in the forest (133.9 – 231 Mg C ha⁻¹), as has been previously reported by Zimmermann *et al* (2010). These grassland soils receive abundant inputs of belowground organic matter from grass roots, while humid and cold conditions lead to slow rates of decomposition, thus promoting high soil carbon storage as has been reported by other studies (Luteyn *et al* 1992, Hofstede *et al* 1995, Zimmermann *et al* 2010, Gibbon *et al* 2010, Muñoz *et al* 2013). As such, these grasslands constitute a valuable terrestrial carbon store and possible sink, and may play an important role in the context of global climate change (Buytaert *et al* 2011).

Undisturbed grasslands are more productive than disturbed grasslands

This study shows that the most undisturbed area (A-IV) had the highest NPP, driven by NPP_{AG} . Some authors have reported that grazing increases productivity, as biomass removal can induce compensatory growth (Körner *et al* 2006), but this had not been studied in tropical alpine grasslands and has been questioned by some other authors (Belsky 1986). Our study did not account for the quantity of biomass removed by grazing in the grazed sites and therefore cannot provide any conclusions about differences in NPP_{AG} between grazed and ungrazed sites. However, our results show that grazing increases NPP_{BG} , perhaps because the grasses allocate more below-ground to get enough carbohydrates and nutrients stored to be able to reshoot faster after aerial removal. Garcia-Pausas *et al* (2011) reported an increase on below-ground productivity with grazing exclusion in the Pyrenees mountains, but different results may be related to the different grasslands and species studied.

Apart from differences for the undisturbed site A-IV, we did not find differences between burnt/unburnt areas or grazed/ungrazed areas, similarly to what other studies in

tropical alpine Andean grasslands have reported. For example, Hofstede *et al* (1995) found that the main effects of burning and grazing on Andean grassland soils were in physical characteristics, while burning itself did not have an effect, either positive or negative, on soil nutrient content. Similarly, Suárez and Medina (2001) did not find significant differences in soil organic matter between burnt and unburnt grasslands soils. This lack of response, however, does not imply that fire and grazing do not alter soil carbon, but perhaps their effects are masked by a long disturbance history and different levels of disturbance frequency and intensity across the tropical alpine Andean grasslands (Piñeiro *et al* 2009b).

Puna and tropical montane forest ecosystems are equally productive

One of the most remarkable findings of this study was that grasslands of the high Andes were as productive as adjacent tropical montane forests. Despite the significantly lower standing biomass stocks in puna grasslands, NPP_{AG} of undisturbed puna sites was equal or exceeded that of the forest sites. This indicates how remarkably productive puna grasslands are, with important implications for our understanding of how these still poorly studied ecosystems function, and of the dynamics of the transition between puna and forest. Several studies have investigated montane treeline dynamics in recent years (Körner 2012). Lutz *et al* (2013) demonstrated that there has been little movement of the treeline in this study region over the last 50 yr, despite a warming climate (Lutz *et al* 2013). They propose several explanations for the unexpected resilience of grasslands to invasion by montane forest vegetation, including high metabolic maintenance costs in high elevation trees (van Oijen *et al* 2010, Marthens *et al* 2012), lack of mycorrhizal associations, increased fire incidence (Lutz *et al* 2013), and tree seedling competition for light in a dense grassland canopy (Rehm and Feeley 2013). The highly competitive production rates of grassland species that we demonstrate here is an indication of the difficulty of tree invasion of grasslands. Grassland species competitiveness for light and nutrients may exceed that of tree seedlings. The low success rate of tree seedling establishment in the puna of our study region was recently demonstrated by Rehm and Feeley (2013). Nonetheless, this conclusion would require further testing and validation along the Andean treeline. Understanding the dynamics of treeline ecology (the ‘grass ceiling’—Rehm and Feeley 2013) becomes particularly important when we consider that montane forest species are likely to face increased pressure for upslope migration in the face of a rapidly changing climate (Feeley *et al* 2012, Tovar *et al* 2013). Another feature to note is that both puna grass species and tree species utilize the C3 synthesis pathway, and are likely to benefit similarly from rising atmospheric CO₂ concentrations. This contrasts with the tropical lowland forest–grassland transition, where C3 trees may benefit disproportionately over C4 grasses under higher CO₂, an explanation that has been

invoked to explain the woody encroachment of savannas observed in much of Africa (Mitchard *et al* 2011).

Concluding remarks

Here we show the importance of tropical alpine Andean grasslands in terms of soil carbon stocks and productivity, which is comparable with their neighbouring cloud forests. There were no significant differences in NPP or soil carbon stocks between grasslands and forests. We also found that the most undisturbed grassland site had higher NPP than the other grasslands sites, but the differences were not due to grazing or burning.

Although these results are from two study areas in the southern Peruvian Andes, they are in accordance with studies being published in other parts of the tropical Andes, and provide a starting point for further investigation of the relationship between disturbances and carbon storage, as well as for the ecological implications of such productive systems on the grassland to forest transition dynamics.

These grasslands are under potential threat because, over the next few decades, they will experience a greater warming effect than their surrounding tropical lowlands, driven by an increase on temperatures and a decrease in humidity (Urrutia and Vuille 2009). This will have immediate effects on soil respiration rates (Muñoz *et al* 2013), species migrations (Feeley *et al* 2012), carbon storage and water provision (Buytaert *et al* 2011). Furthermore, management practices that favour afforestation with alien species like *Eucalyptus* and *Pinus* may have devastating consequences for these ecosystems (Farley *et al* 2013). If conservation policies do not invest on the conservation of these high-altitude grasslands, including recognizing their significant role as a ‘hidden’ carbon reservoir, these areas will increasingly will be degraded as a consequence of climate change and human practices. There is an urgent need to better understand the carbon and water ecosystem services (Buytaert *et al* 2011, Muñoz *et al* 2013) provided by high elevation grasslands, and establish effective soil protection actions.

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