Andean grasslands are as productive as tropical cloud forests

To cite this article: I Oliveras et al 2014 Environ. Res. Lett. 9 115011

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Received 3 June 2014, revised 3 November 2014
Accepted for publication 4 November 2014
Published 20 November 2014

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 (NPPAG), below-ground productivity (NPPBG) and soil respiration ($R_s$) for 2 yr. In the forest, we monitored NPPAG, NPPBG 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 NPPAG and NPPBG, 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.

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

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

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,
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 (Læggaard 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 up slope 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 x 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
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.

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      | Calamagrostis longearistata (74); Festuca dolichophylla (12); Scirpus rigidus (9); 6 spp (5)       |
| A-II | A    | 2005       | No       | Calamagrostis longearistata (65); Festuca dolichophylla (14); Scirpus rigidus (13); Juncus bufonius (2); 6 pp (5) |
| A-III| A    | No         | Low      | Calamagrostis longearistata (57); Scirpus rigidus (20); Cortaderia jubata (11); Disterigma pernothoides (4); Luzula racemosa (3); Festuca dolichophylla (2); 6 spp (3) |
| A-IV | A    | No         | No       | Calamagrostis longearistata (62); Luzula racemosa (11); Juncus bufonius (10); Festuca dolichophylla (8); Scirpus rigidus (8); 5 spp (1) |
| W-I  | Way  | 2003       | Moderate | Ageratina cuscoenzis (33); Calamagrostis longearistata (21); Scirpus rigidus (17); Halenia weddelliana (11); Festuca dolichophylla (5); Hesperomeles spp (3); Werneria nubigena (2); Senecio burkii (1); 7 spp (7) |
| W-II | Way  | 2003       | No       | Calamagrostis longearistata (50); Ageratina cuscoenzis (22); Scirpus rigidus (16); Festuca dolichophylla (8); Halenia weddelliana (2); 2 spp (2) |
| W-III| Way  | No         | Moderate | Ageratina cuscoenzis (47); Calamagrostis longearistata (30); Scirpus rigidus (14); Vaccinium floribundum (4); Festuca dolichophylla (2); 5 spp (3) |
| W-IV | Way  | No         | No       | Ageratina cuscoenzis (48); Calamagrostis longearistata (54); Scirpus rigidus (17); Festuca dolichophylla (4); Werneria nubigena (2); 5 spp (5) |
| WAY  | 3025 m | No         | No       | Weinmannia crassifolia (27); Clusia flaviflora (13); Clusia alata (11); Clethra cuneata (6); Weinmannia bangii (5); Weinmannia reticulata (5); Hesperomeles ferruginea (5); Prunus integrifolia (4) |
| ESP  | 2028 m | No         | No       | Weinmannia bangii (35); Clusia trochoformis (17); Prunus integrifolia (9.2); Meliosma frondosa (4); Weinmannia crassifolia (4); Myrsine coriaceae (4); Symlocos reflexa (3) |

Above-ground productivity (NPP$_{AG}$)

In the puna sites, each plot was divided in 0.25 m$^2$ sub-plots and, every two months, all above ground biomass in one subplot 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\textsubscript{AG} were measured as described in Girardin et al. (2013). However, several components NPP\textsubscript{AG} were only measured on an annual basis. As a result, our estimates of NPP\textsubscript{AG} seasonality are based on equation (1) and our estimates of annual NPP\textsubscript{AG} were based on equation (2):

\[
NPP_{AG,seasonal} = NPP_{ACW>10} + NPP_{canopy},
\]

\[
NPP_{AG} = NPP_{ACW>10} + NPP_{ACW<10} + NPP_{canopy} + NPP_{CWD}.
\]

\(NPP_{ACW>10}\) 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 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\textsubscript{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\textsuperscript{-1} yr\textsuperscript{-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 TMCFs 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\textsubscript{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 TMCF 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 grounded 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 TMCF 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 (\(T_r\))

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\textsubscript{AG}, NPP\textsubscript{BG}, NPP\textsubscript{Total} and \(R_s\) were explored through repeated-measures ANOVA using the ezANOVA function on R 3.0.2 (R Development Core Team 2013).
Results

Productivity

Annual productivity. Total NPPAG was higher in the Acjanaco sites (7.8 ± 0.6 Mg ha⁻¹ yr⁻¹) than in the Wayqecha sites (4.9 ± 0.3 Mg ha⁻¹ yr⁻¹, p < 0.001, figures 2 and S2). Total annual NPPAG 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 NPPAG than the puna sites (5.6 ± 0.5 Mg ha⁻¹ yr⁻¹ versus 6.3 ± 0.6 Mg ha⁻¹ yr⁻¹) for forest and puna sites, respectively but the difference was not significant (P = 0.52).

NPPBG varied within the range of 1.3–2.2 Mg C ha⁻¹ 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). NPPBG was significantly lower in the W-III and W-IV areas (P < 0.001). NPPBG averaged 1.42 ± 0.41 Mg C ha⁻¹ yr⁻¹ in the TMCF sites, with no significant differences between puna and forest sites.

Total average annual puna NPP at Acjanaco (9.6 ± 1.1 Mg C ha⁻¹ yr⁻¹) was significantly higher than NPP at Wayqecha (5.9 ± 0.7 Mg C ha⁻¹ 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 ± 0.61 Mg C ha⁻¹ yr⁻¹ between the two plots, P = 0.075).

Seasonal patterns. There were significant seasonal patterns in puna NPPAG (P < 0.001), NPPBG (P < 0.001), NPP (P < 0.001) and Rs (P < 0.001, figure 4). All puna areas followed the same seasonal pattern with a peak of NPPAG at the beginning of the rainy season (October), followed by a shift in allocation from NPPAG to NPPBG. NPP followed a similar seasonal pattern as NPPAG, and contributed to more than 60% of NPP for most part of the year. However, NPPBG contributed to 50–80% of NPP at the beginning of the rainy season. The undisturbed A-IV area consistently had the highest NPPAG and the lowest NPPBG throughout the year (figure S2). The A site had more NPPAG 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 NPPBG 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 NPPAG 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 ± 2.1 Mg C ha⁻¹ and 2.8 ± 0.2 Mg C ha⁻¹, respectively. All areas had similar AG C stocks (3.4 ± 0.1 Mg C ha⁻¹ on average) excepting the undisturbed area A-IV, which had the highest AG C stocks (5.9 ± 0.5 Mg C ha⁻¹), followed by the burnt, 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 Mg C ha⁻¹ over the two plots (figure 3, Girardin et al. 2013).

Average puna BG C stocks were estimated at 2.8 ± 0.2 Mg C ha⁻¹, slightly lower than AG C stocks (3.8 ± 1.0 Mg C ha⁻¹), and forest BG C were estimated at 7.24 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 ± 25 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 Rs in the A puna sites was significantly lower than in W sites (3.4 ± 0.3 Mg C ha⁻¹ yr⁻¹ versus 3.7 ± 0.3 Mg C ha⁻¹ yr⁻¹, P < 0.001, table S1), but lower Rs rates occurred from March to July only (figure 3). There were also significant differences on Rs between the puna areas (P < 0.001), with Rs 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 Rs than the puna sites (P < 0.001, figure 3, table S1).
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 ($T_{rgb}$) were significantly higher than $T_{rag}$ ($P = 0.0014$), and varied between 1 and 2.8 yr (table 2). $T_{rgb}$ in the A site was significantly lower than W site ($P < 0.001$), with A-IV having the lowest $T_{rgb}$ 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 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.](image-url)
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 (Ramsey 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

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

| Area | $T_{tag}$ | $T_{tbg}$ |
|------|----------|----------|
| 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 |

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 II 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.

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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, Mathews 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 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.

Acknowledgments

This paper is a product of the ABERG research consortium. The authors wish to thank to the research assistants for field assistance, and to MNP forest rangers for allowing us to use their facilities. We also thank the Amazon Basin Conservation Association for institutional support. This material is based upon work supported by the UK Natural Environment Research Council under grant NE/G006385/1.

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