Environmental Conservation (2016) **43** (4): 397–406 © Foundation for Environmental Conservation 2016 doi:10.1017/S0376892916000199

Changes in carbon storage with land management promoted by payment for ecosystem services

THEMATIC SECTION
Forest Ecosystem Services

LEAH L. BREMER[1,2]*, KATHLEEN A. FARLEY[1], OLIVER A. CHADWICK[2] AND CAROL P. HARDEN[3]

[1]*Department of Geography, San Diego State University, San Diego, CA 92182–4493, USA,* [2]*Department of Geography, 1832 Ellison Hall, University of California, Santa Barbara, CA 93106–4060 and* [3]*Department of Geography, University of Tennessee, Knoxville, TN 37996-0925, USA*

Date submitted: 12 June 2015; Date accepted: 20 May 2016; First published online 14 July 2016

SUMMARY

Andean grasslands (*páramos*) are highly valued for their role in regional water supply as well as for their biodiversity and large soil carbon stocks. Several Payment for Ecosystem Services (PES) programmes promote either afforestation or alteration of traditional burning regimes under the assumption that these land management strategies will maximize páramo ecosystem services, including carbon storage. However, knowledge of the effects of incentivized land uses is limited. In an evaluation of how afforestation and elimination of burning affect carbon storage at a site in southern Ecuador, we found the highest above-ground biomass carbon levels at afforested sites (99.3–122.0 t C ha^{-1}), while grassland sites reached 23.9 t C ha^{-1} after 45 years of burn exclusion. Soil carbon storage from 0–20 cm was high across all sites (172.8–201.9 t C ha^{-1}), but was significantly lower with afforestation than with burn exclusion. These findings suggest that, although afforestation is generally favoured when carbon is the primary ecosystem service of interest, grasslands with infrequent burning have important potential as a land management strategy when both above-ground biomass and soil carbon are considered. These results are relevant to the development and adaptation of PES programmes focused on carbon as well as those focused on multiple ecosystem services.

Keywords: Andes, carbon, conservation, grassland, páramo, payment for ecosystem services

INTRODUCTION

Payment for Ecosystem Services (PES) approaches are increasingly advocated as a means to link ecosystem protection and human well-being. Such initiatives provide incentives to landowners to manage land for the protection or enhancement of one or more ecosystem services (Engel *et al.* 2008; Muradian *et al.* 2010). However, whether incentivized land use and management strategies will produce desired outcomes remains uncertain (Ruffo & Kareiva 2009; Naeem *et al.* 2015). Carbon (C)-focused PES projects, in particular, are rapidly growing with elevated international interest in reducing greenhouse gas emissions and increasing terrestrial C sequestration through land management (Trabucco *et al.* 2008; Farley *et al.* 2013). Efforts to enhance terrestrial C storage have primarily focused on enhancing above-ground biomass C through afforestation, reforestation and avoided deforestation (Gibbon *et al.* 2010). Although below-ground C can constitute a large fraction of total C (Lal 2004; Farley *et al.* 2013; Lal 2013), the effects of land-use change on soil C stocks are often poorly understood (Holmes *et al.* 2006; Smith *et al.* 2016). Accordingly, studies are urgently needed that illuminate the effect of land-use and management practices promoted by PES programmes on both above-ground and below-ground C.

Globally, there is a pressing need to quantify links between land management and a range of ecosystem services (Daily *et al.* 2009; Naeem *et al.* 2015). Such studies are particularly lacking in Andean grasslands (páramos), where PES projects constitute a growing approach to conservation (Wunder & Alban 2008; Farley *et al.* 2011; Bremer *et al.* 2014 *a*). In addition to rich biodiversity and importance for regional water supplies, páramo grasslands are valued for their high soil C storage, in part derived from the properties of páramo soils, predominantly Andisols, which stabilize large amounts of soil organic matter (Farley *et al.* 2004; Buytaert *et al.* 2006 *a*; Farley *et al.* 2013). Páramo soil organic C storage is particularly high due to the high organic matter inputs from páramo grassland vegetation combined with the cold and wet climate (Zehetner *et al.* 2003; Tonnejick *et al.* 2010). Given their high C storage and the fact that they are the site of many new PES programmes (Farley *et al.* 2011; Bremer *et al.* 2014 *a*), it is critical to understand the response of páramos to incentivized changes in land use and management. Furthermore, soil C must be included in such an analysis, as the majority of C in these systems is found in this poorly understood below-ground pool (Farley *et al.* 2004; Buytaert *et al.* 2006 *b*; Farley *et al.* 2013).

*Correspondence: Leah L. Bremer, present addresses: University of Hawai'i, Mānoa, Department of Botany, 3190 Maile Way, Honolulu, HI 96822, USA and The Natural Capital Project, Stanford Woods Institute for the Environment, 371 Serra Mall, Stanford, CA 94305, USA, e-mail: lbremer@stanford.edu

Supplementary material can be found online at http://dx.doi.org/10.1017/S0376892916000199

Ecosystem services projects targeting páramo grasslands in Ecuador compensate landowners for afforestation, primarily with pine, or to eliminate burning, which has traditionally been used to promote forage production for livestock. Increasing C storage is either a primary or secondary objective of many of these PES programmes (Farley *et al.* 2011; Farley *et al.* 2013). One important programme is PROFAFOR (Programa FACE de Forestación del Ecuador), the first PES programme targeting páramo grasslands, which focuses on C sequestration through afforestation with *Pinus* species and some Andean species. Second, the SocioPáramo programme (a subprogramme of the larger SocioBosque programme), sponsored by the Ecuadorian government, compensates landowners for excluding burning in páramo grasslands, with the goals of enhancing C storage, biodiversity and water provision as well as contributing to poverty alleviation (de Koning *et al.* 2011; Farley *et al.* 2011; Bremer *et al.* 2014 *b*).

While afforestation of grasslands has been used as a means to increase C sequestration in above-ground biomass, research on soil C following afforestation shows mixed outcomes, with one global synthesis finding either increases or decreases in soil C (Paul *et al.* 2002) and a more recent synthesis finding clear decreases, particularly in the case of pine (Berthrong *et al.* 2009). Mean annual precipitation and plantation age have been found to mediate effects of afforestation on soil C in some studies and to have no effect in others (Guo & Gifford 2002; Paul *et al.* 2002; Berthrong *et al.* 2009; Berthrong *et al.* 2012), making it difficult to predict outcomes for specific ecosystems. In Ecuadorian páramos, studies have found decreases, no change and regional variability in C storage with pine afforestation (Hofstede *et al.* 2002; Farley *et al.* 2004; Chacon *et al.* 2009).

The effects of fire exclusion on C storage in páramo grasslands are even less known, with the limited studies focused primarily on the effects of frequent burning and grazing rather than burn exclusion (Hofstede & Rossenaar 1995; Podwojewski *et al.* 2002), and only one study including sites with medium-term burn exclusion (Farley *et al.* 2013). Globally, fire has variable effects on soil C. It can increase, decrease or have no influence on the amount of soil C, depending on fire intensity, environmental conditions, soil properties and the degree to which organic matter is combusted during a fire (Gonzalez-Perez *et al.* 2004; Zimmermann *et al.* 2010). Frequent burning, coupled with intensive grazing, has been shown to decrease soil C in páramo grasslands (Podwojewski *et al.* 2002), but there is little evidence that burning alone influences soil C in these ecosystems (Hofstede & Rossenaar 1995; Suarez & Medina 2001; Farley *et al.* 2013). However, globally, fire frequency and fire exclusion do influence whether grass-to-shrub transitions occur, and no study has evaluated soil C outcomes of this transition in páramo grasslands. Burn exclusion in grassland ecosystems can lead to woody encroachment, with variable outcomes for the amount and distribution of soil C (Shoji *et al.* 1993; Jackson *et al.* 2002; Neff *et al.* 2009). Understanding the outcomes of these land-cover transitions has important implications for SocioPáramo and other emerging PES programmes that target C sequestration in páramo grasslands by incentivizing burn exclusion.

Improving understanding of the outcomes of páramo land use and management is critical to evaluating whether páramo PES programmes will actually increase C storage. Recent work on changes in land management and social outcomes of SocioPáramo found no identified transfer of burning and grazing to previously ungrazed areas as a result of participating in PES (Bremer *et al.* 2014 *b*). While some participants did intensify grazing in already grazed areas, no major changes in land management occurred outside of the PES study area. Accordingly, we focused on changes in C storage associated with burn exclusion (the direct land-management change promoted by SocioPáramo) and with pine plantations (the direct land-use change promoted by PROFAFOR). We addressed the question: How do afforestation and burn exclusion affect above-ground biomass and soil C storage in páramo grasslands? We quantified above- and below-ground C using a space-for-time sampling design that identified sites with similar long-term land management histories (all were previously páramo grasslands managed for grazing), but varied current land use or management.

METHODS

Study area

This research took place at the Mazar Wildlife Reserve (MWR) in Cañar province (2°33-34'S, 78°44-45'W), Ecuador. MWR is an 1800 ha forest and páramo mixed-use reserve, of which 350 ha are used for alpaca grazing (Fig. 1). Mean annual precipitation is 1326 mm based on data from 1964–2011 at the closest INAMHI (Instituto Nacional de Metrologia e Hidrologia) meteorological station (Rio Mazar Rivera; M0410; 2450 m). Precipitation in the study area was 1503 mm in 2010 (measured for one year by Fundación Cordillera Tropical).

Soils have been characterized as non-allophanic Andisols, dominated by Al-humus complexes (Poulenard *et al.* 2003). Using aerial photos and expert assistance by the 30-year owner and manager of MWR (S. White, personal communication 2010; Fig. 2), we identified six sites representing a chrono-sequence of burn exclusion, including sites where the last burn occurred less than one year ago (M1Y), six years ago (M6Y), 25 years ago (M25Y), and more than 45 years ago (M45Y) (Table S1). We also selected two afforested sites (MP1 and MP2), where pine (*Pinus patula*) had been planted on páramo grasslands approximately 22 years prior to sampling. Plantations are first rotation, with 3 × 3 m spacing. In this study area, plantations are not managed for timber production, but at the time of sampling, the land manager was considering harvesting some of the trees. In other areas of the páramo, such plantations are generally harvested on a 25-year rotation. In general, there is little native vegetation cover under the pines,

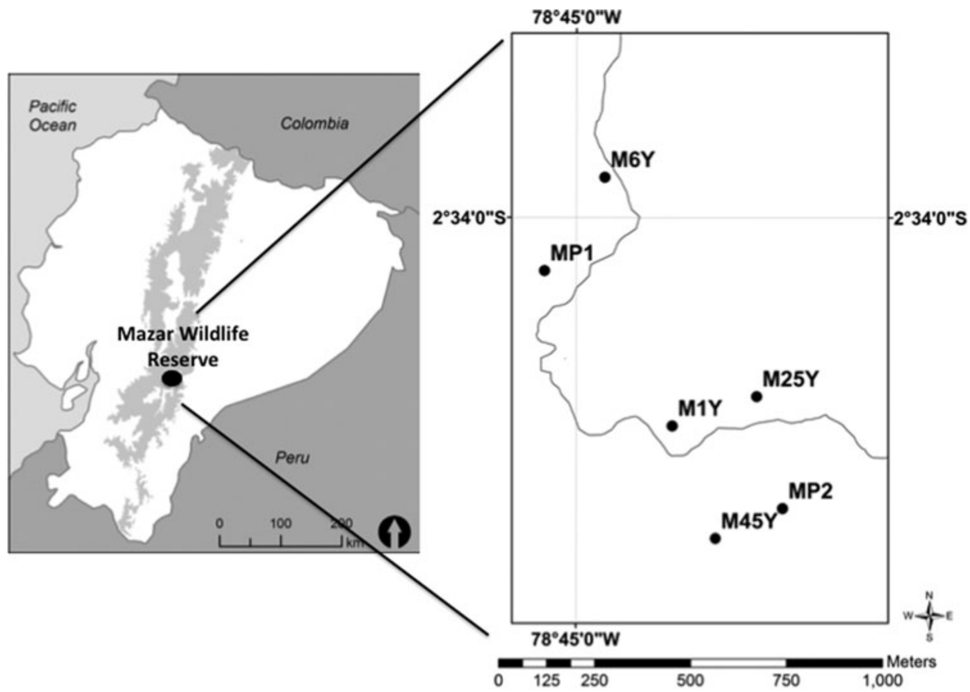

Figure 1 Study sites in the Mazar Wildlife Reserve. Note that the 3400 m contour line is an imprecise estimate based on a 50 m digital elevation model. Elevations measured in the field are reported in Table S1.

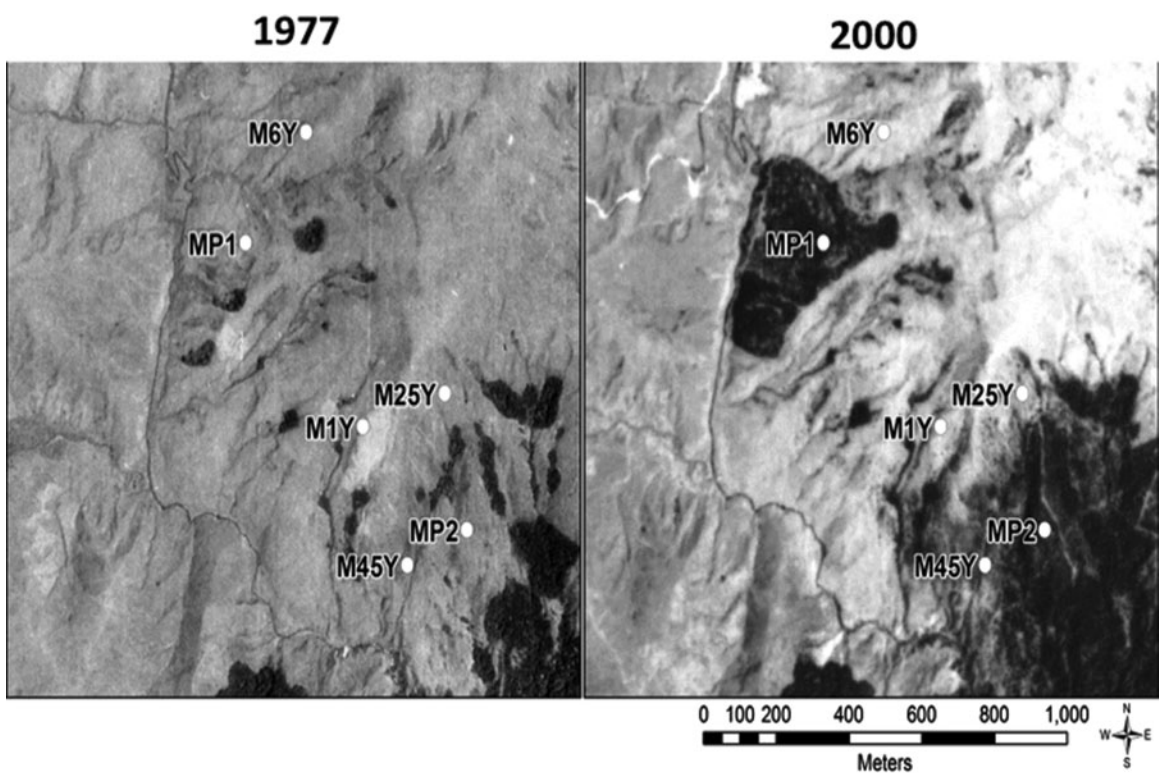

Figure 2 Aerial photo showing land cover in 1977 and 2000 at study sites. Note that the pine and 45 year sites were all grassland in 1977.

but native trees and shrubs have colonized some areas. All sites have similar long-term land management histories, which involved extensive cattle grazing coupled with burning for approximately 80 years followed by 20+ years with variable, but infrequent burning. These sites are unique in Ecuador in that they represent a known chronosequence of burn exclusion sites that are adjacent to pine plantations. This makes MWR one of the few locations suitable for evaluating the outcomes of land management currently being incentivized by PES programmes.

Soil sampling

In each site we established three evenly spaced 20 m transects. Samples were collected at four depths: 0–10 cm, 10–20 cm, 20–30 cm and 30–60 cm. The 0–20 cm samples were collected every 2 m along each transect (n = 33 per site). Three soil samples at 20–30 and 30–60 cm depths, litter samples and bulk density samples (0–20 cm) were taken along each transect (n = 9 of each sample type per site). Soil samples were taken with a soil auger and bulk density samples with a bulk density soil core sampler. One soil pit was also dug in each site, from which we collected two known-volume bulk density samples from each horizon, which were used to calculate total C values for the deeper samples (Fig. S1).

All samples, with the exception of bulk density samples, were air-dried and passed through a 2-mm sieve. Samples were brought back to the University of California, Santa Barbara soil laboratory for grinding and oven drying (60°C). Samples were then transferred to San Diego State University for C and nitrogen analysis using a CHN analyser. All samples were run in duplicate and repeated if duplicates differed by more than 10%. Samples were then oven-dried at 105°C for 24 hours and percent C values adjusted for remaining water weight. Bulk density samples were dried to a constant weight and used to calculate bulk density values for each depth class.

Biomass sampling

We established three 10–20 m plots around each soil transect and calculated the biomass of all trees within them (Fig. S2). Trees were defined as >1.5 m height, >2.5 cm diameter at breast height (DBH) and not branching at the base. For the pine sites, DBH of all pines was measured within each plot and then used to calculate biomass based on established allometric equations for pines (Ravindranath & Ostwald 2008). For native trees, for which established allometric equations were not appropriate, we used a sampling method adapted from Fehse *et al.* (2002) in order to minimize alteration of native vegetation. We first recorded all individual trees in the plot, including species, DBH and height. For each tree species, we sampled two to three individuals. Where there were large differences in height, we subsampled within height classes and assigned masses to unsampled trees based on sampled individuals.

To measure the biomass of sampled trees, we calculated the volume of the bole by measuring the average diameter and height of each branch. We collected a wood sample from each sampled tree and calculated wood density by dividing the mass (obtained by drying to a constant weight at 70°C) by the volume (obtained through displacement). To measure the mass of the crown, 25–30% of the crown was harvested and the wet weight recorded for the entire harvested section. We then collected several subsamples of woody parts and leaves, for which we recorded the wet weight and then dried to a constant temperature at 70°C to calculate the dry/wet ratio, which was then used to calculate the dry weight of the harvested sample and extrapolated to calculate the dry weight of the crown. Weights of the bole and crown were summed to calculate the mass of the tree.

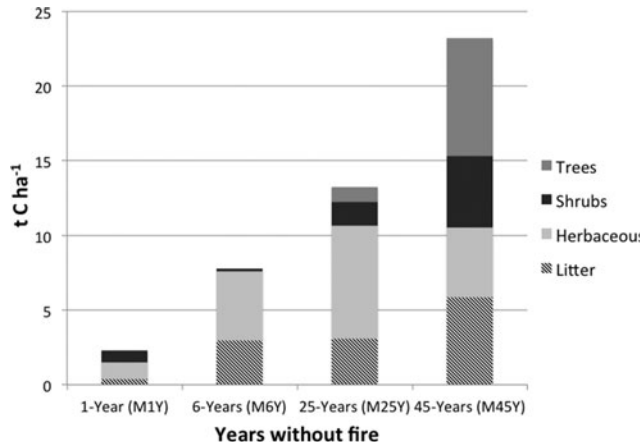

Figure 3 Above-ground biomass carbon (tonnes carbon per hectare). Note: pine sites not included.

To calculate the biomass of shrubs, herbaceous vegetation and litter, we established three randomly located 2 × 2 m plots with nested 1 × 1 m plots within each 10 × 20 m plot (Fig. S2). All shrubs within the 2 × 2 m plots, and all litter and herbaceous biomass in the 1 × 1 m plots were harvested and weighed. For large shrubs and the giant herb *Puya clava-herculis,* 25–50% of the individual was harvested and extrapolated to calculate biomass of the entire shrub. After weighing all harvested biomass according to type (live shrub, dead shrub, live herbaceous, dead herbaceous and litter), we collected and weighed one or two subsamples per plot, per vegetation type. Subsamples were dried at 70°C for 24–48 hours, or until samples reached a constant dry weight, and used to calculate a dry/wet ratio, which was then used to calculate the dry weight of the 2 × 2 m and 1 × 1 m plots. Tree, shrub, herbaceous, litter and total biomass were then extrapolated to calculate biomass (t ha^{-1}) and converted to t ha^{-1} C by multiplying by 0.5.

Statistical methods

ANOVA, followed by Tukey–Kramer HSD *post-hoc* tests, were used to compare percent and total C for surface samples (0–10 and 10–20 cm) where sample size was near or above 30. For deeper soil samples, litter samples (n = 7–9 per site) and above-ground biomass C values, we employed Kruskal–Wallis tests followed by Steel–Dwass all-pairs nonparametric *post-hoc* tests. Non-parametric tests for the greater depth samples were used given smaller sample size, which precluded adequate evaluation of normality.

RESULTS

Above-ground biomass C was highest in the pine sites (99.3 and 122.0 t C ha^{-1} in M1 and M2, respectively) and increased with the length of burn exclusion in the grassland sites (Fig. 3

Table 1 Above-ground biomass carbon and soil carbon (tonnes carbon per hectare). Sites with different letters indicate significant differences in carbon within each pool.

Site	*0–10 cm soil (SE)*	*10–20 cm soil (SE)*	*Litter (SE)*	*Herbs (SE)*	*Shrubs (SE)*	*Trees (SE)*	*Total above-ground biomass carbon*	*Total (0–20 cm soil + above-ground biomass carbon)*
M1Y	96.1 (2.3)^{bc}	76.7 (2.9)^{c}	0.4 (0.2)^{d}	1.1 (0.3)^{bcd}	0.8 (0.5)^{bc}	0 (0)	2.3 (0.4)	175.1
M6Y	89.4 (1.7)^{c}	78.5 (1.8)^{c}	0.3 (0.1)^{d}	4.6 (0.5)^{a}	0.2 (0.1)^{bc}	0 (0)	5.0 (0.9)	172.9
M25Y	106.9 (1.6)^{a}	95.0 (2.2)^{a}	3.1 (0.7)^{c}	7.5 (1.9)^{a}	1.6 (0.6)^{ab}	1.0 (0.5)	13.3 (2.7)	216.2
M45Y	102.7 (2.8)^{ab}	90.7 (2.4)^{ab}	5.9 (0.9)^{b}	4.6 (1.7)^{abc}	4.8 (1.1)^{a}	7.9 (1.9)	23.9 (3.0)	217.3
MP1	96.2 (1.2)^{bc}	94.5 (1.2)^{a}	5.7 (0.8)^{b}	0.3 (1.2)^{de}	0.2 (0.2)^{c}	92.0 (6.8)	99.3 (7.7)	290.0
MP2	89.8 (1.3)^{c}	83.0 (1.1)^{bc}	10.3 (0.8)^{a}	0.0 (0.0)^{e}	0.4 (0.3)^{bc}	111.3 (4.4)	122.0 (4.6)	294.8

and Table 1). Pine sites contained 78.498.1 t C ha^{-1} more above-ground C than the grassland site with the highest biomass (a shrubby páramo last burned over 45 years ago). The pines in the afforested sites were approximately 22 years old at the time of sampling, so above-ground biomass C sequestration of the plantations can be estimated at 4.5 to 5.5 t C ha^{-1} year^{-1}. This is an order of magnitude greater than at grassland sites, where above-ground biomass C storage ranged from 2.3 to 23.9 t C ha^{-1}, an average gain of approximately 0.5 t C ha^{-1} year^{-1} (Fig. 3 and Table 1). The distribution of above-ground biomass also shifted with length of burn exclusion: herbaceous biomass was dominant up to 25 years of burn exclusion, then dominance shifted to tree biomass after 45 years without burning (Fig. 3 and Table 1).

Although large changes in above-ground biomass occurred under different land managements, above-ground biomass C comprised a small portion of total C storage in all sites, constituting only 1–4% of total C (to 60 cm depth of soil) for grassland sites and 15–18% in the pine plantations (Table 1 and Table S2). Soil C (0–20 cm) increased with the length of burn exclusion, reaching the highest levels between 25–45 years since last burn. Soil C (0–20 cm) was significantly lower in the more recently burned sites (1 and 6 years of burn exclusion, with 172.8 and 167.9 t C ha^{-1}, respectively) than in the sites with longer-term burn exclusion (25 and 45 years of burn exclusion, with 201.9 and 193.4 t C ha^{-1}, respectively) ($p < 0.0001$) (Fig. 4 and Table 1).

Soil C at 0–10 and 10–20 cm was significantly lower with afforestation than in the grassland site that had remained unburned for 25 years ($p < 0.05$). Soil C was also significantly lower in one of the pine sites compared to the adjacent grassland with the longest burn exclusion (45 years), which was dominated by shrubs and trees ($p < 0.05$). By contrast, soil C was similar between the pine sites and the recently burned sites (Fig. 4 and Table 1).

At 30–60 cm depth, all sites had similar soil C levels, suggesting that the effects of land management on soil C are not evident at this depth, providing support that pre-existing differences among sites did not exist (Table S2).

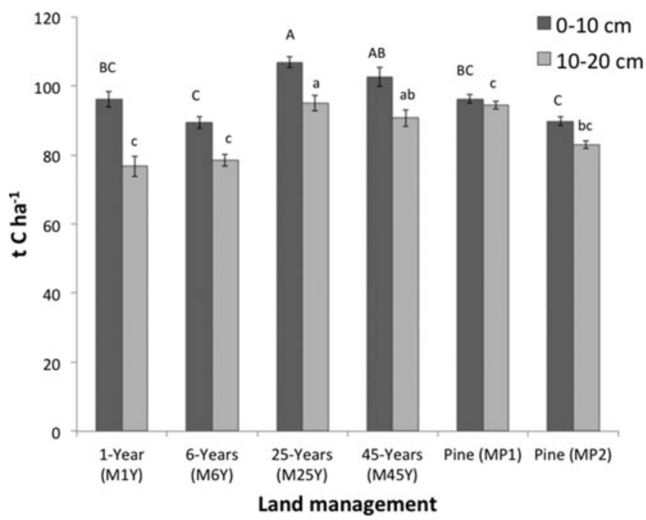

Figure 4 Soil carbon at 0–10 and 10–20 cm depths (tonnes carbon per hectare). Sites with different letters indicate significant differences in soil carbon (upper-case letters used for 0–10 cm and lower-case for 10–20 cm).

DISCUSSION

Our estimates of C stocks in páramo grasslands are indicative of their high soil C storage potential. Between 206.1 and 548.6 t C ha^{-1} are stored in the top 60 cm of soil suggesting that native grasslands are important sinks for C (Gibbon *et al.* 2010; Farley *et al.* 2013). Soil C stocks in the top 60 cm accounted for 96–99% of total C storage in grassland sites and 82–85% of C stocks in afforested sites, pointing to the relative importance of soil C in páramo grasslands, even under afforestation. At the same time, the relatively small changes in soil C storage found in this study suggest that, while vegetation constitutes one control on soil C, other controls, such as climate and parent material, are also important, and also are more likely to vary between regions (Buytaert *et al.* 2007 *a*). This constitutes an important challenge to the ability to use single land-management prescriptions to optimize C storage across large regions in PES programmes. Accordingly, this study can be

https://doi.org/10.1017/S0376892916000199 Published online by Cambridge University Press

used to formulate hypotheses for the effects of burn exclusion and afforestation on soil C in other grasslands, particularly in areas with Andisols, but the multitude of controls on soil C require careful attention to local conditions.

Above-ground biomass C

The clearest effect of changes in land management in this study is the enhancement of above-ground biomass C stocks in the 22 year old pine plantations in páramo grasslands in the reserve. Planting pine contributes to the exchange of below-ground for above-ground biomass C; in comparing the older páramo sites to the pine sites our sites follow this pattern, but both gains in above-ground biomass C and losses of below-ground C were smaller than reported elsewhere (Berthrong *et al.* 2012; Farley *et al.* 2013). Previous studies in the Ecuadorian Andes found larger quantities of above-ground biomass C in a 45-year old native *Alnus* stand and a 40-year old pine plantation (241 t C ha^{-1}and 279 t C ha^{-1}, respectively), while the pine sites in this study stored between 99–122 t C ha^{-1} in above-ground biomass, indicating lower C storage than in other plantation forests in the páramo (Fehse *et al.* 2002; Farley *et al.* 2013).

Given that they are 22 years old, these plantations likely have the potential to sequester more above-ground biomass C with age, which could be accompanied by continued decreases in soil C storage if there is a continued exchange of below-ground for above-ground biomass C. However, above-ground net primary productivity is likely to decrease with stand age (Gower *et al.* 1996; Ryan *et al.* 2004). A recent review of afforestation effects on soil organic C found that plantations left to grow for more than 20–30 years often recover soil C initially lost with plantation establishment (Berthrong *et al.* 2012), but previous studies on pine plantations in the páramo have demonstrated low soil C in a 40-year-old pine plantation (Farley *et al.* 2013) and no sign of reversal by 25 years (Farley *et al.* 2004). Thus, the effect of continued growth of the plantations on soil C stocks remains uncertain. However, in most regions in Ecuador pine plantations are harvested for timber every 25 years and replanted, which could drive long-term decreases in soil C storage even as above-ground biomass C is removed. Pine plantations in páramo grasslands represent a transfer of C to the above-ground biomass pool that is much more likely to be lost through accidental or managed fires (Farley *et al.* 2004). After harvesting pine, woody debris and litter are commonly burned prior to second rotation planting, resulting in emission of some above-ground biomass C to the atmosphere (Farley *et al.* 2004). There has not been any research on soil C dynamics of second rotation pine plantations in páramo grasslands, pointing to a critical area of further research.

Above-ground biomass C stocks in the páramo grassland sites reached up to 23.9 t C ha^{-1} in shrub-dominated sites, which was much lower than those at sites planted with pine, but higher or similar to those previously reported for páramo grasslands (Hofstede & Rossenaar 1995; Farley *et al.* 2013). Previously, 22.9 t C ha^{-1} had been found in a tussock grass-dominated páramo site with 15 years of burn exclusion (in a drier, but similar elevation area), suggesting that grass-dominated páramo can sequester as much above-ground biomass C as a shrubby páramo, even with a much shorter period of burn exclusion (Farley *et al.* 2013). This is a key finding for PES programmes seeking to maximize C storage and improve livelihoods since it provides evidence that longer periods of burn exclusion may not be necessary. Quantifying the relative rates of decomposition and combustibility of herbaceous versus woody páramo species is an important area of future research that would further shed light on páramo above-ground biomass C dynamics.

Thus, while C sequestration efforts have primarily focused on afforestation, reforestation and avoided deforestation, these results provide further support for the idea that native grasslands and shrublands can also have value for their above-ground biomass C stocks (Bekessy & Wintle 2008; Farley *et al.* 2013). Given that afforestation with pines, in particular, has been associated with decreased runoff (Buytaert *et al.* 2007 *b*) and loss of native plant diversity (Van Wesenbeeck *et al.* 2003; Bremer & Farley 2010), greater focus on the C sequestration potential of native grasslands and shrublands is merited (Gibbon *et al.* 2010). In the same MWR sites used in this study, significantly lower levels of soil moisture were found under pine than under grassy páramo, while soil moisture in the shrubby páramo site (burned 45 years ago) was intermediate, but significantly lower than in grass páramo (Harden *et al.* 2013). This suggests a C for water tradeoff with pine, and a lesser but still notable tradeoff with native woody encroachment (Harden *et al.* 2013). Accordingly, this and previous research (Farley *et al.* 2013) suggest that PES could incentivize shorter term burn exclusion – not long enough for conversion to shrubs, but long enough for accumulation of substantial herbaceous biomass – and achieve some above-ground biomass C sequestration, while minimizing water tradeoffs. There have been increasing calls for research on tradeoffs among multiple ecosystem services globally (Goldstein *et al.* 2012; Guerry *et al.* 2015), and this study is one of the few that helps to understand this in the páramo context.

Vegetation controls on soil C

Our results demonstrate that vegetation management has an important, if moderate, influence on soil C storage in páramo soils, and the highest levels of soil C were associated with longer periods without burning. However, given that no additional gain in soil C occurred between 25–45 years of burn exclusion, there appears to be a limit to this benefit, and there is potential for reversal with longer periods of burn exclusion and associated woody plant expansion. This study is the only study of burn exclusion in páramo grasslands that includes sites with more than 15 years without burning. While further research is needed, this finding has important implications for PES programmes as it challenges the idea that long-term burn exlusion is optimal for soil C storage. In Andisols, grassland vegetation has been associated with higher soil C than woody cover (Shoji *et al.* 1993; Tonneijck *et al.* 2010), and losses in C storage have been found with woody encroachment of wet grasslands such as the páramo (Jackson *et al.* 2002). This further suggests that burn exclusion may be beneficial for C storage up to a point, but incentivizing permanent burn exclusion is unlikely to provide increasing benefits and may even result in soil C losses over time. Our results also add to global-scale analyses (Jackson *et al.* 2002), demonstrating that a time component, rather than just the broad categories of shrub versus grass dominated, is needed to assess the influence of burn exclusion on soil C dynamics.

However, our results also suggest greater soil C storage under natural woody vegetation (occurring in sites with burn exclusion) than at pine sites. Previous research found reduced C storage under pines compared to páramo grasslands (Farley *et al.* 2004; Berthrong *et al.* 2009; Farley *et al.* 2013), but did not include páramo sites with high shrub cover as a result of burn exclusion. Farley *et al.* (2013), for example, found greater soil C storage under páramo grasslands with burn exclusion, but the maximum time of burn exclusion was 15 years. Accordingly, our findings provide new evidence that a shrub páramo can also store more soil C than a páramo planted with pine. Our findings also suggest that among grass páramo, shrub páramo and pine, the highest soil C is found in grass páramo that has been protected from burning, but not for long enough for shrub dominance. Thus, burn exclusion to the point where it leads to shrub dominance is not likely to be optimal for soil C storage. This has important implications for programmes like SocioPáramo, which often operate under the assumption that soil C benefits from burn exclusion will continue over 20 or more years.

Soil moisture can be an important control on soil C in páramo grasslands (Buytaert *et al.* 2007 *a*), and changes in evapotranspiration and soil moisture likely played a role in the changes seen with afforestation (Farley *et al.* 2004; Buytaert *et al.* 2007 *b*). Lower soil moisture levels under both pine sites compared with grassland sites have been found previously (Harden *et al.* 2013), with one pine site (MP2) significantly drier than the other (MP1), and soil C was also lower in MP2 compared with MP1. Lower soil moisture levels would be expected to accelerate decomposition of soil organic matter under afforestation given that high moisture levels constrain decomposition in wet sites such as páramos (Poulenard *et al.* 2003; Farley *et al.* 2004; Buytaert *et al.* 2007 *b*; Berthrong *et al.* 2009). Thus, vegetation influences soil moisture, acting as an indirect control on soil C, but climate conditions also vary across páramos regionally (Buytaert *et al.* 2005) and this is an important factor for PES programmes to assess prior to implementing land management prescriptions.

While changes in vegetation cover moderately influenced soil C storage, no direct and immediate impact of fire on soil C storage was detected, a finding that supports the limited research on fire in Andean grasslands (Hofstede 1995; Suarez & Medina 2001; Zimmermann *et al.* 2010). Although above-ground biomass C stores decline with burning, this is largely offset through C sequestered during regeneration (Bowman *et al.* 2009). Thus, while burning will temporarily reduce above-ground biomass C storage, it seems to have little short- to medium-term impact on soil C levels. This finding does not preclude any influence of fire on soil C in páramo grasslands, as fire has the potential to directly alter soil C content through transforming above-ground and below-ground C into more stable char compounds (black C) (Gonzalez-Perez *et al.* 2004; Knicker 2007). However, overall, the finding that burning did not have any direct, measurable impact on soil C suggests that burning can be carried out infrequently (perhaps every 15–25 years) without negatively affecting the soil C stock, and potentially could even increase it. Accordingly, an important conclusion from our research is that infrequent burning may be compatible with ecosystem services projects focused on C. Given that many smallholder and community livelihoods include páramo grazing, allowing infrequent burning and grazing may make PES programmes more effective at simultaneously achieving their ecological and social goals, and may broaden participation (Bremer *et al.* 2014 *a*). By contrast, pine cannot be profitable beyond C payments without harvesting, so pine plantations make less sense as 'working landscapes' for C storage.

It is important to note that, in most cases, burning as a land management strategy in páramos is used in conjunction with cattle, sheep, and, increasingly, alpaca and llama grazing (White & Maldonado 1991; Keating 2007; White 2013). Sites at the MWR were used for alpaca grazing, but these sites are not as heavily grazed and frequently burned as many páramos in Ecuador. While areas with up to 15–20 years since the last burn are used for grazing, it should also be noted that more recently burned areas are associated with higher forage quality. The coupled effect of grazing and fire on forage quality and C storage is an important area for future research.

Operationalizing land management prescriptions in PES programmes

Above-ground biomass C will clearly increase through afforestation and, secondarily, through burn exclusion. However, multiple, interacting factors influence soil C – where most C is stored in these systems – presenting a challenge to the implementation of single land management prescriptions across large regions in PES programmes. The difference between the two pine sites, as well as the smaller magnitude of the changes relative to those found in previous research, underscore this difficulty and illustrate the heterogeneity that can exist within single categories of land management. In a regional study of pine afforestation effects on soil C storage, it was concluded that the effects of plantations are difficult to generalize, as outcomes vary based on environmental factors, history and plantation management (Hofstede *et al.* 2002). We suggest that edaphic and pedogenic factors be added to that list, given that large-scale controls on soil C storage in páramos include volcanic ash deposits and climate (Buytaert *et al.* 2007 *a*). Future research should address how regional controls on soil C storage along with local-scale factors affect the response of Andisols to changes in land management.

CONCLUSIONS AND POLICY RECOMMENDATIONS

PES programmes are prominent on the international sustainability agenda and are rapidly growing around the world (Brockington 2011; Wunder 2013; Bremer *et al.* 2016). However, their implementation is outpacing scientific understanding of links between promoted land uses and targeted ecosystem services, pointing to the critical need for research that examines those links and can be integrated into policy decisions (Ruffo & Kareiva 2009; Naeem *et al.* 2015). There is a complexity in measuring the effects of changes in land use and management in páramo grasslands that is highlighted by the multiple and interacting factors that control C storage. However, despite the difficulty of drawing region-wide generalizations, some recommendations for PES programmes targeting páramo grasslands can be drawn from this research.

Afforestation with pine can be an effective strategy to enhance above-ground biomass C storage, although levels found at MWR were lower than those reported elsewhere for older trees. However, pine plantations continue to be suboptimal as a C sequestration strategy when viewed through a broader lens of tradeoffs among other ecosystem services. The gains in above-ground biomass C found in this study came with losses in soil C and have been associated with negative outcomes for water provision in páramos (Buytaert *et al.* 2007 *b*; Harden *et al.* 2013), suggesting that focusing exclusively on above-ground biomass C storage rather than ecosystem service bundles can compromise other ecosystem functions and services (Lindenmayer *et al.* 2012). Moreover, above-ground biomass C in pines represents a transfer of below-ground to above-ground C, and is much more prone to harvesting or fuel use that will eventually result in the release of stored C.

Our results suggest that burn exclusion can be an effective C storage strategy that can be used as an alternative to afforestation. However, burn exclusion should be managed to minimize shrub encroachment. One of the most important ecosystem services of páramo grasslands is its economic value as forage, and data from the MWR suggest that burn exclusion can lead to a transition to woody-dominated systems that would not be suitable for grazing. Succession to shrubs may happen at different times at different sites, but at the MWR, it appears to occur between 25–45 years without burning. At that point, páramos can be burned to maintain herbaceous cover, an action that will reduce the above-ground biomass C, but is unlikely to impact soil C – where most C in these systems is stored. PES programmes that allow for working landscapes with some level of burning in conjunction with grazing may be a more effective way to prevent conversion of grassland to row crop agriculture, which is likely to have a much greater impact on soil C storage than burning (Guo & Gifford 2002; Buytaert *et al.* 2005; Farley *et al.* 2013). This demonstrates the value of incorporating working landscapes into PES programmes where targeted ecosystem services can be produced simultaneously alongside ecosystem services (e.g., forage) valued by local landowners.

ACKNOWLEDGEMENTS

This study would not have been possible without the support of many people. The authors thank Dr Stuart White for assistance throughout their fieldwork. The authors thank Will Anderson, James Hartsig, Hunter Terrell, Allison Hamada, Joel Jennings, the park guards of Sangay National Park and MWR. The soil lab at the University of Azuay carried out pH analysis of soils and provided facilities for drying and processing soils and biomass. Will Anderson geo-referenced the aerial photos for this paper and Richard Sharp assisted in creating the maps. The authors thank Fundación Cordillera Tropical, Ecociencia and Fulbright Ecuador for institutional support. This material is based upon work supported by a Fulbright Student Grant, the National Science Foundation under Grant No. 0851532 and the SDSU University Grant Program. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the Fulbright Foundation, the National Science Foundation or San Diego State University.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0376892916000199

References

Bekessy, S.A. & Wintle, B.A. (2008) Using carbon investment to grow the biodiversity bank. *Conservation Biology* **22**: 510–513.

Berthrong, S.T., Jobbagy, E.G. & Jackson, R.B. (2009) A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecological Applications* **19**: 2228–2241.

Berthrong, S.T., Pineiro, G., Jobbagy, E.G. & Jackson, R.B. (2012) Soil C and N changes with afforestation of grasslands across gradients of precipitation and plantation age. *Ecological Applications* **22**: 76–86.

Bowman, D., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R. & Pyne, S.J. (2009) Fire in the earth system. *Science* **324**: 481–484.

Bremer, L. & Farley, K. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation* **19**: 3893–3915.

Bremer, L.L., Farley, K.A. & Lopez-Carr, D. (2014 *a*). What factors influence participation in Payment for Ecosystem Services programs? An evaluation of Ecuador's SocioPáramo program. *Land Use Policy* **36**: 122–133.

Bremer, L.L., Farley, K.A., Lopez-Carr, D. & Romero, J. (2014 *b*). Conservation and livelihood outcomes of Payment For Ecosystem Services in the Ecuadorian Andes: what is the potential for 'win–win'? *Ecosystem Services* **8**: 148–165.

Bremer, L.L., Auerbach, D.A., Goldstein, J.H., Vogl, A.L., Shemie, D., Kroeger, T., Nelson, J.L., Benítez, S.P., Calvache, A., Guimarães, J., Herron, C., Higgins, J., Klemz, C., León, J., Sebastián, J., Moreno, P.H., Nuñez, F., Veiga, F. & Tiepolo, G. (2016) One size does not fit all: natural infrastructure investments within the Latin American Water Funds Partnership. *Ecosystem Services* **17**: 217–236.

Brockington, D. (2011) Ecosystem services and fictitious commodities. *Environmental Conservation* **38**: 367–369.

Buytaert, W., Wyseure, G., De Bievre, B. & Deckers, J. (2005) The effect of land-use changes on the hydrological behaviour of Histic Andosols in south Ecuador. *Hydrological Processes* **19**: 3985–3997.

Buytaert, W., Celleri, R., De Bievre, B., Cisneros, F., Wyseure, G., Deckers, J. & Hofstede, R. (2006 *a*). Human impact on the hydrology of the Andean paramos. *Earth Science Reviews* **79**: 53–72.

Buytaert, W., Deckers, J. & Wyseure, G. (2006 *b*). Description and classification of nonallophanic Andosols in south Ecuadorian alpine grasslands (paramo). *Geomorphology* **73**: 207–221.

Buytaert, W., Deckers, J. & Wyseure, G. (2007 *a*). Regional variability of volcanic ash soils in south Ecuador: the relation with parent material, climate and land use. *Catena* **70**: 143–154.

Buytaert, W., Iniguez, V. & De Bievre, B. (2007 *b*). The effects of afforestation and cultivation on water yield in the Andean paramo. *Forest Ecology and Management* **251**: 22–30.

Chacon, G., Gagnon, D. & Pare, D. (2009) Comparison of soil properties of native forests, *Pinus patula* plantations and adjacent pastures in the Andean highlands of southern Ecuador: land use history or recent vegetation effects? *Soil Use and Management* **25**: 427–433.

Daily, G.C., Polasky, S., Goldstein, J., Kareiva, P.M., Mooney, H.A., Pejchar, L., Ricketts, T.H., Salzman, J. & Shallenberger, R. (2009) Ecosystem services in decision making: time to deliver. *Frontiers in Ecology and the Environment* **7**: 21–28.

de Koning, F., Aguinaga, M., Bravo, M., Chiu, M., Lascano, M., Lozada, T. & Suarez, L. (2011) Bridging the gap between forest conservation and poverty alleviation: the Ecuadorian Socio Bosque program. *Environmental Science & Policy* **14**: 531–542.

Engel, S., Pagiola, S. & Wunder, S. (2008) Designing payments for environmental services in theory and practice: an overview of the issues. *Ecological Economics* **65**: 663–674.

Farley, K.A., Kelly, E.F. & Hofstede, R.G.M. (2004) Soil organic carbon and water retention following conversion of grasslands to pine plantations in the Ecuadorian Andes. *Ecosystems* **7**: 729–739.

Farley, K.A., Bremer, L.L., Harden, C.P. & Hartsig, J. (2013) Changes in carbon storage under alternative land uses in biodiverse Andean grasslands: implications for payment for ecosystem services. *Conservation Letters* **6**: 21–25.

Farley, K.A., Anderson, W.G., Bremer, L.L. & Harden, C.P. (2011) Compensation for ecosystem services: an evaluation of efforts to achieve conservation and development in Ecuadorian paramo grasslands. *Environmental Conservation* **48**: 393–405.

Fehse, J., Hofstede, R., Aguirre, N., Paladines, C., Kooijman, A. & Sevink, J. (2002) High altitude tropical secondary forests: a competitive carbon sink? *Forest Ecology and Management* **163**: 9–25.

Gibbon, A., Silman, M.R., Malhi, Y., Fisher, J.B., Meir, P., Zimmermann, M., Dargie, G.C., Farfan, W.R. & Garcia, K.C. (2010) Ecosystem carbon storage across the grassland-forest transition in the High Andes of Manu National Park, Peru. *Ecosystems* **13**: 1097–1111.

Goldstein, J.H., Caldarone, G., Duarte, T.K., Ennaanay, D., Hannahs, N., Mendoza, G., Polasky, S., Wolny, S. & Daily, G.C. (2012) Integrating ecosystem-service tradeoffs into land-use decisions. *Proceedings of the National Academy of Sciences* **109**: 7565–7570.

Gonzalez-Perez, J.A., Gonzalez-Vila, F.J., Almendros, G. & Knicker, H. (2004) The effect of fire on soil organic matter – a review. *Environment International* **30**: 855–870.

Gower, S.T., McMurtrie, R.E. & Murty, D. (1996) Aboveground net primary production decline with stand age: potential causes. *Trends in Ecology & Evolution* **11**: 378–382.

Guerry, A.D., Polasky, S., Lubchenco, J., Chaplin-Kramer, R., Daily, G.C., Griffin, R., Ruckelshaus, M., Bateman, I.J., Duraiappah, A., Elmqvist, T., Feldman, M.W., Folke, C., Hoekstra, J., Kareiva, P.M., Keeler, B.L., Li, S., McKenzie, E., Ouyang, Z., Reyers, B., Ricketts, T.H., Rockström, J., Tallis, H. & Vira, B. (2015) Natural capital and ecosystem services informing decisions: from promise to practice. *Proceedings of the National Academy of Sciences* **112**: 201503751.

Guo, L.B. & Gifford, R.M. (2002) Soil carbon stocks and land use change: a meta analysis. *Global Change Biology* **8**: 345–360.

Harden, C.P., Hartsig, J., Farley, K.A., Lee, J. & Bremer, L.L. (2013) Effects of land-use change on water in Andean Páramo Grassland soils. *Annals of the Association of American Geographers* **103**: 375–384.

Hofstede, R.G.M. (1995) The effects of grazing and burning on soil and plant nutrient concentrations in Colombian Paramo Grasslands. *Plant and Soil* **173**: 111–132.

Hofstede, R.G.M. & Rossenaar, A. (1995) Biomass of grazed, burned and undisturbed Paramo Grasslands, Colombia 2. Root mass and aboveground/belowground ratio. *Arctic and Alpine Research* **27**: 13–18.

Hofstede, R.G.M., Groenendijk, J.P., Coppus, R., Fehse, J.C. & Sevink, J. (2002) Impact of pine plantations on soils and vegetation in the Ecuadorian High Andes. *Mountain Research and Development* **22**: 159–167.

Holmes, K.W., Chadwick, O.A., Kyriakidis, P.C., de Filho, E.P.S., Soares, J.V. & Roberts, D.A. (2006) Large-area spatially explicit estimates of tropical soil carbon stocks and response to land-cover change. *Global Biogeochemical Cycles* **20**: GB3004.

Jackson, R.B., Banner, J.L., Jobbagy, E.G., Pockman, W.T. & Wall, D.H. (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* **418**: 623–626.

Keating, P.L. (2007) Fire ecology and conservation in the high tropical Andes: observations from northern Ecuador. *Journal of Latin American Geography* **6**: 43–62.

Knicker, H. (2007) How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry* **85**: 91–118.

Lal, R. (2004) Soil carbon sequestration to mitigate climate change. *Geoderma* **123**: 1–22.

Lal, R. (2013) Soil carbon management and climate change. *Carbon Management* **4**: 439–462.

Lindenmayer, D.B., Hulvey, K.B., Hobbs, R.J., Colyvan, M., Felton, A., Possingham, H., Steffen, W., Wilson, K., Youngentob, K. & Gibbons, P. (2012) Avoiding bio-perversity from carbon sequestration solutions. *Conservation Letters* **5**: 28–36.

Muradian, R., Corbera, E., Pascual, U., Kosoy, N. & May, P.H. (2010) Reconciling theory and practice: an alternative conceptual framework for understanding payments for environmental services. *Ecological Economics* **69**: 1202–1208.

Naeem, S., Ingram, J.C., Varga, A., Agardy, T., Barten, P., Bennett, G., Bloomgarden, E., Bremer, L.L., Burkill, P., Cattau, M., Ching, C., Colby, M., Cook, D.C., Costanza, R., DeClerck, F., Freund, C., Gartner, T., Goldman-Benner, R., Gunderson, J., Jarrett, D., Kinzig, A.P., Kiss, A., Koontz, A., Kumar, P., Lasky, J.R., Masozera, M., Meyers, D., Milano, F., Naughton-Treves, L., Nichols, E., Olander, L., Olmsted, P., Perge, E., Perrings, C., Polasky, S., Potent, J., Prager, C., Quétier, F., Redford, K., Saterson, K., Thoumi, G., Vargas, M.T., Vickerman, S., Weisser, W., Wilkie, D. & Wunder, S. (2015) Get the science right when paying for nature's services. *Science* **347**: 1206–1207.

Neff, J.C., Barger, N.N., Baisden, W.T., Fernandez, D.P. & Asner, G.P. (2009) Soil carbon storage responses to expanding pinyon-juniper populations in southern Utah. *Ecological Applications* **19**: 1405–1416.

Paul, K.I., Polglase, P.J., Nyakuengama, J.G. & Khanna, P.K. (2002) Change in soil carbon following afforestation. *Forest Ecology and Management* **168**: 241–257.

Podwojewski, P., Poulenard, J., Zambrana, T. & Hofstede, R. (2002) Overgrazing effects on vegetation cover and properties of volcanic ash soil in the paramo of Llangahua and La Esperanza (Tungurahua, Ecuador). *Soil Use And Management* **18**: 45–55.

Poulenard, J., Podwojewski, P. & Herbillon, A.J. (2003) Characteristics of non-allophanic andisols with hydric properties from the Ecuadorian paramos. *Geoderma* **117**: 267–281.

Ravindranath, N.H. & Ostwald, M. (2008) Carbon inventory methods: handbook for greenhouse gas inventory, carbon mitigation and roundwood production projects. pp. 308. Dordrecht, the Netherlands: Springer.

Ruffo, S. & Kareiva, P.M. (2009) Using science to assign value to nature. *Frontiers in Ecology and the Environment* **7**: 3.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P. & Senock, R.S. (2004) An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs* **74**: 393–414.

Shoji, S., Nanzyo, M. & Dahlgren, R. (1993) Volcanic ash soils: genesis, properties, and utilization. In: *Developments in Soil Science 21*. Amsterdam, the Netherlands: Elsevier.

Smith, P., House, J.I., Bustamante, M., Sobocká, J., Harper, R., Pan, G., West, P.C., Clark, J.M., Adhya, T., Rumpel, C., Paustian, K., Kuikman, P., Cotrufo, M.F., Elliott, J.A., McDowell, R., Griffiths, R.I., Asakawa, S., Bondeau, A., Jain, A.K., Meersmans, J. & Pugh, T.A.M. (2016) Global change pressures on soils from land use and management. *Global Change Biology* **22**: 1008–1028.

Suarez, E. & Medina, G. (2001) Vegetation structure and soil properties in Ecuadorian paramo grasslands with different histories of burning and grazing. *Arctic Antarctic and Alpine Research* **33**: 158–164.

Tonneijck, F.H., Jansen, B., Nierop, K.G.J., Verstraten, J.M., Sevink, J. & De Lange, L. (2010) Towards understanding of carbon stocks and stabilization in volcanic ash soils in natural Andean ecosystems of northern Ecuador. *European Journal of Soil Science* **61**: 392–405.

Trabucco, A., Zomer, R.J., Bossio, D.A., van Straaten, O. & Verchot, L.V. (2008) Climate change mitigation through afforestation/reforestation: a global analysis of hydrologic impacts with four case studies. *Agriculture Ecosystems & Environment* **126**: 81–97.

Van Wesenbeeck, B.K., Van Mourik, T., Duivenvoorden, J.F. & Cleef, A.M. (2003) Strong effects of a plantation with *Pinus patula* on Andean subparamo vegetation: a case study from Colombia. *Biological Conservation* **114**: 207–218.

White, S. (2013) Grass páramo as hunter-gatherer landscape. *The Holocene* **23**: 898–915.

White, S. & Maldonado, F. (1991) The use and conservation of natural-resources in the Andes of southern Ecuador. *Mountain Research and Development* **11**: 37–55.

Wunder, S. (2013) When payments for environmental services will work for conservation. *Conservation Letters* **6**: 230–237.

Wunder, S. & Alban, M. (2008) Decentralized payments for environmental services: the cases of Pimampiro and PROFAFOR in Ecuador. *Ecological Economics* **65**: 685–698.

Zehetner, F., Miller, W.P. & West, L.T. (2003) Pedogenesis of volcanic ash soils in Andean Ecuador. *Soil Science Society of America Journal* **67**: 1797–1809.

Zimmermann, M., Meir, P., Silman, M.R., Fedders, A., Gibbon, A., Malhi, Y., Urrego, D.H., Bush, M.B., Feeley, K.J., Garcia, K.C., Dargie, G.C., Farfan, W.R., Goetz, B.P., Johnson, W.T., Kline, K.M., Modi, A.T., Rurau, N.M.Q., Staudt, B.T. & Zamora, F. (2010) No differences in soil carbon stocks across the tree line in the Peruvian Andes. *Ecosystems* **13**: 62–74.