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Soil and fine root chemistry at a tropical Andean timberline

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ABSTRACT

Tropical timberlines are dynamic ecotones influenced not only by climate but often also by human activity. Understanding differences in soils across these boundaries therefore requires explicit consideration of land use. We examined patterns of soil and fine root chemistry at a tropical timberline ecotone in northern Peru nearly three decades after grazing and fire reduction. Soils were collected in forest, edge, and grassland habitat on east- and west-facing slopes and evidence of recent grazing, past fire, and shrub presence was recorded in alpine grasslands. We determined concentrations and mass (to 10 cm) of base cations, phosphorus (P), and inorganic nitrogen (N) in soil, as well as total carbon (C), total N, δ^{13}C, and δ^{15}N in soils and fine roots. Calcium and magnesium concentrations and mass, and soil P and fine root N concentrations decreased from forest to grassland. Lower soil P, soil N, and fine root N concentrations were associated with enriched soil δ^{15}N, indicating enhanced nutrient losses from edge and grassland soils. The stable carbon isotopic composition of soils and fine roots was more enriched in grassland (soil $\delta^{13}C = -24.1‰$; fine root $\delta^{13}C = -25.1‰$) compared to forest (soil $\delta^{13}C = -26.1‰$; fine root $\delta^{13}C = -28.2‰$), except where shrubs were present. In grasslands, topography appeared to influence grazing and shrub expansion; shrubs were more prevalent on the steeper west-facing slopes while cattle dung was found only on the shallower east-facing slopes. The spatially heterogeneous patterns of shrub establishment and surface soil and fine root chemistry across these forest–grassland boundaries provide evidence of legacies of grazing and burning, underscoring the need for further research on land-use legacy effects on belowground processes in tropical timberline ecosystems.

1. Introduction

Tropical timberlines form part of a spatially and temporally dynamic ecotone that encompasses the transition from the upper limit of tropical montane forest to alpine grassland (Young and León, 2007). In the Andes, this forest–grassland boundary stretches thousands of kilometers from Venezuela to northern Chile and Argentina. As such, extraordinary diversity in all of the soil-forming factors—climate, organisms, relief, parent material, and time (Jenny, 1941)—characterizes this tropical timberline ecotone.

In humid and perhumid areas of this vast and variable ecotone, numerous studies document high ecosystem carbon (C) storage (Farley et al., 2013; Gibbon et al., 2010; Tonneijck et al., 2010; Zimmermann et al., 2010). Here, timberline forest and adjacent grassland ecosystems experience cool, wet, humid, and often foggy conditions (Rapp and Silman, 2012) that favor relatively high rates of net primary productivity (NPP). Recent measurements of both above- and belowground NPP indicate that, on average, forests and grasslands at timberline produce 5.6 and 6.3 Mg C ha^{-1} yr^{-1}, respectively (Oliveras et al., 2014). Large amounts of this organic material may be chemically or physically protected through the formation of organomineral associations, low pH and associated high aluminum (Al) concentrations, and large proportions of micro- and mesopores that prevent microbial access to soil organic matter (SOM) (Buytaert et al., 2007; Hofstede et al., 2002; Tonneijck et al., 2010). These processes, coupled with the wet or waterlogged conditions derived from the climate, promote slow litter decomposition and, in turn, organic matter accumulation (Hofstede, 1995).

Stocks of such nutrients as nitrogen (N), sulfur (S), potassium (K), calcium (Ca), and magnesium (Mg) in soils and roots are also often higher at timberline than at lower elevations (Soethe et al., 2007, 2008), though a considerable fraction of these nutrients may not be available to plants (Hofstede, 1995). In Andean grasslands, especially those on volcanic ash soils, adsorption of phosphorus (P) by Al and iron (Fe) oxides results in low overall P availability (Buytaert et al., 2006; Farley and Kelly, 2004). In contrast, some studies indicate increasing soil P and decreasing soil N availability in forests at or near timberline (Fisher et al., 2013; Graefe et al., 2010; Hertel and Wesche, 2008; Soethe et al., 2008). Where nutrients are available, low soil pH and elevated precipitation contribute to leaching losses (Heitkamp et al., 2014).

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Although vegetation may have profound effects on soil chemistry, direct comparisons of forest and grassland soils at tropical timberlines have produced some surprising results. For example, at two sites in southern Peru, soil C stocks and soil nutrient concentrations did not differ across the treeline (Heitkamp et al., 2014; Zimmermann et al., 2010). Comparison of páramo grassland and native forest soils in Ecuador revealed no differences in soil N concentrations or pools (Chacón et al., 2009; Hofstede et al., 2002). Working at the molecular level, Nierop et al. (2007) found that SOM composition varied little between forest and páramo soils and could not explain observable contrasts in soil profile development. There is, however, evidence that vegetation type at tropical timberlines can alter surface soil chemistry through effects on canopy nutrient fluxes (Ponette-González et al., 2010, 2014), litter quantity and quality (Coûteaux et al., 2002; Pérez, 1992), soil moisture and acidity (Farley and Kelly, 2004; Harden et al., 2013; Hofstede et al., 2002), vertical nutrient redistribution (Jobbágy and Jackson, 2004), and weathering (Heitkamp et al., 2014).

In addition to differences in vegetation, human populations have long occupied, utilized, and managed tropical alpine puna and páramo grasslands (Kessler, 2002; Wesche et al., 2000)—in some cases intensively and for thousands of years (Harden, 2006; Horn and Kappelle, 2009; Urrego et al., 2011; White, 2013). Widespread throughout the Andes, the coupled practices of burning and grazing reduce aboveground biomass and vegetation cover through trampling, consumption, and combustion, frequently resulting in the stimulation of root growth and exudation (Hofstede, 1995). These land-use practices also alter nutrient cycling directly through nutrient additions. For example, by accelerating N mineralization and nitrification and releasing P, Ca, Mg, and K stored in biomass, fires increase available N and base cations in the short term (Certini, 2005; Wan et al., 2001). Nutrients consumed by grazers are returned to the soil in the more labile forms of urine and feces (Haynes and Williams, 1993). Grazing and burning also influence soil nutrient availability indirectly through effects on the factors that control decomposition, including soil temperature, moisture, and the quantity and quality of litter (Thomas and Asakawa, 1993).

Fire and grazing result in nutrient loss as well. Nutrients are volatilized during fire and from urea, and those deposited to soil in ash or dung can be lost via wind or water erosion (Certini, 2005; Cingolani et al., 2013). As a result, repeated grazing and burning in tropical landscapes may lead to declining soil base cations, N, and P (Hamer et al., 2013), increasing potential for nutrient limitation over the long term (Davidson et al., 2004).

While there is growing interest in the importance of land use and vegetation to soil characteristics at Andean tropical timberlines, much of the recent research focuses on soil C storage. However, less is known in these systems about other dimensions of nutrient availability and cycling, and the influence that land use might have on variation in soil and plant nutrient and isotopic patterns across forest–grassland transitions and the effects of roots and soils on each other (Nierop and Jansen, 2009). Research on Andean timberline soils is also limited in geographical scope, with few studies available for the northern Peruvian Andes.

In this study, we investigated patterns of soil and fine root chemistry across a tropical forest–grassland transition at a Peruvian Andean timberline nearly three decades after the implementation of grazing reduction and fire exclusion policies. Base cations, inorganic N pools, and extractable P in soil, as well as total C and N in soils and fine roots were examined. We employed stable C and N isotopes to evaluate longer-term changes in vegetation and N cycling, respectively: natural abundance of $\delta^{13}C$ can be used to detect shifts in vegetation between plants with C_3 and C_4 photosynthetic pathways because of differences in the carbon signature of C_3 (−34‰ to −23‰) and C_4 plants (−17‰ to −10‰; Cerling, 1999), while the natural abundance of $\delta^{15}N$ is commonly used as an integrator of N cycling (Robinson, 2001). Plant and soil $\delta^{15}N$ tend to be enriched in systems where N losses exceed N inputs, and vice versa.

Using these indicators, we hypothesized that concentrations of base cations, N, and P in soil and of N in fine roots would be lower in grassland compared to forest because long-term grazing and burning often result in losses of these elements (Davidson et al., 2004). Further, we hypothesized that both soil and fine root $\delta^{13}C$ and $\delta^{15}N$ would be enriched in edge and grassland compared to forest because grassland grazing and burning promote: 1) establishment of C_4 grasses; and 2) hydrologic and gaseous losses that typically lead to an enrichment of soil and plant $\delta^{15}N$ (Pardo and Nadelhoffer, 2010).

2. Materials and methods

2.1. Study region

Río Abiseo National Park (7°45′S and 77°15′W) lies along the eastern slopes of Peru's Cordillera Oriental within the Andean-Amazon basin (Fig. 1, inset). The timberline ecotone is a relatively narrow belt between 3200 and 3800 m (Young, 1993a). This study was conducted above the upper altitudinal limit of continuous montane rainforest in the southern region of the park. Long-term observations of climate at this site do not exist but available data indicate mean annual temperature is likely between 6 and 10 °C (Young, 1992). According to satellite-derived rainfall estimates for 2003–2008, annual rainfall ranges from ca. 1000–1500 mm (CPC MORPhing technique; Joyce et al., 2004) with two distinct periods: a wetter period from October to April and a drier period from May to September. In addition, orographic fog forms throughout the year as a result of west-flowing air masses originating in the Amazon basin.

During the Pleistocene, glaciers in Río Abiseo National Park extended down to 3000 m, covering what is presently the timberline ecotone (Rodbell, 1993). Deglaciation began ~13.3 ka and cirques were ice free by at least 10.3 ± 0.6 ka (uncalibrated ^{14}C dates; Rodbell, 1993). A layer of loess ranging in thickness from 25 to 54 cm was deposited across the landscape following deglaciation (Miller et al., 1993). Today, the lower limit of glaciation is demarcated by a clear boundary between north–south trending U-shaped valleys above ~3000 m and steep-sided V-shaped valleys below.

The present study was conducted in one of the glaciated U-shaped valleys between 3391 and 4067 m elevation (Fig. 1). Although knowledge of the park's geology is limited, bedrock along side slopes of the study valley and of cobbles from till is lithologically similar; both are composed of andesite, dacite, and rhyolite porphyries, are dominated by plagioclase, and have low abundance of amphiboles and pyroxenes (R. Ferring, *personal communication*). Detailed soil mapping has not been done, but soils have histic and nearly histic epipedons; soils are black to dark brown and wet with generally greater than 16% C and low bulk density. Full soil pits were not dug at the sites, so it is unknown whether there are any diagnostic subsurface horizons, but exposures throughout the valley suggest that mineral soils in till parent material extend to at least 1 m depth in grassland areas.

Vegetation in the timberline ecotone is a mosaic of tropical alpine grassland and montane rainforest. Inhabited by the Chachapoya peoples during precolonial times (Church and von Hagen, 2008), this montane rainforest extends up to 3200 m on valley floors and to 3450 m on valley sides, intermixing with grasslands between 3200 and 3800 m. In some valleys, small (<5 ha) isolated forest patches dot the landscape. These forest canopies and their edges have one to two orders of magnitude more woody plant species than equivalent timberline forests in temperate areas (that is, 10–100 species rather than 1–3 species; Young and León, 2007). Within forest patches, common tree genera include *Polylepis*, *Weinmannia*, *Clethra*, and *Myrsine*, while at forest edges shrubs of the genera *Baccharis*, *Brachyotum*, and *Miconia* are abundant. The native C_3 tussock grasses *Calamagrostis*, *Cortaderia*, and *Festuca* dominate tropical alpine grasslands (Young, 1993a). Before park establishment in 1983, Andean herders burned these grasslands every one to

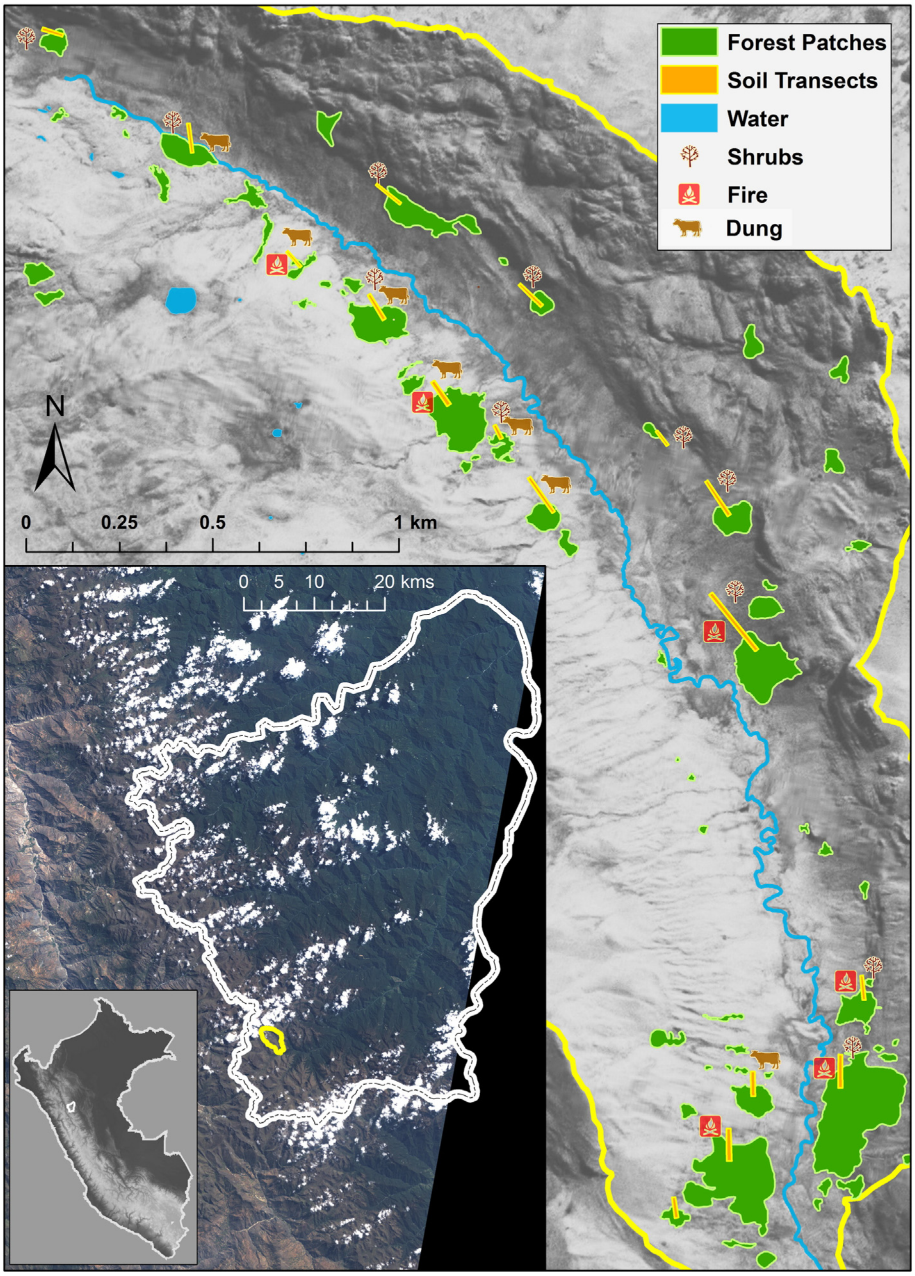

Fig. 1. Map of the study valley in the northern Peruvian Andes, with locations of mapped forest patches and 17 forest–grassland transects. Symbols indicate transects in which visible evidence of shrubs, dung, and past fire was recorded. Water flows from North to South. Note gullying on east- and rock cover on west-facing slopes. Lower left: 15-meter multispectral THEOS image of Río Abiseo National Park (white outline, July 2009) showing the position of the valley (yellow outline) between continuous tropical montane rainforest (right, dark green) and tropical alpine grassland (left, light brown). Inset is map of Peru with Río Abiseo National Park (white outline).

three years to encourage the spread and increase the palatability of grasses for cattle livestock (Young, 1993b). As a result, grasslands contain the fire-adapted C_4 grasses *Paspalum*, *Muhlenbergia*, and *Botriochola* (León et al., 2010), and some forest edges show signs of fire encroachment.

After 1983, land use in the timberline ecotone decreased substantially. Cattle were restricted to a special use zone covering 5% of the total park area, which includes the study valley, and the number of cattle per herder was limited to 30. As a result of these policies, between 1986 and 2002, the cattle population decreased 67%, from ~3000 to ~1000 head (Instituto Nacional de Recursos Naturales, 2003), and burning was prohibited.

2.2. Site selection and transect establishment

In 2010, a total of 63 forest patches ranging in size from 0.025 to 5 ha were mapped across the valley. The valley was then stratified by valley position (low, mid, upper) and aspect (east and west). A total of 17 patches were randomly selected on east- ($n = 9$) and west-facing slopes ($n = 8$; Fig. 1). Five, seven, and five patches were selected in the south-to-north trending lower, mid, and upper sections of the valley watershed, respectively.

In July 2010 and 2011, seventeen forest-edge–grassland transects (3483–3829 m) were laid parallel to slope contours and perpendicular to north-facing patch edges, except in one case where a cliff face did not permit sampling and the opposite edge was sampled (Fig. 1). Distance between neighboring transects ranged from 175 m to 465 m. Forest, edge, and grassland were defined as having >75%, 75–25%, and <25% woody canopy cover, respectively.

2.3. Soil sampling and observations of land use and vegetation

Based on this initial canopy cover assessment, composite soil samples were collected from three 4 m^2 plots in each habitat: at the forest–grassland edge (0 m) and 5 m on either side of the edge (edge habitat); between 10 and 40 m into forest (forest habitat); and between 10 and 40 m into grassland (grassland habitat). The transect length in each habitat was determined by the overall width of the habitat in that transect. In each 4 m^2 plot, we collected three soil cores with 1-m spacing between sampling locations. Overlying leaf litter and a small amount of loose organic debris (Oi) were removed to reveal the upper intact Oa horizon. Soil cores were collected to 20 cm depth, representing the histic epipedon, or to rock using a 2.2 cm diameter soil corer. Soils appeared visually and structurally uniform throughout the entire sampled depth. Samples from each plot were combined in plastic bags, mixed, and air dried in the field prior to shipment to the Ecosystem Geography Laboratory at the University of North Texas.

In 2007, it was estimated that a dozen cattle remained in the valley, a stocking rate of 0.017 cattle ha^{-1}. Therefore, presence of cattle dung was recorded as an indicator of recent grazing. In addition, we noted the presence of remnant trees with visible fire scars, burnt logs, or charcoal on the soil surface. Shrub presence, an indicator of woody plant encroachment, was also noted.

2.4. Elemental and stable isotopic composition of soils and fine roots

Soil samples were homogenized and passed through a 2 mm sieve to separate rocks and organic matter before chemical analysis. Live fine roots (<2 mm) were separated from soil based on color and elasticity following the protocol of Persson and Stadenberg (2010).

Bulk soil samples were shipped to Auburn University where they were analyzed for extractable cations, inorganic N, and pH. Soils were extracted with a Mehlich I (Mehlich, 1953) double acid extract using a 1:4 soil:extractant ratio and analyzed for calcium (Ca), potassium (K), magnesium (Mg), sodium (Na), and phosphorus (P) using ICP OES on a Varian Vista-MPX Radial instrument. Ten grams of soil was extracted for ammonium (NH_4^+) and nitrate (NO_3^-) using 1 M KCl and analyzed colorometrically using a Bran Luebbe Autoanalyzer 3 (Norderstedt, Germany). A 1:1 soil:water ratio was used for pH determination using a Labfit AS3000 meter with a glass electrode. Because precise volumes of soil could not be collected under the field conditions, soil bulk density (D_b) was estimated following the method of Adams (1973)

$$D_b = 100/[(\%OM/OMD_b) + (100-\%OM)/MD_b] \tag{1}$$

where OMD_b is the average bulk density of organic matter (0.223 g cm^{-3}) and MD_b is the average mineral bulk density (1.64 g cm^{-3}; Mann, 1986). Using these bulk density estimates, the mass of each element in the top 10 cm, the depth to which such calculations could be made for all transects, was calculated.

Soil isotopic analyses were conducted at the Kansas State Stable Isotope Mass Spectrometry Lab. A 1 mg subsample of homogenized soil was dried at 60 °C for 24 h, ground to a fine powder, and analyzed for total carbon, total nitrogen, $\delta^{13}C$ and $\delta^{15}N$ on a ThermoFinnigan Delta Plus mass spectrometer (Thermo Fisher Scientific Inc., Waltham, MA, USA). Samples were analyzed using a flour standard. Deviation of standards run as samples from expected values were <0.05‰ for $\delta^{13}C$ and <0.15‰ for $\delta^{15}N$. Replicate samples differed, on average, by 0.06‰ and 0.14‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Live fine roots were washed with deionized water and dried at 70 °C for 48 h, ground to a fine powder, and analyzed for total carbon, total nitrogen, $\delta^{13}C$ and $\delta^{15}N$ at Washington State University Stable Isotope Core facility. Fine root samples were converted to N_2 and CO_2 with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) and analyzed with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, ThermoFinnigan, Bremen, Germany) using acetanilide and corn as standards. Standard deviation of replicate NIST-traceable peach standard was 0.03‰ for $\delta^{13}C$ measurements and 0.12‰ for $\delta^{15}N$.

Stable isotope natural abundances are expressed as

$$\delta(‰) = (R_{sample}/R_{standard}-1) \times 1000 \tag{2}$$

where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Isotopic results are reported relative to Vienna Peedee belemnite atmospheric N_2, for C and N, respectively.

2.5. Statistical analysis

For each transect, soil and fine root elemental and isotopic data were averaged by habitat, the primary unit of analysis, across all replicate transects. To assess the normalcy of data and homogeneity of variances, the Shapiro–Wilk and Levene's tests, respectively, were used. One-way analysis of variance (ANOVA) was used to examine differences in soil nutrient concentrations, the mass of each element in the top 10 cm, and stable isotopic composition among forest, edge, and grassland habitats. In cases with significant differences among habitats, Tukey's honest significant difference was used for pairwise comparisons (two-tailed). Kruskal–Wallis nonparametric ANOVA with Steel Dwass pairwise comparisons was used when sample data did not meet the assumption of normality. Correlations among soil, fine root, and stable isotope concentrations were assessed using Pearson's correlation coefficient and Spearman's Rho.

In alpine grasslands, we compared soil and root properties in areas with and without cattle dung, evidence of past fire, and shrubs using two-sample t-tests, or Welch's approximate t-test when habitats had unequal variance. For data with non-normal distributions, the Mann Whitney-U test was used. Contingency analysis was employed to examine associations among categorical variables, including presence/absence of cattle dung, past fire, shrubs, and aspect. Fisher's exact test was used to test for differences between proportions. All statistical analyses were performed using JMP v11 (SAS Institute, Cary, NC, USA).

3. Results

3.1. Bulk elemental composition, soil nitrogen pools, and $\delta^{15}N$ at timberline

Soil concentrations of Ca and K were significantly lower in grassland ($P = 0.038$, $P = 0.024$, respectively) than in forest, while edge soils had concentrations intermediate between the two (Table 1). A similar pattern was observed for P (Fig. 2a). Edge ($P = 0.009$) and grassland ($P < 0.0001$) habitats both had lower Mg concentrations in soil than forest habitat, whereas Na concentrations did not vary in the ecotone (Table 1). The total mass of extractable Ca and Mg in surficial soil exhibited the same pattern as did concentration; Ca was lower in grassland ($P = 0.046$) than in forest, and intermediate in the edge, while Mg was lower at the edge ($P < 0.05$) and in grassland ($P = 0.0004$) than in forest. Soil K content in grassland was also lower compared to forest, but this difference was not significant ($P = 0.059$). No differences in the mass of P or Na in the top 10 cm of soil were detected among habitats.

The soil inorganic N pool was dominated by NH_4^+–N, with concentrations sevenfold higher, on average, than concentrations of NO_3^-–N across habitats (Table 1). Mean soil NH_4^+–N and NO_3^-–N concentrations increased from forest to edge to grassland, yet two outlier transects with extremely high concentrations of both forms of N affected this spatial pattern; median values showed a different pattern across the forest–edge–grassland transition: 40, 27, and 33 ppm for NH_4^+–N, and 6.3, 6.2, and 7.5 ppm for NO_3^-–N in forest, edge, and grassland, respectively.

Table 1
Mean (SE) extractable elemental and stable isotopic composition of soils and fine roots in forest, edge, and grassland habitat ($n = 17$ transects) at timberline in the northern Peruvian Andes. Aerial mass content is for the top 10 cm. Different letters across rows indicate significant differences ($P < 0.05$).

	Forest	Edge	Grassland
Bulk soil			
P (ppm)	31.1 (4.4)^{A}	21.7 (2.6)^{AB}	18.1 (2.9)^{B}
P (mg m^{-2})	1362 (166.3)^{A}	1112.5 (142.9)^{A}	912.4 (149.6)^{A}
Ca (ppm)	1684.7 (266.9)^{A}	1468.2 (423.6)^{AB}	1441.7 (602.9)^{B}
Ca (mg m^{-2})	76,910.8 (13,258.3)^{A}	73,524.7 (20,311.1)^{AB}	63,546.1 (24,845.2)^{B}
K (ppm)	208 (24.4)^{A}	152.4 (8.1)^{AB}	133.5 (13.8)^{B}
K (mg m^{-2})	9128.6 (898.2)^{A}	7641.7 (420.5)^{A}	6647.6 (684.2)^{A}
Mg (ppm)	194.10 (19.61)^{A}	120.14 (14.53)^{B}	89.21 (12.25)^{B}
Mg (mg m^{-2})	8865 (946)^{A}	6121.6 (847.8)^{B}	4267.3 (501)^{B}
Na (ppm)	68.4 (7.9)^{A}	80.9 (9.5)^{A}	90.1 (12.8)^{A}
Na (mg m^{-2})	3232.7 (456.5)^{A}	4166.4 (556.8)^{A}	4609 (703.4)^{A}
NH_4–N (ppm)	48.83 (11.94)^{A}	56.17 (16.31)^{A}	69.66 (24.69)^{A}
NH_4–N (mg m^{-2})	2442 (481.6)^{A}	2949.8 (755.9)^{A}	3213.9 (1076.4)^{A}
NO_3–N (ppm)	7.54 (1.84)^{A}	8.83 (2.39)^{A}	10.34 (2.56)^{A}
NO_3–N (mg m^{-2})	365.2 (73.6)^{A}	457.1 (94.3)^{A}	488.1 (112.1)^{A}
pH	4.3 (0.11)^{A}	4.4 (0.08)^{A}	4.5 (0.12)^{A}
C (%)	21.15 (1.65)^{A}	18.41 (1.29)^{A}	18.83 (1.39)^{A}
C (g m^{-2})	9123.5 (204.4)^{A}	8776.5 (180.6)^{A}	8897.7 (185.3)^{A}
N (%)	1.31 (0.09)^{A}	1.19 (0.08)^{A}	1.23 (0.08)^{A}
N (g m^{-2})	577 (12.5)^{A}	576.3 (15.7)^{A}	590.5 (16.4)^{A}
δ^{13}C (‰)	−26.14 (0.14)^{A}	−24.57 (0.21)^{B}	−24.12 (0.22)^{B}
δ^{15}N (‰)	5.63 (0.23)^{A}	6.38 (0.24)^{B}	6.52 (0.25)^{B}
Fine roots			
C (%)	45.89 (1.04)^{A}	45.94 (0.39)^{A}	45.59 (0.38)^{A}
N (%)	1.35 (0.09)^{A}	0.89 (0.04)^{B}	0.73 (0.05)^{B}
δ^{13}C (‰)	−28.16 (0.34)^{A}	−26.55 (0.37)^{B}	−25.11 (0.35)^{C}
δ^{15}N (‰)	1.39 (0.23)^{A}	1.66 (0.20)^{A}	1.60 (0.21)^{A}

Soil NH_4^+–N, NO_3^-–N, and total N concentrations and mass in the top 10 cm of the soil did not differ by habitat (Table 1), but fine root N concentrations did (Fig. 2b). Fine root N concentrations were significantly lower in edge ($P < 0.0001$) and grassland ($P < 0.0001$) compared to forest.

The natural abundance of soil δ^{15}N in forest, edge, and grassland habitat ranged from 3.8‰ to 8‰ and was ~1‰ higher, on average, in edge ($P = 0.0828$) and grassland ($P = 0.0146$) relative to forest (Fig. 2c). Several edge transects had δ^{15}N values similar to the mean value for forest (5.6‰; Table 1). Overall, fine roots were more depleted in δ^{15}N than were soils, with values ranging from −0.2‰ to 3.4‰, but unlike soils, fine root values did not differ significantly across the ecotone (Fig. 2d).

There were several significant correlations among soil and fine root concentrations and the natural abundance of δ^{15}N in soil and roots. Soil δ^{15}N was negatively correlated with soil extractable P ($\rho = -0.32$, $P = 0.0235$), soil total N ($\rho = -0.36$, $P = 0.0092$), and fine root N ($\rho = -0.41$, $P = 0.0037$). In addition, fine root δ^{15}N was positively correlated with soil δ^{15}N ($\rho = 0.31$, $P = 0.0297$).

3.2. Soil C and soil and fine root δ^{13}C at timberline

Neither soil C concentrations nor C mass in surficial soil differed significantly among the three habitats (Table 1). Mean soil δ^{13}C, however, was significantly higher in edge (−24.6‰, $P < 0.0001$) and grassland (−24.1‰, $P < 0.0001$) compared to forest (−26.1‰) (Fig. 3a inset). The carbon isotopic composition of soils across all transects and habitats ranged from a minimum −27‰ to a maximum −22.2‰ (Fig. 3a). These soil δ^{13}C values were more variable within edge and grassland than forest habitat, where all values fell below the grand mean of −24.9‰. Values in the edge habitat varied most, by 3.4‰ across transects, with some edges isotopically more similar to forest and others more similar to grassland.

Fine root δ^{13}C was lower and varied more than the δ^{13}C of soil, ranging from a mean of −32‰ to −21‰ (range 11‰) across habitats and

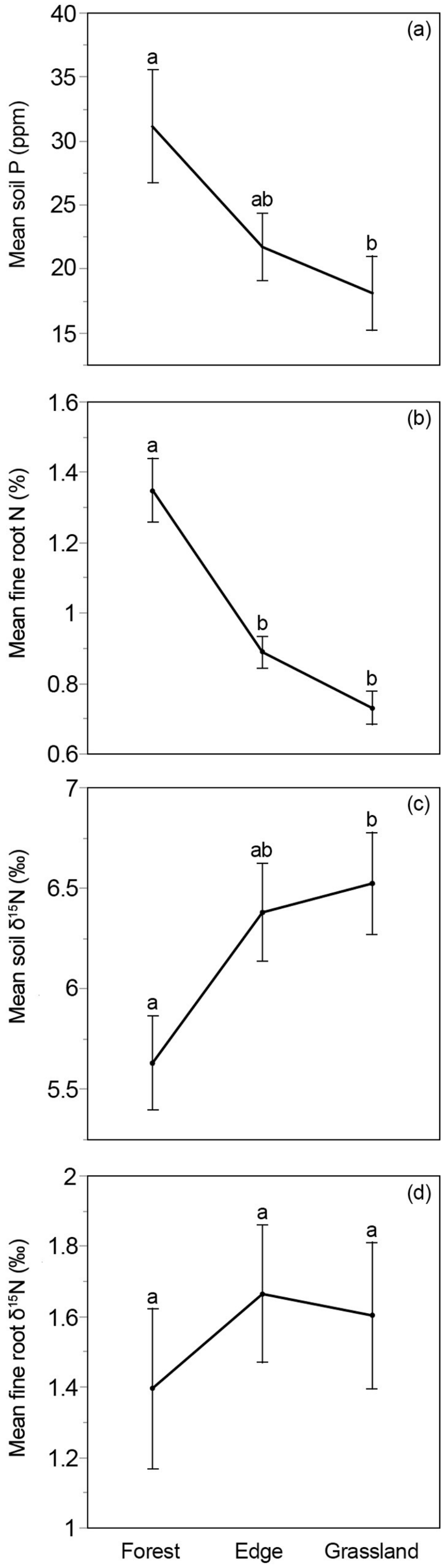

Fig. 2. Concentrations (mean ± SE) of a) P in soils, and b) N in fine roots (<2 mm) in forest, edge, and grassland habitat sampled at timberline in northern Peru ($n = 17$ transects). Mean δ^{15}N (±SE) of c) soils, and d) fine roots in forest, edge, and grassland habitat ($n = 17$ transects). Different letters represent significant differences among habitats (one-way ANOVA, $P < 0.05$).

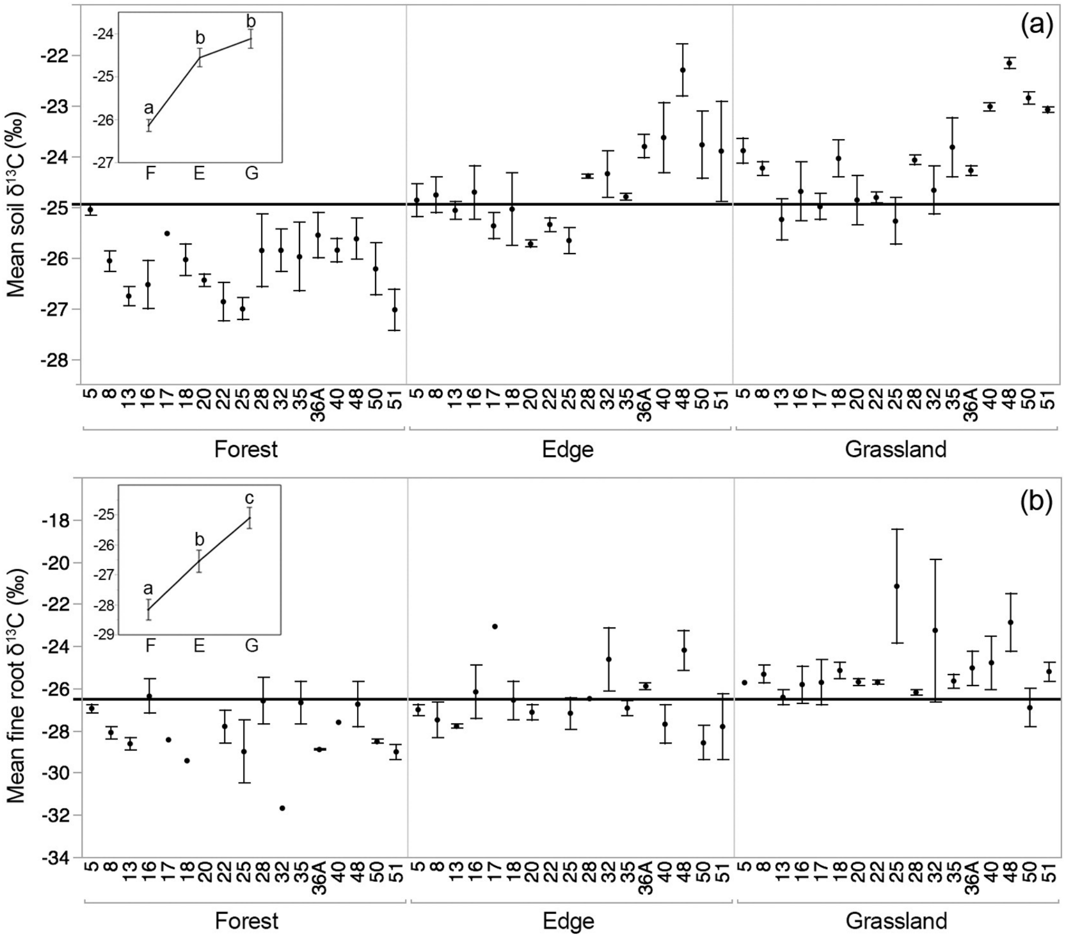

Fig. 3. a) Mean $\delta^{13}C$ ($\pm$SE) values of soils for each patch sampled in forest, edge, and grassland habitat at timberline in northern Peru with grand mean (black line, −24.9‰). Inset: mean $\delta^{13}C$ ($\pm$SE) of soils for forest, edge, and grassland habitat ($n = 17$ transects). Different letters represent significant differences among habitats (one-way ANOVA, $P < 0.01$). b) Mean $\delta^{13}C$ ($\pm$SE) values of fine roots for each patch sampled in forest, edge, and grassland habitat with grand mean (black line, −26.5‰). Note difference in y-axis scale. Inset: mean $\delta^{13}C$ ($\pm$SE) of fine roots for forest, edge, and grassland ($n = 17$ transects). Different letters represent significant differences among habitats (Kruskal–Wallis, $P < 0.01$).

transects (one high and one low outlier excluded, range 6.6‰) (Fig. 3b). The mean $\delta^{13}C$ of fine roots was significantly higher in grassland (−25.1‰, $P < 0.0001$) than in forest (−28.2‰). Yet, unlike soil, fine roots at edges (−26.6‰) were depleted in $\delta^{13}C$ ($P = 0.0066$) relative to those in grassland (Fig. 3b inset; Table 1).

Relationships were found between some of the C and N chemistry variables. Fine root $\delta^{13}C$ was significantly positively correlated with soil $\delta^{13}C$ ($r = 0.51$, $P = 0.0002$), whereas soil C concentrations were significantly negatively correlated with soil $\delta^{13}C$ ($r = -0.4$, $P = 0.0038$). We also found a strong significant positive correlation between soil $\delta^{13}C$ and soil $\delta^{15}N$ ($r = 0.69$, $P < 0.0001$; Fig. 4).

3.3. Grazing, fire, and shrubs and soil and fine root chemistry in grasslands

Evidence of recent grazing, past fire, and shrub encroachment varied spatially across the landscape and, in some cases, was associated with topography (Fig. 1). Shrubs were recorded more frequently than both dung and fire, in a total of eleven (65%) of the grassland transects. All eight of the grassland transects situated on west-facing slopes had signs of shrub encroachment whereas only three grassland transects with shrubs were found on east-facing slopes. This association between shrub presence and aspect was significant (Fig. 5a; $P = 0.009$). Cattle dung was recorded in seven of the grassland transects; all of these were located on east-facing slopes (Fig. 5b; $P = 0.0023$). In addition, we found that concentrations and mass of Na were nearly twofold higher on east- than west-facing slopes, although differences were not significant ($P = 0.092$, $P = 0.194$). We observed evidence of past fire in six sampled grasslands with equal frequency on both sides of the valley (Fig. 5c).

Shrub presence was related to the stable carbon isotopic composition of soil. Mean soil $\delta^{13}C$ was ~2‰ lower in grassland plots where shrubs were present than where they were not ($P = 0.0019$; Fig. 6a). Soil $\delta^{15}N$ tended to be lower in grassland plots with shrubs compared to plots without shrubs, but this difference was not significant ($P = 0.145$; Fig. 6b). Higher soil Ca concentrations and mass ($P = 0.0057$,

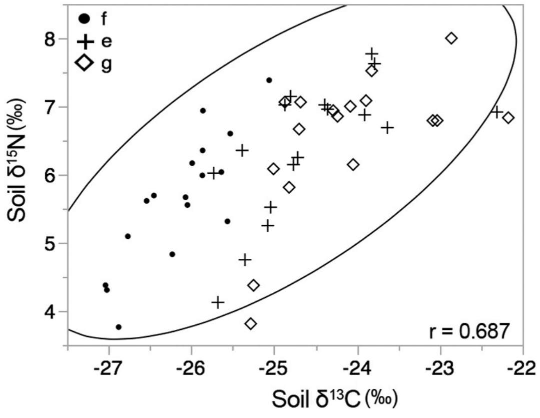

Fig. 4. Scatterplot of soil $\delta^{13}C$ and soil $\delta^{15}N$ ($r = 0.687$). Data are from forest (dot), edge (plus), and grassland (diamond) transects ($n = 17$ transects) at timberline in northern Peru.

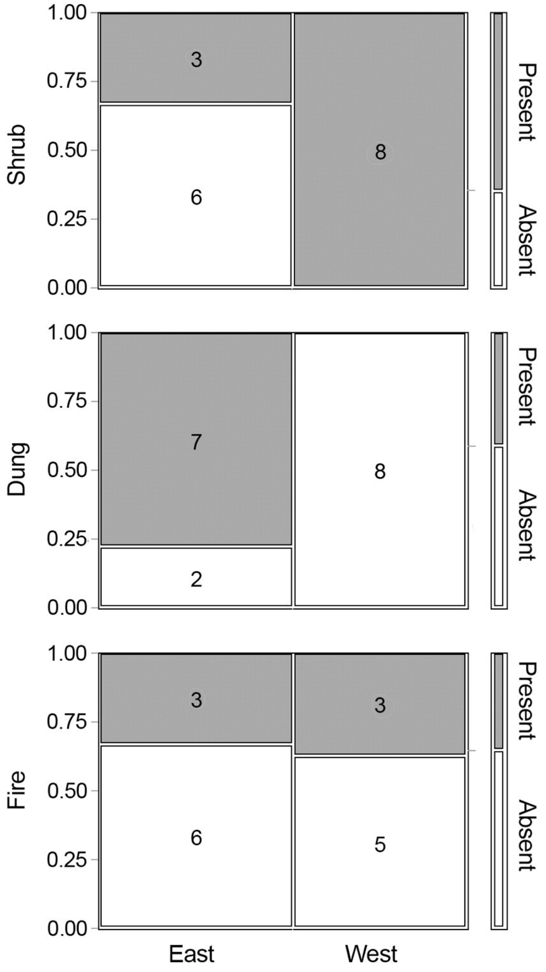

Fig. 5. Mosaic plots showing the frequency of observed shrub presence, cattle dung, and past fire in grassland habitat on east and west-facing slopes in northern Peru. The right y-axis shows the overall proportion of transects with and without recorded evidence of shrubs, dung, and past fire.

$P = 0.0057$) were also measured in grassland plots with than without shrubs.

Soil $\delta^{13}C$ and $\delta^{15}N$ did not differ significantly between transects with and without evidence of recent grazing. Where past fire was observed, there were also no apparent differences in the carbon isotopic composition of soil, although soil $\delta^{15}N$ was often greater ($P = 0.078$). Both forms of land use influenced fine root chemistry, although in contrasting directions. Transects with cattle dung had higher fine root $\delta^{13}C$ (Fig. 7a, $P = 0.0516$) and fine root %N (Fig. 7b, $P = 0.0605$), while transects with evidence of fire had significantly lower fine root $\delta^{13}C$ (Fig. 7c, $P = 0.0129$) and fine root %N (Fig. 7d, $P = 0.0242$), than did transects with no visual evidence of these disturbances.

4. Discussion

4.1. Enhanced losses of base cations, N, and P across a tropical forest–grassland transition

At this remote Peruvian site, forest patches had the highest and alpine grasslands had the lowest concentrations and masses of extractable Ca and Mg in soil, lending support to our hypothesis that soil nutrients would decline from forest into grassland. Given the lack of difference observed in parent material across the forest–grassland boundaries, either enhanced cycling and vertical redistribution of these nutrients by trees (Jobbágy and Jackson, 2004) or leaching from grasslands is a plausible explanation for the lower abundance of base cations under grassland relative to forest (Table 1). A synthesis conducted by Jobbágy and Jackson (2004) showed greater uplift of such nutrients as Ca and Mg under broadleaf forests than grasses, leading to differences in surface soil chemistry between vegetation types. However, because uplift involves nutrient uptake from deep soil layers and redistribution to shallower depths, samples from deeper in the soil profile would be needed to test this hypothesis. At our study site, where conditions are consistently wet, base cation leaching is likely to dominate over vertical uplift (Porder and Chadwick, 2009). Thus, base cations could have been preferentially weathered and leached out of grassland profiles as was found by Heitkamp et al. (2014) in southern Peru.

An alternative—and not mutually exclusive—mechanism is that soil nutrient patterns within the ecotone reflect imprints of past land use (Hamer et al., 2013) that are still detectable after nearly three decades of grazing and fire reduction. Similar to our study, research conducted in montane Ecuador showed substantially lower concentrations of P (6-fold lower), Mg (5-fold lower), and K (2-fold lower) in the surface soils of grazed grassland compared to forest (Chacón et al., 2009; Hofstede et al., 2002). Patterns of soil $\delta^{15}N$ and correlations between soil $\delta^{15}N$ and some aspects of fine root and soil chemistry provide further support for this conjecture. Consistent with findings from highland Ethiopia and New Zealand (Eshetu and Högberg, 2000; Mudge et al., 2014), edge and grassland habitat sampled in this study had soils that were enriched in $\delta^{15}N$ compared to those of forest (Fig. 2c). While there are many plant, soil, and landscape processes that affect the natural abundance of soil $\delta^{15}N$ (Pardo and Nadelhoffer, 2010), our findings indicate that these forest–grassland shifts are likely due to habitat influences on soil N transformations and N losses. Mineralization, nitrification, denitrification, and ammonia volatilization are all fractionating pathways that result in ^{15}N-depleted products (Högberg, 1997). When these compounds are lost via leaching or as gases, residual N becomes enriched in $\delta^{15}N$ (Pardo and Nadelhoffer, 2010). We did not measure

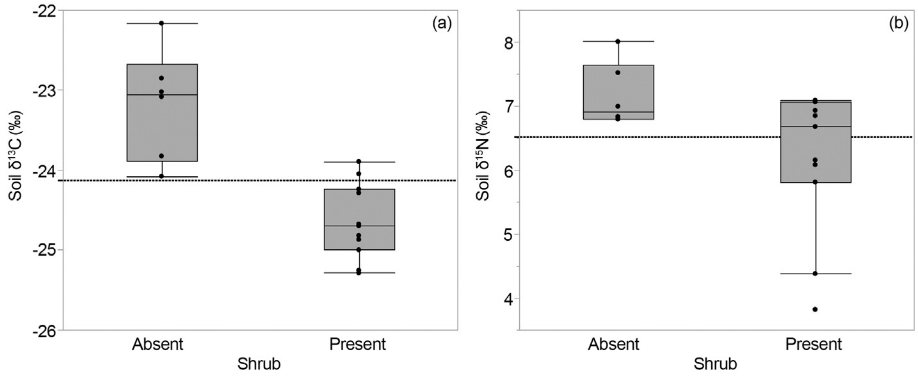

Fig. 6. Soil $\delta^{13}C$ and soil $\delta^{15}N$ in grassland transects with ($n = 11$ transects) and without ($n = 6$ transects) recorded presence of shrubs at timberline in northern Peru. Boxplots show median, 1st and 3rd quartiles, and outliers. Whiskers extend to the outermost data point that falls within 1.5 times the interquartile range in either direction.

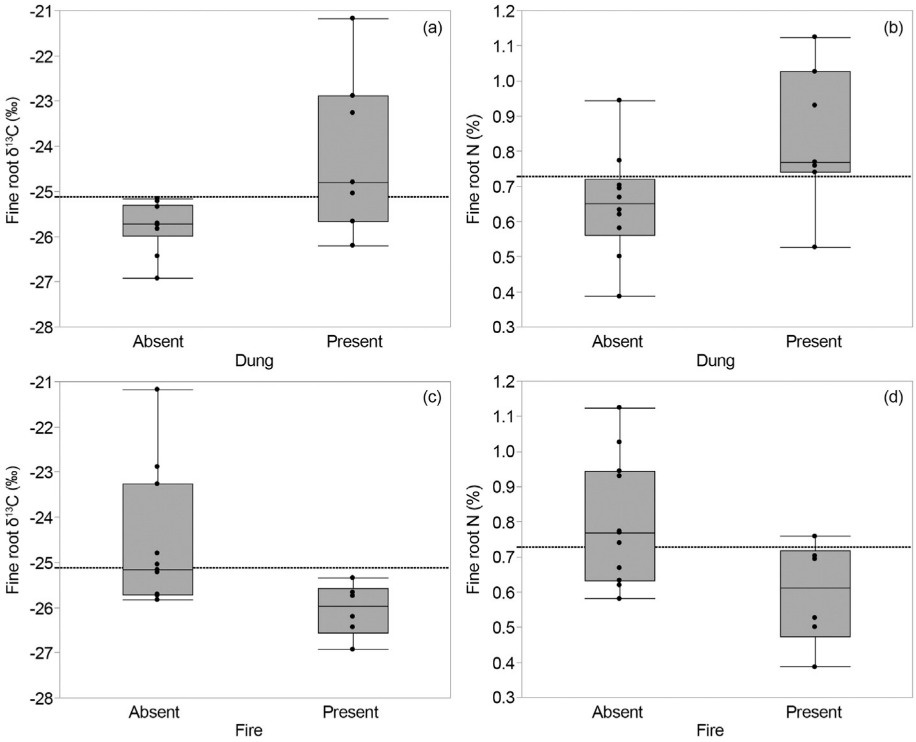

Fig. 7. Carbon isotopic composition and N concentrations of fine roots in grassland transects with and without recorded evidence of cattle grazing ($n = 7$ and $n = 10$ transects, respectively) and past fire ($n = 6$ and $n = 11$ transects, respectively) at timberline in northern Peru. Boxplots show median, 1st and 3rd quartiles, and outliers. Whiskers extend to the outermost data point that falls within 1.5 times the interquartile range in either direction.

soil N mineralization or nitrification rates, and soil N pools did not differ by habitat. However, soil N, soil P, and fine root N concentrations all decreased as a function of increasing soil δ^{15}N, indicating that the nitrogen isotope signature in edge and grassland habitat likely reflects net nutrient losses there (Fig. 2). While it has been suggested that the use of different N sources by plants might also drive changes in soil δ^{15}N across forest–pasture gradients (Piccolo et al., 1994), at this site fine root δ^{15}N did not differ among forest, edge, and grassland habitat. In conclusion, our soil nutrient and stable isotope data suggest that nutrient losses associated with fire and grazing are the primary mechanism contributing to soil chemistry patterns within this tropical timberline ecotone.

4.2. *Woody plant encroachment at timberline after release from fire and grazing*

As we hypothesized, soil carbon isotopic values measured within the timberline ecotone were enriched in edge and grassland compared to forest (Fig. 3). That fine root δ^{13}C and soil δ^{13}C were strongly positively correlated underscores the influence of vegetation, specifically belowground detrital inputs, on the carbon isotopic composition of soils along the forest–grassland transition. The higher values we measured at forest edges and in grasslands could have resulted from the blending of C_3 and C_4 biomass (Rhoades et al., 2000) or from species-specific differences in the isotopic composition of high Andean C_3 vegetation (Szpak et al., 2013).

Environmental factors, including irradiance, temperature, and soil moisture also may alter plant discrimination (Tieszen, 1991) as well as organic matter decomposition (Hofstede, 1995), and in turn soil δ^{13}C patterns under distinct vegetation types. Indeed, there was a strong positive correlation between soil δ^{13}C and soil δ^{15}N across habitats, suggesting increasing fractionation in both C and N as a result of the decomposition process (Nadelhoffer and Fry, 1988; Fig. 4). Higher soil δ^{13}C in edge and grassland was associated with lower C concentrations as well, indicating either lower C inputs to or greater C losses from these habitats.

Regardless of the mechanisms underlying the shift in soil δ^{13}C from forest into grassland, we were surprised to find that fine roots at forest edges had δ^{13}C values that were decoupled from those of soil, a pattern suggestive of fine roots extending beyond canopy edges or forest expanding into grasslands (Fig. 3). The latter hypothesis is supported by remote sensing analyses of vegetation change in protected areas containing tropical Andean timberlines. For example, a recent study of ecotone migration in Manu National Park documented a mean upslope timberline shift of 0.24 m yr^{-1} between 1963 and 2005 (Lutz et al., 2013). In Río Abiseo National Park, forest patches in the grassland zone increased by 607% in area between 1987 and 2001, indicating significant forest recovery and expansion above timberline (Kintz et al., 2006). Moreover, Kintz et al. (2006) detected a 34% increase in shrub area, with grasslands transforming into shrubland. Coupled with the stable C isotope data, these results point to expansion of woody taxa after release from more intensive grazing and fire, or possibly in response to climatic warming.

4.3. *Patchy spatial patterns of encroachment and nutrient cycling in Andean grasslands*

Results from this and another study suggest that spatially variable patterns of land use promote differential rates of woody plant encroachment into grasslands. Matson and Bart (2013) examined shrub distribution in Ecuador 10 years after release from burning and grazing and found higher shrub cover in less frequently disturbed areas. Similarly, here shrubs were more prevalent on west-facing slopes (Fig. 5), where there was less visible evidence of cattle dung and soil concentrations of Na—a nutrient limiting animal growth—were nearly twofold lower. This apparent concentration of grazing on east- and shrubs on west-facing slopes in our valley is likely due to pronounced differences in topography (Fry et al., 2015). The east-facing side of the valley has a high plateau and greater expanse of grazeable area than the western side with its greater proportion of rock cover (Fig. 1).

Soil and plant chemical properties within the Andean grasslands reflect these heterogeneous patterns of woody shrub encroachment and land use. Soils under shrubs had $\delta^{13}C$ and $\delta^{15}N$ values that were intermediate between those of forest and surrounding grassland as well as higher concentrations of Ca, patterns which point to localized accumulation of nutrients beneath shrub canopies (Fig. 6). In contrast, evidence of grazing and burning were primarily associated with changes in fine root C and N (Fig. 7). Grassland areas with cattle dung had roots enriched in $\delta^{13}C$, which we expected given the presence of C_4 taxa (e.g., *Paspalum*, *Muhlenbergia*) within our sampled grasslands, whereas fire-affected areas had fine roots depleted in $\delta^{13}C$, possibly due to root growth by resprouting C_3 grasses (Ansley et al., 2006). The patchy root $\delta^{13}C$ signatures we found are perhaps not surprising; grazing and burning have been found to enhance spatial heterogeneity in fine root biomass C in high-elevation tropical pastures (Potthast et al., 2012).

Recent grazing and past fire were associated with changes in N as well. Fine root N concentrations were generally higher in areas where cattle dung was observed, even though differences in soil $\delta^{15}N$ were not detected, possibly indicating an increase in N availability due to recent grazing (Craine et al., 2009). In contrast, fine roots had lower N concentrations in fire-affected areas. It is well established that in the short term, acceleration of N cycling after fire increases opportunities for N loss and reductions in plant-available N (Wan et al., 2001). For example, in southern Peru, N stocks in alpine grasslands were lower in areas where there was evidence of fire (Zimmermann et al., 2010). To summarize, grazing and burning appear to have contributed to spatial heterogeneity in soil resources within Andean alpine grasslands. In the future, fine-scale legacy-induced soil nutrient heterogeneity could influence the location, form, and dynamics of vegetation within the ecotone (e.g., Smithwick et al., 2009).

While it is not possible to disentangle the many mechanisms (e.g., environmental, litter quality, plant–soil feedbacks) that may have influenced the patterns we document here, our findings still underscore the need to consider land use in interpretations of present and future tropical timberline dynamics (Farley et al., 2013). Similar to Río Abiseo National Park, conservation mandates have resulted in restrictions on grazing and fire in other newly established protected areas in the high Andes. Our findings suggest that woody plant encroachment is likely to vary as a consequence of prior land use (Fig. 5) and increase the patchiness of soil nutrients across the landscape. While in temperate regions seedling mortality and geomorphology are considered fundamental mechanisms driving some patchy treeline forms (Resler, 2006; Smith et al., 2003), our results show that in this tropical region patchiness may also be strongly influenced by land-use processes.

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