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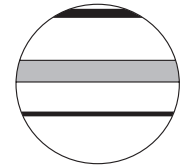
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Abstract

Tussock grass páramo constitutes the dominant vegetation of the high tropical Andes and cordilleras of Costa Rica. Its distribution, composition and the location of the upper forest line are ascribed, by broad consensus, to climate. The zonal argument finds support in the altitudinal movements of páramo during the Pleistocene, clearly responding to changes in precipitation and temperature. I ask here, however, if the principal ecological variables driving post-Pleistocene páramos are circumscribed solely by climate. The combined pollen, charcoal and archaeological evidence generated in recent decades suggests a distinct Holocene etiology. Five principal conclusions emerge: (1) the sedimentary charcoal record establishes that grass páramo is a fired landscape, (2) natural sources of fire, specifically volcanoes and lightning, are incapable of generating the fire regime apparent in the sedimentary charcoal record, (3) burning at most sites intensified significantly between 13,000 and 11,000 cal. yr BP, and maintained heightened levels during the Holocene, (4) archaeological findings suggest that the original settlement of the Andes coincided with the sedimentary charcoal rise, and (5) the subsistence logic of hunter-gatherers argues strongly for firing the vegetation to increase resource productivity and reliability. From the pioneering mixed vegetation after deglaciation, anthropic fire selected in favor of tussocks and against woody species, generating a novel plant association. I propose, therefore, that Holocene grass páramo is not zonal vegetation, but rather a hunter-gatherer landscape.

Keywords

grass páramo, Holocene fire, hunter-gatherer, pollen, sedimentary charcoal, tropical Andes

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Introduction

Neotropical páramos form an archipelago of elongated herbaceous islands covering high mountain terrain between Costa Rica and northern Peru. In sum they occupy over 35,000 km² and extend from 11°N to 8°S latitude (Hofstede et al., 2003; Luteyn, 1999). Botanists and ecologists, struck by the beauty of these landscapes and by the resilience and diversity of their flora, have studied páramos since at least the times of Alexander von Humboldt, 200 years ago (von Humboldt and Bonpland, 2009 [1807]). Humboldt viewed páramo as a response to elevation, in the manner of alpine vegetation, and elegantly schematized the altitudinal distribution of tropical Andean flora from lowlands to perennial snow. Páramos occupied the highest of these vegetation zones, between the upper montane forest and the snowline. The zonal paradigm employed by Humboldt became the measure by which páramos were understood and scientifically explored, and today remains the consensus view.

Twentieth century landscape-scale ecologists universally viewed grass páramo as natural vegetation (Hartshorn, 1983; Troll, 1968; Walter, 1985; Weberbauer, 1945), and most contemporary páramo researchers concur (Bakker et al., 2008; Cleef, 1981; Hooghiemstra, 1984; Hooghiemstra and Cleef, 1995; Horn, 1993; Horn and League, 2005; Körner, 1998; Kuhry et al., 1993; Moscol Olivera and Cleef, 2009a; Moscol Olivera and Hooghiemstra, 2010; Van der Hammen, 1974). In the zonal paradigm the transition from forest to open vegetation and the altitude of the generalized upper forest limit (UFL) primarily reflect temperature constraints, as do the characteristic forms and physiological adaptations of páramo plants. Localized microclimates above the UFL permit the establishment of patch forests, defining an upper tree line. Precipitation regimes control atmospheric and soil humidity and govern, for a given mean temperature, the characteristic life forms and floristics, and influence the altitudinal limits of páramo communities (Sklenář and Lægaard, 2003). Physiological aridity

associated with high transpiration rates, wind and cold provides an explanation for the curious combination of a wet climate and the xeric adaptation of many páramo plants (Leuschner, 2000; Weberbauer, 1945). Secondary to climate, edaphic factors including soil pH, water deficit or excess and nutrient status determine most azonal formations.

In the zonal view three broadly horizontal altitudinal belts are emplaced in ascending elevation on the mountainside (Cleef, 1981; Cuatrecasas, 1968; Hooghiemstra, 1984; Luteyn, 1999): (1) shrub- or sub-páramo, interpreted to be a transitional habitat directly above montane forest; (2) tussock-dominated grass páramo, also called 'páramo proper' or 'true páramo' to emphasize its zonal centrality (Lauer, 1981); and (3) desert páramo, or super-páramo, a formation poor in long-stem tussock grasses and dominated by isolated cushion plants, sclerophyllous dwarf shrubs and acaulescent rosettes, mosses, lichens and open ground (Monasterio, 1979; Sklenář, 2006; Sklenář and Balslev, 2005). Locally specific plant associations can be identified within each altitudinal belt, but the architecture and growth forms of these associations are similar across the broad expanse of northern Andean páramos.

Pleistocene pollen records from the high plain of Bogotá, Colombia, document the altitudinal displacements of páramo and contiguous forest. These records detail how herbaceous vegetation descended and ascended the mountain profile in consort with the waxing and waning of Pleistocene glacial cycles (Groot et al.,

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Figure 1. (a) A grass páramo at 3600–3800 m, Eastern Cordillera, Ecuador. (b) A pure stand of tussock grass at 3600 m, Eastern Cordillera, Ecuador. Plants are 50–70 cm high and form a closed canopy.

2011; Hooghiemstra, 1984; Hooghiemstra and Cleef, 1995; Hooghiemstra and Van der Hammen, 2004; Marchant et al., 2002; Van der Hammen, 1979; Van der Hammen and Cleef, 1986). Contemporary researchers consider the early-Holocene emplacement to be the latest manifestation of prior cycles, on the assumption that the present reflects Pleistocene interglacial conditions (Hooghiemstra et al., 2006). This assumption, however, requires examination. To this end, evidence generated only in recent decades, including new pollen analyses, sedimentary charcoal studies, and the emerging history of early peopling of the Andes, will be appraised.

The term ‘grass páramo’, of central interest here, refers to the exuberant tussock-dominated grasslands found between the UFL and the desert páramo above (Figure 1a, b). This band occupies elevations between a lower limit adjoining the UFL and an upper limit at 4000–4300 m. Mature tussocks at moderate grass páramo elevations establish a closed canopy typically of 70–90% coverage, and reaching 60 cm or more in height. Most shrub páramos retain a tussock coverage of 30–40%. Grass páramo may also include isolated forest patches, gallery forests, and wetlands of variable size within the grassland matrix. The objective of the present discussion is to examine the etiology of grass and brush páramo specifically. Desert páramo at higher elevations and puna grasslands at higher latitudes are not objectives, although they are referenced in the discussion and tables where they provide context for the analysis of grass páramo.

Data sets

Pollen record

At local last glacial maximum (LLGM), 26,000–20,000 cal. yr BP, ice covered the northern Andes down to 3300–3600 m, and for some wetter locations to 2800 m, where ice tongues may locally have been in proximity to montane forest (Clapperton, 1993a, 1993b; Clark et al., 2009; Heine, 2000; Lachniet and Vázquez-Selem, 2005; Thouret et al., 1996; Van der Hammen and Cleef, 1986). At this time the UFL appears to have been situated at about 2000–2400 m (Hooghiemstra and Van der Hammen, 2004; Van der Hammen and Cleef, 1986; Van der Hammen and Hooghiemstra, 2003). By 19,000–18,000 cal. yr BP deglaciation was underway. It proceeded unevenly but in general terms sites at 3700 m were free of ice by 17,000–15,000 cal. yr BP, and at 4000 m by 15,000–12,000 cal. yr BP (Smith et al., 2008). Essentially modern temperatures and circulation patterns were established by 11,000–10,000 cal. yr BP. The observable grass páramo, above the band of UFL displacements and across its entire latitudinal range, achieved its placement during this period.

The Pleistocene movements of forest and herbaceous belts can be traced because the pollen signature of forest and páramo differ notably (Grabandt, 1980, 1985; Grabandt and Nieuwland, 1985; Hansen and Rodbell, 1995; Hansen et al., 2003; Horn, 1993; Horn and League, 2005; Islebe and Hooghiemstra, 1997; Melief, 1985; Moscol Olivera et al., 2009; Niemann et al., 2010; Rodgers and Horn, 1996; Van der Hammen et al., 1981; van 't Veer et al., 1995). Simple percentages of (1) Poaceae, (2) indicator páramo taxa, and (3) arboreal pollen can be employed to distinguish forest from páramo over its broad latitudinal range (e.g. Groot, et al., 2011; Hooghiemstra, 1984). This approach is applied in Table 1 to 50 high elevation pollen cores, in which defining percentages of the three assemblages are considered in consort.¹

For 18 forested sites (or sites deforested for agriculture) in the northern Andes at elevations of 2500–3200 m, replacements of Pleistocene herbaceous vegetation by forest occurred principally between 12,000 and 9500 cal. yr BP. Early-Holocene upslope advance of forest halted at approximately current local UFLs. In general these are found at 3200–3400 m, but range from 2800 m in southern Ecuador (Niemann and Behling, 2009) to 3650 m in northern Ecuador (Bakker et al., 2008) and the wetter páramos of Colombia (Kuhry, 1988a). Holocene UFLs never reached higher than 3650 m at any location yet examined, and remained below 3300–3400 m for most sites.

Cores taken near the modern local UFLs function as sensitive indicators of forest advances and retreats, and these sites have constrained the postglacial variation of UFL elevations. As evident in Table 1, all 32 current shrub and grass páramo sites in the northern Andes and Costa Rica remained in páramo during the entire Holocene, as often concluded by study authors (Bakker et al., 2008; Di Pasquale et al., 2008; Horn, 1993; Horn and League, 2005; Melief, 1985; Moscol Olivera and Hooghiemstra, 2010; Niemann et al., 2010; Salgado-Labouriau and Schubert, 1976; Salgado-Labouriau et al., 1992; Wille et al., 2002). Evidence is absent for a generalized tree cover at current grass páramo elevations as proposed by Lægaard (1992), and supported by others (Hansen and Rodbell, 1995; Hansen et al., 1994; Holtmeier, 2003; Keating, 2000, 2007; Luteyn, 1999; Sarmiento, 2000, 2002; Sarmiento and Frolich, 2002; Young and Keating, 2001). Hence, with the exception of variation around the present UFL, *grass páramo maintained its approximate current distribution since its original emplacement at the Pleistocene/Holocene transition.*

Sedimentary charcoal record

For the zonal school tussock grass dominance is achieved by climatic and edaphic controls alone, and thus fire is of minor import

Table 1. Pollen studies >2500 m elevation, montane tropical America. All páramo sites with adequate dating controls from the northern Andes and Costa Rica are included. Studies are listed by geographic proximity ordered from lower to higher altitude. To facilitate identification, contemporary forest (or agriculture from forest) and near-UFL sites are shaded.

Site name	Altitude (m a.s.l.)	Latitude ^a	Current vegetation	Basal date cal. yr BP ^b [interpolated date]	Date site became forested (cal. yr BP ^c) or <i>Páramo</i> to indicate that site remained as páramo grassland since establishment	Reference
Costa Rica						
La Trinidad I, II	2700	9°50'N	Bog in montane forest	[9800]	9500	Islebe et al. (1996)
La Trinidad III	2700	9°50'N	Bog in montane forest	13,919	11,000	Islebe and Hooghiemstra (1997)
Lago de las Morrenas	3480	9°29'N	Bamboo- and shrub-páramo	11,773	<i>Páramo</i>	Horn (1993)
Venezuela						
Páramo de Mucabají	3540	8°47'N	Páramo	9263	<i>Páramo</i>	Salgado-Labouriau et al. (1992)
Páramo de La Culata	3600	8°45'N	Páramo	8349	<i>Páramo</i>	Salgado-Labouriau and Schubert (1976)
Páramo de Mucabají	3650	8°47'N	Páramo	14,715	<i>Páramo</i>	Salgado-Labouriau (1979, 1986); Salgado-Labouriau et al. (1977)
Páramo Miranda	3920	8°55'N	Superpáramo	13,324	<i>Páramo</i>	Salgado-Labouriau et al. (1988)
Laguna Verde Alta	4215	8°51'N	Superpáramo	14,240	<i>Páramo</i>	Rull et al. (2005)
Colombia						
<i>Eastern Cordillera (Sierra Nevada de Cocuy, High Plain of Bogotá, Páramo de Sumapaz)</i>						
Duitama Plain (Pantano de Vargas)	2510	5°47'N	Agriculture	9109	c. 9800	Gómez et al. (2007)
Ciudad Universitaria	2560	4°67'N	Agriculture	28,576	c. 11,400	Van der Hammen and Hooghiemstra (1995)
El Abra III	2570	5°00'N	Agriculture and secondary forest	14,299	c. 11,400	Schreve-Brinkman (1978); Van der Hammen and Hooghiemstra (1995)
El Abra II B3	2570	5°00'N	Agriculture and secondary forest	13,052	c. 11,200	Van 't Veer et al. (2000)
Laguna Fúquene I, II	2580	5°27'N	Agriculture	24,520	10,700–11,000	Van der Hammen and Cleef (1986); Van der Hammen and Hooghiemstra (1995); Van Geel and Van der Hammen (1973)
Laguna Fuquene III	2580	5°27'N	Agriculture	48,263	10,057	Van der Hammen and Hooghiemstra (2003)
Laguna Fuquene VII	2580	5°27'N	Agriculture	23,479	15,372	Van 't Veer et al. (2000)
Lake Alsacia	3100	4°00'N	Montane forest	17,643	12,100	Melief (1985)
Agua Blanca I	3250	5°00'N	UFL/Páramo w/forest patches	40,856	<i>Páramo</i> ^d	Helmens and Kuhry (1986)
Agua Blanca (PAB II, III)				9296	c. 4900 ^e	Kuhry (1988b)
Ciénaga del Visitador	3300	6°08'N	Páramo	14,870	<i>Páramo</i>	Van der Hammen (1974); Van der Hammen and González (1965); Van der Hammen and Hooghiemstra (1995)
La Guitarra	3450	4°00'N	UFL/Shrub páramo	18,323	<i>Páramo</i> ^f	Melief (1985)
Laguna Ciega	3510	6°30'N	Páramo	24,899	<i>Páramo</i>	Van der Hammen et al. (1981)
La Primavera	3525	4°00'N	Páramo	13,482	<i>Páramo</i>	Melief (1985); Van der Hammen and Cleef (1986); Van der Hammen and Hooghiemstra (1995)

(Continued)

Table 1. (Continued)

Site name	Altitude (m a.s.l.)	Latitude ^a	Current vegetation	Basal date cal. yr BP ^b [interpolated date]	Date site became forested (cal. yr BP ^c) or <i>Páramo</i> to indicate that site remained as páramo grassland since establishment	Reference
Páramo de Palacio	3550	5°16'N	Páramo	9132	<i>Páramo</i>	Van der Hammen (1974); Van der Hammen and Cleef (1986); Van der Hammen and González (1960a)
Peña Negra (PPN I)	3625	5°05'N	Mire w/ grass páramo	14,402 [16,300]	<i>Páramo</i>	Kuhry (1988b)
Laguna Verde (PLV I, II)	3625	5°15'N	Mire w/ páramo	5972 (I); 5942 (II)	<i>Páramo</i>	Kuhry (1988b)
Andabobos	3750	4°08'N	Páramo	16,901	<i>Páramo</i>	Melief (1985); Van der Hammen and Hooghiemstra (1995)
Laguna de los Bobos	3800	6°15'N	Páramo	c. 5000	<i>Páramo</i>	Marchant et al. (2001); Van der Hammen (1974)
El Gobernador	3815	4°00'N	Páramo	8400 [10,500]	<i>Páramo</i>	Melief (1985)
Valle de Lagunillas	3880–4220	6°25'N	Páramo	11,238; 14,149	<i>Páramo</i>	González et al. (1965)
<i>Cordillera Central (Nevado de Ruiz)</i>						
La Laguna	2900	4°55'N	Mixed Weinmannia forest and pastures	22,511	c. 10,100	Helmens et al. (1996)
El Billar I and II	3600	4°54'N	Páramo	15,544	<i>Páramo</i>	Melief (1985); Van der Hammen and Hooghiemstra (1995)
El Bosque Mire	3650	5°45'N	UFL/Montane forest	6553	Before 6553	Kuhry (1988a)
Parque Los Nevados Transect (TPN 26)	3900	4°45'N	Páramo	[6500]	<i>Páramo</i> ^e	Salomons (1986)
Laguna Otún (TPN 21B)	3950	4°47'N	Páramo	8266 [10,500]	<i>Páramo</i> ^h	Salomons (1986)
La Cachucha	4050	5°40'N	Páramo	7100 [10,000]	<i>Páramo</i> ⁱ	Bakker and Salomons (1989); Salomons (1986)
Northern and Central Ecuador						
Surucucho	3180	2°45'S	UFL/Montane forest w páramo above	13,704	11,000 ^j	Colinvaux et al. (1997)
Guandera (G15-II)	3400	0°36'N	Montane forest	6758 [7150]	~6000	Bakker et al. (2008)
Guandera 1 ^k	3540	0°36'N	UFL/Montane forest	12,489	4000–5000	Di Pasquale et al. (2008)
Chorreras	3700	2°45'S	Páramo	c.17,000	<i>Páramo</i>	Hansen et al. (2003)
Quimsacocha	3780	3°02'S	Páramo	7672	<i>Páramo</i>	Jantz and Behling (2012)
Guandera 2 ^k	3810	0°36'N	Páramo	13,006	<i>Páramo</i>	Di Pasquale et al. (2008)
Guandera 3 ^k	3890	0°36'N	Páramo	12,910	<i>Páramo</i>	Di Pasquale et al. (2008)
Pallcacocha	4060	2°45'S	Páramo	15,500	<i>Páramo</i>	Hansen et al. (2003)
Southern Ecuador						
Cocha Caranga	2710	4°02'S	UFL/ shrub páramo above	12,569 [14,500]	14,000–9700 ^l	Niemann and Behling (2009)
El Tiro Pass	2810	3°50'S	Shrub páramo	19,836	<i>Páramo</i>	Niemann and Behling (2008)
Cerro Toledo (CT core)	3150	4°22'S	Shrub páramo	19,999	<i>Páramo</i> ^m	Brunschön and Behling (2009)
Laguna Rabadilla de Vaca	3312	4°15'S	Shrub and grass páramo	10,380 [11,700]	<i>Páramo</i>	Niemann et al. (2009)
Peru						
Laguna Chochos	3285	7°38'S	UFL/Forest close to lake in páramo matrix	14,370 [17,150]	11,500 ⁿ	Bush et al. (2005)

(Continued)

Table 1. (Continued)

Site name	Altitude (m a.s.l.)	Latitude ^a	Current vegetation	Basal date cal. yr BP ^b [interpolated date]	Date site became forested (cal. yr BP ^c) or <i>Páramo</i> to indicate that site remained as <i>páramo</i> grassland since establishment	Reference
Laguna Baja	3575	7°42'S	<i>Páramo</i>	13,915	<i>Páramo</i> ^o	Hansen (1995); Hansen and Rodbell (1995)
Laguna La Compuerta	3950	7°30'S	<i>Páramo</i> (termed 'Wet puna')	30,041 [33,000]	<i>Páramo</i>	Weng et al. (2006)

Notes:

^aLatitude taken from cited study, and Marchant et al. (2001).

^bAll ¹⁴C dates have been calibrated using the Fairbanks0107 curve (Fairbanks et al., 2005). Dates interpolated from dated segments or from sedimentary patterns shared with other cores are given in brackets. Where calendar year dates are given as a range, a mean date is calculated.

^cTo determine if a site remained herbaceous or became forested, the criteria discussed in Note 1 were applied to the pollen diagrams of each study. *Páramo* thus means that *Poaceae* percentage either never descended below 20%, or that during the period in which they were <20%, indicator species totals were greater than 20%. High *Poaceae* percentages associated with human disturbance (mostly late in the Holocene) were discounted as representative of grass *páramo*. Sites near UFL and which may have been briefly forested are discussed in table footnotes. In all cases the dates of forest establishment are estimated from the published pollen sum diagrams.

^dInterpreted by Helmens and Kuhry (1986) to be a 'timberline forest' after 8300 cal. yr BP. But because *páramo* taxa continue to account for 30–40% of pollen, and sub*páramo* taxa for another 20–30%, by the criteria applied here the site was more likely a shrub *páramo* with proximal forest. The current vegetation surrounding the coring site is open shrub *páramo* with forest patches.

^eForests were dominated by *Weinmannia*, but the pollen evidence leaves unclear if the forest cover was continuous or, as now, patchy. The persistence of sub-*páramo* elements (Helmens and Kuhry, 1986) suggests a shrub *páramo* matrix with *Weinmannia* patch forests.

^fInterpreted by Melief (1985) to have been forested by 8800 cal. yr BP, becoming shrub *páramo* at c. 3200 cal. yr BP. However, the persistence of *Poaceae* (20–30%) during the 'forest' phase, and isolated tree pollen peaks reaching only 35–50%, suggest a shrub *páramo*, albeit with forest nearby.

^gShrub *páramo* c. 6250 cal. yr BP, then grass *páramo* to present.

^hShrub *páramo* c. 6000–3000 cal. yr BP, then grass *páramo* to present.

ⁱShrub *páramo* between c. 7500 and 6250 cal. yr BP, then grass *páramo* to present.

^j*Polylepis* forest early; then after 10,000 cal. yr BP dominated by *Weinmannia*.

^kGuandera (Di Pasquale et al., 2008) consists of three sites: One (3540) currently in montane forest and two (3810 m and 3890 m) in *páramo*, noted here as Guandera 1, 2 and 3. Macroscopic charcoal was used to identify the charred remains of characteristic *páramo* and forest species, and thus the plant community.

^lSite at modern UFL. Authors argue that forest was replaced by *páramo* 9700–4200 cal. yr BP, and then reverted to forest. However, the persistence of *Poaceae* (≥20%) in mid- to late-Holocene forests suggests a shrub *páramo* rather than montane forest. Continued burning throughout the 'forest' phases, as evidenced by persistent sedimentary charcoal (except for the last 1200 years), is inconsistent with montane forest.

^mBut UFL close after 8900 cal. yr BP

ⁿLakeside forest was stable since the initial woody colonization of the site, but the *páramo* matrix above and beyond the lake appears to have increased coverage after 6000 cal. yr BP, as suggested by an increase in *Poaceae* to 25–35%.

^oBut UMF close after 10,700 cal. yr BP.

for grass *páramo* etiology (Baruch, 1984; Marchant et al., 2001; Pérez, 1998; Thouret et al., 1996). Anthropogenic fire may alter formerly pristine *páramo* or extend its range, as when brush *páramo* is absent and presumably eliminated by burning (Bader and Ruijten, 2008; Bakker et al., 2008; Hofstede et al., 1995; Moscol Olivera and Cleef, 2009a; Verweij and Beukema, 1992). Environmental regulations of northern Andean countries largely subscribe to the zonal school of *páramo* etiology, with its distinction of natural versus human fires and broad condemnation of the latter (Keating, 2007). Urban public sentiment considers burning to be inimical to the survival of grass *páramo* (Horn, 1998), and associates its occurrence with *páramo* 'destruction'.

A subgroup of researchers holding the zonal view, however, allows that fire is part of *páramo* ecology within the dominant forcing of climate and soils. They note broad plant tolerance to fire and argue or assume that lightning and volcanoes have provided natural sources of ignition (Horn, 1993; Horn and League, 2005; Luteyn, 1999; Moscol Olivera and Cleef, 2009b). Whether this tolerance represents an evolutionary adaptation to fire or the fortuitous availability of traits that allow persistence in a burning regime remains to be determined (Lægaard, 1992). From the zonal perspective of this subgroup, human fire merely augments a natural fire regime adequate to *páramo* creation and maintenance. Anthropogenic fire, and human disturbances in general, may explain grass *páramo* expansion or magnify the dominance of tussocks

but is not considered pertinent to the etiology of the flora (Brunschön and Behling, 2009; Niemann and Behling, 2009; Sklenář and Ramsay, 2001; Thouret et al., 1996). Although the evidence is clear that *páramo* plant community floristics evolved with each glacial cycle (Hooghiemstra and Van der Hammen, 2004), the strong dominance of tussocks in contemporary grass *páramo* is believed to have its analogue in Pleistocene *páramos*. Thus, a contemporary 'undisturbed' grass *páramo* (sensu Hofstede et al., 1995) not only represents a zonal 'true *páramo*', but it also represents a grass *páramo* that is assumed to pre-date the arrival of humans.

Because fire burdens required by the zonal hypothesis are negligible, natural sources of ignition will be largely absent and low concentrations of sedimentary charcoal are predicted. Nonetheless, for zonal advocates who acknowledge fire as an ecological variable secondary to climatic controls, natural fire should be of sufficient intensity to explain the observed fire tolerance of *páramo* plants, and be represented by moderate concentrations of sedimentary charcoal from these natural sources.

Mid 20th century pollen analyses for Andean climatic reconstructions did not report charcoal concentrations until this invaluable line of inquiry was undertaken by Horn (1986, 1989a). Now the inclusion of charcoal data has become standard practice (Horn and Kappelle, 2009). Novel pedoanthracological methods are being introduced (Di Pasquale et al., 2008, 2010), as are higher

time-resolution analyses (League and Horn, 2000). Investigators commonly use charcoal occurrence as a proxy for climate, where an increase in charcoal values over the previous period is taken to represent drier, more seasonal or warmer conditions, because these facilitate burning. Cooler conditions, even when dry, are associated with less burning (Power et al., 2010). In addition to its use as a proxy for climate, the abundance of charcoal informs the vegetation's fire ecology. Table 2 summarizes charcoal data from 22 páramo and upper montane forest/UFL sediment cores and soil profiles, plus three cores from puna.

A number of limitations apply to these data. Although sedimentary charcoal is used to infer fire regimes, concentrations may reflect other factors including hydrology, wind directions, soil residence time and the nature of the vegetation burned (Horn, 1989a). The studies reported in Table 2 resist direct comparison because abundances are calculated in a variety of ways and for different size classes of charcoal particles. The diagnostic value of micro- (<100 µm) and macroscopic (>100 µm) particles is particularly problematic: Although most microscopic charcoal is generated in the local watershed, wind-borne deposition may carry particles from distant sites (Horn and Kappelle, 2009). Nonetheless, with regard to the studies reported in Table 2, the microscopic concentration curves generally parallel macroscopic curves, suggesting that both respond to a local fire regime. An additional difficulty is that intervals between samples vary widely, representing time periods of half a century to half a millennium. As the resolution of the record lessens, the absolute fire frequency becomes more difficult to discern.

But a fundamental observation follows from the data of Table 2: All studies report persistent macroscopic charcoal in páramo soils and sediments from the terminal Pleistocene and throughout the Holocene. No study that looks for charcoal fails to find it in the core or profile, except during periods when the site was under forest (Di Pasquale et al., 2008), and during glacial intervals, when vegetation cover was negligible or absent (Hanselman et al., 2011; Paduano et al., 2003). These data thus suggest that grass páramo fire is ubiquitous and that Holocene fire regimes began before the Pleistocene/Holocene boundary (Di Pasquale et al., 2010). For example, for a Costa Rican páramo core covering the last 11,000 cal. yr, 29 of 30 sediment samples contained at least one fragment greater than 700 µm in size (Horn and League, 2005). Venezuela and Colombia are not represented because to date their pollen analyses of páramo sites have not reported charcoal concentrations. *In the absence of future studies that show little or no charcoal for extended periods, the evidence strongly suggests that Holocene grass páramo is a fired landscape.*

Fire sources

Were grass páramo zonal vegetation, but also to some degree fired, natural ignition sources must exist. In this search a recorded *incident* of ignition, or its mere likelihood, does not establish a sufficient *incidence* of natural fire on a very large and fragmented landscape. Fire must occur at a spatial density and with a return frequency adequate to generate the sedimentary charcoal abundances recorded. Volcanoes and lightning are considered the two principal sources of natural fire in Neotropical mountains. Ignitions caused by sparks from falling rocks, crystal lensing and spontaneous combustion have been documented in other habitats, but there is no evidence to suggest that they occur at the densities and return intervals required for páramo creation and maintenance (Trabaud, 1987; Vogl, 1974). The absence of confirmed reports in the páramo literature of natural fires (Di Pasquale et al., 2008; Horn, 1989b; Luteyn, 1999) underscores the need to critically assess volcanism and lightning as sources for the ubiquity of charcoal in páramo sediments.

Volcanism. Researchers often assume that volcanoes generate fire (Horn and Kappelle, 2009; Keating, 2007; Moscol Olivera and Cleef, 2009a), even though direct observation of fire resulting from volcanic eruptions has not been documented in páramo. Indirect evidence is occasionally cited as, for example, charcoal in a páramo bog core ascribed to the activity of the neighboring Nevado Santa Isabel volcano in Colombia (Kuhry, 1988a). Likewise, charcoal in a páramo profile was linked to volcanism because the core examined showed interbedded Holocene tephra layers (Horn and Kappelle, 2009). But associations of this sort cannot establish causality for a fire regime at the landscape scale. I argue that eruptions are an inadequate source of natural fire for three principal reasons: (1) the localized and non-incendiary nature of most volcanic phenomena, (2) the spatial distribution of northern Andean volcanoes active during the Holocene, and (3) the episodic nature of eruptions.

Volcanoes can cause vegetation fires (Mueller-Dombois, 1981), but their eruptive behavior would generate limited ignition foci. Although pyroclastic flows are hot, their leading edges travel fast and immediately bury what they burn. When a pyroclastic flow stops, it may have cooled to below the ignition temperature, but in any case the potential ignition area is limited to the border of the flow's final emplacement on the original surface. Because pyroclastic flows follow the pre-existing hydrology, they concentrate hot material and carry it quickly downstream and away from headwater páramos. When an eruption includes molten lapilli, deposition is most intense on the flanks and base of the volcano (as is the lightning generated by the pyrocumulus clouds of violent eruptions), where normally no plant matter is available to burn or to carry fire. The principal eruptive products in most cases in the northern Andes are debris flows and ash fallout. These are not associated with fire, and thus a distinct tephra bed reminds us that the páramo in question was not burned but rather buried (Hall and Mothes, 2008).

Second, volcanoes as natural fire sources are limited in their distribution. Were volcanoes a principal explanatory source of natural fire, the location of the major páramo islands should correspond to that of volcanoes active now and throughout the Holocene. This is not the case, as illustrated by the páramos of the Andean depression in southern Ecuador and northern Peru, which have considerable sedimentary charcoal but have not seen volcanism for 2 million years (Beate et al., 2001). Instead charcoal is found everywhere that the mountain terrain achieves páramo elevations of 3200 to 3600 m or higher. In areas of relatively dense volcanic activity, such as central and northern Ecuador, volcanoes active in the Holocene were separated by 20–60 km (Hall and Mothes, 2008; Hall et al., 2008). Isolated páramo fires initiated by volcanic activity would have great difficulty spreading across the intervening distances, because natural obstacles to fire passage make most grass páramos highly fragmented surfaces, even without contemporary human infrastructure (Horn and Kappelle, 2009).

A third reason to doubt volcanoes as sources of páramo charcoal is the sporadic nature of volcanic activity. Intervals between eruptions along Ecuador's volcanic arc, for example, ranged from hundreds to thousands of years during the Holocene (Hall and Mothes, 2008). In the nearly 500 years since the Spanish Conquest, only six of the arc's 68 volcanoes have experienced eruption (Barba et al., 2008). Perhaps within a given eruptive episode fire frequency could be sufficiently high to burn a local páramo repeatedly. But if volcanoes were a singular source of fire, charcoal production should diminish or cease during the prolonged quiescent period between eruptions, a reduction not supported by sedimentary charcoal data.

Lightning. Lightning is more evenly distributed in space and in time than volcanic activity, and would seem at first glance to be a

Table 2. Páramo, puna and UFL Pleistocene/Holocene charcoal records.

Site (core or profile name)/ country/ latitude	Altitude (m a.s.l.)	Current vegetation	Particle size (μm)	Basal date in cal. yr BP ^a Oldest date reported (mean of date range) [Interpolated date]	Date of initial charcoal rise (cal. yr BP ^b) (bold) (subsequent peaks in parentheses; asterisk indicates major rise)	Reference
Lago de las Morrenas (I, 1989-II)/ CR/9°29'N	3477	Páramo	>500	12,360 (11,795)	9500–9100 (4750*, 2600*, 500*)	Horn and League (2005); League and Horn (2000)
Lago Chirripó (1985-II)/ CR/9°29'N	3520	Páramo	>700	4850 (4630)	NA ^c (4450, 2200*, 1100*)	Horn (1989a, 1993); Horn and League (2005)
Guandera ^d (Gua1, Gua2, Gua3)/EC/ 0°36'N	1: 3890 2: 3810 3: 3540	1: Páramo 2: Páramo 3: Forest	400–2000	1: 13,033 (12,489) 2: 13,158 (13,006) 3: 12,994 (12,910)	1: NA ^c (12,500) 2: NA ^c (13,000) 3: NA ^c (12,900)	Di Pasquale et al. (2008)
Guandera ^e (Gua1; Gua2a; Gua2b; Gua3; Gua5; Gua6) /EC/ 0°36'N	1: 3890 2a: 3810 2b: 3810 3: 3540 5: 3530 6: 3790	1: Páramo 2a: Páramo 2b: Páramo 3: Forest 5: Forest 6: Páramo	>400	1: 13,250 (12,250) 2a: 13,200 (12,875) 2b: 13,250 (12,950) 3: 12,895 (12,848) 5: 11,200 (11,130) 6: 11,420 (11,310)	1: NA ^c (12,500) 2a: NA ^c (12,900*) 2b: NA ^c (12,900) 3: NA ^c (12,800) 5: NA ^c (11,200) 6: NA ^c (11,400)	Di Pasquale et al. (2010)
Laguna Pallcacocha/ EC/2°45'S	4060	Páramo	>100	15,000	12,900* (12,100, 11,100*, 9500*)	Hansen et al. (2003)
Laguna Chorreras/ EC/2°45'S	3700	Páramo	>100	17,500	11,100 (9600, 7000, 5300*)	Hansen et al. (2003)
Laguna Surucucho/ EC/2°55'S	3180	Forest near UFL	>25 & <25	13,704	12,000 (9000, 3500*)	Colinvaux et al. (1997)
Laguna Quimsacocha/ EC/3°02'S	3780	Páramo	10–25, 25–50, 50–100, >100	7672	NA ^c (7500, 3900*)	Jantz and Behling (2012)
El Tiro Pass/EC/3°50'S	2810	Shrub páramo	2–150	19,836	8000 (5000, 1900*, 350*)	Niemann and Behling (2008)
Cocha Caranga/ EC/4°02'S	2710	Shrub Páramo near UFL	10–150	[14,500]	9700 (7700*, 6000*, 4200)	Niemann and Behling (2009)
Laguna Rabadilla de Vaca/ EC/4°15'S	3312	Páramo	10–150	10,380 [11,700]	NA ^c (11,500*, 8200*, 3400*)	Niemann et al. (2009)
Cerro Toledo/ EC/4°22'S	3110	Shrub páramo	5–150	20,000	19,000* (16,000, 15,000, 6000)	Brunschön and Behling (2009)
Laguna La Compuerta/ PE/7°30'S	3950	Páramo	<180	30,041	9500* (8400*, 3500)	Weng et al. (2006)
Laguna de Chocho/ PE/7°38'S	3285	Forest and páramo	>100 & <100	14,3709 [17,150]	15,000 (12,000*, 8000, 2000*)	Bush et al. (2005)
Laguna Baja/ PE/7°42'S	3575	Páramo	>100	13,915	13,000*–11,600* (6500, 5600)	Hansen and Rodbell (1995)
Lake Pacucha/ PE/13°36'S	3095	Agriculture/ near UFL	>180	24,000	15,000 (9800*, 5500*)	Valencia et al. (2010)
Lake Titicaca/ PE/16–17°S	3810	Agriculture/ puna	>180	370,000	Interglacials (major rise): 320 kya; 210–190 kya; 135–120 kya. Glacials (limited rise): 240 kya; 60 kya.	Hanselman et al. (2011)
Lake Titicaca/ PE/16–17°S	3810	Agriculture/ puna	>180 & 179–65	27,500	13,200* (11,000, 10,000, 7800*, 5200*)	Paduano et al. (2003)

Notes:

^a¹⁴C ages have been calibrated to calendar years BP using the Fairbanks 0107 curve (Fairbanks et al., 2005). Where authors report date ranges, the oldest date is cited first, followed in parentheses by the mean age for the range. Interpolated dates as provided by authors are given in brackets.

^bDates are interpreted from graphic presentations in the reference, or as stated in textual descriptions. Asterisks indicate the higher absolute charcoal concentration(s) of the series.

^cSites showing high charcoal concentrations at the basal date indicate a significant fire regime but cannot be used to identify a rise.

^dBecause this pedoanthracology study used macro-charcoal fragments to identify forest versus páramo indicator species, and did not examine charcoal concentrations, reported dates show the earliest evidence of burning but do not indicate fire regime intensity. The authors however report that all soil profiles contained charcoal at all depths, except the top organic layer of the contemporary forest (Di Pasquale et al., 2008).

^eThree of the six soil profiles reported in Di Pasquale et al. (2010), located at 3890, 3810 and 3540 m a.s.l., may be those described in Di Pasquale et al. (2008). Earliest charcoal dates between the two studies are quite similar but not identical, suggesting a separate dating procedure for the 2010 results.

suitable natural source of páramo fire. Páramo students frequently invoke lightning (Cleef, 1981; Horn, 1989a, 1989b; Horn and League, 2005; League and Horn, 2000; Luteyn, 1999; Moscol Olivera and Cleef, 2009b; Sarmiento and Frolich, 2002). The Tropics

have the highest global flash rate, which would appear supportive of lightning as a fire source (Horn and Kappelle, 2009; Horn and Sanford, 1992). This, however, ignores important distinctions at regional scales as, for example, the relatively low flash rate in the

tropical Andes compared with the much higher Amazonian forest rate. But the principal difficulty of lightning as a source of páramo fire is its low ignition ratio, which compares the number of lightning strikes with the number of ignitions caused by those strikes (Christensen, 1993). Mid-latitude coniferous forests and prairies support the highest ignition ratios. Andean montane forest and undisturbed lowland forest, in contrast, are practically immune to ignition (Mueller-Dombois, 1981). For this reason no suggestion is made in the literature that páramo was created from undisturbed forest by the direct action of lightning.

But it may be argued that even in a wet mountain climate grass can dry out enough to burn, and thus the lightning ignition ratio will be considerably higher for páramo vegetation than for closed forest. Nonetheless, for grass fires to spread over large areas, two conditions must be met:

- (1) *Strikes must coincide with periods when vegetation is dry.* Since the likelihood of lightning striking any particular point is very small, the occurrence of fire at any point not directly hit by lightning depends on the ability of fire to spread to that point. Thus, if lightning is to spread widely it must occur during a dry period, of which two kinds occur in páramos: The dry season per se (of <1 to 5 months), and a rainless and sunny period of a few days to a week or two that may occur within a rainy season. The dry season is an unlikely period for lightning to occur because the dominant air masses are stable and not conducive to thunderstorms. Lightning is more likely when the air is unstable during the wet season or in the transition between seasons. But tropical mountain thunderstorms form close to the surface in humid air masses that restrict evaporation, and thus virtually all precipitation produced by the cloud reaches the ground (Mueller-Dombois, 1981; Young, 1993). Exceptionally, positive lightning emanating from a cloud top may travel a sufficient horizontal distance to strike outside the precipitation footprint of the cloud, but this phenomenon has not been reported for the high tropical Andes. Instead, when lightning is most likely to occur, vegetation is simultaneously most likely to be wet.
- (2) *Fire must transcend fire obstacles.* The spread of fire is not only impeded by rain but by a variety of obstacles on the ground. Because these obstacles delimit a discrete fire surface, the process of ignition must be repeated for each surface, and thus the number of ignition points required would be very large. This contradicts our impression when observing an expanse of grass páramo, which appears to be an integrated whole because the vegetation is uniformly dominated by tussock grasses. But our observation in fact subsumes many fire surfaces, each burned in a separate ignition event. Especially where the topography is broken, or interrupted by watercourses or rock fields, the number of fire surfaces per unit area will be high. Modern residents in these kinds of páramo who burn their holdings to improve forage for cattle or sheep testify to the need to plant fire in many places. To burn an entire observed expanse of grass páramo requires, therefore, a number of ignitions equal to the number of discrete fire surfaces.

The probability of a given páramo area being burned due to lightning can be summarized: A low probability of lightning

striking any particular point would be multiplied by a low ignition ratio, and this very small number by the inverse of the total number of fire surfaces that comprise an observed páramo. But if grass páramo becomes woodier in the absence of fire (Brandbyge, 1992; Cierjacks et al., 2008; Gade, 1999; Jokisch and Lair, 2003; Lægaard, 1992; Sarmiento and Frolich, 2002) this grand improbability must be further reduced by two elements of the temporal dimension: Mean return interval and deviation around the mean. To be held responsible for burning páramo, lightning must initiate a fire for all discrete fire surfaces with a sufficiently short return frequency, and a low deviation around this value. The lightning return frequency and initiation of localized fires cannot delay much beyond the mean because the facility of a pioneering forest to ignite is considerably less than the grass it replaced, and thus with each failure of fire to return with sufficient frequency, the dominance of woody species increases and the likelihood of fire decreases. In sum, lightning ignitions (as opposed to strikes) would have to be spatially dense, temporally frequent and invariable to a degree that would appear extremely unlikely. *These observations suggest that although natural ignitions are possible, no natural sources of fire can explain the terminal Pleistocene and Holocene sedimentary charcoal records.*

Humans as a source of páramo fire. It appears, by default, that human burning generated virtually all Late Pleistocene and Holocene sedimentary charcoal. If this is the case, then charcoal concentrations for páramo during human occupation should be elevated as compared with those of a pre-human period (Di Pasquale et al., 2010; Hanselman et al., 2011; Pinter et al., 2011; Piperno et al., 1990; Rull, 2009). When associated in a tropical forest setting with disturbance pollen or that of plant domesticates, or with burned phytoliths of disturbance indicators, charcoal reliably represents human-set fires (Behling, 2000; Gómez et al., 2007; Piperno, 2006; Piperno and Jones, 2003; Piperno et al., 1990). This confidence derives from the charred cultural artifacts themselves, but also from the established difficulty of causing ignitions in undisturbed wet forest by natural sources, and the alien nature of fire to wet forest ecology.

Páramo is a more difficult environment in which to segregate the human fire contribution because the vegetation is combustible and the plant community's tolerance of burning may suggest a history of fire exposure. But if a pre-human burning regime can be identified, an initial and sudden rise should represent the first arrival of humans to the sampled site. To qualify undeniably as 'pre-human' would require dates prior to 15,000 cal. yr BP (and perhaps 20,000 cal. yr BP, as discussed below) for elevations currently in páramo. Ideally the concentration curves would include a long pre-human time series, to reliably identify the background frequency and variability of natural fire.

Of the charcoal sites summarized in Table 2, 19 have basal dates older than 12,500 cal. yr BP, and eight of these are $\geq 15,000$ cal. yr BP. They universally reveal a low level of fire in páramo and puna immediately following the LGM. Fire regimes at most sites intensify suddenly during the period c. 13,000–11,000 cal. BP, and three intensify at 15,000 or earlier. Because of their relatively long pre-rise periods and moderate elevations (allowing for early vegetation development and thus an early capacity to be burned), the studies at Chorreras, El Tiro, La Compuerta and Los Chochos are particularly valuable in detecting presumable anthropic inputs to the fire regime (Bush et al., 2005; Hansen et al., 2003; Niemann and Behling, 2008; Weng et al., 2006).²

Parallel to this finding, the sudden rise in the percentage of Poaceae pollen in the final millennia of the Pleistocene may reveal not only a warming climate but also human occupation and burning, given the competitive advantage gained by

bunchgrasses in a fire regime (Brunschön and Behling, 2009; Niemann and Behling, 2009). Accompanying the intensified fire regime and Poaceae increase, the pollen data often signal a reduction of shrubs characteristic of brush páramo, or of *Polyloepis*, in these cases reflecting woody intolerance to burning (Bush et al., 2005; Cierjacks et al., 2008; Weng et al., 2006; Williamson et al., 1986).

Low fire incidence in the earliest core dates certainly reflects limited biomass, especially for higher elevations sites (Mayle et al., 2009). To illustrate, a core covering 370,000 years and three glacial cycles recovered from Lake Titicaca, at 3810 m in the Peruvian Altiplano, establishes that fire was largely absent during glacial periods of up to 50,000 years, but that during interglacials of 15,000 to 20,000 years' duration a vegetation was being burned that resembled modern *puna* (páramo-like grassland) and *puna brava* (super páramo-like) (Hanselman et al., 2011). The macroscopic charcoal concentrations for these interglacials, all presumably resulting from natural ignitions, generated sedimentary charcoal concentrations of 0.1–0.9 mm²/cm³ (with a single outlier of 1.9 mm²/cm³ at 210 kya), and a mean of ~0.3 mm²/cm³.

But how intense a fire regime do these values suggest? Two additional puna studies address this question. From a separate Lake Titicaca core covering the last *c.* 27,500 years, pollen first appears *c.* 21,000 cal. yr BP and charcoal at 17,700 cal. yr BP, with very low abundances (Paduano et al., 2003). Then, at *c.* 13,200 cal. yr BP concentrations suddenly rise to 15 mm²/cm³ and continue at about 10 mm²/cm³ before declining to almost zero in the last 4000 years, perhaps reflecting overgrazing or the agricultural transformation of the zone around Lake Titicaca. These two complementary studies establish that fire was virtually absent during the last three glacial maxima, when plant cover was minimal. But they also indicate that in the presence of *puna* and *puna brava* vegetation during interglacials, burning was very limited as compared with levels reached after 13,200 cal. yr BP, when they increased by orders of magnitude.

This sequence and timing is echoed by the charcoal abundances at Lake Pacucha in southern Peru, now situated in upper montane forest at 3095 m but dominated during the terminal Pleistocene by Poaceae, with abundant Asteraceae and *Polyloepis*. Macroscopic charcoal concentrations remained below 4 mm²/cm³ between 24,000 cal. yr BP and 15,000 cal. yr BP, with a mean of <1 mm²/cm³. They rose suddenly after 15,000 cal. yr BP to 10–15 mm²/cm³ and remained elevated but variable until lowering dramatically 500 cal. yr BP (Valencia et al., 2010).³ From these charcoal studies with basal dates older than ~12,500 cal. yr BP, combined with the severe limitations on natural ignition as argued earlier, *the data indicate that the charcoal rises beginning after 15,000 cal. yr BP at páramo and puna sites initiated a distinct Holocene fire regime, and likely marks the original period of human colonization of these regions.*

A low fire incidence during the LGM in the Andes followed by heightened levels throughout most of the Holocene finds parallels across a variety of Neotropical habitats, as well as austral South America (Haberle and Ledru, 2001; Mayle et al., 2009; Moreno et al., 2010). Human intervention after 14,000–13,000 cal. yr BP is increasingly suggested as the cause for this increase (Di Pasquale et al., 2010; Pinter et al., 2011). Greater biomass, periodically drier climates, higher atmospheric levels of carbon dioxide and rising temperatures beginning in the early Holocene would certainly have facilitated burning (Power et al., 2008, 2010), but in the absence of significant natural ignition sources in Neotropical páramos, the necessary variable in manifesting this potential was *Homo sapiens* (Figure 2).

To explain an early and then persistent administration of fire, we can envision a transient first wave of humans, limited in numbers and currently invisible to us except for their charcoal, moving through the foreland vegetation and using fire as a universal



Figure 2. Cubillín Lake and grass páramo, Ecuador, at 3700 m elevation, with column of smoke from a fire started by sheep herders.

conditioner of their landscape, in the manner of their forbears. By the early Holocene, with the establishment of well-developed and familiar-looking grass páramo, articulated subsistence systems appeared. Territorial bands in larger numbers gained the capacity to sustain their landscape, in the process seeding the soil with charcoal. If this scenario describes the terminal Pleistocene fire regime, the archaeological record should contain evidence for human settlement coincident with the period of fire intensification. This data set is now examined.

Archaeology of early peopling

Archaeologists presently concur that the earliest peopling of South America occurred before 13,000 cal. yr BP (Bruhns, 1994; Cooke, 1998; Faught, 2008; Fiedel, 1999; Gruhn and Bryan, 1991), and many remain open to dates as early as 15,000–20,000 cal. yr BP (Bryan and Gruhn, 2003; Guidon et al., 1996; Lavallée, 2000). Archaeological and recent genetic evidence appear to converge on an original colonization of the Americas by 18,000–15,000 cal. yr BP (Goebel et al., 2008; Pitblado, 2011). At least ten sites in South America have been identified that were first occupied before 12,000 cal. yr BP, and over 30 sites between 12,000 and 10,000 cal. yr BP. A large number of additional sites from this period are now being investigated, many in tropical forest (Borrero, 1996; Bruhns, 1994; Cardale, 2005; López et al., 2003; Miotti and Salemme, 2003). These pre-agricultural populations inhabited a vast array of coastal, riverine, grassland and forest niches by means of locally adapted subsistence systems (Aceituno, 2000, 2002; Aldenderfer, 2008; Bryan, 1973; Dillehay, 2008; Gnecco, 1999; Stothart et al., 2003). Among the earliest sites is Monte Verde, Chile, reliably dated to 14,600 cal. yr BP (Dillehay, 1997; Dillehay and Collins, 1988; Goebel et al., 2008; Meltzer et al., 1997). Although a broad occupation of the Americas by the terminal Pleistocene is now well established, controversy will continue regarding sites with dates prior to 15,000 cal. yr BP, and the interpretation of genetic evidence used to develop a chronology of early diffusion (Bryan and Gruhn, 2003; Gruhn and Bryan, 1991; Pitblado, 2011; Roosevelt et al., 2002).

The earliest peopling of the high Andes provides a beginning point for anthropic inputs to páramo ecology. Were these inputs to occur after páramo had become established, humans would be regarded as disturbance factors. This is the consensus view among zonal advocates. But if humans were present at or before the period of deglaciation then páramo vegetation and human populations in some manner developed together, and the nature of this relationship needs to be elucidated. To this end Table 3 summarizes northern Andean archaeological sites at the Pleistocene/Holocene boundary from Perú, Ecuador and Colombia, and a sampling of sites of this period from the central Andes. I include

Table 3. Terminal Pleistocene/early Holocene hunter-gatherer sites in or proximal to páramo and puna.^a

Site name	Altitude (m)	Date(s) of occupation (cal. yr BP)	Site type	Associated faunal and plant remains
<i>Sabana de Bogotá/Colombia</i>				
Tibitó	2600	11,700	Rockshelter	Extinct horse and mastodon, fox, deer, birds
El Abra	2570	12,400	Rockshelter	White tailed deer and cavia; also armadillo, rabbit, peccary, agouti, birds
Sueva	2600	11,000–10,000	Rockshelter	Modern fauna
Nemocón	2600	11,000	Rockshelter	Modern fauna
Tequendama	2600	10,920	Rockshelter	White tailed and brocket deer; also cavia, armadillo and canids
<i>Highlands/Ecuador</i>				
El Inga (Ilaló, northern EC)	2549	11,000–9000	Open-air camp and obsidian workshop	Mastodons; white tailed and brocket deer, pudu, bear, tapir and small rodents
Chobshi (central EC)	2400	10,010–7535	Rockshelter and tool workshop	White tailed deer, pudu, brocket deer, rabbit, paca, guinea pig, opossum, tapir, Andean bear, porcupine and tinamou; no plant remains recovered due to damp conditions
Cubilán (southern EC)	2800–3100	10,300–9100	Open-air camp and flint workshop	No associated faunal or plant remains recovered
<i>Marañón-Huallaga Divide/Perú</i>				
Manachaqui Cave	3625	12,033	Rockshelter	No remains reported from early horizon
<i>Callejón de Huaylas-Cordillera Negra/Perú</i>				
Guitarrero Cave	2580	12,500–11,000	Rockshelter	Camelids, cervids, viscacha, rabbits and skunk; tubers and rhizomes, beans, <i>Capsicum</i> , <i>Cucurbita</i> , <i>Solanum hispidum</i> and <i>Pouteria lucuma</i> ; remains suggest vertical mobility (access to >4000)
<i>Huánuco Plain/Perú</i>				
Lauricocha	4100	9500	Rockshelter	Mainly deer (various species) and camelids; seasonal exploitation
<i>Junin Plain/Perú</i>				
Pachamachay Panaulauca Uchcumachay	4050–4420	10,500–9000	Rockshelter	Extinct horses and deer for the earliest periods at Uchcumachay, then hunting of a more diversified fauna; specialized vicuña hunting; gathering focused on wetland sites
<i>Ayacucho/Perú</i>				
Pikimachay	2350	14,000–13,000	Rockshelter	Armadillo, sloth, horse, deer

Notes:

^aSources for Lateglacial and early-Holocene sites include summary archaeological reviews (Bruhns, 1994; Cooke, 1998; Dillehay, 2008; Dillehay et al., 2004; Lavallée, 2000; Roosevelt et al., 2002; Scheinsohn, 2003) and specific site studies: *Sabana de Bogotá* (Correal, 1990; Hurt et al., 1972; Ijzereef, 1978; Van der Hammen and Correal, 1978); *Ecuador* (Burger et al., 1994; Lynch, 1989; Lynch and Pollock, 1981; Mayer-Oakes, 1986; Salazar, 1984); *Manachaqui* (Church, 1996); *Guitarrero* (Lynch, 1980; Smith, 1980; Wing, 1980); *Lauricocha* (Cardich, 1976); *Panaulauca*, *Pachamachay*, *Uchcumachay* (Rick, 1980; Wheeler Pires-Ferreira et al., 1976); *Pikimachay* (MacNeish and Vierra, 1983).

puna sites because they form part of the same process of occupation as páramos of the northern Andes, and provide insights into hunter-gatherer subsistence (Bruhns, 1994; Church, 1996; Cooke, 1998; Hurt et al., 1972; Ijzereef, 1978; Lavallée, 2000; Miller and Gill, 1990; Salazar, 1984; Van der Hammen and Correal, 1978). All except two sites are rock shelters, reflecting their utility to hunter-gatherers and the generally dry conditions that permitted the preservation of cultural remains.

Current discussions of the human colonization of páramo routinely assume a temporary and limited use of páramo resources, often combined with an original occupation in the middle to late Holocene (Bakker et al., 2008; Brunschön and Behling, 2009; Ellenberg, 1979; Lægaard, 1992; Moscol Olivera and Hooghiemstra, 2010; Niemann and Behling, 2010). Often this view is based on the assumption that the earliest ceramics or other manifestations of Andean agricultural societies (such as pollen of disturbance indicators or plant domesticates) represent the earliest human occupation (Hansen and Rodbell, 1995; Niemann et al., 2009). But Table 3 reveals that humans had become settled in puna and at the lower edge of páramo by the terminal Pleistocene. These data show that the high Andes participated fully in the earliest peopling of South America, suggesting that páramos were productive habitats (Bruhns, 2003; Lavallée, 2000; Salazar, 1985; Weng et al., 2006). The intensity of this participation remains to be clarified through the discovery of more sites and other

evidence of occupation, but also by calculating the likely human carrying capacity of páramo, and thus its subsistence attractiveness. High-altitude sites would have seen less use in the terminal Pleistocene than in the early Holocene because of the incipient nature of higher-elevation vegetation after glacial retreat, and thus its limited herbivore population and plant food resources (Butzer, 1988; Dillehay et al., 2004; Lanata and Borrero, 1999; Lynch, 1971; Smith, 1980). A similar situation unfolded at the same time along South American coasts as consumable ocean resources developed along rising shorelines. Given that sites at 4000 m in the central Andes and those above 2500 m in the northern Andes were utilized by 12,000 cal. yr BP, it appears that the vegetation between UFLs and retreating ice developed relatively quickly, and was of immediate interest as a subsistence resource.

The limited number of early sites currently described at páramo and near-páramo elevations reflects incipient human populations, but it may also reflect a variety of biases of the record. One is the restricted material culture of hunter-gatherers and the absence of pottery, ceremonial sites, terraces, a formal road network, and settlements to mark their presence in the manner of later agricultural societies. A second bias is the limited number of rock shelters in many páramos, especially as compared with puna. Hunter-gatherer open-air shelters constructed of degradable materials would only leave identifiable remains if fortuitously preserved, as in the bog conditions of Monte Verde (Bocek and Rick,

1984; Dillehay, 1989, 1997; MacNeish and Vierra, 1983). A third bias may be communicational: Some northern Andean hunter-gatherer sites are reported but have not been formally excavated, or are described in national anthropology publications and conference proceedings but have not yet found a wider audience and scrutiny through international peer-reviewed journals (e.g. Salazar, 1985; Weng et al., 2006). Finally, the geographic focus of some active researchers, as would be the case of Correal and Van der Hammen in the Sabana de Bogotá, may produce a cluster of sites. This concentration, combined with an archaeological paradigm disinclined to admit significant early human populations, may generate an erroneous sense of absence elsewhere (Gnecco and Salgado, 1989).

There is no doubt, as well, that early occupants of the northern Andes were mobile and thus neighboring páramos could be exploited for their food resources using base camps at the forest edge or below (Bruhns, 1994; Salazar, 1984, 1985). Vertical mobility is the rule where a dissected topography allows direct access to a variety of elevations (Figure 3). In the pre-agricultural Holocene, as now, rounds that involve walking from forested elevations to páramo and back, even in the course of a day, may have been the norm. Landscape-scale effects of human subsistence activities, especially when fire is a tool, do not require a large or stable resident population.

If these observations are grounded, the eventual identification of additional early hunter-gatherer sites in the northern Andes is likely, some in rock shelters unexamined until now and others in open páramo tied to fortuitously encountered hearths, kill sites, tool-making workshops, garbage pits, and bones and teeth from burials. The first step in this endeavor is to accept the prospect of finding additional signs of early hunter-gatherer occupation and evidence of their impacts. By the very nature of their subsistence and the size of their populations, our inquiry should complement the identification and study of *sites* and *artifacts* with that of *cultural landscapes*, using an expanding array of proxies for vegetation, disturbance, diet, material culture and land use change. By placing páramo hunter-gatherers in the larger context of the Late Pleistocene peopling of essentially all productive environments in South America, a growing array of biological and geochemical proxies that do not require cave settings can be applied to environmental reconstruction.

Pollen analysis will remain of great importance, especially as it becomes more rigorous (Seppä and Bennett, 2003). But the analysis of pollen is now being complemented by the use of fungal spores, diatoms, starch grains, phytoliths, coprolites, soil biomarkers, and other geochemistry indicators (Eckmeier and Wiesenberg, 2009; Jansen et al., 2008, 2010; Montoya et al., 2010; Nierop and Jansen, 2009; Piperno, 2006). These new techniques will supplement and also perhaps challenge the vegetation and land-use reconstructions based to date on pollen and a limited array of non-pollen polymorphs. Many new techniques still need to be calibrated and data bases created of reference specimens and geochemical values. Soil charcoal is one of these landscape markers already in use, and we have seen its value in illuminating páramo origins.

The logic of hunter-gatherer fire

Humans were witnesses of deglaciation in the northern Andes, and likely utilized the foreland habitat below the ice front. The substrate remaining after ice retreated consisted of rock, regolith and sorted materials such as gravel and sand. A mixture of hardy woody and herbaceous species, whose growth was limited initially by unstable inorganic substrates, cold temperatures and freeze-thaw cycles, colonized the newly exposed lands. The species that constituted the incipient vegetation would have come from both



Figure 3. Because they are islands, many grass páramos adjoin upper montane forests and would have permitted hunter-gatherer access to resources from both habitats.

the forest below and from the herbaceous zone between the forest edge and the glacial ice. Over the final millennia of the Pleistocene the mixed vegetation established after ice retreat achieved growing complexity and mass, in tandem with developing soils. Were the early inhabitants passive in their hunting and gathering, accepting the animal and plant foods made available by the climatic shift? Or were they instead inclined to intervene in their environment to make it more diverse and productive, and to enlarge it?

Given the collective ability of hunter-gatherers throughout the world to both adapt to and transform landscapes, it seems likely that páramo hunter-gatherers would have actively manipulated their environment, especially through the use of fire. Such is the case for other open-vegetation hunter-gatherer groups in Asia, Africa and Australia, as in Neotropical lowland settings (Aceituno and Loaiza, 2007; Bird et al., 2008; Gnecco, 1998; Gould, 1985; Kirkpatrick, 1994; O'Connell and Allen, 1995; Piperno et al., 1990; Pyne, 1993; Rull, 2009; Wharton, 1968). Prescribed, moderate-interval burning in páramo would have generated higher plant productivity and herbaceous diversity, resulting in increased graze and thus grazers. Within a fire regime and warming climates, Late-Pleistocene foreland vegetation was progressively transformed to grass páramo. Fire would also have increased the predictability of resources because successional development could be anticipated. Availability is synchronized, for example, when a burn stimulates bunchgrasses to flower and seed as a cohort (Mills, 1986).

As fire initiators, humans may choose the moment and the place to burn that will provide the greatest spread for each ignition point. If for a wet páramo only 20 or 30 days in the year are dry enough for grass to carry fire, humans can target those days with great precision. This is the case now for contemporary páramo cattle and sheep ranchers, as it certainly would have been for hunter-gatherers whose survival depended upon adequate grass and successional stage management. Hunter-gatherers would have known to wait until the morning dew dries, and the daily winds pick up, before starting fires. They would have known to choose adequate points of ignition upwind and at the bottom of slopes, and in the taller grasses. They only needed to carry a smoldering fire stick that would break into flames with a bit of blowing. Easily in a day, and with an expense of energy only slightly greater than that required to walk, a single hunter-gatherer could set fires at multiple points and burn hundreds of hectares over many discrete fire surfaces.

Terminal Pleistocene inhabitants of páramo forelands appear to have hunted species of megafauna until they became locally extinct, by about 11,000 cal. yr BP (Bruhns, 1994; Cooke, 1998;

Correal, 1990; Wheeler Pires-Ferreira et al., 1976). The mega-herbivores occupied primarily open habitats, to which hunters were drawn. Nonetheless, the plant and animal subsistence base likely was broad from the beginning of occupation. Once vegetation became established after ice retreated, hunting centered on camelids and cervids in the central Andes, while in the páramos of the northern Andes the white tailed deer, *Odocoileus peruvianus*, provided most of the animal protein (Ijzereef, 1978; Lynch and Pollock, 1981; Miller and Gill, 1990; Van der Hammen and Correal, 1978; Wing, 1986). White-tailed deer combine browsing and grazing habits and are unusual in their acceptance of a largely grass diet. The universal dependence of early páramo hunter-gatherers on white-tailed deer confirms the herbaceous nature of the environments in which hunters engaged their game. Other important hunted species include the rabbit *Sylvilagus brasiliensis* and the wild guinea pig *Cavia aperea* (Stahl, 2008), both requiring grasslands with forest edges. Montane forest deer (*Mazama* sp. and *Pudu mephistophiles*), paca (*Agouti* sp.), armadillo (*Dasypus novemcinctus*), birds and snails offered additional animal protein (Ijzereef, 1978; Lynch and Pollock, 1981; Miller and Gill, 1990; Wing, 1986). A variety of lithics, including chert, basalt, quartz, and obsidian, plus wood, bone and horn provided material for projectile points and butchering tools. Obsidian was exploited at specific locations and sometimes exchanged over considerable distances in the northern Andes, especially after the mid Holocene (Burger et al., 1994; Van der Hammen and Correal, 1978).

Three changes in the local environment would have permitted the herbivore population, and thus the human carrying capacity, to expand: An increase in the grass component of the open vegetation, a periodic renewal of tussock grasses to maintain their nutritional value, and an enlarged area of grassland vegetation. It is apparent that the periodic application of fire to the vegetation could achieve these three aims simultaneously. Anthropogenic fire in páramo was neither gratuitous nor fortuitous (Niemann and Behling, 2010), but rather supremely purposeful (Mills, 1986; Price and Bowman, 1994).

The strategy of burning, however systematically applied, would nonetheless have left certain areas free of fire because of irregular terrain and natural firebreaks. These protected sites could develop into forest. Early páramo inhabitants would have welcomed forest patches because they provided browse and protection for guinea pig, deer and other species that prosper in edge habitats, while also providing humans a source of firewood, materials for shelter, medicines and plant foods (Ojasti, 1983).

Although fire helped support a robust herbivore population, perhaps more importantly it allowed the maintenance of a diverse and open community of gatherable foods (Bonzani, 1997). For this reason Andean hunter-gatherers are considered primarily broad-spectrum foragers (Bruhns, 1994; Bryan, 1986; Dillehay, 2008). By burning páramo they created a mosaic of different ages of plant succession, and each successional stage provided a singular array of food resources. The first stage, beginning 6 to 8 months after a fire, produced vast quantities of *Calamagrostis* and *Festuca* seeds, similar to wheat and barley in nutritional content and perhaps utilized as food (Pearsall, 1996). Subsequent stages would have included rhizomes and roots, seeds, berries, leaves, flowers and fruits (Pearsall, 1980; Rick, 1980). To illustrate, the excellent preservation conditions of Monte Verde and an acute interest by researchers in reconstructing the diet of its inhabitants permitted the identification of 60 utilized plant species (Dillehay and Rossen, 2002).

The inventory of plant foods in the early páramo diet is poorly known, in part because the archaeological yield of plant remains is marginal in damp environments. But contemporary herders raised in páramo still have considerable knowledge of edible plants (Cardich, 1976; Pérez, 1998). The species they report are

virtually all sun-loving. This finding would be consistent with other heliophytes that dominate the human inventory of cereal and vegetable domesticates. It parallels as well the very early hunter-gatherer strategy in Neotropical forests, where clearings occupied by pioneering species generated gatherable foods, some of which eventually were domesticated (Gnecco, 1998; Piperno et al., 1990). Although as yet little studied, I do not share the view that grass páramo is an autosuccession (Llambí et al., 2003; Sarmiento et al., 2003). Rather, sustained observation of a burned páramo shows site-specific development involving major transformations in plant species composition and structure, over timescales of decades. In sum the mosaic of different-aged successional stages holds great species diversity, which hunter-gatherers could then exploit through mobility. Thus, availability drove mobility rather than scarcity or seasonality as in higher latitudes (Cardich, 1976; Mills, 1986; Salazar, 1984). The successional mosaic would have also created subsistence stability, as has been suggested for hunter-gatherers in the puna (Pearsall, 1983).

Conclusion

Three fundamental observations follow from this discussion:

- (1) *Pleistocene glacial cycles and vegetation movements inform our understanding of the natural constraints on contemporary páramos, but of themselves are inadequate in explaining the origin of tussock-dominated grass páramo.* Although Pleistocene climate oscillations drove the movement of the UFL and the character of the herbaceous vegetation, with human settlement we can no longer argue that the current UFL and páramo plant associations represent simply another interglacial. Because the earliest humans occupying the tropical Andes applied fire to the pioneering vegetation, even in very wet locations, the view must be abandoned that hunter-gatherers were absent or of minor ecological significance, and therefore that the pre-human and human ecologies were similar. Tussock-dominated grass páramos could not exist at their current elevations without periodic fire, and this fire was and remains anthropic.
- (2) *Humans as ecological factors require precise historical grounding.* Food procurement and production link humans to their environment and until modern times generated most anthropic impacts. Because subsistence systems in the high northern Andes have evolved significantly since the first peopling $\geq 13,000$ yr BP, the nature and degree of impact will be specific to each stage in this chronology. The primary distinction is between hunter-gatherer and agricultural societies. The former occupied páramo elevations during the period of grass páramo establishment, 8000–10,000 years before the local advent of agriculture. The land use chronology and the archaeological record do not therefore support scenarios of páramo origins that posit a role for agriculturalists, neither as the original páramo inhabitants (Bakker et al., 2008; Brunschön and Behling, 2009; Moscol Olivera and Hooghiemstra, 2010; Niemann and Behling, 2010; Niemann et al., 2009), nor as agents of deforestation and replacement (Ellenberg, 1979; Lægaard, 1992; Sarmiento, 2002). Sedimentary charcoal evidence indicates, as well, that the first instance of anthropic fire in páramo does not date from the advent of agriculture (Hansen and Rodbell, 1995; Paduano et al., 2003; Wille et al., 2002), but rather began in the Late Pleistocene. Linking grass

páramo development to subsistence systems also brings into focus the danger of applying contemporary observations of human impacts to those made by hunter-gatherers. Intense current páramo fire regimes and deforestation at the UFL, which have been used to suggest that a similar process caused deforestation and replacement earlier in the Holocene, ignores the uniqueness of modern residence patterns, population densities, tools, command of energy, road network and market links. In effect, both the early agriculturalist and contemporary human relationships to grass páramo fail as proxies for the hunter-gatherer relationship.

- (3) *Rather than being framed as either primary or secondary vegetation, grass páramo is best understood as a plant community that co-evolved with humans.* Vegetation reconstructions commonly frame the community in terms of primary or secondary, the former being original and pre-human, and the latter a replacement, often following human disturbance. This standard choice is a valuable instrument, but it also deeply conditions our thinking and has certainly defined the debate on páramo etiology over the last half century. Following Ellenberg (1979) and Lægaard (1992), this debate centered upon the proposal that grass páramo was largely a secondary formation following human removal of a zonal forest. In response, advocates of a natural grass páramo generated ample pollen evidence that almost all existing páramo was never forested, allowing only that grass páramo is a secondary form near a depressed current UFL, where humans are assumed to have eliminated montane forest (Moscol Olivera and Cleef, 2009b; Moscol Olivera and Hooghiemstra, 2010). This explanation attempts to reconcile the zonal and replacement hypotheses by assigning each a location on the altitudinal gradient. In doing so the primary/secondary paradigm is once again brought to bear. I argue that this paradigm has inhibited our ability to adequately reconstruct the vegetation history of grass páramo. If hunter-gatherer fire created grassland from a pioneering mix of vegetation beginning in the terminal Pleistocene, it would be more fruitful to think of humans as biotic factors – part of the original páramo ecology and necessary to its function. From this perspective a hunter-gatherer fire regime ceases to be an external disturbance factor. Specifically, although the variable *fire* is abiotic when generated by lightning or volcanism it becomes biotic when initiated by early humans, just as we might classify *shade* as abiotic when caused by tall canyon walls but biotic when caused by the leaves of competing plants. It follows that a tussock grass páramo should not exclude but rather embrace its hunter-gatherers.

The evidence indicates that hunter-gatherer activities had a decisive bearing on grass páramo origins. In effect, long before the advent of domesticated plants and animals, hunter-gatherers had domesticated a landscape. The pollen, sedimentary charcoal and archaeological data sets are culturally and temporally coherent. I suggest that humans be regarded as a keystone species in grass páramo ecology, and anthropic fire as a fundamental ecological factor.

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Notes

- (1) Modern pollen rain of forest and páramo sites determines the percentage criteria applied to fossil pollen data. Contemporary shrub and grass páramo are reflected in Poaceae contributing 10–60% of the pollen, with percentages as low as 5% in brush páramos and generally $\geq 20\%$ in grass páramos. An abundance of Ericaceae, *Hypericum* and Asteraceae, when combined with significant percentages of Poaceae, suggest a shrub páramo. Páramo sites often include arboreal pollen contributions of 5–20%, and occasionally $\geq 35\%$, blown in from lower-elevation Andean and sub-Andean forests (Van der Hammen and González, 1960b). The sum of indicator páramo taxa may contribute 20–60% of the sample. (These indicators include *Plantago*, *Valeriana*, *Lycopodium*, *Geranium*, *Puya*, *Halenia*, *Distichia*, *Huperzia*, *Senecio*, *Espeletia*, *Jamesonia* and *Gentiana*. Caryophyllaceae, Iridaceae, Ranunculaceae, Apiaceae and Cyperaceae are also particularly common in páramo settings.) Contemporary montane forest vegetation is reflected in arboreal pollen percentages of 30–90%, although most forests have 50–70%. Simultaneously, Poaceae percentages in undisturbed montane forest are usually 0–20%, and the indicator taxa noted above will be absent or very poorly represented (Hansen and Rodbell, 1995). Applying these modern pollen rain data, fossil pollen signatures are here classified as forest when tree taxa pollen percentages are $\geq 40\%$, and páramo when Poaceae is $\geq 20\%$. In residual cases where these minimum percentages are not met, a third criterion is introduced: the described indicators, found almost exclusively in páramo. The higher the percentage of indicator taxa in a residual case, the more likely the signature represents páramo. Sites whose pollen percentages fail to meet the primary criteria as either forest or páramo, or qualify as both, would be located near the transition between these two communities.
- (2) The rise at 19,000 cal. yr BP at Cerro Toledo (4°22'S) appears to be too early to represent human burning, although current archaeological and genetic estimates of first peopling may eventually encompass this date as new evidence accrues (Pitblado, 2011). Another explanation is the particle size range used, of 10–150 μm , which would have allowed for inblown charcoal from natural fires elsewhere (Brunschön and Behling, 2009; Bush et al., 2005). Compared with other sites, the late charcoal rise at c. 9500 cal. yr BP at Laguna La Compuerta (7°30'S) may reflect its higher elevation (3950 m) or Pacific exposure, which limited vegetation establishment and occupation after the local LGM (Weng et al., 2006). The early rise (15,000 cal. yr BP) at Lakes Pacucha (13°36'S) and Chochochos (7°38'S), in contrast, may respond to their lower elevations (3095 m and 3285 m, respectively) and greater biomass, and a very early human occupation from source populations on the Peruvian coast (Aldenderfer, 2008; Pitblado, 2011; Valencia et al., 2010).
- (3) A rapid decline in sedimentary charcoal after 500 cal. yr BP is often evident at páramo sites (e.g. Niemann and

Behling, 2008, 2010; Valencia et al., 2010; Weng et al., 2006), and most likely reflects the demographic collapse of native populations after European contact (Denevan, 1992; Dull et al., 2010; Nevle and Bird, 2008; Nevle et al., 2010). To the extent this decline can be ascribed to depopulation, a tool becomes available to measure the anthropic contribution to the natural fire regime.

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