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Fire in the páramo ecosystems of Central and South America

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18.1 ABSTRACT

Fires periodically burn the grass and shrub-dominated páramo ecosystems found above the treeline in the Andean highlands of northern South America and in the Cordillera de Talamanca of southern Central America. Most modern fires are human-set, the result of purposeful or accidental ignition. Lightning and volcanism are also ignition sources. Páramo fires typically consume all aboveground biomass, leaving charred ground that is recolonized by sprouts from surviving root systems and by seeds that survive the fire or enter afterwards. Plant species in modern páramo communities include many that resprout vigorously following fires, though post-fire growth rates are relatively slow at these high elevations.

Charcoal fragments in profiles of lake and mire sediments and soils document páramo fires that occurred centuries or millennia in the past. The evidence for ancient páramo fires comes both from modern-day páramo ecosystems, and from areas below the modern treeline that supported páramo vegetation and fires during glacial intervals of the late Pleistocene. Some of the charcoal evidence predates human presence and points to a role for natural burning in neotropical páramos. The question of whether páramo fires are human-set or "natural" and the effect fires have had on the distribution of páramo vegetation have long fascinated ecologists and geographers. From a conservation perspective, some of the ensuing debate may be irrelevant. Over long periods, high-elevation fires have shaped páramo plant communities that have conservation value today. The long history of fire in neotropical páramos and the responses of modern páramo species and communities to fire have led to the characterization of páramos as fire-dependent ecosystems.

18.2 INTRODUCTION

To ecologists and geographers, the word *páramo* conjures up images of the cold, wet, windswept slopes of high tropical mountains, above the upper limit of cloud forests but often still in the clouds, so no less soggy underfoot. Thus, the phrase *páramo fire* seems to be a contradiction in terms: How could such wet places ever burn? But the páramos that stretch from the central to northern Andes and appear again on the highest mountains of southern Costa Rica are not perpetually bathed in clouds and mist. For significant numbers of hours or days at a time these treeless peaks and plateaus sit atop the cloud belt, beneath a brilliant blue sky. Soggy ground and plants dry rapidly under strong solar radiation, leaves shrivel and die back, and fires—ignited in a diversity of ways—burn.

The sources and consequences of fires in neotropical páramo have attracted scientific attention since the mid-1900s. Discussions often focus on the role of humans in igniting fires, and discount lightning or other natural ignition sources. First-hand observations of lightning strikes, and paleoecological evidence of fires predating human presence, point to a role for natural burning in neotropical páramos. But for conservation purposes, the question of natural vs. human ignition in the páramo may be irrelevant. Human-set fires over long time periods have helped to create or extend many specific ecosystem types that have conservation value today (Myers, 2006), among them the neotropical páramos.

This chapter considers modern and ancient páramo fires in Central and South America, emphasizing fire sources and behavior, the "naturalness" of neotropical páramo, fire impacts on vegetation, paleoecological evidence of fire history, and challenges for fire management. We have aimed for as comprehensive a review of these topics as the literature and our own observations allow. Sections that seem thin or contradictory should be considered invitations for further research.

18.3 THE PÁRAMOS OF CENTRAL AND SOUTH AMERICA

Areas of mostly open vegetation collectively known as páramo are discontinuously distributed between 8° S and 11° N in the cool highlands of western South America and southernmost Central America (Luteyn, 1999; Hofstede, 2003; Kappelle and Horn, 2005). Neotropical páramo vegetation is sandwiched between the upper limit of cloud or montane forest and, where reached, the snowline or upper limit of plant life, at elevations between about 3,000 m and 5,000 m. It occurs along the crest and on the isolated mountaintops of the northern Andes of Ecuador, Colombia, and Venezuela, with outliers in northernmost Peru and in the Cordillera de Talamanca of Costa Rica and Panama (Luteyn, 1999; Figures 18.1 and 18.2).

Cuatrecasas (1968) divided Andean páramo ecosystems into three broad altitudinal zones: the sub-páramo, the grass páramo or páramo proper, and the super-páramo. As described by Luteyn (1992), the *sub-páramo* is a transition zone composed of species from the forest below and grass páramo above, in which shrubs

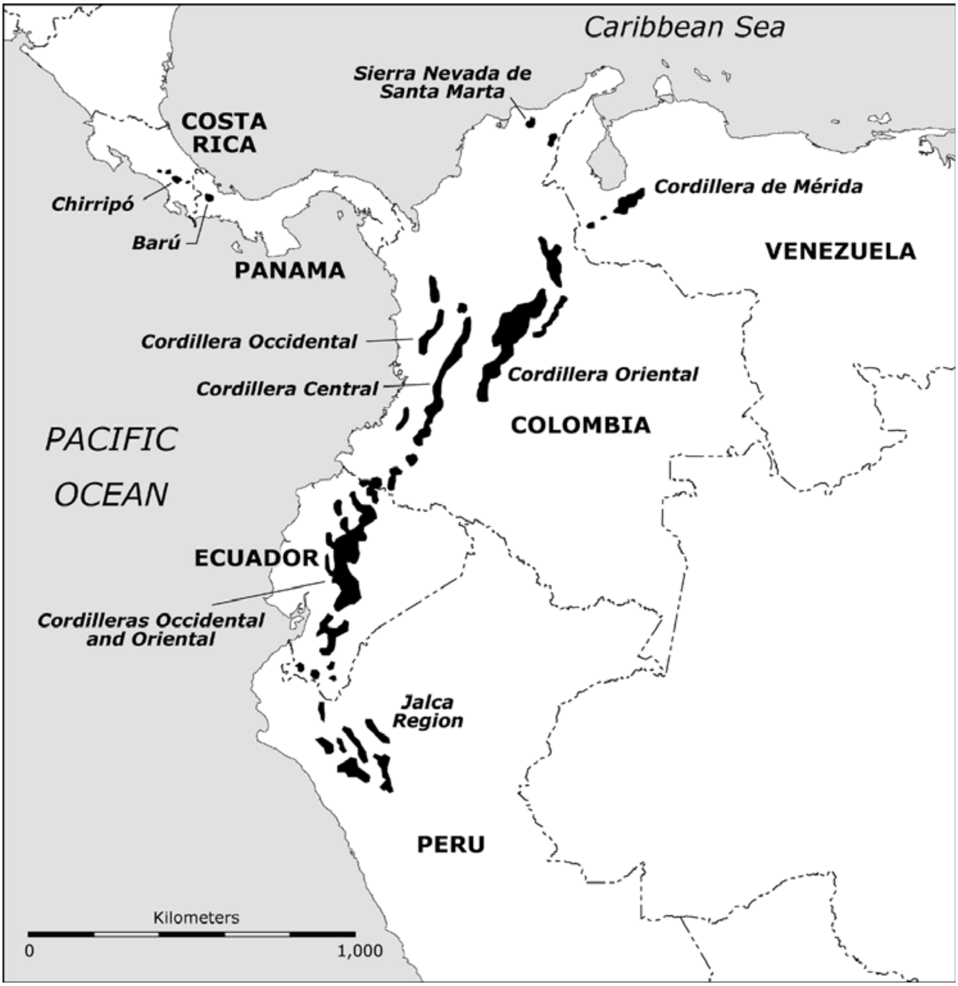

Figure 18.1. The distribution of páramo vegetation in the northern Andes and southern Central America, after Luteyn (1999). The black shading indicates elevations above 3,000 m that are potentially páramo, as originally mapped by Luteyn.

and small trees form mosaics that alternate with shrubby grasslands dominated by bunch grasses or dwarf bamboos.

The *grass páramo* or páramo proper is dominated by bunch grasses (mainly *Calamagrostis* or *Festuca*), or by dwarf bamboos (*Chusquea*) on wetter slopes (Figure 18.3). The vegetation is also rich in shrubs, acaulescent rosette plants, cushion plants, and herbs, and cover is continuous. The high proportion of dead shoots among the living gives the grass páramo an overall yellowish or brownish color (Luteyn, 1992). Giant-stem rosettes of the genus *Espeletia* occur in the grass páramos of Venezuela, Colombia, and northern Ecuador, and boggy or flooded sites support many cushion

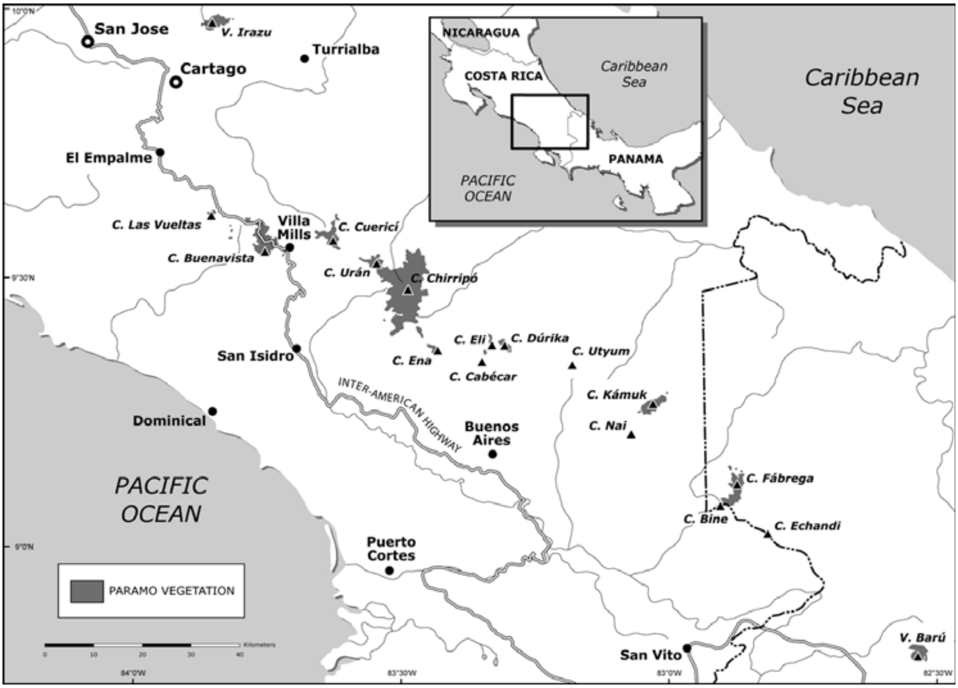

Figure 18.2. The distribution of páramo vegetation in Costa Rica and Panama, and locations mentioned in text.

plants. Large shrubs or small trees of the genus *Polylepis*, with oddly contorted stems and peeling reddish bark, form isolated small woodlands or forest patches within the grass páramo that may reach an elevation of over 4,000 m (Luteyn, 1999). These forest patches of trees up to 8 m high often also contain *Gynoxys* and *Buddleja*,

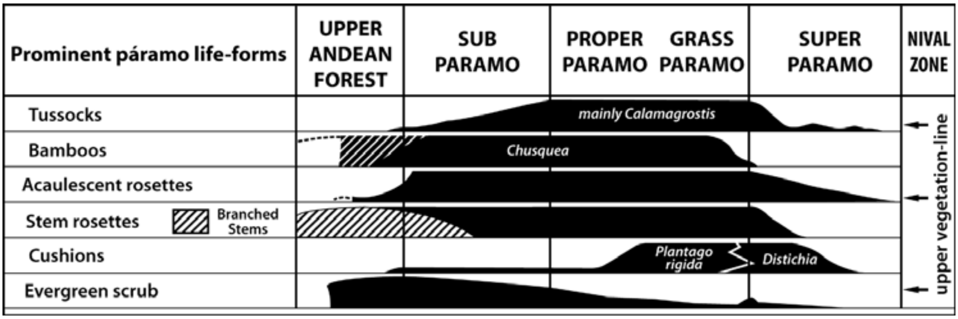

Figure 18.3. Diagram of the altitudinal zonation and optimal development of some life forms in Colombian páramo (after Cleef, 1978 as reproduced in Lauer, 1981). Redrafted from *Mountain Research and Development*, **1**(3/4), 1981 with the permission of the International Mountain Society and United Nations University.

among other taxa (Luteyn, 1999), and preferentially occupy sites that appear to offer protection from fire, such as boulders and talus slopes, and small hollows (Neill, 1999).

Finally, the *super-páramo* is a narrow elevational zone of rocky and sandy soils between the grass páramo and snowline, or top of the mountain where the modern snowline is not reached. Vegetation cover here is discontinuous, but among the herbs that do occur are many endemics (Luteyn, 1992), including large-stem rosettes in Venezuela (Pérez, 1998). In Ecuador, the super-páramo is dominated by shrubs and low cushion plants (Sklenař and Jørgensen, 1999; Keating, 2007). Fires are usually not an influence in the super-páramo, owing to sparse and discontinuous fuels (Sklenař and Ramsay, 2001).

While the zonal páramo classification remains in use, a variety of more detailed classifications have been applied to specific areas of páramo vegetation (páramos), in both the Andes and southern Central America. These include both floristic and physiognomic classifications that vary depending on the aims of the investigators and the methods employed (Luteyn, 1999; Hofstede, 2003; Chaverri and Cleef, 2005; Kappelle *et al.*, 2005). Sarmiento (2002) has criticized the use of the zonal concept in discussing Andean vegetation. We use zonal terminology here in keeping with the ecological literature we cite. In doing so we do not imply that any particular peak will display a clear zonation, that the altitudinal ranges of plant species will correspond with zone boundaries, or that plant distributions will not be complex at the fine scale. Modern land use and human impacts, including agriculture, grazing, and human-set fires, decidedly complicate the zonal classification system and all systems of vegetation classification, especially in the northern Andes, where many páramo areas are inhabited landscapes. These human impacts have engendered controversy over the degree to which páramo represents the *natural* vegetation cover of the areas it now occupies, as described in Section 18.4.

As on mountains everywhere, temperatures in the neotropical páramos decline with increasing altitude, with annual means ranging from about 10°C in the sub-páramo, near the upper forest limit, to as low as 2°C at the upper limit of plant growth, in the super-páramo of the highest peaks (Lauer, 1981; Luteyn, 1999). Unlike the alpine zones of temperate mountains, with their distinct temperature seasonality and frost-free periods, the páramos experience little or no variation in monthly mean temperature, but large diurnal shifts in temperature, and (at some sites) the possibility of frost throughout the year. Lauer (1981) estimated the incidence of frost in the páramo proper of Ecuador to be between 100 and 250 days per year, though the true range of variation may be much greater (Keating, pers. commun., 2008).

Precipitation is greatly influenced by exposure, with annual totals estimated to range from 500 mm to 3,000 mm. Few long-term precipitation records are available from páramo areas, and those that do exist underestimate moisture availability because they do not take into account the moisture that condenses on leaves and drips onto the ground below during periods of persistent ground-level clouds or mist, so-called fog drip or cloud sweep. Luteyn (1999) characterized the páramos of Colombia and Ecuador as humid throughout all or most of the year, owing to the influence of the intertropical convergence zone and orographic uplift of moist air masses, but even these sites have drier weeks and months, as indicated by the Walter-type climate diagrams included in Luteyn (1999). The Venezuelan Andes and Cordillera de Talamanca to the north are, in contrast, more affected by the Northeast Trades, and have a more distinct dry season; however, total annual precipitation in the Buenavista páramo of Costa Rica is significantly higher than any of the sites in Colombia or Ecuador summarized by Lauer (1979) and Luteyn (1999). The driest páramo sites are those of northern Peru, near the transition between neotropical páramo vegetation and the drier and more seasonal puna vegetation of the central Andean highlands (Luteyn, 1999; Luteyn and Churchill, 2000).

18.4 CAUSES OF PÁRAMO FIRES

Human activity appears to be responsible for the majority of contemporary páramo fires. Fires are set intentionally or by accident within the páramo itself, or spread to the páramo from adjacent forests or agricultural fields. The páramos of the northern Andes are inhabited landscapes with varying patterns and histories of human resource use (Parsons, 1982; Pérez, 1998; Sarmiento and Frolich, 2002). Large areas of páramo and high-elevation forest have been cleared for the cultivation of potatoes, grains, and other crops (Luteyn, 1992), and native páramo grasses are grazed by cattle, sheep, horses, and mules. However, grazing intensities are highly variable, with some areas receiving little activity. Many areas that are grazed are regularly burned, at intervals of one to several years, to remove the dead standing biomass of native tussock grasses and promote the growth of young grass shoots more palatable to stock (Lægaard, 1992; Verweij and Budde, 1992; Koenen and Koenen, 2000; Suárez and Medina, 2001; Hofstede, 2003; Keating, 2007). Grazed areas of grass páramo are also burned to reduce the encroachment of shrubs, which are considered undesirable because they reduce grass cover and provide habitats for birds that consume agricultural crops (Knapp, 1991; Keating, 2007). Páramo fires are also set by hunters to flush out small game including birds and rabbits (Stern, 1995), or to improve later hunting by producing areas of tender new shoots that will attract native deer and vicuña (Rust, 2006). Sarmiento and Frolich (2002) cited charcoal production along the forest/páramo margin as another source of páramo fires. They also mentioned that people set fire to páramo during prolonged dry periods in the belief that doing so will induce rainfall. Finally, some highland fires result from acts of arson. Keating (2007) described the setting of fires in grass páramo by schoolboys, for attention or excitement. Pérez (1998) observed some young people setting several tall rosettes on fire in the high páramo of Venezuela, seemingly for amusement. The dry leaf frills burned easily, but the fire did not spread and would be unlikely to do so in the sparsely vegetated super-páramo.

The páramos of the Cordillera de Talamanca in Costa Rica and Panama present a different picture of human land use, but also have a history of burning. Although hundreds of vehicles may travel daily through the Buenavista Páramo along the Inter-American Highway in Costa Rica (Figure 18.2), most visitors to this area, known also as the Cerro de la Muerte, do not stop or leave their cars. A couple of men who collect meteorological data and watch over communication towers on Cerro Buenavista constitute the only year-round páramo residents. Where not bulldozed for communication towers, the summit of Volcán Barú in Panama also supports páramo vegetation. The communications center there is accessible by off-road vehicles on a dirt track and is inhabited by a caretaker or two. The isolated páramos lying between Cerro Buenavista and Volcán Barú, including Cerro Chirripó and the many smaller areas of páramo along the crest of the Cordillera de Talamanca in Costa Rica and adjacent Panama (Cerro Fabrega), are uninhabited. Several hundred tourists visit the Chirripó Páramo each year, most on foot and a few by horse, almost all using a trail that begins at the administration center in San Gerardo de Rivas. Trails to the other páramos are poorly maintained and much less often traveled.

The population of grazing animals is also very low in Talamanca páramo. Over the past 25 years we have seen no more than a few cattle grazing accessible areas of páramo vegetation along the Inter-American Highway. Grazing pressure may have been higher during the early 1970s, when Dohrenwend (1972) reported a herd of 30 cattle in the Buenavista Páramo (although Janzen, 1973a characterized grazing pressure at the time as light). In the early part of the 20th century, prior to the construction of the Inter-American Highway in the 1940s, cattle and pigs were driven over the mountain from San Isidro to Cártago (Figure 18.2), directly through the páramo along a rough dirt track that partly overlapped the current highway route. Although we associate road construction with increased human impact and devastation of natural communities (Laurance *et al.*, 2001), the páramo along the Inter-American Highway was probably more strongly affected by people *prior* to highway construction (Horn, 1989a). The intrepid people who crossed on foot or horseback in those years spent days in the páramo, unlike today's motorists who speed through in minutes. Pre-highway visitors frequently set fires along the way to keep warm in what was, on foot and without proper clothing and rain gear, a very difficult and dangerous trek that could lead to death in some cases, as the name Cerro de la Muerte suggests (Skutch, 1971).

Most recent páramo fires in Costa Rica seem to have arisen accidentally, from carelessly tossed matches or cigarettes, from cooking fires of road and electrical crews along the Inter-American Highway, or from cooking and camp fires of hikers in the more remote páramos. Helicopter and plane crashes have also ignited fires (Horn, 1990). The largest historic páramo fire occurred just seven months after the establishment of Chirripó National Park and burned nearly the entire Chirripó Páramo, together with adjacent montane forest (Chaverri *et al.*, 1976, 1977). Ignited on March 22, 1976 by a hiker ultimately charged with arson, the fire burned for more than a week, charring some 5,000 ha before it was extinguished by rains in early April (Horn, 1990).

Evidence of modern fires in areas that lack human presence, and of ancient fires that predate humans, shows that natural fire from lightning or volcanism is possible. The northern Andes (especially Colombia and Venezuela) and the Talamanca Mountains of Costa Rica and Panama experience a high frequency of thunderstorms with lightning (*http://www.srh.noaa.gov/jetstream/lightning/hirez_72dpi.htm*). Páramo fires can arise from lightning strikes within the páramo itself, or through the upslope spread of fires started by lightning in surrounding montane forests. Lightning has been observed striking the Chirripó Páramo of Costa Rica, as well as forested slopes (Horn 1990), and has ignited at least one recent forest fire (Chaverri and Esquivel, 2005); in the páramos of northern Peru, lightning strikes kill people (B. Leon, pers. commun., 2008) and also cattle (Young, 1993). Sarmiento and Frolich (2002) proposed that frequent night-time heat lightning (without thunder) in the Ecuadorian páramo could lead to natural combustion under dry conditions, but state that this has never been observed. Most researchers consider the probability that lightning will ignite fires in páramo to be low, because the vegetation is often moist when thunderstorms with lightning occur (Bromley, 1971; Keating, 2000, 2007). However, a great complexity of meteorological, geographical, and ecological factors determine the ability of lightning to ignite wildfires (Keane and Finney, 2002). For the neotropical páramos, the possibility needs to be considered that lightning strikes may occur without rain, or may ignite small patches of dry vegetation in protected sites that can smolder for weeks until weather and fuel conditions allow initiation of a flaming surface fire (Keane and Finney, 2002).

Volcanism has been discounted as a source of páramo fires based on the wide spacing of volcanoes and their infrequent eruptions in páramo areas (White, n.d.). But without the modern roads and settlements that fragment today's páramos, fires set by volcanic activity potentially could have spread long distances when weather and fuel conditions were appropriate.

The idea that nature sets considerably fewer fires in tropical highlands than do humans these days is likely correct for the neotropical páramos, and is the accepted wisdom for tropical highlands worldwide (Wesche *et al.*, 2000). Lightning fires do play a role in some modern tropical ecosystems (e.g., in the highlands of Madagascar at 22° S; Bloesch *et al.*, 2002). It is possible that some fires attributed to humans actually result from lightning but are credited to people because they occur in areas occupied or visited by people. Keeley and Bond (1999) hypothesized that the mass flowering that characterizes some bamboos found in neotropical highlands (among other environments) may have evolved in connection with periodic lightning-set fires. While Verweij (1995) speculated that volcanism or lightning may only set one fire per 1,000 years in Los Nevados National Park in the Colombian páramo, it would appear that insufficient data are at hand to support quantitative estimates of natural, as opposed to anthropogenic, fire ignitions in the neotropical páramos.

18.5 THE “NATURALNESS”, FIRE DEPENDENCY, AND CONSERVATION VALUE OF NEOTROPICAL PÁRAMOS

The recognition of the importance of fire, livestock grazing, and other modern human impacts in shaping high-elevation plant communities in the northern Andes has prompted speculation over just how “natural” páramo communities and landscapes may be (Luteyn, 1999). Ellenberg (1979) was an early proponent of the view that deforestation and burning had artificially lowered the upper treeline or timberline throughout the Andean highlands. He argued that the grass-dominated vegetation recognized as páramo in the north and puna in the south had been produced by human activity. Sarmiento (2000, 2002) and Sarmiento and Frolich (2002) have also emphasized the strong imprint of past human activity in Ecuador and throughout the Andean highlands. They have referred to the area as a cultural landscape and argued that its vast grasslands should be considered anthropogenic: "the result of ancient, enduring human impacts, or of managed approaches for using Andean forest resources including burning for grazing and agriculture" (Sarmiento, 2000, p. 429). Lægaard (1992), Sarmiento (2002), and others have regarded patches of *Polylepis* forest within Andean grass páramo as remnants of previously continuous forest cover. This interpretation holds that much of today's grass páramo was once forested, up to the elevation of the highest forest patches.

Others have argued that *Polylepis* and grass páramo have always existed as independent communities in the highlands, expanding and contracting through time in response to climate changes, and that the elevation of the highest present stand of *Polylepis* in a region does not necessarily indicate the former treeline (Luteyn, 1999).

Neill (1999) mentioned vegetation patterns on Sumaco Volcano as possible evidence of natural treeline elevations in the Ecuadorian Andes. Løjtnant and Molau (1982) examined the vegetation of a "virgin" páramo on the remote summit of Sumaco Volcano that they believed had never been subjected to burning or grazing. They described elfin montane forest reaching an upper limit of 3,300 m at the site, and páramo vegetation extending from there to the summit at 3,700 m, an elevational range well below the modern upper limit of *Polylepis* stands in other areas of the Ecuadorian highlands.

The debate over the spatial extent of treeline lowering in the Andes also has an important temporal component (Keating, 2007). Some observers have suggested that high-elevation forests were removed thousands of years ago, while others have speculated that the most dramatic changes did not occur until after the Spanish Conquest. A key consideration is the timing of human settlement in and near páramo areas, which varied by region and requires extrapolation from data sources open to various interpretations. Keating (2007), for example, suggested that people have modified and occupied páramo landscapes in northern Ecuador for thousands of years, while Pérez (1998) concluded that humans did not move into or much affect the Venezuelan páramo until after the Spanish Conquest. Ellenberg (1979) also regarded the post-Conquest period as the time of most dramatic alteration of the neotropical páramos, in contrast with the drier puna environments to the south, where human occupation and impact had occurred for a much longer period. The true reach of human alteration is also a topic of some debate. As recently as 30 years ago, Parsons (1982) commented that vast páramo tracts in the northern Andes remained relatively untouched. Characterizations of páramo human impact need to take into account regional differences in the timing and extent of human settlement and landscape modification in today's páramo regions.

A rather different view of long-term treeline shifts has been proposed by Stuart White (cited in Rust, 2006; *see also http://www.roundriver.org/course_outline.*

html#Outline7). Rather than viewing present grass páramos as the consequence of forest destruction by humans during recent centuries or millennia, White proposed that these areas have been treeless *throughout the current postglacial period.* In his view, treelines that were depressed by glacial cooling during the late Pleistocene never recovered their previous altitude, owing to the early movement of hunters into the grassland zone between the upper forest and retreating ice, and their use of fire to maintain habitat for white-tailed deer, and perhaps tapir. Human-set fires during the postglacial period are thus credited not with carving páramo from forest, but from preventing the natural upslope migration of trees that should have occurred as climate warmed.

Discussion of the role of humans in creating or enlarging areas of páramo vegetation has extended also to the Cordillera de Talamanca. Hartshorn (1983) conjectured that páramo vegetation was originally restricted to the highest peaks in the Cordillera de Talamanca (e.g., Cerro Chirripó), but had extended downward on peaks along the Inter-American Highway due to human-set fires. Janzen (1973a, 1983) maintained that the shrub and bamboo–dominated vegetation of Cerro Buenavista and other peaks along the highway route was not "páramo" but rather just old regeneration following clearing and burning of an original low forest. Rowell and Carbonell (1977), however, argued from biogeographical evidence that the Buenavista Páramo was of considerable antiquity and not the result of recent forest destruction. Their interpretation was based on the presence and generic status of a newly discovered grasshopper species that had evolved in isolation in the páramo habitat. This fits with interpretations of historical biogeography based on today's páramo plants, such as those found in the species-rich genus *Westoniella*, a local endemic in the Asteraceae family (Weber, 1959; Cuatrecasas, 1979; Cleef and Chaverri, 1992).

Recent research on *Polylepis* forests in Ecuador sheds new light on the role of human-set fires in lowering treelines. Bader *et al.* (2007) showed that high solar radiation hinders tree regeneration above the modern treeline because most tree seedlings are shade-dependent. Fire is more important for seedlings of the few tree species that can tolerate high solar radiation, and may be necessary to explain the *complete* lack of forest expansion toward the potential climate-controlled treeline. Bader *et al.* (2007) concluded, however, that natural processes alone can explain both the low elevation and abruptness of many modern tropical treelines. Below the modern treeline, however, fire appears to be a key influence on the edge dynamics of forest patches, as revealed by recent work by Cierjacks *et al.* (2007, 2008), also studying *Polylepis* in Ecuador.

Charcoal fragments and pollen grains preserved in soils and sediments of the neotropical páramos provide a basis for reconstructing long-term fire history and changes in vegetation and treeline. Described in more detail below, these studies show that páramo-like vegetation has occupied neotropical highlands for over 50,000 years, and was particularly widespread during the last glacial period, when treelines were depressed by up to 1,000 m compared with modern values. These studies reveal, at the same time, ample evidence of recurrent fires. The earliest of such fires (*ca.* 35,000 ^{14}C yr BP) predate human settlement and must have derived from lightning or volcanism. Holocene fires may largely reflect human activity, though patterns of fire occurrence also show relationships with climate.

The long history of fire in the neotropical páramos—whether natural or anthropogenic—and the responses of modern páramo species and communities to fire—leads to the characterization of páramos as *fire-dependent ecosystems* (Myers, 2006). As described by Myers (2006), fire-dependent ecosystems are those in which fire is an essential process. Species have evolved adaptations to respond positively to fire and to facilitate the spread of fire, contributing to vegetation that is fire-prone and flammable. If fire is removed or fire regimes greatly altered, the ecosystem will change to something else, and habitats and species will be lost. Myers' view is that the extent of human disturbance in fire-dependent ecosystems does not necessarily diminish their conservation importance, and should not be surprising:

> "In fire-dependent ecosystems, people invariably have played a long-standing role in creating, maintaining, expanding or changing the ecosystems that are desired today for conservation purposes. Many landscapes that are now important to conservation were created, shaped and/or maintained by human burning" (Myers, 2006, p. 17).

Myers' comments above were directed at fire-dependent ecosystems in general, but are highly relevant to the situation in Andean páramo. Luteyn (1999) similarly concluded:

> "Without doubt man has had major impact on the origin and spread of grasslands throughout the Andes, and perhaps he is the single most important reason why grass páramo exists today, where shrub/tree woodlands of *Polylepis*, *Buddleja*, and *Gynoxys* may once have dominated. It is unlikely, however, that we will ever be able to say with confidence what percentage of today's páramo has anthropogenic origins. Whatever the outcome of this discussion, the fact remains that grass páramo currently exists, covers large expanses of the high-elevation Andes, and has great ecological and economic importance" (Luteyn, 1999, p. 31).

Let us turn now to the issues of modern fire behavior and ecological impacts of fire in neotropical páramos. We will then step back to examine what the fossil record can tell us about the history of these dynamics, and how this history, coupled with modern ecological knowledge, can inform fire management in protected areas that support neotropical páramo.

18.6 FIRE BEHAVIOR

The way fire behaves at a site (e.g., the rate of fire spread, spread direction, flame length, and rate of heat release—or fire intensity) is determined by the fire environment including fuel types, amounts, and arrangements; site topography; and weather. Detailed analyses of fire behavior in the neotropical páramos are lacking. Studies of modern páramo fires have largely concerned impacts to vegetation, or in a very few cases, animal populations (e.g., Koenen and Koenen, 2000), and have been conducted after fires have occurred. Based on findings of Hofstede (1995) in the grass páramo in Colombia, Buytaert *et al.* (2006a) speculated that grass páramo fires may often be of low intensity, and thus have little effect on soils. The potential thermal energy of shrub páramo is much higher; Keating (1998) described as intense a large páramo fire that burned primarily shrub páramo in Podocarpus National Park in southern Ecuador in 1985. Only Ramsay and Oxley (1996) have actually measured temperatures during páramo fires, using pyrometers constructed with color-changing crayons deployed prior to experimental burns in Ecuadorian grass páramo. Such studies offer the possibility of greatly enhancing our understanding of key fire parameters that are liable to influence plant survival and post-fire response, such as heat penetration into the soil (Horn, 1997), and should be pursued where opportunities allow. In the grass páramo that Ramsay and Oxley (1996) burned, highest temperatures (to $>500^\circ$C) were reached in the upper leaves of the grass tussocks. Temperatures exceeded 400°C in the middle levels of the tussock, but were often below 65°C in dense leaf bases. Temperatures were variable on the ground between tussocks but at 2 cm below ground did not reach 65°C.

Maarten Kappelle observed a fire in the Buenavista Páramo of Costa Rica in March 1992 (same fire later studied by Horn, 1997, 1998a). The fire moved slowly in the direction of the wind, reaching the edge of the Inter-American Highway in some locations but not crossing it. Botanist Arthur Weston's description of the 1976 fire in the Chirripó Páramo as "fiercely sweeping back and forth across the massif" (Weston 1981, p. 7), suggests a rate of spread and intensity surpassing that of the much smaller fire observed by Kappelle. Within their fire perimeters, however, both fires consumed nearly all shrub crowns and herbs, leaving, in the case of the Chirripó fire, only a few small islands of unburned vegetation (Chaverri *et al.*, 1976).

Philip Keating (pers. commun., 2008) has observed fire behavior in the grass páramo of Ecuador (Keating, 1999, 2007, and unpublished) and is hoping to initiate a project to model the flow of fire in tussock grass páramos using a program called FARSITE which stands for Fire Area Simulator (http://www.firemodels.org/content/view/112/143/). The challenge for this and other attempts to model fire behavior is the lack of better data on fire parameters and plant regeneration dynamics (P. Keating, pers. commun., 2008).

18.7 FIRE SEVERITY AND POST-FIRE VEGETATION DEVELOPMENT

Studies of plant community composition and vegetation stature following páramo fires provide data on post-fire vegetation dynamics in neotropical páramo and a means for assessing the severity of páramo fires. Here we follow the USDA Forest Service's Fire Effects Information System Glossary (*http://www.fs.fed.us/database/feis/glossary.html*) in defining fire severity as the degree to which a site has been altered or disrupted by fire, as per Romme (1980) based on such considerations as changes in the forest floor, the canopy, and the total photosynthetic area. Observations in recent burn sites reveal that most páramo fires, regardless of their intensity, rank as severe in terms of their immediate impact on the ecosystem: fires tend to burn completely within their perimeters, consuming living and dead leaves of all life forms and leaving behind a blackened landscape of burned grass tussocks and leafless stems of shrubs and ferns. While protected buds of many plants may have survived the fire, the complete loss of shrub crowns and photosynthetic tissue of herbs and ferns leads to the classification of these fires as severe.

A growing number of studies have addressed post-fire vegetation development at páramo burn sites. In 1960, P.J. Grubb and J.R. Lloyd examined vegetation on burn sites of different ages within areas of grass tussocks thought to represent the natural grass páramo of Cerro Antisana, Ecuador (Grubb, 1970). They found that fire destroys interspersed shrubs and patches of moss, and leads to colonization by a characteristic group of moss and herb species. Subsequent studies in Ecuador, Colombia, Venezuela, and Costa Rica have quantified post-fire changes in plant composition, cover, and stature. As summarized by Keating (2007), these studies demonstrate that páramo fires can have different effects on vegetation, with outcomes varying according to a range of environmental factors that determine the intensity and extent of a particular fire. Site history (e.g., time since last fire and the nature of other recurrent disturbances) may also be highly significant but is, in most cases, poorly known or unknowable (Horn, 1997; Keating, 2007).

Succession following fires, as well as other disturbances, at páramo sites seems to involve shifts in relative abundance more than species replacement, and could be characterized as "autosuccession" (Llambí *et al.*, 2003; Sarmiento *et al.*, 2003) using the terminology of Muller (1952). Community dominants are present the first year after fire, and limited colonization by other species appears to take place following establishment of the initial community (Horn, 1989b). Tussock grasses survive fire and regenerate from protected meristems within a few weeks or months after burning (Sklenař and Ramsay, 2001), as do many sedges and other herbs (Chaverri *et al.*, 1976). Because some woody species may be killed by fire, burning often favors grasses, at least initially (Williamson *et al.*, 1986; Keating, 1998). However, a single fire is unlikely to convert shrub páramo to grassland, or to completely remove shrubs growing within grass páramo, as many shrubs, along with grasses and forbs, will recolonize by sprouting from protected buds or by seed. As throughout the tropics, more long-term studies are needed in tropical highlands, to reveal the impacts of burning frequency and intensity that may not become apparent over the short time scales of most post-fire regeneration studies.

Lægaard (1992) described and classified the strategies that allow both herbaceous and woody páramo plants to survive fires. He noted that all plants present in grass páramo in Ecuador are able to survive fire, and would not be present were they not, given the ubiquity and frequency of fires. Adaptations include the ability to sprout from buds on stem bases or subterranean corms, rhizomes, or fleshy roots; seeds that germinate after fire; and protection of the apical bud in stem and ground rosettes. The ability of plants to resprout following disturbances or recolonize by seed is an advantage under many circumstances and did not necessarily evolve in response to fire. In páramo plants, some of these adaptations to fire may represent adaptations to aspects of páramo climate (e.g., drought and diurnal temperature fluctuations) that only as a side-effect help the plants survive fire (Lægaard, 1992).

Fire survival and post-fire resprouting by shrubs and bamboo has been investigated at several páramo sites in Costa Rica. Decomposition rates are slow, and the fire-killed aboveground portions of shrubs persist on the landscape as charred skeletons that document past fire and provide a means for estimating the pre-fire vegetation stature and composition (Janzen, 1973b; Williamson *et al.*, 1986; Horn 1989b). Dead stems can be identified to species based on stem architecture and morphology, making it possible to characterize fire responses by species (Williamson *et al.*, 1986). Horn (1989b) classified fire responses using terminology from the California chaparral (Zedler *et al.*, 1983). The bamboo *Chusquea subtessellata* and the ericaceous shrubs *Vaccinium consanguineum* and *Pernettya prostrata* (= *P. coriacea*) exemplify the "sprouter–nonseeder mode" in which most burned plants survive by resprouting but few or no seedlings are produced (Horn 1989b, 1998a); in the case of bamboo even seed set is rare, and many plants may be male-sterile (Horn and Clark, 1992). The shrub *Hypericum irazuense* follows the "sprouter–seeder" pattern; it resprouts less frequently, but establishes abundant seedlings (Horn 1989b, 1997). Janzen (1973b) reported that burned *Hypericum irazuense* (his *H. caracasanum*) shrubs on Cerro Asunción in the Buenavista Páramo resprouted vigorously after a 1969 fire, but all subsequent studies have revealed low (0–20%) resprout success, perhaps because these later fires were more intense burns with greater heat penetration (Horn, 1997). A smaller congener, *Hypericum strictum*, has not been observed to resprout and may be an "obligate seeder"; however, further study is needed. Rodríguez-Beltrán and Ríos (2002) presented a more detailed classification of regeneration modes in Colombian shrub páramo that includes consideration of whether shrubs resprout from buds at the base of the stem or on various types of underground structures.

Some shrubs and herbs are killed by fire and recolonize by seed. In Costa Rican páramo, seedling establishment appears to rely mainly on the influx of seeds from surrounding, unburned areas rather than the survival of seeds in the soil or on plants (Williamson *et al.*, 1986; Horn, 1989b), but soil seedbanks may contribute significantly to post-fire succession at páramo sites in Colombia (Vargas-Río, 1997; Cardenas *et al.*, 2002). Post-fire sprouting of woody species from protected buds may take place at some distance from the base of the original burned plant (Horn, 1989b; Keating, 1998; Rodríguez-Beltrán and Ríos, 2002), making it difficult to distinguish plants established by seed from sprouts from surviving plants (Horn, 1989b).

Hofstede (1995) and Verweij (1995) examined the impacts of burning and grazing on grass páramo in Los Nevados National Park in Colombia. In their study sites and many Andean páramo it is difficult to examine the effects of fire alone on vegetation as burning so often occurs in combination with grazing (Verweij and Kok, 1995). Field observations indicate that fire rarely kills grass tussocks in Colombian grass páramo (Hofstede *et al.*, 1995a). However, burned grass tussocks often tiller on their periphery, resulting in the replacement of a single large tussock by several smaller tussocks. Subsequent fires and grazing determine whether fragmented tussocks recover, remain fragmented, or are replaced by low mats of grass and herbs (Verweij and Kok, 1995).

Based on studies of aboveground and belowground biomass at four sites with different grazing and management histories (the most recent of which had burned four years earlier), Hofstede *et al.* (1995b) and Hofstede and Rossenaar (1995) concluded that burning, in combination with grazing, maintained grass tussocks that in the absence of burning, were converted into ground-covering grass mats. An illegal fire provided Hoftstede (1995b) an opportunity to monitor changes in vegetation structure and nutrient status immediately after burning. This fire was exceptional in only consuming about half of the aboveground vegetation at the site. Many grass tussocks resprouted, but productivity during the first year was not much higher than in an unburned reference area. The input of mineralized nutrients with ashes had only a small and short-lived effect on growth rates. The concentration of nitrogen in grass leaves increased for a short period but phosphorous was still limiting.

Keating (1998) experimentally tested the effects of burning and cutting on grass páramo and cutting on shrub páramo in Podocarpus National Park in southern Ecuador. Burning and cutting alone both led to the elimination of some woody cover and increased grass and herb cover, and the effect was greater when burning and cutting were combined in grass páramo plots. Some woody species that had not been present in plots prior to treatment entered through vegetative spread from plants on the plot edge. Plant height recovery in burned grass plots was higher than in cut plots, either because aboveground portions of some plants survived the fires, allowing regrowth from branchlets 10 cm to 25 cm above the ground surface, or because plant growth was stimulated by fire, by nutrients in the ash from the fire, or by release from competition.

The effect of fire on giant rosette plants in Andean páramo has also garnered attention. Smith (1981) found that fire damaged both juvenile and adult stem rosette *Espeletia schultzii* in Venezuelan páramo. Fire damaged plants 10 cm to 20 cm high by killing the meristem, and taller plants were killed when the dead leaves retained around the stem were burned off, allowing the stem itself to burn (Smith, 1981). In Los Nevados National Park in Colombia, Verweij and Kok (1992) found that that adult mortality of *Espeletia hartwegiana* was higher for taller plants, and that fire-induced stimulation led to higher growth rates on burned sites. In the El Ángel Ecological Reserve in northwestern Ecuador, Suárez and Medina (2001) found that fire increased the density of juvenile stem rosettes of *Espeletia pycnophylla*, due perhaps to the abrupt increase in space, light, and nutrients (especially phosphorous) that may occur after fire. Miller and Silander (1991) found that the fire resistance of giant rosettes of *Puya* in Ecuadorian páramo depended on fire intensity. Both *Puya clava-herculis* and *P. hamata* are able to withstand occasional low-intensity fires but fires of greater intensity will eliminate these plants along with shrubs, promoting greater grass dominance.

Rates of vegetation recovery, in terms of vegetation cover and the stature of individual plants, are slow in páramo ecosystems in comparison with sites at lower elevation. Verweij and Kok (1995) estimated a minimum post-fire recovery period of ten years for tussock grass páramo in Los Nevados, Colombia. In ungrazed páramo in Costa Rica, bare patches of ground can persist for a decade or more following fires (Horn, 1989b). The dominant páramo bamboo in Costa Rica may require 8–10 years to regain its pre-fire stature (Janzen, 1983; Horn, 1989b), while associated dicotyledonous shrubs may require more than a decade to regain pre-fire statures of 1 m to 2 m (Horn, 1989b). Stem diameter recovery, which may be a better indicator of biomass recovery, significantly lags height recovery for most woody species (Horn, 2005).

Keating (2007) examined post-fire plant diversity as a measure of vegetation recovery in Nevado Cotacachi in the Cotacachi–Capayas Reserve of northern Ecuador. Seven months after a November 1996 fire, he found only 12 species of vascular plants (3 woody and 9 herbaceous). Eighteen months later (December 1998), he recorded 27 species (4 woody and 23 herbaceous), but diversity was still much lower than Ramsay (1992) had found in surveys prior to the fire (9 woody and 39 herbaceous species; Keating, 2007). Thus, the effects of the fire would be regarded as negative for biodiversity. However, when Keating censused the area again in July 2005, a very different picture emerged: the burned site now supported 67 species, of which 18 were woody. By nine years post-fire the site had seen a large *net* increase in species richness. The absolute and percentage representation of woody species had risen dramatically, and was now much higher than had been recorded in the area prior to the fire.

During 2000 and 2005, Keating (2007) made extensive plant collections on Cerro Imbabura, a volcanic peak *ca.* 20 km SW of Cotacachi that is surrounded by farms and small villages. Imbabura is not a protected area, and the páramo burns frequently. Nevertheless, in the mosaic of regenerating páramo vegetation on Imbabura, Keating (2007) found 91 vascular plants species (22 woody and 69 herbaceous). No data exist on the intensity of past fires on Imbabura, and it is possible that the higher frequency of fire here results in lower fire intensity than observed on Cotacachi. Nevertheless, the conclusion was inescapable that the high fire frequency on Cerro Imbabura maintains, or perhaps even enhances, species diversity.

18.8 FIRE FREQUENCY

As noted by Keating (2007), fire frequency may be the most important determinant of long-term ecological change within páramo ecosystems. The number of fires per unit time in a particular stand of páramo is likely to influence both fire intensity and the spatial extent of fires (Keating, 2007). Unfortunately, understanding fire frequency requires explicit spatial–historical information that may not be available for most fires, or, if available, may not go back as far in time as would be useful. Managers of protected areas, or nearby residents, may be able to provide some data on past fire occurrence, and studies of post-fire vegetation dynamics will benefit from efforts to assemble all such information, even if the temporal and spatial scale remains coarse. Field observations of vegetation mosaics and shrub stems burned in previous fires can supplement written and oral histories of fire. Fire-killed shrub stems in two stages of decay record the last two fires at some páramo sites in Costa Rica: the more intact dead stems, still with bark, are those killed in the last fire, while more deeply charred stems, missing bark, were killed in the penultimate fire and burned for a second time in the last fire (Williamson *et al.*, 1986; Horn, 1989b). Some shrubs appear to produce annual rings that make it possible to estimate dates of past fires by determining the ages of the oldest living and dead stems that regenerated after these fires (Janzen, 1973b; Horn, 1986; Williamson *et al.*, 1986; Schlachter *et al.*, 2007).

Although we have focused here on the setting of fires in páramo, fuel rather than ignition may drive fire frequency in some stands, because of slow rates of fuel buildup. For example, 20th-century fire recurrence intervals for páramo areas in Costa Rica with well-documented histories range from 6 to 23 years. Six years may be close to the minimum fire recurrence interval possible, owing to slow rates of vegetation recovery and the long persistence of bare ground within these sites. Shorter fire recurrence intervals of 3.0–3.5 years were recorded by Verweij (1995) at grass páramo sites in Colombia. However, she cautioned that this finding does not mean that the vegetation has fully recovered in so short a period, but only that fuels had recovered to the point at which the site could burn again.

Few data exist on how fire at different frequencies affects páramo vegetation. Williamson *et al.* (1986) suggested that repeated fire, at 10-year intervals, is sufficient to preclude shrub dominance in Costa Rican páramo. This interpretation fits general expectations that increased fire frequency in tropical highlands should favor grasses with protected meristems over shrubs (Spehn *et al.*, 2006), but more work is needed at sites with known burn histories. Verweij (1995) found shrub cover to be low in more frequently burned areas of Los Nevados National Park in Colombia, but noted that shrubs did not naturally dominate the páramo communities she studied. She found shrubs to be characteristic and common only in areas in which fire had been negligible or absent in recent decades. Although Andean farmers believe that frequent burning enhances pasture development and thus grazing opportunities, Verweij (1995) found that fire frequencies of more than one fire a decade will degrade forage resources in the long term.

The effect of climate factors on fuel is not, of course, limited to an effect on the rate of fuel accumulation. Climate also affects the moisture content of fuels. Even when human-set, fires in páramo can only occur within a climate window that allows for burning. Our understanding of potential interactions between climate, fires, and fuel is limited both by incomplete knowledge of fire history and by spotty, often short, meteorological records. Circumstantial evidence suggests that a link may exist between large fires in Costa Rica and the severity of the dry season (Horn, 1991). Between 1952 and 1985, meteorological data collected in and near the Buenavista Páramo indicate three years in which the driest month (February or March) recorded less than 0.5 mm precipitation, and in each of these years (1961, 1976, 1985) a large (>100 ha) fire occurred in the Chirripó Páramo and adjacent montane forests. Analyses of fire–climate links in other páramo areas may provide both important insight on modern páramo dynamics and key information for modeling potential fire frequencies in the face of global change.

18.9 CHARCOAL AND POLLEN EVIDENCE OF LONG-TERM FIRE HISTORY

Paleoecological analyses of charcoal fragments and pollen in soils and sediments provide a basis for determining long-term histories and interactions of fire and vegetation in páramo landscapes. Pollen records from lakes and bogs below the modern treeline in Colombia and Costa Rica indicate that these areas supported páramo or páramo-like vegetation during some glacial intervals of the late Pleistocene, when cooler temperatures depressed treelines by up to 1,000 m (Hooghiemstra, 1984; Wijninga, 1996; Islebe and Hooghiemstra, 1997; Horn, 2007). Reduced atmospheric carbon dioxide and shifts in rainfall amounts and seasonality also affected the distributions of páramo and montane taxa during glacial intervals (Boom *et al.*, 2001; Markgraf, 2001; Mora and Pratt, 2002; Mora *et al.*, 2002). Late glacial and Holocene climate conditions interacted with human activity to shape fire regimes in the highlands.

Data on long-term fire history within modern and former páramo environments come primarily from Costa Rica, Ecuador, and northern Peru. Pollen records of vegetation history have been developed from lake and bog sediments in the Venezuelan and Colombian páramo (e.g., Melief, 1985; Rull *et al.*, 1987, 2005; Salgado-Labouriau *et al.*, 1988), but only Gonzalez *et al.* (1966) report sedimentary charcoal, from a site in the Sierra de Cocuy of Colombia. The detailed analyses by Hooghiemstra (1984) and Wijninga (1996) of older sediments from the high plains of Bogotá, which supported glacial age páramo communities, also neglect to mention charcoal evidence of fire history. However, this may reflect the interests of the researchers, rather than a lack of fire over long time scales at the sites investigated. Indeed, studies of Colombian *soil* profiles provide evidence of recurrent páramo fires. Fölster and Hetch (1978) reported charcoal in paleosol (ancient soil) sequences in the Sabana de Bogotá that they associated with glacial age páramo grasslands; three samples yielded dates of 21,900, 23,750, and 30,100 ^{14}C yr BP. Salomons (1986) and Bakker and Salomons (1989) also found macroscopic charcoal in soil profiles in the páramo of Los Nevados National Park. Dated to constrain soil pollen records, the charcoal documents Holocene fires near 2,410, 2,480, 5,710, 6,030, 6,205, 7,260, and 7,440 ^{14}C yr BP. The presence of many interbedded tephra layers suggests that volcanism may have been the source of these páramo fires. Charcoal likely also associated with volcanism was reported by Kuhry (1988) in bog sediments from just below the treeline in the Colombian Cordillera Central.

18.9.1 Records from Costa Rica

Two long pollen records from highland Costa Rica indicate a downslope depression of treeline and expanded areas of páramo vegetation during the late Pleistocene. The records were developed based on cores from two sites located within 2 km of each other near the Inter-American Highway route across the Cordillera de Talamanca: Parque Vicente Lachner Bog (2,400 m elevation; Martin, 1964) and La Chonta Bog (2,310 m elevation; Hooghiemstra *et al.*, 1992; Islebe and Hooghiemstra, 1997). Both records extend beyond the limit of radiocarbon dating (>45,000 ^{14}C yr BP) and show the replacement of local montane forest by open páramo during the last glacial interval, when the treeline is estimated to have been depressed over 1,000 m by cooling of 7°C to 8°C, and today's bogs were lakes surrounded by páramo vegetation (Hooghiemstra *et al.*, 1992; Islebe and Hooghiemstra, 1997). These records show that páramo vegetation has a long history in the Cordillera de Talamanca. Luteyn (1999, p. 138) described the area we call the Buenavista Páramo as only "páramo-like" and "man-made" by fire, following Janzen (1973a, 1983), but the paleoecological record points to the existence of similar vegetation in the area long before human presence.

Charcoal was not quantified as part of the bog studies cited above, but a new core recovered from the La Chonta site in 2001 (Horn and Orvis, unpublished data) contains charcoal dating to the last glacial period. One fragment yielded a radiocarbon date of 35,370 ^{14}C yr BP, significantly predating human arrival in Central America. Based on the pollen study by Hooghiemstra *et al.* (1992), this charcoal should represent an early páramo fire set by lightning or volcanism. A very similar date of 36,640 ^{14}C yr BP was obtained on charcoal in a paleosol located 5 km east of La Chonta Bog at 2,507 m elevation (Driese *et al.*, 2007). Based on the inferred magnitude and timing of páramo expansion during the last glacial interval, this dated charcoal may also represent a natural fire in páramo vegetation.

Evidence of Holocene fires and vegetation change within the Chirripó Páramo derives from studies of the sediments of lake basins formed by glaciation (Orvis and Horn, 2000; Horn *et al.*, 2005). Two short-sediment cores recovered from Lago Chirripó (3,520 m) in 1985 both contained abundant fragments of charcoal attesting to past fires, including macroscopic charcoal (fragments >125 μm) visible to the unaided eye, and smaller, microscopic fragments (Horn 1989c, 1993). The distinction between macroscopic charcoal and microscopic is important because the former size class is regarded as indicating fires that burned within a lake's watershed, while the latter could signal both local and more distant burning, as small charcoal fragments can potentially be dispersed long distances by wind (Whitlock and Larsen, 2001).

Charcoal in the Lago Chirripó cores revealed that fires due to human activity or lightning had affected the páramo for at least 4,000 years (Horn and League, 2005). In 1989, Horn and students recovered two longer cores from Lago de las Morrenas 1 (3,477 m elevation) in an adjacent valley (Horn, 1993; Orvis and Horn, 2000). Both cores reached the glacial flour deposited as ice last retreated from the basin *ca.* 10,000 ^{14}C yr BP. Detailed analyses of microscopic charcoal and pollen confirmed and extended the fire record from Lago Chirripó, and provided evidence of postglacial vegetation. Pollen assemblages demonstrated that the site had been surrounded by treeless vegetation since deglaciation, with no pronounced changes in vegetation. Fires burned repeatedly during the Holocene, with fire activity greatest in the late Holocene, but these fires did not carve páramo from forest. Pollen percentages for grasses and other páramo plants declined upward in the core, while those for certain subalpine, lower montane, and tropical forest taxa increased, suggesting that the extent of páramo vegetation had decreased throughout the Holocene as forest taxa migrated upslope in response to postglacial warming.

League and Horn (2000) later analyzed macroscopic charcoal (>500 μm) in the same Morrenas 1 sediment core used for pollen and microscopic charcoal analysis. The macroscopic charcoal record showed many of the same features, but was an improvement over previous charcoal records because it was based on the analysis of contiguous samples. Samples for the previous study of the Morrenas 1 core were taken at 20 cm intervals that correspond in time to 250 to 500 years. A closer sampling interval was used for the Lago Chirripó core, but fires at both sites could easily have been "missed" between sampling intervals. The Morrenas 1 macroscopic charcoal record is also a better record because it focuses on charcoal fragments >500 μm in size that are sure indicators of local burning. While some of the charcoal on pollen slides from this core could represent fires in montane forests below the páramo, the charcoal >500 μm should largely represent fires within the watershed of the lake.

The macroscopic charcoal record from Lago de las Morrenas 1 is the only high-resolution sedimentary charcoal record of local fires presently available from neotropical páramos. It provides strong evidence of the antiquity of fire in the Chirripó Páramo, and suggests that the frequency of fire has varied over time in response to changes in climate as well as possible human impacts. Macroscopic charcoal influx is highest in the late Holocene (last ~4,200 ^{14}C years), when human population density was higher and when climates of the circum-Caribbean were becoming drier (particularly after about 3,000 ^{14}C yr BP; Hodell *et al.*, 2000). Charcoal influx is lowest between 6,800 and 4,200 ^{14}C yr BP, a time period that overlaps what may have been the wettest interval of the Holocene in the wider Caribbean region (Hodell *et al.*, 2000).

18.9.2 Records from Ecuador and northern Peru

Stratigraphic analyses of microscopic charcoal and pollen in sediment records that date to the last glacial period have been carried out at five lakes and a mire located in or near páramo vegetation in Ecuador and Peru. Five of six sites showed evidence of increasing fire across the late Glacial–Holocene transition, as climate warmed. Holocene charcoal stratigraphy, studied at five sites, differed, with two showing highest fire activity in the middle Holocene, and three showing highest fire activity in the late Holocene, matching the pattern in Costa Rica. The variability among these sediment records may largely reflect true differences in fire history resulting from differences in site conditions and local human history. However, the wide sampling intervals employed in these studies of charcoal on pollen slides, and the different size classes of charcoal investigated, hampers comparisons. Our understanding of páramo fire history in the Andean region would be enhanced by contiguous sampling of macroscopic charcoal in these and other cores, and standardization of procedures for microscopic charcoal counting.

Hansen *et al.* (2003) recovered and analyzed cores from two lakes in Cajas National Park in southwestern Ecuador. Laguna Chorreras (3,700 m elevation, basal date on core *ca.* 14,500 ^{14}C yr BP) is surrounded by tussock grass páramo, with patches of *Polylepis* forest. More open grassland surrounds the higher Laguna

Pallcacocha (4,060 m, basal date *ca.* 12,500 ^{14}C yr BP), where forest patches are less numerous. Pollen assemblages indicate that herb páramo communities with abundant ferns along with *Puya* surrounded both lakes during the late glacial period, probably without nearby *Polylepis* stands but with some woody Asteraceae. Charcoal was negligible near the bases of the cores, indicating few fires, but increased in the late glacial, coincident with other evidence of a dry period. Charcoal on pollen slides was tallied in two size classes, 30–100 μm and >100 μm. At least some of the charcoal in the larger size class probably represents local fires, and the two size classes track each other. The transition to the Holocene (*ca.* 10,000–9,000 ^{14}C yr BP) is marked in both records by increased pollen of montane forest taxa, possibly indicating upslope adjustments in some ranges, followed at Chorreras by increased *Polylepis* pollen. Sediments deposited after 9,000 ^{14}C yr BP were studied only in the Chorreras core. Grass páramo expanded between 7,000 and 3,500 ^{14}C yr BP, as did evidence of fire, which was highest during the middle Holocene. Weed pollen and other signs of disturbance increased after 2,000 ^{14}C yr BP, possibly signaling forest clearance and agriculture, but charcoal concentrations were low and the researchers found no pollen evidence for treeline depression.

Colinvaux *et al.* (1997) examined pollen and microscopic charcoal in two size classes (<25 μm and >25 μm) in a 14 m core from Laguna Surucucho (Llaviucu, 3,180 m), located near the páramo–forest ecotone in Cajas National Park. Basal late glacial sediments are sandy clays that contain pollen assemblages indicating páramo vegetation, perhaps initially super-páramo with low local pollen production. Herb pollen percentages and concentrations increased upcore, possibly indicating a change from super-páramo to páramo vegetation as climate warmed. Before 13,000 ^{14}C yr BP, the clay was replaced by more organic black gyttja and clay, and *Polylepis* pollen increased dramatically, suggesting the presence of Andean woodland in the Surucucho valley. The *Polylepis* increase occurred earlier at Surucucho than at Chorreras, perhaps due to the lower elevation of Surucucho. From *ca.* 12,000 to 10,000 ^{14}C yr BP, *Polylepis* declined and grass pollen increased, indicating the replacement of woodlands by more open vegetation. That this decline was *followed* rather than accompanied by a rise in charcoal argues against fire as the cause of *Polylepis* decline. From 10,000 ^{14}C yr BP onward, pollen percentages and concentrations of forest taxa increased, indicating upslope adjustments of ranges as climate warmed during the Holocene. Charcoal also increased during the Holocene. It was most abundant in the late Holocene, in contrast to the pattern at Chorreras, but this greater abundance was primarily seen in the <25 μm size class, which was ignored at Chorreras. Charcoal concentrations for fragments >25 μm at Surucucho (which may be roughly comparable with the 30–100 μm class at Chorreras) were only slightly higher in the later Holocene.

Niemann and Behling (2008) installed modern pollen traps and raised sediment and soil cores for paleoecological analyses along a transect through Podocarpus National Park in the southeastern Ecuadorian Andes. From El Tiro Pass Bog at 2,810 m in the modern sub-páramo zone they recovered a 1.2 m long core with a basal date of 16,500 ^{14}C yr BP (Niemann and Behling, 2007). Pollen and charcoal counts showed that grass páramo surrounded the site during the late Pleistocene, but fires were rare at this time. Sub-páramo and montane forest expanded slightly during the early Holocene, and fires became common after about 8,000 ^{14}C yr BP, probably both in the region and locally, based on the observation of macroscopic charcoal in the sediments as well as abundant microscopic charcoal on the pollen slides. The authors suggested that upper-montane rainforest surrounded the site for much of the Holocene, under slightly warmer temperatures, with the modern sub-páramo only developing in about the last 3,000 ^{14}C years. They conjectured that fires since 8,000 ^{14}C yr BP may have been predominantly anthropogenic. Increased charcoal after *ca.* 3,000 ^{14}C yr BP was interpreted to represent increased use of fire for slash-and-burn agriculture and hunting in the Loja Valley, and the uplsope movement of escaped fires during drier parts of the year. A marked decrease in fires in the last five centuries is attributed to population decline following the Spanish Conquest (Niemann and Behling, 2007).

In northern Peru, Hansen and Rodbell (1995) studied a 4.2 m long core from Laguna Baja (3,575 m), near the páramo–forest ecotone on the edge of Río Abiseo National Park in the Cordillera Oriental. The record extends to 13,300 ^{14}C yr BP. Herb páramo dominated the site between 11,600 and 10,000 ^{14}C yr BP, during a time of cooler or more seasonal climate. An abundance of charcoal >100 μm along with charcoal 30 μm to 100 μm in size during the páramo interval suggests that many of the fires burned locally. Warming after 10,000 ^{14}C yr BP resulted in rising treelines. Fires increased in the late Holocene, but not to the levels seen during the late glacial.

Weng *et al.* (2006) studied a long sediment core from Laguna Compuerta (3,950 m) on the west Andean slope east of the Laguna Baja site. They described the modern vegetation of the site as wet puna grassland, but Luteyn (1999) mapped a number of occurrences of jalca (the Peruvian name for páramo) in this general region. Charcoal was very rare in sediments deposited before 8,500 ^{14}C yr BP, and generally more abundant in the middle than late Holocene, similar to the pattern seen at Chorreras in Ecuador.

While the studies reviewed above focused on fire and vegetation history throughout the Holocene, Wille *et al.* (2002) investigated a sediment profile from a shallow mire in the páramo of Cerro Atacazo near Quito, Ecuador, that covered only the last *ca.* 800 years. Their detailed study of the Pantano de Pecho at 3,870 m elevation highlighted possible shifts in climate and human activity at these very high elevations not documented by other paleoecological studies. Pollen was analyzed and interpreted in light of analyses of modern vegetation and pollen rain in the páramo surrounding the site, in nearby forest patches, and in the closed forest that presently reaches its upper limit at 3,500 m to 3,600 m elevation. Pollen of Poaceae and other taxa of the grass páramo dominated all levels, with low but consistent percentages of Andean forest taxa and some sub-Andean taxa, aquatics, and others. The record did not show marked changes in pollen percentages but several zones were delineated. These were interpreted in light of the companion studies to suggest an upslope shift in the *natural* upper forest line of several hundred meters between 730 ^{14}C yr BP and 290 ^{14}C yr BP, at which time human disturbance began and the treeline was artificially lowered by 50 m to 100 m. Charcoal was present throughout the record but reached highest values in the last 290 ^{14}C yr, supporting the interpretation of significant local human impact at this time. The authors concluded that post-Conquest deforestation and fire had fragmented what was originally a closed forest between 3,600 m and 3,750 m elevation, but that the mire was surrounded throughout by páramo and that forest patches at the site and at higher elevations had never been part of the continuous forest. They concluded that their dataset did not support the interpretation of Lægaard (1992) that the natural upper forest limit in central Ecuador is from 4,100 m to 4,350 m elevation.

Other evidence of late Holocene treeline shifts (or lack thereof) in Ecuador come from work on soil charcoal by DiPasquale *et al.* (2008). Macroscopic charcoal sieved from soil layers is an important source of information on past fires in both the lowland and highland tropics (e.g., Horn and Sanford, 1992; Sanford and Horn, 2000; Titiz and Sanford, 2007), as well as in temperate regions (Gavin *et al.*, 2007). Soil charcoal studies focus on fragments that are too large to be transported far from the fire source, and, like studies of macroscopic charcoal in lake sediments (e.g., League and Horn, 2000), provide definitive evidence of local burning. Another advantage of soil charcoal studies is that they are not limited by the distribution of lakes or swamps and so can be carried out in vastly more areas. Finally, soil charcoal particles can potentially be identified to species or genera, to provide information on the nature of the plants burned and thus evidence of prior vegetation as well as fire (Hart *et al.*, in press), as was done by DiPasquale *et al.* (2008).

DiPasquale *et al.* (2008) conducted their study at the treeline in the Guandera Biological Station on the western slope of the eastern Cordillera in northern Ecuador. Here the páramo is not grazed but is burned every 3–6 years in the belief that doing so will induce rain. Soil samples were collected from three excavations, one in the cloud forest at 3,540 m elevation, and two in tussock grass páramo (3,810 and 3,890 m elevation; the lower páramo site had a higher cover of shrubs). Soil samples were sieved using screens of 2.0 mm and 0.4 mm to isolate charcoal fragments. A reference collection developed from samples of local woody species was used to identify the charcoal, with particular attention paid to indicator taxa from the forest (trees) and páramo (heliophytic shrubs) that could reveal past treeline shifts. Charcoal from páramo indicator taxa occurred in soil from all three excavations: in the páramo sites from 10,600 or 10,960 ^{14}C yr BP to the present, and in the forest sites from 10,840 to 5,050 ^{14}C BP. No forest taxa were found in any charcoal samples. Thus, the charcoal indicated that all three sites had supported páramo in the late glacial period, and that the modern treeline had only moved up to its present height in the last 5,050 ^{14}C years. The authors concluded that fires had not created páramo from forest, but that burning may have slowed forest expansion, an interpretation in line with the views of White (Rust, 2006).

18.10 ISSUES FOR FIRE MANAGEMENT

Paleoecological records that document the long-term history of fire in páramo ecosystems, together with studies of post-fire dynamics on recent burn sites, have begun to change the way scientists view fire in páramo ecosystems. Fires set by humans or otherwise are beginning to be recognized as an integral component of neotropical páramo landscapes (Myers, 2006). The idea that páramo plants cannot only survive fire but to some extent also seem to require fire, is reflected in the assessment of experts contributing to the Global Fire Assessment sponsored by the Nature Conservancy in collaboration with other groups. They conclude that neotropical páramos are indeed *fire-dependent ecosystems* (Shlisky *et al.*, 2007; *http://giifweb.cnr.berkeley.edu/tnc/about.pl?language=english*). Far from destroying páramo, fire at the appropriate frequency apparently may enhance species and habitat diversity (Sarmiento and Frolich, 2002; Keating, 2007).

We note that these views are not shared by all scientists or land managers (Chaverri and Esquivel, 2005; Spehn *et al.*, 2006), and have yet to be given much attention in management plans for protected areas. They are also markedly at odds with public perception. Páramo fires that are large or burn well-known localities invariably generate newspaper headlines that decry them as ecological disasters (Horn, 1998b; Keating, 2007). Often these fires are reported as "unprecedented" (Horn, 1990). Scientific controversy over the role of fire in páramo ecosystems and public perception of these fires as destructive are part of the context for any consideration of fire management in neotropical páramo.

Fire management in páramo ecosystems includes a range of potential activities. In grazed Andean grass páramo outside protected areas, fire management needs to be considered along with grazing management, and is liable to be strongly driven by economic concerns relating to the maintenance of forage quality. Hofstede (1995), Verweij (1995), Molinillo and Monasterio (1997), and Suárez and Medina (2001), among others, offer important insights from their research on both vegetation dynamics and patterns of human use in pastured páramo.

We focus our comments here on fire management in protected areas in which grazing, if it occurs, is not sanctioned or encouraged, and thus not a major focus of fire management. As suggested by Myers (2006), the development of fire management plans for protected areas requires understanding just what it is that we are trying to protect:

> "Designing and managing ecologically appropriate fire regimes that benefit both people and nature requires the development of fire management goals. People have created protected natural areas, national parks and forest reserves because they contain something of value including needed products and services. These products and services are the conservation 'targets.' They may require fire, be sensitive to it or able to tolerate only certain types of fire or specific fire regimes. Because these areas have something of value that people want to restore, maintain or enhance and these things or processes are affected by fire, fire management goals need to be set for those targets" (Myers, 2006, p. 22).

Fire management of conservation "targets" in the neotropical páramos needs to take into consideration relevant science. Complete fire exclusion appears to be the management goal in many of today's protected areas, but the ecological outcome, were this to be achieved, may not provide the desired products and services. The extensive stands of *Chusquea subtessellata* bamboo that cover the highest peaks of Chirripó National Park in Costa Rica are, in part, a consequence of repeated human-set fires in the 20th century, as well as a long history of earlier fires set by people or lightning that are recorded in lake sediments. Were management objectives of complete fire suppression (Chaverri and Esquivel, 2005) achieved over the next century, the páramo bamboo that now dominates and characterizes the páramo ecosystem might lose ground to slower growing shrub associates (Janzen, 1983). In the grass páramos of the northern Andes, the increased density of woody plants that results from fire suppression (e.g., Jokisch and Lair, 2002) might similarly produce an ecosystem or vegetation structure that is unintended and undesirable, perhaps again through the loss of a species that requires fire, or perhaps because taller shrubs obstruct some open vistas that tourists enjoy.

Management plans that have as their goal the complete elimination of fire from neotropical páramos are not only at odds with history, but may be unrealistic for many páramo areas given modern climate patterns and climate variability. Most páramo areas in the neotropics experience intervals of dry climate that create fuel conditions that foster burning. These may occur seasonally or intermittently, tied with annual shifts in the position of atmospheric systems such as the Intertropical Convergence Zone, or with episodic changes in atmospheric phenomena such as associated with El Niño events. The dry seasons that are a regular part of the modern climate of many páramo areas are likely to vary in severity, potentially affecting fire occurrence and behavior. The large 20th-century fires in páramo and montane forest in Costa Rica that occurred during exceptionally dry years (Horn, 1991) were very difficult or impossible to control precisely because of that climate link. The relationship between fire and drought in protected areas in the neotropical páramos deserves further study, both for understanding historic patterns of fire and for projecting possible changes in fire incidence due to climate change.

Human practices and needs also make fire an inevitable occurrence within protected páramos (Keating, 2007). Keating (2007) concluded that management efforts directed at eliminating fires above 3,300 m elevation in the Cotacachi–Cayapas Ecological Reserve of Ecuador are ‘‘neither desirable nor possible.’’ Fires were bound to occur in the eastern sector, where trying to enforce a ‘‘no-burn’’ policy would only increase conflicts between farmers and park managers. Strict enforcement of such policies could also increase fuel levels to the point that atypically large fires could occur, including fires in super-páramo not usually affected by fire (Keating, 2007). Horn (1998b) made a similar argument for the Chirripó Páramo. She suggested that directing fire management efforts toward limiting fire size would be more appropriate than trying to keep all fires out, and that additional use of firebreaks could be a way to achieve this. Controlled burning might also have a role in efforts to limit fire size in the Chirripó Páramo. The popularity of the Chirripó Páramo as a wilderness destination for Costa Rican and foreign hikers (Horn, 1998b; Chaverri and Esquivel, 2005) and downstream dependence on water sources from the páramo may make this environment one in which freely burning wildfires cannot be accommodated. As suggested by Myers (2006), in such an environment controlled burning may be useful to create fuelbreaks and areas of low fuel load that will facilitate the control of unwanted fires. Such fuelbreaks will also work to keep fire sizes small, which would have a number of other benefits. Small fires would have less of an impact on animal species, would foster faster plant regeneration by reseeding species because of the availability of nearby seed sources, and would impact only portions of watersheds (Horn, 1998b). The patchwork of different aged stands of páramo that would result from a program of controlled burning, and the unplanned smaller fires that might occur, would enhance overall habitat and species diversity.

Such an approach may be worth considering in other protected páramo areas but would have consequences for visitor experiences that need to be taken into account. Many visitors to protected páramo areas may be coming in part to experience a *sense of wilderness* (Botkin, 1990) as well as for the chance to experience physical exertion in a unique high-montane environment (Hofstede, 1995a; Horn, 1998a). Signs of active fire management may be unwelcome to visitors who come to protected areas seeking to experience an environment untouched by modern humans. The perception of pristine or untrammeled wilderness may be very important to visitors, regardless of the true recent history of the protected area. However, visitor needs for wilderness must be balanced against the needs and perceptions of people occupying adjacent lands or inholdings, and the local, regional, and even global need for proper ecological function and for the ecological resources and services that the protected area If one takes the view (Horn, 1998a; Keating, 2007) that fire is for biophysical and human reasons inevitable in protected neotropical páramos, it is better to challenge the perception of a pristine environment through active fire management than to create, through ineffective fire exclusion, conditions that favor larger, more intense fires that may have more severe ecological consequences.

In weighing the diverse social and ecological needs that must shape fire management plans in tropical highlands, policy makers must also take into account the possible effects of global climate change. As described by Foster (2001), the modeling of possible future climate in tropical highlands faces a number of difficulties, including data shortages, a paucity of theory on mountain climate, the spatial and temporal complexity of mountain weather, and the inability of global climate models to accurately model current-day rainfall patterns owing to their inability to resolve topography. Existing projections therefore involve a good deal of uncertainty, which complicates their use in management. Gosling and Bunting (2008) briefly reviewed future climate projections for mountainous regions, including the Andes, based on the work of the Intergovernmental Panel on Climate Change (*http://www.ipcc.ch/*). Models predict that for the period 2020–2029, the Andes will warm by 0.5°C to 1°C along their entire length, with a higher increase (1–1.5°C) in the central Andes. For the later modeling period of 2090–2099, additional warming to at least 2°C above modern values is expected, again with greater increases in the central Andes. Seasonal patterns in precipitation and annual totals are also projected to change. These shifts could accentuate modern differences between Andean páramo and puna as the northern Andes, which are already wetter than the central Andes, are expected to become wetter while the central Andes become drier, and also to warm more (Gosling and Bunting, 2008).

While total precipitation may increase in the Andean páramo, rainfall seasonality is also expected to increase with warming (Buytaert *et al.*, 2006b), along with evapotranspiration. Foster (2001) projected that tropical highlands may experience reductions and shifts in the cloud belt, longer dry seasons, and an increased frequency of drought (Foster, 2001), all of which can increase the incidence of fire.

How these shifts in precipitation and temperature, together with CO_2 fertilization, will affect neotropical páramo within and outside protected areas remains uncertain. While climate warming might be expected to result in higher treelines, thus reducing the extent of páramo, recent research on modern seedling dynamics at the treeline in Andean páramo suggests that microclimatic limitations may hinder treeline advance into the páramo under climate warming, and would do so even in the absence of fires (Bader, 2007; Bader *et al.*, 2007). Thus, warming may not "pinch out" smaller páramos on remote peaks, even if forests at lower elevation are seeing upslope shifts in tree ranges. Parks and reserves created to preserve areas of treeless páramo are likely to continue to support such vegetation into the future. However, in selecting desired outcomes for ecosystem management in neotropical páramo and working to achieve them in a warming world, natural resource managers will face novel and increased challenges due to biophysical changes within and beyond reserve boundaries. Changes in fire regimes will likely be among the biophysical changes that challenge management. As this review demonstrates, research on fire in neotropical páramo has advanced markedly in the last two decades, but much remains to be learned about the roles fire has and should play in these fascinating tropical alpine ecosystems.

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18.12 REFERENCES

Bader, M.Y. (2007) Tropical alpine treelines: How ecological processes control vegetation patterning and dynamics. Ph.D. dissertation, Wageningen University, Wageningen, The Netherlands.

Bader, M.Y., I. van Geloo, and M. Rietkerk (2007) High solar radiation hinders tree establishment above the alpine treeline in northern Ecuador. *Plant Ecology*, **191**, 33–45.

Bakker, J.G.M. and J.B. Salomons (1989) A paleoecological record of a volcanic soil sequence in the Nevado del Ruiz area, Colombia. *Review of Palaeobotany and Palynology*, **60**, 149–163.

Bloesch, U., A. Bosshard, P. Schachenmann, S.H. Rabetaliana, and F. Klötzi (2002) Biodiversity of the subalpine forest–grassland ecotone of the Andringitra massif, Madagascar. In C. Körner and E. Spehn (Eds.), *Mountain Biodiversity: A Global Assessment*. Parthenon Publishing, New York.

Boom, A., G. Mora, A.M. Clee, and H. Hooghiemstra (2001) High altitude C_4 grasslands in the northern Andes: Relicts from glacial conditions? *Review of Palaeobotany and Palynology*, **115**, 147–160.

Botkin, D. (1990) *Discordant Harmonies: A New Ecology for the Twenty-first Century*. Oxford University Press, NewYork.

Bromley, R.J. (1971) Neurolepis, a sensitive indicator of human activity in the high Andes. *American Antiquity*, **36**(4), 475–476.

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

Buytaert, W., R. Celleri, P. Willems, B. De Bièvre, and G. Wyseure (2006b) Spatial and temporal rainfall variability in mountainous areas: A case study from the south Ecuadorian Andes. *Journal of Hydrology*, **329**, 413–421.

Cardenas, C.d.A., C. Posada, and O. Vargas (2002) Banco de semillas germinable de una comunidad vegetal de páramo húmedo sometida a quema y pastoreo (Parque Nacional Natural Chingaza, Colombia). *Ecotropicos*, **15**(1), 51–60.

Chaverri, A. and A.M. Cleef (2005) Comunidades vegetales de los páramos de los macizos de Chirripó y Buenavista, Costa Rica. In M. Kappelle and S.P. Horn (Eds.), *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica [in Spanish].

Chaverri, A. and G.O. Esquivel (2005) Conservación, visitación y manejo del Parque Nacional Chirripó, Costa Rica. In M. Kappelle and S.P. Horn (Eds.), *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica [in Spanish].

Chaverri, A., C. Vaughan, and L.J. Poveda (1976) Informe de la gira efectuada al macizo de Chirripó al raíz del fuego ocurrido en marzo de 1976. *Revista de Costa Rica*, **11**, 243–279.

Chaverri, A., C. Vaughan, and L.J. Poveda (1977) Datos iniciales sobre la fragilidad de un páramo frente a los efectos del fuego. In R. Wolda (Ed.), *Resumenes Recibido para el IV Simposio Internacional de Ecología Tropical, marzo 7–11, 1977, Panama* [in Spanish].

Cierjacks, A., K. Wesche, and I. Hensen (2007) Potential lateral expansion of *Polylepis* forest fragments in central Ecuador. *Forest Ecology and Management*, **242**, 477–486.

Cierjacks, A., S. Salgado, K. Wesche, and I. Hensen (2008) Post-fire population dynamics of two tree species in high-altitude *Polylepis* forests of central Ecuador. *Biotropica*, **40**(2), 176–182.

Cleef, A.M. (1978) Characteristics of neotropical páramo vegetation and its subantarctic regulations. *Erdwissenschaftliche Forschung*, **11**, 365–390.

Cleef, A.M. and P. Chaverri (1992) Phytogeography of the páramo flora of the Cordillera de Talamanca, Costa Rica. In H. Balslev and J.L. Luteyn (Eds.), *Páramo: An Andean Ecosystem under Human Influence*. Academic Press, London.

Colinvaux, P.A., M.B. Bush, M. Steinitz-Kannan, and M.C. Miller (1997) Glacial and postglacial pollen records from the Ecuadorian Andes and Amazon. *Quaternary Research*, **48**, 69–78.

Cuatrecasas, J. (1968) Páramo vegetation and its life forms. In C. Troll (Ed.), Geoecology of the mountainous regions of the tropical Americas. *Colloquium Geographicum*, **9**, 163–168.

Cuatrecasas, J. (1979) Comparación fitogeográfica de páramos entre varias cordilleras. In M.L. Salgado-Laboriau (Ed.), *El Medio Ambiente Páramo*. Centro de Estudios Avanzados/Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela [in Spanish].

DiPasquale, G., M. Marziano, S. Impagliazzo, C. Lubritto, A. De Natale, and M.Y. Bader (2008) The Holocene treeline in the northern Andes (Ecuador): First evidence from soil charcoal. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **259**, 17–34.

Dohrenwend, R.E. (1972) The energetic role of the trade wind inversion in a tropical subalpine ecosystem. Ph.D. dissertation, Syracuse University, New York.

Driese, S.G., K.H. Orvis, S.P. Horn, Z-H. Li, and D.S. Jennings (2007) Paleosol evidence for Quaternary uplift and for climate and ecosystem changes in the Cordillera de Talamanca, Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **248**(1/2), 1–23.

Ellenberg, H. (1979) Man's influence on tropical mountain ecosystem in South America. *Journal of Ecology*, **67**, 401–416.

Fölster, H. and W. Hetch (1978) Paleosol sequences in the Eastern Cordillera of Colombia. *Quaternary Research*, **9**, 238–248.

Foster, P. (2001) The potential negative impacts of global climate change on tropical montane cloud forests. *Earth Science Reviews*, **55**, 73–106.

Gavin, D.G., D.J. Hallett, F.S. Hu, K.P. Lertzman, S.J. Prichard, K.J. Brown, J.A. Lynch, P. Bartlein, and D.L. Peterson (2007) Forest fire and climate change in western North America: Insights from sediment charcoal records. *Frontiers in Ecology*, **5(9)**, 499–506.

Gonzalez, E., T. van der Hammen, and R.F. Flin (1966) Late Quaternary glacial and vegetational sequence in Valle de Lagunillas, Sierra Nevada de Cocuy, Colombia. *Leidse Geologische Mededelingen*, **32**, 157–182.

Gosling, W.D. and M.J. Bunting (2008) A role for palaeoecology in anticipating future change in mountain regions? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **259**, 1–5.

Grubb, P.J. (1970) The impact of man on the páramo of Cerro Antisana, Ecuador. *Journal of Applied Ecology*, **7**(2), 7–8.

Hansen, B.C.S. and D.T. Rodbell (1995) A late-glacial/Holocene pollen record from the eastern Andes of northern Peru. *Quaternary Research*, **44**, 216–227.

Hansen, B.C.S., D.T. Rodbell, G.O. Seltzer, B. Leon, K.R. Young, and M. Abbott (2003) Late-glacial and Holocene vegetation history from two sites in the Western Cordillera of southwestern Ecuador. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **194**, 79–108.

Hart, J.L., S.P. Horn, and H.D. Grissino-Mayer (2008) Fire history from soil charcoal in a mixed hardwood forest on the Cumberland Plateau. *Journal of the Torrey Botanical Society*, **135**, 401–410.

Hartshorn, G.S.. (1983) Plants: Introduction. In D.H. Janzen (Ed.), *Costa Rican Natural History*. University of Chicago Press, Chicago.

Hodell, D.A., M. Brenner, and J.H. Curtis (2000) Climate change in the northern American tropics since the last ice age. In D.L. Lentz (Ed.), *Imperfect Balance: Landscape Transformations in the Precolumbian Americas*. Columbia University Press, New York.

Hofstede, R.G.M. (1995) Recovery after fire in a Colombian páramo grassland: Changes in vegetation structure and soil nutrient status. A chapter in "Effects of burning and grazing on a Colombian páramo ecosystem". Ph.D. dissertation, University of Amsterdam, The Netherlands.

Hofstede, R. (2003) Los páramos del mundo: su diversidad y sus habitantes. In R. Hofstede, P. Segarra, and P. Mena (Eds.), *Los Páramos del Mundo: Proyecto Atlas Mundial de los Páramos*. Global Peatland Initiative/NC-IUCN/Ecociencia, Quito, Ecuador [in Spanish].

Hofstede, R.G.M. and A.J.G.A. Rossenaar (1995) Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. II. Root mass and aboveground:belowground ratio. *Arctic and Alpine Research*, **27**(1), 13–18.

Hofstede, R.G.M., E.J. Chilito, and E.M. Sandoval (1995a) Vegetative structure, microclimate, and leaf growth of páramo tussock grass species in undisturbed, burned and grazed conditions. *Vegetatio*, **119**, 53–65.

Hofstede, R.G.M., C. Mondragón, and O. Rocha (1995b) Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia, I: Aboveground vegetation. *Arctic and Alpine Research*, **27**(1), 1–12.

Hooghiemstra, H. (1984) Vegetational and climatic history of the High Plain of Bogotá, Colombia: A continuous record of the last 3.5 million years. Ph.D. dissertation, University of Amsterdam, The Netherlands.

Hooghiemstra, H., A.M. Cleef, G. Noldus, and M. Kappelle (1992) Upper Quaternary vegetation dynamics and paleoclimatology of the La Chonta bog area (Cordillera de Talamanca, Costa Rica). *Journal of Quaternary Research*, **7**(3), 205–225.

Horn, S. (1986) Fire and páramo vegetation in the Cordillera de Talamanca, Costa Rica. Ph.D. dissertation, University of California, Berkeley, CA.

Horn, S.P. (1989a) The Inter-American Highway and human disturbance of páramo vegetation in Costa Rica. *Yearbook of the Conference of Latin Americanist Geographers*, **15**, 13–22.

Horn, S.P. (1989b) Postfire vegetation development in the Costa Rican páramos. *Madroño*, **36**(2) 93–114.

Horn, S.P. (1989c) Prehistoric fires in the Chirripó highlands of Costa Rica: Sedimentary charcoal evidence. *Revista de Biología Tropical*, **37**(2), 139–148.

Horn, S.P. (1990) Vegetation recovery after the 1976 páramo fire in Chirripó National Park, Costa Rica. *Revista de Biología Tropical*, **38**(2), 267–275.

Horn, S.P. (1991) Fire history and fire ecology in the Costa Rican páramos. In S.C. Nodvin and T.A. Waldrop (Eds.), *Fire and the Environment: Ecological and Cultural Perspectives*. General Technical Report SE-69. USDA Forest Service, Intermountain, Forest and Range Experiment Station, Ogden, UT

Horn, S.P. (1993) Postglacial vegetation and fire history in the Chirripó páramo of Costa Rica. *Quaternary Research*, **40**(1), 107–116.

Horn, S.P. (1997) Postfire resprouting of *Hypericum irazuense* in the Costa Rican páramos: Cerro Asunción revisited. *Biotropica*, **29**(4), 529–531.

Horn, S.P. (1998a) Postfire regrowth of *Vaccinium consanguineum* Klotzch (Ericaceae) in the Costa Rican páramos. *Revista de Biología Tropical*, **46**(4), 1117–1120.

Horn, S.P. (1998b) Fire management and natural landscapes in the Chirripó Páramo, Chirripó National Park, Costa Rica. In K. Zimmerer and K. Young (Eds.), *Nature's Geography: Biogeographical Landscapes and Conservation in Developing Countries*. University of Wisconsin Press, Madison, WI.

Horn, S.P. (2005) Dinámica de la vegetación después de fuegos recientes en los páramos de Buenavista y Chirripó, Costa Rica. In M. Kappelle and S.P. Horn (Eds.), *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica.

Horn, S.P. (2007) Late Quaternary lake and swamp sediments: Recorders of climate and environment. In J. Bundschuh and G.E. Alvarado (Eds.), *Central America: Geology, Resources, Hazards*, vol. 1. Taylor & Francis/Balkema, Leiden, The Netherlands.

Horn, S.P. and L.G. Clark (1992) Pollen viability in *Chusquea subtessellata* (Poaceae: Bambusoideae). *Biotropica*, **24**, 577–579.

Horn, S.P. and B.L. League (2005) Registros de sedimentos lacustres de la vegetación del Holoceno y historia del fuego en el páramo de Costa Rica. In M. Kappelle and S.P. Horn (eds.), *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica.

Horn, S.P. and R.L. Sanford, Jr. (1992) Holocene fires in Costa Rica. *Biotropica*, **24**, 354–361.

Horn, S.P., K.H. Orvis, and K.A. Haberyan (2005) Limnología de las lagunas glaciales en el páramo del Chirripó, Costa Rica. In M. Kappelle and S.P. Horn (Eds.), *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica.

Islebe, G.A. and H. Hooghiemstra (1997) Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews*, **16**, 589–604.

Janzen, D.H. (1973a) Sweep samples of tropical foliage insects: Description of study sites, with data on species abundances and size distributions. *Ecology*, **54**(3), 659–678.

Janzen, D.H. (1973b) Rate of regeneration after a tropical high elevation fire. *Biotropica*, **5**(2), 117–122.

Janzen, D.H. (Ed.) (1983) *Swallenochloa subtessellata* (chusquea, batamba, matamba). *Costa Rican Natural History*. University of Chicago Press, Chicago.

Jokisch, B.D. and B.M. Lair (2002) One last stand? Forests and change on Ecuador's Eastern Cordillera. *Geographical Review*, **92**(2), 235–256.

Kappelle, M. and S.P. Horn (2005) *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica [in Spanish].

Kappelle, M., M. Castro, A. Garrita, L. González, and H. Monge (2005) Ecosistemas de los páramos del área de conservación La Amistad-Pacífico en Costa Rica. In M. Kappelle and S.P. Horn (Eds.), *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica [in Spanish].

Keane, R.E. and M.A. Finney (2002) The simulation of landscape fire, climate, and ecosystem dynamics. In T.T. Veblen, W.L. Baker, G. Montenegro, and T.W. Swetnam (Eds.), *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*, Ecological Studies 160. Springer-Verlag, New York.

Keating, P.L. (1998) Effects of anthropogenic disturbance on páramo vegetation in Podocarpus National Park, Ecuador. *Physical Geography*, **19**, 221–238.

Keating, P.L. (1999) Changes in páramo vegetation along an elevational gradient in southern Ecuador. *Journal of the Torrey Botanical Society*, **126**, 159–175.

Keating, P.L. (2000) Chronically disturbed páramo vegetation at a site in southern Ecuador. *Journal of the Torrey Botanical Society*, **127**(2), 162–171.

Keating, P.L. (2007) Fire ecology and conservation in the high tropical Andes: Observations from northern Ecuador. *Journal of Latin American Geography*, **6**(1), 43–62.

Keeley, J. and W.J. Bond (1999) Mast flowering and semelparity in bamboos: The bamboo fire cycle hypothesis. *The American Naturalist*, **154**(3), 383–391.

Knapp, G. (1991) *Andean Ecology: Adaptive Dynamics in Ecuador*. Westview Press, Boulder, CO.

Koenen, M.T. and S.G. Koenen (2000) Effects of fire on birds in páramo habitat of northern Ecuador. *Ornitologia Neotropical*, **11**, 155–163.

Kuhry, P. (1988) A paleobotanical and palynological study of Holocene peat from the El Bosque mire, located in a volcanic area of the Cordillera Central of Colombia. *Review of Paleobotany and Palynology*, **55**, 19–72.

Lægaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In H. Balslev and J.L. Luteyn (Eds.), *Páramo: An Andean Ecosystem under Human Influence*. Academic Press, London.

Lauer, W. (1979) La posición de los páramos en la estructura del paisaje de los Andes tropicales. In M.L. Salgado-Laboriau (Ed.), *El Medio Ambiente Páramo*. Centro de

Estudios Avanzados/Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela [in Spanish].

Lauer, W. (1981) Ecoclimatological conditions of the páramo belt in the tropical high mountains. *Mountain Research and Development*, **1**(3/4), 209–221.

Laurance, W.F., M.A. Cochrane, S. Bergen, P.M. Fearnside, P. Delamônica, C. Barber, S. D'Angelo, and T. Fernandes (2001) The future of the Brazilian Amazon: Development trends and deforestation. *Science*, **291**, 438–439.

League, B.L. and S.P. Horn (2000) A 10,000 year record of páramo fires in Costa Rica. *Journal of Tropical Ecology*, **16**, 747–752.

Llambí, L.D., M. Fontaine, F. Rada, B. Saugier, and L. Sarmiento (2003) Ecophysiology of dominant plant species during old-field succession in a high tropical Andean ecosystem. *Arctic, Antarctic, and Alpine Research*, **35**(4), 447–453.

Løjtnant, B. and U. Molau (1982) Analysis of a virgin páramo plant community on Volcán Sumaco, Ecuador. *Nordic Journal of Botany*, **2**, 567–574.

Luteyn, J.L. (1992) Páramos: Why study them? In H. Balslev and J.L. Luteyn (Eds.), *Páramo: An Andean Ecosystem under Human Influence*. Academic Press, London.

Luteyn, J.L. (1999) *Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature*, Memoirs of the New York Botanical Garden, Vol. 84. Botanical Garden Press, New York.

Luteyn, J.L. and S.P. Churchill (2000) Vegetation of the tropical Andes. In D.L. Lentz (Ed.), *Imperfect Balance: Landscape Transformations in the Precolumbian Americas*. Columbia University Press, New York.

Markgraf, V. (2001) *Interhemispheric Climate Linkages*. Academic Press, San Diego, CA.

Martin, P.H. (1964) *Paleoclimatology and a Tropical Pollen Profile: VI International Congress on the Quaternary, 1961, Warsaw*, Vol. 2, pp. 319–323.

Melief, A.B.M. (1985) Late Quaternary paleoecology of the Parque Nacional Natural Los Nevados (Cordillera Central), and Sumapaz (Cordillera Oriental) areas, Colombia. Ph.D. dissertation, University of Amsterdam, The Netherlands.

Miller, G.A. and J.A. Silander, Jr. (1991) Control of the distribution of giant rosette species of *Puya* (Bromeliaceae) in the Ecuadorian páramos. *Biotropica*, **23**, 124–133.

Molinillo, M. and M. Monasterio (1997) Pastoralism in páramo environments: Practices, forage and impact on the vegetation in the Cordillera de Mérida, Venezuela. *Mountain Research and Development*, **17**, 197–211.

Mora, G. and L.M. Pratt (2002) Carbon isotopic evidence from paleosols for mixed C_3/C_4 vegetation in the Bogotá Basin, Colombia. *Quaternary Science Reviews*, **21**, 985–995.

Mora, G., L.M. Pratt, A. Boom, and H. Hooghiemstra (2002) Biogeochemical characteristics of lacustrine sediments reflecting a changing alpine neotropical ecosystem during the Pleistocene. *Quaternary Research*, **58**, 189–196.

Muller, C.H. (1952) Plant succession in Arctic heath and tundra in northern Scandinavia. *Bulletin of the Torrey Botanical Club*, **79**, 296–309.

Myers, R.L. (2006) *Living with Fire: Sustaining Ecosystems and Livelihoods through Integrated Fire Management*. The Nature Conservancy Global Fire Initiative, Tallahassee, FL. Available at *http://tncfire.org/documents/Integrated_Fire_Management_Myers_2006.pdf*

Neill, D.A. (1999) Vegetation. In P.M. Jørgensen and S. León-Yánez (Eds.), *Catalogue of the Vascular Plants of Ecuador/Catálago de las Plantas Vasculares del Ecuador*. Missouri Botanical Garden, St. Louis, MO.

Niemann, H. and H. Behling (2007) Late Quaternary vegetation, climate and fire dynamics inferred from the El Tiro record in the southeastern Ecuadorian Andes. *Journal of Quaternary Science*, **23**(3), 203–212.

Niemann, H. and H. Behling (2008) Past vegetation and fire dynamics. In E. Beck, I. Kottke, R. Mosandl, J. Bendix, and F. Makeschin (Eds.), *Gradients in a Tropical Mountain Ecosystem in Ecuador*, Ecological Studies 198. Springer-Verlag, Berlin.

Orvis, K.H. and S.P. Horn (2000) Quaternary glaciers and climate on Cerro Chirripó, Costa Rica. *Quaternary Research*, **54**, 24–37.

Parsons, J.J. (1982) The northern Andean environment. *Mountain Research and Development*, **2**(3), 253–262.

Pérez, F.L. (1998) Human impact on the high páramo landscape of the Venezuelan Andes. In K. Zimmerer and K. Young (Eds.), *Nature's Geography: Biogeographical Landscapes and Conservation in Developing Countries*. University of Wisconsin Press, Madison, WI.

Ramsay, P.M. (1992) The páramo vegetation of Ecuador: The community ecology, dynamics and productivity of tropical grasslands in the Andes. Ph.D. dissertation, School of Biological Sciences, University of Wales, Bangor, U.K.

Ramsay, P.M. and E.R.B. Oxley (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio*, **124**, 129–144.

Rodríguez-Beltrán, W. and O. Vargas-Ríos (2002) Estrategias de regeneración postquema en áreas de vegetación altoandina tipo matorral. *Pérez Arbelaezia*, **13**, 9–32 [in Spanish].

Romme, W. (1980) Fire history terminology: Report of the ad hoc committee. In *Proceedings of the Fire History Workshop, October 20–24, 1980, Tucson, AZ*, RMFRES GTR-81. USDA Forest Service, Intermountain, Forest and Range Experiment Station, Ogden, UT

Rowell, C.H.F. and C.S. Carbonell (1977) *Baeacris talamancensis* gen. and sp. nov. (Acrididae, Melanoplinae), a neotropical montane grasshopper: Its implication for the origin of the dichroplini and the Costa Rican páramo. *Acrida*, **6**(1), 55–73.

Rull, V., M.L. Salgado-Laboriau, C. Schubert, and S. Valastro, Jr. (1987) Late Holocene temperature depression in the Venezuelan Andes: Palynological evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **60**, 109–121.

Rull, V., M.B. Abbott, P.J. Polissar, A.P. Wolfe, M. Bezada, and R.S. Bradley (2005) 15,000-yr pollen record of vegetation in the high altitude tropical Andes at Laguna Verde Alta, Venezuela. *Quaternary Research*, **64**, 308–317.

Rust, R. (2006) *Post-fire Succession in the Alpine Grasslands of Ecuador: A Test of Two Alternative Models of Succession*, Senior Research Project in Biology. St. Mary's College of Maryland, St. Mary's City, MD.

Salgado-Labouriau, M.L., V. Rull, C. Schubert, and S. Valastro, Jr. (1988) The establishment of vegetation after late Pleistocene deglaciation in the Páramo de Miranda, Venezuelan Andes. *Review of Palaeobotany and Palynology*, **55**, 5–17.

Salomons, J.B. (1986) Paleoecology of volcanic soils in the Colombian Central Cordillera (Parque Nacional Natural de los Nevados). Ph.D. dissertation, University of Amsterdam, The Netherlands.

Sanford, Jr., R.L. and S.P. Horn (2000) Holocene rain-forest wilderness: A neotropical perspective on humans as an exotic, invasive species. *Wilderness Science in a Time of Change: Conference, Vol. 3: Wilderness as a Place for Scientific Inquiry, May 23—27, 1999, Missoula, MT*, RMRES-P-15-VOL 3. USDA Forest Service, Intermountain, Forest and Range Experiment Station, Ogden, UT.

Sarmiento, F.R. (2000) Breaking mountain paradigms: Ecological effects on human impacts in man-aged tropandean landscapes. *Ambio*, **29**(7), 423–431.

Sarmiento, F.R. (2002) Anthropogenic change in the landscapes of highland Ecuador. *Geographical Review*, **92**(2), 213–234.

Sarmiento, F.R. and L.M. Frolich (2002) Andean cloud forest tree lines: Naturalness, agriculture and the human dimension. *Mountain Research and Development*, **22**(3), 278–287.

Sarmiento, L., L.D. Llambí, A. Escalona, and N. Marquez (2003) Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes. *Plant Ecology*, **166**, 63–74.

Schlachter, K.J., H.D. Grissino-Mayer, and S.P. Horn (2007) Growth rings in stems of *Vaccinium consanguineum* in the high-elevation páramos of Costa Rica. Poster presented at *Annual Meeting of the Great Plain/Rocky Mountain Division of the Association of American Geographers, Denver, CO, September 28–29*.

Shlisky, A., J. Waugh, P. Gonzalez, M. Gonzalez, M. Manta, H. Santoso, E. Alvarado, A. Ainuddin Nuruddin, D.A. Rodríguez-Trejo, R, Swaty *et al.* (2007) *Fire, Ecosystems and People: Threats and Strategies for Global Biodiversity Conservation*, GFI Technical Report 2007-2. The Nature Conservancy. Arlington, VA. Available at *http://tncfire.org/documents/fire_ecosystems_and_people.pdf*

Sklenař, P. and P.M. Jørgensen (1999) Distribution patterns of páramo plants in Ecuador. *Journal of Biogeography*, **26**, 681–691.

Sklenař, P. and P.M. Ramsay (2001) Diversity of zonal páramo plant communities in Ecuador. *Diversity and Distributions*, **7**(3), 113–124.

Skutch, A.F. (1971) *A Naturalist in Costa Rica*. University of Florida Press, Gaineseville, FL.

Smith, A.P. (1981) Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan Andes. *Smithsonian Contributions to Botany*, **48**, 1–45.

Spehn, E.M., M. Liberman, and C. Körner (2006) Fire and grazing: A synthesis of human impacts on highland biodiversity. In E.M. Spehn, M. Liberman, and C. Körner (Eds.), *Land Use Change and Mountain Biodiversity*. CRC Press/Taylor & Francis, Boca Raton, FL.

Stern, M.J. (1995) An inter-Andean forest relict: Vegetation change on Pasochoa Volcano, Ecuador. *Mountain Research and Development*, **15**(4), 339–348.

Suárez, R.E. and G. Medina (2001) Vegetation structure and soil properties in Ecuadorian páramo grasslands with different histories of burning and grazing. *Arctic, Antarctic, and Alpine Research*, **33**(2), 158–164.

Titiz, B. and R.L. Sanford, Jr. (2007) Soil charcoal in old growth rainforests from sea level to the continental divide. *Biotropica*, **39**(6), 673–682.

Vargas-Ríos, O. (1997) Un modelo de sucesión-regeneración de los páramos después de quemas. *Caldasia*, **19**(1/2), 331–345 [in Spanish].

Verweij, P.A. (1995) Spatial and temporal modeling of vegetation patterns: Burning and grazing in the páramo of Los Nevados National Park, Colombia. Ph.D. dissertation, University of Amsterdam, The Netherlands.

Verweij, P.A. and P.E. Budde (1992) Burning and grazing gradients in páramo vegetation: Initial ordination analysis. In H. Balslev and J.L. Luteyn (Eds.), *Páramo: An Andean Ecosystem under Human Influence*. Academic Press, London.

Verweij, P.A. and K. Kok (1992) Effects of fire and grazing on *Espeletia hartwegiana* populations. In H. Balslev and J.L. Luteyn (Eds.), *Páramo: An Andean Ecosystem under Human Influence*. Academic Press, London.

Verweij, P.A. and K. Kok (co-author) (1995) Effects of fire and grazing on plant populations. A chapter in "Spatial and temporal modeling of vegetation patterns: Burning and grazing in the páramo of Los Nevados National Park, Colombia". Ph.D. dissertation, University of Amsterdam, The Netherlands.

Weber, H. (1959) *Los Páramos Costarricense y su Concatenación Fitogeográfico con los Andes Suramericanos*. Instituto Geográfico Nacional, San José, Costa Rica [in Spanish].

Weng, C., M.B. Bush, J.H. Curtis, K.L. Kolata, T.D. Dillehay, and M.W. Binford (2006) Deglaciation and Holocene climate change in the western Peruvian Andes. *Quaternary Research*, **66**, 87–96.

Wesche, K., G. Miehe, and M. Kaeppeli (2000) The significance of fire for Afroalpine ericaceous vegetation. *Mountain Research and Development*, **20**(4), 340–347.

Weston, A.S. (1981) *The Vegetation and Flora of the Chirripó Páramo*, unpublished report. Tropical Science Center, San José, Costa Rica.

White, S. (not dated) *Grass Páramo as Pyrophilous Vegetation of Human Origin*, unpublished course outline. Available at *http://www.roundriver.org/course_outline.html#Outline7*

Whitlock, C. and C.P.S. Larsen (2001) Charcoal as a fire proxy. In J.P. Smol, H.J.B Birks, and W. Last (Eds.), *Tracking Environmental Change Using Lake Sediments*, Vol. 3: *Terrestrial, Algal, and Siliceous Indicators*. Kluwer Academic, Dordrecht, The Netherlands.

Wijninga, V.M. (1996) Paleobotany and palynology of neogene sediments from the High Plain of Bogotá (Colombia). Ph.D. dissertation, University of Amsterdam, The Netherlands.

Wille, M., H. Hoogiemstra, R. Hofstede, J. Fehse, and J. Sevink (2002) Upper forest line reconstruction in a deforested area in northern Ecuador based on pollen and vegetation analysis. *Journal of Tropical Ecology*, **18**, 409–440.

Williamson, G.B., G.B. Schatz, A. Alvarado, C.S. Redhead, A.C. Stam, and R.W. Sterner (1986) Effects of repeated fire on tropical páramo vegetation. *Tropical Ecology*, **27**, 62–69.

Young, K.R. (1993) National park protection in relation to ecological zonation of a neighboring human community: An example from northern Peru. *Mountain Research and Development*, **13**, 267–280.

Zedler, P.H., C.R. Gautier, and G.S. McMaster (1983) Vegetation response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology*, **64**, 809–818.