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Andean Cloud Forest Tree Lines

Naturalness, Agriculture and the Human Dimension

We challenge the paradigm of natural tree line formation in the equatorial Andes with an alternate view that incorporates the human dimension. We present both direct and indirect evidence of anthropogenic influences on cloud forest tree line location; these human influences should be incorporated in definitions of Andean tree lines as (1) the extensification of grassland for grazing and potato cultivation for the upper limit, and (2) the intensification of the agricultural frontier, fuelwood gathering, and timber extraction for the lower limit. Although we do not claim to fully debunk the prevalent paradigm of tree line dynamics (which is descriptive, depends on the natural sciences, and sees tree lines as physically controlled), we hope to achieve increased recognition for a challenging alternate view of tropical tree lines as functional, resource-use dependent, and human-driven. Management plans and overall tropical montane cloud forest conservation strategies need to consider this new perspective and incorporate a proactive and assertive approach toward restoration of Andean forests in a way that will encourage landscape diversity in tropical mountain ecoregions.

Keywords: *Tree line; mountain agriculture; biodiversity drivers; restoration ecology; Tropandean landscapes;* páramo; *tropical Andes; Ecuador.*

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Introduction

Alpine tree line concepts have historically fallen within the domain of wild mountain ecosystem ecology and focused on temperate environmental factors that influence the growth of montane forests and limit production forestry in northern latitudes with alpine environments. Tree line and "timberline" are used interchangeably, but the term "forest line" is preferred as a synonym for "forest limit" (Sveinbjörnsson 2000). Plant ecologists often use timberline in association with closed-canopy mountain forests, whereas tree line is applied to open-canopy forests (Körner 1998). In the biogeographical literature the altitudinal forest border of mountains is usually referred to as the tree line, whereas the latitudinal continental ecotone is the timberline, reflecting the border effect between forests and grasslands (Armand 1992).

In the tropics, harsh environmental conditions are viewed as the limiting factor for tree growth above a given altitude, mostly correlated with the threshold of 10°C mean July isotherm (Jeník 1997) or the location of the frost line (Sarmiento 1986). At more northern latitudes, and on north-facing slopes, the tree line occurs at a lower altitude (Ives 1978). A subalpine transitional zone or *krummholz* line characterized by increasingly stunted and dwarfed trees is the norm in circumpolar and northern temperate zone mountains (Kullman 1998). Vertical zoning thus results from the relationship between the vegetation type and the zonal climate, where belts are considered to be locally influenced variations dependent on temperate mountain conditions (Whittaker 1952). A combination of elevation, latitude, and local climate defines where the forest–grassland border occurs (Troll 1973). Hence, physically driven tree line presence is the norm at higher latitudes (Stevens and Fox 1991). In this light, Sveinbjörnsson (2000) points out that in North America and Europe 2 major themes emerged: (1) the "presence–absence theme" with new tree line limits as a response to catastrophic events, and (2) the "starvation theme" with tree line formation in response to nutrient availability and resource allocations. These themes are not mutually exclusive, and a combination of both explains locally relevant tree lines in the north.

Although this concept has been considered valid for tropical montane cloud forests (TMCFs), we propose an alternative hypothesis that historical and human factors may in fact have a far more important influence on tree line presence in the tropics than physical factors do. We suggest that a "human driver theme" appears to be the most important one in tropical America. The driving forces of tree line formation in the Tropandean (tropical Andean) ecoregion are past and present human influences, including the direct effects of mountain agriculture and grazing by both introduced and native herbivores, as well as burning regimes and several other indirect effects.

Unlike northern high-montane regions that are virtually uninhabited, tropical high-altitude regions have historically served as human population centers (Westerberg and Christiansson 1999). New evidence points to the anthropogenic nature of the ericaceous belt in the Afroalpine belt, relating the patchy appearance of the tree line to the significance of fire and the role of herbivores (Wesche et al 2000). In the tropical Andes, montane valleys and slopes, as well as highland plateaus, offer a dependable temperate climate with long, mild growing seasons, steady rainfall, and absence of infectious diseases (such as malaria and yellow fever common in the lowland tropics). Thus, these areas have been preferential targets for human settlement since ancient times (Flenley 1979; Gade 1999). People have

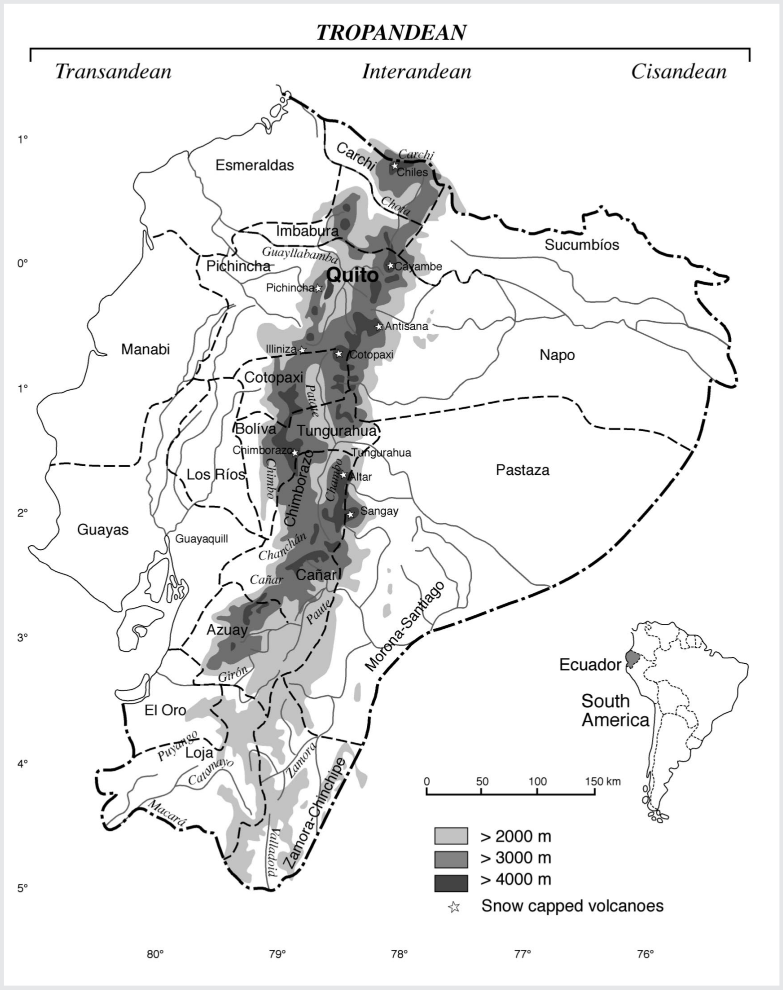

FIGURE 1 A map of the 3 geographical regions in the tropical Andean (Tropandean) ecoregion in Ecuador; 2 longitudinal cordilleras (eastern and western) form the Interandean valleys whose catchment basins (*hoyas*) are separated by transverse ranges (*nudos*). Adapted from Jørgensen and Ulloa-Ulloa (1994) and Sarmiento (2000).

lived for millennia in the high mountains of the neotropics (Budowski 1968; Ellenberg 1979), whereas they have never lived (with the exception of the nomadic Saami in Scandinavian Lapland) in high-temperate and northern mountain areas.

In the Tropandean ecoregion (Figure 1), the mountain environment includes the human imprint immersed in the matrix of cultural landscape, despite 4 axiomatic assumptions, namely: (1) the false "pristineness" of the Transandean montane forests (Sarmiento 1995a); (2) the seeming "naturalness" of the verdant Cisandean forests (Sarmiento 1998); (3) the "irreversibility" of the degraded Interandean forests (Harden 1999); and (4) the "folly" of restoration practices for conversion to healthy forest ecosystems in the equatorial Andes (Sarmiento 1995b; Chepstow-Lusty et al 1998).

All the above are manifestations of the hidden responses (Stern 1983; Flenley 1992) to long-term human impact on tree borderlines in the mountainous landscape of tropical America. These and other mountain ecological principles need elucidation for application in conservation and sustainable development models because they underlie questions to be addressed in future decision making affecting Andean communities.

Tree lines: The scientific rationale

Controversy over the origin of highland grasslands in forested mountains is still unsolved (Mark 1958; Billings 1973; Luteyn 1999). For example, temperate mountains in North America harbor grassy areas locally known as "balds" or openings in the otherwise continuous forest canopy in the highlands. Although balds may have originated at the time of prehistoric megafauna, human activity has expanded them in mountain temperate forests (Weigl and Knowles 1995).

The long-term presence of humans in the mountainous tropics requires us to address a set of other potential determining factors for tropical tree line dynamics. Fires set by humans, agricultural clearing, grazing, and trade routes may be of considerable importance in the establishment and maintenance of tropical balds, particularly *páramos* (Ellenberg 1958; Janzen 1973). In the equatorial Andes, the presence of forest remnants with tall trees (such as those in Table 1) at elevations above 3600 m in remote coves of isolated ranges may be evidence of previous continuous forest formation. Conversely, the presence of both grass balds or *pajonal* (*Calamagrostis* spp, *Festuca* spp, *Cortaderia* spp) and heath balds or *chapparral* (*Hypericum* spp, *Rubus* spp, *Baccharis* spp) on highland plateaus and in areas

TABLE 1 List of some of the tree species found in the study area, representing existing potential forest formation in the Interandean cloud forest of northern Ecuador. (Based on Sarmiento 1988; Palacios and Tipan 1996)

Scientific name	Local name	Family taxon	Life form	Author taxon
Clusia flaviflora	*Guandera*	Clusiaceae	Tree	Engler cf.
Weinmannia auriculifera	*Encenillo*	Cunoniaceae	Tree	Hieron. ex Char.
Weinmannia brachystachya	*Encenillo*	Cunoniaceae	Tree	Willd.
Aequatorium campii	*Peludo*	Asteraceae	Tree	Nordenst
Weinmannia pinnata	*Encenillo*	Cunoniaceae	Tree	L.
Valea stipularis	*Sacha capuli*	Elaeocarpaceae	Tree	L.
Dicksonia sellowiana	*Helecho*	Dicksoniaceae	Tree/shrub	Hook
Cyathea caracasana	*Helecho*	Cyatheaceae	Tree	(Klotzsch) Domin
Aexina macrophylla	*Cafecillo*	Melastomataceae	Tree/shrub	(Naudin) Irlana
Brachyotum ledifolium	*Colca*	Melastomataceae	Tree	(Desr.) Irlana
Brachyotum lindenii	*Colca*	Melastomataceae	Tree	Cogn.
Saurauia bullosa	*Sacha yuyo*	Actinidaceae	Tree/shrub	Wawra
Hyeronima macrocarpa	*Cuacho*	Euphorbiaceae	Tree	Mueel. Arg.
Meriania sanguinea	*Cafecillos*	Melastomataceae	Tree/shrub	Wurdock
Miconia corymbiformis	*Colca*	Melastomataceae	Tree	Cogn.
Miconia ochracea	*Colca*	Melastomataceae	Tree/shrub	Triana
Cedrela montana	*Cedro*	Meliaceae	Tree	J. Moritz ex Turcz.
Ruagea hirsuta	*Cedrillo*	Meliaceae	Tree/shrub	(C.DC.) Harms
***Ilex* spp**	*Guayusa*	Aquifoliaceae	Tree	
Ocotea infrafoveolato	*Aguacatillo*	Laureaceae	Tree	H. v.d. Werlf
Ocotea stuebelii	*Aguacatillo*	Laureaceae	Tree	Mez aff.
Oreopanax micronulotus	*Puma maqui*	Araliaceae	Tree	Harms
Oreopanax palomophyllus	*Puma maqui*	Araliaceae	Tree	Harms
Gynoxis fuliginosa	*Huaiquero*	Asteraceae	Tree	(Kunlin) Cassini
Cybianthus marginatus	*Samal*	Myrsinaceae	Tree/shrub	(Benthorn) Pipoly
Myrcianthes rhopaloides	*Arrayancillo*	Myrtaceae	Tree	(H.B.K.) McVaugh
Piper carpunya	*Cordoncillo*	Piperaceae	Tree	R. & P.
Hesperomeles lanuginosa	*Rosaceae*	Rosaceae	Tree	(R. & P.) Hook
Polelepis sericea	*Yagual*	Rosaceae	Tree	Weddell
Senecio canescens	*Senecio*	Asteraceae	Tree/shrub	H.B.K.
Senecio lotiflorus	*Senecio*	Asteraceae	Tree/shrub	Wedd.
Alnus acuminata	*Aliso*	Betulaceae	Tree	H.B.K.
Brunellia pauciflora	*Falso aluvillo*	Brunelliaceae	Tree	Cuatrec. & Orozco
Prunus rugosa	*Capuli*	Rosaceae	Tree	Kohene
Palicourea amethystina	*Café d' monte*	Rubiaceae	Tree	(R. & P.) DC.
Viburnum triphyllum	*Sombrilla*	Caprifoliaceae	Tree	Benlham
Cestrum peruvianum	*Hierba santa*	Solanaceae	Tree	Wildenow

table continues on next page

Scientific name	Local name	Family taxon	Life form	Author taxon
Sessea corimbosa	*Tomatillo*	Solanaceae	Tree	Goudof
Sessea crassivenosa	*Tomatillo*	Solanaceae	Tree/shrub	Biller
Symplocos quitensis	*Shungi*	Symplocaceae	Tree	Brand
Aegiphila monticola	*Quesilulo*	Verbenaceae	Tree	Moldenke
Freziera canescens	*Zapatillo*	Theaceae	Tree	Bonpland
Escallonia myrtilloides	*Tibar*	Saxifragaceae	Tree	L.
Escallonia paniculata	*Tibar*	Saxifragaceae	Tree/shrub	(R. & P.) Roem & S.
Clethra ferruginea	*Rojillo*	Clethraceae	Tree	(R. & P.) Link
Clethra ovalifolia	*Rojillo*	Clethraceae	Tree	Turcz.
Baccharis macrantha	*Chilca*	Asteraceae	Tree/shrub	H.B.K.
Barnadesia arborea	*Paloespino*	Asteraceae	Tree/shrub	H.B.K.
Diplostephium floribundum	*Alcotana*	Asteraceae	Tree	(Benth) Wedd
Diplostephium glandulosum	*Alcotana*	Asteraceae	Tree	Hieron
Diplostephium rhododendroides	*Alcotana*	Asteraceae	Tree	Hieron
Gynoxis buxifolia	*Huaiquero*	Asteraceae	Tree	Cassini
Schefflera spp	*Chefleras*	Araliaceae	Tree/shrub	

formerly cultivated or grazed indicates previous human influence (Grubb 1970).

The principal assumption on which temperate tree line concepts are based—that altitude is the determining factor—may have little or no validity in the tropical Andes at present, as exemplified by remnant patches of mature Andean forest above the *páramo* areas. Moreover, contemporary pine (*Pinus radiata*) or eucalypt (*Eucalyptus globulus*) plantations in the highland *páramo* demonstrate the potential for viable tree-form vegetation well above the tree line. The Andean tree line often looks very similar to forest borders with agricultural lands where recent clear-cutting is known to have taken place. According to Lægaard (1992), “the forest patches border directly on grass *páramo* vegetation and the forest line is nearly always sharply cut.” Moreover, there is no local terminology for the highland grassland. The Spanish word *páramo* is not vernacular and is open to a variety of interpretations (Luteyn 1999).

Our research findings, some proxy testimony, and experience in the equatorial Andes offer evidence that geological, archaeological, and agricultural history must be considered as the principal framework for understanding where the Andean cloud forest edge occurs. We propose that the current TMCF landscape features 2 distinctive tree lines, as shown in Figure 2.

- An upper tree line that correlates with extensification of the human impact in the more climatically demanding areas of the higher reaches, shortening the extent of TMCFs from above.
- A lower tree line that correlates with intensification of agriculture and fuelwood consumption in the less challenging topography of the foothills, piedmont, and interior highland plateaus, shortening the extent of TMCFs from below.

Study area

A significant 40,000-ha strip of Interandean cloud forest still stands on the eastern central valley slope in the provinces of Imbabura and Carchi in northern Ecuador. With a distinctly unique and highly endemic Interandean flora and fauna, this is perhaps the largest stand of relatively pristine and yet nonprotected forest of this type to be found in the equatorial Andes. The watershed is an extensive catchment basin distributed among 2 main mountain ranges of the eastern Cordillera flowing toward the Interandean valley. Pristine TMCF patches are found as relicts of an earlier widespread forest cover. The valleys of San Gabriel and El Angel to the north and the valleys of Pimampiro, Sigsipamba, and Mariano-Acosta to the south present an agricultural matrix of heavily fragmented forest patches, hedgerows, and open areas covered with crops (mainly potato and corn plantations) or pasture (Figure 3). In the Puruhanta area (located in the northwest corner of the Cayambe-Coca Ecological Reserve), mature Andean

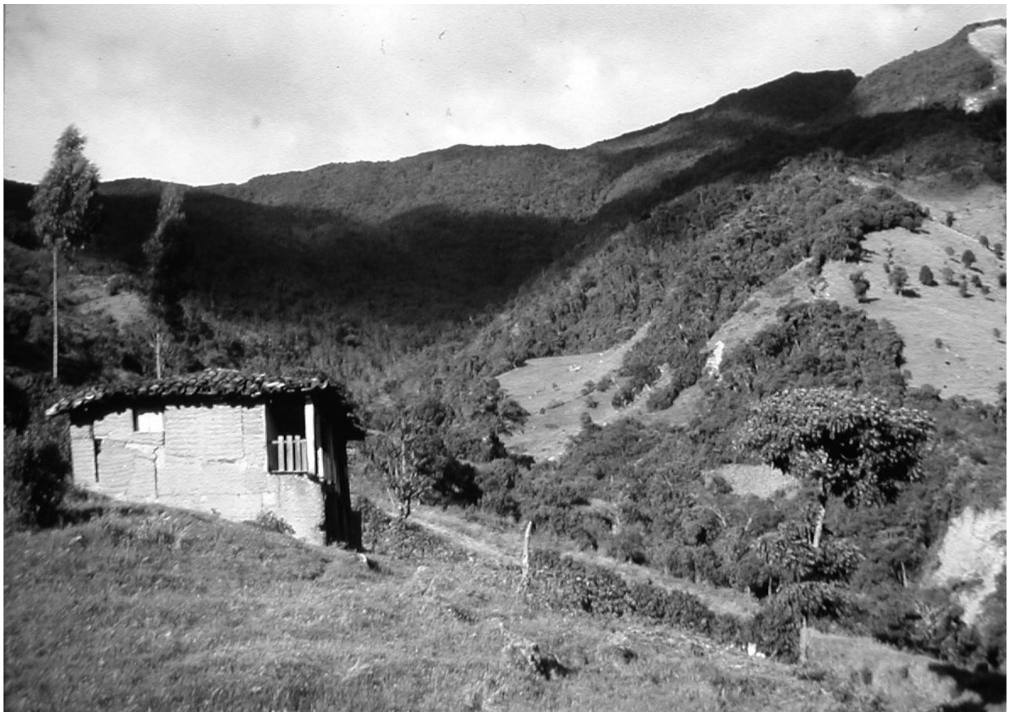

FIGURE 2 A view of the rural landscape of Carchi province, where human activity encroaches on the TMCFs and expands the agricultural frontier, thus raising the lower limit of the tree line. Past activity has been more important in forming the *páramo* and the upper tree line. Past and current pressures make protection of cloud forest remnants crucial in this area. (Photo by T. Sulser)

forests still survive in isolation above 3800 m (Sarmiento 1988) around Chique Lake. The climate pattern, typical of the tropics, is characterized by generally uniform temperatures the year round (mean temperature 12°C) and 2 distinctive moisture regimes—-a rainy season with mean precipitation of 2700 mm/year and a dry season with mean precipitation of 520 mm/year (Cañadas-Cruz 1983). Isolated "islands" of *páramo* display typical grassland vegetation including serotonic ferns and taller herbs such as *frailejones* (*Espeletia pycnophylla*), *orejas de conejo* (*Senecium* spp), and *achupallas* (*Puya clava-herculis*).

The expanding population and opening of new agricultural lands do not appear to have greatly affected the *páramo* border in the eastern range within the study site. A continuous 50-km stretch of intact forest

FIGURE 3 A panoramic view of the rural landscape showing the heterogeneity of land uses and the prominence of potato and corn cultivation. Note native trees surviving along the hedgerows, steep brooks, and other areas unsuitable for agriculture or grazing. (Photo by Larry Frolich)

has prevented extensive use of the *páramo,* which is currently uninhabited. The main human impacts have probably remained the same, if not diminished, since pre-Hispanic times.

Trade routes are now along the Pan-American Highway in the valley floor as opposed to ancient *culuncos,* which followed the ridge tops on the *páramo*–forest tree line. Contemporary travel in the *páramo* is along small trails principally to and from fishing rivers. The *páramo* is purposely burned during long dry periods under the belief that this will induce rainfall and will bring greener grazing grounds. But it could be argued that frequent heat lightning, especially experienced at night, may also lead to natural combustion under dry conditions, albeit this phenomenon has not been documented in the area. As has been argued elsewhere for tropical mountains (Wesche et al 2000), “the overwhelming majority of fires in tropical mountains are man-made, with natural causes contributing at most a minor fraction.” Man-made and man-aged highland environments are 2 considerations of the new paradigms of montology (Sarmiento 2000).

Direct evidence of tree line formation

Mountain agriculture

How different is the páramo *tree line from the agricultural frontier?*

Cash cropping with heavy external chemical inputs, principally of potatoes, but also of wheat, barley, and corn, is a common practice on the eastern Andean slope in the study site. Long enduring customs of terracing, strip contour cultivation, alley cropping, and other traditional techniques such as *wachu rozado* (Frolich et al 1999) are observed. As pointed out by Frolich and Guevara (1999), in Carchi province the agricultural frontier is continuously pushing the lower limits of the tree line upward because of the need for fresh fertile volcanic soils to improve potato yields for an ever-expanding market. The agricultural frontier tree line is now high above the central valley floor because steep slopes have been cleared and converted to farmland for potato cash monocropping. Meanwhile, most of the agricultural biodiversity, and especially heirloom potato varieties, has been lost. Worldwide, the introduction of industrialized agricultural practices has undoubtedly done more to affect cloud forest tree line dynamics than any other single factor.

With time, farm sites become exhausted of nutrients and biologically unbalanced soils are infested by nematodes and other pests that force farmers to increase their use of synthetic pesticides, artificial fertilizers, and manure. Insecurity of land tenure and unclear colonization rules make intensification of agricultural production the driving force in claiming new lands for cultivation from forest areas (Frolich and Guevara 1999). Production is rarely subsistence oriented, and the bulk of the harvest is always hauled away to the cities of Tulcán, Ibarra, and Quito. This economic progress has not occurred without severe collateral environmental and social consequences (Crissman et al 1998).

Mountain grazing

How different is the páramo *tree line from the pasture frontier?*

New research trends identify megafauna herbivores as the initial and principal creative force behind the balds in temperate forested mountains (Weigl and Knowles 1995). In the equatorial Andes, the presence of fossils of megaherbivores, such as mastodonts (*Mastodon cuvierii, M. carchensis*), giant sloths (*Oreomylodon orcessi*), Andean horses (*Equus andium*), and the precursor of modern llamas (*Paleolama* spp), suggests that these Pleistocene foragers may have been instrumental in clearing portions of TMCFs (Owen-Smith 1987), thereby explaining the appearance of grass balds in contemporary tropical Andean forests.

Evidence of precarious animal husbandry in the area can be found in old pottery depicting ungulates and other zoomorphic styles found on ceramic artifacts. Moreover, several cultural centers including Pasto, Capulí, and Quillasingas exhibited clear sedentary patterns of cultivation of crops and animal rearing. Some, such as Pimampiro, developed into impressive trade sites (Molestina 1985). But Carchi was never subjected to Inca rule, and only dubious evidence of the presence of camelid husbandry exists. With the Spanish conquest, vast areas of the high mountain forests were cleared to introduce livestock, mainly sheep and cattle.

In modern times, governmental subsidies offered to dairy industry prompted the replacement of forest with pasture. To this day, cattle grazing is the principal activity for large landholders of the central valley floor. Production of milk, cheese, and other derivatives is more profitable than most crops. In many places good agricultural soils have been converted to pasture using the tenacious introduced African grass *kikuyo* (*Panicum clandestinum*). Other improved species are also planted for grazing purposes, particularly ryegrass and crabgrass. Most farmers and their families are involved in dairy farming, either for subsistence milk production or to complement household income. During the dry season, large herds are sometimes left to graze within the *monte* (or secondary forest within the cloud forest patches). Most often, however, grazing is contained within high pasture areas where controlled burning is routinely exercised all year long, especially during the dry season. Smoke and fire regimes have prompted a species composition favoring smoke-stimulated flowering of ground bromeliads, pyrophytic grasses, and many serotonic forbs and shrubs that resemble the *páramo* assemblage of many fire-tolerant, and even fire-dependent, species.

Burning regime

How different is the tree line from the fire line?

The ancient custom of burning the forest borders for charcoal making is still practiced by *carboneros,* who currently sell their loads of timber-based charcoal in the markets of nearby towns and cities. In-situ production of charcoal is easily identified by cairns or kiln sites, which leave permanent marks in the soil's structure and chemical composition. Burning intensely enough to produce charcoal kills the mycorrhizal components needed to jumpstart succession, creating a crust of burned soil unsuitable for recalcitrant native forest seeds. Thus, recolonization of the cleared, usually round-shaped kiln site by native forest species is delayed and species composition is altered, perhaps thereby preventing full forest succession. Kiln sites maintain the classic encroachment of graminoids and serotonic shrubs typical of a burning regime, and continued burning halts any ecological succession toward a climax forest.

Fire scars and charcoal deposits are interspersed along the forest–*páramo* tree line, providing strong evidence that humans created the abrupt straight line separating the forest from the grassland (Lægaard 1992). The presence of the round-shaped balds or *páramo* islands near the TMCF border zone suggests that accessible border forest was used as an easy source of exportable charcoal and firewood. Firewood gathering in and of itself cannot account for the widespread nature of forest island burning. Pasture management and large-scale charcoal production, on the other hand, benefit big landowners or the middleman and usually result in clearing large patches of forest.

Indirect evidence of tree line formation

Paleoecological data and biogeography

Paleobiogeography in the tropics is understudied relative to northern countries, primarily because of scarce resources and the lack of strong scientific and governmental infrastructure for pursuing such studies. Detailed geological maps based on in-depth pollen and soil analyses, of the kind available for virtually any US county, have not been completed for most of the tropics. Limited data are thus often interpreted on the basis of corollaries with temperate climate studies. Hence, the prevalent view of forest–alpine tree line dynamics is that because we are witnessing glacial recession at the end of an ice age, the tree line is progressively advancing to higher altitudes—as the computerized models elucidating mountain climate change also predict.

But where detailed analyses have been done in the tropics (eg, El Junco in the Galápagos islands, Sabana de Bogotá, Cajas lakes in Ecuador, a crater floor in Panama, and a bog near Cuzco, Peru, etc [see Colinvaux et al 1997, and Wille et al 2002]), they reveal that the situation is not so simple and methodologies as well as paradigms should be revised. Introduced multiple-use trees accompanied human population forays into high altitude, as demonstrated by alders (*Alnus* spp) in Costa Rica (Kappelle 1996) and in Peru and Mesoamerica (Chepstow-Lusty et al 1996).

Palynological history is constrained by the difficulty of finding species-specific markers for some families that may have both shrubs and tree forms. It is difficult to specify the geological history of tree line dynamics. This forces palynologists to generalize the comparison of morphotypes for "forest" versus "prairies." Colinvaux et al (1997) concluded that "Andean vegetation did not respond to glacial cooling or Holocene warming by movement in belts," and proposed that taxa were reassorted according to temperature tolerance: "Vegetation did not move up and down slope as belts. Rather, plant associations were reformed as temperature-sensitive species found different centers of distribution with changing temperature."

The presence of *páramo* endemics (ie, *Espeletia pycnophylla*) is still enigmatic and suggests that vicariance plays an important role. The use of the caulirosula life-form (sensu Cuatrecasas 1957) as an indicator of high *páramo* is particularly relevant for the northern Andes of Colombia or Venezuela, where several species of *Espeletia* exist. But in the equatorial Andes, only 1 *Espeletia* species is encountered in 2 distinct *páramos* (El Angel in the north, and Llanganatis in central Ecuador), making it ambiguous as a good *páramo* indicator.

Archaeological artifacts

When the Spaniards came to the tropical Andes, they discovered an area already widely cultivated and thus affected by extensive human impact (Denevan 1992; Kessler and Driesch 1993). In the equatorial Andes, they encountered impressive remains of previous human intervention in the landscape including abandoned *cangahua* pyramids, terraces, and irrigation channels. Pimampiro at the southern end of our study site was well established as an important commercial center for exchange of goods from the coastal plain (as evidenced by *Spondilus* shells) and from the Amazon region (as evidenced by tropical feathers). In fact, several different types of pottery pieces worked using different techniques from various distant lowland cultures have been found (Molestina 1985). The Mira watershed (across the central valley from our study site) was heavily populated by different cultures such as Capulí, Pastos, and Quillasingas during the Formative and Late Formative periods. Their artifacts are now the principal tools used to analyze the ancient human occupation of the Mira-Chota watershed (Knapp 1991).

Irrigation channels and trade routes

The Interandean basin in our study site is crossed by ancient terracing systems and channels built on sloped terrain, bringing water toward the area of Pimampiro. The scale of this channel and irrigation system suggests a population in the order of several tens of thousands of people who are likely to have lived in the area (Mothes 1987).

The commercial center in Pimampiro and the connecting networks of trade routes to the south and north, as well as to the lower tropical plains of the Amazon (via Puruhanta Lake) and to the Coast (via de Mira Canyon), made the Mira-Chota basin an important cultural center in pre-Hispanic times. Satellite imagery has demonstrated the strategic location of *pucaras* or forts interspersed along the key points in the Interandean valley.

Historical records

The extent of TMCFs within the basin in the colonial era is evidenced by the construction of big colonial houses and churches in nearby cities, particularly Ibarra, Tulcán, San Gabriel, and El Angel, using old growth timber and native lumber from the area. Records kept at the catholic Bishop's office in Ibarra, for instance, attest to the wealth of forest products being exported from the Chota valley and surrounding hills. Today, the Chota valley is void of any significant native forest cover, and most of the surrounding hills are denuded. The overall kingdom of Quito with all its chiefdoms to the north, including those of the Chota-Mira watershed, is reported to have included vast expanses of forests (Salomon 1986).

Fisheries

Human impact on tree lines can also be discerned in freshwater bodies that are surrounded by pristine TMCFs. For instance, Lake Puruhanta (or Chique) in the study site, an otherwise pristine and apparently natural setting, was significantly modified as a result of widespread efforts to develop fishing farms throughout the Ecuadorian highlands and especially in Imbabura province, considered the country's lake district. Despite the apparently pristine surroundings, the area of Puruhanta was significantly altered when inoculation of the exotic trout (*Oncorhynchus mykiss, Salmo gairdnerii*) resulted in the extinction of local native *preñadillas* (*Astroblepus* spp) and *bagrecitos* (*Rhamdia* spp). At the site of a fishing campground, the forest was cut and burned up to the lakeshore, with *páramo* tussock regrowth appearing in the highly restricted site, clearly indicating human intervention (Sarmiento 1988).

Conclusions

The notion of anthropogenic community composition, landscape structure, and ecosystem function is a viable succinct explanation for Andean tree line dynamics, both in the upper and lower boundaries of the native TMCFs (Figure 4). The simplified, temperate-based view of altitudinal vegetation belts moving up and down

FIGURE 4 Distinctive anthropogenic boundary between the forest and the *páramo* in Nueva America. Note the straight line of the slope cut and the avoidance of ravines and brooks not suitable for grazing or agriculture. Often, semicircular shapes are observed as evidence of previous kilns for charcoal extraction. (Photo by L. Frolich)

with climate change has been confronted by a more plausible explanation, consistent with ecological theory, in which individual species are ephemera of habitat, climate, and opportunity (Prentice et al 1991), both in temperate and in tropical ecosystems. Instead of a sinking tree line, a redo of assemblages with cold tolerant species might have kept the equatorial Andes forested throughout the last Ice Age.

Evidence favoring the need to integrate the human dimension in Holocene tree line dynamics in the American tropics comes from different sources (but see Lauer and Klaus 1975). The equatorial Andes with a long prehistorical presence of humans in the mountain landscape thus emerge as a classic example of the anthropogenic nature of tropical montane cultural landscapes, including supposedly pristine primary forests and *páramos*.

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