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Andean montane forests and climate change

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2.1 INTRODUCTION

The montane forest habitats of the Andes support exceptionally high biodiversity, with many species occupying narrow elevational ranges (e.g., Terborgh, 1977). These attributes, combined with the short migratory distances, often < 30 km separates the lowlands from the upper forest line, allows montane forests to be extremely sensitive monitors of climatic change.

Andean montane forests, which we define to encompass temperate and montane rainforests within the tropical zone (after Huber and Riina, 1997), range from *c.* 1,300 m up to *c.* 3,600 m elevation. The mean annual temperature at the lower limit of the montane forest is about 20°C, with minima of *c.* 7°C (Colinvaux *et al.*, 1997). Annual precipitation generally exceeds *c.* 1,000–1,200 mm, and ground level cloud is frequent. Montane forests are diverse in form, composition, and adaptations, and their response to a common forcing, such as a drought event, can vary significantly according to latitude, altitude, aspect, local precipitation, and soil type (Gentry, 1988). A further variable that must be included is that humans have occupied and modified these landscapes for millennia (Erickson, 1999; Kolata *et al.*, 2000). Consequently, uncertainty exists regarding the elevation of the natural upper forest limit in many parts of the Andes (Erickson, 1999; Wille *et al.*, 2002).

In this chapter we will address some of the larger scale issues—for example, the migration of species in response to tectonic and climatic change, the stability of systems despite instability of communities through time, the out-of-phase climatic influence on southern and northern Andean sites during the last glacial maximum (LGM), and the possibility of climate change inducing non-linear responses in ecosystems.

2.2 TECTONIC CHANGES AND THE RISE OF THE ANDES

For the last 20 million years, the Andes have been rising as a result of the subduction of several oceanic plates beneath the South American Plate. The uplift transformed a rather flat continent into one with strong physical separation of lowlands and a host of new habitats ranging from humid foothills to ice covered summits. The rise of the Andes had no less radical an effect on the biogeography of the continent. Drainages of great rivers were reversed (Damuth and Kumar, 1975; Hoorn *et al.*, 1995), and the related orogeny in Central America provided first stepping stones, and ultimately a landbridge connecting a Gondwanan to a Laurasian flora and fauna (Terborgh, 1992; Webb and Rancy, 1996). The great American faunal interchange (Webb, 1997), in which successive waves of taxa moved north and south and then underwent adaptive radiation, began as early as 16 million years ago. Migrations between North and South America peaked following the closure of the Isthmus of Panama, a progressive process that produced a continuous landbridge between 5 and 4 million years ago.

The arrival of eutherian mammals (e.g., monkeys, dogs, bears, sloth, elephantids, camelids, rats, and cats) left a lasting impression on South American systems. Many of these mammals entered unoccupied niches, while others may have gone into direct competition with marsupial counterparts or the indigenous array of flightless, predatory birds. The net result was rather lop-sided with relatively few genera moving into North America, though *Glyptodon*, a re-radiation of sloth species, possum, armadillos, and porcupines were clear exceptions. While, only the latter three have surviving representatives in North America, >50% of mammal genera in South America were derived from Laurasian immigrants (Terborgh, 1992).

In contrast to mammals, where an adaptive advantage lay with eutherian mammals over marsupials, the plants of North and South America shared the same basic biology. Among plants, the pattern of migration and competitive success obeyed the basic biogeographic rule that the species of larger source areas outcompeted those of smaller source areas (Rosenzweig, 1992). Consequently, lowland rainforest taxa from South America surged up into Central America, and became the dominant vegetation of the lowland tropics. Contrastingly, Laurasian elements swept south along mountain chains occupying the climatically temperate zone of Central and South American mountains (Hooghiemstra, 2006; Hooghiemstra *et al.*, 2006).

Many modern genera were extant and clearly recognizable in the pollen of Miocene sediments (23–6 Myr ago) (Jaramillo and Dilcher, 2002). During this time the Andes were rising, attaining about half their modern height, reaching *c.* 2,500–3,000 m about 10 Myr ago (Hoorn *et al.*, 1995). For millions of years, the spine of the Andes comprised forested ridges that trapped clouds. Low passes—such as the Guayaquil gap and the Maracaibo area—maintained lowland connectivity from the Pacific to the interior of the continent until the Mid to Late Miocene (Hoorn *et al.*, 1995). Only in later stages of uplift did large areas of the Andes rise above elevations capable of supporting diverse montane forests (i.e., above 3,300–3,600 m).

Importantly, as the Andes rose, entirely novel habitats were created for the continent. Mid- to high-elevation settings with steep slopes, varying moisture

abundance, light limitation where clouds formed, increased exposure to ultraviolet radiation, and cool temperatures, offered new growing conditions. Speciation occurred among plants and animals as vacant niches were exploited. The radiation of families such as Lauraceae, Rubiaceae, and Ericaceae that filled the Andean forests was a huge biogeographic departure from patterns arising from the diversification of lowland elements. Today, the within-family diversity statistics (i.e. the ranking of families based on their species diversity) of lowland Amazonia and the Congo are much more similar to each other than either is to those of an Andean forest (Gentry, 1988).

Montane-dwelling migrants into this setting from North America had to island-hop through the Caribbean or move from hilltop to hilltop including making passage across a broad lowland plain in central Panama. This gap, without highlands over 1,000 m, was at least 130 km in length and may have acted as a severe filter to large seeded species, such as *Quercus*. Indeed, *Quercus* diversity in Panama was reduced from *c.* 13 species in the west, to one species in eastern Panama (Gentry, 1985).

The southward migrations of arboreal Laurasian taxa (e.g., Annonaceae, *Hedyosmum*, *Salix*, and *Rumex*) were inferred rather than observed, but the arrival of *Myrica*, *Alnus*, and *Quercus*, were apparent in the paleoecological records from the high plain of Bogotá (Hooghiemstra, 1984; Van der Hammen, 1985; Van der Hammen *et al.*, 1992; Van't Veer and Hooghiemstra, 2000). *Myrica* arrived in the Mid Pliocene, whereas *Alnus* first occurred in the Colombian pollen record about *c.* 1.37 million years ago. The last of these three species to arrive was *Quercus*, which first occurred about 478 kyr BP (Van't Veer and Hooghiemstra, 2000), but probably only attained its modern dominance between 1,000 m and 3,500 m elevation about 200,000 years ago (Hooghiemstra *et al.*, 2002). Since the first arrival of these species, *Alnus* spread as far south as Chile, whereas the southernmost distribution of *Quercus* coincided with the Colombian–Ecuadorian border (Gentry, 1993). *Alnus*, a pioneer species, thrived in disturbed settings, whereas *Quercus humboldtii* was a dominant of Andean forest. The arrival of *Quercus* in Colombia clearly impacted previously established taxa such as *Hedyosmum*, *Vallea*, and *Weinmannia* (Hooghiemstra, 1984); species that remained the common components of upper Andean forest from Peru to Colombia.

Progressive cooling during the Quaternary led the upper limit of diverse forest to move downslope, ranging between 3,600 m and 2,800 m during warm periods and probably reaching as low as 2,000 m during peak glacial conditions. The consequent expansion of montane grasslands, through a combination of uplift, cooling, and a reduction in atmospheric CO₂ concentrations, provided habitat for newly arriving holarctic species that enriched Puna and Paramo floras.

The new arrivals to forest and grassland settings created novel communities. Paleoecologists introduced the term no-analog communities to indicate that communities of the past differed from those of the present (e.g., Overpeck *et al.*, 1985). Ecologically, a no-analog community was most significant if it formed a novel community compared with those that preceded it, rather than compared with those of today. The sequential arrival of *Myrica*, *Alnus*, and *Quercus*, each established such novel communities. Furthermore, the faunal interchange between the Americas

altered predator–prey relationships, seed-dispersal, and plant recruitment (Janzen and Martin, 1982; Wille *et al.*, 2002).

Among those seed-dispersers and predators were the megafauna. While the traditional view has been that the megafauna died out in the terminal Pleistocene (Steadman *et al.*, 2005), very real questions exist regarding the exclusion of Holocene ages from those analyses (Hubbe *et al.*, 2007). The probability that relatively low densities of people could have exterminated these large creatures quickly in the forests of the Andes and Amazon is much lower than in the open grasslands of North America or Patagonia. If the later ages for extinction are accepted, the collapse of megafauna appears to have occurred around 9–7 kcal yr BP, a time of strong climatic change and increased fire activity (Paduano *et al.*, 2003; Bush *et al.*, 2007), coupled with increased human impacts on ecosystems (Bush *et al.*, 2007).

Tapir survive in the lowlands and camelids continue to exert a significant grazing influence on montane grasslands. Such a basic observation is an important reminder that the loss of some of the other megafauna could have a substantial impact on the openness of all Neotropical settings and in the transport of large-seeded fruit (Janzen and Martin, 1982; Guimarães *et al.*, 2008). Thus, during the Quaternary, plate tectonics caused a major reorganization of plant and animal communities, featuring long-range migrations, species invasions, and adaptive radiation. In contrast, most responses to glacial–interglacial climate change appear to have been essentially local to sub-continental migrations.

2.3 SENSITIVITY AND QUANTIFYING COOLING

Modern pollen studies are the backbone of any attempt to quantify past vegetation changes. Over the past 25 years, a series of studies in Colombia (Grabandt, 1985), Ecuador (Bush, 1991; Moscol-Olivera *et al.*, 2009), and Peru (Weng *et al.*, 2004), have demonstrated a broad coherence between vegetation types and local pollen inputs. Indeed, apart from low-productivity settings (e.g., the highest grasslands), long-distance transport of pollen forms a very small proportion of the pollen rain. Weng *et al.* (2004) analyzed modern pollen data on an elevational transect in southern Peru and calculated that the accuracy of assigning an elevation to an unknown sample is about ± 260 m at that location. Local moist-air adiabatic lapse rates are almost exactly 5.5°C per 1,000 m of ascent (Weng *et al.*, 2004). From this study it appeared that palynology can be used to provide a temperature estimate of *c.* $\pm 1.5^{\circ}\text{C}$ (Figure 2.1). It will be noted that the samples in Figure 2.1 from 3,350 m and 3,400 m do not fall close to the regression line. Both of these samples were collected from sheltered gullies that contained shrubs of *Weinmannia*, woody Asteraceae, and *Polylepis*, giving these samples a “low” signature in the analysis.

The Weng *et al.* (2004) study was in mature second growth forest, disturbed by road construction. As disturbance-tolerant species tend to produce a lot of pollen and are often generalist species, ongoing study of less disturbed transects may provide even narrower error ranges in temperature estimates.

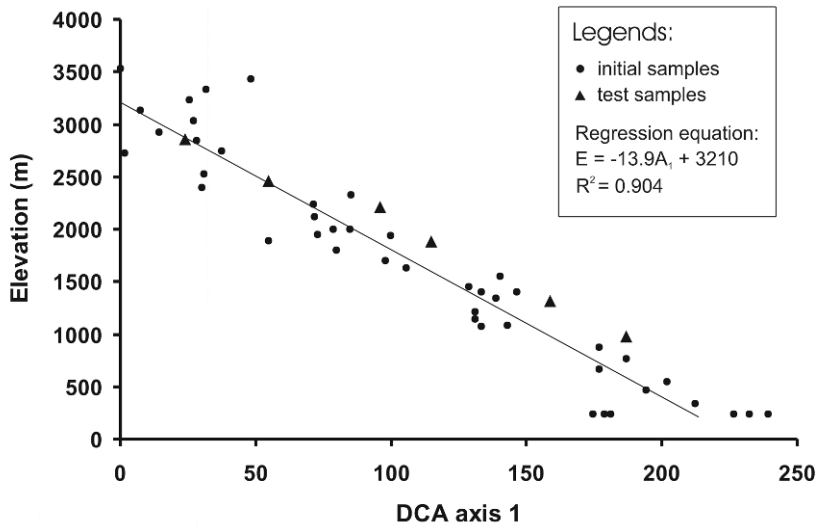


Figure 2.1. Modern pollen rain and elevation. Regression of first axis DCA scores against elevation for log-transformed modern pollen data. All data from a line transect from Amazonia into the Andes in eastern Peru (Weng *et al.* 2004). Black circles represent samples of known elevation (to the palynologist). The six triangles represent a blind study in which the analyst did not know sample elevation.

2.4 SITES IN SPACE AND TIME

Almost all Andean lakes are a product of glaciations, formed less than 20,000 years ago. The lowest of these lakes are usually moraine-dammed and may lie at the upper limit of modern Andean forest (e.g., Lakes Surucuchu (3,180 m elevation; Colinvaux *et al.*, 1997), Chochos (3,300 m; Bush *et al.*, 2005), and Refugio (3,400 m; Urrego *et al.*, 2010a)). However, such lakes that provide paleoecological records from within modern montane forest settings are thinly scattered. The cause of this paucity lies in the geography of the Andes themselves (Figure 2.2). The flanks of the Andes are so steep that the vertical elevation occupied by montane forest is often spanned by just 10–30 km laterally. In the inter-Andean plateaus montane forests are restricted to the wetter and somewhat lower sections of the northern Andes. The small area and lack of glacially-formed lakes within the elevations occupied by modern montane forest, combined with frequent rockslides and active tectonism, contribute to a landscape in which few ancient lakes formed and even fewer survive.

The obvious and important exceptions to this pattern are the great lakes of the Altiplano (e.g., the Salar de Uyuni and Lake Titicaca) and deep grabens such as Lake Junin, but these have probably never lain within forest. The High Plain of Bogotá, at c. 2,550 m elevation contains an extensive series of lakes and marshes that provide much of what we know about the response of montane forest to Quaternary climate change (Torres *et al.*, 2005). Newly described lakes, such as Lakes Pacucha (3,050 m; Hillyer *et al.*, 2009; Valencia *et al.*, 2010) and Consuelo (1,360 m; Bush *et al.*, 2004;

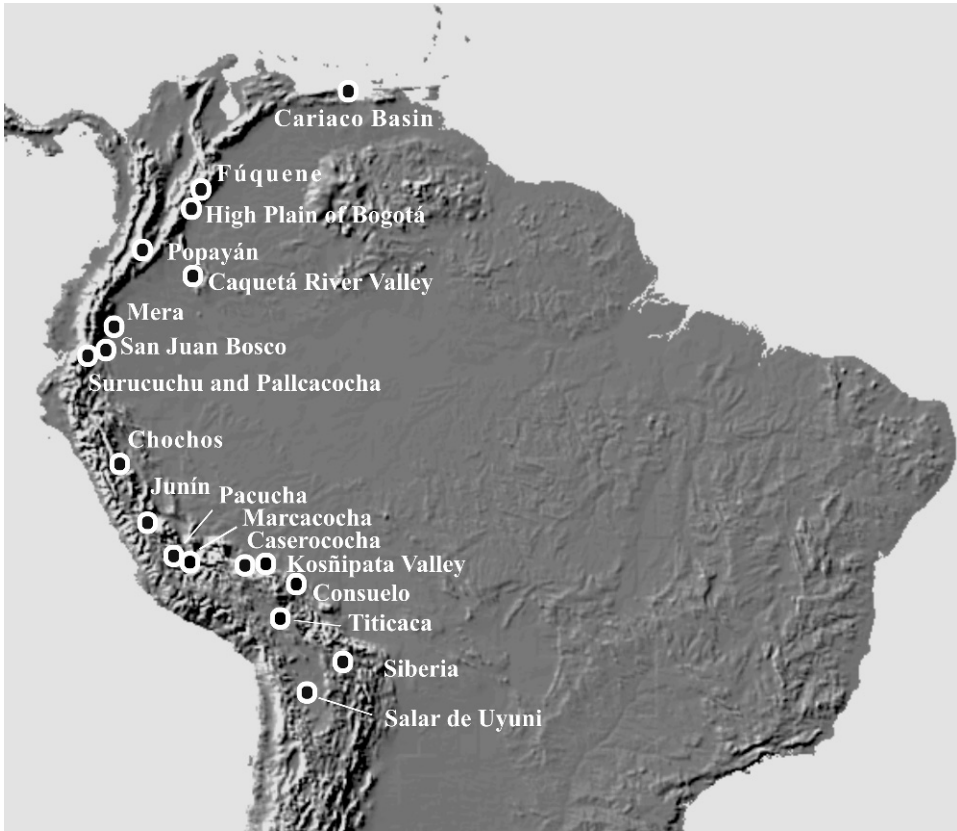


Figure 2.2. The location of sites of paleoecological importance mentioned in the text relative to topography.

Urrego *et al.*, 2010b) augment this understanding by providing additional detail of the last glacial maximum and subsequent deglaciation.

2.5 QUATERNARY GLACIAL-INTERGLACIAL CYCLES

The list of montane forest sites is expanded when we include those that have supported montane forest in the past. During the thermal optima of previous interglacials such as marine isotope stages (MIS) 5e, 7, 9, and 11, it appears that montane forest may have extended upslope by as much as 200 m from its present location (but see below for the case of Lake Titicaca). The influence on the lower limit of montane forest during these episodes is more difficult to establish. Bush (2002) hypothesized that as climates warm the elevation of cloud formation on the flank of the Andes will increase.

Under such warm conditions the change in the elevation of cloudbase may have been greater than the upslope expansion of the montane forest, creating a narrower total elevational range supporting montane forest. Contrastingly, during the glacial periods, montane forest species invaded downslope in response to cooling and the lower formation of cloud. Although the descent of montane taxa and the lowering of the upper forest line appear broadly similar (*c.* 1,500 m) along the Andes, the movement of the lower limit of the cloudbase may be more variable regionally. In the drier lowlands of Colombia this cloudbase may not have moved far downslope (Wille *et al.*, 2001; Hooghiemstra and Van der Hammen, 2004), compared with the wetter systems of Peru and Ecuador (Colinvaux *et al.*, 1996; Bush *et al.*, 2004).

Translating the migration of fossil pollen types in sedimentary records into an estimate of temperature change was pioneered in South America by van der Hammen and González (1960). They documented a periodic 1,500-m descent of vegetation types based on the replacement of forest with grasslands, and then a widening downslope distance to the estimated position of upper forest line. Since that initial study of the High Plain of Bogotá, virtually every Andean record from the last ice age has indicated at least a 1000-m descent of vegetation and often a 1500-m descent of some pollen taxa at the LGM (Figure 2.2). The moist air adiabatic lapse rate (Chapter 10) evident on the Andean flank provided a means to translate this vegetational movement into a change in temperature.

Modern lapse rates vary according to local humidity, ranging between -5.5°C and -6.2°C (Witte, 1994) in Colombia, and *c.* -5.5°C per 1,000 m of ascent in Peru and Ecuador (Colinvaux *et al.*, 1997; Bush and Silman, 2004). Accordingly, for a 1,000–1,500-m descent of vegetation the inferred change in paleotemperature is a cooling relative to the modern values of 5°C to 8.5°C .

Most Andean LGM pollen records are consistent with a cooling of *c.* 8°C in the highest elevations tapering down to a cooling of *c.* $4\text{--}5^{\circ}\text{C}$ in the lowlands. This temperature differential suggests a steeper-than-modern temperature gradient. As there is no suggestion that the Andean slopes were ever without forest, it is improbable that the moist-air adiabatic lapse rate would change very much (Webster and Stretten, 1978; Rind and Peteet, 1985). Evidence from studies of glacial moraines lead to reconstructions of the equilibrium line altitude (ELA) for glaciers. Glaciers in Peru and Ecuador are generally inferred to have ELAs about 800–1,000 m lower than modern counterparts, suggesting a cooling of $4\text{--}5^{\circ}\text{C}$ (Rodbell, 1992; Seltzer, 1992; Smith *et al.*, 2005). Hence the inferred temperature signal from plants at high elevations may contain a more complex signal than first envisaged. Bush and Silman (2004) proposed one such effect in which black-body radiation would elevate sensible heat loss under low atmospheric CO_2 concentrations; an effect that would be more extreme at high elevations. Other additive effects probably contributed to the observed high-elevation cooling.

Within the dating resolution available to us, Neotropical interglacials appear to coincide in timing, and general character, with those documented elsewhere. The interglacials are known as MIS 5e (*c.* 130–116 kyr BP), MIS 7 (*c.* 240–200 kyr BP), MIS 9 (330–300 kyr BP), and MIS 11 (425–390 kyr BP), and generally last about 15,000–40,000 years. While a 100,000-yr cycle appears to underlie the glaciations of the last

half million years, the intensity of interglacial periods appears to be related to precessional amplitude (Broecker, 2006). Three records provided insights into multiple glacial cycles in the Andes: the High Plain of Bogotá, Lake Titicaca (Hanselman *et al.*, 2005), and the Salar de Uyuni, although only the MIS 6 to MIS 1 portion of this record has been published so far (Fritz *et al.*, 2004).

Long sediment cores raised from Lake Titicaca provided a record of vegetational change spanning the last 370,000 years (Hanselman *et al.*, 2011). During interglacials, warming increased local productivity, and the upper Andean forest began to migrate closer to the lake. At the peak of MIS 5e and 9, Titicaca was reduced to a shallow lake with extensive adjacent saltmarsh, while having deeper water and somewhat more mesic vegetation, including *Polylepis* woodland, in its catchment in MIS 7 and 1.

Fire, which these data demonstrated was natural to the high Andes, became a transforming factor and limited the expansion of woody taxa during interglacials. Both the Colombian and Bolivian records indicated that the peak of MIS 5e may have been relatively dry. This drying was especially evident in Lake Titicaca, where the abundance of benthic and saline-tolerant diatoms, and peak abundances of pollen of Amaranthaceae, suggest the lowest lake levels of the last 370,000 years. Amaranthaceae pollen types are commonly derived from salt-tolerant plants, or from plants that grow in areas subject to irregular inundation (Marchant *et al.*, 2002).

At Lake Titicaca substantial differences were evident in the manifestation of the last four interglacials. Trajectories of vegetational change during MIS 1 and 5e were revealed through Detrended Correspondence Analysis (DCA) (Hill, 1979; McCune and Mefford, 1999) for fossil pollen data from Lake Titicaca (Figure 2.3). The scores for Axis 1 were plotted against time since the start of the relevant interglacial. The data were drawn from a deep-water core from Lake Titicaca LT01-2B (240-m water depth), a shallower water core (40-m water depth) from the Huinaymarca sub-basin (Core LT01-3B; Gosling *et al.*, 2008), and a piston core from 130-m water depth that provided a detailed Holocene record from the main basin (core NE98-1PC; Paduano *et al.*, 2003). Core LT01-3B had a hiatus in the middle of the interglacial, but showed a very similar pattern of community change leading into and out of the event as found in the deep-water core LT01-2B. This comparison revealed that while starting similarly, MIS 5e continued on a path to increasing aridity, while in the latter part of the Holocene conditions diverged from this path (Hanselmann *et al.*, 2011).

The evident difference between the interglacials was probably underlain by precessional forcing, however, Bush *et al.* (2010) invoked microclimatic feedbacks as amplifying mechanisms that enhanced the precessional pattern. Lake levels fluctuated on the Altiplano (below) and as deglacial highstands gave way to interglacial lowstands there was a concomitant loss of a regional lake effect.

Lake Titicaca is the world's highest "Great Lake" and it produces a halo of warm ($\sim +4^\circ\text{C}$), moist (doubling local precipitation) conditions that significantly alters local growing conditions. If, as in the time of MIS 5e, the lake area is reduced by more than 50%, some of these moderating influences would be lost, rendering the local area cooler and drier. Triggered by outside forcing such as changes in insolation and sea surface temperature (SST), local positive feedback mechanisms involving

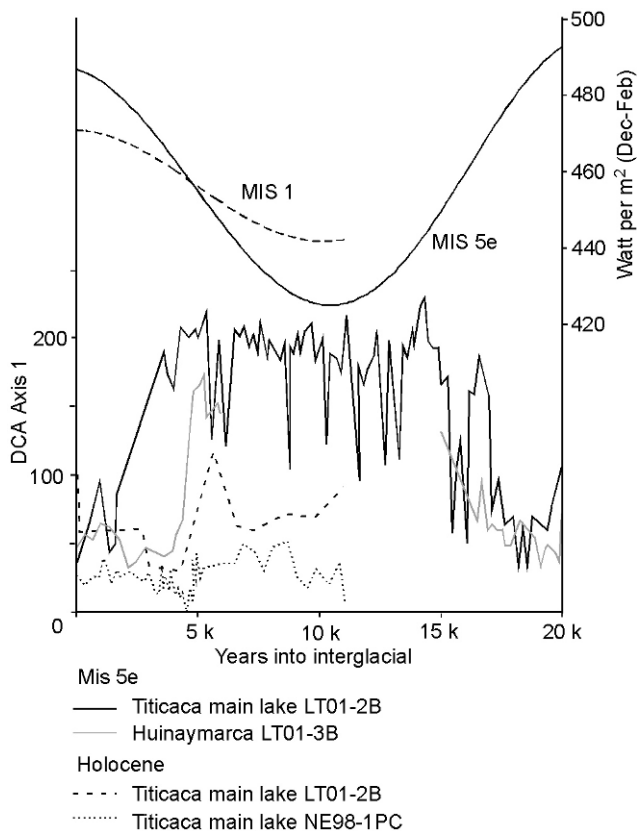


Figure 2.3. A comparison of MIS 5e and the Holocene based on insolation and changes in community composition revealed through DCA. The onset of MIS 5e is taken to be at 136 kyr BP based on the chronology used in Hanselman *et al.* (2005) and 11 kyr BP is taken as the start of the Holocene. Data are from Hanselman *et al.* (2005) and insolation curves from Analyseries 1.2 (Berger, 1992; Paillard *et al.*, 1996).

cloudiness, evaporation, precipitation, and temperature, may have been critical in altering local microclimates.

Bush *et al.* (2010) suggested that at least twice before, during MIS 9 and 5e, the Altiplano had warmed, and then passed a tipping point leading to falling lake levels and aridity (Figure 2.4). Upslope migration of forest stopped, even if temperatures continued to rise as the Altiplano became too dry to support montane forest. Based on the observation that dense Andean forest never reached an elevation of 3800 m, but can grow at 3,500–3,700 m elevations, it is probable that this tipping point occurred within +1–2°C of modern temperatures. This case-study provides an example of how vegetation–climate feedbacks are not always linear.

While it is our expectation that plants will migrate poleward or upslope in response to warming, the interaction of temperature with other climatic parameters,

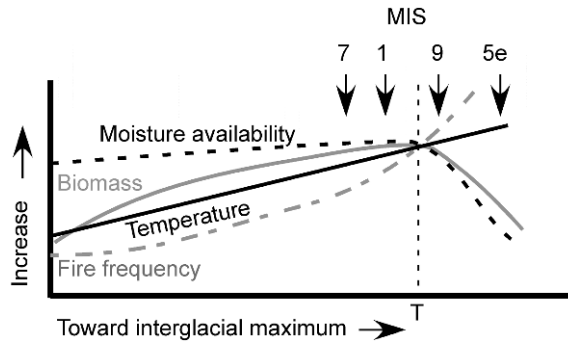


Figure 2.4. Schematic diagram of a non-linear response to warming and a turning point reached in some Andean interglacials based on paleoecological data from Lake Titicaca, Peru/Bolivia. Arrows indicate the approximate peak state of the last 4 interglacials relative to the schema.

in this case precipitation : evaporation ratios and microclimates, can induce non-linear feedbacks that change migrational patterns. Even these responses are not symmetrical as it is possible to slow or halt migration but, as it is believed that plant migrations are often dispersal-limited (McLachlan and Clark, 2005) and outstripped by the rate of climate change, it is unlikely that migration rates can be accelerated.

2.6 THE LAST GLACIAL PERIOD

In the Andes, the termination of the last interglacial was marked by a substantial and rapid cooling, perhaps 3°C , marking the onset of glacial conditions (Van't Veer and Hooghiemstra, 2000). Following this cooling, temperatures bumped up and down, tracking the Milankovitch and Dansgaard/Oeschger Cycles, but gradually declined to the coldest time at the LGM (Hooghiemstra *et al.*, 1993).

The precipitation record for this period is harder to decipher, and inferred lake depth is a major proxy for changes in annual precipitation. Precipitation patterns are often highly localized and, when one is dealing with relatively few sites it is possible that such local effects skew our view of systems. However, if we look outside the montane forest region and include data from ice cores, high Andean lakes, and from the Amazonian plain, a coherent pattern begins to emerge (Table 2.1).

In Colombia, the Funza-2 record terminates about 30 kcal yr BP when the lake dries out. The Fuquene-3 record suggests a progressive lowering of lake level beginning around 60 kyr BP and culminating in a depositional hiatus between c. 22 kcal yr BP and 12 kcal yr BP (Van der Hammen and Hooghiemstra H., 2003). The Altiplano of Peru and Bolivia appears to have become wetter after c. 60 kyr BP (Fritz *et al.*, 2004); given the uncertainties in dating, this may or may not be related to the beginning of the drier conditions in Colombia. However, the

LGM does provide support for asynchrony in wet episodes, as this is a time of flooding in the Altiplano, and low lake-level in Colombia.

At least three giant paleolakes occupied the Altiplano at various times during the Quaternary (Servant, 1977; Baker *et al.*, 1999). The timing of these events is actively discussed (Mourgiart *et al.*, 1997; Baker *et al.*, 2001; Placzek *et al.*, 2006; Gosling *et al.*, 2008). Here we adopt the chronology of Baker *et al.* (2001) as it seems most consistent with other regional records (e.g., Fritz *et al.*, 2004, 2010; Ekdahl *et al.*, 2008; Hillyer *et al.*, 2009), but recognize this issue is far from settled. The most recent, paleolake Tauca, appears to have formed about 26 kcal yr BP (Baker *et al.*, 2001), coincidental with the onset of ice accumulation at Sajama (Thompson *et al.*, 1998). This wet event appears to have lasted until *c.* 16 kcal yr BP when Lake Tauca drained (Baker *et al.*, 2001). The combination of extreme cold and wet conditions during the Tauca period caused ice lobes to advance to within 100 m vertically of the modern Titicaca shoreline (a vertical descent of about 1,300 m; Seltzer *et al.*, 1995, 2002). Baker *et al.* (2001) determined that lake level in the Salar de Uyuni followed the precessional cycle for the last 50,000 years. Highstands corresponded to maxima of insolation occurring during the wet season (December–February), and lowstands during the corresponding minima.

While the evidence of precessional oscillations have a long history in Colombia (Hooghiemstra *et al.*, 1993), on the Altiplano this synchrony is only evident in the last two glacial cycles. Prior to *c.* 60 kyr BP, the Salar de Uyuni was predominantly dry, with only sporadic flooding episodes (Fritz *et al.*, 2004; Chepstow-Lusty *et al.*, 2005). Two plausible scenarios have yet to be tested, one is that the climate was significantly drier prior to 60 kyr BP, and the other is that tectonic change altered the hydrology of the basin at this time, making it more probable that it would hold water (Wille *et al.*, 2001).

In Colombia, the Caquetá River valley (Van der Hammen *et al.*, 1992) documents a relatively wet time between *c.* 50 kcal yr BP and 30 kcal yr BP and a drier LGM, consistent with the records from the High Plain of Bogotá. A record from Popayán (1,700 m; Wille *et al.*, 2000) reveals the presence of either a cool open forest or closed montane forest throughout the last 30,000 years. The data from this site suggest a cooling of 5–7.5°C at the LGM. In Ecuador, the premontane sites of Mera and San Juan Bosco (1,100 m and 970 m, respectively; Bush *et al.*, 1990) match this interpretation closely, suggesting synchrony at least as far south as the equator.

Lake Consuelo, southern Peru, provides a detailed view of the lower Andes during the last glacial maximum (Urrego *et al.*, 2010b). At 1360 m elevation, the modern lake lies at exactly the elevation of cloud formation in this section of the Andes. The modern flora is dominated by lowland elements (e.g., *Alchornea*, *Brosimum*, *Euterpe*, *Ficus*, *Guatteria*, *Maquira*, *Unionopsis*, and *Wettinia*). Premontane elements such as *Dictyocaryum*, *Myrsine*, *Alsophila*, *Oreopanax*, and *Cyathea* are also present. The pollen types of the Holocene reflect this lowland mixture of species, but those of the glacial clearly indicate the presence of a montane forest. *Podocarpus*, *Alnus*, *Hedyosmum*, *Weinmannia*, *Bocconia*, *Vallea*, *Ericaceae*, and *Polylepis/Acaena* replaced the lowland flora. This flora was remark-

Table 2.1. Inferred LGM moisture from described sites in the northern and southern Andes. All ages in cal yr BP.

	Latitude (°S, unless otherwise stated)	Elevation	LGM wet/dry	Onset of deglaciation	Timing of mid-Holocene dry event	Literature source
Venezuela Cariaco Basin	10.5°N	—	Dry	—	—	Peterson <i>et al.</i> (2003), Lee <i>et al.</i> (2009)
Colombia Fúquene	5°N	2,580	Dry	—	—	van der Hammen and Hooghiemstra (2003)
High Plain of Bogotá	4–5°N	2,600	Dry	c. 24,000	—	Hooghiemstra (1984)
Popayán	2°N	1,750	Dry	c. 24,000	—	Wille <i>et al.</i> (2000)
Caquetá River Valley	1°N	c. 400	Dry	—	—	van der Hammen <i>et al.</i> (1992)
Ecuador Mera	0	1,100	Dry	c. 30,000	—	Bush <i>et al.</i> (1990)
San Juan Bosco	0	970	Dry	c. 30,000	—	Bush <i>et al.</i> (1990)
Pallacocha	2	4,060	—	—	c. 7,500–4,000	Hansen <i>et al.</i> (2003)
Surucucho	3	3,180	Wet ^a	—	—	Colinvaux <i>et al.</i> (1997)
Negra	7	3,300	—	c. 15,000	c. 9,000–3,800	Bush <i>et al.</i> (this volume)
Peru Chochos	7	3,285	—	c. 17,000	c. 9,500–7,300	Bush <i>et al.</i> (2005)
Baja	7	3,575	—	—	c. 9,000–6,000	Hansen and Rodbell (1995)
Huascarán	9	6,048	Dry ^a	—	c. 8,400–5,200	Thompson <i>et al.</i> (1995)
Junin	11	4,100	—	—	c. 6,000	Hansen <i>et al.</i> (1994)
Junin	11	4,100	Wet	c. 22,000	—	Seltzer <i>et al.</i> (2002)
Marcacocha	13	3,355	—	—	—	Chepstow-Lusty <i>et al.</i> (2002)
Pacucha	13	3,050	Wet	c. 19,000	c. 10,000–8,700	Valencia <i>et al.</i> (2009), Hillier <i>et al.</i> (2009)
Caserochocha	13	3,900	—	c. 16,500	c. 7,900–4,250	Paduano <i>et al.</i> (2001)

	<i>Latitude (°S, unless otherwise stated)</i>	<i>Elevation</i>	<i>LGM wet/dry</i>	<i>Onset of deglaciation</i>	<i>Timing of mid-Holocene dry event</i>	<i>Literature source</i>
Consuelo	13	1,360	Wet	c. 21,000	c. 8,200–4,000	Bush <i>et al.</i> (2004)
Arequipa	16	2,350–2,750	Wet	—	Mid-Holocene	Holmgren <i>et al.</i> (2001)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	c. 21,000	c. 6,000–4,000	Paduano <i>et al.</i> (2003)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	c. 21,000	c. 8,000–5,500	Baker <i>et al.</i> (2001a)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	c. 22,000	—	Seltzer <i>et al.</i> (2002)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	—	c. 6,000–3,500	Tapia <i>et al.</i> (2003)
Bolivia						
Lago Taypi Chaka Kkota	16	4,300	—	—	c. 8,500–2,500	Abbott <i>et al.</i> (2000, 2003)
Huinamarca	17	c. 3,800	Wet ^a	—	—	Mourguiart <i>et al.</i> (1997, 1998), Mourguiart (1999)
Siberia	17	2,920	Wet ^a	c. 21,000	c. 11,000–4,000	Mourguiart and Ledru (2003)
Sajama	18	6,452	Wet	c. 21,000	c. 9,000–3,000	Thompson <i>et al.</i> (1998)
Salar de Uyuni	20	3,653	Wet	—	—	Chepstow-Lusty (2004), Fritz <i>et al.</i> (2004)
Salar de Uyuni	20	3,653	Wet	—	—	Baker <i>et al.</i> (2001b)

All ages are cal yr BP.

^a As interpreted by the authors of this chapter.

ably constant between *c.* 45 kcal yr BP and 24 kcal yr BP and was probably buffered from precipitation changes by the presence of persistent cloud cover (Urrego *et al.*, 2010). Similar vegetation descents of *c.* 1,300 m and persistent forest cover were recorded in the mid-elevations of the Colombian Andes at Pitalito (1300 m elevation; Will *et al.*, 2001) where upper montane forest rich in *Quercus*, *Hedyosmum*, *Myrsine*, and *Weinmannia* occupied the site during the LGM.

2.7 DEGLACIATION

The timing and rate of Andean deglaciation is somewhat contentious, as it has been suggested that the southern Andes mirrors the Vostok record from Antarctica, while the northern Andes mirrors the Greenland Ice Sheet Project (GISP) record (Seltzer *et al.*, 2002). It appears that the more southern tropical Andes entered a deglacial phase between 21 kcal yr BP and 19 kcal yr BP (within the classic LGM of the northern hemisphere), while the northern Andes may not have warmed until *c.* 16 kcal yr BP. This relatively early deglaciation is manifested in most of the Central Andean records (Figure 2.5).

A further issue that needs to be resolved is whether the warming associated with the deglacial period was protracted and steady or if it occurred rapidly. Abrupt changes in fossil pollen records are certainly apparent in almost all high Andean locations, but whether the sudden change was due to temperature or changes in precipitation and fire regime has yet to be established fully.

On present evidence, the trend out of the last ice age appears to be more gradual in the southern tropical Andes than in the northern Andes. The gradualism of the southern sites could be argued to be buffered by the maximum rate of tree migration (i.e., the forest cannot respond to maintain equilibrium with climatic change). However, abrupt changes in forest abundance are evident in many high Andean settings (e.g., Hansen *et al.*, 2003; Niemann and Behling, 2009; Valencia *et al.*, 2010), where the communities were clearly responding to rapid pulses of climate change.

Further investigation is needed into the role of microrefugia (McGlone and Clark, 2005; Rull, 2009; Mosblech *et al.*, 2011), and how these may have influenced the timing of observed migrations. For the time being, the migrational data appear to support an Antarctic-style deglaciation in the Andes south of *c.* 10°S, while further north (perhaps progressively), paleoclimate records appear to reflect the characteristic climatic oscillations of the North Atlantic and Greenland. Consequently, in Peru and Bolivia the deglacial warming appears to have been on average <1°C per millennium, whereas in the northern Andes a relatively large jump in temperatures at the onset of the Holocene, perhaps 4°C within the space of few hundred years, is thought to have occurred. Thus, these systems have responded to warming events whose rates differed by about an order of magnitude.

The deglacial period highlights periods of rapid landscape change. The upslope expansion of forest taxa and novel climates (*sensu* Williams *et al.*, 2007) jumbled competitive relationships producing short-lived formations that are rare today, or

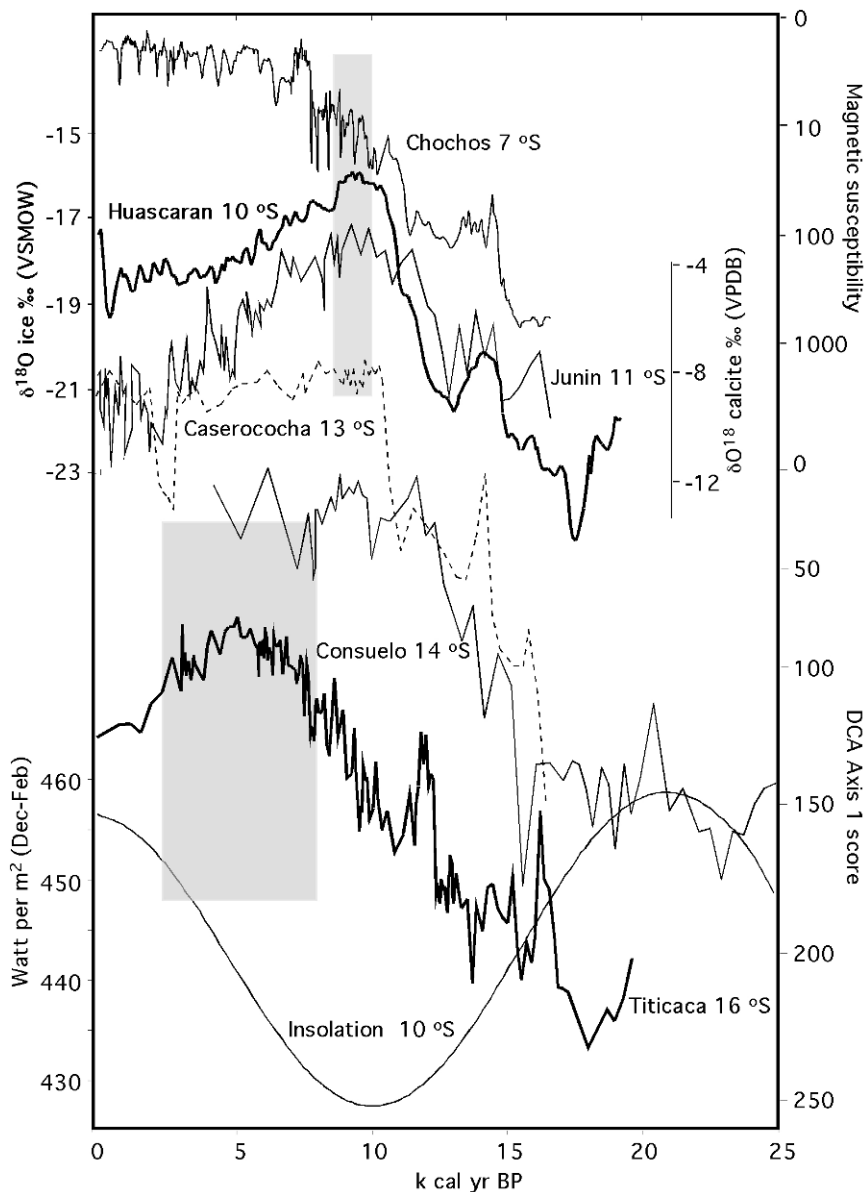


Figure 2.5. Central Andean insolation, and the extent of physical and community change during deglaciation and the Holocene. Datasets are Lake Chochos magnetic susceptibility (note inverted log scale; Bush *et al.*, 2005); Huascarán $\delta^{18}\text{O}$ ice core (Thompson *et al.*, 1995); Lake Junin $\delta^{18}\text{O}$ calcite (Seltzer *et al.*, 2000); Lake Caserococha fossil pollen DCA Axis 1 (Paduano, 2001); Lake Consuelo fossil pollen DCA Axis 1 (Bush *et al.*, 2004; Urrego *et al.*, 2010); Lake Titicaca fossil pollen DCA Axis 1 (Paduano *et al.*, 2003); Insolation (DJF) for 10°S from Analyseries1.2 (Berger, 1992; Paillard *et al.*, 1996). Shaded boxes represent periods of low-lake level or drought recorded at those sites.

possibly without modern analog. However, some of the rapid changes in community structure associated with deglacial settings may indicate a longer no-analog status within the forests. For example, the important tropical families of Moraceae and Urticaceae, which produce copious amounts of pollen, and are important components of every modern mesic Neotropical forest pollen record, do not appear to have been equally abundant in glacial times at any elevation (Valencia *et al.*, 2010). If further research supports this view, the glacial-age rarity of these families, especially the Moraceae, would have had profound impacts on forest ecology.

Evidence for the presence, or absence, of the Younger Dryas event in South America has engendered considerable debate (Heine, 1993; Hansen, 1995; Van der Hammen and Hooghiemstra, 1995; Rodbell and Seltzer, 2000; Van't Veer *et al.*, 2000; Bush *et al.*, 2005). In the sedimentary sequences from Guatemala (Hodell *et al.*, 2008), the Cariaco Basin (Peterson and Haug, 2006), and Colombia reveal a strong and apparently synchronous climatic event corresponding to the Younger Dryas (e.g., Van't Veer *et al.*, 2000). However, other records, such as those of Titicaca and of glacial advances in Ecuador and Peru, reveal an oscillation that predates the Younger Dryas by 500 years (Rodbell and Seltzer, 2000; Paduano *et al.*, 2003). In summary, it appears that the Younger Dryas is better represented in the northern section of the neotropics than south of the equator. In the northern tropics the Younger Dryas appears to be manifested in both temperature and precipitation signals, whereas in the southern tropics, precipitation provides the best cue for this event (Clapperton, 1993; Rodbell and Seltzer, 2000; Smith *et al.*, 2005).

2.8 THE HOLOCENE

Further south in Ecuador, the related sites of Surucuchu (3,180 m; Colinvaux *et al.*, 1997) and Pallacocha (4,200 m; Moy *et al.*, 2002) begin their sedimentary record at *c.* 15 kcal yr BP. These two sites lie in the same drainage basin and each has a markedly laminated stratigraphy. The laminations have been suggested to reflect El-Niño-related storm intensity (Rodbell *et al.*, 1999; Moy *et al.*, 2002). While these sites cannot inform us of climate change in the Pleistocene, they do suggest an affinity with the Colombian sites rather than sites of southern Peru and Bolivia that show a very marked dry event in the Mid Holocene (Wirmann *et al.*, 1992; Ybert, 1992; Paduano *et al.*, 2003; Rowe *et al.*, 2003). Again the southern and northern sites appear to be asynchronous in their precipitation signals, with all sites north of Junin exhibiting a dry start to the Holocene followed by rising lake levels between 10 kcal yr BP and 8 kcal yr BP. Sites in the southern tropical Andes are generally entering a dry phase at that time, and experience low lake levels until *c.* 4 kcal yr BP (Bradbury *et al.*, 2001). The only record from the southern tropical Andes that spans a portion of this event is Lake Siberia (Mourguiart and Ledru, 2003). This record terminates at *c.* 5.1 kcal yr BP, but the period from 10 kcal yr BP to 5 kcal yr BP shows the expansion of grassland, consistent with more open conditions, but the return of some forest taxa in the uppermost samples.

When records resume regionally, human impacts are evident in many sites (e.g.,

Marcacocha (Chepstow-Lusty *et al.*, 2002), Titicaca (Paduano *et al.*, 2003), Pacucha (Valencia *et al.*, 2010), and Junin (Hansen and Rodbell, 1995); the uplands were being transformed by burning and deforestation). The modern upper forest line may be a result of millennia of manipulation. How different a truly natural upper forest line would be from that observed in the modern Andes is a matter of ongoing debate. Ellenberg (1958) suggested that *Polylepis* could have formed extensive woodlands up to elevations of 4,000 m on the wetter slopes and 5,000 m on the drier slopes of the Andes. Though falling from favor for many years, his ideas have been resurrected (e.g., Fjelds , 1992; Kessler, 1995). No resolution has been reached regarding either the natural elevation of upper forest lines, or the past importance of *Polylepis* in Andean floras. Gosling *et al.* (2009) suggested that *Polylepis* was most abundant as a member of transitional communities between full glacial and interglacial conditions. Other evidence of the migration of upper forest lines has been largely equivocal with modest or no migration reported in the last few thousand years in Colombia and Ecuador (Wille *et al.*, 2002; Bakker *et al.*, 2008; Di Pasquale *et al.*, 2008). Two patterns have emerged: the first is that the often stark separation of forest and grasslands is an artifact of millennia of human landuse (Young and Le n, 2006). The second observation is that human impacts on the Andes have been taking place for thousands of years, and that the “natural” state or ecological baseline is often unknown.

While humans altered the highland landscape, it is also probable that climate influenced human populations. The Mid Holocene drought on the Altiplano induced a period termed the “Silencio Arqueol gico” in which there was widespread abandonment (N n ez *et al.*, 2002). Where did these populations go? Into the montane forest? The Lake Siberia record shows an increase in charcoal coincident with the peak of this drought (Mourguiart and Ledru, 2003). Whether these fires resulted from human occupation of a moister site than could be found in the highlands, or whether this area was merely more drought prone has yet to be resolved. Later droughts are implicated in the cultural collapse of civilizations such as the Huari, Tiwanaku, and Chirip  (Brenner *et al.*, 2001; Chepstow-Lusty *et al.*, 2002). Too few records exist to document the effect of these Late Holocene droughts on montane forests and these are data that are badly needed.

2.9 THE PAST AS A KEY TO THE FUTURE

The potential for previous interglacials to serve as a guide to the climatic future of the Holocene has attracted considerable attention (e.g., Ruddiman, 2003; Broecker, 2006). That the full biodiversity of the Andean system appears to have survived the intensity of MIS 5e offers some hope that systems will be able to adjust to the next 50–100 years of projected climate change. Most of the climate simulations project the Amazon Basin to become warmer and drier over the next century, and for a warming of tropical mountains to be about 2–3 C (IPCC, 2007). Estimates of species migrational responses to such climate change suggest that the tropical Andes will be one of the most sensitive regions to biome-level change; that is, the Andes have a high

proportion of pixels representing the region that changes from one biome type to another (Malcolm *et al.*, 2006).

Melting tropical icecaps (Thompson *et al.*, 2002) and the upslope migration of species (Pounds *et al.*, 1999) represent evidence that these changes are already taking effect. The stress of warming, may induce complex interactions (e.g., between droughts, chytrid fungus, and frogs), that may lead to extinctions (Pounds, 2001; Pounds *et al.*, 2006).

The rate of response of communities to climate change has been tested in temperate northern latitudes by rapid warming events such as the termination of the Younger Dryas. That warming was similar in its rate of change to the anticipated warming of the next century. If the tropics were similarly exposed to rapid warming, and there was no corresponding wave of extinction, we might be able to predict a sturdy migrational response that would accommodate climate change. However, such a clear, sharp warming is evident in montane Colombia, but lacking in lowland Peru.

The flat spot in the ^{14}C record that provides relatively large possible calibration solutions between *c.* 10,000 and 11,000 ^{14}C years often frustrates efforts to provide a definitive chronology. From the available records, it appears that there was no rapid warming at the onset of the Holocene in much of Amazonia and the tropical Andes. Species in the biodiversity hotspots of the Peruvian Andes have not contended with change faster than *c.* 1°C of warming per millennium (Bush *et al.*, 2004) and therefore while the range of temperatures projected for the next 50–100 years may be within their Quaternary experience, the rate of climate change probably is not.

2.10 CONCLUSIONS

Paleoecological research in the Andes has provided some exciting insights into the both long-term migrations of species and also responses to rapid climatic oscillations. In Europe and North America the accumulation of thousands of pollen records allowed Holocene migrations to be mapped in great detail. From those studies emerged the understanding that temperate communities are ephemeral, perhaps the most important ecological insight to arise from Quaternary paleoecology. However, simply applying the rules of temperate ecology to the tropics has been shown repeatedly to be unwise. The Andes offer a very different migratory environment to the great plains of Europe and eastern North America. The Amazonian lowlands are often separated from Andean snows by <30 km. The complex topography of Andean valleys, ridges, and streambeds offer a mass of microhabitats that can range from xeric scrub to lush forest in a few tens of meters. The consequence of this heterogeneity is that migration could have been nearly instantaneous rather than lagging by thousands of years. Under these circumstances continuity of habitat availability, rather than ability to migrate in and out of refugia, may be the key to diversity.

Paleoecological records from the Andes show a remarkable continuity of montane forest availability for species. Although the area with ground level cloud moved up and down a mountain, it appears probable that this niche has been a

continuous feature of the environment since the Andean orogeny created uplands high enough to induce cloud formation. Where it can be measured, rates of community change are low for tens of millennia, though communities are changing throughout that time. Novel assemblages arose due to continental-scale, as well as local, migrations, but the overall niche of living within a montane forest may have changed less than its cloud-free counterparts up and downslope.

Regional asynchrony is a feature of the paleoclimatic literature with Lake Junin, Peru (11°S) cited as the southernmost record that had a full glacial precipitational pattern common to sites south of Mexico (Bradbury *et al.*, 2001; further south tropical systems were somewhat out of phase with this northern group of sites). However, Seltzer *et al.*, (2000) argue that moisture change between Lake Junin and sites in the Caribbean were asymmetric in the Holocene. This latter argument is based on the apparent fit of moisture availability and regional wet season insolation. These apparently contradictory assessments can be reconciled by recognizing the temporal migration of the Inter Tropical Convergence Zone (ITCZ) (southward in stadial events and northward in the early Holocene (e.g., Haug *et al.*, 2001)), producing a climatic equator that is not geographically constant. The important points that can be derived from the paleoecological data are that precipitation and temperature patterns varied substantially with latitude along the tropical Andes, and that regions exhibiting synchronous changes in one period could be asynchronous in another.

The paleoecological record needs to be incorporated into conservation thinking to devise appropriate strategies to avert an imminent loss of biodiversity. However, for paleoecology to become genuinely integrated with conservation science we will need to provide more detailed records, especially increasing our taxonomic precision. Furthermore, new paleoecological records from the montane forest region are desperately needed to expand our spatial dataset and test the many emerging theories relating to this fascinating ecosystem.

2.11 ACKNOWLEDGMENTS

This work was funded by National Science Foundation grants ATM 9906107 and 0317539. Two anonymous reviewers are thanked for their help and comments.

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<http://www.springer.com/978-3-642-05382-5>

Tropical Rainforest Responses to Climatic Change

(Eds.) M. Bush; J. Flenley, W. Gosling

2011, XXXIV, 454 p. 100 illus., 9 in color., Hardcover

ISBN: 978-3-642-05382-5