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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) allow 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 about 1,300 m up to about 3,300 km 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. Some caution is needed in grouping all montane forests together and assuming that they will respond similarly to a common forcing as species composition of montane forests varies 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), and there is uncertainty over the elevation of the 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 but instability of communities through time, and whether there is an out-of-phase climatic influence on southern and northern Andean sites during the last glacial maximum (LGM).

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 in which successive waves of taxa moved north and south and then underwent adaptive radiation began as early as 16 million years ago and reached its peak (Webb, 1997) following the closure of the Isthmus of Panama, a progressive process in which the final phase took place between 5 and 4 million years ago.

The arrival of such animals as monkeys, sloths, elephantids, camelids, rats, and cats left a lasting impression on these systems. Many 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 Glyptodont, 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 are derived from Laurasian immigrants (Terborgh, 1992).

This pattern obeys the basic biogeographic rule that the flora of larger source areas will outcompete those of smaller source areas. 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.

Many modern genera were extant and clearly recognizable in the pollen of Miocene sediments (23 to 6 million years 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 million years ago (Hoorn *et al.*, 1995). Thus, these were forest-shrouded systems. Additionally, 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 the Andes rise above elevations supporting diverse montane forests (i.e., above 3,300–3,500 m).

Montane-dwelling migrants into this setting from North America had to island-hop—either literally, or from hilltop to hilltop—including passage across a broad lowland plain in central Panama. This gap without highlands over 1,000 m was at least 130 km and may have acted as a severe filter to large seeded species, such as *Quercus*. Indeed, *Quercus* diversity in western Panama is about 13 species, whereas only one species is present in eastern Panama (Gentry, 1985).

The southward migrations of Laurasian taxa such as Annonaceae, *Hedyosmum*,

Salix and *Rumex* are inferred rather than observed, but the arrival of *Myrica*, *Alnus*, and *Quercus* are apparent in the paleoecological records from the high plain of Bogotá (Hooghiemstra, 1984, 1989; Van der Hammen, 1985; Van der Hammen *et al.*, 1992; Van 't Veer and Hooghiemstra, 2000). *Myrica* arrived in the Middle Pliocene, *Alnus* first occurs in the Colombian pollen record about 1 million years ago. *Quercus* first occurs about 478 kyr BP (Van 't Veer and Hooghiemstra, 2000) but probably only attained its modern dominance between 1,000 m and 2,500 m elevation about 200 kyr BP (Hooghiemstra *et al.*, 2002). Since the first arrival of these species *Alnus* has spread as far south as Chile, whereas the southernmost distribution of *Quercus* coincides with the Colombian–Ecuadorian border (Gentry 1993). *Alnus*, a pioneer species, thrives in disturbed settings, whereas *Quercus humboldtii* is a dominant of mature Andean forests. The arrival of *Quercus* in Colombia clearly impacted previously established taxa such as *Hedyosmum*, *Vallea*, and *Weinmannia* (Hooghiemstra, 1984)—species that are still the common components of upper Andean forest in Peru and Ecuador.

   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 as low as 1,900 m during peak glacial conditions. The consequent expansion of montane grasslands, through a combination of uplift and cooling, provided habitat for newly arriving holarctic species that enriched Puna and Paramo floras.

   The new arrivals to forest and grassland settings created novel communities. The concept of no-analog communities is usually used in reference to suggest that communities of the past differed from those of the present (e.g., Overpeck *et al.*, 1985), but ecologically a no-analog community is most significant if it is the formation of a novel community compared with those that preceded it. The sequential arrival of *Myrica*, *Alnus*, and *Quercus* 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). While many of the megaherbivores died out in the terminal Pleistocene, the surviving camelids 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 had a substantial impact on the openness of all Neotropical settings (Janzen and Martin, 1982). Thus, during the Quaternary there has been a major re-shuffling of community composition, both in plants and animals, that resulted from plate tectonics. Glacial activity added additional layers of migrational change.

2.3   SENSITIVITY AND QUANTIFYING COOLING

Modern pollen studies are the backbone of any attempt to quantify past forest changes. Over the past 20 years a series of studies in Colombia (Grabandt, 1985), Ecuador (Bush, 1991), and Peru (Weng *et al.*, 2004), have provided considerable data against which past migrations can be calibrated. The most recent of these included a blind study to test the sensitivity of pollen as a tool to predict modern forest community. Moss polsters (collected from a 20 m^2 area of forest) at 50–100 m vertical
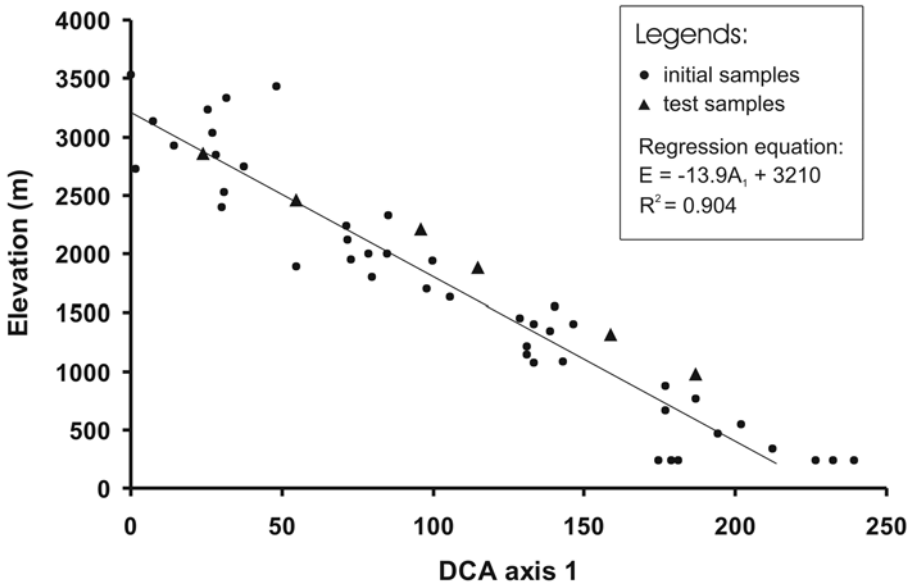
Figure 2.1. Modern pollen rain and elevation. Regression of first axis DCA scores against elevation for log-transformed modern pollen data. All data from a line transect from Amazonia into the Andes in eastern Peru (Weng *et al.*, 2004). *Circles* represent samples of known elevation. The six *triangles* represent a blind study in which the analyst did not know sample elevation.

increments were collected along a transect in the Kosñipata Valley, Peru. The elevational range of the samples was from 300 m to 3,400 m. Despite high pollen diversity (more than 400 types identified) in these samples, >90% of pollen was identified to family level and 30–50% to genus level (Weng *et al.*, 2004). Log-transformed pollen data were analyzed with detrended correspondence analysis (Hill, 1979; McCune and Mefford, 1999) and the resulting Axis 1 scores regressed against elevation (Figure 2.1). In 2001 we collected six further samples and conducted a blind study. The six unlabelled samples were given to the analyst (Weng) to determine the accuracy with which they could be placed into the data set (Figure 2.1). From these results we determined that our accuracy in assigning an elevation to an unknown sample is about ±260 m. Local moist air adiabatic lapse rates are almost exactly 5.5°C per 1,000 m of ascent (Weng *et al.*, 2004). From this we infer that our error in assessing temperature based on palynology is c. ±1.5°C. The Kosñipata transect was 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.

It will be noted that the samples in Figure 2.1 from 3,350 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.

2.4   SITES IN SPACE AND TIME

Sites 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 have survived.

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
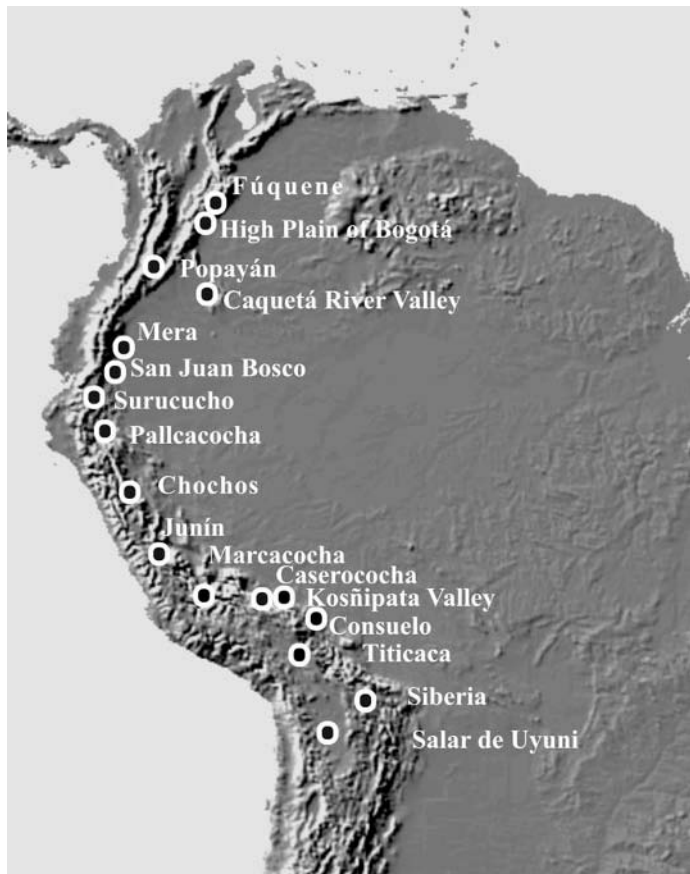

Figure 2.2.   The location of sites of paleoecological importance mentioned in the text relative to topography.

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 of its present location. 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. In the southern Andes at the peaks of these interglacial events, conditions appear to be drier-than-modern, consistent with an upslope movement of the cloudbase. 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).

Van der Hammen and González (1960) documented a 1,500 m descent of vegetation 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 indicates at least a 1,000-m descent of vegetation and often a 1,500-m descent of some pollen taxa at the LGM. The moist air adiabatic lapse rate (Chapter 10)—evident on the Andean flank—provides 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. 5.2°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 modern of 5–8.5°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. 4–5°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 Streten, 1978; Rind and Peteet, 1985). Evidence from studies of glacial moraines leads 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 4–5°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.

2.5 QUATERNARY INTERGLACIALS

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 by their marine isotope stages (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). They generally last about 15–40 kyr. While a 100-kyr 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 exist that provide 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). The amount of ecological change in three fossil pollen records that cover either or both of MIS 1 and MIS 5e from Lake Titicaca reveals that—true to the precessional prediction—MIS 5e is the most extreme of these interglacials (Figure 2.3). 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 kcal . yr BP is taken as the start of the Holocene.
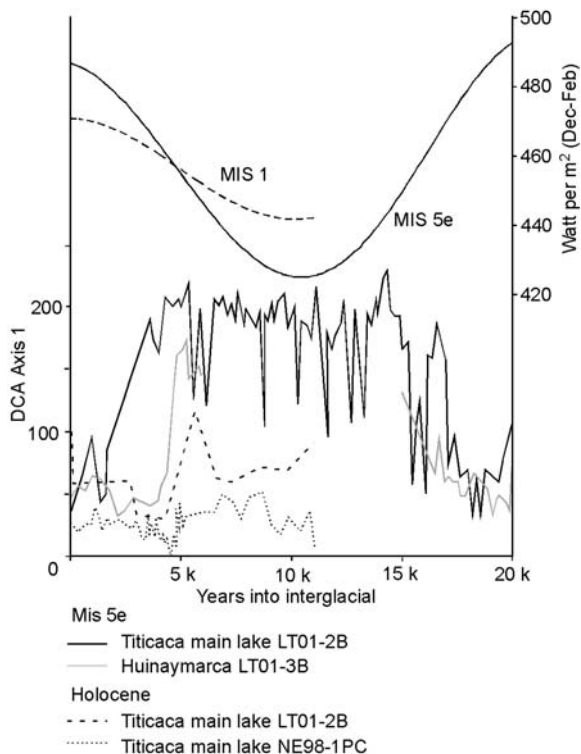

Figure 2.3. A comparison of MIS 5e and the Holocene based on insolation and changes in community composition revealed through DCA. Data are from Hanselman *et al.* (2005) and insolation curves from Analyseries 1.2 (Berger, 1992; Paillard *et al.*, 1996)}.

The data are 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 Huinaymarka sub-basin (Core LT01-3B), and a piston core from 130-m water depth that provides a detailed Holocene record from the main basin (core NE98-1PC; Paduano *et al.*, 2003). The fossil pollen data were combined into a single matrix and ordinated using detrended correspondence analysis (DCA) (Hill, 1979; McCune and Mefford, 1999). The scores for Axis 1 are plotted against time since the start of the relevant interglacial, and therefore provide a comparative trajectory of the amount of ecological change that took place. Core LT01-3B has a hiatus in the middle of the interglacial, but shows a very similar pattern of community change leading into and out of the event as found in the deep water core LT01-2B. That hiatus is entirely consistent with our hypothesis of increased evaporation and reduced precipitation compared with that of the Holocene that marked the peak of MIS 5e.

During 5e, and to a slightly lesser extent in previous interglacials, warming caused the upper Andean forest limit to move about 200 m above its modern elevation. Both the Colombian and Bolivian records indicate that the peak of MIS 5e may have been relatively dry. This drying is especially evident in Lake Titicaca, where the abundance of benthic and saline-tolerant diatoms, and peak abundances of pollen of Chenopodiaceae/Amaranthaceae suggest the lowest lake levels of the last 340,000 years. Chenopodiaceae/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). Parsing out the effects of warming versus reduction in precipitation is not easy, as both would lower lake level. In Colombia the estimate of warming based on migration of tree line appears to have been about 1°C (Van der Hammen and Hooghiemstra, 2003), and this is consistent with the tentative estimate of 1–2°C for Titicaca (Hanselman *et al.*, 2005).

2.6   THE LAST GLACIAL PERIOD

If the pattern of temperature change is traced from the last interglacial to the present, there was a substantial rapid cooling—perhaps 3°C—at the end of the last interglacial that marked the onset of glacial conditions in the Andes (Van 't Veer and Hooghiemstra, 2000). Following this cooling, temperatures bumped up and down, tracking the Milankovitch cycles, but gradually declining 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 and 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 30,000 cal yr BP when the lake dried out. The Fúquene-3 record suggests a progressive lowering of lake level beginning around 60,000 years ago and culminating in a depositional hiatus between

Table 2.1. Inferred LGM moisture from described sites in the northern and southern Andes.

Latitude (°S, unless otherwise stated)	Elevation	LGM (wet/dry)	Onset of deglaciation	Timing of mid-Holocene dry event	Literature source
5°N	2,580	Dry	c. 25,000	—	van der Hammen and Hooghiemstra (2003)
4–5°N	2,600	Dry	c. 24,000	—	Hooghiemstra (1984)
2°N	1,750	Dry	c. 24,000	—	Wille et al. (2000)
1	c. 400	Dry	—	—	van der Hammen et al. (1992)
2	4,060	—	—	7,500–4,000	Hansen et al. (2003)
3	3,180	Wet*	—	—	Colinvaux et al. (1997)
7	3,300	—	c. 15,000	9,000–3,800	Bush et al. (this volume)
7	3,575	—	—	c. 6,000	Hansen and Rodbell (1995)
9	6,048	Dry*	—	8,400–5,200	Thompson et al. (1995)
11	4,100	—	—	c. 6,000	Hansen et al. (1994)
11	4,100	Wet	c. 22,000	—	Seltzer et al. (2002)
13	1,360	Wet	c. 21,000	8,200–4,000	Bush et al. (2004)
16	2,350–2,750	—	—	Wet mid-Holocene	Holmgren et al. (2001)
16–17	3,810	Wet	c. 21,000	6,000–4,000	Paduano et al. (2003)
16–17	3,810	Wet	c, 21,000	8,000–5,500	Baker et al. (2001)
16–17	3,810	Wet	c. 22,000	—	Seltzer et al. (2002)
16–17	3,810	Wet	—	6,000–3,500	Tapia et al. (2003)
16	4,300	—	—	8,500–2,500	Abbott et al. (2000, 2003)
17	c. 3,800	Wet*	—	—	Mourguiart et al. (1997, 1998)
17	2,920	Wet*	c. 21,000	11,000–4,000	Mourguiart and Ledru (2003)
18	6,542	Wet	c. 21,000	9,000–3,000	Thompson et al. (1998)
20	3,653	Wet	—	—	Chepstow-Lusty (2005), Fritz et al. (2004)
20	3,653	Wet	—	—	Baker et al. (2001)

* As interpreted by the authors of this chapter.

c. 22 kcal . yr BP and 12 kcal . yr BP (Van der Hammen and Hooghiemstra, 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 was 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; Placzek *et al.*, 2006). A paleolake 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. Some recent evidence suggests even greater complexity in this sequence of high and low stands suggesting strong swings in precipitation and lake level between 26 and 16 kcal . yr BP (Placzek *et al.*, 2006). The combination of extreme cold and wet conditions during the LGM 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) suggest 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–January–February), and lowstands during the corresponding minima.

Thus, the period centered on 22 kcal . yr BP was wet and the period centered on 33 kcal . yr BP was dry. Indeed, during the 33 kcal . yr BP dry event, lake level in Titicaca dropped by as much as 130 m, certainly the lowest lake levels of the last glacial cycle. This dry event is also documented in the northern Amazon lowlands, though not in southeastern Amazonia (Chapter 3). In Colombia, the Fuquene-2 and Fuquene-7 pollen records (Van Geel and Van der Hammen, 1973; Mommersteeg, 1998) demonstrate that this period was exceptionally wet, providing another good example of antiphasing between the Altiplano and the northern Andes.

While the evidence of precessional oscillations has 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 flooded 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.

The critical question in a discussion of montane forest is: Can these upslope systems provide proxy data about what was happening to the montane forests? The answer to that appears to be a qualified "yes".

In Colombia the Caquetá River valley (Van der Hammen *et al.*, 1992) documents a relatively wet time between c. 50 kyr BP and 30 kyr 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 in southern Peru provides the most detailed view yet of the lower Andes during the last glacial maximum. At 1,360 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—for example, *Alchornea*, *Brosimum*, *Euterpe*, *Ficus*, *Guatteria*, *Maquira*, *Unionopsis*, and *Wettinia*. Premontane elements such as *Dictyocaryum*, *Myrsine*, *Alsophila*, and *Cyathea* are also present (M. Silman, pers. commun.). 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.

   Range data for 24 abundant taxa that could be identified to genus in the pollen record were collected from the TROPICOS database (Bush *et al.*, 2004). A Bayesian analysis of these data in combination with the fossil pollen data generated a probability distribution for the most likely elevation at which the combination of species in a fossil spectrum could occur. Note this analysis does not rely on community structure, as it is based on total documented ranges of species, not on co-occurrence. The outcome of this analysis—the first complete deglacial sequence from the premontane forest region of the southern tropical Andes—revealed a remarkably stable system during MIS 2 and 3 (c. 43–20 kcal.yr BP). These data are particularly interesting as two upslope sites—Siberia (Mourguiart and Ledru, 2003) and the Altiplano (Baker *et al.*, 2001)—both reveal the period prior to the LGM, centered on 33,000 cal yr BP to be dry. Apparently the moisture flow into the montane forests at the base of the Andes was not interrupted, demonstrating continuity of habitat availability for these systems, through one of the driest times of the last glacial cycle.

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 GISP record from Greenland (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 Central Andean records (Figure 2.4).

   The deglaciational path had some bumps in it, though most of the apparent hiccups were probably abrupt changes in precipitation rather than deviations from a steady change in temperature (Bush *et al.*, 2004). A dry event at c. 16.5 kcal.yr BP is recorded strongly in Lake Titicaca, and was followed by a cool, wet event that centers on c. 15.1 kcal.yr BP. This latter event is consistently manifested in Central Andean records, though it is more evident in the records between c. 11°S and 7°S rather than those at higher latitudes.

   Thereafter, the trend out of the last ice age is relatively constant in the southern tropical Andes, whereas the northern Andes appears to reflect the Caribbean and northern hemispheric episodes of abrupt warming and cooling. Consequently, in Peru
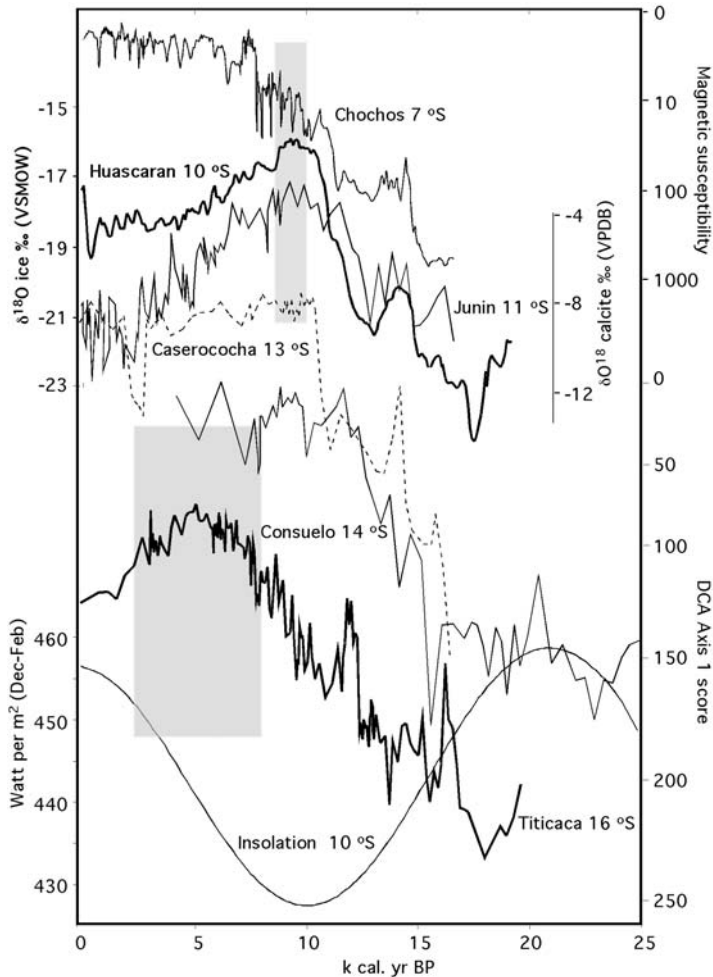
Figure 2.4. Central Andean insolation, and the extent of physical and community change during deglaciation and the Holocene. Datasets are Lake Chochos magnetic susceptibility (note inverted log scale; Bush *et al.*, 2005); Huascaran δ^{18}O ice core (Thompson *et al.*, 1995); Lake Junin δ^{18}O calcite (Seltzer *et al.*, 2000); Lake Caserococha fossil pollen DCA Axis 1 (Paduano, 2001); Lake Consuelo fossil pollen DCA Axis 1 (Bush *et al.*, 2004 and new data from D. Urrego); Lake Titicaca fossil pollen DCA Axis 1 (Paduano *et al.*, 2003); insolation (DJF) for 10°S from Analyseries 1.2 (Berger, 1992; Paillard *et al.*, 1996). VSMOW = Vienna standard marine ocean water; VPDB = Vienna peedee belemnite.

and Bolivia the deglaciational 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 a 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.

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). Some records reveal an oscillation that fits well with the chronology of the North Atlantic event (e.g., Van 't Veer *et al.*, 2000); however, other records—such as that of Titicaca and glacial advances in Ecuador and Peru—reveal an oscillation that pre-dates 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. Furthermore, in most settings if a change is contemporaneous with that of the North Atlantic it is manifested in precipitation change rather than in temperature shifts resulting in some glacial re-advance or retreat (Clapperton, 1993; Rodbell and Seltzer, 2000; Smith *et al.*, 2005).

2.8 THE HOLOCENE

Farther south—in Ecuador—the related sites of Sacurococha (3,180 m: Colinvaux *et al.*, 1997) and Pallcacocha (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 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, which show a very marked dry event in the mid-Holocene (Wirrmann *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—for example, Marcacocha (Chepstow-Lusty *et al.*, 2002), Titicaca (Paduano *et al.*, 2003), and Junin (Hansen and Rodbell, 1995); the uplands were being transformed by burning and deforestation. The modern upper forest line may be a baseline that was created at this time. How different a truly natural upper forest line would be is a matter of ongoing debate. Almost 50 years ago Ellenberg (1958) suggested that *Polylepis* woodland could have been extensive 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., Fjeldså, 1992; Kessler, 1995; Wille *et al.*, 2002). No resolution has been reached regarding either the natural

elevation of upper forest lines, or the past importance of *Polylepis* in Andean floras, but it certainly seems likely that the often stark separation of forest and grasslands is an artifact of millennia of human landuse.

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 Arqueológico'' in which there was widespread abandonment (Núñez *et al.*, 2002). Where did these populations go? Into the montane forest? Perhaps. 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 Chiripó (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 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, 2001). 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 change from one biome type to another (Malcolm *et al.*, 2006).

Melting tropical ice caps (Thompson *et al.*, 2002) and the upslope migration of species (Pounds *et al.*, 1999) are evidence that these changes are already taking effect. The stress of warming may induce complex interactions—for example, between droughts, chytrid fungae, 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 particular 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 seldom evident in tropical records.

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 hot spots 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 <50 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 lagged 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); farther 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 are not necessarily inconsistent as we have yet to discover the proximate causes of glacial age precipitation change in the Andes. 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 in 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 data set and test the many emerging theories relating to this fascinating ecosystem.

Acknowledgements

2.11 REFERENCES

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