

Chapter 12

Millennial-Scale Ecological Changes in Tropical South America Since the Last Glacial Maximum

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Abstract An analysis of rates of ecological change (RoC) from thirteen pollen records from tropical South America is presented here. The analysis aims to identify the periods of fastest change since the last glacial maximum (LGM) and possible driving mechanisms. Despite rapid cooling periods, region-wide profound droughts, fire and human disturbances, RoC analysis showed that the speed of these climate changes never exceed the species response capabilities. Our results legitimize concerns regarding the resilience of species to accommodate future change and emphasize the urgency for integrative environmental measures.

Keywords Rates of ecological change · Climate change · Eastern Andes · Western Amazonia

12.1 Introduction

Human modifications of the landscape coupled with the indirect effects of human-induced pollution resulting in climate change pose synergistic threats to wildlife. While tropical ecosystems have been forced to accommodate prior environmental change (Colinvaux and De Oliveira 2000, Bush et al. 2004b, Mayle et al. 2004, Jansen et al. 2007), it is possible that modern rates of change are so rapid, and ensuing community disruption so severe, that we are poised on the brink of a major extinction event (Brooks et al. 2002, Thomas et al. 2004). While tropical ecosystems are known to be influenced by current climate change (Pounds 2001, Pounds et al. 2006), there are few data regarding tropical past rates of ecological changes and how they compare with modern ones. Under current and projected future climatic conditions, improbably fast migration rates will be required for species to track their fundamental niches (Malcolm et al. 2006). This scenario is further complicated by

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human-induced changes of landscapes such as land use, reduced habitat availability, and barriers to dispersal.

Assessments of rates of ecological changes in Europe and North America showed that temperature and atmospheric CO₂ fluctuations account for the greatest rates of post-LGM (last glacial maximum) ecological change (Jacobsen et al. 1987, Huntley 1990, Williams et al. 2001, Shuman et al. 2005). In temperate systems the rates of ecological change were probably slower than those of climatic fluctuations induced by the meltwater pulse at c. 14 ka, the Younger Dryas (12.5–11 ka), and the 8.2 ka cooling event (all ages are expressed in thousand of calibrated years BP and abbreviated as ka). Consequently, species may have existed in non-equilibrium assemblages, giving rise to the peak occurrence of no-analog communities (e.g. Williams et al. 2004). Orlóci et al. (2006) detected a strong correlation between species compositional change and the Vostok temperature record in several sites worldwide, including two records from eastern South America. Studies from gallery forest and savanna systems in southeastern Amazonia reveal what appears to be an accelerating rate of ecological change within the last 4000 years (Behling et al. 2005, Behling et al. 2007). These increases were correlated with the intensification of human occupation and human-induced fires in the region. However, an integrative regional analysis for western Amazonia, the area with the highest biodiversity, is lacking.

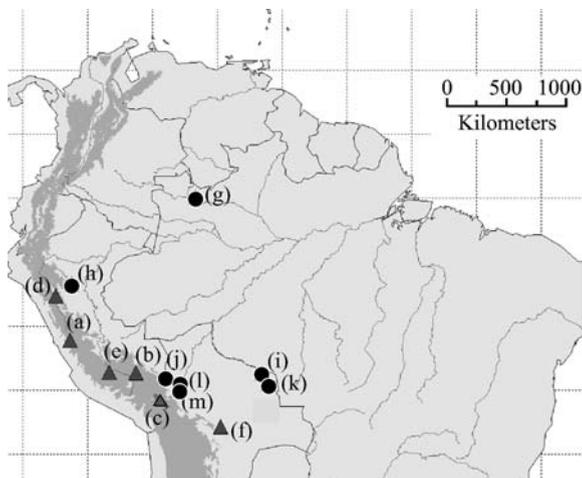
The extent of Holocene ecological variability in tropical South America was traditionally considered small relative to Quaternary glacial and interglacial fluctuations. This idea of relative Holocene stability was founded mostly on high-latitude evidence of stable temperatures since c. 10 ka (Alley 2004). Recent tropical evidence suggested that Holocene environmental change was greater than traditionally thought and that it correlated with abrupt changes in precipitation and increased human occupation (Mayle et al. 2000, De Freitas et al. 2001, Burbridge et al. 2004, Bush et al. 2004b, Mayle and Power 2008). From these observations, Holocene rates of environmental change were hypothesized to be greater than those of the Late Pleistocene.

The purpose of this chapter is to review post-LGM rates of ecological change from western Amazonian and eastern Andean records. We aim to identify periods when the fastest environmental changes took place, and discern whether patterns of change are the same in lowland and high-elevation systems. An analysis of the possible driving mechanisms behind fast rates of change is also presented. In particular, we consider the effects of post-LGM rising temperatures, the role of abrupt cooling events like the Younger Dryas (YD) and the 8.2 ka events, the influence of mid-Holocene dry episodes, and the importance of fire and human occupation as modifying aspects of the landscape.

12.2 Rate-of-Change Analysis

Paleoecological records offer an invaluable opportunity to answer questions regarding the speed of past ecological changes and to improve our understanding of past climate and human-induced variability in western Amazonia and the eastern

Fig. 12.1 Geographic location of sites used for the rates of change (RoC) analysis: Anden records (*dots, a–f*) and western Amazonian records (*triangles, g–m*). (*a*) Junin; (*b*) Caserococha; (*c*) Titicaca; (*d*) Chochos; (*e*) Pacucha; (*f*) Siberia; (*g*) Pata; (*h*) Sauce; (*i*) Bella Vista; (*j*) Consuelo; (*k*) Chaplin; (*l*) Chalalan; (*m*) Santa Rosa



Andes (Orlóci et al. 2002). The rates of change (RoC) are defined here as the amount of ecological change per time unit, determined from pollen records. It is comparable with velocity of change previously calculated by Orlóci et al. (2002). Fossil pollen extracted from lacustrine sediments reflects the community composition around the lake and allows statistical comparisons to be made within and between records (e.g. Birks and Birks 1980). In these analyses, plant compositional changes were derived from fossil pollen analyzed at discrete points in time, herein called time slices. We calculated RoC as the dissimilarity between pollen assemblages from two adjacent time slices divided by the time interval between them. Records were used where the chronology was sufficiently robust to allow plausible linear interpolations between dates and where sample intervals were relatively brief (Figs. 12.1 and 12.2). The underlying assumptions of such analyses were that sedimentation was continuous between time slices and that ecological change was continuous between samples. The RoC analysis was only attempted for core sections meeting these basic requirements. Age models constructed by original authors were used when provided. In records where only radiocarbon dates were available, age models were calculated based on calibrated ages using Calib 5.0.2 (Stuiver and Reimer 1993, Stuiver and Reimer 2005) with linear interpolation between dates.

The dissimilarity between time slices was calculated as the Euclidean distance among scores on the first three axes derived from ordination analyses (Hill and Gauch 1980). This dissimilarity measure represented the geometric (Pythagorean) distance between two samples in the ordination space and corresponded to the change in the forest composition during a given time interval. The units of these dissimilarity measures were fractions of each dataset's total variability, which facilitates relative comparisons among time slices within the same record. However, it should be noted that comparisons among records were done based on the trend of RoC, as comparisons of the absolute magnitudes are meaningless. The DCA was

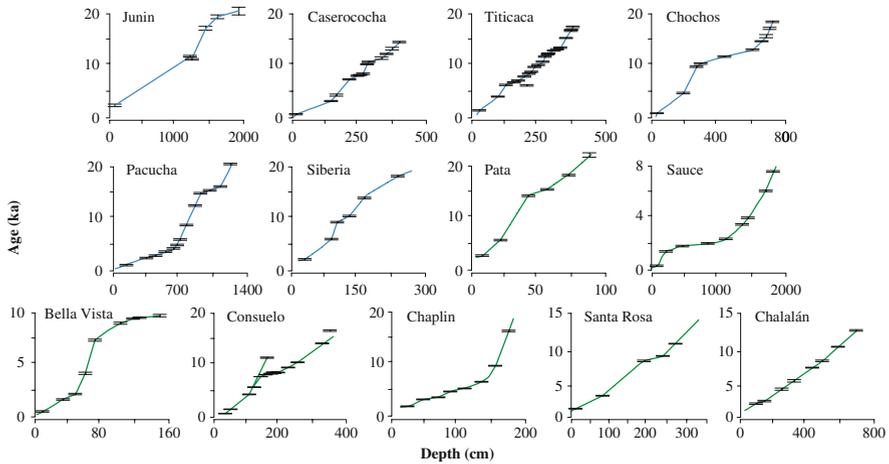


Fig. 12.2 Age-depth curves and age error for thirteen paleoecological records used in the RoC analysis (see Table 12.1 for source and site description)

performed on reduced pollen percentage matrices for thirteen paleoecological sites from western Amazonia and the eastern Andes (Table 12.1 and Fig. 12.1). For all ordinations, iterations were run until a stable solution was reached. The reduced pollen percentage matrices resulted from applying an abundance and persistence filter that preserves the main variability of pollen datasets, while eliminating the noise caused by rare taxa (after Birks and Birks 1980). This filter retained terrestrial taxa with at least 1% (abundance) and occurring in at least 5 time slices per record (persistence). Spores and shoreline elements were excluded to avoid masking terrestrial-vegetation changes. The decision for non-woody taxa such as Cyperaceae was based on their role in the specific modern ecosystems of each site. Cyperaceae were included in the analysis for sites where they were known to be important components of the terrestrial vegetation (e.g. Titicaca, Chaplin and Bella Vista) but excluded for sites where they mostly represent shoreline vegetation (e.g. Consuelo, Pata, Chalaalán).

12.3 Paleoecological Records

The RoC analysis is based on thirteen pollen records from western Amazonia and the eastern Andes spanning at least the last 18 ka (Fig. 12.2 and Table 12.1). Andean sites lie on the eastern slopes of the Andes and parts of the Altiplano ranging from 2900 to 4100 m elevation (Table 12.1). Lowland sites include pollen records between the Equator (Lake Pata in Northwestern Brazil) and 14°S (Lakes Chaplin and Bella Vista in eastern Bolivia) and from 100 m elevation to the modern lower limit of permanent cloud cover (Lake Consuelo 1360 m.a.s.l.) (Table 12.1).

Table 12.1 Description of pollen records from western Amazonia and the eastern Andes used for the rates of change analysis (see Fig. 12.2 for geographic location)

Site*	Latitude	Longitude	Altitude (m.a.s.l.)	Wet-season precipitation (mm)†	Annual precipitation (mm/year)‡	No. of taxa included in analysis	Source
Junin ^a	11°05'S	76°22'W	4100	156	945	49	Hansen et al. 1984
Caserococha ^b	13°39'S	71°17'W	3980	142	726	20	Paduano 2001
Titicaca ^c	16°20'S	65°59'W	3810	190	1136	35	Paduano et al. 2003
Chochos ^d	7°38'S	77°28'W	3285	180	1176	46	Bush et al. 2005
Pacucha ^e	13°36'S	73°19'W	3050	168	911	42	Valencia 2006
Siberia ^f	17°50'S	64°43'W	2920	142	730	49	Mourguiart and Ledru 2003
Pata ^g	0°16'N	66°41'W	300	363	2893	22	Bush et al. 2004a
Sauce ^h	6°43'S	76°13'W	600	161	1419	153	Correa-Metrio 2006
Bella Vista ⁱ	13°37'S	61°33'W	170	276	1562	35	Mayle et al. 2000, Burbridge et al. 2004
Consuelo ^j	13°57'S	68°59'W	1360	362	2395	70	Bush et al. 2004b, Urrego 2006
Chaplin ^k	14°28'S	61°04'W	175	256	1445	26	Mayle et al. 2000, Burbridge et al. 2004
Chalalán ^l	14°25'S	67°55'W	330	278	1883	34	Urrego 2006
Santa Rosa ^m	14°28'S	67°52'W	350	279	1902	36	Urrego 2006

*Nomenclature as in Figs. 12.1 and 12.2; ^{a-f} high-elevation Andean records; ^{g-m} lowland western Amazonian records; † annual precipitation and precipitation wettest quarter from WorldClim dataset (Hijmans et al. 2005)

12.3.1 Andean vs Western Amazonian Changes

Our RoC analysis illustrated clear differences between the timing and intensity of ecological changes in lowland and high-elevation sites during the past 18 ka (Fig. 12.3). Fluctuations in RoC were mostly concentrated in the Holocene period in lowland records while montane sites showed conspicuous oscillations both during the Holocene and the Late Pleistocene. In Lake Junin, located at 4100 m elevation, peaks in RoC occurred between 13 and 11 ka (Fig. 12.3a). This period of rapid change coincided with the final ice retreat identified from moraine patterns in the lake's catchment (Hansen et al. 1984). Lake Caserococha showed the fastest RoC during the Pleistocene-Holocene transition between 13.1 and 8.5 ka (Fig. 12.3b). These fluctuations that began 12.9 ka and lasted until 8.5 ka, pre-date the Younger Dryas (YD) cooling event (12.5–11 ka), suggesting that this relatively short-cooling was not the mechanism behind them (Paduano 2001). Mid-Holocene lowstands were also reported for Lake Caserococha but were not detected as periods of increased changes in the terrestrial vegetation. Lake Titicaca showed relatively steady RoC during the Late Pleistocene (Fig. 12.3c). Although a series of pulses were revealed around the YD episode, these changes have been attributed to the onset of postglacial fires rather than cooling (Paduano et al. 2003). During the Holocene, however, two periods of increased change were observed. The first period dated between 8 and 6 ka, when several peaks in the RoC were associated with reduced-moisture episodes (Paduano et al. 2003, Theissen et al. in press). The second period of increased change took place in the Late-Holocene and corresponded to a shift toward weedy vegetation associated with human activities (Paduano et al. 2003). Timing of this change coincided with the onset of Quinoa cultivation in southern Peru (Chepstow-Lusty et al. 2003).

Laguna de Chochos (3285 m) showed marked oscillations during deglacial phases from c. 14.5 to 11 ka (Fig. 12.3d), while the highest RoC occurred during the early Holocene. Late-Pleistocene peaks coincided with a drought period that lowered lake level between c. 9 and 7.2 ka (Bush et al. 2005). During this period, a *Polylepis* forest dominated the landscape and fire frequency increased at Chochos. At c. 1 ka this record showed a marked increase in RoC, probably related to human occupation of the site (Bush et al. 2005). Human intervention was also inferred to account for the highest RoC in Lake Pacucha (3050 m) (Valencia 2006) between c. 6 and 3 ka (Fig. 12.3e). Increased abundance of *Ambrosia* and *Amaranthaceae-Chenopodiaceae* were attributed to the construction of agricultural terraces and Quinoa cultivation by pre-Colombian peoples (Chepstow-Lusty and Winfield 2000, Valencia 2006). Between 12 and 6 ka, two periods of reduced precipitation at Lake Pacucha were evidenced from the replacement of *Isöetes* and *Myriophyllum* by *Cyperaceae* in the shoreline vegetation (Valencia 2006), reduction of freshwater diatoms, and increased calcium carbonate in the sediments (Hillyer et al. 2009). However, the RoC based on terrestrial vegetation did not differ from that of the background (Fig. 12.3e) suggesting that the terrestrial vegetation response to drought was gradual and that the most significant moisture-balance change occurred as a result of a reduction in wet-season precipitation (Valencia

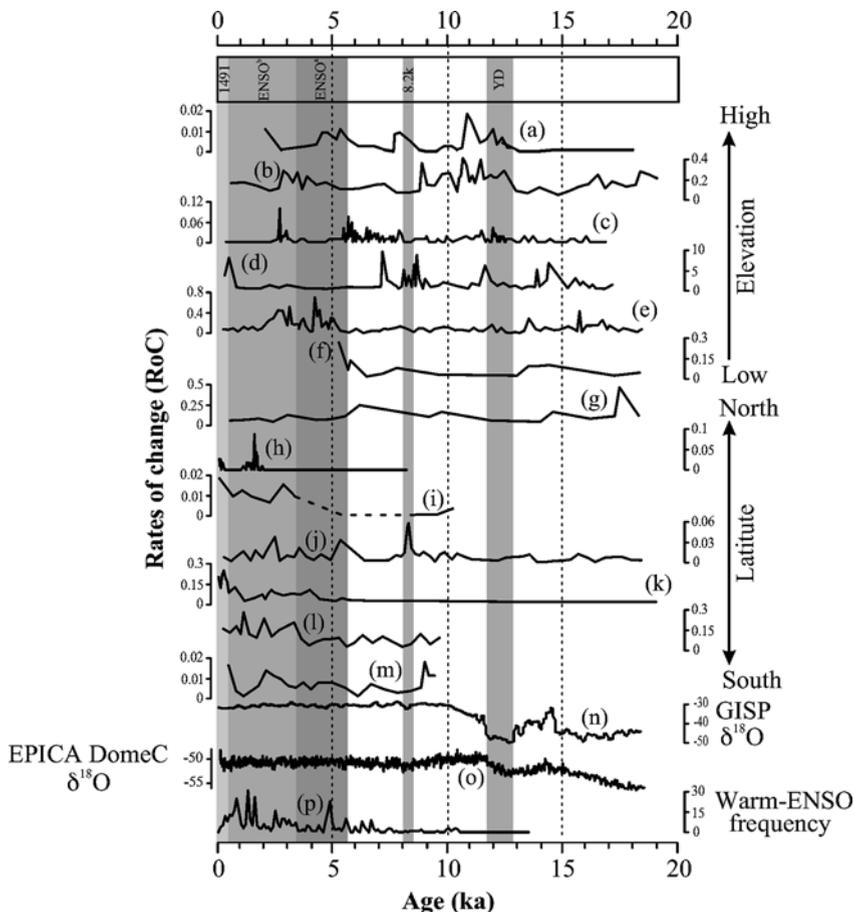


Fig. 12.3 Rates of change from several lacustrine pollen records over the past 18 ka (see Table 12.1 for source and site description). Eastern Andean records plotted on an elevational gradient (a–f); from high to low elevation: (a) Junin; (b) Caserococha; (c) Titicaca; (d) Chochos; (e) Pacucha; (f) Siberia. Western Amazonian records plotted on a latitudinal gradient (g–m), from North to South: (g) Pata; (h) Sauce; (i) Bella Vista; (j) Consuelo; (k) Chaplin; (l) Chalalán; (m) Santa Rosa. Other records plotted for comparison: temperature reconstruction based on stable isotope analysis, (n) from GISP (Alley 2004), (o) from EPICA Dome C (Monnin et al. 2001); (p) number of warm-ENSO events (Moy et al. 2002); YD: Younger Dryas (Broecker 1998); 8.2k: 8.2-ka cooling events (Alley et al. 1997); ENSO^a: period of modern-frequency warm-ENSO events (Sandweiss et al. 1996); ENSO^b: period of intensified warm-ENSO events (Sandweiss et al. 1996); 1491: onset of European colonization. RoC are based on detrended correspondence analyses performed on percentage pollen data and Euclidean distance among ordination axes. Note that RoC scales are relative to total variance within each dataset

2006). In the Lake Siberia record, trends of community change resemble those of lowland records, which may be related to sharing the same Amazonian moisture sources. Post-LGM changes in Siberia were minimal, with slightly increased RoC

between 18 and 16 ka (Fig. 12.3f). This increase was mostly driven by a down-slope migration of the puna-cloud forest limit, characterized by the colonization of *Polylepis-Acaena* (Mourguiart and Ledru 2003). No evidence of drought-caused increases of RoC was observed during the mid-Holocene in Siberia. However, a close examination of charcoal peaks in Siberia (Mourguiart and Ledru 2003, Fig. 12.1) showed a rough coincidence in timing with low lake-level stands in Pacucha (Valencia 2006, Hillyer et al. 2009), suggesting that increased fires may be related to reduced moisture availability in the region. Highest RoC between c. 7 and 5 ka coincided with increased fire frequency associated with the beginning of human activities (Mourguiart and Ledru 2003) or possibly with intensified ENSO activity as proposed by Haberle and Ledru (2001). Unfortunately, in the Siberia record the top 30 cm of the sediment column were lost during coring, hence no record was available for the past 5 ka.

Unlike Andean records which have highest RoC in the Late Pleistocene, records from lowland western Amazonia showed high RoC concentrated in the Holocene (Fig. 12.3 g–m). A few minutes North of the Equator, Lake Pata showed a large Pleistocene RoC peak, not observed in any of the other lowland records (Fig. 12.3 g). This prominent peak was centered around 18 ka and was probably associated with post-LGM temperature increase (Bush et al. 2004a). Following this period of substantial forest change, the Pata record showed another increase in RoC around 6 ka that coincided with increases of herbaceous understory elements suggesting a less dense forest canopy consistent with a reduction in precipitation (Mayle and Power 2008). RoC changes in the Pata record were derived from large time intervals (i.e. as much as 3000 years), hence its low sensitivity to short-lived events such the YD and 8.2 ka events.

Lake Sauce (6°S) provided a high-resolution Holocene record characterized by relatively constant RoC throughout the early and mid-Holocene (Fig. 12.3 h). These virtually constant RoC did not mean that the forest was unchanged, but rather that the speed of these changes was roughly constant. Analyses of El Niño Southern Oscillation (ENSO) activity suggested increased frequency after c. 5.5 ka (Fig. 12.3 p, Sandweiss et al. 2001) and strengthening of the oscillation in the last 1500 years (Fig. 12.3p, Moy et al. 2002). However, the existing records accounted for variability in the warm-phase, El Niño portions of the cycle. The multiproxy record of Lake Sauce showed a strong correlation with the frequency and intensity of both cold and warm ENSO phases in western Amazonia (Correa-Metrio 2007). From 1.8 to 1.1 ka, the high RoC in Sauce (Fig. 12.3 h) coincided with a period that apparently had c. 30 strong El Niño and La Niña events per century; the highest concentration in the last 6 ka (Correa-Metrio 2007). Enhanced ENSO activity in the mid-Holocene was hypothesized to have induced the most rapid changes in terrestrial vegetation in Sauce within the last 6 ka (Correa-Metrio 2007).

The RoC for Lake Bella Vista between 8.5 and 3 ka were plotted as a discontinuous line because we could not establish whether a marked reduction in sedimentation was associated with a sedimentary hiatus (Fig. 12.3i). High RoC are concentrated during the past 3 ka in Bella Vista and sustained until the present. Such large community changes in the Bolivian lowlands were attributed to a reduction in open savannas as forests expanded in response to a gradual increase in mean annual

precipitation (Mayle et al. 2000, Burbridge et al. 2004). The trend of forest expansion is evident in the Lake Chaplin data (Fig. 12.3 k), with the onset of high RoC at c. 3 ka and an intensification of community change around 1 ka. The greater sensitivity of Lake Chaplin, compared with Bella Vista, to Late-Holocene forest expansion may be explained by its proximity to the southern limit of Amazonian forest (i.e. 30 km as opposed to 120 km for Lake Bella Vista) (Mayle et al. 2000, Burbridge et al. 2004). In Lake Consuelo, RoC showed significant differences between the Pleistocene and Holocene periods (Fig. 12.3j). Variability in Pleistocene RoC was much less than that of the Holocene, despite an almost complete forest turnover between 20 and c. 12 ka (Bush et al. 2004b). Even with a 5.5°C Pleistocene cooling relative to modern, the deglacial warming resulted in incremental rather than sudden changes in forest composition. During the Holocene, a significant change in sedimentation rates was identified based on radiocarbon dating of two parallel cores from Lake Consuelo and was attributed to a period of reduced precipitation in the region (Urrego 2006). The effect of this episode on both lake level and forest composition was greater than that caused by any ecological change associated with the LGM or deglaciation. Within the last 3.5 ka, RoC were more variable, with the largest spike around 2.2 ka (Fig. 12.3j). Overall, the results from the RoC analysis of Lake Consuelo suggested that moisture availability, possibly mediated through cloud cover, played the most significant role in rapid ecological change in this system (Bush et al. 2004b).

Also in the western Amazonian lowlands, Lakes Chalalán and Santa Rosa lie c. 450 km West of Chaplin and Bella Vista. RoC in Chalalán and Santa Rosa showed oscillations throughout the Holocene, with a generally increasing trend toward the present (Fig. 12.3 l–m). Lake Santa Rosa showed a peak in RoC during the early stages of the lake, which may be associated with rapid changes in the forest edge due to the stabilization of a new permanent water body (Fig. 12.3m). This tendency was not observed in Lake Chalalán and was attributable to bathymetric differences between these lakes. Today, Santa Rosa is much shallower than Chalalán and has a flat bottom with gentle side slopes. This bathymetric morphology makes its record more sensitive to changes in the forest-edge vegetation. The RoC in Lake Chalalán were relatively small between 8 and 3 ka (Fig. 12.3 l), despite pollen evidence of drier or more-seasonal conditions (Urrego 2006). This evidence included increased abundance of dry forest elements but not a complete replacement of the mesic vegetation. These data suggested that the reduction in precipitation may have been more marked in the wet-season than in the dry season (Urrego 2006). Both the Chalalán and Santa Rosa records suggested that the regional mid-Holocene dry event documented elsewhere (Mayle et al. 2000, Bush et al. 2005) had only a modest influence on these forests. Late-Holocene RoC showed a few shifts in community composition associated with increased precipitation and possibly human disturbance in the last millennium (Urrego 2006).

12.3.2 Drivers of Change

Post-LGM vegetation responses to climate changes in tropical South America remain controversial on issues such as deglacial timing (Seltzer et al. 2002,

Thompson 2005), the effect of warming and moisture fluctuations (Maslin and Burns 2000, Harrison et al. 2003, de Toledo and Bush 2007, Mayle et al. 2007), and the effect of ENSO anomalies on the eastern flank of the Andes (Vuille et al. 2003). Whether rapid cooling events such as the Younger Dryas and the 8.2 ka event are detectable in the southern Neotropics remains to be resolved (Thompson et al. 1998, Alley et al. 2003, Paduano et al. 2003). Fire is another important process driving ecological change in almost all records from the Andes and western Amazonia at millennial timescales. In this section, we discuss these climatic and physical mechanisms focusing on their role in shaping terrestrial plant communities.

12.3.2.1 Temperature

After the LGM, the most important temperature-driven global oscillation associated with the glacial period was probably the onset of deglaciation. The LGM global chronozone is defined as being between 24 and 18 ka (Mix et al. 2001). However, in the Andes and western Amazonia, deglaciation probably began between 22 and 19 ka (Rodbell 1993, Mark et al. 2002, Seltzer et al. 2002, Bush et al. 2004b, Smith et al. 2005). While deglacial warming started some 5000 years earlier in the Neotropics than at Northern high latitudes, the process continued until c. 11 ka (Blunier and Brook 2001, Grootes et al. 2001). From the available paleoecological data, it seems probable that although there was an initial warming as early as 22 ka, this did not become a sustained trend until ca. 18 ka (Bush et al. 2004b). Our RoC analysis begins at 18 ka and a strong response to warming is evident in Lakes Pata (Fig. 12.3 g) and Caserococha (Fig. 12.3 c). At other sites the deglacial signature is more gradual and lacks defined peaks of change.

After the deglaciation, two important post-glacial global temperature reversals were the YD and the 8.2 ka event. The YD was the most significant rapid cooling period that occurred during the last deglaciation in the North Atlantic region, and was clearly recorded in the isotopic temperature reconstruction from GISP (Fig. 12.3n, Alley 2004). The RoC calculated from GISP showed rapid temperature changes before and after the YD (Fig. 12.3 n) indicating the abrupt nature of this episode. In tropical South America, the signal of the YD differed between the northern and central Andes. In the northern Andes of Colombia, this temperature reversal was ubiquitously recorded as a 4 to 6°C cooling (van der Hammen and Hooghiemstra 1995), while in the central Andes and western Amazonia, the impact of the YD remains unclear. In our analysis, high RoC around the YD were observed in Lake Junin, Caserococha and Chocho (Figs. 12.3a,b,d), although rapid cooling has not been suggested as the cause for these changes (Bush et al. 2005). A somewhat uncertain chronology around the YD in the Lake Junin record prevented us from establishing a definitive relationship at this site. At Caserococha and Chocho relatively robust chronologies (Fig. 12.2) and 100- and 200-year resolution, respectively, make these sites appropriate for an investigation of the YD. In Chocho, the RoC signal lagged by c. 1000 year the onset of the YD, while in Caserococha rapid RoC preceded the event. In the three lowland records presented here that span the YD period, no change in RoC was observed that coincided with the event. The

records from Lakes Pata, Chaplin and Consuelo showed relatively low changes during the temperature reversal, indicating that the YD either had no influence on the vegetation of western Amazonia or that it was too short to be recorded. Alternatively, this pattern could be due to poor dating or low sampling resolution. Overall, we were not able to identify changes in Andean or Amazonian records that were directly attributable to the YD event.

The 8.2 ka event was a short-lived cooling event triggered by freshwater inputs to the North Atlantic (Ellison et al. 2006), similar to the YD in its interhemispheric signature although much shorter in duration (c. 200 years) (Alley et al. 1997). No linkage between this rapid episode and terrestrial ecological changes in tropical South America has yet been documented. The marine sedimentary record from the Cariaco Basin reveals the presence of the 8.2 ka event when sedimentary changes suggested a period of enhanced winds or decreased precipitation (Hughen et al. 1996, Alley et al. 2003). Due to the short duration of this temperature reversal, high-resolution, well-dated records are necessary to discern its influence. Furthermore, sedimentation rates need to be high enough to capture such short events. Despite these limitations, we feel it is important to discuss potential linkages between community changes in tropical South America and the 8.2 ka event given the growing evidence of its signature in other tropical systems (Lamb et al. 1995, Mulitza and Rühlemann 2000, Thompson et al. 2002, Lachniet et al. 2004). Within our study region, records with sampling resolution and sedimentation rates high enough to reveal the effects of this event are available from Lakes Titicaca, Chochos and Pacucha.

RoC between 9 and 8 ka in Titicaca were low and preceded a period of increased variability (Fig. 12.3c). In Lake Chochos, the 8.2 ka event fell within a phase of enhanced variability of RoC, although it did not seem to have produced a particular oscillation (Fig. 12.3d). On the other hand, while RoC from terrestrial vegetation in Pacucha did not reveal significant changes around the event, other proxies, e.g. diatoms and CaCO₃ concentrations, reflected an increase in lake level consistent with increased precipitation (Hillyer et al. 2009).

12.3.2.2 Precipitation

The most prominent reduced-precipitation event that has been documented in post-glacial tropical South America is the Mid-Holocene Dry Episode (MHDE) (Mayle and Power 2008). This event has been recorded in several sites both in the northern Andes (Berrio et al. 2002), central Andes (Abbott et al. 1997, Seltzer et al. 1998, Baker et al. 2001, Rowe et al. 2002, Paduano et al. 2003, Theissen et al. in press) and western Amazonia (Mayle et al. 2000, De Freitas et al. 2001, Bush 2005), suggesting that it was regionally widespread. However, the timing and duration of the MHDE were not synchronous among records. In the Andean records used here, the influence of mid-Holocene dry conditions were clear in RoC from Lakes Junin, Caserococha, Titicaca, Chochos and Consuelo (Fig. 12.3). The weakness, or lack of, the MHDE signal in Lake Siberia, could be explained by the buffering effect of a semi-permanent cloud cover. Lake Consuelo, on the other hand, is

presently located right at the lower cloud-base limit (i.e. 1400 m elevation), which may have been displaced upslope as moisture availability was reduced during the mid-Holocene. In Lakes Pacucha, Chalalán, and Santa Rosa the influence of MHDE has been correlated with decreased wet-season precipitation and subtle forest compositional changes (Urrego 2006, Valencia 2006), but not with a complete terrestrial vegetation turnover. This observation could explain the absence of a conspicuous increase of RoC in the records corresponding to the MHDE (Fig. 12.3e,l,m).

Despite the evidence of a regional mid-Holocene dry phase in tropical South America, the driving forces behind this event have yet to be clarified. Hypothesized driving mechanisms include precessional fluctuations in solar forcing of the South American low-pressure systems (Lamb et al. 1995, Seltzer et al. 2000, Garreaud et al. 2003, Harrison et al. 2003, Theissen et al. 2008) and changes in tropical Pacific circulation and millennial-scale fluctuations of ENSO frequency (Sandweiss et al. 1996, Andrus et al. 2002, Riedinger et al. 2002). The RoC analysis could shed light on the effects of this regional drought on the vegetation but does not reveal the mechanism underlying the MHDE in western Amazonia or the eastern Andes. In general, the RoC data identified the MHDE as being a time of substantial and rapid community change in many of the systems studied.

Regarding ENSO, the analysis of community RoC in Lake Sauce supported the correlation with enhanced frequency of both warm and cold ENSO hypothesized by Correa-Metrio (2007). The onset of increased fire frequency in Siberia could also be correlated with intensified ENSO warm-phases since c. 5 ka (Haberle et al. 2001).

12.3.2.3 Fire

Fire has been an important natural mechanism in Andean and western Amazonian sites well before humans occupied the landscape. For instance at Lake Titicaca, fire has been a modifying component of the landscape for 370,000 years (Hanselman 2007). In Lakes Chochos and Siberia, Pleistocene and Holocene vegetation changes were attributed to increased fire frequency (Bush et al. 2005). Similarly, records from Chalalán and Santa Rosa in western Amazonia, showed rapid changes in RoC that correlate with increased fire intensity (Urrego 2006). In general, fluctuations in fire regimes at these sites could be responsible for the large amount of local variability detected in the RoC analysis, indicating the major role that fire has played in shaping tropical South American vegetation.

12.3.2.4 Human Disturbance

Records of human occupation in western Amazonia (Piperno 1990, Bush et al. 2007, de Toledo and Bush 2007) and the eastern Andes (Chepstow-Lusty et al. 2003) date back at least 7 ka and 12 ka, respectively, but only intensify during the Late Holocene. The overall RoC trend observed in both regions was of enhanced variability during last few millennia (Fig. 12.3), consistent with human-derived

modifications of the landscape. The lowland sites of Pata and Consuelo have no known history of human occupation (Bush et al. 2004a), and the Chaplin and Bella Vista records exhibit low late-Holocene charcoal concentrations during a time of forest expansion (Mayle et al. 2000, Burbridge et al. 2004).

Human intervention included deforestation, introduction of weeds, slash and burn, and agricultural practices, indicating that these are not new problems facing the Andes and Amazonia (Willis et al. 2004). Human influence was suggested for Lake Chochos as a deforestation signal as early as 6 ka (Bush et al. 2005) and at Lake Titicaca as an increase in weedy vegetation documented at c. 3.1 ka (Paduano et al. 2003). In Lake Siberia, the onset of human occupation was inferred at c. 7 ka when fire frequency increased (Mourguiart and Ledru 2003) and RoC also rose (Fig. 12.3f). In Lake Pacucha, high RoC at c. 5 ka resulted from an increase in Quinoa and *Ambrosia* (Valencia 2006) both of which are reported as important agroforestry elements of pre-Incan cultures (Chepstow-Lusty et al. 2003).

Our results support theories of human population demise following European colonization of the new world (Roosevelt et al. 1996, Denevan 2003, Heckenberger et al. 2003). RoC increase around 400–500 year BP, which we interpret to indicate the recovery of plant communities following abandonment at Chochos, Sauce, Chalalán and Santa Rosa (Fig. 12.3). Similarly, we expect a second peak during the last two centuries as human populations and European influence expanded exponentially in the region. However, the temporal resolution of most of the records is not high enough to reveal this change. The best evidence for this post-conquest population recovery and landscape change is found in the RoC from Sauce (Fig. 12.3 h), where the paleoecological record has decadal resolution during the past 1000 years.

12.4 Overview

Paleoecological records from the eastern Andes and lowland western Amazonia show great variability both during the Pleistocene and the Holocene. Despite the scattered network of records, RoC peaks appear to be frequent during both the Pleistocene and Holocene in the Andes while being more concentrated in the Holocene period at lowland sites. In light of these differences, we hypothesize that the lack habitat availability makes montane systems like the Andes more sensitive to climate change than the Amazon lowlands. In the lowlands, species have been able to migrate in any direction as local conditions became unfavorable, e.g. species no longer within their bioclimatic envelope. Such migrations could have led populations to migrate in terms of macrotopography, i.e. elevationally within the Andes, or in microtopography, i.e. from terra firme to gallery forests. In the Andes, an upslope migration of species due to warming results in less occupiable space because mountains are effectively cone shaped. In areas where large high-elevation plateaus exist, they lie above modern tree line and could only be occupied by trees if warming is accompanied by increased moisture. Consequently, as migration proceeds

habitat suitable for forest would inexorably decrease, increasing the vulnerability of populations and species to extinction. If true, our hypothesis would have large implications for the conservation of tropical South American ecosystems in the light of future climate change.

Fluctuations in terrestrial plant assemblages are the result of multiple driving mechanisms, including temperature and precipitation changes, fire frequency and ENSO. The marked response to short-sharp cooling events, e.g. the YD and 8.2 ka events, observed at high latitude was not evident in our study area. However, we recognize that the number of suitable records to detect such fine-scale variability is still small. We predict that further high-resolution examination of tropical South American records with high sedimentation rates may reveal pulses of change caused by events like the YD. Evidence of the MHDE is regionally consistent but its impact on ecosystems differed at the local scale according to the extent to which sites were buffered from moisture deficit. While in Lake Conuelo, mid-Holocene dry events were associated with the lifting of the cloud base and vegetation changes indicative of lowered lake levels, in Lakes Pacucha, Chalachán, and Santa Rosa, the changes were not as pronounced. In the two latter sites, reduction of wet-season precipitation has been hypothesized to produce the observed changes. Impacts of MHDE are evident virtually in all records from the eastern Andes and western Amazonia, although the driving mechanisms behind its occurrence remain unclear. The only records with a sedimentation rate and depositional regime suitable to study ENSO variability in the region are those of Lake Sauce, Peru (Correa-Metrio 2007, and Pallacocha) Ecuador (Rodbell et al. 1999, Moy et al. 2002). Those records depict a consistent image of ENSO variability with Lake Sauce providing the first detailed reconstruction of La Niña-dominated phases.

Overall, the RoC analysis showed that the timing of major changes in forest composition was essentially local rather than regional, making widespread patterns the exception rather than the norm. In the eastern Andes and western Amazonia, fire may be a major driver at the local scale, as it was recorded and correlated with changes in all sites with the exception of those from hyper-humid locales (i.e. Pata). Many records show accelerated RoC during the past 3000 years attributable to intensification of human activities. A clear outcome of this analysis is that ecological rates of change from both eastern Andean and the western Amazonian ecosystems have kept pace with the rates of climate changes since the LGM. Such coupling has been possible because rates of climatic change did not exceed the species response capability. Anticipated rates of warming for the next century (IPCC 2002) are likely to challenge the ability of species to keep pace with the geographic movement of their climatic envelope (Malcolm et al. 2006). Landscapes modified by human activities will add barriers impeding needed migration and may trigger an extinction event (Brooks et al. 2002). Our results legitimize concerns regarding the resilience of species to accommodate future change and emphasize the urgency for effective and prompt conservation measures, and the reduction of greenhouse gas emissions.

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