48,000 Years of Climate and Forest Change in a Biodiversity Hot Spot

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A continuous 48,000-year-long paleoecological record from Neotropical lower montane forest reveals a consistent forest presence and an ice-age cooling of ~5° to 9°C. After 30,000 years of compositional stability, a steady turnover of species marks the 8000-year-long transition from ice-age to Holocene conditions. Although the changes were directional, the rates of community change were no different during this transitional period than in the preceding 30,000-year period of community stability. The warming rate of about 1°C per millennium during the Pleistocene-Holocene transition was an order of magnitude less than the projected changes for the 21st century.

The lower montane cloud forests (at elevations of about 1300 to 2000 m) of the eastern Andes are a biodiversity hot spot and among the most threatened habitats on the planet (1). Steep topography and high proportions of endemic species with narrow altitudinal distributions make Andean systems especially sensitive to past and present climate change. Habitat loss through deforestation and an anticipated warming of 1° to 4°C in the present century (2) raise concerns for the long-term survival of these systems. Already, the effects of climate change on tropical montane systems are evident in the contraction of ice caps (3) and the upslope migration of some bird species (4). Amazonian and high Andean ecosystems maintained high diversity even after strong Pleistocene climatic oscillations (5–7), which might be taken to indicate that they would be resistant to future climate change. Here, we show that although the Pleistocene-Holocene warming (about 6°C) was greater than that anticipated within the next century, the rate of climate change was about an order of magnitude less, suggesting that these systems face unprecedented community change. Our data, from an uninterrupted paleoecological record spanning the past 48,000 years from the lower montane forests of the Andes, show that this biodiversity hot spot has a history of profound but not rapid temperature change.

Lago Consuelo (13°57′S, 68°59′W, elevation of 1360 m; Fig. 1), Peru, is a ~10-ha lake in lower montane cloud forest that lies in a small steep-sided catchment underlain by coarse-grained white quartzite (8). Parallel sediment cores that are 8.8 m in length were collected from the center of the lake (water depth of 10.5 m) (9). Pollen analyses (10) were conducted on the sediments and a chronology was established based on 10 accelerator mass spectrometry ^{14}C dates (table S1).

The Lago Consuelo pollen diagram reveals markedly different Pleistocene and Holocene forest types (Fig. 2). Pollen of montane elements that currently do not occur around the lake, such as *Alnus*, *Bocconia*, *Hedyosmum*, and *Vallea* are unique to the Pleistocene. Similarly, lowland elements, such as *Acalypha*, *Alchornea*, *Celtis*, *Trema*, and tree taxa of the Moraceae/Urticaceae attain their maximum representation in the Holocene pollen record. The transition from Pleistocene to Holocene is gradual with a concurrent decline of montane taxa and an increase in the abundance of lowland pollen taxa. The first signal of this transition, at ca. 21,000 calibrated years before present (cal yr B.P.), is the rise of Moraceae/Urticaceae pollen representation above its range for the previous 10,000 years. The first montane tax-

on lost from the pollen record is *Bocconia* at ca. 19,000 cal yr B.P. (Fig. 2). By 17,500 cal yr B.P., a clear steady warming is evident in the pollen record, a trend that continues unabated until 10,000 cal yr B.P.

Fossil pollen data were analyzed using detrended correspondence analysis (11) and purpose-designed transfer functions (12, 13). Inferred paleotemperature data suggest two periods of relatively stable temperatures with a gradual change between states (Fig. 3). Because the pollen record suggests the continuous presence of mesic forest and correspondingly moist air throughout the record, the modern empirically derived lapse rate of 0.0055°C m^{-1} is applied to translate elevation difference into a change in temperature (14). Because temperature and moisture do not have independent influences on elevational distributions, we cannot exclude the possibility that some of the Pleistocene "cooling" and temperature variability may reflect increased precipitation or fog input. However, if the apparent cooling is exaggerated by wet conditions, no "warming" marks the period at ca. 33,000 cal yr B.P., which was the driest time of the late Pleistocene. At this time, Lake Titicaca was about 130 m below its modern level (15) and northern Amazonian lakes were also registering lowstands (7), but at Lago Consuelo, no substantial deviation from surrounding Pleistocene conditions is evident in the transfer function data. We infer that temperature exerted a stronger influence than precipitation on the Pleistocene forests around Lago Consuelo. We conclude that the late Pleistocene was at least 5°C, and possibly as much as 9°C, cooler than the present conditions.

The Pleistocene forests around Lago Consuelo are most similar to modern communities at elevations of about 2500 m (Fig. 3) and exhibit a narrow scatter of high probability solutions around that tendency. At ca. 17,500 cal yr B.P., the transition to Holocene climates is clearly evident as the "paleoelevation" declines steadily until reaching near modern conditions around 10,000 cal yr B.P. During the Holocene, the taxa in forest communities around Lago Consuelo contained species with both high- and low-elevational ranges. This
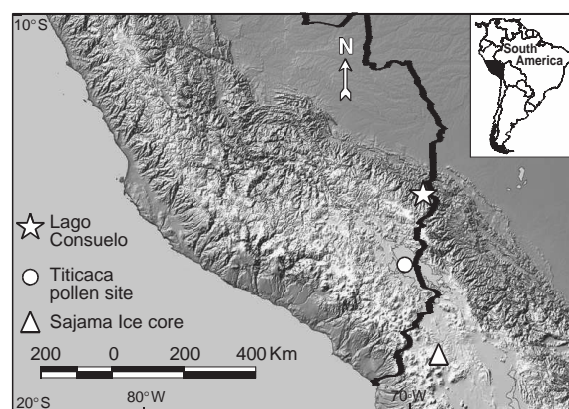
Fig. 1. Location of Lago Consuelo relative to Lake Titicaca and the Sajama ice cap.

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composition results in a broader range of possible temperature solutions compared with those of the Pleistocene. Holocene elevation estimates are scattered around a mean of 1300 m, but the mode is between 700 and 1000 m. This apparent discrepancy with Lago Consuelo's elevation of 1360 m reflects the actual distribution of genera on the Andean flank and the use of presence-absence data in a lowland system. Whereas the high-elevation slopes are rich in palynologically distinct taxa with well-defined elevational ranges, the lower slopes have few such taxa (fig. S2). Indeed, of the genera found in the pollen record, only one, the palm *Dictyocaryum*, has its peak probability of distribution at 1400 m. Given this paucity of mid-elevation markers, lowland taxa with peak distributions at 1000 m or less dominate the mid-Holocene climatic signal.

The lack of empirical data from this region (a problem shared by most Andean analyses) does not allow precipitation and temperature to be estimated separately in the transfer function. Although the transfer function appears to be primarily driven by temperature, some influence of precipitation cannot be discounted. However, the nearly constant sedimentation rate and absence of abrupt changes in sediment type suggest that Lago Consuelo never dried out and that there were no major drought episodes. Although seasonality and temperature changed, wet Andean cloud forest was a continuous feature of this landscape, only retreating upslope during the driest interval of the Holocene. During this event, ca. 9000 to 5000 cal yr B.P., the inferred lifting of the cloud base caused a local replacement of cloud forest taxa with those of wet lowland forest.

Ordination of the fossil pollen data from Lago Consuelo reveals Pleistocene samples that were clustered together and a separate tight clustering of Holocene samples (fig. S3A), suggesting relatively stable communities in the Pleistocene and the Holocene, respectively. The transitional communities connecting these floras form a nearly linear connection. Plotting the compositional dissimilarity (*16*) between past communities and the modern flora reinforces the concept of two distinct and stable forest types of the Pleistocene and Holocene, as well as the gradual change between them (fig. S3B). Another important trend is that the amplitude of community change taking place within the Pleistocene is similar to that taking place within the Holocene. Indeed, the amount of change between samples during the thermally "stable" periods is similar to the change that took place during the transitional period (fig. S3, A to C). The only difference between transitional and stable forest types is whether the changes are directional. These observations are more consistent with hypotheses of stabilizing forces influencing communities (*17*) than hypotheses of neutral drift (*18*). During stable periods, shifts in community composition take place continually and may be either nondirectional or correspond to the vegetation closely tracking short-term climatic oscillations, whereas in transitional stages most variation results from climatically driven vegetation succession.

An important observation from these data is that even during the times of greatest community change in response to the Pleistocene-Holocene transition, the rate of change in forest composition was no greater than that of the average ongoing changes due to either community drift or tracking of small-scale climatic fluctuations. Thus, at any given time, an observer monitoring forest structure would find directional changes ecologically indistinguishable from the more stochastic changes of stable periods. Unlike temperate systems in which long-distance migrations are required for taxa to remain in equilibrium with climate (*19*), species migration in Andean systems probably did not require long-distance dispersal events or any special mechanism beyond normal seed dispersal around a parent. Because of the slopes in Andean systems, species can remain in equilibrium with temperature shifts of 1° to 2°C with migrations of <1 km. Indeed, we hypothesize that the ease with which species can migrate and avoid extinction in response to climate change may be a major factor promoting diversity in these systems.

The slow change in community composition at Lago Consuelo is similar in character to the pollen record of Lake Titicaca, one of the most detailed reconstructions of the Pleistocene/Holocene boundary from the Andes (*20*). Titicaca, which lies above the tree line and immediately upslope of Lago Consuelo, manifested a similar grad-

Fig. 2. Percentage pollen diagram of selected taxa from Lago Consuelo, Peru. Sums based on 300 terrestrial pollen grains. Taxa are ordered according to their apparent sensitivity to warming. Montane elements are listed to the left and lowland elements to the right. Total taxa obtained from the site include 181 terrestrial pollen types (92% of which were identified), 4 aquatic pollen types, and 18 terrestrial fern and moss spore types. Aquatic taxa and spores are excluded from the pollen sum.
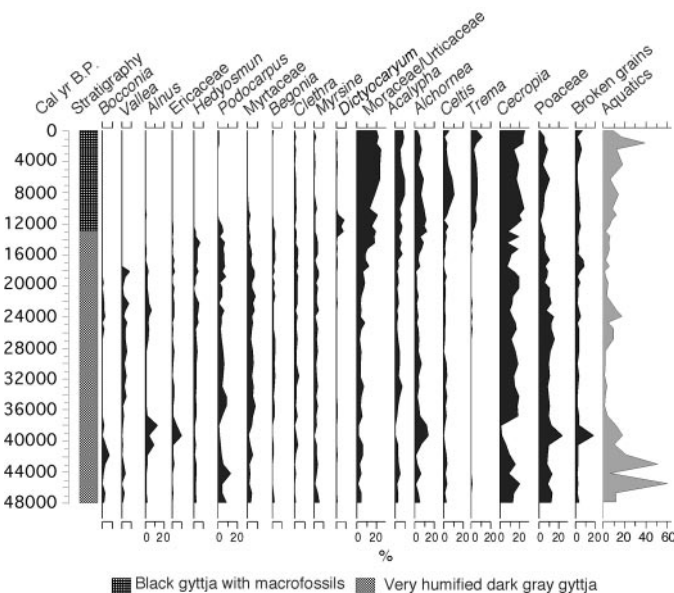
Fig. 3. Most likely equivalent modern elevation and inferred paleotemperature for pollen spectra from Lago Consuelo, Peru. Presence-absence data from 26 taxa with well-characterized modern distributions. Color intensity (blue low to orange high) reflects probability that a sample containing a given set of taxa came from that elevation.
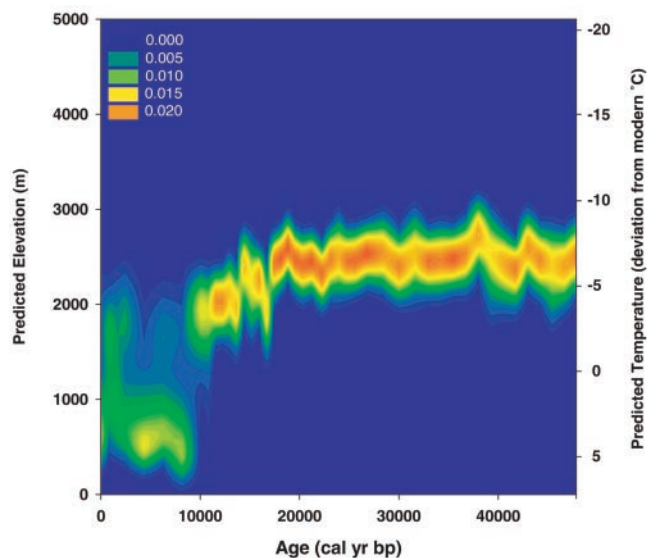
ual warming between 21,000 and 11,000 cal yr B.P. Our data are also consistent with other Andean sites where pollen records show abrupt transitions between forest and puna vegetation (5, 6, 21).

The transition at a given site between the tree line and puna takes place within a climate space of <1°C (22). Thus, a notable change in biome type can be recorded in pollen records without the full Pleistocene-Holocene temperature shift coinciding with the obvious transition between biomes. Our data are consistent with the isotopic record from the only regional ice core that spans the past 20,000 years (14). The stable oxygen isotopic record of the Pleistocene-Holocene boundary from Sajama, Bolivia, exhibits a steady increase in $\partial^{18}O_{(ice)}$ ratios interrupted by one substantial abrupt oscillation in the terminal Pleistocene. Though initially aligned to the Younger Dryas event (3), this oscillation has subsequently been suggested to reflect increased precipitation associated with the formation of Paleolake Coipasa rather than temperature change (15). Thus, no evidence exists of abrupt temperature change in the Sajama record.

In the Holocene, the record at Lago Consuelo is consistent with those of the high Andes (23), coastal Peru (24), and the Bolivian rainforest-savanna ecotone (25) and is consistent with a strong mid-Holocene dry event. Paleotemperature estimates based on species distributions and lapse rate from ca. 8200 and 4000 cal yr B.P. average 1° to 3°C higher than the modern temperature with relatively little statistical error (Fig. 3). However, the apparent temperature increases, manifested by little change in the lowland taxa and lack of montane taxa in the pollen record, could also reflect moisture changes. If this was a time of reduced Andean precipitation, the absence of cloud forest species could be explained by drier conditions, causing the cloud base to lift, rather than or in addition to a simple warming.

These data demonstrate the importance of the buffering force of cloud on these ecosystems. During the strongest drying event of the Pleistocene, aquatic pollen taxa show that the lake level at Lago Consuelo responded somewhat to the drought, but the cloud forest showed no desiccation effect at an elevation of 1360 m (Fig. 2). However, in the mid-Holocene, when the cloud base had lifted to its modern position, a more modest drying event caused the decline of cloud forest elements around the lake. Clearly, although temperature can force elements to migrate vertically, drought will have its most immediate effect on the lower limit of the cloud forest by eliminating moisture interception from clouds, which can provide up to

37% of cloud forest moisture budgets (26).

The Lago Consuelo record establishes several key points. First, cloud forest, although changing between stable community states, existed at or close to this elevation for the past 48,000 years. Second, the temperature change from Pleistocene to Holocene began ca. 19,000 cal yr B.P. and progressed steadily, with no sudden accelerations. Third, rates of forest community change during the most substantial climate change of the past were no greater than during the relative stability of the pre-Industrial Holocene.

Abrupt movement of the Andean tree line at the Pleistocene-Holocene boundary and the presence of many endemic species may provide a misleading impression of community resilience to climate change. Our data suggest that climate changes in these systems have been gradual, perhaps averaging less than 1°C per millennium even during the height of the Pleistocene-Holocene transition. Conservatively, if temperatures change only 1°C this century (the minimum International Panel on Climate Change estimate), that rate would be an order of magnitude higher than the fastest rate observed in this record; the projected climate change in the next 100 years will be fundamentally different from any in the last 50,000 years. Given the relatively short geographic distances between elevations and the concomitantly short migration distances required to move among them, Andean plants with broad elevational distributions should be able to remain in equilibrium with climate. For taxa with narrow elevation ranges, however, the predicted rate of climate change may move them completely outside of their climatic niche space within only one or two plant generations. Coupled with habitat destruction preventing colonization from adjacent metacommunities, Andean plant communities may experience greatly increased extinction rates.

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13. Searches were conducted using TROPICOS (www.mobot.org/tropicos/spectest7.xml). Nonparametric empirical probability distributions were fit for 26 pollen taxa in S-PLUS 6.1 (Insightful Corp., 2002) and are presented in the supporting online material text. We use modern distributional data from herbarium collections grouped at the same level as observed pollen taxa to estimate the probability of a collection of that taxon coming from a given altitude. Taxa were included in the elevation model for a sample when they exceeded 10% or their maximum representation. Cut-offs of 5 and 15% did not affect the conclusions for the model (29). We first estimated the probability Pr (taxon A | elevation). Bayes' theorem was then used with a uniform prior to estimate the most likely elevation from which a given set of taxa originates, Pr (elevation | taxa A, B, C). This method gives a probability distribution of elevation for a group of observed pollen taxa that can also be used to infer a "paleoelevation" for fossil pollen spectra. Taxa used were: *Alchornea, Alnus, Alsophylla, Begonia, Bocconia, Celtis, Clethra, Cyathea, Cystopteris, Dictyocaryum, Gaiadendron, Hedyosmum, Hyeronima, Ilex, Juglans, Myrica, Myrsine, Piper, Podocarpus, Polylepis, Symplocos, Trema, Vallea, Weinmannia, Wettinia,* and *Zanthoxylum.*
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