ing the mid-Pliocene to feed the enhanced production of NADW (*3*, *5*, *6*, *38*). However, our results suggest that the manifestation of the BOC as a characteristic intrusion of cold surface water across the modern South Atlantic (Fig. 1) would have been less pronounced during the mid-Pliocene, because the BC would have upwelled less of the cool SACW. Our mid-Pliocene SST estimates for the BC upwelling system (~26°C) are similar to the average annual SST for the modern oligotrophic waters of the western South Atlantic (~25°C) at the same latitude (Fig. 1). However, global mid-Pliocene warmth would have had a basinwide influence, so that the SST for the western boundary would probably have remained higher than for the eastern boundary (*12*), because our paleoproductivity records and previous studies indicate that a degree of upwelling continued throughout the mid-Pliocene (*18*–*20*).

The processes related to enhanced BC upwelling discussed here may have occurred at the eastern boundaries of the other three major Atlantic and Pacific Ocean basins. These systems could have provided additional long-term sinks for atmospheric CO_2 through the hypothetical mechanism outlined above. The cooling of the Canary Current (*24*, *25*) suggests that the process may have occurred at the North Atlantic's eastern boundary. The development of the $U^{K'}_{37}$ technique for quantitative late Neogene SST reconstruction in sediment cores from a variety of oceanographic settings should allow these and other hypotheses about changes in global and regional paleotemperatures over the past 5 million years to be tested further.

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Millennial-Scale Dynamics of Southern Amazonian Rain Forests

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Amazonian rain forest–savanna boundaries are highly sensitive to climatic change and may also play an important role in rain forest speciation. However, their dynamics over millennial time scales are poorly understood. Here, we present late Quaternary pollen records from the southern margin of Amazonia, which show that the humid evergreen rain forests of eastern Bolivia have been expanding southward over the past 3000 years and that their present-day limit represents the southernmost extent of Amazonian rain forest over at least the past 50,000 years. This rain forest expansion is attributed to increased seasonal latitudinal migration of the Intertropical Convergence Zone, which can in turn be explained by Milankovitch astronomic forcing.

Understanding the long-term dynamics of Amazonian rain forest–savanna boundaries over millennial time scales can provide important insights into Amazonian paleoclimates and may also improve understanding of rain forest biodiversity (*1*). However, the late Quaternary history of forest-savanna dynamics of southern Amazonia is poorly understood, based predominantly on controversial pollen data from two sites. One of these sites, Carajas, is a lake on top of a 700-m plateau (inselberg) in Pará State, Brazil (southeast Amazonia), which is covered by edaphically controlled savanna. The assertion (*2–4*) that the pollen record from this site reflects regional vegetation changes in the Amazon lowlands rather than local vegetation changes on the plateau is controversial (*5*). The paleoecological importance of pollen data from the second site, a valley fill in Katira Creek, Rondônia, Brazil (southwest Amazonia) (*6, 7*), has also proved to be contentious (*5*), with disagreement over whether the pollen record (compiled from only five pollen spectra) reflects regional vegetation history or merely local catchment changes. Although analyses of soil carbon isotopes have revealed late Quaternary fluctuations in southern Amazonian forest-savanna boundaries (*8–10*), determination of the specific kinds of forest communities that existed in the past (e.g., evergreen rain forest versus semideciduous dry forest) has not been possible from carbon isotope data alone. Here, we present paleoecological evidence for rain forest–savanna dynamics of southern Amazonia, quantified both spatially and temporally, spanning the past 50,000 years.

The study area is Noel Kempff Mercado National Park (NKMNP) (Fig. 1, A and B), a protected area of 1.5 million hectares that is located on the Precambrian Shield of eastern Bolivia (*11*), at the southern margin of Amazonia, encompassing an ecotone between humid evergreen rain forest and dry semideciduous forests and savannas (*12*) (Fig. 1, A and B). The region has a strongly seasonal climate produced by latitudinal shifts of the Intertropical Convergence Zone (ITCZ) (*13, 14*) (Fig. 1A), which is the overriding control over the geographical position of the southern limit of Amazonian rain forest, presently located at the southern border of NKMNP (15°S).

Laguna Bella Vista (13°37′S, 61°33′W) (*15*) is ~120 km north of the southern limit of humid evergreen Amazonian forest communities. A 3-m-long sediment core was collected in 1995 from a floating platform toward the center of the lake (2.5-m water depth) by using a modified Livingstone piston corer (*16*), together with a Perspex plastic tube to collect the flocculent surface sediments. Sediment samples (1 cm^3) were processed by standard methods (*17*). Fossil pollen was identified by using a reference pollen collection of ~1000 taxa collected from herbarium material obtained from NKMNP. A chronological framework for the sedimentary sequence was provided by 15 accelerator mass spectrometer (AMS) radiocarbon dates (Fig. 2A) [see Web table 1 (*18*)]. Radiocarbon dates of Holocene age were calibrated into calendar years before the present (cal yr B.P.) (*19*). The sediment record spans at least the past 50,000 years, although no sedimentation occurred at this site during the Last Glacial Maximum (LGM) (~21,000 cal yr B.P.).

The high percentages (~60%) of Moraceae pollen and low percentages of grass (Poaceae) pollen (<10%) in the surface sediment of Laguna Bella Vista provide a signature of the rain forest surrounding the lake today (*20*) (Figs. 1B and 2A). The Pleistocene (ice-age) pollen spectra

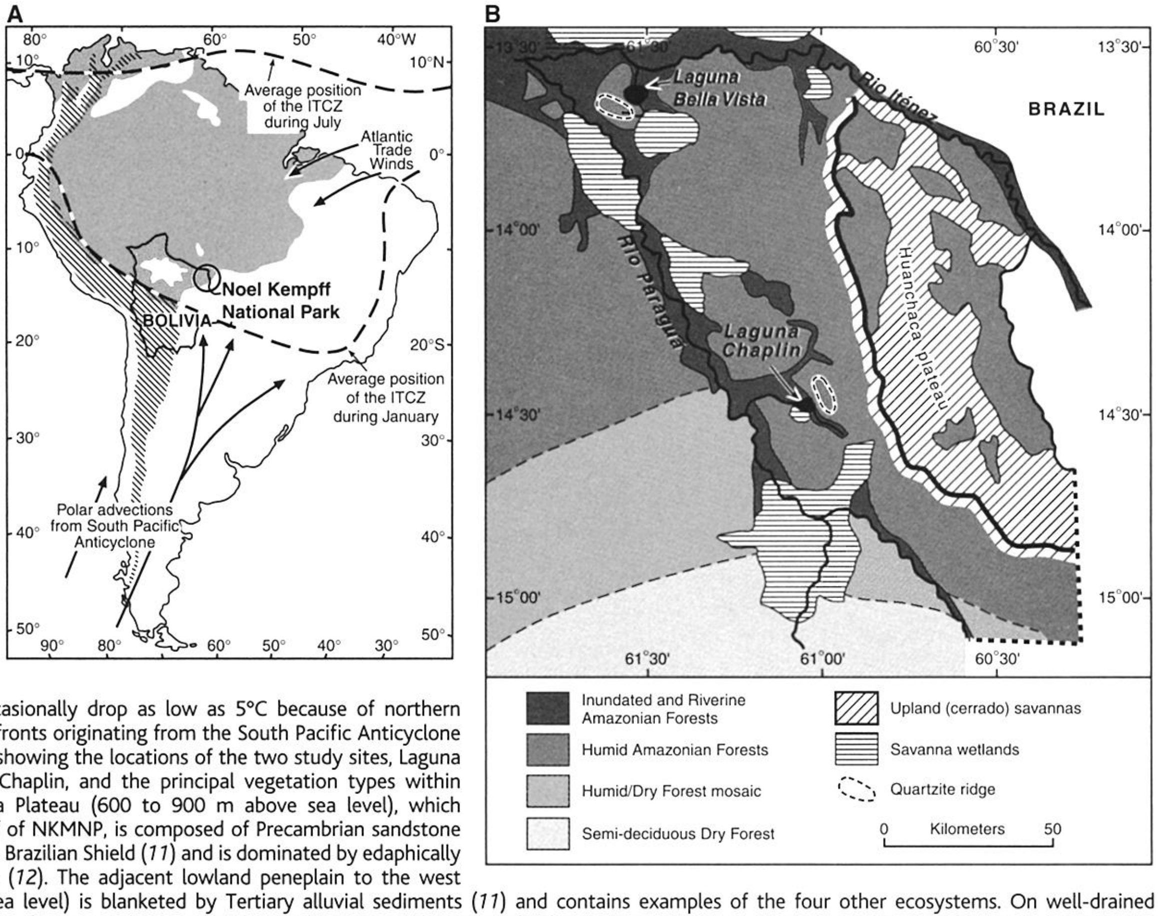

Fig. 1. (**A**) Location of study area in the context of Amazonia and South American climate. The region has a seasonal climate (~1400 to 1500 mm of mean annual precipitation, 25° to 26°C mean annual temperature), influenced by three distinct climate systems (*13, 14*). The ITCZ reaches NKMNP in the austral summer, bringing warm, moist Amazonian air masses responsible for the rainy season. During the austral winter, the ITCZ moves northward and is replaced by dry northerly winds, originating from the anticyclonic circulation of the South Atlantic trade winds, which are responsible for the dry season. Furthermore, winter temperatures occasionally drop as low as 5°C because of northern advections of cold polar fronts originating from the South Pacific Anticyclone over Patagonia. (**B**) Map showing the locations of the two study sites, Laguna Bella Vista and Laguna Chaplin, and the principal vegetation types within NKMNP. The Huanchaca Plateau (600 to 900 m above sea level), which occupies the eastern half of NKMNP, is composed of Precambrian sandstone and quartzite rocks of the Brazilian Shield (*11*) and is dominated by edaphically derived upland savannas (*12*). The adjacent lowland peneplain to the west (200 to 250 m above sea level) is blanketed by Tertiary alluvial sediments (*11*) and contains examples of the four other ecosystems. On well-drained landscapes, Amazonian rain forests predominate in the north, whereas Chiquitano dry forest communities predominate in the south; inundated forests and savannas occupy extensive floodplains throughout the region (*12*).

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[~44,000 to 38,600 radiocarbon years before the present (^{14}C yr B.P.)] are dominated by *Alchornea*, Leguminosae (Papilionoideae), and *Talisia*-type pollen. They are indicative of plant communities that are very different from those of the Holocene (possibly semideciduous dry forests). All three taxa include species present in the Amazonian rain forest, Cerrado (upland grassland, savanna, and woodland), and Chiquitano dry forest biotas. However, the absence or negligible abundance of Moraceae pollen show that these forest communities were not rain forest.

Most of the Holocene sequence is characterized by low percentages of Moraceae pollen (<25%) and peaks in pollen of Poaceae (40%), *Curatella americana*, *Mauritia*/*Mauritiella*, and *Isoetes*. Grasses dominate both well-drained and inundated savannas (*21*). The high percentages of grass pollen are typical of modern pollen spectra from savannas of the Brazilian highlands south of Amazonia (*22*). Preliminary charcoal data from the same core (*23*) reveal that charcoal and grass pollen fluctuations are closely in phase with one another, signifying that this Holocene grass pollen peak is attributable to savanna grasses (which are subject to frequent fire) rather than to aquatic or shoreline grasses. *Curatella americana* is a small tree that dominates well-drained savanna plant communities on lowland landscapes. In NKMNP, this species is typically associated with nonflooded microhabitats (e.g., termite mounds) within seasonally inundated savanna landscapes; it is essentially absent from the upland savannas of the Huanchaca Plateau (*12*). The *Mauritia*/*Mauritiella* pollen can be attributed to two closely related palm taxa, *Mauritia speciosa* and *Mauritiella armata*, that form large mixed colonies characteristic of seasonally flooded marshland (*12*). *Isoetes* is an aquatic herb restricted to lake-margin shallows. Peaks of these palms and aquatics are consistent with lake levels lower than present-day levels, facilitating the expansion of *Isoetes* populations over central portions of the lake and the development of marshland around a shrinking lake margin. Considered as a whole, this Holocene pollen assemblage, before 2790 cal yr B.P., is indicative of a climate drier than today's climate, with lowered lake levels and a landscape dominated by seasonally inundated savannas, with microrelief provided by termite mounds colonized by *C. americana* and levees supporting Moraceae-dominated gallery forests lining the nearby river systems. Evidence that the gallery forests supported at least some species of the Chiqui-

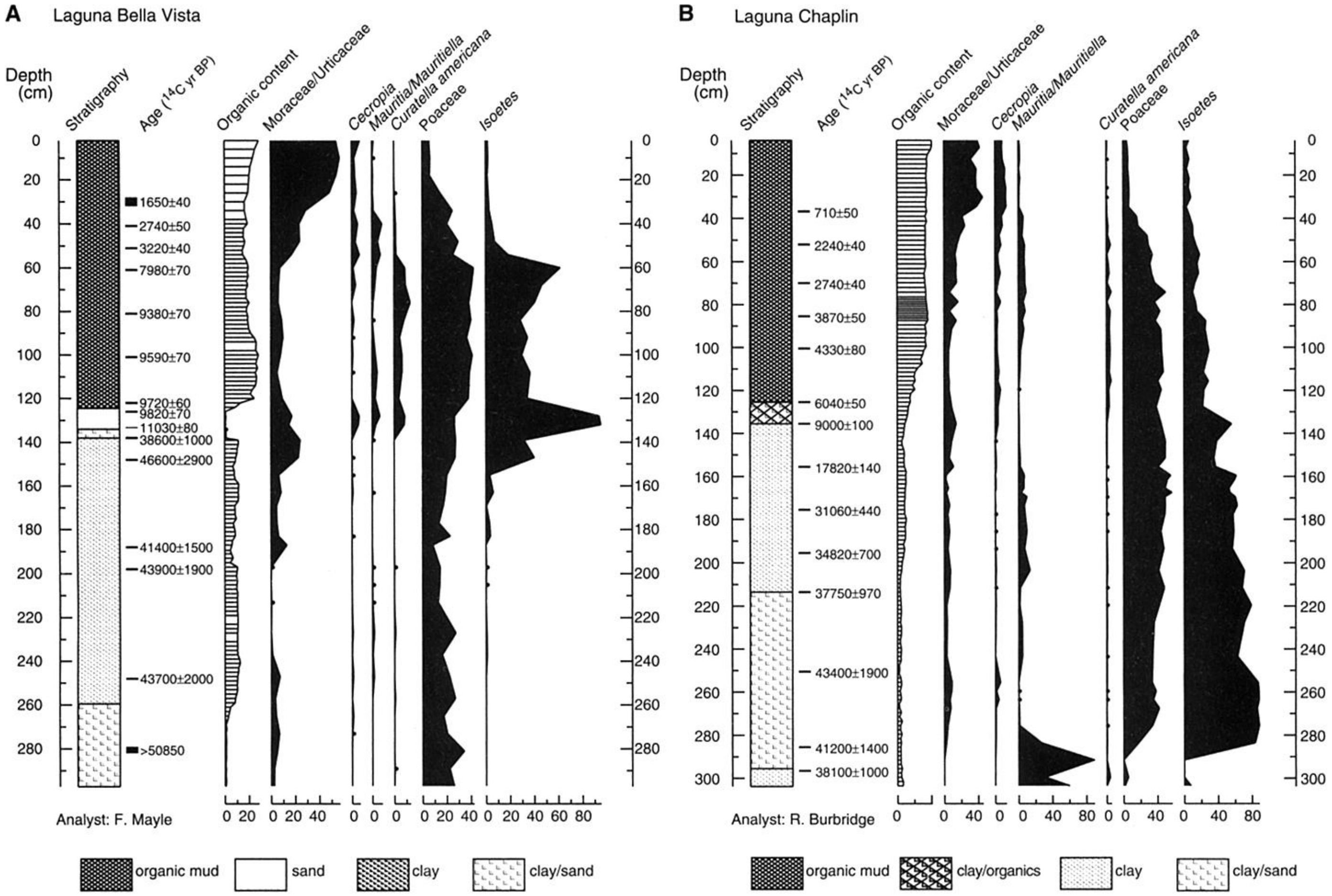

Fig. 2. (**A**) Laguna Bella Vista summary pollen percentage diagram. Percentages are expressed as a proportion of the total land pollen sum (at least 300 grains), including terrestrial fern spores; all aquatic taxa (e.g., *Isoetes* and *Pediastrum*) have been excluded from the pollen sum. Only the most abundant taxa from the full complement of 263 pollen types are shown. Dots on the curves denote <0.5% presence. Analysis of pollen concentration data shows that these percentage changes are not statistical artifacts, but represent real vegetation change. Percent organic content was determined by loss on ignition at 550°C. On the depth scale, 0 cm represents the interface between sediment and water. The pollen record was produced by Mayle [(*23*); see supplemental material for a more detailed pollen diagram (*18*)]. (**B**) Laguna Chaplin summary pollen percentage diagram. Percentages were calculated in the same manner as for (A). Only the most abundant taxa from the full complement of 290 pollen types are shown. Comparison with pollen concentration data reveals that the percentage peak in *Mauritia*/*Mauritiella* pollen at the base of the record is a statistical artifact produced by low concentrations of other pollen taxa at this level. The pollen record was produced by Burbridge [(*26*); see supplemental material for a more detailed pollen diagram (*18*)].

tano dry forest is provided by the peak in pollen of *Astronium fraxinifolium*, a species with a present-day distribution concurrent with dry-forest formations (*24*). The abundance of Moraceae pollen increases steeply from 25% to current levels of 60% between 2740 ± 50 ^{14}C yr B.P. (2790 cal yr B.P.) and 1650 ± 40 ^{14}C yr B.P. (1530 cal yr B.P.), showing that rain forest has expanded into northern NKMNP only within the past three millennia.

To determine the regional importance of the vegetation record from Laguna Bella Vista, we cored another site 100 km farther south. This second site, Laguna Chaplin (14°28′S, 61°04′W) (*15*), was cored in 1998 with a hammer-driven modified Livingstone piston corer (*25*). The morphometry of this basin is very similar to that of Laguna Bella Vista, and the lake is also surrounded by humid evergreen Amazonian forest (Fig. 1B). The sediments were deposited continuously over the past 43,000 years, including the LGM; chronological control was provided by 14 AMS ^{14}C dates (Fig. 2B) [see Web table 2 (*18*)]. Uniformly high grass pollen percentages of 40%, together with peaks in *C. americana* and charcoal (*26*), indicate that savanna communities dominated the catchment of this site continuously from $\sim$40,000 to 2240 ^{14}C yr B.P. The Amazonian rain forest communities surrounding Laguna Chaplin are even younger than those around Laguna Bella Vista, having become established only between 2240 ± 40 ^{14}C yr B.P. (2240 cal yr B.P.) and 710 ± 50 ^{14}C yr B.P. (660 cal yr B.P.), confirming that Amazonian species have expanded their distribution southward in NKMNP in very recent times. This finding is supported by a mapping study (using LANDSAT satellite imagery) (*12*) that places the southernmost boundary of Amazonian rain forest just 20 km south of Laguna Chaplin (Fig. 1B).

Our findings show that Amazonian rain forest communities have only expanded into NKMNP within the past three millennia to reach their current geographical limit at 15°S. Furthermore, our data show that the present-day rain forest boundary in eastern Bolivia constitutes the southernmost extent of Amazonian rain forest in South America over at least the past 50,000 years and that, over most of this period, the ITCZ must have been located north of eastern Bolivia in austral summer, exerting a weaker influence over this region than today, resulting in a longer dry season.

Our evidence for early to middle Holocene savanna in Bolivian Amazonia correlates with stable carbon isotope evidence for savanna expansion between 9000 and 3000 ^{14}C yr B.P. in Rondônia and Amazonas states (western Brazilian Amazonia) (*8–10*) and charcoal evidence for increased fire frequencies between 7000 and 3000 ^{14}C yr B.P. in Pará State (eastern Brazilian Amazonia) (*4, 27*). This correlation shows that Holocene climate aridity did not just affect the vegetation at the southern margin of Amazonia, it affected more central and eastern parts of the Amazon basin as well.

Our pollen evidence for increased precipitation after $\sim$2740 ^{14}C yr B.P. is further corroborated by a rise in the water level of Lake Titicaca between 3600 and 3200 ^{14}C yr B.P. (reaching near-modern levels by 2100 ^{14}C yr B.P.) (*28–30*) and increased snow accumulation on Sajama Mountain at $\sim$3000 ^{14}C yr B.P. (*31*), regions in the Bolivian Andes that are also influenced by the ITCZ. This recent southward shift of the ITCZ can be explained by orbital forcing according to the Milankovitch theory, which predicts a minimum in Southern Hemisphere summer insolation from $\sim$12,000 to 9000 cal yr B.P., with an increase toward the present (*13, 32*).

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