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Pollen-based biome reconstructions over the past 18,000 years and atmospheric CO_2 impacts on vegetation in equatorial mountains of Africa

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ABSTRACT

This paper presents a quantitative vegetation reconstruction, based on a biomization procedure, of two mountain sites in the west (Bambili; 5°56′ N, 10°14′ E, 2273 m) and east (Rusaka; 3°26′ S, 29°37′ E, 2070 m) Congo basin in equatorial Africa during the last 18,000 years. These reconstructions clarify the response of vegetation to changes in climate, atmospheric pressure, and CO_2 concentrations. Two major events characterize the biome changes at both sites: the post-glacial development of all forest biomes ca. 14,500 years ago and their rapid collapse during the last millennium. The rates of forest development between the biomes are different; a progressive expansion of lowland biomes and an abrupt expansion of montane biomes. The trends of pollen diagrams and biome affinity scores are not always consistent in some periods such as the Younger Dryas interval and end of the Holocene Humid Period, because the biomization method is not a simple summarization of the pollen data, but also takes biodiversity into consideration.

Our sensitivity experiment and inverse-vegetation modeling approach show that changes in atmospheric CO_2 concentration unequally influence vegetation in different local environments. The study also suggests that the biome changes prior to the Holocene result from both changes in the atmospheric CO_2 concentration and climate. The development of warm-mixed forest from xerophtic vegetation results from increases in atmospheric CO_2 concentration and near-surface air temperature. Difference in local dryness results in the different biome distributions, with more forest-type biomes at Bambili and more grass/shrub-type biomes at Rusaka.

1. Introduction

Equatorial forests have been considered to be the most stable ecosystems on Earth. From the viewpoint of their great floral and faunal diversity, they must have been in existence over the last several million years even though their extent could have fluctuated with climate and atmospheric composition. However, some previous palaeoecological studies (e.g., Maley and Brenac, 1998; Vincens et al., 1999; Runge, 2002; Lézine et al., 2013a,b; Desjardins et al., 2013) show that the equatorial forest ecosystems in Africa have undergone drastic modifications (floristic, structural and palaeogeographic) in response to climate changes since the last glacial maximum (LGM, ca. 21,000 years ago, 21 ka). These modifications include the possible fragmentation of equatorial forested communities (Maley, 1996), the expansion of species restricted to high elevations today (Dupont et al., 2000) at the LGM and the collapse of the forests around 4–2 ka (Vincens et al., 1999; Lézine, 2007; Marchant and Hooghiemstra, 2004; Lézine et al., 2013a,b). Changes in plant distribution and abundance from the last glacial onwards were also observed in the lowlands all over North Africa, from the Equator to the Northern Tropic (e.g., Lézine et al., 2009; Watrin et al., 2009; Hély et al., 2014). Moreover, ^{13}C measurements on leaf waxes implied the replacement of tropical montane forest by scrub vegetation, the downward migration of alpine treelines and the marked shift towards C4-plant dominance in the tropics during the last glacial period (e.g., Street-Perrot et al.,

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1997; Huang et al., 1999).

Climate factors, such as moisture and heat are commonly invoked to explain the changes in ecosystem composition and structure (e.g., Lézine et al., 2011; Anadón et al., 2014). Other factors, such as atmospheric pressure and atmospheric CO_2 could potentially also have some impacts on the vegetation through physiological processes. Reduced partial pressure of CO_2 and O_2 associated with an increase in altitude related to lower sea level during glacial times could influence photosynthesis (e.g. Friend and Woodward, 1990; Terashima et al., 1995; Sakata and Yokoi, 2002). A decrease in atmospheric CO_2 generally results in a reduction of in the abundance of plants with C3-photosynthesis pathway because of the required increased rates of photorespiration, and an expansion of C4-plants due to their adaptation anatomically and physiologically to low atmospheric CO_2 concentrations (e.g., Ehleringer et al., 1997; Cowling and Sykes, 1999). Simulations with the BIOME3 equilibrium vegetation model also indicated that low atmospheric CO_2 alone could result in the observed replacement of tropical montane forest by scrub vegetation at the LGM (Jolly and Haxeltine, 1997). To understand vegetation changes at tropical high-elevation sites in paleoecological context, we therefore need to understand the effect of changes in the atmospheric CO_2 concentration and air pressure to the vegetation as well as purely climatic effects.

In this study we focus on changes in biomes at roughly similar altitude (2000–2300 m) in tropical Africa: to the West in the Cameroon volcanic line (Bambili) and to the East in the Kivu montane range (Rusaka). Detailed pollen studies at both sites (Lézine et al., 2013a; Bonnefille et al., 1995) have shown that vegetation composition varied considerably through time from 18 ka to the present. The goals of our paper are 1) to discuss biome changes in these mountain areas over the past 18 ka and 2) to investigate the impacts of changes in atmospheric CO_2 concentration on vegetation at the early in the last deglaciation (i.e., 18 ka) using an inverse vegetation-modeling approach. The comparison between two distant sites will enable us to identify the more prominent climate-change events that have affected the Afromontane forests.

2. Equatorial mountains of Africa

2.1. Geographical features

The Cameroon volcanic line is a crescent-shaped chain of highlands and volcanoes that extends from the Gulf of Guinea to the Southwest to the Adamawa plateau to the Northeast. Mean altitude decreases from West (around 2000 m in the "Grassfield" region) to East (around 1000 m in the Adamawa plateaus), punctuated by high mountains, such as Mount Cameroon on the coastline (4095 m) and Mount Oku in the Western plateaus (3011 m). Bambili is a crater lake located in the Western plateaus (05°56′ N, 10°14′ E, 2273 m; Fig. 1) close to Mount Oku where the Afromontane forest is preserved today (Letouzey, 1968, 1985; Momo Solefack, 2009). Regional precipitation, with the rainy season from March to October, is due to the West African monsoon. The temperature is lower relative to lowlands over the tropical Africa due to the altitude of the site.

The Burundi highlands are a part of the Albertine Rift Mountains that enclose the western branch of the East African Rift, following a roughly North-South direction. The mountain ranges include high mountains, such as the Virunga Mountains (4507 m) and the Rwenzori Mountains (5109 m). These altitudes are not reached in Burundi where the highest peak reaches 2684 m only. Rusaka is a swamp lying at 3°26′ S, 29°37′ E and 2070 m in altitude (Fig. 1). The regional climate of Rusaka is related to the South African monsoon, the rainy season is from November to May.

2.2. The African biomes

Fossil pollen data are generally expressed in the form of abundances of individual plant taxa, and detailed pollen descriptions at Bombili and Rusaka have been provided elsewhere (Bonnefille et al., 1995; Lezine et al., 2013a,b). The pollen sequence is continuous and extends from 0 to 18,071 years ago at Bambili and extends from 750 to 18,061 years ago at Rusaka. Here we use biomes, which are geographically and climatically broadly distributed physiognomic vegetation types, for representing vegetation changes in this study. The biomes are represented by assemblages of plant functional types (PFTs) that are defined on the basis of plant traits (e.g., the life form, leaf form, phenology, and bioclimatic tolerances) that reflect their preferable environments, in which the species maximize productivity and minimize environmental stress (Table 1). The use of biomes and PFTs helps to solve the problem of classifying paleoecological records by reducing the number of entities considered and by proving an ecological basis for treating plants from different regions in a comparable way. A method for converting pollen taxa to biomes (i.e. biomization) is described in section 3.1.

The Afromontane vegetation of Africa is discontinuous, with patches separated from one other by lowlands, and thus is referred to as the "Afromontane archipelago" (White, 1983). Despite the geographic discontinuity, they share numerous plant species that are distinct from the surrounding lowland regions. Three main biomes (Table 2), common to all Afromontane regions, are distinguished. They correspond to an elevation gradient from roughly 1600 m to the top of the highlands:

- Warm mixed forest (WAMF) occurs in a lower ombrophilous areas and in the lowland Guineo-Congolian forests;
- Afro-alpine forest (AAF) occurs in an areas at higher elevation typically above 2000 m, with upper limit of the forest is typified by the presence of abundant Ericaceae; and
- Afro-alpine grassland (AAG) is cool afro-alpine grasslands that consist of C3 grasses which are found neR the top of the mountains above 2800 m.

Regional differences between the eastern and western mountain ranges are observed, however, with e.g., *Hagenia*, *Clifforita*, *Afrocrania* and *Junioerus* absent from the western sector (Cameroon), as well as *Artemisia* that has never been collected here.

Lowland African biomes (Table 2) are distributed along a decreasing rainfall gradient from the Guineo-Congolian forests, which ranges from tropical rain forest (TRFO) and tropical seasonal forest (TSFO) (near the Equator), to the Sudanian (to the North)/Zambezian (to the East and South) tropical dry forests (TDFO), to a mixture of woodlands and grasslands (i.e. savanna (SAVA)), to the Sahelian (to the North)/Somalia Masai (to the East) steppes (STEP), and finally to desert (DESE).

In this study, we focus on nine biomes (three biomes for highlands and six biomes for lowlands) on the basis of our own field expertise and local descriptive botanical literature (Troupin, 1982; Letouzey, 1968, 1985; Momo Solefack, 2009).

3. Methods

3.1. Biomization procedure

Biomization is a quantitative procedure that reconstructs biomes on the basis of the characteristic signature in the pollen record of different PFTs (Prentice and Webb, 1998). There are five