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Climate change and topography as drivers of Latin American biome dynamics

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Citation for published version (APA):

Flantua, S. G. A. (2017). *Climate change and topography as drivers of Latin American biome dynamics*.

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Introduction and Thesis Outline

CHAPTER 1

1. Study the past to understand the present and predict the future

The present is a snapshot after a long history of environmental change. A main focus of attention in current society is how to answer the many questions concerning the implications of future environmental change. Numerous studies focus on predicting how species and communities will respond to future climate changes, and climate modellers vigorously try to understand the modern climate to predict how we can expect it to change in the future. However, the short timeframe of ecological and meteorological research does not provide enough information to make reliable long term climate projections. Therefore, evidence from older records that go beyond the time frame we consider “the present” are extremely valuable. The past is used to improve our ability to predict the responses of biological systems to future environmental change.

The ‘paleo’-ecology (Greek *palaio-*, from *palaios*, ancient; from *palai*, long ago) is the ecology of the past (Birks and Birks, 1980). Or more specifically, it is “the branch of ecology that studies (the) past (of) ecological systems and their trends in time using fossils and other proxies” (Rull, 2010). The paleoecological studies can be focusing on any moment in the past (ranging from hundreds to millions of years ago) and therefore forms a strong link between ecology and geology. The paleoecology aims at reconstructing the biota that lived in the past (plants and animals); reconstructing the assemblages and ecosystems that occurred in the past; reconstructing the past landscapes; reconstructing past environments, including climate and possible human impacts.

To reconstruct past environments and species distributions, paleo-data are derived from animal and plant remains. When climate changed in the past, vegetation responded and this is reflected by changes in their abundance, geographic extent, and floral composition of plant associations. Pollen grains produced by these associations are captured and preserved in lake sediments and peat bogs. Paleoecologists make thankful use of these natural deposits. Recovered sediment cores reveal temporal changes in many different biological and physical proxies. Biological proxies include pollen grains, diatoms, shells and beetles, among others.

Most paleoecological evidence is derived from the Quaternary, covering the past 2.58 million years (Gibbard and Cohen, 2008). Pollen of flowering plants are the most abundant fossils found in lake and peat deposits. Changes in fossil pollen assemblages are interpreted in terms of past changes in vegetation while past environmental and climate conditions are inferred based on our knowledge of current species distribution.

2. Regional fossil pollen databases

Computers, internet and online data deposits have facilitated the ability to assemble large amounts of data. Thousands of pollen records have been collected globally (Fig.1) and are currently being incorporated into the global NEOTOMA paleoecology database (www.neotomadb.org). Multi-site analyses of records of past vegetation change address questions about past distributions (Jansson, 2003), species migration, intrinsic changes in vegetation composition, and extrinsic ecosystem responses to climate change (e.g. Willis et al., 2010; Dietl and Flessa, 2011; Williams et al., 2011). Compilations of paleodata are furthermore important for paleoclimatic reconstructions that need data to both improve climate models and to validate model output.

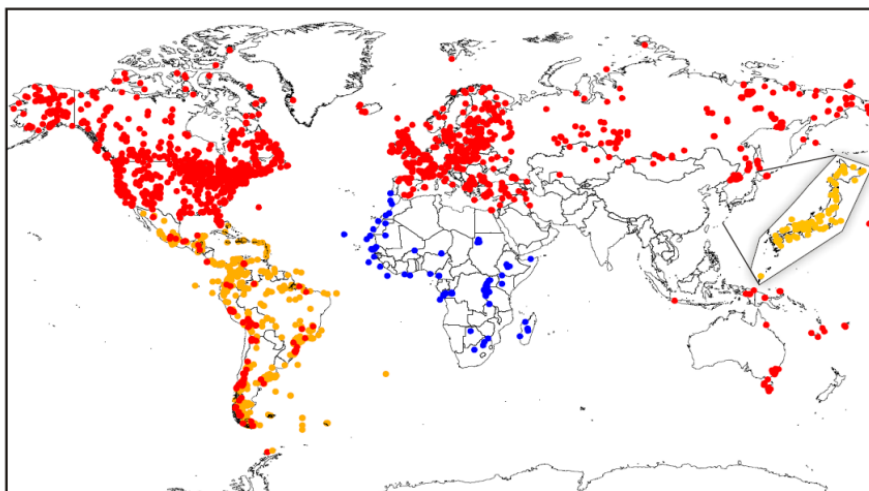


Fig. 1. Pollen sites. Red dots: currently included in the NEOTOMA Paleoeology Database, blue dots: African Pollen Database, yellow dots: known records but not yet included in Neotoma (after: Grimm et al., 2013).

During the past four decades, the dynamic history of Andean ecosystems of northern South America was intensively studied by the palynology research groups of Thomas Van der Hammen and Henry Hooghiemstra. Initially, pollen studies were concentrated in the mountain region of Colombia, but were later extended to the lowlands, exploring not only paleoenvironmental conditions in the region, but also important ecological and biogeographical issues, such as unravelling the Amazonian forest refugia hypothesis (e.g. Hooghiemstra and Van der Hammen, 1998; Hoorn et al., 2010) and the impact of the Intertropical Convergence Zone (e.g. Van der Hammen and Hooghiemstra, 1995). Recent pollen studies have contributed to upper forest line reconstructions in Ecuador (Wille et al., 2002; Moscol-Olivera and Hooghiemstra, 2010), past mean annual temperatures reconstructions (Groot et al., 2011), and methodologies to estimate past biodiversity (Weng et al., 2006; Hoorn et al., 2010).

Importantly, the University of Amsterdam (UvA), and specifically the Research Group of Paleocology and Landscape Ecology at the Institute of Biodiversity and Ecosystem Dynamics has long been the 'basecamp' of the Latin American Pollen Database. The initiative to compile a database of pollen records from Central America, South America and the Caribbean was first launched in 1994 by a research group headed by Vera Markgraf (University of Colorado, US). In 1998 its management moved to the UvA producing in 2009 an overview paper among an international group of collaborators (Marchant et al., 2009). Unfortunately, the database received no further updates after the project ended in 2003.

Through the support by three grants from the Hugo-de-Vries-Foundation (Van Boxel and Flantua, 2009; Flantua and Van Boxel, 2011a; 2011b), the new search for studies was a great success: The new inventory of pollen records showed a number of pollen records much bigger than expected. In the database from 1997, c. 460 sites had been identified; by 2011, I had recovered the metadata from c. 1100 pollen sites and was still working through new publications. This updated Latin American Pollen Database provided exactly the necessary information to develop new research objectives within tropical paleoecology based on the development of multi-site and multi-disciplinary studies.

3. Updated Latin American Pollen Database poses new spatial questions

Compiled data opens a new world of questions that previously were impossible to address by looking at individual records. Having an increasing number of pollen records enhances the ability to produce maps and improves the ability to interpret spatial patterns of temporal change.

There are four main fields of questions that can be raised when temporal data, such as fossil pollen records, are analyzed in a spatial environment, namely: *location*, *conditions*, *trends* and *patterns*. Combining these questions often results in the baseline information or hypothesis development for spatial modelling that rely on datasets, identified patterns and hypothesis to test through advanced models.

Below these spatial analysis questions are further specified in the light of the research questions posed by this thesis:

A. Location: This is the principal spatial question of '**what is located where**'. This information covers the question on the availability and distribution of data for further research. It has a strong exploring and describing approach. In this thesis, I address the following questions aimed at describing locational features:

- 1) What is the spatial and temporal availability and distribution of paleoecological research done by fossil and modern pollen studies in Latin America? (**Chapter 2**)
- 2) Which regions are represented frequently enough in the LAPD to obtain statistically sound vegetation dynamics interpretations? (**Chapter 2**)

B. Condition: Through the use of metadata from each site, additional questions can be raised on the fulfilment of certain 'conditions' of interest. In this case, I focus on **chronological conditions** as a measure of uncertainty before spatial mapping should take place. The following question is addressed in this thesis:

- 3) What is the temporal uncertainty of the Northern Andes and which periods are best suitable to create spatially continuous land cover maps? (**Chapter 3**)
- 4) Does the temporal resolution of the multi-site synthesis allow research on sub-millennium-scale climate variability? (**Chapter 3**)

C. Trends: This aspect of spatial analysis combines information on both location and condition, integrated into questions that focus on identifying **changes over time between sites**. Here a spatial perspective is given to a temporal dataset and comparisons among sites are done in a temporal manner. The following questions on trends are addressed in this thesis:

- 5) Which time periods show synchronous responses of pollen associations and are there regional differences? (**Chapter 4**)
- 6) Is data from palynological site studies suitable for implementation into GIS, where it is synthesized to create spatially continuous maps of past land cover? (**Chapter 5**)

D. Patterns: The spatial patterns analysis I propose to address in this thesis is the assessment that brings the pollen data into relation with other spatial information, for example with climate and topography, and produces new outcomes from the initial dataset. The following chapters use fossil pollen analysis in a spatial environment to support and better understand questions raised by other disciplines. In this case much emphasis is put on understanding mountain biogeography and specifically, to **integrate paleoecological reconstructions on the Pleistocene** into a multidisciplinary framework. Here, the following research questions are raised:

- 7) How do the landscape features in mountains influence the distribution of plant associations under different climate conditions? (**Chapter 6 and Chapter 7**)
- 8) How is contemporary mountain biodiversity influenced by the spatial and temporal dynamics of plant associations during the Pleistocene and specifically in terms of 'historical connectivity'? (**Chapter 7 and Chapter 9**)

- 9) How is contemporary mountain biodiversity influenced by the spatial and temporal dynamics of current climate and deep time geology? (**Chapter 8**)

4. Outline of the Thesis

The general aim of this thesis is to study the temporal and spatial responses of biomes to Pleistocene climate change in Latin America, with the specific aim of creating spatial reconstructions based on fossil pollen records. I provide a combination of spatial and temporal analysis of pollen data in northwest South America, a sub-region of the LAPD, using multi-site and multi-disciplinary integration. I aim to establish a baseline database to foster further research, while revealing the heterogeneity of biome responses to past climate change. Additionally, in this thesis I show the added value of landscape assessments in Geographic Information Systems (GIS) to model past distribution of biomes. The chapters are organized as followed:

The first chapter (**Chapter 2**) has a strong *location* driven approach where the information from the updated Latin American Pollen Database is synthesized. Information from multiple records is compared and an overall view of paleoecological research from Latin American pollen studies is provided.

Chapter 3 emphasises the temporal uncertainty as a *condition* to select a site to a) support more robust quantitative paleoenvironmental reconstructions and b) ensure reliable estimates of the associated uncertainties. For multi-site and multi-proxy comparison, it is important that environmental signals can be identified correctly in multiple records (Seddon et al., 2014). Therefore a method is proposed that provides an additional condition variable that can help identify pollen sites with a certain temporal uncertainty threshold.

In **Chapter 4**, pollen records from South America are compared and synthesized in more detail and combined with climate data to identify *spatial and temporal trends*. The past 2000 years is depicted as the period of interest and a set of conditions on chronology and resolution define the dataset presented. This chapter is structured around climate and vegetation dynamics, but also highlights the human-environment interactions.

Chapter 5 and **Chapter 6** focus on the spatial expansion and contraction of biomes over time, testing different methods of biome mapping or pattern analysis. **Chapter 5** is based on fossil pollen records in the lowlands of Colombia, while **Chapter 6** implements a different kind of method for biome mapping in the Andes. The case studies presented in these chapters support insights into the opportunities and challenges set for paleo-mapping of fossil pollen records.

Chapter 7 and **Chapter 8** focus on mountain biodiversity over long time-scales as the conceptual framework for **Chapter 9**. These chapters also make the step from the previous late Quaternary assessments from the previous chapters to a longer timeframe, namely the Pleistocene. **Chapter 7** highlights the Northern Andes as a strong case study area where long fossil pollen records can provide insights into the Pleistocene dynamics and consequent build-up of biodiversity. Several new conceptual figures support the hypothesis proposed in this chapter that historical connectivity has been an undervalued contributor to contemporary species richness. **Chapter 8** provides an overarching bridge between the Northern Andes in perspective with other mountainous regions around the world, aiming at understanding the relationship between geology, climate and biodiversity on geological time scales.

The final **Chapter 9** strongly aims at testing the conceptual framework presented in Chapter 7 and to further specify conclusions presented in Chapter 8. Here, reconstructions of Pleistocene species dynamics are presented in which the landscape structure of páramos in space and time is modelled. The link between paleoecology and phylogeography is emphasized, with a focus on integrating knowledge to improve our understanding of the biogeographical history of the Northern Andes. It aims at providing an enhanced understanding of ecological and evolutionary dynamics explaining the high species richness of the Northern Andes by using long fossil pollen records.

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