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Climate change and topography as drivers of Latin American biome dynamics

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Synthesis

CHAPTER 10

SYNTHESIS

The aim of this thesis was to study the temporal and spatial responses of biomes to Pleistocene climate change in Latin America, with the specific aim of making spatial paleo-reconstructions based on fossil pollen records. The results of this thesis show that the spatial coverage of pollen records throughout Latin America is impressive and opens up possibilities for spatial mapping of continuous coverages (Chapter 2). Especially the last 10,000 years are well represented. The temporal resolution of sites is especially high in the Northern Andes region, but many sites are disregarded at forehand because of poor chronologies (Chapter 3). Temporal uncertainty is a main limitation to make spatial reconstructions based on fossil pollen records, but a selection of records that fulfil certain quality standards does allow multi-site synthesis work. When comparing changes over time between sites and specifically during the last 2000 years, few regions show synchronous responses of pollen associations. Differences between pollen records are larger within mountainous areas compared to those situated in lowland areas (Chapter 4). This suggests that the latter are more suitable to create interpolated maps between pollen records, but the number of records and their location within the study area influence the quality of the spatially explicit models in GIS (Geographical Information System, Chapter 5). In mountainous areas, biome surface maps can be obtained by making assumptions on the elevational gradient that biomes occupy. This means that on a local scale, biomes follow the same order from the lowlands to the highlands and a similar elevational range is seen throughout a region. Therefore, a single fossil pollen record can be translated into a biome surface map to understand how the landscape features influenced the biomes' distributions in terms of surface availability and 'connectivity' (the potential movement or genetic interchange between different populations) (Chapter 6). As the previous chapter showed that the degree of biome connectivity is a constantly changing feature through time (as species and biomes shift their distributions as a response to climate change), in Chapter 7 I develop a conceptual framework to argue that historical connectivity is a key feature in understanding contemporary (mountain) biodiversity. That historical processes should be taken into account to understand current patterns of species richness also becomes apparent when considering the influence of long term geological processes on mountain biodiversity (Chapter 8). Importantly, spatially explicit models of biome distributions over longer time scale facilitate the integration of disciplines for hypothesis testing on the importance of mountain topography and historical connectivity. The integration of long pollen records and topographic characterization of mountains makes a much stronger assemblage of the biogeographical history, confirming the importance that historical connectivity have had on current species richness patterns (Chapter 9).

In this synthesis chapter I discuss the different research questions I posed in the beginning of the thesis and will link the implications of my results in the context of related research.

A. LOCATION: AVAILABILITY AND DISTRIBUTION OF POLLEN DATA IN LATIN AMERICA

The first question I address covers the basics of spatial analysis, namely '*where are what kind of data*' located. In this case:

1) What is the spatial and temporal availability, and distribution of paleoecological research done by fossil and modern pollen studies in Latin America?

The relevance of this question is shown by the absence of Latin American pollen records in global and regional synthesis work on paleo-reconstructions, e.g. Wanner et al. (2008), Bartlein et al. (2011) and Villalba et al. (2009). To achieve the best projections and predictions of future vegetation responses to ongoing warming and other global changes, we need to make use of the best available data (Wolkovich et al., 2012) and exploit the full potential of palynological data. In terms of availability, the number of records and publications in Latin American has increased substantially during the last decade, with peaks of 60-70 publications per year between 2010 and 2012 (Chapter 2. Fig. 7). The number of fossil pollen records in Latin American exceeds what has been reported for the European Pollen Database (Brewer et al., 2016; 1400 and 1200 respectively), stressing the huge bulk of data potentially available in the tropics. The majority of the fossil pollen records cover the last 10,000 years an overall tendency seen in pollen databases globally. The large number of Holocene (last 11,700 cal yr BP) records are widely distributed throughout Latin America, which is a positive outcome for current initiatives that focus on the last 6000 years (PAGES Landcover6k and LandUse6k workgroups) and the last 2000 years (PAGES2k workgroup).

2) Which regions are represented frequently enough in the Latin American Pollen Database to obtain statistically sound vegetation dynamics interpretations?

Paleoecological research in Latin America shows a clustered spatial distribution of study sites, meaning that certain areas and countries show a higher density of records than would be expected from a random distribution (Chapter 2. Fig. 1). There are modern pollen samples 'hotspots' in Honduras, Uruguay, Argentina, and at the border of Bolivia/Peru. In terms of fossil pollen records, countries like Colombia, Chile and Argentina initially outnumbered other countries until the 90s. During the past two decades large numbers of records have become available in countries like Brazil, Bolivia and Mexico. Geographically many fossil pollen records are found throughout the Andes, from Colombia down to Patagonia, along the coastlines of the Amazon basin, and the area of Yucatán. Research on Caribbean islands has been on the rise, although still scarcely studied compared to most mainland countries.

The question on which regions are represented frequently ‘enough’ is tricky, as thresholds are easily arbitrary. Studies on vegetation dynamics might be focused on a specific ecosystem or biome. Some biomes in the Latin American Pollen Database have been more intensively studied than others, and make up an important part of the database (Chapter 2, Fig. 10). Examples are the cool grass shrublands and grasslands of the high Andes, the páramos and the punas respectively, that have been studied since the early days of paleoecology in Latin America. Also studies in the warm temperate evergreen forest are relatively well represented. However, the latter studies are spread out over a larger geographical distance and spatial uncertainty nevertheless increases. A simple calculation of distance to the ‘nearest neighbour’ (the closest neighbouring fossil pollen record) can indicate the degree of uncertainty in undertaking a comparison between sites within a confound distance and within a certain period of time (Chapter 2, Fig. 3B). On the other hand, even if there is a relative short distance between sample sites, the topographic diversity of a region can add an increased element of complexity that can inhibit a sound spatially explicit model.

What has become apparent throughout this thesis is that there is no “silver-bullet” answer to the posed question here. Although spatially explicit models on vegetation dynamics seem more feasible in highly sampled regions, care should be taken in making interpretations over large spatial scales or topographically rich areas, and importantly without strong age models supporting the comparing records. The importance of quantifying temporal uncertainties is addressed in the following sections.

B. CONDITION: CHRONOLOGIES AND TEMPORAL UNCERTAINTIES

3) What is the temporal uncertainty of the Northern Andes and which periods are best suitable to create spatially continuous land cover maps?

There are 126 records that span the late Pleistocene to the Last Glacial Maximum transition (21,000 cal yr BP), and >20% of the total number of fossil pollen records (~ 1400) cover the Younger Dryas interval and the Pleistocene/Holocene transition (11,700 cal yr BP). There is an uneven coverage of younger time periods which is commonly seen in fossil pollen records as many lakes are formed after the last glaciation. This unexpectedly confirms that the “most recent” periods are best suitable to create spatially continuous land cover maps, but here I specify how this was calculated in this thesis in terms of temporal uncertainty.

During the recent years, the number of ages used for stratigraphic age models has trended upwards, meaning an increasing number of data control points (such as ¹⁴C-dates) are used to support and constructed chronologies (Chapter 2., Fig. 4). There are different ways to take into account the temporal uncertainty of fossil pollen records. For example, the ‘age frequency’ is a measure calculated by taking the number of ages relative to the length of the

time period covered by the pollen record sequence. This metric is used in Chapter 2 (Fig. 5), showing that there is a high spatial variation in temporal uncertainty as estimated by age frequencies. In other words, within the same region researchers have reference records with dissimilar age frequencies. As a result, interpretations on comparisons should be done cautiously.

Another way to estimate temporal uncertainty I addressed in Chapter 3 with a metric that besides age model control points also considers other variables such as the resolution of sampling depths. With this metric I calculated that the average temporal resolution of fossil pollen records in the Northern and Central Andes (Venezuela, Colombia, Ecuador, Peru) was c. 240 years, which falls within the upper range of values found for the European Pollen Database (50 and 250 yr; Giesecke et al., 2014) and which is below the temporal resolution estimated for North America (c. 500 yr), though a different metric was used in the latter (Blois et al., 2011).

4) Does the temporal resolution of the multi-site synthesis allow research on sub-millennium-scale climate variability?

Interest in sub-millennium-scale climate variability has increased recently to understand abrupt climate changes (rapid onset and duration ranging from 200 and 2500 yr; Urrego et al. 2016) during the last 50,000 yr BP. Understanding rapid climate variability could offer insights into current anthropogenic climate change. To support such research records need strong chronological framework that allows the identification of rapid events, and possible temporal leads and lags in responses (Urrego et al., 2014).

In this thesis I addressed this question focusing on a specific area of interest, namely the Northern and Central Andes. Numerous records are available from this region (Chapter 2), but the records and their corresponding age models vary substantially in terms of resolution, chronological control points and period of time assessed. I made a geochronological database gathering all the relevant metadata information on the available age models and recalibrated – where possible – age models to obtain an estimate of the temporal resolution of the fossil pollen records of the region (Chapter 3). After this procedure, the temporal uncertainty was calculated to be c. 240 yr which allows research on sub-millennium-scale climate variability. This mean error is effectively the temporal limit for mapping and engaging into inter-site synthesis research within the Northern and Central Andes.

C. TRENDS: CHANGES OF TIME BETWEEN SITES

5) Which time periods show synchronous responses of pollen associations and are there regional differences?

Andean forelands and Amazon lowlands are less well sampled compared to the Andean region, but records suggest a relatively high resemblance in terms of responsiveness to climate change in the past 2000 years. The lowland regions that are mainly moisture balance driven (lowland Colombia, Amazon basin, southeastern Brazil, and the pampean plains) show a tendency of wetter conditions during the past 1000 years but changes initiate at somewhat different moments in time (e.g. Chapter 4, Figs. 11 and 12). Temperature shifts are detected mostly in the highlands, but no clear pattern of change is clearly detectable with high certainty.

Supported by recent fossil pollen records with an increased temporal resolution and supported by high number of control datapoints (Chapter 2, Fig. 4 and 5), temporal and spatial dissimilarities between records appear to be more the rule than the exception. Previously it was more common practice to compare fossil pollen records from large distances within e.g. the Andes, but results from this thesis suggest that synchronicity in change might be an unlikely feature to look for.

Topographically rich areas, such as the Andes, show a high 'local-site-specific-variability' meaning that fossil pollen records that are within relatively short distance of 10s of kilometres, show remarkable differences in vegetation responses in terms of timing and direction of change (the latter meaning e.g. warmer or colder conditions). This was shown when subdividing South America in subregions and by making inter-, and intra-regional comparison of vegetation and climate dynamics during the last 2000 years (Chapter 4). The effect of topography on local-site-specific-variability is multifaceted. First of all, over the same distance the possible change in climate conditions is higher in mountainous regions than in lowland areas. Profound shifts in temperature or humidity within a few kilometres altitudinal and tens of kilometres latitudinal are common in the Andes (Marchant et al., 2001).

Secondly, the expression of climate modes (interannual to multidecadal climate variability; Chapter 4, Figs. 2-5) is spatially more diverse around mountainous areas. An example is the Northern Andes (Venezuela, Colombia and Ecuador) where moisture supply stems from distinct sources during the year. Here the morphology of the Andes (the three parallel running mountain ranges in Colombia and the high Andean plateau in Ecuador) influences a highly variable expression of climate modes. This is not surprising considering the complex interaction well known to exist between mountains and climate (Chapter 8). As a result, there seems to be a general lack of synchronicity in the responses of pollen associations within mountainous areas (Chapter 4, Figs. 8, 9 and 13), although interpretations should be

cautiously taken as human influence might have interfered with the climate signals, both in highlands as in lowlands.

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?

Spatially continuous maps of past land cover are of interest for a wide range of researchers. For instance, climate models would benefit from an increased understanding of land cover - climate feedback mechanisms (e.g. Villalba et al., 2009; Ahmed et al., 2013), and mapping the extent of human driven change of land cover drives discussions on the timing and the degree of human occupation (e.g. Amazon basin, Piperno et al., 2015; McMichael et al., 2017).

Fortunately, the increasing number of data in publically available databases facilitate continental scale synthesis work to identify temporal and spatial patterns of land cover change (e.g. Europe, Finsinger et al., 2017). Different methodologies to make spatially continuous maps of past land cover or biome types have been developed and implemented in Europe, e.g. REVEALS (Trondman et al., 2015), and pseudobiomisation approach (Fyfe et al., 2015). In South America, Marchant et al. (2002, 2009) engaged in displaying past vegetation dynamics by using the biomisation methodology, showing that plotted datapoints of pollen percentages of taxa can be similarly informative to show temporal changes of environmental change. Continuous past land cover maps are, however, still lacking.

In Chapter 5, I address this question here posed by taking a lowland study area with various fossil pollen records and by looking into interpolation methods that can convert pollen percentages to continuous maps of past land cover. In terms of mapping, one key conclusion was derived from this study, namely that the geographical location of pollen sites is an important determinant to be able to engage into spatially explicit models. Stated another way: pollen sites distributed more evenly over an area of interest facilitate a more effective interpolation, while a lineal transect of data points may only provide a limited amount of information relevant for regional and- spatial interpretations. Also the number of available datapoints influences the outcome of interpolations.

A topographically rich region calls for a different approach. In mountains biome surface maps can be obtained by making assumptions on the elevational gradient that biomes occupy. This means that biomes follow the same order from the lowlands to the highlands, and a similar elevational range is seen throughout a region. Therefore, a single fossil pollen record can be translated into a biome surface map to understand how biomes' distributions

changed through time. An example of this approach was shown in Chapter 6 in a mountainous region on southern Colombia.

In conclusion, the outcome of spatially continuous maps of past land cover can provide enriched insights into patterns not revealed by considering one record alone. Different approaches are suitable for different regions, but without a doubt more data points will make spatial output more robust for climate models and socio-ecological research to benefit from.

D. PATTERNS: POLLEN, MOUNTAINS AND BIODIVERSITY

7) How do the landscape features in mountains influence the distribution of plant associations under different climate conditions? (Chapter 6 and Chapter 7)

Forced by the plethora of changes during the Pleistocene, species migrated to new locations and/or previously unused segments of their ecological range, while other species were overwhelmed by the new constraints and rate of change, and went extinct. Some mountains offered a safe harbour for species to reside and overcome climate variability, but topographic heterogeneity can impose both opportunities and challenges to its residents. The Pleistocene climatic cycles pushed species rhythmically along the mountain flanks, opening temporary dispersal pathways to new regions and/or dividing populations into isolated remnants.

Fragmentation is a spatial phenomenon causing reduction in surface area, increased edge ratio, the separation of habitat patches (increased isolation) and an increased total number of patches. The mountainous landscape is generally thought to cause mainly isolation as a result of fragmented populations. The degree of fragmentation that species endured in the past depends on the degree of *topographic flickering* within the mountain landscape (introduced in Chapter 7 and quantified in Chapter 9). This is determined by surface availability and degree of *connectivity* (the degree of potential flows of species through the landscape) along the elevational gradient, and the amount of time that species resided at certain elevations. These metrics help translate terrain ruggedness into an ecologically meaningful variable that considers spatial and temporal features of the landscape.

By defining the degree of topographic connectivity a spatially explicit model can show where reduced surface area and isolation is expected, leading possibly to extirpation of a biome (e.g. subpáramo in La Cocha-region as shown in Chapter 6 or páramo areas in the Western Cordillera as shown in Chapter 7). However, increased connectivity can also be expected if the topography of the mountain follows a distinct shape than the commonly anticipated 'cone'-shape. For instance, the landscape features of the Ecuadorian mountain

ranges facilitate rather than inhibit species dispersal. Thus, each mountain region has its own surface and connectivity profile along the altitudinal and latitudinal range, causing a complex pattern of possible corridors and barriers at different elevations.

As a result, different climate conditions cause through time a wide variety of spatial configurations of isolated patches, groups of patches and larger core areas. This complex interaction between topographic flickering and temporal climate fluctuations, in this thesis called the 'mountain fingerprint', is proposed to be one of the important causes that species richness differs between different mountain systems.

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)

In this thesis I propose that from a dynamic landscape perspective, there are four mechanistic processes that left an imprint in contemporary mountain biodiversity during these climate shifts, namely fragmentation, colonization, intermixing and hybridization (Chapter 7, Fig.1). Each process has been identified as a trigger for species diversification and has the potential to stimulate species richness and genetic differentiation. A system where all these processes are facilitated and dynamically interchanged is prone to radiations and increase of biodiversity during a relatively short period of time.

Depending on the intrinsic characteristics of the mountain fingerprint, the different mechanisms here proposed occurred in a spatially and temporarily diverse manner, and thus left a complex imprint on contemporary mountain biodiversity. Fragmentation can strongly influence the genetic structure of populations as isolation and consequently allopatric speciation enhance divergence and phylogeographic breaks. Fragmentation occurs in topographically rich areas due to certain elevation thresholds, such as valleys, but restricted cross-mountain gene flow is also caused by high-elevation ridgelines and extensive ice caps during wet glacial periods. Shifting climate conditions becoming optimal for connectivity can facilitate colonization (the successful establishment after dispersal to new areas) and as a consequence species might respond by increased diversification rates (e.g. Collevatti et al., 2015). Historical connectivity between formerly isolated areas also aids intermixing of species. Especially in clusters of isolated patches or population, species diversity can benefit from parallel diversification during isolated phases, while subsequent reconnection during climate optima facilitate interchange of species compositions. This phenomenon is known from oceanic islands (Ali & Aitchison, 2014; Gillespie & Roderick, 2014) and equally applies to isolated of alpine ecosystems in mountainous areas. Finally, connecting refugia or contact zones between refugia (after periods of allopatric speciation)

are also susceptible areas to hybridization, a process that contributes to the overall species richness through the formation of new lineages alongside the parental taxa.

In conclusion, the Pleistocene has been short (2.6 Myr) geologically speaking, but its dynamic character facilitated the accumulation of mountain biodiversity over several climatic cycles. Unsurprisingly, an increasing number of studies emphasize the importance of considering historical processes in understanding contemporary biodiversity (e.g. Araujo et al., 2008; Duncan et al., 2015). Without a doubt, the mountain fingerprint caused a complex pattern of consecutive processes of connecting core areas, species dispersal, disconnecting of populations, and local extinction as a result of the climate fluctuations during the past millions of years. Although these described processes might be difficult to disentangle in contemporary mountain biodiversity, overall differences between mountains could be related to the degree of connectivity that was facilitated within the mountain fingerprint (see conceptual comparison Chapter 9, Fig. 8). The rapidly advancing techniques in phylogenetic studies are expected to further enrich our insights into the Pleistocene legacy on mountain biodiversity, where historical connectivity will be playing an increasingly important role (see Knowles et al., 2016, Kolář et al., 2016)

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

A clear relationship between current climate and the mountain biodiversity is found for regions around the world, where both temperature and precipitation play an important role (Chapter 8). In regions where a strong orographic barrier is formed this relationship is very evident, meaning that the warmer and wetter sides of mountains are hosting more species. This pattern is clearly visible in the Central Andes and along the Himalayas, where respectively the South American monsoon and the South-East Asian monsoon interacts strongly with topography. The relationship between temperature and biodiversity is linear at a global analysis, meaning that with increasing temperature biodiversity follows a similar trend upwards (Chapter 8, Fig. 2). The relationship with precipitation is somewhat similar but after c. 1500 mm rainfall per year species richness tends to decrease. That climate plays a crucial role in shaping contemporary mountain biodiversity is in general terms not a surprising finding as numerous studies have suggested water availability and temperature to be key factors for predicting latitudinal and elevational gradients of biodiversity (e.g. Hawkins et al., 2003; McCain 2005; Field et al. 2009; McCain and Grytnes, 2010). However, when comparing between mountains important contrasting results are seen with varying importance of each variable (precipitation, temperature, and their seasonality) and sometimes contrasting relationships (positive or negative).

The non-linear relationship between species richness and precipitation resembles a hump-shape curve where the highest species richness levels are found around mid-precipitation levels but become negative towards highest precipitation. This pattern is observed in North America, East Africa and somewhat in High Asia (Chapter 8, Suppl. Figs 1-4). Increasing temperatures cause increased species richness in all studied mountains, but temperature range (difference between the highest and lowest temperature during the year) might have a positive, e.g. North America, or negative effect, e.g. High Asia. In North America and the Andes, precipitation seasonality plays a positive role related to species richness, while an opposite pattern is observed in Eastern Africa. This inter-mountain analysis convincingly shows that although temperature and precipitation are strong predictors of global patterns of mountain biodiversity, their interactions vary between mountains.

The relationship between deep time geology and species richness is complex, and there is an ongoing discussion if mountains were biodiversity cradles (where species originated and consequently diversified to other regions; e.g. Dick & Wright, 2005) or museums (where species survived relatively long 'stable' periods of time with low extinction rates, e.g. Harrison and Noss, 2017), or possibly both (López-Pujols et al., 2011). In Chapter 8 a quantitative assessment is presented to deepen our understanding of the relationship between deep-time geological processes and biodiversity.

It is shown that deep-time geological processes, here represented by long-term erosion and apatite fission track cooling ages, are positively related to species richness in regions such as High Asia, where short term erosion plays an equally important role. This is suggested to be related to the region's diverse geological history with areas of high geological activity and terrain ruggedness alongside older formations. It's also a region with substantial environmental heterogeneity reflected in high biodiversity. In the relatively young Northern Andes, relief and short term erosion are the most prominent geological variables, suggesting that recent processes interacting with current topography leave a strong imprint on species richness. Interestingly, in North America and East Africa, cooling age and long term erosion are negatively related with biodiversity. These regions are probably also the oldest formations in the analysis here completed. The highest elevations might be relatively young but mountain building consists mainly of ancient features. Long term erosion processes might have weathered the landscape to such extent that topography lacks ample heterogeneity, and as a result a lack of topographic ruggedness might tamper regional species richness. Considering the geographical and geological differences between mountains it is not surprising that this relationship is not straightforward and has been difficult to disentangle. The future integration of geology, biology and phylogeography is expected to enrich insights into the complex history of mountain biodiversity.

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