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Reconstruction of late Holocene forest dynamics in northern Ecuador from biomarkers and pollen in soil cores

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ABSTRACT

Centuries of human interference have led to large scale reduction of montane forests in the northern Ecuadorian Andes. As a result the natural position of the upper forest line (UFL) in the area is now subject of scientific debate, which is hindering sustainable reforestation efforts. Uncertainty is fuelled by insufficient precision of fossil pollen spectra to reconstruct the natural UFL position. Here we tried to resolve this issue by using biomarkers, i.e. plant species specific patterns of *n*-alkanes and *n*-alcohols, preserved in soils in the northern Ecuadorian Andes as additional proxy to reconstruct the natural UFL position. To unravel preserved biomarker patterns we used the recently developed VERHIB model, and for the first time assessed its applicability in soil archives. Changes in Holocene biomarker-based vegetation composition were directly compared to changes in pollen-based vegetation composition from the same soil profiles. Both proxies proved to be complementary and a combined application allowed for a more accurate reconstruction of past vegetation than with pollen analysis alone. We found that the present-day UFL in the study area has not been significantly depressed by human interference and was at 3650 m maximally during late Holocene times. For the moment of post-glacial forest development we found a migration lag between pollen (earlier) and biomarkers (later). This reflects the difference between the non-transported biomarker signal showing spot-dating (thus in paleoecological studies functionally equalling the information from plant macro-remains in peat bogs), and the upslope wind-blown pollen signal showing an upslope forest expansion up to over a millennium ahead. The combined pollen-biomarker approach in soil cores shows great potential for vegetation reconstruction. However, more research of biomarker consistency and preservation is needed before application in other environments.

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1. Introduction

Prior to the onset of massive human interference, the higher parts of the northern Ecuadorian Andes were characterized by montane forests consisting of upper montane rain forest (UMRF), subalpine rain forest (SARF) and at altitudes above the upper forest line (UFL) tropical alpine grasslands (páramo) (Moscol-Olivera and Cleef, 2009a,b). Centuries of human interference in the area have replaced large stretches of forest at lower altitudes with agricultural land, but are also believed to have depressed the UFL through practices of clear-cutting and burning (Laegaard, 1992; Lauer et al., 2001). Nevertheless, the extent of human induced depression of the UFL remains subject of scientific debate. Two contrasting theories suggest that in northern Ecuador the natural UFL position is at either 3600 m above sea level (Wille et al., 2002; Bakker et al., 2008; Moscol-Olivera and Hooghiemstra, 2010) or 4100 m (Laegaard, 1992; Lauer et al., 2001). This uncertainty illustrates our limited understanding of the response of the UFL in tropical ecosystems to anthropogenic impact and is hindering a sustainable strategy for reforesting areas in the frame of REDD+-driven activities to reduce atmospheric CO_2 (Dulal et al., 2012).

The uncertainty about the altitudinal UFL position relates to the proxies used to reconstruct past vegetation dynamics in tropical montane areas. The most common proxy is the analysis of fossil pollen and/or the stable carbon isotope signal preserved in lacustrine or peat sediments (Street-Perrott et al., 1997; Mayle et al., 2000; Clark and McLachlan, 2003). Also plant macrofossils and pollen influx values may be indicative (Tinner et al., 1996). However, the altitudinal resolution of a UFL reconstruction based on pollen analysis alone is limited by the dispersal of pollen by wind prior to deposition (Tinner et al., 1996; Hicks, 2006; Ortu et al., 2006). Within the context of a UFL reconstruction, pollen analysis is also hindered by the presence of pollen of plant families in which both forest and non-forest species are represented and that cannot be resolved beyond the family level, such as asteraceous pollen (Moscol-Olivera and Cleef, 2009a,b). Stable carbon isotope analysis in bulk organic matter in turn is only useful when the division

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into forest and non-forest species coincides with a division in a dominance of C3 and C4 plants as for instance in a transition of forest to savannah (e.g. Mariotti and Peterschmitt, 1994; Boom et al., 2001). This is not the case in our study area where most plants have a C3 photosynthetic pathway (Moscol-Olivera and Cleef, 2009a,b).

To overcome the mentioned limitations, we previously developed an application of biomarkers as additional proxy to reconstruct past shifts in UFL positions in the Ecuadorian Andes. It is based on patterns of plant-specific *n*-alkanes and *n*-alcohols with chain-lengths of 20–36 carbon atoms originating from the epicuticular wax layers on leaves and roots of higher plants (Kolattukudy et al., 1976) and preserved in suitable archives. The choice for *n*-alkanes and *n*-alcohols followed a thorough screening of a much wider range of extractable lipid classes present in vegetation and soils relevant for our study. These included carboxylic acids, diterpenes, phytosterols and pentacyclic triterpenes (Jansen et al., 2006a, 2007; Jansen and Nierop, 2009). In addition, non-extractable macromolecular components, particularly lignin, were considered (Nierop et al., 2007; Nierop and Jansen, 2009).

The use of *n*-alkanes and *n*-alcohols as biomarkers to reconstruct past vegetation is not new (e.g. Pancost et al., 2002; Hughen et al., 2004; Zech et al., 2009; Gocke et al., 2010). However, in most instances separation has been limited to reconstructing shifts in vegetation based on changes in concentration ratios of a limited number of *n*-alkanes and *n*-alcohols. The main reason is that concentration ratios of lipids of different chain-lengths are species-specific, and not the individual lipids themselves (Jansen et al., 2006a). As a result the preserved biomarker signal represents a mixture of a large number of *n*-alkanes and *n*-alcohols of various chain-lengths. When visually evaluating changes in such patterns it is infeasible to include more than a small selection of *n*-alkanes and *n*-alcohols present.

Therefore, to enable interpretation of the preserved mixed *n*-alkane and *n*-alcohol signal we previously developed the VERHIB model (VEgetation Reconstruction with the Help of Inverse Modeling and Biomarkers). We successfully applied biomarker analysis using the VERHIB model to reconstruct past vegetation composition using a peat sediment core from the northern Ecuadorian study area (Jansen et al., 2010). Upon combination of the results with those from a previous pollen-based reconstruction from the same peat core (Bakker et al., 2008), we found biomarker analysis to add important local detail to the reconstruction of regional vegetation patterns over time obtained through pollen analysis (Jansen et al., 2010).

However, the peat core where the combination of pollen and biomarker analysis with VERHIB was first applied is located at 3400 m, ca. 200 m below the current UFL in the area (Bakker et al., 2008). The only other suitable peat sediment in the area is located at 3810 m, 200 m above the present-day UFL (Moscol-Olivera and Hooghiemstra, 2010). The lack of suitable peat archives at potential past UFL positions hinders particularly the biomarker based vegetation reconstruction owing to the local nature thereof (Jansen et al., 2010). The general applicability of the multi-proxy combination of pollen and biomarker analysis would be greatly enhanced if it were not restricted by the chance occurrence of suitable peat sediments. An application of pollen and biomarker analysis in soil archives would greatly help to unequivocally reconstruct the past UFL in the northern Ecuadorian study area.

Therefore, the aim of the present study was: i) to assess for the first time the applicability of the multi-proxy combination of pollen analysis and biomarker analysis using the VERHIB model to reconstruct past vegetation dynamics from soil archives; and ii) to use the combined approach to resolve the issue of the natural UFL position in northern Ecuador.

2. Experimental setting

2.1. Description of the study area

The study area is located in a nature protection area, Guandera Biological Reserve, in El Carchi province in northern Ecuador on the Eastern Cordillera (Fig. 1). The forest and páramo belong to the Tropical Andes biodiversity 'hotspot' (Myers et al., 2000). Mean annual precipitation (MAP) in the area is around 1900 mm and mean annual temperature (MAT) is 12 °C at 3000 m.a.s.l. and lowers up to 4 °C at 4000 m.a.s.l.

Three soil profiles were used in the present study, located along an altitudinal transect intersecting the present-day UFL situated at 3650 m. Site G1 is located in the UMRF at 3500 m at GPS coordinates in WGS 1948 of N 0°35′27″/W 77°42′1″. Site G5a is located in a SARF forest patch at 3695 m at GPS coordinates N 0°35′41″/W 77°41′36″ and site G5b is situated in the páramo next to the forest patch at 3695 m and GPS coordinates N 0°35′41″/W 77°41′35″ (Fig. 1).

2.2. Present-day vegetation

Guandera Biological Reserve includes ca. 10 km^2 of relatively undisturbed páramo grass- and shrubland characterized by bunchgrass *Calamagrostis effusa* and stem-rosette *Espeletia pycnophylla* (Moscol-Olivera and Cleef, 2009a). The altitudinal vegetation zonation in the area shows at the forest-páramo transition a narrow belt of SARF of low stature in which species of Asteraceae, Ericaceae and *Hypericum* are dominant and with prominent occurrence of the loranthaceous *Gaiadendron punctatum* (Moscol-Olivera and Cleef, 2009b). In downslope direction SARF is transitional to a broad belt of UMRF including *Clusia flaviflora*-dominated forest. Around an elevation of 3550 m within continuous forest, isolated patches of páramo vegetation occur. Outside the reserve nearly all land at lower elevations is used for crop cultivation and cattle grazing. From the zonal forest belts remnants of forest are mostly located between 3300 and 3650 m. In the páramo belt some isolated patches of forest, including the one that harbors soil core G5a, occur up to 3700 m (Moscol-Olivera and Cleef, 2009b).

2.3. Soils

All soil profiles consist of a current soil in a thick tephra deposit overlaying a paleosol in a preceding tephra deposit. Between the current soil and the paleosol an overprinted zone is present that shows characteristics of both as a result of mixing through bioturbation (Tonneijck and Jongmans, 2008). Under the buried paleosol a remnant of a third ash layer is present (Tonneijck et al., 2008).

A striking difference between soil profiles from forest and páramo is a much thicker ectorganic layer (up to 1 m thick) in the forest, compared to a very thin ectorganic layer (<1 cm) in the páramo. As a result, forest soils in the study area classify as Histosols with Andic properties or as Andic Cambisols (Tonneijck et al., 2008), while páramo soils all classify as Andosols according to the World Reference Base (FAO, 2006).

Extensive analysis of the tephra stratigraphy of the soils in the study area revealed that bioturbation occurred over limited vertical distances (≤5 cm) and shifted upwards during soil formation (Tonneijck and Jongmans, 2008). This is the result of a combination of repeated tephra deposition and an extremely high accumulation of soil organic matter (SOM) (Tonneijck et al., 2010). As a result the chronological sequence of the SOM is preserved (Tonneijck and Jongmans, 2008). Table 1 summarizes the key soil properties of the three profiles used in the present study.

3. Materials and methods

3.1. Sampling procedure

At each of the study locations (G1, G5a and G5b) soil pits of approximately 1.5 m^2 surface area and a depth of 1.5 m to 2 m depending on the soil profile were excavated. From the pits, undisturbed soil cores were obtained using metal gutters of 75h × 5w × 4d cm. Samples were stored at 2 °C under field moist conditions prior to analysis.

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