Holocene upper forest line dynamics in the Ecuadorian Andes: a multiproxy study
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7. SYNTHESIS

The main aim of this PhD thesis was to obtain improved knowledge on the natural position of the upper forest line (UFL) at present and during the past 3000 years. We used a combination of vegetation analysis along an altitudinal gradient, analysis of the relationship between vegetation and modern pollen rain, and the analysis of the pollen signal in peat sequences and soils. This approach allowed us to examine the validity of the ‘high upper forest line’ hypothesis proposed by different researchers positioning the UFL under natural conditions at 4000 to 4100 m altitude. As a consequence, the páramo below this altitude is assumed to represent secondary vegetation in a formerly forested area. We also assessed the ‘low upper forest line hypothesis’ which claims a natural position of the UFL between 3600 to 3700 m elevation. As a consequence, páramo vegetation at higher elevations reflects a natural ecosystem which needs protection against unjustified destruction by creating forest plantations.

General conclusions are made by integrating the results of all chapters of this thesis. Results are placed in the broader context of South American palaeoecology and vegetation ecology. We also suggest here some topics for further research concerning UFL dynamics.

1. The multiproxy approach of the RUFLE programme

The original aim of ‘Reconstruction of the Upper Forest Line in Ecuador’, or RUFLE programme was to investigate past human induced lowering of the UFL in the northern Ecuadorian Andes at two locations with contrasting anthropogenic impact. The first study area chosen was the Reserve of Guandera, located near San Gabriel in the Eastern Cordillera. This site reflects one of the last remaining relatively undisturbed montane rain forest areas. The second location was the Ecological Reserve of El Angel located at approximately the same latitude in the Western Cordillera. This area has experienced significant impact from human activities such as burning and deforestation. The fact that both areas are in close proximity and subject to rather similar climatic conditions allows a direct comparison of the results.

The extensive field work needed to collect the basic data among other imponderables did not allow us to include the palaeoecological analysis of site El Angel in this project. But the present study, being a part of the RUFLE programme, succeeded to identify to which altitude the montane forest would have extended in the Guandera area in the absence of anthropogenic disturbance. Thereby, it provides a guideline for the reconstruction of the UFL in Andean ecosystems elsewhere. In addition, results from the present project give answers to the more fundamental question about which part of the UFL dynamics was caused by human interference and which part by natural climate change. As such, our results presented here will not only be of interest to local Ecuadorian scientists and policy makers, but will certainly provide valuable tools to predict the response of the UFL to climatic change.
This thesis also shows the high potential of integrated research when complex interactions between effects of human activities and natural climate change on the forest-páramo ecotone, and its resilience, are studied. Among the proxies complementary to fossil pollen proposed at the beginning of this research, macrofossil analysis was considered as essential because of the potential to reach a higher taxonomic level of plant identification and a better spatial resolution than pollen analysis alone (Birks 2001, 2003). Unfortunately, very few macrofossils were found in the different cores, presumably due to poor preservation conditions or catchment characteristics. Therefore macrofossil analysis was only presented for record G-15 (Chapter 5).

2. Vegetation types and altitudinal distribution

We characterised the structure and floristic composition of modern plant communities to provide a basis for the interpretation of palaeoecological records. Vegetation analysis along the studied altitudinal transects provided us with several key findings:

1) Our analysis shows that all the sampled páramo plots belong to the “paramo proper” belt (sensu Cuatrecasas 1934, 1954). The newly described phytosociological order Espeletio pycnophyllae-Calamagrostietalia effusae unifies all the zonal bunchgrass páramos of the Guandera and El Angel study areas.

2) The lack of similarity in floristic composition found between the seven forest communities detected in our research area and the montane forest communities of Colombia and Ecuador reinforces the biological importance and significance of the upper montane forest ecosystems in El Carchi province. This conclusion is also valid for the páramo cushion bogs described in our study.

3) In contrast with previous phytosociological studies in the region, the high Andean forest in Guandera is functionally part of the humid Andean forest zone (or upper montane forest zone) instead of reflecting a proper community at the association level (e.g. Bussmann 2002, Cleef et al. 1984, 2003, Rangel-Ch. et al. 2005). The Guandera area is also characterised by absence of a structural subpáramo vegetation.

4) Along altitudinal transects the vegetation shows a patchy structure due to four reasons:

   a) Páramo islands in high Andean forest. Open spaces with páramo-like vegetation mainly found in high Andean forest and Andean forest on the western slopes of Guandera Reserve between the UFL and about 3550 m. These páramo islands (Espeletio pycnophyllae-Diplosteophietum floribundi) are situated on exposed ridges in high Andean forest and are composed of a selection of taxa from the high Andean forest and bunchgrass páramo. These taxa represent for the larger part easily pioneering species.

   b) Forest patches in páramo just above the UFL. In Guandera the floristic affinity between
the high Andean forest plots and the forest patches in the páramo is significant to such a high degree that they only differ at the level of variants. This suggests that separation of the forest patch from the continuous forest belt occurred relatively recently, possibly during the last hundreds of years. Alternatively, the forest patch was colonised by species from the high Andean forest.

c) Forest patches in the páramo of El Angel. On small hills or steep slopes located between 3300 and 3700 m extant forest is present as patches smaller than 7 ha surrounded by páramo. Here, the high Andean forest, and the UFL as a consequence, have disappeared by clear cutting leading to a process of “paramización” downslope. Therefore the isolated forest patches at 3740 m around the lake basin of El Voladero could not be compared to the no longer existing high Andean forest stands in El Angel. The forest patches at El Voladero, located at an elevation assumed to be some 100 m above the natural UFL have a longer history of separation from the upper forest belt.

d) Forest patches in agricultural land in Guandera. These forests patches are located around 3300 m and are more diverse in species and more complex in layering compared to forest communities upslope. This was even true while these patches were recovering from recent disturbance (felling).

3. Vegetational evidence of human impact

At present-day the UFL in Guandera is very abrupt. Most probably this is a consequence of frequent and extensive fires in páramo along the high Andean forest. In the course of time repetitive fires have burnt down the shrubby structure of the subpáramo and the treelets and shrub of the uppermost fringe of the high Andean forest. Almost all the woody species became dwarfish and ground covering under the process of ‘paramización’. We estimated the modern UFL has been lowered by some 50 m due to these activities. On the steep slopes of Guandera the present UFL is at 3640 m. We estimated the natural position of the UFL at about 3660 m and subpáramo vegetation reached under natural conditions up to about 3680 m. Burning of the páramo may also explain we found in the pollen records a relatively low number of páramo species during the last centuries. In El Angel, the floristic composition of subassociation paspaletosum bonplandianum (lowermost open bunchgrass páramo), belonging to the association Gynoxyo-Calamagrostietum, suggests that it was probably located on formerly forested land. This suggestion is based on the absence of high Andean forest and the upper part of Andean forest combined with the presence of many weedy species. The presence of distinct species of *Hydrocotyle*, *Aethantus* and some pleurocarpous mosses, in the subassociation of *Paspalum bonplandianum* was an undeniably response to habitat alteration induced by human activities.
4. Modern pollen rain vs upper forest line reconstruction

The relatively undisturbed character of the vegetation in Guandera allowed us to establish relationships between vegetation cover and the proportion of pollen of these vegetation types in the pollen rain. This is the first study exploring this relationship in the northern Ecuadorian Andes. The main altitudinal vegetation zones in Guandera are the páramo, high Andean forest, Andean forest, and cultivated fields and meadows and these zones could be recognised in the modern pollen spectra. This allows to recognise these vegetation types also in the fossil pollen records.

Pollen spectra from moss polsters (including the pollen rain of a number of years) and pollen traps (in our case including the pollen rain of one year) were equally rich in pollen taxa, in total as well as on average per sample. The modern pollen spectrum collected in small patches of a vegetation type resembled the pollen spectrum collected in the surrounding matrix, whether a páramo patch in a forested area, or a forest patch in an area with páramo vegetation. This shows that the contribution from local vegetation sources prevailed above an elevational influence. It also suggests that small patches of forest located in the páramo may be difficult to detect in the pollen rain and the fossil pollen record. Here, analysis of plant biomarkers extracted from soil profiles (Jansen et al. 2008, 2010) can be helpful to better identify on a local scale the prevalent vegetation mostly at the species level. The modern pollen rain from samples collected in cultivated fields and meadows lacked pollen taxa typically found in páramo or forest. This shows that widescale deforestation in the Andes of Ecuador substantially reduces the pollen input from taxa of the Andean forest whereas intensive land-use in the páramo might diminish the proportion of taxa typical for páramo vegetation. We used pollination syndromes to better understand over- and underrepresentation in the pollen rain. Pollen taxa with wind-dispersed pollination syndromes were overrepresented, whereas pollen from entomophilous taxa were underrepresented or even absent. In total 29 out of 42 forest taxa were overrepresented in the pollen rain of páramo sites, while only 4 out of 12 páramo taxa were overrepresented in the pollen rain of forest sites. This points to a more effective upslope transport of pollen from forest into the páramo and a less effective downslope transport of pollen from páramo into forest. The pollen signals of *Clusia* (12-33%), *Ilex* (0.87-4.5%), and *Weinmannia* (18-85%), and to a lesser degree *Peperomia* and *Clethra*, are best to infer local presence of forest. Pollen from *Puya* (0.30-0.88%), Apiaceae (0.25-0.88%), Poaceae (30-70%), and Cyperaceae (13-29%) point at the presence of páramo vegetation.

The relationships we found between pollen rain and vegetation cover are encouraging to reconstruct forest or páramo from fossil pollen records and thus finding evidence of the altitude of the UFL in the past. However, some caution is needed as the data set is spatially and temporally limited (Jackson and Wong 1994). Moreover, it is not certain that the UFL in the past was as sharply defined as is currently the case. Additionally, we must
not systematically expect that forests were always identical to the current ones. Some plants such as *Hypericum laricifolium* or *Coriaria ruscifolia* near the UFL show a significant morphological plasticity reaching the herb layer under open conditions or the tree layer in closed forests (Young and Keating 2001). Also species with a poor pollen distribution do not contribute to a reconstruction of the past vegetation and are ‘palynologically silent’.

5. **Past upper forest line dynamics as a response to environmental change**

This study demonstrates that conventional pollen analysis is one of the most powerful tools for environmental and climatic reconstructions. Limitations of this method however, are the low spatial resolution, and the impossibility to distinguish beyond family level for some taxa.

Pollen of Asteraceae are abundant and cannot be distinguished beyond family level. The source area lies in forest as well as in the páramo and therefore an uncertainty in the determination of UFL positions cannot be avoided. This uncertainty is difficult to evaluate considering the different biotic and abiotic factors involved. Reduce this envelope of uncertainty is important when reconstructions from multiple sites are compared but also to improve comparisons with other proxies like biomarker analysis. The latter method helps to identify species from species-rich families present in more than one plant community, such as the Asteraceae (Jansen et al., 2010).

We reconstructed the altitudinal position of the UFL in Guandera on the basis of information from pollen, non-pollen palynomorphs, and plant macrofossils in a sediment core from a mire at 3400 m (Chapter 5) and 3810 m (Chapter 6), and from a soil monolith at 3820 m altitude (Chapter 6). These three records show the natural response of the forest-páramo ecotone to natural climatic change during the last 3000 years; the record from 3400 m shows the history up to 6000 years before present. During the last six centuries the records show evidence of anthropogenic impact such as presence of *Rumex* pollen reflecting weeds related to agricultural activities, and presence of *Dodonaea* pollen reflecting shrub vegetation on eroded soils. These signals of human impact coincide with the period when major political entities expanded around 800 cal yr BP in this region (Bakewell and TePaske 1981, Seltzer and Hastorf 1990).

Our main conclusion is that during the last three millennia the natural UFL reached a maximum altitude of 3700 m. This estimated elevation as well as the finding that human disturbance seems to have caused an artificial lowering of the UFL by some 50 m is in support of previous palynological studies by Wille et al. (2002) and also congruent with the vegetation analysis we performed in the study area (Chapters 2 and 3).

The pollen record from the soil monolith was not informative for the altitudinal position of the UFL but allowed to demonstrate that páramo vegetation had occurred at 3800 m
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elevation during the last 3000 years. Without doubt this study is in favour of the low UFL hypothesis and substantiated that páramo vegetation above 3700 m elevation represents a natural ecosystem. Where anthropogenic deforestation occurred by clear cutting and burning, páramo vegetation has expanded downslope indeed, a process locally known as ‘paramización’. The degree of downslope páramo expansion varies from some tens of metres (~50 m in Guandera) to an almost complete deforested landscape (such as in El Angel) where a degraded páramo vegetation is at many places transitional to the agricultural zone in the valleys. There is no evidence in the palaeoecological literature of the northern Andes that the validity of this conclusion is restricted to the study area. Therefore we conclude with precaution that our conclusions might be extrapolated to the northernmost Andes. At some places in the northern Andes the UFL attains higher altitudes, e.g. 3900 m in the Páramo de Papallacta, East of Quito (Lauer et al. 2001) and on the western slope of the Sierra Nevada del Cocuy in Colombia (Cleef 1981).

An increasing number of monocultures of rapidly growing trees such as Mexican pine, Australian eucalypt and Acacia decurrens are created in the Andes of Ecuador, Colombia and Venezuela to compensate CO₂ emissions. There is now compelling evidence that forest plantation of exotic tree species should not exceed 3700 m altitude. As a matter of fact native tree species have their limit at the natural UFL, thus at about 3700 m. Vegetation studies in forest plantations located in the páramo have shown that conifers cause a rapid acidification of the soil (Wesenbeeck et al. 2003, Farley and Kelly 2004). Therefore, elimination of present stands of conifer forests does not necessarily guarantee a rapid recovery of the natural páramo vegetation. It should be anticipated that the damage to the páramo ecosystem caused by the current practice of making forest plantations with exotic species in the páramo has a long lasting effect.

6. Predicting UFL migration

In the frame of Global Change studies there is currently much interest to collect understanding on the rate at which the UFL may advance in response to future global warming. Upward movements of montane forest have already been attributed to global warming, particularly affecting mountain ecosystems (Price 1999). In this respect Castaño (2002) showed that predictions and projections are still complex and driven by various factors. In mountains the altitudinal location of the UFL is mainly determined by the mean annual temperature and, to a lesser extent, by the mean annual precipitation. The UFL has its highest position in the Ecuadorian Andes on exposed, wet, and outer slopes of the mountains; on the drier inner slopes the UFL shows its lowest position. The difference is best explained by the effect of cloudiness and mist on the wetter outer slopes, which prevents extreme daily temperature fluctuations (Van der Hammen et al. 1980, 1981, 1995; Pérez-Preciado 1984, Lauer et al. 2001).

If it is assumed that growth and reproduction are mainly controlled by temperature a
rapid advance of the UFL would be predicted. Estimates of the likely migration rate under climatic warming may be based upon some simple rules. As mean annual temperatures are mainly determined by altitude Van der Hammen and González (1963) calculated for the area of the high plain of Bogotá an average lapse rate of 0.66°C /100 m vertical UFL displacement. In Parque Los Nevados transect area of the Colombian Cordillera Central Thouret (1983) found a lapse rate of 0.57 °C / 100 m on a West slope and 0.61 °C / 100 m on an East slope. Using warming rates of 4° to 5°C per century (IPCC 2007) we estimate that the UFL would migrate some 600 to 700 m upslope.

With an advancing UFL, we may expect species with restricted niche areas in the future including fragmentation or loss of habitats, or ultimately going extinct in the case of endemics. More generally, plant communities and species compositions are expected to change both as an effect of a possible climate change as well as an effect of altered competition following UFL shifts. However, it is difficult to predict how individual taxa will behave under such future conditions as seed production and seed dispersal as well as growth physiology of woody species in the upper montane forests of tropical South America are research fields that still remain largely unexplored. In South Ecuador the German-Ecuadorian DFG project has collected first data on these topics (Beck et al., 2008).

7. UFL position and sustainable land use options

The present study was triggered by multiple observations in Venezuela, Colombia and Ecuador that forest plantations were placed at elevations where, according to vegetation ecologist Cleef and paleoecologist Hooghiemstra, under natural conditions no forest occurred, or had occurred during the past millennia. These afforestation activities are almost exclusively based on exotic species like Pinus (and in less degree Eucalyptus), which can grow hundreds of meters above the natural UFL.

Many of these forest plantations aim to compensate CO$_2$-emissions in the frame of the international Kyoto Protocol. At first glance this policy may be considered a positive step as it contributes to reduce the level of soil erosion. However, it was applied in the Ecuadorian Andes without any previous ecological assessment of the consequences in the long term. Before any land use changes are being implemented we believe a ‘baseline study’ is needed to assess the justification of measurements. Through this PhD thesis we have clearly demonstrated that in our study area the natural UFL was maximally at 3700 m during the past 3000 years. We expect to contribute with our results to define sustainable management of the upper Andean forest and páramo ecosystems as well as to increase the extent of areas under conservation. However, we are also aware that the UFL position in other regions of the equatorial Andes can be different.
8. Further research

This study shows the added value of using information from various proxies, and various altitudes to establish past elevations of the UFL. Jansen et al. (e.g. 2008, 2010) developed in the study area the method of biomarker analysis. Plant waxes from leaves accumulating on top of the soil leave a molecular chemical signal in the soil. Tonneijck and Jongmans (2008) and Tonneijck et al. (2008) showed that the stratigraphy of these molecular components was preserved enabling to relate changes in molecular composition to a radiocarbon dated soil profile. Jansen (l.c.) showed that páramo and forest vegetation can be recognised on the basis of the biomarkers left in the soil. Biomarker analysis and pollen analysis in the same core showed that both proxies reveal a consistent result. This method is applicable to humid and humiferous soils and allows for a relatively rapid assessment of large vegetation shifts such as from forest to páramo or vice versa. While a pollen record can only be retrieved from basins, and therefore suitable sites are scarce in the landscape, soil profiles can be collected almost without restrictions and offer from a spatial point of view almost unlimited opportunities. In this way the largest possible number of sites at locations where the past UFL is assumed can be assessed. Biomarker analysis needs further development, for example by increasing the number of plants in the calibration set with a known biomarker spectrum.

With respect to research on the altitudinal position of the UFL several issues deserve further study. More sites in an undisturbed forest setting should be studied for vegetation patterns, modern pollen rain, and pollen-analysis to reduce the uncertainty of the present results. This is in particular true for the new biomarker proxy. An attractive location would be the natural *Clusia flaviflora* forests reported on several crests of the Western Cordillera in the area of Cotocachi-Cayapas Ecological Reserve, Imbabura Province, northern Ecuador (Rodriguez et al. 1994). Also the watershed area of the Paute River in southern Ecuador (Minga et al., unpublished data) offer a valuable setting. In order to evaluate rates of growth and succession in montane forests, permanent plot data are needed to assess the speed of UFL expansion.

Complementary information to estimate the forest dynamics near the UFL may come from altitudinal and temporal charcoal distributions and from diatom analysis, and for the recent past also from satellite data and other remote sensing techniques. Finally, models can be developed to assess the impact of climate change on the UFL incorporating characteristics of an energy balance, physiology, and reproductive biology.