BIOGEOGRAPHIC STUDY OF THE POLYLEPIS FOREST REMNANTS OF THE NORTHEASTERN CORDILLERA ORIENTAL OF ECUADOR AND IMPLICATIONS FOR THEIR CONSERVATION

by

SHEIKA ARAGUNDI LEÓN

(Under the Direction of Kathleen C. Parker)

ABSTRACT

This dissertation aimed to clarify the relative importance of environmental versus human factors in shaping the historic and modern distribution of *Polylepis* forest in the southern part of the northeastern Cordillera Oriental of Ecuador (491 km^2) and to assess the implications of its current distribution range for the genetic variation of the dominant tree species, *Polylepis pauta*, and for its floristic diversity.

Aerial photography interpretation revealed that *Polylepis* forest covered approximately 5% percent of the study area in 1956 and that around 3% of that forest cover was lost by 1999 through attrition and shrinkage. Spatial associations between fire, landslides and *Polylepis* forest loss combined with knowledge of indigenous land use practices, suggests an anthropogenic transition from forest to grassland in the study area. The analysis of allozyme variation from twelve *Polylepis* forest patches showed that the level of genetic diversity maintained by *Polylepis pauta*, coupled with low levels of genetic differentiation between populations within and among watersheds, is consistent with a more continuous historical range of the species in the southern part of the northeastern Cordillera Oriental of Ecuador. Results also identify the Oyacachi basin as the richest in *P. pauta* genetic diversity.

Overall floristic diversity recorded in the *Polylepis pauta* forest patches sampled in the Chalpi, Oyacachi and Papallacta basins was lower than that observed in floristic inventories of *Polylepis* forests of Ecuador, Peru and Bolivia. At the local scale, the Oyacachi basin was more diverse than the other two basins. The elevation range spanned by forest patches showed the strongest relationship to plant species diversity. The continuous forest of the Chalpi basin differed from forest fragments in terms of the lower occurrence of ferns and the high frequency of a grass that is indicative of transition from forest to páramo, *Neurolepis elata*. The virtual absence of *N. elata* from the other watersheds may be an anthropogenic condition. Phytolith analyses of *Polylepis* forest species have considerable potential for studies of the historical range of *Polylepis* forest in the northeastern Cordillera Oriental of Ecuador.

INDEX WORDS: *Polylepis* forest, distribution range, aerial photography, land cover change, allozyme variation, floristic diversity, fragmentation, phytoliths.

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DEDICATION

To the *Polylepis* forests.

The people of the Andes will always be tied to you

by the blessing of your presence,

by the tragedy of your absence.

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CHAPTER 1

BACKGROUND AND RESEARCH SCOPE

1.1 BACKGROUND

*Polylepi*s forests are the highest elevation Andean forests, generally found from 3000-4500 m elevation from Venezuela to central Argentina (Kessler 2002). As their name suggests, they are dominated by trees of the genus *Polylepis*, which consists of about 20 species, all believed to be wind pollinated (Salgado-Labouriau *et al.* 1977, Berry and Calvo 1989, Fjeldså and Kessler 1996) and wind dispersed (Van Schaik *et al.* 1993, Vélez *et al.* 1998). Their occurrence in isolated patches in ravines, steep rocky slopes and boulder fields in the Andes was long thought to be their natural pattern of distribution (Kessler 2002, after an extensive review of scientific papers by German researchers). It was not until the late 1950s that this view was questioned and an anthropogenic origin was suggested for the fragmented occurrence of these high elevation Andean forests (Ellenberg 1958 as cited by Kessler 2002). The hypothesis of a long-term consistent conversion of forest to pasture through frequent burning (Ellenberg 1979) has only started to gain support over the last decade (Fjeldså 1992, Lægaard 1992, Kessler 1995, 2002). Despite extensive research on the natural and human factors that limit *Polylepis* forest distribution (mostly in Venezuela, Peru and Bolivia), a consensus has still not been reached as to the relative importance of environmental vs. anthropogenic causes in determining the distribution of this particular type of forest (Kessler 2002).

The importance of *Polylepis* forests for the provision of environmental services and as refuges of unique biological diversity has been highlighted by several authors over the last decade (Fjeldså and Kessler 1996, Fjeldså 2002b, Herzog and Cahill 2002, Renison *et al.* 2002). From an environmental perspective, being the highest Andean forests, *Polylepis* communities accomplish crucial environmental services where no other trees can grow. As far as biological diversity is concerned, although more homogeneous than the montane forests below them, *Polylepis* communities exhibit high levels of diversity and endemism of epiphytes (Young *et al*. 2002) and birds, and are considered priority conservation sites for these groups (Fjeldså and Kessler 1996, Bruijnzeel and Hamilton 2000, Bubb *et al*. 2004). Wild relatives of certain Andean crops and medicinal species are also known to occur in these forests (Hensen 1991, Hijmans and Spooner 2001). The elucidation of the *Polylepis* forest natural range is not only a matter of theoretical concern; it is also a major issue in environmental and human welfare in this region (Fjeldså and Kessler 1996, Renison *et al*. 2002, Capriles and Flores Bedregal 2002).

Polylepis forests in Ecuador are restricted to the 3000-4100 m altitudinal belt of the central and northern Cordillera Oriental of the Andes (altitudinal limits may vary depending on local physical and climatic conditions; Cañadas 1983, Jørgensen and León 1999). These forests have been estimated to cover approximately 975,000 ha, or 3.78 % of the Ecuadorian territory (Cañadas 1983). Under natural conditions they would be bounded above by drier shrubby to grassy vegetation types and at lower elevations by either drier or humid tropical forest (Cañadas 1983, Balslev 1988, Lægaard 1992). Like most Andean forest relicts, Ecuadorian *Polylepis* forests are under severe pressure from cutting for fuel wood, burning, grazing and agricultural encroachment (Lægaard 1992, Lauer *et al.* 2001).

Despite their consideration as a regional and national biodiversity research priority, and their vital environmental role, knowledge of Ecuadorian *Polylepis* forests remains limited (Aldrich *et al*. 1997, Bruijnzeel and Hamilton 2000, Bubb *et al.* 2004), due in part to their inaccessibility and the difficulty of adequately sampling and identifying species-rich communities (Gentry 1995, Aldrich *et al*. 1997, Bruijnzeel and Hamilton 2000). Compared with *Polylepis* forests in Peru and Bolivia, the Ecuadorian counterparts have been the focus of little research and even less monitoring. Knowledge of the original distribution of *Polylepis* forest and the magnitude of loss over the past four decades of agricultural intensification is critical to assess the threats these forests face. Equally crucial is the assessment of the consequences of fragmentation on their floristic diversity and the genetic diversity of *Polylepis* stands and their potential as sources for restoration.

1.2 RESEARCH SCOPE

The southern part of the northeastern Cordillera Oriental of Ecuador is one of the few regions in the Andes where *Polylepis* forests exist as both patchy and continuous forest, and are still influenced by Andean people (DIVA 1997). The synergistic combination of these factors provides a unique opportunity to cast light on environmental versus human controls of the *Polylepis* forest present and its historical distribution, and to explore the associations of its current range with its diversity.

The area studied encompassed three adjacent river basins in the southern part of the Cayambe Coca Ecological Reserve (hereafter RECAY) and farther south (78°11’55”- 78°2’22”W, 0°10’34”- 0°25’34”), the Oyacachi, Chalpi and Papallacta river basins (approximately 491 km^2). Of these, the Chalpi river basin is the least disturbed, supporting a continuous cover of mountain forest from 2000 to 4000 m elevation. Both the Oyacachi and the Papallacta basins have been disturbed by conversion to pastureland and agricultural encroachment and dam and road construction. The Oyacachi river basin has been inhabited since the mid-16th century by the Oyacachis, a Quechua community whose population (approximately 551 people) occupies 44,500 ha (11.0%) of the RECAY (Ohlson 2001). Their territory, located within the 1800 to 4000 m altitudinal belt, is primarily grass páramo and pastureland (63 %) with smaller areas of forest and agricultural land (Fundación Antizana 1998, Ohlson 2001).

This investigation aimed to clarify the relative importance of environmental *vs.* human factors in shaping the historic and modern distribution of *Polylepis* forest in the southern part of the northeastern Cordillera Oriental of Ecuador (491 km^2) and to assess the implications of its current distribution for its floristic diversity and genetic variation of the dominant tree species, *Polylepis pauta* . The second chapter of the dissertation focuses on cover changes experienced by *Polylepis* forests in the Oyacachi, Chalpi and Papallacta basins over four decades of agricultural intensification between 1956 and 1999. Land cover maps of 1956 and 1999 are generated from interpretation of aerial photography of 1956, 1965, 1993 and 1999 and subtracted in a GIS environment to derive a matrix of cross-tabulated aerial statistics on categories of land cover change. *Polylepis* forest cover changes are then interpreted in the light of the spatial distribution of cover loss or gain and manifestations of environmental processes and human activities.The third chapter investigates the distribution of genetic variation in twelve populations of *Polylepis pauta* distributed in the Oyacachi, Chalpi and Papallacta watersheds to assess whether the levels and patterns of genetic diversity observed are consistent with that expected for a more continuous historical range. Isolation by distance and spatial attributes of forest patches are incorporated into the study to increase our understanding of genetic differentiation among subpopulations of *P. pauta* in the area.The fourth chapter examines the vascular floristic diversity of the *P. pauta* forest patches studied in the previous section with the aims of detecting changes in species diversity with elevation and assessing the relative importance of the spatial attributes of remnants on the distribution pattern of plant diversity within them. Because *Polylepis* forests occur on steep slopes whose susceptibility to landslides, and consequently to canopy openings, increases with elevation, estimation of canopy closure at different elevations is incorporated into the study to provide a more comprehensive explanation of floristic variation within the elevation range encompassed by these forests.The fifth chapter explores the potential of phytoliths to study the historical distribution of *Polylepis* forests. Opal phytoliths extracted from selected *Polylepis* forest species are assessed in terms of both the uniqueness of their morphology and their frequency to produce a set of diagnostic *Polylepis* forest phytoliths which can be used as standards and compared to phytoliths from soil beneath the páramo matrix to determine whether *Polylepis* forests preceded the vast extensions of páramo which today characterize the high Andes.

1.3 SIGNIFICANCE

This work aims to expand our understanding of the influence of natural and anthropogenic factors in shaping the distribution and diversity of forest communities in tropical montane areas. This investigation also intends to increase our knowledge of the consequences of fragmentation on montane species with restricted ranges. In a practical sense, this dissertation presents a multi-scale methodological approach for the study of forest communities in remote areas which can be adapted as necessary as the techniques and procedures used here are refined and imagery resolution is improved.

CHAPTER 2

Four decades (1956 -1999) of *Polylepis* FOREST COVER CHANGE IN THE NORTHEASTERN CORDILLERA ORIENTAL OF ECUADOR

2.1 INTRODUCTION

Although the values of montane forests as protective cover of headwater catchment slopes and stabilizers of water quality and stream flow have long been acknowledged, the rather exclusive additional hydrological benefit of cloud forests on tropical mountains is a more recent finding (Bruijnzeel and Proctor 1995, Aldrich *et al*. 1997, Bruijnzeel 2000). Because of fairly constant interception of fog drip and lower water intake by cloud forests, stream flows originating from these forests tend to be larger and more dependable during dry periods than those from montane forests at higher latitudes (Bruijnzeel and Hamilton 2000, Bubb *et al.* 2004).

In the Andean cordillera a rare type of evergreen forest provides these environmental services at the highest elevation, under conditions that are typically adverse to tree growth, *i.e.*, contrasting daily temperatures, steep slopes and waterlogged peat soils (Fjeldså and Kessler 1996, Fjeldså 2002, Herzog and Cahill 2002, Renison *et al.* 2002). This forest, named '*Polylepis* forest' after the dominant tree genus (*Polylepis* spp.), is generally found from 3000 m to 4500 m elevation from Venezuela to central Argentina (Kessler 2002). Until recently, their notably patchy distribution across the Andean cordillera was considered to be the result of physical factors above the tree line (Kessler 2002 after an extensive review of research on the distributional range of *Polylepis* spp.). In the late 1950's an anthropogenic origin was suggested for the fragmented occurrence of these high elevation Andean forests (Ellenberg 1958 as cited by Kessler 2002, Ellenbergh 1979). Although there is growing evidence that the current relatively disjunct distribution of *Polylepis* forests is more a consequence of anthropogenic activity than biophysical limiting factors, much of this evidence comes from studies carried out in Peru and Bolivia (Fjeldså and Kessler 1996, Hensen 2002, Herzog and Cahill 2002). In fact, the relative importance of biophysical factors appears to vary regionally (Fjeldså and Kessler 1996, Vélez *et al*. 1998, Kessler 2002). Given the critical role that these forests perform in the conservation of water resources, their conversion to agriculture or grazing has the potential to profoundly change the hydrology of the area (Bruijnzeel and Hamilton 2000, Fjeldså 2002). Clarifying the relative importance of environmental *vs*. anthropogenic factors in shaping the distribution of *Polylepis* forests is therefore a matter of environmental and human welfare in this region (Fjeldså and Kessler 1996, Renison *et al*. 2002, Capriles and Flores Bedregal 2002).

Knowledge of Ecuadorian *Polylepis* forest distribution and extent is restricted to records of its presence at specific locations as indicated by *Polylepis* spp. collections at QCA and AAU herbariums of the Universidad Católica del Ecuador and the University of Århus respectively, distribution models based on both climatic variables (Cañadas 1983) and indicator species (Baquero *et al.* 2004), and a coarse-resolution assessment of its extent at a national level (Sierra 1999). In Ecuador, *Polylepis* forests are restricted to the 3000-4100 m altitudinal belt of the central and northern Cordillera Oriental of the Andes (altitudinal limits may vary depending on local physical and climatic conditions; Cañadas 1983, Jørgensen and León 1999) and to cover approximately 975,000 ha, or 3.78 % of the Ecuadorian territory (Cañadas 1983). Under natural conditions it is believed that these forests would be bounded above by drier shrubby to grassy vegetation types and at lower elevations by either drier or humid tropical forest (Cañadas 1983, Balslev 1988, Lægaard 1992).

The southern part of the northeastern Cordillera Oriental of Ecuador is one of the few regions in the Andes where *Polylepis* forests exist as both patchy and continuous forest, and are still influenced by Andean people (Skov 1997). Despite the unique opportunity provided by the synergistic combination of these factors to cast light on human vs. environmental controls of *Polylepis* forest distribution, this issue has not been investigated in this area. Possible reasons for this are the relative inaccessibility of forest patches in the area (this was particularly true before the construction of the road connecting the Oyacachi and the Papallacta settlements in 1994) and limited availability of high resolution satellite and airborne imagery. Attempts to monitor *Polylepis* forest cover with SPOT and Landsat Thematic Mapper imagery in Bolivia yielded poor accuracy and insufficient resolution for change detection and canopy cover assessment (Larrazabal De la Vía 2004). Aerial photography interpretation is a powerful tool to accurately characterize vegetation cover of rugged montane areas (Welch *et al.* 2002) and detect change (Lo and Shipman 1990); however, its use to study *Polylepis* forest has only started to be explored. Although most of the fragmentation of *Polylepis* forests in the northeastern cordillera oriental of Ecuador likely preceded the Spanish conquest (Jameson 1858, Grubb *et al.* 1963), further loss probably has occurred during and after the early 1960’s when agrarian reform was implemented by the Ecuadorian government to promote agricultural development in rural areas (Gondard and Mazurek 2001).

The present study aimed to determine the extent and nature of the changes in *Polylepis* forest cover in the northeastern Cordillera Oriental of Ecuador between 1956 and 1999 through the use of aerial photography and satellite imagery in a GIS environment. Assessing the influence of human factors in the distribution and stand size was the major focus of the present assessment of *Polylepis* forest cover change in the four decades of study.

2.2 MATERIALS AND METHODS

2.2.1 STUDY AREA

The area studied was approximately 491 km² in size and located in the southern part of the northeastern Cordillera Oriental of Ecuador, within the boundaries of the Cayambe Coca Ecological Reserve and farther south (78°11’55”- 78°2’22” W, 0°10’34”-0°25’34” S Figure 2.1). Incorporated into the Ecuadorian National Protected Area System since 1970, the Cayambe Coca Ecological Reserve (hereafter RECAY) encompasses an altitudinal gradient ranging from 750 to 5750 m and includes 81 lakes in an area of 403,000 ha (Fundación Antisana 1998). The study area includes three adjacent river basins in the southern part of the RECAY, the Oyacachi, the Chalpi and the Papallacta basins. Of these three, the Chalpi river basin is probably the least disturbed, supporting a continuous forest cover from approximately 3000 m to 4200 m elevation. The Oyacachi river basin has been inhabited since the mid-16th century by the Oyacachis, a Quechua community whose population (approximately 551 people) occupies 44,500 ha (11.0%) of the RECAY (Ohlson 2001). Their territory, which is located within the 1800 m to 4000 m altitudinal belt, is primarily grass páramo and pastureland (63%) with smaller areas of forest and agricultural land (Fundación Antizana 1998, Ohlson 2001). Significant loss of montane forest to pasture is believed to have occurred from the early 1960's to the early 1990's during the implementation of the agrarian reform by the national government (Gondard and Mazurek, 2001). At present, primary threats to natural resources in the area are deforestation, burning, forest conversion to pasture, construction of dams and roads and uncontrolled hunting and fishing (CDC 1997, Skov 1997, Ohlson 2001).

2.2.2 MATERIALS

The study used a Landsat Thematic Mapper (TM) image from April 1999 (spatial resolution 30m and swath width 135 km) downloaded from the U.S. Geological Survey website, along with 4 sets of aerial photography prints from 1956, 1965, 1993 and 4 digital maps of scale 1:50,000 of contours (2) and lakes (2) obtained from the Instituto Geográfico Militar of Ecuador. The aerial photography set from 1956 had a scale of 1:50,000 and consisted of 5 photographs in one flight line covering approximately two thirds of the longitudinal width of the study area in its central part. The 1965 set had a scale of 1:50,000 and included 21 aerial photographs split into 3 flight lines (7 photos per flight line) covering the whole study area (Figure 2.3). The 1993 and 1999 aerial photography sets had a scale of 1:60,000 and overlapped in approximately one third in the central part of the whole longitudinal width of the study area. The 1993 set consisted of 10 photographs distributed in 2 flight lines over the west sideof the study area, while the 1999 set consisted of 5 photographs of one flight line over the east side of the area surveyed. The digital contours map had a contour interval of 40 m.

2.2.3 ORTHORECTIFICATION OF AERIAL PHOTOGRAPHY

The 1999 Landsat TM image was registered to the Universal Transverse Mercator (UTM) in ERDAS IMAGINE 9.1 software (developed by Leica Geosystems Inc.) using GCS Clarke 1866 geographic projection (Clarke 1866 datum). The digital maps of lakes were used as source of ground control (x and y coordinates) for image registration using polynomial geometric correction. The aerial photography prints were scanned at 1200dots per inch (dpi) in *.TIF file format and photogrammetric orthorectification was performed in ERDAS 9.1 using Direct Lineal Transformation, and Nearest

Neighbor resampling. The registered Landsat TM image was used as the reference file for x and y coordinates, and a 40 m resolution digital elevation model (DEM) derived from the digital contour maps in ArcGIS were used as the reference file for the z values. The Landsat TM image and the orthorectified photographs of 1956 and 1965 were then imported into ArcMap 9.2 for heads-up on-screen digitizing of land cover classes to generate the 1956 land cover map of the area surveyed (Figure 2.2).

The land cover map for 1999 was derived through the same procedure from a mosaic of orthorectified aerial photography for 1993 and 1999. In both cases the significant proportion of overlap between the photographs of the two integrated dates permitted assessment of the degree of similarity of the two dates; this assessment indicated that the aerial photography assemblages of two dates were equivalent to a one-date series (Figure 2.3).

2.2.4 AERIAL PHOTOGRAPHY INTERPRETATION

Land cover classes were interpreted through stereoscopic observation of pairs of original aerial photography prints with a Dietzgen mirror stereoscope (magnification 2.5x to 6x) and a Bausch & Lomb zoom stereoscope (magnification 10x). Land cover classes identified were then traced on acetate and the resulting land cover overlays were used as a referemce for on-screen digitizing of land cover on the orthorectified aerial photographs in ArcMap 9.2 (ESRI 2006).

Ground truth points of *Polylepis* forest, mixed shrub páramo *Polylepis* forest, sparse shrubs/ *Polylepis*, shrubland and páramo were collected during field surveys undertaken from June to July 2006 and 2007 and were used to improve classification accuracy (Figures 2.4 through 2.7). Ground truth points were particularly important for differentiating dense *Polylepis* forest from mixed shrub páramo *Polylepis* forest.

2.2.5 ANALYSIS OF *Polylepis* FOREST COVER CHANGE

Land cover change analysis was carried out in ArcMap 9.2 and consisted of overlaying the land cover maps of 1956 and 1999 and subtracting land cover polygons to produce quantitative areal data of the overall land cover changes. The procedure generated an associated matrix of cross-tabulated categories of land cover change. Losses from one category to another are expressed in the matrix rows and gains in one category at the expense of another in the matrix are expressed as columns. The percentage loss from each category was computed by multiplying the areal loss in each cover class by the percentage (expressed in decimals) of the area surveyed initially represented by that cover class. Land cover classes that involved *Polylepis* spp. were emphasized in the analysis. Land cover changes were then interpreted in the context of spatial distribution, and manifestations of physical processes and human intervention.

2.3 RESULTS

2.3.1 LAND COVER CLASSES

Ten land cover classes were identified from aerial photo interpretation: fire scar, human use, lake, landslide, montane forest, páramo, dense *Polylepis* forest, shrubland, mixed shrub páramo/*Polylepis* forest and sparse shrub/*Polylepis*.

Fire scars were identified on aerial the photographs by their relatively round shapes and sharp boundaries and their location, usually adjacent to *Polylepis* forest remnants. Recently burnt sites looked black and had some texture due to the burned vegetation (Figures 2.8 and 2.9), while older fire scars had a very light tone (reflection of poorly covered dry soil, Figure 2.10 and 2.11). Human-use areas were characterized by their patchy appearance and sharp, straight boundaries separating the elements within the mosaic (Figure 2.12). Lakes appeared as very dark smooth surfaces with sharp boundaries (Figure 2.13). Landslides in areas of high relief had a bright tone and a characteristic narrow elongated shape (Figures 2.14 and 2.15). Montane forest areas were evident on photos as relatively large surfaces along the rivers with a dark gray tone and grainy texture (Figures 2.16 and 2.17). Páramo cover appeared in the form of a light background matrix or as light round patches in the tops of hills and mountains (Figures 2.16 through 2.19). Dense *Polylepis* forest showed as dark patches of fine-grained texture embedded in the páramo matrix (Figure 2.14) and as a darker, less textured belt above the montane forest (Figure 2.16 and 2.17). Delimitation of the boundary between montane and dense *Polylepis* forests (Figures 2.16 and 2.17) often required the use of the10x power of the zoom stereoscope. Mixed shrub páramo/*Polylepis* appeared as dark, nearly black thin threads on a grey to light background of shrub páramo (Figures 2.19 and 2.20). In this land cover class characterized by significant heterogeneity, predominance of woody shrubs such as *Miconia latifolia*, *Monnina loxensis*, *Monticalia myrsinites* and *Gynoxis hallii* and grass species such as *Neurolepis aristata* and *Neurolepis elata* relative to *Polylepis* forest was variable. In some areas within this land cover class, *Polylepis* forest would predominate and look more or less defined, but they were not digitized as they did not appear consistently across the different dates for which aerial photography was available. Sparse shrub/*Polylepis* often occurred at the uppermost part of mountains, immediately below páramo areas and was characterized either by a chunky mosaic of very small dark and gray patches and páramo (Figure 2.21) or by black fine-grained bands in a páramo background (Figure 2.22). Shrubland areas were evident in the lowlands as dark gray surfaces with little or no texture (Figure 2.23). Subtle changes in the density of shrubs vs. *Polylepis* over time in the sparse shrubs/*Polylepis* land cover class can be seen in Figures 2.24 and 2.25.

2.3.2 LAND COVER MAP OF 1956

Dense *Polylepis* forest covered approximately 25 km² (5 %) of the study area in 1956 (Table 2.1). Most of its range was continuous in the western part of the study area, towards the Amazon basin, and heavily fragmented towards the inter Andean valley (Table 2.1, Figure 2.26). Approximately 20 % (98 km², Table 2.1) of the study area, in the southwest quadrant was covered by a continuous belt of mixed shrub páramo/*Polylepis* forest. Sparse shrub/*Polylepis* occurred mostly from the center towards the northwest within a páramo matrix and covered approximately 4 % of the study area. It often coincided with steep terrain heavily affected by fire scars and landslides (Figure 2.26). Thin bands of sparse shrub/*Polylepis* occurred beside landslides and fire scars but were more common by the former; in contrast, broader areas of sparse shrub/*Polylepis* were more common by fire scars. Landslides occurred throughout the whole area surveyed but tended to be narrower and more frequent in the northwest. Several fire scars occurred as very narrow belts (10 to 15 m wide) surrounding forest patches or at the uppermost altitudinal limit of *Polylepis* forest but were not digitized due to image spatial resolution and digitizing constraints. Occurrence of fire scars at the uppermost limit of *Polylepis* forests indicated that ignition in certain cases was initiated at the páramo ridge in the direction of the forest. This observation was confirmed by B. Iñuca (Quichua community leader, pers. com. 2008).

Montane forest formed a continuous belt in the Oyacachi, Chalpi and Papallacta basins covering approximately 18 % of the study area in the west (Table 2.1, Figure 2.26). Páramo occurred as a continuous cover over nearly half the study area stretching from the center towards the west (inter Andean valley) and the northwest. Most of the recorded patches of páramo (Table2.1, Figure 2.26) occurred on the caps of mountains towards the southeast.

Shrubland was usually found at the lowest elevation in the study area and most of its range was restricted to a large continuous patch in the south (Figure 2.26). In this classification, "human use" refers exclusively to human settlements; although a significant part of the páramo is used for free- range cattle ranching, it cannot be discriminated as a separate class and is, consequently, not included in the human use category. Settlements in 1956 were limited to scattered small patches in the Oyachi river valley and two relatively large cleared areas in the Papallacta basin (Figure 2.26).

2.3.3 LAND COVER MAP OF 1999

The land cover of 1999 resembled that of 1956 in several respects despite the presence of the road built in 1994 connecting the Oyacachi and Papallacta valleys. In general terms, the extent of most cover classes maintained the proportions of 1956 (Table 2.2, Figure 2.27). The area surveyed shows the same dichotomy of a forested southwest *vs*. a páramo northwest that was evident in 1956 (Figure 2.27). Most scattered *Polylepis* forest patches in the páramo matrix persisted over the time interval studied (Table 2.2). It is worth noting that most of these retained their shape regardless of their size. Several fire scars of 1956 were still evident in the same locations and covering roughly the same area in 1999. Wide isolated landslides in the southeast also showed a certain degree of persistence from 1956 through 1999 (Figures 2.26 and 2.27).

Major differences were observed in the extent of human settlements. In 1999 settlements in the Oyacachi valley spread up to the upper limit of the montane forest where it merges with *Polylepis* forest. A similar pattern was apparent in the south where human settlements spread beyond the uppermost limit of the montane forest in the western part of the Papallacta valley (Figure 2.27).

2.3.4 LAND COVER CHANGE

Overall land cover transformation between 1956 and 1999 involved less than 6 % of the study area. Most of the changes involved human occupation of previously forested areas (Table 2.3, Figure 2.26) and/or conversion of forests to páramo. Approximately 3 % of dense *Polylepis* forest cover was lost during the four decades studied; most of this percentage corresponded to conversion to páramo and human use (Table 2.3). Most was lost through attrition, *i.e.* loss of entire patches (Forman 1999); however the process was masked by simultaneous fragmentation due to road construction (*i.e.* the number of *Polylepis f*orest fragments remained virtually the same over time, Tables 2.1 and 2.2). Reduction in minimum and average area of polygons from 1956 to 1999 reflects that both forest loss and fragmentation took place (Tables 2.1 and 2.2), probably with some shrinkage of existing patches as well. Areas where dense *Polylepis* forest was lost to sparse shrub/*Polylepis* often coincided with fire scars (Figures 2.26 and 2.27). This was also true for the relatively large areas of sparse shrubs/*Polylepis* lost to shrubland and páramo during the period of study (Table 2.3).Some sparse shrubs/*Polylepis* patches appeared lighter and more coarsely textured in the aerial photography of 1993. These patches were either perforated or surrounded by fires scars (Figures 2.21 and 2.22) but the area affected by fire scars was too small to be digitized and recorded as change. Most of the changes that affected dense Polylepis forest and mixed shrub páramo *Polylepi*s forest occurred in the northwest of the study area, where both land cover classes occurred in a fragmented manner in 1956.

Montane forest was the ecosystem which experienced the most significant loss of area relative to its extent in 1956. Human settlements doubled in extent at the cost of montane forest in the Oyacachi valley and the east side of the Papallacta basin (Table 2.3, Figures 2.26 and 2.27).

2.4 DISCUSSION

Aerial photography interpretation constituted a reliable source of land cover classification and monitoring in the Northeastern Cordillera Oriental of Ecuador. Classification accuracy depended on stereoscopic observation of aerial photos and number of ground truth points. Certain classification constraints brought about by differences in area coverage, scale and levels of exposure of historical photography can be overcome by combining photography of relatively close dates.

The land cover of 1956 showed a sharp dichotomy between forested cover in the southeastern part of the study area and páramo-dominated cover in the northwest. Drier vegetation types are expected to occur as one moves from the headwater catchments of the Amazon basin to the inter Andean valley (Van der Hammen 1985, Balslev 1988); however the presence of scattered *Polylepis* patches in the páramo matrix along with landslides and fire scars may indicate a human influenced transition from a forested to grass-dominated landscape. Landslides have often been associated with surfaces that have been denuded by fire on steep slopes (Cannon *et al*. 1998, Cannon *et al.* 2001). Although landslides were present in the whole area surveyed and they could also be related to geological aspects of the area (*e.g.* slope steepness, as has been the case for other mountain regions at higher latitudes where precipitation is also high, cf. Larsen *et al*. 2006). Landslides also were more frequent in the northwest where fire scars were also more common. The occurrence of fire scars around *Polylepis* forest patches and immediately above the uppermost limit of continuous *Polylepis* forest in the 1965 aerial photography would be consistent with this view.

The landscape dichotomy of 1965 persisted throughout 1999, with the difference that páramo expanded to the northeast through human occupation in the Oyacachi valley. Land cover transformation took place in less than 6% of the study area and most involved human expansion into montane forest and, to a lesser extent, *Polylepis* forest. This pattern of human encroachment at higher elevation in the Andes has been observed in most montane areas of Ecuador as a result of the implementation of the agrarian reform and legalization of land tenure in the early 1960's and thereafter (Gondard and Mazurek 2001).

Dense *Polylepis* forest experienced attrition, further range fragmentation and shrinkage but overall loss was only 3.4 % of the 1956 cover. This finding is consistent with studies carried out in Perú using aerial photography for comparable periods of time, 1930-1997, by Byers (2000) and 1956-2005, by Jameson and Ramsay (2007). The transition of dense *Polylepis* forest, to sparse shrub/*Polylepis* forest and from this latter to shrubland and páramo that was recorded in this study suggests a human-influenced distribution of *Polylepis* forests and *Polylepis*/shrub blends in the study area. A similar kind of transition has been proposed for scattered *Polylepis* spp. occurrence in the Andes of Argentina (Cabido and Acosta 1985, Cingolani *et al.* 2004). Persistence of certain forest patches in the study area might be more a consequence of Andean people's decision to maintain forest shelter for free ranching cattle than special landscape and/or physical factors that would prevent burning, as suggested by other studies (Fijeldsa 2002). *Polylepis* forest expansion in the Oyacachi valley seemed to have been prevented through tree cutting at the edges and clearing of small areas with machetes to allow cattle to enter the forest for shelter (field observation). This practice might have become common after 1997 when fire was forbidden in the area by the national Ministry of the Environment.

The Oyacachi basin, where most of the changes took place, supported an isolated and relatively small Quichua community before road construction which connected Oyacachi to Papallacta in 1994 (EMAAP 1991). Land cover transformations in the study area reflect a slow rate of development characteristic of secluded settlements of the Andes during the implementation of the agrarian reform (Gondard and Mazurek, 2001). From this perspective, the nature of the changes experienced by *Polylepis* forests, *i.e.*, attrition, perforation and shrinkage through fire, were more informative for assessing the relevance of human factors in shaping the 1999 distribution pattern of *Polylepis* forests in the northeastern Cordillera Oriental of Ecuador than the actual extent to which they occurred. Considering the four centuries of human occupation of the Oyacachi basin under a similar rate of land conversion, it is possible that approximately 30 % of dense *Polylepis* forest was lost to páramo.

Several years of observations and reflections of tropical mountain ecosystems led Ellenberg to conclude:

> "In my opinion we should wonder why some forests or tree stands are still left there, instead of wondering why they are so small and rare that they could be looked upon as exceptions. Up to now we know very little about man's influence on ecosystems and not much more about the influence of ecosystems on him. When we seriously accept man as an important item in ecosystem research, we will certainly contribute to a future harmony between man and his environment." (Ellenberg 1979)

Ellenberg's statement not only challenged a long standing theory on limiting factors for forest growth in the Andes, but it also brought human beings into the biogeographical research arena for the first time in the young history of mountain ecosystem research (Kessler 2002). Considerable progress has been made in both areas since Ellenberg's assertion; however, the question remains as to the relative benefits of different high elevation Andean ecosystems in terms of water holding capacity of their soils and their water production potential (cf. Bruijnzeel and Proctor 1995, Bruijnzeel and Hamilton 2000, Fjeldså 2002, Hofstede *et al*. 2002, Buytaert *et al*. 2006, Harden 2006). Amount of water production of the Ecuadorian páramos (estimated from runoff series of small páramo catchments, Buytaert *et al*. 2004) ranges from 600 to 1000 km^3 yr^{-1} which is approximately 2/3 of the annual rainfall (Buytaert *et al*. 2004). Although studies on the hydrology of the Andean páramos show that high water production of the páramo is primarily due to high precipitation regimes, they also acknowledge that the presence of *Polylepis* forest patches in these areas is likely to add water to the hydrological cycle through precipitation from fog and dew interception (Buytaert *et al*. 2005). This mechanism described for tropical mountain cloud forests is known to increase total rainfall input by 5 to 20 %, particularly under high precipitation regimes (Bruijnzeel and Proctor 1995). As the uppermost cloud forests of the Neotropics, *Polylepis* forests play this critical role at the headwater catchments of the Andean cordillera (Fjeldså 2002, Buytaert *et al*. 2006), however, quantitative data are lacking. The páramo has been widely studied and praised for its capabilities for water production (Buytaert *et al*. 2006, Hofstede *et al*. 2002, Harden 2006), but *Polylepis* forest are yet to be researched for their ability to serve human settlements downstream.

Table 2.1: Summary of land cover statistics for the Oyacachi, Chalpi and Papallacta basins in 1956, Northeastern Cordillera Oriental of Ecuador

Land cover classes	Area (km^2)	Percentage of cover	Polygons per class	Minimum Size (km^2)	Maximum Size (km^2)	Average Size (km^2)
FS	2.45	0.50	79	0.0011	0.39	0.03
HU	9.15	1.86	34	0.0022	4.08	0.27
LA	5.14	1.05	81	0.0003	0.47	0.06
LS	2.72	0.55	146	0.0005	0.61	0.02
MF	87.37	17.80	13	0.0075	69.36	6.72
P	226.50	46.14	248	0.0001	203.25	0.91
DP	24.70	5.03	428	0.0004	2.97	0.06
S	4.95	1.01	18	0.0002	4.52	0.28
MPP	106.16	21.63	12	0.1309	56.61	8.85
SSP	21.71	4.42	194	0.0034	2.33	0.11
Total	490.85	100	1253			

Table 2.2: Summary of land cover statistics for the Oyacachi, Chalpi and Papallacta basins in 1999, northeastern Cordillera Oriental of Ecuador

Land Cover classes	Area (km^2)	Percentage of cover	Polygons per class	Minimum Size (km^2)	Maximum Size (km^2)	Average Size (km^2)
FS	0.23	0.05	10	0.0011	0.39	0.03
HU	19.44	3.96	20	0.0022	4.08	0.97
LA	5.13	1.05	80	0.0003	0.47	0.06
LS	1.38	0.28	87	0.0005	0.14	0.02
MF	79.72	16.24	13	0.0025	65.23	6.13
P	233.57	47.58	278	0.0001	211.71	0.84
DP	23.86	4.86	427	0.0003	2.97	0.05
S	11.42	2.33	26	0.0002	3.97	0.44
MPP	97.58	19.87	11	0.1309	55.49	8.87
SSP	18.52	3.77	192	0.0034	2.33	0.09
Total	490.85	100.00	1144			

Legend of Tables 2.1 and 2.2:
FS: Fire scar
HU: Human use
LA: Lake
LS: Landslide
MF: Montane Forest
P: Páramo
DP: Dense *Polylepis* forest
S: Shrubland
MPP: Mixed shrub páramo *Polylepis* forest
SPP: Sparse shrubs/*Polylepis*

Table 2.3: 1956 -1999 Land cover change expressed as percentage of loss/gain per land cover class relative to the total area in the Oyacachi, Chalpi and Papallacta basins, northeastern Cordillera Oriental of Ecuador

	FS	**HU**	**LS**	**MF**	**P**	**DP**	**S**	**MPP**	**SSP**	**Lost**[2]
FS	-[1]	-	-	-	0.47	-	0.01	-	0.01	0.49
HU	-	-	-	0.02	0.01	-	0.01	-	-	0.04
LS	-	0.01	-	0.01	0.28	0.01	-	-	0.01	0.32
MF	-	1.57	-	-	0.02	-	-	-	-	1.59 (8.93)
P	0.02	0.24	0.02	-	-	-	0.01	-	-	0.29
DP	0.01	0.18	0.01	-	0.23	-	0.02	-	0.07	0.52 (3.4)
S	-	0.14	-	-	-	-	-	-	-	0.14
MPP	-	-	-	-	0.12	-	1.30	-	-	1.42 (8.1)
SPP	-	-	0.01 (0.22)	-	0.60 (13.10)	-	0.13 (2.83)	-	-	0.74 (16.15)
Gained	0.03	2.14	0.04	0.03	1.73	0.01	1.48	-	0.09	5.5

FS: Fire scar
HU: Human use
LS: Landslide
MF: Montane Forest
P: Páramo
DP: Dense *Polylepis* forest
S: Shrubland
MPP: Mixed shrub páramo *Polylepis* forest
SSP: Sparse Shrub / *Polylepis*

[1] "-" means no change or change < 0.01%

[2] Number in parentheses represents percentage of loss relative to that class (in row)

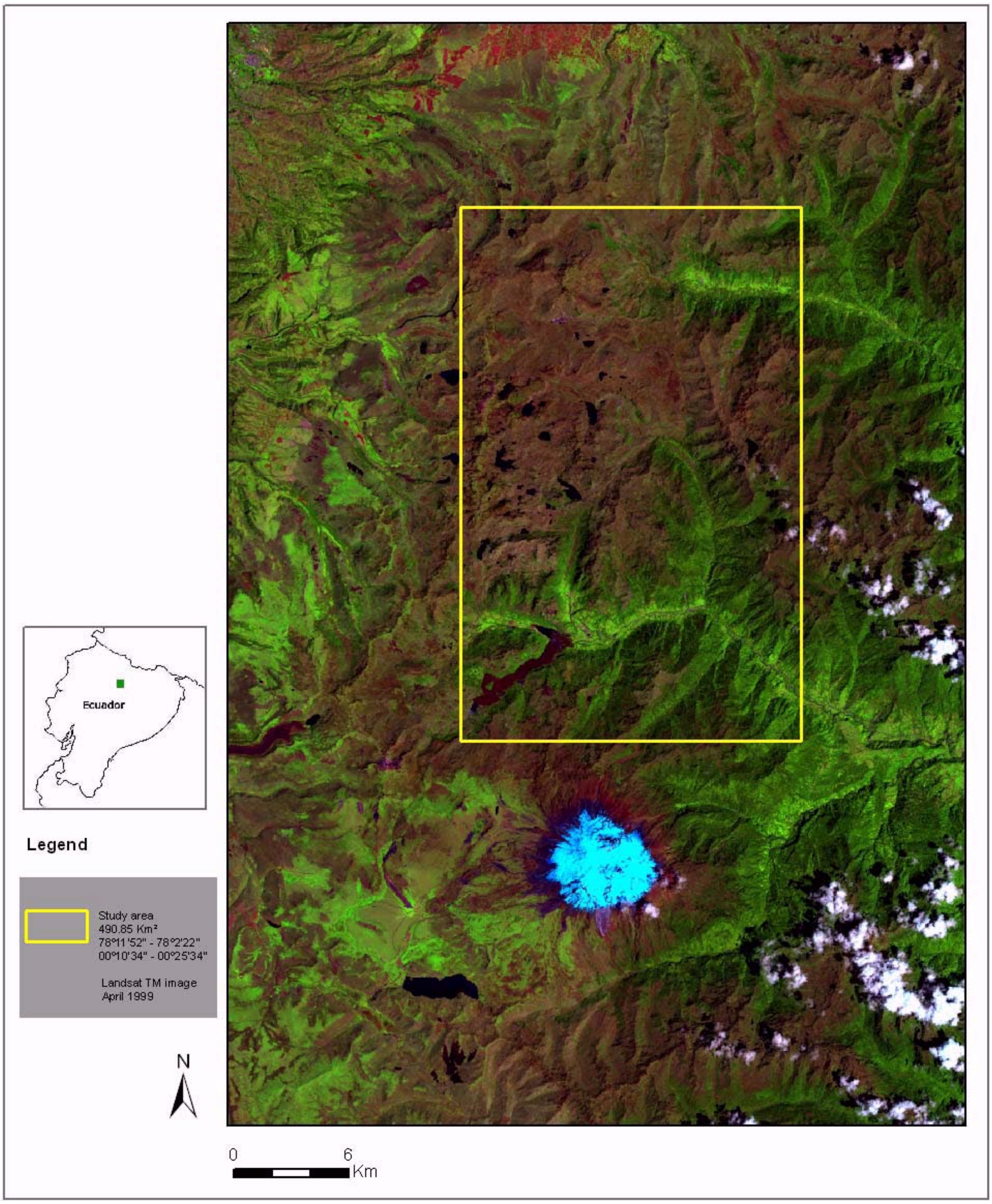


Figure 2.1: Study area, approximately 491 km² in the southern part of the northeastern Cordillera Oriental of Ecuador, within the boundaries of the Cayambe Coca Ecological Reserve and farther south (78°11’55”- 78°2’22” W, 0°10’34”-0°25’34” S)

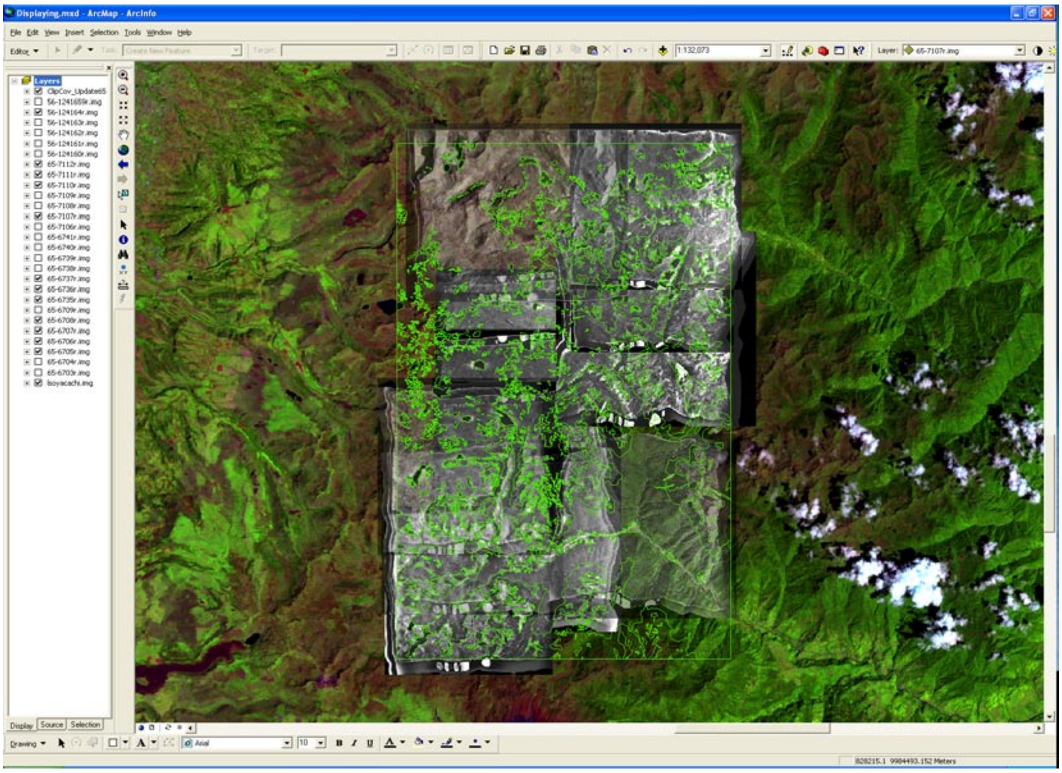


Figure 2.2: 1956 and 1965 aerial photography mosaic after photogrammetric correction and generation of the 1956 land cover map of the Oyacachi, Chalpi and Papallacta basins in ArcMap 9.2

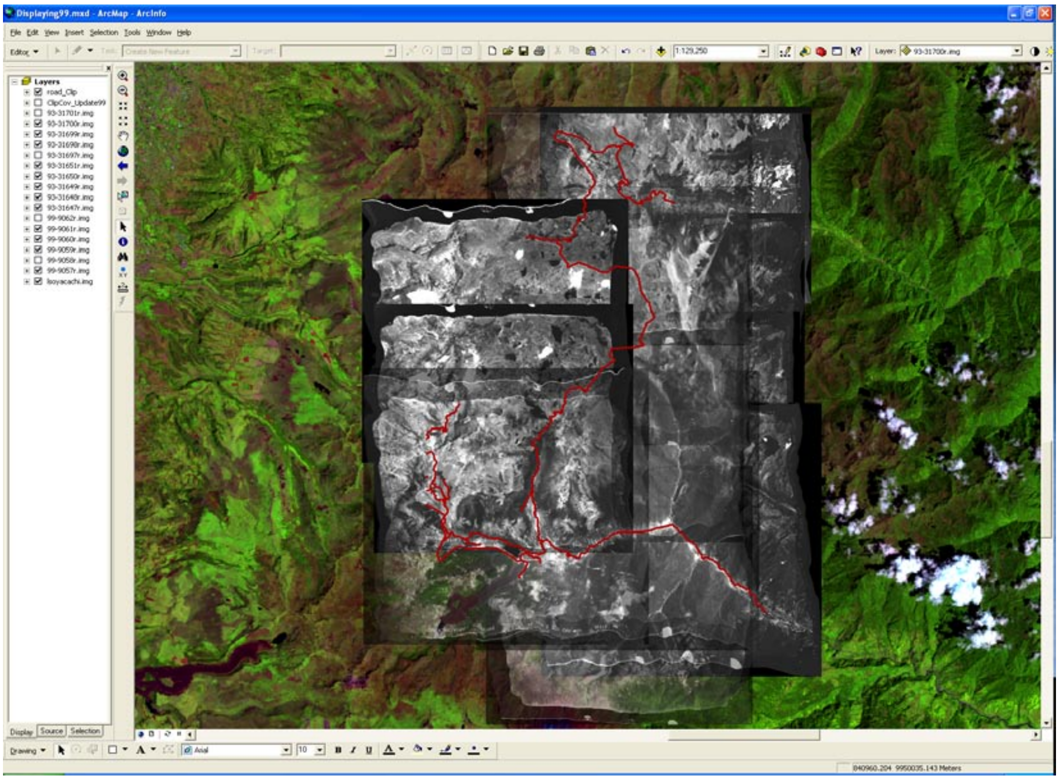


Figure 2.3: 1993 and 1999 aerial photography mosaic after photogrammetric correction and tracing of the road Oyacachi – Papallacta for the 1999 land cover map of the Oyacachi, Chalpi and Papallacta basins, Ecuador (ArcMap 9.2)

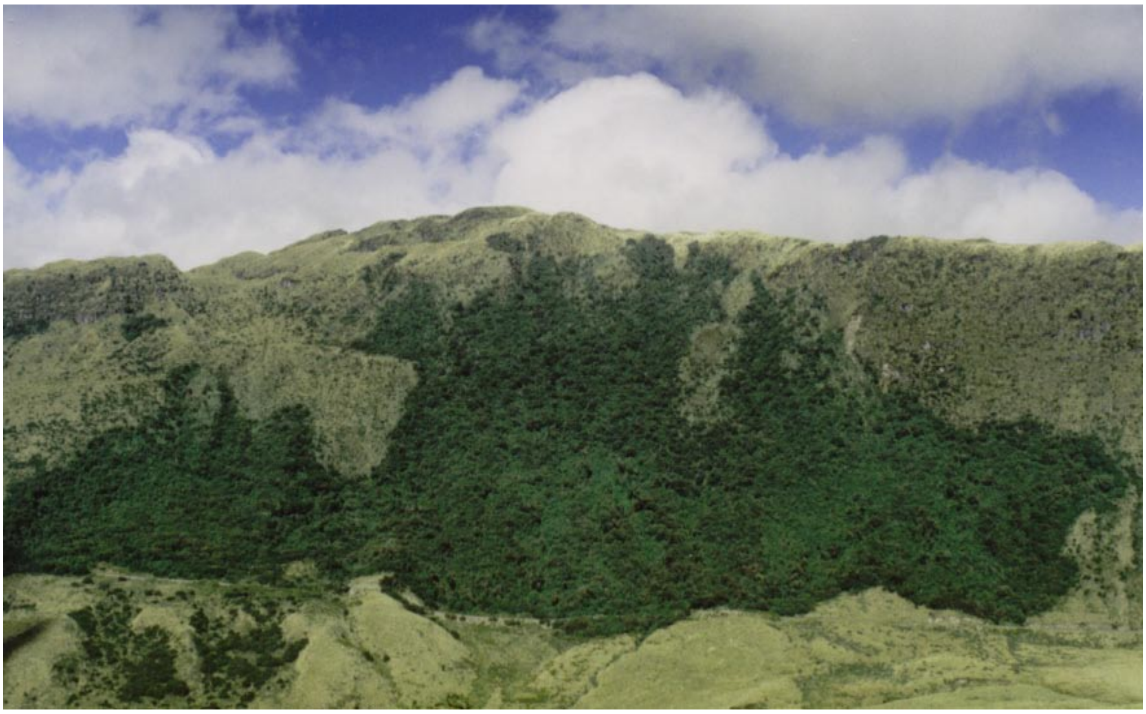


Figure 2.4: Dense *Polylepis pauta* forest patch, Oyacachi river basin, southern part of the northeastern Cordillera Oriental of Ecuador, July 2006

Figure 2.5: Mixed shrub páramo *Polylepis pauta* forest, Chalpi river basin, southern part of the northeastern Cordillera Oriental of Ecuador, July 2006

Figure 2.6: Dense *Polylepis pauta* forest patches southwest facing slope and northeast facing slope, páramo and shrubland (bottom right corner of the image). Papallacta river basin, southern part of the northeastern Cordillera Oriental, Ecuador, June 2007

Figure 2.7: Sparse Shrubs/*Polylepis (P. pauta)*, Oyacachi river basin, southern part of the northeastern Cordillera Oriental, Ecuador, June 2007

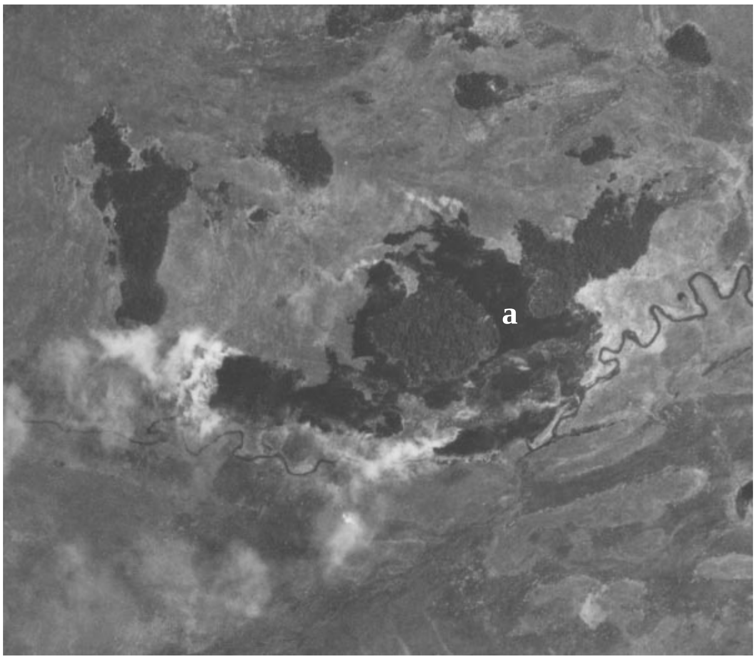


Figure 2.8: Recent fire scar (a), black relatively smooth surface, sharp boundaries and round shapes. Smoke to the left of the image. Aerial photography of 1965, scale 1: 50,000.Oyacachi basin, Ecuador

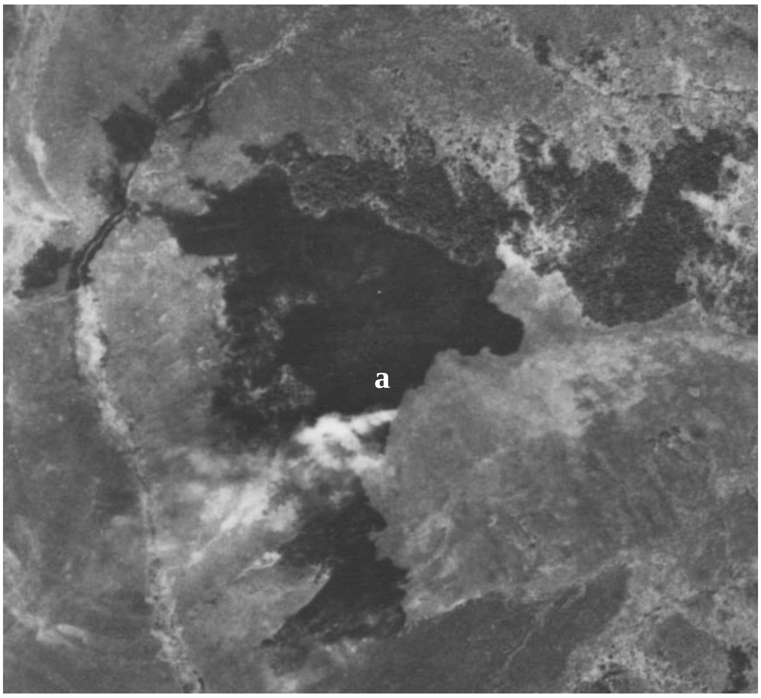


Figure 2.9: Recent fire scar (a) in the middle of *Polylepis* forest. Smoke towards the center of the image, edge of the fire scar. Aerial photography of 1965, scale 1: 50,000.Oyacachi basin, Ecuador

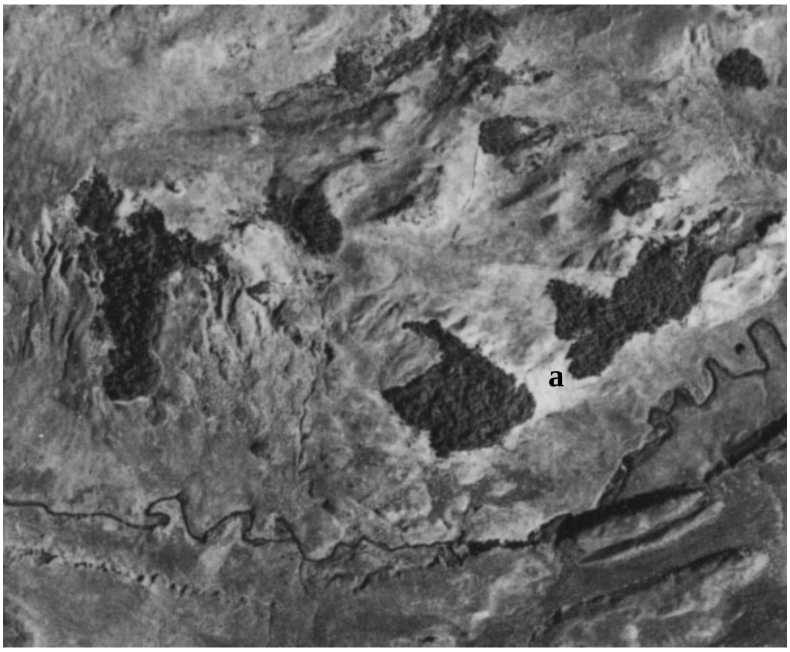


Figure 2.10: Old fire scar (a) slightly lighter than the páramo background. The same sites were burnt in 1965 (Figure 2.4).Aerial photography of 1956, scale 1:50,000.Oyacachi basin, Ecuador

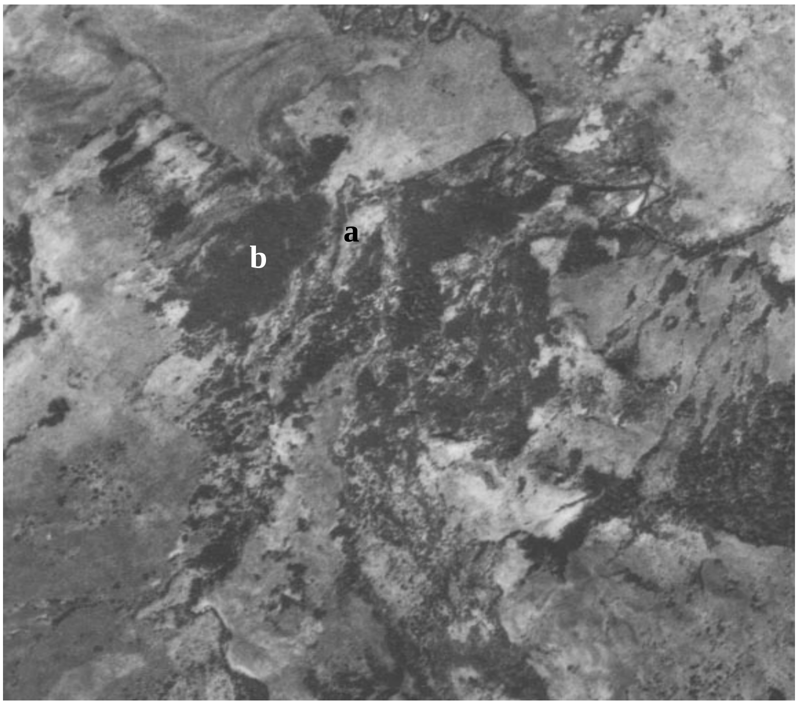


Figure 2.11: Old fire scar (a), very light in the middle of *Polylepis* forest (dark patches, b) and páramo vegetation (light background, c).Aerial photography of 1965, scale 1:50,000.Oyacachi basin, Ecuador

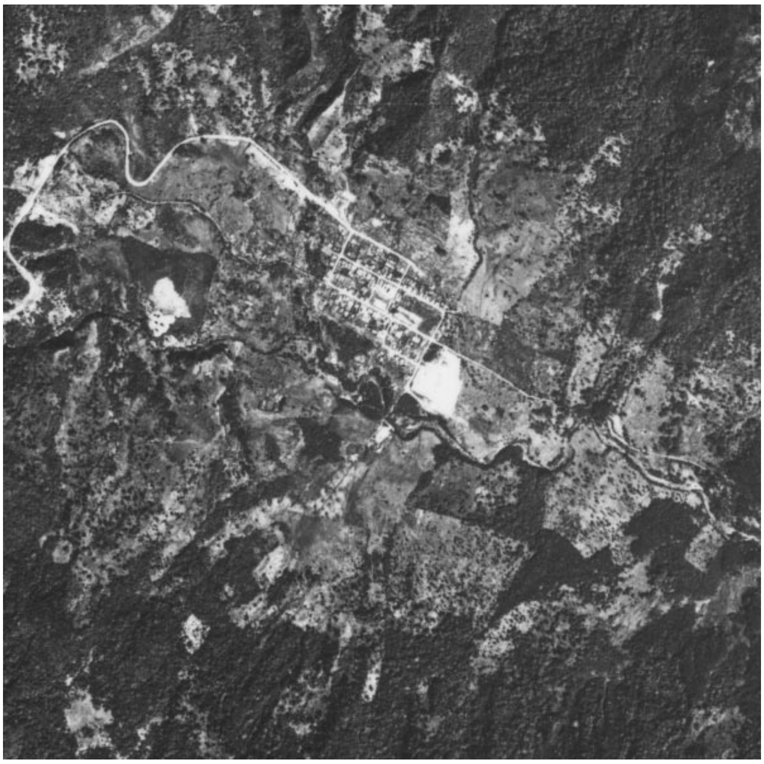


Figure 2.12: Human use areas show patchy with straight boundaries separating elements of the mosaic. Aerial photography of 1999, scale 1:50,000.Oyacachi basin, Ecuador

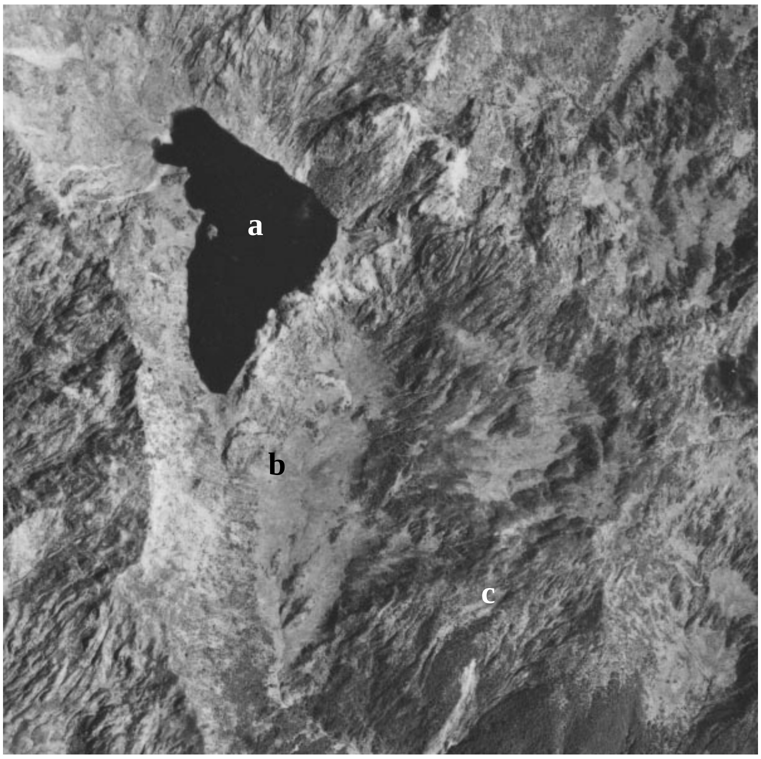


Figure 2.13: Lake (a), páramo (b) to the north and south of the lake and mixed shrub páramo *Polylepis f*orest (c) in the right half of the image. Aerial photography of 1999, scale 1:50,000.Oyacachi basin, Ecuador

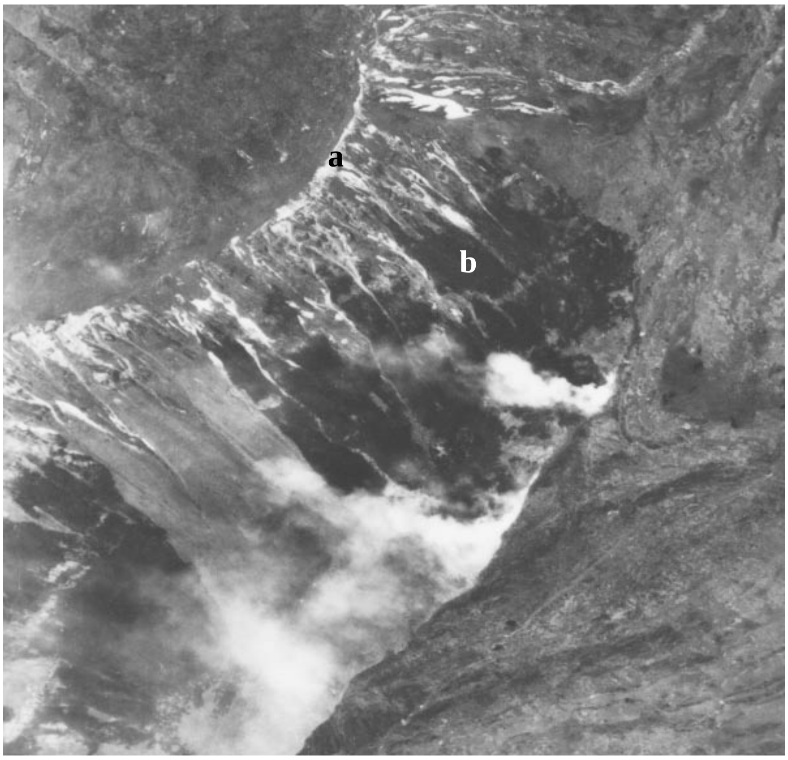


Figure 2.14: Landslides (a) show as light elongated shapes. In this image they are above *Polylepis* forest (dark, b). Note the smoke from burning at the bottom of the patches. Aerial photography 1965, scale 1:50,000. West of the Oyacachi basin, Ecuador

Figure 2.15: Landslides (a) intermingling with sparse shrubs (dark grey, b) and *Polylepis* (black threads and spots, c).Aerial photography of 1965 scale 1:50,000. Oyacachi basin, Ecuador

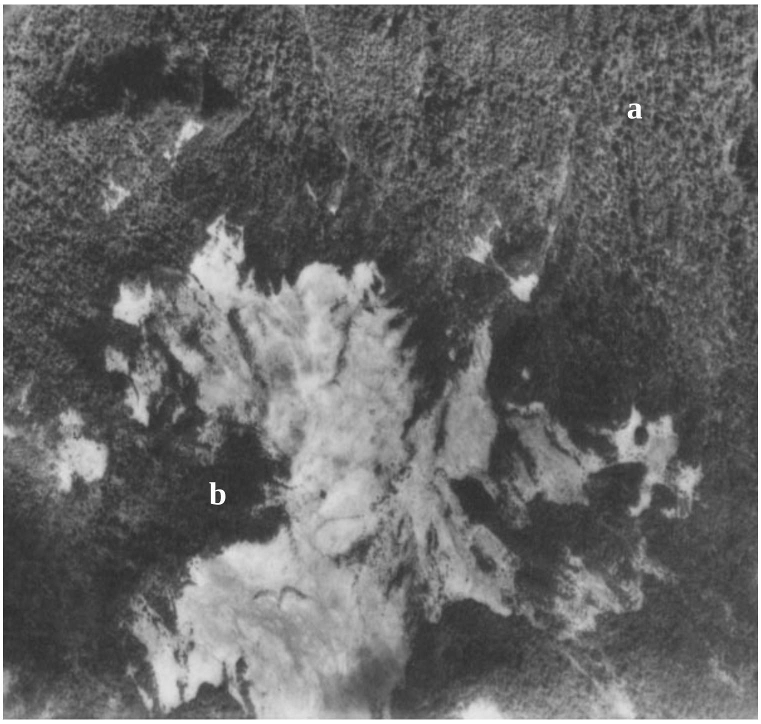


Figure 2.16: Montane forest, dark grey and grain textured (top left and right corners, a), dense *Polylepis* forest darker and of a finer texture (b), surrounding páramo (center of the image). Aerial photography of 1965, scale 1: 50,000.Southern part of the Papallacta basin, Ecuador.

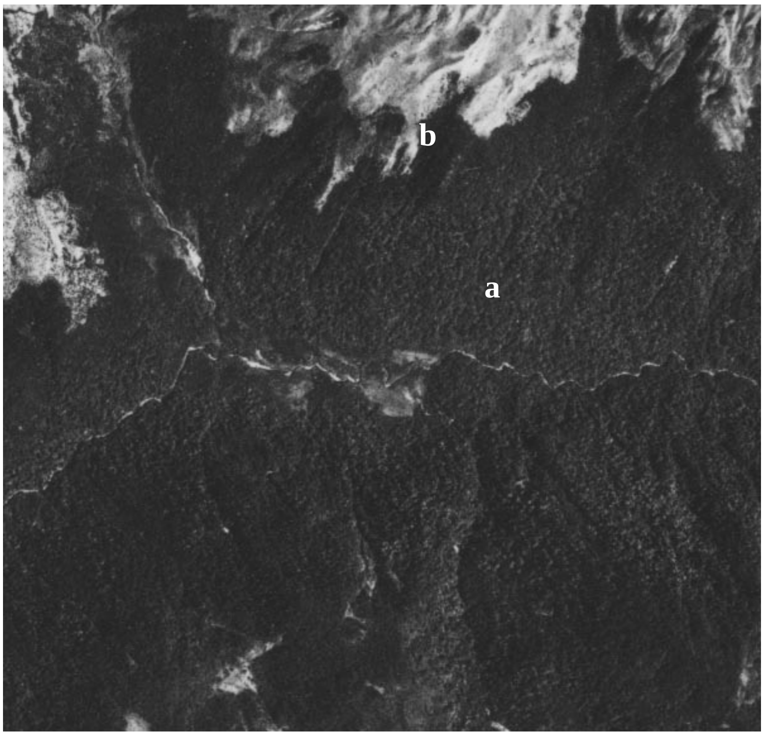


Figure 2.17: Montane forest (bottom to center of the image, a) dark grey tone and more highly textured and dense *Polylepis* forest showing as a darker thin belt towards the top of the image (b). Aerial photography of 1965, scale 1:50,000. Oyacachi river basin, Ecuador

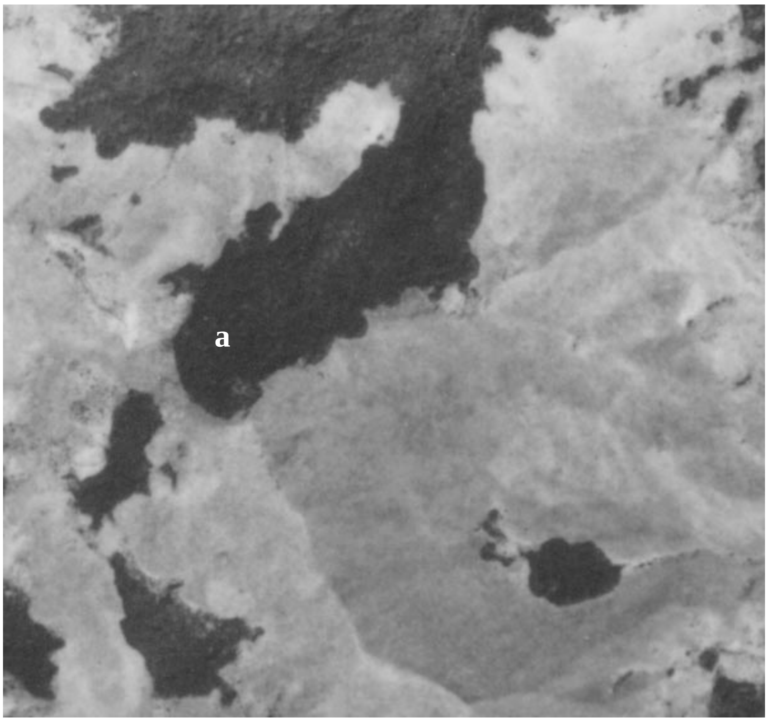


Figure 2.18: Dense *Polylepis* forest patches show dark with fine grain texture and sharp boundaries (a) against the páramo background Aerial photography of 1965 scale 1:50,000.Papallacta basin, Ecuador

Figure 2.19: Mixed shrub páramo *Polylepis* (a), showing as dark vertical threads of *Polylepis* intermingling with lighter bands of shrub/tall grass páramo. Aerial photography of 1965, scale 1:50,000. Oyacachi basin, Ecuador

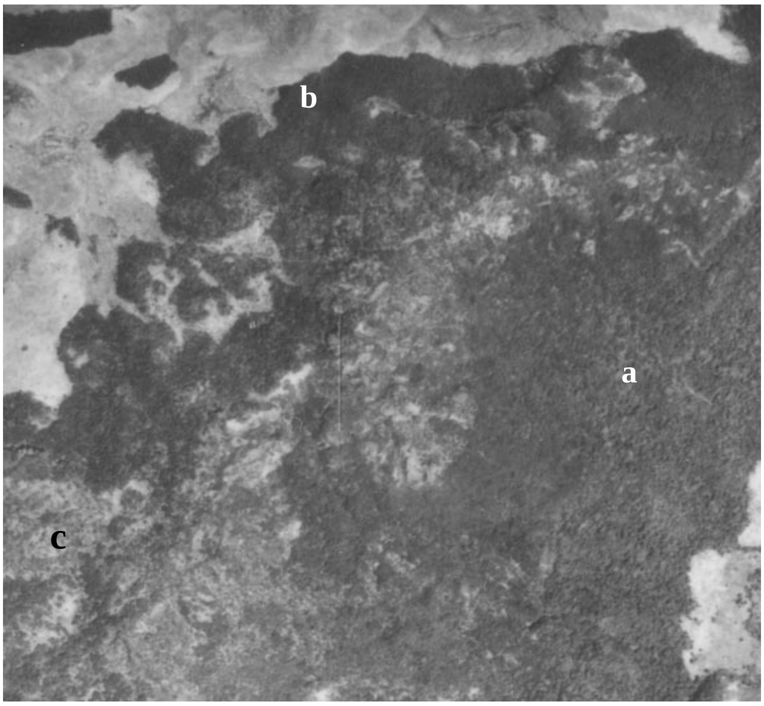


Figure 2.20: Mixed shrub páramo *Polylepis* forest (bottom right corner, a), dense *Polylepis* forest (top right quadrant of the image, b) and sparse shrubs/*Polylepis* (left bottom corner, c).Aerial photography of 1965, scale 1:50,000. Papallacta basin, Ecuador

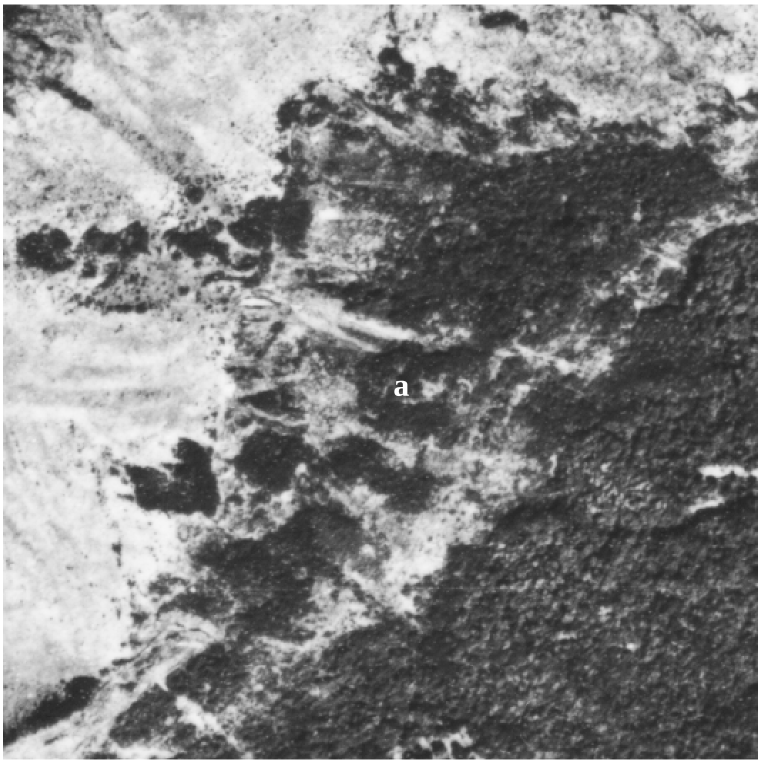


Figure 2.21: Sparse shrubs/*Polylepis* (a) occurring as a mosaic of chunky dark spots of *Polylepis* and lighter more spread areas of shrubs in a páramo matrix in a mountain top. Aerial photography of 1965, scale 1:50,000. West side of the Chalpi basin, Ecuador.

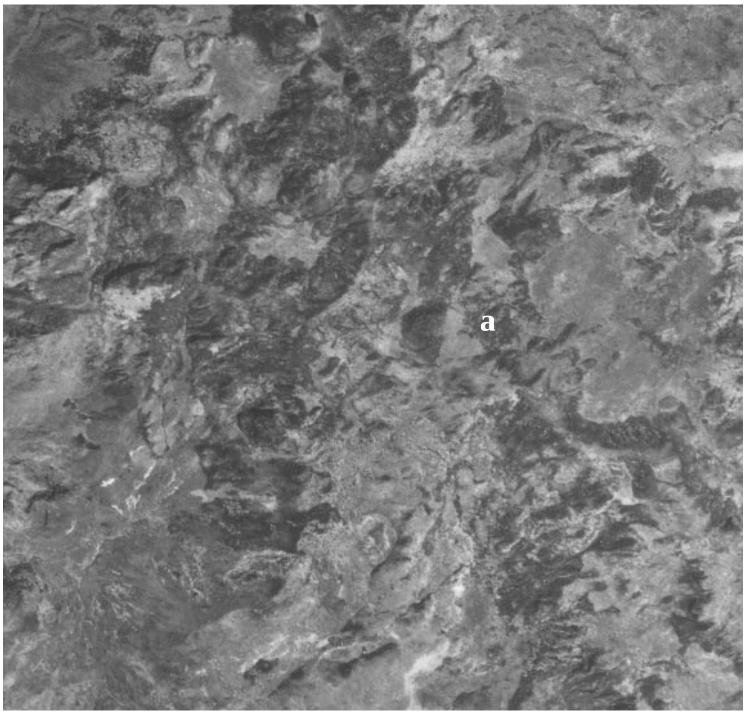


Figure 2.22: Sparse shrubs / *Polylepis* (a) as a snake shaped strip of intermingling shrubs and *Polylepis* in a páramo matrix.Aerial photography of 1965, scale 1:50,000. West side of the Chalpi basin, Ecuador

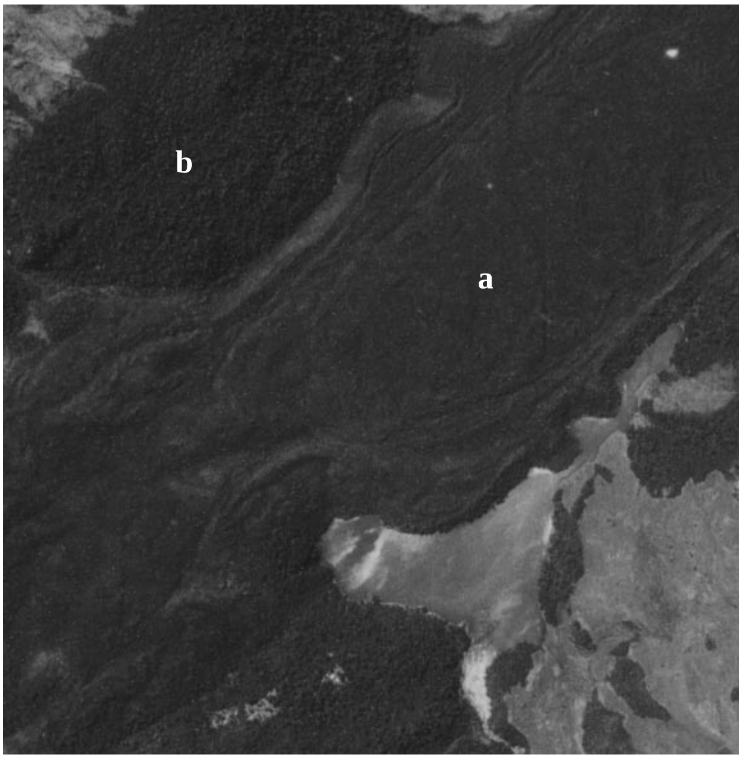


Figure 2.23: Srubland (a) dark gray surface with little or no texture in the center of the image and *Polylepis* forest in the top (b). Aerial photography of 1993, scale 1:60,000. Papallacta basin, Ecuador

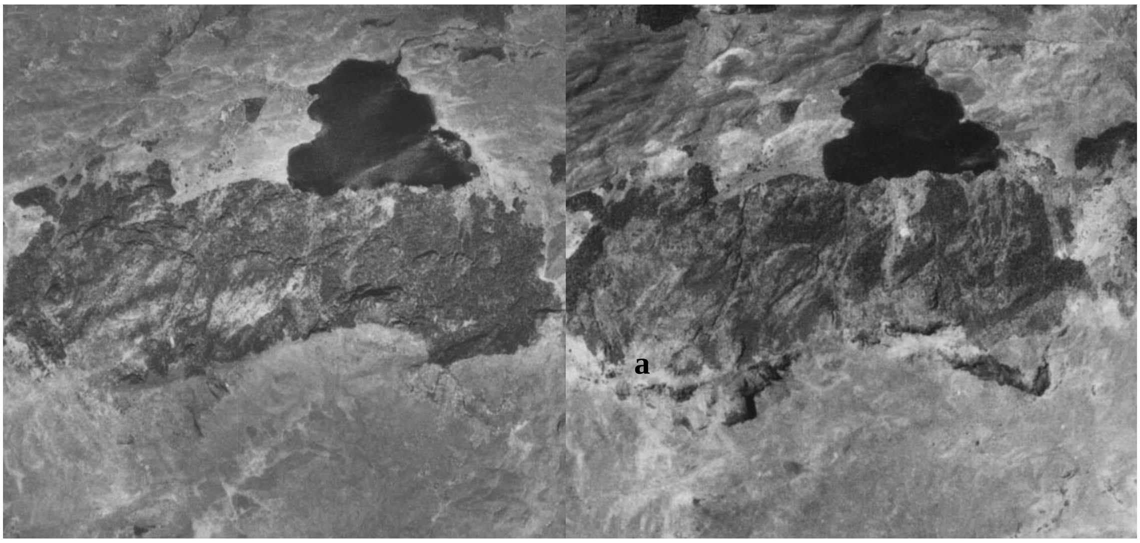


Figure 2.24: Change in density of shrub vs. *Polylepis* in the sparse shrub/ *Polylepis* land cover class between 1965 (left) and 1993 (right). *Polylepis* has become denser and shows as clearly defined patches in 1993 while shrubs have died out and become sparser. Fire scars can be seen at the edge of the sparse shrubs in the 1993 image (a). Laguna Ciega, Papallacta basin, northeastern Cordillera Oriental, Ecuador

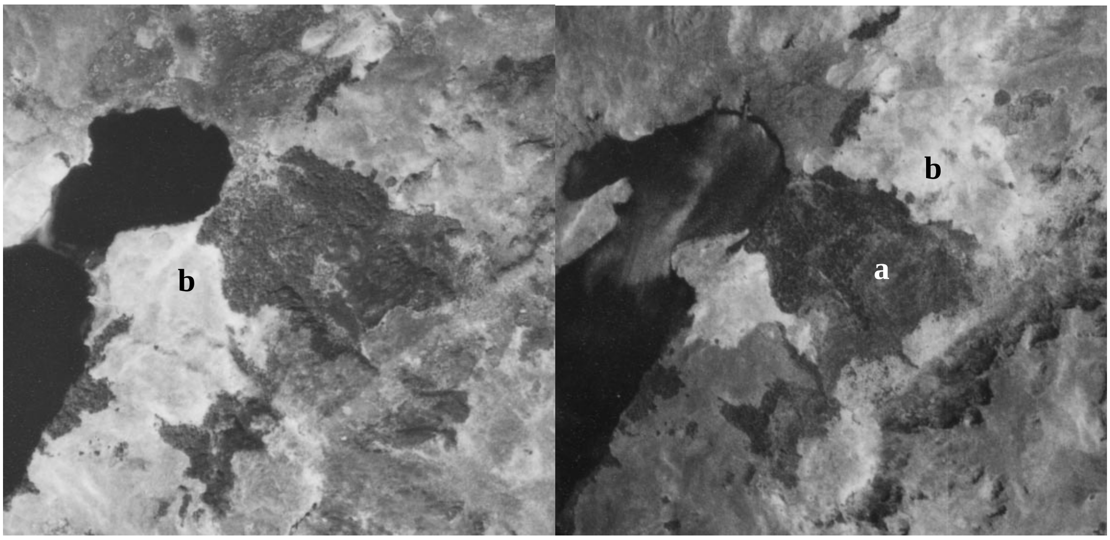


Figure 2.25: Change in extent and density of *Polylepis* vs. shrubs between 1965 (left) and 1993 (right) in the sparse shrubs/ *Polylepis* land cover class. After perforation of the patch, shrubs have replaced *Polylepis*(a) in the right part of the patch and become denser. Fire scars around the patch can be seen in the images of both dates (b). Laguna Sucus, Papallacta basin, northeastern Cordillera Oriental, Ecuador.

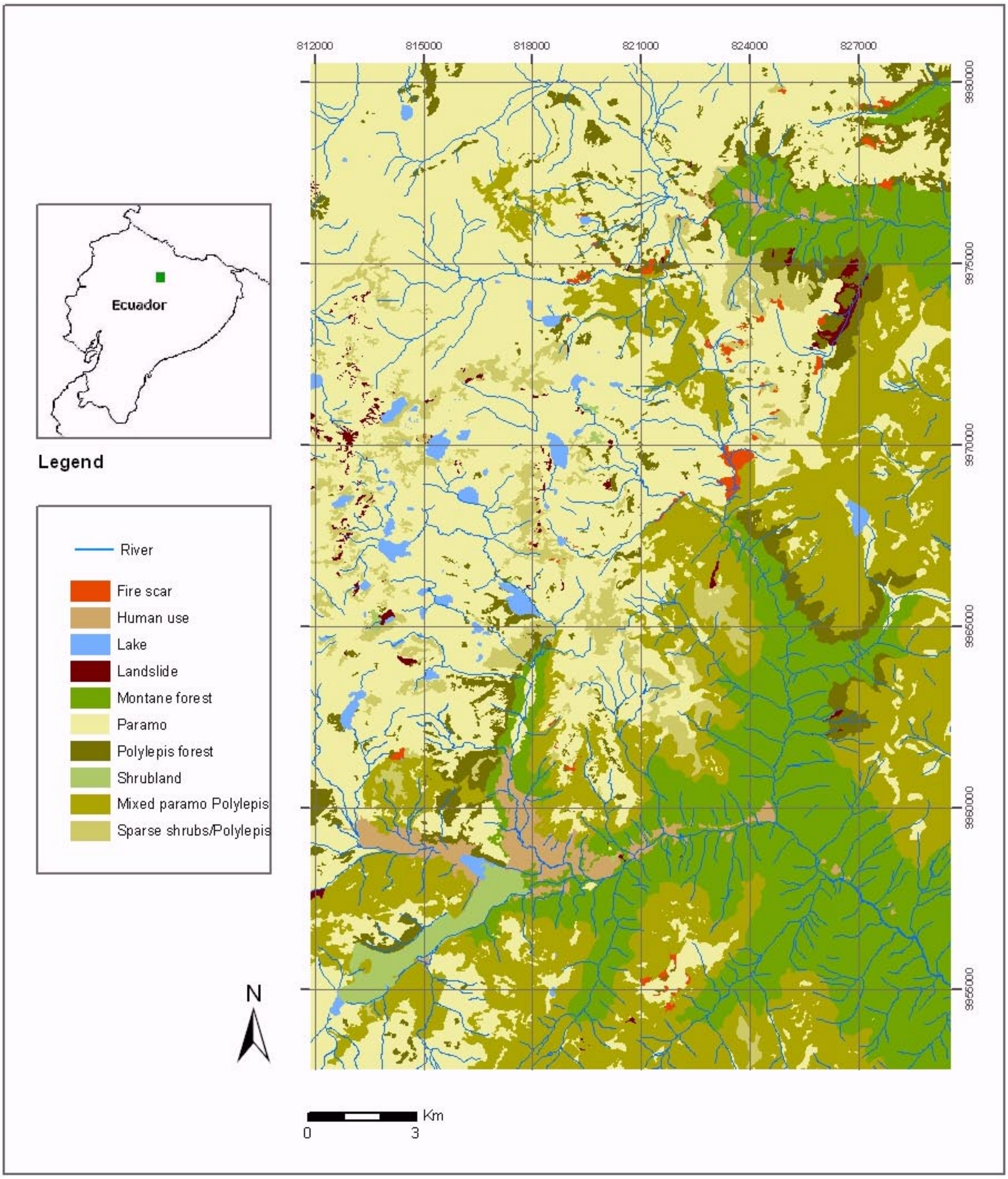


Figure 2.26: 1956 Land cover map of the Oyacachi, Chalpi and Papallacta watersheds, southern part of the northeastern Cordillera Oriental, Ecuador

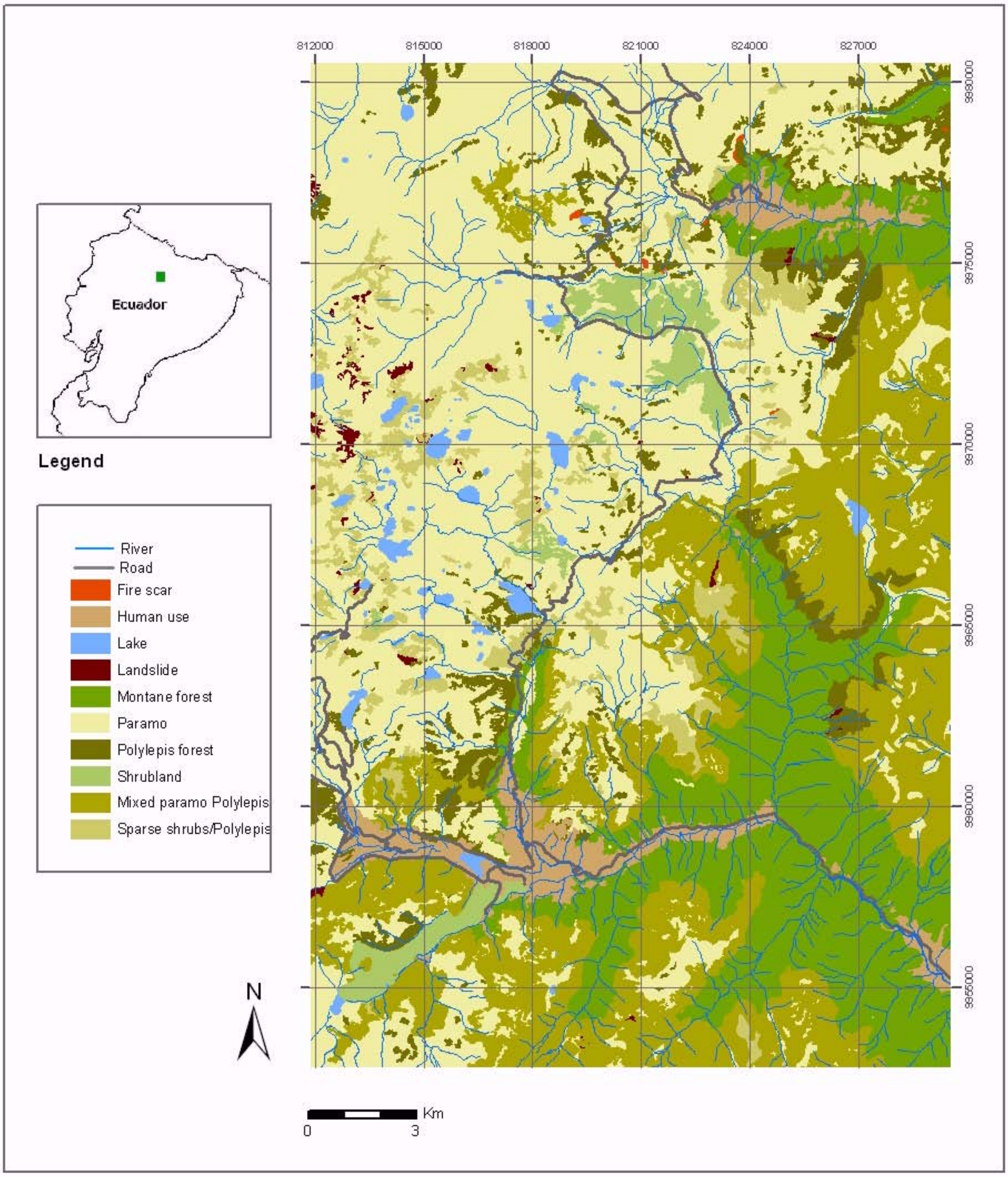


Figure 2.27: 1999 Land cover map of the Oyacachi, Chalpi and Papallacta watersheds, southern part of the northeastern Cordillera Oriental, Ecuador

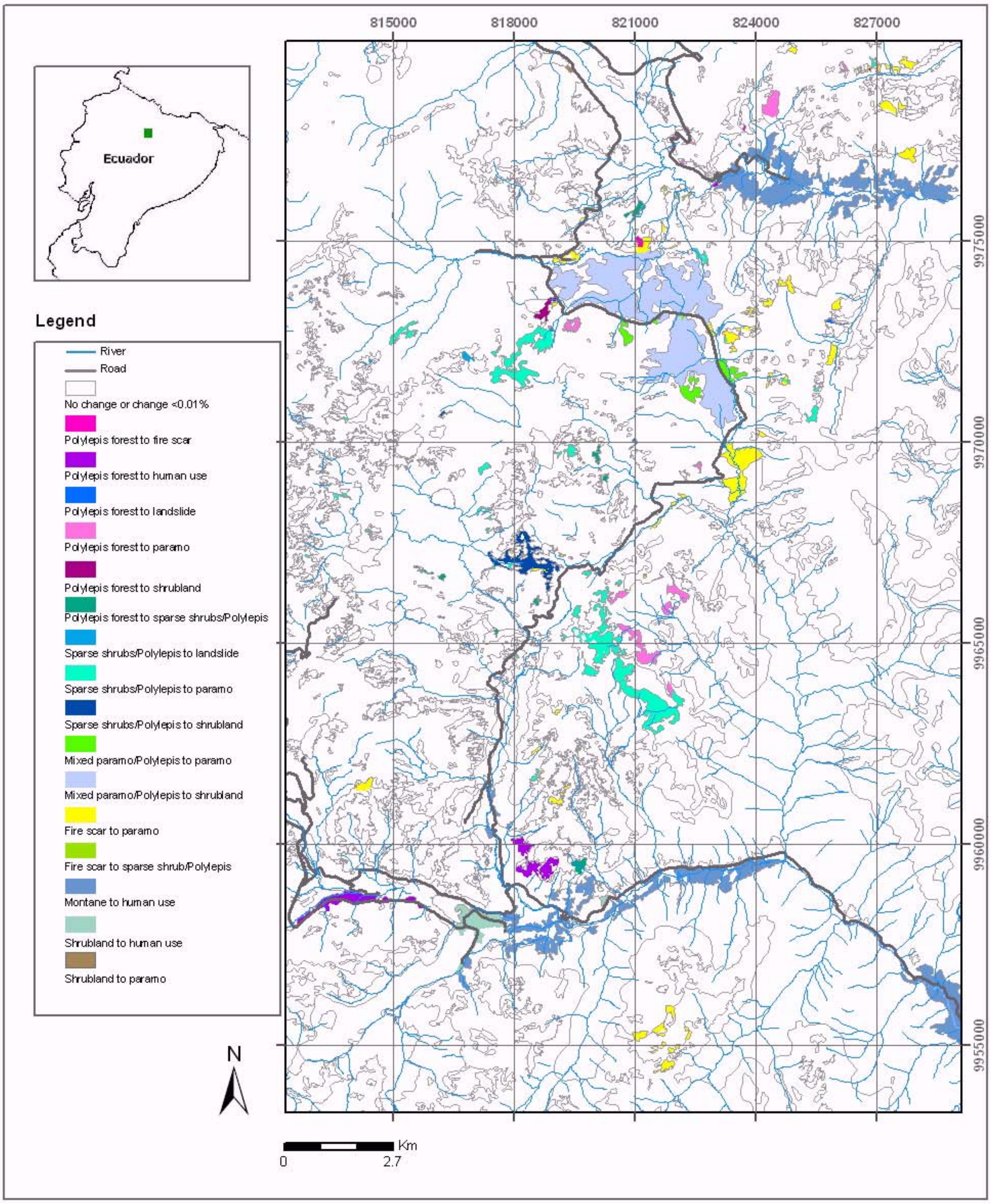


Figure 2.28: 1956-1999 Land cover change map of the Oyacachi, Chalpi and Papallacta watersheds, southern part of the northeastern Cordillera Oriental, Ecuador

CHAPTER 3

GENETIC INSIGHTS INTO THE HISTORICAL DISTRIBUTION OF *Polylepis pauta* (ROSACEAE) IN THE NORTHEASTERN CORDILLERA ORIENTAL OF ECUADOR

3.1. INTRODUCTION

Large continuous populations, remarkable longevity and long distance pollen and seed dispersal are linked to high levels of genetic diversity maintained within and low genetic differentiation among populations of tree species (Hamrick *el al*. 1992, Hamrick and Godt 1996). Divergence from this pattern is expected where a woody species either originated from a reduced number of individuals or has had a historically disjunct range (Hamrick *el al*. 1992, Hamrick 2004, Pither *et al.* 2003, Jump and Puñuelas 2006). Such species are expected to have less variation at the species and population level and more variation among populations than species with broader and more continuous historical ranges (Hamrick *et al*. 1992, Hamrick 2004, Pither *et al.* 2003, Jump and Puñuelas 2006).

The scattered distribution of polylepis forests (named after the dominant tree genus, *Polylepis* spp.) within the 3000 to 4500 m altitudinal belt of the Andean Cordillera from Venezuela to Argentina was long considered their natural pattern of distribution (Kessler 2002, after an extensive review of research on *Polylepis* spp. distribution). It was not until the late 1950s that this view was questioned and an anthropogenic origin was suggested for the sporadic occurrence of these forests in isolated patches along stream ravines and steep rocky slopes (Ellenberg 1958 as cited by Kessler 2002). The hypothesis of a consistent long-term conversion of forest to pasture through frequent burning (Ellenberg 1979), which probably preceded the Spanish conquest (Fjeldså and Kessler 1996, Kessler 2002), has only started to gain support over the last decade (Fjeldså 1992, Kessler 1995, 2002, Lægaard 1992).

Current research on *Polylepis* forest fragmentation has focused on vertebrate species (particularly birds; Fjeldså 2002a, 2002b, Herzog and Cahill 2002, Servat *et al.* 2002) and ecological processes (Fjeldså and Kessler 1996, Velez *et al*. 1998, Kessler 2002). Research into the consequences of fragmentation on genetic variation within the dominant tree species of these forests is limited. This information is critical for the assessment of the long term viability of forest relicts (Saunders *et al*. 1991, Hamrick and Nason 1996, Hamrick and Apsit 2004) and their potential as sources for restoration (Saunders *el al*. 1991, Solbright 1991, Hamrick and Nason 1996, Renison *et al*. 2005).

The objective of this study was to investigate the distribution of allozyme genetic variation within and among populations of *Polylepis pauta* in the southern part of the northeastern Cordillera Oriental of Ecuador and assess whether the observed pattern are consistent with that of a more continuous historical range. Spatial attributes of forest patches were also incorporated to increase our understanding of genetic differentiation among subpopulations of *P. pauta* in the area.

3.2 MATERIALS AND METHODS

3.2.1 STUDY AREA

This study was carried out in the southern part of the northeastern Cordillera Oriental of Ecuador, in the 3500 - 4000 m belt of the Cayambe Coca Ecological Reserve (hereafter RECAY) and further south (78°11’55”- 78°2’22”W, 0°10’34”-0°25’34”S, Figures 2.1 and 3.1). The study area (approximately 491 km²) comprises three adjacent river basins in the southern part of the RECAY, the Chalpi, the Oyacachi, and the Papallacta basins. Of these three, the Chalpi River basin (Figure 3.3) is probably the least disturbed, supporting a continuous cover of mountain forest from 2000 to 4000 m elevation. The Oyacachi (Figure 3.2) and the Papallacta (Figure 3.4) basins have both been disturbed by conversion to pastureland, agricultural encroachment, and dam and road construction. The Oyacachi river basin has been inhabited since the mid-16th century (Ohlson 2001). Although it is not possible to accurately estimate the age of the *Polylepis* forest patches in the study area, some patches might have originated during that period, while others may be of more recent origin (19th century, Jameson 1858, Grubb *et al.* 1963).

3.2.2 THE SPECIES

The Andean genus *Polylepis* encompasses about 20 species of shrubs and trees with imparipinnate leaves and bisexual flowers arranged in racemes (Simpson 1979). All species are believed to be wind pollinated (Salgado-Labouriau *et al.* 1977, Berry and Calvo 1989, Fjeldså and Kessler 1996) and wind dispersed (Van Schaik *et al*. 1993, Vélez *et al.* 1998). *Polylepis pauta*, the tallest species within the genus (15-27 m), is characterized by thin dark orange bark that sheds in bands. The sericeous leaves consist of 7-11 leaflets, and hairs in the abaxial leaflet surface are typically restricted to the veins. The unbranched inflorescence usually holds more than 25 flowers and a floral pedicel is present (Schmidt-Lebuhn *et al.* 2006).

P. pauta is patchily distributed in northern Ecuador, east central and southern Peru (Fjeldså and Kessler 1996) and northern Bolivia (Kessler and Schmidt-Lebun 2006). In the study area the species stretches sporadically from 3640 m to 4000 m elevation in a grass páramo matrix, often co-occurring with species of the genera *Escallonia* and *Gynoxis* near its lower elevation limit. In most of the Chalpi basin, *P. pauta* has a continuous distribution.

3.2.3 FIELD SAMPLING

Four *Polylepis* forest patches (*i.e.*, populations *sensu* Forman 1999) per watershed were selected based on accessibility (Table 2.1).Two areas sampled in the Chalpi basin (C1 and C5) consisted of sites that actually occurred within a large continuous patch. Forty eight individuals, 24 mature (> 100 years) and 24 seedlings, were randomly sampled from a diagonal transect across each forest patch. Thus the whole sample (575 individuals) consisted of 192 individuals in the Chalpi basin, 192 in the Oyacachi basin and 191 in the Papallacta basin (one set of mature individuals consisted of 23 individuals). For each adult, terminal leaflets were cut within 5 to 10 hours after collection of small branches (<20 cm), put into cryogenic tubes and stored in liquid nitrogen. For seedlings, the entire individual was used to ensure sufficient tissue for allozyme analysis. The frozen tissue was shipped to the University of Georgia within a month of collection.

3.2.4 LABORATORY PROCEDURES

Frozen leaflets were crushed in liquid nitrogen and a buffer solution (Alvarez-Buylla and Garay 1994) was added to extract the proteins. The protein extract was absorbed onto chromatography paper wicks, which were stored on microtest plates at -70° C until electrophoretic analysis. A total of 25 loci were identified through the combination of four starch gel buffer systems and 11 enzyme stains (Soltis *et al*. 1983), namely: system 4, isocitrate dehydrogenase (*Idh-1, Idh-2* and *Idh-3*), Fructose-1,6-diphosphatase (*F,6dp-1*) and UTP-glucose-1-phosphatase (*Ugpp-1* and *Ugpp-2*); system 8-, fluorescent esterase (*Fe-1*, *Fe-2*, *Fe-3* and *Fe-4*) and triose-phosphate isomerase (*Tpi-1*, *Tpi-22*, *Tpi-3*, *Tpi-4*, *Tpi-5*,*Tpi-6* and *Tpi-7*); system 11 with malate dehydrogenase (*Mdh-1*), shikimate dehydrogenase (*Skdh-1*) and 6-phophosgluconate dehydrogenase (*6-Pgdh-1*); and system 34, glutamate dehydrogenase (*Gdh-1*), phosphoglucoisomerase (*Pgi-1* and *Pgi-2*), and phosphoglucomutase (*Pgm-1* and *Pgm-2*).

3.2.5. DATA ANALYSIS

Genetic variation at the species (*i.e.*, pooled) and within-population levels was measured in terms of the percentage of polymorphic loci (*P*), mean number of alleles per locus (*A*) and per polymorphic locus (*AP*), effective number of alleles (A_e), and observed (H_o) and expected (H_e) heterozygosities (Hamrick *et al.* 1979; Hamrick and Godt 1989) for the 12 populations in the study area (4 populations per watershed, each consisting of 48 individuals, 24 mature and 24 seedlings). Among-population genetic divergence and level of inbreeding for each polymorphic locus were estimated from calculation of $G_{ST} = [(H_T - H_S)/H_T]$, where H_T is the overall expected heterozygosity and H_S is within-population diversity (Nei 1973, 1977, 1987), and $F_{IS} = [(1-H_o)/H_e]$ (Wright 1965), respectively. Significance of deviations from Hardy-Weinberg equilibrium was assessed with chi-square analysis, $\chi^2 = NF^2$ (a-1) with df = a (a-1)/2, where N is the total sample size and a is the number of alleles at a locus (Li and Horvitz 1953). Genetic parameters were also calculated for watersheds overall, as well as for seedlings and mature individuals across and within watersheds. Statistics of genetic variation were calculated with LYNSPROG (developed by M.D. Loveless, Department of Biology, College of Wooster, Wooster, OH, USA, and A. Schnabel, Department of Biology, Indiana University, South Bend, IN, USA).

To test the effect of distance on genetic divergence, $F_{ST}/(1-F_{ST})$ was regressed against the natural logarithm of geographic distance between population pairs (Rousset, 1977). Isolation by distance was estimated with the software program GENEPOP 3.4 (designed by M. Raymond and F. Rousset, Université de Montpellier II, Montpellier, France). The relationship of genetic distance to the natural logarithm of the geographic distance was analyzed with Pearson product moment correlation and its significance was assessed through t test. Genetic affinity between populations was estimated from Nei's genetic identity and distance (Nei 1972). Graphic clustering of genetically similar populations in the form of a unweighted pair group method using an arithmetic average (UPGMA; Hillis, 1984) dendrogram was produced using NSYST-pc 2.1 software (Rohlf, 1992).

Relationships between genetic parameters, namely H_e, allelic richness (*i.e.*, total number of alleles in each population), percentage of alleles per population (*i.e.*, the proportion of alleles in one population in relation to the total number of alleles recorded for all populations) and several landscape metrics, including patch size, patch relief (*i.e.*, altitudinal range encompassed between the lower and upper patch limits), slope and shape complexity (*i.e.*, a measure of the degree of development of the border of the patch based on perimeter and area given by the Shoreline Development Index designed by Patton,1975), were assessed through Spearman rank correlation coefficient. Landscape metrics were derived from a rectified 1999 Landsat Thematic Mapper image, orthorectified aerial photography (scale 1:60,000) in ArcGIS/ArcMap 9.1 (ESRI, 2006) and coordinates and elevation of the forest patches were obtained with a Garmin GPS III. The error reported for coordinates ranged from 8 to 15 m, thus elevation data were affected by a 16 to 30 m error. *Polylepis* forest patches selected for the study were very distinct from the grass páramo matrix where they occurred and exhibited sharp boundaries; therefore they were identified and delineated directly on the orthorectified aerial photography (Figures 3.2 through 3.4).

3.3 RESULTS

3.3.1 GENETIC DIVERSITY OF *Polylepis pauta*

At the species level, 20 of 25 (i.e. 80%) loci resolved were polymorphic (Table3.2). Monomorphic loci included *Tpi-2*, *Tpi-4*, *Tpi-5*, *Tpi-6* and *Idh-2*. The number of alleles per polymorphic locus ranged from 2 to 4 (average *Ap* = 2.35, Table3.2) and the total number of alleles recorded for all loci and all populations was 59. None of the populations contained all of the alleles; the highest number of alleles recorded for a population was 52 (O4 and O6) and the lowest was 44 (P3, Table3.2). Unique alleles were found in populations C1, C5, O6, O7 and P1.

3.3.2 WITHIN POPULATION VARIATION

The Papallacta populations were genetically less diverse than the other two basins by most genetic measures. The percentage of polymorphic loci ranged from 72% to 80% in the populations of both the Chalpi and the Oyacachi basins and from 60 to 72 in the Papallacta populations (Table 3.2). The number of alleles per polymorphic locus (A_p) was also lower in the Papallacta populations than in the Chalpi and Oyacachi populations. The number of alleles per population showed the same pattern, with pooled values of 55, 57 and 51 for the Chalpi, Oyacachi and Papallacta watersheds, respectively (Table3.2). The Chalpi populations exhibited the highest pooled effective number of alleles per locus (A_e) and expected heterozygocity (H_e) while the Papallacta population had the lowest pooled values for these parameters.Observed heterozygosity (H_o) was lower than expected heterozygosity (H_e) under Hardy-Weinberg equilibrium in all 12 populations, but none of the differences was significant (Table 3.2).

3.3.3 AMONG POPULATION VARIATION

Differences in allele frequencies among populations were significant for 17 of the 20 polymorphic loci (Table 3.3). Overall genetic differentiation among the 12 remnant populations (G_{ST}) was 0.059 (mean H_T = 0.324, mean H_S = 0.304, Table 3.3). Genetic differentiation was generally higher across populations within each watershed than between watersheds. The highest genetic differentiation (G_{ST}) was recorded among the Oyacachi populations and the lowest, among the Papallacta populations (0.067 and 0.024, respectively, Table 4). The proportion of genetic differentiation among watersheds was 0.014 (*i.e.*, individuals within watersheds pooled to produce 3 populations, Table 3.4).

The mean inbreeding coefficient across all 20 polymorphic loci, F_{IS} (=0.038), did not depart significantly from Hardy-Weinberg equilibrium expectations (P>0.05, Table 3.3). Mean within-population genetic diversity (H_S) across watersheds was 0.320 and ranged from 0.284 (Oyacachi) to 0.337 (Chalpi) at the watershed level (Table 3.4).

3.3.4 COMPARISON OF AGE CLASSES

Dividing the 12 populations into mature individuals and seedlings yielded a marginally lower total genetic variation (H_T) for mature individuals (H_T= 0.319) than for seedlings (H_T= 0.328, Table 4) across all watersheds. Mean within-population genetic variation, H_S was similar for the two age classes across watersheds but varied slightly at the watershed level, being highest for the Chalpi basin and lowest for the Oyacachi populations (Table 3.4). Seedlings showed greater differentiation across watersheds than mature individuals (G_{ST} = 0.109 and 0.066, respectively; Table 3.4). Comparison of seedlings and mature individuals within each watershed yielded the highest G_{ST} for the Chalpi populations, while the Oyacachi populations were the least differentiated in terms of these two age classes (0.014 and 0.008 respectively, Table 3.4).

3.3.5 GENETIC IDENTITY AND ISOLATION BY DISTANCE

Correlation analysis indicated that pairwise genetic similarity between the 12 populations, expressed as $F_{ST} / (1-F_{ST})$, was not significantly related to the natural logarithm of geographical distance ($r = 0.14$, $P>0.05$) across basins.

Clustering of the 12 populations in a UPGMA dendrogram (Figure 3.5) revealed a strong affinity between populations from different watersheds. For example, the Chalpi populations had a greater genetic affinity with the populations of Papallacta and Oyacahi than with other Chalpi populations, even though two of them (C1 and C5) were actually part of a continuous patch. The grouping of P2 and P3 and, O1 and O4 were the only cases where populations within a watershed were the most similar. It is worth noting that patches which clustered together either face each other (*e.g.* P2 and P3) or converge at their upper limits roughly at the same elevation (*e.g*. O1 and O4) with no geographical barrier between them (Figures 3.1 trough 3.4).

3.3.6 GENETIC VARIATION AND LANDSCAPE CHARACTERISTICS

The mean number of alleles per polymorphic loci (A_p) showed a significant positive correlation with patch size and patch length (Table 3.5). A similar, but not significant, pattern was observed for expected heterozygosity (H_e), effective number of alleles (A_e) and percentage of alleles (Table 3.5). Although the sample size was consistent across populations, *Polylepis pauta* exhibited a rather uniform spacing within the populations sampled (field observation) and it is likely that larger patches supported larger populations, which would likely include more genetic variation. It is worth noting that larger forest patches also encompassed a broader elevation range ($r_s =0.78$, $P<0.05$).

The mean number of alleles per polymorphic locus (A_p) and the percentage of alleles were also positively correlated with shape complexity, as expressed by the Shore Development Index (*D*; 0.50 and 0.26 respectively, Table 3.5) but not in a significant manner. All genetic variation parameters (P, A_p, A_e, H_e and % of alleles) decreased with increasing patch steepness and average elevation of the patch (except for percentage of polymorphic loci, P,in the case of the latter), although significant negative correlations were recorded only for the percentage of polymorphic loci and the percentage of alleles (Table 3.5). This pattern could be related to the prevalence of vegetative reproduction of trees over sexual reproduction in steeper slopes which are more prone to landslides and consequently larger canopy openings (field observation).

3.4 DISCUSSION

Genetic diversity maintained by *Polylepis pauta* in this geographic region, expressed in terms of total genetic variation (pooled H_e) and percentage of polymorphic loci (P), is higher than that observed for most wind pollinated and dispersed temperate and tropical trees with regional distributions (cf. reviews by Hamrick *et al*. 1992 and Hamrick and Godt 1996). Values of within population variation (mean H_e) recorded for the *P. pauta* populations sampled fall within the range observed for tree species characterized by the above mentioned life history and ecological traits (cf. reviews by Hamrick *et al*. 1992 and Hamrick and Godt 1996). It is worth noting that the Oyacachi basin populations had the highest percentage of polymorphic loci (P), number of alleles per polymorphic locus (A_p) and number of alleles per population. The generally lower percentage of polymorphic loci, mean number of alleles per polymorphic locus, mean number of alleles per locus and percentage of alleles recorded in the Papallacta populations might be the consequence of either a more severe anthropogenic disturbance of this basin as compared to the other two, or to the significantly smaller total area sampled in this basin (0.25 km²) relative to the Chalpi (0.92 km²) and the Oyacachi (0.82 km²) basins. Although differences between observed and expected heterozygosities were observed within each patch, they were not significant.

G_{ST} values obtained from comparing the 12 remnant populations at different spatial scales revealed lower differentiation across watersheds than among populations within each watershed. The Oyacachi basin showed more differentiation among the four populations within the watershed than was the case within either of the other two watersheds. The Oyacachi basin populations also exhibited the largest variation in the altitudinal range they encompassed and the populations were further apart than the populations in the other two basins. The converse was also true; *i.e*., populations with similar elevational range and closer together showed less differentiation (*e.g.* Papallacta basin).

Lower genetic differentiation was recorded for populations of mature individuals than for seedling populations. The higher G_{ST} values among populations of juveniles relative to adults (perhaps the progeny of a few adults), could be explained by the very patchy occurrence of seedlings, with most of them restricted to canopy gaps (field observation, also noted by Enrico *et al*. 2004), which predisposed a patchy collection of samples. Indeed, seedlings were relatively more evenly spread in the populations of the Oyacachi basin where the degree of differentiation between mature individuals and seedlings was the lowest. The absence of such structure in populations of mature individuals is consistent with theoretical predictions for tree populations, characterized by a generally low genetic structure (Hamrick and Godt 1989, 1996; Nybom 2004). Strong selection of seedlings (observed in *Polylepis incana*, *P. pauta*, [Cjerjacks *et al.* 2007], and *P. australis* [Enrico *et al.*2004]) and delayed reproductive maturity in trees could contribute to the attenuation of structure over time (Austerlitz *et al.* 2000; Le Corre and Kremer 2003).

No correlation was found between geographic distance and genetic differentiation, and clustering of populations on the basis of genetic similarity often revealed more affinity between populations of different watersheds than populations within the same basin. The relevance of populations' spatial arrangement may suggest that there is a greater gene exchange among populations in different river basins than within basins due to prevailing wind patterns.

The level of genetic variation shared by *Polylepis pauta* trees in the 12 forest remnants in three adjacent watersheds was used to assess the likelihood of a historically continuous range in the southern part of the northeastern Cordillera Oriental of Ecuador. The levels and distribution of genetic variation in these *Polylepis pauta* populations are more consistent with that of relatively recent fragmentation of a more continuous historical range, where the trees' longevity and aptitude for long-distance pollen and seed flow has buffered the tendency of distant populations to diverge genetically, as theory predicts (cf. Aldrich *et al*. 1998, Bacles *et al.* 2004, Hamrick 2004, Petit and Hampe 2006, Young *et al.* 1993).

Although no research has been published so far on the longevity of *Polylepis* spp. (M. Kessler, pers. comm. August 2008), tree ring chronologies developed from *Polylepis tarapacana* revealed high longevity (705 yr, Argollo *et al*. 2004). No attempts were made in this study to assess the age or longevity of *Polylepis pauta*; based on the size reached by most mature individuals of *Polylepis pauta* sampled (re sprouts were 80 cm DBH), however, it is not out of the question that considerable longevity may characterize this species as well. Similarly, the dispersal distance of *Polylepis* spp. pollen has not been specifically studied; nonetheless, wind pollination and seed dispersal are likely to become more important with increasing altitude in tropical montane floras (Smith and Young 1987; Berry and Calvo 1989), which would further reduce the effects of fragmentation in *Polylepis* forests. Other non-genetic analyses are currently being conducted to explore further the timing of fragmentation of the *Polylepis* forest patches.

The second aim of this study was to explore potential correlations between spatial attributes of forest patches and the distribution of genetic variation of *P. pauta*. Larger forest patches, encompassing a broader altitudinal range, showed higher values for most of the genetic diversity parameters considered in this study (P, Ap , A, A_e , H_e and percentage of alleles). Given the relatively constant spacing of *Polylepis* trees across all patches (field observation), larger patches likely supported larger populations, which could explain the higher intraspecific variation observed in the larger patches. Greater genetic diversity within patches with a greater altitudinal range and the greater differentiation within watersheds that span a greater elevation range supports Smith and Young's (1987) suggestion that genetic differentiation occurs within species with large elevation ranges.

More complex patches (higher Shoreline Development Index, D) showed a tendency to have more alleles and mean number of alleles per locus than compact, more circular ones. This is consistent with enhanced interactions across boundaries provided by more convoluted patch shapes (Forman 1999) which are known to influence pollen movement pattern and actually increase it (Levin and Wilson 1978; Rai and Jain 1982; Handel 1983).

Consistently lower genetic variation (as expressed by P, A_p , A, A_e , H_e and percentage of alleles) was associated with steeper slopes and higher average elevation of the patch; this might stem from the predominance of vegetative over sexual reproduction in steeper areas at higher elevations due to the increased frequency of landslides. Large fallen trees usually root and branch from their horizontal position in large canopy gaps and outgrow seedlings in those gaps (field observation). Most research on the relationships between intraspecific genetic variation and landscape features has focused on connectivity at the metapopulation level (Manel *et al.* 2003, Storfer *et al.* 2007). Relationships between genetic variation and landforms (*e.g.,* terrain topography) constitute a relatively unexplored area of research within the recently emerged discipline of landscape genetics but one that is worthy of further exploration.

Table 3.1: Locations and spatial attributes of the *Polylepis pauta* patches sampled in the southern part of the northeastern Cordillera Oriental of Ecuador

Basin	Patch	Area *A* (km^2)	Altitudinal range (m)	Average elevation	Relief *R* (km)	Perimeter *P* (km)	Slope *S*	*D*
Chalpi	C1	0.27	3720 – 3880	3800	0.16	2.76	0.70	1.50
	C3	0.02	3910– 3960	3935	0.05	0.79	0.39	1.58
	C4	0.08	3760 – 3880	3820	0.12	1.42	0.67	1.42
	C5	0.55	3720 – 3880	3800	0.16	4.07	0.51	1.55
		0.92[1]						
Oyacachi	O1	0.32	3660 – 3880	3770	0.22	3.38	0.75	1.68
	O4	0.03	3880 – 4000	3940	0.12	0.91	0.52	1.49
	O6	0.34	3640 – 3920	3780	0.28	3.61	0.61	1.74
	O7	0.13	3800 – 3880	3840	0.08	2.25	0.57	1.76
		0.82[1]						
Papallacta	P1	0.05	3740 – 3840	3790	0.10	1.32	1.11	1.67
	P2	0.15	3760 – 3920	3840	0.16	2.67	0.89	1.95
	P3	0.01	3800 – 3900	3850	0.10	0.33	1.00	0.94
	P4	0.04	3840 – 3980	3910	0.14	1.07	0.70	1.51
		0.25[1]						

R is the altitudinal range encompassed by the patch

S was computed by dividing the altitudinal range (the line's vertical rise) by the distance of the projected line on the Landsat TM Image (the distance the line travels on the surface)

$D=P/2\sqrt{\pi A}$, *Shoreline Development Index* (Patton, 1975) is a measure of the degree of convolution of a patch based on perimeter and area

[1] Total area sampled per watershed

Table 3.2: Allozyme variation in the 12 *Polylepis pauta* populations sampled in the southern part of the northeastern Cordillera Oriental of Ecuador

Basin	Patch	P	A_p	A	A_e	H_o (SD)	H_e (SD)	*No. of Alleles*[a]	*% of Alleles*
Chalpi	C1	80.00	2.35	2.08	1.52	0.248 (0.013)	0.270 (0.044)	52	88.14
	C3	76.00	2.32	2.00	1.47	0.238 (0.013)	0.251 (0.045)	50	84.75
	C4	76.00	2.26	1.96	1.55	0.268 (0.013)	0.284 (0.045)	49	83.05
	C5	72.00	2.44	2.04	1.52	0.231 (0.012)	0.272 (0.044)	51^1	86.44
	Mean	76	2.34	2.02	1.52	0.246	0.269	50.5	85.59
	Pooled	80.0	2.50	2.00	1.54		0.280 (0.044)	55	93.2
Oyacachi	O1	72.00	2.39	2.00	1.43	0.228 (0.012)	0.234 (0.043)	50	84.75
	O4	80.00	2.35	2.08	1.38	0.219 (0.012)	0.220 (0.040)	52	88.14
	O6	76.00	2.42	2.08	1.42	0.226 (0.012)	0.238 (0.041)	52^1	88.14
	O7	76.00	2.37	2.04	1.36	0.194 (0.012)	0.213 (0.040)	51^1	86.44
	Mean	76	2.38	2.05	1.40	0.217	0.226	51.25	86.87
	Pooled	80.00	2.60	2.28	1.44		0.247 (0.042)	57	96.6
Papallacta	P1	72.00	2.39	2.00	1.41	0.231 (0.012)	0.232 (0.042)	50^1	84.75
	P2	72.00	2.33	1.96	1.44	0.229 (0.012)	0.242 (0.042)	49	83.05
	P3	60.00	2.27	1.76	1.42	0.226 (0.012)	0.225 (0.045)	44	74.58
	P4	72.00	2.33	1.96	1.42	0.220 (0.012)	0.230 (0.041)	49	83.03
	Mean	69	2.33	1.92	1.42	0.227	0.232	48	81.35
	Pooled	72.2	2.44	2.04	1.43		0.238 (0.042)	51	86.4
Mean		73.67	2.35	2.00	1.45	0.230	0.243	49.7	84.61
Pooled		80.0	2.75	2.40	1.48		0.259	59	100
SD		2.53	0.06	0.09	0.059	0.018	0.012	2.103	3.719

P is the percentage of polymorphic loci, *AP* is the mean number of alleles per polymorphic locus, *A* is the mean number of alleles per locus, A_e is the effective number of alleles, Ho is the observed heterozygosity , $\mathrm{H_e}$ is the expected heterozygosity under Hardy –Weinberg equilibrium , No of Alleles refers to total number of alleles found in each population, and % of Alleles is the proportion of alleles in one population in relation to the total number of alleles recorded for all the populations.

[a] Superscript following the number indicates the number of unique alleles found in the population

Table 3.3: Number of alleles observed at each polymorphic locus and genetic diversity and structure statistics of *Polylepis pauta* patches sampled in the southern part of the northeastern Cordillera Oriental of Ecuador

Locus	Alleles[a]	X^2 (df)	H_T	H_S	G_{ST}	F_{IS}
Fe-1	3	113.2 (22) ***	0.6222	0.5830	0.0631	0.0375
Fe-2	4^1	243.0 (33)***	0.4365	0.4025	0.0779	0.1212
Fe-3	4	164.2 (44)***	0.4995	0.4846	0.0300	0.2049
Fe-4	2	45.6 (11)***	0.0357	0.0339	0.0488	-0.0707
F1,6dp-1	2	108.8 (11)***	0.2152	0.1948	0.0946	-0.0803
Gdh-1	2	15.8 (11)	0.0606	0.0598	0.0137	0.0696
Idh-1	3	66.7 (22)***	0.5159	0.5052	0.0207	0.0275
Idh-3	2	30.0 (11)**	0.2692	0.2621	0.0262	0.0031
Mdh-1	2	378.2 (11)***	0.4024	0.2701	0.3289	0.0406
Pgi-1	4^1	122.7 (33)***	0.0343	0.0330	0.0381	-0.0124
Pgi-2	3	71.6 (22)***	0.4364	0.4254	0.0251	-0.1199
Pgm-1	3	60.2 (22)***	0.4189	0.4078	0.0264	0.0417
Pgm-2	3^1	41.2 (22)**	0.4842	0.4715	0.0263	0.0450
6-Pgdh-1	3^1	61.0 (22)***	0.2624	0.2558	0.0252	-0.1013
Skdh-1	4^1	162.4 (33)***	0.6148	0.5782	0.0595	0.0827
Tpi-1	2	58.2 (11)***	0.2658	0.2493	0.0621	0.0249
Tpi-3	2	26.0 (11)**	0.3343	0.3268	0.0226	0.1697
Tpi-7	2	13.3 (11)	0.3432	0.3392	0.0116	0.1233
Ugpp-1	2	14.4 (11)	0.0475	0.0469	0.0125	0.0362
Ugpp-2	2	187. 4 (11)***	0.1883	0.1576	0.1629	0.1504
Mean	2.7		0.3244	0.3044	0.0588	0.0376
SD	0.8013		0.8165	0.1784	0.0731	

H_T is the total genetic diversity for the species; H_S is the mean within-population genetic diversity; G_{ST} is the proportion of the total genetic diversity found among populations. Significance of X^2 test for allele frequencies differences among the 12 populations: *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

[a] Superscripts following the numbers indicate alleles found in only one population

Table 3.4: Among population variation across and within watersheds and between age classes for *Polylepis pauta* populations sampled in the southern part of the northeastern Cordillera Oriental of Ecuador

Basin	Populations sub setting	Number of populations	N	Total Sample size	H_T	H_S	G_{ST}
All three	All populations[1]	12	48	575	0.324	0.304	0.059
watersheds	Among watersheds[2]	3	192	575		0.320	0.014
	All mature individuals	12	24	287	0.319	0.294	0.066
	All seedlings	12	24	288	0.328	0.291	0.109
Chalpi	All	4	48	192	0.350	0.337	0.036
	Mature vs. seedlings	2	96	192		0.346	0.014
Oyacachi	All	4	48	192	0.309	0.284	0.067
	Mature vs. seedlings	2	96	192		0.306	0.008
Papallacta	All	4	48	191	0.334	0.325	0.024
	Mature vs. seedlings	2	96	191		0.330	0.011

N is the number of individuals per population; H_T is the total genetic diversity for the species; H_S is the mean within-population genetic diversity; G_{ST} is the proportion of the total genetic diversity found among populations

[1] Original 12 populations corresponding to the 12 forest patches sampled

[2] The 12 populations sampled pooled across populations, within watershed

Table 3.5: Spearman rank correlation coefficients for genetic variation parameters and spatial attributes of the *Polylepis pauta* patches sampled in the southern part of the northeastern Cordillera Oriental of Ecuador

	Genetic variation parameters				
Patch spatial attributes	P	A_p	A_e	H_e	% Alleles
Patch area (A)	0.17	0.71*	0.32	0.44	0.46
Average Elevation	0.09	-0.62*	-0.20	-0.32	-0.24
Patch relief (R)	0.01	0.49	0.38	0.38	0.25
Slope steepness (S)	-0.59*	-0.10	-0.11	-0.18	-0.54
Shoreline development index (D)	0.06	0.50	-0.28	-0.10	0.26

Significance of Pearson correlation coefficient, r_s: *$P < 0.05$

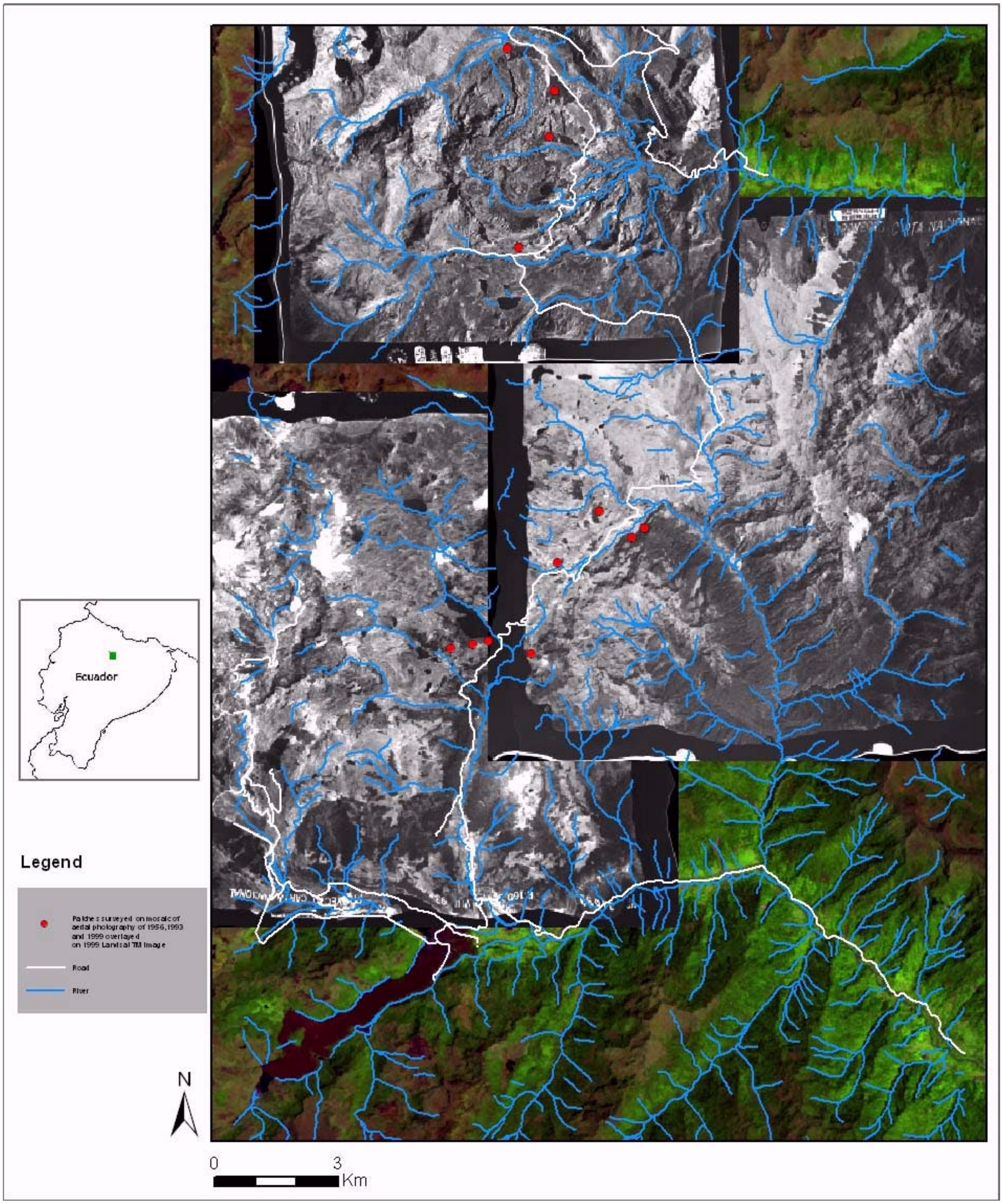


Figure 3.1: *Polylepis* forest patches sampled in the Oyacachi, Chalpi and Papallata basins, southern part of the Northeastern Cordillera Oriental, Ecuador.

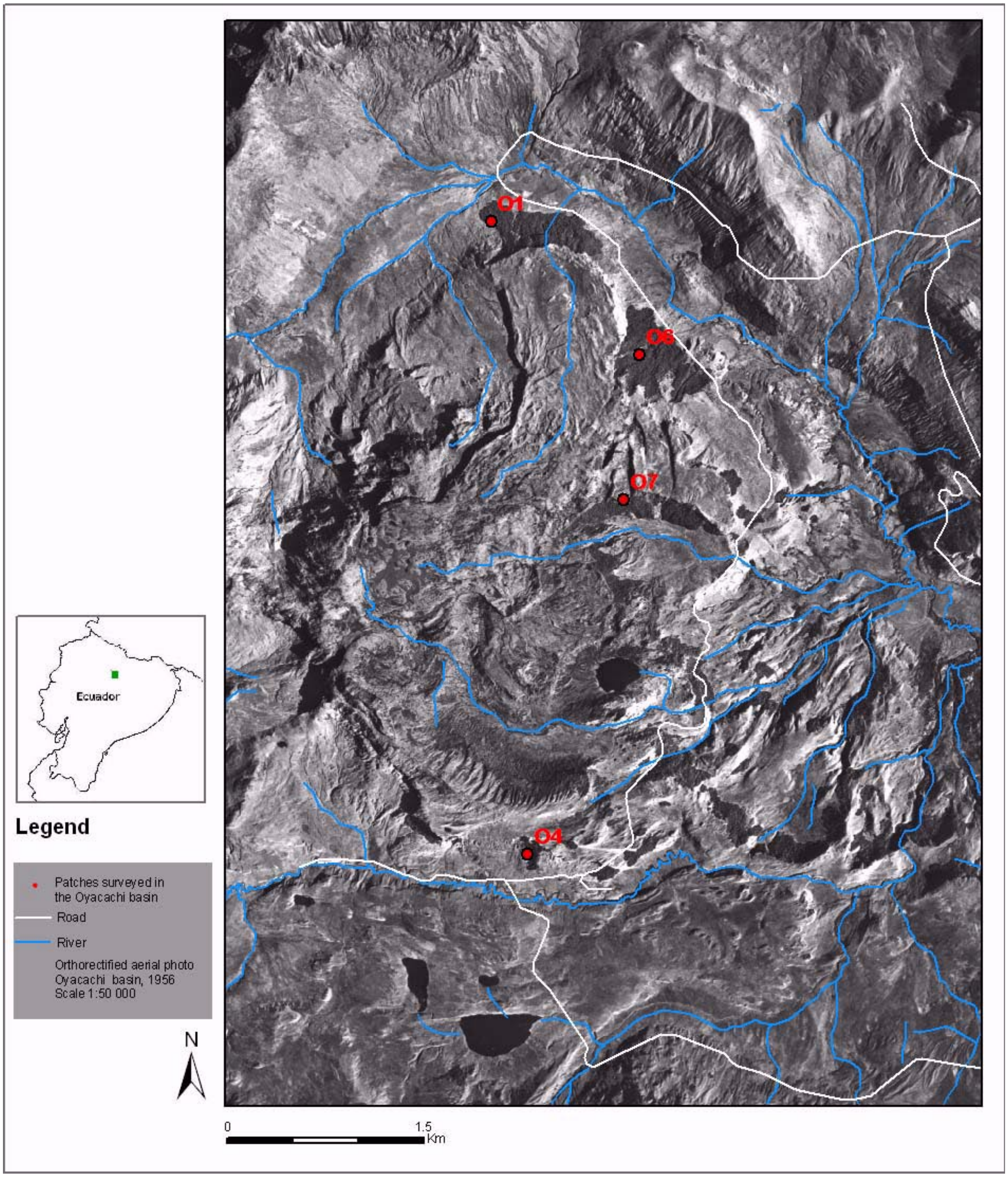


Figure 3.2: *Polylepis* forest patches sampled in the Oyacachi River basin, southern part of the Northeastern Cordillera Oriental, Ecuador.

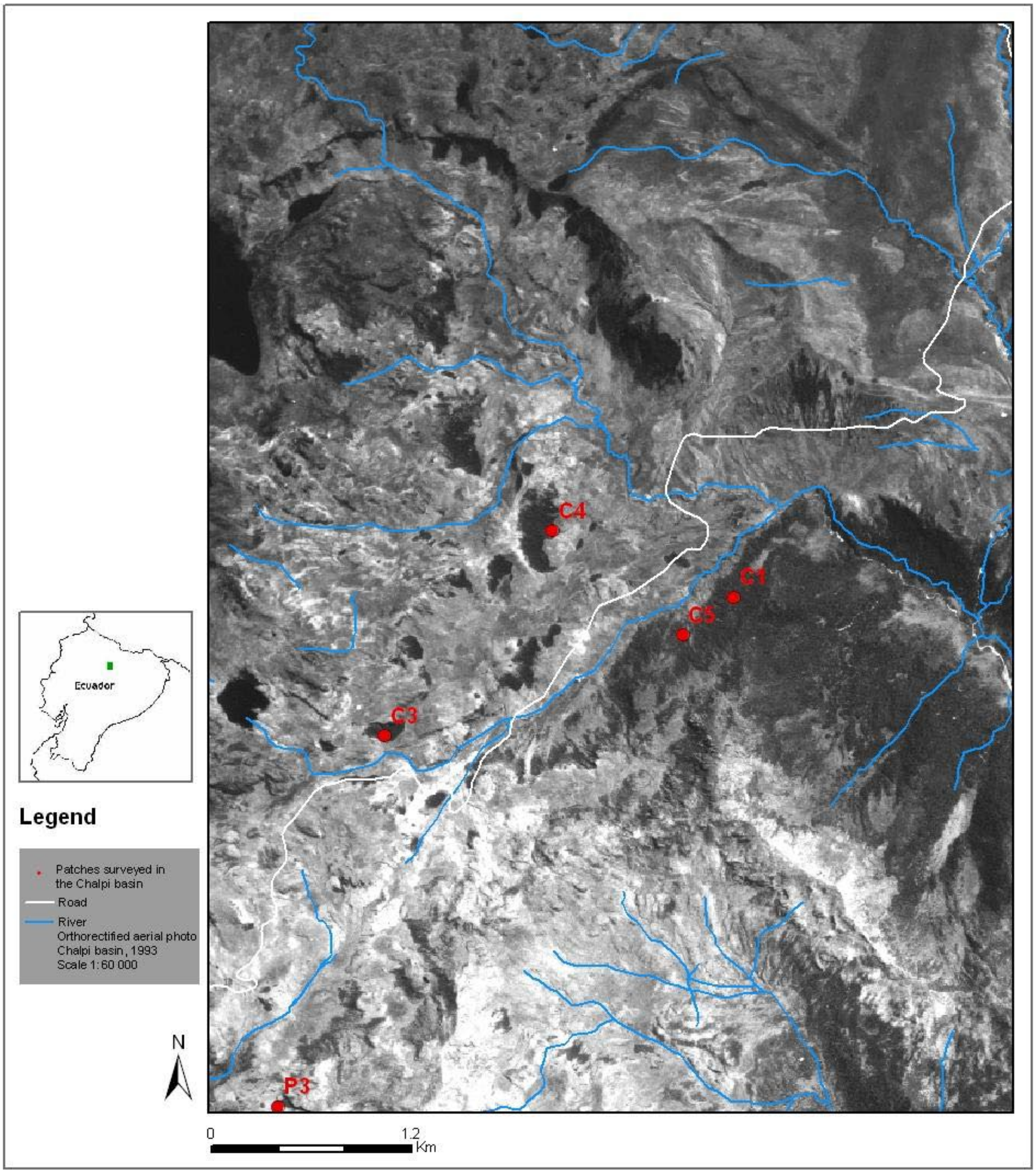


Figure 3.3: *Polylepis* forest patches sampled in the Chalpi River basin, southern part of the Northeastern Cordillera Oriental, Ecuador.

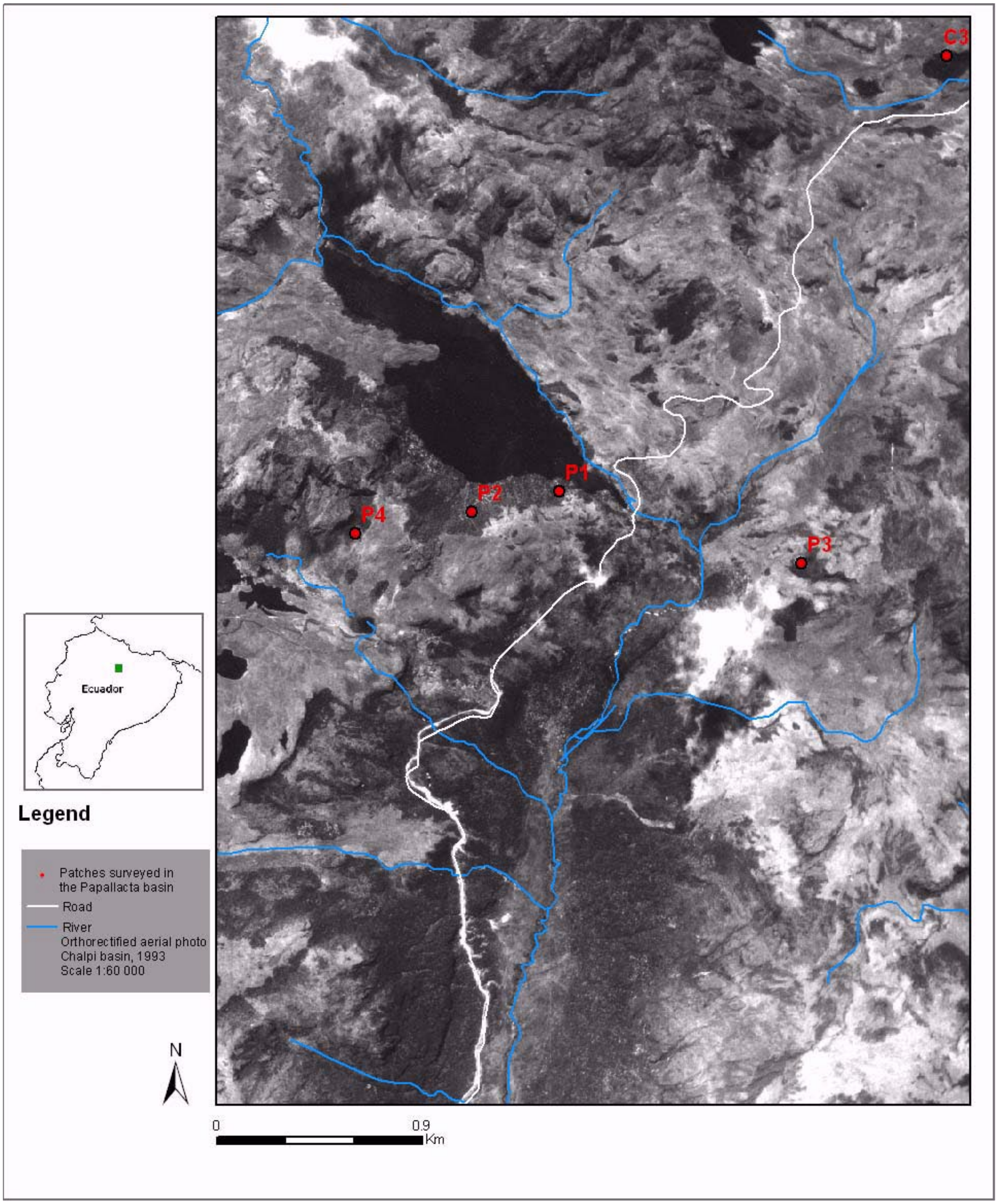


Figure 3.4: *Polylepis* forest patches sampled in Papallata River basin, southern part of the Northeastern Cordillera Oriental, Ecuador.

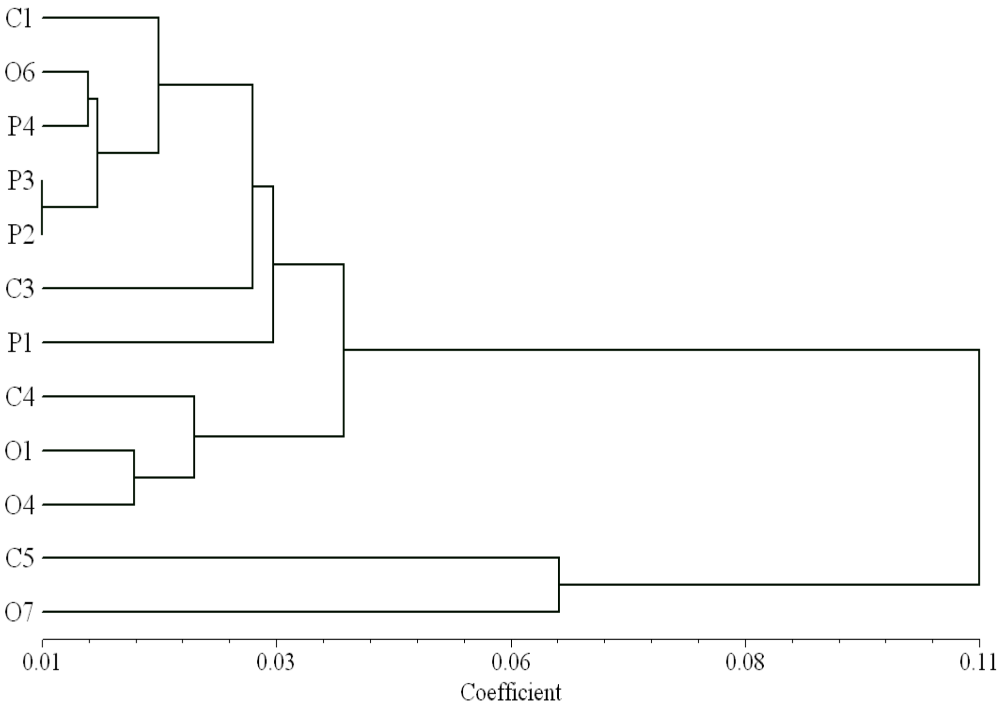


Figure 3.5: UPGMA dendrogram based on Nei's genetic distance for the *Polylepis pauta* populations sampled in the Cayambe Coca Ecological Reserve, Ecuador.

CHAPTER 4

FLORISTIC DIVERSITY OF THE *Polylepis* FOREST REMNANTS OF THE SOUTHERN PART OF THE NORTHEASTERN CORDILLERA ORIENTAL OF ECUADOR:

ASSOCIATIONS WITH ELEVATION AND FRAGMENTATION

4.1 INTRODUCTION

The trend of species diversity decline with increased elevation has been known for nearly two centuries (Humboldt 1849, Wallace 1878, Merriam 1890, Whitthaker 1960, MacArthur 1972, Lomolino 2001) but it is still poorly understood (Lomolino 2001, Rahbek 1995, Spehn *et al*. 2002). Major constraints to a comprehensive understanding of the elevation gradient of species diversity and assessment of its universality are the remoteness of mountain environments and inadequate research approaches to deal with the species-area effect in mountain regions (Rahbek 1995 and 2005, Lomolino 2001). The reduction of land area with increasing elevation has long been linked to elevation gradients in species diversity (Lomolino 2001 and references there in, Körner 2002); however, high elevation communities have seldom been analyzed with a species-area relationship approach (Lomolino 2001) or studied in the context of fragmentation.

Fragmentation is known to affect most biogeographic patterns through erosion of native species diversity as a consequence of habitat loss and increased insularization (Wilcox 1980, Terborgh and Winter 1980, Tilman *et al.* 1994, Forman 1995). However, most studies which confirm theoretical predictions assess relatively recent fragmentation events (cf. review by Hobbs and Yates 2003), which, given the prolonged lag effects of many consequences of fragmentation (Tilman *et al.* 1994, Loehle and Li 1996, McCarthy *et al*. 1997, Terborgh *et al.* 1997), are unlikely to provide a representative depiction of the changes in biogeographic patterns which result from this process (cf. review by Hobbs and Yates 2003).

Studies of the effects of fragmentation on biogeographic patterns are further complicated by the scant information on high elevation communities and the fact that most ecosystems are no longer continuously distributed and, therefore, community departure from that condition cannot be fully assessed. Better assessments of the consequences of habitat loss and insularization on species distribution patterns are possible where fragmentation events are old and have had sufficient time to reach a species-turnover steady state ("equilibrate" *sensu* MacArthur and Wilson 1967, also cf. Turner *et al.* 1996, Kellman *el al.* 1997, Tabarelli *et al.*1999), and where they coexist with a contemporaneous continuous forest.

The southern part of the northeastern Cordillera Oriental of Ecuador possesses some of the few remnants of continuous *Polylepis* forest and several isolated patches (Fundación Antisana 1998); together these constitute a unique opportunity to assess the effects of fragmentation on plant species diversity of a high elevation community. *Polylepis* forests, named after the dominant tree species (*Polylepis* spp.), occur within the 3000-4500 m altitudinal belt of the Andean Cordillera (altitudinal limits vary depending on local physical and climatic conditions; Cañadas 1983, Jørgensen and León 1999), under conditions that are typically adverse to tree growth, *i.e*, extreme diurnal temperature variation, steep slopes, and waterlogged peat soils (Fjeldså and Kessler 1996). Continuous long-term conversion of these forests to pasture through frequent burning is most likely the cause for their patchy occurrence restricted to steep rocky slopes and stream ravines (Ellenberg 1958 as cited by Kessler 2002, Ellenberg 1979, Fjeldså 1992, Lægaard 1992, Kessler 1995, 2002). Under natural conditions they would be bounded above by drier shrubby to grassy vegetation types and at lower elevations by either drier or humid tropical forest (Cañadas 1983, Balslev 1988, Lægaard 1992). Compared with *Polylepis* forests in Peru and Bolivia, Ecuadorian counterparts have been the focus of little research and even less monitoring.

This study aims to document the vascular floristic diversity of *Polylepis pauta* forest patches of the southern part of the Northeastern Cordillera Oriental of Ecuador, determine whether species diversity declines with increased elevation within these forest patches and assess the relative importance of the fragments' spatial attributes on the level and distribution patterns of plant diversity within them. Because *Polylepis* forests occur on steep slopes whose susceptibility to landslides, and consequently to canopy openings, increases with elevation, estimation of canopy closure at different elevations was incorporated into the study to enhance our understanding of floristic variation within the altitudinal range encompassed by these forests.

4.2 MATERIALS AND METHODS

4.2.1 STUDY AREA

The study area falls within the limits of the Cayambe Coca Ecological Reserve, identified as a priority area for the conservation of mountain ecosystem diversity and water resources (Fundación Antisana 1998) and an adjacent area farther south (approximately 491 km²). It encompasses the 3600-4000 m belt of three adjacent river basins in the southern part of the Northeastern Cordillera Oriental of Ecuador (0°10'34" -0°25'34"S; 78°2'22"- 78°11'55" W, Figure 2.1), the Oyacachi,,the Chalpi and the Papallacta basins. The three watersheds are part of the northwesternmost limit of the Amazon basin and occur on moderately developed soils of recent volcanic origin, predominantly Inceptisols (Skov1997). Relief is remarkably heterogeneous and dominated by steep slopes (Skov 1997).

Mean annual precipitation is 1310 mm in the Papallacta basin (derived from 43 years record from the Papallacta precipitation station) and 1290mm in the Oyacahi basin (obtained from 17 years records of the Oyacachi precipitation station), with a peak in July and a relatively dry period in January. There are no records for the Chalpi basin, but a similar trend in annual precipitation peaks and relatively dry periods has been noted (EMAAP 1991). Mean monthly temperature for the study area is 10.6°C and mean relative humidity ranges from 91.0% in October to 93.3% in January (Papallacta precipitation station).

The Chalpi River basin supports a continuous cover of mountain forest from 3000m to 4000 m elevation and is the least disturbed of the three basins. *Polylepis* forest patches of the Oyacachi and

Papallacta river basins might have originated during the first human settlements in the Oyacachi valley (i.e., 16th century, Ohlson 2001), while others may be of more recent origin (19th century, Jameson 1858, Grubb *et al.* 1963).

4.2.2 FIELD SAMPLING

Twelve *Polylepis* forest patches were surveyed throughout their elevation range (approximately 3500m-4100 m, Figure 3.1) on the three adjacent watersheds of the study area during mid-June to mid-July 2006 and 2007. Four patches (*sensu* Foreman 1999) per watershed were selected on the basis of accessibility (Figure 3.1 through 3.4) and sampled using three circular quadrats of 5.65 m radius (circular plots of 100.29 m² each). The three quadrats representing each patch corresponded to three altitudinal categories defined in relative terms, *i.e.*, lowest, middle and highest zone within each patch. Coordinates and elevation of the center of each quadrat were obtained with a Garmin GPS III. The error reported for coordinates ranged from 8 to 15 m, thus elevation data were affected by a 16 to 30 m error. The altitude of the center of each quadrat varied as patches varied in altitudinal occurrence (Table 4.1). Centers of the lowest and highest quadrats were located approximately 20 m from the lowest and highest patch limits, respectively.

All vascular species occurring in each quadrat were collected. Identification of collections was carried out at the herbarium of the Catholic University of Ecuador, Quito, Ecuador (QCA, www.puce.edu.ed/herbario) and the herbarium of the University of Århus, Århus, Denmark (AAU, www.biology.au.dk) during August 2006 and December 2006 and January 2007.

To assess canopy closure (*sensu* Jennings *et al*. 1999) in each quadrat, the circular sampling plot was divided into 4 sub-quadrats, each representing ¼ of the circular plot. Photographs were taken with a Canon 1000FN/AF camera leveled on the ground at the center of each sub-quadrat, with the lens axis vertical. The camera was fitted with a 35-80mm *ƒ*/4-5.6 lens at minimum magnification and ISO 400 film. Aperture width and shutter speed were set to the automatic mode. Selection of this method over the hemispherical photography method was based upon the objectives of the present study and the biophysical features of *Polylepis pauta* forest patches sampled. The goal for the estimation of canopy closure was to assess the potential relationship of crown gaps to elevation and their influence on plant species diversity over a relatively small area (approximately 25 m²). Narrower angles of view are considered to perform better in such cases (Bunnell *et al*. 1989, Guevara-Escobar *et al*. 2005). The photographs produced with this method chosen are less biased by incoming light variation imposed by the biophysical characteristics of the study area than photographs encompassing a broader field of view. *Polylepis* patches studied occurred on steep slopes; canopy height varied from 3 to 12 m within short distances across the study area; and skies were usually overcast. The combined effects of these features in hemispherical photographs are, in general terms, increased reflectance (Roxburgh and Kelly 1995) and light income overestimates (Jennings *et al*. 1999).

4.2.3 DATA PROCESSING AND ANALYSIS

Plant species collected were divided into 3 groups according to their growth form, *i.e.*, herbs and vines, shrubs and treelets, and ferns. Species occurrence was recorded separately by quadrat and by forest patch as presence/absence. Pearson product-moment correlation analysis was used to explore possible direct relationships between plant species richness and quadrat elevation, percentage canopy closure, and the spatial attributes of patches, *i.e.* patch area, length, slope, shape complexity and distance to other patches.

Canopy photographs were scanned as 24 x 36 mm color negatives with a Canon film scanner (CanoScan 4400F) and Adobe Photoshop CS3 software (developed by Adobe System Incorporated, San Jose, California, 2006) Digital images were saved as uncompressed *.TIFF files and then converted to and saved as *.BMP binary files (*i.e.*, 8-bit 2.1 MB black and white pixels images) in Image J 1.38e/Java 1.50_09 software (developed by Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, Maryland, USA). The percentage of canopy closure was computed from the black and the total pixel counts of the *.BMP image histogram in Image J (Figures 4.1 and 4.2).

Two separate cluster analyses were carried out to indicate compositional similarities among quadrats and among patches. Analyses were conducted with the group average linkage method based on presence/absence matrices with relative Sørensen distance (“revitalized Manhattan” in Faith *el al.* 1987). Ordination of quadrats was performed using Detrended Correspondence Analysis (DCA, Hill and Gauch 1980) on the quadrat presence/absence matrix. Rare species were downweighted; the rescaling threshold was set at 0, and the number of segments, at 26. Classification and ordination analyses were performed with PC-ORD 4 (McCune *et al*. 1999). Possible links between resulting DCA axes and elevation and canopy closure were analyzed with the Spearman’s rank correlation coefficient, r_s.

Spatial attributes of forest patches were obtained from aerial photography of 1993 scale 1:50,000 (Figures 3.1 through 3.4), a rectified 1999 Landsat Thematic Mapper (TM) image, a digital contour map in ArcGIS/ArcMap 9.1 (ESRI, 2006) and ground control points obtained in the field with the Garmin GPS III (with an 8 to 16 m error for x and y coordinates and 15 to 30 m error for elevation) . *Polylepis* forest patches selected for the study are very distinct from the grass páramo matrix where they occur and exhibit sharp boundaries (Figures 4.3 through 4.8); so they were identified and delineated directly on the rectified aerial photography with no need for further classification. . Spatial attributes of the patches included area, patch relief (*i.e.*, altitudinal range encompassed between the lower and upper patch limits), slope and shape complexity (*i.e.*, a measure of the degree of development of the border of the patch based on perimeter and area given by the Shoreline Development Index designed by Patton1975). Potential effects of spatial attributes of the patches on species diversity were assessed with the Spearman’s rank correlation coefficient, r_s.

4.3. RESULTS

4.3.1 FLORISTIC DIVERSITY OF *Polylepis* FORESTS OF THE CHALPI, OYACACHI AND PAPALLACTA BASINS

A total of 104 plant species was recorded in 12 *Polylepis pauta* forest patches sampled in the Chalpi, Oyacachi and Papallacta basins (Appendix A). Of these, 44 were herbs and vines, 33 were shrubs and treelets and 27 were ferns. Common species of *Polylepis pauta* forests (Figures 4.9 through 4.11) from the study area (*i.e.* found in more than two thirds of the 36 quadrats sampled) were, among herbs and vines: *Stellaria recurvata* and *Neurolepis aristata* (grass); among shrubs and treelets: *Aetheolaena involucrata*, *Aetheolaena lingulata*, *Gynoyis hallii*, *Miconia latifolia* (Figure 4.12), *Ceratostema alatum* (Figure 4.13) and *Valeriana microphylla*; and among ferns: *Elaphoglossum ovatum, Elaphoglossum vulcanicum* (Figure 4.14), *Hymenophylum myriocarpum*, *Melpomene pilosissima* and *Terpsichore heteromorpha*. Other species found in relatively high frequency (*i.e.* found in more than half of the quadrats sampled) were: *Hydrocotyle alchemilloides*, *Luzula gigantea*, and *Oxalis lotoides* (herbs); *Monticalya myrsinites* and *Pernettya prostrata* (shrubs); and, *Melpomene pseudonutans*, *Polypodium mindense* and *Thelypteris retroflexa* (ferns).

It is worth noting that *Neurolepis elata* (Figure 4.15), whose occurrence has been associated with the upper montane forest transition to páramo (Ohl and Bussmann 2004, Ritcher *et al*. 2008) and mixed forest / shrubland (Renison *et al*. 2006), was very common in the Chalpi basin (Figure 4.16), where it occurred mostly in seeps, and was absent from the plant collections of the other two basins. *N. elata* seems to have previously occurred in the Oyacachi and Papallacta basins as the Quichuas recall collection of this species for roof construction several decades ago (50 years or so ago, E. Parion, pers.com. July 2007). The Chalpi basin, and particularly the continuous forest within this basin, also differed in the frequency of occurrence of certain common herbs and ferns, which were often present in the Oyacachi and Papallacta watersheds but were rare or even absent (*M. pseudomutans*) in the Chalpi basin. For example, the herbs *A. involucrata*, *A. lingulata*, *C. alatum*, *V. microphylla*, *O. lotoides* and the ferns *E. cuspidatum*, *M. pseudomutans* and *P. mindense,* were rather infrequent in the Chalpi basin.

None of the watersheds encompassed all the plant species that were recorded in the study area. The total number of species per patch ranged from 36 to 59 (Table 4.2). At the patch level, shrubs and treelets were the most numerous (12-20 species per patch), followed by herbs and vines (9-21 species per patch) and ferns (9- 15 species per patch, Table 4.2).

The Oyacachi basin was the richest (83 species) of the three basins in terms of basin-wide species diversity, as well as the total number of shrubs and treelet species, herb and vine species, and rare species (*i.e.*, species with only one record in the whole collection, Table 4.2). The Chalpi and the Papallacta watersheds had the same basin-wide species diversity (72 species) but differed in numbers of vine and herb species (higher in the Papallacta basin), and the number of shrub and treelet species (higher in the Chalpi). Fern diversity was similar across all three basins.

4.3.2 *Polylepis* FOREST SPECIES DIVERSITY AT THE QUADRAT LEVEL IN RELATION TO ELEVATION AND CANOPY CLOSURE

At the growth form level, there was no consistent trend in diversity with respect to elevation; exceptionally diverse quadrats for each growth form were found in all three elevation classifications (*e.g.* C5-m, O6-h, P4-l, Table 4.3, where letters after patch code denote elevation within each patch, i.e. h, m and l correspond to the highest, middle and lowest elevation belts of each patch respectively). Canopy closure (the proportion of the sky hemisphere obscured by vegetation when viewed from a single point, Jennings *et al.* 1999) expressed as percentage, ranged from 51.45 to 93.60% across quadrats, with considerable variation among quadrats at the same elevation (Table 4.3).

No significant decline in species number with increased elevation was detected at the quadrats level (r_s = -0.20, p >0.05 Table 4.4). Canopy closure decreased with increased elevation but not in a significant manner (r_s = -0.17, p >0.05), and its variation was not significantly related to plant growth form diversity (Table 4.4).

Cluster analysis of 36 quadrats based on relative Sørensen distance was performed to identify compositional similarities related to elevation; this grouped together middle and lowest elevation quadrats within the same watersheds and across watersheds (*e.g.* middle and lowest elevation quadrats of C1, C3 and C5 and O7 and O4 and uppermost quadrats of C1 and O1 and C4; Figure 4.17). Higher elevation quadrats were grouped only twice in the dendrogram, suggesting less compositional affinity among them than among middle and lower elevation quadrats.

DCA ordination based on the species presence/absence matrix produced a similar clustering pattern, also revealing a compositional similarity between the Oyacachi and the Chalpi basins (Figure 4.18). Higher elevation quadrats (ranked 01 to 12 of a total of 36) grouped towards the upper part of the ordination space, lower elevation ones (ranked 24 to 36) clustered in the bottom and middle elevation quadrats (ranked 13 to 24) occupied the center (Figure 4.18). Similarities in species composition among patches in the same watershed were also evident in the ordination space (Figure 4.18). This was particularly evident for the Chalpi remnants which occurred in a continuous way (C1 and C5 quadrats were clustered towards the bottom left quadrant of the ordination space, orange symbols, Figure 4.18), patches that were closer to each other (O1 and O6 quadrats were grouped to the bottom right quadrant of the ordination plot, green symbols Figure 4.18) and patches in the same watershed (Papallacta quadrats clustered on the bottom left quadrant of the ordination space)

Correlation analysis indicated that compositional patterns depicted on the DCA ordination were related to elevation and, to a lesser extent, canopy closure. Significant positive correlations ($P<0.05$) were observed between percent canopy closure and DCA axis 1 scores and between elevation and DCA axis 2 scores (Table 4.5).

4.3.3 RELATIONSHIP OF SPATIAL ATTRIBUTES OF POLYLEPIS FOREST PATCHES TO PLANT SPECIES DIVERSITY

Species richness was greater in patches that had a greater elevation span (Table 4.6). Patch area was significantly correlated to patch relief ($r_s=0.78$, $p<0.05$) although area *per se* did not show a significant positive correlation with overall species diversity. Species numbers in all three growth forms were positively correlated with patch area, altitudinal range encompassed by the patch (relief) and slope, but no significant correlation was found for any growth form category (Table 4.6). Species numbers decreased in a significant manner (except for shrubs and treelets' decline) with increasing average elevation of the forest patch (Table 4.6). The same relationship although not significant was found for species numbers and shape complexity (given by the Shoreline Development Index, *D*).

From the continuous *vs*. fragmented perspective, the continuous remnants of the Chalpi basin, C5 and C1, ranked 5th and 6th respectively in terms of overall species diversity, after two large fragments of the Oyacachi basin and two rather small patches of the Papallacta basin (Tables 4.2 and 4.3). Patch relief did not fully explain the lower diversity found in the Chalpi patches as the species rich patches of the Papallacta watershed covered an even narrower altitudinal range than the Chalpi patches (Table 4.1). The high frequency of a tall grass, *N. elata* in the Chapi and its relative rarity in the Oyacachi and Papallacta patches studied may be influencial in this difference.

Hierarchical cluster analysis of the 12 *P. pauta* forest patches on the basis of their floristic composition showed more affinity among patches within the same watershed (O1 and O6, P1 and P2 and C1 and C5) than across watersheds. Within watersheds, continuous forest areas (*e.g.*, C1 and C5) and fragments (*e.g.*, P1 and P2, O1 and O6) that were closer together were more compositionally similar and, therefore, paired first (Figure 16). Further clustering grouped the Chalpi and the Oyacachi communities, and the Oyacahi and the Papallacta communities, in decreasing order of similarity (Figure 4.19). At both scales, within and across watersheds, clustering was consistent with the spatial distance between *P. pauta* forest patches in the study area (Figures 3.1, Table 4.1).

DISCUSSION

Overall species diversity recorded in the *Polylepis pauta* forest patches sampled in the Chalpi, Oyacachi and Papallacta basins was similar to that observed in a floristic inventory carried out by Laur *et al*. (2001) in *P.pauta* forests of Ecuador, south of the Papallacta basin (Laur *et al*. 2001 recorded 120 species) . Similarly, diversity of ferns observed in this study was comparable to the number inventoried by Øllgaard and Navarrete (1997) in a 240 x 5 m transect of *Polylepis* forest in Oyacachi. The higher diversity recorded by other floristic inventories in Peru (cf. Servat *et al*. 2002, Cordillera de Vilcanota, Cuzco) and Bolivia (cf. Fernandez-Terrazas and Ståhl 2002, Cordillera de Cochabamba) may stem from the fact that these studies surveyed all together *Polylepis* forests dominated by different species of the genus *Polylepis* (*P. besseri* and *P. subsericans* in Perú and *P. besseri*, *P. racemosa* and *P.tomentella* in Bolivia). Floristic inventories of *Polylepis* forest in Bolivia using 1 x 100m and 2 x 500 m transects indicate that the smaller survey plots are sufficient to record alpha diversity in *Polylepis* forests (cf. Fernandez-Terrazas and Ståhl 2002).

At a more localized scale, the Oyacachi basin was appreciably more diverse than the other two basins. *Polylepis* forests are known to vary in floristic richness, structure and patterns of occurrence according to local environmental conditions (Fjeldså and Kessler 1996, Kessler 2002). Local physical and climatic heterogeneity associated with the latitudinal and altitudinal range encompassed by the *Polylepis* species have been linked to differences in floristic composition (Kessler 1995, Fjeldså and Kessler 1996). The study area encompasses significant topographic heterogeneity and subtle differences in climatic regimes. It is not out of question, therefore, that these may contribute to the floristic differences observed among these basins. The presence of certain common herbaceous species such as *L. gigantea* and *Pennisetum clandestinum*, often associated with disturbance, in the *Polylepis* forest patches of Papallacta and Oyacachi might be a consequence of cattle incursions into patches to seek shelter from the rain (field observation, Susana León-Yanez, pers. comm., 2007). Both the Papallacta and, to a lesser extent, the Oyacachi basins have a long history of forest conversion to pasture, and this is likely expressed through the occurrence of disturbance-related species. The high frequency of occurrence of *N. elata* and *N. aristata* in the Chalpi and Papallacta basins respectively is probably associated with the greater frequency of high-intensity rainfalls that characterize their precipitation regime, which makes the slopes of these basins more prone to landslides and forest disruption. *N. elata* forms big clumps of giant rosettes in waterlogged soils along forest edges and often invades the forest interior (field observation and aerial photography interpretation, Chapter 2). Its frequent presence in these basins (particularly the Chalpi basin) could be one of the causes for the lower species diversity observed in this basin.

Species diversity decline with increased elevation, although observed, was not significant at the quadrat level in *Polylepis pauta* patches studied. This is not necessarily inconsistent with previous investigations on tropical mountain diversity gradients which have noted a significant decrease in overall plant species diversity with increasing altitude (Van der Hammen *et al*. 1989, Gentry 1995, Lieberman *et al*. 1996, Kessler 2002b). Scale has been recognized to have a strong influence on detection of altitudinal patterns of diversity (Rahbek 1995 and 2005), and it is likely that the elevation range encompassed by the *Polylepis* forest patches studied was too narrow for this broad-scale diversity pattern to express in a significant manner at the quadrat level. Furthermore, the error associated with elevational data obtained from the Garmin GPS III could have exacerbated the scale issue. In fact, the ordination of quadrats showed compositional similarities between quadrats at the same elevation and species diversity declined significantly with increased average elevation of the forest patch. This suggests that subtle gradual shifts in floristic composition may be accompanying the elevation gradient represented in this study, with a similarly subtle decrease in species diversity. In the same context, of all the spatial attributes of forest patches considered in this study, the elevation range spanned by the patch showed the strongest relationship to overall plant species diversity. Although *Polylepis* forests are generally viewed as a more homogeneous type of forest than lower elevation mountain forests in the tropics (Balslev 1988, Fjeldså 2002a, 2002b, Laur *et al*. 2001), the positive correlation observed in this study between patch length (*i.e.*, elevation range encompassed by the patch) and floristic diversity is consistent with theoretical predictions for steep climatic gradients characteristic of tropical mountain ecosystems (Van der Hammen *et al*. 1989, Gentry 1995, Lieberman *et al*. 1996).

Floristic composition was more similar among middle and lower elevation quadrats than among uppermost quadrats. The consistently reduced canopy cover at higher elevations could be generating local environmental heterogeneity which in turn cause floristic dissimilarities. The generally more open canopy observed in the Papallacta basin may be linked to the severity of anthropogenic disturbance this basin has undergone in recent decades compared to the others (EMAAP 1991).

The continuous forests of the Chalpi basin differed from fragmented patches in the notable frequency of *N. elata*, absent in the other watersheds and their relatively lower number of fern species. *N. elata*, considered a forest to páramo transition species (Ohl and Bussmann 2004, Ritcher *et al*. 2008), occurred in narrow seeps vertically oriented, intermingling with *Polylepis* forest. Its absence or very low frequency in the Oyacachi and Papallacta watersheds may be due to drier microhabitat conditions caused by forest removal a human-influenced condition.

Table 4.1: Locations and spatial attributes of the *Polylepis pauta* patches sampled in the southern part of the northeastern Cordillera Oriental of Ecuador used to study floristic diversity associations with fragmentation

Basin	Patch	Area A (km^2)	Altitudinal range (m)	Average elevation	Relief R (km)	Perimeter P (km)	Slope S	D
Chalpi	C1	0.27	3720 – 3880	3800	0.16	2.76	0.70	1.50
	C3	0.02	3910 – 3960	3935	0.05	0.79	0.39	1.58
	C4	0.08	3760 – 3880	3820	0.12	1.42	0.67	1.42
	C5	0.55	3720 – 3880	3800	0.16	4.07	0.51	1.55
		0.92[1]					0.57[2]	
Oyacachi	O1	0.32	3660 – 3880	3770	0.22	3.38	0.75	1.68
	O4	0.03	3880 – 4000	3940	0.12	0.91	0.52	1.49
	O6	0.34	3640 – 3920	3780	0.28	3.61	0.61	1.74
	O7	0.13	3800 – 3880	3840	0.08	2.25	0.57	1.76
		0.82[1]					0.60[2]	
Papallacta	P1	0.05	3740 – 3840	3790	0.10	1.32	1.11	1.67
	P2	0.15	3760 – 3920	3840	0.16	2.67	0.89	1.95
	P3	0.01	3800 – 3900	3850	0.10	0.33	1.00	0.94
	P4	0.04	3840 – 3980	3910	0.14	1.07	0.70	1.51
		0.25[1]					0.92[2]	

A is the area of the forest patch; L is distance encompassed by altitudinal range; R is distance encompassed by altitudinal range; S was computed by dividing the altitudinal range (the line's vertical rise) by the distance of the projected line on the Landsat TM Image (the distance the line travels on the surface); $D=P/2\sqrt{\pi A}$, *Shoreline development index* (Patton, 1975), which is a measure of convolution of the patch based on perimeter and area.

[1] Total area sampled per watershed

[2] Mean slope per watershed

Table 4.2: Floristic diversity (expressed as the number of species) of 12 *Polylepis* forest patches sampled in the southern part of Cayambe Coca Ecological Reserve, Ecuador.

Basin	*Patch*	*Herbs & Vines*[a]	*Shrubs & Treelets*	*Ferns*	*All species*
Chalpi	C1	15^{1}	15	12	42
	C3	13^{1}	16	9	38
	C4	9	16	15^{1}	40
	C5	16^{1}	12	15	43
	Mean	13.25	14.75	12.75	40.75
	Total	26^{3}	25	21^{1}	72^{4}
Oyacachi	O1	21^{2}	23	15^{1}	59
	O4	15	13	14^{1}	42
	O6	21^{1}	20^{1}	14^{1}	55
	O7	13	12	11	36
	Mean	17.5	17	13.5	48
	Total	32^{3}	30	21^{3}	83^{7}
Papallacta	P1	12	17^{1}	11	40
	P2	11	15	14	40
	P3	21^{2}	18	15	54
	P4	16	16	14	46
	Mean	15	16.5	13.5	45
	Total	29^{2}	23^{1}	20	72^{3}

[a] Superscript following the number indicates the number of rare species, i.e., with only one record found in only that forest patch

Table 4.3: Elevation, canopy cover and plant growth form diversity at 36 quadrats of *Polylepis pauta* forest patches sampled in southern part of the northeastern Cordillera Oriental of Ecuador

Basin	*Quadrat Name*[1]	*Elevation* (m)	*% of Canopy Closure*[2]	*Herbs & Vines*[3]	*Shrubs & Treelets*	*Ferns*	*All Species*
Chalpi	C1-h	3850	86.83	12^{1}	9	7	28
	C3-h	3959	68.63	8^{1}	13	3	24
	C4-h	3844	80.55	5	10	10^{1}	25
	C5-h	3818	87.36	5	7	8	20
	Mean		80.84	7.5	9.75	7	24.25
	C1-m	3760	87.86	7	11	7	25
	C3-m	3926	79.12	7	9	6	22
	C4-m	3811	92.58	4	10	9	23
	C5-m	3779	73.20	9^{1}	10	11	30
	Mean		83.19	6.75	10	8.25	25
	C1-l	3739	82.42	8	12	7	27
	C3-l	3913	78.10	7	11	7	25
	C4-l	3775	90.87	9	9	3	21
	C5-l	3726	74.43	9	9	11	29
	Mean		81.46	8.25	10.25	7	25.5
Oyacachi	O1-h	3853	91.13	9	10	10	29
	O4-h	3942	78.98	8	10	8	26
	O6-h	3758	79.27	16^{1}	16	8	40
	O7-h	3878	76.61	10	10	8	28
	Mean		81.50	10.75	11.5	8.5	30.75
	O1-m	3715	88.66	16^{1}	17	9^{1}	42
	O4-m	3926	77.96	10	8	8^{1}	26
	O6-m	3713	93.60	9	8	9^{1}	26
	O7-m	3852	76.39	8	10	8	26
	Mean		84.15	10.75	10.75	8.5	30
	O1-l	3664	91.48	10^{1}	13	7	30
	O4-l	3905	86.22	5	9	10	24
	O6-l	3644	80.64	16	11	11	38
	O7-l	3810	69.57	6	9	10	25
	Mean		81.98	9.25	10.5	9.5	29.25
Papallacta	P1-h	3835	59.4	11	12^{1}	7	30
	P2-h	3872	65.21	7	12	9	28
	P3-h	3900	67.42	11^{1}	11	8	30
	P4-h	3969	82.93	9	10	6	25
	Mean		68.76	9.5	11.25	7.5	28.25
	P1-m	3805	51.45	4	12	7	23
	P2-m	3845	63.19	9	15	11	35
	P3-m	3852	79.85	10	12	10	32
	P4-m	3940	88.12	12	11	8	31
	Mean		70.65	8.75	12.5	9	30.25
	P1-l	3750	55.90	6	12	7	25
	P2-l	3816	77.15	7	9	10	26
	P3-l	3817	73.04	16^{1}	15	11	42
	P4-l	3861	85.50	10	12	12	34
	Mean		72.90	9.75	12	10	31.75

[3] Superscript following the number indicates the number of unique records, *i.e.*, rare species.

Table 4.4: Spearman rank correlation coefficients (r_s) between plant growth form diversity and both canopy closure and elevation

	Floristic diversity			
	Herbs & Vines	*Shrubs & Treelets*	*Ferns*	*All Species*
Elevation	-0.08	-0.13	-0.20	-0.20
% Canopy Closure	0.12	-0.29	-0.06	-0.09

*Significance of Spearman rand correlation coefficient, r_s: $P< 0.05$

Table 4.5: Spearman rank correlation coefficients (r_s) between axes scores for quadrat-based DCA ordination and both elevation and canopy closure

	Axis 1	Axis 2
Eigenvalue	0.192	0.104
Elevation	-0.06	0.31*
% of Canopy Closure	0.70*	-0.19

*Significance of Spearman rank correlation coefficient, r_s: $*P< 0.05$

Table 4.6: Spearman rank correlation coefficients between spatial attributes of patches and plant growth form diversity of 12 *Polylepis pauta* forest patches sampled in the southern part of the northeastern Cordillera Oriental of Ecuador

	Growth forms			
Forest patches spatial attributes	*Herbs & Vines*	*Shrubs & Treelets*	*Ferns*	*All Species*
Patch Area *(A)*	0.18	-0.11	0.24	0.30
Average elevation	-0.91*	-0.51	-0.63*	-0.98*
Relief *(R)*	0.39	0.14	0.50	0.70*
Slope steepness*(S)*	0.01	0.48	0.16	0.32
Shoreline development index *D*	-0.12	-0.03	-0.35	-0.21

A is patch area*; R* is distance encompassed by altitudinal range*; S* was computed by dividing the altitudinal range (the line's vertical rise) by the distance of the projected line on the Landsat TM Image (the distance the line travels on the surface)*; d* is the average distance to patches in the same watershed.; $D=P/2\sqrt{\pi A}$, *Shoreline development index* (Patton, 1975), which is a measure of convolution of the patch based on perimeter and area.

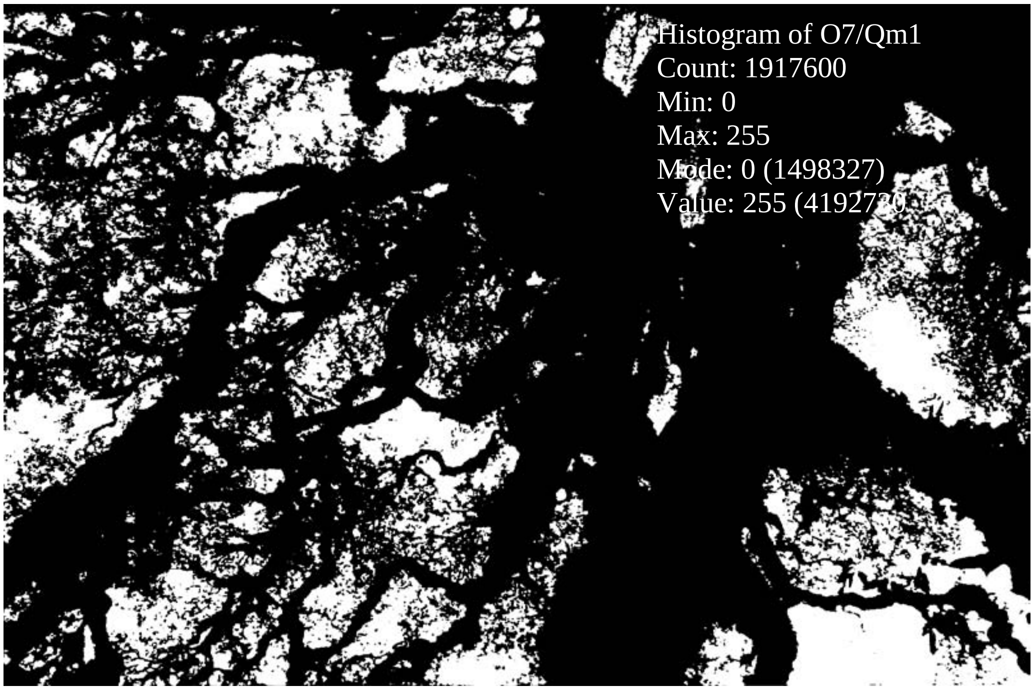
[1] Total area sampled per watershed

[2] Mean slope per watershed

[3] Mean of average distance between patches within the same watershed

Significance of Spearman rank correlation coefficient, r_s: $*P< 0.05$

Figure 4.1: Canopy closure photography of one of four sub quadrats of the middle elevation quadrat (Qm1) of patch 7 (O7) of the Oyacachi basin, southern part of the northeastern Cordillera Oriental, Ecuador. The image is a scanned * .TIF file of the color negative.



```
Histogram of O7/Qm1
Count: 1917600
Min: 0
Max: 255
Mode: 0 (1498327)
Value: 255 (4192730
```

Figure 4.2: Canopy closure binary image, 8-bit *.BMP, from previous photograph of sub quadrat 1 of the middle elevation quadrat (Qm1) of patch O7. The histogram from Image J 1.38 software provides the total number of pixels (Count) and the number of black (255 value) and white (0 value) pixels.

Figure 4.3: *Polylepis pauta* forest patch O1, Oyacachi river basin of the southern part of the northeastern Cordillera Oriental of Ecuador, June 2006

Figure 4.4: *Polylepis pauta* forest patches O6 (left) and O1 (right), Oyacachi river basin, southern part of the northeastern Cordillera Oriental of Ecuador, July 2006

Figure 4.5: *Polylepis pauta* forest patch O4, Oyacachi river basin, southern part of the northeastern Cordillera Oriental of Ecuador, July 2006

Figure 4.6: *Polylepis pauta* continuous forest, Chalpi river basin, southern part of the northeastern Cordillera Oriental of Ecuador, July 2006

Figure 4.7: *Polylepis pauta* forest patches C3 , Chalpi River basin, southern part of the northeastern Cordillera Oriental, Ecuador, June 2007

Figure 4.8: *Polylepis pauta* forest remnant P3, Papallacta river basin, southern part of the northeastern Cordillera Oriental of Ecuador, June 2007

Figure 4.9: *Polylepis pauta* tree, Oyacachi , Ecuador, June 2006

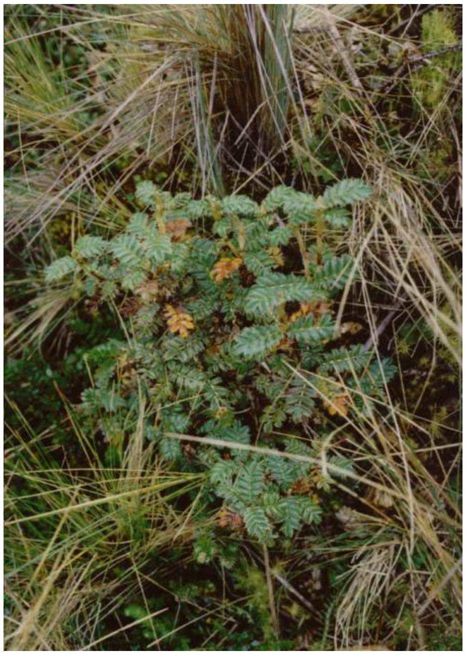


Figure 4.10: *Polylepis pauta* sapling, Oyacachi, Ecuador, June 2006

Figure 4.11: *Polylepis pauta* bark, Oyacachi, Ecuador, July 2006

Figure 4.12: *Miconia lloensis*, Chalpi, Ecuador, July 2007

Figure 4.13:*Ceratostema alatum*,
Chalpi, Ecuador, July 2007

Figure 4.14: *Elaphoglossun vulcanicum*,
Papallacta, Ecuador, June 2007

Figure 4.15: *Neurolepis elata*,
Chalpi basin, Ecuador, July 2007

Figure 4.16: *Polylepis pauta*, *N.aristata*
N.elata and shrub páramo vegetation,
Chalpi, Ecuador, June 2007

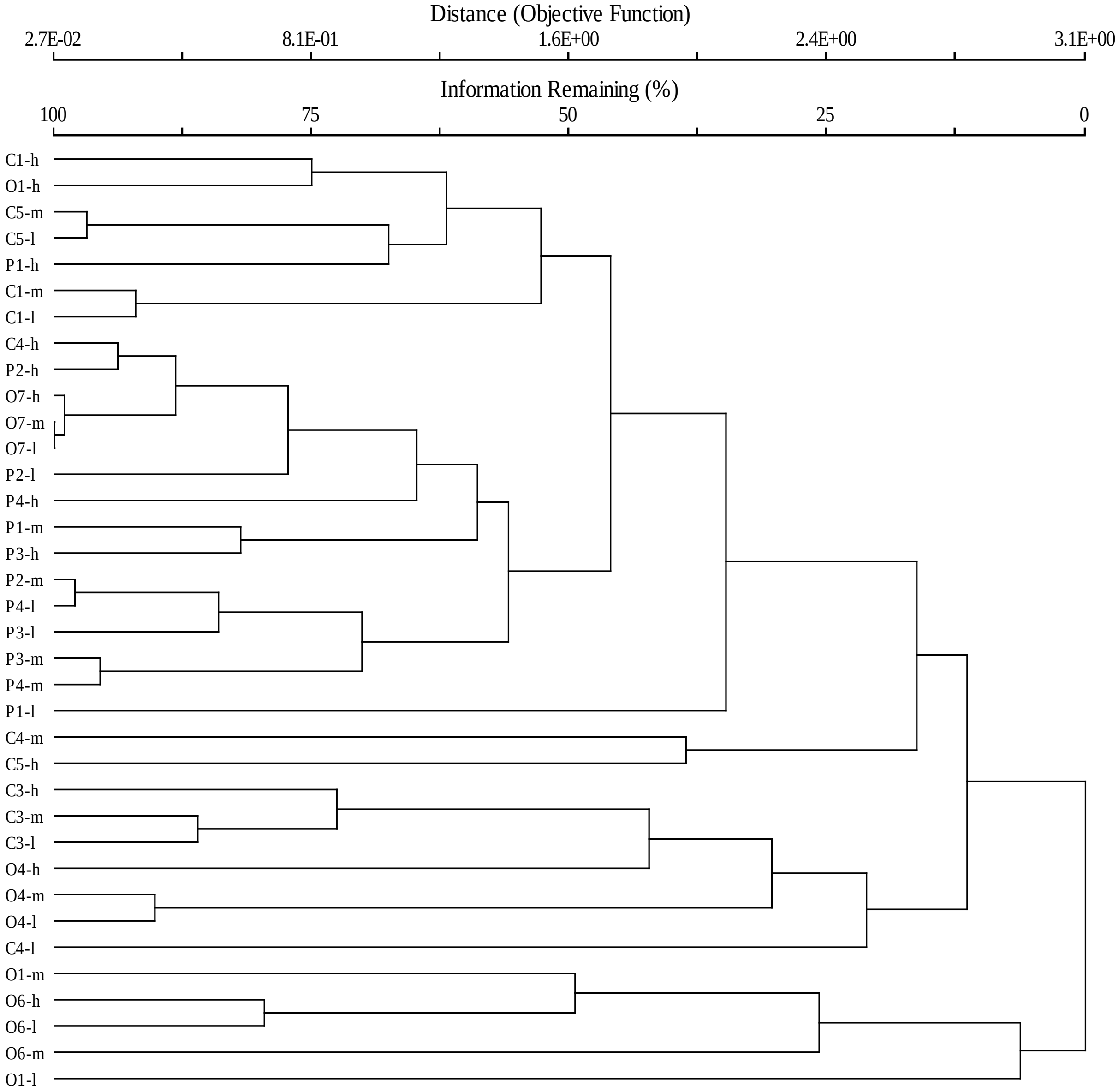


Figure 4.17: Hierarchical cluster analysis dendrogram based on relative Sørensen distance between 36 quadrats in 12 *Polylepis pauta* forest patches in the southern part of the northeastern Cordillera Oriental of Ecuador

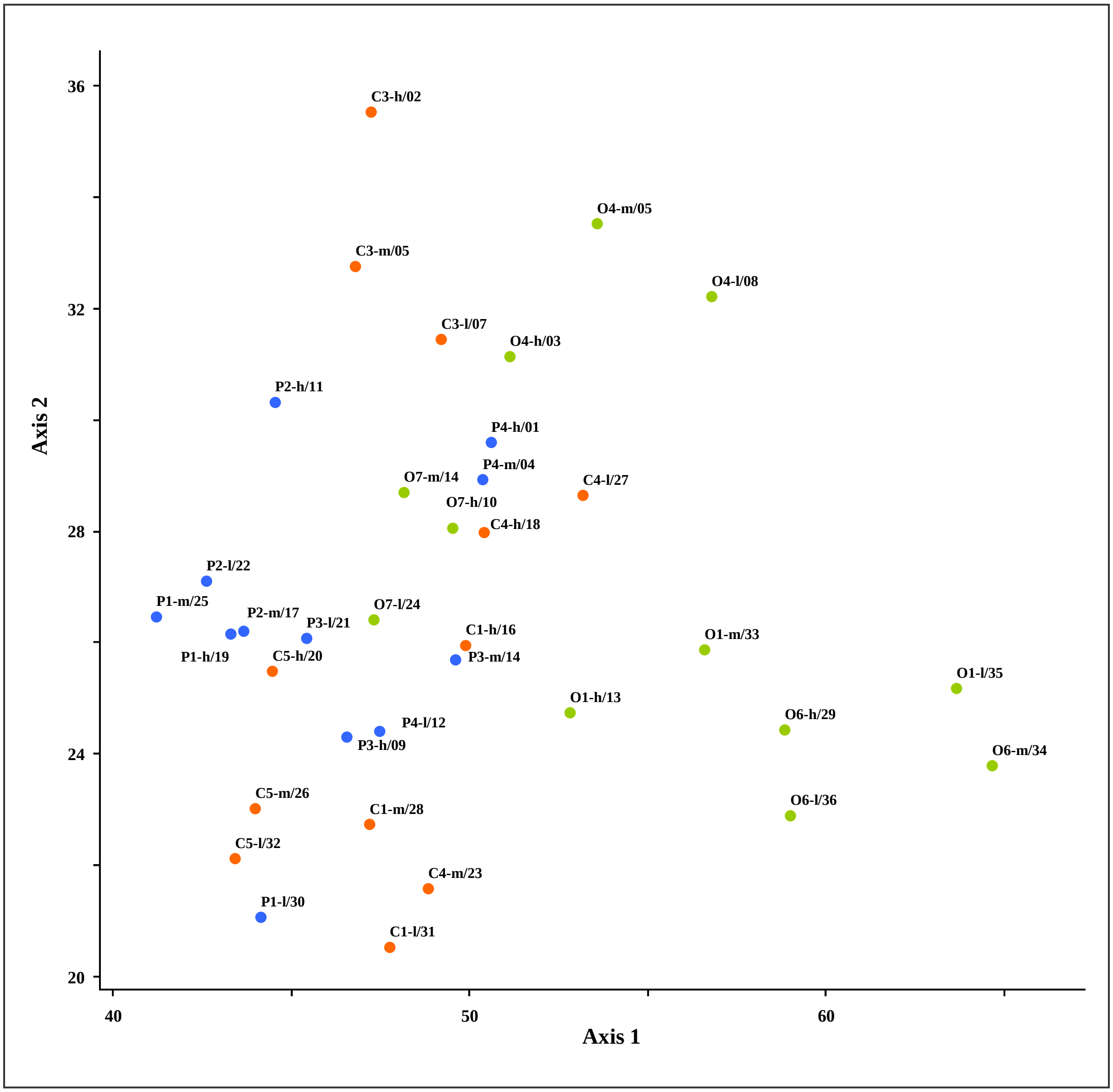


Figure 4.18: DCA of the 36 quadrats based on the species presence/absence matrix for *P. pauta* forest patches sampled in the southern part of the northeastern Cordillera Oriental of Ecuador. The Chalpi, Oyacahi and Papallacta quadrats are represented in orange, green and blue respectively. Letters following the patch code denote elevation range within the patch (*i.e.* high, middle and low). All quadrats are ranked according to elevation from 01 (highest) to 36 (lowest). Higher elevation quadrats (ranked 01-12) are grouped towards the upper part of the ordination space, middle elevation ones (ranked 13 to 24) towards the center and lower ones (ranked 25 to 36) in the bottom.

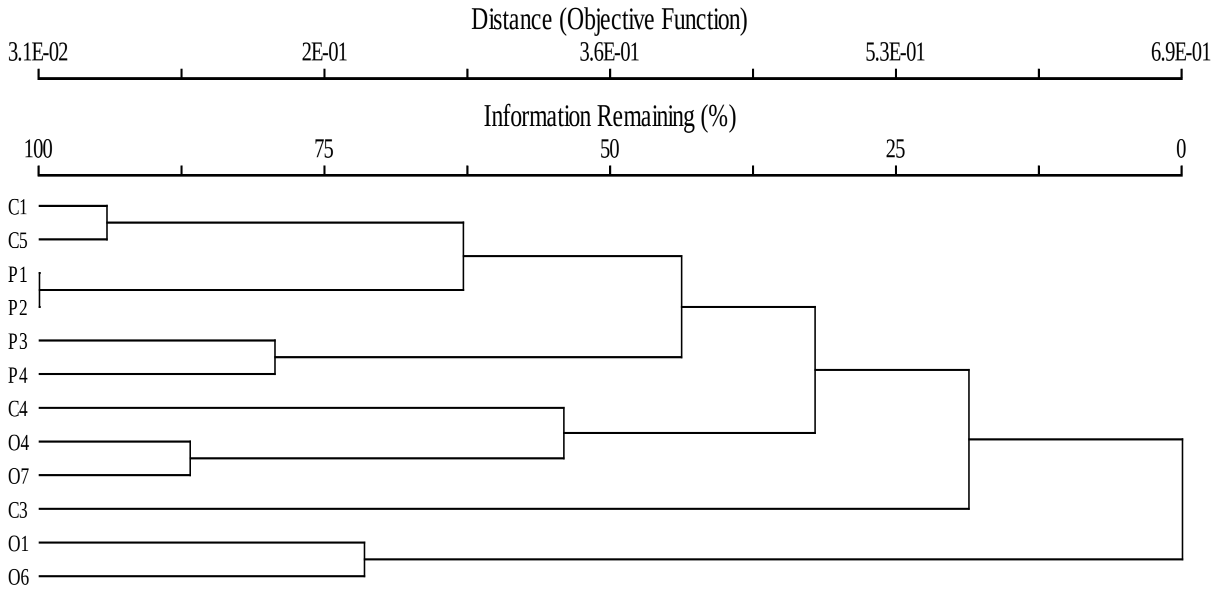


Figure 4.19: Hierarchical cluster analysis dendrogram based on relative Sørensen distance between 12 *Polylepis pauta* forest patches in the southern of the northeastern Cordillera Oriental of Ecuador

CHAPTER 5

THE POTENTIAL OF PHYTOLITHS FOR DOCUMENTING THE HISTORICAL RANGE OF *Polylepis pauta* IN THE SOUTHERN PART OF THE NORTHEASTERN CORDILLERA ORIENTAL OF ECUADOR

5.1. INTRODUCTION

The scattered distribution of *Polylepis* forests in the Andean cordillera has been examined in the context of human disturbance by several authors over the last decade (Fjeldså and Kessler 1996, Hensen 2002, Herzog *et al*.2002). The importance of these forests in providing environmental services and refuges of unique biological diversity (Fjeldså and Kessler 1996, Fjeldså 2002b, Herzog and Cahill 2002, Renison *et al.* 2002), coupled with evidence of human-induced decline of their occurrence (Fjeldså and Kessler 1996, Hensen 2002, Herzog and Cahill 2002, Chapter 2), has encouraged conservation and restoration efforts that have rarely been successful (Renison *et al*. 2004, Renison *et al*. 2005). The failure of *Polylepis* forests to spread over the vast expanse of grass páramo which surrounds them despite fire suppression and reforestation (Renison *et al*. 2004, Cierjacks *et al*. 2007) has challenged ecologists to look for a more accurate delimitation of their historical range and to improve our knowledge of the physiological adaptations of different species within the genus.

Considerable research is being carried out in both fields (Hansen *et al*. 1984, Hansen *et al*. 1994, Hansen *et al*. 1995, Renison *et al*. 2005, Argollo *et al*. 2006, Renison *et al*. 2006). So far, most studies have used pollen records to determine the historical range of the genus *Polylepis* (Hansen *et al*. 1984, Hansen *et al*. 1994, Hansen *et al*. 1995, Chepstow-Lusty *et al*.2005), although pollen identification has been possible only at the level of family for most taxa of interest (Hansen *et al*. 1995, Boyd 2005). A more recent alternative to pollen records, which has been successfully used during the past three decades, is the analysis of phytoliths. Unlike most pollen fossils, fossil micrometric minerals precipitated in plant tissues (phytoliths as defined by Meunier and Colin 2001) and found in soils and sediments (Piperno 1985, 2006a,b) can be resolved to the level of subfamily (in the case of grasses, Boyd 2005), or even genus, in some cases (Piperno 2006a,b).

Furthermore, phytoliths are considered to become incorporated into the soil through *in situ* decay (Dimbleby 1978, Piperno 1988, Mulholland 1989), thus providing a frequently more accurate approach to the study of historical local distributions of plants species and community composition than pollen analyses (Boyd 2005). Thus fossil phytholiths have been successfully used in the reconstruction of agricultural activity, vegetation dynamics and paleoenvironments (Pearsall 1978, Pearsall and Piperno 1990, Piperno1985, 2006, Fisher *et a*l.1995, Alexandre *et al*. 1997, Kelly *et al*. 1998, McGlone 2001, Boyd 2005).

In the Andean region, phytoliths have traditionally been used in archeological research to study agricultural development in pre-Hispanic times; they have contributed enormously to our knowledge of crop diversity and human dynamics and the extent of human occupation before the Spanish conquest (Pearsall 1978, Pearsall and Piperno 1990, Piperno1985 and 2006a, Piperno 2008). Although conversion of agriculture often involved forest clearance, the transition of forest to agricultural land, historical ranges of forests and tree species have rarely been considered in phytolith research (cf. Mercader *et al*.2000, Piperno 2006a, Tsarsidou *et al*. 2007). This might be in part due to the fact that the morphology of woody plant phytoliths, particularly trees, is very similar (Piperno 2006b). Thus successful research on woody species has to date relied on phytoliths from seeds and fruits of the species (Piperno 1989).

This study explores the potential of opal phytoliths as indicators of the historical local-scale distribution of *Polylepis pauta* forests through the analysis of opal phytoliths from dominant plant species in four growth-form categories, *i.e.* trees, shrubs, ferns and grasses. Phytoliths were extracted also from organic matter of the soil beneath a *Polylepis* forest to qualitatively estimate which species are more likely to be major contributors of soil sediment and thus serve as a reference for studying the distribution of *Polylepis pauta* forest prior to human disturbance (*i.e.*, approximately 1500 ago).

5.2 MATERIALS AND METHODS

5.2.1 SOURCE AREA

The area from which *Polylepis* forest species were collected was approximately 491 km² in the southern part of the northeastern Cordillera Oriental of Ecuador, within the boundaries of the Cayambe Coca Ecological Reserve (hereafter RECAY) and farther south (78°11’55”- 78°2’22” W, 0°10’34”- 0°25’34” S Figure 2.1). The study area includes three adjacent river basins in the southern part of the RECAY, the Oyacachi, the Chalpi and the Papallacta basins. Of these three, the Chalpi river basin is probably the least disturbed, supporting continuous forest cover from approximately 3000 m to 4000 m elevation. The Oyacachi River basin has been inhabited since the mid-16th century by the Oyacachis, a Quechua community whose population (approximately 551 people) occupies 44,500 ha (11.0%) of the RECAY (Ohlson 2001). Their territory, which is located within the 1800 m to 4000 m altitudinal belt, is primarily grass páramo and pastureland (63 %) with smaller areas of forest and agricultural land (Fundación Antizana 1998, Ohlson 2001).

5.2.2 PLANT MATERIAL AND SOIL ORGANIC MATTER

Terminal branches and mature leaves of 12 vascular species (Table 5.1) from twelve *Polylepis pauta* forest patches were collected from June to July 2006 and 2007. Plant species selected for phytolith extraction included specimens in three growth form categories and were assessed in terms of their frequency in the twelve patches surveyed and their capability to produce diagnostic phytoliths. The data base from the University of Missouri Paleoethnobotany Laboratory and comprehensive reviews by of phytolith studies by Meunier and Colin (2001) and Piperno (2006a,b) were consulted to identify diagnostic phytoliths. Organic matter from the forest soil was separated to obtain a sample for phytoliths extraction.

5.2.3 PHYTOLITH EXTRACTION

Phytoliths from *Polylepis* forest species were extracted using a procedure known as "dry ashing". A total of 12 samples of approximately 12g of air dry plant tissue were put into porcelain crucibles and submitted to ignition at 450-500° C in a muffle furnace for 2 hours. Once they cooled, 5 ml of *aqua regia* (*i.e.*. HCl + HNO3 in 3:1 proportion) were added to each sample and allowed to react for 2 minutes in order to remove chemical precipitates in the ash. Samples were then rinsed with distilled water. The rinsing procedure involved centrifuging samples in 45 ml of distilled water and siphoning to remove the water. Samples were rinsed three times, and then they were dried in a low-temperature (approximately 50°C) oven. The same procedure was used to extract phytoliths from organic matter separated from forest soil.

5.2.4 PHYTOLITH ANALYSIS

Phytoliths extracted from *Polylepis* forest species were spread onto microscope slides with a soft tapping motion of a thin brush containing phytoliths. The brush was loaded with phytolith extract three times to cover each slide. The morphology of phytoliths was documented by microphotography with a standard Zeiss light microscope equipped with a 40x zoom lens and fit with a Nikon high-resolution digital camera. Both contrast and fluorescent photography were performed, but only fluorescent photography provided three dimensional outlines of the samples. Images were saved as *.TIF files and used for identification and assessment of potential historical range reconstruction.

A total of three slides were screened per sample. Phytoliths were identified on the basis of their morphology, the type of plant tissue represented by the sample and their taxonomy at the family level (cf. Piperno 2006b). Other keys to phytolith identification use morphology and surface ornamentation, with highly specific detail (cf. Bowdery *et al*. 2001). This latter type of classification is useful for achieving maximum resolution in vegetation dynamics studies that examine species in the same family (often grass species, Boyd 2005). Because the present study aimed at a categorical distinction between forest and grass species, this level of detail was not necessary. Phytoliths of the Poaceae family (which dominate the páramo of the study area) have been widely studied and photographic keys to grass phytoliths are available in the literature and in electronic databases from herbariums and academic institutions. Phytolith size was estimated from the area they occupied in the field of view of the x 40 lens of the microscope. Determination of phytolith abundance was categorical (*i.e*., rare, common and abundant) and based on the average number of phytoliths of a certain category observed per slide. The categories were defined as follows: rare = <10, common = ≥10 to <20 and abundant = > 20 (Table 5.1). Both specificity and frequency where considered to assess the potential of phytoliths as standards for historical *Polylepis* forest distribution reconstruction from soil samples.

A second part of the analysis consisted of screening phytoliths extracted from organic matter of the forest soil to assess which of the forest species analyzed were likely to be major contributors to soil particles.

5.3 RESULTS

5.3.1 DIAGNOSTIC PHYTOLITHS OF *Polylepis* FORESTS

A significant number of phytoliths were obtained from most of the species selected, and most of them were diagnostic (Table 5.2) for the grass *vs*. forest dichotomy. Facetate phytoliths were the most common type, produced by virtually all species studied (Table 5.2, Figures 5.1f, 5.2b, 5.3c and 5.3b). Most facetate phytoliths differed in size within and among species but some exhibited a characteristic morphology (e.g. *Polyposium mindense*, Table 5.2). Rondel phytoliths were shared by all fern species studied, although size and frequency varied across species. These phytoliths which were observed in three forms, plain, striated and as alignments of both- were remarkably common and large in *Terpsichore heteromorpha* samples. Morphologically distinctive phytoliths among ferns were found in the samples from *Blechnum loxense* (Figure 5.6) and *Elaphoglossum ovatum* (Figure 5.9 and 5.11). The tracheids of *M. pilossissima* were the most fluorescent of all phytoliths identified although they are not diagnostic (Figure 5.7). *Polylepis pauta* yielded four types of phytoliths, epidermal polyhedral (Figure 5.1), facetates, epidermal vascular tissue phytoliths and sclereids. Polyhedral phytoliths showed a distinctive layered pattern and a high degree of fluorescence. Judging from the regularity of the layer pattern and the consistent clustering (Figure 5.1), these phytoliths could be diagnostic at the species level. It is worth noting that although *P. pauta* is characterized by pubescent leaves, hair-base phytoliths and hairs, which are common in species with pubescent leaves, (Piperno 2006b) were rare in the *P. pauta* extracts from *Neurolepis elata*, very common grass of the Chalpi basin, produced epidermal stomata phytoliths typical of grass species.

Screening of phytoliths from forest organic matter yielded an assemblage dominated by facetate phytoliths of different sizes, disaggregate mesophyl and polyhedral phytoliths and abundant fragments of pipe-shaped striated phytoliths from ferns.

5.4 DISCUSSION

Most opal phytoliths extracted from selected *Polylepis pauta* forest species were distinctive and common. *P. pauta* aggregates of polyhedral phytoliths were not as abundant in soil organic matter as were fragments of striated pipe shape, rondel phytoliths and, to a lesser extent, decorated spheres from ferns. Fern phytoliths displayed significant variation in shape and size, as previous works on pteridophytes have shown (Lentfer 2003 cited by Piperno 2006b). Given the frequency with which diagnostic phytotololiths are found in fern leaves, as well as the abundance of ferns in *Polylepis pauta* forests, fern phytoliths appear to have considerable potential for studying the historical range of *Polylepis* forests. Although some fern phytoliths do not seem to be well preserved in Neotropical soils (Piperno 2006b), this is more likely to be an issue in studies that deal with community composition and where genus or species level identification is required. Additionally the soil in *Polylepis* forests is different in many respects from that of lowland forests, particularly in the rate of decay of organic matter given the lower temperatures at high elevations (Renison *et al.* 2005). Despite these limitations, *P. pauta* and fern phytoliths have a considerable potential to document the occurrence of *Polylepis* forest at a local scale, and to assess whether this forest type preceded the vast extensions of grass páramo that today characterize the Andes. *Neurolepis elata* seems to co-occur naturally with *Polylepis* spp. and it is considered a forest –transiton species (Ritcher *et al*. 2008). A finer classification of the phytoliths from *N .elata* would be necessary in order to distinguish it from the grass species which form the páramo matrix around *Polylepis* forest and thus interpret adequately the distribution of mixed páramo *Polylepis* communities.

Table 5.1: Species selected from *Polylepis pauta* forest of the northeastern Cordillera Oriental of Ecuador for phytolith extraction

Family	Growth form	Species
Rosaceae	Tree	*Polylepis pauta*
Ericaceae	Shrub	*Ceratosteme alatum*
Ericaceae	Shrub	*Pernetya prostrata*
Grosulariaceae	Shrub	*Escalonia myrtilloides*
Melastomataceae	Shrub	*Miconia latifolia*
Blechnaceae	Fern	*Blechnum loxense*
Dryopteridaceae	Fern	*Elaphoglossum ovatum*
Dryopteridaceae	Fern	*Elaphoglossum vulcanicum*
Polypodiaceae	Fern	*Melpomene pillossissima*
Polypodiaceae	Fern	*Teprsichore heteromorpha*
Polypodiaceae	Fern	*Polypodium mindensi*
Poaceae	Grass	*Neurolepis elata*

Table 5.2: Diagnostic phytoliths of *Polylepis pauta* forest species, northeastern Cordillera Oriental, Ecuador

Species	Type of phytolith [1]	Figure	Diagnostic	Frequency
Polylepis pauta	Epidermal (leaves)	5.1	yes	abundant
	Facetate	5.2	no	abundant
	Epidermal (bark)	5.3	no	abundant
	Sclereids (bark)	5.4	yes	rare
Ceratostema alatum	Facetate	-	no	common
Pernetya prostrata	Facetate	-	no	common
Escalonia myrtiloides	Facetate	-	no	common
Miconia latifolia	Facetate	-	no	common
Blechnum loxense	Rondels	5.5	no	common
	Striated pipe shape	5.6	yes	common
	Tracheids	5.7	no	common
	Facetate	5.8	no	common
	Epidermal	5.8	no	rare
Elaphoglossum ovatum	Decorated spheres	5.9	yes	common
	Mesophyll	5.10	no	common
	Rondels	5.11	no	common
	Hat-shaped	5.11	yes	rare
Elaphoglossum vulcanicum	Rondels	5.12	no	common
	Facetate	5.13	Yes	common
	Epidermal	5.13	Yes	abundant
Melpomene pillossissima	Rondels	5.14	yes	rare
	Facetate	5.15	no	common
Tersichore heteromorpha	Epidermal	5.16	yes	rare
	Rondels (aligned)	5.17	yes	abundant
	Rondels (isolated)	5.18	no	abundant
Polypodium mindensi	Facetate tracheids	5.19	yes	rare
	Facetate	5.20	no	rare
	Rondels	5.20	yes	rare
Neurolepis elata	Epidermal (type 1)	5.21	yes	common
	Epidermal (type 2)	5.22	yes	rare

[1] Based on guide to phytoliths identification by Piperno (2006b)

[3] Frequency is defined in terms of number of average number of phytoliths observed per slide. Rare = <10, common = ≥10 and <20 and abundant = > 20

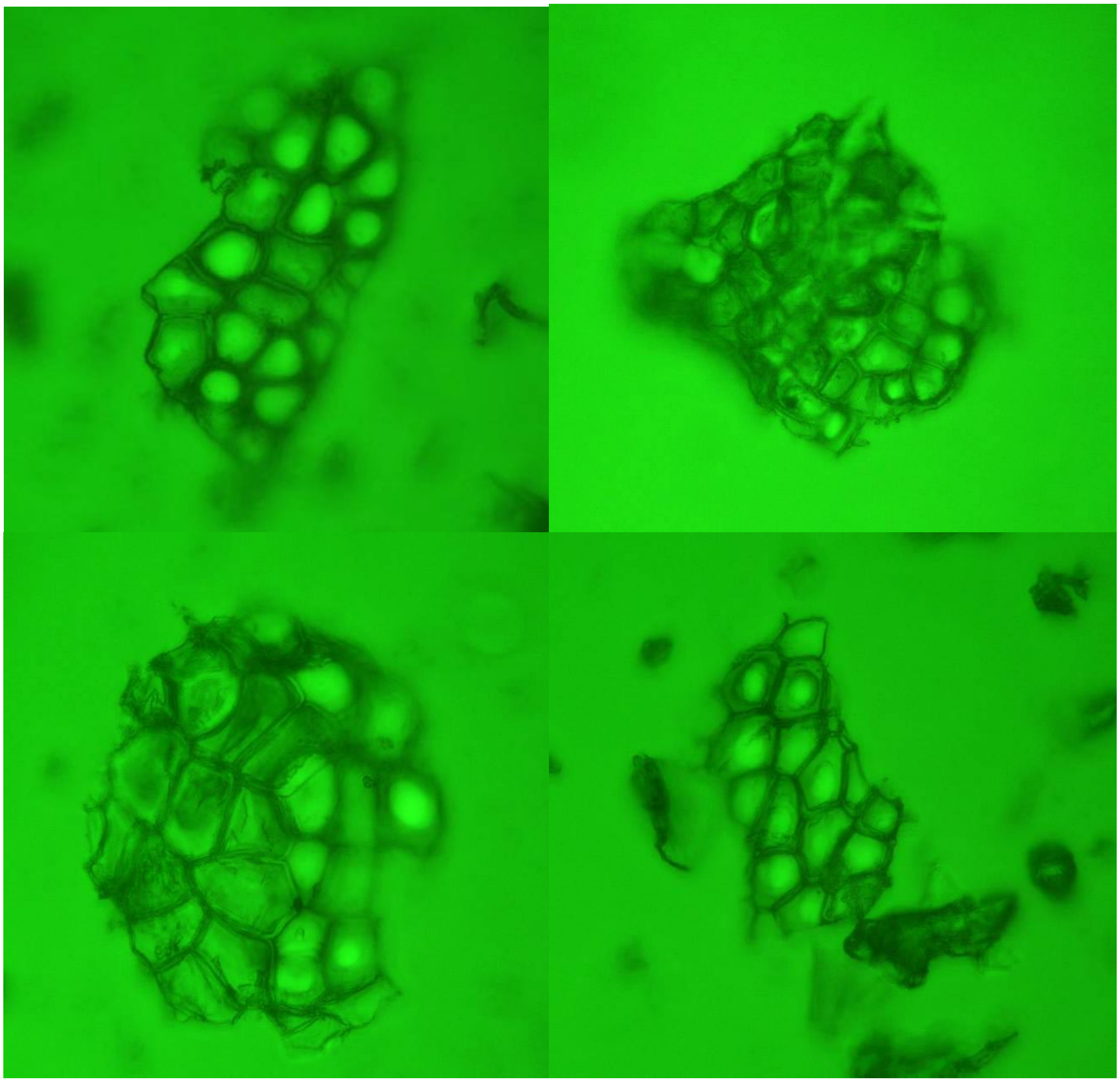


Figure 5.1: Light micrographs (40x zoom lens) of multicellular aggregation of polyhedral epidermal phytoliths from leaves of *Polylepis pauta* . Fragments are approximately 50 µm to 60 µm in length.

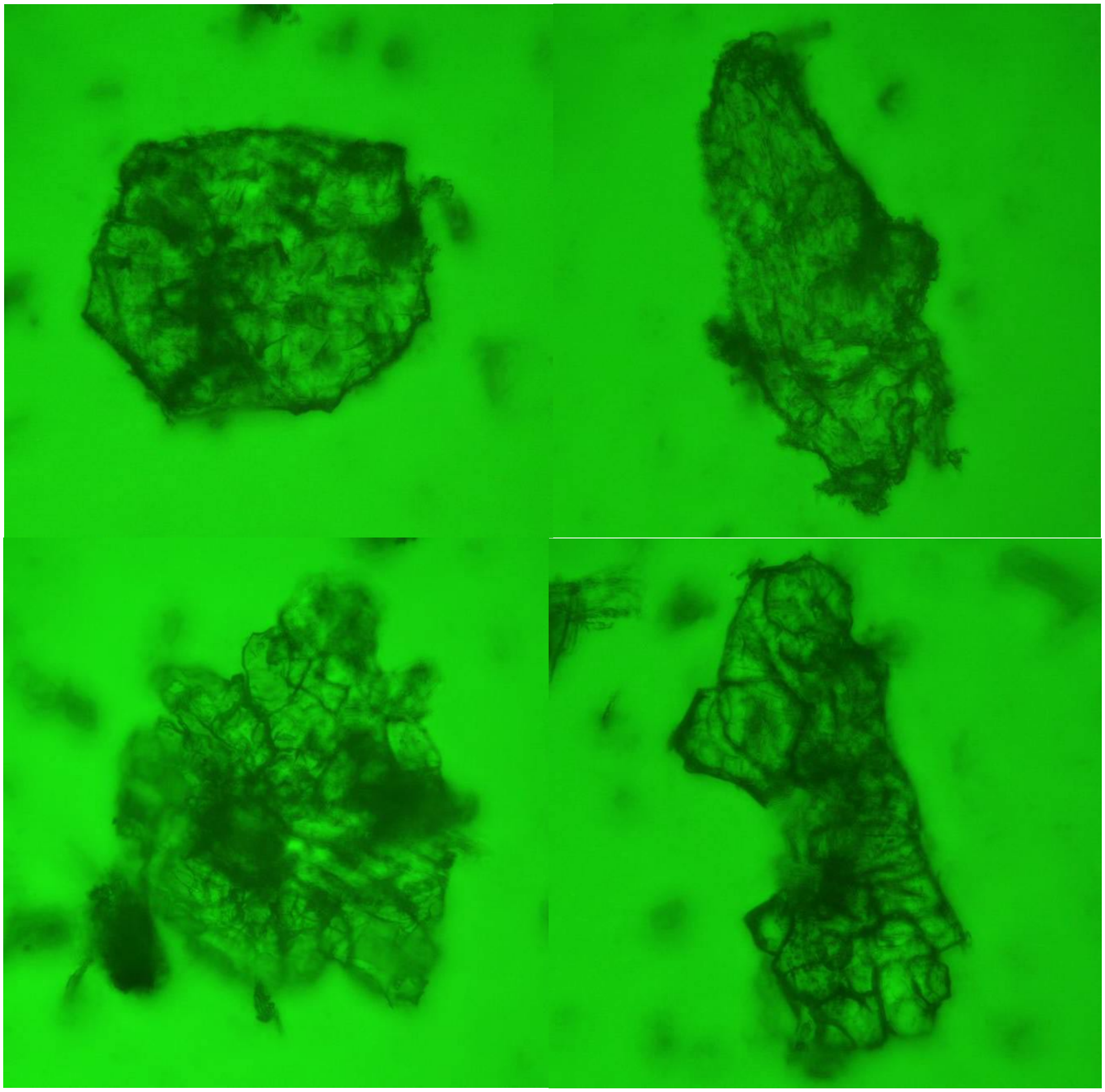


Figure 5.2: Light micrographs (40x zoom lens) of facetate phytoliths from leaves of *Polylepis pauta*. The size of these phytoliths ranges from 40µm to 60µm.

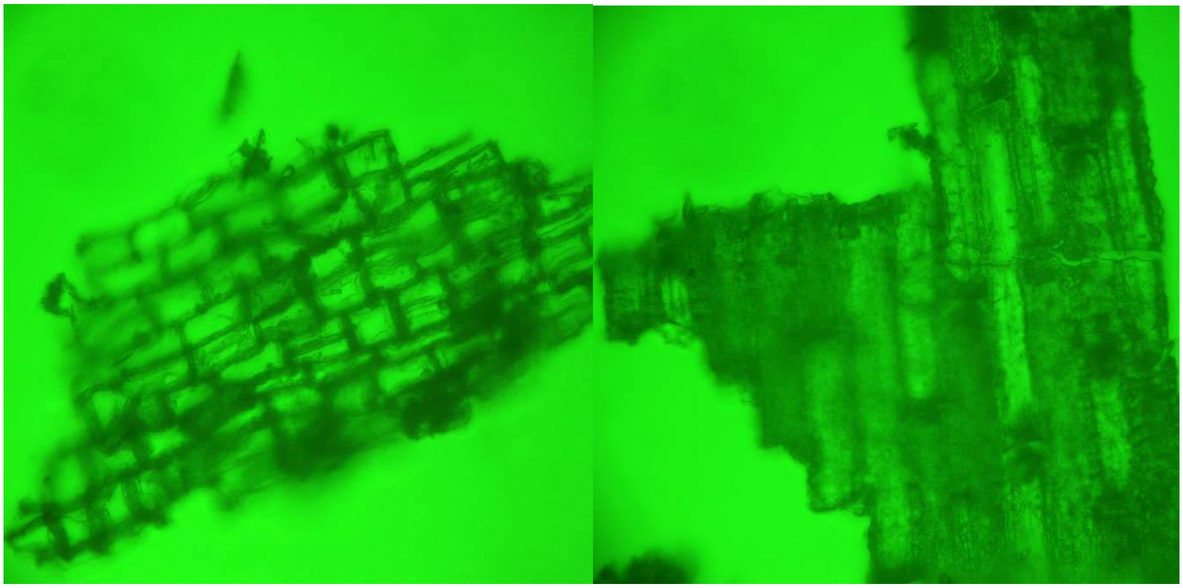


Figure 5.3: Light micrographs (40x zoom lens) of epidermal phytoliths from twigs of *Polylepis pauta*. The size of each cell ranges from 10µm to 20µm.

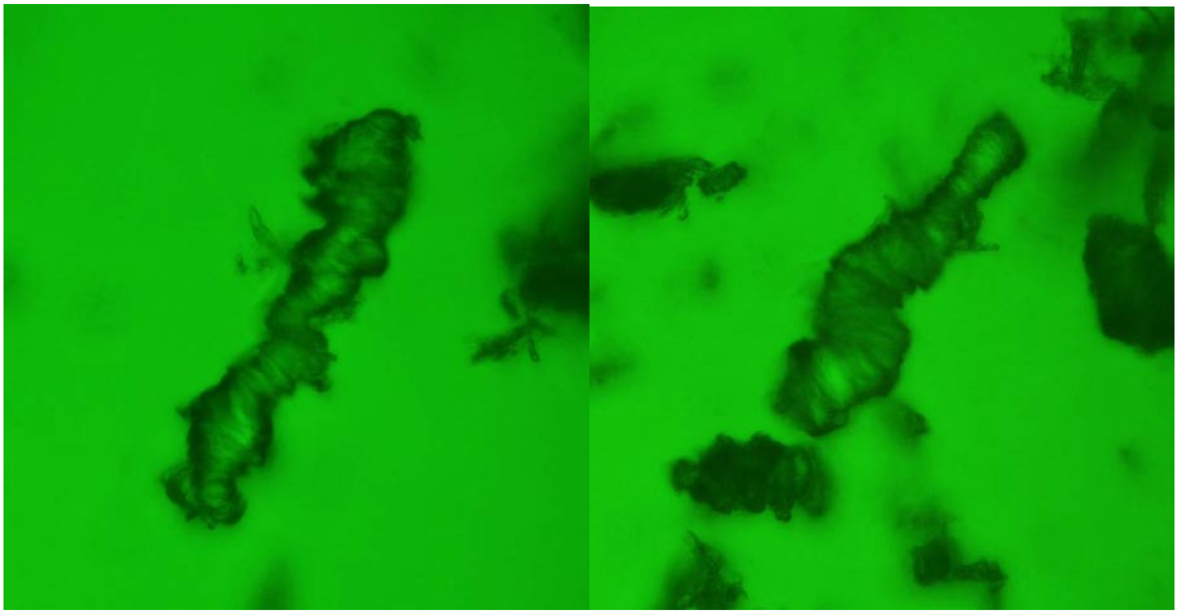


Figure 5.4: Light micrographs of phytoliths (sclereids) from twigs of *Polylepis pauta*. The width of these phytoliths is aproximately 20 µm and the length varies from 40 to 60µm.

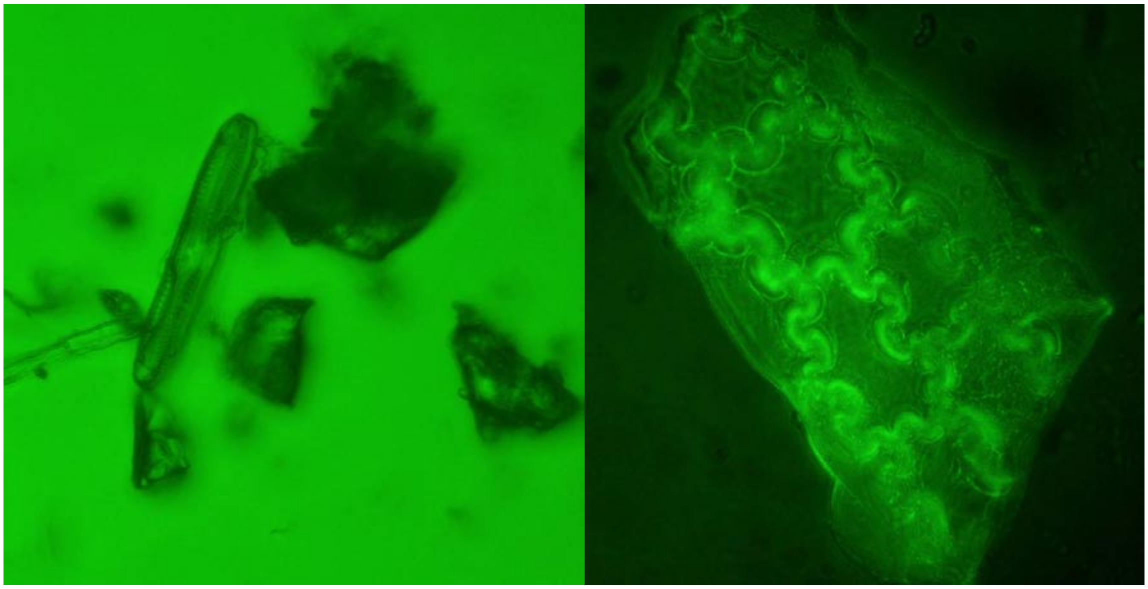


Figure 5.5: Light microgaphs (40x zoom lens) of rondel phytolith (left) and multicellular aggregation of epidermal phytoliths (right) of the fern *Blechnum loxense*. The size of rondel phytoliths ranges between 10µm and 60 µm, and the length of epidermal phytoliths is around 30µm.

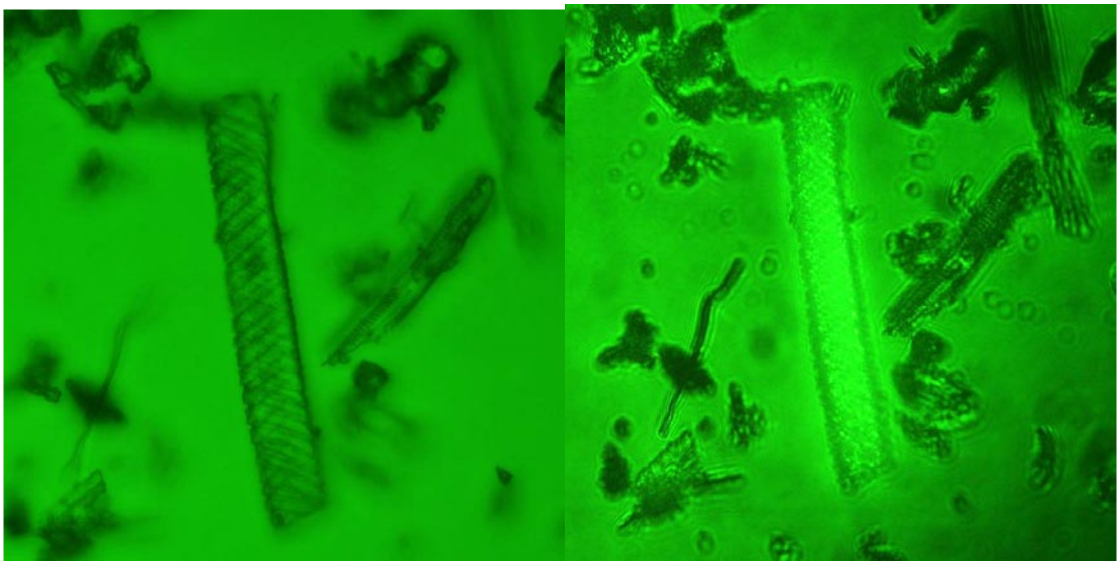


Figure 5.6: Light microgaphs (40x zoom lens) of striated pipe shape phytoliths of the fern *Blechnum loxense* showing surface pattern (light contrast, left) and fluorescens (UV rays, right) .The diametre is aproximatly 10µm and the length ranges from 40µm to 60 µm.

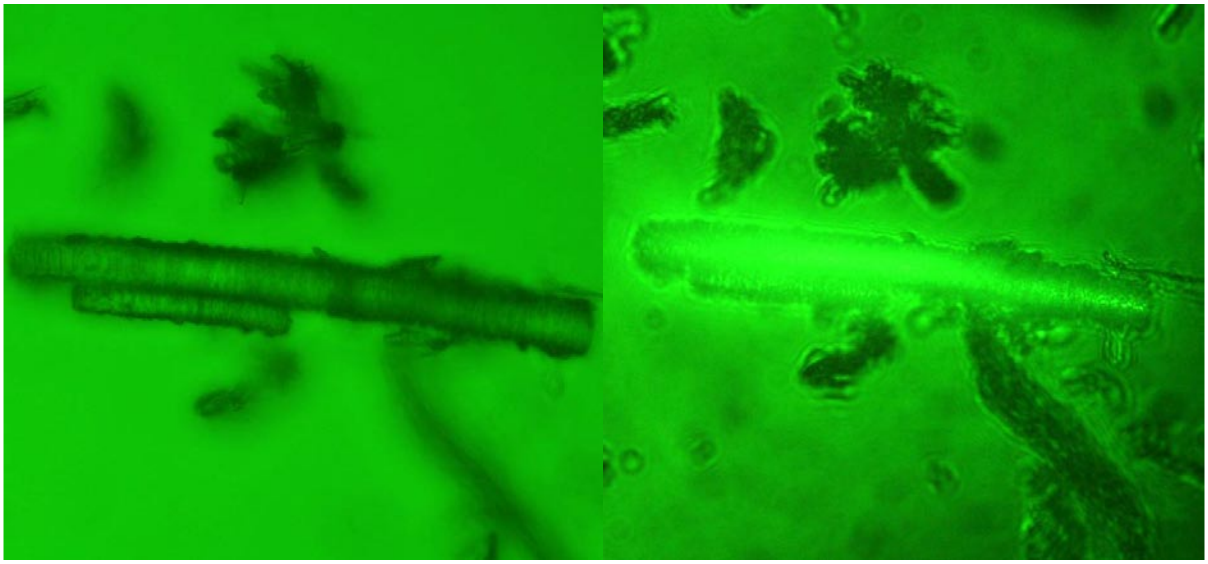


Figure 5.7: Light microgaphs (40x zoom lens) of tracheids of the fern *Blechnum loxense* showing surface pattern (light contrast, left) and fluorescens (UV rays, right) .The diametre of these phytoliths is aproximatly 10µm and the length ranges from 40µm to 70 µm.

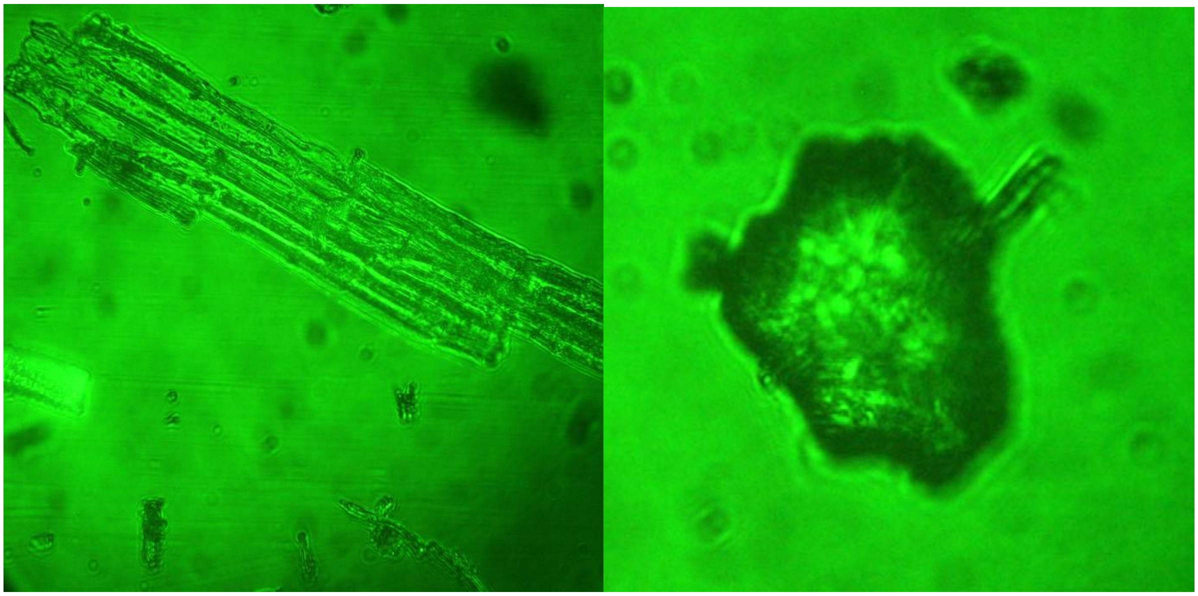


Figure 5.8: Light microgaphs (40x zoom lens) of epidermal (left) and facetate (right) phytoliths of the fern *Blechnum loxense*.The length of these epidermal phytoliths is aproximately 40µm and the size of facetate phytoliths of *B. loxense* ranges from 40µm to 60µm.

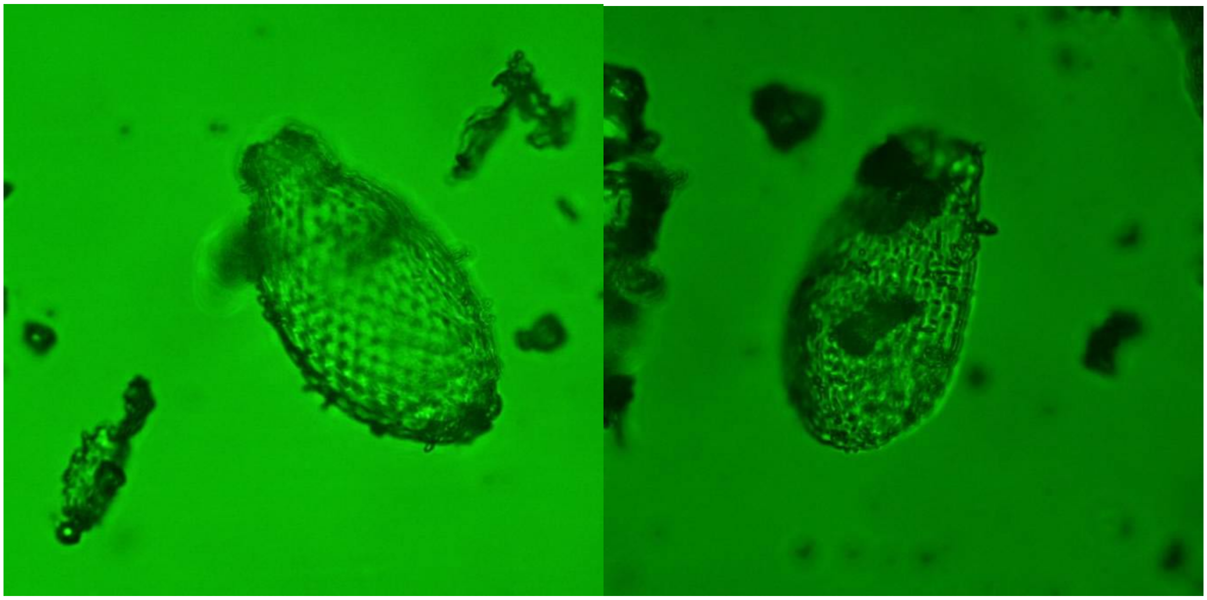


Figure 5.9: Light microgaphs (40x zoom lens) of decorated spheres from the fern *Elaphoglossum ovatum*. These phytoliths are approximatly 60µm long and 50µm in diametre.

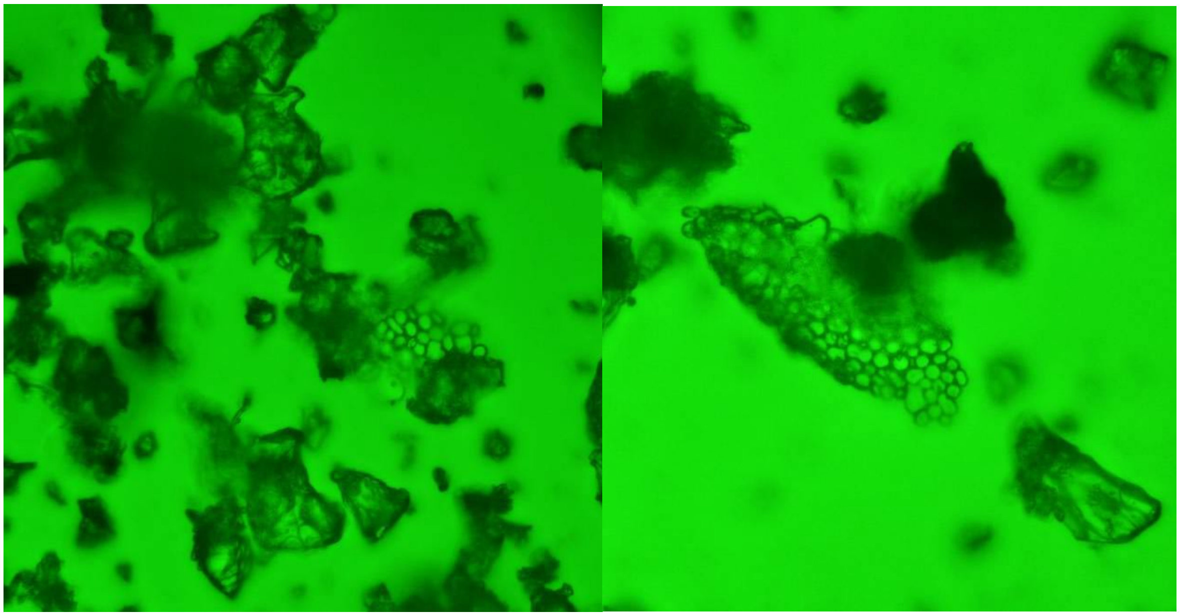


Figure 5.10: Light microgaphs (40x zoom lens) of facetate and mesophyll (right) phytoliths from the fern *Elaphoglossum ovatum*. The size of each cell of mesophyll phytoliths is approximatly 10µm. Facetate phytoliths of *E. ovatum* are 30µm to 40µm.

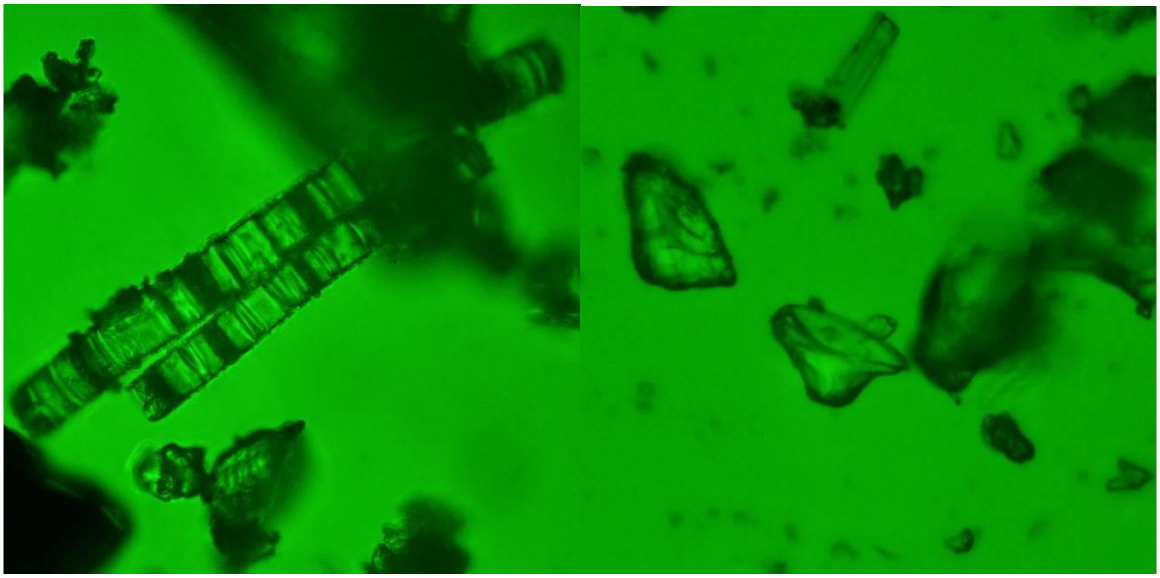


Figure 5.11: Light microgaphs (40x zoom lens) of aligned rondel (left)and hat-shaped phytoliths from the fern *Elaphoglossum ovatum*. Rondel phytoliths of *E. ovatum* are from 20µm to30µm in diamatre and form alignments that are between 50µm to 70µm in length. Hat-shaped phytoliths of *E. ovatum* are approximatly 20µm in diametre.

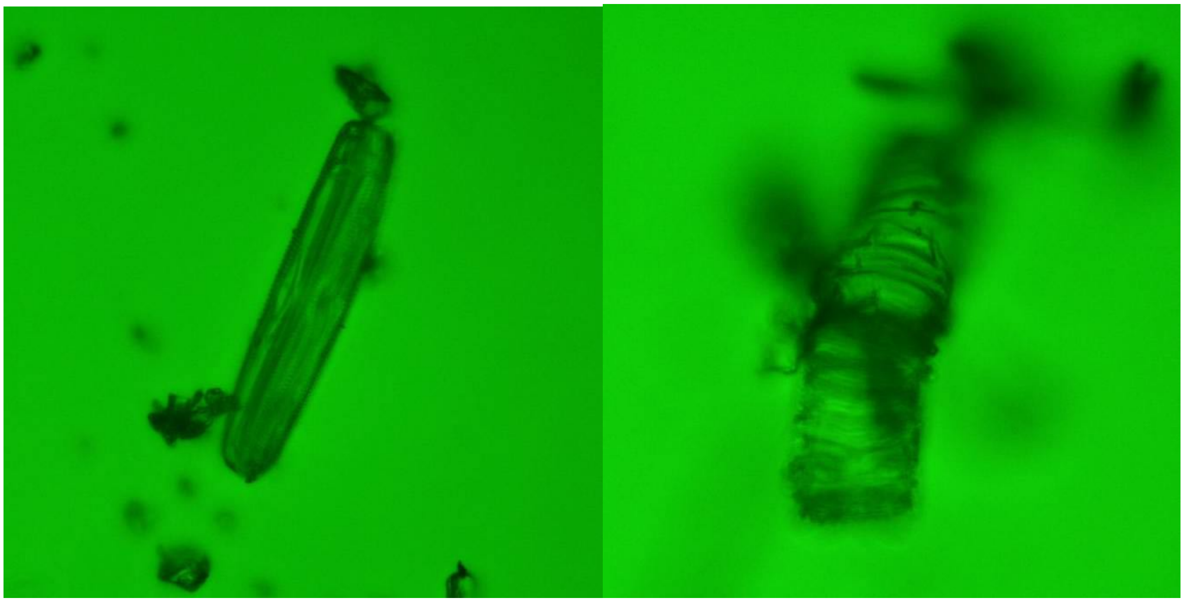


Figure 5.12: Light microgaphs (40x zoom lens) of rondel (left) phytolith and aligned rondels (right) of the fern *Elaphoglossum vulcanicum*. The diametre of rondel phytoliths of *E. vulcanicum* ranges from 20µm to 60µm and alignments are up to 50µm in length.

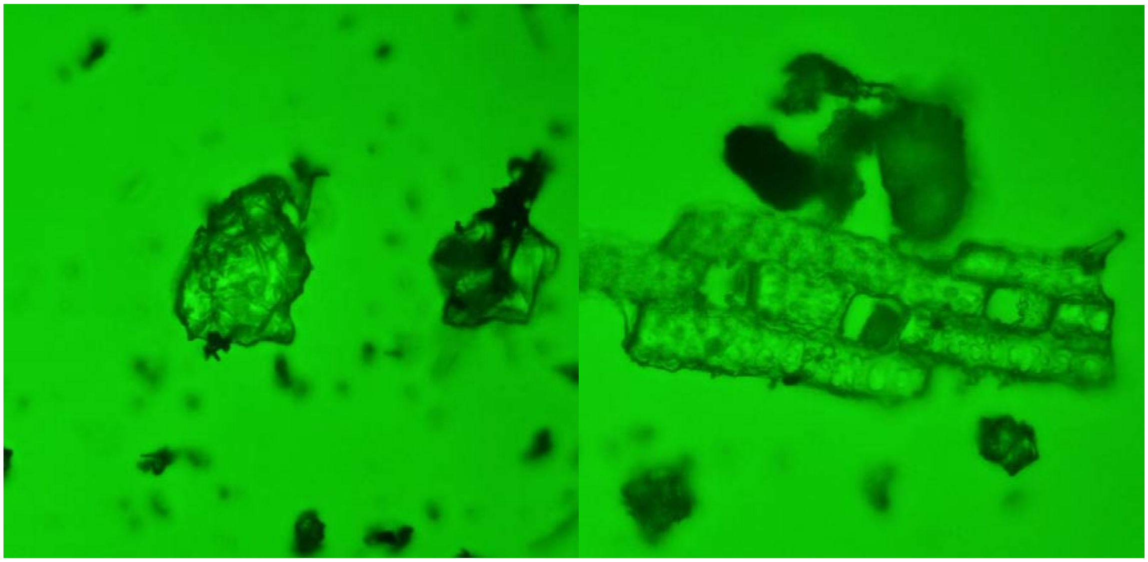


Figure 5.13: Light microgaphs (40x zoom lens) of facetate phytoliths and charcoal (left) and epidermal phytoliths (right) of the fern *Elaphoglossum vulcanicum*. The size of facetate phytoliths of *E. vulcanicum* range from 20µm to 40µm in and epidermis phytholith fragmet is aproximatly 60µm in legth.

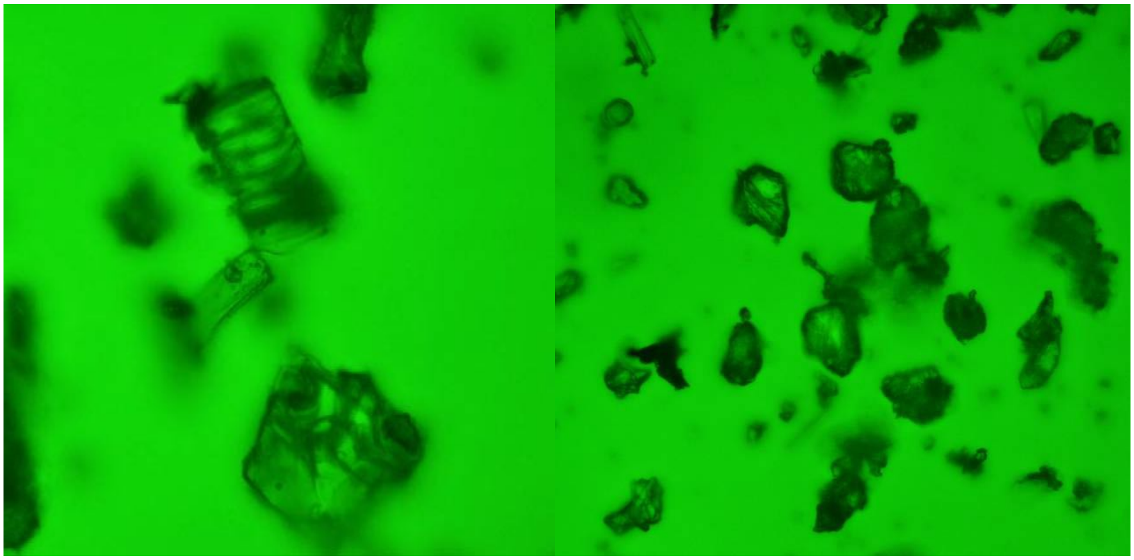


Figure 5.14: Light microgaphs (40x zoom lens) of aligned rondel phytoliths (left, 20µm in width and aproximately to 40µm in length) and facetate phytoliths (rigth, aproximately 20µm) of the fern *Melpomene pilossissima*.

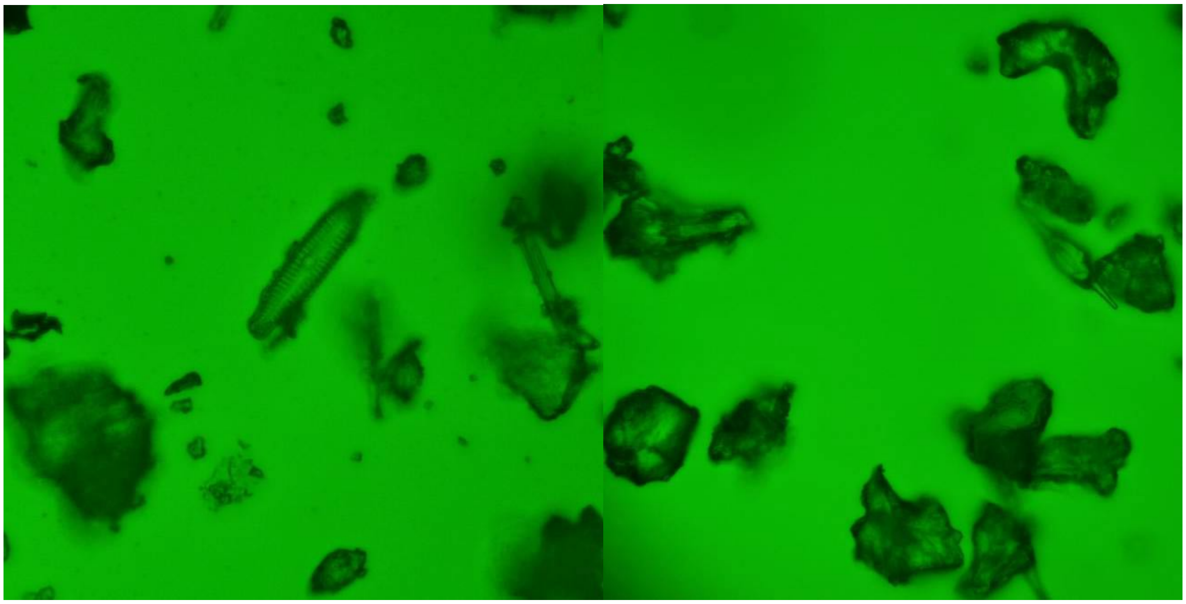


Figure 5.15: Light microgaphs (40x zoom lens) of straited rondel phytolith (left, approximatly 20µm in diametre) width and aproximately to 40µm in length) and facetate phytoliths (rigth, aproximately 20µm) of the fern *Melpomene pilossissima*.

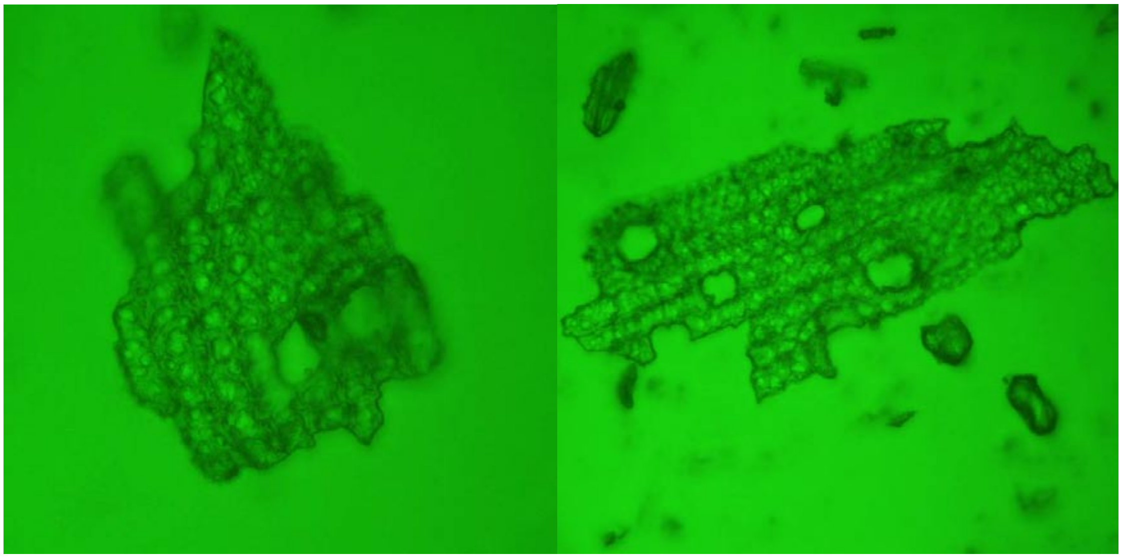


Figure 5.16: Light microgaphs (40x zoom lens) of epidermal phytoliths of the fern *Terpsichore heteromorpha*, fragments are approximatly 50µm (left) to 60 µm in length .

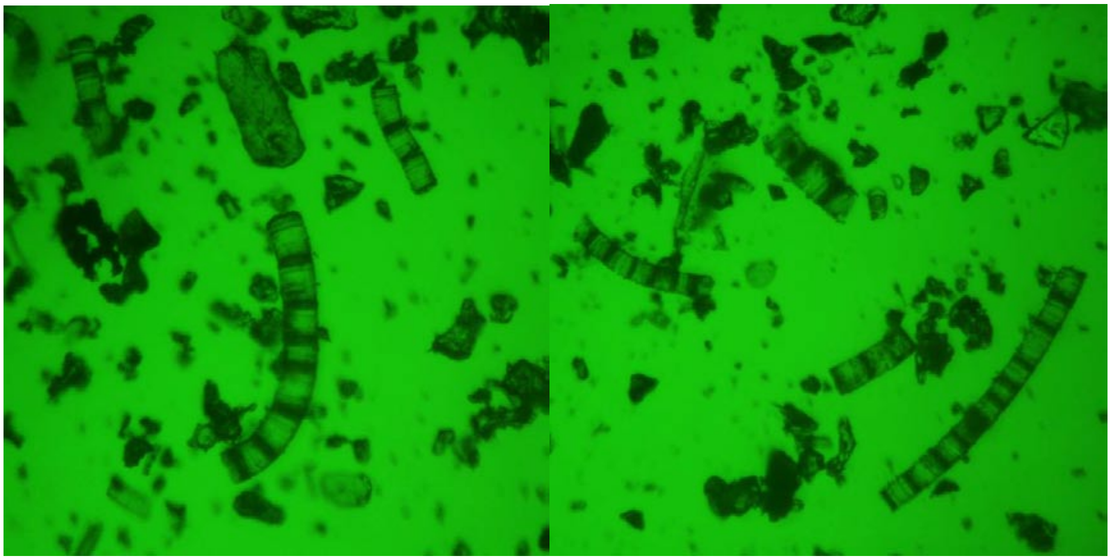


Figure 5.17: Light microgaphs (40x zoom lens) of aligned rondel phytoliths of the fern *Terpsichore heteromorpha*. The diametre of rondel phytoliths of *T.heteromorpha* ranges from 20µm to 60µm and alignments of small rondels (20µm in diametre) are up to 70µm in length.

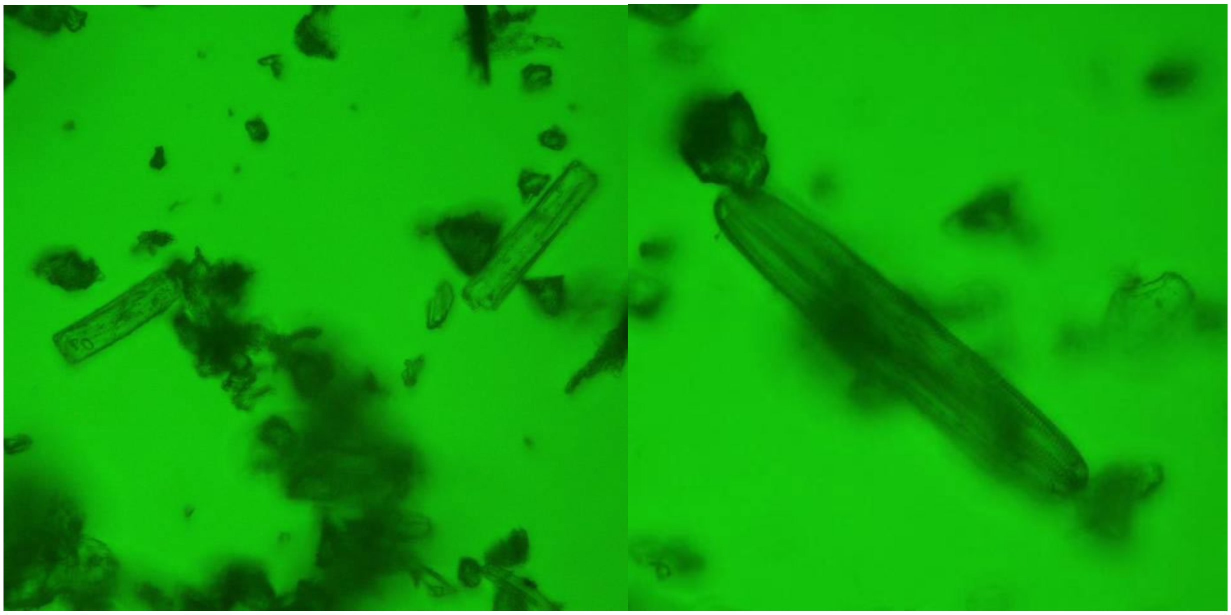


Figure 5.18: Light microgaphs (40x zoom lens) of rondel phytoliths of the fern *Terpsichore heteromorpha*. Their diametre ranges from 20µm to 60µm.

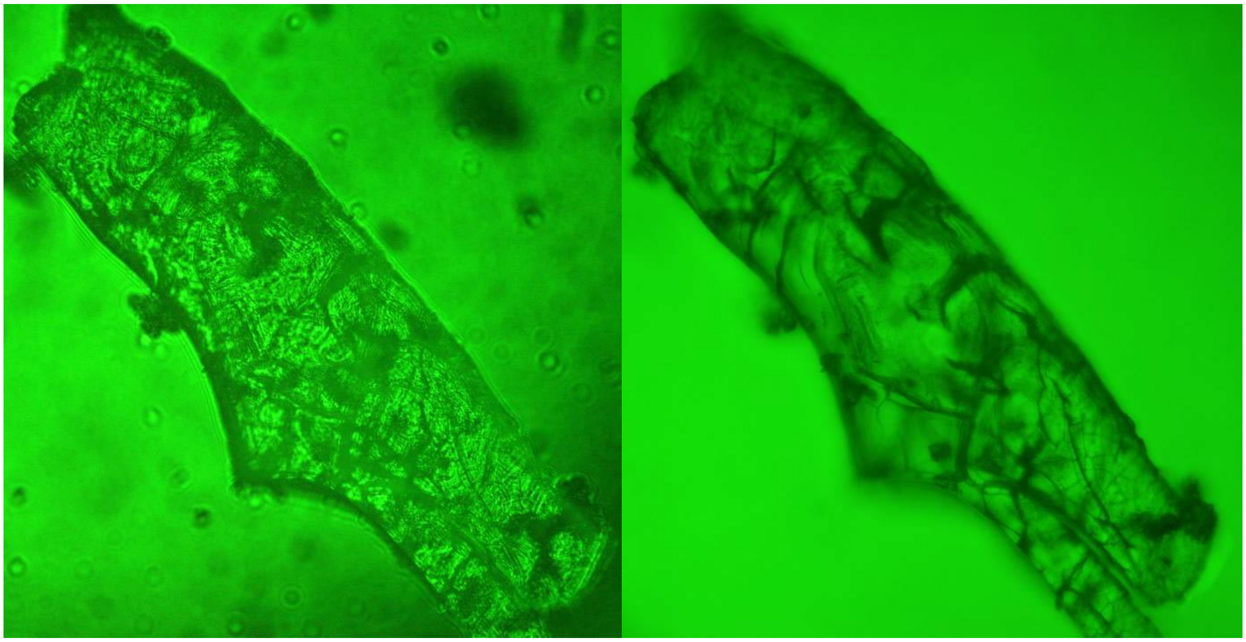


Figure 5.19: Light micrographs (40x zoom lens) of facetate tracheid of the fern *Polypodium mindense*, showing fluorescens (left) and surface pattern (right), it is aproximatly 80µm in length

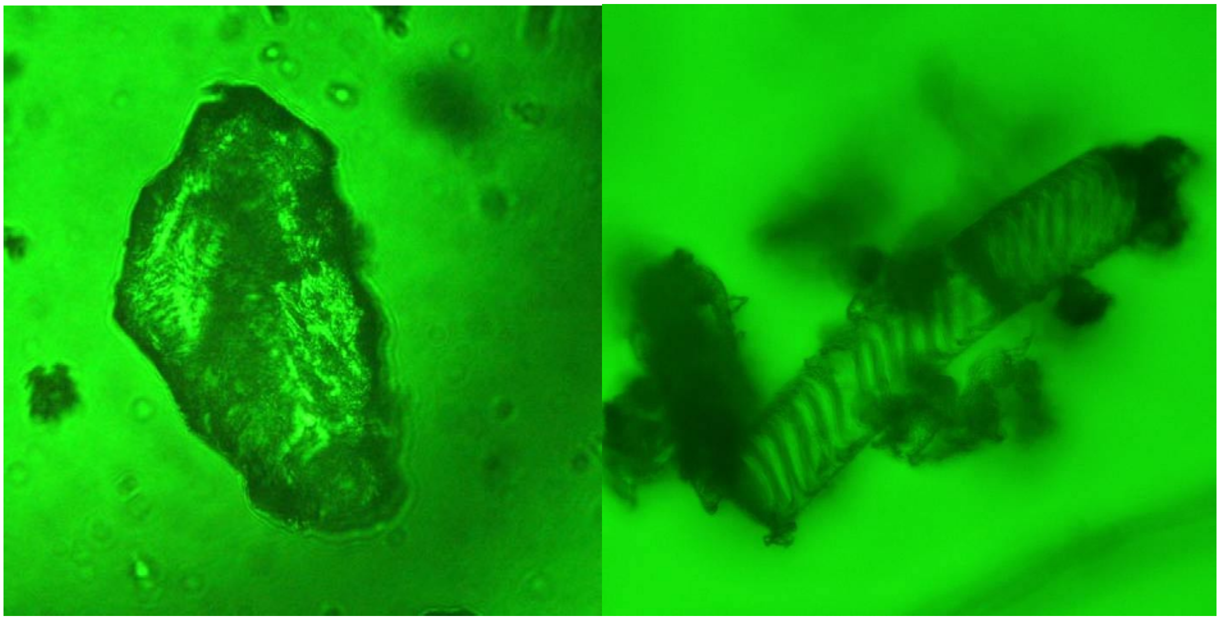


Figure 5.20: Light micrographs (40x zoom lens) of facetate phytolith (left, approximatly 50 µm in length) and aligned rondel phytoliths (right, approximatly 60 µm in length) of the fern *Polypodium mindense*. Their diameter ranges from 20µm to 60µm.

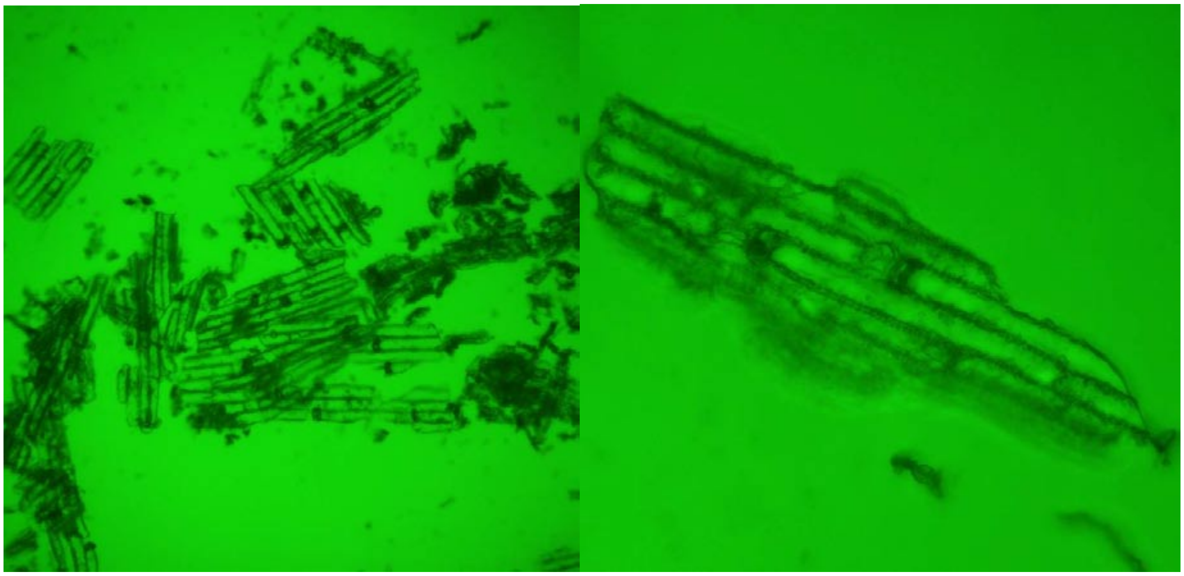


Figure 5.21: Light micrograghs (16x and 40x zoom lenses for the left and ritght micrographs respectively) of phytoliths in epidermal tissue of the grass *Neurolepis elata* . The fragments are approximatly 60 µm in length.

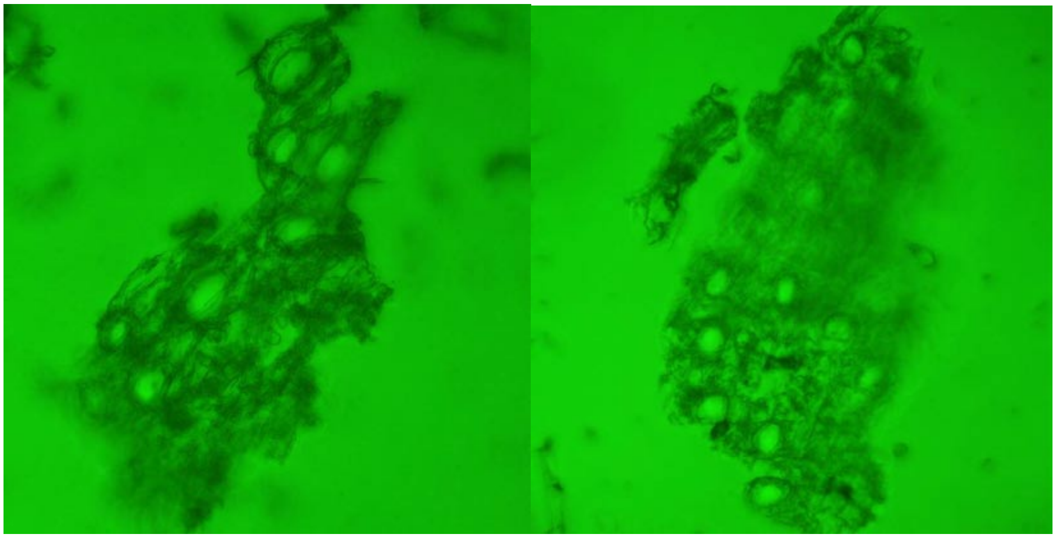


Figure 5.22: Light micrograghs (40x zoom lens) of epidermal phytoliths of the grass *Neurolepis elata* . The fragments are approximatly 60 µm in length.

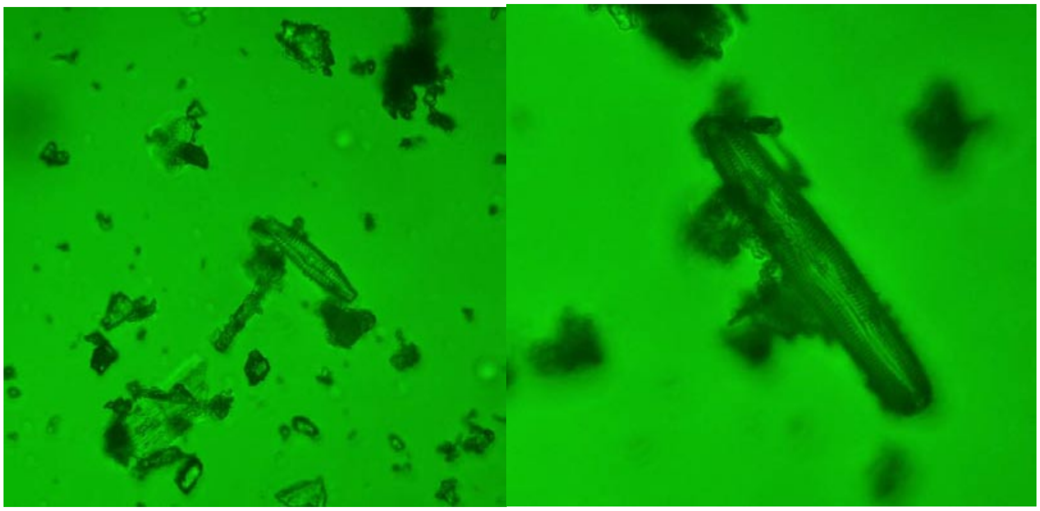


Figure 5.23: Light micrograghs (40x zoom lens) of straited rondel phytoliths (left, approximatly 30µm in diameter and right aproximatly 60 µm in diameter length) extracted from soil organic matter beneath *Polylepis* forest.

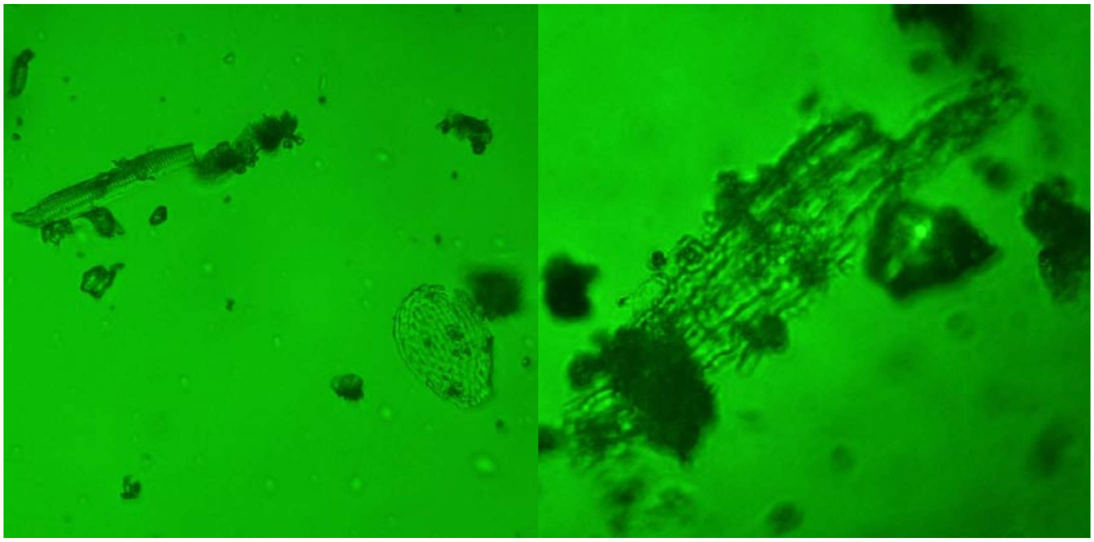


Figure 5.24: Light micrograghs (40x zoom lens) of sclereid (70µm in length)decorated sphere (60µm µm left) and ehpidermal phytoliths (right, fragment is aproximatly 60 µm in length) present in soil organic matter beneath *Polylepis* forest.

CHAPTER 6

CONCLUSIONS

Scattered patches of *Polylepis* forests occur within the 3000 m to 4500 m altitudinal belt of the Andean Cordillera from Venezuela to Argentina; they have been hypothesized to be remnants of a once continuous forest whose range became fragmented through anthropogenic processes that probably preceded the Spanish conquest (Ellenberg 1979, Fjeldså 1992, Kessler 1995, 2002, Lægaard 1992). The importance of *Polylepis* forests in the provision of environmental services and as refugia for unique biological diversity (Fjeldså and Kessler 1996, Fjeldså 2002b, Herzog and Cahill 2002, Renison *et al.* 2002) has rendered the issue of their ancestral range a matter of human and environmental welfare in the Andes (Fjeldså and Kessler 1996, Renison *et al*. 2002, Capriles and Flores Bedregal 2002).

This dissertation used a multidisciplinary approach to assess the relevance of environmental versus human factors in shaping the historical and modern distribution of the *Polylepis pauta* forests in the southern part of the northeastern Cordillera Oriental of Ecuador, with a focus on three watersheds (the Oyacachi, Papallacta, and Chalpi basins). Interpretation of historical aerial photography was used to assess the extent and nature of recent changes in *Polylepis* cover in the study area. The degree of genetic similarity between *Polylepis pauta* trees from fragments in different watersheds was determined through allozyme genetic analyses to assess whether the observed patterns were consistent with an historical more continuous distribution of the species in the study area. Floristic surveys were carried out to investigate associations of vascular floristic diversity within forest remnants with elevation and fragmentation. Finally, opal phytoliths were extracted from *Polylepis* forest species and from organig mater of soil underneath the forest to explore their potential for investigating whether *Polylepis* forests historically preceded the grass páramo within the 3000 m to 4100 m Andean belt. Findings from each approach yielded consistent implications for *Polylepis* forest conservation in Ecuador.

Aerial photography interpretation proved to be a reliable approach to land cover classification and monitoring in the Northeastern Cordillera Oriental of Ecuador. Land cover maps from 1956 and 1999 derived from aerial photography assemblages of 1956 and 1965 and of 1993 and1999, respectively, showed a sharp dichotomy between a forested cover in the southeastern part of the study area and páramo-dominated cover in the northwest. The presence of scattered polylepis patches in the páramo-dominated northwest, along with landslides (often associated with burnt sites in mountain regions with high intensity precipitation, Cannon *et al*. 1998, Cannon *et al.* 2001) and fire scars, may indicate a human-influenced transition from a forested to a páramo landscape. The occurrence of fire scars around *Polylepis* forest patches and immediately above the uppermost limit of continuous *Polylepis* forest in the 1965 aerial photography would be consistent with this view. Dense *Polylepis* forest experienced attrition, further range fragmentation and shrinkage; but overall loss was only 3.4 % of the 1956 cover. This finding is consistent with studies carried out in Perú using aerial photography for comparable periods of time, 1930-1997 by Byers (2000) and 1956-2005 by Jameson and Ramsay (2007). The transition of dense polylepis forest to sparse shrub/polylepis forest, and from this latter vegetation type to shrubland and páramo, which was recorded in this study, suggests a human-influenced distribution of *Polylepis* forests and *Polylepis*/shrub mixtures in the study area. A similar transition has been proposed for scattered *Polylepis* spp. occurrence in the Andes of Argentina (Cabido and Acosta 1985, Cingolani *et al.* 2004). The Oyacachi basin, where most of the changes took place, supported an isolated and relatively small Quichua community before the road construction which connected Oyacachi to Papallacta in 1994 (EMAAP 1991). Land cover transformations in the study area reflect the slow expansion characteristic of secluded Andean settlements during the implementation of agrarian reform (Gondard and Mazurek, 2001).

Genetic diversity maintained by *Polylepis pauta* in the study area, expressed in terms of total genetic variation (H_{es}) and percentage of polymorphic loci (P), was higher than that observed for most wind-pollinated and wind-dispersed temperate and tropical trees with a regional distribution (cf. reviews by Hamrick *et al*. 1992 and Hamrick and Godt 1996). Values of within population variation (H_{ep}) recorded for the *P. pauta* populations sampled fell within the range observed for tree species with similar life history and ecological traits (cf. reviews by Hamrick *et al*. 1992 and Hamrick and Godt 1996). G_{ST} values obtained from comparison of the 12 remnant populations at different spatial scales revealed lower differentiation across watersheds than among populations within each watershed. The lower genetic differentiation recorded for populations of mature individuals than for seedling populations is consistent with theoretical predictions for tree populations characterized by a generally low genetic structure (Hamrick and Godt 1989, 1996; Nybom 2004). Strong selection of seedlings (observed in *Polylepis incana*, *P. pauta*, [Cjerjacks *et al.* 2007], and *P. australis* [Enrico *et al*.2004]) and delayed reproductive maturity in trees could contribute to the attenuation of structure over time (Austerlitz *et al.* 2000; Le Corre and Kremer 2003). The levels and distribution of genetic variation in the *Polylepis pauta* populations are consistent with those expected with relatively recent fragmentation of a more continuous historical distribution, where trees' longevity and aptitude for long-distance gene flow have buffered the tendency of distant populations to diverge genetically, as theory predicts (cf. Aldrich *et al*. 1998, Bacles *et al.* 2004, Hamrick 2004, Petit and Hampe 2006, Young *et al.* 1993). In contrast if this forest patches date back to the recovery form the last glacial epoch, we would expect to have seen greater genetic differentiation among forest patches.

Genetic variation among populations was significantly related to spatial attributes of patches. Specifically, larger forest patches, encompassing a broader altitudinal range, showed higher values for most of the genetic variation parameters considered in this study (P, A_p, A, A_e, H_e and percentage of alleles). The greater diversity within patches with a larger altitudinal range and the greater differentiation within watersheds that span a greater elevation range support Smith and Young's (1987) suggestion that genetic differentiation occurs within species with a large elevation range. More convoluted patches had a higher percentage of polymorphic loci, percentage of alleles and mean number of alleles per locus than compact, more circular ones. This is consistent with enhanced interactions across boundaries provided by more complex patch shapes (Forman 1999) which are known to influence successful pollen movement pattern and actually increase gene flow among patches (Levin and Wilson 1978; Rai and Jain 1982; Handel 1983). Consistently lower genetic variation (as expressed by P, A_p, A, A_e, H_e and percentage of alleles) was associated with steeper slopes; this might stem from the predominance of vegetative reproduction in steeper areas at higher elevation ranges, which are more prone to landslides (field observation).

Overall vascular species diversity recorded in the *Polylepis pauta* forest patches sampled in the Chalpi, Oyacachi and Papallacta basins was similar to that observed in other floristic surveys carried out in *P. pauta* forests in Ecuador south of the Papallacta basin (cf. Laur et al. 2001) but lower than others carried out in Peru (cf. Servat *et al*. 2002, Cordillera de Vilcanota, Cuzco) and Bolivia (cf. Fernandez-Terrazas and Ståhl 2002, Cordillera de Cochabamba) in forests of *P. besseri*, *P. subsericans*, *P. racemosa*, *P. tomentella*. At a more localized scale, the Oyacachi basin was appreciably more diverse than the two other basins examined in this study. *Polylepis* forests are known to vary in floristic richness, structure and patterns of occurrence according to local environmental conditions (Fjeldså and Kessler 1996, Kessler 2002). The study area encompasses a significant topographic heterogeneity and subtle differences in climatic regimes. It is not out of question, therefore, that these may contribute to the floristic differences among the three basins. The presence of certain common herbaceous species such as *L. gigantea* and *Pennisetum clandestinum*, often associated with disturbance, in the *Polylepis* forest patches of Papallacta and Oyacachi might be a consequence of cattle incursions into patches to seek shelter from the rain (field observation, Susana León-Yanez, pers. comm., 2007). Both the Papallacta and, to a lesser extent, the Oyacachi basins have a long history of forest conversion to pasture, and this is likely expressed through the occurrence of disturbance-related species. In contrast with previous research on tropical mountain diversity gradients (Van der Hammen *et al*. 1989, Gentry 1995, Lieberman *et al*. 1996, Kessler 2002b), a straightforward pattern of species diversity decline with increased elevation was not evident in *Polylepis pauta* forest remnants studied. No significant negative correlation was found between species diversity and elevation, but DCA ordination of quadrats showed compositional similarities between quadrats at the same elevation. Another possible reason for the absence of a correlation between elevation and species diversity is that the elevation range encompassed by the polylepis forest remnants studied was too narrow for this broad-scale diversity pattern to express. Scale has been recognized to have a strong influence on detection of elevational patterns of diversity (Rahbek 1995 and 2005). Of all the spatial attributes of forest patches considered in this study, the elevation range spanned by the patch showed the strongest relationship to plant species diversity. Although *Polylepis* forests are generally viewed as a more homogeneous type of forest than lower elevation mountain forests in the tropics (Balslev 1988, Fjeldså 2002a, 2002b, Laur *et al*. 2001), the positive correlation observed in this study between patch length (*i.e.*, elevation range encompassed by the patch) and floristic diversity is consistent with theoretical predictions for steep climatic gradients characteristic of tropical mountain ecosystems (Van der Hammen *et al*. 1989, Gentry 1995, Lieberman *et al*. 1996). The continuous forests from the Chalpi differed from fragmented relicts in the notable frequency of *N. elata*, absent in the other watersheds, and their lower number of fern species relative to the other two basins. *N. elata*, considered a forest to páramo transition species (Ohl and Bussmann 2004, Ritcher *et al*. 2008), occurred in downhill seeps, forming big clumps of giant rosettes in waterlogged soils, often invading forest interior and intermingling with *Polylepis* forest (cf. Ritcher *et al.* 2008 for similar observations in the northern half of the Cordillera Real, Ecuador). The species is used for thatching in Ecuador, and was formerly collected in the Oyacachi basin some decades ago (50 or 60 years ago, E. Parion pers com. 2007). Its absence or very low frequency in the Oyacachi and Papallacta watersheds may be a human-influenced condition.

Several years of observations and reflections of tropical mountain ecosystems led Ellenberg (1979) to conclude:

> "In my opinion we should wonder why some forests or tree stands are still left there, instead of wondering why they are so small and rare that they could be looked upon as exceptions. Up to now we know very little about man's influence on ecosystems and not much more about the influence of ecosystems on him. When we seriously accept man as an important item in ecosystem research, we will certainly contribute to a future harmony between man and his environment."

Ellenberg's statement not only challenged a long standing theory on limiting factors for forest growth in the Andes, but it also brought human beings into the biogeographical research arena for the first time in the young history of mountain ecosystem research (Kessler 2002). Considerable progress has been made in both areas since Ellenberg's assertion; however, the relative benefits derived from *Polylepis* forest vs. páramo extensions are still disputed.

Interpretation of historical aerial photography in this study revealed that *Polylepis* forests were lost to paramo or transformed into scattered *Polylepis* and shrubs through fire. Although associations between fire and landslides in the study area need further exploration, the apparent spatial coincidence of these establishes the need to study the actual potential of *Polylepis* forest in soil and water conservation. Páramo extensions have been widely studied and praised for their capabilities in this respect (Hofstede *et al*. 2002, Harden 2006), but *Polylepis* forests are yet to be researched in their aptitude to serve human settlements downstream.

From the species conservation perspective, the genetic resilience which characterizes trees in the face of fragmentation (cf. reviews by Hamrick *et al*. 1992 and Hamrick and Godt 1996) seems to be favoring *Polylepis pauta*. The genetic variation exhibited by this species across the study area was seemingly well spread over the three basins. The populations of Oyacachi which had a slightly higher genetic diversity would be better suited to serve as a source material for restoration.

The floristic survey of patches and continuous remnants of *Polylepis* forest showed a strong link between elevation range encompassed by remnants and their vascular floristic diversity. This is an issue that is worth considering in conservation efforts of *Polylepis* forests in the region.

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APPENDICES

Appendix A: List of vascular plant species[1] recorded in 12 *Polylepis pauta* forest patches of the southern part of the northeastern Cordillera Oriental of Ecuador

Family	**Growth form**	**Species name** [2,3]
Angiosperms	**Herbs & vines**	
Apiaceae	H	*Hydrocotyle alchemilloides* A. Rich.
Apiaceae	H	*Hydrocotyle bonplandii* A. Rich.
Apocynacea	V	vine, not determined
Asteraceae	H-S	*Aetheolaena mojandensis* (Hieron) B. Nord.
Asteraceae	H	*Bacharis genisteloides*
Asteraceae	H	*Laciocephalus* sp. (musilago)
Asteraceae	V	*Mikania lloensis* Hieron.
Asteraceae	H-S	*Muticia* sp. / Gynoxis sp.
Asteracea	S	*Pentacalia arbutifolia*
Asteraceae	H	*Senecio clavus* Cuatrec.
Asteraceae	H	*Senecio formosus*/ Laciocephalus
Asteraceae	H	*Senecio scrobicarioides* D.C.
Brassicaceae	H	*Cardamine jamesonii* Hooker
Bromeliaceae	H	*Puya cf hamata* L.B.Sm.
Campanulaceae	H	*Siphocampylus rupestris* E.Wimm
Caryophilaceae	H	*Cerastium* sp.
Caryophyllaceae	H	*Stellaria recurvata* Willd.ex Schltdl.
Caryophyllaceae	H	*Stellaria ovata* Willd.ex.Schltdl.
Commelinaceae	H	*Callicia* sp.
Cyperaceae	H	*Carex* sp. / *Rhyncospora* sp.
Geraniaceae	H	*Geranium angelense* Halfdan-Nielsen
Geraniaceae	H	*Geranium equadorense*
Gunnerceae	H	*Gunnera magellanica*
Juncaceae	H	*Luzula gigantea* Desv.
Orchidaceae	H-epiphyte	*Epidendrum* sp.1
Orchidaceae	H-epiphyte	*Epidendrum* sp.2
Orchidaceae	H-epiphyte	*Stellis* sp.
Oxalidaceae	H-V	*Oxalis lotoides* Kunth.
Piperaceae	H-epiphyte	*Peperonia hispidula* (Sw.) A.Dietr.
Piperaceae	H	*Peperomia violacea* C.DC.
Piperaceae	H	*Peperomia hartwegiana* Miq.
Poaceae	H	*Neurolepis elata*
Poaceae	H	*Neurolepis aristata* (Munro) Hitchc.
Poaceae	H	Pennisetum clandestinum Hotchst. ex Chiov
Ranunculaceae	H	*Ranunculus* sp.
Rosaceae	H	*Lachemilla holosericea* (L.M. Perry) Rothm.
Rubiaceae	V	*Gallium hypocarpium* (L.) Endl. ex Griseb.
Scrophulariaceae	H	herb, not determined
Scrophulariaceae	H-S	*Bartsia strict*a (H.B.K.) Benth.
Solanaceae	V	*Solanum brevifolium* Dunal
Solanaceae	H-S-V	*Jaltomata viridiflora* (Kunth) M. Nee & Mione
Solanaceae	H-V	*Solanum* sp.
Urticacea	H	*Urtica echinata* Benth.
Valerianaceae	H	*Valeriana adscendens* Turcz.

ANGIOSPERMS	SHRUBS & TREELETS	
Araliaceae	S-T	*Oreopanax seemannianus* Marchal
Asteraceae	S-V	*Aetheolaena involucrata* (Kunth) B. Nord.
Asteraceae	S	*Aetheolaena lingulata* (Schltdl.) B. Nord.
Asteraceae	S-V	*Aetheolaena otophora* (Wedd.) B.Nord.
Asteraceae	S	*Bacharis* sp.
Asteraceae	S	*Diplostephium rupestre* (Kunth) Wedd.
Asteracea	S-T	*Diplostephium hartwegii* Hieron
Asteracea	S-T	*Gynoxys acostae* Cuatrec.
Asteracea	S-T	*Gynoxys buxifolia* (Kunth) Cass.
Asteracea	S-T	*Gynoxys hallii* Hieron
Asteraceae	S	*Monticalia myrsinites* (Turcz.) C. Jeffrey
Asteraceae	S	*Monticalia vaccinioides* (Kunth) C. Jeffrey
Ericaceae	S	*Ceratostema alatum* (Hoerold) Sleumer
Ericaceae	S	*Pernettya prostrata* (Cav.) D.C.
Grossulariaceae	S-T	*Escallonia myrtilloides* L.f.
Grossulariaceae	S	*Ribes ecuadorense* Jancz.
Grossulariaceae	S	*Ribes lehmannii* Jancz.
Grossulariaceae	S	*Ribes hirtum* H.B.K.
Loranthaceae	S	*Tristerix longebracteatus* (Desr.) Barlow & Wiens
Melastomataceae	S-T	*Brachyotum alpinum* Cogn.
Melastomataceae	S-T	*Miconia latifolia* (D.Don) Naudin
Nyctanaceae	S-V	*Colignonia scandens* Benth
Polygalaceae	S	*Monnina loxensi*s Benth.
Polygonaceae	S	*Muehlenbeckia tamnifolia* (Kunth in H.B.K.) Meisner
Rosaceae	S-T	*Hesperomeles obtusifolia* (Pers.) Lindl.
Rosaceae	S	*Rubus coriaceus* Poiret
Rosaceae	T	*Polylepis pauta* Hieron
Rosaceae	S-V	*Rubus nubigenus* Kunth
Solanaceae	S-T	*Solanum cf nutans* Ruiz & Pavon
Solanaceae	S-T	*Solanum stenophyllum* Dunal
Asteraceae	S-V	*Bacharis latifolia* / Eucharis sp.
Valerianaceae	S	*Valeriana microphylla* Kunth
Violaceae	S	*Viola* sp.

PTERIDOPHYTES	FERNS	
Blechnaceae	F	*Blechnum Loxense*
Dennstaedtiaceae	F	*Hypolepis bogotensis* H. Karst
Dryopteridaceae	F	*Elaphoglossum albescens*
Dryopteridaceae	F	*Elaphoglossum confusum*
Dryopteridaceae	F	*Elaphoglossum cuspidatum*
Dryopteridaceae	F	*Elaphoglossum ensiforme*
Dryopteridaceae	F	*Elaphoglossum lingua* (C. Presl.) Brack
Dryopteridaceae	F	*Elaphoglossum ovatum*
Dryopteridaceae	F	*Elaphoglossum rimbachii* (Sod.) Christ
Dryopteridaceae	F	*Elaphoglossum vulcanicum*
Dryopteridaceae	F	*Elaphoglossum* sp.1
Dryopteridaceae	F	*Elaphoglossum* sp.2
Equisetaceae	H	*Equisetum bogotense* Kunth
Hymenophyllaceae	F	*Hymenophylum myriocarpum*
Lycopodiaceae	F-M (Firmoss)	*Huperzia lindenii* (Spring) Trevis
Polypodiaceae	F	*Campyloneurum amphostenon*
Polypodiaceae	F	*Grammitis* sp.
Polypodiaceae	F	*Melpomene pilosissima*
Polypodiaceae	F	*Melpomene pseudonutans* H. Christ & Rosenti
Polypodiaceae	F	*Polypodium mindense*
Polypodiaceae	F	*Polypodium monosorum*
Polypodiaceae	F	*Terpsichore heteromorpha*
Polypodiaceae	F	*Terpsichore lanuginosa*
Polypodiaceae	F	*Terpsichore* sp.
Pteridaceae	F	*Jamesonia scammanae*
Pteridaceae	F	*Radiovittaria stipitata*
Thelypteridaceae	F	*Thelypteris retroflexa*

[1] Identification of plant specimen collections is based on the Catalogue of the Vascular Plants of Ecuador by Jørgensen and León -Yanez 1999)

[2] One specimen of each species collected has been deposited at the UGA herbarium (2008)

[3] Assistance with the identification of plant specimens was provided by: Henrik Balslev (AAU), Simon Lægaard (AAU), Susana León-Yánez (QCA), Hugo Navarrete (QCA) and Benjamin Øllgaard (AAU).