Holocene upper forest line dynamics in the Ecuadorian Andes: a multiproxy study
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2. Vegetation composition and altitudinal distribution of Andean rain forests in El Angel and Guandera reserves, northern Ecuador

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Marcela C. Moscol Olivera and Antoine M. Cleef

ABSTRACT

Patterns of vascular plant species composition and structure of the remaining rain forest of the Andean Cordillera in northern Ecuador were studied in two reserves: Guandera and El Angel. Thirty three plots located between 3300 and 3700 m were examined along two altitudinal transects crossing the Upper Forest Line (UFL). The phytosociological subdivision using TWINSPLAN revealed two communities for Guandera and five communities for El Angel on the basis of both floristic composition and percentage of cover. The distribution pattern of these forest communities clearly corresponds to a humidity gradient declining East to West from Guandera to El Angel. The high Andean and the Andean rain forest zones of Guandera were not floristically discernable by our analysis at the community level. The Guandera forest patches in páramo (3550-3700 m) are in terms of structure and floristic composition similar to the high Andean forest below the UFL (3600-3620 m), differing only at the level of variants. This indicates that the separation of the forest patch is relatively recent or that the forest patch was easily colonised by direct input from the high Andean forest located at ca. 50 m from the patch. No direct floristic affinity was detected between the forest types identified in our study area and 14 other forest sites of Colombia and Ecuador. The sharp and abrupt present-day UFL in Guandera (at 3640 m) is probably a consequence of frequent and extensive fires. All this suggests that the natural UFL was at slightly higher altitude in the undisturbed setting. In El Angel, the natural UFL as well as the high Andean forest have disappeared by clear cutting leading to a process of “paramización”. Thus the isolated asteraceous forest patches at 3740 m could not be compared to the high Andean forest stands in El Angel. The Andean forest patches in El Angel currently suffer from continuous wood extraction and are becoming depleted.

Key words: Upper Forest Line, Montane Rain Forest, (high) Andean rain forest, human impact, phytosociology, altitudinal zonation, Ecuador.

Abbreviations: DS = Diagnostic species; RUFLE = Reconstruction of Upper Forest Line in Ecuador; UFL = Upper Forest Line.
RESUMEN

Los patrones de composición florística y estructura de las plantas vasculares de los remanentes de bosques andinos en la Cordillera de los Andes del Norte del Ecuador fueron estudiados en dos reservas: Guandera y El Angel. Examinamos 33 parcelas ubicadas entre 3300 y 3700 m snm a lo largo de dos transectos altitudinales que cruzan el límite superior del bosque. La subdivisión fitosociológica usando TWINSPLAN reveló dos comunidades para Guandera y cinco comunidades para El Angel en base a su composición florística y porcentaje de cobertura. El patrón de distribución de estas comunidades boscosas corresponde claramente a un gradiente de humedad que declina del Este al Oeste de Guandera hacia El Angel. El Bosque Altoandino y el Bosque Andino en Guandera no pudieron ser separados florísticamente por nuestro análisis a nivel de comunidad. En Guandera, los parches de bosque en el páramo (3550-3700 m) son similares a las parcelas de bosque Altoandino justo debajo del límite superior del bosque (3600-3620 m) en cuanto a estructura y composición florística se refiere, difiriendo sólo a nivel de variantes. Esto indica que la separación del parche de bosque es relativamente reciente o que este parche fue fácilmente colonizado por la influencia del bosque Altoandino situado a aprox. 50 m. No se detectó afinidad florística directa entre bosques objeto del presente estudio y 14 otros lugares boscosos de Colombia y Ecuador. El nítido y abrupto límite superior del bosque actual en Guandera (a 3640 m) es probablemente una consecuencia de incendios frecuentes y extensos. Todo esto sugiere que el límite superior del bosque estuvo a una altitud ligeramente superior en condiciones de ausencia de intervención humana. En El Angel, el límite superior del bosque en condiciones naturales así como el bosque Altoandino han desaparecido por acción de la tala dando a lugar a un proceso de paramización. Por consiguiente, una comparación entre los parches de bosque de Asteráceas a 3740 m y el bosque Altoandino no pudo ser posible. Los parches de bosque Andino en El Angel son objeto de continua extracción de madera y están en vías de desaparición.

INTRODUCTION

Tropical rain forests contain the greatest biodiversity on Earth (World Conservation Monitoring Centre 1992; Heywood 1995). In this context, equatorial montane rain forests of the Andes are also among the most threatened of all habitats (Myers et al. 2000). Unfortunately, they are among the most poorly described habitats as well (Gentry 1995; Webster 1995).

According to Webster (1995), half of all species of the flora of Ecuador are found in the montane rain forests. While in Colombia estimates of the remaining primary montane rain forests range from 27% (Cavelier & Etter 1995) to less than 10% (Henderson et al. 1991), in Ecuador the process of deforestation has had even greater consequences. Official sources
report that montane forests in Ecuador have no more than 7% of their pristine habitat remaining (CENDES & CORMADERA 1991). Other studies of deforestation in Ecuador calculate even more alarming figures, indicating that due to the increasing human impact during last decades only 4% of the forests on the western Andean slope remains and almost nothing is left of natural forests of the Central Valley (Dodson & Gentry 1991). Apparently more conserved are the montane rain forests on the eastern slopes of the Andes (Lauer & Rafiqpoor 2002).

Many of the remaining large clusters of Ecuadorian montane rain forest are found in protected areas, such as Sangay National Park or Cayambe-Coca Ecological Reserve (Mena 1995). However, significant areas of montane rain forest also occur outside of protected areas and include zones such as the forests near El Angel Ecological Reserve and Guandera Biological Reserve in El Carchi Province. In order to achieve the conservation of these remaining areas there is an urgent need to gather information on the status of plants and habitats in such areas, so that conservation actions can be proposed. In this context, there have been several floristic and phytosociological studies about cool neotropical montane forests centered on the northernmost Andes (e.g. Cuatrecasas 1934, 1958; Gentry 1982a, 1982b, 1986a; Sugden 1982a, 1982b; Cleef et al. 1984; Huber 1986; Rangel-Ch. & Lozano 1989; Henderson et al. 1991; Rangel-Ch. et al. 2005; Cuello & Cleef 2009). However, quantitative studies of vascular plants of Andean forests in Ecuador are few (Grubb et al. 1963; Grubb & Whitmore 1966, 1967; Jørgensen 1991; Valencia & Jørgensen 1992; Madsen & Øllgaard 1994; Young & Keating 2001), especially those focusing on phytosociology (Bussmann 2001; Lauer et al. 2001).

This study is part of a larger research programme that focuses on the reconstruction of the upper forest line (UFL) in Ecuador. The main aim is to reconstruct the present-day altitudinal position of the UFL under natural conditions, and to improve our understanding about forest-páramo ecotones during the past three millennia.

Within this framework, a first reconstruction of the altitudinally shifting UFL during late Holocene time was published by Wille et al. (2002), and more detailed studies were undertaken (e.g. Moscol Olivera & Hooghiemstra, 2010). Finally, such increased understanding of the forest-páramo ecotone is crucial to make scientifically based decisions stating to which altitude reforestation efforts may be carried out. At present-day, tree plantations can be found in the páramo, which may be ecologically inexpedient situation if such páramo is above the natural UFL position. The research area of our programme is based in and around the El Angel Ecological Reserve and Guandera Biological Reserve in El Carchi Province. Unfortunately, for the specific area of El Carchi Province, no detailed description of the forest vegetation for scientific and conservation purposes has been published yet. Only a flora account exists with respect to the Guandera Reserve (Palacios & Tipaz 1996).

The current study was specifically designed to answer the following questions:
(1) What are the patterns of vascular plant species composition and structure in the study area according to differences along the altitudinal and humidity gradient? Are the high Andean and the Andean rain forest zones in the study area floristically discernable by our analysis? And, are forest patches in páramo floristically similar to the continuous forest below the UFL in terms of structure and floristic composition?

(2) Is there any floristic affinity between the forest types identified in our study area and those recorded in other sites in the equatorial Andes? How do they compare?

(3) What are the effects of human disturbance on the uppermost Andean rain forests of El Carchi?

(4) What is the evidence of the (potential) upper forest line (UFL) at both study sites in terms of structure and floristic composition?

The altitudinal range of 3300 to 3700 m has been sampled at both study sites in El Carchi Province along two altitudinal transects crossing the UFL. Here we report a first phytosociological approximation of the current Andean and high Andean rain forests based mainly on our field observations and on studies from elsewhere in the equatorial Andes. Furthermore, we explain possible determinants of forest patterns considering the importance of historical factors in addition to current environmental conditions.

Environmental conditions of the present-day UFL have been studied by Körner and co-workers mainly in Europe, but also in other parts of the world (Körner 1998, 2007; Körner & Paulsen 2004; Paulsen et al. 2000). However the record from equatorial UFLs is limited. Bader (2007) is most useful in the context of the present study.

METHODS

Study area

Among the last remaining montane rain forests in the Andes of northern Ecuador, two research locations were selected in El Carchi Province: Guandera Biological Reserve and El Angel Ecological Reserve including the adjacent Los Encinos Scientific Station, as well as their surrounding privately held areas with woody species cover (Fig. 1).

The study area is part of the sometimes called “global epicenter of biodiversity”, the biologically richest and most diverse of Earth’s biodiversity and hotspots (Mittermeier et al. 1998, Myers 1990). The montane forests in El Carchi Province are unusual in that they contain a high proportion of restricted range species (Borcksenius 1997) and are still habitat of singular and threatened fauna like the rare spectacled bear Tremarctos ornatus (Kattan et al. 2004).
Vegetation analysis of Andean rain forests in El Angel and Guandera

Fig. 1. Study area in northern Ecuador; relevant sites mentioned in the text are shown: (1) El Angel; (2) Guandera; (3) Papallacta; (4) San Francisco Reserve; (5) Puracé; (6) Valle de la China - Alto del Cóndor; (7) Parque Nacional Los Nevados; (8) Tatamá.
Precipitation in our study area is high all year round. However, Guandera receives almost twice the amount of annual precipitation El Angel does (annual means 1900 mm and 1000 mm, respectively).

Since there are no official meteorological stations currently operational in the study area, we based our climatic characterization on the existent maps from the Ministerio de Agricultura y Ganadería (MAG). Diurnal temperature fluctuations are strong, at least as experienced in Guandera (Fig. 2, Bader et al. 2007) while average temperatures are low and fluctuate little through the year.

![Image: Isohyetal map of the study area showing the humidity gradient between Guandera and El Angel. Numbers in bold indicate precipitation in mm/year. Based on the source map from the Ministerio de Agricultura y Ganadería (MAG).](image)

The predominant soils in the study area classified as Andosols (FAO 1998), soils formed in volcanic ash and typically rich in organic matter. Preliminary results characterizing soil properties in El Angel and Guandera (Tonneijck et al. 2006) show high levels of organic carbon for the A and B horizons (4-25%), low bulk densities (< 0.85 g/cm³, which is diagnostic) and acid to very acid pH values (3.2 - 4.9).
Vegetation analysis of Andean rain forests in El Angel and Guandera

Volcanic systems in Ecuador and Southern Colombia are part of the 'Northern Volcanic Zone', extending from 5ºN to 2ºS (Stern 2004). The northern part of the Ecuadorian Andes is covered by Cenozoic volcanic rocks (Hörmann & Pichler 1982). Those of the Western Cordillera belong to a calc-alkaline andesite-dacite series, while in the Eastern Cordillera they are members of the andesite-dacite-rhyodacite series (Hörmann & Pichler 1982; Stern 2004). The soil profiles in the study area were formed within three distinct tephra deposits of Holocene age (Tonneijck et al. 2008).

We base the names of the Andean forest zones used in this study on Cuatrecasas (1934, 1958), Acosta Solís (1968), Cleef et al. (1984), Cleef et al. (2003) and Rangel-Ch. et al. (2005). They correspond to the equatorial montane rain forest zonation by Grubb (1977). This author recognised three altitudinal montane rain forest on tropical mountains, e.g. the Lower Montane Rain Forest (LMRF), the Upper Montane Rain Forest (UMRF) and the Subalpine Rain Forest (SARF). In the northern Andes these forests are known as Subandean rain forest or ‘bosque subandino’, Andean rain forest or ‘bosque andino’ and high Andean rain forest or ‘bosque altoandino’ respectively, as initially defined by Cuatrecasas (1934; 1958).

**Guandera**

Guandera is a private reserve of the non-governmental organization (NGO) Jatun Sacha Foundation, located approximately 11 km east of San Gabriel in the Eastern Cordillera (Fig. 2). It encompasses complex natural habitats, predominantly high altitude grasslands or "páramo" (covering around 1000 ha) with *Espeletia pycnophylla* stem rosettes, and extensive areas of relatively intact Andean rain forest. The remaining forest (Andean forest and high Andean forest) on the western slope of Guandera is found between 3300 m and 3640 m. Below 3300 m, the area has been almost completely deforested for cattle and agriculture; mainly in the form of fenced meadows and potato cultivation. Above 3640 m, the prevailing bunchgrass páramo is interrupted occasionally by scattered forest islands occurring up to about 3700 m.

*Clusia flaviflora* trees dominate the Andean forest around 3500 m (Palacios & Tipaz 1996), while a fringe of high Andean forest extends above this level up to the lower limit of the páramo at about 3650 m.

In this paper, we use the general name ‘Guandera’ to refer to the reserve and its surrounding areas (buffer zone and privately held areas at the lowest part of the transect), while ‘Guandera Reserve’ indicates the protected area proper.

**El Angel**

Separated from Guandera Reserve by a fertile agricultural central valley, the El Angel Ecological Reserve is situated on the southern slopes of the volcanic basin El Voladero,
probably a caldera in the southern outliers of Volcano Chiles massif in the Western Cordillera. This reserve together with the adjacent Los Encinos Scientific Station cover approximately 16,000 ha of páramo characterised by *Espeletia pycnophylla* stem rosettes. For centuries and especially since the road El Angel-Tulcán was built, this area has been experiencing direct impacts from human activities. This includes the annual burning of several hectares of páramo, native vegetation clearing and conversion of land into agriculture, exploitation of forest products and cattle grazing. It is most likely that páramo now occurs in many areas that were once under natural high Andean rain forest and/or Andean rain forest (Ellenberg 1979, Lægaard 1992), a phenomenon known as ‘paramización’ (Verweij & Kok 1992, Hernández 1997, Van der Hammen 1998, Rangel-Ch. 2000, Hofstedte et al. 2002). The still extant forest in this area is present as patches (each patch being smaller than 7 ha) surrounded by páramo, on small hills or steep slopes located between 3300 and 3700 m.

In this study, we use the general name ‘El Angel’ to refer to the reserve and its surrounding areas (Los Encinos Scientific Station, the buffer zone and privately held areas at the lowest part of the transect), while ‘El Angel Reserve’ indicates the protected area proper.

**Site selection**

In each locality, a field survey was performed over the altitudinal range studied to select sites and subjectively define units differing visually in forest vegetation structure and composition, but having as much as possible a similar aspect and slope. In Guandera, the vegetation units selected were: forest patches at low altitude (approx. 3300 m), *Clusia* forest (approx. 3500 m), high Andean forest (approx. 3600 m) and forest patches at high altitude (between 3550 and 3700 m).

In El Angel, the following vegetation types were chosen to be sampled: forest patches at low altitude (approx. 3300 m), *Clethra* forest (approx. 3450 m), Asteraceae forest patch (approx. 3450 m) and forest patches at high altitude (between 3600 and 3700 m).

**Data collection**

We established three replicate 10 m x 50 m plots randomly located in every selected vegetation unit of homogeneous forest. The rectangular size plot was chosen because of the steep terrain. In the case of forest islands smaller than 500 m², the entire area was sampled (400 m² or less) avoiding the forest borders.

Following the guidelines by Van der Hammen et al. (1989), for every plot, a complete species list of vascular plants (and dominant bryophytes in some cases) was recorded along with their corresponding cover percentage for each species and each stratum, each stratum being defined by a predominant growth form and height. Quantitative records were made of altitude, slope and aspect. Estimates of percentage cover of bare soil, litter
thickness and maximum tree diameter (dbh) were also recorded. Additional information on human impact was documented by visual observations in situ or informal talks with various farmers and/or landowners living near the reserves.

Five forest strata or structural layers were taken into account: tree layer, grouping trees taller than 10 m; treelet layer, between 5 m and 10 m height; shrub layer, formed by species between 50 cm and 5 m tall, including some herbaceous plants; herb layer, referring to species between 10 cm and 50 cm tall, and ground layer, assembling all individuals under 10 cm height. The peripheral outline of the canopy of each species was taken as the basis for estimating cover percentages.

**Plant identification**

Voucher specimens (fertile when possible) of vascular plants, that could not be identified in the field, were collected under the number of the first author. Specimens were subsequently identified to species with the help of taxonomic keys and preserved plant collections housed at the Herbario Nacional del Ecuador (QCNE) and Herbario QCA of the Pontificia Universidad Católica del Ecuador, where the collected specimens are currently stored. A number of collections were not identified; mostly as a result of loss by flooding of the storage area. Nomenclature for vascular plants follows Jørgensen & León (1999). Dominant terrestrial bryophytes were recognised at genus level, as far as previous experience allowed for. They were not collected or studied in detail.

**Data analysis**

For our locations, the data of all plots (species and their percentage cover) were sorted and clustered according to the TWINSPAN computer package (Hill 1979), into final vegetation types.

The TWINSPAN arrangement was an important tool for a first grouping of forest types recognizing similarities and differences between relevés and forest types along the altitudinal transect and regionally between both transects. Then, following conventional phytosociological techniques, hand refinement was used to produce a final table with the conventional diagonal structure. Species occurring only once and having less than 3% of cover were omitted from the analysis, but listed at the base of Table 1.

The resulting vegetation types or plant communities were hierarchically ranked and described following the method of Zürich-Montpellier school, also called Braun-Blanquet approach (Westhoff & van der Maarel 1973). Because a small part of the plant collections were lost by the previously mentioned flooding of the storage, the community descriptions may lack (diagnostic) species. Therefore the community concept has been implemented; and vegetation classification following Weber et al. (2000) was not applied.

We used the term ‘diagnostic species’ (DS) instead of ‘character species’, because this is the first phytosociological study of montane rain forests in the region. We are unaware...
which vascular species are really exclusive. With respect to bryophyte species, plot sampling was not complete and therefore information as to diagnostic bryophyte species has to be used with care.

We compared the described montane forest types with forests documented elsewhere in the equatorial Andes in order to detect floristic affinities. We assembled a presence table containing 18 Andean forest sites distributed over 6 main geographical localities from Central Colombia to southern Ecuador. *Quercus* forests were excluded from this analysis because this taxon does not occur in Ecuador. The 18 Andean forest sites have been studied by Rangel-Ch. et al. (2005), Cuatrecasas (1934) Cleef et al. (2003), Rangel-Ch. & Franco (1985), Rangel-Ch. & Lozano (1986), Moscol Olivera & Cleef (this study), Lauer et al. (2001) and Bussmann (2002). The presence matrix was subjected to TWINSPAN (Hill 1979) with 4 cut levels. Bryophytes were not considered in the analysis except for *Sphagnum*, because they were not taken into account at each forest site. We included records with a relatively low number of taxa and/or species (e.g. Rangel-Ch. & Franco 1985, Rangel-Ch. & Lozano 1989) and in our own data we did not consider some species lacking complete identification. These facts may have an influence on the final results of the TWINSPAN analysis.

**RESULTS**

**Phytosociological analysis**

In total 33 Andean forest plots -15 from Guandera and 18 in El Angel- were used in this study.

TWINSPAN allowed to delineate seven forest communities (numbered 1 to 7), which clustered into three groups at the level of community group on the basis of both floristic composition and percentage of cover (Table 1). The Andean and high Andean rain forest communities of Guandera and El Angel are described below.

**Order group of *Blechnum schomburgkii-Weinmannia cochensis* Andean rain forest communities**

Grupo del orden de comunidades de bosque andino de *Blechnum schomburgkii* y *Weinmannia cochensis*

Table 1

**Physiognomy:** Humid Andean and high Andean rain forests with a well developed tree or treelet layer (canopy height varying between 5-8 m in high Andean to 25 m in Andean forest) and usually high levels of terrestrial and epiphytic bryophyte cover. Ferns and tree ferns are common.
Composition: DS in terms of abundance are the tree ferns *Blechnum schomburgkii* (transgr.) and *Dicksonia sellowiana* (transgr.) and the tree(-let) *Weinmannia cochenensis*. Other less frequent DS concerned: *Axinœa macrophylla*, *Clethra crispa*, *C. rotunda*, *Miconia bracteolata*, *Myrsina coriacea*, *Nertera granadensis*, *Oligactis cf. pichinchensis* and *Weinmannia auriculifera*.

Ecology and distribution: This order group of Andean forests comprises the Andean forest and high Andean forest types from 3300 to 3735 m altitude, where high humidity levels are maintained by frequent fog and precipitation.

The Andean rain forests of this order group are only known in our study area. In El Angel, the Andean forests of the *Blechnum schomburgkii - Weinmannia cochenensis* order group have almost entirely been destroyed by human activities. Only some forest areas are found distributed on and around the humid southwestern and western slopes of Guandera, as well as on the western slopes of El Angel, where they represent remnants of the more humid forests between 3450 m and 3735 m.

1. *Diplostephium rhododendroides - Gynoxys fuliginosa* high Andean dwarf forest Bosque alto-andino de *Diplostephium rhododendroides* y *Gynoxys fuliginosa*

Table 1, col. 1-3; Fig. 3; representative rel. 1

Physiognomy: Forest patches in páramo of low stature (5-7 m tall) with spherical dark green dense canopies. *Gynoxys fuliginosa* (maximum dbh up to 30 cm) is usually dominant. Only an occasional emergent tree could be observed (with cover <3%). Four well-defined layers are present: (1) treelet layer, up to 8 m height, ranging in cover from 10 to 30% ; (2) shrub layer, well developed, about 2-3 m height, covering between 55 and 80% of the area, (3) herb layer (including saplings), up to 1 m height, sparse to moderately dense, reaching up to 50% cover, and (4) ground layer (height <10 cm) consisting mostly of hygrophytic bryophytes, covering between 50 to 70% of the area.

Composition: DS are *Baccharis teindalensis*, *Brachyotum lindenii*, *Diplostephium rhododendroides*, *Solanum stenophyllum* and *Valeriana laurifolia*. Other DS include: *Fuchsia vulcanica* (transgr.) and *Gynoxys* sp. 2 (transgr.). Some 50 vascular species in total were recognised in these patches of dwarf forest. Quite a number of these DS were shared with the upper montane forests downslope in El Angel Reserve and surroundings (Table 1).

This dwarf forest type is documented by three relevés, which do not belong to one of both Andean forest community groups in El Angel, but could be ranked under the order group of *Blechnum schomburgkii - Weinmannia cochenensis* forests.

Ecology and distribution: The patches of asteraceous dwarf forest of this community are present at about 3740 m on the steep and high slopes of El Angel Reserve, especially in
the area surrounding El Voladero lakes and bogs. Here they only occur as small isolated dwarf forests in protected sites with favorable climatic and soil conditions in zonal *Espeletia- Calamagrostis* bunchgrass páramo.

**Fig. 3.** Extrazonal forest patches in El Voladero area of El Angel Reserve at 3750 m.
Table 1. Phytosociological classification of the forests in Guambinda and El Angel study areas, northern Ecuador.

<table>
<thead>
<tr>
<th>Order group</th>
<th>Community</th>
<th>Subcommunity</th>
<th>D. S. of Guambinda</th>
<th>D. S. of El Angel</th>
<th>Vascular flor.</th>
<th>Litter cover</th>
<th>Bare soil</th>
<th>Field nr. relevé</th>
<th>Column nr. relevé</th>
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</tbody>
</table>

**D. S. of Guambinda: community**

- *D. S. of Schefflera sodiroi - Weinmannia concinna communit*
  - *Miconia sp. 4*
  - *Epidendrum sp.* 3
  - *Monnina crassifolia
  - *Prunus rugosa*
  - *Polypodium*
  - *Vaccinium floribundu*

**D. S. of El Angel: community**

- *D. S. of Wejunsta punctatum*
  - *Miconia theaezan*
  - *Elleanthus*
  - *Gasteranthus*
  - *Pernettya prostrata*
  - *Gynoxys fuliginosa*

**D. S. of Schefflera sodiroi - Weinmannia concinna community**

- *Myrsine coriacea*
  - *Maxillaria*
  - *Gynoxys*
  - *Elaphoglossum*
  - *Diplostephium rh.*

**D. S. of Wejunsta punctatum**

- *Clethra crisp*
  - *Pieris japonica*
  - *Myrica rubra*
  - *Latecaea setigerca*

**D. S. of Vittaria**

- *Prunus laurocerasus*
  - *Vaccinium vitis-idaea*

**D. S. of Prunus laurocerasus**

- *Myrica rubra*
  - *Vaccinium vitis-idaea*
  - *Latecaea setigerca*

**D. S. of Myrica rubra**

- *Clethra crisp*
  - *Pieris japonica*

**D. S. of Latecaea setigerca**

- *Prunus laurocerasus*
  - *Vaccinium vitis-idaea*
  - *Myrica rubra*
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<th>Order group</th>
<th>Community group</th>
<th>Neocalamites acuminata - Clethra parallelinervia</th>
<th>Clethra ovalifolia</th>
<th>Diplostephium rh.</th>
<th>Pleurothallis sp. 1</th>
<th>Axinaea affinis</th>
<th>D.S. of Weinmannia pinnatifida subcommunity</th>
<th>D.S. of Guzmania bakeri subcommunity</th>
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- **Rows:**
  - Data representing the composition of subcommunities within each community group.
Vegetation analysis of Andean rain forests in El Angel and Guandera

*Disterigma acuminata* - *Clusia flaviflora* Andean rain forest community group

Grupo de comunidades de bosque andino de *Disterigma acuminata* y *Clusia flaviflora*

Table 1, col. 4-18

**Physiognomy:** Physiognomically similar to the Andean and high Andean forests of the *Blechnum-Weinmannia* order group.

**Composition:** DS for this community group include: *Axinaea affinis*, *Brunellia pauciflora*, *Disterigma acuminatum*, *Gaiadendron punctatum*, *Miconia corymbiformis*, *Neurolepis aristata* (transgr.), *Ocotea infrafoveolata*, *Oreopanax palamophyllus*, *Polypodium loriceum*, *Ribes* cf. *andicola*, *Symplocos quitensis* and *Weinmannia rollottii*.

This community group consists of two Andean forest communities: (1) *Schefflera sodiroi* - *Weinmannia cochensis* and (2) *Ilex colombiana* - *Clusia flaviflora*, described below.

Ecology and distribution: The forests of this community group are present in a permanently humid zone, with very frequent rain, cloudiness and fog. Epiphytism, specially of liverworts is most common, but also locally bromeliaceous epiphytes might determine the general appearance. The Andean and high Andean rain forests of this community group were found comprising the whole forest belt occurring currently on the humid southwestern and western slopes of Guandera, between the agricultural land (presumably formerly forested area) below 3300 m and the páramo areas above 3650 to 3700 m. Forests of this community group are also expected to occur elsewhere in northern Ecuador. *Clusia flaviflora* has a range between northern Ecuador and Bolivia (Missouri Botanical Garden’s nomenclatural database w3 Tropicos).

2. *Schefflera sodiroi*-Weinmannia cochensis Andean rain forest community

Comunidad de Bosque andino de *Schefflera sodiroi* y *Weinmannia cochensis*

Table 1, col. 4-7; representative rel. 4

**Physiognomy:** Humid and frequently clouded Andean forest recovering after selective felling, with trees up to 10 m in the lower part of the area and up to 15 m in the area below the *Clusia flaviflora* dominated forest. Five distinct well-defined structural layers include: (1) tree layer, covering up to 20% and consisting of a mixture of woody species (maximum dbh of 22 cm), only in the zone above 3350 m, (2) treelet layer, up to 9 m tall; the majority of the arboreal species (reaching 80% of cover) is represented, (3) generally dense shrub layer (up to 3 m tall) with *Blechnum* tree ferns, (4) herb layer, up to 1 m height, with a variable cover ranging from 20 to 50%, and (5) ground layer (up to 5 cm) comprising mostly terrestrial bryophytes covering up to 20% of the area.

**Composition:** *Clusia flaviflora* is less common than in the other forest community of this forest community group. The number of canopy tree species amounts up to 10. DS are *Anthurium pulchrum*, *Brunellia tomentosa* (rare), *Chusquea lehmannii*, *Gasteranthus* cf.
ecuadorensis, and Schefflera sodiroi. Clethra revoluta, Ilex andicola, Myrsine coriacea, Prunus rugosa were DS in the lowermost forests of this community (3300-3350 m). Brunellia pauciflora and a páramo invader, Paspalum bonplandianum, are DS for the uppermost forests.

Other diagnostic features concern the high cover values of Myrsine coriacea and Weinmannia rollottii and the absence (or very low cover values) of e.g. Hedysosmum cumbalense, Mikania stuebeli, Myrsine andina and Oreopanax seemannianus. Rubus nubigenus and Pernettya prostrata were commonly found in lower strata. Baccharis latifolia shrub (a species usually associated to disturbance) was also present.

Four relevés document this Andean forest community.

**Ecology and distribution:** These undisturbed forests were more diverse in species and more complex in layering in comparison to upslope forest communities, even when they were recovering from recent disturbance (felling), and might remain only as patches at lower altitudes. The litter layer is well developed and both vascular and bryophyte epiphytes, are a common feature.

Andean rain forests of this community are found on the steep and humid western to southwestern slopes of Guandera, between 3300 m (location of Jatun Sacha station) and 3450 m. Downslope are agricultural lands. This Andean forest type is only known from the Guandera Reserve and its buffer zone.

### 3. Ilex colombiana-Clusia flaviflora Andean rain forest community

**Comunidad de bosque andino de Ilex colombiana y Clusia flaviflora**

Table 1, col. 8-18; Fig. 4; representative rel. 12

**Physiognomy:** Andean rain forest with a canopy height up to 25 m. Included are the high elevation contiguous forests as well as forest patches in páramo, both sharing the presence of Clusia flaviflora and the predominance of Ilex colombiana, accounting for up to 60% of the tree cover. Striking epiphytism is displayed by bromeliads, orchids, ferns, and mosses.

Commonly, five structural layers are present: (1) high tree layer (closed canopy), covering up to 120% (due to crown overlap) and usually dominated by Clusia flaviflora and Ilex colombiana (both with an average dbh of 30 cm, maximum dbh up to 95 cm); (2) treelet layer, up to 10 m height, covering up to 20%; (3) shrub layer, moderately dense, with varying cover of 15 - 25% and about 1-2 m height, (4) herb layer with a height up to 50 (-100) cm, dense to moderately dense, attaining up to 80% cover, mainly composed by terrestrial bromeliaceous rosettes or ferns; and (5) ground layer (under 10 cm) with a variable cover from 10 to 40%, including bryophytes and other vascular indicators of moisture and shadow.
Composition: This Andean forest community was characterised by the high cover of *Clusia flaviflora* (transgr.) and *Ilex colombiana* (exclusive in Table 1), both codominant canopy species. Other DS include: *Desfontainia spinosa*, *Disterigma alaternoides* (exclusive), *Guzmania bakeri*, *Miconia chlorocarpa* and *M. theaezans*. Two subcommunities have been recognised on basis of the floristic composition and abundance: (1) *Guzmania bakeri* and (2) *Galadendron punctatum*.

Ecology and distribution: The rain forests belonging to this Andean forest community have only been found on the western slopes of Guandera Reserve, between 3500 to 3700 m. They constitute the uppermost forest belt in this area and comprise also the isolated forest patches above the UFL. Litter layers under these forests are of impressive thickness and form part of black humic soils on top of a mineral profile. The majority of composing woody plants are found to possess hard leaves, which form a thick ectorganic layer as they decompose slowly (Nierop et al. 2007).

*Clusia flaviflora* dominated forests are reported to occur on restricted crests of the Western Cordillera in the area of Cotocachi-Cayapas Ecological Reserve, Imbabura Province, northern Ecuador (Rodríguez et al. 1994) as well as on the watershed of Paute river, southern Ecuador (Minga et al. unpublished data). *Clusia flaviflora* is more widespread in the tropical humid Andes, being reported from mixed forests on the Eastern Cordillera of La Paz department, Bolivia (Paniagua-Zambrana et al. 2003) and the Yungas of west-central Bolivia (Araujo-Murakami et al. 2006).

![Fig. 4. Guandera Reserve - view on the Ilex colombiana - Clusia flaviflora community.](image-url)
*Ilex colombiana-Clusia flaviflora* Andean rain forest community

3.1. *Guzmania bakeri* subcommunity

**Subcomunidad de *Guzmania bakeri***
Table 1, col. 13-18; Fig. 5; representative rel. 17

**Physiognomy:** *Clusia flaviflora* (80-100% cover) is the prominent species in the canopy layer, represented by 20 to 25 (35) m tall and 50 to 95 (235) cm dbh trees, the oldest in the area. Epiphyte cover on tree trunks was also the highest in forests of this subcommunity. Striking was the bromeliaceous rosette *Guzmania bakeri*, usually dominating the herb layer, with cover values ranging from 8 to 80%. This species was also abundant as an epiphyte. For other physiognomic characteristics see further the *Ilex-Clusia* Andean forest community.

**Composition:** DS are: *Guzmania bakeri*, *Miconia chlorocarpa*, *M. ochracea* and also *Weinmannia rollottii* (transgr.).

**Ecology and distribution:** In terms of habit and composition, the epiphyte communities in the Andean forests of this subcommunity, indicate particularly high and rather permanent humid conditions.

*Fig. 5.* Interior of the *Clusia flaviflora* dominated forest - Guandera Reserve 3520 m.
The Andean rain forests of this subcommunity are only represented at altitudes between 3500 and 3520 m on the western slopes of Guandera Reserve.

**Ilex colombiana-Clusia flaviflora Andean rain forest community**

### 3.2 Gaiadendron punctatum subcommunity

**Subcomunidad de Gaiadendron punctatum**

Table 1, col. 8-12; Fig. 6; representative rel. 8

**Physiognomy:** Ecotonic forest of low stature (height up to 16 m) and dbh up to 35 cm. This subcommunity includes the zone of dense and sometimes almost impenetrable high Andean rain forest or ‘bosque altoandino’ occurring above the *Clusia* dominated forest and just below the open páramo. The so-called ‘forest islands’ or forest patches in the páramo zone belong to this vegetation type as well. Canopies are frequently contracted and spherical shaped. The small leaf size of woody species varies from microphyllous to nanophyllous along the Guandera transect.

![Fig. 6. High Andean rain forest in Guandera Reserve next to the páramo and the Upper Forest Line at 3640 m.](image)

**Composition:** DS are: Asteraceae sp. 13, *Disterigma alaternoides*, the parasitic tree *Gaiadendron punctatum* (also occurring as seedlings in the adjacent páramo), *Thibaudia parvifolia* and the climbing parasitic shrub *Tristerix longibracteatus*. This subcommunity includes high Andean forests and related forest patches in páramo, each of them being differentiated as variants. However, more relevés are needed to confirm the floristic differences between both habitats (Table 1).
Ecology and distribution: high Andean forests of *Gaiadendron punctatum* subcommunity are found spanning altitudes between 3550 and 3700 m, usually on steep slopes with an inclination of 10° to 20° on the western side of Guandera Reserve.

**Grosvenoria rimbachii-Clethra crispa Andean forest community group**

Grupo de comunidades de bosque Andino con *Grosvenoria rimbachii* y *Clethra crispa*

Table 1; col. 19-25

**Physiognomy:** Similar to the order group, but with a lower terrestrial and epiphytic bryophyte cover and lower tree layer’s height usually not as high as for the forests of *Disterigma acuminata* - *Clusia flaviflora* Andean forest community group. Emergent trees attain up to 25 m in height, but mean canopy height is about 12 m.

**Composition:** DS are *Clethra crispa* and *Grosvenoria rimbachii* in the tree layer. At least 33 species are in common with the isolated *Diplostomium rhododenroides-Gynoxys fuliginosa* community dwarf forests, which were provisionally not ranked under this Andean forest community group but directly under the order group referred to above. This community group comprises two Andean forest communities: (1) *Weinmannia lenticifolia* - *Clethra crispa* and (2) *Weinmannia pinnata* - *Clethra crispa*, which are described below.

Ecology and distribution: Atmospheric humidity appeared to be less prominent in El Angel Andean forests than in those of the *Disterigma-Clusia* community group limited to Guandera.

The rain forests of this Andean forest community group were the tallest recorded in the Guandera and El Angel study area. They contain valuable timber such as *Clethra crispa* and species of *Weinmannia*. Along the present-day UFL in El Angel tree felling and extraction was observed to be a common practice.

The Andean rain forests of this community group are generally found between 3450 and 3575 m on the steep northwestern slopes of El Angel.

4. **Weinmannia lenticifolia-Clethra crispa Andean forest community**

Comunidad de bosque andino de *Weinmannia lenticifolia* y *Clethra crispa*

Table 1, col. 19-22; representative rel. 20.

**Physiognomy:** A dense, up to about 20 (-23) m tall forest, with basically the same physiognomy as described for the Andean forests of the *Grosvenoria rimbachii - Clethra crispa* community group. Trunk diameters average 25 cm dbh but the largest recorded was 90 cm. Very high levels of crown overlap characterise the canopy.

Structurally, five strata are recognised: (1) dense tree layer with variable cover (moderate to very high), attaining up to 150% (due to crown overlap) when dominated by big crowns of *Weinmannia cochensis* (average dbh of 10 cm, maximum dbh of 85 cm); (2) treelet layer, up to 8 m in height, more variable than the previous layer in terms of cover (ranging
from 10% to about 150% cover); (3) shrub layer, covering 20-35% and a height of about 2-4 m; (4) herb layer, up to 1 m height, moderately dense to sparse, attaining up to 55% cover, and (5) ground layer (under 10 cm) consisting mostly of hygrophytic bryophytes, with a variable cover ranging from 10 to 50%.

**Composition:** The highest diversity of *Weinmannia* species (7 in this community; 10 in total) is recorded in the study area. DS include: *Clethra parallelinervia*, *Dioscorea glandulosa*, *Diplazium* sp. 2, *Elaphoglossum* sp. 9, *Gaultheria reticulata*, *Rubus adenotrichos*, *Weinmannia fagaroides*, *W. lenticifolia* and *W. mariquitae*. DS against the *Weinmannia pinnata-Clethra crispa* are: *Blechnum schomburgkii*, *Clethra revoluta*, *Diplostephium glandulosum*, *D. rhododendroides*, *Escallonia myrtilloides*, *Fuchsia vulcanica*, *Gaultheria glomerata*, *Gynoxys buxifolia* and *Munnozia jussieui*. The isolated dwarf forest patches of *Diplostephium rhododendroides-Gynoxys fuliginosa* around El Voladero lakes share quite a number of species with the forests of this Andean community. Indeed the floristic distance between them was the shortest of all other forest types studied in El Angel Reserve.

**Ecology and distribution:** A true dwarf high Andean forest (as transition to grasspáramo) has not been observed near the Los Encinos Scientific Station, but the existence of some surviving patches of this forest could not be rejected. In this forest type less moisture was observed than in the forests of Guandera, but slightly more than in the forest remnants along the road close to the small town of El Angel.

The Andean rain forests of *Weinmannia lenticifolia-Clethra crispa* community are situated between ca. 3500 and 3575 m as forest patches in páramo on the northwestern to northeastern slopes of the buffer zone of El Angel Reserve, in part in the protected area of Los Encinos Scientific Station. They are situated close to the páramo, mostly in an impoverished type of *Espeletia pycnophylla-Calamagrostis effusa* bunchgrassland (Moscol Olivera & Cleef 2009a).

### 5. *Weinmannia pinnata-Clethra crispa* Andean forest community

**Comunidad de bosque andino de Weinmannia pinnata y Clethra crispa**

Table 1, col. 23-25; Fig. 7; representative rel. 24

**Physiognomy:** Physiognomically similar to the previous Andean forest community of the same *Grosveneria rimbachii-Clethra crispa* community group in terms of layer’s height, dbh, density and epiphytic cover. The height (up to 25 m) of the canopy of the forest of *Weinmannia pinnata-Clethra crispa* community made it markedly different from other forests at the same elevation. Usually, the forests are made up of four layers: (1) tree layer showing incomplete canopy closure (25-75%), composed of *Clethra crispa* (emerging conspicuously), *Hedysorum cumbalense* and *Miconia bracteolata* as dominant species (maximum dbh of 45 cm); the heliophytic shrub *Macleania rupestris*, co-dominant in this stratum and leaning on adjacent shrubs and trees for support; (2) treelet layer, up to 9 m
height, with low to moderate crown overlap, varying in cover from 15% to 85%; (3) shrub layer (cover up to 20%) consisting mainly of saplings of the dominant canopy species as well as a few individuals of *Vallea stipularis* attaining here their uppermost altitudinal limit for the study area; (4) herb layer, up to 1 m in height, combining commonly shade preferring herbs like *Anthurium* sp. 2 and the bromeliad ground rosette *Greigia* sp. 2 with individuals of *Macleania rupestris* and *Clethra revoluta* in their very early successional stages; (5) ground layer (under 10 cm height) generally consisting of bryophytes; their cover is between 15 to 30%. The litter layer is well developed, covering up to 70% of the ground surface.

**Composition:** DS (almost exclusive in Table 1) include: *Viburnum triphyllum*, *Weinmannia multijuga*, *W. pinnata* and *W.* sp. 4. DS against the former former Andean forest community are *Blechnum auratum*, *Berberis pichinchensis*, *Calceolaria gossypina*, *Hackelia revoluta*, *Miconia bracteolata*, *Rubus nubigenus*, *Sessea crassivenosa* and *Vallea stipularis*.

*Fig. 7.* Forest remnant in El Angel Reserve at 3450 m, representing the *Weinmannia pinnata* - *Clethra crispa* community.

**Ecology and distribution:** The forests of this community represent the last remnants of a severely disturbed mature rain forest at 3450 m. Access to El Angel Reserve is easy and its buffer zone remains ineffectively protected for the purposes of biodiversity conservation. Thus, the extraction of wood as firewood and as construction material by the local population was observed to be a common practice. Consequently, the trees display low dbh in average, with a single emergent tree left.
Different successional stages are frequently present. Cut trunks, paths and tracks are found throughout the forest remnants. Andean rain forests of this community are present only as small fragments covering hills surrounded by páramo at ca. 3450 m on the northern and northwestern slopes of El Angel Reserve buffer zone. This forest community has not been reported anywhere else before.

*Brachyotum ledifolium*-*Vallea stipularis* Andean forest community group

*Grupo de comunidades de bosque andino de Brachyotum ledifolium y Vallea stipularis*

Table 1, col. 26-33

**Physiognomy:** The Andean rain forests of this community group are conspicuously low in stature (up to 12 m) and do not display a well-developed canopy structure. Coverage of epiphytic bryophytes is low to intermediate (35 - 50%); vascular epiphytes are almost absent. Climbers are rare as well. Trunks in these secondary forests are usually thin, reaching no more than 20 cm of dbh (exceptionally 40 cm). The ground floor mainly consists of dessication-tolerant species and the cover is very limited to moderate, attaining a maximum of 20%. The Andean forests of this community group, when dominated by Asteraceae (species of *Diplostephium* and *Gynoxys*), are easily distinguished as their crowns had a tendency to be grayish to grayish-green due to the whitish hairs covering their foliage.

**Composition:** Species richness is relatively low in comparison to the other more humid upper Andean rain forests of the El Angel-Guanda area. Diagnostic is the high presence of the following species: *Bomarea multiflora, Brachyotum ledifolium, Escallonia myrtilloides, Gynoxys buxifolia, Hesperomeles obtusifolia, Llerasia hypoleuca, Monnina pseudopilosa, Pernettya prostrata, Rubus nubigenus and Vallea stipularis*. Most of these species are transgressive but have higher presence and/or cover in this community group. Also DS with lower presence are: *Baccharis latifolia, Gynoxys hallii, Peperomia saligna* and *Valeriana hirtella*.

This Andean forest community group includes two communities: (1) *Blechnum auratum - Diplolomphium floribundum* (with two variants) and (2) *Otholobium mexicanum – Vallea stipularis* and has yet to be ranked to an order group.

**Ecology and distribution:** Human intervention (cutting, clearing for arable land, etc.) is much more common in the lower part of the transect, as the local population of the Central Valley just below the limit of El Angel Reserve bases its economy on agricultural and cattle production (López Sandoval 2004). The forest remnants are composed of different successional phases. Successional dynamics are strongly displayed in these stands also because of past and present cutting and/or extraction. We observed slender stems and low height in some of the forest stands, usual characteristics of forest recovery after clear cutting.
The forests belonging to this community group occur at altitudes between 3300 m and 3450 m, as isolated stands on steep slopes (up to 20º), between cultivated agricultural land or pastures, and the páramo. They represent the Andean forest type at lowest elevation in El Angel. They are only reported from the lowest part of El Angel Reserve buffer zone and the Central Valley next to it.

6. **Blechnum auratum-Diplostephium floribundum** Andean forest community

Table 1, col. 26-30; representative rel. 27

**Physiognomy:** High Andean dwarf forests of low stature (up to 12 m height), usually with characteristic grayish and spherical canopies. The maximum dbh attains 40 cm, but most of the thickest trees do not exceed 25 cm of dbh. This dwarf forest community is dominated by Asteraceae (mostly species of *Diplostephium* and *Gynoxys*). There are also small forest fragments in páramo, located near the forests of the *Weinmannia pinnata-Clethra crispa* community.

**Composition:** DS include: *Blechnum auratum*, *Diplostephium floribundum* (transgr.), *Miconia jahnii*, *M. salicifolia*, *Monnina pseudopilosa* (transgr.), *Rubus nubigenus* (transgr.), *Ribes ecuadorense*, *Berberis pichinchensis* and *Valeriana microphylla*. *Diplostephium floribundum* is a DS at the class level (class not formally described), and attains the highest cover in the forests of this community.

Two variants are present: (1) *Cybianthus marginatus* (rel. Moscol 127, 129, 130) and (2) *Hesperomeles ferruginea* (rel. Moscol 48, 91), which need more relevés to be fully described.

**Ecology and distribution:** This dwarf high Andean forest is situated in a wide valley, occupied in its lowest part by low asteraceous forest (species of *Diplostephium* and *Gynoxys*) on humid ground. The forest plots of this community are transitional (gradient of edaphic humidity) to the lowermost asteraceous stand on very humid ground. The community has much affinity with the previous one of *Weinmannia pinnata-Clethra crispa*, as evidenced by the high number of shared species.

The relevés of the *Blechnum auratum-Diplostephium floribundum* high Andean dwarf forest are situated around 3450 m, near the first guard post of El Angel Reserve driving upslope from the town of El Angel.

7. **Otholobium mexicanum-Vallea stipularis** Andean forest community

Table 1, col. 31-33; representative rel. 32
Physiognomy: Patches of low height forest on very steep slopes between (less sloping) agricultural land. The forest was generally between 5-8 m in height. Old stumps of thick stems have remained on the forest floor pointing to selective cutting and wood extraction of the biggest stems. In general the successional forest is dense, with branches close to the steep sloping surface. The dry litter layer is limited in thickness and cover.

Composition: DS are: *Aegiphila ferruginea*, *Badilloa salicina*, *Cornus peruviana*, *Miconia papillosa*, *Otholobium mexicanum*, *Oreopanax ecuadorensis*, *Piper barbatum*, *P. andreanum*, *Tournefortia scabra* and *Viburnum hallii*. *Vallea stipularis* was diagnostic by its high cover (as compared to the previous community). *Coriaria ruscifolia*, *Columellia oblonga*, *Lamourouxia virgata* and *Phytolacca bogotensis*, are frequent after disturbance. The forest remnants of this community are mostly in stages of succession with occasionally a single old remnant emerging tree. There is weak floristic affinity with the humid forests of the order group of *Blechnum-Weinmannia cochensis* (Table 1).

Ecology and distribution: For the forests of this community, steepness of the terrain was frequently more than 20° and runoff was seen quickly discharging to the stream below. The dry litter layer found was a signal of drier atmospheric conditions. The Andean forest patches of the *Otholobium mexicanum-Vallea stipularis* community are only found at 3300 m on the steepest habitats of the agricultural landscape near the town of El Angel, along the road to Tulcán.

Summarizing, general floristic patterns documented by Table 1 concern the predominance of *Weinmannia cochensis* at canopy level, *Blechnum* treeferns, *Macleania rupestris* and *Miconia tinifolia* in the shrub layer and a wealth of ferns and orchids as epiphytes and in the ground layer. This pattern is characteristic for the order group of the most humid upper montane forests. In Guandera, the most humid Andean forests show predominance of *Clusia flaviflora* and *Ilex colombiana* at canopy level. In the shrub layer are common: *Disterigma acuminatum* (also attached to stems and canopy climbing), *Neurolepis* sp. and more diversity of *Oreopanax* species in subcanopy or canopy. Bromeliaceous rosettes of *Guzmania bakeri* occur in the ground layer and as epiphytes. As natural in these cool and humid Andean forests, bryophyte cover is prominent at ground level, covering trees up to 4-5 m. Liverwort species are the most important group in terms of cover and biomass. This pattern is also consistent in the other forests except in the drier forests close to the town of El Angel with a limited bryophyte cover.

On the southernmost slopes of Volcano Chiles, South of El Voladero lakes, *Clethra crispa* is the leading species at canopy level in the forest of Los Encinos Scientific Station and in El Angel Reserve. Here the highest diversity of *Weinmannia* species is also recorded (up to 9 species versus 2 species in the more humid Guandera forests). *Hedyosmum cumbalense* and *Oreopanax seemannii* are prominent subcanopy trees associated with the shrub
Grosvenoria rimbachii. This assemblage corresponds to the community group of *Grosvenoria-Clethra crispa*.

The drier Andean forest remains near the town of El Angel stand out by the prominent presence of *Vallea stipularis* and *Diplostephium floribundum* in the tree layer, *Baccharis macrantha* and *Hesperomeles obtusifolia* in the subcanopy layer, *Brachyotum ledifolium* and *Otholobium mexicanum* in the shrub layer and a species of *Galium* prominent in the ground layer.

**DISCUSSION**

**Limitations of the methods**

The final phytosociological ranking of the Andean forests and high Andean forests of the Guandera-El Angel study area resulted in one order group (*Blechnum schomburgkii-Weinmannia cochensis*), three community groups and seven communities (Table 2). The forest remnants along the road from the town of El Angel close to the first guard post of El Angel Reserve, at 3450 m belong to another community group including two different communities.

We did not formally describe a class group, because we are uncertain about the delimitation. Possible DS for the class group are the species headed in importance of cover and presence by *Miconia tinifolia* (Table 1). A problem is that the last described *Otholobium-Vallea* community is not part of this supposed class group. A follow-up vegetation survey in the region is needed to provide more regional detail and hopefully a satisfactory classification up to class level. On the other hand it may be possible as well (and likely more realistic) to expect that the *Blechnum-Weinmannia cochensis* order group will belong to a forest class covering Andean forests on the moderately humid to very humid slopes of the equatorial Andes in northern Ecuador and southern Colombia.

The vegetation was described on the basis of a low number of relevés. The plots also were the same as those in the Ecoandes transects in Colombia, i.e. 500 m$^2$ (Cleef et al. 1984, Cleef et al. 2003, Rangel-Ch. et al. 2005, Cleef et al. 2008). Measurements of minimum plot size taken by Bussmann (2001, 2002) in floristically much richer montane rain forests in San Francisco Reserve / Zamora-Chinchipe (southern Ecuador) resulted in lower surface values than expected for minimum areas: 64 m$^2$ for Andean forest including high Andean forest. However, we assume that the forest patterns described in this paper are already sufficiently visible.
**Table 2.** Overview of hierarchical forest communities of Guandera and El Angel, northern Ecuador.

<table>
<thead>
<tr>
<th>Forest Community Group</th>
<th>Species Combinations</th>
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<tr>
<td><strong>Blechnum schomburgkii-Weinmannia cochensis ORDER GROUP OF ANDEAN RAIN FOREST COMMUNITIES</strong></td>
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<tr>
<td>1. <em>Diplostephium rhododendroides</em> - <em>Gynoxys fuliginosa</em> high Andean dwarf forest community</td>
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<tr>
<td><strong>Disterigma acuminata - Clusia flaviflora</strong> ANDEAN RAIN FOREST COMMUNITY GROUP</td>
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<td>2. <em>Schefflera sodiroi</em> - <em>Weinmannia cochensis</em> Andean rain forest community</td>
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<td>3. <em>Ilex colombiana</em> - <em>Clusia flaviflora</em> Andean rain forest community</td>
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<td>3.1 <em>Guzmania bakeri</em> subcommunity</td>
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<td>3.2 <em>Gaiadedron punctatum</em> subcommunity</td>
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<tr>
<td><strong>Grosvenoria rimbachii - Clethra crispa</strong> ANDEAN RAIN FOREST COMMUNITY GROUP</td>
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<td>4. <em>Weinmannia lenticifolia</em> - <em>Clethra crispa</em> Andean forest community</td>
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<td>5. <em>Weinmannia pinnata</em> - <em>Clethra crispa</em> Andean forest community</td>
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<td><strong>Brachyotum ledifolium - Vallea stipularis</strong> ANDEAN FOREST COMMUNITY GROUP</td>
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<tr>
<td>6. <em>Blechnum auratum</em> - <em>Diplostephium floribundum</em> Andean forest community</td>
<td></td>
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<tr>
<td>7. <em>Otholobium mexicanum</em> - <em>Vallea stipularis</em> Andean forest community</td>
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</table>

**General patterns of Andean forest composition along environmental gradients: Guandera vs. El Angel.**

From the seven new phytosociological communities recorded in this study, we found only two Andean forest communities in the Guandera transect. The lowermost one is the *Schefflera sodiroi-Weinmannia cochensis* Andean forest community, which lowest border adjoins the current agricultural land at 3300 m and therefore is under influence of human disturbance. The border between this forest community and *Ilex colombiana - Clusia flaviflora* forest community is near 3450 m, expanding upslope and still showing the floristic aspect and patterns of a pristine forest habitat at this altitude.

In El Angel, Andean forest communities with species of *Weinmannia* and *Clethra crispa* (*Grosvenoria-Clethra crispa* community group) constitute the uppermost forests in the studied transect. They are subdivided into two communities: (1) *Weinmannia lenticifolia-Clethra crispa* and (2) *Weinmannia pinnata-Clethra crispa*. The border between both forest communities is estimated at about 3500 m. Floristic differences between both communities can be attributed to altitude (equivalent with mean annual temperature), but
perhaps also to the location of the sampling place as *Weinmannia pinnata-Clethra crispa* forest has been sampled some kilometers to the West near the first guard post of El Angel Reserve, which implies more human impact. The lowest patches of *Otholobium-Vallea* Andean forest at 3300 m are near the town of El Angel. The highest distribution of this forest type is assumed at or near 3400 m.

Interesting is the observation that the arrangement of the forest types in Table 1 also corresponds to a humidity gradient from humid forests close to the Amazon Basin (Guandera) to medium humidity in the forests of Los Encinos (below El Voladero lakes), and lower humidity at the first guard post of El Angel Reserve (3450 m) and the rather dry forest remnants with *Vallea stipularis* at 3300 m directly above the town of El Angel. This corresponds to a gradient of the annual precipitation mean of 1700-1900 mm near Guandera to 1000-1250 mm near El Angel between 3300-3500 m (Fig. 2). Without doubt high humidity levels (also caused by vertical precipitation and water input by fog) are reflected in the humid forests of the *Blechnum-Weinmannia cochensis* order group.

The westernmost border of the humid upper montane forests is located between Los Encinos rain forests and those of the first guard post above the town of El Angel. The forests of the last mentioned locality at 3450 m, and those close to El Angel town at 3300 m, belong to the same community group (Brachyotum ledifolium-Vallea stipularis). On the basis of the relevés of Table 1 higher level communities could not be recognised; for such purpose more regional relevés would need to be collected in the surroundings of El Angel town, which was beyond the scope of the present study. The Andean forests in El Angel anyway are drier along this E-W humidity gradient with an estimated 30-50% less yearly precipitation than in Guandera.

Comparing Guandera and El Angel transects, there is a striking similarity in altitudinal borders between the different forest types. However, diversity of Andean forest types is slightly larger in El Angel transect: 3 communities vs. 2 in Guandera (Table 1).

In Guandera, we found that high Andean forest is part of the humid Andean forest zone represented by the *Disterigma-Clusia flaviflora* community group and the *Blechnum-Weinmannia cochensis* order group. We did not find many arguments in the present analysis to define a proper high Andean forest community: the subcommunity of *Gaiadendron punctatum* is part of the uppermost *Ilex-Clusia flaviflora* Andean forest community. In most of the cases previously studied high Andean forest constitutes a proper community at the association level (e.g. Bußmann 2002, Cleef et al. 1984, Cleef et al. 2003, Rangel-Ch. et al. 2005).

The high Andean forest may be considered as a subzone of the Andean forest zone because the floristic composition (Cuatrecasas 1934, 1958; Van der Hammen 1984, 2003, 2005, 2008) and ecosystem processes such as nutrient cycling and decomposition (Grubb, 1977), syndromes of pollination and seed dispersal (Cuello 2010) are rather similar. Near
the UFL, forest structure or height, is markedly lower and some tree species (*Diplostephium rhododendroides*, *Gynoxys fuliginosa*, *Gaiadendron punctatum*) are better adapted to cold and changes in UFL position and are dominant or codominant. Sometimes the border between high Andean forest and Andean forest is really sharp (Cuatrecasas 1934, Cleef et al. 1984, Cleef et al. 2003, Rangel-Ch. et al. 2005) and easily mapped (Kloosterman et al. 2003), occasionally is it also gradual.

The floristic affinity between the high Andean forest plots in Guandera and the forest patches in the páramo is highly significant to the point that they only differ at the level of variants. This indicates that the separation of the forest patch is relatively recent, estimated during the last hundreds of years, or that the forest patch was easily colonised just by input from the high Andean forest at close distance.

The isolated dwarf forest patches near El Voladero lakes in El Angel páramo possibly experienced a longer separation. Their floristic affinity is based on 33 species shared with the Andean forests downslope, mainly those of the *Weinmannia lentiscifolia-Clethra crispa* Andean forest community. However, more affinity is to be expected with the high Andean forests downslope. High Andean forest stands have not been found at lower altitude. This is the result of long lasting patch-like logging and finally complete deforestation. As a follow-up the process of “paramización” allows for the establishment of a *Espeletia pycnophylla* bunchgrass páramo (Moscol Olivera & Cleef, 2009).

**An interregional comparison with other forests in the equatorial Andes**

In order to elucidate the phytosociological position of the community groups of Andean forests defined for the Guandera and El Angel study area, an interregional comparison was made. In total we gathered the presence values of over 900 species in a presence matrix. The species number was reduced to an input of over 600 taxa by combining rare and/or endemic species under the genus name adding 'spp'.

The presence matrix was subjected to TWINSpan with 4 cut levels and separated the Ecuadorian and Colombia Andean forests by the first division. The TWINSpan subdivision is represented in Fig. 8. Interesting to note is the similarity between the San Francisco Reserve / Zamora-Chinchipe site (Bussman 2002) and our study area. The Papallacta relevés taken by Lauer et al. (2001) have less similarity with our data probably due to the presence of some páramo taxa included in the Papallacta forest records. Surprisingly the Puracé Andean forests, and those of our study area are poorly related, probably also because of unsufficient sampling in the Puracé area. Apparently more relationship exists between the wet West Cordilleran Tatamá Andean forests and the very humid high Andean and Andean forests of Tolima volcano: the sites Alto del Condor and Valle La China (Cuatrecasas 1934).
Fig. 8. Twinspan dendrogram based on the species composition of 18 Andean forest communities in Ecuador and Colombia. Relevant study sites and syntaxa mentioned in the text are: (1) Papallacta 1 (4 rel., 3160–3370 m), "Tournefortion" (Lauer et al. 2001); (2) Papallacta 2 (5 rel., 3450–3700 m), "Miconietum salicifolii" (Lauer et al. 2001); (3) Reserva San Francisco (15 rel., 2770–3050 m), Bussmann (2002); (4) Guanangra 1 (4 rel., 3300–3450 m), Schefflera - Weinmannia community (Moscol Olivera & Cleef 2009b); (5) Guanangra 2 (11 rel., 3500–3700 m), Ilex - Clusia community (Moscol Olivera & Cleef 2009b); (6) El Angel 1 (7 rel., 3450–3570 m), Grosvenoria - Clethra community group (Moscol Olivera & Cleef 2009b); (7) El Angel 2 (8 rel., 3300–3450 m), Brachyotum - Vallea community group (Moscol Olivera & Cleef 2009b); (8) Valle de la China (1 rel., 2800–3300 m), Cuatrecasas (1934); (9) Tatamá 1 (3 rel., 3520–3700 m), Weinmannio - Miconietum (Rangel-Ch. et al. 2005); (10) Tatamá 2 (3 rel., 3300–3500 m), Clusio-Clethretum (Rangel-Ch. et al. 2005); (11) Tatamá 3 (5 rel., 3300–3440 m), Schefflero - Miconietum (Rangel-Ch. et al. 2005); (12) Alto del Cóndor (1 rel., 3500–3600 m), Cuatrecasas (1934); (13) Puracé-Irlanda (2 rel., 3230–3480 m), Rangel-Ch. & Lozano (1986); (14) Puracé 1 (1 rel., 3640 m), Rangel-Ch. & Franco (1985); (15) Puracé 2 (1 rel., 3480 m), Rangel-Ch. & Franco (1985); (16) Puracé 3 (3 rel., 2915–3180 m), Rangel-Ch. & Franco (1985); (17) P. Los Nevados 1 (2 rel., 2940–3185 m), Cleef et al. (2003); (18) P. Los Nevados 2 (2 rel., 3335–3550 m), Cleef et al. (2003).
There are no full records of Nariño humid Andean forests, just north of the study area, with an array of *Brunellia* canopy species. Because of visual similarity in structure and composition we suppose a close relationship with the El Carchi study area.

All sites do have a large body of taxa/species in common, however we noted also that there are less species in common with the Andean forest sites in Colombia. This assemblage of taxa could perhaps be diagnostic for a class. However, the order Purdiaeetalia nutantis, recognised by Bussmann (2002) in southern Ecuador does not include the Andean forests of the El Carchi study area. Bussmann (2001) studied at the northern extreme of Podocarpus National Park (Zamora-Chinchipe Province), the whole sequence from Subandean rain forest at 1800 m to about 3300 m in páramo as did earlier Madsen & Øllgaard (1994) in the Andean rain forests in the Loja region.

In the San Francisco Reserve (Zamora-Chinchipe Province), Purdiaeetalia nutantis is distributed between 2100 and 2650/2750 m. These forests are mainly composed of a low (5-10 m) cyrillaceous tree *Purdiaea nutans* (Purdiaeetum nutantis Bussmann 2001), but locally also by *Clusia latipedis* (Clusietum latipedis Bussmann 2001) reaching up to 15 m. There is, according to the description, a strong physiognomical match with the Guandera forest of *Ilex-Clusia flaviflora*. Above this forest belt in the San Francisco Reserve site there is another one of ‘Jalca’ or ‘Ceja andina’ of the order Clusio ellipticae - Weinmannietalia cochensis (Bussmann 2001) with an alliance and association of the same combination of both species.

In a Central-southern Colombian transect study (Rangel-Ch. & Lozano 1989) from the Magdalena Valley up to the volcano Puracé, the high Andean forest has been classified as Weinmannio brachystachyae-Miconietum cuneifoliae (Rangel-Ch. & Lozano 1989). This dwarf forest association is very similar in structure and generic composition to the Guandera high Andean forest. Also an Andean forest community of *Weinmannia mariquitae* and *Miconia cuneifolia* has been described from the northern sector of Puracé Park by Rangel-Ch. & Lozano (1986). Downslope Puracé volcano in the lower part of Andean forest and the upper part of Subandean forest *Quercus humboldtii* forest (Monotropo uniflorae - Quercion humboldtii; Rangel-Ch. & Lozano 1989) is present. *Quercus* forests are also close to the El Carchi study area; they have been reported by Cuatrecasas (1958) near Ipiales, only at one kilometer distance of the Ecuador-Colombia border, located only at 15 kilometer distance of our study area. Turning back to Ecuador, the last remnants of Andean forest at 3260-3300 m on the steep slopes of Paschoa volcano (35 km south of Quito) were also part of this comparative analysis (Valencia & Jørgensen 1992). Most of the western slopes of Paschoa are still covered by Andean forest including rare native tree species, like *Ceroyxylon parritrens, Podocarpus oleifolius*, and *Polylepis reticulata*. However, this forest does not display many floristic similarities with the forests of our study area.
Finally, the study of Young & Keating (2001), documenting the characteristics of upper montane forests remaining between 3330 m and 3650 m in Cotacachi-Cayapas Ecological Reserve in northern Ecuador were also taken into account. In this case, floristic similarities with our study are related to the presence at elevations around 3400 m of species of *Oreopanax*, *Myrsine* and *Gynoxys*.

**Forest response to human disturbance**

We can distinguish between different types of human impact in the Guandera-El Angel study area, as discussed below for each locality.

In Guandera forests we observe a strong decrease of human influence (cutting, extraction) with increasing altitude. In general, almost no significant human influence has been observed upslope of the biological station at 3300 m. In contrast, the UFL on the western slope of Guandera is unnaturally sharp (see Fig. 9 and also the photographs in Bader 2007, p. 28 and 54). This can only be explained by burning, most probably repeated burning with intervals of some years. The area of Guandera has been used by local people living adjacent to this area. They walk across the reserve to gain access to rivers for fishing purposes (Christopher James, pers. comm. 2004). It is likely that these inhabitants may have set fire in the bunchgrass vegetation to chase out rabbits and other native wildlife. The fires would have been moving along the UFL or would have extinguished at this level without entering the humid forest edge. We hypothesise that there was originally more open low shrub and dwarf shrub close to the UFL as a kind of subpáramo transition (Moscol Olivera & Cleef, 2009a). Woody elements such as low shrubs in bunchgrass vegetation are apparently more sensitive to recurrent fire (Hofstede et al. 1998, Salamanca et al. 2003). Sensivity implies slow recovery and tendency to gradual disappearance (Cleef et al. 2008). The sharp present-day UFL at 3650 m in Guandera is a consequence of frequent and extensive fires (Bader 2007; Moscol Olivera & Cleef, 2009a).

In the course of the years, repetitive fires have burnt down the shrubby structure of the subpáramo and the treelets and shrub of the uppermost fringe of the high Andean dwarf forest. The fires were downslope limited by the actual UFL, marking a sharp border between dwarf forest with conspicuous treelets of *Gaiadendron punctatum* up to 4-5 m height. This current UFL structure also indicates that the natural UFL is situated at some higher altitude, where the high Andean dwarf forest supposedly grades into a shrubby matrix of about 1.50-2.00 m height ending up in low shrub and a shift to dominance of the bunchgrasses of the open grass páramo. This is the natural altitudinal sequence from the UFL going upslope (Cleef 1981). On active volcanoes, shrubby subpáramo is frequently absent by burning as a consequence of pyroclastic events (Salamanca et al. 2005).
Our vegetation analysis (Moscol Olivera & Cleef, 2009a) of the lowermost páramo (3650-3700 m) with most woody species has documented species of the genera *Arcytophyllum*, *Baccharis*, *Blechnum*, *Brachyotum*, *Diplostephium*, *Disterigma*, *Gaiadendron*, *Gynoxys*, *Hesperomeles*, *Miconia*, *Monticalia*, *Myrteola*, *Pentacalia*, *Pernettya*, and *Vaccinium*. This altitudinal interval corresponds largely to the subassociation typicum (with *Brachyotum lindenii*) of the association Jamesonio-Calamagrostietum effusae. The woody species almost all became dwarfish and ground covering under the process of ‘paramización’.

At 3700 m, we know from the G5b sampling site in open bunchgrass páramo (Jansen et al. 2008) that during the last few thousands years only open grass páramo prevailed. In terms of absolute altitude in this reconstruction on the steep Guandera slope (30-40 degrees) with the present UFL at 3640 m, we estimate the natural UFL at about 3660 m and subpáramo until about 3680 m (Fig. 10). The high Andean forest patch in a concave depression in the terrain on the same slope may have persisted long time probably connected in the lower part to the natural UFL.

Natural fires by lightning are occurring as well, especially in the border area to the perhumid bamboopáramo on the opposite eastern Amazonian slope of Guandera. Di Pasquale et al. (2008) reported Holocene fires dating back to 5000 to 11,000 years ago. They presented a record of charcoal of *Pernettya prostrata* that do not necessarily confirm their statement of presence of páramo 5000 ¹⁴C yr BP at 3540 m because this dwarf shrub is present from the uppermost Andean forest up into the superpáramo.
Holocene upper forest line dynamics in the Ecuadorian Andes

Fig. 10. Guandera Andean forest - grass páramo transect with schematic representation of the current UFL (A) and the reconstructed natural UFL (B); 1: *Ilex* - *Clusia flaviflora* Andean forest; 2: high Andean forest (variant with *Gaiadendron punctatum* of *Ilex* - *Clusia flaviflora* forest); 3a: bunch grass páramo (*Jamesonia imbricata* - *Calamagrostis effusa*) with *Brachyotum lindenii* (‘paramización’); 3b: bunch grassland (natural grass páramo with dense bunches); 4: *Xyris* - *Oreobolus* peat bog; 5: Bamboo páramo with *Neurolepis aristata*; 6: Natural shrub páramo; 7: Natural dwarfshrub páramo.
In Guandera *P. prostrata* has been observed in all forest types described here with low presence and cover (Table 1).

The Andean forest sites studied in El Angel are dramatically impacted by humans (Arellano 2000, López Sandoval 2004). This implies that we are not dealing with a natural UFL. The present human-shaped upper Andean forest border consists rather of isolated remnant forest structures. The structure is open under the canopy where in the recent past selective logging for timber and also some clear cutting took place. Older sites have a closed understory by a tangle of bamboos and lianas and/or successional tree growth. The last condition is most common and probably due to the establishment of the El Angel Ecological Reserve in 1992. Probably, systematic felling of the high Andean and Andean forests has taken place since the arrival of the conquistadores more than 400 years ago (López Sandoval 2004). However, we presume that most felling took place in the past century and that the páramo grassland gradually extended downslope. This topic is dealt with in more detail in Moscol Olivera & Cleef (2009a).

The low asteraceous forest at 3450 m on the sloping valley bottom above the El Angel-Tulcán road near the first guard post of the reserve has a tendency to become azonal (*Blechnum-Diplostephium floribundum* high Andean forest community). Under the low canopy of 5-6 m there is runoff and temporarily a lot of discharge during showers. This explains the selection of an asteraceous tree species with low height and able to cope with high phreatic levels.

**Vegetation belts and Upper Forest Lines**

The UFL (often erroneously called ‘treeline’) in our context marks the border between the ecosystems or biomes of open páramo and montane forest. A ‘tree line’ in this context is situated at much higher elevation than UFL and is the line which connects the uppermost extrazonal tree habitats, e.g. rock shelters where a single or few trees may grow in páramo because of special habitat conditions with respect to temperature (Troll 1973).

Fig. 11 shows the different types of succession of vegetation belts and physiognomy of UFL in an ideal context (A) without human intervention and as displayed in our study area (B to D). Slope has been neglected for practical purposes. Fig. 11 A schematically shows a UFL at about 3650 m with the sequence Andean forest, high Andean forest, UFL, shrub páramo, dwarfshrub páramo and grass páramo. On the volcanoes of El Carchi a well developed subpáramo (shrub páramo, dwarfshrub páramo) has not been observed. On the outer slopes with wet climate towards Amazonas probably a subpáramo is still rather intact because of low fire incidence. In Fig. 11 B, we see a clear cutting of high Andean forest and the upper part and patches of the Andean forest. Successional regrowth on open patches is frequent with development of dense bamboo vegetation. A floristic impoverished *Calamagrostis effusa - Espeletia pycnophylla* community colonised the forest land after removal of the harvested stems.
Fig. 11. Types of succession of vegetation belts and physiognomy at the Upper Forest Line ecotone.
Vegetation analysis of Andean rain forests in El Angel and Guandera

Woody debris decomposed and the remains collected in depressions of the morrainic landscape. This picture has been observed in El Angel area. In Fig. 11 C, irregular pattern of cut over Andean forest is displayed. Some single canopy and subcanopy trees are left.

Successional dwarf forest is already present alternating with remains of natural Andean forest and bamboo patches. Many paths are crossing the Andean forest remains in Fig. 11, B and C. This case has been observed in El Angel area. Finally Fig. 11 D, a sharp UFL is present as a consequence of fires (like the one observed at about 3650 m on the western slope of Guandera). This type of UFL is very common on equatorial high mountains surrounded downslope by settlements and farm houses (Lægaard 1992, Kappelle 2005). Such an artificially looking UFL is also known from elsewhere on high mountains where the lowermost páramo has suffered from fire.

The páramo shown in Fig. 11 is invading (B and C) and finally has established on former forest land (D).

**Present forest patterns versus the UFL position**

The floristic composition and the structure of El Carchi forests revealed several features that allowed us to make some inferences about the past UFL position. Comparing both transects we may assume that the UFL at Guandera was at slightly higher altitude than found today, a setting reconstructed by Bakker et al. (2008) and Moscol Olivera & Cleef (2009a). The border between high Andean and Andean forest in Guandera is located at about 3550 m or even slightly higher; this concerns the border between the forests of both subcommunities of *Ilex colombiana-Clusia flaviflora* forest of the montane rain forest belt in Guandera.

In El Angel there is no evidence of high Andean forest, nor the slightest evidence where the border between high Andean forest and Andean forest was located under undisturbed conditions. Judging the irregular human-made forest border in El Angel and the impressive height of the rain forest left, it is clear that deforestation has already completely cleared the former fringe of high Andean forest. Probably the high Andean forest zone was somewhat broader than in the Guandera transect, as the latter often has a much steeper slope. The extrazonal asteraceous forest patches around the El Voladero lakes at 3750 m probably are similar to the clear cut high Andean forest zone.

The UFL on the western slope of Guandera is located at about 3650 m, however a high Andean forest patch (rel. nr. 10) is present in the páramo at 3700 m (Fig. 9). This forest patch occurs in a depression of the main slope. The connection between the UFL and the extrazonal forest patch has been lost. Also the phytosociological clustering (Table 1) indicates that there were only small differences in floristic composition and abundance (at variant level) between the high Andean forest below the UFL and the forest patch in the páramo (Fig. 9).
In general, the UFL reaches slightly higher on Amazon exposed slopes (Bader 2007, Lauer et al. 2001), probably because extreme minimum temperatures are less frequent compared to similar altitudes on inner Andean slopes. In contrast Lauer et al. (2001) situated the current UFL in Papallacta (Fig. 12) at 3700 m on the eastern slopes facing Amazonia and at 3800 m on the opposite western slope. Interpretation is difficult because the lower part of the grass páramo ('Festucion') in Papallacta is apparently replacing the uppermost forest. The current UFL in Guandera implies that the natural UFL was at (slightly) higher altitude. Some climate components were mentioned to be involved in shaping the UFL in our study area (Bader et al. 2007). Excess radiation in páramo as a key factor hindering tree regeneration in Guandera (Bader et al. 2007) may be correct on an experimental basis (seedling’s transplantation), but we do not believe that it explains the abruptness of UFL in Guandera. Instead we think that seedlings of UFL trees would perform better when they arrive in the natural germination ‘bed’ of a shrubby subpáramo with protective low woody structure and foliage. A small belt of shrubby subpáramo does not exist physiognomically; only some dwarfed shrub species are floristically detectable making in a stratified way relevés of the páramo vegetation along the altitudinal transect. Tree seedlings can hardly survive in the open bunchgrass matrix contiguous to the UFL.

Fig. 12. Altitudinal forest zonation in El Angel Reserve and Guandera Reserve and a comparison with settings at site Papallacta located near Quito (Lauer et al. 2001).
For the El Angel sites we cannot discuss the present-day UFL; in its absence we have to reconstruct the position of this ecotone. However, our reconstruction is only based on vegetational evidence from the páramo study (Moscol Olivera & Cleef, 2009a). This evidence from the phytosociological table and the species composition of páramo plots suggests that most probably the natural UFL has been around the level of 3650 m. Above this elevation páramo grassland are natural according to our evidence. The devastating forest clearing in El Angel of high Andean and Andean forest concerns a large area spanning 200 m in altitude and which is invaded by an impoverished bunchgrass- Espeletia pycnophylla páramo. As Espeletia stems in general only attain 1.50-2.0 m, remarkably enough the Espeletia plants in El Angel may be considered as adult.

Finally, some extrazonal patches of asteraceous forest at about 3750 m around El Voladero lake basin were sampled. In contrast to the extrazonal forest patch near the Guandera UFL, which is almost similar to the high Andean forest below the UFL (and belongs to the same Ilex-Clusia flaviflora forest community), the El Voladero patches differ more from the Andean forest remains of Los Encinos in spite of sharing twenty species (Table 1). Direct comparison to the adjacent local high Andean forest, which has disappeared is not possible.

These facts imply that the El Voladero forest patches, which are located some 100 m in altitude above the assumed natural UFL in El Angel have a longer history of separation from the upper forest belt. However, it must be kept in mind that the asteraceous canopy species of this forest patches have wind dispersed seeds.

CONCLUSIONS

This study helps elucidating the floristic composition and patterns of plant communities in one of the regions holding the best preserved forest areas in northern Ecuador. In the most humid site of Guandera two forest communities were recognised by the present study. In El Angel five Andean forest communities were found along a gradient from more humidity towards the East (Los Encinos) to more dryness in the southwestern part near the town of El Angel. The described forest communities belong to two community groups in El Angel and to one community group in Guandera. The extrazonal forest patch at 3700 m in Guandera differed only at the variant level from the upper continuous high Andean forest located some 50 m downslope. In El Angel possible similarities involving the isolated asteraceous forest patches of El Voladero could not be examined as there are no more high Andean forest stands to be compared with because of the evident clear cutting in the past. The high Andean forest in Guandera belongs to the same forest community as the Andean forest. For other studies in Colombia, Venezuela, and southern Ecuador both forest types belong to one single syntaxon at the association level. The high Andean and
Andean forest stands studied belong to one order group of forest communities of which the regional distribution is largely unknown.

The interregional comparison of Andean and high Andean forest communities of Colombia and Ecuador did not show a direct floristic relationship. Low similarity was detected between the forests in our study area and those of San Francisco Reserve / Zamora-Chinchipe and Papallacta.

The sharp present-day UFL in Guandera is most likely a consequence of frequent and extensive fires. Over the course of the years repetitive fires have burnt down the shrubby structure of the subpáramo and the treelets and shrub of the uppermost fringe of the high Andean dwarf forest. Almost all the woody species became dwarfish and ground covering under the process of ‘paramización’.

Our reconstruction on the steep Guandera slope with the present UFL at 3640 m, results in an estimation of the natural UFL at about 3660 m and subpáramo until about 3680 m. The high Andean forest patch in a concave terrain depression on the same slope may have persisted long time probably connected in the lower part to the natural UFL.

In El Angel, the natural UFL and the adjacent the high Andean forest have disappeared as a result of clear cutting. Also the upper part of the Andean forest zone has been partly removed. The Andean forest remains are patchy-like distributed along the present border of Andean forest and grass páramo. The downslope expanding páramo grassland “paramización” is in fact the result of a large scale process of human interference. The Andean forest patches in El Angel suffer from wood extraction and a continuous human presence and influence. The driest *Otholobium-Vallea* forest patches are the most degraded, remaining only on the most steepest slopes.

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